ISSN 1573-160X, *PHYSICAL OCEANOGRAPHY*, Vol. 32, Iss. 3, pp. 347-360 (2025)
Original Russian Text © I. V. Kovalyova, 2025,
published in *Morskoy Gidrofizicheskiy Zhurnal*, 2025, Vol. 41, Iss. 3, pp. 331–345

Original article

Parameterization of the Dependence of Integral Phytoplankton Biomass on Chlorophyll Concentration at the Black Sea Surface Based on Expeditionary Research Data

I. V. Kovalyova

A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
✉ *ilonavk@ibss-ras.ru*

Abstract
Purpose. The purpose of the study is to present an algorithm for calculating the integral phytoplankton biomass in the Black Sea euphotic layer using expeditionary data, and to perform a comparative analysis of the variability of the studied characteristics obtained by means of calculations in two ways: using direct measurements of chlorophyll concentration along the horizons, and based on the parameterization results.
Methods and Results. The algorithm for calculating the integral biomass of phytoplankton is presented. Data from Crimean coastal waters at the depths of 20–1500 m, collected during R/V *Professor Vodyanitsky* cruises for different seasons of 2018–2022, were used in this study. The estimates resulted from parameterization and those obtained from calculations based on direct measurements of the individual input parameters at different depths are compared. The results of parameterization statistical analysis show that the determination coefficients varied in the range 0.70–0.74. In the photosynthesis zone, the monthly averages of integral phytoplankton biomass (calculated from the expeditionary data) in June and October constitute 768 ± 283 and 2277 ± 726 mg C/m^2, respectively. In the upper mixed layer, in June they are 556 ± 270 mg C/m^2, and in October – 2023 ± 725 mg C/m^2. The parameterization-derived monthly averages for the whole water area under study differ from the ones calculated using the direct measurements of input parameters at different depths by 0.9–4%. The chlorophyll a concentration profiles for individual months in 2018–2022 are considered and mathematically described using the function obtained in earlier studies. In autumn, maximum values of chlorophyll a are observed mainly in the upper mixed layer. In summer, they occur at the lower boundary of the euphotic zone, where up to ~ 0.1% of light reaching the sea surface penetrates.
Conclusions. The above parameterization of integral phytoplankton biomass is applicable to all the seasons, easy to use and agrees well with the results of calculations based on direct measurements of chlorophyll concentration at different depths. In the future, the calculation algorithm will be refined to facilitate computations based on satellite data.

Keywords: integral biomass, phytoplankton, Black Sea, calculation algorithm, chlorophyll a concentration profiles

Acknowledgements: The study was funded by the Russian Science Foundation and the Government of Sevastopol (Grant No. 24-27-20014, “Transformation of the structure and functional characteristics of the Black Sea phytoplankton off the Crimea coast in modern environmental conditions. Fundamental role and applied importance”, https://rscf.ru/project/24-27-20014/). The work was carried out at the Center for Collective Use of R/V *Professor Vodyanitsky*. The author expresses gratitude to N. V. Minina, Leading Engineer, for collecting data during the cruises.

For citation: Kovalyova, I.V., 2025. Parameterization of the Dependence of Integral Phytoplankton Biomass on Chlorophyll Concentration at the Black Sea Surface Based on Expeditionary Research Data. *Physical Oceanography*, 32(3), pp. 347-360.

Introduction

Phytoplankton form the primary link in the trophic chain of aquatic ecosystems. One of the most important indicators of this is biomass. Changes in phytoplankton biomass affect the development of all subsequent trophic levels. Many studies have been carried out for many years on changes in phytoplankton biomass over time and its spatial distribution in the sea [1–12]. Microalgae biomass is usually determined by direct measurement of cell volume, followed by recalculation in various dimensions [1, 3, 4, 13, 14]. In addition to these direct methods, models are being developed that allow the ratio of chlorophyll to organic carbon and phytoplankton biomass to be estimated [9, 15–17]. Models for calculating phytoplankton biomass using a minimum number of easily accessible input parameters can significantly simplify the task, especially when analyzing spatial and temporal changes. Models for calculating phytoplankton parameters are also necessary for studies that use satellite data. Estimates of integral phytoplankton characteristics in the photosynthetic zone are of particular interest. For example, simple, user-friendly models for calculating integral primary production have been developed for the Black Sea [1] [18, 19]. However, similar calculation algorithms for integral phytoplankton biomass with easily accessible input parameters have been presented poorly in the literature. Although model data are inferior in accuracy to direct measurements, direct estimation methods are labor-intensive. Calculating the integral phytoplankton biomass in the euphotic zone and the upper mixed layer (UML) allows for the prompt and extensive analysis of water ecosystems and their use in calculations with satellite observation data.

The study aims to present an algorithm for calculating integral phytoplankton biomass in the euphotic layer of the Black Sea using expeditionary data, and to conduct a comparative analysis of the variability of the studied characteristics obtained through two calculation methods: direct chlorophyll concentration measurements along the horizons and parameterization results.

Materials and methods

The measurements used in this paper were carried out at the Collective Use Data Center of R/V *Professor Vodyanitsky* during cruises No. 122 (June 7 – July 2, 2022) and No. 124 (October 3–20, 2022) in the Black Sea off the southern and southeastern coasts of Crimea. Sampling was performed at station depths of 32–1500 m, with samples collected at 10–20 m below the surface, near the thermocline at deep-water stations, and in the bottom layer at stations with depths of ≤ 100 m.

Surface light intensity was measured daily between 08:00 to 20:00 using a LI-1500 illuminance recorder with a LI-190R quantum sensor (LI-COR, USA). Daily integral irradiance was then calculated.

[1] Demidov, A.B., 2001. [*Seasonal Variations in Primary Production and Chlorophyll a in Open Areas of the Black Sea*]. Thesis Cand. Biol. Sci. Moscow: Moscow State University, 188 p. (in Russian).

The UML was determined using data from an IDRONAUT OCEAN SEVEN 320 Plus M probe, based on a water density increase of 0.07 relative to the surface [20].

The relative water transparency was assessed using a Secchi disk during daylight hours. The euphotic zone depth ($Z_{eu} = 3Z_s$) [2], where up to 1% of the light falling on the surface penetrates, was determined based on the Secchi disk visibility depth (Z_s) data. The light diffusion attenuation indicator k_d (m^{-1}) was estimated using the formula obtained from the data [3, 4]:

$$k_d = 4.6/Z_{eu}\ (r^2 = 0.96).$$

The methodology for determining the concentration of chlorophyll a (hereinafter referred to as ‘chlorophyll a’ throughout this paper), the measurement data collected during the voyages and the areas of water studied are described in [21].

To analyze the chlorophyll concentration profiles, data obtained on R/V *Professor Vodyanitsky* during cruises No. 105, 106, 108, 110, 122 and 124 in November–December, April, July–August, October, June and October 2018–2022 are used. Concentration measurements were usually taken at 10 m intervals down to a depth of 40–50 m and, in some cases, deeper.

Statistical data processing was carried out using Excel, SigmaPlot, Grapher, and OriginLab software.

Results

In this study we modified the previously developed algorithm for calculating phytoplankton biomass in the surface layer of the Black Sea [15], which was adjusted in [22], to estimate integral indicators. Input parameters were calculated for each horizon and then the biomass was integrated by depth.

The following equation to calculate phytoplankton biomass B_z (mg C/m^3) at z depth (m) was used:

$$B_z = \mathrm{Chl}_z/\mathrm{Chl{:}C}_z, \tag{1}$$

where Chl_z (mg/m^3) is the chlorophyll concentration at z depth; $\mathrm{Chl{:}C}_z$ is the ratio of chlorophyll concentration to organic carbon, calculated at each horizon:

$$\mathrm{Chl{:}C}_z = 0.0072(E_z a_{ph\,z})^{-0.395}\ (r^2 = 0.78), \tag{2}$$

$$a_{ph\,z} = 0.017\ \mathrm{Chl}_z^{\ -0.29}. \tag{3}$$

[2] Man’kovskiy, V.I., Soloviev, M.V. and Man’kovskaya, E.V., 2009. [*Hydrooptical Properties of the Black Sea. Handbook*]. Sevastopol: MHI NAS of Ukraine, 92 p. (in Russian).

[3] Vedernikov, V.I., 1989. [Primary Production and Chlorophyll in the Black Sea in Summer-Autumn Period]. In: M. E. Vinogradov and M. V. Flint, eds., 1989. *Structure and Production Characteristics of Plankton Communities of the Black Sea*. Moscow: Nauka, pp. 65-83 (in Russian).

[4] Voznyak, B., Kopter, R. and Vedernikov, V.I., 1986. [Input of Photosynthetically Active Radiation into the Euphotic Zone of the Black Sea in April–May 1984]. In: IO AN SSSR, 1986. *Study of the Ecosystem of the Pelagic Zone of the Black Sea*. Moscow: IO AN SSSR-KOTS “World Ocean”, pp. 198-221 (in Russian).

The equation parameters for Chl:C were obtained from algae cultures in laboratory experiments under different illumination conditions, as described in [15]. To estimate Chl:C at different horizons, the illumination at each depth was determined using the following equation:

$$E_z = 0.94E_0\exp(-k_d z), \qquad (4)$$

where E_z, E_0 (mol quanta/m^2·day) represents the intensity of photosynthetically active radiation (PAR) at depth z and at the sea surface, respectively; the coefficient 0.94 accounts for 6% surface light reflection [5]; $a_{ph\,z}$ (m^2/mg Chl) is the indicator of light absorption by algae pigments, normalized to the chlorophyll concentration.

The integral biomass of phytoplankton was calculated using distribution equations for the necessary indicators. For chlorophyll concentration, the Gaussian curve proposed in [23] was used:

$$\mathrm{Chl}_z = (h/\sigma(2\pi)^{1/2})\exp[-(z - z_m)^2/2\sigma^2], \qquad (5)$$

$$h = (55.73 \pm 1.40)\mathrm{Chl}_0^{(0.56 \pm 0.008)} \ (r^2 = 0.75), \qquad (6)$$

$$z_m = (11.1 \pm 0.75) - (10.46 \pm 0.45)\ln(\mathrm{Chl}_0) \ (r^2 = 0.61), \qquad (7)$$

where h is the total chlorophyll content (mg/m^3) in the maximum layer; σ (m) is the index of the deep chlorophyll maximum width; z_m (m) is the depth of the chlorophyll maximum; Chl_0 (mg/m^3) is the chlorophyll concentration in the surface layer. When estimating the depth of the chlorophyll maximum, according to function (7), it is assumed that the maximum will always be at the surface if $\mathrm{Chl}_0 > 2.89$ mg/m^3. However, when calculating equation (5), z_m is used as function (7). The maximum width of the σ is equal to 20 ± 10 m at $\mathrm{Chl}_0 < 1$ mg/m^3 and 13 ± 8 m at $\mathrm{Chl}_0 > 1$ mg/m^3 [23]. This value was calculated to be 68% of the chlorophyll peak height according to the law of Gaussian distribution. Formula (5), when applied to the input components, is valid for chlorophyll concentration values in the surface layer typical of the Black Sea. This distribution is typical of the warm period of the year (April–October, and sometimes November); whereas for the cold period (December–March) it is considered that chlorophyll is distributed uniformly [18, 23]. The nutritional conditions during the development of the model were assumed to be optimal.

For each depth, the parameters $a_{ph\,z}$, Chl:C_z, B_z, E_z were calculated, taking into account the direct measurements obtained during the cruises. The integral biomass calculation was carried out in two ways: the first included direct measurements of chlorophyll concentration in the algorithm; the second used equation (5) to calculate the distribution of this parameter with depth; the remaining parameters were calculated identically. Then, the biomass was integrated by depth for the euphotic zone and UML.

[5] Mankovsky, V.I., 1996. *Fundamentals of Ocean Optics. Methodical Manual*. Sevastopol: MHI NAS of Ukraine, 119 p. (in Russian).

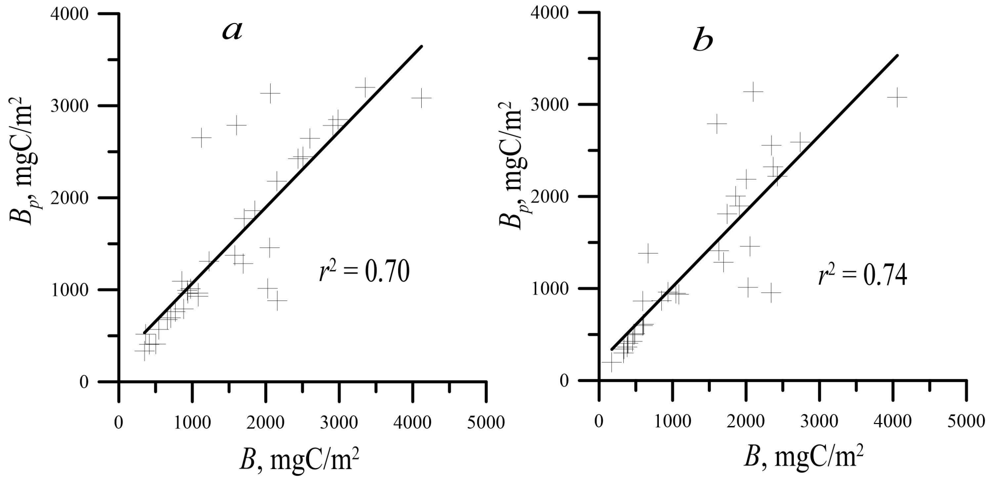
The results of the integral phytoplankton biomass comparison, obtained by calculation using the presented algorithm and equation (5), showed high consistency with the biomass calculated using direct measurements of chlorophyll concentration for the coastal area along Crimea and the open coast (depths greater than 500 m) of the northern Black Sea. The statistical characteristics of the compared values for the photosynthesis zone and the UML are presented in Fig. 1 and in the accompanying table.

Statistical indicators and average values obtained by the algorithm and calculated using direct measurements of chlorophyll concentration at horizons for the integral phytoplankton biomass averaged based on the data collected in cruises No. 122 and 124 of R/V *Professor Vodyanitsky*

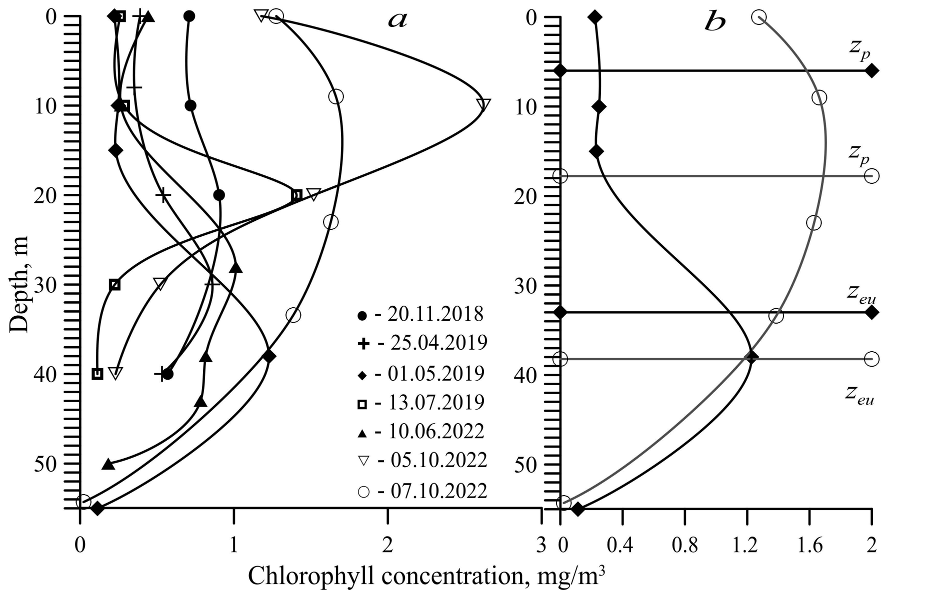
Zones	r	r^2	F	P	$\langle B \rangle_{122}$	$\langle B \rangle_{124}$	$\langle B_p \rangle_{122}$	$\langle B_p \rangle_{124}$
Euphotic zone	0.84	0.70	75.4	< 0.0001	768 ± 283	2277 ± 726	776 ± 276	2212 ± 759
UML	0.86	0.74	89.5	< 0.0001	556 ± 270	2023 ± 725	561 ± 240	1942 ± 719

N o t e: r is the correlation coefficient, r^2 is the determination coefficient, F is the Fisher criterion, P is the importance level, $\langle B \rangle$ and $\langle B_p \rangle$ (mg C/m^2) are the average values of integral phytoplankton biomass obtained using direct measurements and parameterization results, respectively.

The differences between the model and the measured data for the chlorophyll concentration profiles are reflected in the results of the biomass calculation using the two methods. These differences appear when the maximum chlorophyll concentration on the surface is quite high and then decreases sharply with depth, or when there are low values on the surface and a maximum with a high chlorophyll concentration at depth. Significant differences in the results of the biomass calculation by the two methods are also observed in the presence of two-peak chlorophyll concentration profiles. Compared to direct measurements, model calculations can overestimate or underestimate phytoplankton biomass by up to one and a half times in the cases described above. However, the number of chlorophyll concentration profiles that deviate so markedly from the parameterized description is small: 18% according to data from two cruises in the euphotic zone, and 15% in the UML. Measurements were carried out almost daily during the cruises at various stations in the coastal and deep-water areas near the Crimean coast. Consequently, when averaging is applied, the results obtained using the distribution function and those obtained using direct measurement data will be smoothed and approximated (Table and Fig. 1).

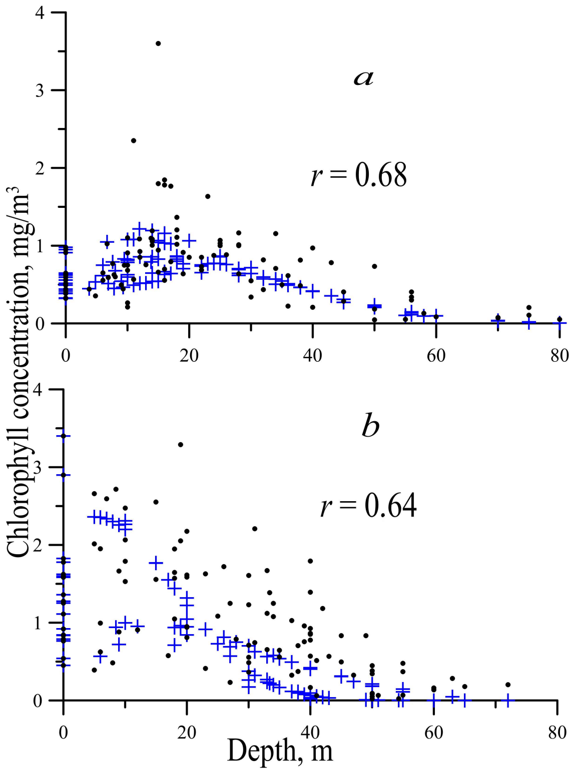


F i g. 1. Comparison of the values of integral phytoplankton biomass obtained by parameterization (B_p) and calculated using direct measurements of input parameters (B) for the euphotic zone (*a*) and UML (*b*)



F i g. 2. Change in chlorophyll concentration with depth based on the data obtained during the cruises of R/V *Professor Vodyanitsky* in 2018–2022: a – for selected days in different months; *b* – showing data from 7 October 2022 (○) and 1 May 2019 (♦) with UML (z_p) and euphotic zone (z_{eu}) boundaries

The present paper analyzes 88 chlorophyll concentration profiles from April to December. Some examples are shown in Fig. 2. Over the entire period under consideration, two-peak profiles were observed 9 times and a three-peak profile was observed once. These profiles were mainly observed in October (6 times), as well as in June (3 times) and August (once). Maximum chlorophyll concentrations were usually observed within the UML zone in October, November and December (Fig. 2). However, during cruise No. 110 in October, the maximum was more often noted at the lower boundary of the UML or below this zone. In June and April, the maximum chlorophyll concentration was below the UML at the lower boundary of the euphotic layer (Fig. 2), and was sometimes below 1% of the PAR illumination falling on the sea surface. In July–August, the chlorophyll peak was also observed within the euphotic zone or at its lower boundary. Equation (5) of the chlorophyll concentration distribution [23], presented above, provided a description of the profiles that was close to the measurement data. According to our data, which used all the points from two cruises, testing showed r = 0.68 in June and r = 0.64 in October (Fig. 3). Of the 218 points used in the calculations for the two cruises (No. 122 and 124), the correlation coefficient varied for 21 profiles in the range of 0.80–0.99, for five profiles – in the range of 0.60–0.8, for five profiles – in the range of 0.30–0.60 and for three profiles it was less than 0.10.



F i g. 3. Change in chlorophyll concentration with depth in cruises No. 122 (*a*) and 124 (*b*) of R/V *Professor Vodyanitsky* (data obtained using the distribution function (5) are indicated with a cross, and the direct measurement data – with a circle)

The relationship between σ and Chl_0, the UML, the euphotic zone depth and the temperature of the sea surface layer, as well as with E_0 and k_d, was considered. The σ indicator showed the best agreement with the UML, euphotic zone depth and Chl0, but no reliable correlation with the analyzed parameters was revealed in the sample. According to the multiple correlation results, the influence of the three specified parameters explained 20% of the variability in σ, while the influence of six parameters explained 25%. The average value of σ was 25 ± 10 m across all the months considered, varying in the 2–48 m range. In the autumn months, the σ width was comparable with the UML values; however, in the summer months, it could exceed them several times over. Compared with the width of the euphotic zone, the σ parameter was almost always smaller than or comparable with it. It can be assumed that σ depends on the amount of nutrients and the characteristics of the hydrological conditions since no obvious correlation was found with the six considered parameters. These parameters were chosen for estimating σ because they can be easily determined and calculated using satellite data, which will facilitate more extensive studies in the future.

Also, studies of chlorophyll concentration profiles revealed that the maximum concentration in spring (from April) and summer can be observed at approximately up to the 0.1% light penetration from the surface values. Accordingly, the euphotic zone boundary will be below 1% PAR in these months.

Discussion

There are very few data on the integral biomass of phytoplankton in the literature, particularly with regard to the Black Sea. For example, the authors of [24] estimate the integral biomass of diatoms using models from [17, 25], comparing the results with chlorophyll concentrations obtained from satellite data. An earlier study [26] used a simplified approach to calculate integral biomass when analyzing expeditionary studies carried out in winter and spring. However, the calculation methods used in these studies did not consider the depth distribution of important phytoplankton characteristics and optical indicators when estimating biomass. The calculations were carried out in different areas and the results were difficult to compare with each other.

The phytoplankton biomass distribution function is given in [23]. This requires nitrate concentration and water temperature measurements by horizon, which are not always possible. Another function from this paper requires the determination of optical depth and provides rough estimates of integral biomass compared to direct measurements, as indicated by the authors themselves. For example, we compared calculated integral phytoplankton biomass data using the specified function, which includes optical depth and integral biomass values obtained by our algorithm, with data obtained by direct chlorophyll concentration measurements at different horizons. We analyzed 34 biomass profiles obtained from the results of cruises No. 122 and 124 of R/V *Professor Vodyanitsky* in June and October. Their comparison showed the consistency of the two calculation methods for June ($r^2 = 0.63$) and October ($r^2 = 0.19$). It was also found that, compared to our calculations, the values obtained using the biomass function from [23] in October were often approximately twice as high.

Direct determinations of phytoplankton biomass, particularly integral determinations, are labor-intensive and carried out extremely rarely. No such measurements have been taken in the Black Sea for 10–15 years. Therefore, it is not possible to obtain or compare direct measurements of integral biomass with calculation results due to the absence of such measurements. The consistency of the measured and calculated phytoplankton biomass values for the surface layer obtained using the algorithm described earlier in [15, 22, 27] has been demonstrated. The distribution function (5) of chlorophyll concentration was also compared with direct measurement data at the horizons in the present paper and in [23]. Based on this consistency, it is assumed that the calculated values at the horizons, taking into account different illumination, are adequate.

Our research builds upon the works of [15, 23]. The algorithm we have developed for calculating integral biomass is based on laboratory and expeditionary studies. It is easy to use and shows good comparability with calculation data, including direct measurements of chlorophyll concentration at different horizons (Table). The algorithm considers the depth distribution of important input parameters such as Chl, a_{ph}, Chl:C, as well as the illumination variation with depth. The algorithm used for the surface layer was developed based on 10 species of algae found in the Black Sea (*Nitschia sp., Pseudonitschia delicatissima, Skeletonema costatum, Talasiossira parva, Coscinodiscus granii, Phaeodactilum tricornutum, Prorocentrum micans, Isochrysis galbana, Dunaliella tertiolecta, Glenodinium foliaceum*), including species from the dominant taxonomic groups (diatoms and dinoflagellates), which were available for experimentation. For these species, the aforementioned dependencies of the physiological and structural parameters of microalgae and their average coefficients were obtained (equations (1) – (7)). In this model, the nutritional conditions are assumed to be optimal at different illumination levels.

In our algorithm, we rely on measurements of chlorophyll concentration and the previously obtained dependence of the average specific content of chlorophyll in cells of different types of algae in individual groups. The Chl:C estimation in the model from [15] was performed by taking into account light absorption by microalgae, enabling an approximate total phytoplankton biomass estimate despite the absence of other species in the parameterization.

One limitation of our algorithm is that it does not consider coccolithophores, which dominate at the beginning of summer [11, 28–30]. Therefore, phytoplankton biomass values may be underestimated during their ‘blooming’ period. According to the results of our earlier studies presented in [21], coccolithophores dominated in June compared to other microalgae groups. The integral biomass data calculated in two ways showed high consistency, and the phytoplankton biomass values were not low. This can be explained by the relatively close average specific chlorophyll content values in the cell [6] of the considered diatoms and coccolithophores. The algorithm provides general estimates of phytoplankton biomass without dividing microalgae into groups and types. Therefore, the results should be analyzed taking into account the limitations and assumptions of this model.

[6] Stelmakh, L.V., 2017. [*Patterns of Phytoplankton Growth and Its Consumption by Microzooplankton in the Black Sea*]. Doctor of Biological Sciences Dissertation. Sevastopol, 310 p. (p. 37) (in Russian).

Analysis of the chlorophyll concentration profiles reveals that, in most cases, maximum formation occurs in the UML zone in autumn. This may be due to increased mixing of water masses, the flow of biogenic substances into the upper water layers, and expansion of the UML zone. At the same time, dissolved organic matter resulting from the activity of marine organisms remains in the surface layer. Decreased solar radiation also allows the photosynthesis zone to rise higher, enabling the development of algae species that experienced photoinhibition in the UML zone in summer. The same reasons can also cause two peaks to form in the chlorophyll profiles during this period. The formation of chlorophyll maxima in April and in the summer outside the UML, at the lower boundary of the euphotic zone, is mainly associated with high levels of illumination, pronounced temperature stratification in the water column, and a narrow UML zone. For example, in June, peaks in the chlorophyll profiles were observed at less than 1% illumination, which indicates euphotic zone expansion due to the high level of PAR falling on the sea surface.

Mathematically describing chlorophyll concentration profiles remains problematic in cases where there are two or even three maxima in the water column or the profile is atypically single-peaked. This problem is simplified by the fact that complex profiles are uncommon, and differences are smoothed out during averaging. The same thing happens when recalculating other phytoplankton parameters.

When constructing models of the Black Sea that take many factors into account, such as hydrological conditions and nutrient levels (including nitrogen, phosphorus and silicon compounds), it is necessary to take contact measurements of these parameters. Studies and data collection were conducted over several years to identify relationship between parameters such as dominant species and nutrients, taking wind activity into account [12], as well as the relationship between river runoff and phytoplankton community structure [31]. Considering all these factors will lead to the development of more complex models in the future. However, not all of the specified input parameters will currently or in the near future be available to estimate integral values based on satellite data. Although there are complex global models of marine ecosystems that include a large number of input parameters [17, 32–34], they do not describe all cases either and also have their own assumptions, limitations and errors.

Our current task is to create a simple algorithm for estimating total phytoplankton biomass and integral values within the water column, taking into account the average ratios of specific chlorophyll within cells of certain dominant microalgae groups (equation (2)). The proposed algorithm is applicable to all seasons and considers the distribution of chlorophyll concentration (equation (5)) from April to November, as well as its uniform distribution from December to March [23]. The results were analyzed using data from two seasons. Thus, the average monthly integral phytoplankton biomass values obtained from our parameterization differ by 0.9–4% from those obtained from calculations using measured input parameters at different depths (Table). With a limited supply of individual nutrients, deviations in the Chl:C ratio are possible. In real conditions, changes in species composition also occur. However, the parameterization proposed in this paper does not take such factors into account. The algorithm only allows estimation of variability in total phytoplankton biomass based on the average characteristics described above (equations (1) – (7)). The proposed parameterization can be applied to estimate integral biomass. This calculation algorithm will be useful for future calculations based on satellite data that take into account the hydrooptical characteristics of the Black Sea [35].

Conclusion

The presented algorithm was used to calculate the integral biomass of phytoplankton in the coastal and open coastal zones (at depths over 500 m) of the northern Black Sea. The results of the integral biomass calculation obtained using two methods are in good agreement: one method used data from direct measurements of input parameters at different depths in expeditionary studies, while the other method used equations for the distribution of input parameters. According to the statistical analysis, the determination coefficients for the data from the two cruises are 0.7 and 0.74, respectively. The average monthly values and standard deviations of the integral phytoplankton biomass, calculated based on the results of expeditionary studies, are 768 ± 283 mg C/m^2 in the photosynthesis zone in June and 2277 ± 726 mg C/m^2 in October, and 556 ± 270 mg C/m^2 in June and 2023 ± 725 mg C/m^2 in October in the upper quasi-homogeneous layer. The average monthly values calculated using the two methods varied by 0.9–4%.

The presented algorithm includes distribution equations for all input parameters and is user-friendly and convenient for working with satellite data. Analysis of chlorophyll concentration profiles revealed that the peak is typically observed in the UML zone in autumn and at the lower boundary of the euphotic layer in April – July, when up to 0.1% of the PAR reaching the sea surface is absorbed. Multiple correlation analysis revealed no reliable correlation between the width of the deep maximum of chlorophyll concentration in the water layer and any of the following six parameters: chlorophyll concentration at the surface; UML and euphotic layer depth; temperature; illumination on the sea surface; and the diffuse light attenuation coefficient. It was found that these parameters influence the variability of the width of the chlorophyll maximum by 25%.

REFERENCES

1. Selifonova, Zh.P. and Yasakova, O.N., 2012. Phytoplankton of Areas of the Seaports of the Northeastern Black Sea. *Marine Ecological Journal*, 11(4), pp. 67-77 (in Russian).
2. Krasheninnikova, S.B., Minkina, N.I., Samyshev, E.Z. and Shokurova, I.G., 2019. The Influence of the Complex of Environmental Factors on the Phytoplankton and Zooplankton Biomass in the Black Sea in Spring. *Ekologiya i Stroitelstvo*, (4), pp. 14-21. https://doi.org/10.35688/2413-8452-2019-04-002
3. Stelmakh, L.V. and Mansurova, I.M., 2020. Long-Term Dynamics of Phytoplankton and Chlorophyll a Concentration in the Surface Layer of the Coastal Waters of the Black Sea (Sevastopol Region). *Issues of Modern Algology*, 1(22), pp. 66-81. https://doi.org/10.33624/2311-0147-2020-1(22)-66-81 (in Russian).

4. Stelmakh, L.V., 2019. Effect of Phytoplankton Adaptation on the Distribution of Its Biomass and Chlorophyll-a Concentration in the Surface Layer of the Black Sea. *Monitoring Systems of Environment*, 1(5), pp. 106-114. https://doi.org/10.33075/2220-5861-2019-1-106-114 (in Russian).
5. Morozova-Vodyanitskaya, N.V., 1948. [Phytoplankton of the Black Sea. Part I. Phytoplankton in the Sevastopol Region and a General Overview of the Phytoplankton of the Black Sea]. In: SBS, 1948. *Trudy Sevastopolskoj Biologichskoj Stantsii*. Moscow-Leningrad: AS USSR Publishing. Vol. 6, pp. 39-172 (in Russian).
6. Morozova-Vodyanitskaya, N.V., 1954. [Phytoplankton of the Black Sea. Part 2. Phytoplankton in the Sevastopol Region and a General Overview of the Phytoplankton of the Black Sea]. In: SBS, 1948. *Trudy Sevastopolskoj Biologichskoj Stantsii*. Moscow-Leningrad: AS USSR Publishing. Vol. 8, pp. 11-99 (in Russian).
7. Marañón, E., Holligan, P.M., Varela, M., Mouriño, B. and Bale, A.J., 2000. Basin-Scale Variability of Phytoplankton Biomass, Production and Growth in the Atlantic Ocean. *Deep Sea Research Part I: Oceanographic Research Papers*, 47(5), pp. 825-857. https://doi.org/10.1016/S0967-0637(99)00087-4
8. Pérez, V., Fernández, E., Marañón, E., Morán, X.A.G. and Zubkov, M.V., 2006 Vertical Distribution of Phytoplankton Biomass, Production and Growth in the Atlantic Subtropical Gyres. *Deep Sea Research I: Oceanographic Research Papers*, 53(10), pp. 1616-1634. https://doi.org/10.1016/j.dsr.2006.07.008
9. Behrenfeld, M.J., Boss, E., Siegel, D.A. and Shea, D.M., 2005. Carbon-Based Ocean Productivity and Phytoplankton Physiology from Space. *Global Biogeochemical Cycles*, 19(1), GB1006. https://doi.org/10.1029/2004GB002299
10. Stelmakh, L.V., 2015. Spatial and Temporal Variability of Carbon to Chlorophyll a Ratio in Phytoplankton of the Surface Layer in Shallow Water Areas of the Black Sea (Crimea). *International Journal on Algae*, 17(4), pp. 385-396. https://doi.org/10.1615/InterJAlgae.v17.i4.60
11. Mikaelyan, A.S., Pautova, L.A., Chasovnikov, V.K., Mosharov, S.A. and Silkin, V.A., 2015. Alternation of Diatoms and Coccolithophores in the North-Eastern Black Sea: A Response to Nutrient Changes. *Hydrobiologia*, 755(1), pp. 89-105. https://doi.org/10.1007/s10750-015-2219-z
12. Silkin, V.A., Pautova, L.A., Giordano, M., Chasovnikov, V.K., Vostokov, S.V., Podymov, O.I., Pakhomova, S.V. and Moskalenko, L.V., 2019. Drivers of Phytoplankton Blooms in the Northeastern Black Sea. *Marine Pollution Bulletin*, 138, pp. 274-284, https://doi.org/10.1016/j.marpolbul.2018.11.042
13. Zhitina, L.S., Ilyash, L.V., Belevich, T.A., Klyuvitkin, A.A., Kravchishina, M.D., Tolstikov, A.V. and Tchultsova, A.L., 2016. Phytoplankton Structure in the White Sea after Summer Bloom: Spatial Heterogeneity in Relation to Hydrophysical Conditions. *Sibirskiy Ecologicheskiy Jurnal*, 23(6), pp. 888-899. https://doi.org/10.15372/SEJ20160608 (in Russian).
14. Menden-Deuer, S. and Lessard, E.J., 2000. Carbon to Volume Relationships for Dinoflagellates, Diatoms, and Other Protist Plankton. *Limnology & Oceanography*, 45(3), pp. 569-579. https://doi.org/10.4319/lo.2000.45.3.0569
15. Finenko, Z.Z., Kovalyova, I.V. and Suslin, V.V., 2018. A New Approach to Estimate Phytoplankton Biomass and Its Variability in the Black Sea Surface Water Layer Based on Satellite Data. *Uspekhi Sovremennoi Biologii*, 138(3), pp. 294-307. https://doi.org/10.7868/S0042132418030079 (in Russian).
16. Abakumov, A.I. and Pak, S.Ya., 2021. Modeling of Photosynthesis Process and Assessing of Phytoplankton Dynamics Based on Droop Model. *Mathematical Biology and Bioinformatics*, 16(2), pp. 380-393. https://doi.org/10.17537/2021.16.380 (in Russian).

17. Oguz, T., Ducklow, H.W. and Malanotte-Rizzoli, P., 2000. Modeling Distinct Vertical Biogeochemical Structure of the Black Sea: Dynamical Coupling of the Oxic, Suboxic, and Anoxic Layers. *Global Biogeochemical Cycles*, 14(4), pp. 1331-1352. https://doi.org/10.1029/1999GB001253
18. Finenko, Z.Z., Suslin, V.V. and Churilova, T.Ya., 2009. The Regional Model to Calculate the Black Sea Primary Production Using Satellite Color Scanner SeaWiFS. *Morskoy Ekologicheskiy Zhurnal*, 8(1), pp. 81-106 (in Russian).
19. Kovalyova, I.V. and Suslin, V.V., 2022. Integrated Primary Production in the Deep-Sea Regions of the Black Sea in 1998–2015. *Physical Oceanography*, 29(4), pp. 404-416. https://doi.org/10.22449/1573-160X-2022-4-404-416
20. Kubryakov, A.A., Belokopytov, V.N., Zatsepin, A.G., Stanichny, S.V. and Piotukh, V.B., 2019. The Black Sea Mixed Layer Depth Variability and Its Relation to the Basin Dynamics and Atmospheric Forcing. *Physical Oceanography*, 26(5), pp. 397-413. https://doi.org/10.22449/1573-160X-2019-5-397-413
21. Stelmakh, L.V., Mansurova, I.M., Farber, A.A., Kovaleva, I.V. and Borisova, D.S., 2024. Structural and Functional Parameters of the Black Sea Phytoplankton during the Summer Bloom of the Coccolithophore Emiliania Huxleyi. *Regional Studies in Marine Science*, 76, 103594. https://doi.org/10.1016/j.rsma.2024.103594
22. Kovalyova, I.V. and Suslin, V.V., 2023. Seasonal Variability of Biomass and Specific Growth Rate of Phytoplankton for 2016-2020 in the Deep-Water Zone of the Black Sea. *Sovremennye Problemy Distantsionnogo Zondirovaniya Zemli iz Kosmosa*, 20(4), pp. 250-262. https://doi.org/10.21046/2070-7401-2023-20-4-250-262 (in Russian).
23. Finenko, Z.Z., Churilova, T.Ya. and Li, R.I., 2005. Vertical Distribution of Chlorophyll and Fluorescence in the Black Sea. *Morskoy Ekologicheskiy Zhurnal*, 4(1), pp. 15-46 (in Russian).
24. Kubryakova, E.A., Kubryakov, A.A. and Stanichny, S.V., 2018. Impact of Winter Cooling on Water Vertical Entrainment and Intensity of Phytoplankton Bloom in the Black Sea. *Physical Oceanography*, 25(3), pp. 191-206. https://doi.org/10.22449/1573-160X-2018-3-191-206
25. Mellor, G.L., 2001. One-Dimensional, Ocean Surface Layer Modeling: A Problem and a Solution. *Journal of Physical Oceanography*, 31(3), pp. 790-809. https://doi.org/10.1175/1520-0485(2001)0312.0.CO;2
26. Finenko, Z.Z., Mansurova, I.M., Kovalyova, I.V. and Georgieva, E.Yu., 2021. Development of Phytoplankton in the Winter-Spring Period in the Coastal Waters of Crimea. *Marine Biological Journal*, 6(1), pp. 102-114. https://doi.org/10.21072/mbj.2021.06.1.08 (in Russian).
27. Finenko, Z.Z., Mansurova, I.M. and Suslin, V.V., 2022. Temporal Dynamics of Phytoplankton Biomass in the Surface Layer of the Black Sea According to Satellite Observations. *Oceanology*, 62(3), pp. 358-368. https://doi.org/10.1134/S0001437022030043
28. Pautova, L.A., Mikaelyan, A.S. and Silkin, V.A, 2007. Structure of Plankton Phytocoenoses in the Shelf Waters of the Northeastern Black Sea during the Emiliania Huxleyi Bloom in 2002–2005. *Oceanology*, 47(3), pp. 377-385. https://doi.org/10.1134/S0001437007030101
29. Mikaelyan, A.S., Silkin, V.A. and Pautova, L.A., 2011. Coccolithophorids in the Black Sea: Their Interannual and Long-Term Changes. *Oceanology*, 51(1), pp. 39-48. https://doi.org/10.1134/S0001437011010127
30. Silkin, V.A., Pautova, L.A., Pakhomova, S.V., Lifanchuk, A.V., Yakushev, E.V. and Chasovnikov, V.K., 2014. Environmental Control on Phytoplankton Community Structure in the NE Black Sea. *Journal of Experimental Marine Biology and Ecology*, 461, pp. 267-274. https://doi.org/10.1016/j.jembe.2014.08.009
31. Sergeeva, V.M., Mosharov, S.A., Shulga, N.A., Kremenetskiy, V.V., Khlebopashev, P.V. and Matorin, D.N., 2023. Response of the Coastal Phytoplankton Community to the Runoff from Small Rivers in the Northeastern Black Sea. *Diversity*, 15(7), 857. https://doi.org/10.3390/d15070857

32. Vichi, M., Pinardi, N. and Masina, S., 2007. A Generalized Model of Pelagic Biogeochemistry for the Global Ocean Ecosystem. Part I: Theory. *Journal of Marine Systems*, 64(1-4), pp. 89-109. https://doi.org/10.1016/j.jmarsys.2006.03.006

33. Dorofeev, V.L., Korotaev, G.K. and Sukhikh, L.I., 2017. Analysis-Forecast System of the Black Sea Ecosystem State. *Problems of Ecological Monitoring and Ecosystem Modelling*, 28(2), pp. 71-85. https://doi.org/10.21513/0207-2564-2017-2-71-85 (in Russian).

34. Belyaev, V.I. and Konduforova, N.V., 1990. *Mathematical Modelling of the Ecological Shelf Systems*. Kiev: Naukova Dumka, 240 p. (in Russian).

35. Suslin, V.V., Churilova, T.Ya. and Pryahina, S.F., 2012. The Black Sea IOPs Based on SeaWiFS Data. *Ecological Safety of Coastal and Shelf Zones and Comprehensive Use of Shelf Resources*, 26(2), pp. 204-223 (in Russian).

Submitted 16.08.2024; approved after review 03.03.2025;
accepted for publication 13.03.2025.

About the author:

Ilona V. Kovalyova, Senior Researcher, Algae Eco-Physiology Department, A.O. Kovalevsky A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS (2 Nakhimova Ave., Sevastopol, 299011, Russian Federation), CSc. (Biol.), **ORCID ID: 0000-0001-5430-2002**, **Scopus Author ID: 57211264299**, **ResearcherID: AAB-4397-2019**, **SPIN-code: 2356-4570**, ilonavk@ibss-ras.ru

The author has read and approved the final manuscript.
The author declares that she has no conflict of interest.