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Photosynthetic Parameters of Phytoplankton and Primary Production in Coastal Waters of the Black Sea: Seasonal Features

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Abstract

This paper studies seasonal variability of phytoplankton photosynthetic parameters in the Black Sea coastal waters near the Crimean Peninsula. Primary production was estimated using a full spectral approach that took into account phytoplankton spectral light absorption coefficient, spectral downwelling irradiance and quantum yield of photosynthesis. In the coastal waters near the village of Katsiveli, the annual dynamics of chlorophyll a concentration was characterized by maximal values in winter and minimal (half as many) in summer, while in the waters near Sevastopol, the maximum was recorded in early October and March, which is likely due to the "bloom" of phytoplankton. High annual variability of both the phytoplankton spectrally weighted chlorophyll a specific absorption coefficient (~ 3 times) and maximum quantum yield of photosynthesis (~ 7 times) was noted, with maximal values in summer and winter, respectively. In the vertical profile, the minimal values of the quantum yield were observed in the sea surface layer associated with the high photosynthetically active radiation incident on the sea surface. The variability in photosynthetic parameters, caused by phytoplankton adaptation to changing environmental factors, resulted in a strong annual variability of primary production, which varied ~ 8-fold over the study period. The obtained patterns of variability of the basic photosynthetic parameters of phytoplankton (the ability to absorb light quanta and use them in photochemical reactions) are necessary for understanding the mechanism of formation of primary production in the studied water region.

Keywords: chlorophyll a, quantum yield of photosynthesis, light absorption, photosynthetically available radiation, spectral downwelling irradiance

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Фотосинтетические характеристики фитопланктона и первичная продукция в прибрежных водах Черного моря: сезонные особенности

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Аннотация

Исследована сезонная изменчивость фотосинтетических характеристик фитопланктона в прибрежных водах Черного моря у побережья Крымского полуострова. Первичную продукцию оценивали с использованием полного спектрального подхода, учитывающего спектральные показатели поглощения света пигментами фитопланктоном, спектральную освещенность и квантовый выход фотосинтеза. В прибрежных водах у поселка Кацивели годовая динамика концентрации хлорофилла *a* характеризовалась максимальными значениями зимой и минимальными (в два раза меньше) летом, тогда как в водах вблизи Севастополя максимум концентрации хлорофилла *a* был отмечен в начале октября и в марте, что, вероятно, обусловлено «цветением» фитопланктона. Отмечена высокая годовая вариабельность как удельной эффективности поглощения света пигментами фитопланктона (примерно в три раза), так и максимального квантового выхода фотосинтеза (примерно в семь раз) с наблюдаемыми максимальными значениями летом и зимой соответственно. В вертикальном распределении квантового выхода минимальные значения были отмечены в поверхностном слое, что связано с высокой фотосинтетически активной радиацией, падающей на поверхность моря. Вариабельность фотосинтетических характеристик, обусловленная адаптацией фитопланктона к изменяющимся факторам среды, привела к значительной годовой изменчивости первичной продукции, которая за исследуемый период варьировала примерно в восемь раз. Полученные закономерности изменчивости основных фотосинтетических характеристик фитопланктона (способности поглощать кванты света и использовать их в фотохимических реакциях) необходимы для понимания механизма формирования первичной продукции в исследуемой акватории.

Ключевые слова: хлорофилл *a*, квантовый выход фотосинтеза, поглощение света, фотосинтетически активная радиация, спектральная освещенность

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Introduction

Phytoplankton uses the sunlight energy during the primary synthesis of organic matter from inorganic compounds, the daily rate of which is called primary production (PP) [1]. PP ensures functioning of all trophic levels in food web of water ecosystems [1, 2]. The rate of photosynthesis depends on photosynthetically available radiance (PAR), the nutrient supply and temperature [2]. The coastal waters of the Black Sea (BS) are subject to strong anthropogenic impacts [3], which results in an increase in the concentration of nutrients, organic and suspended matter in the sea [4]. Elevated nutrient (mineral compounds of nitrogen, phosphorus and silicon) concentrations in the upper mixed level (UML) contribute to higher photosynthesis rates and enhance the growth of planktonic microalgae [5]. The photosynthetic and productive characteristics of phytoplankton determine the functioning of all other levels of the aquatic ecosystem's food web. Therefore, assessment of the current state of phytoplankton productivity in the BS coastal waters is highly relevant. Light intensity and its spectral properties change with depth in the sea associated with light absorption and scattering by optically active components (OAC), namely phytoplankton, colored dissolved organic matter (CDOM), non-algal particles (NAP) and pure water [6]. Consequently, a spectral approach to primary productivity (PP) estimation provides more accurate estimates than other approaches, which are based on PAR (i. e. light intensity integrated for wavelengths of 400–700 nm) [7, 8]. For the BS region, a full spectral algorithm was developed [9]. This approach considers the spectral properties of downwelling irradiance, light absorption by phytoplankton and the quantum yield (efficiency of absorbed photon use in photosynthesis), which determines the accuracy of the PP estimate [9–11].

This study focuses on the seasonal dynamics of PP, chlorophyll a concentration, photosynthetic parameters of phytoplankton, namely spectrally weighted chlorophyll a-specific phytoplankton absorption coefficient and the quantum yield of photosynthesis in the BS coastal waters. Additionally, the aim of this study is to investigate the influence of the spectral composition of light on the spectrally weighted chlorophyll a-specific phytoplankton absorption coefficients.

Methods

Study area

The study was carried out in the BS coastal waters. The BS is an inland sea, the easternmost of the seas of the Atlantic Ocean basin. In the southwest it connects to the Sea of Marmara through the Bosphorus Strait, in the northeast it connects to the Sea of Azov through the Kerch Strait. The BS is one of the largest and deepest inland seas. Its greatest depths are in the range of 2210–2258 m. About 1000 large and small rivers flow into the BS. Due to the large river runoff, the BS surface waters salinity is 18‰ [12].

Bio-optical properties and phytoplankton photosynthetic parameters were measured at two fixed stations in the coastal waters of the Crimean Peninsula:

1. A station located about a mile offshore outside of Sevastopol Bay (44°38′ N, 33°29′ E) with a depth of ~50 m (to the bottom) (22.02.2022; 16.06.2022; 13.07.2022; 06.10.2022; 09.11.2022; 29.11.2022; 07.03.2023; 21.03.2023);

2. The oceanographic platform of the Marine Hydrophysical Institute (MHI) of the Russian Academy of Sciences located in the coastal waters ~ 0.37 mile offshore from the village of Katsiveli with a depth of ~ 30 m (to the bottom) (44°23′ N, 33°59′ E) (08.06.2023; 24.01.2024).

Water sampling

The downwelling irradiance spectra $E_d(\lambda)$ were measured in increments of 1 m within the euphotic zone using a RAMSES submersible spectroradiometer (TrioOS, Germany). The euphotic zone depth (Z_{eu}) is limited to the depth at which 1% photosynthetically available radiation (PAR) penetrates. Water samples (5 L) were collected using Niskin bottles at the depths selected based on water transparency and temperature profiles. Water transparency was assessed based on Secchi disk depth (Z_s).

Pigment Analysis

The sum of chlorophyll a and pheopigment concentrations (TChl-*a*) was determined by the spectrophotometric method [13, 14] with 90% acetone using Whatman GF/F glass fiber filters (25 mm diameter, 0.7 μm size pore). The optical density (OD) of the acetone-extracted phytoplankton pigments was measured with a Lambda 35 dual-beam spectrophotometer (PerkinElmer).

Absorption Measurements

The spectral light absorption coefficients of phytoplankton ($a_{\mathrm{ph}}(\lambda)$), NAP ($a_{\mathrm{NAP}}(\lambda)$) and CDOM ($a_{\mathrm{CDOM}}(\lambda)$) were measured in accordance with modern protocols [15, 16] using a Lambda 35 dual-beam spectrophotometer (PerkinElmer) equipped with an integrating sphere. The chlorophyll a-specific phytoplankton light absorption coefficient of ($a^*_{\mathrm{ph}}(\lambda)$) ($\mathrm{m^2 \cdot mg^{-1}}$) was calculated by dividing $a_{\mathrm{ph}}(\lambda)$ by TChl-*a*.

Spectrally weighted chlorophyll a-specific absorption coefficients of phytoplankton $\bar{a}^*_{\mathrm{ph}}(z)$, $\mathrm{m^2 \cdot mg^{-1}}$, were calculated as

$$\bar{a}^*_{\mathrm{ph}}(z) = \frac{\int_{400}^{700} a^*_{\mathrm{ph}}(\lambda, z) \cdot E_d(\lambda, z) d\lambda}{\int_{400}^{700} E_d(\lambda, z) d\lambda \cdot \mathrm{TChl}\text{-}a}.$$

Primary production

PP, $\mathrm{mgC \cdot m^{-3} \cdot d^{-1}}$, was determined according to the full spectral approach [9]:

$$\mathrm{PP} = 12000 \cdot \phi(z) \cdot \mathrm{PUR_{psp}}(z),$$

where 12000 – moles to mg carbon conversion ratio; ϕ – the quantum yield of photosynthesis, and $\mathrm{PUR_{psp}}$ – the amount of quanta absorbed by photosynthetically active pigments, per TChl-*a* unit.

The ϕ values ($\mathrm{mol\ C \cdot mol\ quanta^{-1}}$), were calculated as [17]:

$$\phi\,(z) = \phi_{\max}(z) \cdot \tanh\left(\frac{I_k(z)}{\mathrm{PAR}(z)}\right),$$

where $\phi_{\max}$ is the maximum quantum yield of photosynthesis; I_k is the light intensity saturating relative electron transfer rate (rETR), which corresponds to I_k for the photosynthesis rate [17].

The ϕ_{max}, mol C·mol quanta^{-1}, was assessed based on the parameters of variable chlorophyll a fluorescence:

$$\phi_{max} = \left(\frac{F_v}{F_m}\right)/(K_c \cdot 2),$$

where F_m is the maximal fluorescence of chlorophyll a with closed reaction centers (RC) of photosystem II (PSII); F_v is the difference between F_m and the minimal fluorescence of chlorophyll a with open RC PSII (F0); K_c is the number of electrons required to fix a single CO_2 molecule [18]; 2 is the number of photons required for the transfer of one electron along the photosynthetic electron transport chain [2].

F_m, F0 and rETR were measured in the laboratory with a chlorophyll fluorescence kinetic measurement system (fluorimeter Smart) developed at the Department of Biophysics, Faculty of Biology, Lomonosov Moscow State University [19].

K_c, mol electrons·mol C^{-1}, was calculated in accordance with [20]:

$$K_c = 0.85PAR + 6.55.$$

I_k, µmol quanta·m^{-2}·s^{-1}, was calculated as [21]:

$$I_k = \frac{rETR_{max}}{\alpha},$$

where $rETR_{max}$ is the maximal value of rETR; α is the tangent of the initial slope of the light curve of rETR. The light curve of rETR was fitted using the equation [22]:

$$rETR = rETR_{max}\left(1 - \exp\left(\frac{\alpha \cdot PAR}{rETR_{max}}\right)\right) \cdot \exp\left(\frac{\beta \cdot PAR}{rETR_{max}}\right),$$

where β is the tangent of the slope of the curve on the declining section.

PUR_{psp}, µmol quanta·m^{-3}·s^{-1}, was calculated as [23]:

$$PUR_{psp}(z) = k_{psp} \cdot PUR(z),$$

where k_{psp} is a coefficient reflecting the contribution of photosynthetic pigments to light absorption by all pigments, PUR is the number of quanta absorbed by all phytoplankton pigments. The k_{psp} was calculated as [23]:

$$k_{psp} = (1 - NPSP) / (1 + NPSP),$$

where NPSP is the weight fraction of photoprotective pigments in the total amount of phytoplankton pigments. The NPSP, g·g^{-1}, was calculated using its dependence on the daily average light intensity in the UML (PAR_{uml}) [24]:

$$NPSP = 0.0202\ (PAR_{uml} - 2.92).$$

PAR_{uml}, µmol·quanta·m^{-2}·s^{-1}, was calculated as [23]:

$$PAR_{uml} = PAR_0 \cdot \frac{1 - \exp\left(-4.6\frac{Z_{uml}}{Z_{eu}}\right)}{4.6\frac{Z_{uml}}{Z_{eu}}},$$

where PAR_0 is the daily PAR incident on the sea surface [25]; Z_{uml} is the depth of the upper mixed layer. Z_{uml} was determined using a temperature gradient [26].

PUR, µmol quanta·m^{-3}·s^{-1}, was calculated as:

$$PUR(z) = \int_{400}^{700} Ed(z, \lambda) \cdot a_{ph}(z, \lambda)d\lambda.$$

Results and discussion

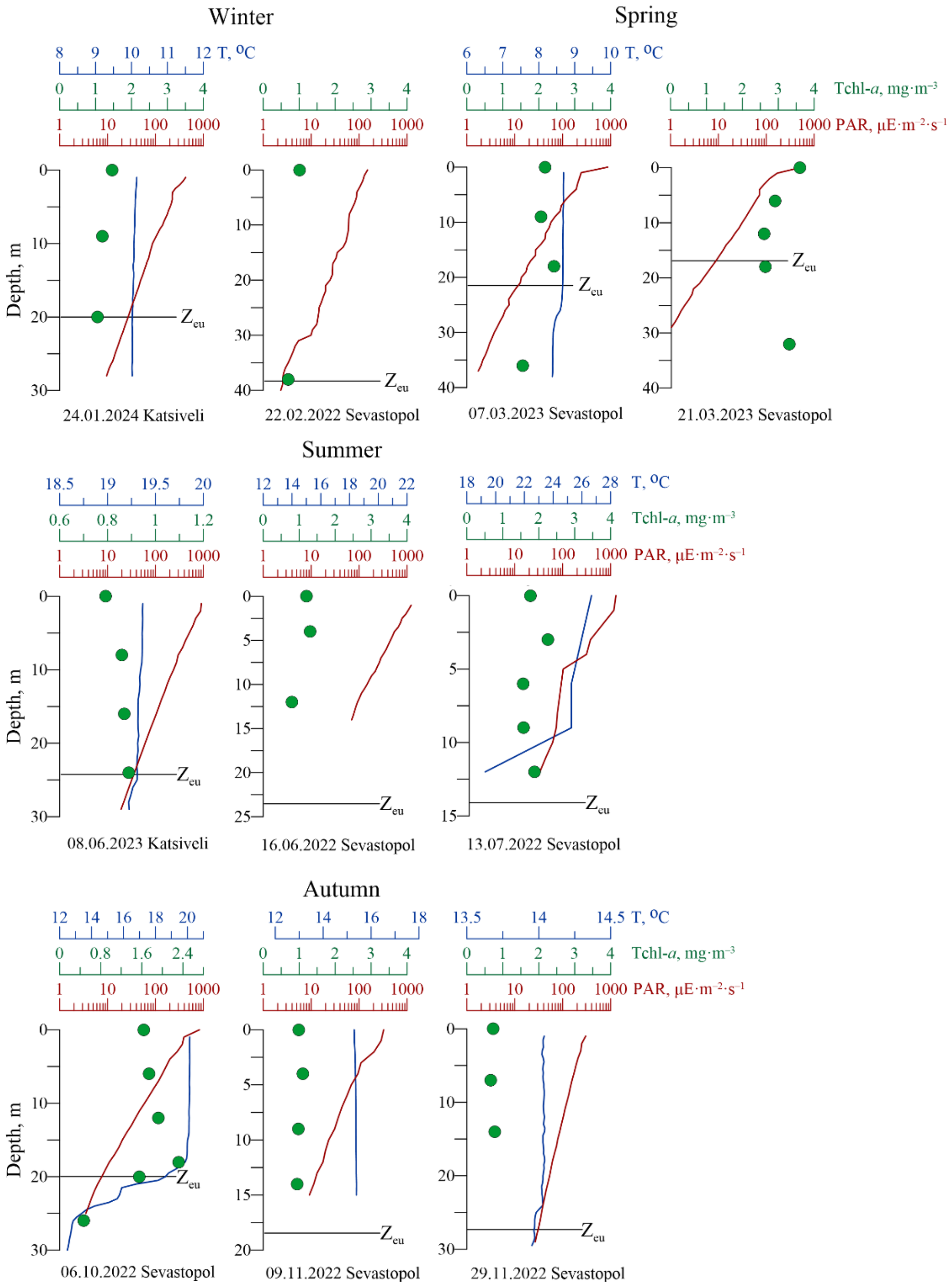
Hydrological parameters

In summer (June, July 2022), the sea surface temperature (SST) varied in the range from 19 to 25°C and the average PAR_0 equaled 59 ± 1 mol quanta·m^{-2}·day^{-1}. At the station located near Sevastopol, the seasonal thermocline was well-developed (vertical temperature gradient > 2°C·m^{-1}). It divides the euphotic layer into two layers: the UML and thermocline with a part of the euphotic zone located below. During stratification, the UML waters are characterized by higher light intensity, temperature and dissolved oxygen concentration in comparison to the waters under the thermocline [27]. The coastal waters in the Katsiveli area were characterized by the absence of a thermocline in early June. The water temperature was 19°C over the entire water column. This is probably due to the high dynamic activity of the coastal waters near the Southern Coast of Crimea [28, 29]. In autumn, SST varied from 15 to 20°C, the average PAR_0 equaled 27 ± 8 mol quanta·m^{-2}·day^{-1}. Water stratification was only observed in early October. In winter, SST varied from 10 to 14°C and the PAR_0 on average was 22 ± 5 mol quanta·m^{-2}·day^{-1}. In spring, SST was 9°C, and the averaged PAR_0 was 32 ± 5 mol quanta·m^{-2}·day^{-1}. During the winter and early spring, the water was well-mixed due to convection and winds at both stations. The water transparency and Z_{eu} at the stations significantly differed by season (Fig. 1).

Spectral downwelling irradiance and euphotic zone

Light is the main factor for photosynthesis. An electron needs the energy of a photon of the visible spectrum to move from the ground state to the excited state [2]. The attenuation of light with depth, as well as the change in the spectral characteristics of light, occurs due to scattering and absorption of light by suspended matter, CDOM and pure water [6] (Fig. 2, *a*). A comparison of the $E_d(\lambda)$ spectrum shape showed (Fig. 2) that the wavelength of the $E_d(\lambda)$ spectrum maximum at a depth of 1% PAR shifted from ~ 495 nm to ~ 561 nm, since the surface total non-water light absorption at 438 nm ($a_{tot\text{-}w}(438) = a_{ph}(438) + a_{NAP}(438) + a_{CDOM}(438)$) increased from 0.204 m^{-1} in February to 0.328 m^{-1} in October (Fig. 3, *a*).

The light attenuation depends on the OAC content in water [6]. A decrease in the OAC content is accompanied by an increase in the water transparency, and light penetrates to greater depths than in waters with lower transparency [6]. The transparency determines the Z_{eu} (Fig. 3, *b*). In summer, at the beginning of June, with $a_{tot\text{-}w}(438)$ equal to 0.138 m^{-1} in the surface layer, Z_{eu} was 24 m. With a double increase in $a_{tot\text{-}w}(438)$ (0.253 m^{-1}) in mid-July, the Z_{eu} decreased by ~ 1.6 times (15 m). In winter, a different pattern was noticed: with relatively identical $a_{tot\text{-}w}(438)$ values in the surface layer, Z_{eu} was in the range from 28 to 38 m (Fig. 3, *b*). As a result, link Z_{eu} vs. $a_{tot\text{-}w}$ was weak in the surface layer, likely due to the inhomogeneous vertical distribution of OAC and to the influence of light scattering (Fig. 3, *b*). Suspended matter both absorbs and scatters light. Therefore, an increase in microalgae biomass and NAP in water (Fig. 3, *c*) can lead to a decrease in Z_{eu} due to an increase in the contribution of backscattering to light attenuation. It is worth noting that the effect of backscattering on transparency is manifested to a greater extent in the presence of mineral particles [30].



F i g . 1 . Vertical profiles of temperature T (blue line), photosynthetically available radiance PAR (red line) and chlorophyll a plus pheopigment concentrations TChl-*a* (green circles) near Sevastopol and Katsiveli

Р и с . 1 . Вертикальные профили температуры *T* (синяя линия), фотосинтетически активной радиации *PAR* (красная линия) и суммарной концентрации хлорофилла *a* и феопигментов *TChl-a* (зеленые кружки) вблизи Севастополя и Кацивели

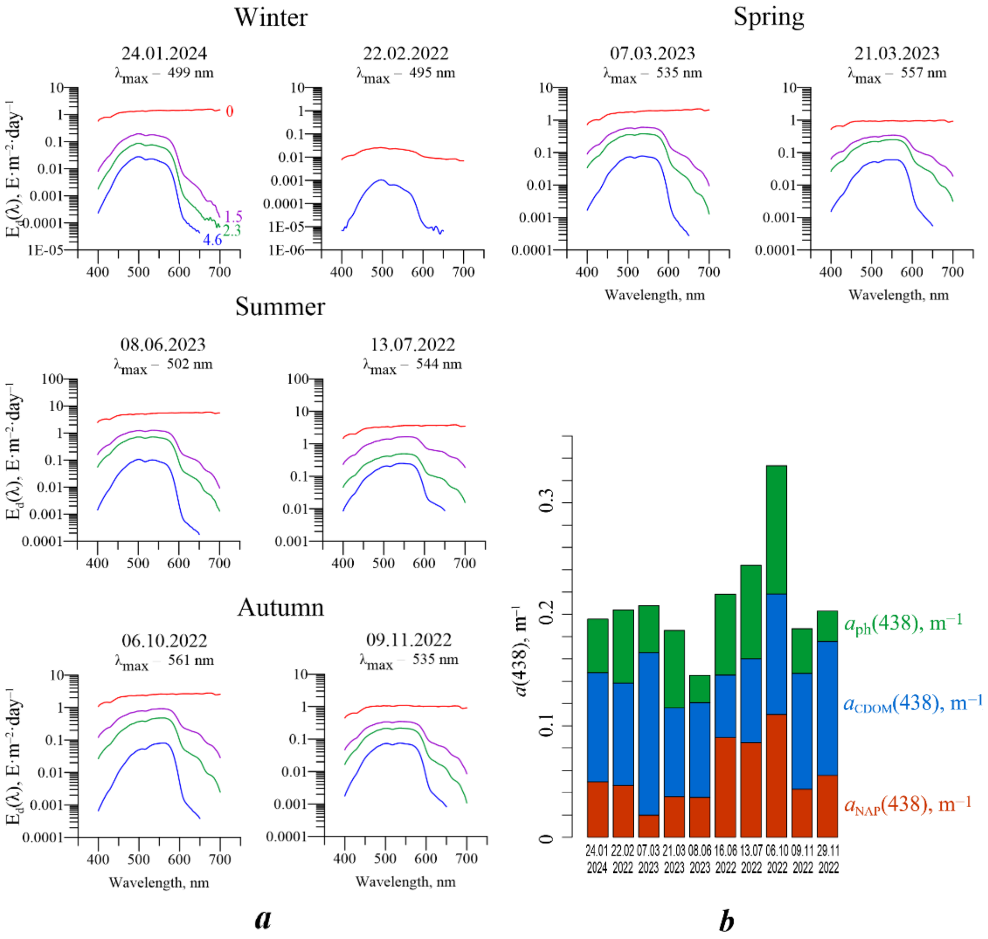


Fig. 2. Spectral downwelling irradiance $E_d(\lambda)$ at optical depths of 0 (red curve), 1.5 (purple curve), 2.3 (green curve), 4.6 (blue curve) (*a*); light absorption at 438 nm by non-algal particles $a_{NAP}(438)$ (red), colored dissolved organic matter $a_{CDOM}(438)$ (blue) and phytoplankton $a_{ph}(438)$ (green) (*b*) at the surface of the Black Sea

Рис. 2. Спектральное излучение, проникающее в толщу воды Ed (λ) на оптической глубине 0 (красная кривая), 1.5 (фиолетовая кривая), 2.3 (зеленая кривая), 4.6 (синяя кривая) (*a*); поглощение света на длине волны 438 нм неживым взвешенным веществом $a_{NAP}(438)$ (красный), окрашенным растворенным органическим веществом $a_{CDOM}(438)$ (синий) и фитопланктоном $a_{ph}(438)$ (зеленый) (*b*) на поверхности Черного моря

Pigment concentration

In summer, in coastal waters near Sevastopol, the vertical TChl-*a* distribution was relatively uniform throughout the studied layer (including the UML and the thermocline layer) (Fig. 4, *a*). On average, TChl-*a* in the UML was 1.5 ± 0.4 mg·m^{-3}, which exceeded the winter values at this station by almost 2 times (0.8 ± 0.2 mg·m^{-3} in the UML). At the station near Katsiveli, the opposite situation was observed: winter TChl-*a* values (1.2 ± 0.2 mg·m^{-3} in the UML) were 2 times higher than summer

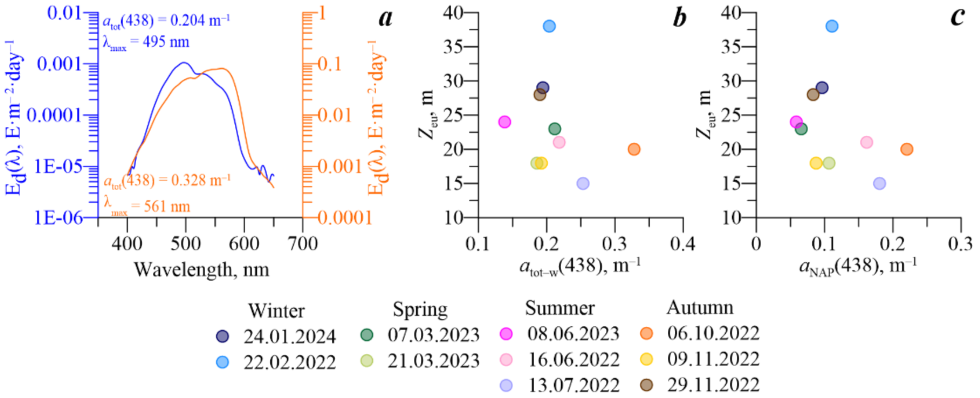


Fig. 3. Spectral downwelling irradiance $E_d(\lambda)$ at the euphotic zone depth Z_{eu} on 22.02.2022 (blue line) and 06.10.2022 (orange line) (*a*); relationship between the total non-water light absorption at 438 nm $a_{tot-w}(438)$ and Z_{eu} (*b*); relationship between the non-algal particles absorption coefficients at 438 nm $a_{NAP}(438)$ and Z_{eu} (*c*)

Рис. 3. Спектральное излучение, проникающее в толщу воды $Ed(\lambda)$ на глубине зоны фотосинтеза Z_{eu} 22.02.2022 и 06.10.2022 (*a*); зависимость между общим поглощением света (без учета поглощения водой) на длине волны 438 нм $a_{tot-w}(438)$ и Z_{eu} (*b*); соотношение между показателями поглощения света неживым взвешенным веществом на длине волны 438 нм $a_{NAP}(438)$ и Z_{eu} (*c*)

ones (0.6 ± 0.1 mg·m^{-3} in the UML). Such an increase of TChl-*a* in winter compared to summer is typical for the deep-water areas of the Black Sea [31, 32]. The maximum TChl-*a* values for the study period were recorded in March (2.3 ± 0.5 mg·m^{-3} in the UML) and at the beginning of October (3.1 ± 0.2 mg·m^{-3} in the UML) (Fig. 4, *a*). The obtained data are consistent with the known patterns of phytoplankton bloom. Spring bloom is often observed in March in the coastal waters of the Black Sea due to the nutrients supply and increase of solar radiance [33, 34]. Autumn phytoplankton bloom is caused by an increase in the nutrients supply [33].

Spectrally weighted chlorophyll a specific absorption coefficient of phytoplankton

Change of $\overline{a}^*_{ph}(z)$ with depth in different seasons is shown (Fig. 4, *b*). The $\overline{a}^*_{ph}(z)$ values in the surface layer (0–1 m) almost tripled from the minimal values (0.009 m^2·mg^{-1}) in early March to the maximal values (0.024 m^2·mg^{-1}) in summer (Fig. 4, *b*). In March, the $\overline{a}^*_{ph}(z)$ increased from 0.009 to 0.015 m^2·mg^{-1}. The maximal values (0.023–0.024 m^2·mg^{-1}) were recorded in summer at both stations near Katsiveli and Sevastopol. In autumn $\overline{a}^*_{ph}(z)$ was lower (0.018 m^2·mg^{-1}) than in summer. In winter the $\overline{a}^*_{ph}(z)$ values differed between stations by a factor of two: 0.021 m^2·mg^{-1} near Sevastopol and 0.012 m^2·mg^{-1} near Katsiveli.

In the surface layer, where $E_d(\lambda)$ spectra have the same shape (Fig. 2), the seasonal dynamics of $\overline{a}^*_{ph}(z)$ depends only on $a^*_{ph}(\lambda)$ (equation 1). The minimal values of the $a^*_{ph}(438)$ were noted in winter near Katsiveli (0.032 m^2·mg^{-1}) and in spring near Sevastopol (0.023 m^2·mg^{-1} and 0.035 m^2·mg^{-1}) (Fig. 5, *b*). The maximal values of $a^*_{ph}(438)$ (0.058 m^2·mg^{-1}) were recorded in summer (June, July) at both stations.

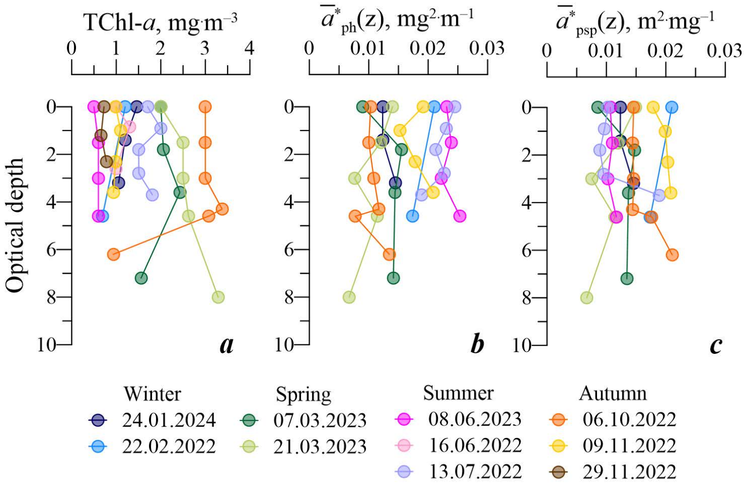


Fig. 4. Vertical distribution of the chlorophyll a plus pheopigment concentrations TChl-*a* (*a*); the spectrally weighted chlorophyll a-specific phytoplankton absorption coefficient $\bar{a}^*_{\mathrm{ph}}(\mathrm{z})$ (*b*); and $\bar{a}^*_{\mathrm{ph}}(\mathrm{z})$ calculated for photosynthetically active pigments $\bar{a}^*_{\mathrm{psp}}(\mathrm{z})$ (*c*) in the Black Sea coastal waters

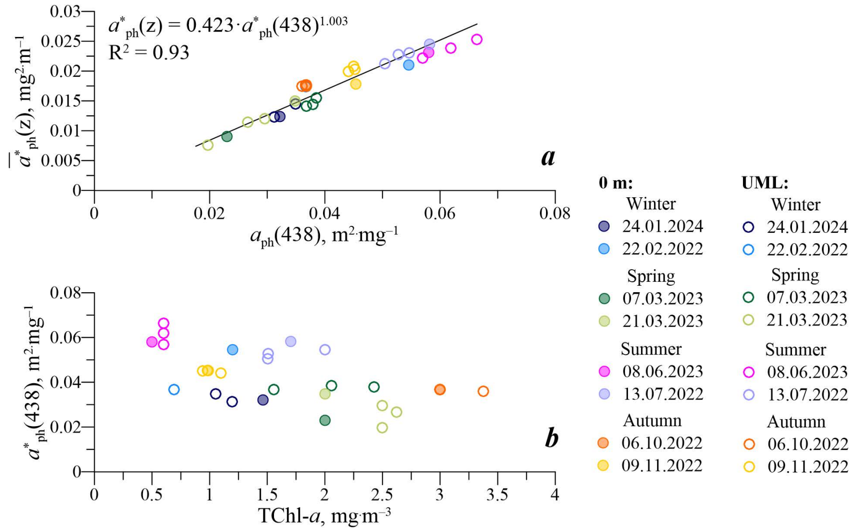
Рис. 4. Вертикальное распределение суммарной концентрации хлорофилла *а* и феопигментов *TChl-a* (*a*); удельная (нормированная на *TChl-a*) эффективность поглощения света всеми пигментами фитопланктона $\bar{a}^*_{\mathrm{ph}}(z)$ (*b*); и $\bar{a}^*_{\mathrm{ph}}(z)$, рассчитанная для фотосинтетических пигментов $\bar{a}^*_{\mathrm{psp}}(z)$ (*c*) в прибрежных водах Черного моря

High winter values of $a^*_{\mathrm{ph}}(438)$ in the coastal waters of Sevastopol (0.055 m^2·mg^{-1} in February) are most likely associated with the predominance of small-celled algae species. In autumn, intermediate values of $a^*_{\mathrm{ph}}(438)$ were observed: 0.037 m^2·mg^{-1} in October and 0.045 m^2·mg^{-1} in November.

The changes in $a^*_{\mathrm{ph}}(\lambda)$ are caused by the “pigment package effect”, which is associated with intracellular pigment concentration and phytoplankton cell size composition [35]. The intracellular pigment concentration changes as a result of microalgal adaptation to environmental factors (PAR, the nutrient availability, temperature) [36], which vary throughout the year. The PAR$_0$ varies from 22.1 ± 4.6 E·m^{-2}·day^{-1} in winter to 59.4 ± 0.9 E·m^{-2}·day^{-1} in summer [25]. As a result of adaptive changes in the intracellular composition and concentration of pigments, $a^*_{\mathrm{ph}}(\lambda)$ differed seasonally [37].

Seasonal changes in $a^*_{\mathrm{ph}}(438)$ (2.5 times) led to almost the same (2.7 times) changes in $\bar{a}^*_{\mathrm{ph}}(\mathrm{z})$. A positive correlation was obtained between $\bar{a}^*_{\mathrm{ph}}(\mathrm{z})$ and $a^*_{\mathrm{ph}}(438)$ (Fig. 5, *a*).

In addition to photosynthetically active pigments, phytoplankton cells also contain photoprotective pigments that absorb excess solar radiation to protect the RC cells from photodestruction [38]. This applies to a greater extent to microalgae living in the sea surface layer. In spring, the daily PAR incident at the sea surface averaged 32.4 ± 5.5 mol quanta·m^{-2}·day^{-1}, while NPSP averaged 0.014 ± 0.010 g·g^{-1}. In summer, when the PAR values were maximal – on average 59.4 ± 0.9 mol quanta·m^{-2}·day^{-1},



F i g . 5 . Dependence of the spectrally weighted chlorophyll a specific absorption coefficient by phytoplankton $\overline{a}^*_{ph}(z)$ on the chlorophyll a specific light absorption coefficient of phytoplankton at 438 nm $a^*_{ph}(438)$ (*a*); dependence of $a^*_{ph}(438)$ on chlorophyll a plus phaeopigment concentrations TChl-*a*(z) (*b*)

Р и с . 5 . Зависимость удельной (нормированная на *TChl-a*) эффективности поглощения света всеми пигментами фитопланктона $\overline{a}^*_{ph}(z)$ от удельного (нормированного на *TChl-a*) показателя поглощения света пигментами фитопланктона на длине волны 438 нм $a^*_{ph}(438)$ (*a*); зависимость $a^*_{ph}(438)$ от суммарной концентрации хлорофилла *a* и феопигментов *TChl-a*(*z*) (*b*)

NPSP increased to 0.39 ± 0.28 g·g^{-1} as a result of adaptation. In autumn, PAR decreased to 27.0 ± 7.9 mol quanta·m^{-2}·day^{-1}, which led to a decrease in NPSP to 0.096 g·g^{-1}. The lowest level of PAR$_0$ was observed in winter – 22.1 ± 4.6 mol quanta·m^{-2}·day^{-1}, for these conditions no photoprotective pigments were obtained.

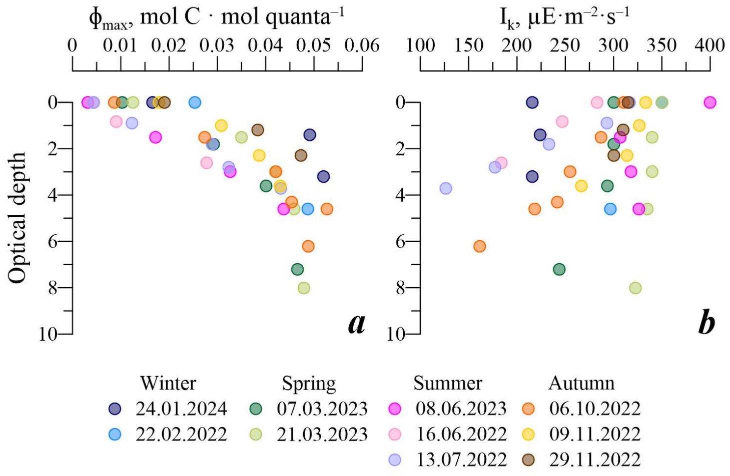
Only light quanta absorbed by photosynthetically active pigments are used during photosynthesis [2]. The annual dynamics of NPSP (0–0.39) led to varying degrees of change in $\overline{a}^*_{psp}(z)$ relative to $\overline{a}^*_{ph}(z)$. In summer, near Katsiveli and Sevastopol, the values of $\overline{a}^*_{psp}(z)$ in the sea surface layer were 2.2 and 2.4 times less than the value of $\overline{a}^*_{ph}(z)$, correspondingly (Fig. 4, *c*). The value of $\overline{a}^*_{psp}(z)$ in early October in the sea surface layer was 1.2 times less than $\overline{a}^*_{ph}(z)$. Winter and spring $\overline{a}^*_{psp}(z)$ values were almost equal to $a^*_{ph}(0)$ due to low (almost zero) content of photoprotective pigments. As a result, the values of $\overline{a}^*_{psp}(z)$ changed 2.3 times from 0.009 m²·mg^{-1} in early March to 0.021 m²·mg^{-1} in late February (Fig. 4, *c*). Thus, the variability range of the $\overline{a}^*_{psp}(z)$ values was narrowed compared to that of $\overline{a}^*_{ph}(z)$.

Quantum yield of photosynthesis

Values of ϕ depend on the environmental conditions. Theoretically, ϕ_{max} is ~ 0.125 mol C·mol quanta^{-1} [39], whereas in practice, ϕ_{max} is lower [40], which is associated with the inhibitory effect of high PAR and nutrients availability [41].

In the sea surface layer, where the PAR values are maximal, the lowest values of ϕ_{max} were noted: from 0.003 mol C·mol quanta^{-1} in early June to 0.025 mol C·mol quanta^{-1} in late February. The ϕ_{max} increased with depth due to decreasing PAR. As a result, the ϕ_{max} near the bottom of the euphotic zone increased from 0.044 mol C·mol quanta^{-1} in early June to 0.053 mol C·mol quanta^{-1} in early October (Fig. 6, *a*).

Seasonal variability of I_k values is associated with the acclimation of phytoplankton to changes in the light level in the sea [2]. In summer, in coastal waters near Sevastopol, I_k values varied from 280 µmol quanta·m^{-2}·s^{-1} in June to 320 µmol quanta·m^{-2}·s^{-1} in July in the surface layer. The I_k decreased with depth by 1.5 and 2.5 times in June and July, respectively (Fig. 6, *b*). The average I_k value in the UML was 270 ± 30 µmol quanta·m^{-2}·s^{-1}. The I_k values were higher in autumn (on average 290 ± 30 µmol quanta m^{-2}·s^{-1} in the UML) and varied in the sea surface layer from 310 µmol quanta·m^{-2}·s^{-1} in October to 330 µmol quanta·m^{-2}·s^{-1} in November. At the beginning of October, a more pronounced decrease in I_k with depth was noted than in November (Fig. 6, *b*). High winter values were noted in the UML of the Sevastopol coastal waters (on average 310 ± 25 µmol quanta m^{-2} s^{-1}). In the sea surface layer by the end of November, I_k was equal to 315 µmol quanta·m^{-2}·s^{-1}, and at the end of February it was 350 µmol quanta·m^{-2}·s^{-1}. A more uniform vertical distribution of this parameter was observed in winter. The I_k values at the beginning of spring were similar to those in winter (315 ± 30 µmol quanta·m^{-2}·s^{-1} in the UML). In the surface layer, the I_k was 300 µmol quanta·m^{-2}·s^{-1} in early March and increased up to 350 µmol quanta·m^{-2}·s^{-1} in late March.



F i g. 6. Vertical distribution of the maximum quantum yield of photosynthesis ϕ_{max} (*a*) and the light intensity saturating the photosynthesis I_k (*b*) in the Black Sea coastal waters

Р и с. 6. Вертикальное распределение максимального квантового выхода фотосинтеза ϕ_{max} (*a*) и интенсивности света, насыщающего фотосинтез I_k (*b*), в прибрежных водах Черного моря

In summer, the I_k values in the coastal waters of Katsiveli averaged 320 ± ± 15 μmol quanta·m^{-2}·s^{-1} in the UML (340 μmol quanta·m^{-2}·s^{-1} at 0 m), which exceeded I_k values near Sevastopol. The vertical distribution of the I_k was uniform near Katsiveli, which is due to the absence of thermal vertical stratification. In winter, the lowest I_k values were recorded in the coastal waters of Katsiveli over the entire study period: 220 ± 5 μmol quanta·m^{-2}·s^{-1} in the UML. In summer and early October, a decrease in the I_k with depth by ~ 2 times was noted in the coastal waters of Sevastopol due to temperature stratification of the waters. During the rest of the study period, when temperature vertical stratification was not observed, the depth-dependent variability of the I_k values was insignificant. The variability of the I_k values among seasons and with depth noted in the study is a result of phytoplankton adaptation to light conditions and depends on the so-called light history of phytoplankton [42]. Within the UML, phytoplankton is in constant vertical movement, and therefore, the photosynthetic parameters of phytoplankton are determined by the average light intensity for this layer [23, 43]. Temperature (density) gradient is a barrier to the vertical mixing of water. As a result, phytoplankton in the layers (above and below the thermocline) exist under different environmental factors, such as light intensity, nutrients and temperature. This determines the pronounced variation in the phytoplankton photosynthetic parameters with depth [44].

One of the key parameters for estimating PP is ϕ [2]. It expresses the efficiency of phytoplankton carbon fixation per quantum of light absorbed by the photosynthetic apparatus of the cell [45]. The ϕ varied with depth and by season. Light conditions determine the content of photoprotective pigments, which reduce the ϕ values [2, 17]. Due to the high PAR values in the sea surface layer, the ϕ values were minimal: at the station near Katsiveli in summer, the ϕ was equal to 0.005 mol C·mol quanta^{-1}, whereas at the station near Sevastopol, the average summer values were lower and equaled 0.003 ± 0.003 mol C·mol quanta^{-1}. Within the UML, ϕ increased by ~ 6 times at both stations. Autumn ϕ values reached 0.005 mol C·mol quanta^{-1}, increasing with depth in the UML by ~ 8 times. In winter, when the PAR values were minimal, the ϕ was maximal: at the station near Katsiveli, the ϕ in the sea surface layer was equal to 0.007 mol C·mol quanta^{-1} (increasing in the UML by ~ 7 times), while at the station near Sevastopol it was 0.010 mol C·mol quanta^{-1} (increasing in the UML by ~ 5 times) and 0.012 mol C·mol quanta^{-1} (increasing in the UML by ~ 5 times) on 22.02.2022 and 29.11.2022, respectively. With the increase of PAR in spring, the ϕ values began to decrease and amounted to 0.007 ± 0.001 mol C·mol quanta^{-1} in the sea surface layer, increasing within the UML by ~ 6 times (Fig. 7, *a*). It was found that in winter in the sea surface layer near Sevastopol, the ϕ values were ~3 times higher than in summer. Such significant seasonal dynamics of the ϕ is a consequence of the phytoplankton acclimation to changing light conditions.

A comparison of the ϕ values with PUR^{*}_{psp} showed a relationship between these parameters, which was described by a power function (Fig. 7, *b*).

Primary production

For the entire study period, the same types of vertical PP profiles were observed with a maximum in the sea surface layer. The profiles varied significantly throughout the year: from 11 mgC·m^{-3}·day^{-1} in early November to 84 mgC·m^{-3}·day^{-1} in early

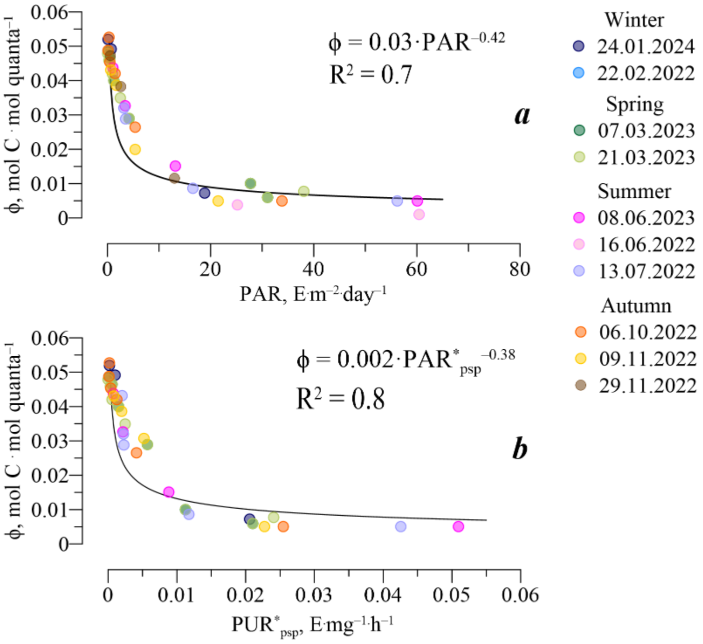


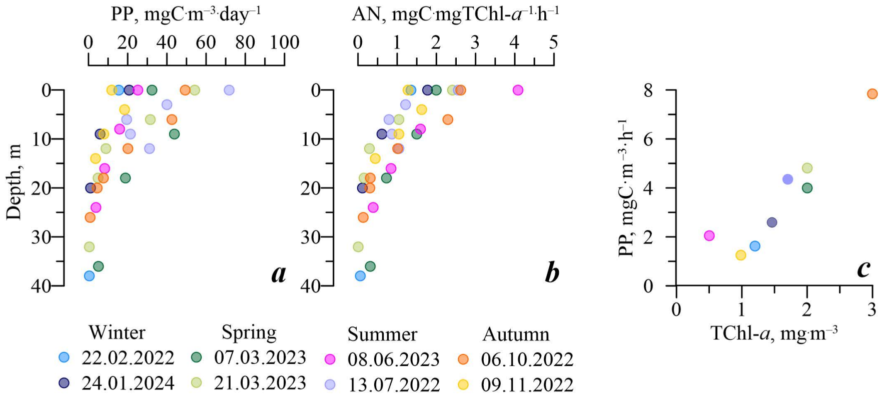
Fig. 7. Dependence of the quantum yield of photosynthesis ϕ on PAR in the UML (*a*) and on the amount of quanta absorbed by photosynthetically active pigments, per chlorophyll a unit PUR^*_{psp} in the UML (*b*)

Рис. 7. Зависимость квантового выхода фотосинтеза ϕ от *PAR* в верхнем перемешанном слое (*UML*) (*а*) и от количества квантов, поглощенных фотосинтетически активными пигментами, в расчете на единицу хлорофилла *а* PUR^*_{psp} в *UML* (*b*)

October (Fig. 8, *a*). The winter PP values at the stations near Katsiveli and Sevastopol equaled 21 $\text{mgC·m}^{-3}\text{·day}^{-1}$ and 16 $\text{mgC·m}^{-3}\text{·day}^{-1}$, respectively. During March, the PP increased from 43 $\text{mgC·m}^{-3}\text{·day}^{-1}$ to 58 $\text{mgC·m}^{-3}\text{·day}^{-1}$.The summer PP values were higher in the coastal waters of Sevastopol (72 $\text{mgC·m}^{-3}\text{·day}^{-1}$) than in those of Katsiveli (34 $\text{mgC·m}^{-3}\text{·day}^{-1}$).

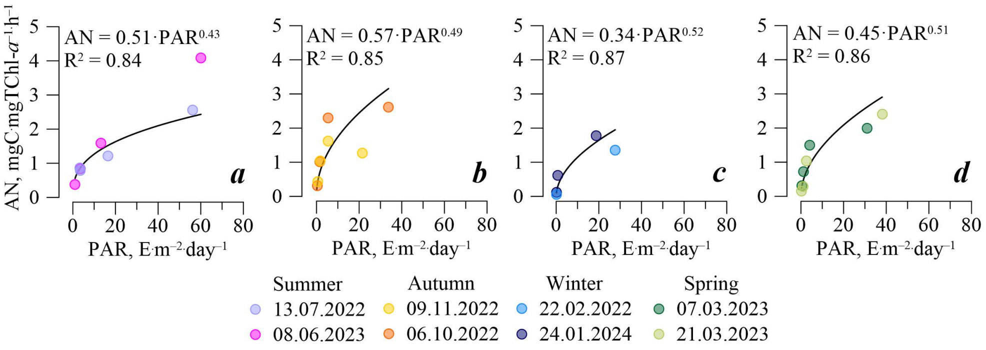
The maximal photosynthesis rate in the sea surface layer was observed in October (7.8 $\text{mgC·m}^{-3}\text{·h}^{-1}$), and relatively high values were also observed in March (4.0 $\text{mgC·m}^{-3}\text{·h}^{-1}$ and 4.5 $\text{mgC·m}^{-3}\text{·h}^{-1}$) and July (4.4 $\text{mgC·m}^{-3}\text{·h}^{-1}$) (Fig. 8, *c*). The high photosynthesis rate corresponded to the maximum TChl-*a* values and minimum ϕ values. In summer, the TChl-*a* values varied between stations by 3.4 times, while the PP values differed by 2 times. In November, a decrease in the TChl-*a* values also led to a 6-fold decrease in the PP values.

The values of assimilation number (AN) in the sea surface layer increased from early November (1.3 $\text{mgC·mgTChl-}a^{-1}\text{·h}^{-1}$) to July (2.6 $\text{mgC·mgTChl-}a^{-1}\text{·h}^{-1}$) at the station near Sevastopol and from winter (1.8 $\text{mgC·mgTChl-}a^{-1}\text{·h}^{-1}$) to summer



F i g . 8 . Vertical distribution of the PP (*a*) and the assimilation number AN (*b*); dependence of the PP on chlorophyll a plus phaeopigment concentrations TChl-*a* at 0 m (*c*)

Р и с . 8 . Вертикальное распределение *PP* (*a*) и ассимиляционного числа (*AN*) (*b*); зависимость *PP* от суммарной концентрации хлорофилла *a* и феопигментов *TChl-a* в поверхностном слое при 0 м (*c*)



F i g . 9 . Dependence of the AN on the PAR in the UML of the Black Sea coastal waters in summer (*a*), autumn (*b*), winter (*c*) and in spring (*d*)

Р и с . 9 . Зависимость *AN* от *PAR* в *UML* прибрежных вод Черного моря летом (*a*), осенью (*b*), зимой (*c*) и весной (*d*)

(4.0 mgC·mgTChl-a^{-1}·h^{-1}) at the station near Katsiveli (Fig. 8, *b*). The analysis showed that the AN varied among seasons, which was more pronounced in the sea surface layer (Fig. 8, *b*). The AN depends mainly on light intensity and to a lesser extent on other abiotic factors such as temperature and nutrients availability [42]. A comparison of the AN with the light intensity allowed us to reveal dependencies for individual seasons (Fig. 9):

$$\text{for summer, AN} = 0.51\ \text{PAR}^{0.43},\ n = 9,\ r^{r2} = 0.83; \tag{3}$$

$$\text{for autumn, AN} = 0.57\ \text{PAR}^{0.49},\ n = 10,\ r^{r2} = 0.85; \tag{4}$$

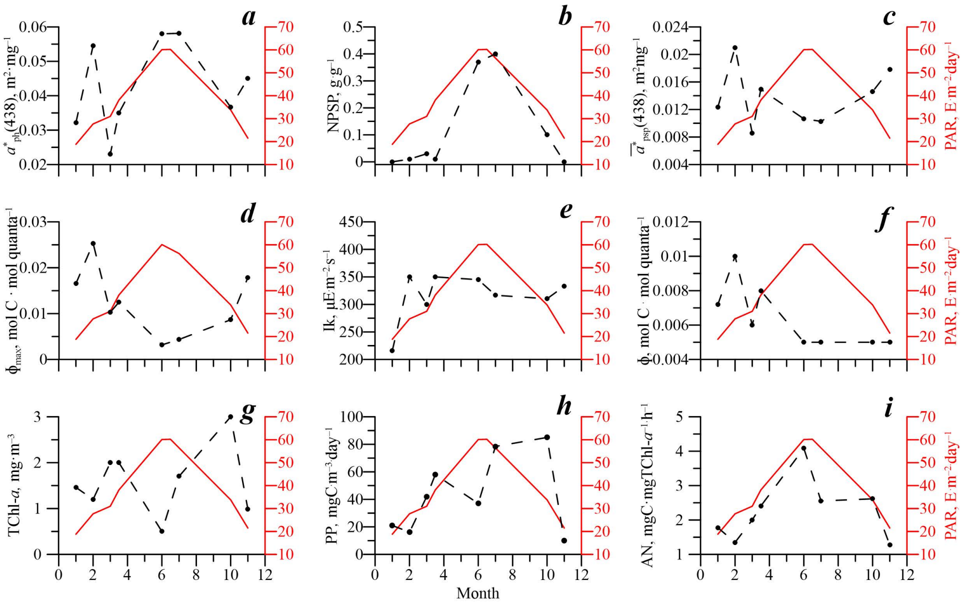
$$\text{for winter, AN} = 0.34\ \text{PAR}^{0.52},\ n = 5,\ r^{r2} = 0.87; \tag{5}$$

$$\text{for spring, AN} = 0.45\ \text{PAR}^{0.51},\ n = 8,\ r^{r2} = 0.86. \tag{6}$$

The revealed dependencies of the AN on the PAR (equations 3–6) reflect seasonal differences in the AN under the same light conditions (Fig. 9).

Annual cycle

In the most productive surface layer of the sea (Fig. 8, *a*), ϕ_{max} varied ~ 7-fold during the year, which exceeded the degree of variability of other photosynthetic parameters. An analysis of the seasonal dynamics showed that ϕ_{max} (Fig. 10, *d*) was related inversely to PAR_0, whereas I_k was directly related to PAR_0 and showed



F i g . 1 0 . Annual cycle of the studied parameters. The red line is photosynthetically available radiance PAR at surface water. The dashed lines denote chlorophyll a-specific light absorption coefficient of phytoplankton $a^*_{ph}(438)$ (*a*); intracellular content of photoprotective pigments and their share NPSP in the total amount of phytoplankton pigments (*b*); the spectrally weighted chlorophyll a specific absorption coefficient calculated for photosynthetically active pigments $\overline{a}^*_{psp}(z)$ (*c*); maximum quantum yield of photosynthesis ϕ_{max} (*d*); the light intensity saturating the photosynthesis I_k (*e*); quantum yield of photosynthesis ϕ (*f*); chlorophyll a plus phaeopigment concentrations TChl-*a* (*g*); primary production PP (*h*); assimilation number AN (*i*)

Р и с . 1 0 . Годовой цикл исследуемых параметров. Красная линия – фотосинтетически активная радиация *PAR* в поверхностном слое вод. Штриховыми линиями обозначены: удельный (нормированный на *TChl-a*) показатель поглощения света пигментами фитопланктона $a^*_{ph}(438)$) (*a*); внутриклеточное содержание фотозащитных пигментов и их доля *NPSP* в общем количестве пигментов фитопланктона (*b*); удельная (нормированная на *TChl-a*) эффективность поглощения света фотосинтетическими пигментами фитопланктона $\overline{a}^*_{psp}(z)$ (*c*); максимальный квантовый выход фотосинтеза ϕ_{max} (*d*); интенсивность света, насыщающего фотосинтез I_k (*e*); квантовый выход фотосинтеза ϕ (*f*); суммарная концентрация хлорофилла *a* и феопигментов *TChl-a* (*g*); первичная продукция *PP* (*h*); ассимиляционное число *AN* (*i*) a twofold seasonal variation (Fig. 10, *e*). Since the ϕ depends on the ϕ_{max} and I_k (equation 2), and since ϕ_{max} was the most variable seasonally, the ϕ was directly related to PAR, yet to a lesser extent than ϕ_{max} (Fig. 10, *f*). The intra-annual variability of $a^*_{ph}(438)$ in the surface layer spanned a factor of three and was directly related to PAR_0, except the high a^*_{ph} values in February (Fig. 10, *a*), which may be associated with small-celled species of phytoplankton [35], in particular coccolithophores. The abundance of coccolithophores in the phytoplankton increased in the last decade in the Black Sea [46]. However, the seasonal dynamics of $\overline{a}^*_{psp}$ (Fig. 10, *c*), which determines the rate of photosynthesis, differed from a^*_{ph}. This was due to the proportion of photoprotective pigments (Fig. 10, *b*), which depended directly on the light intensity in the UML [23]. In the annual cycle of $\overline{a}^*_{psp}$, a peak was observed in February. The peak is associated with the dominance of small-cell phytoplankton species, and the decline in March is due to the bloom of large diatoms. However, in general, a U-shaped type of cycle was observed with relatively lower values in summer, with their increase in other seasons. The annual AN cycle (Fig. 10, *i*) differs in type from ϕ and $\overline{a}^*_{psp}$. This is due to the fact that AN also depends on the light intensity. Consequently, the light factor has a predominant influence on the intra-annual dynamics of the AN. The TChl-*a* in the sea surface layer varied 6 times during the year. The annual cycle of TChl-*a* has two peaks (Fig. 10, *g*): spring and autumn, which is associated with the bloom of phytoplankton in these seasons. The intra-annual variability of PP was 8-fold and was similar to the annual cycle of TChl-*a* (Fig. 10, *i*).

Conclusions

We analysed seasonal dynamics of photosynthetic characteristics of phytoplankton in the BS coastal waters near the Crimean Peninsula. The seasonal variability of PP was caused by acclimation of phytoplankton to environmental conditions. The PAR incident on the sea surface increased approximately threefold from winter (22 ± 5 mol quanta·m^{-2}·day^{-1}) to summer (59 ± 1 mol quanta·m^{-2}·day^{-1}). This caused photoadaptive transformations in the pigment complex of microalgae, namely changes in the concentration of chlorophyll a and accessory pigments, including photoprotective pigments, which affect the capacity of phytoplankton to absorb light in the sea and use it during photosynthesis. The seasonal variability of the TChl-*a* occurred. High values of TChl-*a* in the sea were observed in early October and in March, which may be associated with phytoplankton bloom, while low values were observed in summer (twice as little). The $\overline{a}^*_{ph}(z)$ varied significantly among seasons: from minimal values in spring (on average 0.012 m^2·mg^{-1}) to maximal values in summer (on average 0.024 m^2·mg^{-1}) with intermediate values in autumn and winter (on average 0.017 m^2·mg^{-1}). The variability of the $\overline{a}^*_{ph}(z)$ is mainly due to the intra-annual variability of the a^*_{ph}. The $\overline{a}^*_{psp}$ was minimal in summer (on average 0.010 m^2·mg^{-1}) due to the highest relative content of photoprotective pigments (on average 0.35 g·g^{-1}). The ϕ in the surface layer varied among seasons by ~ 3 times from the lowest values in summer (0.003 mol C·mol quanta^{-1}) to the highest values (0.010 mol C·mol quanta^{-1}) in winter, which is associated with the annual dynamics of sea surface insolation. The variability of ϕ within the euphotic zone was greatest (up to 8.7 times) compared to other parameters. PP values varied widely in the sea surface layer, decreasing with depth. The AN changed during the year by ~ 2 times from 1.3 to 4 mgC·mgTChl-a^{-1}·h^{-1}, which is associated with its dependence on PAR.

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