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DEVELOPMENT OF PHYTOPLANKTON IN THE WINTER-SPRING PERIOD IN THE COASTAL WATERS OF CRIMEA

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The analysis of phytoplankton in the winter-spring period is important for investigating peculiarities of its annual dynamics and the Black Sea ecosystem overall functioning. Phytoplankton state in the winter-spring period in the Black Sea shelf zone is less studied than that of the summer-autumn season; conducting such a research is especially important for solving several problems, related to the productivity of the last links of the food chain, the formation of water hydrochemical regime, and the carbon cycle in the sea. The aim of the work is to assess the effect of seasonal conditions on the development of phytoplankton and its production estimates in the winter-spring period in the coastal waters of Crimea. The article presents the results of studies of hydrophysical (water temperature, density, and relative transparency) and biological indicators (chlorophyll *a* concentration, its fluorescence, taxonomic composition, and phytoplankton production estimates) in the Black Sea shelf zone in January – April 2016–2019. The studies were carried out at 50 stations, located in the coastal waters of Crimea from the Karkinitsky Bay to the Kerch Strait. Chlorophyll *a* concentration was measured by the standard fluorometric method, species composition was determined by microscopy, and phytoplankton specific growth rate was calculated according to the previously developed model. In winter (January – February), the values of chlorophyll *a* content and upper mixed layer depth were the highest (0.42–0.52 mg·m^{-3} and 44–58 m, respectively); in spring (March – April) they were 2–3 times lower. In January – February, the coccolithophore species *Emiliania huxleyi* (Lohmann) W. W. Hay & H. P. Mohler, 1967 predominated; in March – April, in different years, either dinoflagellates and diatoms or coccolithophores, dinoflagellates, and diatoms prevailed. In winter, chlorophyll *a* vertical distribution at most stations was uniform; in spring, unimodal profiles with a depth maximum prevailed, the location of which was not related to temperature and density gradients. Relative changes in chlorophyll *a* concentration and fluorescence with depth were usually the same. Phytoplankton production and daily production/biomass ratio (P/B) increased from winter to spring. There was no correlation between the values of integral production, biomass, and maximum specific growth rate of algae. Maximum specific growth rate was the least variable indicator. During the winter-spring period, algae in the photosynthetic zone divided on average once every 2–5 days.

Keywords: taxonomic composition, phytoplankton abundance and biomass, chlorophyll *a*, fluorescence, algae maximum specific growth rate, temperature, water density, Black Sea

Winter-spring period is the season of great importance for the Black Sea ecosystem: convective mixing of the upper sea layer is observed, and active transport of nutrients from deeper sea layers to the photosynthetic zone occurs, where nutrients, being consumed by phytoplankton, change their state from dissolved to suspended (Krivenko & Parkhomenko, 2014). This process results in formation of new production, supporting the growth of heterotrophs (Krivenko et al., 1998). The intensity of this formation depends on climatic conditions. As it is considered, the transport of nutrients is more intensive in cold and severe winters, and the conditions for organic matter biosynthesis during photosynthesis are more favorable than in mild ones (Finenko et al., 2009 ; Mikaelyan et al., 2017). Primary production, formed in the winter-spring period, determines the regeneration processes throughout the year, *inter alia* in the warm season.

A wide range of research in phytoplankton community is required for solving several problems, related to the productivity of the final links of the food chain, the formation of water hydrochemical regime, and the carbon cycle in the sea. Number of seasonal phytoplankton investigations, carried out off the Crimean Peninsula, is rather high, but planktonic algae state in the winter-spring period has been poorly studied (Arashkevich et al., 2015 ; Stelmakh, 2010 ; Finenko at al., 2019 ; Mikaelyan et al., 2017). Since there is no long-term monitoring, it is difficult to understand the effect of climatic conditions on the level of development of planktonic algae. At the same time, the results of direct and satellite measurements of chlorophyll *a* concentration in the surface layer indicate the presence of interannual changes in the development of phytoplankton (Finenko at al., 2014 ; Yunev et al., 2002). Physical and geographical conditions affect the development of plankton community, with its peculiarities in deep and shallow sea areas, but there is clearly not enough data for carrying out the biogeochemical zoning.

The aim of the work is to assess the effect of seasonal conditions on the level of the development of phytoplankton and its production estimates in the winter-spring period in the coastal waters of Crimea.

MATERIAL AND METHODS

Phytoplankton studies were carried out during the 83rd, 84th, 93rd, and 106th cruises of the RV "Professor Vodyanitsky" in the coastal waters of Crimea from the Karkinitsky Bay to the Kerch Strait at stations with a total depth of 16–93 m, as well as on three transects, which began at Cape Tarkhankut, the southern coast of Crimea, and the Kerch Strait and ended in the open Black Sea (January – May 2016–2019) (Fig. 1). The measurements of chlorophyll *a* (hereinafter Chl) concentration, its fluorescence, water temperature, density, and relative transparency were performed at 52, 11, 38, 23, and 34 stations, respectively (Table 1). Vertical profiles of these indicators were established for 75–100 % of the total number of stations.

Samples were taken with a plastic bathometer or with a cassette of CTD bathometers of a Neil Brown Mark III probe. When choosing the depths, a vertical profile of fluorescence or temperature [the data, obtained from a Neil Brown Mark III or Ocean Seven 320 Plus (Idronaut) probe] and relative water transparency were taken into account. Continuous fluorescence monitoring in the shelf zone was carried out throughout the water column, while in deep-water areas – up to 100–150 m. The data on temperature and salinity, measured by high-precision submersible digital probes, were vertically interpolated with a step of 1 m and used for calculating potential density by the UNESCO formula. The lower boundary of the upper mixed layer (hereinafter UML) is considered as a depth, at which potential water density exceeds surface water density by 0.07 kg·m^{-3} (Kubryakov et al., 2019). The depth of the mixed layer for each station was estimated by the depth of the maximum water density gradient. Relative water transparency was determined in the daytime by a Secchi disk. When irradiance was not measured at various depths, the depth of the euphotic zone (Z, m) was calculated as follows:

$$Z = 3 \times S \,, \qquad (1)$$

where S is the depth of Secchi disk visibility, m.

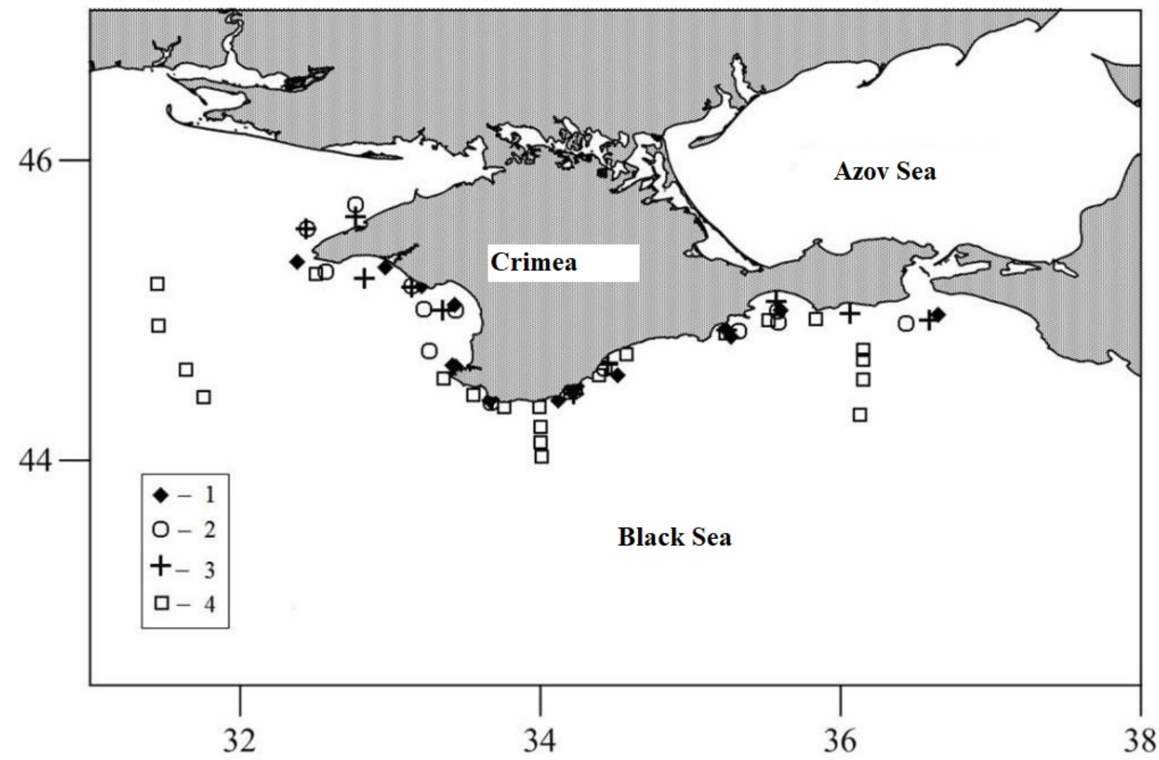

Fig. 1. Map of the stations, where the work was carried out: 1 – 27 January to 03 February, 2016; 2 – 19 to 25 April, 2016; 3 – 28 March to 04 April, 2017; 4 – 18 April to 13 May, 2019

Seawater samples of 0.25–1.50 L were filtered immediately after sampling at a vacuum (< 0.2 atm) through Sartorius membrane filters with a pore diameter of 0.65 μm and a working surface diameter of 47 mm or through glass microfiber filters GF/F (Whatman) with a 22-mm working surface. Comparison of the results, obtained with two types of filters used, showed their similarity. The filters were dried on filter paper in the dark for 15 minutes, folded in four with a sediment inward, and foil-wrapped; then, they were stored in a freezer at −18 °C for no longer than three weeks. Measurements of pigment concentration were performed under laboratory conditions onshore. Chl was extracted with 3–5 ml of a 90 % aqueous solution of acetone. To improve pigment extraction, the filters were mechanically rubbed with a glass rod and stored in a refrigerator in the dark at +8 °C for 18 hours (Phytoplankton Pigments in Oceanography…, 1997). Then, the filters were rubbed again and centrifuged by a laboratory clinical centrifuge OPn-3 UKhL 4.2 for 5 minutes at 3000 rpm. Acetone extracts were put into a quartz cuvette, in which fluorescence measurements were performed before and after acidification with two drops of 1.2 M HCl. Fluorescence measurements were carried out using a laboratory fluorometer. A KGM 12-100 halogen lamp was used as a source of excitation of pigment fluorescence. Fluorescence was excited by a CC8 blue-light filter with a maximum transmission of 440–450 nm. Fluorescence was recorded by an FEU-27 photomultiplier, fed from a stabilized voltage source of a VS-22 type. A red-light filter KS17 with a wavelength of 670 nm was used to record fluorescence signal. The signal from FEU load resistance was fed through a preamplifier to the input of a UT60A digital multimeter, used as a recording device. The fluorometer was pre-calibrated, as in (Yunev & Berseneva, 1986 ; Lorenzen, 1967), based on chromatographically pure chlorophyll *a* by Sigma (USA); its initial concentration was determined by a Specord UV-Vis spectrophotometer with the specific light absorption coefficient of 87.67 $L \cdot g^{-1} \cdot cm^{-1}$ (Phytoplankton Pigments in Oceanography…, 1997).

Table 1. Data on the work, carried out in the coastal waters of Crimea in the winter-spring period

Cruise No.	Dates	Total number of stations / Number of stations with vertical profiles with determination of:					
		depth of Secchi disk visibility	temperature	density	chlorophyll *a*	fluorescence	phytoplankton
83	27 January – 03 February, 2016	10/10	15/15	8/8	16/14	7/7	14/0
84	19–25 April, 2016	12/11	13/13	5/5	14/13	4/4	13/0
93	28 March – 04 April, 2017	–	–	–	–	–	13/0
106	19 April – 1 May, 2019	12/7	10/10	10/10	22/11	–	–
In total		34/28	38/38	23/23	52/39	11/11	40/0

To calculate phytoplankton production estimates (biomass, specific growth rate, and maximum and integral photosynthesis rates), we used the models, described earlier (Finenko et al., 2018 ; Finenko at al., 2019).

To determine phytoplankton taxonomic composition and quantitative characteristics, 2-L water samples were concentrated by reverse filtration through track-etched membrane filters with a pore diameter of 1 μm. The resulting concentrate (40–50 mL) was fixed with 0.1 mL of Lugol's iodine. The samples were stored in a refrigerator at +8 °C. Determinations of species composition and phytoplankton cells size were carried out under a light trinocular microscope XY-B2 using a Nauman's chamber. Biomass was calculated by cell volume, using the standard method (Radchenko et al., 2010).

RESULTS

Chlorophyll a content in the upper mixed layer and predominant phytoplankton species. In January – February, in the shelf zone off the western coast of Crimea from Cape Tarkhankut to Cape Fiolent, the UML extended from the surface to the bottom (16–90 m, on average (44 ± 34) m); only at one station in the Kalamitsky Bay (depth of 26 m), the UML thickness was 14 m. In winter, in all the studied areas, the coccolithophore species *Emiliania huxleyi* (Lohmann) W. W. Hay & H. P. Mohler, 1967 predominated (52–94 % of the total phytoplankton abundance). Its ratio in the total biomass was 24–57 %. At several stations in the eastern area, *Skeletonema costatum* (Greville) Cleve, 1873 prevailed in abundance and biomass (60–70 and 26–30 %, respectively).

Chl content in the UML varied 0.40 to 0.60 mg·m^{-3}, averaging (0.47 ± 0.07). Off the southern coast of Crimea, with a depth range of 70–80 m, the UML thickness varied 50 to 80 m; in the deep-water area, it was 37 m, averaging (58 ± 18) m. Mean Chl concentration for this area in the UML was (0.42 ± 0.11) mg·m^{-3}. Off the eastern coast, with station depth of 25–60 m, the lower boundary of the UML was on average at (31 ± 9) m, and Chl content was (0.52 ± 0.18) mg·m^{-3}. In general, mean Chl values in the UML in all the studied areas did not differ significantly. No correlation was established between the UML depth and mean Chl concentration in it.

Work, carried out at the end of April 2016 on the shelf off the western coast of Crimea, showed that the UML thickness and Chl concentration in it decreased significantly, compared to the estimates of the winter period: up to (15 ± 12) m and (0.15 ± 0.08) mg·m^{-3}, respectively. Off the southern and eastern coast of Crimea, mean values of the UML and Chl content in it were the same: (16 ± 2) and (14 ± 4) m and (0.22 ± 0.04) and (0.22 ± 0.09) mg·m^{-3}, respectively. Mean values of Chl concentration in these areas are slightly higher than those off the western coast.

In late April – early May 2019, the UML thickness in the coastal and deep-water areas decreased, compared to that of 2016, and averaged (9 ± 4) m. Chl content in the eastern sea area, near the Kerch Strait, did not change during this period; however, in the western area, it was almost 1.5 times higher, and in the central area – 2 times higher than in the spring of 2016.

Thus, in the coastal waters of Crimea, Chl values were usually higher in winter than in spring.

In the early spring of 2017, *E. huxleyi* predominated in abundance off the southern coast of Crimea (47–57 %), while in other areas different Flagellata species prevailed (36–69 %). In the early spring period, at most stations in the western area and at several stations in the central and eastern areas, dinoflagellate *Heterocapsa triquetra* (Ehrenberg) F. Stein, 1883 predominated in biomass (18–59 %), as well as diatoms *Coscinodiscus janischii* A. W. F. Schmidt, 1878 (29–64 %), *Chaetoceros curvisetus* Cleve, 1889 (23 %), and *Pseudosolenia calcar-avis* (Schultze) B. G. Sundström, 1986 (29 %).

At the end of April 2016, *E. huxleyi* again predominated in abundance (41–96 %) in most of the water area; only at two stations, the diatom *Pseudo-nitzschia delicatissima* (Cleve) Heiden, 1928 prevailed (35–36 %). In the western and central areas, algae of different taxonomic groups predominated in biomass: coccolithophore *E. huxleyi* (22–50 %), dinoflagellates *Ceratium furca* (Ehrenberg) Claparède & Lachmann, 1859 (46–51 %) and *Ceratium tripos* (O. F. Müller) Nitzsch, 1817 (20 %), and diatoms *P. delicatissima* (13 %) and *P. calcar-avis* (27–43 %). Throughout the eastern area, *P. calcar-avis* prevailed (23–32 %).

Vertical distribution of chlorophyll a concentration. In winter and spring, Chl vertical distribution was analyzed by its content at different depths and by continuously recorded fluorescence. Comparison showed as follows: in 64 % of cases, change in relative values of Chl concentration and fluorescence with depth was of the same character, whereas in 36 % it was multidirectional (Fig. 2). The reason for this discrepancy may be that with an increase in Chl content with depth, relative fluorescence (normalized to a chlorophyll unit) decreases. Generally, vertical profiles of Chl fluorescence were less variable than the profiles of its concentration. It should be noted that for the entire dataset, no reliable correlation was revealed between Chl content and its fluorescence.

In winter, the lower boundary of the mixed layer almost reached the bottom or was 10–20 m higher. Temperature and density gradients in the water column were low: as a rule, they did not exceed 0.1 degree·m^{-1} and ranged 0.01–0.10 kg·m^{-3}·m^{-1}, respectively. Under such conditions, Chl vertical distribution at 60 % of the total number of stations was uniform; in other cases, Chl concentration either increased with depth or decreased. At several stations, maximum content was registered in the 0–10-m layer (deeper its values decreased).

In spring, the stability of the water column increased, and this resulted in a decrease of the UML thickness on average 3-fold, compared to that of the winter of 2016; temperature and density gradients remained low. Under these conditions, a distribution of Chl along the depths was uniform only in 30 % of cases; at the other stations, Chl content increased mainly from the surface to the lower boundary of the photosynthetic zone. In the winter of 2016, the photosynthesis layer averaged (25 ± 5) m;

in the spring, the value ranged 21 to 51 m, averaging (35 ± 10) m. In winter, this layer contains 12 mg·m^{-2} of Chl, which is 63 % of the integral value in the UML. In other words, 37 % of Chl from its total content is outside the photosynthetic zone. In spring, the total Chl content in the photosynthetic zone averages 7 mg·m^{-2}, and all of it is in the euphotic layer. In the spring of 2019, the stability of the water column was higher than in the spring of 2016; the UML thickness averaged (9 ± 4) m; temperature and density gradients remained at the same level. Meanwhile, a decrease in the UML thickness did not result in an increase in Chl concentration in the surface layer. At most stations, unimodal vertical distribution of Chl was observed. In the 0–20-m layer, its content varied slightly; deeper, an increase was registered, with a maximum at 30–48 m, being on average (38 ± 6) m (Fig. 3). As a rule, Chl maximums were recorded at a depth, where 0.2–1.0 % of light from the surface penetrates. Chl concentration at its maximum reached 1.23 mg·m^{-3} and was on average 2.8 times higher than Chl content in the UML. The maximums are not related to temperature and density gradients; they may result from algae adaptation to low light intensities, which is possible only with weak turbulent mixing.

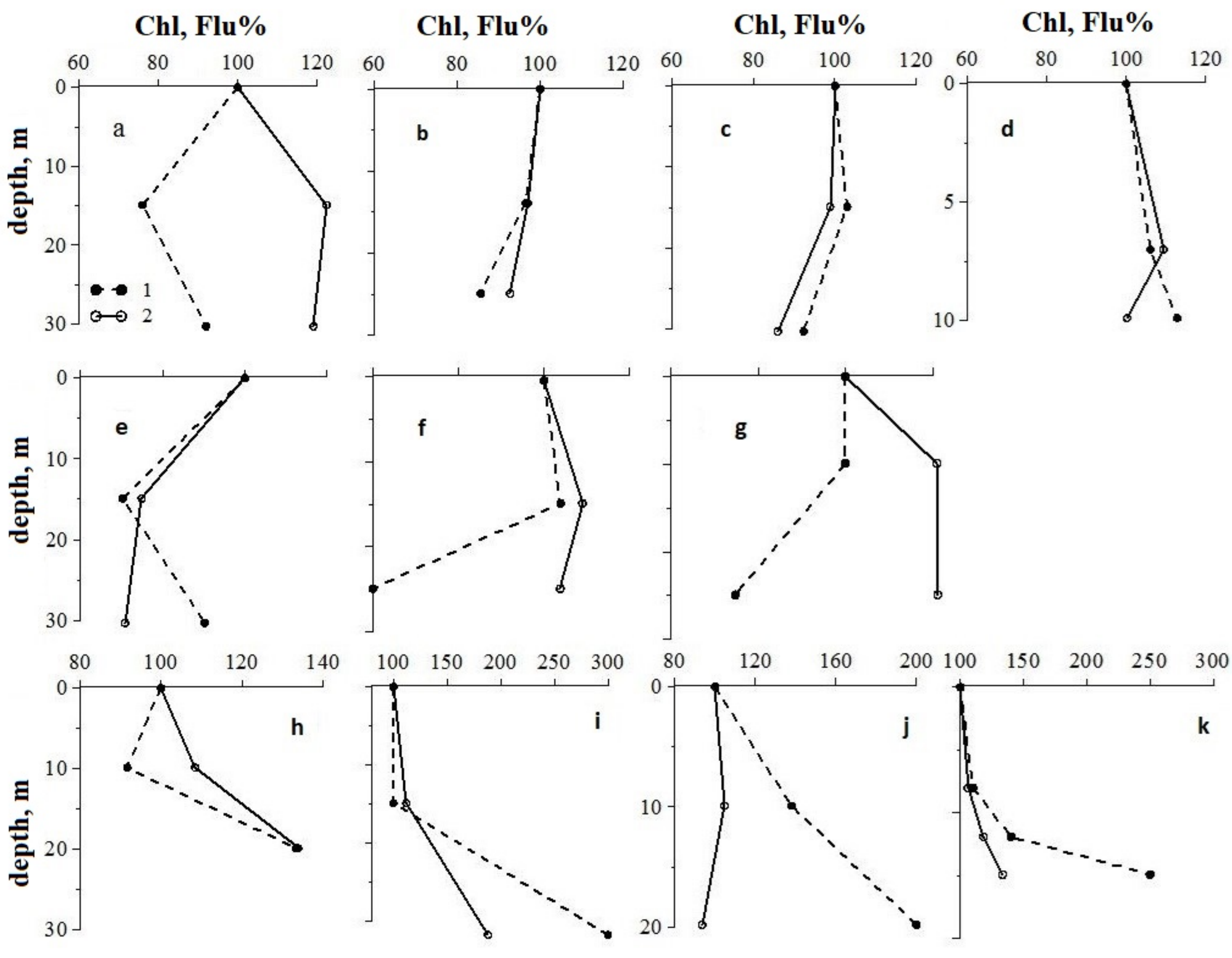

Fig. 2. Vertical distribution of chlorophyll *a* concentration (1) and fluorescence (2) in relative units (% of surface values) in January – February 2016 (a – at Cape Tarkhankut; b – in the Kalamitsky Bay; c – at Cape Fiolent; d – off the coast of Yevpatoriya; e, f – in Yalta area; g – in Alushta area) and at the end of April 2016 (h, i – in the Karkinitsky Bay; j – in the Kalamitsky Bay; k – off the coast of Yevpatoriya)

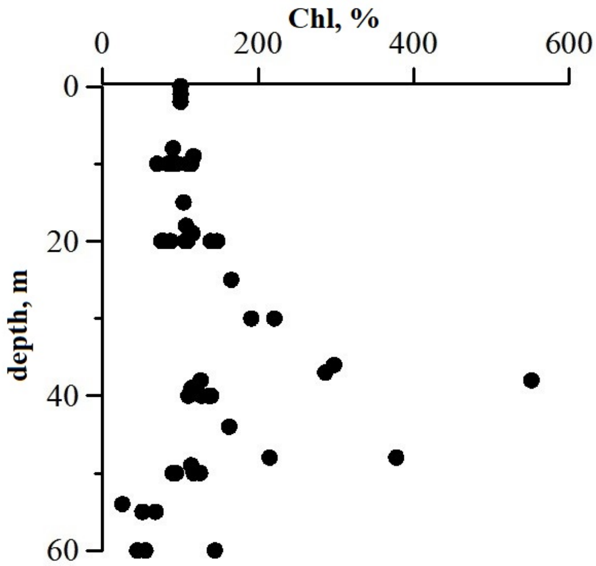

Fig. 3. Vertical distribution of chlorophyll *a* concentration in relative units (% of surface values) in spring 2019

It is apparent from the above data, that in spring the interannual differences in Chl content in the UML amounted 1.5–2.0 times for the western and southern sea areas. During that period, a vertical Chl structure with a depth maximum begins to form. In some cases, algae are able to adapt to extremely low irradiance (0.06 mol·m^{-2}·day^{-1}). Off the southern coast of Crimea, Chl concentration in the photosynthetic zone and outside it was the same; in the eastern area, only 30 % was in the irradiance zone.

In winter, at stations within the depth range of 16–50 m, the UML in 70 % of cases extended to the bottom; at 2 stations, it was at a depth of 14 and 31 m. At the same time, vertical distribution of Chl content was uniform only in 60 % of cases, and in the rest it either increased with depth or decreased. At stations within the depth range of 50–100 m, the lower boundary of the UML either reached the bottom or was at 42–53 m. When the UML reached the bottom, vertical distribution of Chl was uniform, or concentrations were the highest in the surface layer and decreased with depth.

Phytoplankton production estimates. The main production estimates of the phytoplankton community varied considerably in winter and spring (Table 2). In winter, phytoplankton physiological activity was low: primary production averaged 94 mg C·m^{-2}·day^{-1}, and daily production/biomass ratio (P/B) for the photosynthesis layer was 0.2. At the same time, the values of phytoplankton maximum specific growth rate and Chl concentration were relatively high. Low intensity of solar radiation, minimum temperature, and relatively shallow depth of the photosynthetic zone were the main limiting factors: because of them, algae in the photosynthetic zone divided once every 5 days.

In spring, mean intensity of solar radiation increased almost 4-fold, and the thickness of the photosynthetic zone increased 1.4 times on average. As a result, in 2016, the values of primary production and daily P/B ratio increased on average 2 times compared to those in winter. In 2019, primary production and biomass in the water column almost doubled compared to that of the spring of 2016; it resulted in P/B ratio and phytoplankton maximum specific growth rate remaining at the same level.

It allows us to conclude that the change in production, biomass, and maximum phytoplankton growth rate in the winter-spring period are not always synchronized. In spring, in the photosynthetic zone, algae divide approximately once every 2 days. Values of P/B and maximum specific growth rate differ insignificantly, which indicates that the onset of light saturation by the growth rate is observed at extremely low irradiance.

Table 2. Phytoplankton production estimates in the coastal waters of Crimea in the winter-spring period (numerator denotes minimum and maximum values; denominator denotes mean value ± standard deviation)

Season	PP, mg C·m^{-2}·day^{-1}	B, mg C·m^{-3}	B_i, mg C·m^{-2}	P/B, day^{-1}	μ, day^{-1}
Winter (2016)	49.8–143.3 / 93.9 ± 29.2	10.4–26.9 / 15.8 ± 4.3	218.0–659.3 / 412.1 ± 127.3	0.21–0.24 / 0.23 ± 0.01	0.59–0.73 / 0.66 ± 0.04
Spring (2016)	50.6–315.1 / 174.1 ± 71.9	4.7–18.0 / 11.8 ± 4.5	118.2–735.1 / 411.1 ± 200.1	0.35–0.52 / 0.44 ± 0.07	0.41–0.68 / 0.50 ± 0.08
Spring (2019)	208.2–522.4 / 309.1 ± 123.9	14.2–36.9 / 22.4 ± 9.0	450.5–1283.4 / 752.1 ± 353.8	0.39–0.46 / 0.44 ± 0.03	0.49–0.58 / 0.55 ± 0.03

Note: PP is phytoplankton integral primary production; B is phytoplankton mean biomass in the photosynthetic zone; B_i is integral biomass in the photosynthetic zone; P/B is daily production/biomass ratio for the photosynthetic zone; μ is phytoplankton maximum specific growth rate.

DISCUSSION

In the coastal waters of Crimea, Chl concentration in the UML in winter varied within narrow limits, averaging (0.47 ± 0.12) mg·m^{-3}. These values are 2.0–2.5 times lower than in deep-water areas (Finenko et al., 2017). Discrepancies in Chl values can result from different mechanisms of nutrient input into the photosynthetic zone. In the deep-water area, they come mainly with the rise of deep water, whereas in the coastal areas they inflow due to coastal runoff and mineralization of organic matter by heterotrophs. In winter, at low water temperatures, their metabolism is minimal, which results in a low mineralization rate. The weak flow of nutrients determines low Chl concentrations and phytoplankton biomass values in the coastal area. On the contrary, in deep-water areas, the water column stability decreases in winter, and dynamic activity of water increases; as a result, favorable conditions are created for the nutrient input into the photosynthetic zone.

In winter, the thickness of the mixed layer in Crimean coastal waters reached 75 m. Under these conditions, maximum Chl content was registered, and three types of its vertical distribution were observed. At most stations (60 %), it was uniform. At the other stations, maximum Chl content either increased with depth or decreased. During this period, deep-water areas are characterized by a uniform distribution of Chl in the UML (30–40 m), which is limited by the main pycnocline (Finenko et al., 2005). Below the mixed layer, Chl concentration decreases sharply.

In spring, a relatively high interannual variability of Chl content was observed in deep-water areas, with mean values in April varying, according to satellite data, 0.28 to 1.48 mg·m^{-3} (Finenko at al., 2014). In the coastal areas, variability of Chl concentration during this period was lower, with mean values within the range of 0.19–0.33 mg·m^{-3}. At this time, the UML decreases on average 3.5-fold compared to winter value, and the stability of the water column increases. These conditions are believed to be favorable for spring development of phytoplankton (Chiswell, 2011); however, in the coastal waters of Crimea in 2016, it was not registered. The results of hydrochemical measurements showed that the amount of inorganic nitrogen and phosphorus compound in the UML is low: mean nitrates concentration was (0.21 ± 0.11) μM, and phosphates one – (0.04 ± 0.02) μM. In the Black Sea, the Michaelis – Menten half-saturation constants (Ks) for nitrates in spring are on average (0.15 ± 0.05) μM (Krivenko, 2008), and for phosphates – (0.035 ± 0.010) μM (Parkhomenko, 2009). As can be seen, concentrations of these substances in water and Ks values are approximately the same. Therefore, they could have a limiting effect on the development of phytoplankton.

In spring, a depth Chl maximum begins to form in the coastal and deep-water areas (Finenko et al., 2005). During this period, the number of stations with a uniform distribution of Chl was 2 times less than in winter; at the other stations, the distribution was mainly unimodal. The depth maximum was recorded at mean temperature of (9.0 ± 0.6) °C and conditional density of (14.3 ± 0.2); it was on average 2.8 times higher than Chl concentration in the UML. According to the results of fluorescence measurements in the southern sea area, the maximum fluorescence intensity was observed at depths with temperature of (6.9 ± 0.3) °C and conditional density of (14.4 ± 0.1); the maximum fluorescence intensity was on average 2.7 times higher than that near the surface (Krivenko, 2008). The location of the depth maximum was closely related to the boundary of the nitratocline layer. In general, in the southern sea area and off the coast of Crimea, the depth maximum is at the same conditional density and has the same intensity of development; it is not related to density gradients.

Phytoplankton maximum specific growth rate depends on abiotic factors, as well as on size and taxonomic composition of phytoplankton (Chen & Liu, 2010). In the coastal areas, the values of the specific growth rate, calculated for the layer with optimal light conditions, varied within narrow limits during the study period. In winter, coccolithophore *E. huxleyi*, with a small cell size, predominated, and the maximum growth rate was on average (0.66 ± 0.04) day^{-1}. Generally, in spring, after mild winters, relatively large algae prevailed: at half of the stations, it was diatom *P. calcar-avis*, and at quarter – dinoflagellates of the genus *Ceratium*. With the given taxonomic composition of the phytoplankton community, the maximum growth rate decreased and averaged (0.50 ± 0.08) day^{-1}; daily P/B ratio for the photosynthesis layer increased on average 2 times. In winter, the rate of algae division is 3 times lower in the photosynthesis layer than that near the surface. In spring, these values differed insignificantly. One of the reasons for the multidirectional change is as follows: in winter, intensity of solar radiation is low, and algae growth rate rapidly decreases with depth. In spring, intensity of solar radiation increases several times, and the growth rate in the photosynthetic zone changes very little; as a result, P/B ratio turns out to be higher than in winter and approaches the values of the maximum growth rate. The maximum values of the growth rate, recorded in January – April in the Sevastopol Bay (Finenko et al., 2017), and those calculated by us in the coastal waters of Crimea were the same, while the taxonomic composition of the phytoplankton community was different. In the bays near Sevastopol in February – April, with the predominance of diatoms, the maximum growth rate varied 0.40 to 0.75 day^{-1}, averaging 0.50 day^{-1}; in the open coastal area opposite the Kruglaya Bay, it was slightly higher: on average 0.85 day^{-1} (Stelmakh et al., 2009). In the Sevastopol Bay, with dinoflagellates predominating in the community, the growth rate was on average 1.5 times lower than with the predominance of diatoms (Stelmakh, 2016). Thus, the values of the specific growth rate, obtained by the dilution method and calculated by us, proved to be quite close. The previously developed model for assessing phytoplankton specific growth rate can be used for rapid determination of the functional activity of the phytoplankton community.

Conclusions:

1. In winter, in the coastal waters of Crimea, chlorophyll *a* concentration and the depth of the upper mixed layer are the highest, and Chl content in the UML does not significantly differ at the western, southern, and eastern coast. During that period, in the studied water area, the coccolithophore *E. huxleyi* mostly predominated. In spring, Chl concentration and the depth of the UML were 2–3 times lower than in winter. In March – April, in different years, either dinoflagellates and diatoms or coccolithophores, dinoflagellates, and diatoms prevailed.
2. In winter, vertical distribution of Chl concentration at most stations was uniform. In spring, unimodal profiles with a depth maximum prevailed, location of which was not related to temperature and density gradients; Chl content was on average 3 times higher than in the UML. Generally, relative changes in Chl concentration and fluorescence with depth have the same character. Vertical profiles of Chl fluorescence were less variable than the profiles of its content; for the entire dataset, no reliable correlation was revealed between them.
3. The values of phytoplankton production and daily P/B ratio increase from winter to spring. The values of integral production, biomass, and specific growth rate vary disproportionately to each other. Functional estimates of the phytoplankton community in the coastal and deep-water areas are approximately the same. In spring, in the photosynthetic zone, algae divide almost once every 5 days. P/B ratio and maximum specific growth rate values differ insignificantly, which indicates as follows: the onset of light saturation by the growth rate is observed at extremely low irradiance.

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РАЗВИТИЕ ФИТОПЛАНКТОНА В ЗИМНЕ-ВЕСЕННИЙ ПЕРИОД В ПРИБРЕЖНЫХ ВОДАХ КРЫМА

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Исследование фитопланктона в зимне-весенний период имеет важное значение для изучения особенностей его годовой динамики и функционирования экосистемы Чёрного моря в целом. Состояние фитопланктона в шельфовой зоне в зимне-весенний период по сравнению с таковым в летне-осенний сезон изучено слабо, поэтому проведение подобного исследования особенно важно для решения ряда проблем, связанных с продуктивностью конечных звеньев пищевой цепи, формированием гидрохимического режима вод и циклом углерода в море. Цель работы — оценить влияние сезонных условий на развитие фитопланктона и его продукционные показатели в зимне-весенний период в прибрежных водах Крыма. В статье представлены результаты исследований гидрофизических (температура, плотность, относительная прозрачность воды) и биологических параметров (концентрация хлорофилла *a*, его флуоресценция, таксономический состав и продукционные характеристики фитопланктона) в шельфовой зоне Чёрного моря в январе — апреле 2016–2019 гг. Исследования проведены на 50 станциях, расположенных в прибрежных водах Крыма от Каркинитского залива до Керченского пролива. Концентрация хлорофилла *a* определена стандартным флуориметрическим методом, видовой состав — с помощью микроскопирования; удельная скорость роста фитопланктона рассчитана по разработанной ранее модели. Зимой (январь — февраль) концентрация хлорофилла *a* и глубина верхнего квазиоднородного слоя были максимальными (0,42–0,52 мг·м$^{-3}$ и 44–58 м соответственно), весной (март — апрель) — в 2–3 раза ниже. В январе — феврале доминировала примнезиевая водоросль *Emiliania huxleyi* (Lohmann) W. W. Hay & H. P. Mohler, 1967; в марте — апреле в разные годы преобладали динофитовые и диатомовые водоросли либо примнезиевые, динофитовые и диатомовые. Зимой вертикальное распределение хлорофилла *a* на большинстве станций было равномерным; весной преобладали одномодальные профили с глубинным максимумом, расположение которого не было связано с градиентами температуры и плотности. Относительное изменение концентрации хлорофилла *a* и флуоресценции с глубиной имело, как правило, одинаковый характер. Продукция фитопланктона и суточный коэффициент P/B (production/biomass ratio) повышались от зимы к весне. Корреляция между величинами интегральной продукции, биомассой и максимальной удельной скоростью роста водорослей отсутствовала. Максимальная удельная скорость роста была наименее изменчивым показателем. В течение зимне-весеннего периода водоросли в зоне фотосинтеза делились в среднем 1 раз в 2–5 суток.

Ключевые слова: таксономический состав, численность и биомасса фитопланктона, хлорофилл *a*, флуоресценция, максимальная удельная скорость роста водорослей, температура, плотность воды, Чёрное море