

Quasi-tropical cyclone caused anomalous autumn coccolithophore bloom in the Black Sea

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Abstract. Short-period action of the quasi-tropical cyclone in September 2005 caused strong autumn coccolithophores bloom in the Black Sea lasted for more than 1.5 months. The cyclone induced intense upwelling of deep waters with temperature on 10-13°C lower than surrounding waters and acceleration of the Rim Current up to extreme values of 0.75 m s⁻¹. The Rim current transported nutrient-rich waters from the north-western shelf to the zone of the cyclone action. Mixing of the shelf and upwelled waters triggers the initial growth of remote sensing reflectance (R_{rs}) indicating the beginning of the coccolithophore bloom. After two weeks, the bloom shifted directly to the zone of maximum upwelling in the western cyclonic gyre, where R_{rs} reached values of 0.018 sr⁻¹, corresponding to estimates of 10⁷ cells l⁻¹. Advection by the Rim Current spread the bloom over the entire south part of the Black Sea on more than 1000 km from its initial source.

1 Introduction

15 Vertical mixing and upwelling caused by the action of tropical cyclones uplift nutrients to the euphotic layer and induce intense sporadic phytoplankton blooms in the World Ocean (for example, Babin et al., 2004; Chacko, 2017; Han et al., 2012; Kubryakov, Stanichny, et al., 2019; Lin et al., 2003; Miller et al., 2006; Morozov et al., 2015; Tsuchiya et al., 2013). An important tracer of such changes is the chlorophyll-*a* concentration (Chl), which can be determined from satellite measurements. Intense nutrients entrainment leads to the rapid rise of Chl, which can be observed several months after the action of the storm in various ocean areas (for example, Shi et al., 2007; Wu et al., 2008), including the Black sea (Kubryakov, Stanichny, et al., 2019a). In some cases, the action of atmospheric cyclones causes the growth of specific types of phytoplankton. For example, (Zhu et al., 2014) showed that the storm action in Taihu lake led to an intensive growth of potentially toxic cyanobacteria.

At the same time, there is almost no information on the impact of tropical cyclones on the development of coccolithophores. Coccolithophores are one of the dominant phytoplankton types in the ocean. Their specific feature is the ability to form calcified plates – coccoliths, which play a significant role in the ocean carbon pump (Balch et al., 2011; Hernández et al., 2018, 2020; Krumhardt et al., 2017; Rost and Riebesell, 2004) and formation of calcareous sediment layers (Coolen, 2011; Hay et al., 1990; Honjo, 1976). Coccolithophores cause significant light scattering and increasing the reflectance of the water, which makes it possible to study them using satellite data (Balch et al., 1996; Cokacar et al., 2001, 2004; Hooligan et al., 1983;

30 Hopkins et al., 2015; Kopelevich et al., 2014; Krumhardt et al., 2017; Mikaelyan et al., 2011; Shutler et al., 2013; Suslin et al., 2012; Tyrell and Merico, 2004). The Black Sea has some of the strongest coccolithophore blooms in the world (Mikaelyan et al., 2005, 2011, 2015; Cokacar et al., 2001, 2004; Pautova et al., 2007; Yasakova and Stanichny, 2012; Kopelevich et al., 2014; Korchemkina et al., 2014) with cell concentrations can reach $30 \cdot 10^6$ cells l^{-1} (Mihnea, 1997). The most intense coccolithophore blooms in the Black Sea are observed in the spring and summer (Cokacar et al., 2001, Mikaelyan et al., 2015). Weaker blooms are also observed in winter, both from satellite data and measurements of Bio-Argo buoys (Kubryakov, Zatsopin, et al., 2019) and *in situ* measurements (Hay et al, 1990; Sorokin, 1983; Stelmakh et al., 2009; Stelmakh, 2013; Sukhanova, 1995; Turkoglu, 2010; Yasakova et al., 2017).

This paper documents for the first time the impact of an anomalous quasi-tropical atmospheric cyclone on the development and evolution of autumn coccolithophore blooms in the Black Sea on the base of the analysis of satellite optical, infrared and altimetric data. This case was recorded after an anomalous intense atmospheric cyclone in September 2005, described in (Efimov et al., 2007, 2008). The action of the cyclone caused significant changes in the basin dynamics, which promote horizontal and vertical entrainment of nutrients into the upper layer of the sea and caused the intense coccolithophore bloom, accompanied by the noticeable of Chl.

2 Data and methods

45 For the analysis of the coccolithophore bloom in the Black Sea, the Level 2 MODIS-Aqua daily maps of remote sensing reflectance at a wavelength of 555 nm (R_{rs}) and Chl for September-November 2005 with a spatial resolution of 1 km and a time of 1 day were used. High R_{rs} values are caused by increased backscattering on particles. In the coastal zone, especially at river mouths, the main reason for the increase in R_{rs} values is terrigenous particles. In the central part of the oceans and, in particular, in the Black Sea, intense growth of R_{rs} values are caused by scattering on coccoliths during the coccolithophore bloom (Cokacar et al., 2001, 2004; Kopelevich et al., 2014).

The equation $N=0.8 \cdot 10^9 \cdot b_{bp}(700)^{1.21}$ and the linear relationship between $R_{rs}(555)$ and $b_{bp}(700)$ $R_{rs}=0.7 \cdot b_{bp}(700)$ obtained on the base of comparison of Bio-Argo and satellite measurements (Kubryakov, Zatsopin, et al., 2019) were used to estimate the coccolithophore cells concentration from R_{rs} values. Estimates that are comparable in order of magnitude can be obtained using the formula from (Churilova and Suslin, 2012; Suslin et al., 2012). According to the used parameterization, the concentration value is more than $1 \cdot 10^6$ cells l^{-1} , i.e. bloom corresponds to the value of $R_{rs}=0.005$ sr^{-1} . The area of coccolithophore bloom was estimated as a total area with values of $R_{rs} \geq 0.005$ sr^{-1} .

Wind velocity measurements of the scatterometer SeaWinds of the satellite QuikSCAT for September-November 2005 with a spatial resolution of $0.25^\circ \times 0.25^\circ$ and a time resolution of 1 day was used. The value of the Ekman pumping was defined as

$$W_{ek} = \frac{1}{\rho_w \times f} rot(\tau), \text{ where } \rho_w=1000 \text{ kg m}^{-3} \text{ is the water density, } \tau = c_d \rho_a \cdot |v| \cdot v \text{ is the wind stress, } c_d=1.3 \cdot 10^{-3} \text{ is}$$

60 the drag coefficient, $\rho_a=1.3 \text{ kg m}^{-3}$ is the air density, v is the wind velocity.

Regional dataset on altimetry-derived daily mapped sea level anomalies (MSLA) with $1/8^\circ$ resolution produced by AVISO was downloaded from CMEMS (Copernicus Marine Environment Monitoring Service). MSLA was added to the mean dynamic topography (Kubryakov and Stanichny, 2011) to compute surface geostrophic velocities in the sea. The obtained dataset was validated in (Kubryakov et al., 2016) with drifters and hydrological data. The analysis of the sea surface temperature (SST) was carried out using measurements of AVHRR (Advanced Very High-Resolution Radiometer) radiometers with a spatial resolution of 1 km.

3 Results

3.1 Impact of a quasi-tropical cyclone on physical processes in the Black Sea

From 25 to 29 September 2005, an anomalous intense quasi-tropical cyclone was observed in the atmosphere over the Black Sea from satellite images (Fig. 1a). It had a cloud-free eye and distinct spiral cloud bands and was no more than 300 km in diameter. Wind velocity in the cyclone reaches $20\text{--}25\text{ m s}^{-1}$ according to the QuikSCAT satellite data (Fig. 1b). Its development occurred after weak wind conditions and was associated with overheating of the sea surface and increased moisture fluxes over the western part of the Black Sea. A detailed analysis of the dynamics of this cyclone and its causes was carried out in (Efimov et al., 2007, 2008).

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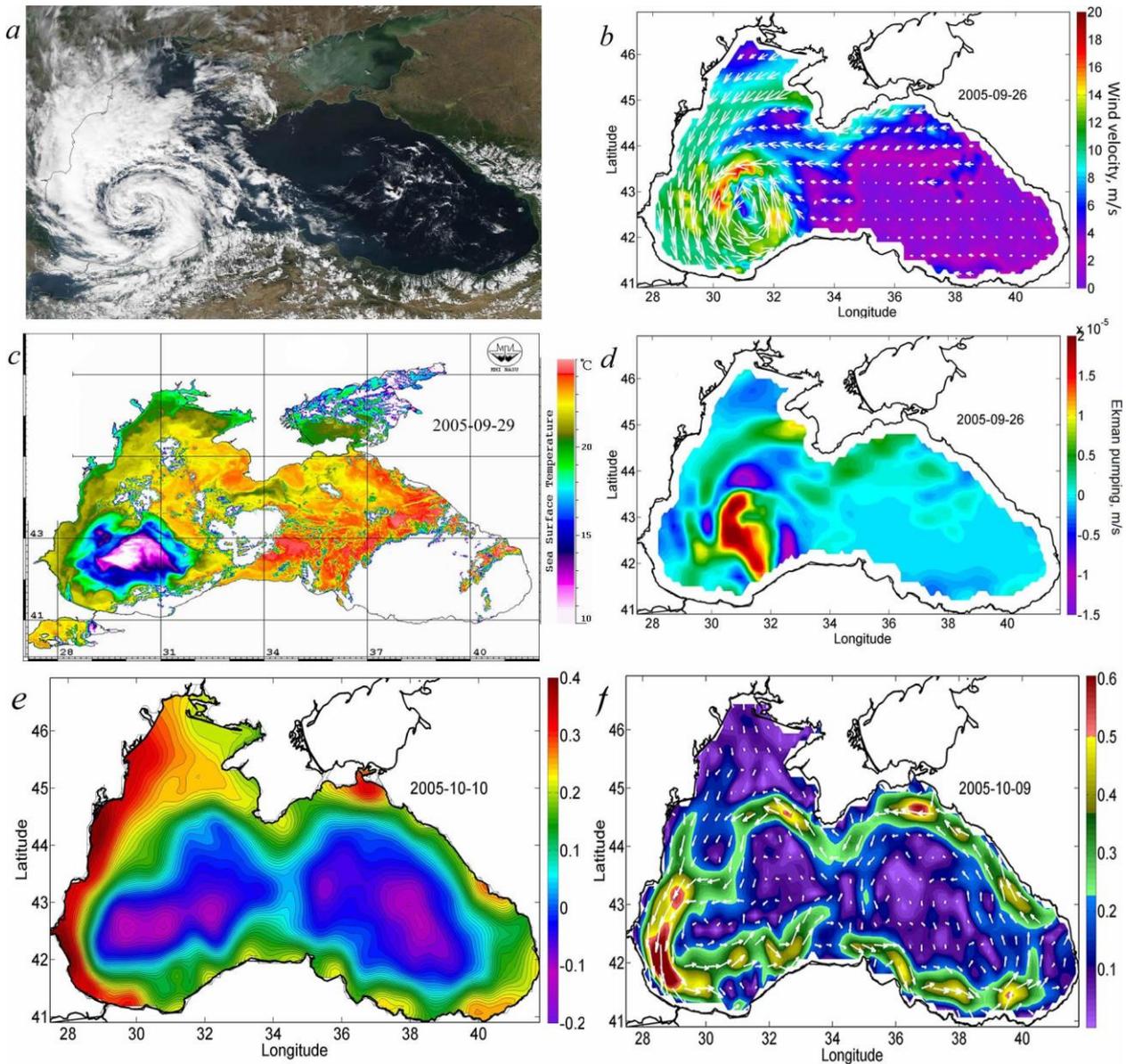


Figure 1: (a) – satellite image of MODIS-Aqua in the visible range for 27 September 2005 (data obtained from the Worldview portal); (b) – wind velocity (m s^{-1}) of the scatterometer SeaWinds of the satellite QuikSCAT on 26 September 2005; (c) – SST ($^{\circ}\text{C}$) for 29 September 2005, according to the AVHRR radiometer; (d) – Ekman pumping velocity (m s^{-1}) on 26 September 2005, calculated from the scatterometer SeaWinds of the satellite QuikSCAT; (e) – sea level, m at 10 October 2005; (f) – flow velocity, m s^{-1} at 9 October 2005.

Cyclonic wind vorticity led to Ekman pumping and divergence in the upper mixed sea layer, which caused the uplift of deep waters to the surface. The Ekman pumping, on 26 September was $2 \cdot 10^{-5} \text{ m s}^{-1}$ (Fig. 1d) with an observed maximum of $2 \cdot 10^{-4} \text{ m}$ (Efimov et al., 2007). The atmospheric cyclone was situated over the western cyclonic gyre of the Black Sea circulation. The center of the gyre was observed in altimetry maps as an area of a decreased sea level reflecting the uplift of isopycnals

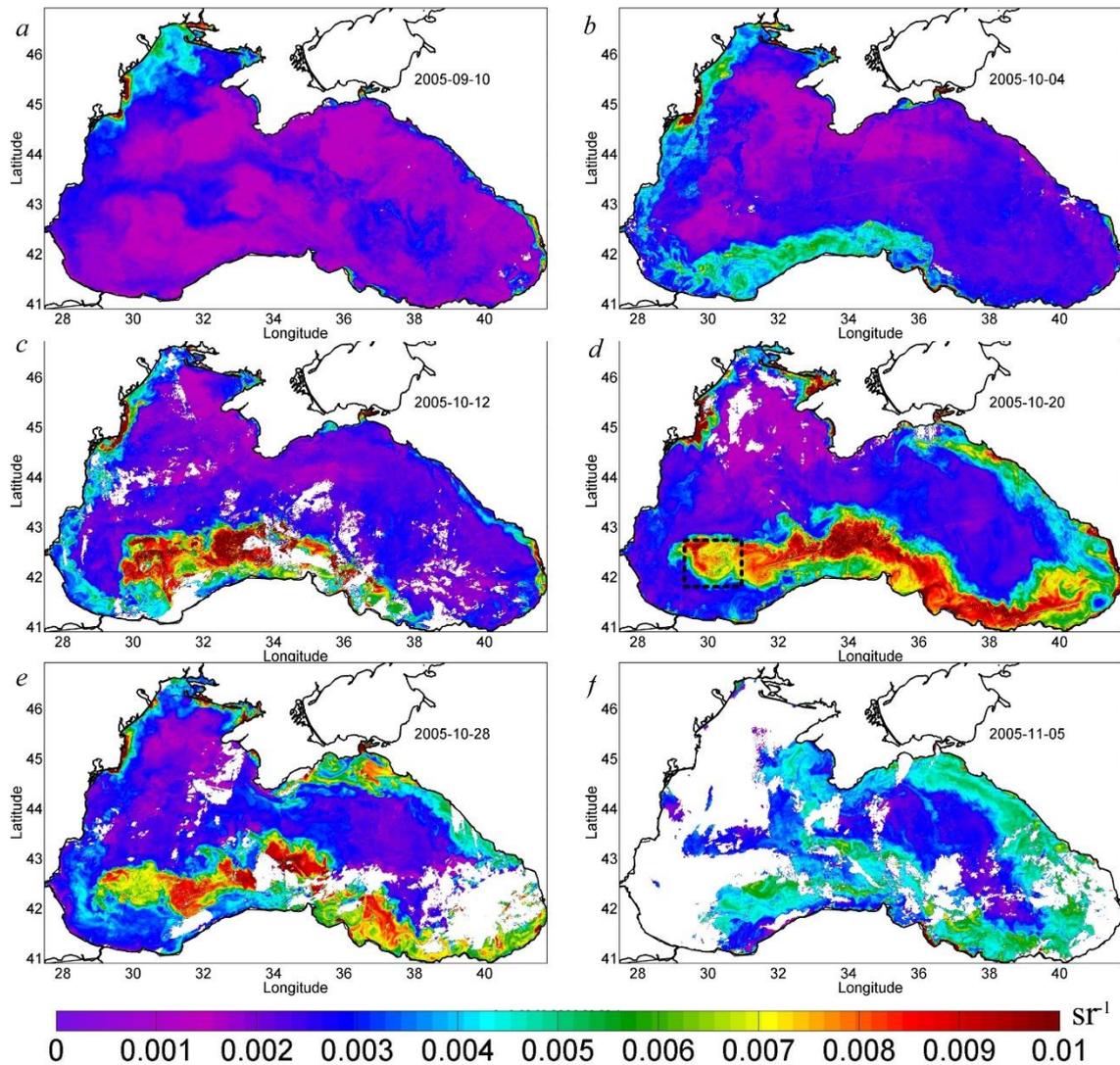
85 (Fig. 1e). On average the pycnocline and nitrocline in the centers of cyclonic gyres in the Black Sea are elevated by 20 m relative to the periphery of the sea (Ivanov and Belokopytov, 2013).

A quasi-tropical atmospheric cyclone caused additional intense upwelling, accompanied by strong mechanical wind mixing. The action of Ekman pumping pushed the waters from the central part of the basin to its periphery strongly increasing the sea level gradients over the Black Sea continental slope. Particularly, the sea level on the western shelf of the basin rose from 0.2
90 to 0.4 cm and on its eastern part from 0.05 cm to 0.2 cm (Fig. 1e). The compensating upward vertical motions caused intense entrainment of deep cold waters in the sea surface layer. According to the AVHRR radiometer data, on 29 September, the SST in the central-western part decreased by more than 12°C (Fig.1d). The maximum cooling was observed in the center of the cyclonic gyre in the south-western part of the sea, where SST reached 10°C which was on 13-15°C lower than in surrounding waters (23-25°C). The isotherm 10°C in the Black Sea in September are located under the seasonal thermocline at depths of
95 30-40 m. Thus, the action of the atmospheric cyclone led to the rise of isopycnic surfaces by 30-40 m and the outcropping of deep isopycnals layers on the sea surface. Taking into account the active thermal mixing of waters due to the action of the cyclone and solar heating in this period of a year, it can be assumed that the waters were uplifted from even larger depths.
Strong river inflow brings a large amount of colored dissolved organic matter to the sea (Vladimirov et al., 1997), that is why the euphotic zone of the Black Sea is shallow and is about 40 m (Vedernikov and Demidov, 1993). The underlying layers
100 contain a large amount of nitrates (Konovalov and Murray, 2001), which were uplifted into the sea surface layer in September 2005.
Therefore, nutrients

Upwelling and the rise of the sea level caused a significant intensification of the cyclonic Rim current. Its velocity over the continental slope increased twofold from the values of 0.25 to 0.45 m s⁻¹ (Fig. 1f). The highest values of geostrophic velocity were recorded in the south-western part of the sea, where they reached extremely high values for the Black Sea exceeding 0.6
105 m s⁻¹ with a maximum of 0.75 m s⁻¹ (Fig. 1f).

3.2 Impact of quasi-tropical cyclone on biological processes in the Black Sea

Satellite measurements show that such changes in the basin dynamics significantly affected the bio-optical characteristics of the Black Sea. Before the passage of an atmospheric cyclone, R_{rs} in the Black Sea was less than 0.004 sr⁻¹, except the north-western shelf affected by the main river's inflow (see Fig. 2a). This value is typical for this season and indicates that the surface
110 layer of the sea central part contains low concentrations of particles that cause backscattering. R_{rs} in the western central part stayed low until the action of the quasi-tropical cyclone at the end of September (see the purple line in Fig. 3), which caused a significant decrease of SST in this area (blue line in Fig. 3). The values of Chl in the sea central part were also low, less than 0.7-0.8 mg m⁻³ (see Fig. 3, 4). Immediately after the action of an atmospheric cyclone in late September, Chl increased significantly throughout the western part of the sea and on 4 October Chl reached its maximum values (1.3 mg m⁻³) in the
115 western central part of the basin (green line in Fig. 3). This fast rise of the Chl in the zone of the cyclone action was partly caused by the entrainment of phytoplankton from the layer of its subsurface maximum (Kubryakov, Stanichny, et al., 2019), which is usually situated at depths of 15-30 m during this period (Vedernikov and Demidov, 1993).



120 **Figure 2:** 8-daily maps of remote sensing reflectance R_{rs} , sr^{-1} , centered at (a) 10 September 2005, (b) 4 October 2005, (c) 12 October 2005, (d) 20 October 2005, (e) 28 October 2005, (f) – 5 November 2005. The black rectangle shows area “A” with coordinates: 41.66-42.78° N, 29.43-31.38° E.

At the same time, the rise of R_{rs} to the values of $5\text{--}6 \cdot 10^{-3} \text{ sr}^{-1}$, corresponding to the level of coccolithophore bloom, was first observed in the south-western part of the sea (Fig. 2b). The increase of R_{rs} was observed only in a limited area south of the cyclone's action over the sea continental slope. Rise of R_{rs} was also observed in the southern western part of the sea. In this area, it was only observed on the shelf/slope boundary in the intermediate zone between the shelf and the central part of the sea and was absent near the coast. At the same time in the sea central part, the R_{rs} values were low. The confinement of bloom to the area of mixing of the shelf and deep waters was also observed on the next dates (Fig. 2c, d).

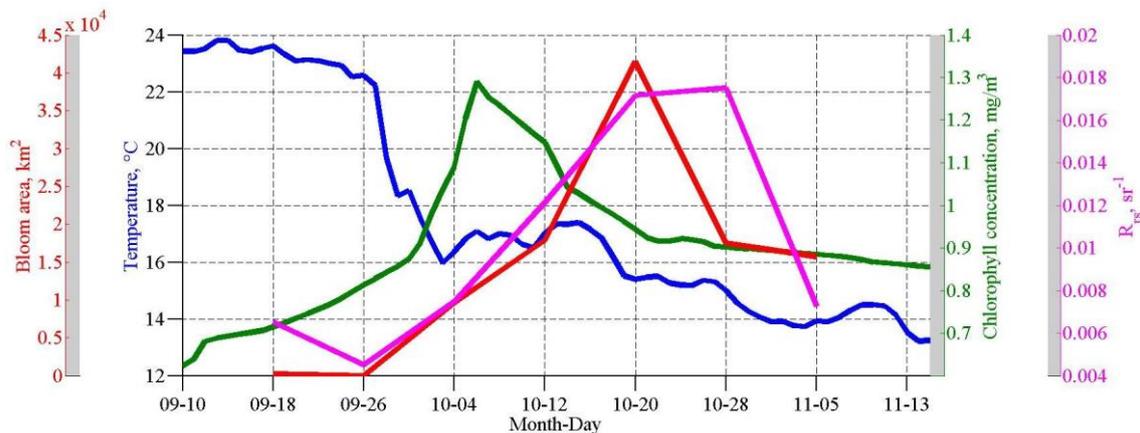


Figure 3: Average variability of SST according to the AVHRR radiometer (blue line), R_{rs} (purple), chlorophyll-a concentration (green) according to MODIS data in the center of the western cyclonic cycle (rectangle “A” in Fig. 2d); maximum area of coccolithophore bloom (red) in the sea.

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The reason for the initial increase in R_{rs} values was not vertical, but horizontal advection. The intensification of the Rim Current led to increased transport of river plume water from the north-western part of the sea in a cyclonic direction along the sea coast. This flow was well traced in Chl maps (Fig. 4a, b, c). At the beginning of September 2005, an area of high Chl ($>3 \text{ mg m}^{-3}$) associated with the spread of a plume of Danube was observed near the western coast to the north of 42° N (Fig. 4a). After the Rim Current intensification under the impact of the atmospheric cyclone at the beginning of October 2005 the waters of the plume were transported along the coast to the south-western part of the sea (Fig. 4b). Exactly in this area the growth of R_{rs} was first observed (Fig. 2b, c). Note that the position of high R_{rs} values and Chl did not coincide at that time. High R_{rs} values were observed directly to the south of the cyclone zone, while Chl gradually decreased from its source at the north-western shelf (Fig. 2c, 4c).

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A week later, at 8-15 October R_{rs} value rapidly increased (Fig. 2c) and the bloom area has doubled (Fig. 3, red line). The maximum R_{rs} increased to 0.012 sr^{-1} , which corresponded to $5.8 \cdot 10^6 \text{ cells l}^{-1}$. The area of most intense bloom was observed in the continental slope south of the western gyre and the regions west of it. Chl was characterized by a similar distribution (Fig. 4c, d). Part of the turbid Danube waters during this period moved across the isobates and penetrated a considerable distance into the central part of the sea (Fig. 2c, 4c). The offshore boundary of the front of turbid waters was characterized by several mesoscale features, indicating intense processes of horizontal exchange. These features were probably caused by the baroclinic instability of the Rim Current, caused by its significant intensification under the impact of the atmospheric cyclone. As a result, a large amount of nutrients from the shelf area were transferred into the central part of the sea. The area of the intense horizontal mixing was characterized by the maximum R_{rs} values, which were observed over the basin continental slope. At the same time the rise of R_{rs} along the coast was significantly less pronounced. It indicated that the most favorable conditions for coccolithophore bloom initially occurred in the zone of mixing of shelf waters and deep waters in the center of the western

155 cyclonic gyre. Besides, this distribution indicates that the rise of the R_{rs} was not associated with the terrigenous particles caused by storm-driven coastal erosion.

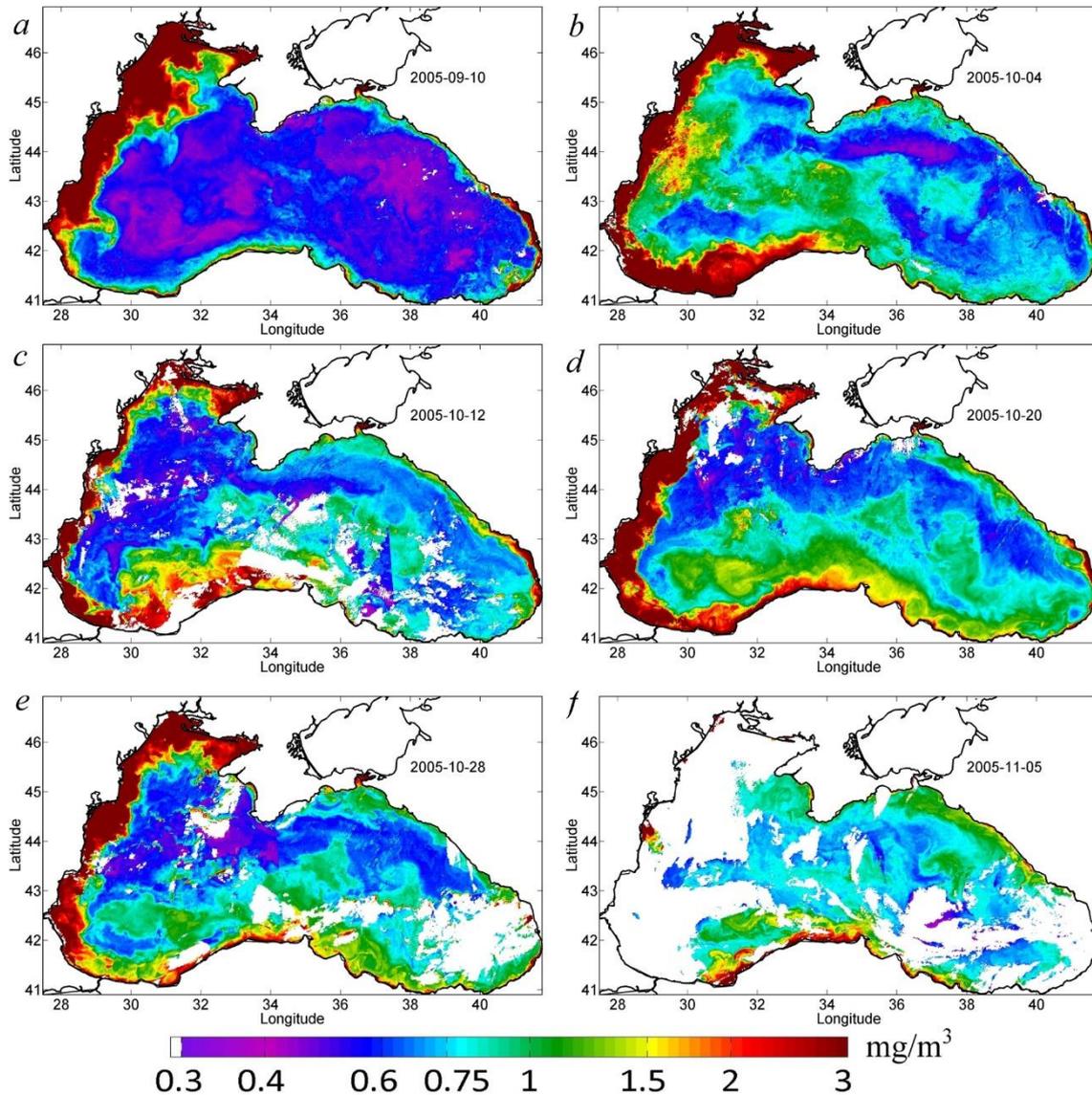


Figure 4: 8-daily maps of chlorophyll-a concentration, mg m^{-3} , centered at (a) 10 September 2005, (b) 4 October 2005, (c) 12 October 2005, (d) 20 October 2005, (e) 28 October 2005, (f) – 5 November 2005.

160 In the next week (from 16 to 23 October), the bloom position shifted from the coast to the center of the western gyre – zone of maximal vertical entrainment (Fig. 2d). Here stable bloom area with a diameter of about 100 km developed. The region of high values of the R_{rs} parameter extended from this area eastward along the continental slope up to the eastern coast of the basin up to 41.5° E (Fig. 2d). The total length of the bloom area was more than 1200 km (Fig. 2d). After 2-3 weeks after the

cyclone's action, the average and maximum values of the R_{rs} parameter reached the highest value (Fig. 3, purple line). In some areas, the R_{rs} value was higher than 0.018 sr^{-1} , which corresponds to an estimate of $9 \cdot 10^6 \text{ cells l}^{-1}$. Bloom area at this time reached a maximum of about $40 \cdot 10^3 \text{ km}^2$ (Fig. 3, red line). In the same areas, Chl increased to a value of $1 \cdot 1.3 \text{ mg m}^{-3}$, which was three times higher than in early September (Fig. 4d). Thus, the growth of calcified phytoplankton was observed simultaneously with the development of phytoplankton with a high content of Chl, which is mainly diatoms for the Black Sea (Mikaelyan et al., 2015).

Waters with high R_{rs} and Chl values were transported by the Rim Current from the area of the cyclone action to the eastern coast of the basin. At the velocity of 0.45 m s^{-1} (Fig. 1e), the particles will be transported on 1000 km in 3 weeks, which coincides well with satellite optical measurements (Fig. 2). The advection by the Rim Current transport both raised nutrients and already formed phytoplankton cells to the east. At the same time, the maximum bloom position was continuously observed in the zone of the maximal vertical entrainment during a month after the action of the quasi-tropical cyclone. Thereby, the upwelling in the center of the west cyclonic gyre was a permanent source of nutrients and phytoplankton growth, from which the bloom stretched to the eastern shore. Indeed, decreased SST in this area was observed until the end of October, which also indicates the stability of upwelling.

At the end of October, the intensity of coccolithophore bloom in the western cyclonic cycle weakened indicating the relaxation of upwelling and the lowering of nitrocline. In this period, the maximum value of R_{rs} decreased to 0.007 sr^{-1} and shifted to the east to $31 \cdot 32^\circ \text{ E}$ longitudes (Fig. 2e). Chl also decreased to $8 \cdot 1.2 \text{ mg m}^{-3}$ (Fig. 4e). At the beginning of November, R_{rs} fell to $0.005 \cdot 0.006 \text{ sr}^{-1}$, indicating the termination of the bloom (Fig. 2f). The termination occurs at the time of the beginning of late-autumn phytoplankton (probably, diatoms) bloom, reflected in the rise of Chl over the whole central part of the basin (Fig. 4f). Such bloom in the Black Sea is usually associated with the deepening of a mixed layer to the upper border of nitrocline (Mikaelyan et al., 2017, 2018; Silkin et al., 2019).

4 Discussion and conclusions

The action of an anomalous atmospheric quasi-tropical cyclone caused a strong coccolithophore bloom, which lasted for more than a month and covered the entire southern part of the Black Sea. The bloom of coccolithophores was observed simultaneously with the rise of Chl associated in the Black Sea with a high concentration of diatoms (Mikaelyan et al., 2015). The natural cause of phytoplankton bloom is the entrainment of nutrients in the euphotic layer caused by rapid changes in basin dynamics. Usually the entrainment of nutrients, particularly, in winter causes a rapid growth of diatoms, which have the highest growth rate and are more concurrent than the coccolithophores (Goldman, 1993; Lomas and Glibert, 1999). Particularly, early summer coccolithophore bloom in the Black develops only after the termination of spring bloom of diatoms due to the depletion of the nitrates entrained in the upper layer in winter (Mikaelyan et al., 2015, 2018). It is believed that coccolithophores can use mixotrophy (Balch, 2018; Poulton et al., 2017) and further can grow on the base of remineralized organic matter and remains of phosphates after diatom bloom (Mikaelyan et al., 2011, 2015). Several studies show that amount

of phosphates largely determines the interannual variability of the intensity of coccolithophore blooms in the Black Sea (Mikaelyan et al., 2011, 2015; Silkin et al., 2009, 2014). The phosphates are remained in the upper layer of the Black Sea, as the N/P ratio in the deep part of the basin is very low 2-6 (Konovalov et al., 2005; Tugrul et al., 2014).

200 This is related to the removal of nitrates from the sea in the form of free nitrogen due to the intense chemical in the suboxic layer of the basin (Konovalov et al., 2008; Tugrul et al., 2014). At the same time intense river discharge provides a large amount of nitrates and organic matter in the basin shelf parts (Cociasu and Popa, 2005; Ludwig et al., 2010). Besides, in summer-early autumn season subsurface layers of the Black Sea contains a high concentration of dissolved organic matter (Kubryakov, Zatsepin, et al., 2019).

205 In the case we have considered, the nutrients were supplied simultaneously from two sources – the shelf zone under the impact of advection by the Rim Current and the deep layers under the impact of Ekman pumping. Satellite data showed that such processes caused the development of both types of phytoplankton simultaneously. Coccolithophores grew firstly in the zone of the horizontal mixing of shelf and deep waters. These mixing diluted the shelf waters with a high amount of nitrates and organics with deep waters rich in phosphates promoting the favorable conditions for the coccolithophore bloom. In the deep part of the basin upwelled water contains nitrates, which were available for diatoms consumption, and excess of phosphates, as well as dissolved organic matter, available for coccolithophores. Such simultaneous blooming was observed earlier in May-June by *in situ* measurements in the Black Sea (Mikaelyan et al., 2018; Pautova et al., 2011; Silkin et al., 2011, 2019) and other ocean areas (Balch, 2018). Note that both diatoms and coccolithophore blooms in September-October is atypical in other years. However, several previous studies (Kubryakov, Zatsepin, et al., 2019; Mikaelyan et al., 2017) showed that autumn storms can lead to an increase of Chl in the Black Sea surface layer as a result of the entrainment of phytoplankton from its subsurface maximum layer and the entrainment of new nutrients from nitrocline. September's coccolithophore bloom was recorded earlier in two studies (Stelmakh et al., 2009; Stelmakh, 2013), but the reasons for them remained unclear.

220 In the considered case, the action of an atmospheric cyclone caused an intense bloom of calcified phytoplankton – coccolithophore, which plays an important role in the ecosystem of the North Atlantic, Barents Sea, Southern Ocean and other areas (Balch et al., 1996, 2019; Hopkins et al., 2015; Krumhardt et al., 2016; Moore et al., 2012; Shutler et al., 2013; Tyrrell and Merico, 2004). Extreme atmospheric pressure led to the development of coccolithophores in October, which is unusual for this type of phytoplankton, which grows in the Black Sea in May-June or December. Such events can play a role in the observed interannual variability of the coccolithophores in the different ocean regions documented in many studies (Krumhardt et al., 2016; Shutler et al., 2013). Coccolithophore bloom may contribute to the emergence of a microbial loop – the transition of trophic energy to small species and subsequent changes in the entire trophic structure of the region (Brussaard, 2004; Kubryakov, Zatsepin, et al., 2019). Detailed information about the response of the taxonomic composition and characteristics of phytoplankton to short-term physical processes is necessary for understanding the functioning of marine ecosystems. Such information can be provided only on the base of continuous monitoring, based, e.g. on the measurements of flow cytometers.

Data availability

We acknowledge the use of (1) moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Ocean Color Data produced
230 by NASA Goddard Space Flight Center. DOI: data/10.5067/AQUA/MODIS/L2/OC/2018; (2) DUACS delayed-time altimeter
gridded maps of sea level anomalies over the Black Sea ([https://cds.climate.copernicus.eu/cdsapp#!/dataset/sea-level-daily-
gridded-data-for-the-black-sea-from-1993-to-present?tab=overview](https://cds.climate.copernicus.eu/cdsapp#!/dataset/sea-level-daily-gridded-data-for-the-black-sea-from-1993-to-present?tab=overview)) produced and distributed by the Copernicus Climate
Change Service; (3) QuikScat (or SeaWinds) data are produced by Remote Sensing Systems and sponsored by the NASA
Ocean Vector Winds Science Team and are available at <http://www.remss.com/missions/qscat/>; (4) AVHRR data were
235 received and reprocessed at Marine Hydrophysical Institute, Russia, and are available from
http://dvs.net.ru/mp/data/200509bs_sst.shtml.

Author contribution

Sergey Stanichny and Arseny Kubryakov were involved in planning and supervised the work, Elena Kubryakova and Arseny
Kubryakov processed the satellite data, performed the analysis, Elena Kubryakova drafted the manuscript and designed the
240 figures. All authors discussed the results and commented on the manuscript.

Competing interests

The authors declare that they have no conflict of interest, no competing financial interests.

Acknowledgments

Data acquisition and processing were made with the support of the Russian Science Foundation (grant No. 19-77-00029). The
245 study of the impact of a tropical cyclone on the phytoplankton bloom development was supported by the Russian Science
Foundation (grant No. 20-17-00167). Investigation of the evolution of autumn coccolithophore bloom was supported by
Russian Foundation for Basic Research (grant No. 20-35-70034).

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