**Temporal variability of coccolithophore *Emiliania huxleyi* blooms in the open Black Sea: Evaluation by satellite data (1998−2020)**

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**1. Introduction**

Coccolithophores, small single-celled algae, are one of the most abundant eukaryotic phytoplankton in the oceans (Tyrrell and Merico, 2004; Winter et al., 1994; Young, 1994; Ziveri et al., 2004). These algae are primarily distinguished by their ability to synthesize external calcium carbonate plates (coccoliths), which enclose the spherical cells (Balch et al., 1991; Holligan et al., 1993; Monteiro et al., 2016). The most common bloom-forming species of coccolithophores in the oceans is *Emiliania huxleyi*(*E.* *huxleyi*), the smallest coccolithophore species (about 5–10 m diameter), which is considered one of the major calcifiers in the pelagic ocean and during seasonal blooms (coccolithophore abundance exceeding 106 cells L-1; Balch et al., 1991) can occupy huge areas (up to 100,000 km2 and more) of ocean surface (Brown and Yoder, 1994; Holligan et al., 1993; Westbroek et al., 1989; Iglesias-Rodrıguez et al., 2002).

Moreover, large blooms of these algae significantly affect the optical properties and ecological dynamics of the mixed layer of the upper ocean (Brown and Yoder, 1994; Tyrrell et al., 1999). Plated cells and detached coccoliths have a strong non-selective light scattering (Brown and Yoder, 1994; Holligan et al., 1993), that allow identification of coccolithophore blooms occupying the surface layer from satellite color scanners, as well as mapping and tracking their distribution pattern. Thus, the key parameter in the algorithms that were developed for the quantitative assessment of *E.* *huxleyi* blooms intensity has become the particulate backscattering coefficient (bbp) (Gordon and Balch, 1999; Gordon et al., 2001).

Using these algorithms, it was shown that *E.* *huxleyi* only reaches bloom proportions in specific areas of the oceans, despite the fact that it is an extremely cosmopolitan phytoplankton species and has been identified in the majority of the world’s oceans (Brown and Yoder, 1994; Winter et al., 1994; Iglesias-Rodríguez et al., 2002). For example, satellite observations revealed spectacular, seasonally repeating pattern of coccolithophore blooms in the North Atlantic (including its marginal seas) (Balch, 2004 and references therein; Brown and Yoder, 1994;Iglesias-Rodrıguez et al., 2002) and the Bering Sea (Broerse et al., 2003; Merico et al., 2004). Generally, the highest densities of *E.* *huxleyi* in all ocean regions are reached at high carbonate saturation and at times of high solar radiation, maximum water column stratification as well as nutrient depletion in the surface waters usually following the spring diatom blooms (e.g., Balch et al., 1991;Townsend et al., 1994; Tyrrell and Merico 2004).

The Black Sea, where *E. huxley* typically comprise 90–99% of the total number of coccolithophores (Mikaelyan et al., 2011), is probably the European marginal sea with the most intense blooms of this species, especially towards the end of the 20th century (Iglesias-Rodrıguez et al., 2002). Intense *E. huxley* blooms were also recorded in the Barents Sea (Giraudeau et al. 2016) as well as in the Dardanelles and the Sea of Marmara (Turkish Straits System) (Turkoglu 2008; 2010), whereas in other Mediterranean Sea regions, coccolithophore abundance did not exceed 103–105 cells L-1 during the year (Dimiza et al., 2008; Godrijan et al. 2018; Oviedo et al., 2015; Triantaphyllou et al, 2004; 2010). Interestingly, intense blooms with an abundance of cells reached 2.51×106 cells L−1 were observed for another coccolithophore (*Syracosphaera halldalii*) in a salt-wedge estuary of Krka River (Adriatic Sea) in August and October 2017 ([Skejić](https://onlinelibrary.wiley.com/authored-by/Skeji%C4%87/Sanda) et al., 2021). However, coccolithophores are of little importance in the Baltic Sea compared to other European seas (Thomsen, 2016). The vast majority of recorded coccolithophores are from the western Baltic and the confluence region between the Baltic Sea and the North Sea, i.e. the Danish Straits. A few species (e.g. *Emiliania huxleyi)* contribute in terms of algal abundance and productivity within the area, although they never attain bloom proportions*.*

Satellite studies of spatio-temporal changes in coccolithophore blooms in the open Black Sea as well as their underlying drivers began with SeaWiFS ocean color data (Cokacar et al., 2001, 2004) followed by MODIS scanners data (e.g., Burenkov et al., 2011; Kopelevich et al., 2014; 2018; Kubryakov et al., 2019; Kubryakova et al., 2018; Mikaelyan et al., 2015; Oguz and Merico, 2006). Summing up recent studies (Kubryakov et al., 2021; Kubryakova et al., 2021; Mikaelyan et al., 2020; Vostokov et al., 2022), it can be concluded that (1) E. *huxleyi* blooms in the open Black Sea are observed regularly twice a year: in May–July and October–February; (2) both periods are characterized by considerable year-to-year variability in bloom patterns: in some years, late spring-summer blooms can cover the entire open sea, last up to three months, and *E.* *huxleyi* abundance can be as high as 10-20×106 cells L-1; (3) the autumn-winter period is characterized by less intense coccolithophore blooms, although they can also cover almost the entire open part of the sea and last 1-2 months; (4) the intensity of late spring-summer *E.* *huxleyi* blooms is mainly linked to the intensity of nutrients uplift from deep layers as a result of winter convection and, therefore, to the intensity of the winter ̶ early-spring diatoms blooms, which are estimated from satellite chlorophyll *a* (Chl *a*) data.

However, we propose to reconsider the current perception of the temporal changes in *E. huxleyi* abundance and mechanisms supporting coccolithophore blooms in the open Black Sea. Our proposition is primarily based on the fact that previous studies of coccolithophore abundances used standard products for oceanic waters – level 2 or 3 remote sensing reflectance at 555 nm (RRS(555)) from one MODIS band (<https://oceancolor.gsfc.nasa.gov/atbd/rrs/>). At the same time, the optical properties of the Black Sea (Case 2 waters) differ considerably (mainly due to higher concentrations of dissolved organic matter) from the oceans (Case 1 waters). Therefore, to determine bio-optical parameters for the open Black Sea waters, including particulate backscattering coefficient, more precise regional bio-optical algorithms have been developed, which use RRS in two or more bands and take regional water properties into account (e.g. Suslin et al., 2007; 2012; 2016; Kopelevich et al., 2014; 2018). For instance, Suslin et al. (2018) showed that a regional algorithm for Chl *a* in the Black Sea (Suslin and Churilova, 2016) had a much smaller relative error (30-50%) compared to that (200-400%) of the standard NASA algorithm, derived by using data for the Atlantic Ocean (O’Reilly et al., 1998).

Secondly, a recent study has shown that Chl *a* is inappropriate for describing the seasonal variations in phytoplankton biomass, and the peak of phytoplankton biomass (blooms) in the open Black Sea occurs not in winter ̶ early-spring, but much earlier, in September (Yunev et al., 2021). Thus, using Chl *a* as a proxy of phytoplankton biomass and the standard ocean color product (<https://oceancolor.gsfc.nasa.gov/atbd/rrs/>) for the analysis of *E.* *huxleyi* blooms in the open Black Sea could potentially lead to a misrepresentation of the temporal variation in the coccolithophoreabundance and misperception of the mechanisms sustaining its late spring-summer blooms.

Here, we present data on the *E.* *huxleyi* abundance and bloom events for the open part of the Black Sea within the period 1998-2020 based on: 1) satellite data, 2) a regional algorithm that was calibrated from measured in situ coccolithophore abundances and 3) an algorithm to partition coccolithophoreabundance data into a base seasonal variation and outliers, which were termed as *E.* *huxleyi* blooms. The objective was to describe recent temporal changes in *E.* *huxleyi* abundance with particular focus on bloom development.

***2.* Material and methods**

*2.1. Satellite measurements and algorithm*

Due to the ability of coccolithophores to scatter light at all wavelengths, any band in the visible spectrum can potentially be used, but typically a band in the green part of the spectrum, e.g., λ= 555 nm, is employed (IOCCG 2006; 2014). Values for the particulate backscattering coefficient at 555 nm () were obtained from remote sensing reflectance (RRS) that included atmospheric correction. RRS data were obtained from SeaWiFS and MODIS-Aqua/Terra instruments (NASA-1, 2, 3, 2023) and processed using a regional algorithm based on Black Sea inherent optical properties (IOPs) (Suslin et al., 2016). The basic principle of this regional algorithm is the estimation of from RRS measured at the six spectral wavelengths (λ): 490, 510, and 555 nm for SeaWiFS, and 488, 531, and 547 nm for MODIS-Aqua/Terra.

The first step of this algorithm is to obtain the total light absorption coefficient (α*tot*) for the above wavelengths:

α*tot*(λ) = α*w*(λ) + α*ph*(λ) + α*CDM*(λ), (1)

where α*w*(λ) is clear seawater absorption coefficient obtained from Pope and Fry (1997) for all λ; α*ph*(λ) is phytoplankton absorption coefficient obtained from Suslin and Churilova (2016) for λ= 490 nm and from Churilova et al. (2017) for other λ; α*CDM*(λ) is the absorption coefficient of non-living organic matter (dissolved organic matter and detritus) obtained from Suslin and Churilova (2016) for λ= 490 nm and from Churilova et al. (2007, 2008) for other λ’s.

The second step is to calculate the total backscattering coefficient at the six wavelengths (*bb*(λ)) by solving a system of three equations with three unknowns for every , namely, the remote sensing reflectance (, (IOCCG, 2006):

(3)

Then, *bbp(λ)* is calculated for each spectral wavelengths according to the equation (Kopelevich 1983):

*bb(λ)* = *bbw(λ)*+ *bbp(λ)*, (5)

where *bbw(λ)* is the clear seawater backscattering coefficient (Smith and Baker 1981).

The final step of the local algorithm is to find the optimal solution of the particulate backscattering coefficient at 555 nm (), which describes the spectral course of *bbp(λ)* with minimum standard deviation (SD). To reduce the effect of measurement and atmospheric correction errors, is calculated from six values: , , for SeaWiFS, and , , for MODIS-Aqua/Terra, using a general relationship in marine optics (Kopelevich 1983):

, (6)

where is the spectral slope for *bbp(λ)*. The optimal solution for and is found by minimizing the squared difference between the six wavelength-specific values of and the predictions from the equation above.

5-day composite for rectangular areas of 0.3° longitude and latitude (estimated from about 25–2500 pixels) were aggregated by averaging into one region representing the whole open part of the Black Sea with depths >1000 m. Aggregation of satellite data into one region was motivated by the fact that our previous study of phytoplankton seasonality in the open Black Sea (Yunev et al., 2021) did not reveal any differences between sub-regions characterized by different hydrodynamic activity (upwelling and downwelling) in terms of phytoplankton biomass in the surface layer. Consequently, it is reasonable to assume that *E.* *huxleyi* abundance (N*Eh*) does not exhibit any differences between sub-regions as well. The loss of satellite information due to cloud cover (~1–2 % and ~5% of 5-d composites for April–October and November–March, respectively) was minimized by combining data from three satellite instruments with multiple overflights per day (Suslin and Churilova 2016).

*2.2. Linking in situ observations with satellite data*

In situ *E. huxleyi* abundances (Supplementary Table S1) were derived from two sources: Bulgarian (BG) monitoring surveys during 1999 – 2019 from May to November and Romanian (RO) monitoring surveys during 2018–2020 from May to August (87 stations in the outer shelf and the open sea). Stations shallower than 50 m were excluded due to the existence of so-called "straylight" in the sea regions closer than approximately 2 km from the shore (Barnes et al., 1995). Straylight means the influence of closely located land areas on the spectrum of the upward radiation recorded on the satellite, which significantly deteriorates the quality of atmospheric correction, i.e., RRS recovery, which, in turn, leads to deterioration of the recovery.

The BG and RO labs follow the same standard sampling procedures and lab processing techniques for phytoplankton analysis (Moncheva and Parr, 2005/2020) and QC/QA of the data (Moncheva, 2010). For determination of *E. huxleyi* abundances phytoplankton samples were collected by 5l Teflon Niskin bottles attached to CTD - SBE 911 - Rosette System equipped with in situ fluorometer (Chelsea Minitraca) from 1m below the surface. 1l sea water in plastic bottle was fixed immediately after sampling with 4% formaldehyde, buffered with sodium borate (Na2B4O7) to pH 7.5, were concentrated down to 50 cm3 by slow decantation after storage for at least 20 days in a cool and dark place. Taxonomic identification and cell counts and morphometric measurements were performed under inverted microscope (Nikon T300E) connected to a video-interactive image analysis system ((L.U.C.I.A, Version 4.8, Laboratory Imaging Ltd, Prague) at 400x magnification by the Utermöhl (1958) method in Sedgwick-Rafter counting chambers. Depending on the concentration of phytoplankton (pre-screening under the microscope) the 50 ml sample is either further analysed in the Utermöhl chambers, or diluted and analysed in the Sedgwick-Rafter counting chambers (taking sub-sample of 0.5 - 0.2 ml using automatic pippetes and diluting with filtered sea water (GFF filters)). For each sample, a minimum of 400 cells were counted, measured and identified to the lowest taxonomic level possible, using specific manuals, monographs and phytoplankton Atlas (Sournia, 1986; Round et al., 1990; Chrétiennot-Dinet, 1990; Tomas, 1997; 2012, Young et al., 2003), including recent electronic sources (https://[www.mikrotax.org/Nannotax3](https://www.mikrotax.org/Nannotax3), <http://oceandatacenter.ucsc.edu/home/outreach/PhytoID_fullset.pdf>, [https://www.maine.gov/dmr /sites /maine.gov.dmr/files/docs/PhytoplanktonIdentificationGuide6-DMRGuideat10x.pdf](https://www.maine.gov/dmr%20/sites%20/maine.gov.dmr/files/docs/PhytoplanktonIdentificationGuide6-DMRGuideat10x.pdf)). For counting the large-size and rare species the whole chamber was examined.

The taxonomic validation was performed using the World Register of Marine Species (WoRMS) and Algae Base. Where identification to species level was not possible the “Cf.” qualifier was used to indicate a specimen relevant to the species claimed and the numbered “sp.” was used to denote an organism relevant to the identified genus (giving the dimension measures of the cell in brackets). In addition to using a common methodology, the experts of the two labs have participated in joint cruises, intercalibration exercises conducted under various projects (UP-GRADE Black Sea, SESAME, MISIS, ANEMONE etc.) in which common data acquisition and common data bases were targeted. This produces comparable results, allowing for analysis of the combined data set. The numerical data of *E. huxley* (N*Eh*, cells L-1) include counts of intact coccospheres, or partly disrupted coccolith envelope (common during blooms, due to the detachment of coccoliths), without naked cells.

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**Fig. 1.** Locations of in situ N*Eh* measurements.

An empirical calibration relationship between N*Eh* and the 5-day composite , corresponding to the sampling time and location for N*Eh*, was established for translating satellite observations into abundances:

(7)

This relationship has an intercept for equal to *b+c* that describes a background value of due to other substances than *E.* *huxleyi*. For low values of N*Eh* the relationship is almost linear, as expected, becoming gradually curvilinear with increasing abundance of *E.* *huxleyi*. This deviation from proportionality between N*Eh* and at higher abundances is due to increasing scattering, particularly backscattering, from the coccoliths. The three parameters were estimated by non-linear ordinary least squares regression with uncertainty associated with both N*Eh* and .

Abundances of *E.* *huxleyi* were predicted from satellite observations *(*N*Eh*(RS)) employing the parameter estimates in Eq. (7).

*2.3. Coccolithophore bloom identification*

Time series of the average 5-day composite N*Eh*(RS) for the open Black Sea (depth >1000 m) were separated into a base seasonal pattern and outliers. Outliers were defined as observations exceeding the 99th percentile of the normal distribution using a periodic spline function (gam (bs = “cp”) in R-package mgcv) to describe the expected seasonal variation (Carstensen et al., 2015). The periodic spline allows for flexibility in describing the seasonal variation. The algorithm rests on the assumption that the base seasonality of N*Eh*(RS) is normal distributed with a seasonal mean described by a periodic spline function. The algorithm was initialized by setting all observations to the base population, and the periodic spline for the seasonal variation was estimated. Occurrences of N*Eh*(RS) exceeding the 99th percentile of the prediction interval of the periodic spline were identified as outliers, defined as *E. huxleyi* blooms. The periodic spline was estimated again on the remaining base observations and the 99th percentile of the prediction interval was used to single out additional outlier observations. This re-estimation of the periodic spline was continued until all base observations were below the 99th percentile of the prediction interval, and all outlier observations exceeded this upper limit.

The frequencies of *E.* *huxleyi* occurrences and blooms within a given season or month were calculated as the number of total coccolithophores relative to the number of observations and the number of bloom observations relative to the number of total coccolithophore occurrences, respectively. Bloom intensity was calculated as the deviation of bloom observations from the expected monthly mean N*Eh*(RS). Trends in the frequency of E. *huxleyi* occurrence and blooms were investigated using a logistic regression.

*2.4. Environmental coccolithophore bloom contributory parameters*

To investigate potential relationships between *E.* *huxleyi* bloom characteristics (frequency and duration) and environmental variables in the open Black Sea we turned to variables commonly used in open ocean studies (e.g., Iglesias-Rodrigues et al., 2002; Raitsos et al., 2006): sea surface temperature (SST), mixed layer depth (MLD), solar radiation (E0), critical irradiance (Ecr) and wind stress (τ). Additionally, we used the intensity of winter convective mixing, which could be estimated by the annual renewal intensity of the Cold Intermediate Layer (CIL) waters. Convective mixing is the main external source of nutrients (through their input from deeper waters) to sustain the intense development of *E.* *huxleyi* in the open Black Sea surface waters in winter.

SST data were obtained from satellite observations: for the period 1998–2000 from PO.DAAC data archive (<http://podaac.jpl.nasa.gov/sst/>); for the period 2000–2020 from OceanColor data archive (<https://oceancolor.gsfc.nasa.gov/>). The hydrodynamic model by Dorofeev and Sukhikh (2017) was employed to estimate the MLD as the depth at which the potential water density increased by 0.1 kg m-3 from the surface values. The model is based on assimilation of data from remote sensing of sea surface temperature and free surface elevation.

Monthly composites of PAR (standard satellite product with proven quality for the Black Sea; Suslin et al., 2015) were obtained from OceanColor data archive (<https://oceancolor.gsfc.nasa.gov/>) for the three optical scanners SeaWiFS and MODIS–Aqua/Terra. The critical irradiance parameter, characterizing ‘stratification relative to light level’ (Raitsos et al., 2006), was calculated using the formula (Iglesias-Rodrigues et al., 2002):

Ecr=Zeu×Eo/Zm, (8)

where, Zeu is the depth of the euphotic zone, Eo is the surface solar radiation and Zm is the MLD.

Sea surface wind stress, produces horizontal surface currents that enhance vertical mass flux through Ekman pumping, influences the stratification of the surface layer and, consequently, the conditions favorable or unfavorable for coccolithophores bloom (Raitsos et al., 2006). Wind stress magnitude (τ) was calculated from the square of monthly averaged wind speed at 10 m above the sea surface (*Va*) (Kara et al., 2007):

τ = *ρa* ×*CD*

where *ρa* is the average air density of ~1.3 kg m-3 and *CD* is the dimensionless drag coefficient that varies with wind speed (Yelland and Taylor, 1996):

for (11)

for . (12)

The 10-m height wind speed data (3-hour temporal resolution) were obtained from coastal observations at the Crimean meteorological stations of Chernomorskoye, Evpatoriya, Yalta, Feodosiya and Kerch, which are sufficiently representative as equivalent of offshore wind conditions (Ivanov and Belokopytov, 2013).

The intensity of the CIL renewal was estimated from SST winter data measured in the centers of the eastern and western cyclonic gyres (where large part of CIL waters forms) according to the SST data processing procedures described in Belokopytov (2011). For our purpose, the relative cooling index CCIL was used:

CCIL = (13)

where *Ti* is the monthly average temperature of surface water in February, *T*C is the climatology (1961–1990) for surface water temperature in February, *T*max is the upper temperature bound for CIL water (equal to 8°), *T*min is the temperature of intense CIL renewal waters (equal to 5° for the western and eastern gyres), and *K*= –2is a normalizing coefficient. The value *C*CIL = 1 corresponds to the maximum CIL renewal, values around 0 correspond to mean conditions, and the value *C*CIL = –1 corresponds to a week mixing, whereas *C*CIL = –1.5 is regarded as practically absence of CIL water renewal.

The relationship between bloom frequency and environmental variables was examined between interannual changes in the monthly average data for June, when the bloom intensity is usually largest. Besides, interannual variability of bloom frequency in June and SST in February was also examined due to the belief that excessive late spring-summer coccolithophore blooms are linked to the winter severity (Kubryakov et al., 2019; 2021; Kubryakova et al., 2021; Mikaelyan et al., 2015; 2020; Vostokov et al., 2022). The relationship between bloom duration and environmental variables was examined between interannual variation in the duration of the late spring-summer E. *huxleyi* blooms and the monthly average environmental variables for June. Relationships of bloom frequency and duration versus environmental variables were investigated using GAMs with logistic transformation for frequency and log transformation for duration.

**3. Results**

*3. 1. Linking satellite data and in-situ measurements*

The match-up between 5-day composite rectangles and in-situ N*Eh* measurements resulted in 87 observations that were fitted with non-linear relationship (Fig. 2). Although these included both outer shelf and open sea, there was no apparent difference between these two. The parameters of the non-linear regression were all significant (P<0.05). The estimated model suggested a mean background of 2.51×10-3 m-1. The relationship is almost linear for N*Eh*<106 cells L-1, becoming increasingly curvilinear for higher abundances. The root-mean-square deviation (RMSD) and the [coefficient of variation](https://en.wikipedia.org/wiki/Coefficient_of_variation) (CV) for N*Eh* were ±0.28×106 cells L-1 and ~50%, respectively.

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**Fig. 2.** Relationship between and in situ measured *E.* *huxleyi* abundance.

*3.2. Seasonal and interannual variations in abundance and bloom events*

The separation of *E.* *huxleyi* abundance into base seasonal variation and outliers provided an opportunity to describe the seasonal patterns separately for the base N*Eh*(RS) and blooms (Fig.3). The base N*Eh*(RS) in the open Black Sea had two peaks: late spring-summer (May–July) and winter (December–February). The N*Eh*(RS) values during the late spring-summer peak (~0.91×106 cells L-1) were approximately 1.5 times higher than the winter peak and three times higher than low abundance periods in spring (March–April) and late summer-autumn (August–November). Although *E.* *huxleyi* was observed throughout the annual cycle, the occurrence and bloom frequencies varied substantially across seasons and years (Fig. 4).

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**Fig. 3.** Seasonal patterns of N*Eh*(RS) from April to March (1998–2020) with observations partitioned into a seasonal base distribution () and blooms () in the open Black Sea. Dark solid line shows the estimated mean seasonal cocolithophore abundance for non-bloom observations and the grey solid line is the 99th percentile of the non-bloom prediction interval, separating non-bloom and bloom observations.

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**Fig.4.** Interannual variation in occurrence () and bloom () frequency of *E.* *huxleyi* for different seasons: (A) late spring-summer (May-July), (B) winter (December-February), (C) spring (March-April) and (D) late summer-autumn (August-November). The solid and dotted lines in (B), (C) and (D) show significant trends (P<0.05) for the occurrence and bloom frequency of *E.* *huxleyi*.

The late spring-summer peak period is characterized by the almost persistent presence of *E.* *huxleyi* (90±9%), but also by large changes in the bloom frequency, ranging from low-bloom years (2-3% in 2001, 2003, 2009, 2010 and 2018) to high-bloom years (53% in 2002, 73% in 2012, 62% in 2017, and 59% in 2019) (Fig. 4A). These differences were even more pronounced in June (Supplementary Fig. S1), when bloom frequency reached 100% in the high-bloom years, covering the entire open sea (Supplementary Fig. S6). There are also large changes in the bloom duration during this peak period, ranging from 15-25 days to 65-70 days (Fig. 5). In most cases, the blooms begin in the second half of May and end in the first half of July. The coccolithophore abundance of the late spring-summer blooms typically exceeded the base seasonal variation by 1.5–3 times, reaching abundances up to ~2.11×106 cells L-1 (Fig. 3).

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**Fig.5.** Interannual variation in the duration of the late spring-summer *E.* *huxleyi* blooms (depicted as vertical lines).

The winter peak period was characterized by a significant negative trend in the *E.* *huxleyi* occurrence frequency from approximately 93% in 1998–2000 to 46% in 2018–2020 (Fig. 4B). This was paralleled by decreasing bloom frequencies, typically ranging from 5 to 28% before 2007, decreasing to 1–3% in subsequent years, and with no blooms observed in 2015–2017 (Fig. 4B). The coccolithophore abundance of winter blooms exceeded the base seasonal variation slightly more than the late spring-summer blooms (by 2–3.5 times), but the abundance of the blooms was similar for the two periods (Fig. 3).

During the spring and late summer-autumn periods, there was a significant decrease in the *E.* *huxleyi* occurrence frequency from 70% to 17% and 86% to 13% for the two periods, respectively (Fig. 4C and D), corresponding to approximately four and seven-fold decreases, which is more drastic than the two-fold decrease for the winter peak period (Fig. 4B). Blooms were almost completely absent in spring and late summer-autumn periods, not exceeding 3% and in some years not observed at all. Although these blooms were rare, they still reached abundances similar to the late spring-summer and winter blooms, averaging 1.51×106 cells L-1 (Fig. 3).

*3.3. Relationships between E. huxleyi blooms and environmental conditions*

In the open Black Sea, all investigated environmental variables exhibited pronounced seasonal variability (Fig. 6), but only MLD and Ecr attained minimum (13.7 m) and maximum (409 E m-2 day-1) values in June, respectively. In comparison, Eo had maximum (643 E m-2 s-1) in July, SST had maximum (25.5 0C) in August, and τ had minimum values (0.025–0.026 Pa) from May to July. Significant relationships between interannual changes of bloom frequency in June (Supplementary Fig. S1) and bloom duration in late spring-summer peak period (Fig. 5), on the one hand, and environmental variables in June (Supplementary Table S2), on the other, were found for mixed layer depth (Fig. 7A and C) and critical irradiance (Fig. 7B and D), whereas both bloom frequency and bloom duration were not linked with neither sea surface temperature, solar radiation nor wind stress (Supplementary Fig. S2 and S3; all P>0.05).

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**Fig. 6.** Seasonality of abiotic characteristics in the open Black Sea (1998-2020) shown as monthly means for mixed layer depth (A), critical irradiance (B), solar radiation (C), sea surface temperature (D), and wind stress (E).

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**Fig. 7.** Relationships: 1) *E.* *huxleyi* bloom frequency versus mixed layer depth (A) and critical irradiance (B), and 2) the late spring-summer *E.* *huxleyi* bloom duration versus mixed layer depth (C) and critical irradiance (D) in June (n=23; 1998–2020).

*E.* *huxleyi* bloom frequency in June was also not linked with sea surface temperature in February (Supplementary Fig. S4A), what most probably indicates absence of connection between excessive Junes bloom (Supplementary Fig. S1) and the winter severity. Moreover, the studied period was characterised by a positive trend of February SST (Supplementary Fig. S5), which was part of the positive trend that actually started after the cold winter of 1992 (the coldest of the last century; Oguz and Velikova, 2010). In turn, the increase in winter SST caused a decrease in the intensity of waters renewal in the CIL (according to the decrease in the relative cooling index, Fig. 8) and hence in the intensity of the winter convective mixing. In fact, all winters of the studied period (except for the winters of 2006, 2012 and 2017) had the intensity of convective mixing below the mean climatic intensity, and excepted winters were very close to the mean climatic intensity. Analysis of the relationship between interannual changes in *E. huxleyi* bloom frequency in June and changes in CCIL also showed no link between summer and winter characteristics (Supplementary Fig. S4B).

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**Fig. 8.** Long-term variability of the relative cooling index in the open Black Sea in February. Linear trends for CCIL are shown with solid (1998-2020) and dotted (1992-2020) lines. The dash-dotted line shows the mean climatic state (1961–1990).

**4. Discussion**

Remote sensing and development of appropriate algorithms to retrieve the *E.* *huxleyi* characteristics from satellite data has revolutionized the study of the spatial and temporal variability of coccolithophores in different areas of the ocean. However, acquisition of and comparison with ground truthing data remains understudied. The greatest inconsistency between optical and biological data can be observed when algorithms for the recovery of *bbp*, developed for clear ocean waters, are applied to coastal or inland waters (IOCCG 2006; 2014). Taking into account the findings of the International Ocean Colour Coordinating Group (IOCCG 2006; 2014), we used a regional algorithm based on the Black Sea inherent optical properties (Suslin et al., 2016).

The study of the match-up between the satellite and in situ N*Eh* measurements (Fig. 2) showed that predictions of N*Eh* for the open Black Sea from satellite data have a relative error equal to ~50%, which is comparable to the error of predicting Chl *a* when applying a regional algorithm (30-50%; Suslin and Churilova 2016), and secondly that there is a threshold value of the satellite equal to 2.51×10-3 m-1, corresponding to the minimum N*Eh* in situ (approximately 500 cells L-1), that can be sensed by the satellite. Thus, the results of the match-up between the satellite and in situ N*Eh* measurements presented above, together with the statistically valid separation of bloom events through using the algorithm (Carstensen et al., 2015), contributed to more accurate and precise predictions of N*Eh* to gain new insights into the mechanisms driving *E.* *huxleyi* blooms.

*4.1. The late spring-summer E. huxleyi blooms*

*E.* *huxleyi* blooms during the late spring-summer period is a typical feature of the seasonal succession of phytoplankton in the open Black Sea after the mid-1990s. This is well documented from field studies (Mikaelyan et al., 2005; 2011; Stelmakh and Georgieva 2014; Stelmakh and Gorbunova, 2018) and remote sensing observations (Cokacar et al., 2001, 2004; Oguz and Merico, 2006; Mikaelyan et al., 2015; Kopelevich et al., 2018). Different environmental conditions conducive to coccolithophore blooms have been proposed (Balch et al., 1991;Buitenhuis et al., 2008; Townsend et al., 1994; Tyrrell and Merico 2004; Tyrrell et al., 2007) and will be discussed in the following.

Buitenhuis et al. (2008) found an optimum temperature for *E.* *huxleyi* growth of ~20 °C, which corresponds to SST in June for the open Black Sea (Fig. 6D). However, the largest coccolithophore blooms are typically observed in summer but at broad ranging temperatures, e.g. <15 °C in the North Atlantic (Iglesias-Rodrıguez et al., 2002) or ~12 °C in the Bering Sea (Merico et al., 2004). We found that interannual variations in June SST could not explain *E.* *huxleyi* bloom frequency and duration (Figs. S2A and S3A), indicating that temperature does not have any significant influence on coccolithophore blooms in the open Black Sea.

Stratification is one of the most important variables controlling the succession of phytoplankton communities (e.g., Margalef, 1997). Stratification enhances light conditions for phytoplankton growth, driving a succession in phytoplankton communities from diatoms to coccolithophores that exhibit higher tolerance for high irradiances (Balch et al., 1992; Nanninga and Tyrrell, 1996). Photosynthesis experiments have shown that diatoms and dinoflagellates experience light saturation at ~400 to 500 E m-2 s-1 and photoinhibition at higher irradiances (Nanninga and Tyrrell, 1996). In contrast, the light saturation of *E.* *huxleyi* growth rate is 3 to 4 times higher than that of diatoms and dinoflagellates and photoinhibition is not pronounced even at higher light intensities due to the light-scattering properties of coccoliths surrounding the cells (Nanninga and Tyrrell, 1996). Specifically, *E.* *huxleyi* was found to have genes present in the core genome, which encode a variety of photoreceptors that facilitates tolerance to high light by minimizing reactive oxygen species (ROS) accumulation and preventing oxidative damage (Read et al., 2013). Consequently, high irradiance in the surface layer in summer (Fig. 6B, С) provides a significant advantage for the development of *E.* *huxleyi* compared to other algal species.

The development of a seasonal thermocline in the open Black Sea beginning mid-May (Yunev et al., 2022) also reduces the vertical inputs of inorganic nutrients from depth. Low nutrient concentrations are found in the surface layer; 0.15-0.2 M for nitrate and 0.2–0.4 μM for phosphate, yielding N:P ratios (4.4-5.5:1) substantially lower than the Redfield ratio (16:1) (Mikaelyan, 1995; Mikaelyan et al., 2011; Stelmakh and Gorbunova 2018). Such conditions limit the intensive growth of diatoms and dinoflagellates in the late spring-summer months, but not for *E.* *huxleyi*. With its small size and genes in the core genome for inorganic phosphate and nitrogen uptake and assimilation (Hagino et al., 2011; Read et al., 2013), coccolithophore can grow at a maximum rate even at very low nutrient concentrations. Half-saturation constants (Ks) for nitrate is 0.1 μM (Eppley et al., 1969) and maybe even as low as 0.001 μM for phosphate (Riegman et al., 2000).

*E.* *huxleyi* has one more physiological trait that can contribute to bloom development under low nutrient conditions. It is the ability of *E. huxleyi* to grow successfully on ammonium, i.e., on regenerative nitrogen (Glibert et al., 2016). It should be noted that the abundance of ~0.91×106 cells L-1 during summer months (Fig. 3) corresponds to a biomass of ~10 µg L-1, using the carbon content (11 pg) of E. *huxleyi* cell sizes of 4-6 µm (Olenina et al., 2006). For comparison, the total biomass of other algal species is ~40 µg L-1 (Yunev et al., 2021), i.e. ~4 times higher. So, coccolithophore blooms in the open Black Sea could be sustained by nutrient regeneration. Besides, by combining batch culture experiments with a simple numerical model it has been also shown that *E.* *huxleyi* has the capacity to divide up to several times in the absence of external nutrients by using internal nutrient stores (Perrin et al., 2016).

Seasonal studies of phytoplankton in the Marmara Sea and the Dardanelles (Turkish Straits System) in 2003/2004 showed that *E.* *huxleyi* was the most frequent species among the coccolithophores, just as in the Black Sea, and also exhibited two bloom periods: summer (beginning of June to mid July) and winter (mid December to late January) (Turkoglu 2008; 2010). The summer bloom (cell density ranging from 3.58×107 to 2.55×108 cells L-1) occurred under similar environmental conditions as for the Black Sea: high irradiance, establishment of a seasonal thermocline that prevented mixing with nutrient-rich deep waters, depleted inorganic nutrients within a thin upper layer (0–15 m) and low N:P ratios (mean 9.11 ± 3.95) (Turkoglu 2008). However, in contrast to the Black Sea the strong nutrient depletion was caused by a large diatom bloom right before the *E.* *huxleyi* bloom (Turkoglu 2008). Diatom blooms preceeding coccolithophore blooms have also been observed in other marine systems (Balch et al., 1991;Broerse et al., 2003**;** Holligan et al., 1993; Townsend et al., 1994; Tyrrell and Merico 2004), making the Black Sea somewhat of an exceptional case.

In other regions of the Mediterranean Sea, such as the Aegean, Cretan, Adriatic, the northernmost Ionian and northern Tyrrhenian regions the abundance of *E.* *huxleyi* did not exceed 103–105 cells L-1 at any time, despite it is a dominant phytoplankton species (Dimiza et al., 2008; Oviedo et al., 2015; Triantaphyllou et al, 2004; 2010). The main reason for the absence of summer coccolithophore blooms in these areas of the Mediterranean Sea is most probably the deep location of the thermocline during summer months (between 60-80 m depth and deeper) (Tselepides at al., 2000) and, consequently, the thickness of the upper quasi-homogeneous layer exceeding 3-4 times the appropriate thickness for the possibility of blooms during the late spring-summer peak (e.g., Balch et al., 1991;Townsend et al., 1994; Tyrrell and Merico 2004).

The most notable feature of the late spring-summer *E.* *huxleyi* bloom in the open Black Sea is the interannual variability (Fig. 4). For example, the bloom frequency in June 2001 was only 3%, compared to 96% in June 2002, and in June 2003, it was very low again (8%) (Supplementary Fig. S1). This high variability in bloom frequency is observed throughout the entire studied period (Fig. 4) and could be explained by variations in MLD and Ecr (Fig. 7). At the same time, it should be noted that Ecr includes MLD in its formulation (Iglesias-Rodrigues et al., 2002.) Therefore, it is logical to assume that changes in MLD are responsible for the observed bloom characteristics during the late spring-summer peak. In turn, MLD is controlled by the density stratification of water masses and wind impact with opposite effect on MLD. Strong density gradients prevent vertical mixing by wind. So, the balance between density stratification and wind stress must regulate the MLD and, consequently, the frequency and duration of coccolithophore blooms.

Importantly, the Black Sea is a dilution basin with a positive fresh water balance and therefore low salinity and low density averaging  = 12.6 in the surface layer (Ivanov and Belokopytov, 2013), whereas the waters of Mediterranean origin spilling through the Bosporus Strait have density = 26–28. The water column of the open Black Sea is characterized by the occurrence of two pycnoclines. A seasonal thermocline forms from April to November within the layer of 15–20 m, reaching density difference in July–August (the vertical gradient up to 1.5 sigma-t m-1, mean value of 0.2–0.3 sigma-t m-1; Ivanov and Belokopytov, 2013). A permanent halocline is located between 70 and 150 m depth. Raitsos et al. (2006) found no relationship between summer *E. huxleyi* blooms and wind stress for the North Atlantic. In the open Black Sea, wind stress is minimal during summer months (Fig. 6) and 2-3 times lower than in the subarctic North Atlantic (Ivanov and Belokopytov, 2011), contributing to water column stability and thus, supporting coccolithophore bloom formation in the open Black Sea.

Thus, a combination of optimal environmental conditions and the presence of a number of favorable physiological traits, giving *E*. *huxleyi* a competitive advantage over other phytoplankton species, provide an opportunity for the coccolithophore to bloom in the open Black Sea at low inorganic nutrient concentrations during the late spring-summer period. The main factor responsible for the high variability in *E. huxleyi* bloom frequency and duration, which is observed throughout the entire studied period, is changing density stratification of the upper mixed layer. The frequency of coccolithophore bloom shifted from a few percent to 100% and bloom duration shifted from 15 to 70 days, once the mixed layer depth became shallower than 12– 14 m (Fig. 7).

Previously proposed mechanisms for the late spring-summer blooms of *E.* *huxleyi* (Kubryakov et al., 2019; 2021; Kubryakova et al, 2018; 2021; Mikayelyan et al., 2015; 2020), involving a sequence of event (extremely cold winters, intense winter convection, high vertical entrainment of "new" nutrients, intense diatom bloom in February-March) were not supported by our results (Supplementary Fig. S4). Firstly, the winter-spring diatom blooms have been absent in recent decades due to reduced upward transport of nitrate resulting from warming (Yunev et al., 2021). Secondly, the absence of winter-spring diatom blooms leads to the questions: Were there really extremely cold winters and intense winter convection, and, as a result, high vertical entrainment of "new" nutrients in the open Black Sea after the mid-1990s? We believe that the answers to these questions are found in the results of interannual changes in frequency of the *E.* *huxleyi* occurrences and blooms during the cold season.

*4.2. The winter E. huxleyi bloom*

Environmental conditions during winter in the open Black Sea are opposite to those observed during the late spring-summer period (Fig. 6), i.e. they do not correspond to commonly reported conditions promoting coccolithophore blooms (e.g., Balch et al., 1991;Townsend etal., 1994; Tyrrell and Merico 2004). Nevertheless, our analysis of seasonal changes of *E.* *huxleyi*abundance clearly shows a second peak of base N*Eh*(RS) (December - February) (Fig. 3) and coccolithophore winter blooms in the first half of the study period (Fig. 4B). Similarly, rather intense *E.* *huxleyi* winter blooms (cell density ranging from 1.60×107 to 5.03×107cells L-1) were observed in the Dardanelles under conditions of low light, low temperatures, strong winds and deeper mixing (Turkoglu 2010). Winter coccolithophore development (but not in bloom abundance) have also been documented for the central Portuguese margin (Guerreiro et al., 2013), Yellow and East China seas (Sun et al., 2014) as well as the Northern South China Sea (Jin et al., 2019). These other regions were characterised by two common features.

Firstly, in all of them, like in the Black Sea, *E. huxleyi* also developed actively during the warm season. Hence, the same species can grow actively in the same region under very different environmental conditions. One of the most probable reasons could be that *E.* *huxleyi* can be divided into several morphological forms called morphotypes, based on differences in coccolith structure (Cook et al., 2011; Hagino et al., 2011), and that there is a pronounced seasonality in the presence of different morphotypes (Smith et al., 2012). For example, the heavily calcified form of the *E.* *huxleyi* population shifted from <10% (summer) to >90% (winter) in the Bay of Biscay (Smith et al., 2012). The authors also suggested that the shifts in carbonate chemistry alone unlikely caused the morphotype shift (pH and CaCO3 saturation are lowest in winter). Future molecular phylogenetic studies in the Black Sea could shed more light this hypothesis. Thus, although the presence of two bloom periods could be caused by shifts in morphotypes, the causative explanation for this shift remains unknown.

Secondly, in all cited regions, the development of *E.* *huxleyi* in winter was mainly attributed to the input of “new” nutrients into the surface layer. In the open Black Sea, around late October/early November, as a result of cooling and increased wind activity, the seasonal thermocline breaks down (Ivanov and Belokopytov, 2013) and there is a possibility for transport of nutrient-rich deep water to the surface layer by convective mixing (Oguz et al., 2003; Yunev et al., 2005). At the same time, the overall low frequency of *E.* *huxleyi* blooms during the winter peak period, which did not exceed 28% until 2007 and decreased to 1-3% in subsequent years (Fig. 4B), indicates that nutrients transport from deeper water through convective mixing cannot support more intense coccolithophore bloom. This is also indicated by the decreasing trend in the relative cooling index (CCIL) with values well below the average climatic state for most years (Fig. 8). Taking into account a rather deep location of the nutriclines in the open Black Sea (Konovalov and Murray, 2001; Yunev et al., 2005), it is unlikely that upward nutrients transport could sustain intensity winter blooms of *E.* *huxleyi*. Even years with the coldest winters and convective mixing intensity close to the mean climatic intensity (Fig. 8) could not sustain frequent blooms, i.e. 2% in 2012 and no bloom at all in 2017 (Fig. 4B).

The development of *E.* *huxleyi* in winter can be observed in other regions, where winter nutrient concentrations in the surface layer are generally low, albeit enough to support coccolithophore growth. Eutrophication of the Dardanelles since the 1980s and the relatively shallow location of the nutricline created favorable conditions for intense winter blooms, not only of *E.* *huxleyi*, but also of diatoms (Turkoglu 2010). The lack of diatom winter blooms in the open Black Sea (Yunev et al, 2021), in comparison to the peak presence of base N*Eh*(RS) (Fig. 3) and coccolithophore blooms exceeding 106 cells L-1 (Fig. 4B), suggests high growth rates for the winter trait of *E.* *huxleyi* despite low nutrient concentrations, giving it a competitive advantage over diatoms.

Experiments show that *E. huxleyi* can grow at high rates under highly variable light conditions from ∼6 to 2500 µE m-2 s-1 (Balch et al., 1992; van Bleijswijk et al., 1994; Nielsen, 1995; Nanninga and Tyrrell, 1996). This means that *E. huxleyi* is competitive at high light levels in summer, as well as low light levels in winter. Finally, the presence of several morphological forms of coccolithophore and the existence of seasonality in the presence of different morphotypes (which has not been shown for other algae), could also give *E. huxleyi* a competitive advantage in winter.

Thus, despite the unfavorable environmental conditions to bloom development in the open Black Sea during the cold season, the low intense winter coccolithophore blooms in the first half of the study period still occur due to some of its physiological traits, namely the ability to grow at high rates under low light conditions and low nutrient concentrations, which give *E. huxleyi* a competitive advantage over diatoms. Negative trends of occurrence and bloom frequency in cold season of the post-eutrophication period (after the early/mid 1990s) coincides with the trend of the relative cooling index in February, which indicates a decrease in nutrients input from the deep layers. This testifies that during the winter months, nutrients coming from the depth are the most likely source for coccolithophore development and sporadic winter bloom in the open Black Sea.

**5. Summary**

In this study, using a regional algorithm based on the Black Sea inherent optical properties, the relative error in determination of the *E. huxleyi* abundance in the open Black Sea from satellite data was estimated for the first time to be ~50%. It is also the first to investigate seasonal changes of *E.* *huxleyi* separately in the base abundance and blooms owing to using an algorithm to partition coccolithophoreabundance data into a base seasonal variation and outliers, which were termed as *E.* *huxleyi* blooms. Our results indicate that *E.* *huxleyi* was observed in the open Black Sea throughout the year, but the frequency of its occurrence and the frequency of blooms varied considerably. The base coccolithophore abundance had two peaks: late spring-summer (May–July) and winter (December–February). Base abundance values during the late spring-summer peak were ~0.91×106 cells L-1 and approximately 1.5 times higher than the winter peak and three times higher than low abundance periods in spring (March-April) and late summer-autumn (August-November). The late spring-summer peak period was also characterized by the almost constant presence of *E.* *huxleyi* (90±9%), but significant interannual variations in bloom frequency, which ranged from 2-3% to more than 70% throughout 1998 ̶ 2020. In this peak period, blooms typically exceeded the base seasonal variation by 1.5–3 times, reaching up to ~2.11×106 cells L-1. On the contrary, the winter peak period was characterized by significant negative trends in frequency of *E.* *huxleyi* occurrences and blooms, the latter in the range 5–28% before 2007 and decreasing to 1–3% in subsequent years.

Interannual variability of *E.* *huxleyi* bloom frequency in June (when the most prominent changes of coccolithophore bloom frequency were observed) and bloom duration during the late spring-summer period versus environmental conditions in June highlighted that density stratification of the upper mixed layer is the main environmental factor responsible for significant changes in coccolithophore bloom characteristics. Small changes in MLD and Ecr (not exceeding 25%) were associated with large changes in the frequency of E. *huxleyi* bloom from a few percent to 100% and bloom duration from 15 to 70 days. Our study also suggests that the low intensity of winter *E.* *huxleyi* bloom results from weak convective mixing and the deep location of nutrients maxima, factors unlikely to stimulate intense surface coccolithophore bloom through uplift of nutrients from depth.

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