

Article

Seasonal and Long-Term Variability of Coccolithophores in the Black Sea According to Remote Sensing Data and the Results of Field Investigations

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Abstract: Based on satellite data from the SeaWiFS, MODIS-Aqua, and MODIS-Terra scanners, the long-term dynamics of coccolithophores in the Black Sea and their large-scale heterogeneity have been studied. During the twenty years in May and June, mass development of coccolithophores population of different intensities was recorded annually. Summer blooms of coccolithophores reached peak levels in 2006, 2012, and 2017, after abnormally cold winters. It was noted that in conditions of low summer temperatures, the blooming of coccolithophores could be significantly reduced or acquire a local character (2004). In the anomalous cold summer of 2001, coccolithophore blooms was replaced by the mass growth of diatoms. Over twenty years, numerous signs of coccolithophores mass development in the cold season have been revealed. Winter blooms develop mainly in warm winters with periods of low wind activity. The formation of a thermocline and the surface layer's stability are essential factors for initiating winter blooms of coccolithophores. It was noted that after the winter blooms of coccolithophores, their summer growth was poorly expressed. It is shown that during periods of rapid growth, the bulk of coccolithophores is concentrated in the upper mixed layer and thermocline. During the blooming period, the share of coccolithophores in phytoplankton biomass constituted 70–85%. The intensity of coccolithophore's blooms is associated with the previous diatoms' growth level. The effect of eddies circulation on the distribution and growth of coccolithophores is considered.

Keywords: remote sensing; phytoplankton; coccolithophores; long-term variability; chlorophyll; climatic conditions



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1. Introduction

As the primary productive link of the marine ecosystem, phytoplankton affects the fundamental biogeochemical processes in the ocean [1,2]. Coccolithophores are an essential component of marine phytoplankton. Seasonal and long-term dynamics of coccolithophores largely determine the processes of sedimentation of carbonates [1] and are an essential component of the geochemical carbon cycle in marine basins. The mass growth of coccolithophores is accompanied by the assimilation of vast amounts of dissolved carbonates and CO₂, followed by the transition of carbon compounds into a suspended form. This process affects the parameters of CO₂ exchange between the ocean and the atmosphere [3].

The particular importance of coccolithophores for the Black Sea ecosystem is defined by the drastic changes in the phytoplankton structure taking place over recent decades. These changes are expressed by replacing traditional dominant diatoms with coccolithophores, which are represented mainly by *Emiliania huxleyi* [4]. During the summer growing season, the coccolithophores abundance reaches 10 million cells/L and more, while their share in phytoplankton biomass exceeds 90%. This process directly impacts functioning of the food chains of the Black Sea ecosystem. Due to the low nutritional value of coccolithophores for zooplankton [5], the expansion of their dominance in the primary link of the food

web may affect the production characteristics of higher trophic levels. Substituting small diatoms ($l < 50 \mu\text{m}$) with coccolithophores can also change the direction of energy flows in the marine ecosystem [6].

The trophic status of The Black Sea as an internal inland sea basin significantly depends on the nutrients coming from the river runoff. An essential feature of the Black Sea circulation is the Eastern and Western cyclonic eddies (Figure 1) situated in the central parts of the sea. The Black Sea characteristic feature is the Rim Current 40–80 km wide, which runs along the continental slope and forms a general cyclonic circulation [7–9]. The Rim Current, meandering, forms numerous mesoscale cyclonic and anticyclonic eddies over the continental slope and in the open part of the sea [10]. As well as coastal anticyclonic eddies, they involve coastal waters in the general circulation [11]. Eddies circulation within the Rim Current provides an active water exchange between coastal and open sea areas. A characteristic feature of the hydrological structure is the formation of a seasonal thermocline in summer and its destruction during winter convection due to cooling of the surface layer and wind mixing [12,13].

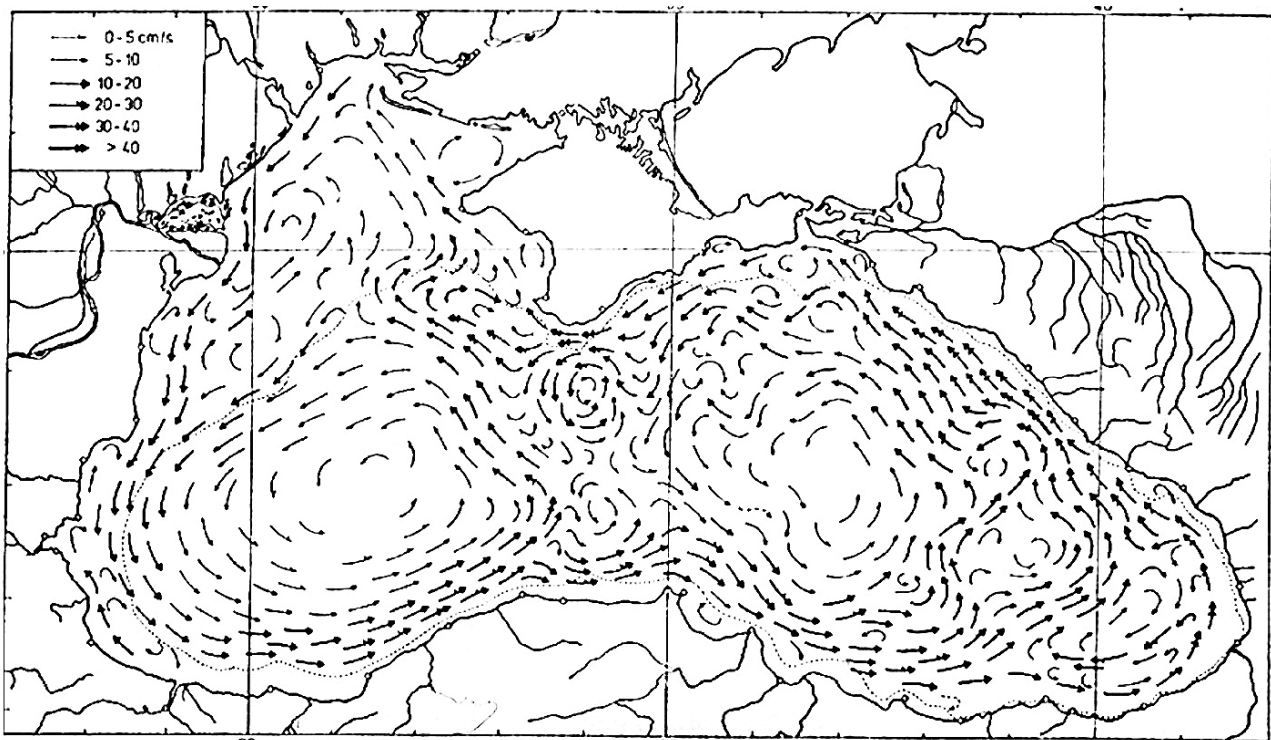


Figure 1. General scheme of circulation in the surface layer in the Black Sea. Neumann, 1942 [14].

The ecosystem of the Black Sea is sensitive to environmental changes and anthropogenic impacts. For several decades, it has been significantly influenced by factors of a different nature: eutrophication, climate change, uncontrolled fishing, and invasive species [15–18]. About 80% of the river flow in the Black Sea (more than 250 km^3) falls on the northwestern part of the sea, where signs of eutrophication are often observed [19,20]. In-situ observations and remote sensed chlorophyll data showed that the annual dynamics of phytoplankton were close to a U-shaped line [21–23] with maximal growth in the cold period of the year. The spring maximum of phytoplankton in the coastal zone is also expressed in maximum chlorophyll concentrations [23]. At the same time, the growth of coccolithophores is poorly combined with an increase in the concentration of chlorophyll. Therefore, the abundance of coccolithophores is usually assessed by other bio-optical parameters, making it possible to consider their dynamics separately. Over the last decade, special fundamental research has been carried out to identify the parameters and causes of restructuring occurring in the phytoplankton of the Black Sea [6,24–26]. Long-term changes

in the composition of nutrients, which led to changes in the structure of phytoplankton, have been studied. The role of nitrogen and phosphorus ratios in the competitive relationships of various algae species has recently been determined, and physiological mechanisms regulating the phytoplankton structure were also discovered [27–29]. An important area of research of coccolithophores in the Black Sea is the development of regional algorithms for estimating the concentration of algae according to remote sensing data [30–37].

At the same time, many fundamental and anomalous phenomena have not been recorded by traditional methods due to the lack of regular observations of the coccolithophores, especially in open areas of the sea. Remote sensing creates an opportunity for studying the main patterns of seasonal and inter-annual variability of phytoplankton continuously throughout the sea, to identify long-term trends and regional features. The multisensory approach provides the study of structural changes in the phytoplankton of the Black Sea [23] and their relationship with hydrometeorological environmental factors [35,36]. The use of satellite data has made it possible to fill the existing gaps in the study of seasonal and long-term dynamics of phytoplankton. At the same time, seasonal cycles of coccolithophores, their relationship with climatic changes and current hydrometeorological conditions have remained insufficiently studied. The winter blooms of coccolithophores, recorded by satellite scanners [23,35,37,38] and confirmed by field observations, have also been poorly investigated. In recent years, new data on the growth of coccolithophores in winter and winter-spring periods have also been obtained based on satellite data and field observations [39]. This makes it possible to supplement the understanding of algae's seasonal dynamics significantly.

The objectives of this work are to consider the main features of coccolithophores dynamics over twenty years based on remotely sensed data, to record the most significant regular and abnormal events in seasonal and long-term cycles of algae growth with a view to their further in-depth study, to fill in the existing gaps in the study of coccolithophores in the Black Sea based on new data from field and satellite observations. An essential part of this work is to consider the patterns of seasonal and long-term variability depending on current hydrometeorological conditions and climatic changes.

According to satellite sensing data, the variability of chlorophyll concentrations is usually analyzed when studying phytoplankton dynamics. The primary data sources are based on measurements of SeaWiFS, MODIS-Aqua, MODIS-Terra color scanners [21–25,30–35,37,40]. Due to the specific structure of the cells, coccolithophores are usually weakly expressed in the chlorophyll images. Thus, this group of algae is usually estimated in remote sensing reflectance at a wavelength of 551, 555 nm, backscattering, and the PIC concentration (concentration of suspended inorganic carbon) calculated by an algorithm [41–44]. In general, all the bio-optical parameters mentioned describing the large-scale variability of coccolithophores similarly. Suspended inorganic carbon (PIC) is the main component of the material composition of coccolithophores. Therefore, it has been repeatedly used as a parameter for assessing algae's spatial and temporal variability [4,45,46]. PIC also demonstrates a good correlation with biomass of coccolithophores ($R = 0.86$) during summer blooms (May–July) in the Black open sea [4]. Thus, accessible data on suspended inorganic carbon as an indicator of coccolithophore concentrations was considered optimal for solving the tasks. It is considered that the development of coccolithophores population to the level of 10^6 cells per liter marks the blooming. This boundary has a very conditional character but is used by authors [6,24]. When evaluating coccolithophores by PIC content, the blooming boundary will correspond to the values close to 0.001 mmol/m^3 .

The regional algorithm developed for the Black Sea [32,33] needs many initial satellite data processing and additional calculations, which is not justified for solving the main tasks on a twenty-year observation interval. Calculations by the regional algorithm [32] were used in this work in a test mode to confirm (demonstrate) its application for the future detailed study of mesoscale variability of coccolithophores.

2. Materials and Methods

Distribution maps reflecting dynamics of coccolithophores were created using PIC data (level 3) [41,44,47] and SeaDAS software to provide an optimal color scale. Satellite data on surface temperature and wind speed (Sea winds, QuikSCAT) were used to assess the long-term variability of hydrometeorological conditions.

To analyze the seasonal and long-term variability of coccolithophores and temperature conditions in different areas of the Black Sea, we used data averaged over the marked regions (satellite polygons) shown in Figure 2.

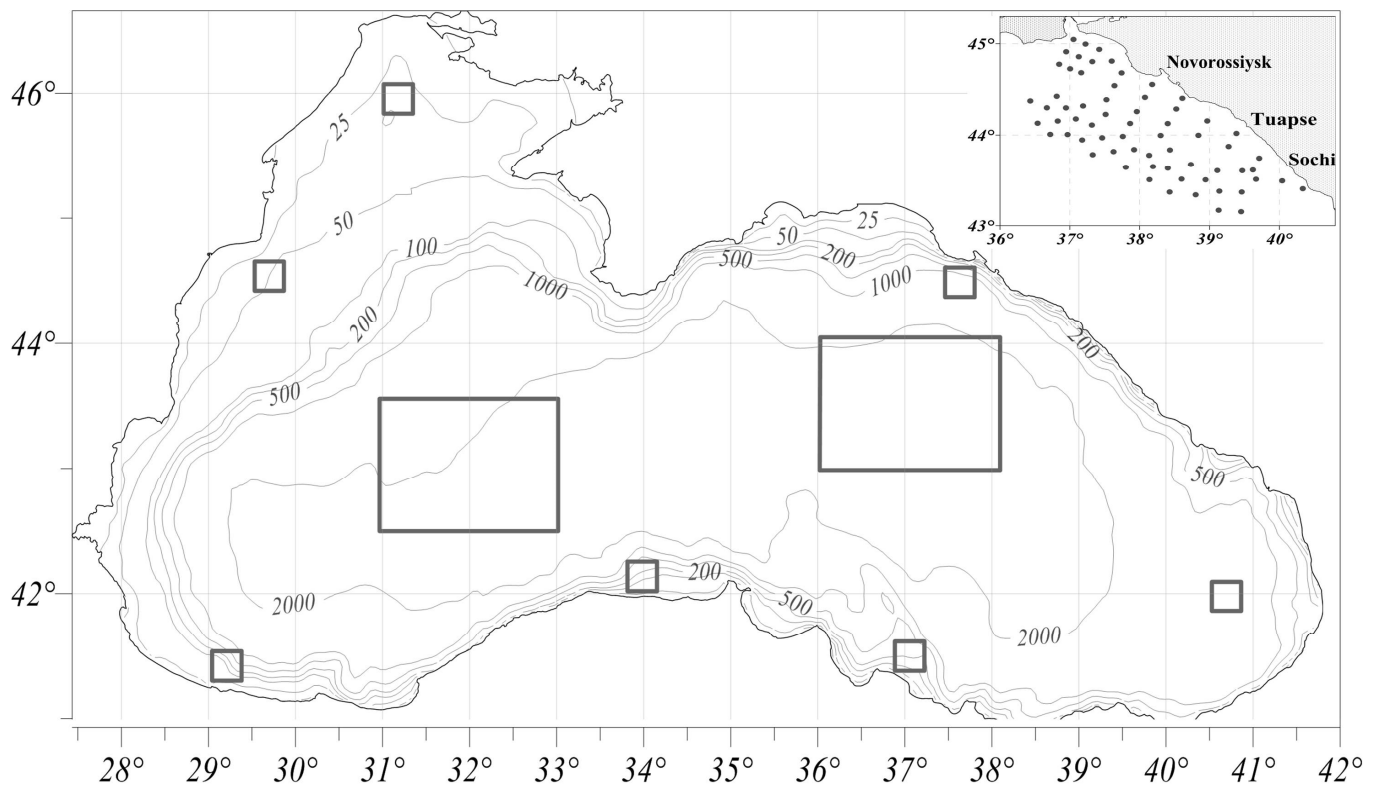


Figure 2. Location of the long-term satellite observations areas and sampling stations of field studies in the Black Sea.

The field data on coccolithophore variability and hydrophysical factors were studied at stations located in various production zones of the north-eastern part of the sea (Figure 2) using the methods described below.

2.1. Sampling

Hydrophysical and hydrochemical parameters and quantitative characteristics of the phytoplankton community (i.e., taxonomic structure, species abundance) were determined during regular expeditions of the research vessels “Rift” and “Professor Shtokman” in the north-eastern part of the Black Sea. Stations of sampling and hydrophysical probing are shown in Figure 2. SBE 19plus CTD profiler (Sea-Bird Electronics, Inc., Bellevue, WA, USA) and TURNER SCUFA fluorimeter were used to measure the vertical distribution of temperature, salinity, density, and fluorescence. Water samples for phytoplankton analysis were collected using 5-L Niskin bottles mounted on a carousel water sampler (SBE 32). Samples were taken from the surface, the middle of the upper mixed layer, the seasonal thermocline, and below the thermocline. Phytoplankton samples (0.5, 1 volume) were fixed with neutralized formaldehyde (final concentration 1.0%). A lower final concentration of formaldehyde was used for better preservation of cells, while taking into account their being processed within one month from the moment of sampling. The samples were

stored in the dark, at room temperature, for two weeks. After that, the samples were slowly decanted.

2.2. Phytoplankton Analysis

Ergoval light microscope (Karl Zeiss, Jena, Germany) with a magnification of 160× and 400×, was used to identify species and cell counting. Cells with linear dimensions <20 microns were counted using a Nautott chamber (0.05 mL). The counts were considered statistically sufficient if at least 100 cells of each species were counted. Camera Naumann (1 mL) was used to count larger cells; usually, the entire Nauman chamber was counted.

Species identification was based on morphology, according to [48,49], as well as to the World Register Marine species <http://www.marinespecies.org> (accessed on 15 December 2021). Cells with an unknown taxonomic affiliation ranging in size from 4 to 10 µm microns were classified as “small flagellates,” assuming that this is a size class. Cell biomass was evaluated according to [50]. The total biomass was calculated as the sum of the biomass of all species. The dominant species was the one whose biomass was the highest at this station. The total number of phytoplankton samples used in our study was about 1000.

Field observation data were used to a limited extent, mainly to demonstrate the typical structure of phytoplankton and hydrological conditions during distinct periods of coccolithophore growth. For statistical analysis of data sets, Pearson’s correlation coefficient was used.

3. Results

3.1. Seasonal and Long-Term Dynamics of Coccolithophores

The long-term dynamics of coccolithophores expressed as PIC concentrations show that every year from May to July, there are periods of mass coccolithophores growth of different intensities (Figure 3a,b), reaching the level of blooms with about a two-four-year periodicity. The seasonal variability of coccolithophores in the open part of the Black Sea averaged over twenty years is shown in Figure 3c.

Among all the coccolithophores summer blooms in twenty-year period, three years with a peak level of growth are distinguished—2006, 2012, 2017 (Figures 3a,b and 4).

A joint analysis of satellite data on the interannual dynamics of PIC and surface layer temperature (T °C) showed that peak summer blooms of coccolithophores were preceded by the coldest winters (Figure 5). In this case, the water temperature in winter indicates the intensity of winter convection and the enrichment of the surface layer with nutrients.

At the same time, in 2004, after a relatively cold winter, the summer blooming of coccolithophores was also observed, but it was poorly expressed and localized mainly in the eastern part of the sea. It should be noted that the summer growth of coccolithophores in 2004 took place at low temperatures of the surface layer (Figure 5). The negative anomaly of the summer temperature indicates unusual hydrological conditions for the growing period.

Moreover, the hydrological conditions of the abnormally cold summer of 2001 led to coccolithophores being totally replaced in summer blooming by the massive growth of diatoms, which was reflected in the remotely sensed chlorophyll distribution (Figure 6). The low temperature was not a direct impact factor but indicated a violation of the surface layer stability, including due to active mixing. It also indicates significant changes in the hydrological structure and the surface layer stratification necessary for coccolithophores’ growth in summer.

It is interesting to mention that the Caspian Sea, located in the same climatic zone as the Black Sea, also demonstrated an abnormal blooming of diatoms in the summer of 2001, the most powerful over twenty years of satellite observations (Figure 7).

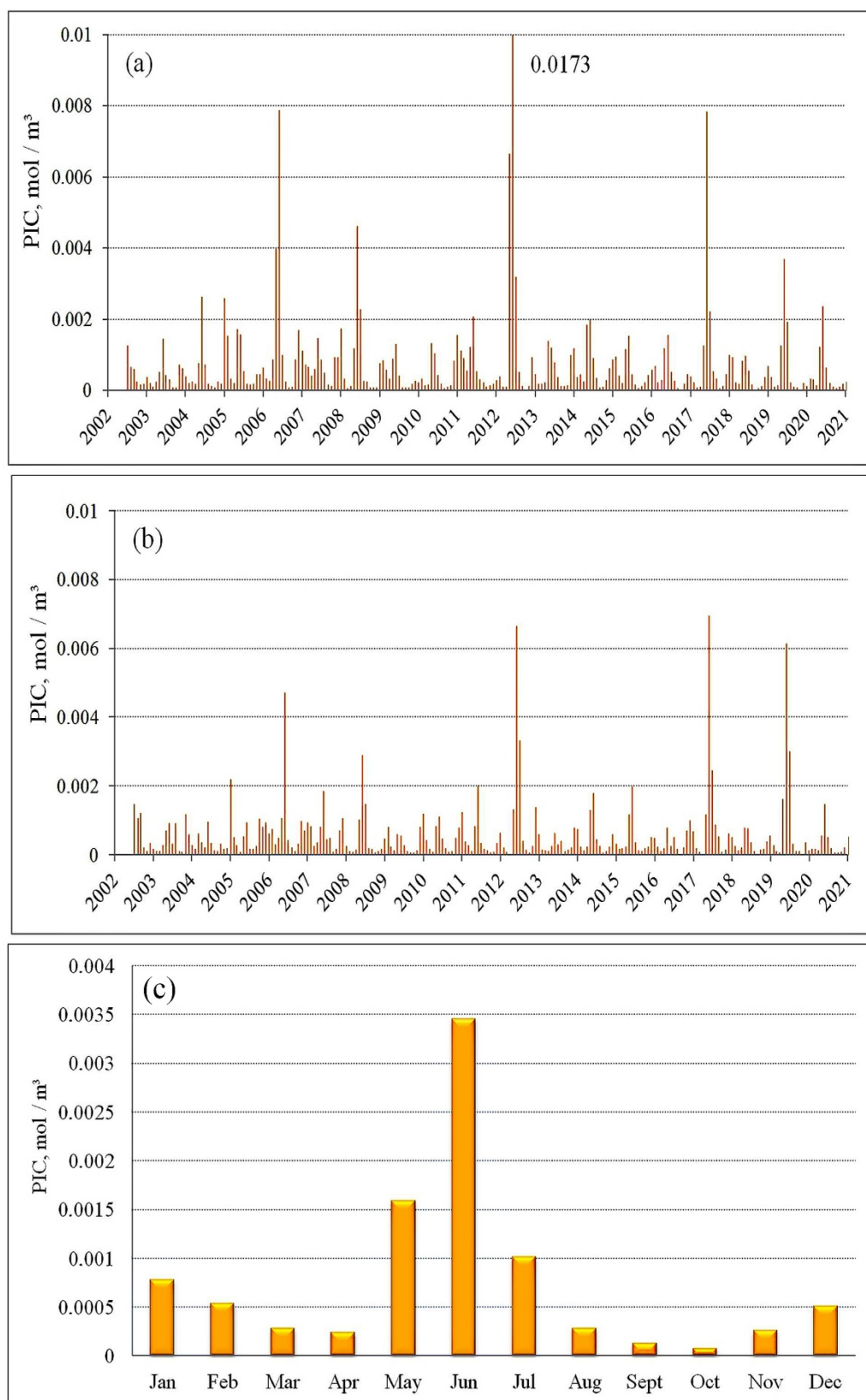


Figure 3. Long-term dynamics of coccolithophores in the Black Sea expressed as PIC concentrations: Eastern gyre (a), Western gyre (b) and averaged seasonal changes in PIC content in the open Black Sea (c) according to the MODIS-Aqua.

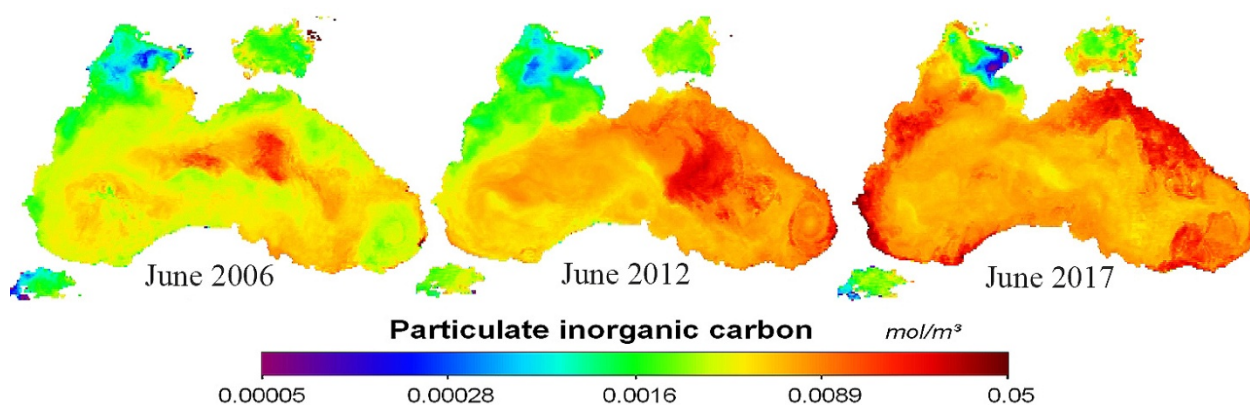


Figure 4. Distribution of suspended inorganic carbon in the Black Sea during the coccolithophore blooms in June 2006, 2012, 2017 according to the MODIS-Aqua (monthly average data).

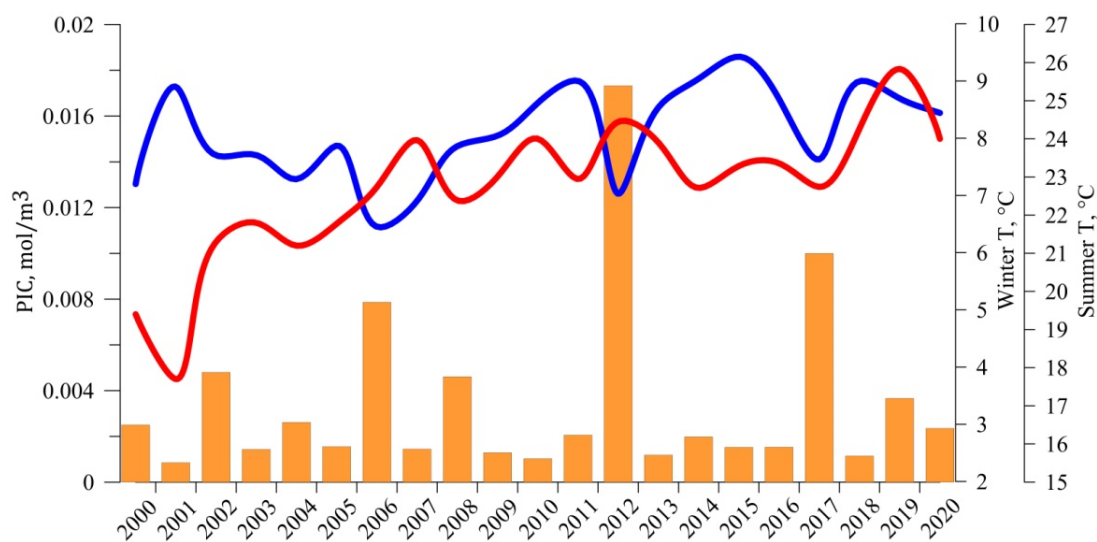


Figure 5. Dynamics of summer coccolithophore blooms (Average PIC values for June), minimum winter temperatures (February average)—blue line and summer temperatures (June average)—red line in the eastern Black Sea according to SeaWiFS and MODIS-Aqua.

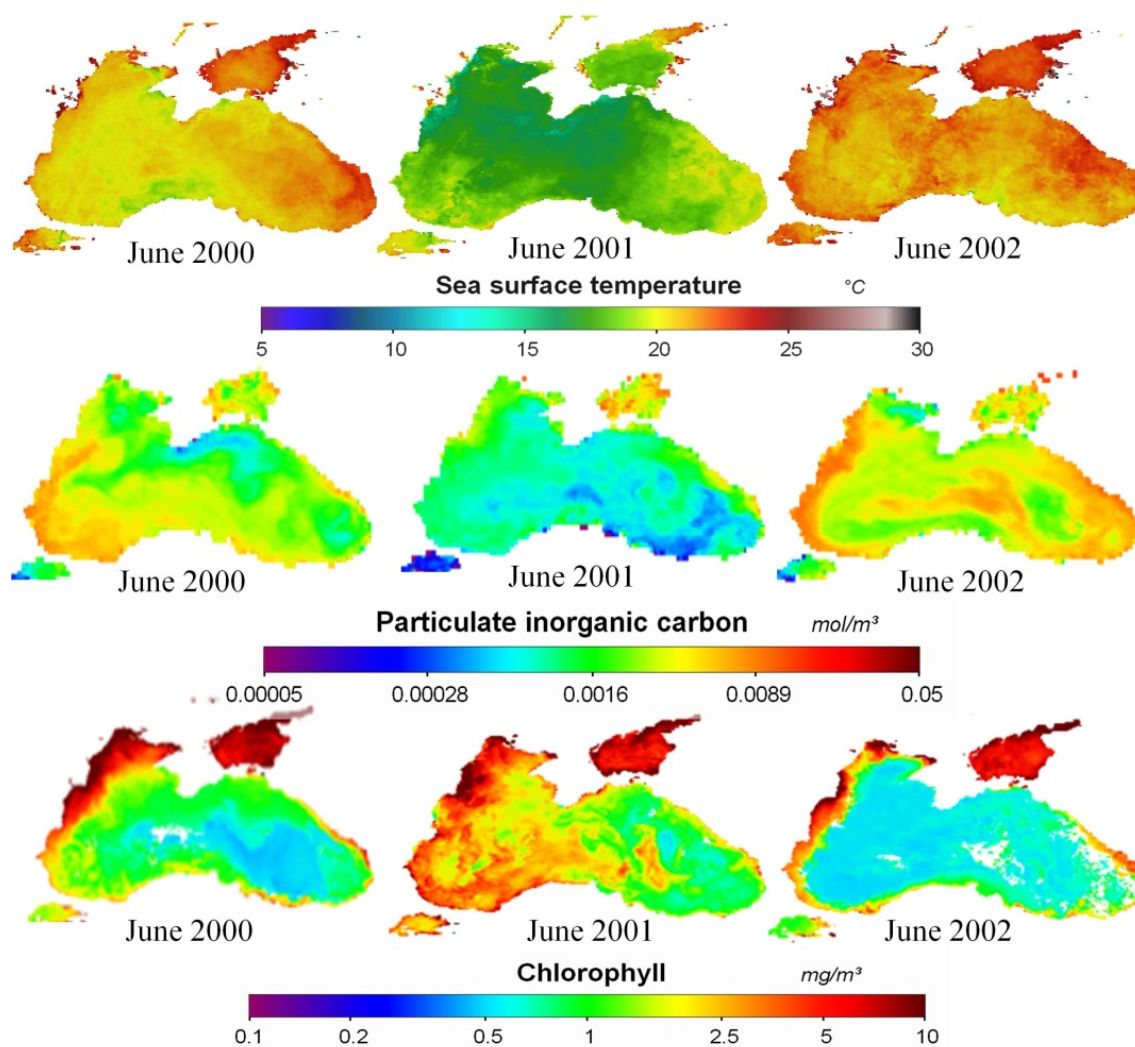


Figure 6. Changes in surface temperature, PIC, and chlorophyll in June 2000–2002.

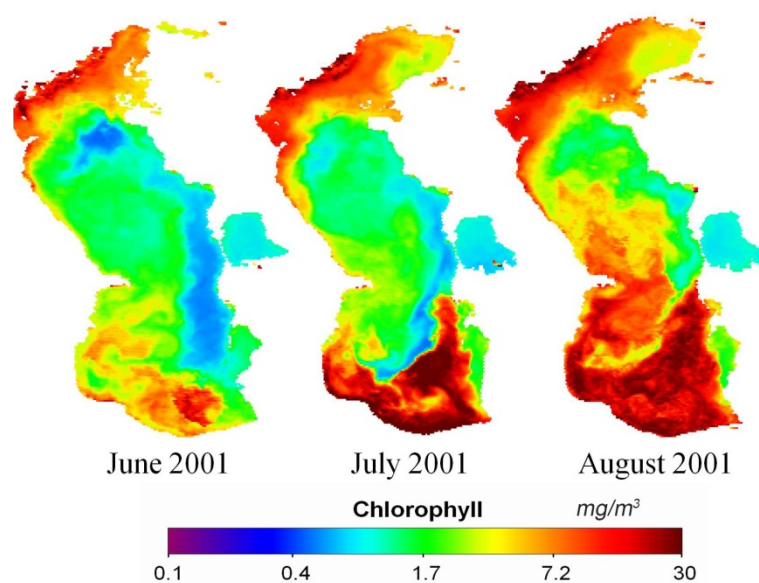


Figure 7. Chlorophyll distribution in the Caspian Sea in June, July and August 2001 according to Modis-Aqua.

3.2. Patterns of Large-Scale Distribution of Coccolithophores during the Summer Growing Season

The distribution of coccolithophores in the sea area during summer blooms is highly heterogeneous and characterized by significant temporal variability. Therefore, to assess large-scale heterogeneity, it is advisable to use one-day images in combination with maps of monthly averages. The patterns of algae distribution are determined by mesoscale circulation and regional hydrological conditions promoting or inhibiting algae growth. Satellite data show significant differences in the development of coccolithophore blooms in the western and eastern parts of the sea. These differences are also noted in the diagrams of seasonal variability of PIC in the Western and Eastern gyres (see Figure 3a,b). It is noted that for most of the years (1999, 2004, 2005, 2006, 2012), the summer growth of coccolithophores was more pronounced in the eastern part of the sea, which was characterized by more stable stratification of the surface layer and favorable temperature conditions (Figure 8).

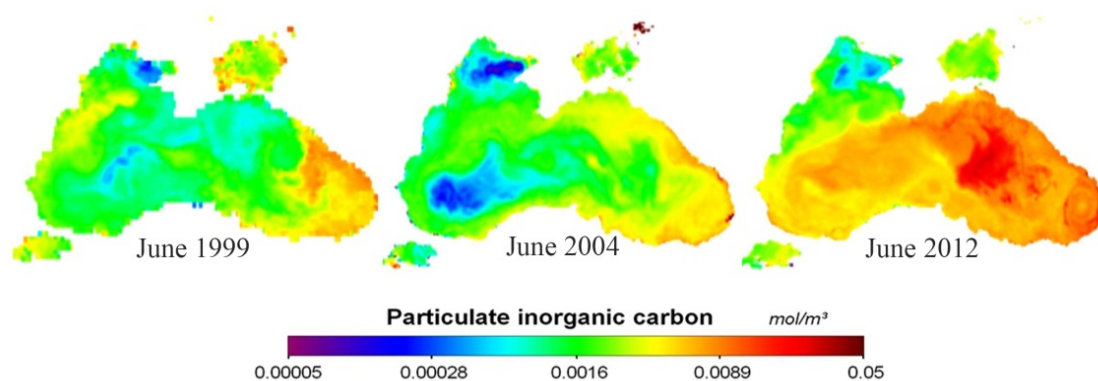


Figure 8. Distribution of coccolithophores (PIC) in 1999, 2004, 2012 blooming periods according to the MODIS-Aqua (June averages).

There were also few cases (1998, 2000, 2002) when blooms began to develop in the western and southern parts of the sea (Figure 9).

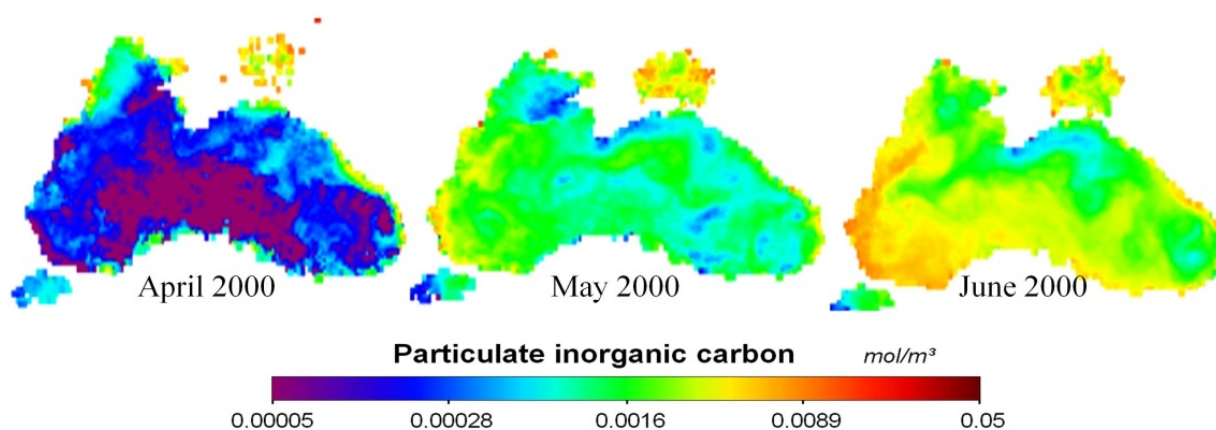


Figure 9. Growth of coccolithophores (PIC) in 2000 according to the MODIS-Aqua (monthly average values).

An essential issue in studying phenology of coccolithophores is determining the initiation areas of blooms. According to long-term observations, in most cases, the initiation of blooms occurs in the eastern and north-eastern periphery of the sea. In the years of peak blooms development (2006, 2012), summer growth of coccolithophores was also initiated mainly in the eastern half of the Black Sea and later spread to the entire sea area.

The mass growth of coccolithophores in the summer of 2017 differed significantly from the peak blooms of 2006 and 2012 in spatial distribution and initiation areas. First of all, during the bloom initiation in May 2017, intensive algae growth was observed along

the entire basin's perimeter and was not recorded well in the waters of the central gyres (Figure 10a). During the period of the most coccolithophores concentration in June 2017 (see Figures 4 and 10b), extensive areas and blooming spots were also located mainly on the periphery of the sea, in the Rim Current zone. The deep penetration of coccolithophores into the northwestern shelf in 2017 is also abnormal, so the blooms of coccolithophores did not usually occupy this shelf region during the summer growing season.

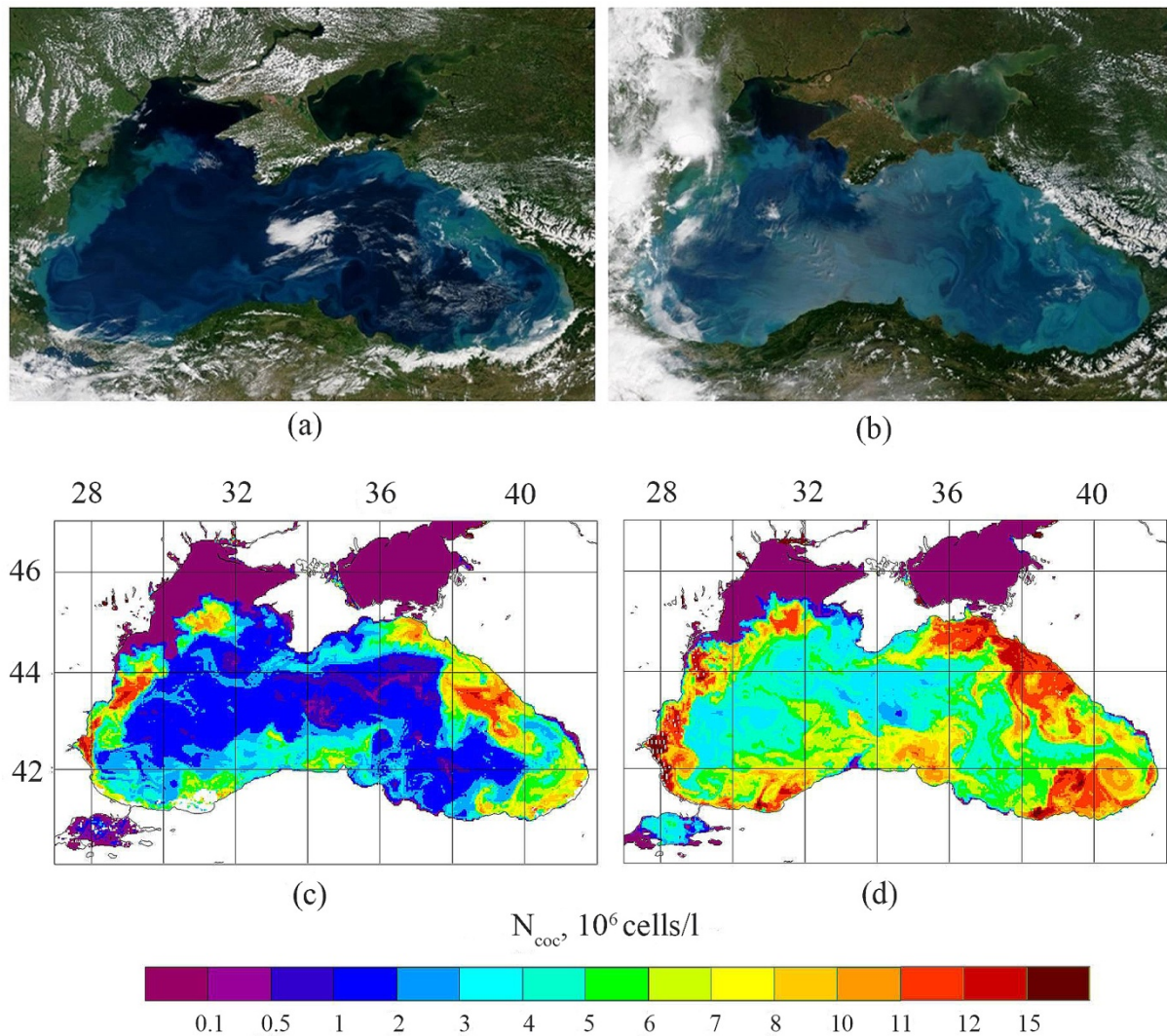


Figure 10. Coccolithophore blooms in the Black Sea in May (29 May 2017) and June (8 June 2017) (a,b)—true color (<https://visibleearth.nasa.gov>, accessed on 15 December 2021), (c,d)—(N_{coc}) number of coccolithophores by the regional algorithm.

Calculations on the base of regional algorithm (Figure 10c,d) confirm the reality of the observations made. The uniqueness of the 2017 coccolithophores bloom is also illustrated by the long-term variability of PIC concentrations in the western shelf waters of the Black Sea (Figure 11). According to satellite data, coccolithophore blooms in western coastal areas were less pronounced in other years.

The cause of this phenomenon may be specific hydrodynamic and hydrochemical conditions in the summer of 2017, favorable for penetration and growth of coccolithophores in the coastal zone of the sea.

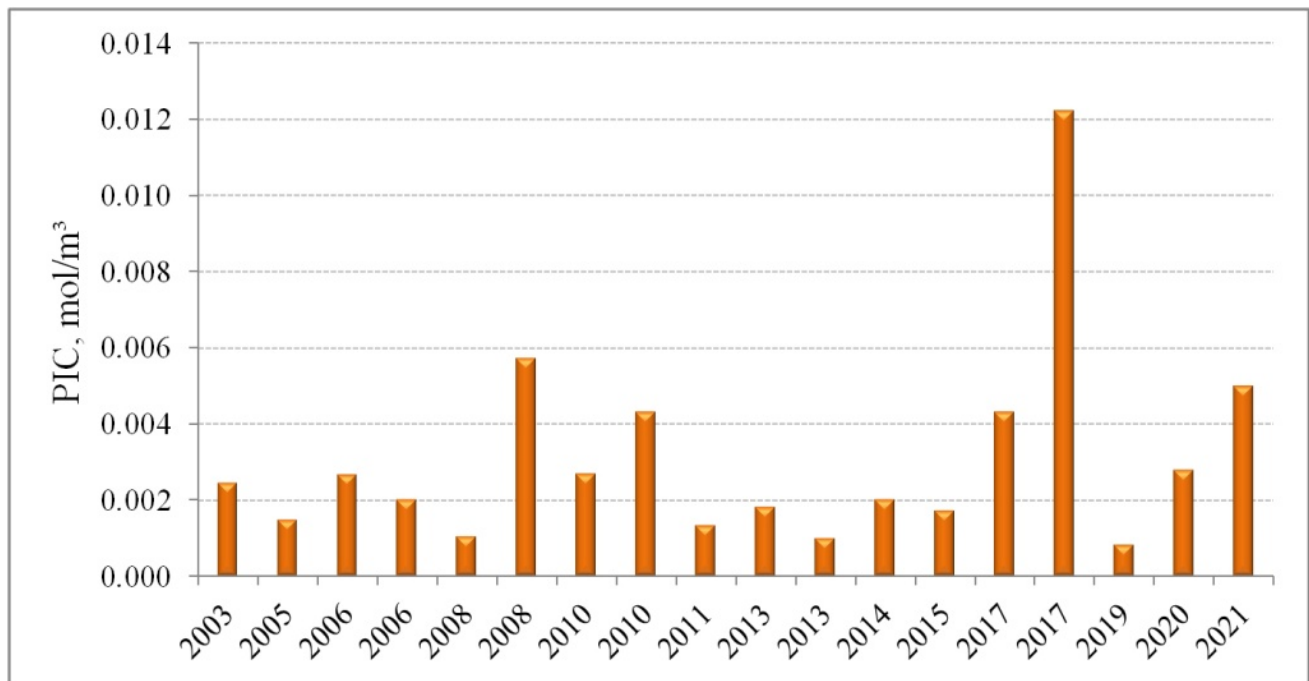


Figure 11. Long term changes in average monthly PIC concentrations in June in the waters of the western shelf of the Black Sea.

3.3. Regional and Local Features of Coccolithophores Growth in Summer

The dynamics of coccolithophores in open areas and the coastal zone may be different. Shelf and open areas of the sea differ in hydrochemical and hydrophysical characteristics, which determines the dynamics of coccolithophores. The southern, eastern, and north-eastern shelves of the Black Sea are characterized by a small extent and are greatly affected by the water masses of the open sea. The existing general circulation system includes many eddies that form along the coastal zone on the outer contour of the Rim Current. They contribute to the active exchange of shelf waters with the water masses of the open sea. The distribution of coccolithophores in the coastal zone is influenced by eddies activity and meandering of the Rim Current itself, which can be seen on satellite images.

The western and northwestern sea shelves have a large extent and varying degrees of involvement in the general circulation of the Black Sea. Shelf waters are affected by biogenic river runoff, which largely determines the formation and production status of phytoplankton [19,34]. Under these conditions, the growth and distribution of coccolithophores in offshore waters are primarily determined by competitive relationships with populations of other species in the leading complex of shelf phytoplankton. The evidence of this interaction is demonstrated by some satellite images (Figure 12). In these images, the distribution of coccolithophores is reflected in white tones, and the predominance of phytoplankton (mainly diatoms) with high specific chlorophyll content is reflected in the images in dark green (Figure 12).

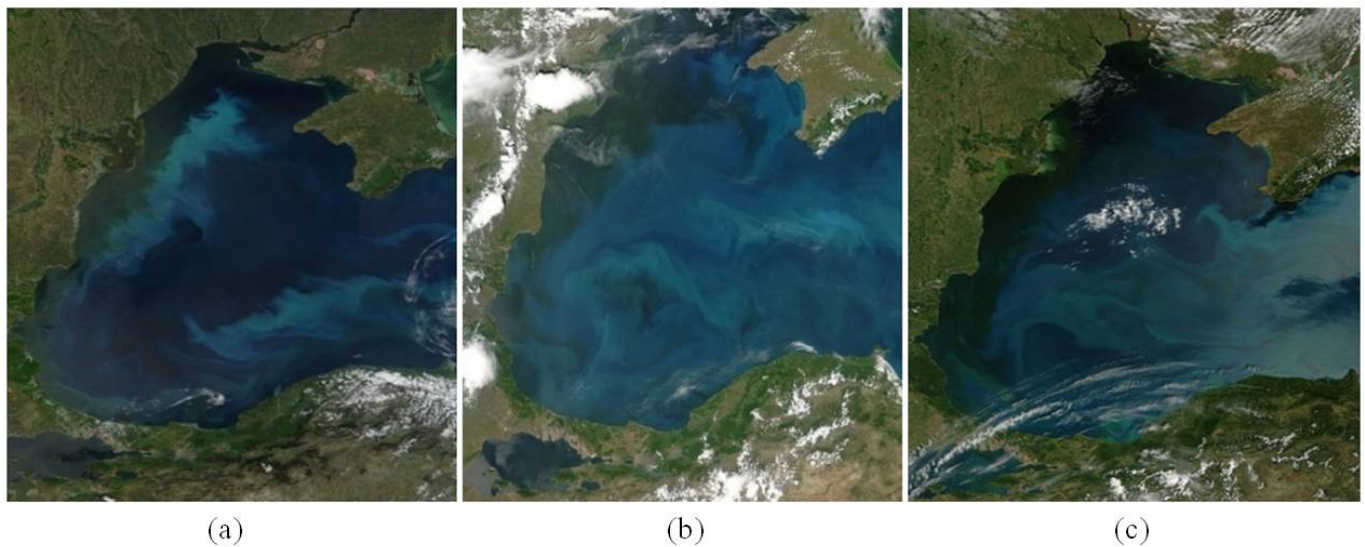


Figure 12. Summer blooms of coccolithophores in the western part of the Black Sea in 2002 (10 May 2002) (a), 2006 (20 June 2006) (b), and 2012 (18 June 2012) (c) Source (<https://visibleearth.nasa.gov>, accessed on 15 December 2021).

The satellite images shown in Figure 12 also demonstrate numerous eddy formations that appeared in the color and brightness of the sea surface. Mesoscale eddy currents associated with the Rim Current redistribute the blooming spots of coccolithophores, giving them a specific shape. The effect of eddy dynamics is expressed in the spatial distribution of coccolithophores over the water area. Eddies can also change hydrophysical and hydrochemical conditions, creating local upwelling zones and provide nutrient enrichment. So quasi-stationary eddies can create favorable conditions for coccolithophores or suppress their growth forming the regional and local features of algae distribution.

The different influences of eddy circulation on coccolithophores can be traced by the example of the Batumi anticyclone situated in the eastern part of the sea (See Figure 1). This quasi-stationary anticyclonic gyre being one of the main features of the Black Sea circulation demonstrates the opposite variants of coccolithophores concentration dynamics observed during the summer blooming period (Figure 13).

In 2006 and 2008, during the period of maximum growth of coccolithophores in the entire sea, the bloom in the zone of the Batumi anticyclone was practically absent. Also, the specific frontal zone was recorded to the west of the Batumi gyre, in which the color of the sea indicating coccolithophores abundance changed abruptly. On the contrary, during the summer period of 2012 and 2017, pronounced blooming spots of coccolithophores were observed within the Batumi anticyclone. Their spiral shape corresponded to the anticyclonic nature of the circulation in the Batumi gyre (Figure 13). The stable spiral shape of a powerful coccolithophore blooming spot in June 2012 and 2017 was also traced on the maps of average monthly PIC concentrations (see Figure 4), demonstrating stability throughout the season.

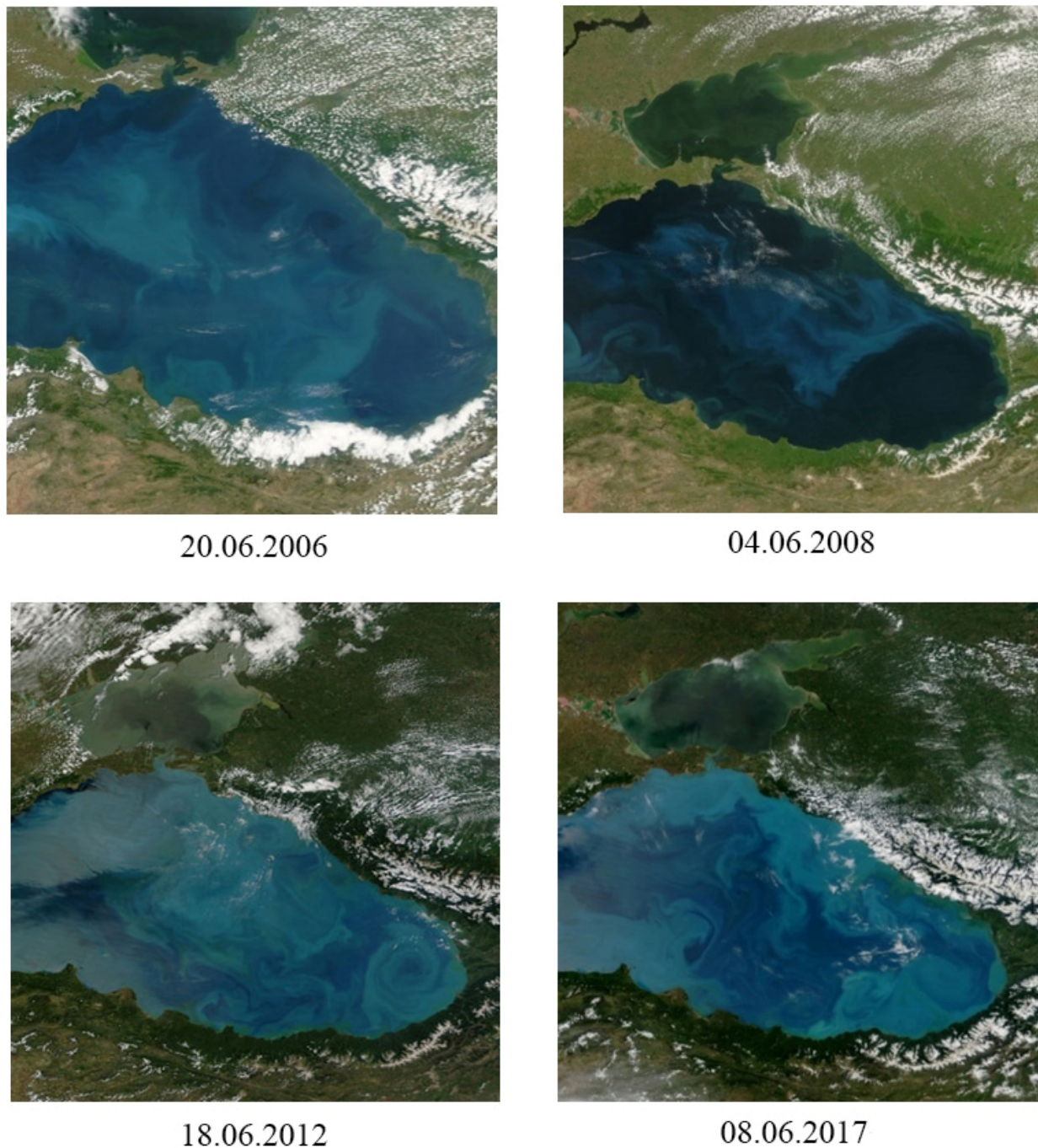


Figure 13. Distribution of coccolithophores in Batumi anticyclone during the summer blooms of 2006, 2008, 2012, 2017. Source (<https://visibleearth.nasa.gov>, accessed on 15 December 2021).

In addition to the interannual differences, the cardinal changes in the coccolithophore were recorded during one-year summer bloom development. So, in May 2008, after forming a blooming spot in the Batumi anticyclone, the degradation of the blooming area was already recorded in June (Figure 14). Moreover, the degradation mentioned took place in the opposite phase to further coccolithophores development in the total sea area.

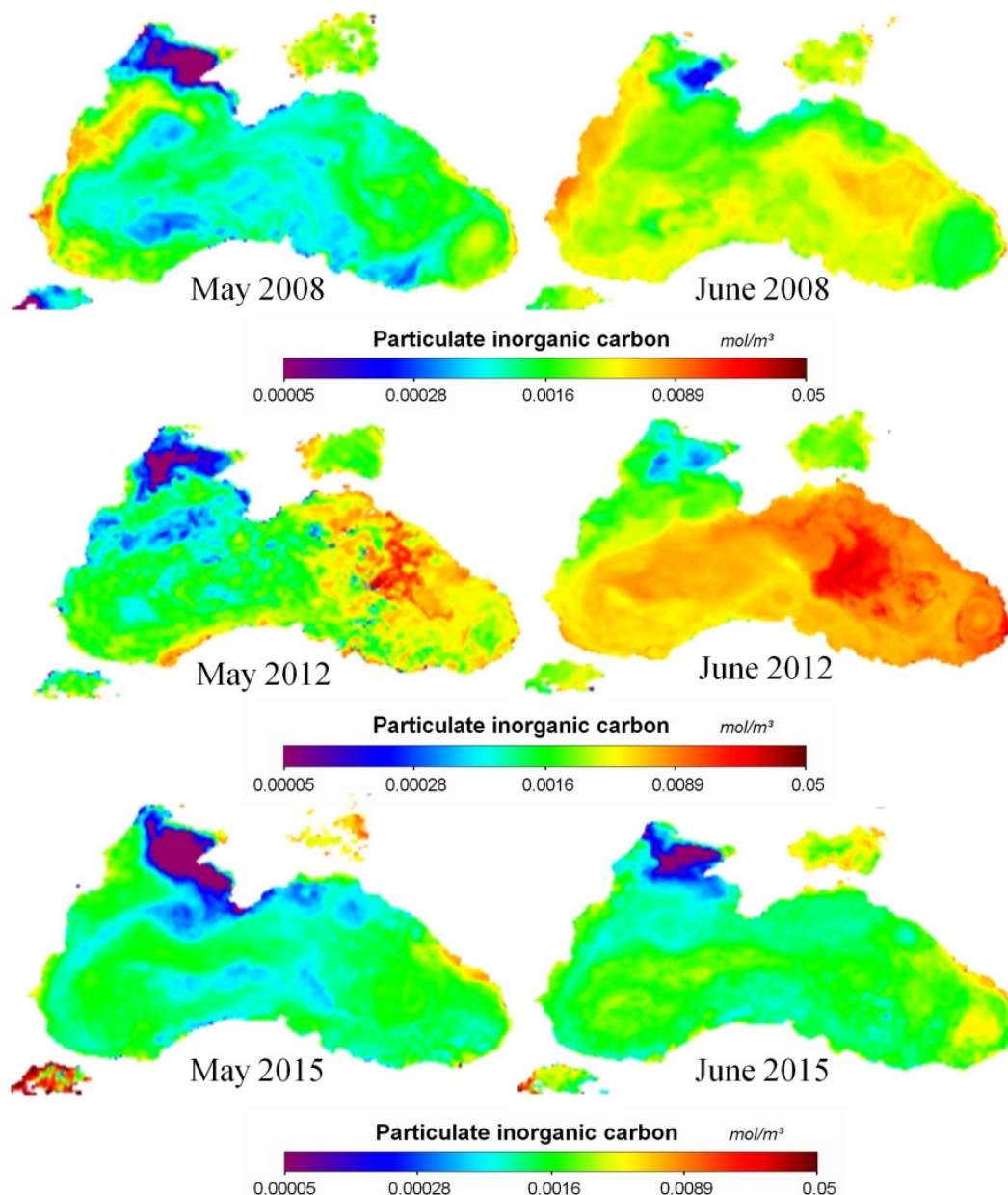


Figure 14. Development of coccolithophore blooms (PIC average monthly values) in the zone of the Batumi anticyclone in May and June 2008, 2012, 2015, according to the MODIS-Aqua data.

In the other case, during the blooming initiation in May 2012, the growth of coccolithophores in the Batumi anticyclone was minimal (Figures 14 and 15). Furthermore, in June, a powerful spiral-shaped blooming spot was recorded in the cycle. Calculations using a regional algorithm (Figure 15c,d) confirm the evidence mentioned.

Similarly, in May 2015, there was no essential growth of coccolithophores in this area. In June, against the background of generally weak population development in the entire sea, a blooming spot in the zone of the Batumi anticyclone was observed (See Figure 14).

The reason for the seasonal and interannual diversity of coccolithophores within the Batumi anticyclone can be various hydrophysical and hydrochemical conditions at different stages of the cycle development. River runoff can also influence coccolithophore's growth, strengthening stratification and providing additional nutrients. Eddies can also involve the inshore waters to open sea circulation. The bloom observed in 2015 in the nearest to Batumi cycle coastal area affected by river runoff may confirm the latter argument.

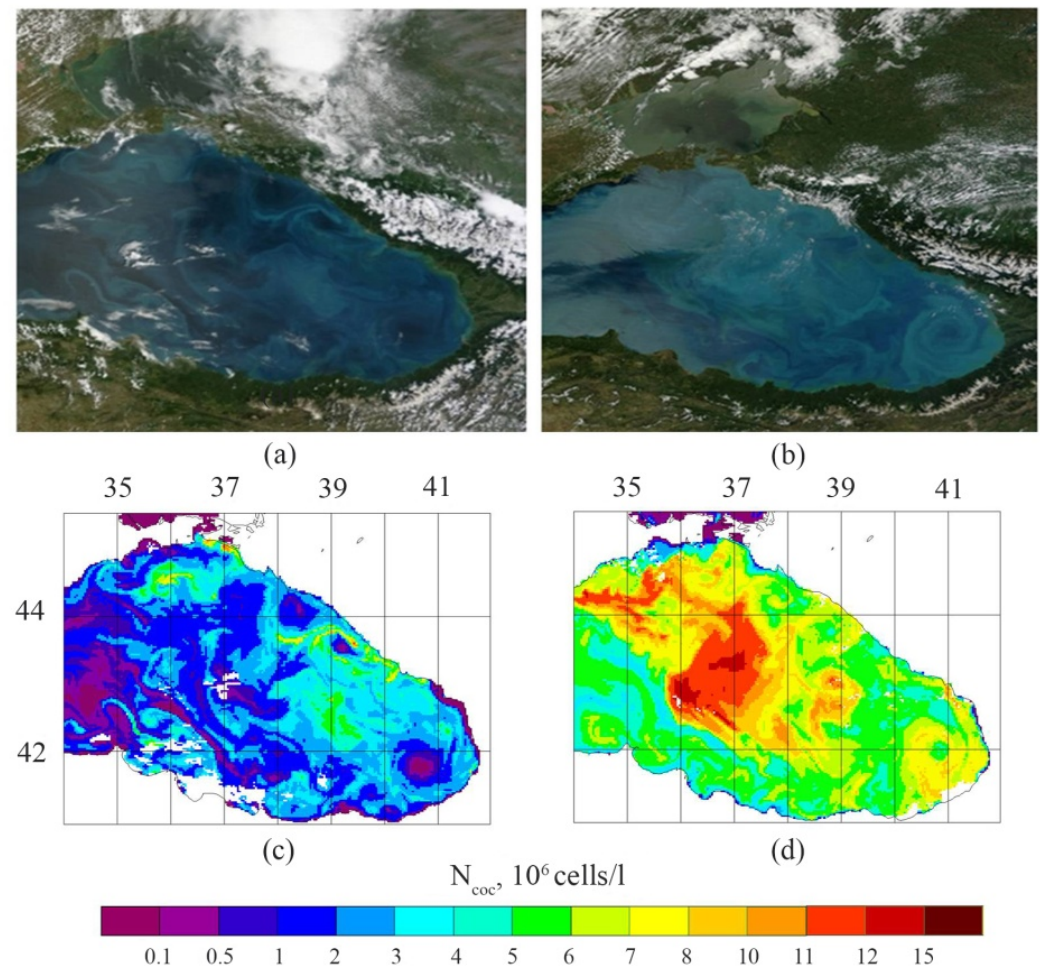


Figure 15. Development of coccolithophore blooms in the zone of the Batumi anticyclone in May and June 2012 according to the MODIS-Aqua; on the left—May (18 May 2012), on the right—June (18 June 2012) (a,b)—true color images; (c,d)—(N_{coc}) number of coccolithophores by the regional algorithm.

3.4. Hydrological Conditions and Phytoplankton Structure during the Summer Growing Season of Coccolithophores

Long-term satellite and field observations have shown that in the summer, favorable hydrometeorological conditions are created for the mass growth of coccolithophores in almost the entire Black Sea area. Summer blooms, as a rule, develop during the period of active warming of the surface layer and the formation of a seasonal thermocline.

Figure 16 reflects the vertical distribution of biomass, structure of phytoplankton, and the hydrophysical characteristics in the surface layer during the beginning of the summer coccolithophore's bloom. This period is characterized by a sharp gradient thermocline, which maintains the stability of the water column providing bloom development in large water areas.

At the initial stage of bloom development, the bulk of algae with a total predominance of coccolithophores is concentrated in the surface mixed layer and thermocline. Later, coccolithophores can spread to greater depths due to settling and turbulent mixing. The share of coccolithophores in phytoplankton biomass in the surface layer during this period is more than 80%. The presence of residual amounts of coccolithophores at depths of 100 m or more may be associated with the previous winter population development.

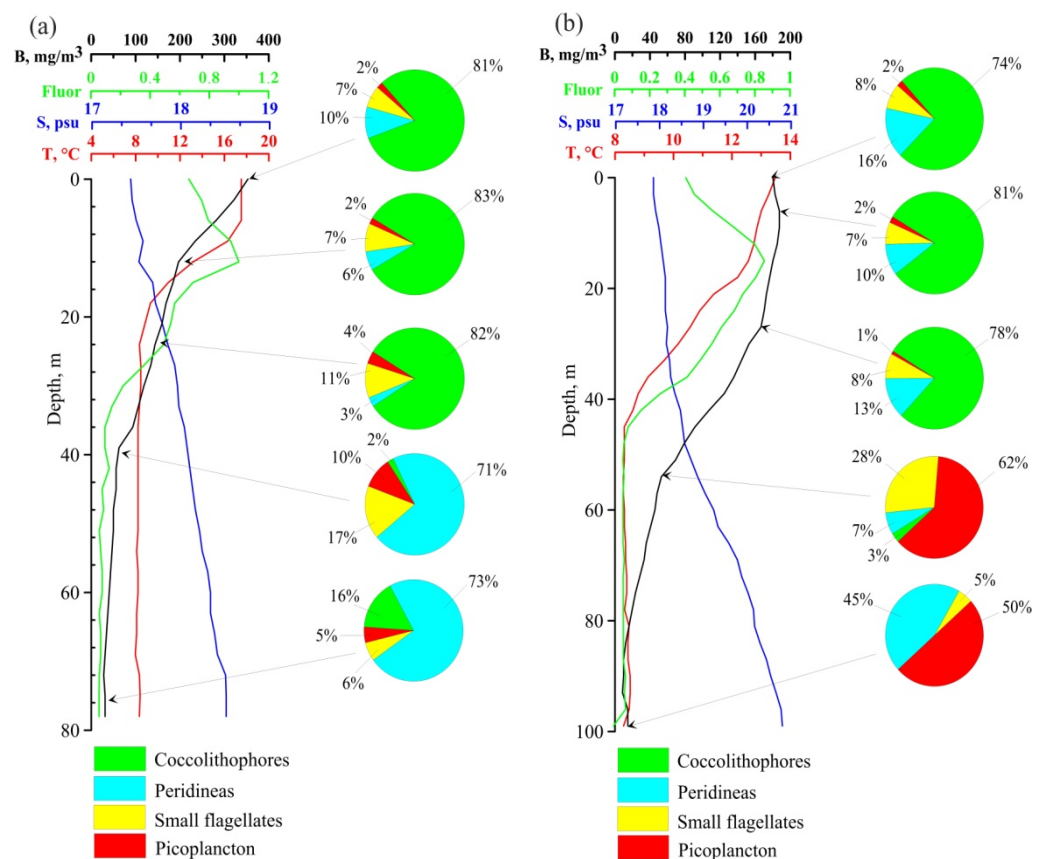


Figure 16. Vertical distribution of temperature (T), salinity (S), fluorescence (Fluo), total biomass (B) and phytoplankton structure during the summer and winter growing season in the north-eastern part of the Black Sea; (a)—June 2011; (b)—December 2010.

3.5. Spatial Dynamics of Coccolithophores during the Winter Growing Season. Winter Blooms of Coccolithophores

In recent years, the winter and winter-spring blooms of coccolithophores and the accompanying hydrometeorological conditions have been studied based on remotely sensed data and field observations. A retrospective analysis of satellite data indicated numerous winter blooms of coccolithophores from 1998 to 2020 considered unusual for the Black Sea. Comparing the data of field coccolithophore observations during the winter period with remote sensing PIC data made it possible to interpret the numerous signs of mass coccolithophore growth in the cold period of the year. As a result, numerous winter blooms of coccolithophores were identified, which took place in the entire Black Sea (2001, 2003, 2005–2006, 2007, 2011, 2012, 2014 years), or locally (1998, 1999, 2001, 2002, 2004, 2009, 2013, 2015–2019).

Analysis of satellite data showed that the winter growth of coccolithophores occurs, as a rule, in warm and calm winters during periods with stable stratification of the surface layer. It should be noted that, unlike summer, winter blooms of coccolithophores do not always cover the entire water area of the sea. First of all, this is due to the lower stability of hydrological conditions in winter, which are necessary for algae growth. In most cases, local blooms are observed mainly in the north-eastern and eastern sea parts. These sea areas are shown to be a warm sector and are protected from the effects of cold north-easterly winds that strengthen winter convection and destroy the stratification of the surface layer. Depending on the current hydrometeorological conditions of the year favorable for coccolithophores, the winter-blooming area may be located in the eastern, southern, south-eastern, or north-eastern part of the sea (Figure 17).

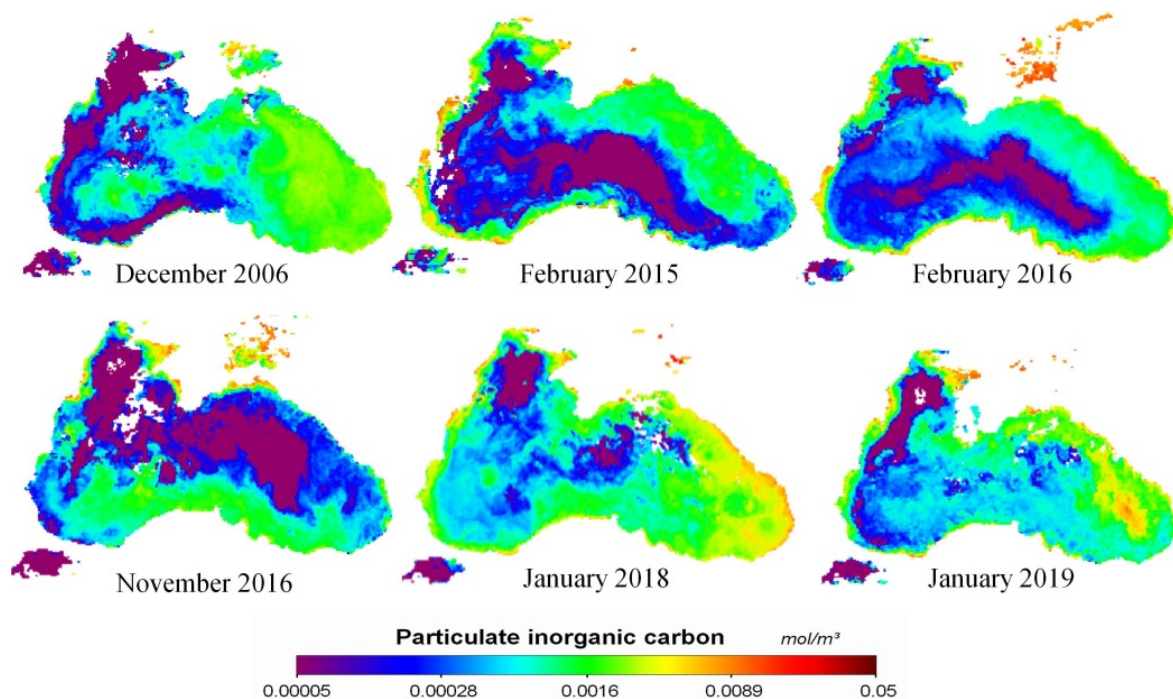


Figure 17. Winter blooms of coccolithophores (PIC) according to the MODIS-Aqua.

The hydrological conditions and the structure of phytoplankton during the winter and winter-spring blooming of coccolithophores were studied in the north-eastern part of the Black Sea (See Figure 16).

The mass growth of coccolithophores, recorded during field investigations at the end of December 2010, occurred in warm winter and low windy weather. Blooming was preceded by a short storm period, which contributed to the turbulent involvement of deep waters in the surface-producing layer. In the subsequent low-wind period, the formation of a thermocline and stable stratification occurred, allowing algae to remain in the zone of light optimum. During the winter-blooming period of December 2010, phytoplankton with a total predominance of coccolithophores was concentrated in the upper mixed layer and thermocline. At a depth of 40 m or more, in the winter of 2010, coccolithophores were practically absent in the plankton. According to satellite data, the expedition studies in December 2010 took place during the initiation of the winter-blooming of coccolithophores, which further developed during the three months from January to March.

A joint analysis of satellite data and the results of field observations showed that conditions of cold winters with active convection prevent mass growth of coccolithophores, as a rule. The weakened wind mixing and stable stratification in warm winters are essential factors for the initiation of coccolithophores blooming. The dynamics of coccolithophores' growth in the years with warm and cold winters are shown in Figure 18a,b.

The seasonal succession of coccolithophores in the years with warm winters was characterized by a pronounced period of growth in February–March and smoothed summer blooming, with a peak in June (Figure 18a). Moreover, the coccolithophores concentration in the warm winter of 2011 (Figure 18b) is comparable with the summer values in May and June. A different situation is observed in years with cold winters when temperature convection is enhanced by wind mixing. The relevant data shows (Figure 18b) that in the cold winter conditions of 2012 with temperatures of about 6 °C coccolithophores' growth was poorly expressed compared to the summer peak. After the cold winter, in summer 2012, one of the most intensive blooms for the entire twenty-year observation period occurred. These examples demonstrate two different types of seasonal succession of coccolithophores, depending on the hydrometeorological conditions of the previous winters.

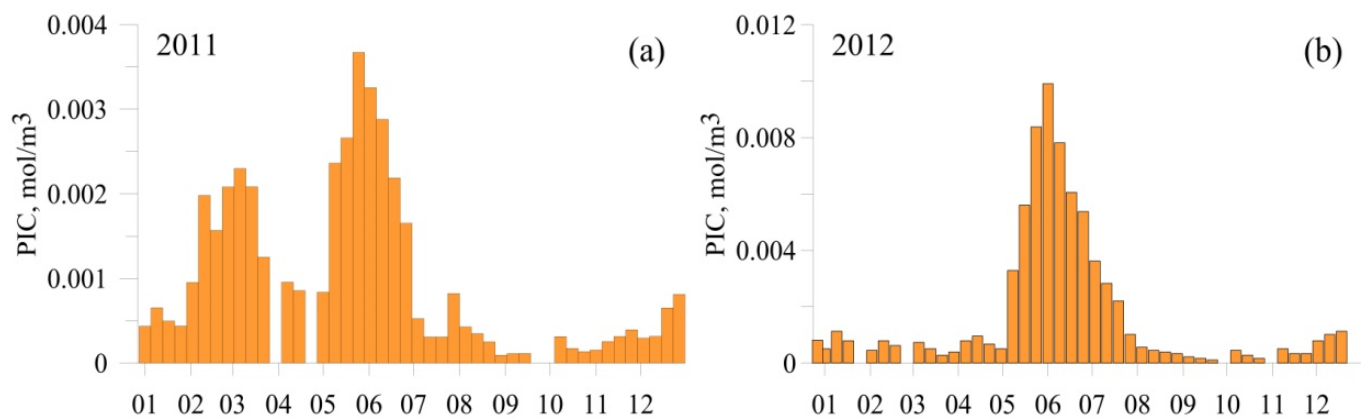


Figure 18. Dynamics of coccolithophores during winter and summer blooms assessed by PIC concentration in the years with warm (a) and cold (b) winters according to the MODIS-Aqua.

4. Discussion

As numerous studies have shown, coccolithophores play a significant role in the Black Sea phytoplankton, occupying a dominant position at the beginning of the summer period [6,23–25]. Summer blooms of coccolithophores are a characteristic feature of the seasonal succession of phytoplankton. At the same time, significant interannual differences in the growth of coccolithophores are recorded. The reason for the variation mentioned is a diverse combination of climatic and current hydrometeorological factors that determine the parameters of winter convection, providing nutrient enrichment of the surface layer. It was shown that summer blooms reach the highest level after the coldest winters. This pattern [4,23] is reproduced with new data and persists on the background of a steady trend of minimum winter temperatures increase. From 2000 to 2020, a positive correlation was noted between monthly average PIC concentrations in June and the minimum sea surface temperatures in February ($R = 0.59$). It is evident that the winter temperature, in this case, is an indicator of the intensity of winter convection and the enrichment of the photosynthesis layer with nutrients. A positive correlation of PIC with minimum winter temperatures was also noted by several authors [4,23,32]. At the same time, after the cold winter of 2007, there was no intensive summer development of coccolithophores. It should be noted that peak blooms of coccolithophores along 20 years never follow each other but take place within a 2–4-year interval, which also applies to this case. The reasons detection needs more detailed consideration of all factors affecting the initiation of peak summer blooms in addition to intense convection in the previous winter. Among them, the interaction of blooming coccolithophores and diatoms, the depletion of the pool of nutrients after blooms, surface layer stratification, and others are important. This interaction will be the subject of additional research.

Wind mixing plays an equally important role in enriching the surface layer, enhancing the effect of temperature convection in the winter season. Wind action and, consequently, active turbulent mixing, led to the enrichment of the producing layer with nutrients and algae cells redistribution after blooming within the euphotic layer. At the same time, in summer, this can interfere with the growth of coccolithophores, reducing the stability of the water column and promoting the removal of cells from the light optimum zone and dilution of the community. In addition, the turbulent enrichment of the photosynthetic layer with nutrients can disrupt the stoichiometry of nitrogen and phosphorus of the summer period and create favorable conditions for the growth of algae species competitive with coccolithophores. This situation was observed in the abnormally cold summer of 2001 when diatoms replaced the coccolithophore bloom. Diatoms can develop under temperature convection and turbulence conditions and adapt to changing lighting conditions. As such, they can effectively use nutrients involved in the photic layer due to mixing. The stock of nutrients renewed in the photosynthetic layer in winter largely determines phytoplankton succession during the year [6,23]. The level of coccolithophore concentrations in the

summer period is also influenced by the parameters of the phytoplankton community in the preceding winter-spring season. The peak growth of coccolithophores in 2006, 2012, and 2017, which occurred after cold winters, was preceded by a relatively low level of winter diatoms growth. This pattern is confirmed by a negative correlation ($R = -0.32$) of average PIC values during the summer coccolithophore blooms and the remote sensed average chlorophyll concentrations during the winter diatoms development in the open regions of the sea. In general, the interaction of diatom and coccolithophore blooms in the cycle of seasonal succession is of great importance and requires a more detailed study.

An additional driver for the coccolithophore's growth may be the influx of nutrients from river runoff. Several authors believe that biogenic runoff can significantly affect the growth of coccolithophores in the coastal zone and cause blooms along the north-eastern coast of the Black Sea [24]. River runoff enhances stratification creating favorable conditions for the initiation of the bloom. The river waters can also be a reason for local coccolithophore blooms in the case of specific nutrient composition with the predominance of mineral phosphorus. This chemical structure of waters leads to the advantage of coccolithophores concerning other types of phytoplankton. Otherwise, diatoms will have a competitive advantage in river flow areas. At the moment, the analysis of satellite data without synchronous measurements of nutrient content does not allow us to unambiguously identify the impact of biogenic river runoff on the growth of coccolithophores.

On the contrary, in the western part of the sea, in the zone of the Danube influence, the vast growth of diatoms and other phytoplankton species is recorded, as evidenced by the high chlorophyll content, on most of the western shelf of the sea. The enrichment of the surface layer with nutrients in summer due to wind mixing and eddy activity in the open sea also led to the mass growth of diatoms, which was reflected in the chlorophyll concentrations observed [35,36,46]. Abnormal hydrometeorological conditions of the cold summer of 2001 led to the mass growth of diatom plankton in almost the entire sea area, which was observed during the season characteristic of coccolithophore blooming. This phenomenon requires further in-depth research, including an analysis of the hydrological regime in summer and the climatic conditions of 2001 in general. The Caspian Sea, located in the same climatic zone, also demonstrated in the summer of 2001 an abnormal blooming of diatoms, the most powerful over twenty years of satellite observations. These patterns are of fundamental importance for understanding the nature of hydrometeorological conditions that determine the succession of phytoplankton and variability of coccolithophores.

As was noted, there has been a general trend of replacing diatoms by coccolithophores in phytoplankton in the last decades [4]. It is known that each group of algae has its range of stoichiometric ratios of the main nutrients, optimal for their growth [26–29]. Studies of the long-term variability of nutrients have shown that the existing changes in the stoichiometry of nitrogen and phosphorus compounds in seawater create additional competitive advantages for coccolithophores [4,6].

Winter blooms of coccolithophores in the Black Sea are the least studied phenomenon in the seasonal succession of the marine ecosystem [37,46]. At the same time, the extended growth of coccolithophores in the cold season plays a crucial role in substituting diatoms with coccolithophores in the ecosystem of the Black Sea. Despite the considerable spatial and temporal variability of phytoplankton for the Black Sea, some general patterns of change in dominant complexes during the year can be fixed. The predominance of small diatoms ($l < 50 \mu\text{m}$) in the winter-spring period, coccolithophores in the late spring and early summer season, and large diatoms in summer and autumn are of the most importance. In this sense, the total or local substitution of diatoms with coccolithophores in winter is an abnormal phenomenon of great importance for the functioning of the food chain of the Black Sea ecosystem, as well as the sedimentation regime of organic and inorganic carbon. The absence of stable density stratification during winter blooms of coccolithophores can accelerate sedimentation processes and contribute to the preservation of organic matter in sedimentary material, reducing the time of its destruction in the oxygen zone. The role of winter blooms in the geochemical carbon cycle needs additional assessment.

A joint analysis of satellite data and the results of field observations showed that in conditions of cold winters and active winter convection, the mass growth of coccolithophores is not observed. When the water column is stabilized by warm and calm winters, conditions for active growth of coccolithophores are created [46,51]. The absence of wind mixing, which destroys stratification in winter, is an essential factor for the initiation of coccolithophore blooms. At the same time, the absolute temperature values of both warm (8–10 °C) and cold (6–8 °C) winters are not a factor limiting the mass growth of algae. The same result was recorded before in the North Atlantic [52]. Under favorable conditions, blooms can also occur locally, forming spots or elongated areas. The shape and extent of blooms are always mediated by dynamic factors, often of an eddy nature. An essential role in the formation and distribution of blooms is played by the meandering of the Rim Current, which provides an exchange between the coastal waters enriched by nutrients and open areas of the sea. Active transfer and redistribution of algae by the Rim current can lead to the fact that the areas of initiation of blooms do not coincide with the areas of their further growth. Local inhomogeneity in the distribution of phytoplankton can also be created by quasi-stationary eddies, initiated by short-term wind effects, such as tropical cyclones and Novorossiysk tunnel flow [35,36,53–55]. Strong northern and north-eastern winds and tropical cyclones can locally change the hydrophysical conditions of phytoplankton growth, including coccolithophores, contributing to the enrichment of the surface mixed layer with nutrients which can lead to outbreaks of algae growth [35,36,56]. In some cases, these events can be stable and reflected on the satellite maps with monthly averaging [35]. The effect of mesoscale eddies on phytoplankton also depends on the type of eddy formation and the stage of its development [56,57]. The effect of eddies circulation on coccolithophores, as a factor initiating blooms has yet to be studied. The available data indicate a multidirectional impact of eddies on the dynamics of coccolithophores. In the case of Batumi anticyclone, it may also be a result of a periodical change in the type of the eddy circulation from anticyclonic to cyclonic.

The results obtained provide for identifying priority fields and areas for further research. Using the updated regional algorithm will allow analyzing the quantitative distribution of algae and its mesoscale variability during seasonal succession in open and nearshore regions depending on river runoff. Particular attention should be paid to the influence of eddy circulation on the phytoplankton communities' development, including coccolithophorids.

Further field data studies will reveal the features of hydrochemical and hydrophysical conditions responsible for summer and winter coccolithophores blooms. A detailed study of the vertical structure of the phytoplankton community and the use of regional algorithms will provide for quantifying the total abundances and biomass of coccolithophores in the photosynthetic zone and estimate sedimentation parameters based on remotely measured characteristics of the surface layer.

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