# MATHEMATICAL MODELLING
# МАТЕМАТИЧЕСКОЕ МОДЕЛИРОВАНИЕ





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## Mathematical Model of Plankton Dynamics Accounting for the Transformation of Nutrient Compounds, Suspended and Dissolved Substances

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**Abstract**

***Introduction.*** In the context of increasing anthropogenic pressure and imbalance of nutrients, the development of phytoplankton dynamics models becomes particularly relevant. The proposed approach integrates the description of oxygen and carbon dioxide cycles, which is critically important for assessing the risks of cyanobacterial water "blooms" and reservoir deoxygenation.

***Materials and Methods.*** An approach to constructing a comprehensive mathematical model is considered. Unlike existing analogues, this model simultaneously accounts for the dynamics of three functionally distinct phytoplankton groups with their specific preferences for nitrogen and phosphorus sources, as well as the complete silicon cycle, which is critically important for diatoms. The model integrates gas exchange processes, enabling the assessment of plankton dynamics' impact on the oxygen regime of the aquatic environment and acidity, which are key indicators of ecosystem health.

***Results.*** Stationary solutions were obtained for the problem of plankton dynamics, considering the transformation of nutrient compounds, suspended and dissolved substances, including oxygen and carbon dioxide. Depending on external conditions (light, temperature, input nutrient concentrations), several qualitatively different stable stationary states are possible.

***Discussion.*** The obtained results can be used for forecasting the consequences of reservoir eutrophication and water "blooms"; assessing the seasonal succession of plankton communities; developing strategies to reduce anthropogenic load on water bodies; and evaluating the role of marine and freshwater ecosystems in $CO_2$ absorption and oxygen production.

***Conclusions.*** Understanding the conditions under which the system reaches a particular stationary state (equilibrium) allows us to predict the long-term consequences of anthropogenic impact and develop effective management solutions.

**Keywords:** plankton dynamics, nutrients, dissolved oxygen, carbon dioxide, stationary solution

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*Оригинальное эмпирическое исследование*

# Математическая модель динамики фитопланктона с учетом трансформации биогенных соединений, взвешенных и растворённых веществ

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**Аннотация**

***Введение.*** В условиях возрастающей антропогенной нагрузки и нарушения баланса биогенных элементов особую актуальность приобретает разработка моделей динамики фитопланктона. Предлагаемый в настоящей работе подход интегрирует описание циклов кислорода и углекислого газа, что критически важно для оценки рисков «цветения» воды цианобактериями и деоксигенации водоемов.

***Материалы и методы.*** Рассмотрен подход к построению комплексной математической модели, которая в отличие от существующих аналогов одновременно учитывает динамику трех функционально различных групп фитопланктона с их специфическими предпочтениями к источникам азота и фосфора, а также полный цикл кремния, критически важный для диатомей. Модель интегрирует ключевые показатели здоровья экосистемы — кислотность и процессы газообмена, что позволяет оценивать влияние динамики планктона на кислородный режим водной среды.

***Результаты исследования.*** Получены стационарные решения задачи динамики планктона с учетом трансформации биогенных соединений, взвешенных и растворённых веществ, в том числе кислорода и углекислого газа. В зависимости от внешних условий (свет, температура, входные концентрации биогенных веществ) возможны несколько качественно различных устойчивых стационарных состояний.

***Обсуждение.*** Полученные результаты могут быть использованы для прогноза последствий эвтрофикации водоемов, «цветения» вод, оценки сезонной сукцессии планктонных сообществ; разработки стратегий снижения антропогенной нагрузки на водоемы; оценки роли морских и пресноводных экосистем в поглощении $CO_2$ и продуцировании кислорода.

***Заключение.*** Проанализированы условия, при которых система приходит к тому или иному стационарному состоянию (равновесию), что позволит спрогнозировать долгосрочные последствия антропогенного воздействия и разрабатывать эффективные управляющие решения.

**Ключевые слова:** динамика планктона, биогенные вещества, растворенный кислород, углекислый газ, стационарное решение

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**Introduction.** The ecosystem of a water body is a complex organized structure in which different groups of aquatic organisms interact both with organic substances and with environmental factors such as salinity, temperature, and others. The level of dissolved oxygen has a substantial effect on the ecosystem, since oxygen deficiency may lead to mass mortality of living organisms. Growth in industrial production and the discharge of industrial waste and pollutants into water bodies sharply increase the load on aquatic ecosystems. For example, in recent decades the carbon cycle has had a significant impact on aquatic ecosystems, because the level of carbon dioxide uptake by the world ocean has been increasing. This, in turn, affects both the pH of water and the chemical reactions occurring in the water column, which substantially influence the vital activity of living organisms.

Phytoplankton, as the main producer in most aquatic ecosystems, plays a key role in global biogeochemical cycles by producing oxygen and absorbing carbon dioxide. However, under anthropogenic impact, primarily eutrophication, i. e. enrichment of waters with biogenic elements (nitrogen and phosphorus), the natural balance of plankton communities is disturbed. This disturbance is often manifested as massive water blooms, which may be caused by different phytoplankton groups. Blooms of cyanobacteria (blue-green algae) are especially hazardous, since many of them produce toxins dangerous

to aquatic organisms, animals, and humans. In addition, the decomposition of dead plankton biomass leads to deoxygenation of water, resulting in "dead zones", hypoxic and anoxic areas unsuitable for aerobic organisms [1]. A shift in dominant phytoplankton species, for example from diatoms to cyanobacteria, is an indicator of serious changes in ecosystem status.

A key aspect of aquatic ecosystem functioning is the transformation of substances. The input of mineral forms of phosphorus and nitrogen stimulates phytoplankton growth. The death and excretion of organic matter initiate degradation processes that are closely related to the dynamics of dissolved oxygen ($O_2$) and carbon dioxide ($CO_2$). The oxygen regime in surface waters is formed mainly by production processes, whereas in near-bottom waters it is determined primarily by the biochemical decomposition of bottom sediments [2]. Dissolved oxygen is not only a source for the respiration of aquatic organisms but also a factor determining the completeness and rate of organic matter mineralization in a water body. A characteristic feature of the oxygen regime of the Sea of Azov is its instability, which is determined by a number of permanent and seasonal factors: absorption of atmospheric oxygen by the surface water layer, uneven inflow of river and Black Sea waters, development and decline of organism activity, circulation processes that control the penetration of oxygen into near-bottom layers, and other processes [3].

In this regard, the relevant task is not merely to forecast the growth of phytoplankton biomass, but to provide integrated modeling of the plankton community structure and the associated biogeochemical cycles. Mathematical modeling becomes an indispensable tool for solving this problem, since it makes it possible to integrate heterogeneous data on physical, chemical, and biological processes and to predict the response of the system to changing external conditions.

Classical models, such as the Monod equation or the Michaelis-Menten model, describe the dependence of phytoplankton growth rate on the concentration of a single limiting substance (nitrogen or phosphorus) [4]. More complex models take into account simultaneous limitation by several resources. To describe phytoplankton adaptation to changing conditions, models of phytoplankton growth have been developed in which the growth rate depends on the internal content of nutrients in the cell, rather than only on their concentration in the surrounding environment (the Droop model) [5].

The competitive exclusion model (Gause's law or principle) predicts that, in a stationary state, only as many species can survive as there are limiting resources [6]. This stimulated the development of models that include additional factors allowing a larger number of species to coexist: spatial heterogeneity, temporal variability of parameters, allelopathy, and the presence of predators (zooplankton). In the context of the present study, models that consider competition among phytoplankton with different strategies for consuming nutrients, for example the ability of cyanobacteria to fix atmospheric nitrogen, are of particular importance.

The works of such researchers as Riley, Steele, and Lorenz laid the foundations for including biogeochemical processes in ecosystem models [7, 8]. Models of the nitrogen cycle incorporating nitrification and denitrification were developed, including WASP (Water Quality Analysis Simulation Program) [9] and ERSEM (European Regional Seas Ecosystem Model) [10]. In the 1990s and 2000s, models of plankton dynamics were integrated with biogeochemical models, which made it possible to describe seasonal variability in species composition and the related changes in elemental cycles.

The dynamics of $O_2$ and $CO_2$ are traditionally modeled through the balance of photosynthesis, respiration, and air-water gas exchange [11]. The complexity lies in the need to account for diurnal dynamics, which are often averaged in models intended for long-term forecasts. Recently, increasing attention has been paid to modeling the carbonate system (pH, alkalinity) and its effect on the growth of different phytoplankton species.

Classical models, such as the NPZ (Nutrient-Phytoplankton-Zooplankton) model [12], focus on the interaction among nutrients, phytoplankton, and zooplankton. However, they often treat biogenic elements in a simplified way, for example by representing "nitrogen" or "phosphorus" as a single pool.

More complex models take into account the transformation of different forms of elements. For example, the nitrogen cycle is detailed by considering nitrification (oxidation of ammonium to nitrites and then to nitrates) and denitrification [13]. This is critically important because different phytoplankton species have different preferences for nitrogen sources: diatoms prefer nitrates, many green algae prefer ammonium, and some cyanobacteria are able to fix atmospheric nitrogen ($N_2$), which gives them a competitive advantage in nitrogen-poor waters.

Similarly, to describe the dynamics of diatoms adequately, the silicon cycle must be taken into account, since their frustule consists of silica ($SiO_2$). Models that ignore silicon limitation may substantially overestimate forecasts of diatom biomass.

Models that include oxygen and $CO_2$ dynamics represent the next level of complexity. They make it possible to assess the consequences of eutrophication not only in terms of algal biomass, but also in terms of ecosystem health (oxygen regime) and its role in the carbon cycle. Such models are often based on stoichiometric ratios (Redfield ratios [11]) among carbon, nitrogen, and phosphorus in plankton biomass.

Despite the existence of integrated models, such as the ERSEM family of models, the literature still lacks models that simultaneously account for competition among several specific phytoplankton species with different nutritional strategies, the complete silicon cycle, and gas dynamics within a closed system of equations. The present study aims to fill this gap by constructing an integrated model and conducting a systematic analysis of its stationary states, which is a fundamental task for understanding the resilience of aquatic ecosystems to anthropogenic impact.

**Materials and Methods**

**1. Mathematical model of plankton dynamics.** The proposed model of plankton dynamics is based on a system of transport equations for nutrients [11, 13, 14]:

$$\frac{\partial q_i}{\partial t}+\frac{\partial (uq_i)}{\partial x}+\frac{\partial (vq_i)}{\partial y}+\frac{\partial ((w+w_{s,i})q_i)}{\partial z}=\frac{\partial}{\partial x}\left(\mu\frac{\partial q_i}{\partial x}\right)+\frac{\partial}{\partial y}\left(\mu\frac{\partial q_i}{\partial y}\right)+\frac{\partial}{\partial z}\left(\upsilon\frac{\partial q_i}{\partial z}\right)+R_{q_i}+C_{q_i}, \quad (1)$$

where $q_i$ is the concentration of the $i$-th component, mg/L (the components are listed in Table 1); $\mathbf{V} = \{u,v,w\}$ are the components of the water-flow velocity vector, m/s; $w_{s,i}$ is the gravitational settling velocity of the $i$-th component if it is suspended; μ, υ are the horizontal and vertical components of the turbulent exchange coefficient, m²/s; $R_{q_i}$ is the source function for nutrients, mg/(L·s); $C_{q_i}$ is the flux of oxygen and carbon dioxide from the atmosphere, mg/(L·s).

The model under consideration accounts for the following factors (components), presented in Table 1 and forming the system of equations (1).

Table 1

Components of the mathematical model (1)

| $i$ | Sym. | Name |
|---|---|---|
| 1. | $F_1$ | concentration of green algae (*Chlorella vulgaris*) |
| 2. | $F_2$ | concentration of blue-green algae (*Aphanizomenon flos-aquae*) |
| 3. | $F_3$ | concentration of diatoms (*Sceletonema costatum*) |
| 4. | $PO_4$ | concentration of phosphates, mineral phosphorus |
| 5. | $POP$ | concentration of suspended organic phosphorus |
| 6. | $DOP$ | concentration of dissolved organic phosphorus |
| 7. | $NO_3$ | concentration of nitrates |
| 8. | $NO_2$ | concentration of nitrites |
| 9. | $NH_4$ | concentration of ammonium |
| 10. | $Si$ | concentration of dissolved inorganic silicon (silicic acid, $Si(OH)_4$) |
| 11. | $O_2$ | concentration of dissolved oxygen |
| 12. | $CO_2$ | concentration of carbon dioxide (gaseous carbon dioxide, dissolved organic carbon, and total inorganic carbon) |

In the further consideration of the model, the following assumptions are adopted:

1. Temperature and light regime are specified as external control parameters.

2. Hydrodynamic processes are taken into account. The velocity vector of the aquatic environment is calculated on the basis of a mathematical model of shallow-water hydrodynamics [15].

3. Zooplankton and higher aquatic vegetation are excluded from consideration in order to focus on primary production and decomposition processes.

4. The input of nutrients ($PO_4$, $NO_3$, $NH_4$, $Si$) from external sources is constant.

5. Nitrification proceeds in two stages: oxidation of $NH_4^+$ to $NO_2^-$ and oxidation of $NO_2^-$ to $NO_3^-$.

6. Mineralization, nitrification, and respiration processes depend on temperature according to the Van't Hoff law.

7. The stoichiometric ratios of elements in phytoplankton biomass ($C$:$N$:$P$:$Si$) are assumed to be constant for each species.

**2. Equations for phytoplankton.** The chemical-biological reactions for phytoplankton describing the nutrient source function can be written as follows [11, 14]:

$$R_{F_i}=C_{F_i}\left(1-K_{F_iR}\right)q_{F_i}-K_{F_iD}q_{F_i}-K_{F_iE}q_{F_i},\ i=\overline{1,3}, \quad (2)$$

where $C_{F_i}$ is the growth rate of the $i$-th phytoplankton species; $K_{F_iR}$ is the specific respiration rate of the $i$-th phytoplankton species; $K_{F_iD}$ is the specific mortality (natural death) rate of the $i$-th phytoplankton species; $K_{F_iE}$ is the specific phytoplankton excretion rate.

The growth rate of the $i$-th phytoplankton species is modeled with multiple-resource limitation: for $F_1$ and $F_2$, silicon limitation is absent; for $F_2$, fixation of molecular nitrogen ($N_2$) may be taken into account, which removes nitrogen limitation at low $NH_4$ and $NO_3$ concentrations (this can be represented by introducing an additional term $K_{N_2F_2}$, that depends on $O_2$ concentration, since fixation is inhibited by oxygen), but $N_2$ is not considered in the present study; for $F_3$, silicon limitation is mandatory; for $F_3$, $NH_4$ uptake is preferred over $NO_3$ uptake (suppression effect).

Taking these constraints into account, the following function is obtained to describe the phytoplankton growth rate:

$$C_{F_{1,2}} = K_{NF_{1,2}} f_T(T) f_I(I) f_S(S) \min\{f_P(q_{PO_4}), f_N(q_{NO_3}, q_{NO_2}, q_{NH_4})\},$$
$$C_{F_3} = K_{NF_3} f_T(T) f_I(I) f_S(S) \min\{f_P(q_{PO_4}), f_N(q_{NO_3}, q_{NO_2}, q_{NH_4}), f_{Si}(q_{Si})\}, \quad (3)$$

where $K_{NF_i}$ is the maximum specific phytoplankton growth rate; $f_T(T), f_I(I), f_S(S)$ are functions describing the dependence of the growth rate of a particular phytoplankton species on temperature, illumination, and salinity, respectively; $f_P(q_{PO_4})$, $f_N(q_{NO_3}, q_{NO_2}, q_{NH_4})$, $f_{Si}(q_{Si})$ are functions describing the dependence of the phytoplankton growth rate on the water content of phosphorus, nitrogen compounds, and silicon, respectively.

Liebig's law of the minimum, in the form $\min\{f_P(q_{PO_4}), f_N(q_{NO_3}, q_{NO_2}, q_{NH_4})\}$ and $\min\{f_P(q_{PO_4}), f_N(q_{NO_3}, q_{NO_2}, q_{NH_4}), f_{Si}(q_{Si})\}$ is used to account for the combined limiting effect of several nutrient compounds.

The dependence of phytoplankton growth on temperature and salinity is described by:

$$f_T(T) = \exp\left(-\alpha\{(T - T_{opt})/T_{opt}\}^2\right), f_S(S) = \exp\left(-\beta\{(S - S_{opt})/S_{opt}\}^2\right), \quad (4)$$

where $T_{opt}$ is the temperature, $S_{opt}$ is the salinity optimal for a particular phytoplankton species, and $\alpha > 0$ and $\beta > 0$ are the coefficients determining the width of the phytoplankton tolerance intervals for temperature and salinity, respectively.

The dependence of phytoplankton growth on illumination is described by Steele's model:

$$f_T(T) = (I/I_{opt})\exp(1 - I/I_{opt}), \quad (5)$$

where $I_{opt}$ is the optimal light intensity for photosynthesis.

The phosphorus limitation function is:

$$f_P(q_{PO_4}) = \frac{q_{PO_4}}{q_{PO_4} + K_{PO_4}}, \quad (6)$$

where $K_{PO_4}$ is the phosphate half-saturation constant.

The nitrogen-compound limitation function is:

$$f_N(q_{NO_3}, q_{NO_2}, q_{NH_4}) = f_N^{(1)}(q_{NO_3}, q_{NO_2}, q_{NH_4}) + f_N^{(2)}(q_{NH_4}),$$
$$f_N^{(1)}(q_{NO_3}, q_{NO_2}, q_{NH_4}) = \frac{(q_{NO_3} + q_{NO_2})\exp(-K_{psi} q_{NH_4})}{K_{NO_3} + (q_{NO_3} + q_{NO_2})}, \quad (7)$$
$$f_N^{(2)}(q_{NH_4}) = \frac{q_{NH_4}}{K_{NH_4} + q_{NH_4}},$$

where $K_{NO_3}$ is the nitrate half-saturation constant; $K_{NH_4}$ is the ammonium half-saturation constant; $K_{psi}$ is the ammonium inhibition coefficient.

The silicon limitation function is:

$$f_{Si}(q_{Si}) = \frac{q_{Si}}{q_{Si} + K_{Si}}, \quad (8)$$

where $K_{Si}$ is the silicon half-saturation constant.

**3. Equations for the transformation of nutrients**

**3.1. Phosphorus cycle.** Equation for phosphates ($PO_4$): the chemical-biological reaction describing the source function for phosphates ($PO_4$) can be written as follows [11, 14]:

$$R_{PO_4} = -\sum_{i=1}^{3} s_P C_{F_i}(1 - K_{F_i R}) q_{F_i} + K_{PN} q_{POP} + K_{DN} q_{DOP}, \quad (9)$$

where $s_p$ is the normalization coefficient corresponding to the stoichiometric ratio, $K_{PN}$ is the *POP* phosphatization coefficient; $K_{DN}$ is the *DOP* phosphatization coefficient. The first term in (9) reflects phosphate uptake by phytoplankton. It should also be noted that mineralization (hydrolysis) of *DOP* to phosphates occurs faster than mineralization of *POP*.

Equation for suspended organic phosphorus (*POP*):

$$R_{POP} = \sum_{i=1}^{3} s_P K_{F_i D} q_{F_i} - K_{PD} q_{POP} - K_{PN} q_{POP}, \quad (10)$$

where $K_{PD}$ is the specific *POP* autolysis rate. The first term in (10) reflects the input of *POP* from dead phytoplankton biomass, while the second and third terms represent loss due to the transition of a part of *POP* to *DOP* during decomposition and mineralization (phosphatization) of *POP*.

Equation for dissolved organic phosphorus (*DOP*):

$$R_{DOP} = \sum_{i=1}^{3} s_P K_{F_i E} q_{F_i} + K_{PD} q_{POP} - K_{DN} q_{DOP}. \quad (11)$$

The first term in (11) reflects the input of *DOP* due to lysis and exosmosis of dead phytoplankton biomass; the second term represents the transition of a part of *POP* to *DOP* during decomposition; and the third term represents mineralization of *DOP* to phosphates.

**3.2. Nitrogen cycle.** Equation for ammonium ($NH_4$): the chemical-biological reaction describing the source function for ammonium ($NH_4$) can be written as follows [11, 14]:

$$R_{NH_4} = -\sum_{i=1}^{3} s_N C_{F_i} \left(1 - K_{F_i R}\right) \frac{f_N^{(2)}\left(q_{NH_4}\right)}{f_N\left(q_{NO_3}, q_{NO_2}, q_{NH_4}\right)} q_{F_i} + \sum_{i=1}^{3} s_N \left(K_{F_i D} + K_{F_i E}\right) q_{F_i} - K_{42} q_{NH_4}, \quad (12)$$

where $s_N$ is the normalization coefficient corresponding to the stoichiometric ratio, $K_{42}$ is the specific rate of ammonium oxidation to nitrites during nitrification (in the general case, it depends on the concentrations of ammonium and oxygen). The first term in (12) reflects ammonium uptake by phytoplankton.

Equation for nitrites ($NO_2$):

$$R_{NO_2} = -\sum_{i=1}^{3} s_N C_{F_i} \left(1 - K_{F_i R}\right) \frac{f_N^{(1)}\left(q_{NO_3}, q_{NO_2}, q_{NH_4}\right)}{f_N\left(q_{NO_3}, q_{NO_2}, q_{NH_4}\right)} \cdot \frac{q_{NO_2}}{q_{NO_2} + q_{NO_3}} q_{F_i} + K_{42} q_{NH_4} - K_{23} q_{NO_2}, \quad (13)$$

where $K_{23}$ is the specific rate of nitrite oxidation to nitrates during nitrification. The first term in (13) reflects nitrite uptake by phytoplankton (usually insignificant), the second term represents the inflow due to the first stage of nitrification (oxidation of ammonium to nitrites), and the third term represents the outflow due to the second stage of nitrification (oxidation of nitrites to nitrates).

Equation for nitrates ($NO_3$):

$$R_{NO_3} = -\sum_{i=1}^{3} s_N C_{F_i} \left(1 - K_{F_i R}\right) \frac{f_N^{(1)}\left(q_{NO_3}, q_{NO_2}, q_{NH_4}\right)}{f_N\left(q_{NO_3}, q_{NO_2}, q_{NH_4}\right)} \cdot \frac{q_{NO_3}}{q_{NO_2} + q_{NO_3}} q_{F_i} + K_{23} q_{NO_2}. \quad (14)$$

The first term in (14) reflects nitrate uptake by phytoplankton, while the second term represents the inflow due to the second stage of nitrification (oxidation of nitrites to nitrates).

**3.3. Silicon cycle.** The chemical-biological reaction describing the source function for dissolved silicon (*Si*) can be written as follows [11, 14]:

$$R_{Si} = -s_{Si} C_{F_3} \left(1 - K_{F_3 R}\right) q_{F_3} + s_{si} K_{F_3 D} q_{F_3}, \quad (15)$$

where $s_{si}$ is the normalization coefficient corresponding to the stoichiometric ratio. The first term in (15) represents silicon uptake by diatoms, and the second term represents the inflow due to dissolution of biogenic silicon from the frustules of dead diatoms.

**4. Equations for dissolved gases**

**4.1. Dissolved oxygen**

$$R_{O_2} = s_O \sum_{i=1}^{3} s_P C_{F_i} \left(K_{F_i R} - 1\right) q_{F_i} + s_O \left(K_{PN} q_{POP} + K_{DN} q_{DOP}\right) + \gamma_{O_2}^{(1)} K_{42} q_{NH_4} - \gamma_{O_2}^{(2)} K_{23} q_{NO_2} + C_{O_2}, \quad (16)$$

where $s_O$ is the normalization coefficient corresponding to the stoichiometric ratio, $\gamma_{O_2}^{(1)}$ is the oxygen consumption coefficient for the first stage of nitrification (oxidation of ammonium to nitrites), $\gamma_{O_2}^{(2)}$ is the oxygen consumption coefficient for the second stage of nitrification (oxidation of nitrites to nitrates), and $C_{O_2}$ is gas exchange with the atmosphere. The first term in (16) reflects $O_2$ production during photosynthesis and $O_2$ consumption for phytoplankton respiration; the second and third terms reflect the participation of $O_2$ in phosphatization; and the fourth and fifth terms reflect the participation of $O_2$ in nitrification. To describe oxygen gas exchange between the atmosphere and the ocean, we use [16]:

$$C_{O_2} = k_{O_2} \left(\frac{Sc}{660}\right)^{-0,5} \left(C_{O_2 eq} - q_{O_2}\right), \quad (17)$$

where $k_{O_2}$ is the relative gas-exchange rate, which can be calculated as a function of wind speed, $k_{O_2}(u) = 0.365u^2 + 0.4u$ [16], where $u$ is wind speed; *Sc* is the Schmidt number, which reflects the ratio between kinematic viscosity and the turbulent exchange coefficient; for oxygen at 20 °C, *Sc* = 660; and $C_{O_2 eq}$ is the equilibrium oxygen concentration, calculated as a function of temperature and salinity according to UNESCO standards (1986) [17]; at 20 °C it is 31 mL/L.

**4.2. Carbon dioxide**

$$R_{CO_2} = s_C \sum_{i=1}^{3} C_{F_i} \left( K_{F_i R} - 1 \right) q_{F_i} + C_{CO_2}, \tag{18}$$

where $s_C$ is the normalization coefficient corresponding to the stoichiometric ratio, $C_{CO_2}$ is gas exchange with the atmosphere. The first term in (18) reflects $CO_2$ consumption during photosynthesis and $CO_2$ release during phytoplankton respiration.

To describe carbon dioxide gas exchange between the atmosphere and the ocean, we use the following formula [18]:

$$C_{CO_2} = k_{CO_2} \left( C_{CO_2 eq} - q_{CO_2} \right), \tag{19}$$

where $k_{CO_2}$ is the exchange coefficient calculated from near-surface wind speed using empirical formulas according to [19], and $C_{CO_2 eq}$ is the equilibrium carbon dioxide concentration calculated by Henry's law: $C = kP$, where $P$ is the partial pressure of carbon dioxide and $k$ is Henry's constant, which depends on the gas and the liquid.

**5. Specification of initial and boundary conditions.** For system (1), we prescribe the vector field of water-flow velocities calculated on the basis of a mathematical model of shallow-water hydrodynamics [15, 20], the salinity field S and temperature field T, as well as the initial values of the concentration functions $q_i$, where the index i corresponds to the components presented in Table 1:

$$q_i (x, y, z, 0) = q_t^0 (x, y, z), \ (x, y, z) \in \bar{G}, \ t = 0, \tag{20}$$

$$\mathbf{V}(x,y,z,0) = \mathbf{V}_0(x,y,z),\ T(x,y,z,0) = T_0(x,y,z),\ S(x,y,z,0) = S_0(x,y,z).$$

We consider the mathematical model (1)–(19) in the computational domain $G$, which is a closed basin bounded by the undisturbed water surface $\Sigma_0$, the bottom $\Sigma_H = \Sigma_H (x, y)$ and the cylindrical (lateral) surface σ over the time interval $0 < t \le T$. $\Sigma = \Sigma_0 \cup \Sigma_H \cup \sigma$ is the piecewise smooth boundary of the domain $G$. Let $\mathbf{n}$ be the outward normal vector to the surface Σ, and $u_{\mathbf{n}}$ be the component of the water-flow velocity vector normal to Σ.

For the concentrations of all substances except $O_2$ and $CO_2$, we assume that there is no substance input through the upper boundary of the computational domain:

$$\frac{\partial q_i}{\partial z} = 0, \ i = \overline{1,10}. \tag{21}$$

For dissolved oxygen and carbon dioxide, gas exchange with the atmosphere is calculated according to formulas (17) and (19):

$$\frac{\partial q_{11}}{\partial z} = C_{O_2} (q_{11}), \ \frac{\partial q_{12}}{\partial z} = C_{CO_2} (q_{12}). \tag{22}$$

On the lateral boundary σ, the following conditions are specified for the concentrations of all substances presented in Table 1:

$$q_i = 0, \text{ если } u_{\mathbf{n}} < 0; \ \frac{\partial q_i}{\partial \mathbf{n}} = 0, \text{ если } u_{\mathbf{n}} \ge 0. \tag{23}$$

At the bottom $\Sigma_H$ the following conditions are specified for the concentrations of all substances presented in Table 1:

$$\frac{\partial q_i}{\partial z} = \varepsilon_i q_i, \tag{24}$$

where $\varepsilon_i$ is the absorption coefficient of the $i$-th component by bottom sediments.

The proposed model (1)–(24) can be used to simulate the movement and accumulation of dissolved oxygen and carbon dioxide in the water column and to study their effect on the ecosystem of a water body.

**Model parameter selection.** To refine the parameters of the phytoplankton-dynamics model accounting for the transformation of nutrient compounds, suspended and dissolved substances, including oxygen and carbon dioxide, we find stationary solutions of the model (1)–(24). For the computational experiment, a program was written in the *R* programming language. It implements the solution of the system of ordinary differential equations (ODEs) (2), (9)–(16), (18) by the fourth-order Runge-Kutta method, constructs plots of the resulting stationary solutions for the concentrations of phytoplankton, nutrient compounds, suspended and dissolved substances, and checks the stability of the obtained stationary solutions. Numerical experiments were performed under the assumption that phytoplankton development depends on a single limiting substance.

The input values of the parameters of the phytoplankton-dynamics model accounting for the transformation of nutrient compounds, suspended and dissolved substances, including oxygen and carbon dioxide, as well as the initial concentrations of phytoplankton, nutrient compounds, suspended and dissolved substances, are presented in Table 2. Limitation by temperature, salinity (4), and illumination (5) was not taken into account: $T = T_{opt}$, $I = I_{opt}$, $S = S_{opt}$.

Table 2

Values of phytoplankton-dynamics model parameters and initial concentrations of the studied substances

| Sym. | Name | Value | Unit |
|---|---|---|---|
| Model parameters | | | |
| Green alga (*Chlorella vulgaris*) | | | |
| $K_{NF_1}$ | maximum specific growth rate | 2.8000 | 1/day |
| $K_{F_1R}$ | specific respiration rate | 0.1500 | 1/day |
| $K_{F_1D}$ | specific mortality rate | 0.0500 | 1/day |
| $K_{F_1E}$ | specific excretion rate | 0.1500 | 1/day |
| $K_{PO_4}$ | phosphate half-saturation constant | 0.2400 | |
| $K_{NO_3}$ | nitrate half-saturation constant | 0.3000 | |
| $K_{NH_4}$ | ammonium half-saturation constant | 0.2000 | |
| Blue-green alga (*Aphanizomenon flos-aquae*) | | | |
| $K_{NF_2}$ | maximum specific growth rate | 2.8000 | 1/day |
| $K_{F_2R}$ | specific respiration rate | 0.1500 | 1/day |
| $K_{F_2D}$ | specific mortality rate | 0.0500 | 1/day |
| $K_{F_2E}$ | specific excretion rate | 0.1500 | 1/day |
| $K_{PO_4}$ | phosphate half-saturation constant | 0.2400 | |
| $K_{NO_3}$ | nitrate half-saturation constant | 0.3000 | |
| $K_{NH_4}$ | ammonium half-saturation constant | 0.2000 | |
| Diatom (*Sceletonema costatum*) | | | |
| $K_{NF_3}$ | maximum specific growth rate | 2.8000 | 1/day |
| $K_{F_3R}$ | specific respiration rate | 0.1500 | 1/day |
| $K_{F_3D}$ | specific mortality rate | 0.0500 | 1/day |
| $K_{F_3E}$ | specific excretion rate | 0.15 | 1/day |
| $K_{PO_4}$ | phosphate half-saturation constant | 0.2400 | |
| $K_{NO_3}$ | nitrate half-saturation constant | 0.3000 | |
| $K_{NH_4}$ | ammonium half-saturation constant | 0.2000 | |
| $K_{Si}$ | silicon half-saturation constant | 3.0000 | |
| Phosphorus cycle | | | |
| $K_{PD}$ | specific *POP* autolysis rate | 0.0150 | 1/day |
| $K_{PN}$ | *POP* phosphatization coefficient | 0.0200 | 1/day |
| $K_{DN}$ | *DOP* phosphatization coefficient | 0.1000 | 1/day |
| $s_P$ | normalization coefficient | 0.0100 | |
| Nitrogen cycle | | | |
| $K_{42}$ | specific rate of ammonium oxidation to nitrites | 0.9000 | 1/day |
| $K_{23}$ | specific rate of nitrite oxidation to nitrates | 2.5000 | 1/day |
| $K_{psi}$ | ammonium inhibition coefficient | 1.4600 | 1/day |
| $s_N$ | normalization coefficient | 0.0160 | |
| Silicon cycle | | | |
| $S_{Si}$ | normalization coefficient | 0.0230 | |
| Dissolved oxygen | | | |
| $s_O$ | normalization coefficient | 0.0500 | |
| $\gamma_{O_2}^{(1)}$ | oxygen consumption coefficient for the first stage of nitrification | 0.0500 | 1/day |
| $\gamma_{O_2}^{(2)}$ | oxygen consumption coefficient for the second stage of nitrification | 0.0015 | 1/day |
| $C_{O_2eq}$ | equilibrium oxygen concentration[1] | 9,1000 | mg/L |

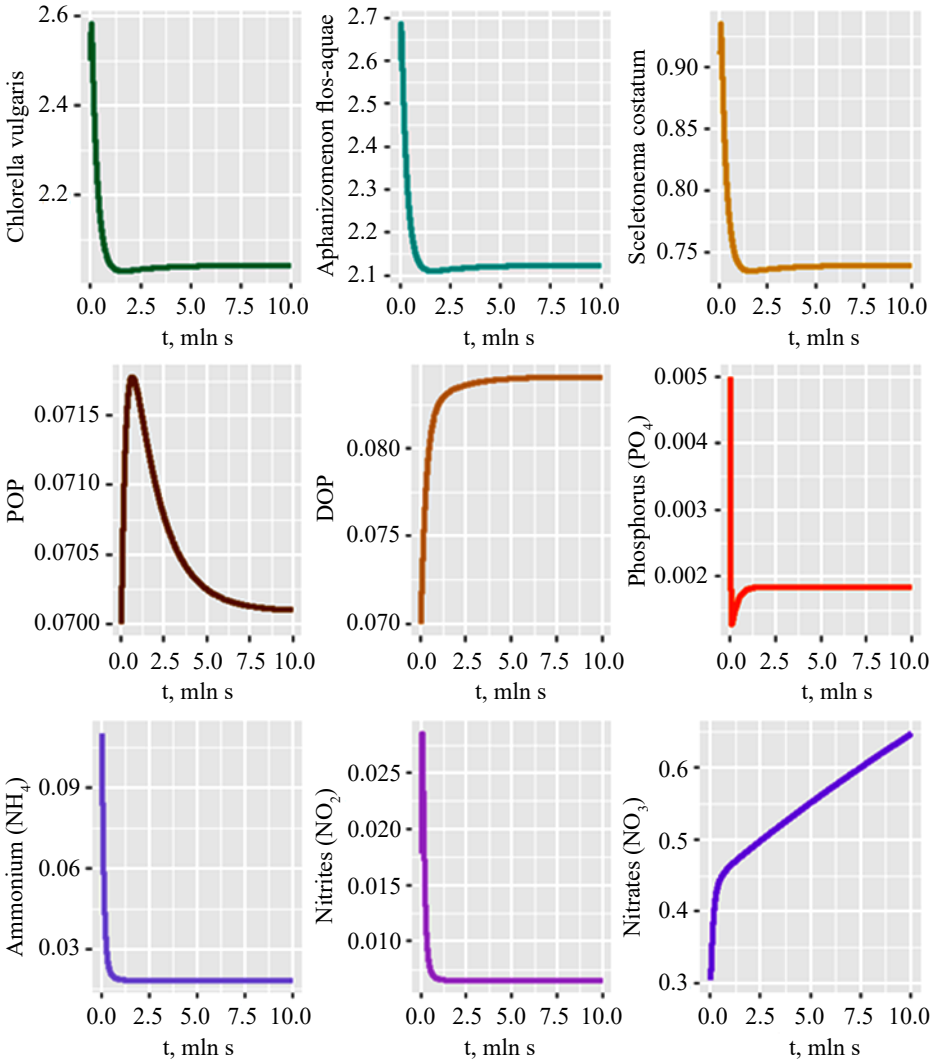
[1] For simplicity, the equilibrium oxygen concentration was calculated based on an empirical temperature dependence formula: $C_{CO_2eq}(T) = 14.6 - 0.42 \cdot T + 0.008 \cdot T^2$, $T = T_{opt} = 25$ °C.

End of Table 2

| Sym. | Name | Value | Unit |
|---|---|---|---|
| Model parameters | | | |
| Carbon dioxide | | | |
| $s_C$ | normalization coefficient | 0.0020 | 1/day |
| $C_{CO_2eq}$ | equilibrium carbon dioxide concentration | 1.5000 | mg/L |
| Initial concentrations | | | |
| $q_1$ | initial concentration of green algae | 2.5000 | mg/L |
| $q_2$ | initial concentration of blue-green algae | 2.6000 | mg/L |
| $q_3$ | initial concentration of diatoms | 0.9100 | mg/L |
| $q_{PO_4}$ | initial concentration of phosphates | 0.0050 | mg/L |
| $q_{POP}$ | initial concentration of suspended organic phosphorus | 0.0700 | mg/L |
| $q_{DOP}$ | initial concentration of dissolved organic phosphorus | 0.0700 | mg/L |
| $q_{NO_3}$ | initial concentration of nitrates | 0.3040 | mg/L |
| $q_{NO_2}$ | initial concentration of nitrites | 0.0178 | mg/L |

Fig. 1 presents the simulation results for the stationary regime of the ODE system under the assumption that phytoplankton development is limited by phosphorus, nitrogen, and silicon. The limitation functions are calculated on the basis of (6)–(8).

The computational experiments show that, for the initial concentrations and equation parameters specified in Table 2, stationary regimes arise for the ODE system (2), (10)–(17), (19), which describes the case of a spatially uniform distribution of substances.



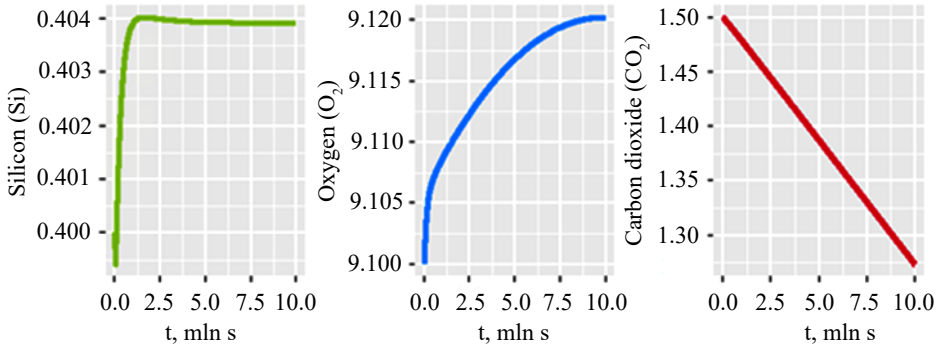



Fig. 1. Stationary regimes of the phytoplankton-dynamics model

Over time, the dynamics become smooth and oscillations decrease until a stationary state is reached. For nitrates in Fig. 1, an increase in concentration is observed, but it does not exceed $10^{-6}$ mg/L. The decrease in carbon dioxide concentration in Fig. 1 also does not exceed $10^{-5}$ mg/L. These results illustrate the stable distribution of algae and oxygen in the water body achieved by the model.

**Silicon deficiency scenario.** On the basis of the refined model parameters, several scenarios of phytoplankton dynamics accounting for the transformation of nutrient compounds, suspended and dissolved substances, including oxygen and carbon dioxide, are considered. As the first scenario, we consider the case of a low silicon concentration. The model parameters and initial concentrations were specified according to Table 2, except for the silicon concentration, which was set to $q_{Si} = 0.01$ mg/L. The simulation results are presented in Fig. 2. As shown by the obtained results, silicon deficiency substantially affected the concentration of diatoms, which by the end of the simulation period did not exceed $2 \cdot 10^{-9}$ mg/L. At the same time, the concentrations of green and blue-green algae were higher than in Fig. 1 (with the initial silicon concentration $q_{Si} = 0.4$ mg/L).

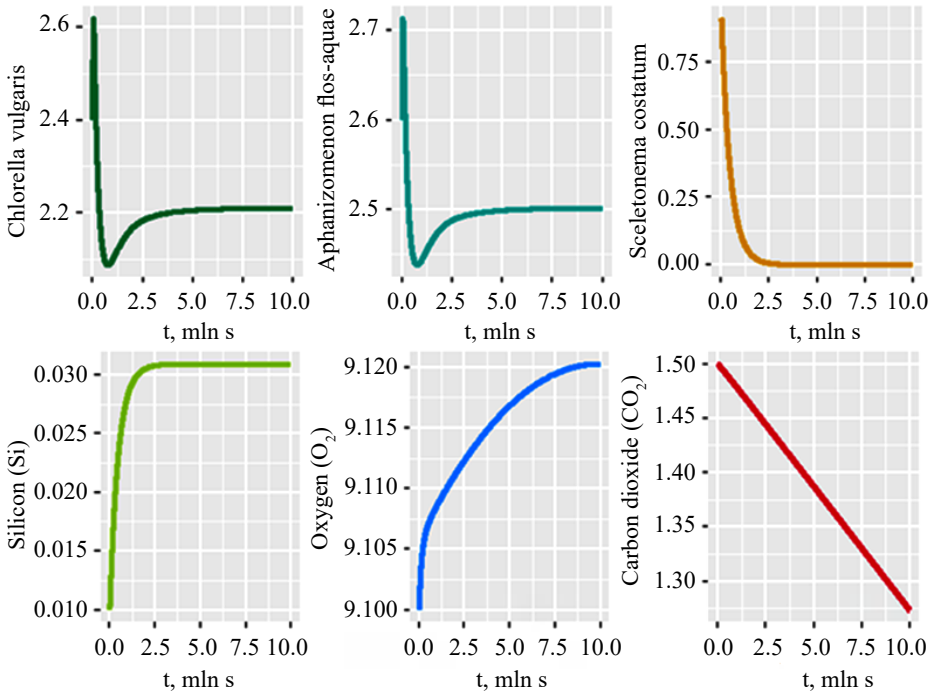



Fig. 2. Stationary regimes of the phytoplankton-dynamics model under silicon deficiency

**Nitrogen deficiency scenario.** As the second scenario, we consider the case of nitrogen deficiency. The model parameters and initial concentrations were specified according to Table 2, except for the concentrations of nitrates, nitrites, and ammonium, which were set to $q_{NO_2} = 0{,}001$ mg/L, $q_{NO_3} = 0{,}001$ mg/L, $q_{NH_4} = 0{,}01$ mg/L.

The simulation results are presented in Fig. 3. The deficiency of nitrogen compounds substantially reduced the biomass of all three phytoplankton species (to $7.7 \cdot 10^{-5}$ mg/L, $8 \cdot 10^{-5}$ mg/L, and $2.8 \cdot 10^{-5}$ mg/L for green, blue-green, and diatom algae, respectively) and also affected the concentrations of other nutrient and dissolved substances.

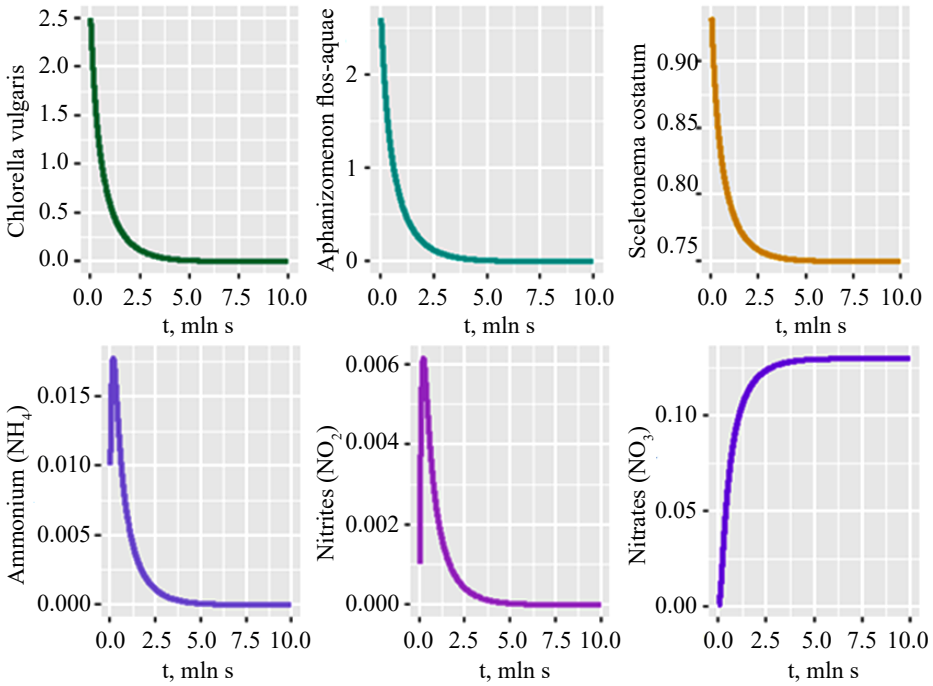



Fig. 3. Stationary regimes of the phytoplankton-dynamics model under nitrogen deficiency

**Phosphorus deficiency scenario.** As the third scenario, we consider the case of phosphorus deficiency. The model parameters and initial concentrations were specified according to Table 2, except for the concentrations of phosphates and suspended and dissolved organic phosphorus: $q_{PO_4} = 0.0005$ mg/L, $q_{POP} = 0.007$ mg/L, $q_{DOP} = 0.007$ mg/L.

The simulation results are presented in Fig. 4. The deficiency of phosphorus compounds reduced the biomass of all three phytoplankton species, although not as strongly as nitrogen deficiency.

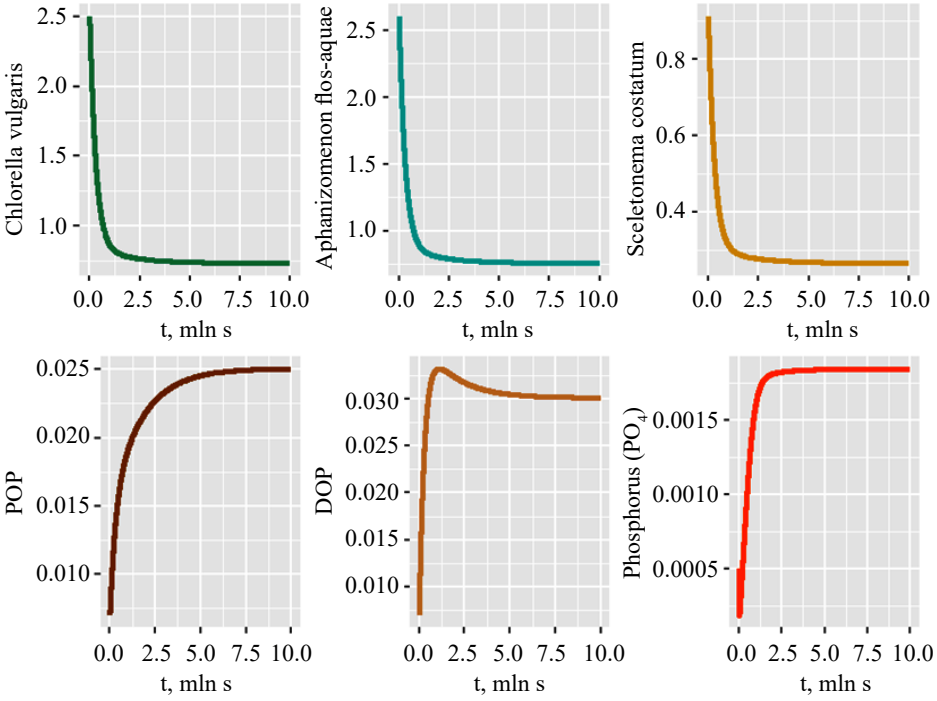



Fig. 4. Stationary regimes of the phytoplankton-dynamics model under phosphorus deficiency

Nutrient abundance scenario. As the fourth scenario, we consider the case of abundant compounds of all nutrients. The model parameters were specified according to Table 2. The initial concentrations of substances were as follows: $q_1 = 2.5$ mg/L; $q_2 = 2.6$ mg/L; $q_3 = 0.91$ mg/L; $q_{PO_4} = 0.05$ mg/L; $q_{POP} = 0.7$ mg/L; $q_{DOP} = 0.7$ mg/L; $q_{NO_3} = 0.09$ mg/L; $q_{NO_2} = 0.17$ mg/L; $q_{NH_4} = 0.8$ mg/L; $q_{Si} = 2$ mg/L; $q_{O_2} = 9.1$ mg/L; $q_{CO_2} = 2.5$ mg/L.

The simulation results are presented in Fig. 5. As expected, an abundance of nutrients leads to accelerated growth of all three phytoplankton species. The final concentrations of substances are as follows: $q_1$ = 15.14 mg/L; $q_2$ = 15.75 mg/L; $q_3$ = 5.51 mg/L; $q_{PO_4}$ = 0.0018 mg/L; $q_{POP}$ = 0.52 mg/L; $q_{DOP}$ = 0.624 mg/L; $q_{NO_3}$ = 4.786 mg/L; $q_{NO_2}$ = 0.052 mg/L; $q_{NH_4}$ = 0.145 mg/L; $q_{Si}$ = 1.89 mg/L; $q_{O_2}$ = 9.44 mg/L; $q_{CO_2}$ = 0.819 mg/L.

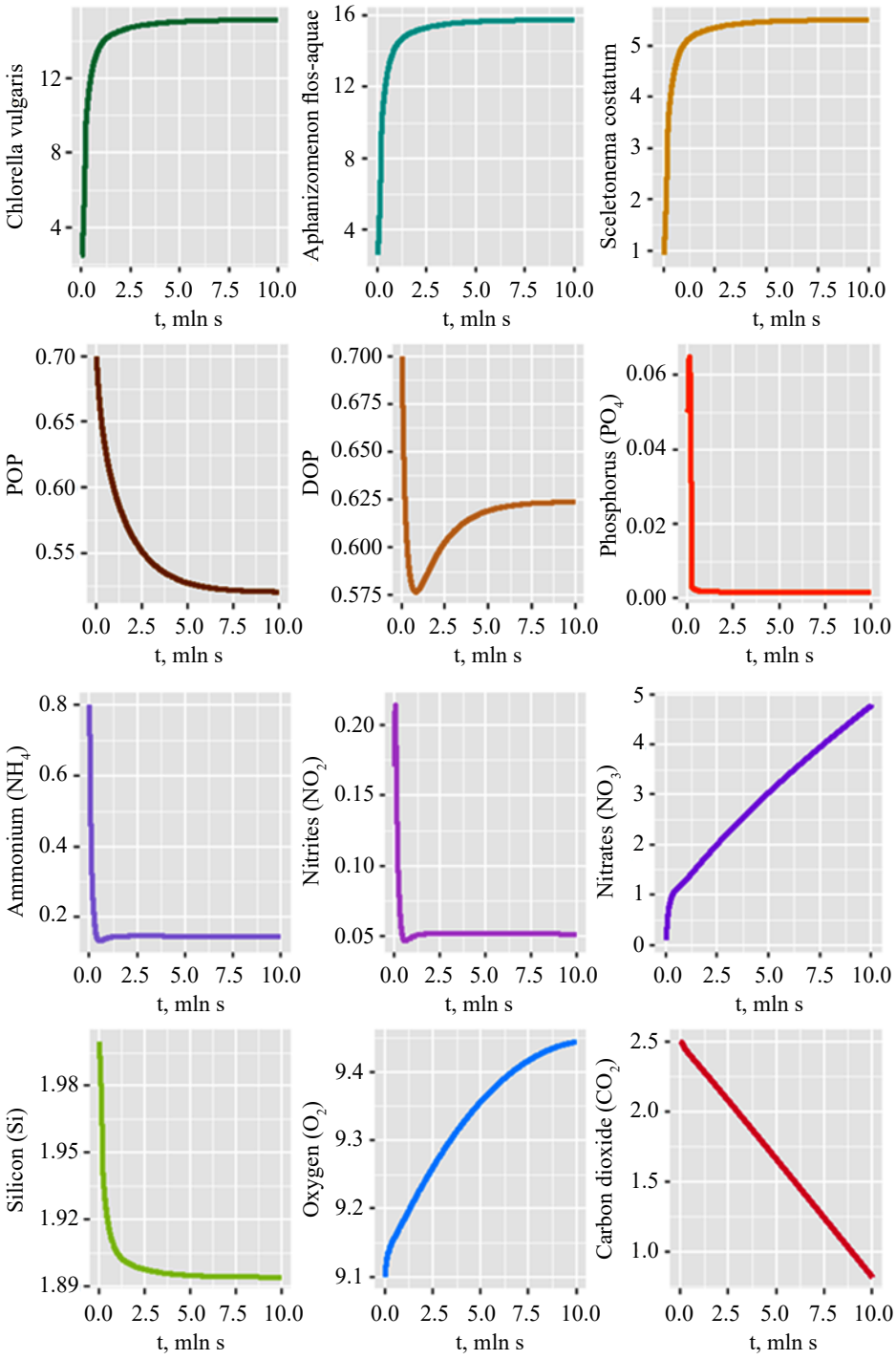



Fig. 5. Stationary regimes of the plankton-dynamics model under nutrient abundance

**Discussion.** In the course of the study, an integrated mathematical model of plankton dynamics was considered with allowance for the transformation of nutrient compounds, suspended and dissolved substances, including oxygen and carbon dioxide. The model is characterized by a high level of detail in the description of biogeochemical cycles, which makes it possible to describe processes in real aquatic ecosystems more adequately.

The main result of the study is a qualitative investigation of stationary solutions of this model. Various scenarios of nutrient concentrations were considered. The obtained solutions are consistent with data from field experiments.

It was established that the key factors determining the structure of the plankton community at equilibrium are the ratios of biogenic elements. The rate of gas exchange with the atmosphere and $O_2$-dependent nitrification processes are critical feedbacks that can stabilize or destabilize the system.

**Conclusion.** The results of the study make it possible to forecast the consequences of anthropogenic impact on water bodies. For example, the model predicts that a set of measures may be required to shift the system to a more favorable state, such as diatom dominance. Such measures may include reducing the input of phosphorus compounds, managing silicon runoff, and intensifying water mixing to improve the oxygen regime.

Further research should focus on increasing the model complexity by including zooplankton, detailing light-transmission processes, accounting for spatial heterogeneity, and validating the model against field data.

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