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

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Abstract. A quasi-tropical cyclone (QTC) observed over the Black Sea on 25-29 September 2005 caused an exceptionally strong anomalous autumn coccolithophore bloom that lasted for more than 1.5 months. QTC induced intense upwelling, causing a decrease in sea surface temperature of 15°C and an acceleration of the cyclonic Rim Current up to extreme values of 0.75 m s^{-1}. The Rim Current transported nutrient-rich Danube plume waters from the north-western shelf to the zone of the

10 cyclone action. Baroclinic instabilities of the plume boundary caused an intense submesoscale process, accompanied by mixing of the shelf and upwelled waters. These processes triggered the initial growth of remote sensing reflectance (R_{rs}) on the offshore front of the plume, indicating the beginning of the coccolithophore bloom. Further, the bloom shifted to the zone of the strongest upwelling in the western cyclonic gyre. Intense vertical entrainment of nutrients in this area caused, first, the increase of chlorophyll-*a* concentration (Chl), which then was followed by strong bloom of coccolithophores. Advection by the Rim

15 Current spread the bloom over the entire south part of the Black Sea on more than 1000 km from its initial source. One month after the QTC action, R_{rs} in these areas reached a value of 0.018 sr^{-1}, corresponding to an estimate of a coccolithophore concentration of 10^7 cells l^{-1}.

1 Introduction

Vertical mixing and upwelling caused by the action of tropical cyclones uplift nutrients to the euphotic layer and induce intense,

20 sporadic phytoplankton blooms in the World Ocean (for example, Babin et al., 2004; Chacko, 2017; Han et al., 2012; Kubryakov et al., 2019c; 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 et al., 2019c). In some

25 cases, the action of atmospheric cyclones causes the growth of specific groups 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 atmospheric cyclones on the development of coccolithophores. Coccolithophores are one of the dominant phytoplankton groups 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;

30 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 increase the reflectance of the water, which makes it possible to study them using satellite data (Balch et al., 1996; Cokacar et al., 2001, 2004; Holligan et al., 1983; Hopkins et al., 2015; Krumhardt et al., 2017; Shutler et al., 2013).

One of the strongest coccolithophore blooms in the World Ocean are observed in the Black Sea (Tyrell, Merico, 2004) in the
35 early summer period (May-June) (Cokacar et al., 2001, 2004; Mikaelyan et al., 2005, 2011, 2015; Kopelevich et al., 2014). Cocoliths protect the cells from photoinhibition, which gives them an advantage to grow in summer during high insolation and low mixed layer depth (Tyrell, Merico, 2004). Usually, the cell concentration (N) during summer blooms in the Black Sea is $\sim 2\text{-}6\cdot10^6$ cells l^{-1} (Mikaelyan et al., 2005, 2011, 2015; Pautova et al., 2007), but in certain years it can reach very high values $N=10\text{-}30\cdot10^6$ cells l^{-1} (Korchemkina et al., 2014; Mihnea, 1997; Yasakova and Stanichny, 2012). Weaker blooms are detected
40 in the winter period (Hay et al., 1990; Kubryakov et al., 2019c; Kubryakova et al., 2021; Mikaelyan et al., 2020; Sorokin, 1983; Stelmakh et al., 2009; Stelmakh, 2013; Sukhanova, 1995; Türkoğlu, 2010; Yasakova et al., 2017). Recent Bio-Argo (Kubryakov et al., 2019c) and satellite studies (Kubryakova et al., 2021) showed that winter blooms usually start in December with a peak in January and are observed almost every year. N is usually lower in winter than in summer ($N=0.5\text{-}2\cdot10^6$ cells l^{-1}) (Kubryakov et al., 2019c; Stelmakh et al., 2009; Stelmakh, 2013).

45 In autumn 2005, satellite data detected a very strong bloom of coccolithophores, anomalous both by its intensity and timing. This bloom was observed after an action of very intense Quasi-Tropical Cyclone (QTC) observed over the Black Sea in September 2005 (Efimov et al., 2008; Yarovaya et al., 2008). Tropical cyclones (or typhoons) are usually originated at latitudes less than 30° (see the review in Emanuel, 2003). However, an anomalous atmospheric cyclone formed over the Black Sea basin at 40°E on 25-29 September (Fig. 1a) had all the characteristic features of the tropical cyclones. It had spiral cloud bands,
50 warm core, pronounced eye of the cyclone, and high wind velocity reaching 25 m s^{-1} (Efimov et al., 2007, 2008). Similar cyclones were documented rarely in the Mediterranean Sea (Pytharoulis et al., 1995; Homar et al., 2003), but never before over the Black Sea. Later, a detailed statistical study of the characteristics of the atmospheric cyclones over the Black Sea (Efimov et al., 2009) showed that cyclones with such large intensity were detected over the Black Sea only 3 times during 30-year period. One of the unique characteristics of the QTC in September 2005 was its quasi-stationarity. It acted on the Black
55 Sea for more than 4 days, which led to significant changes in the Black Sea dynamics and ecosystem.

This paper documents for the first time the impact of such an anomalous quasi-tropical atmospheric cyclone on the development and evolution of autumn coccolithophore bloom in the Black Sea on the base of satellite optical, infrared, and altimetric data.

2 Data and methods

60 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 deep part of the Black Sea, the rapid growth of R_{rs} is mainly caused by scattering on coccoliths during the coccolithophore bloom (Cokacar et al., 2001, 2004; Kopelevich et al., 2014). Another strong source of backscattering and the reflectance increase in the enclosed Black Sea

65 is lithogenic particles originating from the river discharge; due to coastal erosion; resuspension of bottom sediments. These processes mainly occur in the shelf area of the basin (see more details in Section 3.3).

In the areas of coccolithophore bloom, their cell concentration (N, cell l^{-1}) can be estimated on the base of backscattering or R_{rs} data (see Gordon & Balch, 1999). In this paper, we use the equation

$$N = 0.8 \cdot 10^9 \cdot b_{bp}(700)^{1.21} \tag{1}$$

70 and the linear relationship between $R_{rs}(555)$ and backscattering coefficient (b_{bp}, m^{-1}) $b_{bp}(700)$ – $R_{rs}=0.7 \cdot b_{bp}(700)$ – to give an estimate of coccolithophores concentration on the base of satellite data. It should be noted that this formula is very approximate and gives only rough estimates of N. The backscattering during coccolithophore bloom represents a mixture of the signals from the plated coccolithophores and detached coccoliths. The number of coccoliths per cell can vary strongly. In this paper, we use an average value of 30 coccoliths per cell. However, this value can change from 10 (Balch et al., 1991) to more than

75 50 (Mikaelyan et al., 2005). In the coastal areas, R_{rs} represents the mixture of signals from riverine particles and coccoliths (Kopelevich et al., 2014). These signals can be separated using a two-parametric model (Kopelevich et al., 2014), which is based on the data on absorption coefficient of yellow substance (a_g) and R_{rs}. Unfortunately, we do not have data on the a_g in September-October 2005. That is why, in our study, we used a more simple approach (Equation 1) to give only approximate estimates of the maximum observed N and the area of a bloom. The phytoplankton bloom is usually subjectively defined as

80 the conditions when N exceeds 10^6 cells l^{-1}. According to Equation 1, it 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}. To exclude the impact of lithogenic particles on the shelf, we used only pixels located in the deep part of the basin (depths more than 500 m).

We used daily Level 2B array of QuikScat wind data provided on a non-uniform grid within the swath at 12.5 km pixel resolution for September-November 2005. Data was downloaded from https://podaac.jpl.nasa.gov/dataset

85 /QSCAT_LEVEL_2B_OWV_COMP_12. The ekman pumping was defined as $W_{ek} = \dfrac{1}{\rho_w \cdot f} rot(\vec{\tau})$, where

$\rho_w = 1000$ kg m^{-3} is the water density, $\vec{\tau} = c_d \rho_a \cdot |v| \cdot v$ is the wind stress, $c_d = 1.3 \cdot 10^{-3}$ is the drag coefficient, $\rho_a = 1.3$ kg m^{-3} is the air density, v is the wind velocity.

A regional dataset on altimetry-derived daily mapped sea level anomalies with 1/8° resolution produced by AVISO. The satellite altimeter data (product identifier: SEALEVEL_BS_PHY_L4_REP_OBSERVATIONS_008_042) is made freely

90 available by the Copernicus Marine Environmental Monitoring Service (ftp://my.cmems-du.eu/Core/SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_042/). Mapped sea level anomalies were added to the mean dynamic topography (Kubryakov and Stanichny, 2011) to compute surface geostrophic velocities in the sea. The obtained dataset was validated by 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 and Discussion

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

From 25 to 29 September 2005, an anomalous intense QTC was observed in the atmosphere over the Black Sea on satellite imagery (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 20–25 m s^{-1} according to the QuikSCAT satellite data (Fig. 1c). Its development occurred after weak wind conditions and was associated with overheating of the sea surface, which caused increased moisture fluxes over the western part of the Black Sea. Importantly, QTC was observed over the western part of the Black Sea for more than 4 days. A detailed analysis of the dynamics of QTC and the reasons for its formation was carried out in (Efimov et al., 2007; Yarovaya et al., 2008).

Cyclonic wind vorticity led to ekman transport directed from the QTC and ekman pumping. Particularly, ekman pumping, on 26 September in the zone of QTC action exceeded $4 \cdot 10^{-5}$ m s^{-1} (Fig. 1d), while in (Efimov et al., 2008), authors documented absolute maximum reaching $20 \cdot 10^{-5}$ m s^{-1}. QTC was situated over the western cyclonic gyre of the Black Sea circulation. The center of the western cyclonic gyre was observed in altimetry maps as an area of a decreased sea level reflecting the uplift of isopycnals (Fig. 2a). On average, in the Black Sea, the pycnocline and nutricline in the centers of the western cyclonic gyre are elevated by 20-30 m relative to the periphery of the sea (Ivanov and Belokopytov, 2013). Ekman pumping caused additional intense upwelling in this area, which was accompanied by strong wind mechanical mixing. As a result, according to the AVHRR radiometer data, on 29 September, the SST in the central-western part decreased by more than 10°C (Fig. 1b), reaching an exceptionally low value for September of 10°C. The maximum cooling was observed in the center of the cyclonic gyre in the south-western part of the sea, where SST fell to 10°C, which was 13-15°C lower than the surrounding water SST (23-25°C). In the Black Sea, the isotherm 10°C in September is located under the seasonal thermocline at depths of 30-40 m. Thus, the action of the QTC led to the rise of isopycnic surfaces by 30-40 m and the outcropping of deep isopycnal layers into the sea surface. Taking into account the active thermal mixing of waters due to the action of the cyclone and intense solar heating in this period of the year, it can be assumed that the waters were uplifted from even larger depths.

Nutricline in the Black Sea is relatively shallow, and its upper border is located at a depth of 50-60 m (Konovalov and Murray, 2001; Tuğrul et al., 2015). The euphotic zone in the Black Sea in September is about 40-50 m (Kubryakov et al., 2020). Thereby the impact of QTC caused an uplift of nutricline on 30-40 m to the euphotic zone, accompanied by its erosion driven by strong wind mechanical mixing.
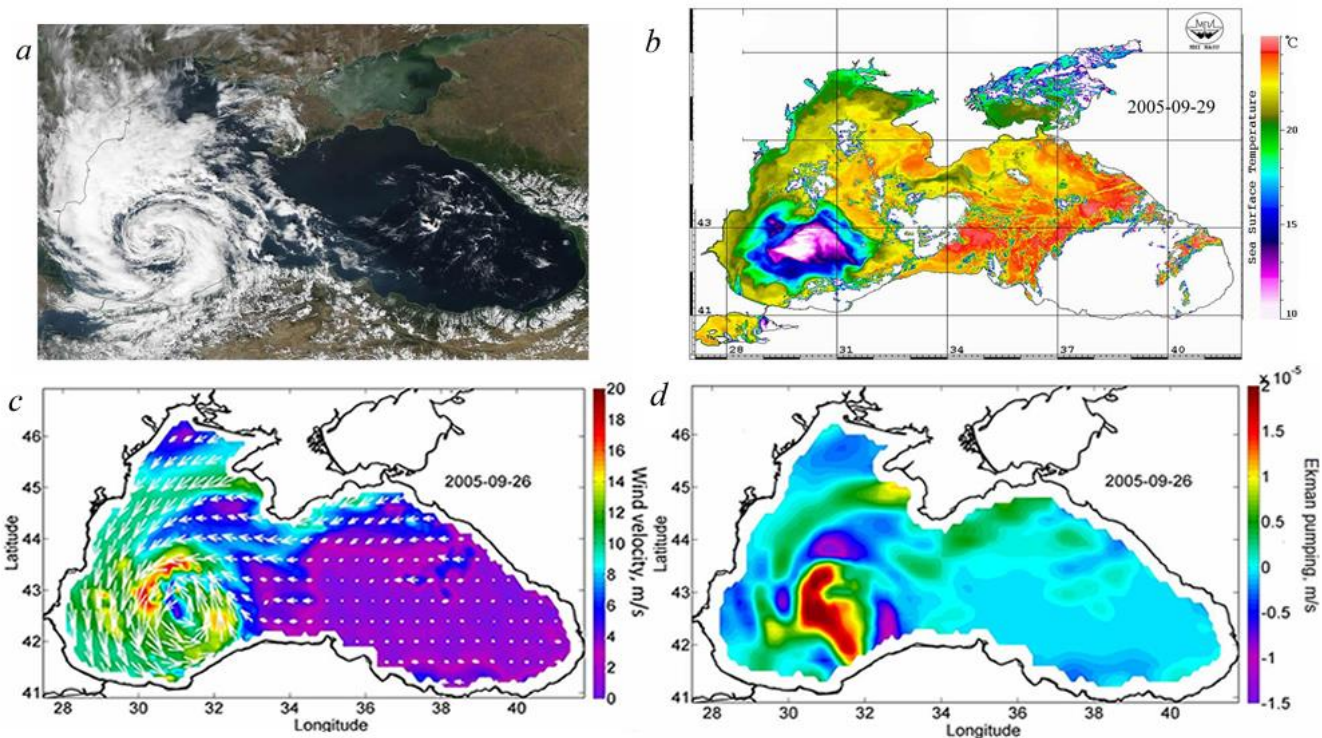
Figure 1: (a) – satellite image of MODIS-Aqua in the visible range for 27 September 2005 (data obtained from the Worldview portal); **(b)** – AVHRR SST (°C) for 29 September 2005; **(c)** – wind velocity (m s^{-1}) of the scatterometer SeaWinds of the satellite QuikSCAT on 26 September 2005; **(d)** – ekman pumping velocity (m s^{-1}) on 26 September 2005, calculated from QuikSCAT data.

The action of ekman transport 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 by 20 cm from 0.2 to 0.4 cm (Fig. 2a, c). At the same time, in the west-central part of the basin, the sea level dropped by 20 cm (Fig. 2a, c). The rise of sea level gradients caused a strong intensification of the large-scale cyclonic circulation of the Black Sea – the Rim Current. Its velocity over the continental slope increased on average twofold from the values of 0.25 to 0.45 m s^{-1} (Fig. 2b, d). 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 m s^{-1} with a maximum of 0.75 m s^{-1} (Fig. 2d).

The maximum intensity of the geostrophic velocity was observed about 2 weeks after the action of the cyclone on 6-10 October (Fig. 3, black line). This delay is related to the time needed for the sea level to adjust to the changes in ekman transport. Such time estimated from altimetry data is 1-2 weeks (Grayek et al., 2010; Kubryakov et al., 2016), which is in close agreement with the time lag observed in the present case. As horizontal and vertical circulation are coupled, the same delay would be observed between the time of cyclone action and the maximum upwelling. Thus, we might suggest that the vertical entrainment of nutrient-rich waters from deep layers also reaches its maximum after 2 weeks from QTC action.
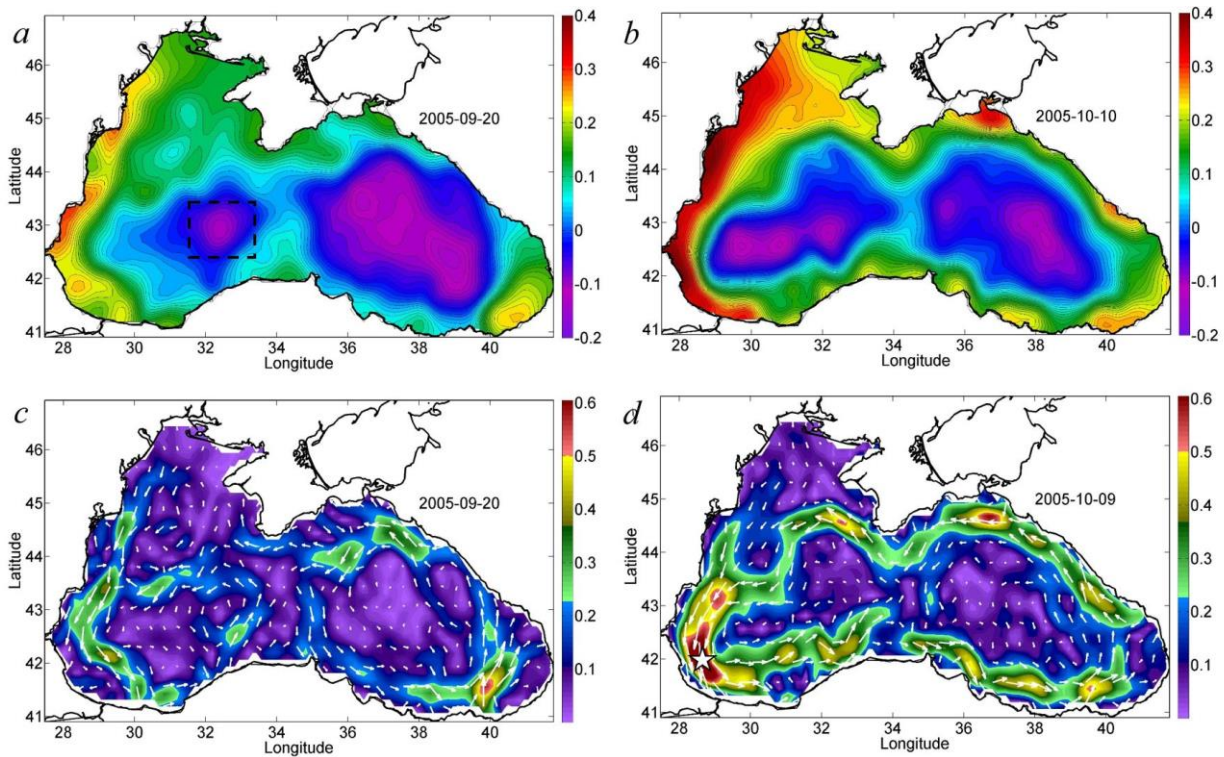
Figure 2. Altimetry-derived map of sea level and geostrophic velocity before **(a, c)** and after **(b, d)** the action of the cyclone. Sea level (m) at: **(a)** – September 20, 2005, **(b)** – October 10, 2005; geostrophic velocity (m s^{-1}) at: **(c)** – September 20, 2005, **(d)** – October 9, 2005. The black rectangle shows the position of the western cyclonic gyre. Velocity magnitude in Fig. 2c, d is shown by color scale.

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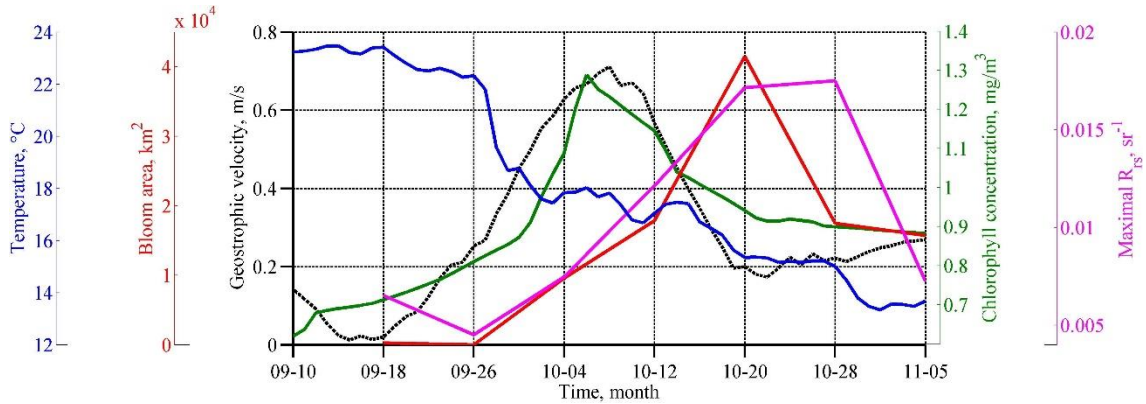
Figure 3: Temporal evolution of SST (°C, blue line), R_{rs} (sr^{-1}, purple), Chl (mg m^{-3}, green) averaged in the central-western part of the basin (see black rectangles in Fig. 5c, d); area of coccolithophore bloom (km^2, red) compute only; geostrophic velocity over the Black Sea continental slope in the point 41.9375N and 28.4375E, see white star in Fig. 2d (m/s, black).

3.2 Impact of quasi-tropical cyclone on Chl

Satellite measurements show that such changes in the basin dynamics significantly affected the bio-optical characteristics of the Black Sea. Before the passage of the atmospheric cyclone, the values of Chl in the central part of the basin were relatively low, less than 0.7-0.8 mg m^{-3} (see Fig. 3, 4). High values of Chl exceeding 3 mg m^{-3} at this time were observed in the north-west shelf of the basin (red rectangle in Fig. 4a). The increase of Chl in this area is related to the discharge of several rivers with the major impact of the Danube plume (Yankovsky et al., 2004; Karageorgis et al., 2014). It should be noted that the Danube plume and shelf waters of the Black sea correspond to turbid Case 2 waters. The determination of the Chl in Case 2 waters is a difficult task, and it is likely overestimated mainly due to the presence of colored dissolved organic matter. Therefore, for the description of the time variability of Chl in Fig. 3, we used only data in the central part of the basin. At the same time, increased values of Chl can be successfully used as a tracer of plume waters (see, for example, Sur et al., 1994, 1996; Kubryakov et al., 2018). At the beginning of September 2005, Danube waters with high satellite Chl occupied the north-western part of the basin. The southern border of the plume was located in the south-western part of the basin near 42°N. Immediately after the action of QTC in late September, Chl increased significantly in the western central part of the sea (red ellipse in Fig. 4b). Here, on 4 October, Chl reached relatively high values (1.3 mg m^{-3}) (green line in Fig. 3). However, on the next MODIS 8-daily map (Fig. 4c), Chl in this zone decreased to the pre-storm values. One of the possible reason of such rise of Chl is entrainment of phytoplankton from its summer subsurface maximum, which cause its rapid but short-period increase in surface layers (Babin et al., 2004; Kubryakov et al., 2019c).

QTC also impacted significantly on the propagation of the Danube plume waters. The intensified Rim Current transported the plume in the cyclonic direction from the south-western part to the south-central coast (marked as the black arrow in Fig. 4b). On 5 October (Fig. 4b), the zone with high Chl (>3 mg m^{-3}) reaches 34°E. At this time, this zone looked like an alongshore band of high Chl values with about 50 km width extending from the Danube mouth to the south-central coast of the Black Sea. Similar action of the Rim Current transport on the transfer of Danube plume to the southern part of the basin was documented in several previous studies (see, e.g. Özsoy and Ünlüata, 1997; Yankovsky et al., 2004; Kubryakov et al., 2018).
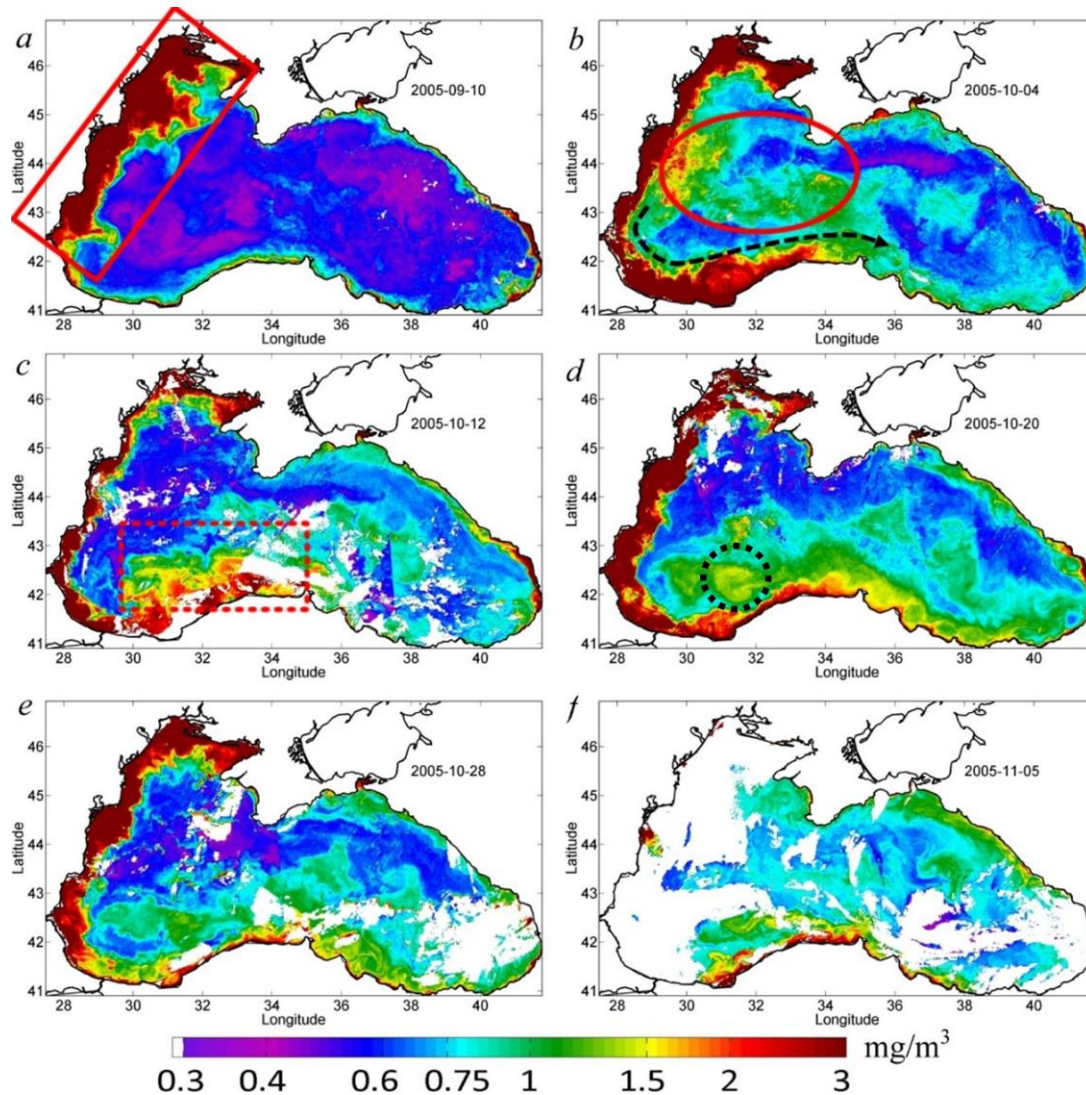
Figure 4: 8-day maps of Chl concentration, mg m^{-3}, centered at **(a)** 10 September 2005, the red rectangle (solid line) shows the position of the Danube plume; **(b)** 4 October 2005, the red oval shows the zone of the rapid increase od Chl in the western central part of the basin; **(c)** 12 October 2005, the red dashed rectangle show the position of the cross-shelf mixing area; **(d)** 20 October 2005, black dashed circle show the maximum of Chl in the western cyclonic gyre; **(e)** 28 October 2005; **(f)** – 5 November 2005.

Significant intensification of the Rim Current in the southwest Black Sea up to extreme values of 0.75 m s^{-1} caused its baroclinic instability related to strong horizontal shear. The offshore boundary of the front of turbid waters was characterized by several mesoscale features – eddies and filaments (see zoomed MODIS map in Fig. 5a). These processes intensified the horizontal exchange in this part of the basin. As a result, on 12 October 2005, the area of the high Chl values in the south-eastern part of the sea significantly widened and reached a width of 100-150 km (red dashed rectangle in Fig. 4c). The difference between the Chl maps in Fig. 4b and Fig. 4 c shows that near the coast (in the area of the red dashed rectangle), Chl decreased, while to the north increased. It evidences about the dilution of the plume due to its horizontal mixing with offshore waters with

relatively low values of Chl (Chl<0.75 mg m^{-3}). Such distribution indicates that a significant part of the brackish and nutrient-rich plume water moved across the isobaths and penetrated in the southwest central part of the sea. A week later, at 16-24 October, this wide zone of increased Chl (Chl>1.5 mg m^{-3}) disappeared, and the width of the plume decreased significantly (see zoomed Fig. 4d).
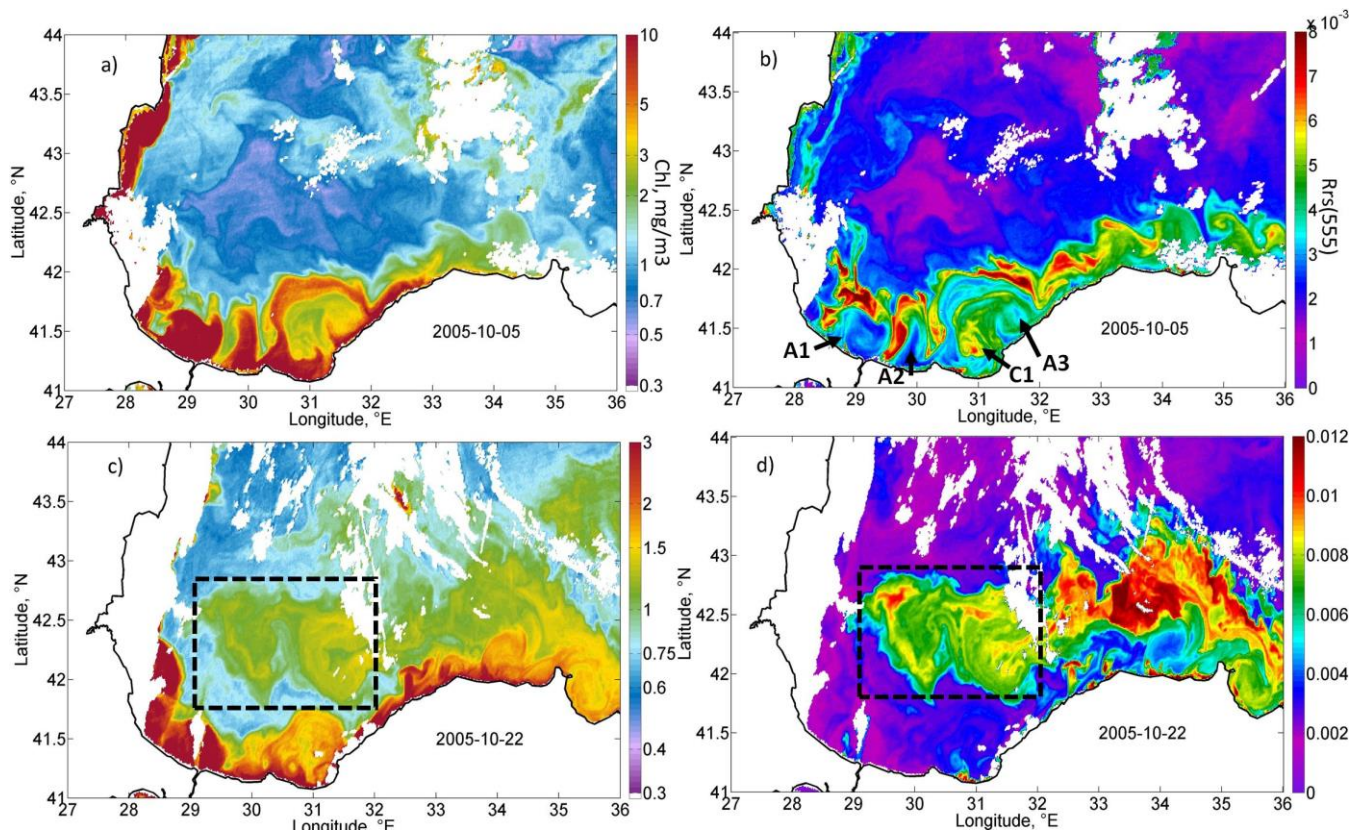
Figure 5. Zoomed daily MODIS maps demonstrating two stages of coccolithophore blooms development: MODIS daily map of Chl **(a)** and R$_{rs}$ **(b)** on 5 October 2005 demonstrating the initial rise of R$_{rs}$ on the offshore periphery of the Danube plume; MODIS daily map of Chl **(c)** and R$_{rs}$ **(d)** on 22 October 2005 demonstrating the rise of R$_{rs}$ in the western gyre of the Black Sea (black dashed rectangles).

At this time, high values of Chl appeared in the central-western part of the sea (Fig. 4d, 5c). The highest values of Chl (black circle in Fig. 4d, black rectangle in Fig. 5c) were located in the area maximum upwelling in the western cyclonic gyre, corresponded to the zone of minimal SST in Fig. 1b. Further, waters with high Chl values were transported from this area by intense Rim Current to the east. As a result, the region of high values of the Chl extended eastward along the continental slope up to the eastern coast of the basin – 41.5°E (Fig. 4d, e). In these areas, Chl increased to a value of 1-1.3 mg m^{-3}, which was two times higher than in early September (Fig. 4d). At the end of October, Chl in the areas affected by the QTC began to decrease. It fell about twofold to the values of 0.75 mg m^{-3} (Fig. 4e).

At the beginning of November, Chl in the whole central part of the Black Sea rose again to 1 mg m^{-3} (Fig. 4f). This rise probably indicates the beginning of late-autumn phytoplankton bloom, which is associated with the deepening of a mixed layer to the upper border of the nutricline (Mikaelyan et al., 2018; Kubryakov et al., 2020).

3.3 Impact of quasi-tropical cyclone on coccolithophores bloom

However, the strongest impact of the cyclone was observed in the field of R_{rs}. Exceptionally high rise of R_{rs} was observed in the western cyclonic gyre and south deep part of the basin (Fig. 6a). The comparison of the R_{rs} map on 28 October 2005 with the climatic-averaged map for October 2003-2019 (Fig. 6a, b) demonstrates this anomalous event. In the usual year, R_{rs} in the Black Sea in October does not exceed 0.001 sr^{-1}, except the area located near Danube mouth, the Kerch strait, the most coastal areas near Caucasian rivers, and shallow north-western shelf (see black rectangles in Fig. 6b). These areas are the source of lithogenic particles in the Black Sea caused by riverine or the Azov Sea inflow, resuspension of bottom sediments, and coastal erosion (see Constantin et al., 2017; Aleskerova et al., 2017, 2019; Kubryakov et al., 2019a).

A significantly different spatial distribution of R_{rs} was observed after the action of QTC. R_{rs} was highest not near the coast or river mouths, but in the deep western part of the basin with depths more than 1500 m over the south continental slope. In this area, R_{rs} reached more than 0.010 sr^{-1}, which is 10 times higher than climatological values.

In the south part of the basin, there are several small rivers, but their plumes usually do not extend on more than 10 km from their mouth (Kostianoy et al., 2019). In the considered cases (Fig. 6a), the width of high R_{rs} values near the south part of the basin was about 100 km. They were located not near a specific river mouth but extended over the whole periphery of the basin. Therefore, the observed rise of R_{rs} should have a biological origin. In the Black Sea, such a rise of R_{rs} is often observed during coccolithophore blooms (Cokacar et al., 2001). The above arguments suggest that in the presented case, we observe unusual coccolithophore blooms in October in the Black Sea.
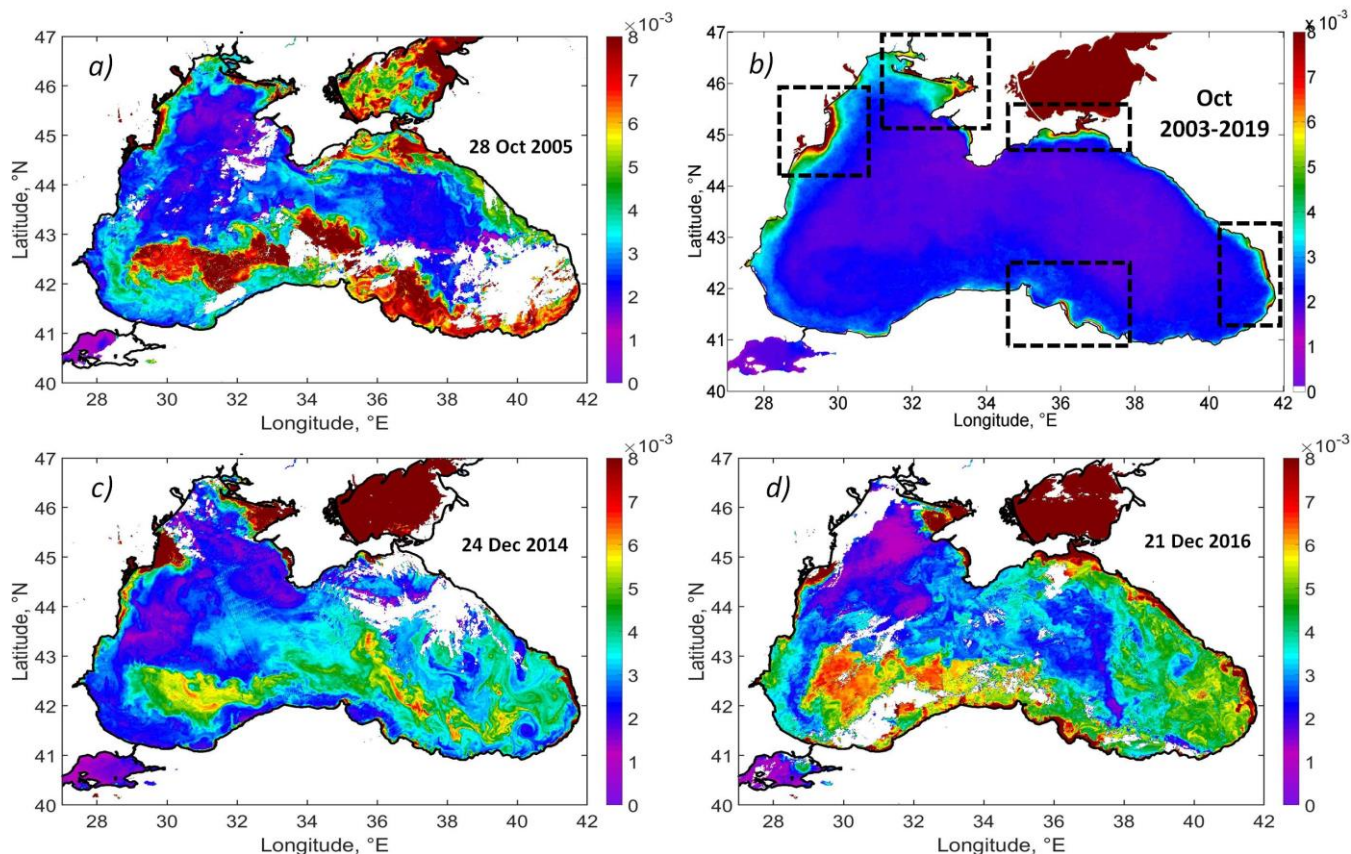
Figure 6. (a) MODIS RRS map on 28 October 2005 showing the intense coccolithophore bloom developed after the action of QTC; **(b)** climatic R_{rs} map for October of 2003-2019 (black rectangles show the main sources of the lithogenous articles in the Black Sea); similar to the case of October 2005 coccolithophore blooms observed on the maps of R_{rs} on 24 December 2014 **(c)** and 21 December 2016 **(d)**.

The detailed evolution of R_{rs} in September-October 2005 is demonstrated in Fig. 7. Before the passage of the atmospheric cyclone, R_{rs} in the Black Sea was less than 0.004 sr^{-1} (Fig. 7a). This value is typical for this season and indicates that the surface layer of the sea central part contains a low concentration of particles that cause backscattering. The exception was the shallow north-western shelf affected by the discharge of the major rivers.

In the western central part, R_{rs} was low until the action of the QTC (see the purple line in Fig. 3). At the beginning of October 2005, the rise of R_{rs} was first observed in the south-western part of the sea (red rectangles in Fig. 7b). In this place, it increased to the values of $5\text{-}6 \cdot 10^{-3}$ sr^{-1}, corresponding to the level of coccolithophore bloom. The initial rise of R_{rs} was detected in a limited area located over the south continental slope of the basin to the south and west from the area of QTC action. This increase was only observed on the shelf/slope boundary in the intermediate zone between the shelf and the central part (see red rectangles in Fig. 7b).
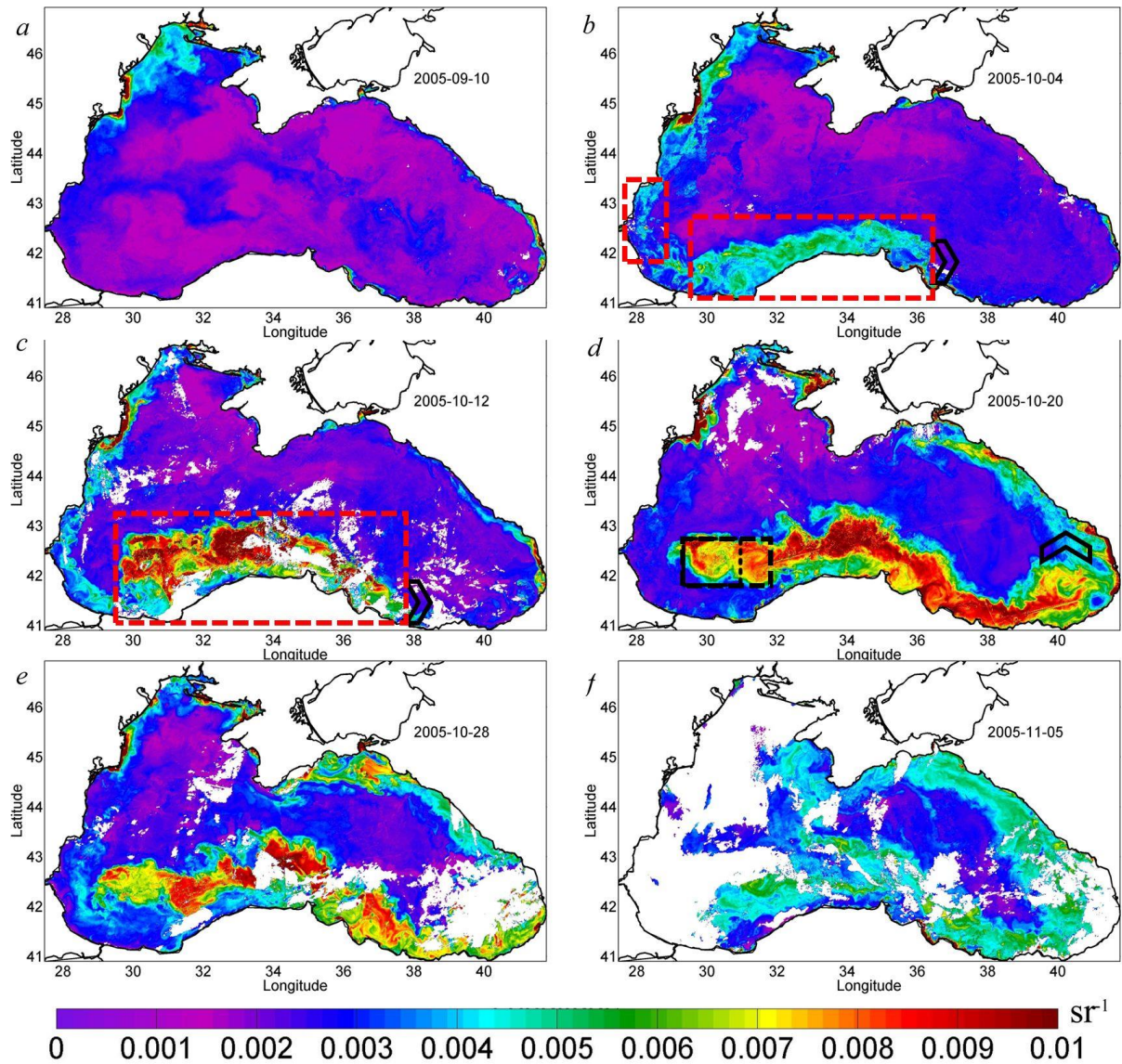
Figure 7: 8-day maps of remote sensing reflectance R_{rs}, sr^{-1}, centered at **(a)** 10 September 2005; **(b)** 4 October 2005 the red rectangle shows the area of the initial start of the bloom; **(c)** 12 October 2005, the red rectangle shows a mixing area; **(d)** 20 October 2005, the black rectangle shows the center of the deep bloom in the western cyclonic gyre **(e)** 28 October 2005, **(f)** – 5 November 2005. The black arrow shows the position of the eastern boundary of the bloom.

A detailed daily map of R_{rs} for 5 October 2005 (Fig. 5b) shows that the maximum R_{rs} was observed in the thin zone on the offshore periphery of the Danube plume. At the same time, near the coast and in the western central part in the epicenter of QTC action, high value of R_{rs} rise at this time were absent. This frontal zone is a subject of the intense horizontal mixing between brackish nutrient-rich plume waters and saline waters of the central part, which may be one of the possible triggers of phytoplankton bloom. High R_{rs} values were located mainly in the frontal instabilities formed on the boundary of the plume.

Such instabilities were possibly formed due to the impact of strong horizontal shear on the periphery of the intensified Rim Current. Mixing between plume and saline waters additionally intensified buoyancy gradients and baroclinic submesoscale instabilities observed in Fig. 5a, 5b. Submesoscale motions can induce very strong vertical velocities reaching more than 10-100 cm s^{-1} (Mahadevan, 2016), which can provide intense upward nutrient fluxes. In the center of anticyclones (see, for example, anticyclones A1 and A2 in Fig. 5b), where vertical motions were directed downward, R_{rs} was low. At the same time, on their periphery, where vertical velocities are probably directed upward, a strong rise of R_{rs} was observed. Another prominent feature in Fig. 5b is the mushroom structure consisted of cyclone C1 and anticyclone A3. The cyclonic part of this structure had significantly higher R_{rs} than its anticyclonic part. These observations suggest the important impact of submesoscale vertical fluxes in cyclonic structures on the initial rise of R_{rs}. Analysis of MODIS daily maps showed that in this area from 5 to 7 October of 2005 R_{rs} valued almost doubled. At the same time, R_{rs} was lower near the coast, which indicates that its rise was not related to the lithogenic particles caused by river discharge or storm-driven coastal erosion.

A week later, at 8-15 October, R_{rs} rapidly increased (Fig. 7c), and the bloom area has doubled (Fig. 3, red line). We note that the bloom area was estimated using only pixels in the deep part of the basin (depth more than 500 m) to exclude the impact of the lithogenic particles. The maximum R_{rs} increased to 0.012 sr^{-1}, which corresponded to N=5.8·10^6 cells l^{-1}. The area of most intense bloom was observed over the continental slope south of the western gyre and the regions west of it (see red rectangle in Fig. 7c). This distribution was very similar to the one observed in Chl (Fig. 4c, d).

In the next week (from 16 to 23 October), the bloom position shifted from the coast offshore to the center of the western gyre (Fig. 5d, 7d). The position of this gyre can be observed as an area of decreased SST (Fig. 1b) and low sea level (Fig. 2b) in satellite measurements. This area corresponded to the zone of maximal vertical mixing and intense vertical entrainment of nutrients from deep isopycnals layers. Here stable bloom area with a diameter of about 100 km developed (see black rectangles in Fig. 5d, 7d). At the same time, R_{rs} values in the south-eastern coastal zone decreased to the background values.

Further, the advection by the Rim Current transported both raised nutrients and already formed phytoplankton cells from the central-western gyre to the east. The region of high values of the R_{rs} extended from this area eastward along the continental slope to the eastern coast of the basin up to 41.5°E (Fig. 7d, e). The black arrow in Fig. 7 marks the propagation of the eastward boundary of the plume. At the velocity of 0.45 m s^{-1} (Fig. 2d), the particles should be transported on 1000 km in three weeks. Such transport caused the extension of the bloom up to the eastern coast of the Black Sea in agreement with satellite optical measurements (Fig. 7e). As a result, the total length of the bloom area on 20 October 2005 was more than 1200 km (Fig. 7d). The western boundary of the bloom was stationary and located in the center of the western cyclonic gyre (black rectangle in Fig. 7d). Therefore, the losses of coccolithophore cells caused by horizontal advection in this local zone were probably compensated by their growth due to intense vertical fluxes of nutrients. It indicates that the upwelling in the center of the western cyclonic gyre was a continuous source of nutrients for phytoplankton until the end of October, from which the bloom stretched to the eastern shore. Indeed, decreased SST in this area was observed until the end of October, indicating the stability of upwelling. Such prolonged duration of upwelling (2-3 weeks) can be related to the: 1) delay between the action of ekman pumping and upwelling; 2) the time needed for the relaxation of the upwelling after the wind action.

The average and maximum values of the R_{rs} reached the highest values 2-3 weeks after the action of QTC on 20 October 2005 (Fig. 3, purple line). At this time, in some areas of the central Black Sea (e.g. 43°E, 34°N), the R_{rs} was higher than 0.018 sr^{-1}, which corresponds to an estimate of 9-10·10^6 cells l^{-1}. Bloom area reached a maximum of about 40·10^3 km^2 (Fig. 3, red line). At the end of October, the intensity of coccolithophore bloom in the western cyclonic cycle weakened (Fig. 7e). In this period, the maximum value of R_{rs} decreased to 0.007 sr^{-1}. At the beginning of November, R_{rs} fell to 0.005-0.006 sr^{-1}, indicating the termination of the bloom (Fig. 7f). The termination occurred at the time of the beginning of late-autumn phytoplankton bloom, reflected in the rise of Chl over the whole central part of the basin (Fig. 4f).

4 Discussion

The action of the QTC caused a strong coccolithophore bloom in October 2005, which lasted for more than 1.5 months and covered the entire southern part of the Black Sea. Analysis of R_{rs} variability in 2003-2019 showed that this situation was unique for the early autumn period, when R_{rs} usually is low (< 0.002 sr^{-1}, see Fig. 6b). Only in rare cases – in October of 2006 and 2014 – we observe the increase of R_{rs} up to 0.005 sr^{-1}, still two times lower than 0.010 sr^{-1} in 2005. Somewhat similar to October 2005, blooms were observed in satellite data in December 2014 and 2016 (Fig. 6c, d). These figures demonstrate similar spatial patterns of R_{rs} extending from the western cyclonic gyre over the south continental slope. Such winter blooms were also triggered by intense western storms (see Kubryakova et al., 2021) over the western cyclonic gyre. These illustrations show that the discussed in this paper processes may define the biological characteristics of the basin in other years. However, in both of these cases, R_{rs} was smaller than in 2005 and usually does not exceed 0.007, compare to 0.01 sr^{-1} in 2005. Also, such blooms were observed later in winter – in December, the month characteristic for the winter coccolithophore blooms (Kubryakova et al., 2021).

Such an analysis demonstrates that in October 2005, we observed an exceptional situation in the Black Sea – early autumn bloom of coccolithophores with estimated cell concentrations exceeding 10·10^6 cells l^{-1}. This situation was caused by the action of the anomalous, extremely strong QTC in September 2005. Unfortunately, currently there is no in-situ microscopic information about coccolithophore blooms and especially their time evolution after intense atmospheric storms. The results of this study showed that such processes could impact significantly on the taxonomic composition of the phytoplankton and deserves a specialized in-situ investigation.

The phytoplankton bloom in the autumn-winter period in the Black Sea is related to the vertical entrainment of nutrients from their subsurface maximum. Usually, this process causes a rapid growth of diatoms in November-December (Sorokin, 1983; Mikaelyan et al., 2017; Silkin et al., 2019; Kubryakov et al., 2020), which have a higher growth rate than the coccolithophores (Goldman, 1993; Lomas and Glibert, 1999). Several authors demonstrated the rapid increase of Chl in the Black Sea after strong storm events in summer (Nezlin, 2006; Kubryakov et al., 2019c) and the autumn period (Mikaelyan et al., 2017, 2020). However, in October 2005, we observed another case: the atmospheric cyclone caused only a slight rise of Chl, which was followed by the very strong coccolithophore blooms (see Fig. 3).

310   There are several possible reasons for such intense coccolithophore blooms in the observed case. Very intense upwelling and wind mixing caused the entrainment of a huge amount of nutrients from the nutricline. These layers of the Black Sea are characterized by a low N/P ratio, which is about 2-6 (Konovalov et al., 2005; Tuğrul et al., 2014). Low N/P is caused by intense removal of nitrates by denitrification process in the suboxic layer of the basin (Konovalov et al., 2008; Tuğrul et al., 2014). Nitrates entrained to the surface are first rapidly consumed by diatoms, which have a higher growth rate than coccolithophores

315   (Goldman, 1993). This process caused the increase of Chl, which reached its peak one week after the QTC (Fig. 3). However, as the N/P ratio (2-6) was significantly smaller than the Redfield ratio (16), part of the phosphate remained in the upper layer. Due to lower growth rates of coccolithophores, the observed rise of R_{rs} was more gradual. Two-three weeks after the QTC, Chl decreased to its pre-storm values. The decrease of Chl indicates termination of the bloom due to mortality of grazing and transformation of nutrients in the organic form. According to Stelmakh et al. (2009), the lysis of the organic matter by small

320   diatoms on the final stage of their bloom promotes the growth of *Emiliania huxleyi* in the Black Sea. Coccolithophores can use osmotrophy and utilize dissolved organic nitrogen (Benner and Passow, 2010; Poulton et al., 2017). *Emiliania huxleyi* contains several specific enzymes and proteins, which may switch their diet from inorganic to organic (Dyhrman & Palenik, 2003). A large amount of remained phosphates and organic nitrogen caused the maximum development of the coccolithophore blooms 3-4 weeks after the QTC. Such a situation is usually observed in the Black Sea in spring, when winter convection is

325   followed by intense spring bloom of diatoms in March, and then by May-June coccolithophores bloom (Mikaelyan et al., 2015; Kubryakov et al., 2019c). The hypothesis explaining the observed diatom-coccolithophore sequence in the Black Sea was proposed in (Mikaelyan et al., 2015) and is supported by in-situ chemical and biological data of (Mikaelyan et al., 2015; Silkin et al., 2009).

Long-term analysis of MODIS data in 2003-2019 (Kubryakova et al., 2021) showed that winter coccolithophore blooms are

330   also often observed 1-2 weeks after intense storm action. According to (Kubryakova et al., 2021), such blooms were especially strong in years with increased cross-shelf exchange. One of the possible reasons for such a relation is the grazing pressure by zooplankton on diatoms. Shelf waters of the Black Sea are characterized by a high concentration of zooplankton, which can exceed its concentrations in the deep part of the basin 10 times (Kovalev et al., 1999). The grazing pressure on the diatoms or dinoflagellates by zooplankton usually is higher than on coccolithophores (Nejstgaard, 1997; Stelmakh, 2013), which may

335   give them an advantage during high concentrations of predators. Stelmakh (2013) showed that in the Black Sea, grazing in diatom-dominated regions was about 90%, while in coccolithophore-dominated, it was three times lower (30%) in agreement with estimates obtained by Olson and Strom (2002).

The largest seasonal peak of zooplankton in the Black Sea is observed in September-October (Kovalev et al., 2003; Stelmakh, 2013). Therefore, QTC was observed during a seasonal maximum of zooplankton. QTC caused intense cross-shelf exchange

340   (see Fig. 5), which promote additional penetration of zooplankton from the shelf to the central part of the basin. All the above processes may suppress the rise of diatoms despite the strong nutrients fluxes and may give an advantage to coccolithophores. The initial rise of R_{rs} was observed at the frontal zone separating the brackish, nutrient-waters of the Danube plume and saline waters of the central Black Sea. Acceleration of the Rim Current up to extreme velocities of 0.75 m s^{-1} caused an increase of

horizontal and vertical shear. The vertical shear of the Rim current is one of the important reasons for the rise of the vertical
345 turbulent mixing (see Podymov et al., 2020). The rise of horizontal shear also triggered the formation of several submesoscale eddies (see Fig. 5) in the coastal zone of the Black Sea (Zatsepin et al., 2019). These eddies intensified cross-shelf exchange and the horizontal transport of Danube plume waters in the deep part of the basin. Danube plume waters are rich in organic and inorganic nutrients (Saliot et al., 2002; Kondratev et al., 2015, 2019). The mixing zone became the first area where coccolithophores started to grow up to bloom conditions. The overflow of the brackish plume on the saline waters additionally
350 increases the baroclinic instabilities (Luo et al., 2016) and intensifies submesoscale motions. Recent studies demonstrated that such processes could cause very intense vertical motions, which may be the important reason for the rise of the primary productivity on the fronts (Oguz et al., 2015; Mahadevan, 2016). Such submesoscale vertical fluxes can explain the spatial distribution of R_{rs} in Fig. 5a and also help to explain its earlier rise compared to the central part of the basin. Therefore, a cross-frontal mixing may cause the initial growth of coccolithophores due to several reasons: 1) vertical fluxes of nutrients caused
355 by baroclinic submesoscale instabilities; 2) penetration of nutrient or dissolved organics from brackish plume waters in the deep saline part of the basin; 3) penetration of zooplankton from the shelf, which suppresses the growth of other types of phytoplankton.

The most intense coccolithophore blooms in the Black Sea are observed in May-June. At this period, the cell concentration is usually $N=2-6 \cdot 10^6$ cells l^{-1} (Mikaelyan et al., 2011, 2015), which is 2-4 times higher than in weaker winter blooms ($N=0.5-$
360 $2 \cdot 10^6$ cells l^{-1}) (Kubryakova et al., 2021). The coccolithophore blooms usually occupy the upper mixed layer, which in winter is 2-3 times larger than in summer, which suggests that the total cell amount in the water column is similar in the winter and summer period (Kubryakov et al., 2019b). In October 2005, we observed very high surface values of R_{rs} reaching 0.018 sr^{-1}, which correspond to the estimated N reaching $10 \cdot 10^6$ cells l^{-1}. The mixed layer in October is usually about 2 times higher than in early summer, which suggests that the intensity of the observed autumn coccolithophore bloom in October 2005 was
365 comparable to the record blooms detected in the summer of 1993 (Mihnea, 1997) and 2012 (Yasakova and Stanichny, 2012).

5. Conclusions

The action of the QTC in September 2005 caused an intense bloom of coccolithophore in the Black Sea basin with satellite-estimated concentration reaching $10 \cdot 10^6$ cells l^{-1}. Satellite data showed that the bloom was caused by intense upwelling driven by ekman pumping during the action of QTC. The upwelling was maximum in the western cyclonic gyre of the Black Sea,
370 where isopycnals were uplifted to the surface. After QTC, SST in this area decreased to 10°C, which was on 10-13°C lower than surrounding waters, indicating intense vertical entrainment of nutrients in the euphotic layer. This process led to the increase of Chl, which was followed by strong bloom of coccolithophores. The bloom was continuously observed in the area of upwelling in the west cyclonic gyre for more than 1.5 months. Intense cyclonic Rim Current spread the bloom from this permanent source of nutrients, and at the end of October, the bloom covered the entire south part of the Black Sea.

375 The initial growth of coccolithophores after the QTC was observed in the frontal zone between the central part of the Black Sea and the plume of the Danube. Rapid intensification of the Rim current after the QTC led to the intense cross-shelf mixing of these waters, accompanied by the generation of the number of submesoscale instabilities. The initial growth of R_{rs} were detected in these submesoscale structures of cyclonic signs, which indicate that intense vertical motions in frontal submesoscale cyclones were another important source of the nutrients for the coccolithophore blooms at its initial stage.

380 We hypothesize that the possible reasons for domination of coccolithophores in the observed case were: a) higher grazing pressure on the other phytoplankton (such as diatoms) by zooplankton, which have its seasonal maximum in September-October; b) ability of coccolithophores to use osmotrophy and utilize organic nitrogen; c) low N/P ration in the Black Sea nutricline, which led to the fast depletion of nitrates for diatoms blooms.

As described here, extreme atmospheric events can play an important role in the observed interannual variability of the
385 coccolithophores and related carbonate fluxes in many other ocean areas, such as the Northern Atlantic and the Southern Ocean, where storms are significantly more frequent. Such coccolithophore blooms may significantly impact on the seasonal succession of marine phytoplankton. Particularly, they can trigger the following microbial loop – the transition of trophic energy to small species and subsequent changes in the entire trophic structure of the region (Brussaard, 2004; Kubryakov et al., 2019b). Detailed information about the response of the phytoplankton community to short-term physical processes is
390 necessary for understanding the functioning of marine ecosystems. Such information can be provided only on the base of continuous data of the taxonomic composition of phytoplankton, based, e.g. on the measurements of moored flow cytometers. These data are crucial for the validation of satellite algorithms for phytoplankton species detection (such as Xi et al., 2020) and biogeochemical numerical models, which will help to provide more insights into the mechanisms of the ecosystem response to intense atmospheric forcing.

395 **Data availability**

We acknowledge the use of (1) moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Ocean Color Data produced 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 produced and distributed by the Copernicus Climate
400 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) AVHHR data were received and reprocessed at Marine Hydrophysical Institute, Russia, and are available from http://dvs.net.ru/mp/data/200509bs_sst.shtml.

Author contribution

405 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 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.

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415 **References**

Aleskerova, A. A., Kubryakov, A. A., Goryachkin, Y. N., Stanichny, S. V., and Garmashov, A. V.: Suspended-Matter Distribution Near the Western Coast of Crimea under the Impact of Strong Winds of Various Directions. Izvestiya, Atmospheric and Oceanic Physics, 55(9), 1138-1149, https://doi.org/10.1134/S0001433819090044, 2019.

Aleskerova, A. A., Kubryakov, A. A., Goryachkin, Y. N., and Stanichny, S. V.: Propagation of waters from the Kerch Strait
420 in the Black Sea, Physical Oceanography, 6, 47-57, DOI: 10.22449/1573-160X-2017-6-47-57, 2017.

Babin, S. M., Carton, J. A., Dickey, T. D., and Wiggert, J. D.: Satellite evidence of hurricane-induced phytoplankton blooms in an oceanic desert, J. Geophys. Res., 109, C03043, https://doi.org/10.1029/2003JC001938, 2004.

Balch, W. M.: The ecology, biogeochemistry, and optical properties of coccolithophores, Annual review of marine science, 10, 71-98, https://doi.org/10.1146/annurev-marine-121916-063319, 2018.

425 Balch, W. M., Bowler, B. C., Drapeau, D. T., Lubelczyk, L. C., Lyczkowski, E., Mitchell, C., and Wyeth, A.: Coccolithophore distributions of the North and South Atlantic Ocean, Deep Sea Research Part I: Oceanographic Research Papers, 151, 103066, https://doi.org/10.1016/j.dsr.2019.06.012, 2019.

Balch, W. M., Drapeau, D. T., Bowler, B. C., Lyczskowski, E., Booth, E. S., and Alley, D.: The contribution of coccolithophores to the optical and inorganic carbon budgets during the Southern Ocean Gas Exchange Experiment: New
430 evidence in support of the "Great Calcite Belt" hypothesis, J. Geophys. Res., 116, C00F06, https://doi.org/10.1029/2011JC006941, 2011.

Balch, W.M., Holligan, P.M., Ackleson, S.G., & Voss, K.J.: Biological and optical properties of mesoscale coccolithophore blooms in the Gulf of Maine. Limnology and Oceanography, 36(4), 629-643, https://doi.org/10.4319/lo.1991.36.4.0629, 1991.

435 Balch, W. M., Kilpatrick, K. A., and Trees, C. C.: The 1991 coccolithophore bloom in the central North Atlantic. 1. Optical properties and factors affecting their distribution, Limnology and Oceanography, 41(8), 1669-1683, 1996.

Benner, I., and Passow, U.: Utilization of organic nutrients by coccolithophores, Marine Ecology Progress Series, 404, 21-29, https://doi.org/10.3354/meps08474, 2010.

Brand, L. E.: The salinity tolerance of forty-six marine phytoplankton isolates, Estuarine, Coastal and Shelf Science, 18(5),
440 543-556, https://doi.org/10.1016/0272-7714(84)90089-1, 1984.

Brussaard, C.P.D.: Viral control of phytoplankton populations — a review, Journal of Eukaryotic Microbiology, 51(2), 125-138. https://doi.org/10.1111/j.1550-7408.2004.tb00537.x, 2004.

Chacko, N.: Chlorophyll bloom in response to tropical cyclone Hudhud in the Bay of Bengal: Bio-Argo subsurface observations, Deep Sea Research Part I: Oceanographic Research Papers, 124, 66-72.
445 https://doi.org/10.1016/j.dsr.2017.04.010, 2017.

Cokacar, T., Kubilay, N., and Oguz, T.: Structure of Emiliania huxleyi blooms in the Black Sea surface waters as detected by SeaWiFS imagery, Geophysical Research Letters, 28(24), 4607-4610, https://doi.org/10.1029/2001GL013770, 2001.

Cokacar, T., Oguz, T., and Kubilay, N.: Satellite-detected early summer coccolithophore blooms and their interannual variability in the Black Sea, Deep Sea Research Part I: Oceanographic Research Papers, 51(8), 1017-1031,
450 https://doi.org/10.1016/j.dsr.2004.03.007, 2004.

Constantin, S., Constantinescu, Ș., and Doxaran, D.: Long-term analysis of turbidity patterns in Danube Delta coastal area based on MODIS satellite data, Journal of Marine Systems, 170, 10-21, https://doi.org/10.1016/j.jmarsys.2017.01.016, 2017.

Coolen, J.: 7000 years of Emiliania huxleyi viruses in the Black Sea. Science, 333(6041), 451-452, DOI:
455 10.1126/science.1200072, 2011.

Efimov, V. V., Shokurov, M. V., Yarovaya, D. A., and Hein, D.: Statistics of mesoscale cyclonic eddies over the Black Sea, Physical Oceanography, 19(4), 211, https://doi.org/10.1007/s11110-009-9052-8, 2009.

Efimov, V. V., Stanichnyi, S. V., Shokurov, M. V., and Yarovaya, D. A.: Observations of a quasi-tropical cyclone over the Black Sea, Russian Meteorology and Hydrology, 33(4), 233-239, https://doi.org/10.3103/S1068373908040067, 2008.

460 Eppley, R. W., Rogers, J. N., and McCarthy, J. J.: Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton 1, Limnology and oceanography, 14(6), 912-920, https://doi.org/10.4319/lo.1969.14.6.0912, 1969.

Goldman J.C.: Potential role of large oceanic diatoms in new primary production, Deep-Sea Research, 40, 159–168, https://doi.org/10.1016/0967-0637(93)90059-C, 1993.

Gordon, H. R., and Balch, W.M. (Eds.): MODIS detached coccolith concentration. MODIS Algorithm Theoretical Basis
465 Document, University of Miami, 1999.

Grayek, S., Stanev, E. V., and Kandilarov, R.: On the response of Black Sea level to external forcing: altimeter data and numerical modelling. Ocean Dynamics, 60(1), 123-140, https://doi.org/10.1007/s10236-009-0249-7, 2010.

Han, G., Ma, Z., and Chen, N. Hurricane Igor impacts on the stratification and phytoplankton bloom over the Grand Banks, Journal of Marine Systems, 100, 19-25, https://doi.org/10.1016/j.jmarsys.2012.03.012, 2012.

470 Hay, B.J., Honjo, S., Kempe, S., Ittekkot, V.A., Degens, E.T., Konuk, T., and Izdar, E.: Interannual variability in particle flux in the south-western Black Sea, Deep Sea Research Part A. Oceanographic Research Papers, 37(6), 911-928, https://doi.org/10.1016/0198-0149(90)90103-3, 1990.

Hernández R., A. S., Flores, J. A., Sierro, F. J., Fuertes, M. A., Cros, L., and Trull, T. W.: Coccolithophore populations and their contribution to carbonate export during an annual cycle in the Australian sector of the Antarctic zone, Biogeosciences,

475 15, 1843–1862, https://doi.org/10.5194/bg-15-1843-2018, 2018.

Hernández R., A. S., Trull, T. W., Nodder, S. D., Flores, J. A., Bostock, H., Abrantes, F., Eriksen, R. S., Sierro, F. J., Davies, D. M., Ballegeer, A.-M., Fuertes, M. A., and Northcote, L. C.: Coccolithophore biodiversity controls carbonate export in the Southern Ocean, Biogeosciences, 17, 245–263, https://doi.org/10.5194/bg-17-245-2020, 2020.

Holligan, P. M., Viollier, M., Harbour, D. S., Camus, P., and Champagne-Philippe, M.: Satellite and ship studies of

480 coccolithophore production along a continental shelf edge, Nature, 304(5924), 339-342, https://doi.org/10.1038/304339a0, 1983.

Homar, V., Romero, R., Stensrud, D. J., Ramis, C., and Alonso, S.: Numerical diagnosis of a small, quasi-tropical cyclone over the western Mediterranean: Dynamical vs. boundary factors, Quart. J. Roy. Meteor. Soc., 129, 1469–1490, https://doi.org/10.1256/qj.01.91, 2003.

485 Honjo, S.: Coccoliths: production, transportation and sedimentation, Marine Micropaleontology, 1, 65-79, https://doi.org/10.1016/0377-8398(76)90005-0, 1976.

Hopkins, J., Henson, S.A., Painter, S.C., Tyrrell, T., and Poulton, A.J.: Phenological characteristics of global coccolithophore blooms, Global Biogeochemical Cycles, 29(2), 239-253, https://doi.org/10.1002/2014GB004919, 2015.

Ivanov, V. A., and Belokopytov, V. N. (Eds.): Oceanography of the Black Sea, ECOSY-Gidrofizika, Sevastopol, 2013.

490 Karageorgis, A. P., Gardner, W. D., Mikkelsen, O. A., Georgopoulos, D., Ogston, A. S., Assimakopoulou, G., ... and Pagou, K.: Particle sources over the Danube River delta, Black Sea based on distribution, composition and size using optics, imaging and bulk analyses, Journal of Marine Systems, 131, 74-90, https://doi.org/10.1016/j.jmarsys.2013.11.013, 2014.

Kondratev, S. I.: Peculiarities of Nutrients Distribution in the Coastal Waters near the Danube Estuary in 1997–2013. Physical Oceanography, 5, 10.22449/1573-160X-2015-5-32-48, 2015.

495 Kondratev, S. I.: Three Typical Hydrological-Hydrochemical Situations Near the Danube River Mouth Based on the Marine Hydrophysical Institute Research Expeditions in 1997-2013. Physical Oceanography, 26(4), 10.22449/1573-160X-2019-4-326-340, 2019.

Konovalov, S. K., and Murray, J. W. Variations in the chemistry of the Black Sea on a time scale of decades (1960–1995), Journal of Marine Systems, 31(1), 217-243, https://doi.org/10.1016/S0924-7963(01)00054-9, 2001.

500 Konovalov, S. K., Fuchsman, C. A., Belokopitov, V., and Murray, J. W.: Modeling the distribution of nitrogen species and isotopes in the water column of the Black Sea, Marine Chemistry, 111(1-2), 106-124, https://doi.org/10.1016/j.marchem.2008.01.006, 2008.

Konovalov, S. K., Murray, J. W., and Luther III, G. W.: Black Sea Biogeochemistry, Oceanography, 18(2), 24-35, 2005.

Kopelevich, O., Burenkov, V., Sheberstov, S., Vazyulya, S., Kravchishina, M., Pautova, L., ... and Grigoriev, A.: Satellite
505 monitoring of coccolithophore blooms in the Black Sea from ocean color data, Remote sensing of environment, 146, 113-123, https://doi.org/10.1016/j.rse.2013.09.009, 2014.

Korchemkina, E.N., and Lee, M.E.: The anomalous optical characteristics of the Black Sea waters in July 2012 and their relationship to the concentration of mineral suspended matter in the water, Marine Hydrophysical Journal, 2, 67-72, 2014 (in Russian).

510 Kostianoy, A. G., Lebedev, S. A., Soloviev, D. M., and Tepe, Y.: On river plumes along the Turkish coast of the Black Sea, Ecologica Montenegrina, 25, 63-78, DOI:10.37828/em.2019.25.7, 2019.

Kovalev, A. V., Mazzocchi, M. G., Kideyş, A. E., Toklu, B., and Skryabin, V. A.: Seasonal Changes in the Composition and Abundance of Zooplankton in the Seas of the Mediterranean Basin. Turkish Journal of Zoology, 27(3), 205-219, 2003.

Kovalev, A. V., Skryabin, V. A., Zagorodnyaya, Y. A., Bingel, F., Kideyş, A. E., Niermann, U., and Uysal, Z.: The Black Sea
515 zooplankton: composition, spatial/temporal distribution and history of investigations, Turkish Journal of Zoology, 23(2), 195-210, 1999.

Krumhardt, K. M., Lovenduski, N. S., Freeman, N. M., and Bates, N. R.: Apparent increase in coccolithophore abundance in the subtropical North Atlantic from 1990 to 2014, Biogeosciences, 13, 1163–1177, https://doi.org/10.5194/bg-13-1163-2016, 2016.

520 Krumhardt, K. M., Lovenduski, N. S., Iglesias-Rodriguez, M. D., and Kleypas, J. A.: Coccolithophore growth and calcification in a changing ocean, Progress in Oceanography, 159, 276-295, 2017.

Kubryakov, A. A., and Stanichny, S. V.: Mean Dynamic Topography of the Black Sea, computed from altimetry, drifter measurements and hydrology data, Ocean Science, 7(6), 745-753, https://doi.org/10.5194/os-7-745-2011, 2011.

Kubryakov, A. A., Aleskerova, A. A., Goryachkin, Yu. N., Stanichny, S. V., Latushkin, A. A., and Fedirko, A. V.: Propagation
525 of the Azov Sea waters in the Black sea under impact of variable winds, geostrophic currents and exchange in the Kerch Strait. Prog. Oceanogr., 176, 102119, https://doi.org/10.1016/j.pocean.2019.05.011, 2019a.

Kubryakov, A. A., Mikaelyan, A. S., and Stanichny, S. V.: Summer and winter coccolithophore blooms in the Black Sea and their impact on production of dissolved organic matter from Bio-Argo data, Journal of Marine Systems, 199, 103220, https://doi.org/10.1016/j.jmarsys.2019.103220, 2019b.

530 Kubryakov, A. A., Mikaelyan, A. S., Stanichny, S. V., and Kubryakova, E. A.: Seasonal stages of chlorophyll-a vertical distribution and its relation to the light conditions in the Black Sea from Bio-Argo measurements. Journal of Geophysical Research: Oceans, 125, e2020JC016790. https://doi.org/10.1029/2020JC016790, 2020.

Kubryakov, A. A., Stanichny, S. V., Zatsepin, A. G.: Interannual variability of Danube waters propagation in summer period of 1992–2015 and its influence on the Black Sea ecosystem, Journal of Marine Systems, 179, 10-30, https://doi.org/10.1016/j.jmarsys.2017.11.001, 2018.

Kubryakov, A. A., Stanichny, S. V., Zatsepin, A. G., and Kremenetskiy, V. V.: Long-term variations of the Black Sea dynamics and their impact on the marine ecosystem, Journal of Marine Systems, 163, 80-94, https://doi.org/10.1016/j.jmarsys.2016.06.006, 2016.

Kubryakov, A. A., Zatsepin, A. G., and Stanichny, S. V.: Anomalous summer-autumn phytoplankton bloom in 2015 in the Black Sea caused by several strong wind events, Journal of Marine Systems, 194, 11-24, https://doi.org/10.1016/j.jmarsys.2019.02.004, 2019c.

Kubryakova, E. A., Kubryakov, A. A., and Mikaelyan, A. S.: Winter coccolithophore blooms in the Black Sea: Interannual variability and driving factors. Journal of Marine Systems, 213, 103461, https://doi.org/10.1016/j.jmarsys.2020.103461, 2021.

Lin, I., Liu, W. T., Wu, C. C., Wong, G. T., Hu, C., Chen, Z., ... and Liu, K. K.: New evidence for enhanced ocean primary production triggered by tropical cyclone, Geophysical Research Letters, 30(13), https://doi.org/10.1029/2003GL017141, 2003.

Lomas M.W., and Glibert P.M.: Interactions between NH_4^+ and NO_3^- uptake and assimilation: Comparisons of diatoms and dinoflagellates at several growth temperatures, Marine Biology, 133, 541–551, https://doi.org/10.1007/s002270050494, 1999.

Luo, H., Bracco, A., Cardona, Y., and McWilliams, J. C.: Submesoscale circulation in the northern Gulf of Mexico: Surface processes and the impact of the freshwater river input, Ocean Modelling, 101, 68-82, https://doi.org/10.1016/j.ocemod.2016.03.003, 2016.

Mahadevan, A.: The impact of submesoscale physics on primary productivity of plankton, Annual review of marine science, 8, 161-184, https://doi.org/10.1146/annurev-marine-010814-015912, 2016.

Mihnea, P.E.: Major shifts in the phytoplankton community (1980–1994) in the Romanian Black Sea, Oceanologica Acta, 20, 119–129, 1997.

Mikaelyan A.S., Kubryakov, A.A., Silkin, V.A., Pautova, L.A., and Chasovnikov, V.K.: Regional climate and patterns of phytoplankton annual succession in the open waters of the Black Sea, Deep Sea Res. Part I, 142, 44-57, https://doi.org/10.1016/j.dsr.2018.08.001, 2018.

Mikaelyan, A. S., Mosharov, S. A., Kubryakov, A. A., Pautova, L. A., Fedorov, A., and Chasovnikov, V. K.: The impact of physical processes on taxonomic composition, distribution and growth of phytoplankton in the open Black Sea. Journal of Marine Systems, 208, 103368, https://doi.org/10.1016/j.jmarsys.2020.103368, 2020.

Mikaelyan, A.S., Pautova, L.A., Chasovnikov, V.K., Mosharov, S.A., and Silkin, V.A.: Alternation of diatoms and coccolithophores in the north-eastern Black Sea: a response to nutrient changes, Hydrobiologia, 755(1), 89-105, https://doi.org/10.1007/s10750-015-2219-z, 2015.

Mikaelyan, A.S., Pautova, L.A., Pogosyan, S.I., and Sukhanova, I.N.: Summer bloom of coccolithophorids in the northeastern Black Sea, Oceanology, 45(1), S127–S138, 2005.

Mikaelyan, A.S., Shapiro, G.I., Chasovnikov, V.K., Wobus, F., and Zanacchi, M.: Drivers of the autumn phytoplankton development in the open Black Sea, Journal of Marine Systems, 174, 1–11, https://doi.org/10.1016/j.jmarsys.2017.05.006, 2017.

Mikaelyan, A.S., Silkin, V.A., and Pautova, L.A.: Coccolithophorids in the Black Sea: their interannual and long-term changes, Oceanology, 51(1), 39-48, https://doi.org/10.1134/S0001437011010127, 2011.

Miller, W. D., Harding Jr, L. W., and Adolf, J. E.: Hurricane Isabel generated an unusual fall bloom in Chesapeake Bay, Geophys. Res. Lett., 33, L06612, https://doi.org/10.1029/2005GL025658, 2006.

Moore, T.S., Dowell, M.D., and Franz, B.A.: Detection of coccolithophore blooms in ocean color satellite imagery: A generalized approach for use with multiple sensors, Remote Sensing of Environment, 117, 249-263, https://doi.org/10.1016/j.rse.2011.10.001, 2012.

Morozov, E., Kondrik, D., Fedorova, A., Pozdnyakov, D., Tang, D. L., and Pettersson, L.: A spaceborne assessment of cyclone impacts on Barents Sea surface temperature and chlorophyll, International Journal of Remote Sensing, 36(7), 1921-1941, https://doi.org/10.1080/01431161.2015.1029098, 2015.

Nejstgaard et al.: Feeding and reproduction by *Calanus finmarchicus*, and microzooplankton grazing during mesocosm blooms of diatoms and the coccolithophore *Emiliania huxleyi*, Mar Ecol Prog Ser, 47, 197-217, DOI: 10.3354/meps147197, 1997.

Nezlin, N. P.: Seasonal and interannual variability of remotely sensed chlorophyll, in: The Black Sea Environment, edited by Kostianoy A.G., Kosarev A.N., Springer, Berlin, Heidelberg, 333-349, https://doi.org/10.1007/698_5_063, 2006.

Oguz, T., Macias, D., and Tintore, J.: Ageostrophic frontal processes controlling phytoplankton production in the Catalano-Balearic Sea (Western Mediterranean), PLoS One, 10(6), e0129045, https://doi.org/10.1371/journal.pone.0129045, 2015.

Olson, M. B., and Strom S. L.: Phytoplankton growth, microzooplankton herbivory and community structure in the southeast Bering Sea: Insight into the formation and temporal persistence of an *Emiliania huxleyi* bloom, Deep-Sea Res. II, 49, 5969–5990, 2002.

Ostrovskii, A. G., and Zatsepin, A. G.: Intense ventilation of the Black Sea pycnocline due to vertical turbulent exchange in the Rim Current area, Deep Sea Research Part I: Oceanographic Research Papers, 116, 1-13, https://doi.org/10.1016/j.dsr.2016.07.011, 2016.

Özsoy, E., and Ünlüata, Ü.: Oceanography of the Black Sea: a review of some recent results, Earth-Science Reviews, 42(4), 231-272, https://doi.org/10.1016/S0012-8252(97)81859-4, 1997.

Pakhomova, S.V., Rozanov, A.G., and Yakushev, E.V.: Dissolved and particulate forms of iron and manganese in the redox zone of the Black Sea, *Oceanology*, 49, 773, https://doi.org/10.1134/S0001437009060046, 2009.

Pautova, L. A., Mikaelyan, A. S., and Silkin, V. A.: Structure of plankton phytocoenoses in the shelf waters of the northeastern Black Sea during the Emiliania huxleyi bloom in 2002–2005, Oceanology, 47(3), 377-385, https://doi.org/10.1134/S0001437007030101, 2007.

Pautova, L. A., Silkin, V. A., Mikaelyan, A. S., and Lukashova, T. A.: The growth of new species in the Black Sea: Chaetoceros throndsenii (Marino, Montresor and Zingone) Marino, Montresor and Zingone in natural and experimental conditions, International Journal on Algae, 13(3), 277-288, DOI:10.1615/InterJAlgae.v13.i3.60, 2011.

Podymov, O., Zatsepin, A., Kubryakov, A., and Ostrovskii, A.: Seasonal and interannual variability of vertical turbulent exchange coefficient in the Black Sea pycnocline in 2013–2016 and its relation to variability of mean kinetic energy of surface currents, Ocean Dynamics, 70(2), 199-211, https://doi.org/10.1007/s10236-019-01331-w, 2020.

Poulton, A. J., Holligan, P. M., Charalampopoulou, A., and Adey, T. R.: Coccolithophore ecology in the tropical and subtropical Atlantic Ocean: New perspectives from the Atlantic meridional transect (AMT) program, Progress in Oceanography, 158, 150-170, https://doi.org/10.1016/j.pocean.2017.01.003, 2017.

Pytharoulis L., Craig G.C., Ballard S.P.: Study of the hurricane-like Mediterranean cyclone of January 1995, Phys. Chem. Earth (B)., 24, 627–632, https://doi.org/10.1016/S1464-1909(99)00056-8, 1999.

Rost B., and Riebesell U.: Coccolithophores and the biological pump: responses to environmental changes, in: Coccolithophores, edited by Thierstein H.R., Young J.R., Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-06278-4_5, 2004.

Saliot, A., Derieux, S., Sadouni, N., Bouloubassi, I., Fillaux, J., Dagaut, J., ... and Deliat, G.: Winter and spring characterization of particulate and dissolved organic matter in the Danube–Black Sea mixing zone. Estuarine, coastal and shelf science, 54(3), 355-367, https://doi.org/10.1006/ecss.2000.0652, 2002.

Shi, W., and Wang, M.: Observations of a Hurricane Katrina-induced phytoplankton bloom in the Gulf of Mexico, Geophys. Res. Lett., 34(11), https://doi.org/10.1029/2007GL029724, 2007.

Shutler, J. D., Land, P. E., Brown, C. W., Findlay, H. S., Donlon, C. J., Medland, M., Snooke, R., and Blackford, J. C.: Coccolithophore surface distributions in the North Atlantic and their modulation of the air-sea flux of CO_2 from 10 years of satellite Earth observation data, Biogeosciences, 10, 2699–2709, https://doi.org/10.5194/bg-10-2699-2013, 2013.

Silkin, V. A., Abakumov, A. I., Pautova, L. A., Mikaelyan, A. S., Chasovnikov, V. K., and Lukasheva, T. A.: Coexistence of non-native and Black Sea phytoplankton species: Discussion of invasion hypotheses, Russian Journal of Biology Invasions, 2(4), 256-264, https://doi.org/10.1134/S2075111711040102, 2011.

Silkin, V. A., Pautova, L. A., Giordano, M., Chasovnikov, V. K., Vostokov, S. V., Podymov, O. I., ... and Moskalenko, L. V.: Drivers of phytoplankton blooms in the northeastern Black Sea, Marine pollution bulletin, 138, 274-284. https://doi.org/10.1016/j.marpolbul.2018.11.042, 2019.

Silkin, V. A., Pautova, L. A., Pakhomova, S. V., Lifanchuk, A. V., Yakushev, E. V., and Chasovnikov, V. K.: Environmental control on phytoplankton community structure in the NE Black Sea, Journal of Experimental Marine Biology and Ecology, 461, 267-274, https://doi.org/10.1016/j.jembe.2014.08.009, 2014.

Silkin, V.A., Pautova, L.A., and Mikaelyan, A.S.: Role of phosphorus in the regulation of Emiliania huxleyi (Lohm.) Hay et Mohl. (Haptophyta) blooms in the northeastern Black Sea, International Journal on Algae, 11(3), 211-221, DOI: 10.1615/InterJAlgae.v11.i3.20, 2009.

635 Sorokin, Y. U. I. (Eds.): The Black Sea, In ecosystem of the world, estuaries and enclosed seas, Elsevier, Amsterdam, 1983.

Stanev, E., Grayek, S., Claustre, H., Schmechtig, C., and Poteau, A.: Water intrusions and particle signatures in the Black Sea: a Biogeochemical-Argo float investigation, *Ocean Dynamics*, 67, 1119–1136, https://doi.org/10.1007/s10236-017-1077-9, 2017.

Stelmakh, L.V.: Microzooplankton grazing impact on phytoplankton blooms in the coastal seawater of the southern Crimea
640 (Black Sea), International Journal of Marine Science, 3(15), DOI: 10.5376/ijms.2013.03.0015, 2013.

Stelmakh, L.V., Senicheva, M.I., and Babich, I.I.: Ecological and physiological bases of Emiliania huxleyi bloom in Sevastopol Bay, Ekologiya Morya, 77, 28-32, 2009 (in Russian).

Sukhanova N.: Phenomenon of the mass development of coccolithophores during the late autumn period in the Black Sea, Dokl. Akad. Nauk, 340 (2), 256–259, 1995 (in Russian).

645 Sur, H. İ., Ilyin, Y. P., Özsoy, E., and Ünlüata, Ü.: Coastal/deep ocean interactions in the Black Sea and their ecological/environmental impacts, J. mar. Sys, 7, 293-320, https://doi.org/10.1016/0924-7963(95)00030-5, 1996.

Sur, H. İ., Özsoy, E., and Ünlüata, Ü.: Boundary current instabilities, upwelling, shelf mixing and eutrophication processes in the Black Sea, Progress in Oceanography, 33(4), 249-302, https://doi.org/10.1016/0079-6611(94)90020-5, 1994.

Suslin V.V., Churilova T.Ya., and Pryakhina S.F.: Regional technique for restoring the primary hydro-optical characteristics
650 of the Black Sea according to the SeaWiFS color scanner, Ekologicheskaya bezopasnost' pribrezhnoy i shel'fovoy zon morya [Ecological safety of coastal and offshore zones of the sea], 26(2), 204-223, 2012 (in Russian).

Tsuchiya, K., Kuwahara, V. S., Yoshiki, T., Nakajima, R., Miyaguchi, H., Kumekawa, N., ... and Toda, T.: Phytoplankton community response and succession in relation to typhoon passages in the coastal waters of Japan, Journal of Plankton Research, 36(2), 424-438, https://doi.org/10.1093/plankt/fbt127, 2013.

655 Tuğrul, S., Murray, J. W., Friederich, G. E., and Salihoğlu, İ.: Spatial and temporal variability in the chemical properties of the oxic and suboxic layers of the Black Sea, Journal of Marine Systems, 135, 29-43, https://doi.org/10.1016/j.jmarsys.2013.09.008, 2014.

Türkoğlu, M.: Winter bloom of coccolithophore Emiliania huxleyi and environmental conditions in the Dardanelles, Hydrology Research, 41(2), 104-114, https://doi.org/10.2166/nh.2010.124, 2010.

660 Tyrrell, T., and Merico, A.: *Emiliania huxleyi*: bloom observations and the conditions that induce them, in: Coccolithophores, edited by Thierstein H.R., Young J.R., Springer, Berlin, Heidelberg, 75-97, https://doi.org/10.1007/978-3-662-06278-4_4, 2004.

Wu, Y., Platt, T., Tang, C. C., Sathyendranath, S., Devred, E., and Gu, S.: A summer phytoplankton bloom triggered by high wind events in the Labrador Sea, July 2006, Geophys. Res. Lett., 35(10), https://doi.org/10.1029/2008GL033561, 2008.

665 Xi, H., Losa, S.N., Mangin, A., Soppa, M.A., Garnesson, P., Demaria, J., Liu, Y., d'Andon, O.H.F., Bracher, A.: Global retrieval of phytoplankton functional types based on empirical orthogonal functions using CMEMS GlobColour merged products and further extension to OLCI data. Remote Sensing of Environment, 240, 111704, doi:10.1016/j.rse.2020.111704, 2020.

Yarovaya, D. A., Efimov, V. V., Shokurov, M. V., Stanichnyi, S. V., and Barabanov, V. S.: A quasitropical cyclone over the

670   Black Sea: observations and numerical simulation. Physical Oceanography, 18(3), 154-167, https://doi.org/10.1007/s11110-008-9018-2, 2008.

Yakushev, E. V., Pollehne, F., Jost, G., Kuznetsov, I., Schneider, B. and Umlauf, L.: Analysis of the water column oxic/anoxic interface in the Black and Baltic seas with a numerical model, Marine Chemistry, 107(3), 388-410, https://doi.org/10.1016/j.marchem.2007.06.003, 2007.

675   Yankovsky, A. E., Lemeshko, E. M., and Ilyin, Y. P.: The influence of shelfbreak forcing on the alongshelf penetration of the Danube buoyant water, Black Sea, Continental shelf research, 24(10), 1083-1098, https://doi.org/10.1016/j.csr.2004.03.007, 2004.

Yasakova, O.N., and Stanichny, S.V.: Abnormal blooming by Emiliania huxleyi (Prymnesiophyceae) in the Black Sea in 2012, Morskyi Ekolohichnyi Zhurnal, 11(4), 54, 2012 (in Russian).

680   Yasakova, O.N., Okolodkov, Y.B., and Chasovnikov, V.K.: Increasing contribution of coccolithophorids to the phytoplankton in the northeastern Black Sea, Marine pollution bulletin, 124(1), 526-534, https://doi.org/10.1016/j.marpolbul.2017.07.037, 2017.

Zatsepin, A., Kubryakov, A., Aleskerova, A., Elkin, D., and Kukleva, O.: Physical mechanisms of submesoscale eddies generation: evidences from laboratory modeling and satellite data in the Black Sea, Ocean Dynamics, 69(2), 253-266,

685   https://doi.org/10.1007/s10236-018-1239-4, 2019.

Zhu, M., Paerl, H. W., Zhu, G., Wu, T., Li, W., Shi, K., ... and Caruso, A. M.: The role of tropical cyclones in stimulating cyanobacterial (Microcystis spp.) blooms in hypertrophic Lake Taihu, China, Harmful Algae, 39, 310-321, https://doi.org/10.1016/j.hal.2014.09.003, 2014.