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Variability of Photosynthetic Parameters of the Surface Phytoplankton in the Black Sea

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Abstract—The effect of physical, chemical, and biological variables on the spatial and temporal variability of the maximum photosynthesis intensity ($P^B_{\max}$) and the initial slope of light curves α^B were studied. Throughout the year, the values of the photosynthetic parameters varied within one order of magnitude, i.e., $P^B_{\max}$ from 1 to 11 mgC mgChl^{-1} h^{-1} and α^β from 0.04 to 0.20 mgC mgChl^{-1} h^{-1}/(W m^{-2}). The spatial and temporal variability of $P^B_{\max}$ and α^B were lower than that of the chlorophyll concentration. The seasonal dynamics of the $P^B_{\max}$ values is characterized by their growth from winter to summer and their decrease by the end of the year. The annual changes in $P^B_{\max}$ are controlled by temperature, and they have a weak dependence on the phytoplankton adaptation to incident solar radiation. The share of the temperature in the overall variability of $P^B_{\max}$ and I_k is 56–70%, and the temperature dependencies of these parameters are described by exponential functions. The temporal dynamics of α^B are nitrate- and chlorophyll *a*-dependent. The temporal changes in the maximum quantum yield of phytoplankton photosynthesis ($\phi_{\max}$) calculated by α^B and the average specific light absorption by algae in the photosynthetically active radiation range ($\bar{a}^*_{ph}$) were analyzed. It was shown that $\phi_{\max}$ and $\bar{a}^*_{ph}$ were chlorophyll concentration-dependent parameters, but their changes are in the opposite direction. The $\phi_{\max}$ values increase with a rise in the chlorophyll concentration, whereas the $\bar{a}^*_{ph}$ values decrease. Over a wide range of chlorophyll concentration values (from 0.1 to 20 mg/m^3), the relationship between the α^B values and the chlorophyll concentration can be approximated by a dome-shaped curve with a maximum at about 3 mg/m^3.

INTRODUCTION

The key parameters determining the relationship between the photosynthesis rate (P) and the light (I) are the initial slope of the light curve α ($\Delta P/\Delta I$) and the maximum photosynthesis rate ($P_{\max}$). These parameters normalized with respect to the chlorophyll *a* concentration (α^B and $P^B_{\max}$) are usually used in models for the estimation of the primary production values from the satellite-based chlorophyll measurements and determination of the effect of the environmental factors on the specific phytoplankton production.

During the past few years, active efforts were aimed at the extension of our understanding of the character of variations of photosynthetic phytoplankton parameters. In many publications, the α^B and $P^B_{\max}$ variabilities are considered in connection with seasonal [21, 47, 48] and regional [19, 26, 28, 29, 34, 38, 49] features, as well as with the daily periodicity [23, 25], taxonomic and size composition diversity of phytoplankton [9, 17, 52], and the temperature and light adaptation [1, 7, 11, 20]. The results of the studies showed that, in the World Ocean, the photosynthetic parameter values vary over a wide range, namely, $P^B_{\max}$ from 1 to 24 mgC mgChl^{-1} h^{-1} and α^B from 0.03 to 0.40 mgC mgChl^{-1} h^{-1}/(W m^{-2}). The minimum values are characteristic of high latitudes, while the maximums are related to the coastal communities of subtropical and tropical waters. These values do not confirm the hypothesis on the constancy of the α^B values, which was derived from the fact that the initial slope of the light curves was dependent only on photochemical reactions.

The most important factors determining the values of the photosynthetic parameters in natural phytoplankton populations are the light, temperature, nutrient concentration, and pigment content in algae. One of the methods of the study of the effect of a combination of the factors on the variations of the α^B and $P^B_{\max}$ values may help the comparison of their values in the areas with different environmental conditions. The generalization of a great amount of evidence allowed us to distinguish four vast areas in the World Ocean, namely, the Polar area, the areas of the western and trade winds, and the coastal zone, within which provinces were recognized [36, 48]. The classification of provinces is based on the differences between some physical factors influencing the dynamics of the phytoplankton community, photosynthetic parameters, and the parameters determining the vertical chlorophyll distribution. As a result, provinces were recognized where, during certain seasons, the photosynthetic parameters change within relatively narrow limits [47, 48]. The use of these data, in combination with the results of the satellite-based measurements of chlorophyll concentration, gave us the possibility to calculate the primary production values for specific areas and for the World Ocean as a whole. So far, such estimates have had poor precision. For the open oceanic waters, the error is 60%, while for the coastal waters it increases up to 100% [26]. As a rule, one of the reasons is related to the limited number of *P–I* experiments used for the calculations of the primary production values. Based on them, it is difficult to estimate the spatial and temporal variability of the parameters studied in all the identified provinces. In addition, in the pelagic zone of the ocean, no well-defined boundaries of the areas varying from season to season and from year to year are available. For extrapolation of the α^B and $P^B_{\max}$ values measured at selected stations to the scales correlated with the inhomogeneous character of the satellite-based chlorophyll distribution, reliable quantitative data for the interrelation of the photosynthetic parameters with the environmental features, changes in the pigment composition, and physiological and morphological characteristics of phytoplankton are required.

The shortage of data on the variability in the photosynthetic parameters of phytoplankton in the Black Sea makes it difficult to use remote sensing observations for calculation of the primary production values to the scale of the entire sea, because the previous studies were restricted in space and time [1, 8, 9].

The aim of this paper is to examine the effect of the key physical, chemical, and biological factors on the annual and spatial variability of the photosynthetic parameters of the Black Sea phytoplankton, which are considered as a ground for development of algorithms for calculation of the satellite-based primary production values.

MATERIALS AND METHODS

The studies were carried out over twelve oceanographic cruises in the Black Sea, at stations located between 41°30′–45°30′ N in different months and years (Fig. 1). The greatest number of measurements was performed in the deep-water areas of the sea from December to January (1988 and 1992), from March to April (1988 and 1995), from June to July (1996 and 1990), and from August to September (1980 and 1992). At every station, the chlorophyll concentration, temperature, and incident solar radiation at the sea surface

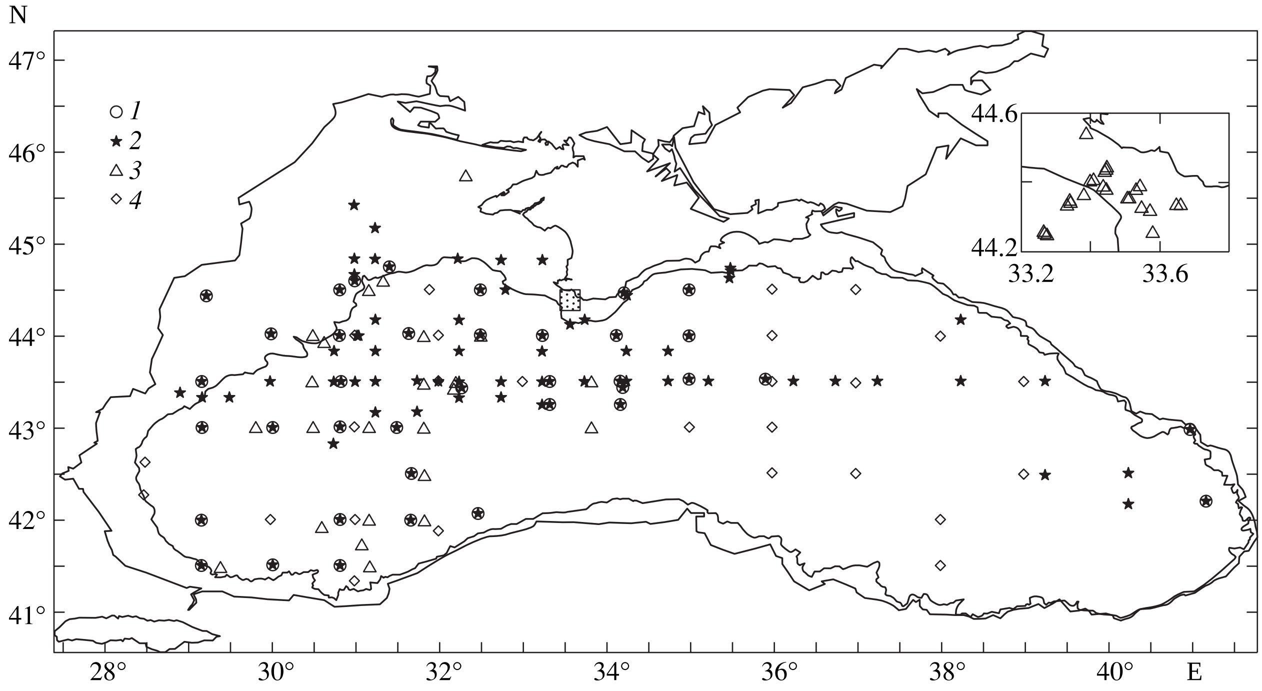

Fig. 1. Layout of the stations where photosynthetic parameters of the surface phytoplankton were measured (200-m depth contour line is indicated): *1*—winter (36 stations); *2*—spring (52 stations); *3*—summer (45 stations); and *4*—fall (31 stations).

were measured, and the experiments estimating the effect of light on phytoplankton photosynthesis were conducted. In total, 164 experiments were carried out, of them, 36 in winter, 52 in spring, 45 in summer, and 31 in fall.

In June 1996, the spectral light absorption by the surface phytoplankton was determined at 20 stations located off the southern coast of the Crimea (Fig. 1) and at 2 stations in the deep-water (42°55′–43°00′ N and 30°48′–31°08′ E) and shelf (44°00′–44°10′ N and 33°01′–33°13′ E) parts of the sea during the period from 1998 to1999. In total, 73 measurements were carried out.

Measurement of phytoplankton photosynthetic parameters. For detection of the photosynthetic parameters of phytoplankton, water samples were exposed to different light intensities for two–three hours at the temperature that was observed within the surface layer. As a light source, white fluorescent lamps with a spectral composition close to that of sunlight were used. In the studies performed before 1990, the photosynthesis rate was determined at eight light intensities, namely, from 1 to 150 W m^{-2}. Different levels of irradiance were produced by filters with a neutral spectral transmission characteristic. In the later studies, an incubator, where the photosynthesis rate was measured at 16 light levels, from 1 to 200 W m^{-2}, was used. A halogen lamp served as a light source. In front of the lamp, a blue filter and a 5% solution of $CuSO_4$ were placed to remove the light with wavelengths greater than 760 nm. Attenuation of the density of incident light flux at the flask surface was provided by sequential arrangement of the samples at different distances from the light source. To enhance the light attenuation between the flasks, light filters with a neutral spectral transmission characteristic (K = 50%) were used. The spectral composition of the efficient radiation was close to that of fluorescent lamps and sunlight in the PhAR range.

Measurement of light. In the course of the laboratory experiments, the light incident on a plane flask surface and inside it was studied. To measure the light inside the flasks, light pipes with a condensing sphere (a bubble of opal glass) fixed at the pipe end were employed. Another end of the light pipe was connected to a photocell. The incident light was measured by means of a quantometer and luxmeter calibrated against the readings of a quantometer in the photosynthetically active radiation range. For transition from units of irradiance to energetic units, an empirically found relationship, namely, 1000 lk $\approx$17.2 μE m^{-2} s^{-1} $\approx$ 3.47 W m^{-2}, was used.

The intensity of the incident solar radiation was measured using a nonselective thermoelectric pyranometer from sunrise to sunset in the days when the experiments were set up. The average value for a light day was calculated. For the transition from the absolute energetic values ($E_{350-3000\ \text{nm}}$) to photosynthetically active radiation ($E_{350-700\ \text{nm}}$), a coefficient of 0.45 was used.

Measurement of the phytoplankton photosynthesis rate. The rate of photosynthesis was measured by the difference between the values of $H^{14}CO_3^-$ absorption by phytoplankton in the light and dark flasks in two replicates. After completion of the experiment, the samples were filtrated under moderate vacuum (down to 0.25 atm) through a membrane filter with a mesh size of 0.45 μm. The isotopes absorbed by filters were washed with 5 ml of a 1% HCL solution and 10 ml of a sea water ultrafiltrate. The radioactivity of the filters was measured in a scintillating liquid by means of a Rack Beta counter. The carbon content in all the forms of carbon dioxide was calculated by standard formulas [4]. For the photosynthetic zone, this value ranged from 33 to 36 mgC/l.

Measurement of chlorophyll *a* concentration. In order to improve the data comparability, aliquots were simultaneously taken from the 10-l bottle water sample. These aliquots were used for determination of the chlorophyll *a* concentration and the rate photosynthesis. Samples 1–2 l in volume were filtrated through a membrane filter with a mesh size of 0.45 μm. Pigments were extracted with 90% acetone over 18 h. After centrifugation of the extract, the chlorophyll *a* and phaeophytin concentrations were measured by a standard fluorometric method [28], according to the technique described in [10].

In the studies performed in June 1996, the chlorophyll concentration was measured by the light absorption by phytoplankton at the wavelength of 680 nm. The set of comparative measurements (n = 32) showed that, in the range of concentrations from 0.2 to 1.1 mg/m^3, the light absorption values (a_{ph}, m^{-1}) at this wavelength are directly proportional to the chlorophyll *a* content measured by the fluorometric method, namely,

$$a_{ph}(680) = 0.0189\ \text{Chl} \quad r^2 = 0.92. \qquad (1)$$

Light absorption by phytoplankton. Water samples 1–2 l in volume were filtrated through GF/F filters, and prior to the measurements, they were kept in a Dewar flask with liquefied nitrogen at a temperature of –70°C. The spectrum of light absorption by particulate matter ($a_p(\lambda)$), where λ is the wavelength, $400 \le \lambda \le 750$ nm), was measured under laboratory conditions by means of a spectrophotometer by the Yentsch method [53] in the modification of Mitchell and Kiefer [40, 41]. The amount of light absorbed by phytoplankton ($a_{ph}(\lambda)$) was measured following [33], i.e., by the difference between the spectral characteristics of particulate matter and those of the particles without pigments. For the transition from the values of the optical density of the suspended matter on the filter to the values of its optical density in suspension, the equation from [39] was used.

Maximum quantum yield of phytoplankton photosynthesis. In the experiments carried out in June

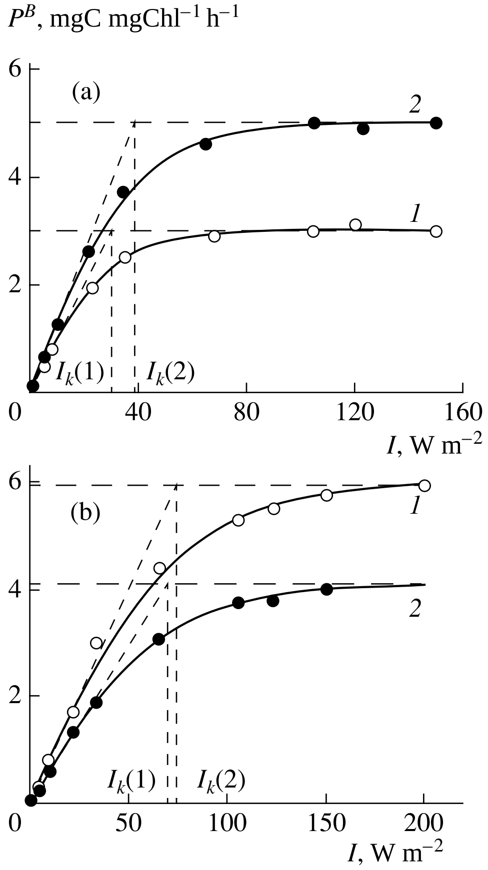

Fig. 2. Typical relationships between the light and intensity of photosynthesis (P^B) of the surface phytoplankton (a) in (*1*) the winter and (*2*) spring seasons and (b) in (*1*) the summer and (*2*) fall seasons. Horizontal dashed lines correspond to the maximum values of photosynthesis intensity ($P^B_{\max}$); vertical dashed lines correspond to the intersections of the extrapolated linear segments with those of the levels of the photosynthesis saturation (I_k).

1996 (in the vicinity of Balaklava), the maximum quantum yield of photosynthesis ($\phi_{\max}$) was determined by the formula

$$\phi_{\max} = \alpha/\bar{a}_{\mathrm{ph}}, \qquad (2)$$

where α is the initial slope of the light–photosynthesis rate curve; $\bar{a}_{\mathrm{ph}}$ is the value equal to the quantity of absorbed quanta, which is normalized to the flux of the incident quanta in the range of the photosynthetically active radiation calculated by the formula

$$\bar{a}_{\mathrm{ph}} = \frac{\int_{400}^{700} a_{\mathrm{ph}}(\lambda)d\lambda Q(\lambda)d(\lambda)}{\int_{400}^{700} Q(\lambda)d(\lambda)}. \qquad (3)$$

The spectral properties of the light energy in the experiment ($Q(\lambda)$) were determined as the product of the energy spectrum of the light source ($E(\lambda)$), the spectrum of the light absorption by a 5% solution of $CuSO_4$–$S(\lambda)$, and the blue filter spectrum ($F(\lambda)$):

$$Q(\lambda) = E(\lambda)F(\lambda)S(\lambda). \qquad (4)$$

Mathematical description of the photosynthesis–light relationship. To describe the photosynthesis–light dependence, the empiric equation offered by Platt *et al.* [45] was used:

$$P^B = P^B_s[1 - \exp(\alpha^B I/P^B_s -)]\exp(\beta I/P^B_s), \qquad (5)$$

where P^B is the photosynthetic intensity (mgC mgChl^{-1} h^{-1}) at the density of a light flux I (W m^{-2}); P^B_s is the scaling factor (mgC mgChl^{-1} h^{-1}); α^B is the initial slope of the light curve [(mgC mgChl^{-1} h^{-1})/(W m^{-2})]; and β is the photoinhibition parameter [(mgC mgChl^{-1} h^{-1})/(W m^{-2})]. In the absence of photosynthesis inhibition ($\beta = 0$), P^B_s is equal to the maximum intensity of photosynthesis ($P^B_{\max}$). For calculation of the coefficients, a standard Sigma-Plot software package was used. The parameter I_k corresponds to the intersection of the extrapolated linear segment with the level of photosynthesis saturation, $I_k = P^B_{\max}/\alpha^B$.

RESULTS

Spatial variability of phytoplankton photosynthetic parameters. Figure 2 shows typical curves for the relationship between the intensity of photosynthesis (P^B) and light (I). Throughout the year, at variations of the power of the light flux in the experiments from 0.5 to 150–200 W m^{-2}, no photoinhibition of the light flux took place. The curves had a similar shape and varied only in the initial inclination and in the maximum value. During the winter–spring period, the P^B values measured reach their peak and flatten out. In the summer, the maximum P^B values obtained in the experiments differ from the calculated $P^B_{\max}$ values by less than 10%. Despite a certain variability in the experimental data, they are described well by the curve calculated by equation (5). When α^B and the $P^B_{\max}$ parameters were estimated, the coefficient of variation ranged within 5–20% and was 10% on average. According to the definition, I_k is a derivative from the calculated values α^B and $P^B_{\max}$ and the accuracy of its estimate depends on that of the determination of these parameters.

During the cold period of the year (from December to March), the water temperature within the surface layer ranges in relatively narrow limits, namely, from 7 to 11°C, while the photosynthetically active radiation incident at the sea surface (I_0) varies from 28 to 130 W m^{-2}.

Table 1. Seasonal changes in the photosynthetic parameters (α^B, $P^B_{\max}$, and I_k) of phytoplankton, average intensity of incident solar radiation in the range of photosynthetically active radiation per light day (I_0), temperature (*T*), and chlorophyll *a* concentration (Chl. *a*) within the surface layer of the Black Sea (0–2 m). The first line is the average value, the second line is the standard deviation, and the third line is the limits of variations

Month, year	α^B	$P^B_{\max}$	I_k	I_0	I_0/I_k	*T*	Chl. *a*	*N*
January, 1989, 1992	0.11	2.80	25	68	2.80	8.0	0.89	20
	(0.014)	(0.53)	(4)	(19)	(0.4)	(0.9)	(0.41)	
	0.07–0.13	1.82–3.75	17–30	35–90	1.6–3.5	6.5–10.0	0.30–4.80	
February 1992	0.17	2.80	16	44	2.74	7.7	1.46	3
	(0.01)	(0.26)	(3)	(10)	(0.5)	(0.3)	(0.12)	
	0.16–0.18	2.60–3.10	14–19	28–50	2.3–3.3	7.8–8.0	1.32–1.53	
March 1989, 1995	0.13	4.82	39	107	2.72	9.19	2.14	22
	(0.03)	(1.05)	(12)	(20)	(1.2)	(1.0)	(0.60)	
	0.07–0.13	2.00–6.00	28–85	60.0–130	0.3–4.3	7.0–11.0	0.37–3.54	
April 1995	0.08	3.92	50	139	2.70	11.6	0.41	18
	(0.016)	(1.13)	(18)	(27)	(0.6)	(2.3)	(0.30)	
	0.05–0.13	2.54–6.60	23–63	40–184	1.1–3.7	10.0–12.0	0.10–1.00	
May 1990	0.07	4.64	66	165	2.50	15.0	0.33	5
	(0.010)	(0.56)	(8)	(24)	(0.5)	(1.0)	(0.20)	
	0.05–0.08	3.85–5.20	55–70	130–200	2.0–3.0	14.0–16.0	0.15–0.60	
June 1989, 1996	0.08	5.51	69	210	2.47	19.7	0.25	20
	(0.011)	(1.50)	(7)	(38)	(0.34)	(1.6)	(0.10)	
	0.07–0.09	4.00–7.00	60–76	168–230	1.8–3.5	5.0–23.0	0.12–0.38	
July 1990	0.08	5.94	74	193	2.76	20.0	0.36	25
	(0.018)	(2.1)	(25)	(25)	(0.72)	(2.0)	(0.25)	
	0.05–0.12	3.00–11.10	45–108	150–229	1.2–4.2	18.0–22.5	0.13–1.67	
August 1992	0.08	7.70	93	245	2.0	23.0	0.18	4
	(0.006)	(0.95)	(41)	(21)	(0.20)	(0.0)	(0.05)	
	0.08–0.09	7.00–9.10	60–168	221–257	1.7–2.2	23.0	0.14–0.25	
September 1980	0.07	4.14	58	172	2.0	20.0	0.16	23
	(0.016)	(1.10)	(6)	(32)	(0.40)	(1.3)	(0.20)	
	0.04–0.12	2.00–7.80	50–65	140–215	1.8–3.6	18.0–22.0	0.03–1.10	
October 1990	0.09	3.88	45	119	2.64	16.0	0.43	5
	(0.017)	(0.81)	(15)	(21)	(0.30)	(0.0)	(0.10)	
	0.06–0.10	2.95–4.70	30–60	98–140	2.2–3.2	16.0	0.33–0.55	
November 1989	0.10	2.71	28	78	2.36	13.0	0.71	3
	(0.017)	(0.53)	(5)	(15)	(0.20)	(0.0)	(0.21)	
	0.08–0.12	2.20–3.30	22–38	60–93	2.4–3.0	13.0	0.51–0.89	
December 1988	0.10	2.42	24	61	2.54	9.0	0.85	14
	(0.021)	(0.60)	(5)	(27)	(0.42)	(1.0)	(0.15)	
	0.06–0.11	1.70–3.35	18–31	33–88	2.0–3.1	8.0–10.0	0.62–1.08	

Note: $P^B_{\max}$—mgC mgChl^{-1} h^{-1}; α^B—mgC mgChl^{-1}/(W m^{-2}); I_k and I_0—W m^{-2}; *T*—temperature, °C; Chl *a*—chlorophyll *a* concentration, mg/m^3.

Under these conditions, the α^B values measured at some stations differ by a factor of three, i.e., from 0.06 to 0.18. In a similar way, the $P^B_{\max}$ values changed from 1.7 to 6.0 (Table 1). The values of the photosynthetic parameters measured in the deep part of the sea and in the areas of the continental slope were close. On average, the coefficient of variation for α^B was 17% and for $P^B_{\max}$ it was somewhat greater—25%.

During the summer period, the maximum values of α^B were found in the area of the continental slope, in the northwestern and southern parts of the sea (0.11 ± 0.015). In the deepwater part of the sea and on the shelf of the southern coast of the Crimea, they were lower (0.07 ± 0.018). The $P^B_{\max}$ values varied in synchronism with those of α^B. Similar regional differences were found in September. In the northwestern part of the continental slope, the mean values of α^B and $P^B_{\max}$ were equal to 0.11 ± 0.015 and 6.20 ± 1.51, respectively, whereas in the deepwater areas they were 0.06 ± 0.014 and 3.92 ± 0.80, respectively. As we can see, during the summer period, the values of the photosynthetic parameters of phytoplankton in the waters of the continental slope, where greater chlorophyll concentrations were observed, were 1.5 times as great as in the deepwater areas. Owing to the coupled action of the variations of the α^B and $P^B_{\max}$ values, a relative stability of the mean values of the I_k parameter (56–65 W m^{-2}) was observed. The coefficients of variation for photosynthetic parameters were equal both under the conditions of a moderately calm sea in the summer and under the intensive turbulent mixing in the winter (15–25%).

Seasonal dynamics of the photosynthetic parameters. Throughout the year, the average monthly $P^B_{\max}$ values increase from 2.40 to 7.70 from December to August, and then they decrease (Table 1). The maximum α^B values are characteristic of the winter–spring period (from December to March), whereas in the period from April to October they are rather stable. Depending on the environmental conditions, the $P^B_{\max}$ values range within wider limits than those of α^B. The latter reliably differ between the cold and warm periods of the year at a level of significance equal to 0.01.

The average values of I_k regularly increased from the winter (16–25 W m^{-2}) to the summer (69–93 W m^{-2}).

The effect of light and temperature on the photosynthetic parameters. The coefficients of simple correlation of the α^B, $P^B_{\max}$, and I_k parameters with temperature and light are given in Table 2. During either period of the year, the coefficients of correlation between the $P^B_{\max}$ and α^B values and the $P^B_{\max}$ and I_k values are reasonably high and reflect the coupling of the light and dark reactions of photosynthesis. During the winter–spring period, a significant correlation of α^B and T and of α^B and I_o ($r = 0.48$ and $r = 0.35$, respectively) is observed, while during the summer–fall period, it is absent. The $P^B_{\max}$ values correlate with T and I_o during both periods of the year, but for the cold period, the coefficients of correlation are 1.5 times higher than for the warm period (Table 2). The I_k parameter correlates with T and I_o during the winter–spring period ($r = 0.65$ and $r = 0.50$, respectively), but for the summer–fall period only the correlation between I_k and T ($r = 0.55$) is reliable.

The effect of solar radiation (I_o) on the photosynthetic parameters of phytoplankton was estimated in the experiments carried out in the cold (from December to March) and warm (from June to September) periods of the year at different I_o values and a relatively constant temperature (8–10 and 19–21°C, respectively). When, during the winter–spring period of the year, the solar radiation values change by a factor of 2–5, no reliable correlation between $P^B_{\max}$, α^B, I_k and I_o was observed

Table 2. Correlation matrix for the data obtained for the surface layer. Coefficients of correlation (r) were calculated from 63 measurements carried out from December to March (gray background) and for 90 measurements carried out from April to October

	α^B	$P^B_{\max}$	I_k	I_0	T
α^B	1	0.57	0.17	0.35	0.48
$P^B_{\max}$	0.55	1	0.79	0.76	0.86
I_k	0.28	0.61	1	0.50	0.65
I_0	0.04 ns	0.46	0.15 ns	1	0.57
T	0.08 ns	0.57	0.55	0.39	1

Note: T—temperature at which the experiments were conducted; I_0—average solar radiation per light day in the range of photosynthetically active radiation (W m^{-2}); I_k, α^B, and $P^B_{\max}$—photosynthetic parameters; *ns*—not reliable value at significance level $p = 0.05$.

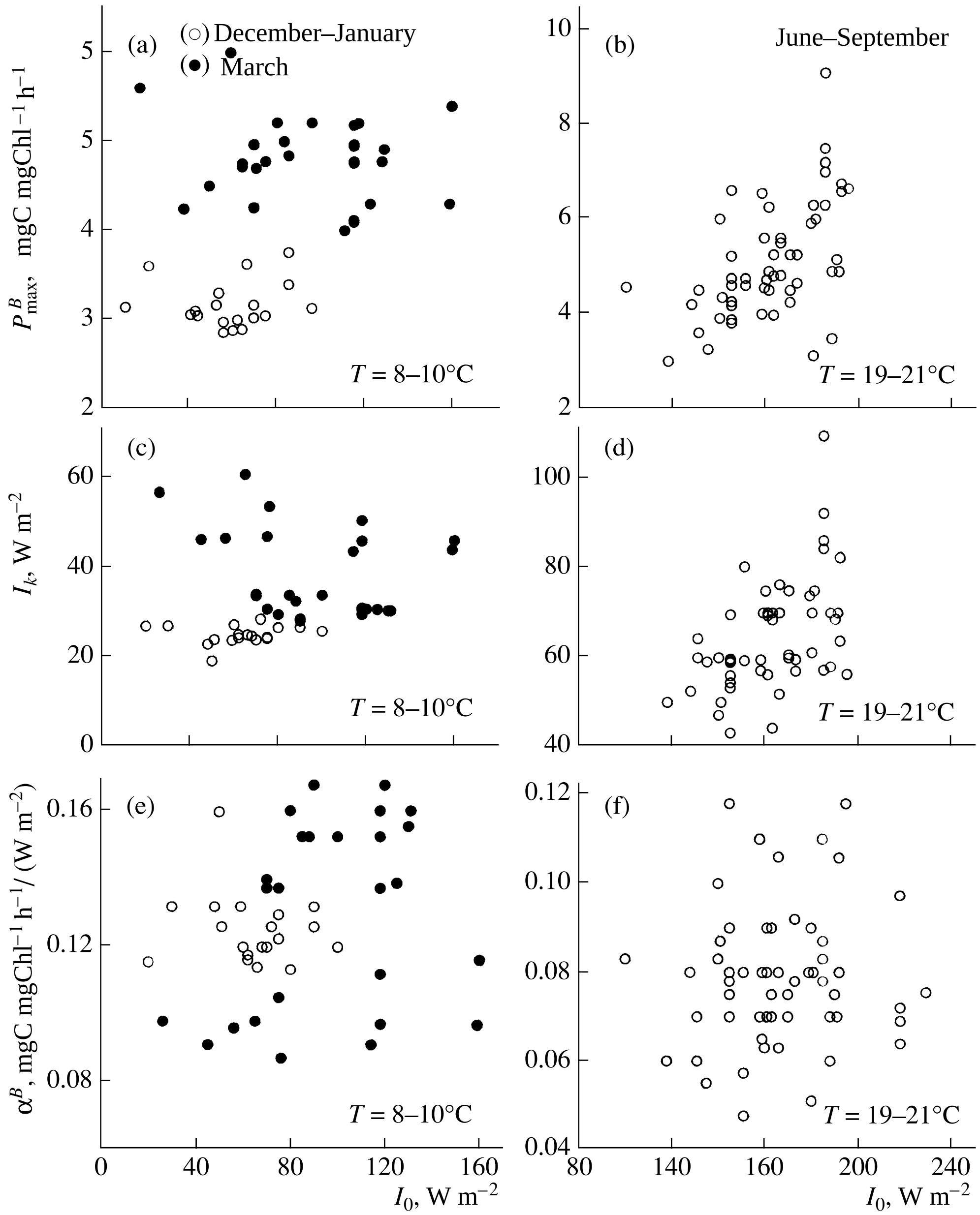

Fig. 3. Variability of the (a, b) P^B_{max}, (c, d) I_k, and (e, f) α^B values of the surface phytoplankton in the cold and warm periods of the year at different intensities of solar radiation (I_0) incident at the sea surface.

(Fig. 3). During the summer–fall period, a weak correlation of P^B_{max} and I_k with I_0 was found, because only 25% of the points were described by a linear relationship ($r^2 = 0.25$ and $r^2 = 0.28$, respectively). Since phytoplankton adaptation to different intensities of incident radiation was not followed by the regular dynamics of photosynthetic parameters, one can assume that the seasonal fluctuations of the P^B_{max}, α^B, and I_k values are controlled by temperature. To check this assumption, the results of the measurements conducted throughout the temperature interval in the cold and warm periods of the year were used. From the data shown in Fig. 4a, we can see that within the biokinetic interval of temperatures, during the winter–spring and the summer–fall periods, the fluctuations of the P^B_{max} values are related to the temperature and are described by the exponential function:

$$P^B_{max} = 1.68\exp(0.074T) \quad n = 40, \quad r^2 = 0.58, \tag{6}$$

$$P^B_{max} = 2.46\exp(0.076T) \quad n = 21, \quad r^2 = 0.72, \tag{7}$$

$$P^B_{max} = 0.82\exp(0.085T) \quad n = 60, \quad r^2 = 0.56. \tag{8}$$

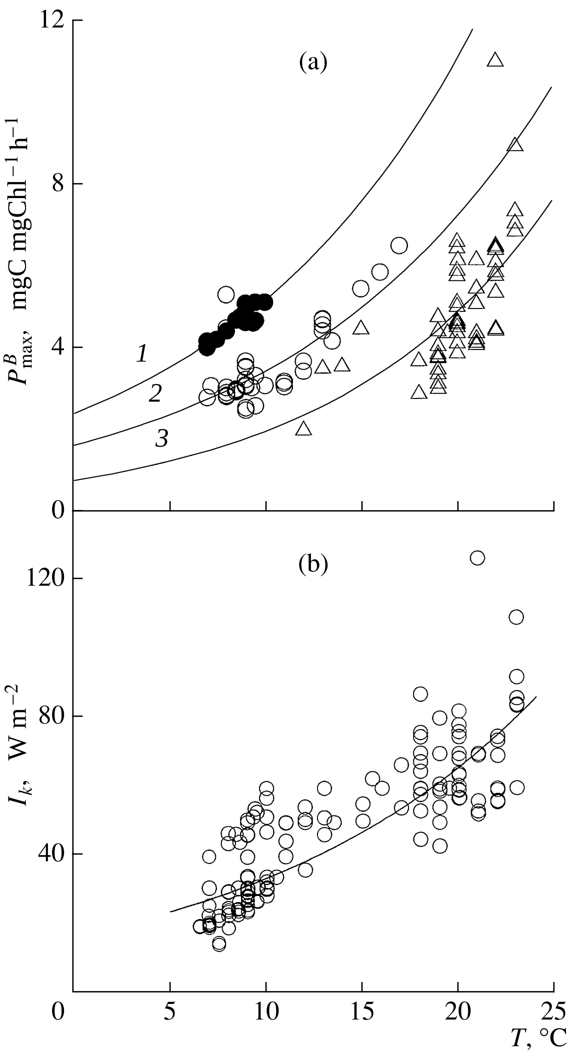

Fig. 4. Effect of temperature on (a) variations of $P^B_{\max}$ values (*1*) at the beginning (December to January) and the end (April) of the winter–spring phytoplankton vegetation, (*2*) at the maximum of the winter–spring phytoplankton vegetation (February to March), and (*3*) at the summer phase of phytoplankton vegetation; (b) variations of the I_k values during all the seasons.

Equation (6) was obtained for the beginning of the winter–spring phytoplankton vegetation period (from December to January) and for the time after its completion (April); equation (7) was acquired for the winter–spring peak of phytoplankton vegetation period (from February to March); and equation (8) was obtained for the summer period (from June to September).

Attention is drawn to the fact that in the above equations corresponding to Q_{10} = 2.1–2.3, the difference between the exponents is very small. Therefore, the phytoplankton adaptation to low and high temperatures does not cause variations in the temperature coefficient $P^B_{\max}$. A comparison of the $P^B_{\max}$ values in the winter–spring and summer phytoplankton at the average temperature of its dwelling (8 and 22°C, respectively) shows that they are two times lower in the winter–spring phytoplankton than in the summer. However, after changing the maximum intensity of photosynthesis of the summer phytoplankton from 22 to 8°C according to equation (8), it becomes three–four times lower than in phytoplankton during the winter–spring period. These differences can either be accepted as a proof for the increase in the maximum photosynthesis intensity of phytoplankton, adapted to low temperatures, or be understood as a result of the different extents of phytoplankton supply by biogenic elements. Since most of the measurements, excluding those conducted in March, were carried out at relatively low nitrate and phosphate concentrations within the surface layer (<0.15 μM), one can assume that they equally influenced $P^B_{\max}$ at all the temperatures. In March, when diatoms featured mass vegetation at a relatively high nitrate concentration within the mixed layer, which reached 0.4–2.0 μM at individual stations, greater $P^B_{\max}$ values were observed at the same temperatures as compared to January.

The light intensity values at which the onset of the light saturation in terms of photosynthesis (I_k) is observed also depend on the temperature (Fig. 4b), and, for all the seasons, the I_k—temperature relationship is described by a common equation:

$$I_k = 17.4\exp(0.066T), \quad n = 164, \qquad r^2 = 0.70, \quad \text{at} \quad 6.5 \le T \le 23°\text{C}. \tag{9}$$

Because $\alpha^B = P^B_{\max}/I_k$ from equations (6)–(9) it follows that at the temperature increase from 10 to 20°C, α^B can increase by 14% on average. As we can see, the share of temperature in the total α^B variability is negligible.

Throughout the year, the averaged monthly ratio I_0/I_k has small variations, because with the growth of temperature, simultaneously, the intensity of incident solar radiation increases, and on average, the I_k value is 38% of I_0, or $I_k = (0.38 \pm 0.09)I_0$.

Ratio between the rate of phytoplankton photosynthesis and chlorophyll concentration. For four periods of the year, when the water temperature (T) within the surface layer ranged by not more than 3–5°C (the first period lasted from December to February, the second was March, the third period lasted from April to May, and the fourth lasted from June to October, Figs. 5a, 5b), the correlation between the rate of photosynthesis and the chlorophyll concentration (Chl) was found. At such an integration of the data obtained, the maximum rate of photosynthesis $P_{\max}$ (mgC m^{-3} h^{-1}), depending on the chlorophyll concentration (excluding March), is described by a power function:

$$P_{\max} = 2.87\ \mathrm{Chl}^{1.25} \quad \text{at} \quad 0.3 \le \mathrm{Chl} \le 2.2, \qquad (10)$$
$$6.5 \le T \le 9.5, \quad r^2 = 0.93, \quad n = 36,$$

$$P_{\max} = 4.73\ \mathrm{Chl}^{1.01} \quad \text{at} \quad 0.3 \le \mathrm{Chl} \le 3.5, \qquad (11)$$
$$7.0 \le T \le 11.0, \quad r^2 = 0.96, \quad n = 23,$$

$$P_{\max} = 5.22\ \mathrm{Chl}^{1.27} \quad \text{at} \quad 0.1 \le \mathrm{Chl} \le 1.0, \qquad (12)$$
$$10.0 \le T \le 14.0, \quad r^2 = 0.93, \quad n = 23,$$

$$P_{\max} = 5.91\ \mathrm{Chl}^{1.16} \quad \text{at} \quad 0.07 \le \mathrm{Chl} \le 1.7, \qquad (13)$$
$$18.0 \le T \le 23.0, \quad r^2 = 0.89, \quad n = 76.$$

Equations (10)–(13) are given for the first to the fourth periods, respectively. For the first, third, and fourth periods of the year, the exponents are approximately the same, but the coefficient of proportionality increases by a factor of 1.8 with the temperature growth. During all the periods of the year, excluding March, the value of the power coefficient differs from unity (at $p < 0.05$) and $P_{\max}$ shows a nonlinear increase as the chlorophyll concentration increases. In this case, the growth in the chlorophyll concentration by a factor of 10 causes an increase in the maximum intensity of photosynthesis ($P^B_{\max}$) by a factor of 1.5–2.0. Thus, phytoplankton responds to the variations in the environmental conditions, first of all, by rather great fluctuations in its biomass and smaller changes in specific production.

The relationship between the rate of photosynthesis on the initial part of the light curve (α, mgC m^{-3} h^{-1}/(W m^{-2})) and the chlorophyll concentration is also described by a power-law function (Fig. 5c). However, unlike the $P_{\max}$ values, the values of the exponent and coefficient of proportionality are barely recognized during all the periods of the year, namely, 1.17–1.31 and 0.10–0.12, respectively. Therefore, the data obtained in all the seasons can be integrated. Then,

$$\alpha = 0.11\ \mathrm{Chl}^{1.28} \quad \text{at} \quad 0.07 \le \mathrm{Chl} \le 5.0, \qquad (14)$$
$$7 \le T \le 23 \quad r^2 = 0.95, \quad n = 164.$$

From equations (10)–(14) it follows that throughout the year, excluding March, a linear relationship between $P_{\max}$ and α is observed. In March, the relation between these parameters is described by a power-law function $P_{\max} = 27.4\alpha^{0.80}$.

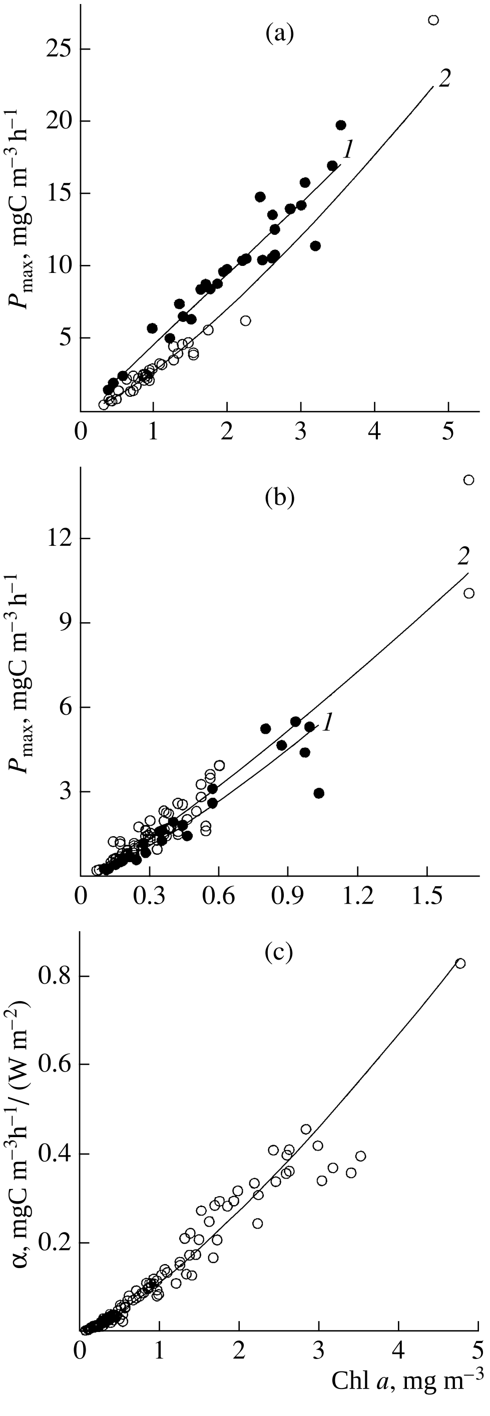

Fig. 5. Relationship of (a, b) the maximum photosynthesis rate $P_{\max}$ and (c) the initial slope of the photosynthesis–light curve to chlorophyll a concentration. (a) *1*—March; *2*—December–January; (b) *1*—April–May; *2*—June–October; and (c)—January–December.

Ratio between the α^B values and chlorophyll concentration. Equation (14) shows that the parameter α^B also depends on the chlorophyll concentration. The data obtained for all the seasons are given in Fig. 6. Despite a rather wide dispersion of the points, they show that the form of the relationship between the α^B values and the chlorophyll concentration adheres to a power-law function over the interval of the values measured:

$$\alpha^B = 0.11\ \mathrm{Chl}^{0.29} \quad \text{at} \quad 0.07 \le \mathrm{Chl} \le 5.0, \qquad (15)$$
$$r^2 = 0.68, \quad n = 164.$$

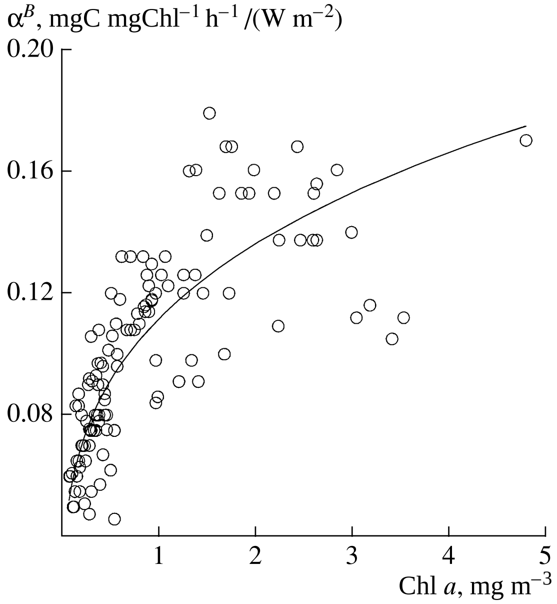

Fig. 6. Relationship between the initial slope of the photosynthesis–light curve (α^B) and chlorophyll *a* concentration.

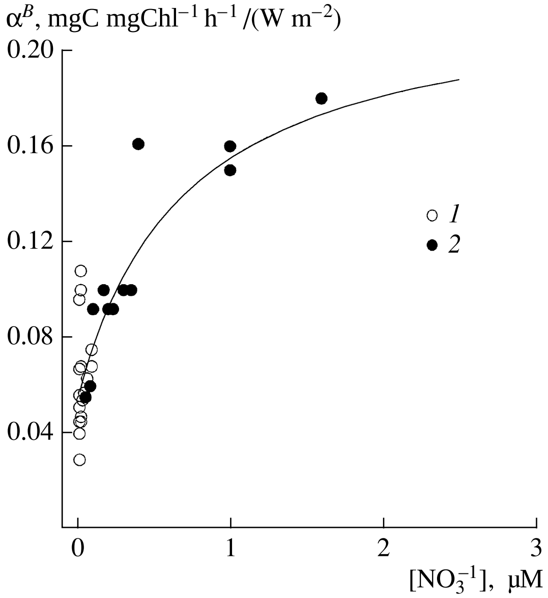

Fig. 7. Initial slope of the photosynthesis–light curve (α^B) as a function of nitrate concentration. *1*—June; *2*—February and March.

From equation (15) it follows that the α^B values grow twofold as the chlorophyll concentration increases from 0.07 to 3.0 mg m^{-3}.

Relationship between the α^B values and nitrate concentration. As has been shown above, the light and temperature weakly control the α^B fluctuations; therefore, the data obtained in the different seasons were integrated for the analysis of the relationship between the α^B and nitrate concentration values. The parallel measurements of the nitrate concentration values and the α^B values were conducted at individual stations in the coastal area off the southern part of the Crimea in the summer and also during the winter–spring period in the southeastern and central parts of the sea. The nitrate concentration values within the 0- to 15-m layer varied from 0 to 2.0 μM, and the α^B values ranged from 0.04 to 0.21 mgC mgChl^{-1} h^{-1}/W m^{-2}. The minimum values of α^B and the nitrate concentration were observed in the summer, while the maximum ones were confined to the period from February to March. Clearly, these differences are not occasional and reflect the α^B variations in the water with the nitrate concentration (Fig. 7). For description of this dependence, a modified equation of the Michaelis–Menthen type was used:

$$\alpha^B = 0.055 + (0.17N/0.7 + N) \quad r^2 = 0.75, \qquad (16)$$

where N is the nitrate concentration, μM.

At low nitrate concentrations (0.01–0.10), the α^B values for the summer and spring phytoplankton are fairly close but they are trebled when, in the period from February to March, the concentration reaches 2 μM.

Quantum yield of photosynthesis. The measurements of the maximum rate of photosynthesis and light absorption by the surface phytoplankton carried out simultaneously off the southern coast of the Crimea in June showed that the $\phi_{\max}$ values vary from 0.005 to 0.015 and make up 0.011 ± 0.003 mole C (mole quanta)$^{-1}$ on average. For calculation of the quantum yield in other areas, where such simultaneous measurements of the rate of photosynthesis and light absorption by phytoplankton were not available, the results of 53 determinations of the spectral light absorption by the surface phytoplankton were used. They were carried out at two fixed stations in the deepwater and coastal areas of the sea in different seasons of 1998–1999. The data analysis showed that in the Black Sea a power-law dependence between the coefficients of light absorption by phytoplankton (a_{ph}, m^{-1}) at the wavelengths of 440 and 678 nm and the chlorophyll concentration in the range from 0.1 to 2.5 mg m^{-3} is valid:

$$a_{\mathrm{ph}}(440) = 0.040\mathrm{Chl}^{0.63} \quad r^2 = 0.63, \qquad (17)$$

$$a_{\mathrm{ph}}(678) = 0.020\mathrm{Chl}^{0.81} \quad r^2 = 0.85. \qquad (18)$$

The average (over the spectrum) specific coefficient of light absorption by phytoplankton in the range from 400 to 700 nm ($\bar{a}^*_{\mathrm{ph}}$) is

$$\bar{a}^*_{\mathrm{ph}} = 0.015\ \mathrm{Chl}^{-0.38}. \qquad (19)$$

Using equations (17)–(19) and the data on the chlorophyll concentration within the surface layer obtained at 164 stations, we calculated the average ratios

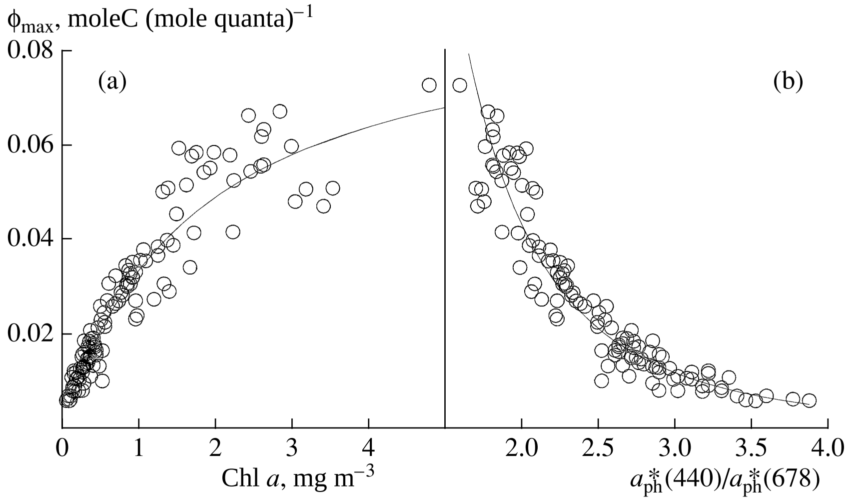

Fig. 8. Maximum quantum yield of photosynthesis of the surface phytoplankton (ϕ_{max}) as a function of (a) the chlorophyll *a* concentration and (b) the ratio between the values of the specific coefficient of light absorption by phytoplankton at 440 and 678 nm.

between the specific coefficients of light absorption by pigments at 440 and 678 nm, $\bar{a}^*_{ph}$ (400–700 nm) for every station, and the maximum quantum yield:

$$\phi_{max} = k(\alpha^B/\bar{a}^*_{ph}), \qquad (20)$$

where k is the coefficient of conversion from gram to mole, hour to second, and watt to mole quanta equal to 0.005; $\bar{a}^*_{ph}$ is the average specific light absorption by phytoplankton normalized to chlorophyll *a* in the range from 400 to 700 nm (m^2 (mg Chl)$^{-1}$).

Throughout the year, the ϕ_{max} values estimated varied within the limits of an order of magnitude, namely, from 0.005 to 0.06 mole C (mole quanta)$^{-1}$. For the winter, spring, and summer and fall, they were 0.032 ± 0.01, 0.034 ± 0.02, and 0.013 ± 0.006 on average, respectively. As we can see, for the summer period, the estimated values were roughly similar to the measured ones. Using all the data, we obtained that the ϕ_{max} values regularly increase as the chlorophyll concentration grows (Fig. 8a) and the kinetics of the process can be described by Michaelis–Menthen equation:

$$\phi_{max} = 0.093\,\text{Chl}/1.76 + \text{Chl}, \quad r^2 = 0.90. \qquad (21)$$

At the same time, it was found that, between the ϕ_{max} values and the specific ratio of the absorbed light at 440 and 670 nm, an inverse relationship is observed (Fig. 8b). A comparison of the character of variations in the ϕ_{max} and $\bar{a}^*_{ph}$ values with the chlorophyll concentrations shows that they go in opposite directions: with a rise in the chlorophyll concentration, the ϕ_{max} values increase, while the $\bar{a}^*_{ph}$ values decrease. As a result, the efficiency of photosynthesis (α^B) equal to the product ($\phi_{max}\bar{a}^*_{ph}$) increases as the chlorophyll concentration increases up to 3 mg m^{-3}.

DISCUSSION

During the early studies carried out in the Black Sea, the photosynthesis intensity–light dependence was determined in the in situ experiments [8]. In the deep-water areas of the sea, the P^B_{max} value for the surface phytoplankton increased from 3.50 ± 1.33 to 6.72 ± 1.77 mgC mgChl^{-1} h^{-1} from April to September. Close values were obtained in the studies conducted later, in the summer–fall period [1–3]. The seasonal dynamics of P^B_{max} in the deepwater areas of the sea and in Sevastopol Bay are similar [6, 8]. During the spring period, the P^B_{max} values range from 1.8 to 4.2, in the summer–fall period they vary from 5 to 15, while in the winter they are not greater than 2.5 mgC mgChl^{-1} h^{-1}.

The average values of P^B_{max} for the Black Sea and oceanic phytoplankton of the temperate latitudes are reasonably close. According to the results from many measurements performed in the winter–spring period between 38° and 50°N in the coastal and deep-water regions of the Atlantic Ocean, the average P^B_{max} values ranged from 2.7 ± 1.3 to 3.7 ± 1.3, while in the summer they varied from 5 to 7 mgC mgChl^{-1} h^{-1} [47]. The measurements carried out in the spring (from April to May) at 20°W and from 35° to 50°N showed that the P^B_{max} values reach 6–10 mgC mgChl^{-1} h^{-1} at a temperature of 16°C [38]. In the subtropical Atlantic waters, the same values were found from April to May [35]; they are approximately twofold greater than in the Black Sea in the spring period, but they are obtained at a higher temperature. The $P^B_{\max}$ values for the winter–spring phytoplankton of the Black Sea, reduced to 16°C according to equations (6)–(7), will be within the same limits (6.1–9.5 mgC mgChl^{-1} h^{-1}). In the fall (September to October), the $P^B_{\max}$ values ranged from 4 to 6 mgC mgChl^{-1} h^{-1} at a temperature of 20–22°C, which was close to the measured and calculated data for the summer Black Sea phytoplankton.

In the Black Sea, in selected seasons, the spatial variability of $P^B_{\max}$ and α^B on the scale of a few hundred kilometers does not exceed 25% (the coefficient of variation), whereas the variability of the chlorophyll concentration is greater (from 30 to 125%, Table 1). The temporal variability of $P^B_{\max}$ (40%) and α^B (30%) is similar being two–three times lower than that of the chlorophyll concentration (106%). Thus, at the level of the mesoscale variability, the rate of photosynthesis normalized to the chlorophyll concentration is a more stable parameter than the phytoplankton biomass.

The studies carried out in the Atlantic Ocean (from 50°N to 50°S) point to the fact that the large-scale variability of the $P^B_{\max}$ (84%) and chlorophyll concentration (102%) values are about the same [38]. The mesoscale variability of $P^B_{\max}$ and α^B in the subtropical area of the Atlantic Ocean ranged from 16 to 60% [35] and, on average, was two times lower than on the scale of several thousands of kilometers. The high variability of the $P^B_{\max}$ parameter in this area is related to the inclusion into the analysis of the data obtained at different depths. Since in the tropical and subtropical waters the $P^B_{\max}$ values decrease with depth [11, 38], one can believe that they reflect the variability within the water column rather than within the surface layer.

By our data, a weak correlation between the $P^B_{\max}$ and I_0 values ($r^2 = 0.25$) was observed only in the summer–fall period, whereas for the winter–spring period it was not observed. Previously, owing to the data of the in situ experiments in the Black Sea, it was shown that, in the summer period, a positive correlation between incident radiation and light photosynthetic optimum is frequently found [5]. By the results of a great number of experiments with different species of algae, which were carried out at a rather constant temperature (18–22°C) and a sufficient nutrient supply, the relationship between the density of the light flux (I_0), to which the algae were adapted, and $P^B_{\max}$ can be described by the function [22] $P^B_{\max} = a + b\log(I_0)$, where $P^B_{\max}$ is expressed in mgC mgChl^{-1} h^{-1}, $a = 1.58$, and $b = 0.88$ at $1 \le I_0$, W m^{-2} ≤ 250. Therefore, when the monthly average I_0 values vary from 60 to 250 W m^{-2}, which was found in the period of our studies, the expected $P^B_{\max}$ values should be equal to 5.2 and 6.4, respectively. Thus, at a constant temperature, the fourfold change in the average values of solar radiation from the winter to the summer (from 60 to 250 W m^{-2}) may increase the $P^B_{\max}$ values only by a factor of 1.2. During this period, the increase in the average value of $P^B_{\max}$ was threefold (Table 1). Therefore, the threefold growth of the $P^B_{\max}$ values results from the change in the water temperature from 7–9 to 20–23°C. The Q_{10} coefficient calculated for this temperature interval is equal to 2.1. In the phytoplankton living under conditions of low or elevated temperatures, Q_{10} is equal to 2.0 and 2.3, respectively (Fig. 4). The generalization of a great amount of data obtained practically over the whole range of temperatures in the ocean (from –1 to 28°C) showed that the $P^B_{\max}$ value increases as the temperature grows within the interval from –1 to 20°C ($Q_{10} = 2.35$) and decreases in the range from 20 to 28°C [12]. The same or close values of Q_{10} were gained in the early studies carried out in the coastal waters off New York [34], Nova Scotia [44], and in Tokyo Bay [30, 51].

According to our studies, the share of temperature in the total variability of $P^B_{\max}$ was 50–70%. In the subtropical waters of the Atlantic Ocean, it ranged from 40 to 60%, but when analyzing the combined effect of the temperature and nutrient concentration (nitrogen, phosphate, and silicates) on the variations in the $P^B_{\max}$ values, the coefficient of determination increases to 0.70–0.84 [35].

In the Black Sea, the temporal dynamics of the α^B values differs from the seasonal changes in the $P^B_{\max}$ values. Comparatively high values were found from November to March (0.10–0.20); in the summer, they are two times lower on average. Not much of the data obtained before for the summer and fall periods is within the same limits [1, 8]. An analysis of the data showed that the α^B parameter was not governed by light, and the temperature contribution to the total variability of the α^B parameter was small (Table 2). At the same time, it was found that the α^B values increase with the growth of nitrate concentration up to 2 μM (Fig. 7). A similar character of the relationship was found during the spring phytoplankton vegetation in the Sargasso Sea, when the nitrate concentration in the water decreases [46]. The data obtained in the Indian Ocean [49] may be regarded as an argument in favor of the assumption that nitrates control the variations in the α^B values. Although the dispersion of the values is very wide, the data in the Sargasso Sea and in the Indian Ocean are described by the same curve. The relations between the α^B values and nitrate concentration for the oceanic and Black Sea phytoplankton have the same form, but the coefficients entering into the equations differ. At low concentrations of NO_3 within the surface layer (about 0.05 μM), the α^B values for the Black Sea and oceanic phytoplankton [46, 49] coincide and equal 0.06 mgC $mgChl^{-1}$ h^{-1}/W m^{-2} on average. At high concentrations of NO_3 (about 3 μM), the α^B values for the Black Sea reach 0.2 mgC $mgChl^{-1}$ h^{-1}/W m^{-2}, which is two times greater than in the Sargasso Sea. In the spring, in the subtropical Atlantic and in the southern subtropical zone of convergence, the α^B values are 0.18–0.40 mgC $mgChl^{-1}$ h^{-1}/W m^{-2} at the same nitrate concentrations (1–3 μM) [19, 35]. While it is difficult to attach particular significance to one of the nutrients, nevertheless, we note that, in different areas, at equal NO_3 concentrations, some differences in the α^B values are found. They can depend on the light absorption by phytoplankton and which are related to the changes in the size and taxonomic algae composition.

It is well known that the algae with large intracellular content of pigments and the cells of large size have lower specific coefficients of light quanta absorption than the algae with small cellular sizes or low content of pigments [31, 42]. An increase in the intracellular content of pigments is followed by the enlarging of chloroplasts and increasing of the amount of tilackoids and the extent of their packaging, which results, by analogy with an optically dense system, in the self-shading of pigments and in the drop in the specific spectral coefficient of light absorption. The power coefficients in the α^B–chlorophyll concentration and a^*_{ph}–chlorophyll concentration relationships are different (equations (15) and (19)). As a result, with increases in the chlorophyll concentration in a wide range of values (0.1–20 mg m^{-3}), the α^B values in the Black Sea calculated as the product ($\phi_{max}\bar{a}^*_{ph}$), will first grow (up to 3 mg m^{-3}) and then decrease. For oceanic phytoplankton, the maximum α^B values are found at a concentration of 0.4–0.6 mg m^{-3}, but in the field of low and high concentrations, they decrease by a factor of 1.3–1.8 [43]. Thus, we can assume that, in the range of the chlorophyll concentrations from 0.1 to 20 mg m^{-3}, the pattern of the variations of the α^B values in the Black Sea will take a dome-shaped form with a single maximum in the left-hand part of the curve.

A comparison between the average values of ϕ_{max} for the Black Sea phytoplankton and the data measured in other areas of the ocean shows that they do not fall beyond the expected limits given in Fig. 8. For example, in the waters of the California Current with a chlorophyll concentration of 0.2–0.4 mg m^{-3}, the ϕ_{max} average for the surface phytoplankton was 0.027 ± 0.019 mole C (mole quanta)$^{-1}$ [50]. In the spring and fall, in the subtropical Atlantic, the ϕ_{max} averages ranged from 0.017 to 0.034 at a variation of the chlorophyll concentration from 0.1 to 0.3 mg m^{-3} [35]. In the mesotrophic and eutrophic waters of the tropical Atlantic, the chlorophyll concentration values ranged from 1 to 5 mg m^{-3} and the ϕ_{max} values varied from 0.035 to 0.05 mole C (mole quanta)$^{-1}$; in the oligotrophic areas with a chlorophyll concentration <0.1 mg m^{-3}, it decreased to 0.005 mole C (mole quanta)$^{-1}$ [11].

In the Black Sea, at low ratios $a^*_{ph}(440\text{ nm})/a^*_{ph}(678\text{ nm})$ (1.5–2.0), the ϕ_{max} value reaches 0.07 mole C (mole quanta)$^{-1}$ and is close to that obtained in the period of the spring bloom and after it in the Sargasso Sea [16]. In the Indian Ocean, at the same ratio of the absorbed light, i.e., $a^*_{ph}(440\text{ nm})/a^*_{ph}(678\text{ nm})$, the ϕ_{max} values were lower than in the Black Sea by a factor of 1.5. These differences are determined by the prevalence of small algae having higher specific coefficients of light absorption [49]. As the ratio $a^*_{ph}(440\text{ nm})/a^*_{ph}(678\text{ nm})$ rises to 3.0–3.5, the quantum yield decreases about five times (Fig. 8b). It is conceivable that this is related to the different nutrient supply of phytoplankton at low and high chlorophyll concentrations. In the laboratory experiments, at the nitrogen-limited rate of algae growth, the ϕ_{max} values decrease [15]. The deficiency of nitrogen decreases the activity of the reaction center of the photosystem and the ratio of the reaction centers of photosystem II to pigments [33]. As a result, the light absorbed by algae is transformed into chemical energy with a lower efficiency. The high density of the light flux causes a decrease in the efficiency of photosynthesis due to the increase in the photoptotective pigments–photosynthetic pigments ratio [18]. The drop in the quantum yield at low chlorophyll concentrations can be determined by partial absorption of the light of limited photosynthetic utility by photoptotective pigments.

Thus, the assessment of a sufficiently great amount of experimental data, for the first time for the Black Sea, allowed us to find temporal and regional variations in the photosynthetic parameters and to reveal the features of their variability depending on the factors that control their variability. The data analysis points to the fact that the key factor determining the temporal variations of the P^B_{max} values is the temperature, while the α^B parameter depends on the nitrate and chlorophyll concentrations and also on the specific light absorption by phytoplankton (a^*_{ph}).

For the first time, temporal variations of the maximum quantum yield of the Black Sea phytoplankton photosynthesis (ϕ_{max}) were studied. The comparison between the pattern of variations of the ϕ_{max} and $\bar{a}^*_{ph}$ values and that of the chlorophyll concentrations shows that they proceed in opposite directions; namely, the ϕ_{max} values grow with the increase in the chlorophyll concentration values, whereas the $\bar{a}^*_{ph}$ values decrease. The results of calculations show that the relationship between the α^B and chlorophyll concentration values

(0.1–20 mg m^{-3}) can be approximated by a one-peaked curve with a maximum at 3 mg m^{-3}.

The relationships found can form a basis for the justification of algorithms for the calculation of the primary production in the Black Sea in terms of the chlorophyll concentrations and densities of the light flux at different depths. They give a possibility to forecast the temporal and spatial variability of photosynthetic parameters within the surface layer of the Black Sea by remote sensing of the chlorophyll concentration and temperature. For the estimation of phytoplankton production within the water column, the α^B parameter is of greater importance. In the Black Sea, on the scale of several hundred kilometers, the α^B values vary by a factor of 1.5–3. Taking these differences into account improves the accuracy of the phytoplankton production calculations from satellite-based data. For the correct estimation of the primary production within the photosynthetic layer, we should also consider the vertical variability of the photosynthetic efficiency.

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REFERENCES

1. Akimov, A.I., Stel'makh, L.V., Churilova, T.Ya., *et al.*, Light Adaptation of Marine Phytoplankton, *Okeanologiya*, 1992, vol. 32, no. 1, pp. 84–91.
2. Vedernikov, V.I. and Demidov, A.B., Vertical Distribution of Primary Production and Chlorophyll in the Black Sea in Different Seasons, *Okeanologiya*, 1997, vol. 37, no. 3, pp. 414–423.
3. Vedernikov, V.I., Primary Production and Chlorophyll in the Black Sea in the Summer-Fall Period, *Structure and Productional Characteristics of the Planktonic Communities of the Black Sea*, Moscow: Nauka, 1989, pp. 65–84.
4. Vedernikov, V.I., Features of Distribution of Primary Production and Chlorophyll in the Black Sea in the Spring and Summer Periods, *Izmenchivost' ekosistemy Chernogo morya: estestvennye i antropogennye faktory* (Variability of the Black Sea Ecosystem: Natural and Anthropogenic Factors), Moscow: Nauka, 1991, pp. 128–147.
5. Skopintsev, B.A., *Formirovanie sovremennogo khimicheskogo sostava vod Chernogo morya* (Formation of the Current Chemical Composition of Black Sea Water), Leningrad: Gidrometeoizdat, 1975.
6. Stel'makh, L.V., Intensity of Photosynthesis in Two Size Fractions of Phytoplankton in the Eutrophic Waters of Sevastopol Bay, *Gidrobiol. Zh.*, 1992, vol. 28, no. 3, pp. 14–20.
7. Finenko, Z.Z., Adaptatsiya Vodoroslei k Osnovnym Faktoram Okeanicheskoi Sredy, *Okeanologiya. Biologiya okeana T. 1* (TRaNSl), Moscow: Nauka, 1977, pp. 9–18.
8. Finenko, Z.Z., Phytoplankton Production, *Osnovy produktivnosti Chernogo morya* (Productivity Basis in the Black Sea), Kiev: Naukova Dumka, 1979, pp. 88–97.
9. Finenko, Z.Z. and Krupatkina, D.K., Primary Production and Size Structure of Phytoplankton in the Black Sea in the Winter–Spring Period, *Plankton Chernogo morya* (Plankton of the Black Sea), Kiev: Nauk. Dumka, 1993, pp. 74–92.
10. Yunev, O.A. and Berseneva, G.P., Fluorimetric Method for Determination of Chlorophyll *a* and Phaeophytine *a* in Phytoplankton, *Gidrobiol. Zh.*, 1986, pp. 89–95.
11. Babin, M., Morel, A., Claustre, H., *et al.*, Nitrogen- and Irradiance-Dependent Variations of the Maximum Quantum Yield of Carbon Fixation in Eutrophic, Mesotrophic, and Oligotrophic Marine Systems, *Deep-Sea Res. I*, 1996, vol. 43, no. 8, pp. 1241–1272.
12. Behrenfeld, M.J. and Falkowski, P.G., Photosynthetic Rates Derived from Satellite-Based Chlorophyll Concentration, *Limnol. Oceanog*, 1997, vol. 42, no. 1, pp. 1–20.
13. Bricaud, A., Babin, M., Morel, A., *et al.*, Variability in the Chlorophyll-Specific Absorption Coefficients of Natural Phytoplankton: Analysis and Parameterization, *J. Geophys. Res.*, 1995, vol. 100, no. C7, pp. 13 321–13 332.
14. Bricaud, A., Morel, A., Babin, M., *et al.*, Variation of Light Absorption by Suspended Particles with Chlorophyll *a* Concentration in Oceanic (Case 1) Waters: Analysis and Implications for Bio-Optical Models, *J. Geophys. Res.*, 1998, vol. 103, no. C13, pp. 31033–31044.
15. Cleveland, J.S. and Perry, M.J., Quantumn Yield, Relative Specific Absorption, and Fluorescence in Nitrogen-Limited *Chaetoceros gracilis*, *Mar. Biol.*, 1987, vol. 94, no. 3, pp. 489–497.
16. Cleveland, J.S., Perry, M.J., Kiefer, D.A., *et al.*, Maximal Quantum Yield of Photosynthesis in the Northwestern Sargasso Sea, *J. Mar. Res.*, 1989, vol. 47, no. 10, pp. 869–886.
17. Cote, B. and Platt, T., Day-to-Day Variations in the Spring–Summer Photosynthetic Parameters of Coastal Marine Phytoplankton, *Limnol. Oceanogr.*, 1983, vol. 28, no. 2, pp. 320–344.
18. Culver, M.E. and Perry, M.J., The Response of Photosynthetic Absorption Coefficients to Irradiance in Culture and in Tidally Mixed Estuarine Waters, *Limnol. Oceanogr.*, 1999, vol. 44, no. 1, pp. 24–36.
19. Dower, K.M. and Lucas, M.I., Photosynthesis–Irradiance Relationships and Production Associated with a Warm-Core Ring Shed from the Agulhas Retroflection South of Africa, *Mar. Ecol. Prog. Ser.*, 1993, vol. 95, pp. 141–154.
20. Falkowski, P.G., Light-Shade Adaptation and Assimilation Numbers, *J. Plankton Res.*, 1981, vol. 3, no. 2, pp. 203–216.
21. Finenko, Z.Z., Production in Plant Populations, *Marine Ecology*, Kinne, O., Ed., New York, 1978, vol. 5, pp. 13–87.
22. Geider, R.J., Quantitative Phytoplankton Physiology: Implications for Primary Production and Phytoplankton Growth, *ICES Mar. Sci. Symp.*, 1993, vol. 197, pp. 52–62.
23. Harding, L.W., Prezelin, B.B., Sweeney, B.M., *et al.*, Diel Oscilations of the Photosynthesis–Irradiance (P–I) Relatonship in Natural Assemblages of Phytoplankton, *Mar. Biol.*, 1982, vol. 67, no. 1, pp. 167–178.

24. Harrisson, W.G. and Platt, T., Variations in Assimilation Number of Coastal Marine Phytoplankton: Effects of Environmental Co-Variates, *J. Plankton Res.*, 1980, vol. 2, no. 4, pp. 249–261.
25. Harrisson, W.G. and Platt, T., Photosynthesis-Irradiance Relationships in Polar and Temperate Phytoplankton Populations, *Polar Biol.*, 1986, vol. 5, pp. 153–154.
26. Hoepffner, N., Sturm, B., Finenko, Z.Z., *et al.*, Depth-Integrated Primary Production in the Eastern Tropical and Subtropical North Atlantic Basin from Ocean Color Imagery, *Int. J. Remote Sensing*, 1999, vol. 20, no. 7, pp. 1435–1456.
27. Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., and Strickland, J.D.H., Fluorometric Determination of Chlorophyll, *J. Cons. Inst. Explor. Mer.*, 1965, vol. 30, pp. 3–15.
28. Hood, R.R., Abott, M., and Huyer, A., Phytoplankton and Photosynthetic Light Response in the Coastal Transition Zone off Northern California in June 1987, *J. Geophys. Res.*, 1991, vol. 96, no. C8, pp. 14769–14780.
29. Hood, R.R., Light Response of Phytoplankton in the South Atlantic Ocean: Interpretation of Observations and Application to Remote Sensing, *J. Geophys. Res.*, 1995, vol. 100, no. C6, pp. 10927–10942.
30. Ichimura, S., Environmental Gradient and Its Relation to Primary Productivity in Tokyo Bay, *Records Oceanog. Works, Japan*, 1967, vol. 9, no. 1, pp. 115–128.
31. Kirk, J.T.O., A Theoretical Analysis of the Contribution of Algal Cells to the Attenuation of Light within Natural Waters, II, Sppherical Cells, *New Phytol.*, 1975, vol. 75, pp. 21–36.
32. Kischino, M.M., Takahashi, N., Okami, S., *et al.*, Estimation of the Spectral Absorption Coefficients of Phytoplankton in the Sea, *Bull. Mar. Sci.*, 1985, vol. 37, pp. 634–642.
33. Kolber, Z., Zehr, J., and Falkowski, P.G., Effects of Growth of Irradiance and Nitrogen Limitation on Photosynthetic Energy Conversion in Photosystem II, *Plant Phisiol*, 1988, vol. 88, pp. 923–929.
34. Krupatkina, D.K., Finenko, Z.Z., and Shalapyonok, A.A., Primary Production and Size-Fractionated Structure of the Black Sea Phytoplankton in the Winter–Spring Period, *Mar. Ecol. Prog. Ser.*, 1991, vol. 73, pp. 25–31.
35. Kyewalyanga, M.N., Platt, T., Sathyendranath, S., *et al.*, Seasonal Variations in Physiological Parameters of Phytoplankton Across the North Atlantic, *J. Plankton Res.*, 1998, vol. 20, no. 1, pp. 17–42.
36. Longhurst, A., Seasonal Cycles of Pelagic Production and Consumption, *Progr. Oceanogr.*, 1995, vol. 36, pp. 77–167.
37. Mandelli, E.F., Burkholder, T.E., Doheny, R., *et al.*, Studies of Primary Productivity in Coastal Waters of Southern Long Island, New York, *Mar. Biol.*, 1970, vol. 7, no. 2, pp. 153–160.
38. Maranon, E. and Holligan, P.M., Photosynthetic Parameters of Phytoplankton from 50°N to 50°S in the Atlantic Ocean, *Mar. Ecol. Prog. Ser.*, 1999, vol. 176, pp. 191–203.
39. Mitchell, B.G., Algorithms for Determining the Absorption Coefficient of Aquatic Particulates Using the Quantitative Filter Technique (QFT), *Ocean Optics X* Spinrad, R., Ed., SPIE Bellingham, Washington, 1990, pp. 137–148.
40. Mitchell, B.G. and Kiefer, D.A., Determination of Absorption and Fluorescence Excitation Spectra for Phytoplankton, *Marine Phytoplankton and Productivity*, Holm-Hansen, O., Bolis, L., and Giles, R., Eds., Springer, 1984, pp. 157–169.
41. Mitchell, B.G. and Kiefer, D.A., Chlorophyll *a* Specific Absorption and Fluorescence Exitation Spectra for Light-Limited Phytoplankton, *Deep-Sea Res.*, 1988, vol. 135, no. 5, pp. 639–663.
42. Morel, A. and Bricaud, A., Theoretical Results Concerning Light Absorption in a Discrete Medium, and Application to Specific Absorption of Phytoplankton, *Deep-Sea Res. Part a*, 1981, vol. 28A, no. 10, pp. 1375–1393.
43. Morel, A., Antoine, D., Babin, M., *et al.*, Measured and Modeled Primary Production in the Northeast Atlantic (EUMELI JGOFS Program): The Impact of Natural Variations in Photosyntecic Parameters on Model Predictive Skill, *Deep-Sea Res. I*, 1996, vol. 43, no. 8, pp. 1273–1304.
44. Platt, T. and Jassby, A.D., The Relationship between Photosynthesis and Light for Natural Assemblages of Coastal Marine Phytoplankton, *J. Phycol.*, 1976, vol. 12, no. 4, pp. 421–430.
45. Platt, T., Gallegos, C.L., and Harrison, W.G., Photoinhibition of Photosynthesis in Natural Assemblages of Marine Phytoplankton, *J. Mar. Res.*, 1980, vol. 38, no. 4, pp. 687–701.
46. Platt, T., Sathyendranath, S., Ulloa, O., *et al.*, Nutrient Control of Phytoplankton Photosynthesis in the Western North Atlantic, *Nature*, 1992, vol. 356, pp. 229–231.
47. Platt, T., Caverhill, C., and Sathyendranath, S., Basin-Scale Estimates of Oceanic Primary Production by Remote Sensing: The North Atlantic, *J. Geophys. Res.*, 1991, vol. 96, no. C8, pp. 15147–15159.
48. Sathyendranath, S., Longhurst, A., Cavergill, C., *et al.*, Regionally and Seasonally Differentiated Primary Production in the North Atlantic, *Deep-Sea Res.*, 1995, vol. 42, no. 10, pp. 1773–1802.
49. Sathyendranath, S., Platt, T., Stuart, V., *et al.*, Some Bio-Optical Characteristics of Phytoplankton in the NW Indian Ocean, *Mar. Ecol. Prog. Ser.*, 1996, vol. 132, pp. 299–311.
50. Schofield, O., Prezelin, B.B., Bidigare, R.R., *et al.*, In situ Photosynthetic Quantum Yield Correspondence to Hydrographic and Optical Variability Within the Southern California Bight, *Mar. Ecol. Prog. Ser.*, 1993, vol. 93, pp. 25–37.
51. Takahashi, M., Fujii, F., and Parsons, T.R., Simulation Study of Phytoplankton Photosynthesis and Growth in the Fraser River Estuary, *Mar. Biol.*, 1973, vol. 19, no. 1, pp. 102–116.
52. Toon, R.K., Lohrenz, S.E., Rathbun, C.E., *et al.*, Photosynthesis–Irradiance Parameters and Community Stricture Associated with Coastal Filaments and Adjacent Waters in the Northern Arabian Sea // *Deep-Sea Res.*, 2000, part II, vol. 47, nos. 7–8, pp. 1249–1277.
53. Yentsch, C.S., Measurement of Visible Light Absorption by Particulate Matter in the Ocean, *Limnol. Oceanogr.*, 1962, vol. 7, no. 2, pp. 207–217.