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MARINE BIOLOGY

Spatial Distribution and Daily Dynamics of Phytoplankton in Nhatrang Bay of the South China Sea

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Abstract—During a spatial survey, the species structure, phytoplankton abundance, and chlorophyll concentration (chl.) were determined at three depths at nine stations. With the help of a pulse submersible fluorometer, vertical profiles of the fluorescent characteristics of phytoplankton, temperature, and underwater irradiance over the upper 18-m layer were recorded at 21 stations. It was shown that, in terms of the values of biomass (*B*) and chlorophyll *a*, the waters of the bay can be referred to as mesotrophic. Seaward, the values of biomass and chlorophyll *a* per 1 m^2 increased. In the southern part of the bay, the values of chlorophyll averaged over the surface layer were higher than those in the northern part, whereas the values of biomass were close. The values of biomass and chlorophyll were higher within the near-bottom layer. With respect to the number of species and their abundance, diatomaceous algae prevailed. *Guinardia striata* made the maximum contribution to the total biomass of phytoplankton. At different stations, phytoplankton were characterized by high similarity. In the surface sea layers, the algae experienced stress from photoinhibition over the major part of the light time of the day. Within the near-bottom layer, photosynthetic activity remained at a high level throughout the entire light period. During the day, the biomass per 1 m^2 changed by more than one order of magnitude. Such a significant fluctuation was determined, in addition to biotic factors, by the dynamics of the biomass within the near-bottom layer due to the movement of the water masses during the tidal cycle.

INTRODUCTION

Phytoplankton of the tropical part of the Pacific Ocean is characterized by a certain structural unity [13]. The greatest differences are inherent to the neritic communities, which are determined by the features of the thermohaline characteristics of the waters, prevailing directions of the vertical and horizontal movements of water masses, by the vertical distribution of the water density and transparency, by the content of nutrients, and other factors [29]. In particular, in some tropical coastal ecosystems, the seasonal dynamics of phytoplankton is determined by the duration and intensity of upwelling [40], whereas in the others it is determined by the supply of nutrients with the riverine waters and precipitation during the raining season [4]. Regarding provision with nutrients, the neritic tropical phytoplankton can be limited by a deficiency of either phosphorus [28] or nitrogen [41]. The diversity of the tropical coastal ecosystems determined the necessity of extension of the number of phytoplankton communities examined and revealed the main factors that are responsible for the seasonal dynamics, spatial distribution, and functional characteristics of plankton algae.

In Nhatrang Bay of the South China Sea, the variations in the abundance of the plankton algae throughout the year are determined by the supply of nutrients with the riverine runoff during the raining season (October–December) [4]. During this period, the biomass of phytoplankton reaches its maximum values. During the rainy season, the nonhomogeneity of waters of the bay in terms of the hydrochemical parameters, which determines the heterogeneity of the spatial distribution of phytoplankton, is high. The chlorophyll *a* concentration, abundance, and biomass of algae decrease from the pre-estuarine areas towards the open sea. The maximum biomass of algae is confined to the upper sea levels, as within the near-bottom layers the phytoplankton development is short of light. After the rains stop (during the dry season), the phytoplankton biomass decreases, and by May it reaches the minimum values over the entire year [4]. To date, the spatial distribution and functional characteristics of phytoplankton in Nhatrang Bay during the dry season and, in addition, the daily dynamics of algae have not yet been examined.

This study is aimed at the following: (1) to evaluate the abundance and functional parameters of phytoplankton in different areas of Nhatrang Bay during the dry season (in March, as an example); (2) to reveal the features of the spatial and vertical distribution of algae and their functional parameters in the dry season, and (3) to examine the daily dynamics of phytoplankton.

MATERIAL AND METHODS

Materials for the studies were collected at 21 stations in Nhatrang Bay of the South China Sea in March 1998 (Fig. 1).

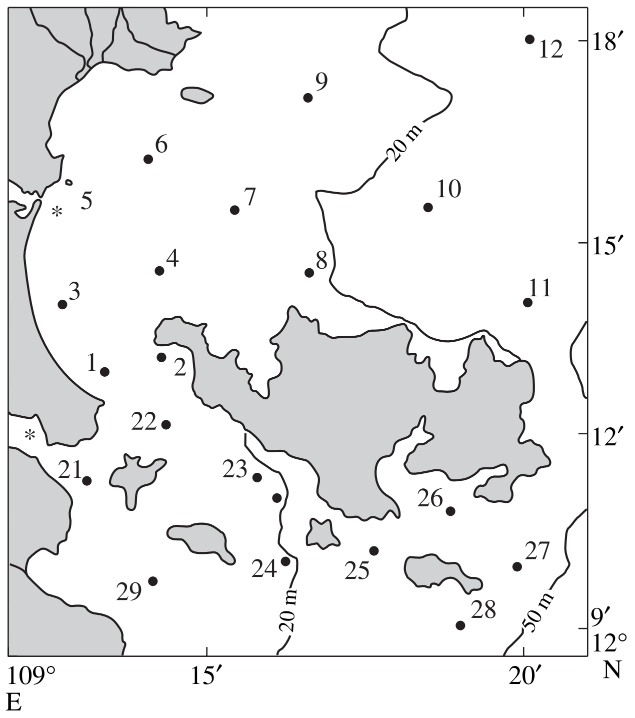

Fig. 1. Location of stations in Nhatrang Bay. The areas of inflow of large rivers are denoted by asterisks.

General Characteristics of the Research Area

Two large rivers and a few small rivers flow into Nhatrang Bay (Fig. 1). The largest island of the bay is located in the central part of the water area; with respect to it, the water area is divided into northern and southern parts. Up to 109°16′ E, sea depths do not exceed 20 m. The 50-m depth contour goes beyond 109°20′ E (Fig. 1).

The tides are semidiurnal with a great daily disparity. At high tide the coastal currents are directed towards the south and north from the area of the location of station 5. During the ebb their directions are reversed. The winds in March are of a permanent northeastern direction. The mean monthly amount of precipitation in the dry season is 421 mm/m^2 [2]. A few small coral reefs are located in the bay; the bottom, especially in the southern part, is partially covered with silty sediments [14].

Fluorescent Parameters, Temperature, and Irradiance

At all the stations, transparency was measured with a Secchi disk and, in addition, with the help of a double-flash pulse submersible fluorometer within the 12- to 18-m layer (depending on the sea depth); in addition, the vertical profiles of the phytoplankton properties, temperature, and underwater irradiance were recorded. A submersible pump-and-probe fluorometer developed at the Biophysics Department, Moscow State University [8] recorded the parameters in a continuous mode (at a frequency of 1 Hz). The fluorometer measured the constant fluorescence (F_0) and relative yield of the variable fluorescence (F_v/F_m) in algae at natural irradiance. The parameter F_0 is proportional to the coefficient of absorption of blue light with the light-absorbing algal pigments [36] and reflects their total concentration [9]. The relative yield of the variable fluorescence (F_v/F_m) shows the efficiency of the primary photochemical transformation of the light energy in the reaction centers of photosystem 2 [7, 30] and can be considered as a parameter of the photosynthetic activity of phytoplankton [17, 30].

Water Sampling

At nine stations (Table 1) water samples were taken at three depths for measuring salinity, concentrations of nutrients and chlorophyll *a*, and, in addition, for quantitative accounting of phytoplankton. The sampling was performed (Table 1) from subsurface, near-bottom, and "intermediate" levels; the latter corresponded to half of the sea depth (stations 1, 5, 7, 9, 11, 12, and 24) or of the depth of the disappearance of the Secchi disk (stations 21 and 26). Further, the water layer from the surface to the "intermediate" depth is referred to as the surface layer.

Salinity, Concentrations of Nutrients, and Chlorophyll *a*

The salinity was calculated from the results of the measurements of the water density introducing a correction for the sample temperature. The content of the mineral forms of phosphorus and nitrogen (ammonium, nitrite, and nitrate) was determined by standard hydrochemical methods [10]. The chlorophyll *a* concentration was estimated by the spectrophotometric method [5].

The Quantitative Accounting of Phytoplankton

For the quantitative accounting of phytoplankton, samples 2–3 l in size were concentrated through reverse filtration (filters with a mesh size of 1.9 μm) and fixed with a 2% formaline solution. To determine the species composition, abundance, and biomass of phytoplankton, the samples were counted under a light microscope in a Naujotte chamber (0.05 ml in volume). The wet biomass was determined by geometric similarity. To estimate the values of biomass (B) in carbon units, the cellular content of organic carbon was calculated by allometric equations in relation to the volume of cells [43]. The biomass of algae being, according to the published data, obligate heterotrophs (species of the genera *Protoperidinium, Oxyrrhis*, and others) were not included in the total phytoplankton biomass.

Table 1. Sea depths at the stations, sampling depths, phytoplankton biomasses (*B*), and chlorophyll *a* concentrations

Nos. of stations	Sea depth, m	Sampling depths, m	*B**, mg C/m^3	*B*, mg C/m^2	Chl.*, µg/m^3
Northern part of the bay					
5	12.3	0.5; 5; 9 (12**)	$\frac{1.2}{4.8}$	37	$\frac{103}{165}$
7	18.0	0.5; 6.5; 18	$\frac{2.1}{11.6}$	123	$\frac{68}{181}$
9	18.2	0.5; 6.5; 17	$\frac{1.9}{12.0}$	127	$\frac{105}{335}$
11	42.1	0.5; 7.5; 15 (42**)	$\frac{2.7}{-}$	199	$\frac{82}{267}$
12	38.2	0.5; 7.5; 12 (38**)	$\frac{2.3}{-}$	191	$\frac{71}{517}$
Southern part of the bay					
1	20.8	0.5; 6; 20	$\frac{2.3}{6.9}$	95	$\frac{74}{151}$
21	14	0.5; 3; 13	$\frac{3.0}{3.1}$	43	$\frac{161}{243}$
24	24.5	0.5; 5.5; 24	$\frac{1.6}{5.3}$	83	$\frac{109}{204}$
26	18.5	0.5; 9.5; 18	$\frac{1.9}{7.9}$	84	$\frac{86}{210}$

*Numerator—mean value in the surface layer (0 m to intermediate depth); denominator—mean value in the near-bottom layer.
**Sampling depth for determination of chlorophyll *a* concentration.

Daily Dynamics of the Abiotic Factors and Phytoplankton

At the daily station C, vertical profiles of the fluorescent characteristics of phytoplankton, the temperature, and the underwater irradiance were recorded during the day every three hours beginning from 9:00 local time. At the same interval, from sea levels of 0.5, 5, and 18 m, samples for determination of the chlorophyll *a* concentration and quantitative accounting of phytoplankton were taken.

Phytoplankton Similarity

Phytoplankton similarity at different stations was evaluated by the Chekanovskii index [11]. The calculations were made with the use of the ECOS v. 1.3 software (developed by A.I. Azovskii, Moscow State University). The cluster analysis was performed by the method of “mean adjunction” with the use of the SYSTAT-7 program.

The scheme of directions of the tidal movements of water masses in Nhatrang Bay and, in addition, the data on the tidal fluctuations of the sea level at the point with coordinates 13°45′ N and 109°13′ E, which were kindly given to us by the associates of the Institute of Oceanography, Vietnam, were used in this paper.

RESULTS

Abiotic Conditions

The temperature of the surface water layer varied from 26.6 to 27.6°C. A slight reduction of the temperature (less than 1.4°C) began at sea depths of 15–20 m. Salinity also changed slightly, namely, from 33.1 to 34.5‰. The maximum irradiance (1000 µE/m^2 s) within the subsurface layer was reached at noon. The depth of the photic layer calculated with the use of the Secchi disk for the stations with a sea depth greater than 18 m, was 40 m. At all the stations with a sea depth of 18 m and less, the irradiance within the near-bottom layer exceeded 1% of the subsurface irradiance. Therefore, in the parts of the water area studied, the photic layer covered the entire water column down to the bottom. At the “intermediate” depths, the irradiance ranged from 21 to 49% of its subsurface value.

The concentrations of the mineral forms of nitrogen (N_{min}) and phosphorus (P_{min}) within the surface layer varied from 1.6 to 45 µmol and from 0.1 to 7 µmol, respectively. At the underlying depths, the concentra-

Table 2. Date and time of the evaluations of the fluorescent parameters, mean values of the constant fluorescence (F_0) in the 0- to 18-m layer, and relative yields of the variable fluorescence (F_v/F_m) of phytoplankton

Nos. of stations	Date, local time	F_0, conventional units	F_v/F_m
Northern part of the bay			
2	March 24, 1998, 15:30	0.46	0.62
3	15:10	0.31	0.59
4	14:55	0.42	0.50
5	14:20	0.22	0.60
6	13:50	0.05	0.08
7	13:10	0.17	0.19
8	12:55	0.14	0.29
9	12:00	0.03	0.69
10	11:25	0.07	0.27
11	7:30	0.22	0.51
12	9:45	0.24	0.47
Southern part of the bay			
1	March 24, 1998, 15:55	0.53	0.64
21	March 25, 1998, 12:30	0.46	0.55
22	12:05	0.21	0.38
23	11:40	0.15	0.25
24	10:57	0.27	0.55
25	10:40	0.06	0.07
26	9:30	0.35	0.54
27	9:07	0.38	0.48
28	8:50	0.38	0.39
29	8:10	0.53	0.59

tion of N_{min} ranged within the above noted limits, whereas the content of P_{min} did not exceed 0.4 μmol. The basic portion in the N_{min} pool was that of ammonium nitrogen, the share of the nitrate nitrogen reached 5% and less; nitrites were found in a very small proportion. The exceptions are stations 24 and 26, where the share of the nitrate nitrogen varied from 21 (station 24, near-bottom layer) to 60% (station 26, 0 to 9.5 m). The atomic ratio $N_{min} : P_{min}$ changed from 2 to 520. At most stations, $N_{min} : P_{min}$ was greater than 30; according to the commonly accepted views [41], this points to the limitation of the phytoplankton growth by the shortage of P_{min}.

Phytoplankton Biomass and Chlorophyll a Concentration

In terms of the phytoplankton abundance and chlorophyll concentration (Table 1), the waters of the bay should be referred to as moderately productive waters. Towards the open sea, the algal biomass within the surface layer of the northern part of the bay increases, while in the southern part it decreases. Both the phytoplankton biomass and the value of the integral biomass (per 1 m^2) increase seaward in both parts of the bay. The averaged values of chlorophyll within the surface layer obtained for the northern and southern parts of the bay are higher than those for the northern part, whereas the biomass values were close.

Fluorescent Parameters of Phytoplankton

The low mean values of the constant fluorescence ($F_0 < 0.20$ conventional units) were noted in the 0- to 18-m layer at stations 6–10 in the northern part of the bay and at stations 23 and 25 in its southern part (Table 2). Similar to the values of chlorophyll within the surface layer, the averaged values of F_0 in the southern part are higher than those in the northern part.

The relative yield of the variable fluorescence (mean values for the 0- to 18-m layer) changed from 0.08 to 0.69. The averaged values of F_v/F_m for the southern and northern parts of the bay were close, namely, 0.42 and 0.44, respectively. The values of F_v/F_m greater than 0.4 point to the comparatively high photosynthetic activity of phytoplankton [8, 30]. The low values of F_0 and F_v/F_m noted at station 25 (Table 2) can be caused by the fact that the station was located above a living coral reef. It is known that the quantity of algae inhabiting above the coral biocoenoses is lower than that in the adjacent waters [15].

Phytoplankton Structure

Altogether, 110 species of algae were noted, among which 80 species are diatoms, 28 species belong to the Dinophyta algae, and, in addition, single representatives of the bluegreen algae and coccolithophorids were found. With respect to the number of species, such genera as *Chaetoceros* (34 species), *Rhizosolenia* (5 species), *Gymnodinium* (5 species), and *Thalassiosira* (5 species) were the most diverse.

The basic contribution to the total biomass of phytoplankton throughout the entire water area of the bay is provided by diatoms (Table 3). With respect to the biomass, *Guinardia striata* prevails; its contribution to the phytoplankton biomass varied from 16 to 60%. At selected stations, the contribution of the following algae exceeded 10%: *Pseudosolenia calvar-avis*, *Cerataulina pelagica*, *Rhizosolenia bergonii*, *R. imbricata*, *Guinardia flaccida*, *Detonula pumila*, *Leptocylindrus minimus*, *Proboscia alata*, *Pseudo-nitzschia pungens*, *Hemiaulus sinensis*, *Bacteriastrum furcatum*, *Pleurosigma* sp., and *Gymnodinium* sp. (Table 3). The algae listed are also among the mass and prevailing forms during other periods of the seasonal phytoplankton growth [4].

Table 3. Contribution of the three most abundant algae to the total biomass of phytoplankton (B, %)

Nos. of stations	Depth, m	B, %
1	0.5	*Guinardia striata*—33; *Pleurosigma sp.*—17; *Cerataulina pelagica*—10
	6	*Pseudosolenia calvar-avis*—40; *Guinardia striata*—27; *Gymnodinium* sp.—9
	20	*Guinardia striata*—40; *Pseudosolenia calvar-avis*—22; *Proboscia alata*—11
5	0.5	*Gymnodinium* sp.—25; *Guinardia striata*—20; *Pseudo-nitzschia pungens*—10
	5	*Guinardia striata*—46; *Rhizosolenia bergonii*—17; *Guinardia delicatula*—9
	12	*Guinardia striata*—37; *Guinardia flaccida*—17; *Gymnodinium sp.*—14
7	0.5	*Guinardia striata*—29; *Detonula pumila*—16; *Hemiaulus sinensis*—10
	6.5	*Guinardia striata*—51; *Bacteriastrum furcatum*—8; *Proboscia alata*—6
	17	*Guinardia striata*—40; *Cerataulina pelagica*—18; *Detonula pumila*—12
9	0.5	*Guinardia striata*—50; *Leptocylindrus minimus*—12; *Bacteriastrum furcatum*—10
	6.5	*Guinardia striata*—60; *Chaetoceros affinis*—8; *Leptocylindrus minimus*—4
	18	*Guinardia striata*—51; *Cerataulina pelagica*—10; *Guinardia flaccida*—9
11	0.5	*Guinardia striata*—40; *Guinardia flaccida*—16; *Chaetoceros affinis*—7
	7.5	*Guinardia striata*—25; *Pseudosolenia calvar-avis*—25; *Chaetoceros affinis*—7
	15	*Guinardia striata*—41; *Guinardia flaccida*—14; *Cerataulina pelagica*—8
12	0.5	*Guinardia striata*—58; *Rhizosolenia hebetata*—6; *Cerataulina pelagica*—4
	7.5	*Guinardia striata*—42; *Bacteriastrum furcatum*—10; *Hemiaulus sinensis*—5
	15	*Guinardia striata*—42; *Rhizosolenia imbirica*—13; *Pseudosolenia calvar-avis*—8
21	0.5	*Guinardia striata*—27; *Pseudosolenia calvar-avis*—23; *Guinardia flaccida*—7
	3	*Guinardia striata*—32; *Leptocylindrus minimus*—9; *Dactyliosolen fragilissimus*—4
	13	*Guinardia striata*—41; *Pseudosolenia calvar-avis*—16; *Leptocylindrus minimus*—5
24	0.5	*Guinardia striata*—27; *Pseudosolenia calvar-avis*—23; *Gymnodinium* sp.—7
	5.5	*Guinardia striata*—24; *Gymnodinium* sp.—21; *Rhizosolenia hebetata*—7
	23	*Guinardia striata*—47; *Cerataulina pelagica*—9; *Guinardia flaccida*—5
26	0.5	*Guinardia striata*—16; *Cerataulina pelagica*—13; *Leptocylindrus minimus*—11
	9.5	*Guinardia striata*—54; *Cerataulina pelagica*—13; *Rhizosolenia styliformis*—8
	16	*Guinardia striata*—44; *Rhizosolenia bergonii*—7; *Cerataulina pelagica*—5

The contribution of the Dinophyta algae into the total biomass of phytoplankton is low. At stations 5, 1, 21, and 24, the proportion of *Dinophyta* was 30, 22, 16, and 22%, respectively. The abundance of coccolithophorids did not exceed 100 cells/l.

The similarity of phytoplankton at the different stations calculated from the integral (per 1 m^2) values of the biomass of the algal populations is rather high (Fig. 2). The phytoplankton at the coastal stations 1 and 5 and also at station 7 are characterized by the least similarity. The differences can result from the fact that these stations are located in the pathway of the tidal water movements.

Vertical Distribution of Phytoplankton

At most of the stations, the algal biomass within the near-bottom layer exceeded that in the overlying layers (e.g. station 9, Fig. 3a). At stations 21 (Fig. 3c) and 24, the minimum biomass is noted at the "intermediate" depth. The chlorophyll distribution matched the vertical distribution of the biomass (coefficient of correlation was 0.65). As to the vertical distribution of F_0 within the 0- to 18-m layer, three types of profiles were observed, namely: (1) an increase with depth (station 10); (2) a decrease with depth (stations 3 and 5), and (3) the presence of two peaks of F_0, namely, in the subsurface

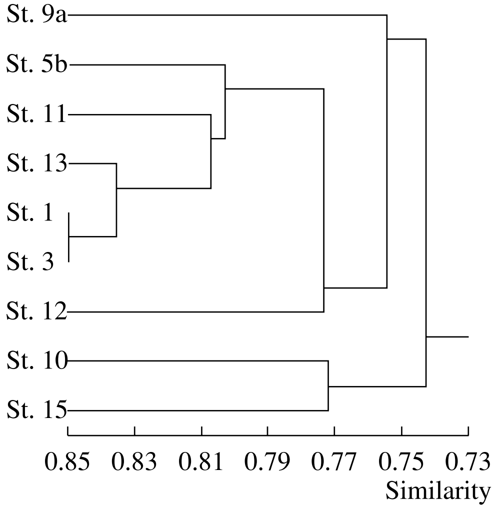

Fig. 2. Classification of stations with respect to the species structure of phytoplankton.

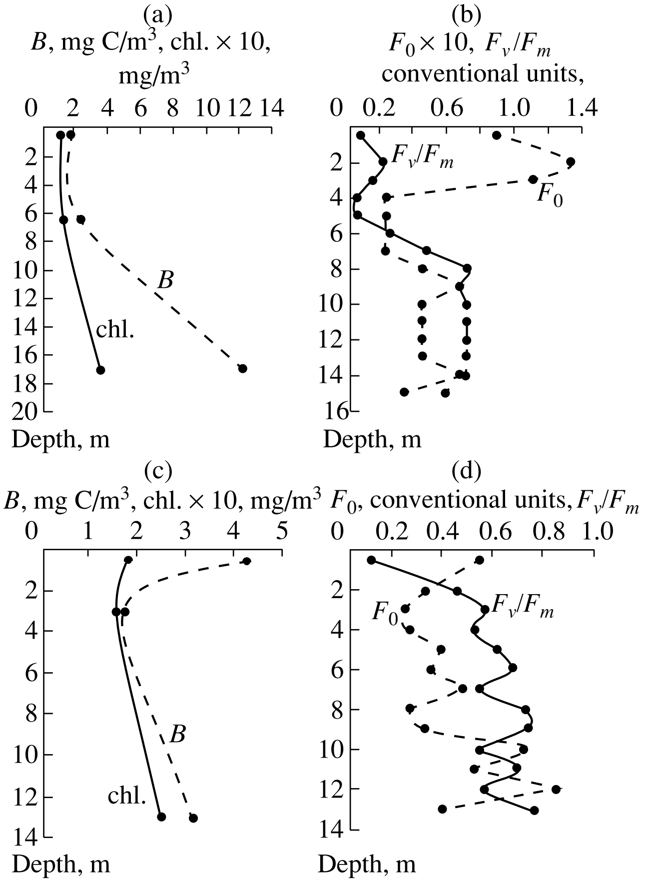

Fig. 3. Vertical distribution of phytoplankton biomass (B), chlorophyll a concentration, constant fluorescence (F_0), and the relative yield of variable fluorescence (F_v/F_m) at (a, b) station 9 and (c, d) station 21.

layer and deeper than 15 m (the rest 18 stations). In addition, at 13 stations the subsurface peak of F_0 is greater than that located deeper. The observed difference of the profiles of F_0 from those of the biomass and chlorophyll (e.g., stations 9 and 21, Fig. 3) can be caused by the photoinhibition of the algae within the surface layer with light of high intensity. When photoinhibition takes place, an increase in the F_0 yield proceeds because of the increase in the proportion of the closed reaction centers of photosystem 2 [1]. In addition, at high irradiance values, the algae accumulate carotinoids [23], which can also cause an increase in F_0 being an indirect indicator of the content of all the photosynthetic pigments [9, 36].

At all the stations, the vertical distribution of the relative output of the variable fluorescence within the 0- to 18-m layer was characterized by an increase in the values of the ratio F_v/F_m with depth (e.g., stations 9 and 21, Figs. 3b and 3d). Its lower values within the subsurface layer point to the photoinhibition of algae by light of high intensity.

In addition to *Guinardia striata* and *Cerataulina pelagica*, whose abundance was greatest within the near-bottom layer, no regular change in the biomass of other species with depth was revealed. No large-sized algae (with a cellular volume greater than 30×10^3 μm^3) such as *Pseudosolenia calvar-avis, Rhizosolenia bergonii*, and *R. imbricata* were encountered within the surface layer. Only at the shallow-water station 21, was the alga *P. calvar-avis* noted in the subsurface layer. In the samples taken from 0.5 and 3 m, great amounts of particulate matter were present, which points to an intense water mixing in this area. The latter can determine the presence of the large-celled algae within the surface layer.

Daily Phytoplankton Dynamics

The algal biomass and chlorophyll content per 1 m^2 reach their greatest values during the night hours (Fig. 4a). In this case, the increase in the algal abundance over the water column is mainly caused by the growth in the biomass within the near-bottom layer (Fig. 4b). During the light time of the day, within the surface layers, phytoplankton is subjected to the photoinhibition; this is confirmed by a decrease in the values of F_v/F_m (Fig. 5) after sunrise (from 06:00 local time) with a practically unchanged chlorophyll concentration and a certain increase in the biomass (Fig. 4b). At noon, the values of F_v/F_m within the 0- to 10-m layer drop to zero (Fig. 6a). By 15:00 local time, as the incident radiation decreases (Fig. 4a), the layer where phytoplankton is photoinhibited reduces to the upper 2 m, while the photosynthetic activity of the algae at the underlying depths is restored (Fig. 6b).

During the light time of the day, within the near-bottom layer, the irradiance varied from 5 to 14% of the subsurface value, and F_v/F_m remained at high level (Fig. 5). With regard to this, it should be concluded that a decrease in the biomass observed within the near-bottom layer after 12:00 local time (Fig. 4b) is determined by factors other than irradiance. Such factors can be the grazing out by phytophagous zooplankton and/or the supply of water with a lower abundance of phytoplankton during a low tidal wave. Of these two factors, the movement of water masses is likely to play a determining role, because the decrease in the total biomass is governed by the reduction in the biomass of the size fraction greater than 30×10^3 μm^3. Meanwhile, the abundance of nannophytoplankton, on which zooplankton mostly feeds [37], only slightly changes (Fig. 7).

An increase in the phytoplankton abundance within the near-bottom layer after 21:00 local time falls on the ebb following a high tidal wave (Fig. 4c). As a rule, the division of the algal cells is confined to the dark time of the day [30]. However, the growth rate of the dominant (in terms of biomass) alga *Guinardia striata* calculated from the minimum (18:00 local time) and maximum (3:00 local time) values of the biomass was 2.51 divisions per day, which considerably exceeds the greatest values (0.71 division per day) published for this species [18]. An increase observed in the biomass of other mass algae such as *Cerataulina pelagica, Hemiaulus hauckii, H. sinensis, Leptocylindrus danicus*, and *L. minimus* was also from 1.4 to 3.5 times higher than the values of the maximum growth rate of these species calculated by allometric equations [19]. The above listed information gives the grounds to conclude that the increase in the algal biomass within the near-bottom layer is determined by cell division and the supply of water masses with a higher phytoplankton abundance during the ebb following a high tidal wave.

DISCUSSION

The low concentrations of mineral phosphorus and high values of the atomic ratio $N_{min} : P_{min} > 30$ over the greater part of the area of the bay suggest that the phytoplankton growth is restricted by the deficiency of P_{min}. This agrees with the conclusion of a number of authors [29], who have stated that the phosphorus limitation is typical of relatively closed tropical shallow-water bays and lagoons. In the open waters of the tropical area of the Pacific Ocean, the concentration of mineral forms of nutrients amounts, as a rule, to 0.02 μmol N and 0.21 μmol P, and phytoplankton is limited by the shortage of nitrogen [28]. In the shallow-water coastal ecosystems, a combined effect of several processes causes the conditions with the phosphorus limitation. (1) In the zone of coral reefs, absorption and sedimentation of phosphorus by carbonate-rich deposits take place. The predominant phosphorus flux from the water mass to the bottom biotopes of the coral ecosystems was shown [42], whereas the ratio between N_{min} and P_{min} released from the sediments is equal to 30 and higher [27]. (2) Many of the benthic cyanobacteria fix molecular nitrogen. Subsequently, N_{min} and organic nitrogen enter the water column [27, 35]. (3) The

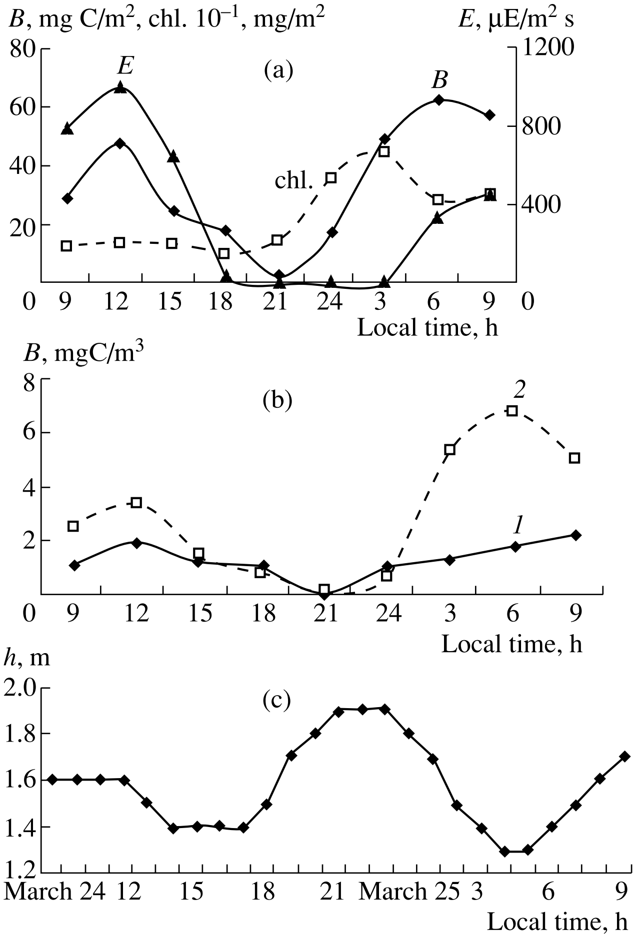

Fig. 4. (a) Daily dynamics of the subsurface irradiance (*E*), integral (per 1 m^2) values of phytoplankton biomass (*B*), and chlorophyll *a* concentration at station C, (b) daily dynamics of phytoplankton biomass within the (*1*) subsurface and (*2*) near-bottom layers at station C, and (c) tidal fluctuations of the sea level (*h*) at the point at 13°45′ N and 109°13′ E.

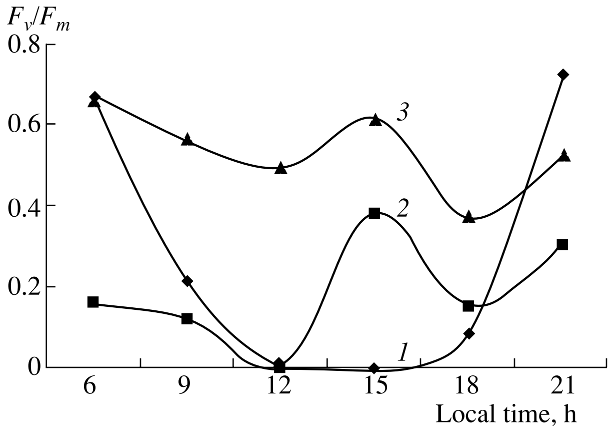

Fig. 5. Daily dynamics of the relative yield of variable fluorescence (F_v/F_m) at depths of (*1*) 0.5, (*2*) 5, and (*3*) 18 m at station C.

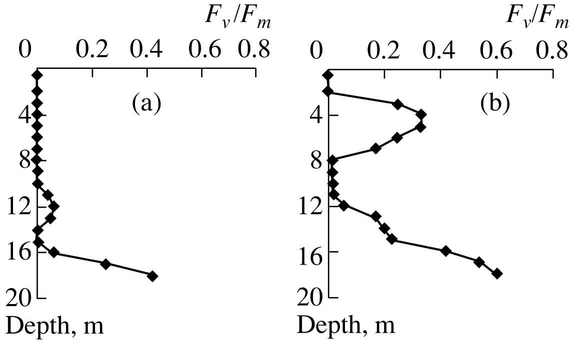

Fig. 6. Vertical distribution of the relative yield of variable fluorescence (F_v/F_m) at station C at (a) 12:00 local time and (b) 15:00 local time.

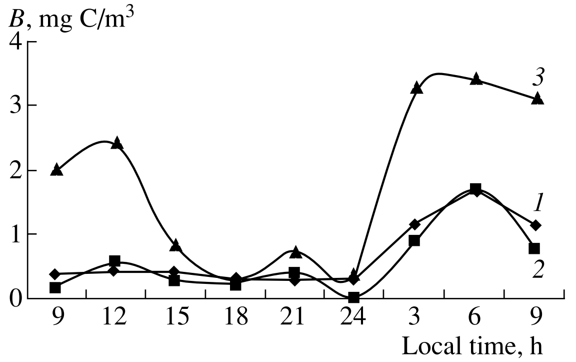

Fig. 7. Daily dynamics of the biomass (*B*) of algae with a cell volume less than (*1*) 5 × 10^3 μm, (*2*) (5–30) × 10^3 μm^3, and (*3*) more than 30 × 10^3 μm^3 at a depth of 18 m at station C.

coastal waters of the South China Sea are characterized by a high bacterial biomass [16]; assuming that, in the bacterial biomass, the ratio N : P < 16 [33], this determines the preferable removal from the environment of dissolved phosphorus as compared to nitrogen.

The phosphorus limitation of algae affects the efficiency of the light reactions of photosynthesis and the intensity of its dark photosynthetic reactions. In particular, at a deficit of phosphorus, the rate of photosynthesis and regeneration of substrates in the Calvin–Benson's cycle decreases [45]. In addition, the suppression of nucleic acid synthesis at the level of transcription is observed [30]. This causes a decrease in the rate of synthesis of pigments and proteins of the photosynthetic apparatus and, therefore, leads to a reduction in the efficiency of the light reactions of photosynthesis [30]. However, at the background of the phosphorus limitation registered by the P_{min} concentration and the ratio N_{min} : P_{min}, and, in addition, at the decrease in the algal biomass in March [4], the phytoplankton of the bay was characterized by high (0.4–0.7) values of the quantum efficiency of the reaction centers of photosystem 2. This can be explained by the following reasons:

(1) The requirements of algae in phosphorus are covered due to the utilization of organic phosphorus (P_{org}) by means of the extracellular splitting off the phosphate group from the molecules of different esters of the phosphorus acid, with the subsequent consumption of phosphates [25, 26]. The turnover time of P_{org} in the coastal waters is so small that it provides the support of the relatively high primary production at a low concentration of P_{min} [20]. In the oligotrophic waters of the tropical area of the Pacific Ocean, a considerable portion of P_{org} is available for degradation [34] and represents an important source of phosphorus for phytoplankton [32].

(2) At the downward trend of the biomass of nanno- and microphytoplankton, the high values of F_v/F_m can be caused by an increase in the abundance and proportion of picoplankton forms. In selected tropical ecosystems of the Pacific Ocean, picoplankton occupies the dominant position among autotrophic organisms [21, 22, 24], and in a number of areas its contribution to the total fluorescence of phytoplankton reaches more than 60% [38]. In addition, picoplankton has a competitive advantage in assimilation of P_{org} compared to nanno- and microplankton [20].

(3) Support for the high photosynthetic activity can be provided by the intracellular reserves of phosphorus. In large algae, the intracellular pools of nutrients are greater than those in small-cell algae [39]. Therefore, the ability to support metabolism due to the intracellular reserves is typical, first of all, of the populations of large-cell algae. This is in agreement with the prevalence (with respect to biomass) of the alga *Guinardia striata* in the phytoplankton of the bay.

(4) The decrease in the phytoplankton biomass at the high photosynthetic activity of algae, to a certain extent, can be caused by the strengthening of the grazing pressure of the phytophagous zooplankton. In March, in the bay, an increase in the abundance and biomass of zooplankton is noted [12].

The prevalence of ammonium nitrogen in the pool of N_{min} and the essential role of P_{org} in the feeding of phytoplankton (this conclusion is based on indirect arguments) gives grounds to suggest that, during the dry season, the vital activity of the phytoplankton from Nhatrang Bay is provided by nutrients due to their recycling, and the production regenerated makes up the main portion of the total production of organic matter.

With respect to the abundance of phytoplankton and chlorophyll content, the waters of the bay should be referred to as mesotrophic waters. The moderate level of productivity was also noted in other coastal ecosystems of Vietnam [15]. For Nhatrang Bay, the same authors gave two values of the daily primary production belonging to the period from March to May, namely, 6 mg C/m^2 (in the zone of a living border reef) and 210 mg C/m^2 (50–100 m away from the reef).

The values of the abundance and biomass of phytoplankton from Nhatrang Bay in March match the algal abundance off the Panama coast during the period of absence of upwellings and low concentration of nutrients [40]. Meanwhile, the content of the mineral phosphorus in the waters of Nhatrang Bay is lower than that off the Panama coast, which is also a direct support of the conclusion about the essential role of organic phosphorus in the feeding of phytoplankton of the bay.

With respect to the number of species and abundance, diatoms dominate throughout the entire water area of the bay. The prevalence of diatoms is typical of many tropical coastal ecosystems [40, 44]. The algae *Guinardia striata, Pseudosolenia calvar-avis, Cerataulina pelagica, Rhizosolenia bergonii, R. imbricata, Guinardia flaccida, Detonula pumila, Leptocylindrus minimus, Proboscia alata, Pseudo-nitzschia pungens, Hemiaulus sinensis, Bacteriastrum furcatum, Pleurosigma* sp. and *Gymnodinium* sp. gave the greatest contribution to the total biomass of phytoplankton. These algae, as well as many other species encountered in March, grow year round [4, 6]. The permanent presence of the algae in plankton, which become dominant during certain periods, is a characteristic property of phytoplankton in the coastal tropical ecosystems [40]. In the coastal waters of the temperate and high latitudes, most of the algae entering into the composition of the dominant forms appear in plankton a short time before they reach the maximum abundance [3].

In all the areas of the bay studied, the biomass of algae and the concentration of chlorophyll within the near-bottom layer exceeded those in the overlying layers, while at most of the stations a subsurface peak of the vertical distribution of the yield of the constant fluorescence is noted. The difference of the F_0 profiles from those of distribution of the phytoplankton biomass and chlorophyll concentration is caused by the photoinhibition of algae growth by light of high intensity within the surface layer. The increase in the F_0 yield takes place due to the increase in the proportion of the closed reaction centers of photosystem 2 [1], and, in addition, can be determined by the rise in the cellular content of subsidiary pigments, e.g., carotinoids. In addition to the light-accumulating role, carotinoids perform the function of protection of photosynthetic apparatus from damaging by photooxidation [46]. An increase in the irradiance causes accumulation of carotinoids [23], whereas the cellular content of chlorophyll *a* decreases [31].

In the surface layers, phytoplankton is subjected to the stress of photoinhibition throughout the major part of the light period of the day. Within the subsurface layer, the photosynthetic activity begins to decrease soon after sunrise (from 6:00 local time) and to noon, it drops to zero within the 0- to 10-m layer. As the incident radiation decreases, the photosynthetic activity of algae is restored at depths deeper than 2 m and within the subsurface layer by 15:00 and 18:00 local time, i.e. prior to sunset, respectively. The diatomaceous algae are capable of restoring the high functioning efficiency of the photosynthetic apparatus in a few hours after exposure to great doses of irradiance from the visible light. In so doing, the reparative period increases with the growth of the dose and the duration of irradiance [1]. Within the near-bottom layer, the photosynthetic activity remains at a high level throughout the whole light period.

Throughout the day, in the southern part of the bay, the algal biomass per 1 m^2 varied 26-fold. Such considerable variation in the phytoplankton abundance is caused by the dynamics of algae within the near-bottom layer. In addition to the biotic factors (grazing out by zooplankton and division of cells), the changes in the algal biomass within the near-bottom layer depend, to a great extent, on the tidal movements of the water masses. In relation to the height and phase of the tidal wave, water with different abundances of algae goes through certain sites of the water area. The phytoplankton biomass varies more strongly over the area in the near-bottom layer than within the surface layer, and so, due to the tidal currents, the daily variations in the biomass are better manifested at the near-bottom level.

A comparison of the patterns of distribution of plankton algae over the area during the dry season and during the rainy season shows that the spatial distribution of phytoplankton depends on the intensity of the riverine runoff. During the raining season, the nonhomogeneity of the bay waters with respect to hydrochemical parameters, which determines the nonhomogeneity of the phytoplankton spatial distribution, is high [4]. Towards the open sea, the phosphorus limitation of the phytoplankton growth at pre-estuarine locations is replaced by its limitation due to the shortage of mineral nitrogen. The chlorophyll concentration, abundance, and biomass of algae decrease seaward from the pre-estuarine locations. The greatest biomass of algae is confined to the upper layers; within the near-bottom layers phytoplankton growth is limited by the deficiency of light. [4]. During the dry season, towards the open sea, the phytoplankton biomass and chlorophyll concentration per 1 m^2 increase. Within the near-bottom layer, the abundance of algae is higher. The algae living in the surface layer are subjected to stress from photoinhibition. In different areas of the bay, the phytoplankton is characterized by a high degree of similarity.

CONCLUSION

In Nhatrang Bay, during the period with small precipitation (dry season) and the least supply of riverine waters, the phytoplankton biomass and chlorophyll concentration per 1 m^2 increase seaward. The algal abundance is higher within the near-bottom layer. The chlorophyll concentrations averaged over the northern and southern parts of the bay are higher than that in the northern, while the values of the alga biomass are close. With respect to the number of species and abundance, diatoms dominate over the entire water area, the proportion of the Dinophyta algae is very small, and the species diversity and abundance of coccolithophorids are low. In different parts of the bay, the phytoplankton is characterized by a high degree of similarity. During the day, the algal biomass per 1 m^2 changes by more than one order of magnitude. Such a considerable variation in the phytoplankton abundance over the water column is determined by the alga dynamics within the near-bottom layer.

The phytoplankton structure and its photosynthetic activity is determined by the following principal factors: (1) the movements of water masses during the tidal cycle; (2) the photoinhibition of phytoplankton within the surface layer during the major part of the light period of the day; (3) a limitation of the alga growth due to the shortage of mineral phosphorus and provision of the requirements of this element due to recycling and using the dissolved organic phosphorus, and (4) grazing pressure imposed by phytophagous zooplankton and fauna of the coral reefs.

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