Article

Annual Dynamics of Phytoplankton in the Black Sea in Relation to Wind Exposure

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Abstract: Studies of the annual dynamics of phytoplankton in the NE Black Sea at two stations on the shelf and the continental slope were conducted in 2016, 2017, and 2019. The species composition of phytoplankton has not undergone significant changes compared to previous decades. The coccolithophore *Emiliania huxleyi*, small flagellates, and diatoms determined the abundance of phytoplankton; and diatoms, coccolithophores, and dinoflagellates determined the total biomass. The annual dynamics of the satellite-derived chlorophyll-a showed peaks in spring and autumn, and sometimes in summer. During the stratified water column period, strong winds in most cases led to a detectable increase in chlorophyll-a. The annual dynamics of phytoplankton followed the pattern: small diatoms (spring) → coccolithophores (late spring, early summer) → large diatoms (summer, autumn). Such a pattern was typical for the previous decades. Coccolithophores dominated in weak SE winds, diatoms in NE winds. The combined effect of sustained offshore wind and strong current can cause diatom blooms during stratified water, even if the wind velocity is moderate.

Keywords: phytoplankton; Black Sea; species composition; wind; diatoms; dinoflagellates; coccolithophores

Citation: Silkin, V.; Mikaelyan, A.S.; Pautova, L.; Fedorov, A. Annual Dynamics of Phytoplankton in the Black Sea in Relation to Wind Exposure. *J. Mar. Sci. Eng.* **2021**, *9*, 1435. <https://doi.org/10.3390/jmse9121435>

Academic Editor: Carmela Caroppo

Received: 31 October 2021

Accepted: 9 December 2021

Published: 15 December 2021

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1. Introduction

Marine phytoplankton play a decisive role in the functioning of the biological carbon pump, which is responsible for the transfer of atmospheric carbon to the deep layers of the ocean [1,2]. The ocean is the primary carbon depositor [3] and is an essential regulator of the planet's climate [4,5]. Atmospheric carbon dissolved in water is absorbed by phytoplankton during photosynthesis; as a result, organic compounds are synthesized, which determine the functioning of the organic pump. However, there are species of phytoplankton—coccolithophores, which, in addition to creating organic matter, convert inorganic carbon into calcite, forming the so-called carbonate pump. In the ocean, diatoms are mainly responsible for the first pump, and coccolithophores are responsible for the second [6–8]. Therefore, the dominance of one or another component of phytoplankton determines the nature of the biological pump. The annual dynamics of phytoplankton exhibit pronounced seasonality; there is a regular recurring change of dominants. Without identifying the regulators that determine the shift of dominants, it is impossible to understand the basic pattern of the formation of the phytoplankton structure. This task is not trivial since there are seasonal and interannual trends in structural changes in phytoplankton and many potential regulators. This problem can only be successfully resolved with the help of regular and long-term field and remote sensing studies of the annual dynamics of phytoplankton. Potential regulators of phytoplankton dynamics can be divided into abiotic and biotic. The first includes the nutrients concentration, irradiation, and turbulence. The consensus of opinion is that nitrogen limits production in marine ecosystems [9,10]. The classical concepts of regulating the annual dynamics of phytoplankton are based on the change of mixing regimes in the ocean and the associated vertical transport of nutrients [11]. Light intensity can also shift the structure of phytoplankton [12].

The central biotic regulators of phytoplankton structure and productivity are considered to be the pressure of herbivores [13–15] or the influence of viruses [16]. Recently, hypotheses have emerged that suggest a change in the structure of phytoplankton due to non-static predator–prey dynamics [17,18].

However, climate change also significantly determines the structural and functional organization of phytoplankton [19]. Climate change is not just temperature change; it can change meteorological parameters, the most important of which is wind [20]. The wind speed regulates the intensity of the Ekman pumping, and the wind direction significantly impacts the nature and properties of macro- and mesoscale hydrodynamics. These physical processes determine the rate of flow of nutrients into the photic zone while simultaneously changing the depth of the seasonal thermocline and, as a result, the light regime in the upper mixed layer (UML) [21]. The structure of phytoplankton in the Black Sea is significantly determined by the speed and direction of the wind [22]. Therefore, long-term phytoplankton data need to be supplemented with data from meteorological observations.

The Black Sea is an inland body of water with a relatively weak influence from the ocean, affecting the sea's salinity, which does not exceed 19 on the surface [23]. The trophic status of this reservoir has a latitudinal zonality, 80% of river runoff is concentrated in the western part, which is the most eutrophicated [24–27]. In the eastern part, the phytoplankton biomass is significantly lower [28].

A feature of the hydrodynamics of the Black Sea is the presence of the Rim Current (RC), which runs along the periphery along the continental slope. It has a cyclonic circulation and forms the central Western and Eastern cyclonic gyres as well as mesoscale cyclonic and anticyclonic eddies along the slope [29–31]. The current speed of the RC ranges from 0.1 to 1 m s^{−1} and is determined by the intensity and direction of the winds. The dominant wind directions in the northeastern Black Sea are northeast and southeast [32].

Considerable data on the species composition, abundance dynamics, and biomass of phytoplankton have accumulated from the Black Sea. However, most of this material relates to the western part of the sea [33,34]. Studies conducted in the last century in the northeastern part of the Black Sea were episodic. The exception is the long-term observations of the structure of phytoplankton in Novorossiysk Bay [35]. There are two examples of annual surveys to study the structure of phytoplankton in coastal and adjacent waters near Gelendzhik [36] and Anapa [37]. These studies have shown that 2–3 peaks of phytoplankton abundance and biomass are observed in these areas. The first spring bloom is in February–March and is determined by the intensive growth of diatoms. The second bloom is in autumn, less powerful, and also associated with the growth of the diatoms. Sometimes there is a third peak both in bays and in the open sea due to the growth of either diatoms or dinoflagellates.

Studies of recent decades have shown that in the 2000s, there was a significant transformation of the structure of phytoplankton [38,39]. Spring blooms of diatoms have become less intensive; simultaneously, the role of the coccolithophore *Emiliania huxleyi* has increased, the blooms of which began to be recorded practically every year in late spring or early summer. The role of dinoflagellates has decreased, and all changes in the composition of dominants are now taking place within the framework of the “diatoms–coccolithophores” system [40,41].

In addition, intensive autumn–winter growth of coccolithophores was recorded in the open waters in November–February [33,42–44]. Winter diatom bloom was observed in February [28].

Remote sensing methods based on measuring the concentration of chlorophyll-a (Chl) and particulate inorganic carbon (PIC) have significantly supplemented the possibility of the study of the seasonal changes and interannual trends of phytoplankton [45–48]. Algorithms for calculating the coccolithophore abundance from satellite data have been developed for the Black Sea [49], making it possible to differentiate diatom and coccolithophore blooms. However, these methods have limitations and work well with the support of ship observations.

This work continues the previous studies of phytoplankton seasonal dynamics in the northeastern part of the Black Sea [22,41]. We analyze the annual dynamics of phytoplankton during three years. For the shelf and continental slope areas, we used field data on phytoplankton composition. For the area adjacent to the continental slope, we used Chl obtained from a satellite scanner. A distinctive feature of this work is the emphasis on meteorological factors, namely, the influence of wind speed and direction on the amount and structure of phytoplankton.

2. Methods

2.1. Field Sampling

Phytoplankton samples were collected on a standard section from Golubaya Bay (near the city of Gelendzhik) from the R/V Ashamba. Two stations were located above a sea bottom depth of 100 and 500 m (Figure 1). The number of sampling depths varied from 6 to 8. The vertical distribution of phytoplankton down to a depth of 70 m was studied in layers: in the UML, the seasonal thermocline (ST), and sub-thermocline layer. A total of 251 phytoplankton bathometric samples were collected and processed. The CTD “Sea Bird” (Sea-Bird Electronics, Inc., Bellevue, WA, USA) was used for hydrophysical measurements. Water samples were collected using 5-L Niskin bathometers. Samples were fixed with neutralized formaldehyde, and the final concentration was 0.8–1.0%. Samples were stored in the dark, at room temperature, for a minimum of two weeks and slowly decanted after that [50,51]. Species identification was based on cell morphology [52,53]. Species names were checked <http://www.algaebase.org> and <http://www.marinespecies.org> (accessed on 15 October 2021).

Figure 1. Map of the study area. The dots show the locations of two stations at 100 m and 500 m. The rectangle shows the area for the satellite scanner’s estimates of chlorophyll-a concentration.

A method based on the geometric shape of cells was used to calculate biovolume [50,51,54]. Wet weight was calculated from the cell biovolume, assuming cell density was equal to 1 g mL^{-1} . Biomass was expressed in units of wet weight (mg m^{-3}). A species was considered dominant if its biomass was more than half of the total phytoplankton biomass at a given station. The second most biomass species was considered subdominant. The bloom level was taken as a cell abundance equal to $10^6 \text{ cells L}^{-1}$, or a total phytoplankton biomass equivalent to 1000 mg m^{-3} [55].

2.2. Remote Sensing Data

To study the effect of wind on the growth of phytoplankton, data on the Chl were used. They were obtained using the MODIS-Aqua satellite scanner (<http://oceancolor.gsfc.nasa.gov>, accessed on 15 October 2021, 13, resolution 4 km) in 2016, 2017, and 2019. We used 8-day composite images since such temporary averaging allows data to be available for most of the year, avoiding the problem of cloudy days. Chl measurements were carried out in a rectangular region located in the Gelendzhik area along the coast of the North Caucasus ($44^\circ 35.6' \text{ (N)}$, $37^\circ 52.1' \text{ (E)}$; $44^\circ 26.6'$, $38^\circ 06.7'$; $44^\circ 23.8'$, $38^\circ 02.5'$; $44^\circ 32.8'$, $37^\circ 48.0'$) at a distance of 4–5 km from the coast. This region is a continental slope.

The Black Sea is a region with a high concentration of organic matter that distorts the Chl signal. In this regard, several local algorithms have been developed to extract Chl from satellite images [56]. In the current study, we used an algorithm developed on the basis of Chl data collected in the northeastern part of the sea [57] where our study region was located:

$$\text{Chl} = 0.354 \times \text{Chl_sat} - 0.003 \quad (1)$$

where Chl_sat is the concentration of chlorophyll-a according to MODIS-Aqua images.

2.3. Meteorological Data

Data on wind speed and direction for the analysis of its effect on shelf phytoplankton were taken at the Gelendzhik meteorological station. For open waters, the data on wind speed were obtained from the Anapa meteorological station (<http://pogoda-service.ru>, accessed on 15 October 2021). This station is located in a flat valley, which the North Caucasus does not shelter, and therefore more adequately reflects wind conditions in the open sea. To identify the dominant winds, progressive vector diagrams (PVD) were constructed using MATLAB 7.1.0, according to conventional methods [58].

3. Results

3.1. Wind on the Shelf and Adjacent Area

The main contribution to the wind on the shelf was made by the NE and SE winds (Table S1). The first determine the wave dynamics for most of the year, and they prevailed in the second half of the year. The second occur in March, April, and May. The wind regime usually changed in mid-June. In 2016, the E–SE winds became dominant in February; in June, the NE winds prevailed. In 2017, compared to 2016 and 2019, the overall repeatability of E, SE, and W winds was relatively high over the year; N and NE winds had less repeatability.

The highest wind speed was observed in January and February, 2016 and 2017; in 2019, no storms were recorded. The lowest wind speed is usually in the summer. June 2017 was characterized by absolute windlessness, while in 2016, a wind of a relatively high intensity was recorded.

3.2. Hydrological Structure

In the winter months, when the air temperature is below the water temperature, the sea surface cools, and, as a result, vertical convection develops (Figure 2). In addition, storm winds contribute to intensive vertical mixing, recorded in the first two months. Usually, after mid-February, the sea surface warms up under the influence of an ever-increasing influx of solar radiation and warm air masses. The ST is formed usually in mid-March,

separating the UML and the underlying colder and denser waters. In summer, there is a deepening of the lower border of the ST. This layer is broken down in late autumn, usually mid-November, due to the decrease in temperature and increasing wind-induced mixing.

Figure 2. Vertical distribution of temperature at the station above a depth of 500 m in 2016, 2017, and 2019.

3.3. Chl Dynamics in the Open Waters

During three years of observations, Chl varied from maximum values in winter to minimum values in summer (Figure 3). The annual trend corresponded best to the second-degree polynomial. This fit was good in 2016 ($r = 0.73$) and 2019 (0.84) and worse in 2017 (0.39). The latter could be due to the lack of data since it was cloudy for many 8-day periods. An annual trend line was used as a mean to estimate Chl anomalies, which were correlated with periods of strong wind exposure.

Figure 3. Seasonal dynamics of chlorophyll-a (Chl) concentration against the background of strong wind (number of days with wind $> 8 \text{ m s}^{-1}$ in an 8-day period) during 2016, 2017, and 2019. The trend line is a polynomial function. Vertical gray lines show the boundaries between hydrological periods with a non-stratified (winter) and stratified (spring, summer, autumn) water column. Cycles indicate the coincidence of strong wind effects and Chl increases above the annual trend line.

Weak wind does not significantly increase turbulent mixing in the water column. To increase intensive mixing in the UML and pulsed turbulent mixing in the thermocline and below, a strong wind is required for a more or less long period. In this regard, we analyzed the duration of strong winds of more than 8 m s^{-1} during 8-day periods corresponding to the 8-day images of the Chl.

There are two fundamentally different hydrological seasons in the Black Sea with an unstratified (winter) and stratified (spring, summer, autumn) water column. Several strong wind events (from 3 to 4) were observed during the stratified period each year.

During each storm, an average daily wind speed of more than 8 m s^{-1} was observed for 1–7 days. In most cases (10 out of 12), Chl showed a positive anomaly (Figure 3, cycles). In two cases, in October 2016 and August 2017, a one-day storm coincided with a negative Chl anomaly. A correlation was found between the number of days with strong wind during 8-day periods and the Chl anomaly. It was weak, but significant ($r = 0.3$, $n = 84$, $p < 0.005$). In contrast to the stratified period, no correlation was found between these parameters in the unstratified period.

3.4. Species Composition of Phytoplankton in the Shelf and Slope Areas

In all years, phytoplankton was characterized by the same taxonomic composition (Tables 1 and 2). The high diversity of the community (up to 114 species) was formed primarily by dinoflagellates, which annually dominated the number of species (up to 72, 60–69% of the total number of species). The *Protoperidinium* genus was represented annually by a large number of species (up to 17). The interannual variations in the species composition of dinoflagellates were small—Jaccard index of similarity of the species structure reached 90%.

Table 1. Taxonomic composition of phytoplankton abundance *.

Taxon	2016		2017		2019	
	N	%	N	%	N	%
Bacillariophyceae	14	18.9	27	23.7	25	27.5
Dinophyceae	51	68.9	74	64.9	55	60.4
Prymnesiophyceae	4	5.4	6	5.2	5	5.5
Cryptophyceae	1	1.4	1	0.9	1	1.1
Dictyochophyceae	3	4.0	4	3.5	3	3.3
Chlorophyceae	-	-	1	0.9	1	1.1
Euglenophyceae	1	1.4	1	0.9	1	1.1
Total	74	100	114	100	91	100

* N—number of species; %—the proportion of total number of species.

In second place, in terms of number of species in all the years were diatoms (up to 27 species). The level of similarity of diatom species between the years was significantly lower—within 50%. Interannual differences were mainly determined by variations in the number of randomly occurring planktonic species from the genera *Navicula*, *Nitzschia*, and *Amphora*. During the entire study period, the species of the genus *Chaetoceros* were not recorded in phytoplankton.

3.5. Cells Abundance

In all years, the abundance of phytoplankton was determined by the coccolithophore *Emiliana huxleyi* (April–early June), small flagellates with cells of 6–10 μm (June and August–September), and large centric diatom *Pseudosolenia calcar-avis* (summer maximum in July–August). (Table 2). The highest bloom of *E. huxleyi* over the slope was noted in June 2017 ($7.7 \times 10^6 \text{ cells L}^{-1}$) at a depth of 5 m. The minimum bloom of this species was recorded in April–May 2016 ($1.1\text{--}1.2 \times 10^6 \text{ cells L}^{-1}$) at the surface. Summer maximum abundance of *P. calcar-avis* differed significantly between years. The highest abundance of this species was recorded in August 2017 ($1.1 \times 10^5 \text{ cells L}^{-1}$). In other years,

the abundance of *P. calcar-avis* was an order of magnitude lower (1.0 and 2.1×10^4 cells L^{-1} in July 2019 and June 2016, respectively), although it still prevailed in terms of biomass.

Table 2. Abundance (cells L^{-1}) of dominant phytoplankton species in 2016, 2017, and 2019.

Species	2016	2017	2019
Dominants			
Small flagellates (size 6–10 μm)	2.1×10^6 June	8.4×10^5 June	1.0×10^6 June, August, September
<i>Emiliana huxleyi</i>	1.1 – 1.2×10^6 April–May	7.7×10^6 June	3.3 – 3.7×10^6 May–June
<i>Pseudosolenia calcar-avis</i>	2.1×10^4 June	1.1×10^5 August	9.6×10^3 July
<i>Pseudo-nitzschia delicatissima</i>	-	-	1.1×10^6 May
<i>Proboscia alata</i>	-	-	1.8×10^3 September
Sub-dominants			
<i>Thalassionema nitzschioides</i>	6.4 – 6.1×10^3 June, September	1.2×10^4 August	3.4×10^3 May
<i>Cryptomonas</i> sp.	-	2.3×10^4 September	3.6×10^4 June
<i>Gyrodinium fusiforme</i>	1.1×10^4 June	1.0×10^3 August	2.3×10^4 May
<i>Scrippsiella acuminata</i>	7.8×10^3 June	2.2×10^3 August	8.2×10^3 June
<i>Prorocentrum micans</i>	1.4×10^3 November	1.2×10^3 July	1.4×10^3 November
<i>Prorocentrum cordatum</i>	2.4×10^2 June, July, September	-	1.0×10^3 November
<i>Prorocentrum balticum</i>	-	-	4.4×10^3 May
<i>Pseudo-nitzschia delicatissima</i>	1.8×10^4 August	3.6×10^4 August	-

As for other diatoms, the small pennate diatom *Pseudo-nitzschia delicatissima* was only recorded as the dominant species in May 2019. Its accumulations (1.1×10^6 cells L^{-1}) were located at the lower boundary of the ST at a depth of 23 m. Another centric diatom, the large-celled *Proboscia alata*, was noted as part of the dominant complex (both in abundance and biomass) at the end of September 2019 (Table 2).

3.6. Biomass

In all years, maxima of the total phytoplankton biomass were characteristic of the upper 25–0 m water layer (2017, 2019, and 2016, respectively). The two highest biomass were recorded in June (1.4 g m^{-3}) and August 2017 (1.6 g m^{-3}) (Figure 4). In June, high biomass was formed by *Emiliana huxleyi*, whose contribution to the total biomass reached 96.5% (Figure 5). In August, the phytoplankton biomass was 98.5% formed by the large diatom *Pseudosolenia calcar-avis* (Tables 3 and 4, Figures 3 and 4). In 2019, this pattern persisted—coccolithophores and *P. calcar-avis* made the main contribution to the formation of the maximum total biomass (*E. huxleyi*, 88–95%, May–June; *P. calcar-avis*, 52%, July). However, the community's biomass was lower this year than in 2017 during the bloom period of coccolithophores (0.6 – 0.8 g m^{-3}) and during the growth of *P. calcar-avis* (0.6 g m^{-3}) (Figure 4).

Figure 4. Dynamics of phytoplankton biomass in the NE the Black Sea at the station above a depth of 500 m.

Figure 5. Taxonomic composition of phytoplankton biomass at the end of spring and in the early summer during the period of bloom of *Emiliania huxleyi* in 2016, 2017, and 2019.

Table 3. Monthly maximum of the total biomass (B, mg m^{−3}) of phytoplankton in 2016, 2017, and 2019.

Year	March	April	May	June	July	August	September	October	November	December
2016	456.3	245.9	236.6	317.4	166.3	143.4	506.8	110.8	95.3	92.0
2017		60.6		1428.5		1638.5	854.1			
2019		94.0	610.1	801.2	610.1	190.1	120.6	93.1	122.7	86.4

Table 4. Contribution (%) of diatoms, dinoflagellates, coccolithophores, and chrysophytes to the monthly maximum of the total phytoplankton biomass in 2016, 2017, and 2019. Values in bold show predominance of single species.

Taxon	March	April	May	June	July	August	September	October	November	December
2016										
Diatoms	1.0	0	0	5.8	0.6	4.6	0.7	3.1	6.5	0.1
Dinoflagellates	81.5	6.7	2.8	42.6	9.7	41.1	15.2	61.2	24.8	29.6
<i>E. huxleyi</i>	9.0	89.7	81.1	36.6	72.9	10.9	0	7.9	44.1	50.8
<i>Dinobryon balticum</i>	-	-	-	-	-	-	80.0	-	-	-
Small flagellates	5.8	2.8	12.7	13.0	14.1	32.6	16.7	14.8	20.2	8.0
2017										
Diatoms		0		0		98.5	97.2			
Dinoflagellates		4.8		0.9		0.9	1.2			
<i>E. huxleyi</i>		82.5		96.5		0.3	13.0			
Small flagellates		11.8		2.5		0.5	1.3			
2019										
Diatoms		4.8	0.35	1.2	52.0	14.0	5.0	0.7	18.3	
Dinoflagellates		20.3	9.2	11.3	23.0	37.3	17.3	7.0	54.3	
<i>E. huxleyi</i>		36.8	87.8	84.9	17.7	24.4	29.0	74.5	4.6	
Small flagellates		38.0	2.6	2.6	7.2	27.0	48.6	17.7	29.2	

In 2016, the maximum biomass was the lowest for all years (0.46 and 0.5 g m^{−3} in March and September, respectively) (Table 3). This was associated with a weak bloom of *Emiliania huxleyi* and small cell size of *Pseudosolenia calcar-avis*. The leading role in the biomass was played by small dinoflagellates of the spring complex (up to 82% of the maximum total biomass, March) and chrysophyte *Dinobryon balticum* (80%, September) (Table 4). As in 2017 and 2019, coccolithophores made a decisive contribution to the total biomass during their bloom period in April–May (up to 90%). However, the contribution of *P. calcar-avis* was insignificant (5.8%) during its maximum growth in June, whereas the bulk of the biomass was formed by dinoflagellates (42.6%).

3.7. Effect of Wind on Phytoplankton in the Slope Area

Phytoplankton biomass and its taxonomical composition were associated with storm periods and moderate but frequent winds or their absence (Figure 6). In June 2017, the high biomass consisted mainly of coccolithophores (84%). Before the sampling date of 7 June, daily winds were generally less than the 4-month average (4.3 m s^{−1}). In a highly stratified water column with a shallow UML (6 m), coccolithophores developed. The period of weak winds lasted from May to mid-July, which is confirmed by the prevalence of negative diurnal wind anomalies and a decrease in the cumulative sum of anomalies. After 15 July,

there were several 3–5 day periods with moderate wind ($5\text{--}7\text{ m s}^{-1}$). The general increase in the influence of wind is reflected in the rise in the cumulative sum of wind anomalies. On 15 August, the depth of the UML increased to 13 m indicating the result of the wind-induced mixing. Bloom of diatom *Pseudosolenia calcar-avis* was observed, which contributed 96% to the total phytoplankton biomass. After 22 August, the wind weakened, as evidenced by the decrease in the cumulative sum of wind anomalies. On 4 September, the depth of the UML was 20 m. However, the bloom ended, and the biomass of phytoplankton was low, although diatoms composed the bulk of biomass (63%).

Figure 6. Daily wind anomalies from average speed for 4-month (bars) and cumulative sum of wind anomalies (line) during the period from 12 May to 12 September 2017. The diagrams show the average biomass (mg m^{-3}) of the main groups of phytoplankton in the upper 10-m layer on 7 June, 15 August, and 4 September 2017 (data are shown by arrows).

4. Discussion

4.1. Wind Effect on Annual Chl Dynamics

There are two hydrological seasons in the Black Sea: unstratified and stratified. The most probable establishment of an ST (stratified period) occurs in mid-March, and its destruction (not stratified) in mid-November [59,60].

The data on chlorophyll concentration obtained by remote sensing methods show that, in general, the annual dynamics followed a U-shaped curve with a peak in spring and autumn and a minimum in summer. This corresponds to other researchers' data in the Black Sea obtained using direct and remote observation methods [29,45,61].

In the stratified period of the year, the growth of phytoplankton in the euphotic zone is mainly limited by nutrients. Wind-induced mixing of the UML increases the erosion of the upper thermocline, which usually increases the concentration of nutrients in the UML. In addition, the kinetic energy of mixing penetrates the thermocline and below, increasing turbulent diffusion and upward flow of deep nutrients into the photic zone [62]. As a

result, it promotes phytoplankton growth. However, this scheme works if the mixing is strong enough. In the Black Sea, a strong wind of more than 8 m s^{-1} with a total duration of 2–3 days per week determines the timing of the autumn bloom of phytoplankton [46]. In summer, the density gradients in the thermocline are the strongest. However, storms can destroy the thermocline. In July 2006, a strong 3-day wind of more than 10 m s^{-1} led to a deepening of the UML from 8 m to 22 m [63]. Our analysis showed that storms lasting from one to four days cause positive Chl anomaly in 83% of cases (Figure 2), which is in line with theoretical concepts.

It should be noted that our analysis was based on a rough comparison between a wind event and abiotic response. Eight-day periods may be too long or too short to detect an increase or decrease in Chl levels. For example, in some cases, the prominent rise in Chl was observed in the next period after the storm (Figure 3: April and October 2016, April 2017, and November 2017). Nevertheless, the obtained significant correlation between solid wind and Chl anomalies confirms the positive role of wind in stimulating the primary productivity of the basin during the period of water column stratification. It is known that very intense mixing during a powerful wind, such as a typhoon, dramatically increases the level of Chl [63,64]. It was previously shown that four successive storms in August 2015 caused an extreme bloom of phytoplankton in the Black Sea [43]. Our results showed that even a single period of strong winds regularly led to a detectable increase in Chl in the Black Sea. In the unstratified water period, the relationship between wind mixing and phytoplankton is reversed. During this period, the growth of phytoplankton is mainly limited by light. Thus, increasing the depth of the UML leads to a decrease in the cumulative illumination received by the cells and a decrease or prevention of phytoplankton growth. This follows from Sverdrup's fundamental Critical Depth Hypothesis [65].

Typically, the spring bloom of phytoplankton occurs at the end of winter, when convection stops and the formation of a seasonal thermocline reduces the depth of the UML. Sometimes, a near-surface bloom occurs before the appearance of a seasonal thermocline in the temporary upper layer, which forms if the wind is weak and mixing is suppressed [66,67]. In the Black Sea, due to strong vertical stratification, the phytoplankton bloom often occurs in winter. It was shown that calm weather in winter leads to creating a temporary thin upper layer in which phytoplankton grows. Strong winds also affect the spring bloom. For example, storms delay spring blooms on the Northwest European shelf [68]. Modeling has shown that increased wind mixing during the bloom period decreases its value in the polar and northern subtropical regions [69]. Although we did not find a significant negative relationship between solid winds and positive Chl anomaly for unstratified water, some examples show this pattern during the spring bloom period (Figure 3: February–early March 2016 and 2019).

4.2. The Structure of Phytoplankton

The taxonomic composition of phytoplankton in 2016, 2017, and 2019 did not change significantly compared to previous years. Diatoms and dinoflagellates made a decisive contribution to species diversity. Dinoflagellates were represented by the largest number of species, among which the genus *Protoperidinium* had the maximum number of species as in previous years [39]. A characteristic feature of the current research period was the complete absence of species from the genus *Chaetoceros*. In previous years, these species played a significant role in phytoplankton and were even dominant [22,39]. Since *Chaetoceros* species previously dominated phytoplankton in late spring at relatively high concentrations of nitrogen and silicate, their disappearance from phytoplankton may indicate changes in the hydrochemical regime.

The main role in the formation of phytoplankton abundance belonged to the coccolithophore *Emiliania huxleyi*; the maximum abundance was recorded in 2017 ($7.7 \times 10^6 \text{ cells L}^{-1}$). This value is slightly lower than the maximum abundance ($8.2 \times 10^6 \text{ cells L}^{-1}$) recorded in 2004 (our data), which indicates the continued favorable conditions for growth of this

species. It should be noted that the role of dinoflagellates in the formation of the subdominant complex has increased.

Phytoplankton biomass comprises mainly of three systematic groups—diatoms, coccolithophores, and dinoflagellates (Table 4). The role of dinoflagellates in the biomass has increased. The total phytoplankton biomass was determined by the growth of dinoflagellates in March and October 2016, and November 2019. In 2017, they did not play a significant role. The largest biomass was found in summer, and it was associated with the intensive growth of the large diatom *Pseudosolenia calcar-avis*. The maximum biomass of this species of 1.6 g m^{-3} was reached in August 2017. This value is almost two times lower than that we found earlier in August 2012 (3.3 g m^{-3}). The maximum biomass of coccolithophores was registered at the beginning of June 2017, and it was also slightly lower than in the same season of 2004. In general, biomass values observed in the current research may indicate a trend of decreasing eutrophication of the NE Black Sea.

4.3. Wind Regime

In the Black Sea, hydrological structure is determined by two meteorological parameters, namely air temperature and wind direction and speed [70]. Wind and thermal atmospheric conditions are responsible for hydrophysical processes in the upper layers, namely the formation of the ST in the spring–summer–autumn period and its destruction in winter.

The wind regime observed in 2016, 2017, and 2019 did not differ significantly from previous years, as seen from the progressive vector diagram (Figure 7). From 2010 to 2015, the annual cycle was dominated by NE winds. The wind direction changes in the spring months. The interannual differences were in the shift of the timing of the change of the wind regime.

Figure 7. Progressive vector diagrams of the monthly averaged wind in the research area for the period 2010–2015. Vectors between dots show the prevailing wind direction.

4.4. Annual Dynamics of Phytoplankton

The data obtained made it possible to identify the main pattern of the annual dynamics of phytoplankton. First of all, there are coccolithophores, which contribute mainly to biomass in late spring and early summer. The second and more productive component is large diatoms. Every year in summer and autumn, the large diatom *Pseudosolenia calcar-avis* causes the highest peak of phytoplankton biomass. Remote sensing shows that the most powerful peak in the Chl is observed every year in winter and early spring. Previous observations have shown that the small diatom *Pseudo-nitzschia delicatissima* develops in this period [22,28]. Thus, the annual dynamics of phytoplankton follows a pattern:

small diatoms (spring) → coccolithophores (late spring, early summer) → large diatoms (summer, autumn).

The first Chl maximum of the year associated with the bloom of small diatoms can be formed by different species depending on the place of sampling—bay, shelf, or open sea [23,28,35,37,71,72]. It was shown that over the past three decades, the pennate diatom *Pseudo-nitzschia delicatissima* is the most likely contributing species [22,28]. To date, several hypotheses explain the launch of this spring bloom. The most widespread with the longest history is the Critical Depth hypothesis [65] (Sverdrup, 1953), which explains the absence of bloom during winter. It follows that after the end of winter convective mixing, the depth of the UML becomes less than the compensation depth of population, when the growth rate is reached that exceeds the rate of total losses, bloom begins. This explains well the onset of bloom both in coastal waters and in the open ocean [73–75]. To date, there is criticism of this hypothesis, and a number of new hypotheses have been proposed, which are essentially some modifications of Sverdrup's theory [67,76–78]. The Pulse Bloom hypothesis is of particular interest since it explains bloom in winter and low biomass of small diatoms during spring bloom in the Black Sea [46]. Convective mixing and intense winds, usually recorded in January and February in the Black Sea [79], create supply of nutrients in the upper layers. The spring bloom begins at relatively high nitrogen and phosphorus concentrations and ends with a significant decrease, primarily in nitrogen concentration [22]. At the same time, the silicate concentration remains relatively high [22]. After the bloom of diatoms, the dominance passes to dinoflagellates, as was observed in March 2016. In April and May, phytoplankton biomass begins to be determined by coccolithophores, but they show maximum growth in late May and early June. Weak SE winds characterize this period; in June 2017, they were minimal, making it possible to raise the seasonal thermocline relatively high (7–10 m). In the UML, low nitrogen concentrations and a low nitrogen–phosphorus ratio (below the Redfield ratio) were observed at high silicate concentrations (up to 8 μM) [22]. This environment is a condition for accumulating of high biomass of coccolithophores in the UML, which was observed in 2017 and 2019 (Table 3, Figure 3).

Some hypotheses explain the dominance of large diatoms. They can be divided into biotic and abiotic factors. According to the first type of hypothesis, dominance is due to a narrowing of the spectrum of potential predators due to the size of large-celled diatoms compared to small-celled phytoplankton species [14,15,80]. In addition, the risk of virus attack on such large cells will likely be low [16]. However, this hypothesis cannot explain the complete absence of small diatoms, and why only one species remains in the community.

The central abiotic hypothesis states that large cells can accumulate nutrients and gradually use them in conditions of scarcity. Such species can dominate in the periodic provision of nutrients [22,81–84]. The weakness of this hypothesis is that such a mechanism can work for two–three cell generations (several days) [17], while the time between fluxes of nutrients may be longer. Indeed, during the dominance of large diatoms, the frequency of wind pumping can be more than one week. In all the years studied, the character interval between storms in the stratified period was 2–4 weeks (Figure 3).

In a dynamic environment with a deep thermocline, the light intensity varies widely from photoinhibition level in the near-surface layer of water to light limitation at the ST lower boundary. According to another hypothesis, large diatoms can change the specific light absorption coefficient due to moving chloroplasts [12]. This ability allows them to change the amount of energy absorbed depending on the intensity of the light. A low light absorption coefficient in near-surface waters avoids the destruction of chloroplasts; a high coefficient makes it possible to absorb light at low light fluxes effectively. This mechanism seems to be one of the main reasons for predominating large diatoms in the summer-autumn period. Another essential condition is an increased flow of deep nutrients to the photic zone due to intense mesoscale dynamics in these seasons [85].

Our data show that the dynamics of Chl were the opposite to the dynamics of the phytoplankton biomass (Figures 2 and 3). In summer, we observed the lowest Chl while the biomass was at its maximum. This is due to two factors. The first is the absorption of light by the cell depending on cellular Chl and the cell size [86,87]. With an increase in cell size, the relative cellular Chl decreases [88,89] while the ratio of the carbon-chlorophyll ratio increases [90]. Secondly, the absorption of light by the cell is determined by the so-called package effect; it is associated with self-shading [91,92]; with an increase in cell size, the package effect reduces the specific light absorption coefficient [93]. These dependencies indicate that the satellite-derived Chl does not correctly reflect the annual dynamics of phytoplankton biomass in the Black Sea [90], where the summer growth of large diatoms results in a high total phytoplankton biomass.

4.5. Wind Effect on Annual Dynamics of Phytoplankton

The decisive influence of strong winds on the intensive mixing of the UML is well known, which, as a rule, leads to enrichment with nutrients that stimulate the growth of phytoplankton. Strong winds determine the timing of the autumn bloom of phytoplankton [46,66]. During the period of water stratification, typhoons and strong storms cause the development of phytoplankton [63,64]. The effect of moderate winds or calm has been less studied. In the Black Sea, May–June is the most windless month. This pattern is illustrated by wind statistics in 2017 (Figure 6). This period is favorable for the growth of coccolithophores, which is observed every year and is associated with strong stratification and low nitrogen concentration [22,41]. Thus, the absence of storms determines the conditions for the predominance of coccolithophores in phytoplankton during this period of annual succession (Figure 5).

The increase in the average wind velocity in the second half of summer is not associated with an increase in the frequency of storms (Figure 3). However, the cumulative effect of moderate wind mixing can cause the bloom of diatoms (Figure 6). In addition, prolonged exposure to wind increases the Rim Current velocity [70]. The higher speed of current increases turbulent diffusion, which enhances the upward fluxes of deep nutrients. Wind direction is also crucial in the shelf–slope area. In July–August, 45–55% of the winds were in the northeastern direction. This offshore direction may cause an upwelling of deep water along the continental slope and shelf. For example, in August 1978, a strong northeastern wind resulted in the bloom of diatoms in the slope area [36]. In July–August, the average wind velocity in 2017 ($4.43 \pm 0.25 \text{ m s}^{-1}$) was not significantly higher than that in 2016 ($4.04 \pm 0.13 \text{ m s}^{-1}$) and 2019 ($4.16 \pm 0.2 \text{ m s}^{-1}$). However, combined with the cumulative effect of long-term exposure in an area with strong currents and offshore direction, moderate winds can cause severe algal blooms, as was the case in August 2017 (Figure 6).

5. Conclusions

Three-year studies of the annual dynamics of phytoplankton in the northeastern part of the Black Sea have shown:

1. The species composition of phytoplankton has not undergone significant changes compared to previous years. The phytoplankton numerical abundance was deter-

- mined by coccolithophore *Emiliania huxleyi*, small flagellates, and diatoms. Diatoms, coccolithophores, and dinoflagellates formed the biomass.
2. The annual dynamics of satellite-derived Chl followed a U-shaped curve with a minimum in summer. Chl peaks are recorded in spring and autumn, and sometimes in summer. During the stratified water column period, strong winds regularly lead to a detectible increase in Chl. In the unstratified water period, a relationship between wind mixing and the amount of phytoplankton was not found.
 3. The annual dynamics of phytoplankton had the following pattern: small diatoms (spring) → coccolithophores (late spring, early summer) → large diatoms (summer, autumn). Such a pattern was typical for the previous decades.
 4. The combined effect of sustained offshore wind and strong current may cause bloom of diatoms during the stratified water period, even if the wind velocity is moderate.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/jmse9121435/s1>, Table S1: Monthly and annual wind frequency for the periods 2016, 2017, and 2019.

Author Contributions: V.S. conceptualized and wrote the paper; A.S.M. analyzed remote sensing data and wrote the paper; L.P. provided the field data and wrote the paper; A.F. conducted field studies. All authors have read and agreed to the published version of the manuscript.

Funding: Ministry of Science and Higher Education of the Russian Federation (theme No. 0128-2021-0013), Analysis of influence of wind on phytoplankton—Russian Science Foundation grant (project No. 20-17-00167); Analysis of seasonal changes of phytoplankton - the Russian Foundation for Basic Research (project No. 19-05-50090).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Conflicts of Interest: The authors declare that they have no known competing financial interest or personal relationships that could have appeared to influence the work reported in this paper.

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