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MARINE CHEMISTRY

Mathematical Modeling of Biogenic Substance Transformations and Recycling in a Subtropical Coastal Marine Ecosystem

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Abstract—A mathematical model describing the biotransformations of organic and mineral compounds of biogenic elements (P, N, and Si) and dissolved organic carbon was applied for a theoretical analysis of the recycling of nutrients in the coastal zone of the Canary water upwelling. The aim of this study was to quantitatively estimate the effect of nutrient recycling on the dynamics of the biomasses of microorganisms as a matter basis for the biological productivity of the marine environment. Model calculations were carried out for four near-shore areas off the Moroccan Sahara using the morphometric data (mean depths, water volumes, and areas) and long-term monthly mean values of the parameters of the marine environment (temperature, light intensity, water transparency, and depth of the thermocline). In the calculations, no account was taken for the flow rates across the boundaries between the areas and only indirect account for the vertical exchange was taken. At the absence of nutrient transfer, the model reproduces particular features of the dynamics of nutrient and detritus concentrations and the biomasses of microorganisms resulting from the internal recycling of organic and mineral substances only. In order to characterize the processes of the biotransformation, the internal fluxes and turnover times of organic and mineral components were estimated together with the biomasses and biological productivities of microorganisms.

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INTRODUCTION

The conditions of functioning of marine ecosystems in subtropical and tropical latitudes show no significant seasonal differences in the principal physical parameters of the marine environment (water temperature and light inteasity) in the surface layer. Here, the activity of marine microorganisms during the year is permanently high and depends on the conditions of the supply of nutrients from the deep layers to the surface and on the rates of the turnover (recycling) of nutrients in the marine environment. The near-shore areas of the regions cited are characterized by quasi-stationary water upwellings, which define the vertical inhomogeneity in the distribution of the biomasses of microorganisms and nutrient concentrations and form particular conditions for the recycling of nutrients and organic matter in the marine environment [1, 11].

The objective of this study was to quantitatively estimate the process of consumption and transformation of the matter by microorganisms of the lower trophic chain (bacteria, phyto- and zooplankton) in the course of the nutrient recycling and to understand how they integrate this matter into their biomass and how this biomass depends on the environmental parameters. This problem may be solved if one applies ecological models that are capable of reliably reproducing the mutual interactions between the microorganisms of the lower trophic levels and accounting for the influence of the environment conditions of their dwelling on their development. Nutrients (compounds of elements such as C, N, P, and Si) serve as the food base for hydrobionts, who include them into the composition of their cellular structure.

In this study, special attention was paid to the estimation of the biological productivity of the marine environment using the modeling results. As a rule, when studying marine ecosystems, the greatest attention is focused on the formation of the primary production defined by the phytoplankton activity. It is subdivided into "new" production that is formed by phytoplankton from the allochtonous part of the nutrients supplied from external sources and the "regenerated" production formed in the course of the recycling of nutrients in the surface layer. The principal substrates for the "new" production are the nitrogen of nitrates (NO_3), dissolved gaseous nitrogen (N_2), and dissolved inorganic phosphorus (DIP), while those for the "regenerated" production are ammonium nitrogen (NH_4) and dissolved forms of organic nitrogen (DON) and phosphorus (DOP) [13].

Nutrient recycling in the euphotic zone is defined by the particular features of the processes of its transformation, in which microorganisms of the lower trophic

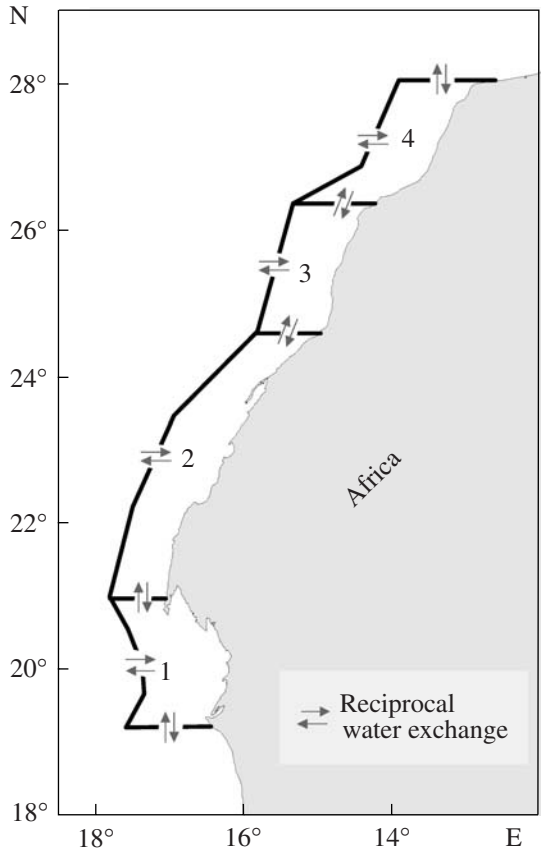

Fig. 1. Schematic map of the region of the studies.

levels (bacteria and phyto- and zooplankton) take part. The nutrient turnover proceeds in the surface layer at least ten times before a part of it (in the form of particulate matter) is removed from the cycle by precipitation processes [13]. The studies of the conditions of functioning of marine ecosystems should concern not only the issue of the formation of the primary production but also the production of bacteria and zooplankton, since a significant portion of the phytoplankton biomass is transformed into the biomass of other links of the trophic chain. In the tropical and subtropical regions, the production cycles of microorganisms of lower trophic levels develop continuously, which means that the intensities of the oppositely directed processes that determine the growth and elimination of the biomass of microorganisms are approximately equal [4].

The biological productivity (BP) is one of the most important characteristics of marine ecosystems. Methods for calculating the primary production rates are developed on the basis of the changes in the measured nutrient concentrations [9]. The essence of these methods lies in the fixation of the initial and final concentrations of mineral components of P and N (or O_2), and the values of the daily production (or the biomass yield over the season) are calculated accounting for the assumed intervals of the variability in the concentrations of the above substances. However, this approach to the estimation of primary production is virtually inapplicable for subtropical and tropical regions since, in these areas, the nutrient content in the surface layer of the ocean is close to analytical zero over the major part of the year. Precisely this was the reason why the numerous attempts to find the relation between the phytoplankton biomass and the nutrient contents in the subtropical and tropical zones of the ocean failed [13]. An account of the vertical nutrient transfer from deeper layers to the euphotic layer allows one to characterize the "new" production and does not account at all for the continuous and multiple turnover (recycling) of nutrients, which in low latitudes forms an additional (and significant) "regeneration" production in the marine environment. Only the existence of internal nutrient fluxes due to recycling may help to explain this additional increment in the phytoplankton biomass at an actually low total content of nutrients in the oceanic environment.

In this study, in order to estimate the BP values for microorganisms, we used the information about the internal fluxes of organic and mineral nutrient compounds that are involved into the turnover by microorganisms, which were calculated with the model.

According to the FAO classification, the region considered is called the Central East Atlantic or the region of the Canary Upwelling. Here, we assess a minor water area in the near-shore zone of the region conventionally referred to as the Moroccan Sahara (Fig. 1) from 28° to 19°15′ N east of 20° W. The extension of the shelf zone is 380 km at a width of 30–80 km; its area up to the 200-m depth contour equals 65 th. km^2 [14]. The entire area studied is subdivided into four parts (Table 1).

Table 1. Morphometric characteristics of the areas distinguished off the coasts of the Moroccan Sahara

Region	Latitude, N	Volume, km^3	Area, km^2	Mean sea depth, m
1	19°15′–21°00′	5.3	21.5	247
2	21°00′–24°36′	13.2	44.3	298
3	24°36′–26°20′	7.4	23.8	311
4	26°20′–28°00′	6.1	20.6	296

BRIEF CHARACTERISTICS OF THE CNPSi MODEL—AN INSTRUMENT FOR ANALYSIS OF OCEANOLOGICAL INFORMATION

The studies of the conditions of the transformation and recycling of nutrients in the region off the Moroccan Sahara were performed with the use of the CNPSi mathematical model, which describes the interrelated biohydrochemical cycles of N, P, and Si and the transformation of dissolved organic carbon (DOC) and O_2 in

a two-layered marine ecosystem [6]. The CNPSi model is capable of reproducing the differences that exist in the distributions and concentrations of the chemical and biological characteristics in different sea areas. It provides calculations of the concentrations of DOC; O_2; and N-, P- and Si-containing substances in the course of their biotransformation in an aquatic medium with a community of microorganisms (bacteria and phyto- and zooplankton) and at the development of exchange processes at the water–bottom and water–air interfaces. In this case, we took no account for the matter transfer across the boundaries of the area distinguished (shown by the arrows in Fig. 1); it will be accounted for in future calculations. Using the modeling results, we estimated the intra-annual variations in the biomasses of the above-listed microorganisms and in the concentrations of dissolved inorganic forms of P (DIP), N (ammonium NH_4, nitrite NO_2, and nitrate NO_3), and Si (DISi); in the organic forms of these elements (DOP, DON, and DOSi, respectively); and in the detritus contents in the units of P (PD), N (ND), and Si (SiD).

The model reproduces the spectrum of the processes of biotransformation of organic matter and nutrients characteristic of aquatic ecosystems and their turnover: heterotrophic bacteria *B* assimilate organic compounds of nutrients and form a stock of mineral substances in the aquatic medium, three dominating groups of phytoplankton (*F1*, *F2*, and *F3*) consume mineral substances and produce organic matter, and two groups of zooplankton (phytophagous *Z1* and predatory *Z2*) influence the development of the processes of biotransformation of the matter affecting the dynamics of the microorganisms.

In order to maintain the matter balance, the biomasses of the microorganisms are presented in units of organogenic elements (C, N, P, and Si). The biomass of heterotrophic bacteria is calculated in units of C (B_C), N (B_N), P (B_P), and Si (B_{Si}); the values of *F1* and *Z1* are presented in units of Si ($F1_{Si}$ and $Z1_{Si}$), N ($F1_N$ and $Z1_N$), and P ($F1_P$ and $Z1_P$); while those of *F2*, *F3*, and *Z2* are given in units of N ($F1_N$, $F2_N$, and $Z2_N$) and P ($F1_P$, $F1_P$, and $Z2_P$).

In the model, the marine ecosystem is represented by two layers. In the upper layer, the dynamics of the microorganism biomasses is limited by the nutrient contents, while, in the lower layer, it is controlled by the light conditions in the aquatic medium. Precisely these factors are the most important for subtropical and tropical regions of the ocean [13]. The boundary between these layers is specified from the vertical distribution of the water temperature.

For each of the areas distinguished (Fig. 1), the CNPSi model estimates the instant transitional states in the rates of changes and values of the concentrations of substances depending on the impacts defined by the environmental factors. The results of the modeling allow one to recognize the particular features of the dynamics of the biomasses and concentrations of chemical substances with respect to the set of environmental conditions and finally characterize the features of the development of the processes of biotransformation of nutrients and organic matter in the marine ecosystems considered using a rather complete set of calculated characteristics (rates of individual processes, internal and external matter fluxes, their balance, and the internal biogenic load caused by the nutrient recycling). Thus, the model allows one to answer the most important questions of biooceanology: what biomasses of microorganisms may be formed in the aquatic medium at corresponding nutrient concentrations, what are the specific rates of their growth, which environmental factors mainly control them, and which microorganisms interact with each other and with the environment.

Precisely the application of the CNPSi model, which was tested when studying marine ecosystems [5, 7, 8], allows us to assess the particular features of the nutrient dynamics and conditions of the development of biological productivity with account for the nutrient recycling and with no account for their supply owing to the water transport and upwelling. The complete description of the model equations is presented and discussed in [6]; in the general form, the model equations are presented in the Appendix to this paper.

INPUT DATA FOR MODEL CALCULATIONS

In order to study the conditions of the recycling of nutrients in the Atlantic region considered, we introduced into the model the morphometric characteristics and the monthly parameters of the conditions of the environment (the temperature and transparency of the water, the light inteasity of the sea surface, and the photic period) for areas 1–4. In our study of the transformation and turnover of nutrients, we took no account for the parameters of the water exchange at the boundaries of the areas distinguished and for the nutrient concentrations in the ocean waters neighboring areas 1–4. The temperature and transparency of the seawater were estimated based on the scientific reports of various expeditions of the Atlantic Scientific–Research Institute for Marine Fisheries and Oceanography held in this region of the Atlantic during 1960–2000. The other parameters were specified mainly from reference books (for example, [2]).

Areas 1–4 differ in their morphometric parameters (Table 1).

In Table 2, we present monthly values of the parameters of the condition of the marine environment for areas 1–4. In individual months, the vertical position of the thermocline ranged within 35.0–103.0 m. The ranges of the surface water temperatures in areas 1–4 were 14.46–19.34, 15.04–19.34, 14.80–19.19, and 18.00–21.33°C, respectively; in the lower layer, the corresponding ranges were 12.51–15.26, 13.84–16.37, 13.23–15.18, and 13.37–14.36°C. These data indicate

Table 2 Mean annual values of the parameters of the marine environment over months for regions 1–4 off the coasts of the Moroccan Sahara

Region	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Depth of the thermocline, m												
1	84.9	91.0	44.3	89.4	89.4	89.4	49.5	35.0	44.5	54.0	65.0	74.0
2	103.0	50.5	90.7	76.5	61.5	45.8	51.4	49.6	61.0	71.0	82.0	92.5
3	60.8	49.6	49.5	64.7	27.0	67.1	57.2	75.3	72.0	69.0	67.5	64.0
4	34.0	34.4	36.5	38.0	39.5	42.2	41.6	39.0	37.4	36.5	35.5	35.0
Temperature, °C												
1	17.64 14.32	14.46 14.30	17.54 14.84	16.97 12.51	18.20 13.34	19.34 14.18	18.31 14.27	18.18 15.26	18.02 15.02	17.93 14.80	17.80 14.65	17.75 14.45
2	16.55 13.84	15.04 15.51	17.90 14.21	16.82 14.30	18.05 15.00	19.28 15.77	19.34 16.37	19.11 15.77	18.30 15.30	18.07 14.95	17.55 14.60	17.03 14.20
3	17.18 15.18	14.80 13.23	18.76 14.11	16.81 14.07	16.45 14.06	18.97 14.65	19.19 14.14	18.95 14.67	18.60 14.70	18.25 14.83	17.90 14.95	17.53 15.05
4	18.95 13.93	18.32 13.80	18.20 13.70	18.13 13.55	18.05 13.43	18.00 13.37	19.49 13.99	20.42 14.17	21.33 14.36	20.74 14.29	20.13 14.17	19.55 14.05
¨Light inteasity, cal/(cm^2 day)												
1	143.0	152.0	235.0	281.0	330.0	331.0	295.0	265.0	235.0	210.0	185.0	165.0
2	142.7	152.5	235.8	280.6	330.0	331.0	295.0	265.0	235.0	210.0	185.0	165.0
3	146.0	143.3	205.2	246.3	280.0	295.0	295.0	275.0	245.0	220.0	195.0	175.0
4	127.9	151.7	194.3	249.0	262.0	265.0	240.0	215.0	190.0	170.0	152.0	140.0
Photic period, dimensionless												
1	0.463	0.466	0.501	0.544	0.550	0.565	0.561	0.552	0.535	0.515	0.490	0.470
2	0.463	0.466	0.509	0.544	0.550	0.584	0.562	0.552	0.535	0.515	0.490	0.470
3	0.459	0.459	0.500	0.544	0.568	0.576	0.566	0.556	0.532	0.505	0.485	0.459
4	0.464	0.467	0.500	0.538	0.570	0.583	0.572	0.563	0.535	0.510	0.490	0.465
Transparency, m												
1	11.0	11.0	9.5	9.0	9.0	9.1	8.3	7.0	7.0	7.5	8.5	10.0
2	12.3	13.3	10.5	10.7	10.5	12.3	12.2	9.0	9.3	9.8	10.5	11.5
3	16.8	17.0	15.3	12.8	11.0	12.0	15.2	16.0	16.3	16.6	16.9	17.1
4	14.7	17.0	10.2	7.5	10.0	12.0	14.7	11.0	12.0	12.6	13.0	14.0
Atmospheric precipitation, km$^3 \times 10^3$												
1	0.11	0.04	0.02	0.0	0.0	0.0	0.06	0.56	0.80	0.41	0.11	0.13
2	0.13	0.31	0.13	0.0	0.0	0.0	0.04	0.58	0.22	0.84	0.09	0.31
3	0.31	0.38	0.29	0.10	0.02	0.0	0.0	0.0	0.14	0.29	0.40	0.67
4	0.84	0.47	0.37	0.29	0.06	0.02	0.08	0.04	0.12	0.39	0.76	0.88

Note: Above are the temperature values for the upper layer and below are those for the lower layer.

that the amplitudes of the variations in the mean monthly surface water temperatures decrease in the northward direction from 4.88 to 3.33°C and those in the lower layer decrease from 2.75 to 0.99°C. The highest values of the surface water temperature in areas 1–4 fall in June, July, and September, respectively. In the lower layer, the months with the maximal temperatures are August, July, January, and September. The least temperature values in areas 1 and 3 are observed in the period from January to April and in area 4 in June. The light inteasity was highest in June (265–331 cal/(cm^2 day)) and the lowest in January (127.9–146 cal/(cm^2 day)). For the model calculations, the initial concentrations of individual nutrients were assumed to be equal in all the areas.

The calculations should demonstrate to what extent the differing factors of the marine environment in areas 1–4 (at the absence of replenishment of the nutrient stock by the supply from adjacent regions and water upwelling) influence the dynamics of the chemical and biological components. The calculated nutrient concentrations and biomasses of microorganisms are determined by the conditions of the nutrient recycling, and the particular features of their dynamics are characterized by the values of the times of the turnover of the variables, the internal nutrient fluxes, and the parameters of the productivity of the microorganisms. Note that the calculated variations in the nutrient concentrations and biomasses of hydrobionts are purely theoretical since they characterize the conditions at the absence of the horizontal transport and water upwelling. Therefore, the calculated nutrient concentrations cannot be directly compared to those under the actual conditions in the near-shore zone off the Moroccan Sahara, where the horizontal transport and water upwelling are characteristic and well-manifested phenomena. Therefore, the calculated data may be used only for a theoretical analysis of the influence of environmental factors and nutrient recycling on the dynamics of chemical and biological variables.

RESULTS OF THE MODELING AND THEIR ANALYSIS

Calculations with the model allowed us to estimate the theoretical interannual variations in the nutrient concentrations in areas 1–4. In order to retain the possibility of functioning of the ecosystems in areas 1–4, the nutrient losses in the upper layer that are caused by the detritus sedimentation were replenished by a compensational supply of mineral substances to the upper layer. Under natural conditions, this nutrient supply is provided by the processes of transfer (horizontal and vertical, owing to the water upwelling) and by the nutrient recycling. Figure 2 shows the changes in the concentrations of the forms of P (DIP, DOP, and PD) in the areas considered throughout the year. In areas 2–4, one can see a clear similarity in the variabilities of the DIP concentrations: a sharp drop from 40 to 5–10 μg P/l at

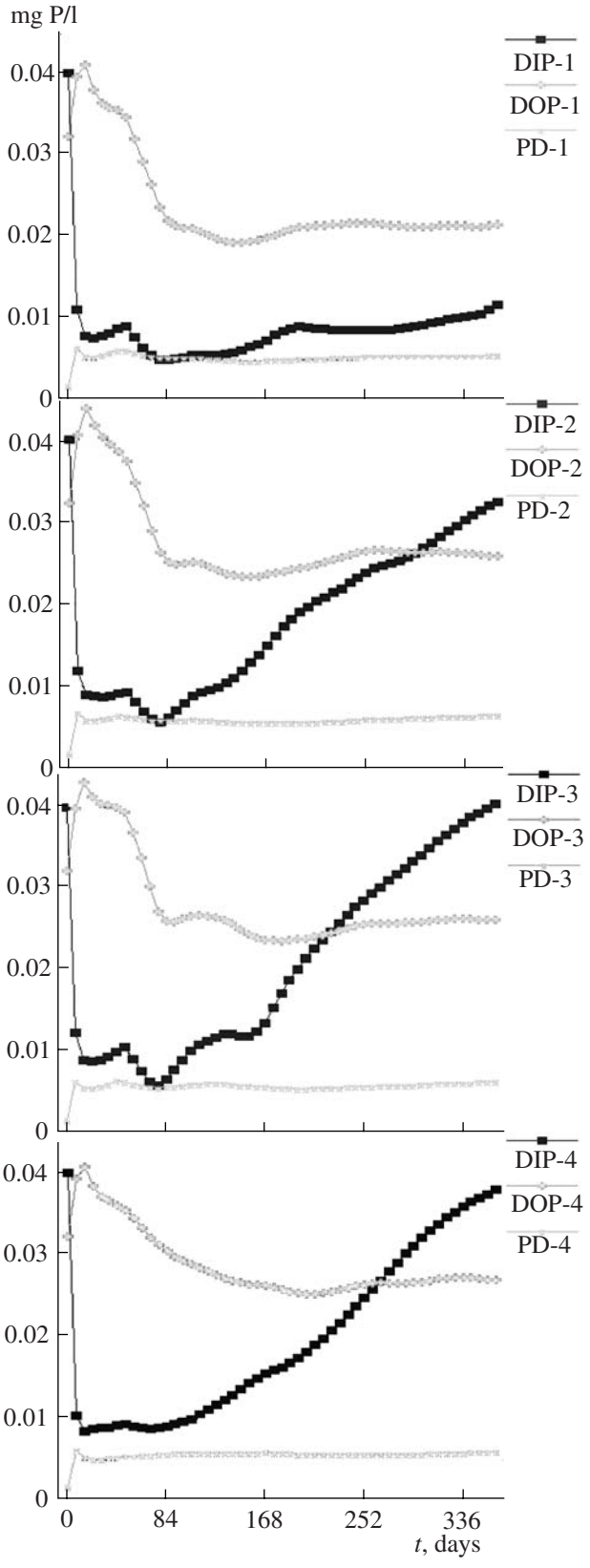

Fig. 2. Calculated intra-annual dynamics of the concentrations of the forms of P (DIP, DOP, and PD) in areas 1–4.

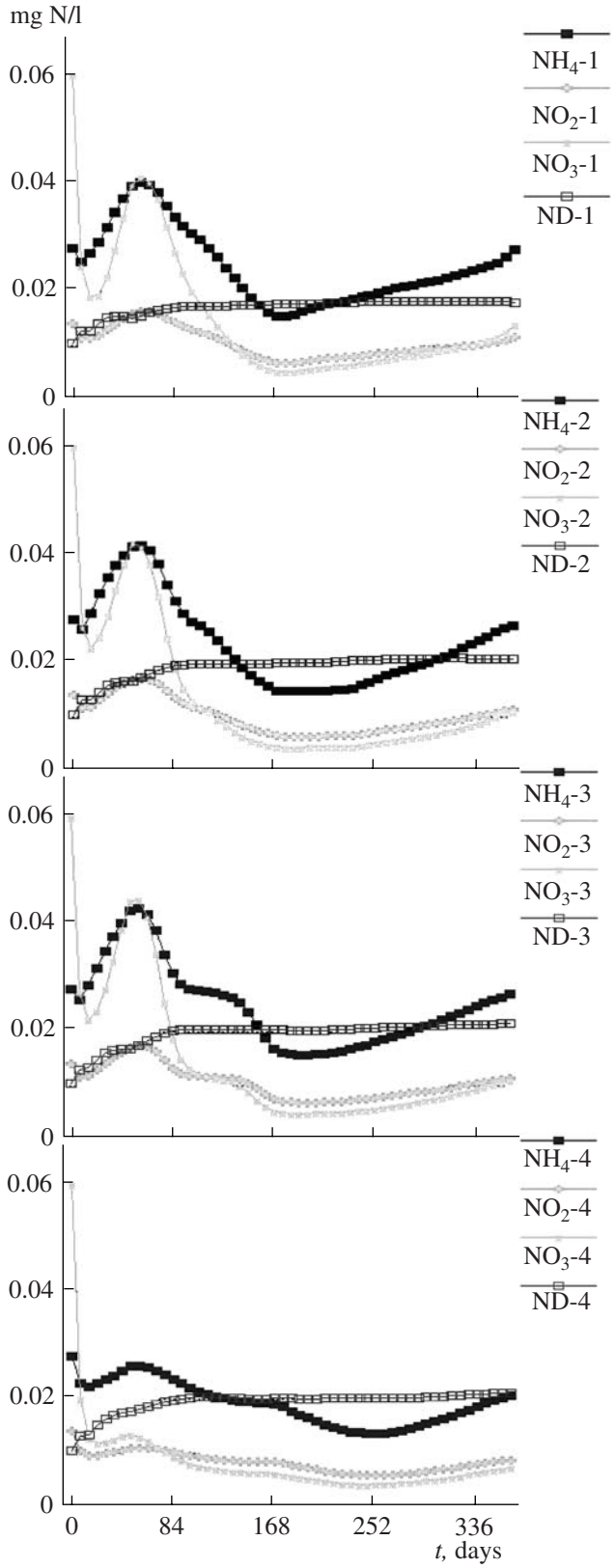

Fig. 3. Calculated intra-annual dynamics of the concentrations of the forms of N (NH_4, NO_2, NO_3, and ND) in areas 1–4.

the beginning of the year and a gradual growth by the end of the year up to 32–40 μg P/l. In area 1, there was no such growth in the DIP concentrations by the end of the year, and, at the end of December, it comprised only 12 μg P/l.

The DOP concentrations feature similar changes in areas 1–4 throughout the year: from the beginning of the year, an increase in the DOP concentrations from 32 to 40-45 μg P/l is noted and then they gradually decrease down to 20–21 μg P/l (area 1) and 25–27 μg P/l (areas 2–4); up to the end of the year, the DOP concentrations almost do not change while undergoing insignificant fluctuations.

Over the greater part of the year, the PD contents in areas 1–4 slightly change with small oscillations within 5–6 μg P/l (Fig. 2).

The calculated interannual dynamics of the mineral forms of N (NH_4, NO_2, and NO_3) and ND in areas 1–4 are shown in Fig. 3. In areas 1–3, a similarity in the amplitudes and dynamics of the concentrations of the N forms cited throughout the year are noted. Area 4 is characterized by a significantly lower amplitude of the variations in the N form concentrations.

In areas 1–3, the contents of the mineral forms of N at the beginning of the year (the first 7–14 days) decrease: the content of NO_3 falls from 60 to 20–21 μg N/l and that of NH_4 decreases from 28 to 26 μg N/l. By the end of February, the concentrations of NH_4 and NO_3 grow up to 40-42 μg N/l. By the middle of the year, a decrease in the concentrations of NH_4 and NO_3 is observed down to 15–17 and 5–7 μg N/l, respectively, and, by the end of the year, they gradually grow up to 27–28 and 10–12 μg N/l, respectively. The annual dynamics of the NO_2 virtually follow the tendencies in the NH_4 changes, though the range of the concentration changes is significantly smaller than that of NH_4.

In area 4, a clearly expressed decrease in the concentrations of NO_3 (from 60 to 12 μg N/l) and NH_4 (from 28 to 21 μg N/l) is observed at the beginning of the year. Later on, a certain growth in the concentration of NH_4 up to 25 μg N/l is noted, which is followed first by a gentle decrease down to 17 μg N/l (by day 252) and then by a rise in the concentrations of NH_4 up to 20 μg N/l at the end of the year. The concentrations of NO_3 throughout the year vary within 5–12 μg N/l and, by the end of the year, comprise 7 μg N/l. Over the greater part of the year, the concentrations of NO_2 vary synchronously with those of NO_3.

In areas 1–4, the content of ND almost similarly change throughout the year: from the beginning of the year, it somewhat decrease and then gradually grow up to 19 μg N/l in area 1 and up to 20 μg N/l in areas 2–4 (Fig. 3).

The calculated annual dynamics of the biomasses of the three groups of phytoplankton and of phytophagous and predatory zooplankton in areas 1–4 are shown in Fig. 4 in units of N. The seasonal dynamics of the phytoplankton biomasses feature individual particularities.

In particular, in each area, one observes intermediate peaks and lows in the phytoplankton biomasses; their values and the times of their appearance also differ. Meanwhile, on the whole, in areas 1–3, the annual dynamics of the phytoplankton biomasses demonstrate certain similar features, while, in area 4, they strongly differ from those in other areas. The calculated dynamics of the biomasses of the zooplankton show no significant seasonal differences in different areas (Fig. 4).

In order to characterize the characteristics of the particular features of the processes of nutrient biotransformation, we calculated the values of the turnover periods for the phytoplankton biomasses $F1_N$, $F2_N$, and $F3_N$ (τ_{F1_N}, τ_{F2_N}, and τ_{F3_N}, respectively) and those of the mineral components of the nutrients in areas 1–4.

The changes in τ_{F1_N} throughout the year occur in the ranges of 4.52–12.02, 4.55–12.21, 4.70–12.14, and 4.94–13.02 days in areas 1–4, respectively. The interannual variations in τ_{F2_N} are stronger and comprise 4.78–24.56, 5.67–23.67, 5.28–23.61, and 5.01–18.49 days in areas 1–4, respectively, and those in τ_{F3_N} are even higher being 5.34–28.92, 5.77–29.91, 5.23–28.88, and 4.14–20.88 days in areas 1–4, respectively. The variations in the turnover periods of the phytoplankton biomasses are mainly defined by the daily variability in the light inteasity of the water surface, which, in low latitudes, has the greatest effect on the phytoplankton activity and its capability of performing the processes of nutrient transformation. Another important factor is the grazing out of phytoplankton biomasses by zooplankton [13].

Since, in the latitudes under consideration, no temperature influence on the phytoplankton activity is recognized (throughout the year, the temperature remains high and varies within a narrow interval), the next significant factor of the influence on the phytoplankton is the concentrations of nutrients such as compounds of P, N, and Si, whose calculated contents in the water significantly change throughout the year (Figs. 2, 3). The calculated values of the turnover periods τ for nutrients characterize the rate of their turnover in the aquatic medium; their values are listed in Table 3. Since the values of τ change throughout the year, in order to more adequately represent this information, we subdivided the entire year into four intervals (the beginning of the year up to 72.8 days, 74.2–151.2, 152.6–259.0, and 260.4–365 days), for which the ranges of the τ variability for individual nutrients in areas 1–4 are shown (Table 3). Different nutrients differ in the values of τ and the ranges of their variations throughout the year, which is related to the different conditions of their transformation and turnover depending of the conditions of the marine environment.

The turnover of the components of detritus (ND and PD) proceeds at the highest rate; correspondingly, the values of their turnover periods τ_{PD} and τ_{ND}, as well as

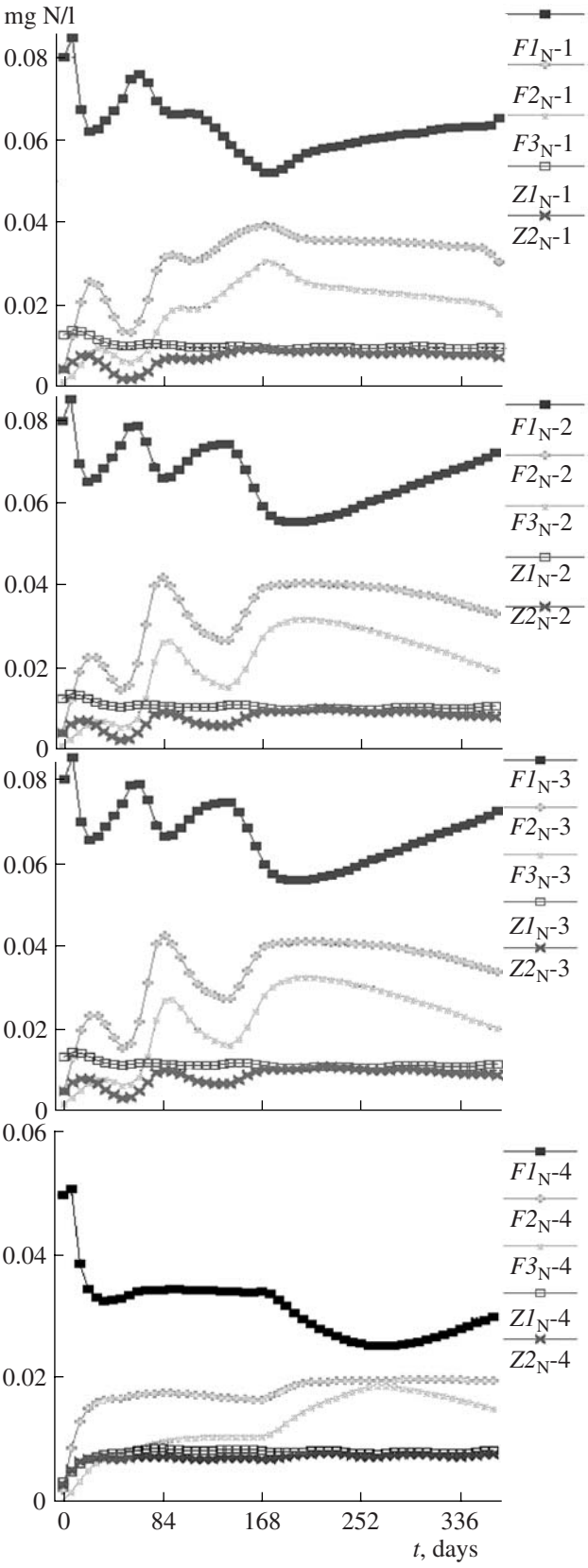

Fig. 4. . Calculated intra-annual dynamics of the biomasses of phytoplankton ($F1_N$, $F2_N$, and $F3_N$) and zooplankton ($Z1_N$ and $Z2_N$) in areas 1–4.

Table 3. Ranges of the nutrient turnover time (τ, days) changes in areas 1–4 in selected periods of the year (modeling results)

Nutrient concentration	Period of the year, days	Area 1	Area 2	Area 3	Area 4
DIP, mg P/l	5.6–72.8	0.57–3.38	0.58–3.46	0.63–3.54	0.92–3.03
	74.2–151.2	0.49–2.23	0.53–3.72	0.55–3.50	0.91–4.06
	152.6–259.0	0.72–3.06	1.38–6.73	1.20–7.88	1.50–7.04
	260.4–365.0	0.89–3.45	2.41–8.12	2.95–9.69	2.58–9.40
NH_4, mg N/l	1.4–72.8	3.10–6.71	3.54–6.59	3.48–6.67	2.20–5.84
	74.2–151.2	1.78–5.78	1.51–5.37	2.01–5.16	1.62–3.93
	152.6–259.0	1.49–3.52	1.18–2.94	1.30–3.40	1.05–3.25
	260.4–365.0	1.86–4.48	1.41–4.09	1.50–3.94	1.09–3.09
NO_2, mg N/l	1.4–72.8	2.75–3.33	2.81–3.15	2.72–3.17	2.55–3.07
	74.2–151.2	2.59–2.91	2.58–2.93	2.68–2.98	2.65–2.75
	152.6–259.0	2.49–2.74	2.41–2.65	2.45–2.80	2.15–2.75
	260.4–365.0	2.66–2.85	2.58–2.92	2.55–2.84	2.14–2.53
NO_3, mg N/l	1.4–72.8	0.38–7.12	1.68–7.19	0.68–7.25	0.80–5.14
	74.2–151.2	0.62–5.86	0.48–4.72	0.68–4.58	0.57–2.27
	152.6–259.0	0.44–1.86	0.36–1.43	0.40–1.65	0.32–1.62
	260.4–365.0	0.60–2.77	0.44–2.26	0.48–2.09	0.33–1.55
DISi, mg Si/l	2.8–72.8	26.16–159.7	26.06–149.5	26.35–145.7	28.67–150.3
	74.2–151.2	64.63–169.7	62.78–160.2	62.53–153.2	67.54–163.5
	152.6–259.0	75.08–170.9	73.00–164.8	70.96–163.2	75.72–175.7
	260.4–365.0	67.06–165.9	64.34–161.2	66.64–159.7	83.59–177.0
DOC, mg C/l	1.4–72.8	2.47–18.32	2.42–18.36	2.33–18.32	2.10–18.14
	74.2–151.2	3.74–10.52	3.85–11.79	3.67–12.71	3.46–10.67
	152.6–259.0	10.55–18.19	11.83–21.15	12.81–23.34	10.72–20.88
	260.4–365.0	17.62–27.14	20.53–32.08	22.67–33.24	20.34–29.71
DON, mg N/l	2.8–72.8	8.81–16.61	8.52–16.50	8.50–16.46	9.15–16.10
	74.2–151.2	8.86–11.35	8.80–11.91	8.73–12.09	9.20–11.30
	152.6–259.0	11.27–11.98	11.92–13.61	12.14–14.57	11.32–13.56
	260.4–365.0	11.67–12.96	13.17–15.30	14.08–16.22	13.27–14.89
DOP, mg P/l	1.4–72.8	3.47–7.50	3.49–7.93	3.58–7.74	4.19–7.29
	74.2–151.2	2.96–4.60	3.28–4.55	3.32–4.59	3.61–5.29
	152.6–259.0	3.01–4.11	3.32–4.27	3.23–4.13	3.40–4.28
	260.4–365.0	3.01–4.09	3.31–4.28	3.30–4.21	3.44–4.45
ND, mg N/l	1.4–72.8	0.62–0.84	0.65–0.88	0.66–0.87	0.64–0.85
	74.2–151.2	0.62–0.79	0.64–0.82	0.65–0.83	0.65–0.81
	152.6–259.0	0.61–0.79	0.64–0.82	0.65–0.82	0.65–0.81
	260.4–365.0	0.63–0.80	0.66–0.84	0.67–0.84	0.66–0.83
PD, mg P/l	1.4–72.8	0.54–0.94	0.55–0.96	0.56–0.96	0.57–0.85
	74.2–151.2	0.47–0.71	0.49–0.74	0.51–0.76	0.51–0.71
	152.6–259.0	0.47–0.68	0.47–0.70	0.49–0.69	0.49–0.70
	260.4–365.0	0.50–0.70	0.52–0.72	0.52–0.71	0.51–0.69
SiD, mg Si/l	1.4–72.8	3.14–12.62	3.23–12.57	3.18–12.49	2.88–9.35
	74.2–151.2	7.69–11.84	7.87–11.80	8.30–11.63	7.03–9.40
	152.6–259.0	6.63–9.86	6.27 –10.06	6.67–11.07	5.84–9.41
	260.4–365.0	6.83–9.52	6.42–10.16	6.71–9.65	5.80–7.51

the amplitudes, are the lowest. For areas 1–4, the total range of the changes in the τ_{ND} and τ_{PD} values comprises 0.61–0.88 and 0.47–0.96 days, respectively.

Meanwhile, the turnover of SiD proceeds slower than that of ND and PD, and the values of the period of the SiD turnover (τ_{SiD}) are comparable with those characteristic of the organic components (DOC and DON). In area 4, the turnover of SiD is implemented somewhat faster than in the other areas studied. Throughout the year, in all the areas, the rate of the SiD turnover is the greatest in the period of 152.6–259.0 days.

In the initial period, the dynamics of the τ values for the organic components in areas 1–4 are the same. Only in the values of τ for the DOC, DON, and DOP are there slight differences. From the beginning of the year, the intensity of the organic component turnover grows, and, on days 30–70, the highest rate of the organic component turnover is reached characterized by the values τ_{DOC} = 2.10–2.47 days, τ_{DON} = 8.50–9.15 days, and τ_{DOP} = 3.47–4.19 days. In the subsequent periods, the rates of the organic components turnover decrease and the replenishment of their stock proceeds at the expense of the processes of detritus decomposition and biological production, which actively develop throughout the year. From the beginning of the year, certain differences in the τ values for organic components in different areas become noticeable. The faster and slower organic component turnovers are observed in areas 1 and 3, respectively, while areas 2 and 4 are characterized by intermediate rate values. In the second half of the year, the amplitudes of the changes in the τ values for the organic components generally decrease; the turnover of Ai DOP is the fastest (τ_{DOP} = 3.01–4.45 days), while the turnover of DON and DOC proceeds somewhat slower (τ_{DON} = 11.27–16.22 days and τ_{DOC} = 10.55–33.24 days) (Table 3).

The turnover of the DIP in all the areas is implemented at elevated rates. It is especially intensive in the period of 74.2–151.2 days: the values of τ_{DIP} for this period vary in the range of 0.49–4.06 days in different areas. In other periods, the rate of the DIP turnover is somewhat lower and the amplitude of the τ_{DIP} changes is greater. On the whole, the turnover of the DIP is best implemented in area 1: here, throughout the year, τ_{DIP} varies in the range of 0.49–3.45 days, while, in areas 2–4, τ_{DIP} changes within 0.53–8.12, 0.55–9.09, and 0.91–9.40 days, respectively.

The turnover of NH_4 is more active in the period of 152.6–259 days; the values of τ_{NH_4} for this period in areas 1–4 vary within 1.05–3.52 days. NH_4 changes most rapidly in this period in areas 2 (over 1.18–2.94 days) and 4 (over 1.05–3.25 days) (Table 3).

The turnover of NO_2 in all the periods in areas 1–4 proceeds at an approximately similar rate; the total range of the τ_{NO_2} changes comprises 2.14–3.33 days. NO_3 is characterized by somewhat lower turnover rates and greater amplitudes of the τ_{NO_3} changes at the beginning of the year (days 0–70): in areas 1–4, τ_{NO_3} changed in the ranges of 0.38–7.17, 1.68–7.19, 0.68–7.25, and 0.60–5.14 days, respectively. With the beginning of the spring, the turnover of NO_3 accelerates. It proceeds most intensity in the period of 260.6–365 days (the total amplitude of τ_{NO_3} in this period is 0.33–2.77 days). In area 4, the turnover of NO_3 is generally faster than in other areas (Table 3).

Note that the calculated values of the turnover periods of NH_4 and NO_3 are close to the values estimated for the Black Sea ecosystem: in the summer, when the rates of the consumption of NH_4 and NO_3 by microplankton are maximal, the turnover periods of the fractions considered are 0.208 ± 0.125 and ~0.5 days, respectively [3].

The total range of the changes in τ_{DISi} in areas 1–4 comprises 26.06–177.0 days. The highest amplitudes of τ_{DISi} (26.06–159.7 days) fall in the initial period of the year (0–70 days); later, the amplitude decreases and the values of τ_{DISi} vary within the range of 62.53–177.0 days. In area 3, the turnover of DISi proceeds faster than in other areas (Table 3).

The organic and mineral components contained in the aquatic medium form the matter basis for the formation of the BP of the community in the sea. For the microorganisms assessed in the model (bacteria and phyto- and zooplankton), the values of their BP were calculated from the internal matter fluxes (in units of C, Si, N, and P) estimated in the model calculations. Thus, these calculations imply that the most important environmental factors (the temperature, the light inteasity, the concentrations of nutrients consumed by microorganisms, and their delivery to the medium in the course of the nutrient recycling) influence the principal processes of the nutrient biotransformation and formation of the biomass of microorganisms. The multiple cycling of nutrients allows the microorganisms to maintain their activity even under low nutrient concentrations. In this case, the role of the internal processes of nutrient transformation is estimated from the calculated fluxes of nutrient transformation in the course of the nutrient consumption by microorganisms, excretion of the products of metabolism to the aquatic medium, formation of detritus, and grazing out of bacteria and phytoplankton by zooplankton (Table 4).

The calculations show that the consumption of N by bacteria in the waters of the areas studied comprises 7.849–8.853 g N/(m^3 year) (97.6–97.8% is consumed in the form of DON, and 2.2–2.4% is consumed in the form of ND). The bacterial consumption of P comprises 2.278–2.722 g P/(m^3 year) (in the form of DOP and PD, 74.6–76.8 and 23.2–25.4%, respectively, is consumed). The N : P ratio in the components consumed by bacteria is (3.2–3.5) : 1.

Table 4. Internal nutrient fluxes provided by the activity of microorganisms in areas 1–4 in the region of the Moroccan Sahara

Name of the flux, substance, units	Areas 1–4 in the region of the Moroccan Sahara			
	1	2	3	4
Consumption of substances by heterotrophic bacteria *B*:				
DON, g N/(m^3/year)	7.659	8.465	8.631	8.647
ND, g N/(m^3/year)	0.190	0.199	0.197	0.206
DOP, g P/(m^3/year)	1.700	2.002	2.052	2.027
PD, g P/(m^3/year)	0.578	0.651	0.670	0.612
DOC, g C/(m^3/year)	17.965	19.216	19.690	19.532
O_2, g O_2/(m^3/year)	36.477	39.410	40.011	40.485
Release of substances by heterotrophic bacteria *B*:				
DON, g N/(m^3/year)	1.538	1.698	1.731	1.736
DOP, g P/(m^3/year)	0.135	0.157	0.161	0.157
DIP, g P/(m^3/year)	1.216	1.416	1.452	1.408
NH_4, g N/(m^3/year)	0.854	0.944	0.961	0.964
UR, g N/(m^3/year)	1.025	1.132	1.154	1.157
DISi, g Si/(m^3/year)	6.197	6.720	6.826	6.909
Detritus formation *B*:				
PD, g P/(m^3/year)	0.831	0.867	0.992	0.950
ND, g N/(m^3/year)	4.120	4.554	4.639	4.628
SiD, g Si/(m^3/year)	7.795	8.436	8.557	8.654
Consumption of substances by phytoplankton *F1*, *F2*, and *F*:				
NH_4, g N/(m^3/year)	1.544	1.795	1.720	1.996
NO_3, g N/(m^3/year)	2.753	2.695	2.777	2.576
DIP, g P/(m^3/year)	1.892	2.081	2.114	2.075
DOP, g P/(m^3/year)	0.309	0.231	0.216	0.215
DISi*, g Si/(m^3/year)	6.478	6.733	6.833	6.058
Release of substances by phytoplankton *F1*, *F2*, and *F3*:				
DON, g N/(m^3/year)	0.143	0.149	0.150	0.136
DOP, g P/(m^3/year)	0.202	0.212	0.213	0.200
NH_4, g N/(m^3/year)	0.025	0.026	0.026	0.024
Detritus formation by *F1*, *F2*, and *F3*:				
PD, g P/(m^3/year)	1.776	1.869	1.877	1.852
ND, g N/(m^3/year)	3.841	4.020	4.058	4.057
SiD*, g Si/(m^3/year)	7.071	7.318	7.425	6.612
Consumption of substances by zooplankton *Z1* and *Z2*:				
DOP, g P/(m^3/year)	0.154	0.175	0.178	0.210
PD, g P/(m^3/year)	0.249	0.272	0.277	0.299
B_P, g P/(m^3/year)	0.072	0.081	0.087	0.092
F_P, g P/(m^3/year)	0.207	0.211	0.215	0.210
DON, g N/(m^3/year)	0.249	0.284	0.295	0.275
ND, g N/(m^3/year)	0.189	0.211	0.215	0.249
B_N, g N/(m^3/year)	0.227	0.240	0.240	0.264
F_N, g N/(m^3/year)	0.243	0.247	0.254	0.294
Release of substances by zooplankton *Z1* and *Z2*:				
DON, g N/(m^3/year)	0.080	0.086	0.088	0.091
DOP, g P/(m^3/year)	0.066	0.072	0.073	0.078
NH_4, g N/(m^3/year)	0.076	0.083	0.084	0.086
DIP, g P/(m^3/year)	0.116	0.125	0.127	0.130
Detritus formation by *Z1* and *Z2*:				
PD, g P/(m^3/year)	0.488	0.528	0.538	0.587
ND, g N/(m^3/year)	0.747	0.809	0.824	0.896
SiD**, g Si/(m^3/year)	0.183	0.198	0.201	0.202
Individual processes:				
Destruction of PD to DOP, g P/(m^3/year)	1.746	1.958	1.990	2.008
Destruction of ND to DON, g N/(m^3/year)	6.205	6.988	7.160	7.103
Sedimentation PD, g P/(m^3/year)	0.530	0.491	0.477	0.479
Sedimentation ND, g N/(m^3/year)	2.144	2.000	1.964	2.044
Sedimentation SiD, g Si/(m^3/year)	2.183	1.923	1.887	1.619
Oxidation UR to NH_4, g N/(m^3 year)	1.013	1.119	1.143	1.149
Oxidation NH_4 to NO_2, g N/(m^3/year)	1.177	1.127	1.198	0.993
Oxidation NO_2 to NO_3, g N/(m^3/year)	1.345	1.291	1.363	1.149
Expense of O_2 for oxidation of NH4, g O_2/(m^3/year))	4.025	3.855	4.097	3.395
Expense of O_2 for oxidation of NO_2, g O_2/(m^3/year)	1.533	1.472	1.554	1.310

Notes: * accounting only for *F1*;
** accounting only for *Z1*.

As a function of the year, the phytoplankton consumes 4.315–4.605 g N/(m^3 year) (in the form of NH_4, NO_2, and NO_3 35.8–43.3, 0.6–0.7, and 56.0–63.8%, respectively). The phytoplankton consumption of P lies within 2.201–2.330 g P/(m^3 year); in so doing, the proportions of DIP and DOP consumed by phytoplankton are 86.0–90.7 and 9.3–14.0%, respectively. The N : P ratio in the nutrients consumed by the phytoplankton equals (1.9–2) : 1.

For the zooplankton, the composition of the substrates consumed is rather diverse. The consumption of N by zooplankton generally lies in the range of 0.908–1.082 g N/(m^3 year). 25.4–29.4% is consumed in the form of DON; 25.2–27.2% and 24.9–25.0% (in units of N) is consumed in the form of the biomasses of phytoplankton and bacteria, respectively; and 20.8–23.0% is consumed in the form of ND.

The consumption of P by zooplankton lies in the range of 0.682–0.811 g P/(m^3 year); of it, 25.9–30.3% is the consumption of the phytoplankton biomass (in units of P), 36.5–36.9% is detritus, 22.6–25.9% is consumed in the form of DOP, and 10.6–11.3% is the biomass of bacteria (in units of P). The N : P ratio in the substrates consumed by zooplankton comprises (1.3–1.4) : 1 (Table 4).

The principal role in the nutrient consumption by the community belongs to bacteria. They consume 7.659–8.647 and 0.190–0.206 g N/(m^3 year) (or 96.7–96.8 and 45.3–50.1%) in the form of DON and ND, respectively, and 1.700–2.052 and 0.578–0.670 g P/(m^3 year) (or 78.6–83.9 and 67.2–70.8%) in the form of DOP and PD, respectively. The annual DON consumption by zooplankton comprises 0.249–0.295 g N/(m^3 year) (or 3.1–3.3%), and that of ND makes up 0.189–0.249 g N/(m^3 year) (49.9–54.7%). The DOP consumption by zooplankton is estimated at 0.154–0.210 g P/(m^3 year) (7.1–8.5%), and that of PD is estimated at 0.249–0.299 g P/(m^3 year) (29.2–32.8%). The contribution of phytoplankton to the DOP consumption is 0.215–0.309 g P/(m^3 year) (or 8.8–14.3%) (Table 4).

In the course of their life activity, microorganisms release products of their metabolism to the aquatic medium, which are repeatedly involved by them into the turnover and are used as food. Under the conditions of the marine environment characteristic of areas 1–4, the metabolic excretions of bacteria, phytoplankton, and zooplankton provide 1.538–1.736, 0.136–0.150, and 0.080–0.091 g N/(m^3 year) (or 18.0–19.3%, 1.5–1.8, and 1%), respectively, in the form of DON. The bulk of the DON (6.205–7.160 g N/(m^3 year) or 77.9–78.4%) is produced at the destruction of detrital N in the aquatic medium (Table 4).

The formation of DOP in the aquatic medium owing to the metabolic excretions of bacteria, phytoplankton, and zooplankton comprises 0.135–0.161, 0.200–0.213, and 0.066–0.078 g P/(m^3 year) (or 6.3–6.6, 8.2–9.4, and 3.0–3.2%), respectively. The principal way of the DOP formation in the aquatic medium is related to the destruction of PD, which provides the formation of 1.746–2.008 g P/(m^3 year) (or 81.2–82.9%) (Table 4).

The formation of mineral components of P and N also occurs because of the activity of microorganisms. Bacteria and zooplankton release DIP as a metabolic product at rates of 1.216–1.452 and 0.116–0.130 g P/(m^3 year) (or 91.3–92.0 and 8.0–8.7%), respectively (Table 4).

The metabolic release of NH_4 by bacteria, phytoplankton, and zooplankton is 0.854–0.964, 0.024–0.026, and 0.076–0.086 g N/(m^3 year) (or 43.4–43.5, 1.0–1.3, and 3.8–3.9%), respectively. The principal way of the NH_4 formation in the marine environment is the destruction of urea formed in the processes of the microorganism metabolism (it represents one of the first products of destruction of protein compounds). In this case, the reaction of the urea hydrolysis results in the formation of (1.013–1.149 g N/(m^3 year) or 51.5–51.7%) salts of NH_4 (Table 4).

The total production of NH_4 in areas 1–4 comprises 1.968–2.223 g N/(m^3 year) and that of DIP is 1.332–1.579 g P/(m^3 year). The NH_4 to DIP ratio in the mineral components formed comprises (1.4–1.5) : 1.

Because of the oxidation of NH_4 in the marine medium, in areas 1–4, 0.993–1.198 g N/(m^3 year) are formed in the form of nitrite N, while, at the oxidation of NO_2, 1.149–1.363 g N/(m^3 year) of nitrate N are formed. The oxidation of NH_4 and NO_2 takes 3.395–4.097 and 1.310–1.554 g O_2/(m^3 year), respectively (Table 4).

In the marine environment, owing to the activity of microorganisms, continuous formation of detritus proceeds. The major contribution to this process is made by phytoplankton and bacteria. The total amount of PD formed in areas 1–4 comprises 3.085–3.407 g P/(m^3 year); in so doing, the contributions of bacteria, phytoplankton, and zooplankton are 55.1–57.4, 26.6–29.1, and 14.3–16.1%, respectively. The amount of ND formed makes up 8.708–9.581 g N/(m^3 year); the contributions of bacteria, phytoplankton, and zooplankton to this value are 47.3–38.7, 42.3–44.1, and 8.6–9.4%, respectively (Table 4).

During the year, in the marine environment, about 15.049–16.183 g Si/(m^3 year) is produced in the form of SiD and the contributions of bacteria, phytoplankton, and zooplankton are estimated at 57.8–55.9, 42.8–47.0, and 1.2–1.3%, respectively. The Si : N : P ratio in the total detritus formed by microorganisms in areas 1–4 ranges within (4.6–5.0) : (2.8–2.9) : 1. The Si : N : P ratio for the detritus formed by bacteria throughout the year comprises (8.6–9.7) : (4.7–5.3) : 1, that for phytoplankton is (3.6–4) : 2.2 : 1, and the values related to zooplankton are (0.3–0.4) : 1.5 : 1 (Table 4).

Calculations show that, throughout the year, in areas 1–4, the losses of PD, ND, and SiD because of sedimentation are 0.477–0.530 g P/(m^3 year), 1.964–2.144 g N/(m^3 year), and 1.619–2.183 g Si/(m^3 year), respectively. Note that, on average, these losses are

lower than PD, ND, and SiD formed owing to the activity of microorganisms by factors of 6.4, 4.4, and 8.4 (Table 4). In order to keep the conditions stable for the matter transformation, the values of the matter supply to the upper layer that compensate for the losses of the mineral components of nutrients in the course of the detritus sedimentation were specified for each of the areas as 0.511 g P/(m^3 year) in the form of DIP, 2.227 g N/(m^3 year) in the form of N_{min}, and 1.826 g Si/(m^3 year) in the form of DISi. The calculations carried out using the maximal gradients of the nutrient concentrations as estimated in [12] showed that the possible vertical nutrient flux caused by the upwelling in this region of the Atlantic may be 3–4 times as high as the flux that compensates for the nutrient losses from the upper layer because of the sedimentation processes. Thus, in this case, we assume that the calculations of the nutrient dynamics in areas 1–4 indirectly account for the possible delivery of nutrients to the upper layer owing to the vertical exchange.

The information acquired during the calculations suggests a significant contribution of the community of microorganisms to the implementation of the processes of nutrient recycling. If no nutrients are supplied from external sources, its internal recycling smoothes the differences in the formation of N and P compounds. As a result, the N : P ratios for individual fractions differ from their standard values, which indicates changes in the provision of microorganisms with nutrients. The components of nutrients and the detritus that are formed in the marine environment due to the activity of microorganisms are repeatedly involved into the turnover and provide a high activity of the community even during the periods when the nutrient content in the medium is the least (close to analytical zero). This gives grounds to affirm that, in the tropical and subtropical zones, the activity of the microorganism functioning in an ecosystem is defined mainly by internal nutrient fluxes rather than by the concentrations of nutrients in the aquatic medium. The nutrient recycling also controls the conditions of the BP formation in the marine environment.

In the model operations, for areas 1–4, the values of the BP of microorganisms per unit of water volume were calculated at each step and summed up. This way, each month, we accounted for the differences in the environment factors that influenced the regime of the nutrient recycling and the formation of the biomass of microorganisms. When processing the file with calculated BP values per unit of water volume, first, the BP of the microorganisms was determined for each month and, then, the annual values were calculated for each area. These values of the production were then converted to the resulting production for each month with account for the thickness of the upper (active) layer (in thousands of tons of the element per month). Later on, these values were summed up, and, this way, the annual production was estimated for each of the groups of hydrobionts in thousands of t (in units of C, Si, N, and P). The calculated annual values of the BP of the hydrobionts for areas 1–4 are presented in Table 5.

The calculations showed that, generally, the values of the annual BP (per unit of water volume) for bacteria (BP_B), phytoplankton of the second (BP_{F2}) and third (BP_{F3}) groups, and predatory zooplankton (BP_{Z2}) are higher in area 4, while those for the first group of phytoplankton (BP_{F1}) and phytophagous zooplankton (BP_{Z1}) are higher in area 3. Generally, in area 1, the values of the BP of microorganisms and those of their internal fluxes are lower than in other areas. This kind of distribution of the hydrobionts' production values is evidently defined by the environmental factors and the conditions of the internal nutrient turnover. This set of conditions determines the region of the formation of the microorganism biomasses and their activity in the nutrient transformation and maintenance of the continuous nutrient turnover in the marine medium.

On the whole, the estimated weight proportions of the annual bioproductivity values (in units of C, Si, N, and P) in different aquatic areas change within narrow ranges; meanwhile, the differences distinguished allow one to infer that the conditions of the formation of the biomasses of microorganisms in the areas studied are not constant. For example, in areas 1–4, the proportions of the bacterial production in units of C, Si, N, and P are $BP_{B_C} : BP_{B_{Ni}} : BP_{B_N} : BP_{B_P} = (6.3–6.8) : (5.7–6.2) : (3.3–3.5) : 1$, and these relatively small differences in the proportions of the BP_B production are caused by the differences in the bacteria provision with forms of P (DOP and PD).

For the first group of phytoplankton (diatom algae), the proportions of the production in units of Si, N, and P in areas 1–3 are $BP_{F1_{Si}} : BP_{F1_N} : BP_{F1_P} = 4.4 : 1.8 : 1$, and, in area 4, the proportions are (4.7 : 1.8 : 1). These proportions suggest an evident distinction in the turnover conditions of the stock of silicon compounds in area 4 as compared to areas 1–3 and a constancy of the conditions of circulation of mineral components of N and P in these areas. The latter suggestion is confirmed by the constancy of the proportions of the estimated total values of the production of three phytoplankton groups (primary production) in units of N and P in areas 1–4, which comprises $(BP_{F1_N} + BP_{F2_N} + BP_{F3_N}) : (BP_{F1_P} + BP_{F2_P} + BP_{F3_P}) = 2.0 : 1$. Similarly constant in the areas studied are the proportions of the total production of zooplankton (phytophagous and predatory) in units of N and P—$(BP_{Z1_N} + BP_{Z2_N}) : (BP_{Z1_P} + BP_{Z2_P}) = 1.4 : 1$.

On the whole, in areas 1–4, the annual production of bacteria is higher than that of the primary production by factors of (1.8–1.9) and (1.1–1.2) in units of N and P, respectively. The estimated values of the annual primary production are higher than the annual production of zooplankton by factors of (4.1– 4.6) and (2.8–3.2) in

units of N and P, respectively. The proportions between the values of the microorganism production calculated in the course of the modeling result from the differences in the environmental factors in the near-shore areas (off the Moroccan Sahara) that define the turnover of nutrients and the proportions of their concentrations.

In order to compare the values of the "regenerative" production (with account for the changes in the environmental factors and nutrient recycling) obtained in this study with the estimates of the phytoplankton BP available from publications, the annual values of $B\,P_{F1N}$, $B\,P_{F2N}$, and $B\,P_{F3N}$ (in units of N) were converted to units of C. To do this, we used the stoichiometric atomic ratio C : Si : N : P = 106 : 23 : 16 : 1 known for marine phytoplankton. The above values of the BP for each of the phytoplankton groups were multiplied by 106 and 12 (molecular weight of C) and divided by 16, 14 (molecular weight of N), and 365 (number of days in a year). The total BP values for the three phytoplankton groups within each area were summed up, and the values of the total BP_{FN} were obtained for areas 1–4 equal to 133.4, 139.4, 141.0, and 142.0 g C/(m^3 days). Note that our calculated values of the BP_{FN} are by a factor of 1.6–2.2 higher than those estimated for individual periods with the use of the radiocarbon method (64–84 g C/(m^3 days) and by a factor of 1.7–2.4 higher than those estimated from the drops in the concentrations of phosphates, nitrates, and O_2 [9].

Assuming the thickness of the photosynthetic layer in this region equal to 25 m [9], we obtain that the values of the "regenerative" $B\,P_{FN}$ in areas 1–4 comprise 3.3–3.6 g C/(m^2 days). Taking into account that, in the regions of intensive water upwellings the values of the total ("new" and "regenerative") primary production comprise 10–20 g C/(m^2 days) and more [10], the value of $B\,P_{FN}$ = 3.3–3.6 g C/(m^2 days) obtained in this study, which refers to the entire year and is related to the "regenerative" component of the primary production, may be regarded as quite admissible for the region considered.

The values of the primary production of the microorganisms calculated per unit of water volume were also converted into total production values (thousands of tons in units of C, Si, N, and P) for each area with account for the monthly changes in the volumes of the subsurface waters in these areas. As the volume in area 2 was greater than in the other areas, the values of the microorganism production obtained precisely in area 2 were the highest in terms of all the parameters; with respect to the production values, areas 1 and 3 occupy an intermediate position, and the lowest annual production values are characteristic of area 4 (Table 5).

Table 5. Annual values of the bioproductivity of microorganisms in areas 1–4 in the region of the Moroccan Sahara calculated with the help of the hydroecological model

Microorganisms	Units	1	2	3	4
$B1_C$	g C/m^3 / th.t C	30.868 / 456.784	33.232 / 1071.243	33.810 / 486.175	34.208 / 261.853
$B1_{Si}$	g Si/m^3 / th.t Si	28.027 / 413.140	30.371 / 969.669	30.381 / 443.255	31.200 / 239.163
$B1_N$	g N/m^3 / th.t N	15.628 / 222.773	17.247 / 524.960	17.563 / 253.409	17.614 / 136.485
$B1_P$	g P/m^3 / th.t P	4.533 / 64.741	5.273 / 161.736	5.410 / 78.138	5.245 / 40.711
$F1_{Si}$	g Si/m^3 / th.t Si	13.949 / 207.046	14.469 / 475.679	14.686 / 208.804	12.996 / 99.454
$F1_N$	g N/m^3 / th.t N	5.740 / 83.437	5.972 / 189.927	6.033 / 85.179	5.027 / 38.871
$F1_P$	g P/m^3 / th.t P	3.169 / 46.404	3.320 / 106.188	3.339 / 47.007	2.775 / 21.429
$F2_N$	g N/m^3 / th.t N	1.805 / 25.483	1.861 / 55.278	1.900 / 27.996	2.362 / 18.245
$F2_P$	g P/m^3 / th.t P	0.813 / 11.437	0.838 / 24.806	0.852 / 12.556	1.064 / 8.229
$F3_N$	g N/m^3 / th.t N	1.026 / 14.401	1.128 / 32.098	1.124 / 16.837	1.735 / 13.397
$F3_P$	g P/m^3 / th.t P	0.405 / 5.561	0.446 / 12.570	0.442 / 6.172	0.712 / 5.519
$Z1_{Si}$	g Si/m^3 / th.t Si	0.367 / 5.343	0.397 / 12.459	0.404 / 5.800	0.404 / 3.113
$Z1_N$	g N/m^3 / th.t N	1.148 / 6.924	1.239 / 38.974	1.259 / 18.037	1.234 / 7.603
$Z1_P$	g P/m^3 / th.t P	0.845 / 11.400	0.914 / 28.103	0.928 / 13.319	0.915 / 5.550
$Z2_N$	g N/m^3 / th.t N	0.706 / 9.971	0.786 / 22.939	0.787 / 11.716	0.985 / 9.971
$Z2_P$	g P/m^3 / th.t P	0.527 / 7.436	0.571 / 17.041	0.584 / 8.671	0.718 / 7.436

CONCLUSIONS

Using systematized data of long-term observations, a theoretical estimate was performed with a mathematical model of the influence of the factors of the marine environment varying throughout the year (such as the temperature, the light inteasity, the transparency, and the depth of the thermocline) of the nutrient dynamics, their internal fluxes, and bioproductivity in areas 1–4 in the near-shore zone off the Moroccan Sahara. The calculations indirectly accounted for the compensational nutrient losses owing to the detritus sedimentation.

Areas 1 and 4 differ from other areas in the dynamics of the mineral forms of P and N (in particular, NH_4 and NO_3). The values of the turnover periods for organic and mineral components and the ranges of their variability during the year significantly differ. This is defined by the different rates of the nutrient transformation depending on the environmental factors. The fastest is the turnover of the detritus components ND and PD (over 0.61–0.88 and 0.47–0.96 days, respectively). The turnover of organic components (DOC, DON, and DOP) rapidly develops at the beginning of the year (over 2.10–2.47, 8.50–9.15, and 3.47–4.19 days, respectively). In the middle of the year, the turnover of organic components is slower, being determined by the rates of the replenishment of the organic matter stock from the destruction of detritus and due to production processes. The turnover of the organic component in areas 1 and 3 is the most and the least intensive, respectively.

The times of the active turnover of mineral components in different areas of the near-shore zone are significantly different. The turnover of DIP is most actively implemented in the period of 74.2–151.2 days, and the τ_{DIP} values in different areas in this period vary within 0.49–4.06 days. On the whole, the DIP turnover is faster in area 1. The turnover of NH_4 is more active in the period of 152.6–250 days, and the values of τ_{NH_4} in areas 1–4 during this period vary in the range of 1.05–3.52 days. The fastest is the NH_4 turnover in area 2. The turnover of NO_2 in areas 1–4 proceeds at approximately similar rates with variations in the values of τ_{NO_2} within 2.14–3.33 days. The most active NO_3 turnover is observed in the period 260.6–365 days; in this period, the values of τ_{NO_3} in areas 1–4 vary in the range of 0.33–2.77 days. The most active turnover of NO_3 occurs in area 4. The DISi turnover in areas 1–4 is implemented over 26.06–177 days, and, on the whole, it is more active in area 2.

The oscillations in the turnover periods of the phytoplankton biomasses are mainly determined by the daily changes in the light inteasity of the aquatic medium and by its grazing out by zooplankton. The fastest biomass turnover is characteristic of the first group of phytoplankton (over 4.52–12.02, 4.55–12.21, 4.70–12.14, and 4.94–13.02 days in areas 1–4, respectively). The turnover of the biomasses of the second and third groups of phytoplankton proceeds slower and is limited by the conditions of the nutrient turnover in the marine environment.

The values of the N : P ratio in the components consumed by bacteria, phytoplankton, and zooplankton are (3.2–3.5) : 1, (1.9–2) : 1, and (1.3–1.4) : 1, respectively. Bacteria play a significant role in the consumption of organic (dissolved and particulate) substances. The bulk of the dissolved organic components of N and P are created at the decomposition of detritus.

Under the subtropical (and tropical) conditions, the intensity of the functioning of the ecosystem is defined by the internal fluxes (recycling) of nutrients rather than by their concentrations. The intensity of the nutrient recycling controls the conditions of the formation of the marine environment.

The conditions of the development of bacteria and phyto- and zooplankton are also characterized by the calculated values of their monthly and annual production in units of C, Si, N, and P (based on the internal matter fracture zones in different regions). In areas 1–4, the values of the annual production of bacteria in units of N and P are generally higher than the total phytoplankton by factors of 1.8–1.9 and 1.1–1.2, respectively. The annual production values of phytoplankton are higher than those of zooplankton by factors of 4.1–4.6 and 2.8–3.2 in units of N and P, respectively. The values of the annual production of bacteria, the second and third groups of phytoplankton, and predatory zooplankton are the highest in area 4, and those of the first group of phytoplankton and phytophagous zooplankton are higher in area 3. This is related to the environmental factors that define the internal nutrient turnover in the areas studied in the near-shore zone off the Moroccan Sahara.

The "regenerative" portion of the primary production, which is defined by the nutrient recycling at the given environmental parameters, in areas 1–4, comprises 3.3–3.6 g C/(m^3 day). This estimate seems quite reasonable since, according to the published data, the value of the total ("new" and "regenerative") primary production in the regions of intensive water upwellings comprises 10–20 g C/(m^3 day).

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APPENDIX

1. The equation for the description of the changes in the concentrations of the substances C_{ijk} in the CNPSi model has the following general form:

$$dC_{ijk}/dt = R_{ijk} + LOAD_{ijk} + TR_{ijk}, \quad (1)$$

where i is the model counter of the areas distinguished (the maximal number of areas is 10); j is the model counter of the layers distinguished (j = 2); k is the counter of the model components assessed (k = 29); and R_{ijk}, $LOAD_{ijk}$, and TR_{ijk} are the rates of the changes in the concentrations of the substances C_{ijk} owing to the biotransformation of the components, owing to the matter supply from external sources, and owing to the spatial (horizontal and vertical) matter transfer, respectively (all these values are in mg of the element/day).

2. Structure of the equations for the description of the matter biotransformation, R_{ijk}:

(a) Dynamics of the biomasses B_k:

$$dB_k/dt = (UP - L - S)B_k - GZO, \quad (2)$$

$$UP = K(T, Light)/(1 + B_C/PoolC + B_N/PoolN + B_P/PoolP + B_{Si}/PoolSi), \quad (3)$$

$$PoolC = \Sigma d_k C_k; \quad PoolN = \Sigma d_k N_k;$$

$$PoolP = \Sigma d_k P_k; \quad PoolSi = \Sigma d_k Si_k;$$

$$L = rUP; \quad r = aUP/(1 + bUP) + (1 - a/b);$$

$$S = q + mr + gB/UP.$$

(b) Mechanism of the regulation of the microorganism activity:

a. Biomass/substrate relation
(B_C/PoolC; B_N/PoolN; B_P/PoolP; B_{Si}/PoolSi);

b. r = f(UP);

c. S = f(r, UP);

d. L = f(UP), S = f(UP).

c. Dynamics of chemical substances C_{ijk} and detritus:

Organiv fractions –

$$dC_{ijk}/dt = L_o B_k - UP_o B_k + K_k D, \quad (4)$$

Mineral fractions

$$dC_{ijk}/dt = L_m B_k - UP_m B_k, \quad (5)$$

Detritus D –

$$dC_{ijk}/dt = \Sigma S_k B_k - K_k D - \Sigma UP_d B_k - K_{sed} D, \quad (6)$$

where UP, L, S, and G are the specific rates of the total substance consumption, total release of the products of metabolism, biomass dying out, and its grazing out by zooplankton, respectively, with all the values in day^{-1}; $UP = UP_o + UP_m + UP_d$ (UP_o, UP_m, and UP_d are the consumption of organic fractions, mineral fractions, and detritus, respectively, by microorganisms (day^{-1})); $L = L_o + L_m$ (L_o, and L_m are the release of organic and mineral substances, respectively, by microorganisms (days-1)); PoolC, PoolN, PoolP, and PoolSi are the stocks of the C, N, P and Si compounds, respectively, for microorganisms; and K, d_k, a, b, q, m, and g are the constants.

3. Equations for the calculation of the rates of the matter supply $LOAD_{ijk}$:

$$LOAD_{ijk} = fl_{ijk}(Q_{pr}C_r/V_i) + CZ_{ijk} + W_{ijk}, \quad (7)$$

$$W_{ijO_2} = -K0_{14}(O_2 - O_{2n}), \quad (8)$$

$$O_{2n} = 14.61996 - 0.4042T + 0.00842T^2 - 0.00009T^3, \quad (9)$$

$$W_{ijN_2} = -K0_{33}(N_2 - N_{2atm}), \quad (10)$$

$$N_{2atm} = 22.33 \exp(-0.0207T). \quad (11)$$

The first, second, and third terms in the right-hand part of Eq. (7) show the rates of supply of the substances to the area studied with the atmospheric moisture, from distributed sources, and owing to the exchange with the atmosphere (for dissolved gases), respectively, in mg element/(l days); V_i is the water volume in the basin studied, km^3; O_{2n} and N_{2atm} are the concentrations of the oxygen and nitrogen dissolved in the water at their saturation, respectively; T is the temperature of the aquatic medium, °C; and $K0_{14}$ and $K0_{33}$ are the constants of the rates of the water aeration by oxygen and nitrogen, respectively, at the expense of the exchange with the atmosphere.

4. Equations for the transport term TR_{ijk}:

$$TR_{ijk} = fl_k[TRIN_{ijk} + TRUP_{ijk} + TRSEC_{ijk} + TROUT_{ijk}], \quad (12)$$

$$TRIN_k = QWIN_{ij}CIN_{ki}/V_{ij}, \quad (13)$$

$$TRUPk = abs(QWUP_i)(CM_{ki3\text{-}j} - Y_k)/V_{ij}, \quad (14)$$

$$TRSEC_{ki} = [(QW_{ij}CM_{kj}) - (QW_{ij}Y_k)]/V_{ij}, \quad (15)$$

$$TROUT_k = -(QWOUT_{ij}Y_k)/V_{ij}, \quad (16)$$

where $TRIN_{ijk}$, $TRUP_{ijk}$, and $TRSEC_{ijk}$ are the rates of the matter supply to the areas considered with water flows, owing to the vertical exchange with the underlying layer, and owing to the transfer from adjacent regions within the marine ecosystem, respectively; $TROUT_{ijk}$ are the matter losses with water flows across the outer boundaries of the aquatic system (all the values are in mg of the element/(l day); $QWIN_{ij}$ are the water discharges of the external flows in corresponding areas of the sea, km^3/month; $QWUP_i$ is the component of the vertical transfer, km^3/month; $QWOUT_{ij}$ are the water discharges at the outer boundary of the sea for the calculations of the matter losses from the marine ecosystem, km^3/month; QW_{ij} are the water discharges across the boundaries of the sea areas distinguished, km^3/month; Y_k are the instant concentrations of substances in corresponding sea areas in the water layer considered, mg of the element/l; $CM_{ki3\text{-}j}$ are the instant concentrations of substances in corresponding sea areas in the upper (or lower) layer of the water column, mg of

the element/l (required for the calculations of the amounts of matter participating in the vertical transfer); CIN_{ki} are the concentrations of the components assessed in the water flows, mg of the element/l; V_{ij} are the water volumes of the areas and layers considered, km^3; and fl_k are the parameters controlling the advective matter transfer (dimensionless).

Thus, the CNPSi models allows one to calculate, for individual areas of the aquatic ecosystem under consideration, the following parameters: the intra-annual dynamics of the concentrations of chemical and biological parameters of the environmental conditions, the instant rates of the processes responsible for the changes in the concentrations of the substances, the internal and external matter fluxes, the periods of turnover for all the chemical and biological components assessed in the model, the specific production rates of hydrobionts, and the values of the productivity of the community of aquatic microorganisms assessed in the model that implement the biotransformation of nutrients and organic matter. Based on the information acquired with the CNPSi model, it is possible to correctly calculate the balances of nutrient compounds in various areas of the ecosystem under study.

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