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Drivers of the autumn phytoplankton development in the open Black Sea

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ABSTRACT

The dynamics of the autumn development of phytoplankton in the Black Sea were investigated using satellite-derived chlorophyll-*a* concentration (Chl), which was estimated for two regions in the deep sea over a 20-year period. We analysed 8-day composite Chl images along with changes in: (i) nutrient concentration obtained from in-situ measurements, (ii) sea surface temperature (SST), (iii) photosynthetically available radiation (PAR) obtained from satellite imagery, (iv) wind speed from the re-analysis of meteodata and (v) the depth of the upper mixed layer (UML) calculated from a 3D numerical model of the Black Sea. The peak in Chl was identified most frequently in the first half of November. A positive correlation between the duration of strong wind events and phytoplankton development was revealed, which was associated with the deepening of the UML, and replenishment of the photic zone with nutrients.

The impact on phytoplankton was significant when the cumulative duration of strong wind (>8 m s^{-1}) exceeded 60 h over the preceding 8 days. In such cases, the frequency of the Chl peaks increased up to 30–50% with an average of 20%. Strong wind was shown to determine the timing of the autumn bloom, but not its strength. From a positive relationship between the maximum Chl and nitrate concentration we found instead that the intensity of the autumn bloom was mainly defined by nitrate replenishment in the photic zone. On average, the timing of the seasonal maximum of Chl in the first half of November coincided with the deepening of the UML to the bottom of the seasonal thermocline (*ca* 25 m). Elution of nitrate from deeper layers, where its concentration is substantially higher, mitigated the nutrient limitation of phytoplankton growth. At the same time, a sharp decrease in PAR after mid-November resulted in the limitation of light for phytoplankton growth. Inter-annual variations of Chl in spring and autumn were shown not to be correlated. For example, the basin-wide autumn blooms were observed in some years when the spring blooms were absent. As the bloom cannot be based on regenerated nitrate, the amount of 'new' nitrate in the photic zone should have a positive trend in autumn. However, the sources and mechanisms of the basin-wide increase of nitrate concentration in the upper layer in autumn are not clear.

1. Introduction

In common with other temperate regions, the mass development of phytoplankton in autumn is a typical feature of seasonal succession in the Black Sea and has been observed in many studies; see the references below in this paragraph. The majority of these studies were carried out in coastal waters (see reviews in Sorokin, 2002; Nesterova et al., 2008) and only a few in the open sea. In the open sea basin, the autumn development of phytoplankton has been observed mainly from October to December, due to large-celled diatoms (Belogorskaya and Kondratieva 1965; Berseneva et al., 2004; Morozova-Vodyanltskaya, 1954, 1957; and others). A large quantity of phytoplankton in autumn has also been manifested in increased concentrations of chlorophyll-*a* (hereafter Chl) (Berseneva et al., 2004; Chu et al., 2005, Finenko et al., 2014; Kovaleva, 2014; Oğuz et al., 2003; Vedernikov, Demidov, 1993; Yilmaz et al., 1998; Yunev et al., 2002) and high primary production (Demidov, 2008; Sorokin, 2002; Vedernikov and Demidov, 1993; Vedernikov and Demidov, 1997; and others).

The main deficiency in previous studies of phytoplankton variability in open Black Sea waters has been an absence of continuous observations. In most cases, a set of unrelated data were obtained for different years and different sea regions, making it difficult to investigate the details of phytoplankton dynamics in a given area. To resolve this problem we have used satellite-derived Chl. The use of Chl as an index of phytoplankton biomass has some restrictions (Land et al., 2014). For instance, the concentration of chlorophyll in a single cell (cell-Chl) varies several times during a year. According to plant physiology, cell-Chl increases under low irradiance and high nutrient concentrations and decreases under the opposite conditions (see e.g. review by Finenko et al., 2003). This results in the highest carbon-to-chlorophyll ratio in phytoplankton in summer and the lowest in winter. In the Black Sea, the increase of this

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ratio from winter to summer has been estimated as 5:1 (Berseneva et al., 2004) and 10:1 (Stel'makh and Babich, 2003). Such a wide range of variation in cell-Chl, the annual cycle of which coincides with changes in Chl, complicates analysis of the real annual cycle of phytoplankton biomass on the basis of this dynamic. In order to avoid such uncertainty, in this paper we focus on the time evolution of Chl within the autumn period only, which is characterized by similar species composition and light-nutrient conditions. In this analysis, the temporal changes in cell-Chl will not mask changes in phytoplankton biomass. Despite these restrictions, the use of Chl, even without additional information on the taxonomic composition of phytoplankton, has a number of advantages; it allows us to explore phytoplankton dynamics, the timing and the magnitude of peaks in phytoplankton biomass (Land et al., 2014). It is also important that during periods of phytoplankton mass development, the surface Chl is a good proxy for standing stock in the water column (Vedernikov and Demidov, 1997).

Along with the spring period, the autumn growth comprises a substantial portion of annual primary production (e.g. Finenko et al., 2009). However, prior to the 1990s, the magnitude of the spring bloom was about 2 times higher than the autumn bloom (Demidov, 1999; Vedernikov and Demidov, 1993; Yunev et al., 2002). During the individual cold years of the 1960s the maximum of the total phytoplankton biomass in spring was 10 times higher than in autumn (Mashtakova and Roukhiyainen, 1979). From the 1970s to the 1990s, monthly Chl in February–March was estimated as 2.5–2.8 μg l^{-1} (Vedernikov and Demidov, 1993), 1.6–2.7 μg l^{-1} (Demidov, 1999), 1.9 μg l^{-1} (Yunev et al., 2002), 1.8 μg l^{-1} (Chu et al., 2005). The monthly Chl in October–November was substantially lower: 0.5–0.55 μg l^{-1} (Vedernikov and Demidov, 1993), 0.45–0.6 μg l^{-1} (Yunev et al., 2002), 1.2 μg l^{-1} (Chu et al., 2005), 0.6–0.8 μg l^{-1} (Demidov, 2008). After 1995, the difference between the spring and autumn blooms decreased. This gave rise to the hypothesis that the decrease was caused by climate change reducing the intensity of winter convection and, as a result, the amplitude of the spring bloom (Burenkov et al., 2011; Oğuz et al., 2003).

After the spring bloom of phytoplankton, nutrients in the photic zone are not completely consumed. Substantial quantities of nutrients remain in the seasonal thermocline and below (Chu et al., 2005). It was shown that during the cold regional climatic period from the mid-1980s to mid-1990s, when there was extremely intensive winter convection, this stock of nutrients supported a high biomass of phytoplankton during the warm months of the year (Mikaelyan et al., 2013). One can expect that after severe winters, the bulk of nutrients are maintained in the sub-thermocline layers during summer and penetrate into the photic zone during autumn convection. Therefore, a correlation between the severity of winter and the phytoplankton biomass in the following autumn may exist.

In this paper we analyse 8-day composite Chl images along with changes in (i) nutrient concentration obtained from in-situ measurements, (ii) sea surface temperature (SST), (iii) photosynthetically available radiation (PAR) obtained from satellite imagery, (iv) wind speed from the re-analysis of meteodata and (v) the depth of the upper mixed layer (UML) calculated from a 3D numerical model of the Black Sea in order to identify the main drivers of the autumn phytoplankton mass development in the open Black Sea. We have also compared the strength of the autumn and spring bloom over a recent 18 year period.

2. Material and methods

Sampling for nutrient measurements was carried out in the eastern part of the Black Sea from 1998 to 2013 (Fig. 1). Samples were collected either in a vertical series at a number of depth levels or only at the sea surface. The depth levels for chemical sampling were chosen on the basis of CTD profiles with the aim of collecting samples from distinct water layers. In order to minimise the influence of coastal waters, measurements were only used for analysis at locations where the seabed is deeper than 1000 m. Concentrations of macronutrients (P–PO_4^{-3}, N–NO_3^-, N–NO_2^-, N–NH_4^+ and Si) were measured at 196 stations from September to November (Table 1). Total inorganic nitrogen (N_{tot}) was estimated as the sum of all nitrogen types. Not all types of nutrients were measured in all years. Inorganic phosphorus and nitrogen concentrations were obtained for 10 years (1998–2001, 2004, 2007, 2008, 2011–2013). The nutrient analyses were conducted using either a segmented continuous-flow Techicon II autoanalyser, or by photocolorimetric methods (Bordovskiy and Chernyakova, 1992; Grashoff et al., 1999).

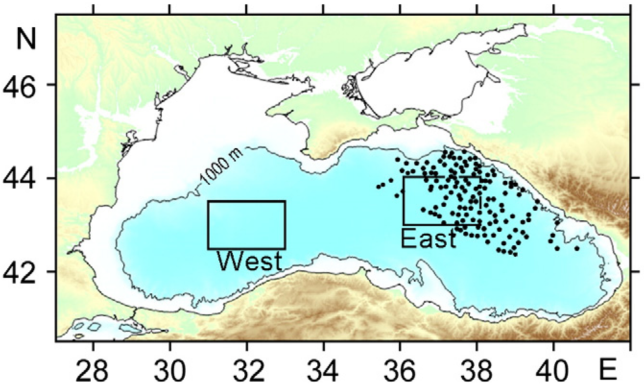

Fig. 1. Study regions in the Black Sea. Rectangles showing the western (West) and the eastern (East) regions used for satellite observations and model simulations. Dots show the locations of CTD-profiles and sampling for nutrient measurements.

The Chl and abiotic parameters were obtained in two rectangular regions in the central Black Sea (Fig. 1) in the autumn season, which is here defined as a period from October to mid-December. The regions (each with an area of 19,000 km^2) were situated in the deep basin. Both regions were selected to coincide with the most probable positions of the western and the eastern cyclonic gyres (Belokopytov, 2011; Oğuz et al., 1993; Toderascu and Rusu, 2013). The study areas covered the central parts of the gyres (West: 42.5°–43.5° N, 31°–33° E; East: 43°–44° N, 36°–38° E).

Data for Chl were taken from Aqua MODIS (level 3 products, at 4 km resolution) from 2002 to 2016. From 1997 to 2001, data were obtained from SeaWiFS (level 3 products, at 9 km resolution). It is known that the standard NASA algorithms overestimate absolute values of Chl in the open waters of the Black Sea, but reflect relative changes in this parameter quite accurately (Burenkov et al., 1999). Local algorithms, which were developed for the specific optic properties of Black Sea waters, give more correct relative and absolute values of Chl. Comparisons with the field data showed that sometimes one model is better, sometimes another (Suslin et al., 2008). To maintain reliability, we used two alternative local algorithms in the calculation of Chl. The first was based on the empirical relationships between the standard NASA satellite Chl and Chl obtained in field measurements in the open Black Sea (Stanichny, 2014), using the following equations:

$$\mathrm{Chl{-}Std} = 0.663\mathrm{SeaWIFs\_Chl} - 0.07 \tag{1}$$

$$\mathrm{Chl{-}Std} = 0.538\mathrm{AquaMODIS\_Chl} - 0.03 \tag{2}$$

Data obtained via this approach are designated hereafter as the Chl-Std.

The second approach was based on algorithms developed by Shirshov's Institute of Oceanology (SIO) and tuned for the special conditions of the open waters of the Black Sea (Kopelevich et al., 2011):

$$\mathrm{SeaWIFs{:}\ Chl{-}SIO} = 0.88\,[0.987R_{RS}(510)/R_{RS}(555)]^{-2.24} \tag{3}$$

$$\mathrm{AquaMODIS{:}\ Chl{-}SIO} = 0.83\,[0.996R_{RS}(531)/R_{RS}(547)]^{-4.36}, \tag{4}$$