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Phytoplankton Dynamics and Biogeochemistry: Model Studies

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Abstract: The seasonal dynamics of the NE Black Sea phytoplankton follow the following pattern: small diatoms (spring) → coccolithophorid *Emiliana huxleyi* (late spring–early summer) → large diatoms (summer). Our hypothesis states that nitrogen and phosphorus concentrations regulate the seasonal phytoplankton dynamics. A minimum number of parameters is enough to understand the mechanisms of dominant species change. Based on the concept of intracellular regulation, the following parameters were evaluated: the minimum nitrogen and phosphorus quotas; half-saturation constants for nitrogen and phosphorus uptake; the maximum specific growth rate of the dominant phytoplankton species. Computational experiments on the model show the following: (1) in spring, a species with a high maximum specific growth rate becomes dominant; (2) in late spring and early summer, a species with a low minimum nitrogen quota and a low half-saturation constant for nitrogen uptake is observed; (3) in summer, a low minimum phosphorus quota and a low half-saturation constant for phosphorus uptake allow the species to become dominant.

Keywords: phytoplankton; biogeochemistry; seasonal dynamic; model; diatoms; coccolithophores



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1. Introduction

Oceanic phytoplankton is responsible for half of the carbon assimilated from the atmosphere [1], exerting a significant regulatory influence on the planet's climate. As a complex system of interconnected biogeochemical processes for capturing atmospheric inorganic carbon, its transformation, and transportation to depth, the biological carbon pump plays a fundamental role in climate regulation [2,3]. Inorganic carbon is a crucial matter in the reactions of photosynthesis to form organic matter, and this is an organic pump. Carbon can also participate in calcite formation reactions, which is the carbonate pump. The ratio between carbonate and organic pumps depends on the structure of phytoplankton and, above all, the ratio of diatom phytoplankton and coccolithophorids [4]. Diatoms are responsible for the organic pump's functioning; coccolithophores determine the carbonate pump's operation. Therefore, a change in the ratio is fundamental for the functioning of a biological carbon pump.

The nutrient concentrations determine the phytoplankton community structure [5]. Data on the seasonal dynamics of phytoplankton in the Black Sea confirm this conclusion [6]. An analysis of a large dataset collected over 20 years (from 2002 to 2021) in the northeastern part of the Black Sea showed that (1) small diatoms mainly predominate in spring (from the end of February); (2) the coccolithophorid *Emiliana huxleyi* dominates in late spring and early summer; (3) large diatoms dominate in summer and autumn [6–9]. Small diatoms, most often from the genus of *Pseudo-nitzschia*, include species with a cell volume of up to 1000 microns³; large diatoms are species with a cell volume above 10,000 microns³. In the NE Black Sea, large diatoms are represented by two species of *Pseudosolenia calcar-avis*

and *Proboscia alata*. The shift in dominance from one species to another is controlled by the availability of nutrients and their stoichiometry, which mainly depends on the stability of the water column [9].

It is necessary to build mathematical models to understand the mechanisms of processes that underlie the seasonal dynamics of phytoplankton. The base of this model is the dependence of the specific growth rate of phytoplankton on the concentration of the limiting factor. The so-called concept of extracellular regulation implies the dependence of the specific growth rate on the concentration of the growth-limiting nutrient, and it is most often expressed by the Monod equation [10]:

$$\tilde{\mu}_{ij} = \frac{\tilde{\mu}_{ij}^m C_j}{\tilde{K}_{ij} + C_j} \quad (1)$$

Here, $\tilde{\mu}_{ij}$ and $\tilde{\mu}_{ij}^m$ are the current and maximum specific growth rates of the i -th species depending on the j -th nutrient; C_j is the current concentration of the j -th nutrient; \tilde{K}_{ij} is the half-saturation constant of the i -th species with the j -th nutrient.

This equation has only two physiological parameters: the maximum specific growth rate and the half-saturation constant.

In another more complex concept of intracellular regulation, two processes are considered—the uptake of the growth-limiting nutrient and growth as a function of the intracellular content of the limiting nutrient. It was shown [11] that the dependence has the following form:

$$\mu_{ij} = \mu_{ij}^m \left(1 - \frac{q_{ij}}{Q_{ij}} \right) \quad (2)$$

Here, μ_{ij} and μ_{ij}^m are the current and maximum specific growth rates of the i -th species depending on the j -th nutrient; Q_{ij} and q_{ij} denote the current and minimum cellular quotas for the j -th nutrient in the biomass of the i -th species.

The Michaelis–Menten function describes the nutrient uptake rate depending on the nutrient concentration in the medium:

$$v_{ij}(C_{ij}) = \frac{v_{ij}^m C_j}{K_{ij} + C_j}. \quad (3)$$

$v_{ij}(C_{ij})$ and v_{ij}^m denote the current and maximum uptake rates of the j -th nutrients of the i -th species; K_{ij} denotes the half-saturation with the j -th nutrient of the i -th species.

This work is a continuation of our previous article [9], in which it was shown that the seasonal change in dominants is determined by the nitrogen and phosphorus concentrations in water and their ratios. Here, we find the minimum number of parameters, which is enough to understand the mechanisms of dominant species change in the seasonal dynamics of phytoplankton. Based on the concept of intracellular regulation, the following parameters are fundamentally important:

The minimum nitrogen and phosphorus quotas;

Half-saturation constants for nitrogen and phosphorus uptake;

The maximum specific growth rate of the dominant phytoplankton species.

We aimed to evaluate these parameters and, using computational experiments on the model, show the consistency of these results with accumulated field and experimental data.

2. Model

2.1. Modeling Protocol and Parameterization

The creation of a model based on the concept of intracellular regulation involves the assessment of four physiological parameters, namely the maximum specific growth rate (it is not equal to the parameter in the Monod equation), the minimum quota of the

growth-limiting nutrient, and the parameters of the uptake process—the maximum uptake rate and the half-saturation constant.

What essential properties of these species must be required to become absolute dominants in the appropriate season? In order to displace other species, the dominant species must have a higher growth rate. According to the R-competition theory [12,13], the dominant species should have the ability to grow at a lower concentration of the growth-limiting nutrient, and a minimum half-saturation constant becomes necessary for dominance. For species whose sizes differ significantly, it is necessary to consider the ability of cells to accumulate nutrients, which significantly affects species dynamics [14,15].

The model describes the dynamics of phytoplankton species in the upper mixed layer (UML) in the presence of a seasonal thermocline. In this case, the UML is a relatively isolated system. Vertical exchange determines the production processes: nutrients come from the lower layer. The growth of cells of a species is limited by a nutrient that is minimally available for this species.

As a result, the model describes the dynamics of phytoplankton biomass (or cell abundance), the concentration of nutrients in the water, and the nutrients in the biomass (or in cells) in the form of:

$$\begin{aligned}\frac{dW_i}{dt} &= \left[\min_j \mu_{ij} (Q_{ij}) - D \right] W_i \\ \frac{dC_j}{dt} &= D(C_{0j} - C_j) - \sum_{i=1}^n v_{ij}(C_j) W_i \\ \frac{dQ_{ij}}{dt} &= v_{ij}(C_j) - Q_{ij} \min_j \mu_{ij} (Q_{ij}, I_z)\end{aligned}\quad (4)$$

This system is based on the concept of intracellular regulation of phytoplankton growth, and the specific growth rate depends on the nitrogen and phosphorus content according to the Droop equation (Equation (2)).

Here, W_i and C_j represent the biomass concentration of the i -th species and the concentration of the j -th nutrient, respectively; C_{0j} —concentration of the j -th nutrient in the thermocline; Q_{ij} is the content of the j -th nutrient in the biomass of the i -th species; D is the rate of water exchange in the UML.

The uptake rate of the j -th nutrient by the i -th species $v_{ij}(C_j)$ is described using Equation (3). The maximum specific growth rate μ_{ij}^m depends on the amount of absorbed light energy of photosynthetically active radiation (PAR) by the biomass and the efficiency of its use during growth:

$$\begin{aligned}\mu_{ij}^m &= k \cdot \vartheta \cdot I_{av} \cdot a_{Chl} \frac{\beta_{Chl}}{W_{cell}} - \mu_o \\ I_{av} &= I_0 \cdot \frac{1 - e^{-z_t k_d}}{z_t k_d}\end{aligned}\quad (5)$$

Here, W_{cell} is cell biomass (g dry weight cell^{−1}), I_{av} is the average irradiance in the UML (W m^{−2}), a_{Chl} is the chlorophyll-specific light absorption coefficient (m² (g chl)^{−1}), β_{Chl} is chlorophyll content in the cell (g chl cell^{−1}), ϑ is the ratio of daylight hours to 24 h (dimensionless), k_d is the light attenuation coefficient (m^{−1}), z_t is the depth of the UML (m), and I_0 is the surface irradiance (W m^{−2}).

In the steady state, when the i -th species is limited by the j -th nutrient, the concentration of this nutrient is calculated as

$$C_j = \frac{K_{ij} D \mu_{ij}^m q_{ij}}{v_{ij}^m (\mu_{ij}^m - D) - \mu_{ij}^m q_{ij} D} \quad (6)$$

It follows that the residual concentration of the growth-limiting nutrient depends on the properties of the cell: directly proportional to the half-saturation constant K_{ij} of the

nutrient uptake, it increases with an increase in the maximum growth rate of μ_{ij}^m and the minimum quota q_{ij} . In addition, the concentration of the nutrient is inversely proportional to the maximum rate of uptake in this nutrient v_{ij}^m .

Thus, the system of equations describes the dynamics of the biomass of the three dominant phytoplankton species, the concentration of nitrogen and phosphorus in water, and the nitrogen and phosphorus content in the biomass of the studied species.

For each computational experiment, the initial conditions are equal biomass in the studied species (100 mg wet weight m^{-3}). This biomass value was selected based on long-term field observations; the species becomes dominant with this biomass. The maximum specific growth rate of the species was estimated from numerous experimental data on cultivating natural phytoplankton populations under laboratory conditions [9,16]. The nitrogen and phosphorus concentrations at the entrance were determined as the average long-term (2002–2023) data for each season [6,9]. The initial nitrogen and phosphorus content conditions in the biomass were equal to their minimum quotas, i.e., the cells were limited in these nutrients. The minimum quotas were calculated from the minimum protein content in the phytoplankton biomass [17]. In photoautotrophs, structural nitrogen is primarily associated with the content of chloroplasts. The specific volume of chloroplasts (the ratio of the volume of chloroplasts to the cell volume) was calculated. Morphological measurements show that *Emiliania huxleyi* has the lowest index, with one chloroplast per cell. The second source of information was laboratory experiments on the cultivation of natural populations [9,16], from which the optimal N/P ratio for the dominance of the studied species was determined. These ratios were used to estimate the minimum quota ratios.

Regular quotas were increased by 30% to study the response of phytoplankton dynamics to changes in minimum quotas. The maximum uptake rate was varied from $\mu_m q$ to $\mu_m 4 q$ to assess the sensitivity of phytoplankton dynamics to changes in this parameter. The half-saturation constants were estimated using Equation (6). The upper mixed layer (UML) water exchange rate is assumed to be 10%, the most realistic rate for late spring and early summer. In summer, this parameter is slightly higher. Our computational experiments show no significant changes in dynamics in 10 to 20% of water exchange. The beginning of spring is characterized by temporary instability of the water column, which leads to a decrease in the biomass of the dominant species. We chose an exchange value of 10% to show the characteristic trends of species dynamics in the absence of instability.

2.2. Conceptual Scheme

We use a model (a system of Equation (4)) to study the dynamics of biomass of three species: *Emiliania huxleyi* (Eh), a small diatom species, *Pseudo-nitzschia delicatissima* (Pn), and large diatom species of *Proboscia alata* (Pa).

Long-term observations of phytoplankton dynamics and experimental studies with a natural phytoplankton population revealed the following patterns: small diatoms dominate at relatively high concentrations of nitrogen and phosphorus and a ratio close to the Redfield ratio; coccolithophorids become dominant at low concentrations of nitrogen and N/P below the Redfield ratio. Large diatoms successfully grow at low concentrations of phosphorus, and N/P is significantly higher than the Redfield ratio [6,9] (Figure 1). Turning to the intracellular nitrogen and phosphorus content, the above patterns can be expressed as follows: $Q_N : Q_P \approx 16$ is the zone of dominance of small diatoms; $Q_N : Q_P < 16$ is the zone of dominance of coccolithophorids; $Q_N : Q_P > 16$ is the zone of dominance of large diatoms (Figure 2). The consequence of these results is the following relations between the parameters of the Droop model (2) for the three species under consideration.

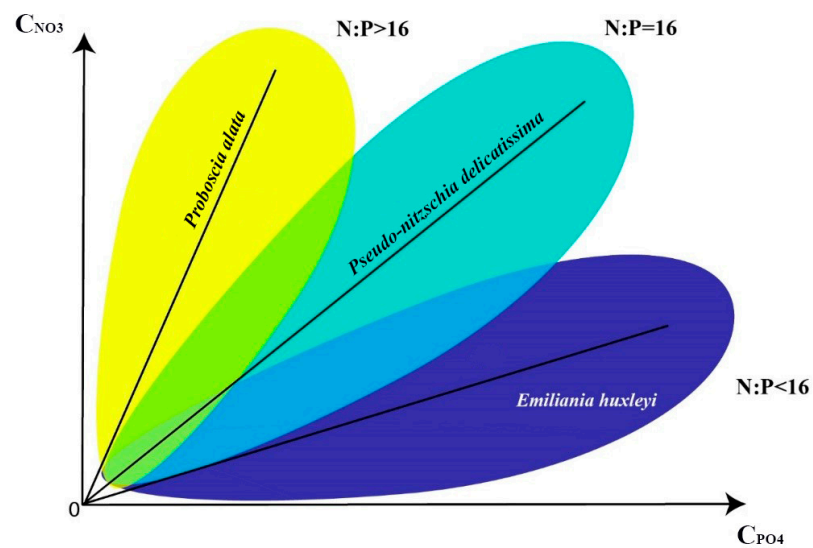


Figure 1. Conceptual scheme of phytoplankton species dominance in the coordination of nitrogen and phosphorus concentration in the water, obtained as a result of field and experimental studies.

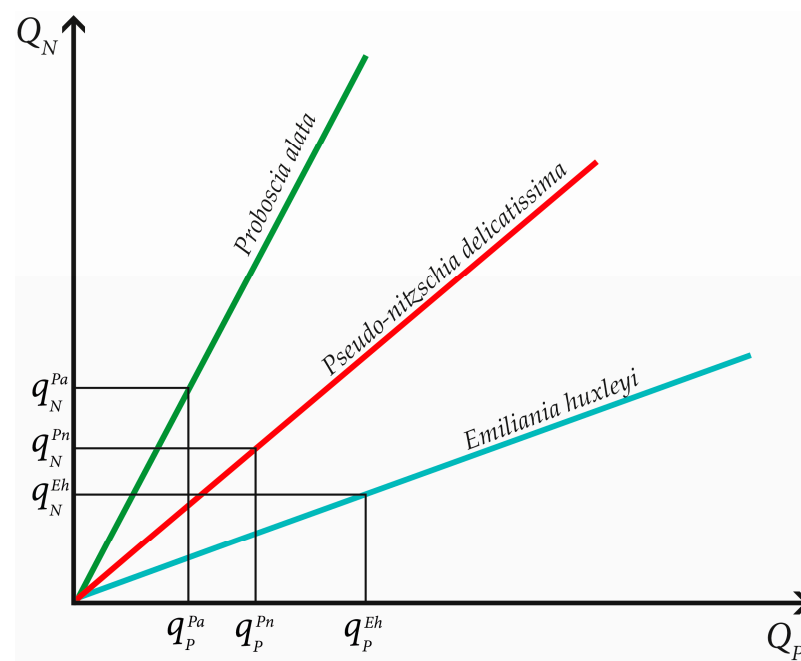


Figure 2. The ratio between the nitrogen and phosphorus content in biomass of dominant phytoplankton species.

The minimum nitrogen quotas for the three species under consideration are subject to inequalities

$$q_N^{Eh} < q_N^{Pn} < q_N^{Pa} \quad (7)$$

and the same phosphorus quotas are related by opposite inequalities (Figure 2):

$$q_P^{Eh} > q_P^{Pn} > q_P^{Pa} \quad (8)$$

The same relations are valid for the half-saturation constant (Figure 3):

$$K_N^{Eh} < K_N^{Pn} < K_N^{Pa}, K_P^{Eh} > K_P^{Pn} > K_P^{Pa} \quad (9)$$

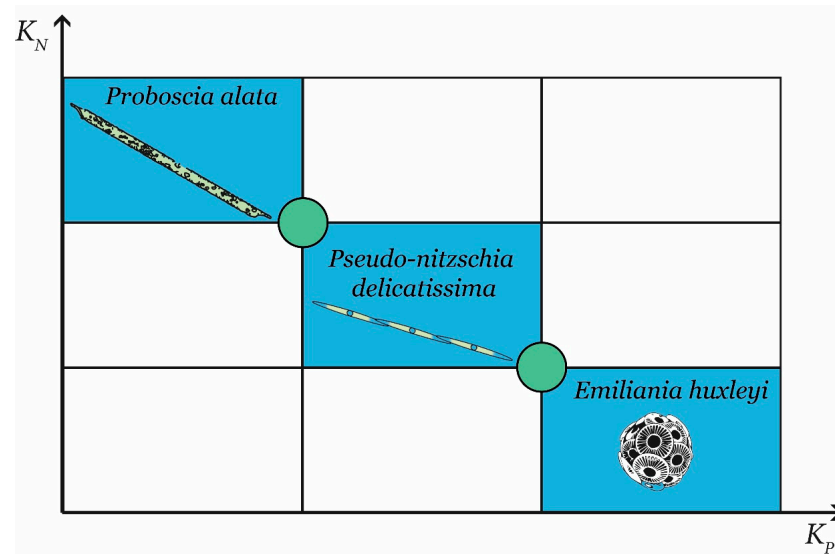


Figure 3. The ratio of the half-saturation constant.

The model parameters and units of measurement are described in Table 1, and their estimates are shown in Table 2.

Table 1. Symbols, descriptions, and units of the model parameters.

Symbol	Description	Units
μ_{NO3}^m	Maximal specific growth rate under nitrogen limitation	day ⁻¹
μ_{PO4}^m	Maximal specific growth rate under phosphorus limitation	day ⁻¹
v_{NO3}^m	Maximal nitrogen uptake rate	g N (day g wet wt) ⁻¹
v_{PO4}^m	Maximal phosphorus uptake rate	g P (day g wet wt) ⁻¹
K_{NO3}	Half-saturation constant for nitrogen uptake	g m ⁻³
K_{PO4}	Half-saturation constant for phosphorus uptake	g m ⁻³
q_N	Minimal nitrogen quota	g N (g wet wt) ⁻¹
q'_N	q_N increased by 30%	g N (g wet wt) ⁻¹
q_P	Minimal phosphorus quota	g P (g wet wt)
D	the rate of water exchange in the UML	day ⁻¹
C_{0NO3}	Dissolved inorganic nitrogen concentration	μmol L ⁻¹
C_{0PO4}	Dissolved inorganic phosphorus concentration	μmol L ⁻¹

Table 2. The estimated model parameters for dominant species.

Para-Meters	Spring			The End of Spring-Early Summer			Summer		
	<i>Eh</i>	<i>Pn</i>	<i>Pa</i>	<i>Eh</i>	<i>Pn</i>	<i>Pa</i>	<i>Eh</i>	<i>Pn</i>	<i>Pa</i>
μ_{NO3}^m	1.5	3.5	1.5	1.5	2.3	1.5	1.5	1.5	1.5
μ_{PO4}^m	1.55	3.5	1.22	1.55	2.3	1.22	1.55	1.5	1.22
v_{NO3}^m	0.00225	0.0105	0.006	0.00225	0.0069	0.006	0.00225	0.0045	0.006
v_{PO4}^m	0.00031	0.00035	0.00002	0.00031	0.00023	0.00002	0.00031	0.00015	0.00002
K_{NO3}	0.0042	0.0112	0.028	0.0042	0.0112	0.028	0.0042	0.0112	0.028
K_{PO4}	0.031	0.016	0.001	0.0031	0.0016	0.001	0.0031	0.0016	0.001
q_N	0.0015	0.003	0.004	0.0015	0.003	0.004	0.0015	0.003	0.004
q_P	0.0002	0.0001	0.00002	0.0002	0.0001	0.00002	0.0002	0.0001	0.00002
q'_N	0.001	0.002	0.003	0.001	0.002	0.003	0.001	0.002	0.003
C_{0NO3}		1.8			0.55			1.3	
C_{0PO4}		1.1			0.1			0.01	
D					0.1				

With the help of computational experiments, the consistency of the above parameter ratios should be shown.

3. Results

3.1. Results of Computational Experiments

Computer experiments with the model simulate the dynamics of a phytoplankton community with seasonal changes in external conditions. These conditions are described by the values of the parameters from Table 2, considering the seasonal features.

3.2. The Spring

Blooms of small-cell diatoms occur in late February and early March. This period is characterized by relatively low illumination and a shorter day [9]. Long-term data show that the nitrogen and phosphorus concentrations are 1.8 and $1.1 \mu\text{M L}^{-1}$, respectively [9].

In this scenario, the absence of a reaction of all phytoplankton species to changes in light intensity is considered, or the maximum specific growth rate remains unchanged (Table 2). *Pseudo-nitzschia delicatissima* gains an advantage and contributes mainly to the phytoplankton biomass (Figure 4). Reducing the nitrogen quota leads to a decrease in biomass.

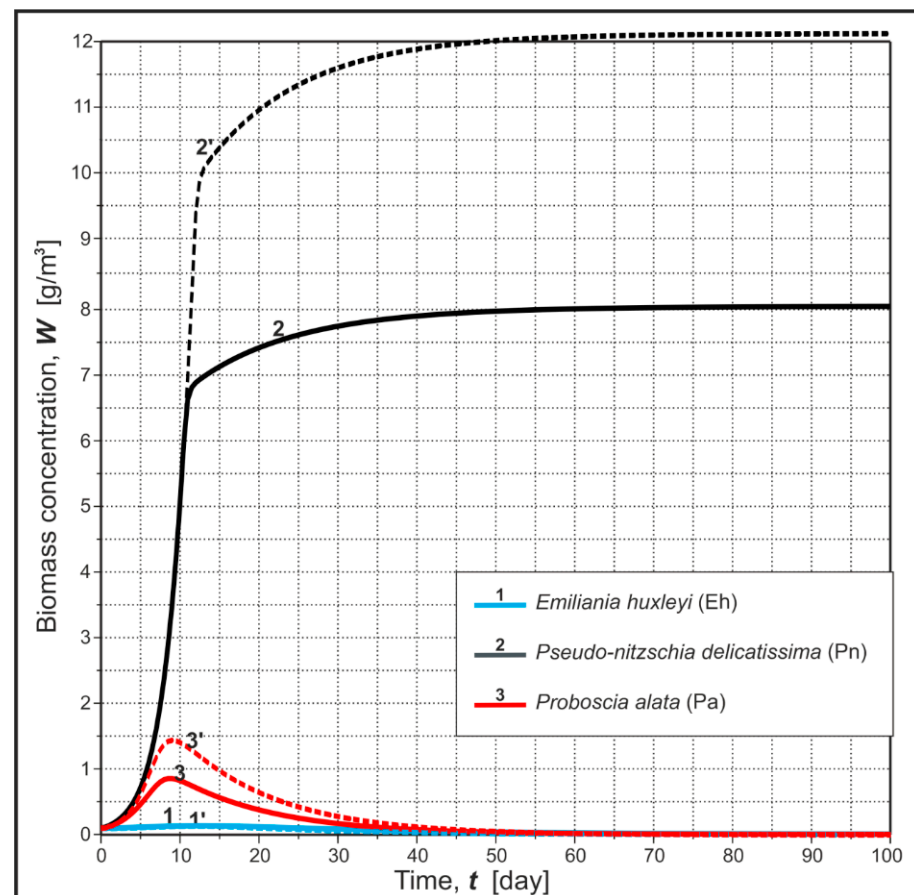


Figure 4. Dynamics of the primary phytoplankton dominants in the spring with the regular nitrogen quota (broken line) and increased by 30% (solid line).

A fourfold increase in V_{max} leads to the short-term dominance of *Proboscia alata* at the beginning of the experiment (Figure 5). The dominance of *Pseudo-nitzschia delicatissima* begins only after 35 days.

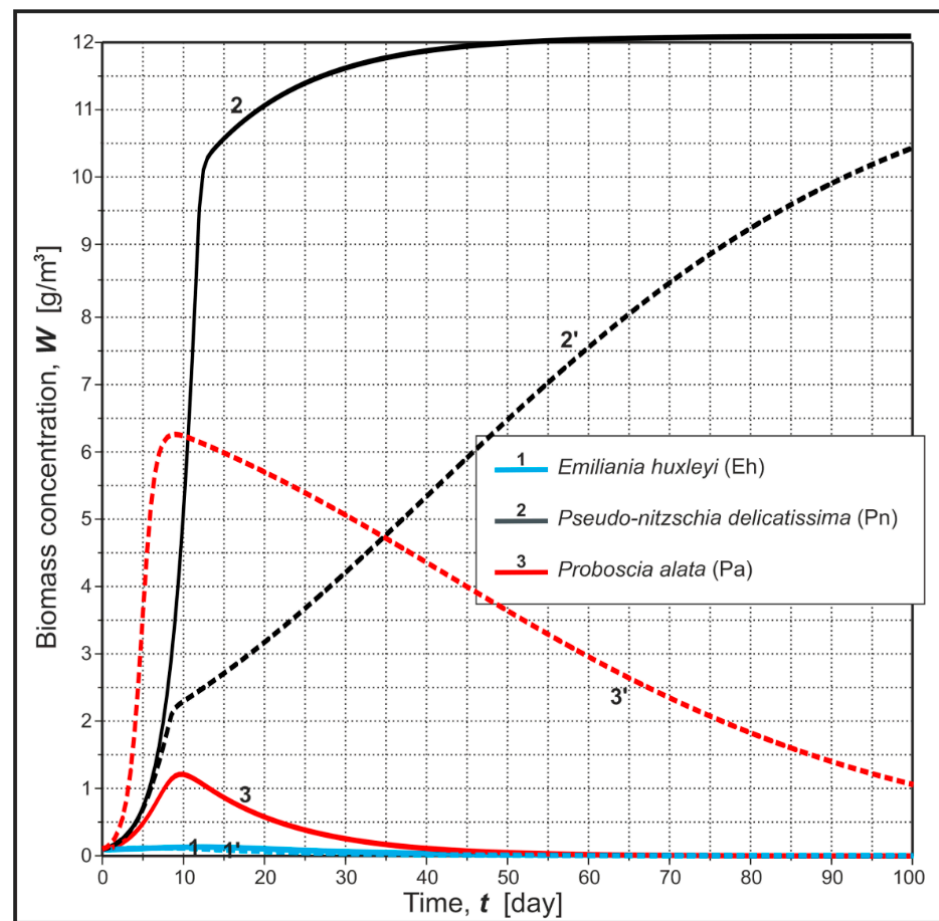


Figure 5. Dynamics of the primary phytoplankton dominants in the spring at the regular maximum nitrogen uptake rate V_{max} (solid line) and increased by four-times (broken line).

3.3. The End of Spring–Early Summer

High sea surface light fluxes and low UML nitrogen concentrations characterize this period. In addition, due to the high backscattering coefficient, the light absorption coefficient increases almost three-times. For example, during the coccolithophorids bloom in June 2023, this parameter increased to 0.29 m^{-1} . As a result, the average irradiance in the UML is significantly reduced, which leads to a significant decrease in the maximum specific growth rate (Table 2). In this case, *Pseudo-nitzschia delicatissima* may dominate in the initial stages (Figure 6). *Emiliana huxleyi* becomes dominant after 20 days of maintaining this regime. Changing the minimum quotas only leads to the level of accumulated biomass.

The hypothesis of nitrogen limitation. Small diatoms reduce the chlorophyll concentration in the cell with nitrogen deficiency, decreasing their maximum specific growth rate up to 1.5 day^{-1} (Equation (5)). In this case, *Emiliana huxleyi* gains an advantage in the initial stages; this species becomes the dominant species as soon as five days after the experiment's beginning (Figure 7).

Increasing the maximum rate of nitrogen uptake increases the competitiveness of *Pseudo-nitzschia delicatissima* and *Proboscia alata* at the initial stages (Figure 8).

3.4. Summer

Summer is characterized by high irradiance and surface water temperature, a deep thermocline, and a high nitrogen–phosphorus ratio [9]. Under such conditions (Table 2), *Proboscia alata* becomes the dominant species (Figure 9). Changing the minimum quotas leads to a change in the level of accumulated biomass and the rate of its change.

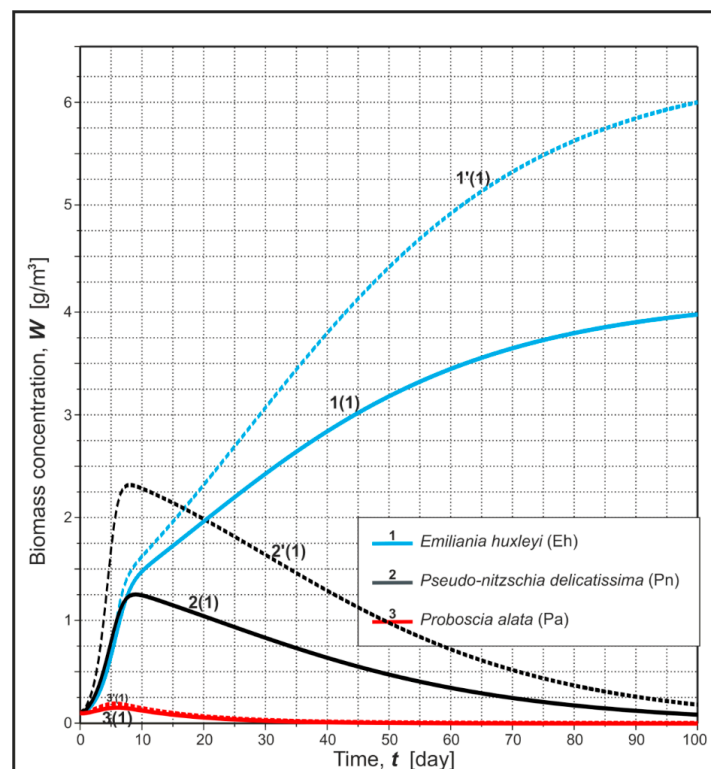


Figure 6. The dynamics of the primary phytoplankton dominants in late spring–early summer with a change in the specific growth rate due to a decrease in the average irradiance in the UML and at the regular nitrogen quota (broken line) and increased by 30% (solid line).

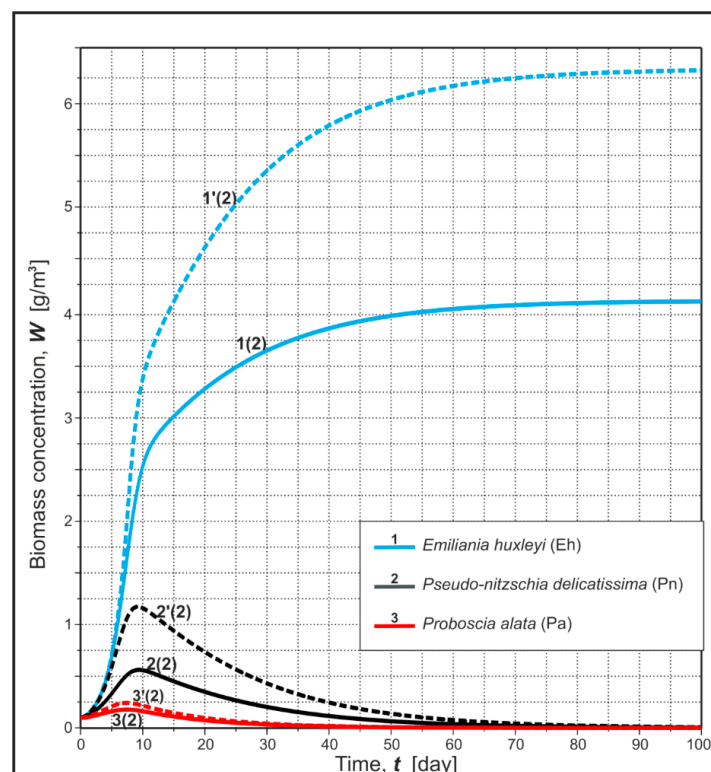


Figure 7. Dynamics of the primary phytoplankton dominants in late spring–early summer with nitrogen limiting the growth of small diatoms at the regular nitrogen quota (broken line) and increased by 30% (solid line).

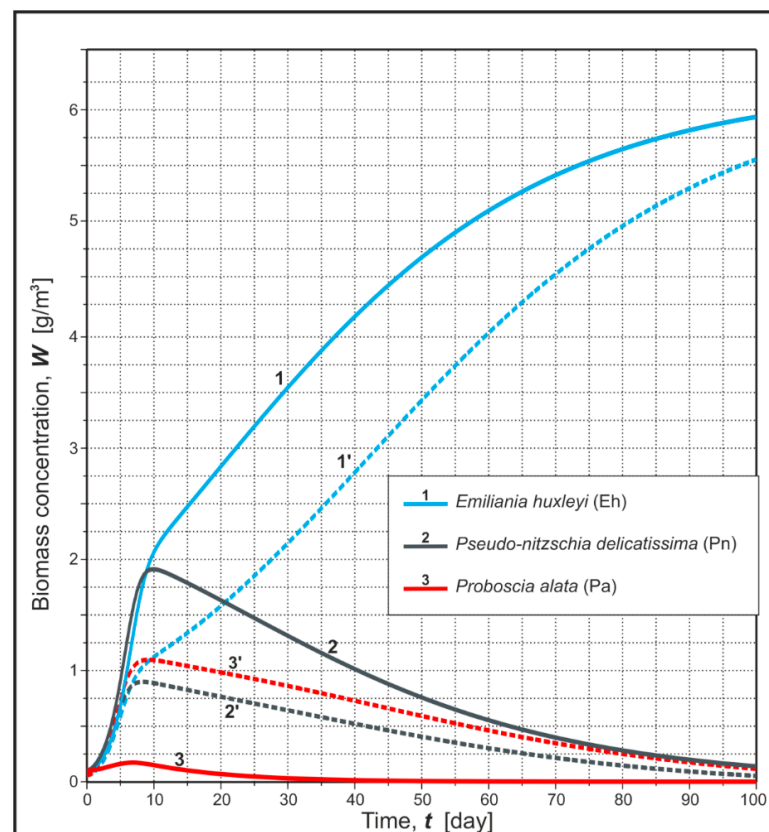


Figure 8. Dynamics of the primary phytoplankton dominants in late spring–early summer with a change in the specific growth rate due to a decrease in the average irradiation in the UML and at the regular maximum nitrogen uptake rate V_{max} (solid line) and increased by four times (broken line).

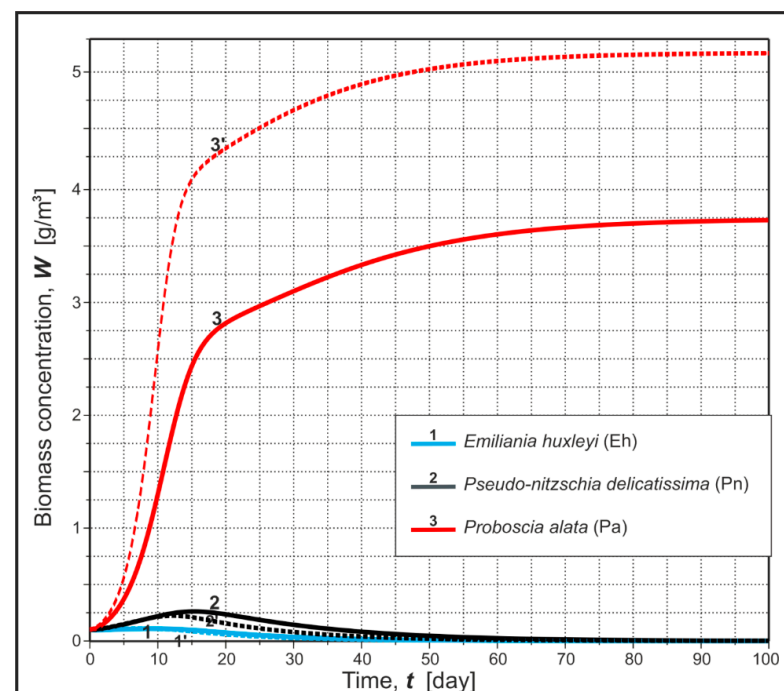


Figure 9. Dynamics of the primary phytoplankton dominants in summer with the regular nitrogen quota (broken line) and increased by 30% (solid line).

An increase in the maximum nitrogen and phosphorus uptake rate by four-times does not significantly affect phytoplankton dynamics (Figure 10).

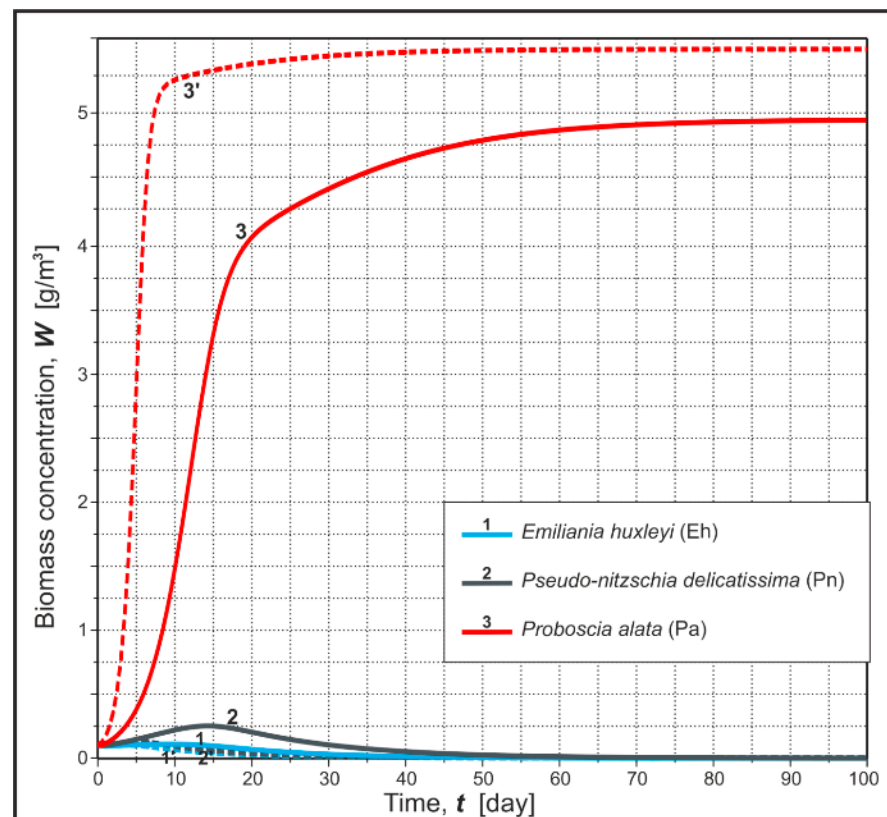


Figure 10. Dynamics of the primary phytoplankton dominants in summer at the regular maximum nitrogen uptake rate V_{max} (broken line) and increased by four times (solid line).

4. Discussion

Long-term studies have shown the unidirectional seasonal dynamics of phytoplankton in the northeastern part of the Black Sea, from small diatoms through coccolithophorids to large diatoms [6,9]. At certain stages of the dynamics, one species sometimes makes up 99% of the total biomass. Thus, there is an ecological filter that allows the Baas–Becking paradigm (1934) [18] to be realized, according to which “everything is everywhere, but the environment selects.” Here, we tried to answer the question of what properties of a species allow it to pass through this filter and become the dominant species. There is a minimum set of parameters reflecting the properties necessary for dominance:

The minimum nitrogen and phosphorus quotas;
 Half-saturation constants for nitrogen and phosphorus uptake;
 The maximum specific growth rate of the dominant phytoplankton species.

For each season, there is a different set of parameters necessary for the dominance of the species.

4.1. Spring

In spring, *Pseudo-nitzschia delicatissima* gains an advantage, and the main factor that contributes to winning this competition is the maximum specific growth rate. At relatively high concentrations of nutrients, the dynamics of species biomass is determined by this parameter, which depends on the amount of energy absorbed (Equation (5)). This species has high values for this parameter due to its high specific light absorption coefficient [19]. Coccolithophorid *Emiliana huxleyi* also has high specific light absorption coefficients [19]. However, this species’ maximum specific growth rate is relatively low since the relative

costs of absorbed energy for calcification are high [20–22]. In conditions of low irradiance at the end of winter and short daylight hours, these physiological growth limitations in *E. huxleyi* are critical for the dynamics of this species. *Proboscía alata* has a very low specific light absorption coefficient, and the specific growth rate is low in low-irradiance conditions. The only way to increase competitive abilities is to increase the specific light absorption coefficient by reducing the cell's radius.

Spring bloom is a ubiquitous phenomenon in the ocean [23], coastal waters and estuaries [24,25], and under ice in Arctic waters [26]. According to Sverdrup's classical hypothesis, it begins when the critical depth is sufficient for photosynthesis to exceed respiration and the growth rate is above zero [27]. Such an effect can only be provided by species with a high specific light absorption coefficient, i.e., small-cell species. Our model studies show that these species have a minimum nitrogen and phosphorus quota ratio close to the Redfield ratio.

4.2. The Late Spring and Early Summer

In late spring and early summer, the dominance of *Emiliania huxleyi* is observed annually, while the contribution to the total phytoplankton biomass reaches 99%. It seems crucial to answer what physiological mechanisms provide high competitive abilities compared to other phytoplankton species. The dominance of coccolithophorids is characterized by conditions that differ from other seasons of the year by a low-nitrogen concentration and a relatively high-phosphorus concentration. Our model studies show that this species has relatively low-nitrogen and high-phosphorus quotas. In addition, our computational experiments show that a necessary property for the dominance of coccolithophorid is a low half-saturation constant for nitrogen uptake and a high one for phosphorus. The low value of the half-saturation constant in *E. huxleyi* compared to diatoms has been shown experimentally for a long time [28]. Equation (6) shows species with a low quota, and a half-saturation constant should have a low residual nitrogen concentration. According to Tilman's concept [12,13], this species gains competitive advantages when limiting the growth process with nitrogen. Considering that nitrogen is the main limiting factor in the ocean [29–32], the widespread distribution of coccolithophorids becomes clear [33,34].

A low-nitrogen quota indicates a relatively low protein content with a growth rate close to zero. A high-phosphorus quota indicates a high ribosome content, and according to the Growth Rate Hypothesis, such species should have a maximum specific growth rate [35,36]. However, coccolithophorids have a relatively low specific growth rate compared to diatoms, particularly *Pseudo-nitzschia delicatissima*. Phosphorus limitation causes an intensification of the calcification process [37,38]. Therefore, high-phosphorus concentrations are necessary to minimize calcification, and the absorbed light energy is sent to the growth processes. Nitrogen limitation also enhances calcification processes, but this condition is necessary because *Emiliania huxleyi* can win the competition only under these conditions.

In diatoms, the process of cell frustule formation from silica is less energy consuming than the calcification process in coccolithophorids [39]. Up to 30% of absorbed lights are believed to be spent on calcification processes [40,41]. These phenomena create additional advantages for diatoms, but when nitrogen is limited, diatoms lose the competition.

4.3. Summer

A minimum phosphorus quota and a very low half-saturation constant for the phosphorus uptake are essential for the dominance of large diatoms. This fact ensures a low residual phosphorus concentration (Equation (6)) and, according to Tilman's concept [12,13], high competitiveness of large diatoms.

Relatively high nitrogen concentrations in the water allow large diatom cells to accumulate it, which is facilitated by a high content of vacuoles [42]. Since the maintenance of large cells is more energy intensive than that of small cells, it requires a higher content of light-collecting structures that contain more nitrogen than phosphorus. As a result, the minimum nitrogen quota is relatively higher here than other dominants. In large cells, the

ribosome content is relatively low, contributing to a low phosphorus content and a high N/P ratio.

4.4. Seasonal Phytoplankton Dynamic as the Dynamic of Parameters of the Model

Thus, our computational experiments show that the hypothesis expressed in ratios 1, 2, 3, and Figures 2 and 3 is reasonable. The maximum specific growth rate of dominant species tends to decrease continuously from the end of the winter and the beginning of spring to summer. The nitrogen quota has a minimum value in the late spring and early summer. In summer, it has a maximum value. The phosphorus quota has an inverse pattern. The N/P ratio in the water has the same dynamics as the ratio of quotas. The ratio of minimum quotas as a species-specific indicator is highly variable [43]. The half-saturation constant for nitrogen has average values in spring; in late spring and early summer, it takes the lowest values, and in summer, it increases again. This fact does not contradict the literary sources [28,44,45]. The low values of this parameter in late spring and early summer are due to the ability of coccolithophorids to uptake nitrogen at lower concentrations than diatoms, which was shown earlier [28]. It is also shown that the half-saturation constant for nitrogen is lower in small diatoms than in large ones [44,45]. Our estimates of the half-saturation constant for nitrogen uptake in *Pseudo-nitzschia delicatissima* are close to those obtained for other species of this genus [45].

The phosphorus half-saturation constant is highest in late spring and early summer, and the lowest in summer. Evidence shows that large diatoms have a higher half-saturation constant for phosphorus than small ones [44]. However, our research shows that summer dominants in the Black Sea grow at very low (near analytical zero) phosphorus concentrations.

It has been shown in experiments on monocultures that the ratio of nitrogen and phosphorus content in the cell changes proportionally to the change in the ratio in the medium at the entrance [46]. The optimal N/P ratio in the water, according to the criterion of specific growth rate, is approximately equal to the ratio of their minimum quotas [47]. The ability of a species to adapt beyond the optimal ratios of nitrogen and phosphorus determines the physiological plasticity of the species or “homeostatic ability” [48]. In a natural ecosystem, when the N/P ratio in the environment changes, species are replaced with corresponding ratios of minimum quotas [43]. This phenomenon can be called ecological plasticity.

Nutrient-limiting growth leads phytoplankton cells of these two types to trigger mechanisms of physiological plasticity, which leads to a decrease in the specific growth rate and loss of competitiveness. The lack of physiological plasticity leads to the replacement of dominant species.

The parameters we identified allow us to complement the main competitive strategies that allow species to occupy a leading position in the ecosystem [48]: in the spring, R-strategists with a high maximum specific growth rate and a ratio of minimum quotas close to the Redfield ratio gain an advantage; in late spring and early summer, K-strategists who can grow to dominate at low-nitrogen concentrations and have a minimum quota ratio less than the Redfield ratio; in summer, the space is occupied by species capable of accumulating nitrogen and, at the same time, having the ability to grow at low concentrations of phosphorus, so the ratio of minimum quotas is greater than the Redfield ratio.

Specific parameters and identified strategies make it possible to predict phytoplankton's structure with nitrogen and phosphorus concentration changes and their ratios. At relatively high concentrations of these substances, small diatoms will dominate. This phenomenon will be observed with increased eutrophication. Coccolithophorids become dominant at low-nitrogen concentrations and N/P below the Redfield ratio. Such a reaction is possible with climate changes associated with warming, and the expected increase in the stratification of the water column will reduce the vertical intake of nutrients into the euphotic layer (for example, Ref. [49]). At N/P above the Redfield ratio, large diatoms dominate in the UML, which occurs with a buried thermocline and periodic wind mixing. This forecast is somewhat different from the forecasts of other authors [50,51]; they predicted

the dominance of diazotrophs at N/P above the Redfield ratio. Regional peculiarities can explain this difference.

5. Conclusions

Long-term studies have shown that the seasonal change in dominants follows a specific pattern. In this study, we attempted to test the hypothesis that this pattern of seasonal changes is regulated by nitrogen and phosphorus concentrations and their ratio in seawater. Applying the concept of intracellular regulation based on the Droop equation allowed us to identify the minimum set of model parameters describing seasonal dynamics. These parameters were evaluated using field and experimental studies. Computer calculations have shown that the minimum quotas for nitrogen and phosphorus, the half-saturation constant for nitrogen and phosphorus uptake, and the maximum growth rate of dominant species are fundamental. At the same time, the species with the maximum growth rate wins in spring; in late spring and early summer, this is the species with the minimum nitrogen quota and the minimum half-saturation constant for nitrogen uptake; in summer, the species with the minimum phosphorus quota and the minimum half-saturation constant for phosphorus uptake are competitive. The results obtained do not contradict the stated hypothesis.

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