Modeling of the Biochemical Processes in the Benthic Phytocenosis of the Coastal Zone

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Introduction. A simulation model of bottom phytocenosis based on object-oriented approach to marine ecosystems was proposed.

Data and methods. The dynamic model of macroalgae growth is based on the system of ordinary differential equations describing the processes of photosynthesis and production of organic matter, nitrogen and phosphorus uptake, and extraction of organic matter and oxygen into the environment. Photosynthetically active radiation (PAR), water temperature, a content of nutrients in the water were chosen as the control variables.

Results. The model allows an estimation of nitrogen and phosphorus content in algae tissues, rate of photosynthesis, actual parameters of uptake nutrients and extraction of organic matter depending on the control variables. Analytical solutions for the steady state of a system at constant control variables were obtained. Parameterization of photosynthetic and kinetic parameters of seaweed using their dependencies of the specific surface of thalli was proposed. The growth of red macroalga Gracilaria biomass over a year was simulated with a preset dynamics of control variables (for the Southern Coast of Crimea). Yearly oxygen production, nitrogen and phosphorus uptake and accumulated quantity of these elements in algae tissues were calculated; the volume of organic matter coming to the next trophic level (benthic organisms and finfish) was estimated. The results correspond to the published observational ecosystem data in the region under study.

Discussion and conclusion. The developed model will be used as a separate unit simulating the dynamics of bottom phytocenosis in a three-dimensional object-oriented physical-chemical-biological model of the marine ecosystem.

Keywords: marine ecosystem, object-oriented modeling, macroalgae, photosynthesis, metabolic processes, specific surface of thalli.

Introduction

In the coastal shallow zone a key role in the fluxes of matter and energy is played by macroalgae and seagrass. In the benthic phytocenoses of the shallow zone up to 90% of total organic matter is produced during the autotrophic processes. Unlike pelagic ecosystems where phytoplankton is the main producer,

the main source of organic matter in shallow water areas is bottom vegetation [1]. Correspondingly, the macroalgae of benthic phytocenoses produce most of the dissolved oxygen, which is used then for the oxidation of suspended and dissolved organic matter, significant amount of which is produced in shallow coastal ecosystems. Extracting from the sea water and accumulating a lot of chemical elements (including xenobiotics) macroalgae are involved in biological water purification. Competing with phytoplankton for nutrients, phytobenthos also contributes to water purification. Phytoplankton cells quickly die off replenishing the pool of suspended organic matter, the oxidation of which consumes oxygen, while the macroalgae absorb the nutrients and remove them from the cycle for a long time. Thus, the bottom vegetation is actively involved in the bottom layer biochemical processes. A chance of occurrence of hypoxia or anaerobic conditions in this area largely depends on the density and spatial distribution of the phytobenthos.

In recent decades, in the coastal zone ecosystems severe oxygen deficiency, leading to extremely negative consequences, is recorded more frequently. This phenomenon develops in the near-bottom area, but under adverse conditions, it could also spread to the pelagic zone. Its main cause is imbalance between the oxygen supply (due to the water mixing and photosynthetic activity of autotrophs) and the consumption by oxidation of organic matter accumulating in the bottom area.

Hypoxia is compounded by the intense anthropogenic impact which affects the considered ecosystems. In order to assess the risk of suffocation occurrence in this region and permissible anthropogenic load, the research on the contribution of hydrophysical and biogeochemical processes to the formation of the zones of oxygen deficiency and hydrogen sulfide contamination are required. These studies should be carried out by sharing data from expeditionary observations and numerical modeling methods. Simulation experiments with 3D physical-chemical-biological ecosystem model, which takes into account biochemical processes in the bottom layer, provide quantitative assessments of permissible load. Currently, a large array of *in situ* and laboratory data on metabolic processes in benthic phytocenoses is accumulated. Many of the published works on this topic are devoted to the study of photosynthesis, as well as to extraction of nutrients from the environment by algae and their accumulation in algae tissues (which accompany the abovementioned process) and the search for appropriate parameterizations [2−6].

The found regularities formed the basis for the development of mathematical models of algae biomass dynamics depending on external impacts. One of the first studies on the numerical modeling of benthic phytocenosis state is the work [7]. It proposes a model of Zostera sea grass growth depending on light and mineral nitrogen concentration. The light intensity effect on the rate of extraction of ammonium and nitrates, the relative importance of the leaves and the root system of the plant in this process are also analyzed.

In [8], which develops the phytoplankton growth models from [9, 10], the growth of algae biomass in ponds with an inflow of runoff waters from greenhouses saturated with nutrients, is mathematically described. The model variables are the concentration of nutrients in the water and in algae cells, the amount of sugars and dry matter

produced per unit of time during the photosynthesis. The control variables are the rate of nutrient flux at the pond entrance and exit, water temperature, frequency and volume of algae extracted from the pond. It is assumed that pond waters are well-mixed and the algae growth is slow and uniform. Therefore, the mentioned variables are the time functions and do not depend on spatial coordinates.

The work [11] is dedicated to the simulation of phytocenosis biomass dynamics of marine macrophytes which includes plants of three functional groups: floating algae, rhizophites, and epiphytes. Each of these groups combines many species of macroalgae, which in certain seasons are predominant in the phytocenosis. Spatial distribution of species in this model is not taken into account (as in [8]). The interaction between the phytocenosis and environment is not taken into account as well. The data on nutrient concentrations in the water and substrate pore waters are set in the model from observational data.

Abovementioned sources were used in the present work for developing the balance model of benthic phytocenosis functioning in the shallow area of the Crimean coast.

Materials and methods

Two species of brown alga Cystoseira: *Cystoseira barbata* and *Cystoseira crinita* form the structure of benthic phytocenoses at the depths from 0.5 to 10 m. Cystoseira phytocenosis is a complex community with a large active surface due to micro- and macro-epiphytes settling on the substrate and algae thalli. Among the related species, red, brown and green algae are observed. Cystoseira reserves in the Black Sea coastal zone (which are of commercial interest) reduce due to a water transparency decrease. As a result of water transparency decrease, the lower boundary of Cystoseira growth gradually goes up (in 60–70s of the XX century the lower boundary of Cystoseira distribution was indicated at 15–20 m depths, now it is no deeper than 10 m) and the width of the algae belt decreases [1, 12].

The activity of metabolic processes between the algae and the surrounding aquatic environment is assessed using the specific surface index, i.e. the ratio of the thalli surface area to their mass or occupied volume (S / W). If the alga has a complex hierarchical structure, the total surface area of the branches of each organization level $S_k = \sum_i S_i$ and their total weight $W_k = \sum_i W_i$ are assessed separately. After that, the biological indicator of specific surface area of a set of macroalgae organs of a given level is calculated: $(S / W)_k = S_k / W_k$. Total specific surface is calculated by summing the surface areas at all levels of organization and relating them to the total plant weight. The specific surface area of the population and the community as a whole are assessed in the same way [13].

The biological specific surface index, other things being equal, determines the intensity of photosynthesis and metabolic processes occurring in the tissues of algae. Thus, the photosynthetic characteristics, the rate of dissolved nutrients absorption and their accumulation in tissues, the intensity of oxygen release and the growth rate of alga depend on S / W index [2–6, 14]. In [15], 38 species of macroalgae were considered and it was shown that when combining them into functional groups having close S / W index values, clear power-law dependencies of the abovementioned characteristics on the S / W specific surface with power

exponents from 2/3 to ¾ are indicated. In addition to the morphological parameters, the production characteristics of marine algae are generally affected by other factors the main of which are: radiation flux, temperature, concentration of nutrients in the water and its temporal variability, the velocity of current.

In the phytocenoses of the Crimean coastal zone the structural dominant is Cystoseira, the mass of which is much higher than the masses of accompanying species, and the functional dominants are epiphytes (red and green algae) as their specific surface area is 2–3 times higher than that of basiphyte*. Therefore, for an adequate assessment of the volume of substances absorbed and released by the phytocenosis, it is necessary to take into account the intensity of the production processes of all species forming the phytocenosis.

A numerical model of benthic phytocenosis functioning will be constructed using the technology of object-oriented modeling (OOM), previously used for developing the models of the pelagic plankton community [16]. This technology is very suitable for describing the hierarchical structure of phytocenosis consisting of several levels of basiphyte organization and a number of epiphytic algae species. Each of these sets has its own biological parameters of specific surface and leaf-area index. It is enough to present these sets as sets of objects with given different properties in order to achieve the completeness of the mathematical description of the phytocenosis.

We set the basic element of a spatially-distributed object-oriented model in the form of a cylinder with h height and r base radius ("biological object" class). Thus, we model the nearest living space for a set of plant organs of one organization level (in case of a complex hierarchical plant structure) or plants of the same species (for annual macroalgae) growing on a substrate within the area of the cylinder base. The properties of the base object are its coordinates, radius and height, as well as macroalgae biomass. We assume that the mass spatial distribution inside the object is uniform. Objects of different types can coexist in the same space competing for resources. The shadowing of the phytocenosis understory can be simulated by setting a functional relationship between the biomass of epiphytes and branches of overstory and radiation flux magnitude at the bottom.

We will separately introduce into the model a class of objects "species" which describes the varieties of macroalgae (or organs of a complexly organized plant) in terms of their production and biochemical characteristics. These characteristics include: the content of nutrients (carbon, nitrogen and phosphorus) in the tissues, the interval of variability of thallus specific surface and surface index, typical photosynthetic parameters (maximum rate, slope and light compensation point of the photosynthesis curve, light saturation level, dark respiration), kinetic parameters (the maximum rate of nutrients uptake, half-saturation constants) and their dependence on temperature and salinity, maximum and minimum content of nutrients in the plant tissues.

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* Saburin, M.Yu., 2004. Phytocenoses of the Black Sea Cystoseira: Structure, Restoration and Application Perspectives: Abstract of a Thesis, PhD (Biology): 03.00.18. Moscow: MSU, 20 p. (in Russian).

Using two above-described classes as the ancestor class, we form a child class "macrophytes", which will include all the listed properties. The methods of this class are the subroutines numerically integrating the equations of mathematical model of photosynthesis and biomass growth of seaweed of this type, as well as calculating the matter fluxes and the corresponding changes in the environment. This work is devoted to the derivation of the equations of this mathematical model − one of the methods of general benthic phytocenosis object-oriented model and to the justification of necessary parameterizations and the analysis of numerical test experiments.

Description of the model

Mathematical model of alga biomass dynamics B (g (DW)/m^2) is based on the balance equation

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

where P_r is a specific growth rate; E is a specific rate of dissolved organic matter release; m is a coefficient taking into account the destruction and separation of alga branches, as well as the grazing by marine animals.

The macroalgae are the autotrophs and increase their mass during the photosynthesis of organic matter. The photosynthesis rate depends on several factors, the main of which is the intensity of the incident flux of photosynthetically active radiation (PAR) I. In ecology this value is generally measured in micromoles of photons per unit area per unit time (μmol photons/m^2 s). We express the specific rate of P_p photosynthesis in units of oxygen released per hour by one gram of dry matter of the alga (mg O$_2$ / g (DW) h). The function of this quantity on the radiation intensity is called in the ecology a *PI*-curve and can be approximated by the formula

$$P_p = (P_{\max} + R_d)(1 - e^{\frac{-\alpha I^{1,7}}{(P_{\max} + R_d)E_c}}) - R_d, \tag{2}$$

where $P_{\max}$ is the maximum photosynthesis rate (mg O$_2$ / g (DW) h); α is a slope of *PI*-curve at small values of radiation flux; R_d is a dark respiration, i.e. the amount of oxygen which the seaweed uptakes from the environment and spends on breathing in the absence of the photosynthesis; E_c is a light compensation point of *PI*-curve, i.e. luminous flux at which oxygen consumption for respiration is balanced by the oxygen release during the photosynthesis (Fig. 1, *a*).
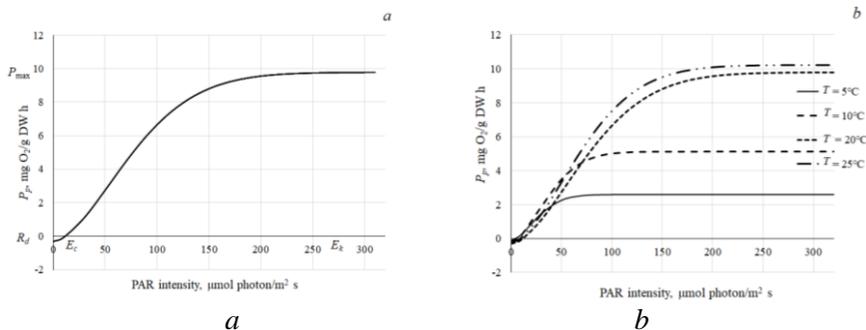
F i g. 1. Dependence of the photosynthesis specific rate upon the radiation (*a*); *PI*-curves for Gracilaria at different water temperature (*b*)

P_p value in mg O_2 / g (DW) h is easily converted to the specific production of new organic matter in carbon units (mg C / g (DW) h). Using the data on the average carbon content in the algae tissues [17], we can express them in the units of dry weight, since the literature provides the data on the maximum possible rates of physiological processes relative to the units of the algae dry weight.

PI-curve parameters depend on water temperature and salinity. In [18, p. 747] the field data on the variability of red alga Gracilaria photosynthetic parameters affecting by changes in temperature, salinity and light intensity are given. Using these data, we constructed *PI*-curves for 20‰ salinity value (Fig. 1, *b*). As can be seen from the figure, the temperature impact is very significant and photosynthesis rate in winter and summer may differ several times with the same solar radiation level.

The intensity of radiation flux that reaches the plants of the benthic phytocenosis depends on the depth, as well as the amount of suspended mineral and organic particles in the water (including phyto- and zooplankton). In addition, the phytocenosis understory is affected by a shadowing effect from the plants of the overstory. All this must be taken into account in the model for adequate description of biochemical processes and, accordingly, the flux of matter between the phytocenosis and the environment.

In addition to the PAR and water temperature, the photosynthesis rate is limited by the content of essential minerals in algae tissues. Following [10, 11], we introduce the function of the photosynthesis rate dependence on the content of nutrients in alga cells, applying the empirical relationship proposed first in [19] for the phytoplankton growth rate, slightly modifying it to take into account the maximum possible nutrient content in algae tissues:

$$P_r = P_p \left(\frac{Q - Q_{min}}{Q_{max} - Q_{min}} \right), \tag{3}$$

where Q is a nutrient content in the tissues; P_p is a photosynthesis rate at the maximum nutrient content Q_{max}; Q_{min} is the minimum nutrient concentration in the tissues at which the production processes suspend (in order to simplify the model, here we combine two phases of the photosynthesis process — the formation of sugars and the organic matter synthesis — into one). For taking into account the

impact of two main nutrients that provide the growth of algae tissues (nitrogen and phosphorus), we use Liebig limiting factor law:

$$P_r = P_p \min(f(Q_N), f(Q_p)), \qquad (4)$$

$$f(Q_P) = \frac{Q_p - Q_P^{\min}}{Q_P^{\max} - Q_P^{\min}}, \qquad (5)$$

$$f(Q_N) = \frac{Q_N - Q_N^{\min}}{Q_N^{\max} - Q_N^{\min}}, \qquad (6)$$

where Q_P and Q_N are the content of phosphorus and nitrogen in the algae tissues (µmol/g (DW)); $Q_P^{\min}$, $Q_N^{\min}$, $Q_P^{\max}$ and $Q_N^{\max}$ are the minimum and the maximum concentration of nitrogen and phosphorus. Extraction rate of dissolved mineral forms of nitrogen (V_N) and phosphorus (V_P), depending on their concentration in the sea water, is usually represented in the form of Michaelis – Menten law

$$V_N = V_N^{\max} \frac{[N]}{K_N + [N]}, \quad V_P = V_P^{\max} \frac{[P]}{K_P + [P]}, \qquad (7)$$

where $V_N^{\max}$, $V_P^{\max}$ are the maximum possible uptake rates at rather high nutrient concentration in the water (saturation level), [P], [N] are the concentrations of phosphorus and nitrogen in the sea water; K_P, K_N are the half-saturation constants. When placing the algae with a low content of nitrogen or phosphorus in the water rich in this nutrient, the uptake rate is high and then it gradually decreases to a certain stable level. Upon reaching the saturation (maximum possible content in the tissues), further absorption of the element from the environment ceases. By analogy with the regularities empirically determined for phytoplankton [20], following the authors of [11], we introduce a ratio connecting the uptake rate with the concentration of nutrients in tissues:

$$V_{N_r} = V_N^{\max} (1 - \frac{Q_N - Q_N^{\min}}{Q_N^{\max} - Q_N^{\min}}), \qquad (8)$$

$$V_{P_r} = V_P^{\max} (1 - \frac{Q_P - Q_P^{\min}}{Q_P^{\max} - Q_P^{\min}}). \qquad (9)$$

As the nutrients are extracted from the environment, they are accumulated in the algae tissues and the synthesis of new organic matter takes place. This process also requires the nutrients extracted from the water. The change in the nitrogen and phosphorus concentration in the tissues, by analogy with the phytoplankton growth model [10], will be written in the form of ordinary differential equations

$$\frac{dQ_N}{dt} = V_{N_r} \frac{[N]}{K_N + [N]} - P_r Q_N, \qquad (10)$$

$$\frac{dQ_P}{dt} = V_{P_r} \frac{[P]}{K_P + [P]} - P_r Q_P. \qquad (11)$$

With a sufficient content of nutrients in the sea water, their content in the tissues stabilizes (Fig. 2). It can be assessed by setting to zero the left parts of equations (10), (11). At first, we are to find a solution for the element that limits the algae growth. Stationary nitrogen content Q_{lim}^{st} in algae tissues is calculated by solving a quadratic equation

$$P_{max}(Q_{lim}^{st2}) + (V_{lim} - P_{max}Q_{lim}^{min})Q_{lim}^{st} - V_{lim}Q_{lim}^{max} = 0, \tag{12}$$

where V_{lim} is determined according to the formula (7). Calculating the stationary content of the element that limits the growth, we find the stationary content of non-limiting element:

$$Q_{unlim}^{st} = \frac{V_{unlim}Q_{unlim}^{max}}{P_{max}(Q_{unlim}^{max} - Q_{unlim}^{min})f(Q_{lim}^{st}) + V_{unlim}}, \tag{13}$$

where

$$f(Q_{lim}^{st}) = \frac{Q_{lim}^{st} - Q_{lim}^{min}}{Q_{lim}^{max} - Q_{lim}^{min}}. \tag{14}$$

T a b l e 1

Numerical values of the parameters and the external conditions in the equations (8)−(11) preset for calculating the curves in Fig. 2, $P_r = 0.002$ (h^{-1})

Biogenic element	Q_{min}, μmol/g (DW)	Q_{max}, μmol/g (DW)	Half-saturation constant, μM	V_{max}, μmol/g (DW) h	Nutrient concentration in the water, μM
N(NO$_3$)	714	1700	30.7	20.0	5.00
P(PO$_4$)	40	92	2.7	1.2	0.31

As it can be seen from the obtained relations (12), (13), stationary values of nitrogen and phosphorus content in the tissues are due to the balance between the uptake of these elements from the sea water and their spending on the growth of new tissues (production processes). Depending on the ratio of empirical values of the maximum uptake rate, half-saturation constant and the maximum alga growth rate, under certain external conditions (PAR, concentration of nutrients in the sea water, temperature) certain concentrations of nitrogen and phosphorus in alga tissues are settled. Table 1 presents the data used for the calculation of the model stationary state (Fig. 2). In this calculation the kinetic parameters for brown alga *Fucus vesiculosus* according to the data from [14] were used. As it can be seen on the graph (Fig. 2, *d*), phosphorus is the limiting element in this case.
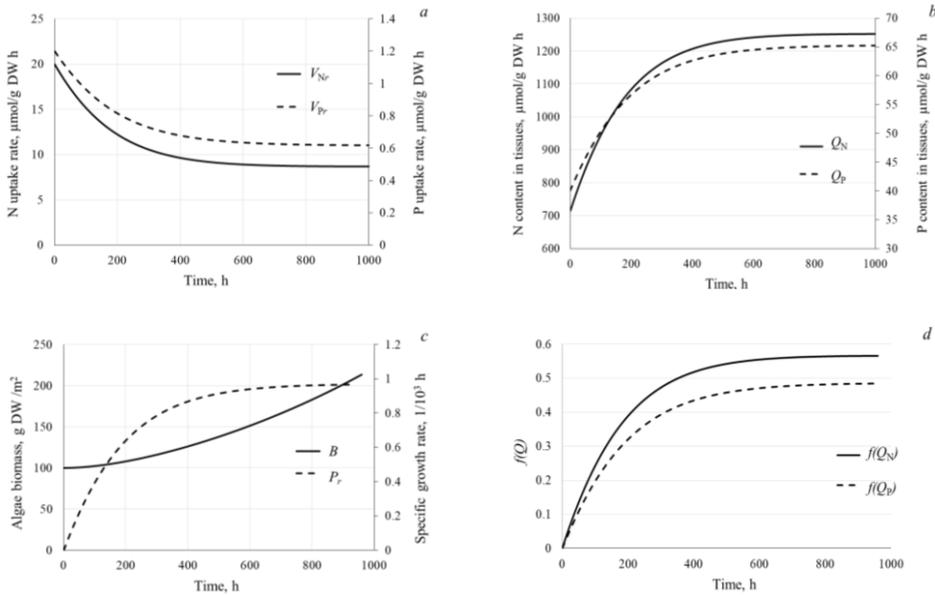
F i g. 2. Calculation of steady state nitrogen and phosphorus content in the tissues of growing algae at constant concentrations of biogenic elements in seawater using the model (1)-(11): a – actual uptake rates; b – nitrogen and phosphorus content in alga tissues; c – algae biomass B and its specific growth rate P_r; d – growth limitation function $f(Q_N), f(Q_P)$

We consider the impact of external conditions on the stationary content of nitrogen and phosphorus in the alga tissues. In Fig. 3, a the growth of Q_N^{st} depending on the concentration of inorganic nitrogen compounds in the sea water is shown. If N / P ratio preservs, the stationary phosphorus content in the tissues increases similarly to Q_N^{st}. The alga growth rate increases as expected. The value of Q_N / Q_P ratio slightly changes in this case, remaining within 18−20 range. At a significant difference of Q_N / Q_P from the Redfield ratio, the alga growth rate of slows down due to an imbalance between the nutrients (Fig. 3, b). N / P ratio value in algal tissue increases due to a decrease in the phosphorus content.
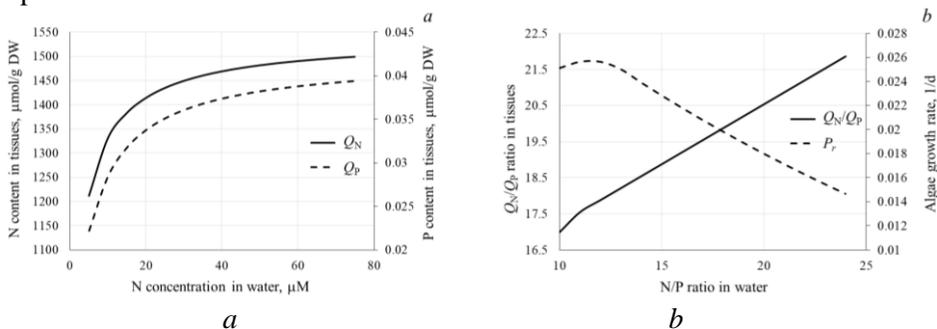
F i g. 3. Impact of growth of nutrient concentration in water on steady state content in alga tissues at constant N / P in water (a); impact of N / R ratio increase in water on steady state nutrients content in alga tissue and its growth rate (b)

We considered in detail the ratios required for calculation of actual specific alga growth rate P_r from equation (1), which take into account the processes of photosynthesis, respiration and the extraction of nutrients from the sea water. Rate of these processes, in its turn, depends on the concentration of elements in the tissues. The second term of the right side of equation (1) is the release rate of organic compounds. According to data of studies [21, 22], the intensity of excretion of organic metabolites by macroalgae is a function of temperature and irradiance. It is proportional to growth rate P_r in the daytime, which indicates a relation between the photosynthesis and exchange processes. At night, the release of organic metabolites does not stop but its rate is significantly decreases. The work [22] provides information on the correlation of respiration rate and release of metabolites at night time. Based on these data, we express the intensity of organic compounds release in units of carbon in the form of a linear dependence

$$E = k_1 P_r \qquad (15)$$

in the daytime

$$E = k_2 R_d \qquad (16)$$

in the dark.

The amount of released organic nitrogen and phosphorus in the composition of the metabolites will be assessed in Q_N / Q_P proportion. The last term of equation (1) depends on the intensity of the algae destruction and grazing by marine animals. The mortality coefficient m should be determined empirically from the results of observations, and it cannot be derived from any theoretical constructions. In the literature, it is customary to preset the mortality to be proportional to the algae biomass. The work [23, p. 747] provides the data for several groups of algae: proportionality factors vary within the range from 0.005 to 0.02 (1 / day).

Empirical coefficients in the parameterizations (2), (7) essentially determine the model stationary state of nitrogen and phosphorus content and C: N: P ratio in alga tissues. The lack of one or another nutrient or its low uptake rate inhibits the growth of algae due to the fact that the balance between nitrogen and phosphorus in the tissues is disrupted. The knowledge of empirical characteristics of metabolic processes (kinetic and photosynthetic parameters) is extremely important for the practical application of the model (1) – (11) in order to assess the fluxes of matter and energy in the coastal zone ecosystem. As mentioned above, these parameters significantly depend on the morphological characteristics of the alga, described by the ratio of surface area to weight SA / W. The maximum rates of nutrient uptake V^{max} increase with the expansion of specific surface area, the half-saturation constants have a negative correlation with this morphological characteristic [5, 24]. In the literature, a lot of assessments of V^{max} and K_P, K_N are given; however, the spread in values of these parameters even for the same macroalgae species is very large. Different authors give assessments that differ by an order of magnitude. Apparently, this is due to the unequal conditions of the experiments. The kinetic parameters are assessed according to the Michaelis – Menten curve, which approximates the obtained uptake rates at various nutrient concentrations in the

environment. The uptake process is affected by temperature, salinity, the concentration of nutrients in the water, the initial nutrient content in alga tissues and the morphological features of macroalgae living in this region. In [25], the data on the maximum rates and half-saturation constants for two mass species of algae, determined from the measurements of uptake rates of ammonium, nitrates and phosphates in 0–30, 30–60, 60–120, 120–180 min time intervals, are presented. The obtained estimates differ by a factor of 5–10. The variability of experimental conditions and regional algae morphology peculiarities determine the variability of these characteristics.

More representative dependences are obtained by averaging these characteristics within the morphofunctional groups [15]. In the given work the regression equations for nitrogen content in the tissues, respiration rate, net and specific photosynthesis rates, as well as the specific growth rate depending on the SA / V ratio obtained from the processing of empirical data for 38 macroalgae species, are presented. We derived similar regression equations for kinetic parameters on the basis of the analysis of data given in [14, 26]. According to the classification [27], the following morphological and functional groups of macroalgae are distinguished by the type of thallus: 1 – with thin tubular and sheet-like thallus; 2 – with delicately branched filamentous thallus; 3 – with a coarsely branched thallus; 4 – with leathery blades or cartilaginous branches (Table 2).

T a b l e 2

Kinetic parameters K_m (µM) and V^{max} (µmol/g DW h) for the morphofunctional group of algae

Species of macroalgae	SA / V	K_P	V_P^{max}	K_{NO3}	$V_{NO_3}^{max}$	K_{NH4}	$V_{NH_4}^{max}$
Morphofunctional group 1							
Chaetomorpha linum	237.0	10.35	21.52	3.00	30.00	13.00	132.00
Dictyosiphon foeniculaceus	408.5	2.12	11.13	4.34	63.79	3.60	54.43
Enteromorpha ahlneriana	529.0	1.51	4.59	1.73	27.80	16.64	150.00
Enteromorpha intestinalis	315.0	8.10	13.90	43.70	237.30	66.40	439.10
Enteromorpha prolifera	529.0	–	–	7.81	122.20	8.53	138.40
Ulva lactuca	400.0	3.65	8.77	5.00	20.00	20.50	225.50
Morphofunctional group 2							
Ceramium tenuicorne	191.0	1.00	0.78	3.91	18.67	16.93	143.43
Cladophora glomerata	569.0	0.48	3.61	5.27	115.72	32.68	327.83
Cladophora serica	645.0	1.00	6.58	5.00	17.00	13.00	122.00
Pterocladia capillacea	80.0	–	–	14.19	14.2	45.00	65.00
Rhodomela confervoides	207.9	1.03	0.64	4.46	12.14	23.86	38.07
Elachista fucicola	1042.3	–	–	1.94	17.57	20.93	133.86
Pilayella littoralis	1694.0	15.40	44.20	116.4	300.1	66.6	466.70

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Morphofunctional group 3							
Apophlaea lyallii	14.9	–	–	9.26	2.19	42.08	11.56
Chordaria flagelliformis	100.0	–	–	5.10	5.93	4.35	61.95
Codium fragile	8.9	–	–	5.00	9.00	25.00	81.00
Gracilaria foliifera	30.0	–	–	2.48	9.71	1.6	23.82
Gracilaria pacifica	30.0	–	–	6.00	4.00	10.00	30.00
Phyllophora truncata	8.9	–	–	9.21	1.69	7.93	9.71
Morphofunctional group 4							
Chorda filum	17.0	0.62	1.38	0.60	6.63	3.44	23.64
Fucus distichus	30.0	–	–	3.50	20.00	4.00	60.00
Fucus spiralis	34.0	5.34	0.75	6.70	17.56	7.47	23.51
Fucus vesiculosus	33.7	11.17	1.05	24.69	9.29	14.93	24.62
Furcellaria lumbricalis	20.5	2.97	0.13	15.29	3.19	6.53	4.88
Scytothamnus australis	19.2	–	–	17.74	10.26	42.8	76.24
Xiphophora gladiata	15.6	–	–	20.97	5.19	36.69	8.72

In Fig. 4 the dependence of the maximum extraction rate and its relation to the half-saturation constant, averaged within the group, on the specific surface of thalli are represented in a double logarithmic scale. The obtained functions provide preliminary assessments of characteristics which are of interest to us. Further, these dependencies can be refined by carrying out special laboratory experiments.
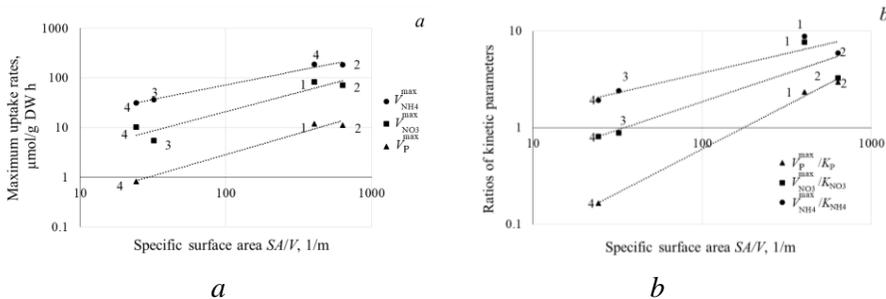
F i g. 4. Graphs of dependence of the kinetic parameters averaged within the framework of the morphofunctional group upon the thalli mean specific surface (numbers denote the group)

Discussion of the results

As a test, we present the calculations of the annual dynamics of all above-mentioned characteristics of Gracilaria, kinetic and photosynthetic parameters of which are known from the literature data [18, 28], at preset water temperatures, insolation and nutrient concentrations in the water (Fig. 5). The coefficient m in equation (1) is preset to be equal to 0.007 1/day. [23], $k_1 = 0.25$, $k_2 = 1$ (15, 16).
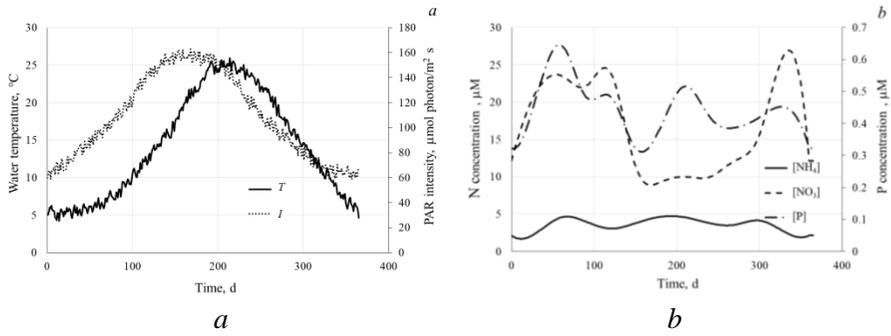
F i g. 5. Annual variability of the external (control) variables: water temperature – *1*, PAR intensity – *2*, concentrations of ammonium – *3*, nitrates – *4* and phosphates – *5* in seawater (port of Yalta, 2005 – 2010, based on the data from [29])

Fig. 6 illustrates the results of numerical integration of the system of equations (1)–(11), (15), (16) during one year with 1 h step. At the initial moment the near-minimum nitrogen and phosphorus content in the alga tissues is preset, and therefore in the first few days a rapid saturation of tissues takes place: high extraction rate leads to stabilization of nitrogen and phosphorus content at the level (Fig. 6 *c*, *d*) determined by external conditions and alga kinetic parameters. Quasi-stationary nitrogen content level is established faster than the one of the phosphorus. On this basis, we can conclude that the growth of algae in these conditions is limited by the phosphorus concentration in the water. Molar ratio of carbon, nitrogen and phosphorus in the algae tissues varies from 390: 21: 1 to 510: 25: 1.
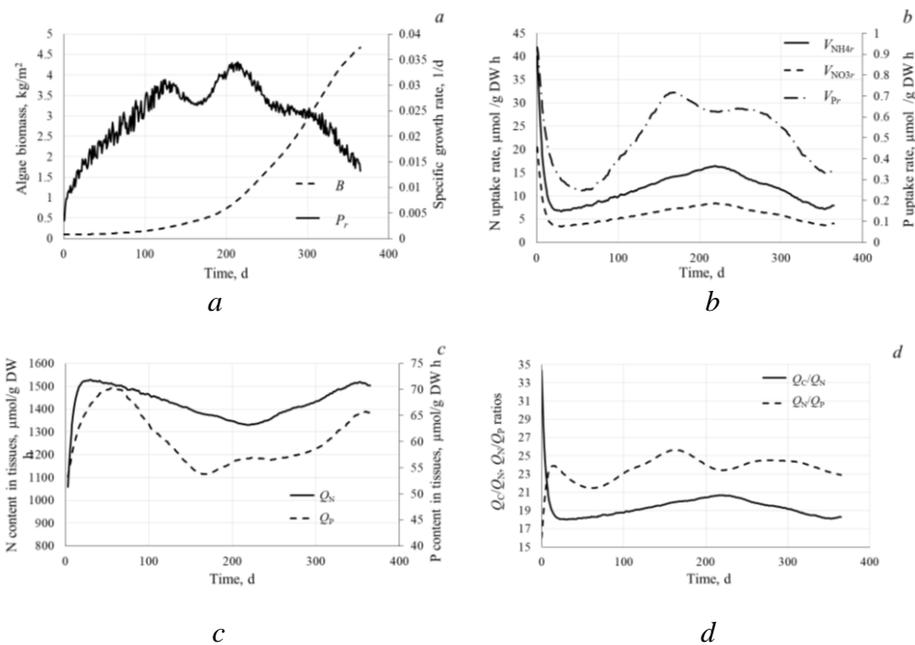
F i g. 6. Results of the numerical simulation experiment

The calculations of oxygen released by algae during the year, as well as amount of nitrogen and phosphorus uptaken from the sea water were carried out. Based on 1 ton of dry algae weight, 7.32 tons of oxygen were released per year, 180 kg of inorganic nitrogen and 17 kg of phosphorus were uptaken. Of that amount, 74 kg of nitrogen and 7 kg of phosphorus were accumulated in the macroalgae tissues, 53 kg of nitrogen and 5 kg of phosphorus were released in the form of dissolved organic matter. 53 kg of nitrogen and 5 kg of phosphorus came to the next trophic level (finfish and benthic organisms). Comparison of these estimates with the published data [23, 30] shows that model calculations provide absolute and relative values close to the field data.

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All the authors have read and approved the final manuscript.

The authors declare that they have no conflict of interest.