

Influence of circulation processes on cyanobacteria bloom and phytoplankton succession in the Baltic Sea coastal area

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Abstract

Many studies related to the influence of eddies on the primary production chain of marine ecosystems have been conducted; however, this effect tends to be regionally specific, especially in coastal dynamic waters. In the Baltic Sea, mesoscale and submesoscale eddies are a ubiquitous feature of water circulation during summer, when diazotrophic cyanobacteria blooms occur in surface waters due to the excess of phosphorus in seawater. Climatic change may increase the frequency and duration of these negative events in the marine ecosystem. We examined the taxonomic composition, abundance, and primary production of phytoplankton in the southeastern Baltic Sea during the occurrence of the packed eddy system at the end of the abnormally warm summer of 2018. Massive cyanobacteria growth was observed in the plume of the eutrophic Vistula Lagoon in the Gulf of Gdansk. The only species diazotrophic *Dolichospermum flos-aquae* ((Bornet & Flahault) P. Wacklin, L. Hoffmann & Komárek, 2009) vegetated along the western coast of the Sambia Peninsula. Its colonies reached the highest biomass nearby the dumping site of the Amber Mining Plant in Yantarny, Kaliningrad Region, Russia. The cyanobacteria colonies dispersed in the outgoing jet of a relatively warm eddy dipole. *Chrysochromulina* spp. (Lackey, 1939) was dominant in these nitrogen-rich waters. In contrast, cryptophyte species dominated in the relatively cold waters of the dipole anticyclone that resulted in a fourfold decline in primary production. The decrease in the number of mobile phytoplankton species was revealed within the “old” eddies near the northern coast of the Sambia Peninsula and the Curonian Spit. Meanwhile, species of the spring–autumn complex *Coscinodiscus granii* (Gough, 1905), *Peridiniella catenate* ((Levander) Balech, 1977) and other developed in the community. This implies that the appearance of eddies can cause phytoplankton succession in the coastal area. The mechanism of their influence was similar to the action of other physical factors perturbing a relatively stationary environment. Capture of cyanobacterial colonies by eddies led to an improvement of the ecological situation in the area, as cyanobacteria transported their biomass outside the coastal area. However, the opposite direction processes obviously were the deterioration of light conditions, increased water turbidity, and organic matter concentration.

Key words: phytoplankton, cyanobacteria, bloom of *Dolichospermum flos-aquae*, primary production, chlorophyll *a*, ocean color, eddies, Baltic Sea, Gulf of Gdansk.

Introduction

Over the last decade, it was assumed that the eutrophication problem in the Baltic Sea had been gradually receding due to the efforts of the countries to reduce the amount of nutrients from anthropogenic sources entering the sea from its catchment area (HELCOM 2018; Murray *et al.* 2019; Zdun *et al.* 2021). Nevertheless, this problem was reminded again in the unusually warm summer of 2018, when the strongest blooms of diazotrophic cyanobacteria repeatedly occurred in the sea (Figure 1). These blooms were among the largest in recent years and were observed both in areas of the open sea and near the coasts (Finnish..., 2023; Earth.... 2023, Gogolev *et al.* 2019; Krek *et al.* 2021a; Karlson *et al.* 2022).

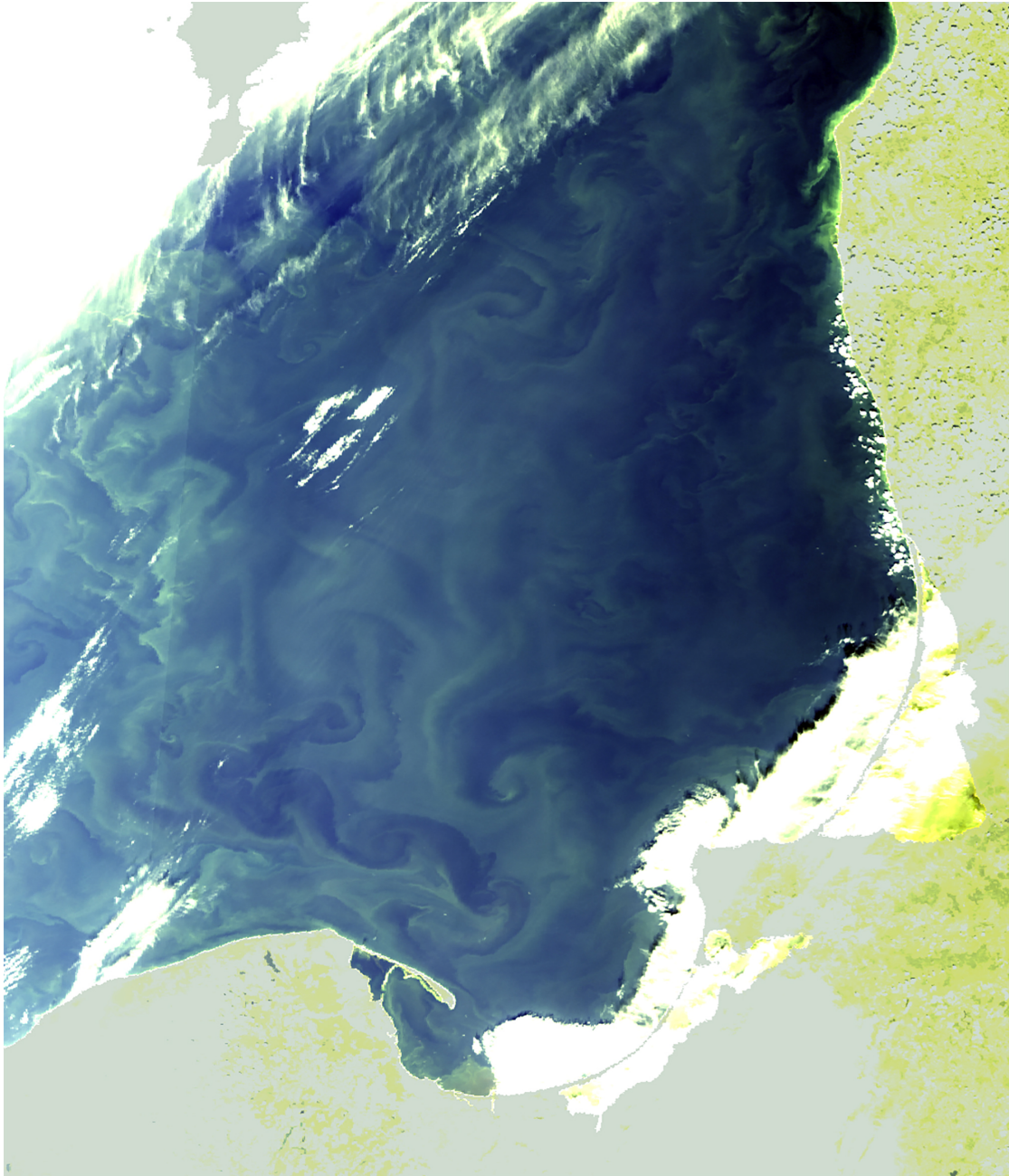


Figure 1. Phytoplankton patches on the surface of the southern Baltic Sea. Fragment of a color-synthesized image of the Baltic Sea surface in the visible range from OLCI-Sentinel-3 satellite scanner data of June 27, 2018.

The population of coastal cities is affected by the negative consequences accompanying the blooms: hydrogen sulfide smell from decomposition of microalgae biomass in the littoral zone, fish mortality and poisoning of small animals by phytotoxins (nodularin, microcystin), and deterioration of recreation conditions on beaches (Lehtonen *et al.* 2003; HELCOM 2009; Kankaanpää *et al.* 2009; Schoffelen *et al.* 2018; Karlson *et al.* 2021). The main condition for bloom development is hot, windless weather and sufficient concentration of dissolved phosphorus entering the euphotic layer prior to bloom initiation during periods of intensive vertical mixing.

A particular source of phosphorus within the Russian part of the southeastern Baltic Sea coastal area is terrigenous input (Figure 2). According to published estimates, agriculture, domestic sewage, animal and poultry waste provided the bulk of the nutrient load on coastal waters (Gorbunova *et al.* 2018). The region's physiogeographical features favour cyanobacteria blooms: the gentle underwater coastal slope between the northern coast of the Sambia Peninsula and the Curonian Spit, the turn of the coastline and the adjoining underwater hill (Rybachy Plateau prevents the export of phytoplankton cells (Kudryavtseva & Aleksandrov 2019; Kudryavtseva *et al.* 2022)). In the area from Cape Taran to Cape Gvardeysky, the shore and bottom are susceptible to intensive erosion (Emelyanov 1986; Bukanova *et al.* 2018). In the area of Cape Gvardeysky, there is a source of nutrients, which is associated with anthropogenic activities of domestic wastewater treatment facilities (the exhaust pipe locates near here).

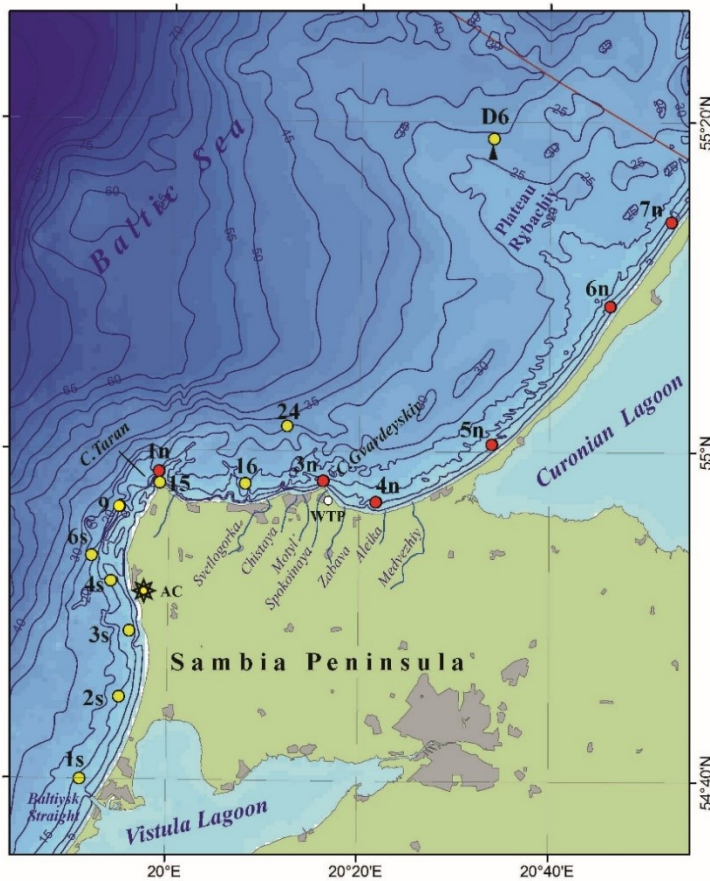


Figure 2. Study area and locations of station in the southeastern Baltic Sea (a)

Conditional symbols:

Yellow circles correspond to the stations conducted on August 22, 2018. Red circles correspond to the stations conducted on August 23, 2018.

White circle is Wastewater Treatment Plant (WTP) on the northern coast of Sambia Peninsula. Amber Mining Plant (AC) is indicated as an asterisk on the western coast.

Dolichospermum flos-aquae bloom at the western coast of Sambia Peninsula (b).



The underwater slope of the western coast of the Sambia Peninsula and the Vistula Spit is characterized by sharp depth drops. Unlike the northern coast, there are no small rivers here, thus the supply of fresh water is apparently lower. Near the Yantarny village, rock used in amber mining is dumped into the sea (Bukanova *et al.* 2018; Krek *et al.* 2018; Lavrova *et al.* 2019). In the southernmost part of the western coast of the peninsula, seawater mixes with the fresh waters of the Vistula Lagoon, which are discharged from the navigable Baltic Sea Canal. The concentration of biogenic nutrients in the lagoon exceeds the permitted concentrations of nitrogen and phosphorus (Aleksandrov 2009; Aleksandrov & Gorbunova 2012).

On satellite images, the plum area is 7–10 km from the canal site. According to CTD probing and ADCP profiling, its vertical thickness varies from 1 to 4 m (Nazirova & Krayushkin 2021).

Relatively noticeable fronts are observed at the boundary between the coastal and open sea areas, the position of which is subject to significant fluctuations associated with meandering alongshore currents, and different intensities of wind and wave impact in the southeastern Baltic Sea (Hydrochemical... 1994; Morozov *et al.* 2008). A specific feature of marine circulation during the warm season is the appearance of eddies with typical horizontal scale of 1–20 km, which play an important role in the redistribution of freshwater from continental runoff between the coastal and open sea areas (Gurova & Chubarenko 2012; Ginzburg *et al.* 2015). The mechanism of their formation is related to the disturbance of the stability of the alongshore current (Zhurbas *et al.* 2017, 2019a, 2019b). Cyclonic eddies with a cold core are formed by offshore winds, which induce upwelling events, while anticyclonic eddies with a warm core are generated by downwelling-favourable winds. Cyclonic and anticyclonic eddies are components of “mushroom-like” currents (vortex dipoles, combinations of a vortex pair: cyclone and anticyclone). Current velocities in eddies increased from 5–10 up to 70–80 cm/s (Krayushkin *et al.* 2018). The maximum number of mesoscale eddies is located in the upper 15-m layer (up to 90% of the flow depth), and the lifetime ranges from 1 to 7 days (Dargahi 2019).

Most of the known papers are devoted to analysing the manifestation of spatial and temporal characteristics of eddy structures on the surface of the Baltic Sea based on satellite images (Lavrova *et al.* 2008; Gurova & Chubarenko 2012; Ginzburg *et al.* 2015; Bukanova *et al.* 2022). However, eddies are an important physical factor which regulates biological production, typically through changes in nutrient concentration (Bibby *et al.* 2008; Hu *et al.* 2014; McGillicuddy 2016). Long-term observations in the southeastern Baltic Sea revealed that primary production (PP) was greatly influenced by hydrometeorological conditions in the Cape Taran area. Their variability was under the influence of the changes in wind direction, frequent upwelling, and the appearance of submesoscale eddies (Kudryavtseva & Aleksandrov 2019; Krek *et al.* 2021b). The impact of eddies on the PP and phytoplankton remains poorly explored in the study area.

Our study aims to improve the understanding of coastal eddies influence on the southeastern Baltic Sea ecosystem. For this purpose, we investigated the taxonomic composition, abundance and biomass of phytoplankton, as well as their growth intensity at the end of the abnormally warm summer of 2018, when strong blooms of cyanobacteria on the sea surface were recorded.

Data and Methods

The survey was conducted on August 22 and 23, 2018. On the first day, the vessel *Nord-3* left the port in the area of Cape Gvardeysky and in the evening completed its journey in the Baltic Canal. The first station (st. 24) was performed at 7:00 (UTC), and the last station (st. 1s) was performed at 19:00 (Figure 2). St. D6 was performed at the Lukoil offshore oil platform D6, samples from which were taken at 8:00. On the second day, another vessel, the *Neman*, left Cape Gvardeysky and finished at the Curonian Spit. First station st. 3n was performed at 7:30. The northernmost station on the route (st. 7n) was completed at 12:00. After that, the vessel turned to the south-west to Cape Taran (st. 1n), which was reached at 16:15.

On the first day, phytoplankton and water samples for hydrochemical analysis were collected in the surface layer (except st. 16 and 24, where phytoplankton integrated samples were collected). Samples for measurement of PP and determination chlorophyll *a* concentrations (Chl *a*) were taken from depths ranging from 1 to 95% of photosynthetically active radiation (PAR). On the second day, Chl *a*, chemical and microbiological samples were collected from the surface and near-bottom depth, and phytoplankton samples were collected from the surface. The measurements were carried out with a 90M CTD probe (Sea & Sun Technology, Germany).

PP was measured by the radiocarbon method (Steemann Nielsen 1952) in the modification described in (Kudryavtseva *et al.* 2011). Chl *a* concentration was measured using a spectrophotometer UNICO 1201 (United Products & Instruments, Inc., USA). Hydrochemical analyses were performed by standard methods (Grashoff *et al.* 1999). The taxonomic composition of phytoplankton was determined under a light microscope with magnification $\times 400$, $\times 1000$. Reference books and the World Register of Marine Species website (2023) were used for species identification. The amount and biomass of bacteria were determined by epifluorescence microscopy using acridine orange as a dye (Francisco *et al.* 1973; Kudryavtseva *et al.* 2012).

The averaged vertical attenuation coefficient of downwelling irradiance (K_d) was determined measurements of water transparency using a Secchi disk (D) from the ratio $K_d=1.3/D$ (Matciak 1997).

The optical images of the sea surface were collected from the Multi Spectral Instrument (MSI) on-board Sentinel-2 (spatial resolution 20 m, processing level 1C, SNAP 8.0 software) and the Ocean and Land Color Instrument (OLCI) scanner aboard the Sentinel-3A satellite (spatial resolution 300 m, processing level 2, SNAP 8.0 software) and obtained from <https://scihub.copernicus.eu>. Sea surface temperature (SST) values were taken from the infrared data of the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard the Aqua satellite (spatial resolution 1 km, processing level 2, SeaDAS 8.2 software, the data source is <https://oceancolor.gsfc.nasa.gov>). Chl *a* concentration was calculated from to the MODIS-Aqua data (the source is <https://oceancolor.gsfc.nasa.gov>) using a regional algorithm for the southeastern Baltic Sea (Bukanova *et al.* 2011). The flux of photosynthetic active radiation (PAR) per day was derived from the OLCI Sentinel-3A satellite scanner data.

Results

Water circulation according to the infrared and optical satellite images

During the results obtained on 22–23 August 2018, a system of packed eddies existed in the coastal area of the Sambia Peninsula and the Curonian Spit. Their manifestations are shown on the satellite images in the infrared and visible spectral ranges (Figure 3). On the first day of studies, a dipole eddy was observed to south of Cape Taran, providing an outflow of relatively warm water about 20 km long from the coast (st. 4s, 6s and 9; SST_{max} 21.9 °C). The flow of water in the dipole anticyclone (A1) resulted in the supply of relatively cold water from the open sea to the northern coast of the Sambia Peninsula in the area of Cape Taran (st. 15/1n; SST_{min} 21.1 °C). At the root of the Curonian Spit, a second anticyclone (A2) with a diameter of ~25 km was formed (st. 4n and 5n; SST 21.6 °C). Its appearance resulted in the outflow of water from the coast in the area of Cape Gvardeysky (st. 3n, 16 and 24; SST 22.1 °C). The third anticyclone (A3) was visible in the area of the Rybachy Plateau and st. D6 was located at the center of the eddy circulation (SST 21.0 °C) (Figure 3a).

On the second day of research, eddies A1 and A2 moved 5–10 km along the northeastern coast of the Sambia Peninsula and transformed into elongated swirling structures. SST rose by 0.8 °C at Cape Taran and by 0.2 °C near the central part of the Curonian Spit. A decrease of SST by 0.7 °C was observed at Cape Gvardeysky and by 0.1°C at the root of the spit (Figure 3c).

The mean SST increase over the CTD temperature measurements was 0.5 ± 0.2 °C. The discrepancy reached 1 °C at the shallowest st. 6n and 0.6 °C at st. 3n, performed 4.5 hours before the satellite pass. Other stations demonstrated that SST was higher by 0.4 ± 0.1 °C than the measured by the CTD-probe.

Areas of eddies with higher concentration of suspended particles on the sea surface corresponded to warm water flows in the infrared images, that was clearly visible in the color-synthesized RGB image for August 23, whilst the areas of relatively cold water spreading matched with the relative absence of surface suspended particles (Figure 3c, d).

Light transmission in the water column

During the studies, the PAR values ranged from 46.0 to 46.5 mol quanta·m⁻²·day⁻¹. Water transparency did not exceed 1.5–2 m in the areas of maximum suspended particles concentrations along the western coast of the Sambia Peninsula and in the Baltic Canal plume. Values >5 m were observed at the boundary between the coastal area and the open sea (st. 24 and D6). At a distance of 1–3 km from the coast, light attenuation by seawater increased in the areas affected by relatively cold waters in comparison with the areas influenced by relatively warm currents, where light attenuation declined. The Secchi disc data were confirmed by measurements of water turbidity by a sensor mounted on a CTD-probe (Figure 4). The large suspended particles concentration at the sea surface layer probably decreased in warm water currents due to water dilution and accelerated sedimentation. Small particles with neutral buoyancy, which scattered light more efficiently, were obviously present in relatively cold water.

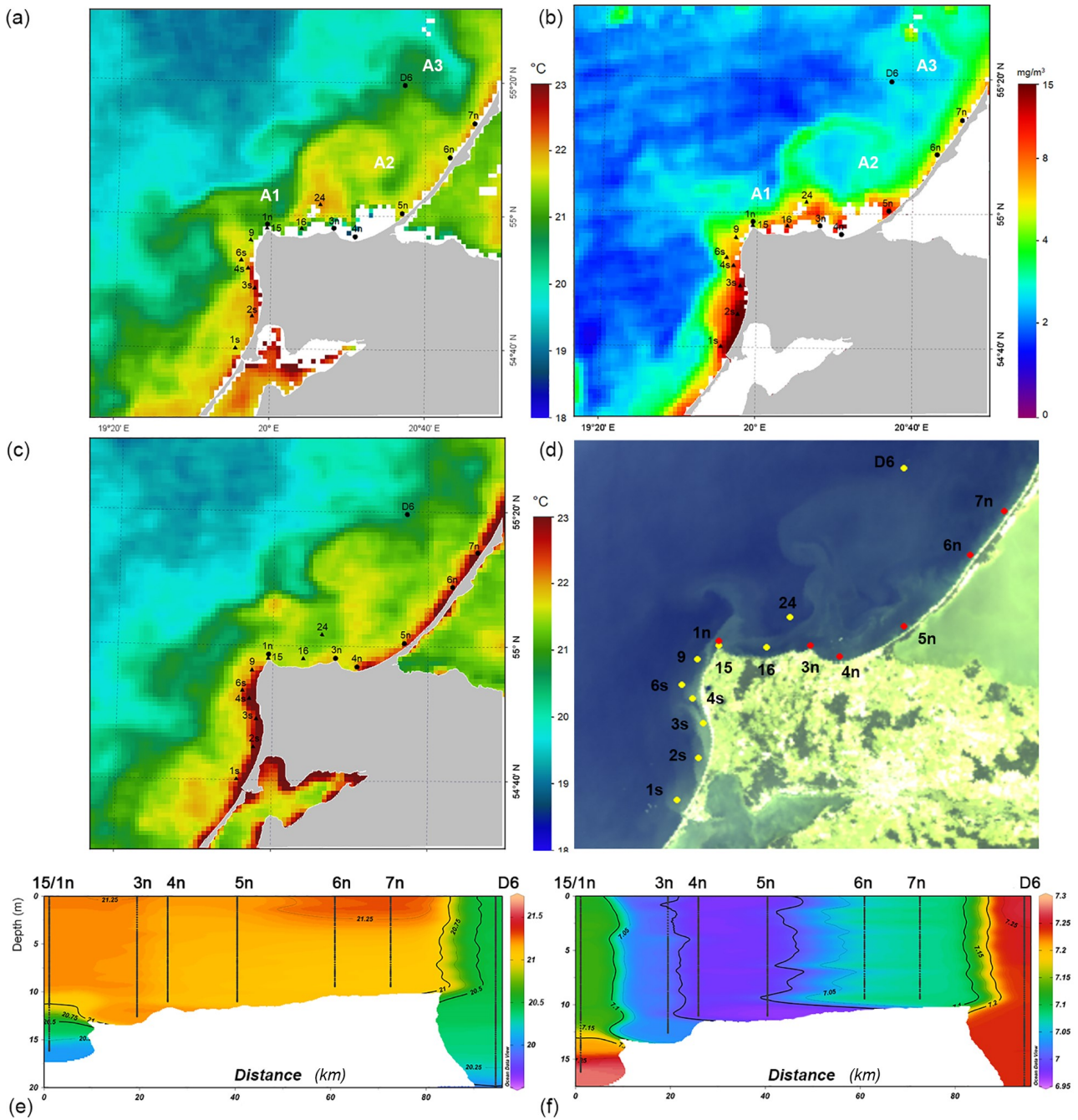


Figure 3. Sea surface temperature (a) and chlorophyll *a* concentration (b) on August 22 (11:30 UTC), and sea surface temperature (c) on August 23, 2018 (12:10 UTC), all from MODIS-Aqua satellite data; (d) fragment of optical satellite image (red, green, blue composite) derived from the Ocean and Land Color Instrument (OLCI) on Sentinel-3A satellite from August 23, 2018 (9:25 UTC); (e) temperature (°C) and salinity (f) transects along the northern coast of the Sambia Peninsula and Curonian Spit on August 23, 2018.

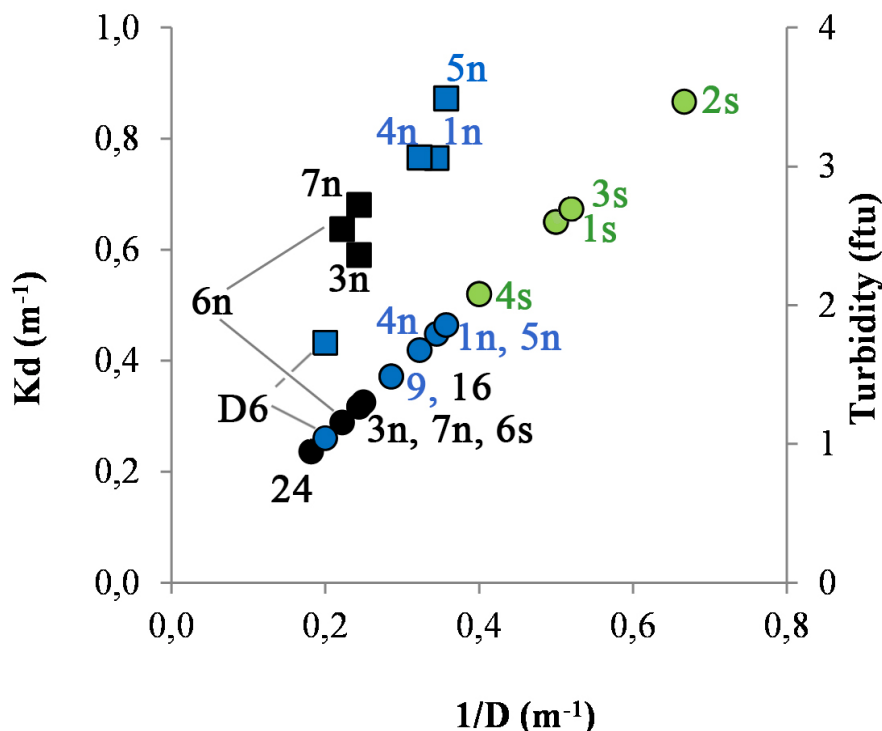


Figure 4. Photosynthetic active radiation attenuation coefficient (K_d) and inverse Secchi depth (D , circles) vs. turbidity and inverse Secchi depth (squares) at stations with cyanobacteria blooms (green symbols), under the influenced of cold water stations (blue symbols) and under the influenced of warm water stations (black symbols), respectively. Turbidity is given in units according to the turbidity standard for Formazine (Formazin Turbidity Unit, ftu).

Phytoplankton taxonomic composition, abundance and biomass

Conglomerates of suspended particles on the sea surface near the western coast of the peninsula were associated with the bloom of diazotrophic *Dolichospermum flos-aquae* ((Bornet & Flahault) P. Wacklin, L. Hoffmann & Komárek, 2009), which biomass reached 4 g/m^3 at st. 3s (Figure 5). The rise in *Dolichospermum flos-aquae* and other *Dolichospermum* spp. biomass up to 0.06 g/m^3 was recorded at the northern coast of the Sambia Peninsula at the mouth of warm water jets near Cape Gvardeysky and near Cape Taran (st. 3n and 1n). In relatively cold water of A1 eddy (st. 15), the abundance of colonies was negligible (0.001 g/m^3), or they were absent completely (st. 4n and D6). The areas of intense *D. flos-aquae* bloom indicated the waters with high concentrations of total nitrogen in water (TN), that was clearly visible along the western coast (up to $58\text{--}65 \mu\text{M}$ at st. 1–3s). In areas under the influence of relatively cold water flows, the TN concentration decreased noticeably (up to $25\text{--}26 \mu\text{M}$ at st. 1n, 4n and D6).

Together with *Dolichospermum* spp. the group of freshwater brackish-water (moderately warm-water) complex of species dominated along the western coast, which included *Aphanizomenon flos-aquae* (Ralfs ex Bornet & Flahault, 1886) with biomass up to 0.1 g/m^3 , *Chroococcus* (Nägeli, 1849) spp. (up to 0.03 g/m^3), *Merismopedia* (Meyen, 1839) spp. (up to 0.02 g/m^3), *Monoraphidium* (Komárková-Legnerová, 1969) spp. (up to 120 thousand cells/ m^3), and heterotrophic dinoflagellates of the genera *Gymnodinium* (F. Stein, 1878) and *Protoperidinium* (Bergh, 1881) (up to 0.04 g/m^3 and 0.06 g/m^3 , respectively). Diatoms did not vegetate at the western coast of the peninsula, except a small-cell *Cyclotella choctawhatcheeana* (Prasad, 1990) (up to $80 \cdot 10^3$ cells/ m^3), which was founded everywhere within the coastal area together with numerous small microalgae of the genus *Pyramimonas* (Schmarda, 1849) (up to $400 \cdot 10^3$ cells/ m^3). The abundance of *Chrysochromulina* (Lackey, 1939), the genus of haptophytes, increased significantly in relatively warm eddy currents both near the western and northern coasts (up to $728 \cdot 10^3$ cells/ m^3).

The plume of the Baltic Canal (st. 1s) was distinguished by the greatest diversity of green algae and cyanobacteria (33 species) and the absence of *C. choctawhatcheeana* in the samples. Differences in phytoplankton composition from other stations indicated the outflow of the Vistula Lagoon waters to the sea during the study period. Such species as *Lagerheimia genevensis* ((Chodat) Chodat, 1895), *Oocystis borgei* (J.W. Snow, 1903), *Neglectella solitaria* ((Wittrock) Stenclová & Kastovsky, 2017), *Woronichinia compacta*

((Lemmermann) Komárek & Hindák, 1988), *W. elorantae* (Komárek & Komárková-Legnerová, 1992), *Pseudopediastrum* (E. Hegewald, 2005) were not found at other stations or did not reach a very high abundance in plume.

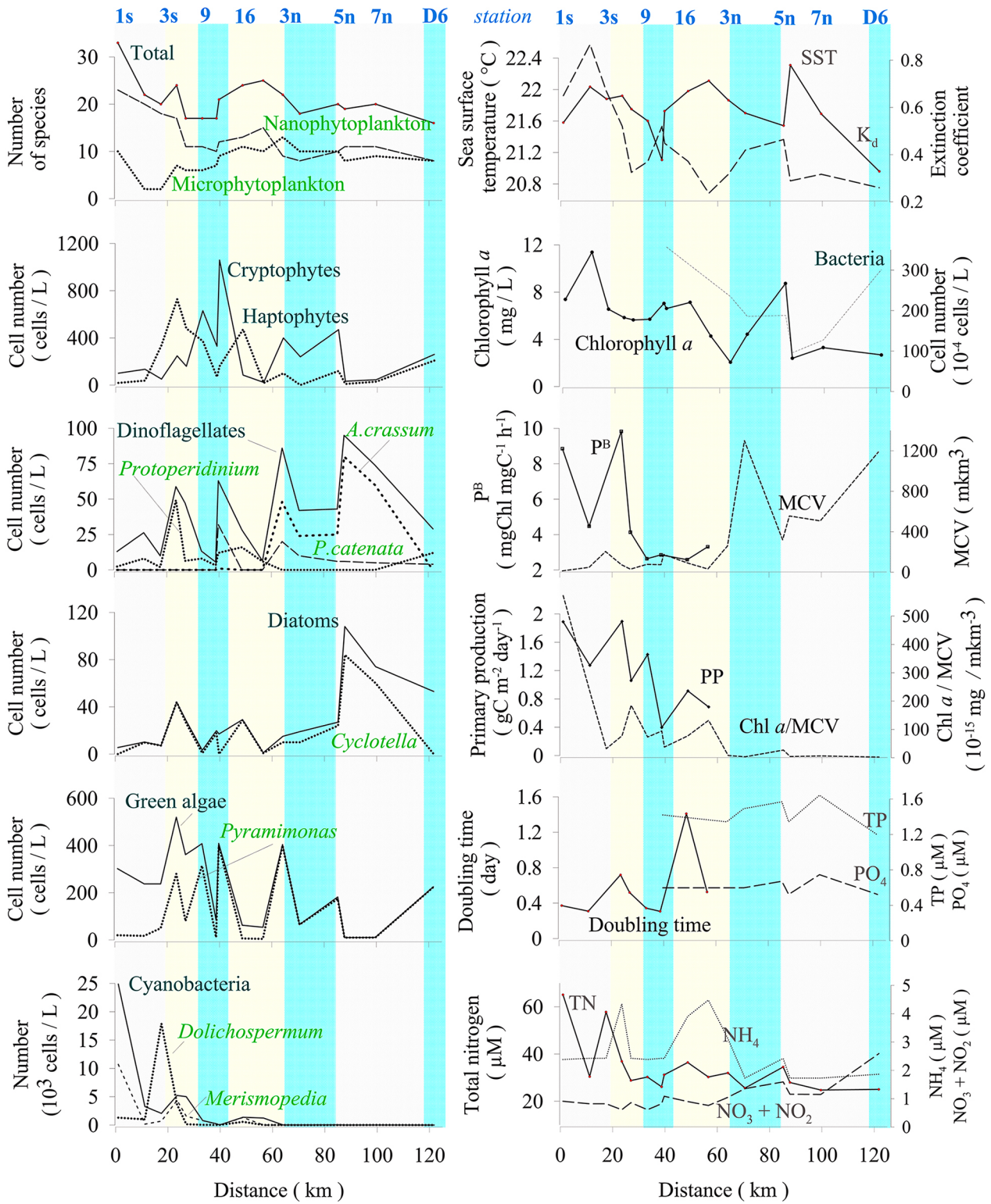


Figure 5. Spatial variations of optical, physical, chemical, and biological parameters along the coast of the Sambia Peninsula and the Curonian Spit. The yellow background corresponds to warm waters in eddies, the blue background corresponds to cold waters, and the grey background corresponds to waters outside eddies.

The following species of the marine temperate warm water (autumn) complex prevailed northeast of Cape Taran: diatoms *Actinocyclus normanii* ((Gregory) Hustedt, 1957), *A. octonarius* (Ehrenberg, 1837), and *Chaetoceros* (C.G. Ehrenberg, 1844) spp. (Figure 6). Dinoflagellates were represented by heterotrophic *Amphidinium crassum* (Lohmann, 1908), *Scrippsiella acuminata* ((Ehrenberg) Kretschmann, Elbrächter, Zinssmeister, S. Soehner, Kirsch, Kusber & Gottschling, 2015), and *Peridiniella catenata* ((Levander) Balech, 1977) with extremely small cells, probably in the growth phase. The large-cell *Coscinodiscus granii* (Gough, 1905) vegetated in the centre of A3 eddy (st. D6, 0.6 g/m³), where the concentration of the sum of nitrates and nitrites (NO₃+NO₂) reached 2.2 μM, and eastward Cape Gvardeysky in A2 eddy (st. 4n, 0.4 g/m³), where the sum of NO₃+NO₂ concentration exceeded 1.4 μM. Moreover, inhabitants of turbid waters dominated in A1 and A2 eddies – cryptophytes of genera *Teleaulax* (Hill, 1991) and *Komma caudata* ((L. Geitler) D.R.A. Hill, 1991). Their abundance reached 71% and 60% of the biomass at Cape Taran (st. 9, 15 and 1n), and 67% and 62% at the root of the spit. In the center of A3 eddy, the relative contribution of cryptophytes to the biomass was low due to the presence of *C. granii*, but the relative contribution to the total abundance was also high (60%). Finally, in relatively cold eddy water (near Cape Taran and at st. D6), bacterial abundance, as well as cryptophyte abundance, demonstrated increased values (>3000 10³ cell/mL).

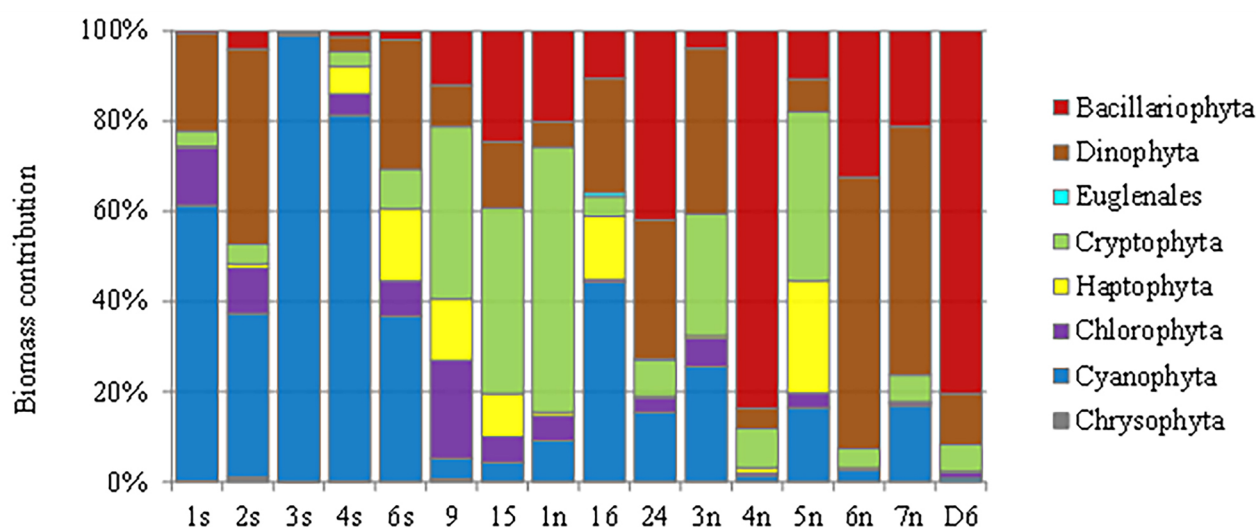


Figure 6. Phytoplankton biomass contribution in the upper 1 m layer (station 16 and 24 – integrated samples over euphotic depth).

Spatial and temporal variability of a vertical distribution of primary production and chlorophyll a concentration

The features of the vertical profiles of Chl *a* in the eddy dipole along the western coast of the Sambia Peninsula were as follows: 1) a relatively extended area with high Chl *a* concentration in warm waters; 2) small thickness of the layer with high Chl *a* concentration in relatively cold waters (5.6–7.1 mg/m³ at the surface and 1.5–2.0 mg/m³ at a depth of 3–4 m already) (Figure 7). A day after the eddy dipole displacement, when the tip of Cape Taran (st. 15 and 1n) was under the influence of relatively warm water, the Chl *a* concentration in the surface layer varied slightly (from 6.6 to 7.1 mg/m³), however, its integral concentration in the euphotic layer remarkably increased (from 19 to 73 mg/m²). On the second day, a noticeable decrease of Chl *a* concentration in the surface layer (from 7.1 to 2.1 mg/m³) and its integral concentration in the euphotic zone (from 87 to 30 mg/m²) was observed near Cape Gvardeysky (st. 16 and 3n), in agreement with the decrease of water temperature. These estimates confirmed the results of hydro-optical observations, which showed that warm flows could mix and dilute large particles of organic matter, such as cyanobacterial bloom near the coast.

The integrated PP of the summer species complex exceeded 1.8 gC/(m²·d) in the Baltic Canal plume (st. 1s) and in the areas with high biomass accumulation of *Dolichospermum* (st. 3 s and 4s). Optimal conditions for photosynthesis were found in the upper 1 m layer, where chlorophyll *a* - specific PP (P^B) reached high values of 8.9–9.8 mgC/(mgChl·h). In the dipole area near Cape Taran, the integrated PP decreased rapidly up to a value of 0.4 gC/(m²·d) in relatively cold water of A1 eddy (st. 15). Whereby, the

highest P^B values were obtained at a depth of 4–7 m (2.6–2.9 mgC/(mgChl·h)). Near the northern coast of the Sambia Peninsula, peaks in P^B values were again observed in the surface layer, however, they also did not exceed 2.6–3.3 mgC/(mgChl·h). They were consistent with an integrated PP values that reached 0.9 gC/(m²·d) at st. 16 and 0.6 gC/(m²·d) in a warm water jet at st. 24. Finally, the community biomass doubling time was lower in warm streams (0.7–1.4 d) than in non-eddy areas, where it reached 0.3 d. Thus, the appearance of eddies obviously had a negative effect on the photosynthesis of the community in which cyanobacteria were leading. Their growth could be inhibited when entering the area of eddy water movement. This is confirmed by close statistical relationships, which are given in the Table 1.

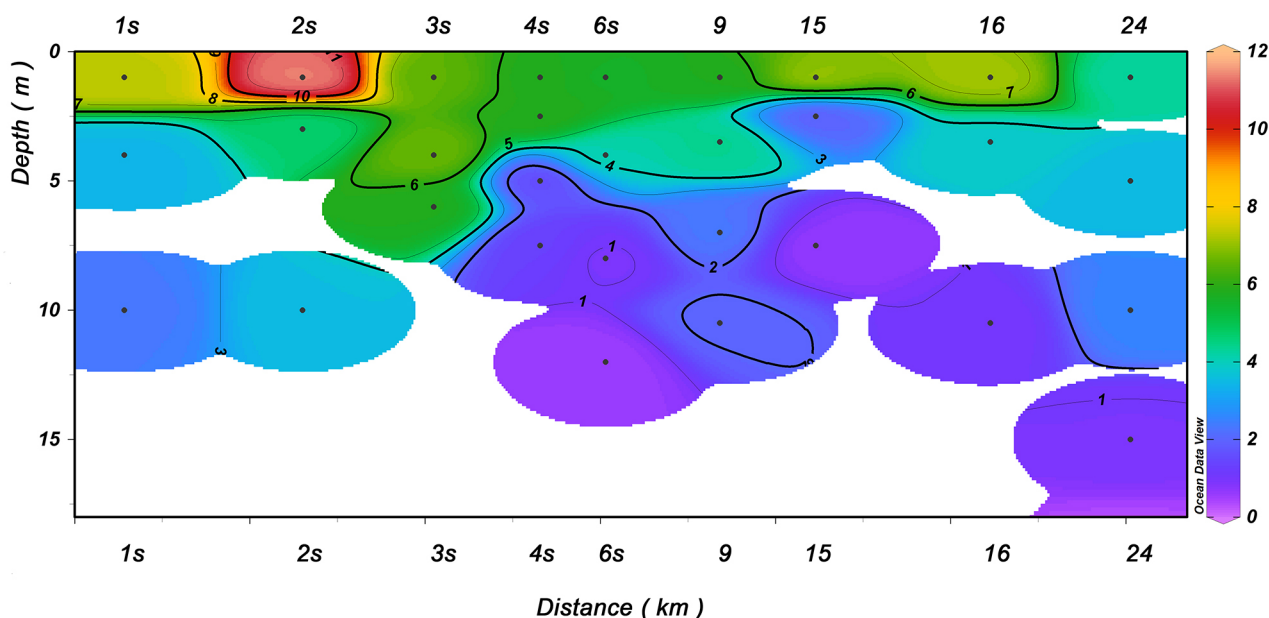


Figure 7. Vertical distribution of chlorophyll *a* concentration along the coastal area of the Sambia Peninsula on August 22, 2018.

Carbon to chlorophyll a ratio and chlorophyll a to mean cell volume ratio

Phytoplankton responded to deteriorating light conditions by increasing the content of Chl *a* in cells. The maximum Chl *a* content in cells was recorded in the area of turbid water discharge from the Baltic Canal and reached $572 \cdot 10^{-15}$ mgChl/ μm^3 (st. 1s). Chl *a* to mean cell volume (MCV) ratio could correspond to the change of dominating phytoplankton groups at other stations. In relatively warm water, Chl *a*/MCV ratio values reached $185 \cdot 10^{-15}$ mgChl/ μm^3 , whereas in communities of relatively cold eddy water, the ratio decreased to $3 \cdot 10^{-15}$ mgChl/ μm^3 (st. 1n/15). Regression analysis showed a direct positive relationship between Chl *a*/MCV ratio and cyanobacteria abundance in the coastal area and an indirect negative relationship with salinity, which may reflect lower Chl *a* content in cells of phytoplankton inhabiting waters pumped by eddies to the coastal area from distant marine areas and from deeper waters.

The presence of eddies apparently had less influence on C/Chl *a* ratio. It reached the greatest value near the western coast, where the maximum biomass of *Dolichospermum* was observed (st. 3s). The high determination coefficients for C/Chl *a* ratio and PP are a confirmation of the high intensity of carbon assimilation in the cyanobacteria bloom area.

Lifetime of coastal eddies structures

Satellite images for 2018–2023 revealed that the appearance of similar "mushroom-like" eddies opposite the western coast of the Samba Peninsula, which we observed in August 2018, is quite rare. Visualization of such eddies on optical satellite images is hampered by frequent dense cloud cover, especially in a cold period of a year (Nazirova & Krayushkin 2021). We found only one eddy dipole occurred on 3 May 2019 near Cape Taran. Its lifetime did not exceed 2 days similar to the period of our studies in August (Figure 8).

Table 1. Coefficients of determination between the phytoplankton productive parameters and abiotic factors.

<i>parameter</i>	P^B	<i>PP</i>	<i>DT</i>	<i>Chl a</i>	<i>Carbon biomass</i>	<i>MCV</i>	<i>Chl /MCV</i>
<i>PAR</i>	0,63	0,40	-	-	-	-	-
<i>K_d</i>	-	-	-	0,66	-	-	-
<i>Salinity</i>	-	-	-	-	-	-	0,83*
<i>TN</i>	0,42	0,42	-	-	0,39	-	0,40
<i>NH₄</i>	-	-	-	-	-	0,29*	-
<i>NO₃+NO₂</i>	-	-	-	-	-	0,61	-
<i>Chl a/MCV</i>	0,27	-	-	-	-	-	-
<i>C/Chl a</i>	0,71	0,54	-	-	-	-	-
<i>Carbon biomass</i>	0,78	0,62	-	-	-	-	-
<i>Total phytoplankton abundance</i>	0,65	0,56	-	-	-	-	0,47
<i>Nanophytoplankton abundance</i>	0,65	0,56	-	-	-	-	0,47
<i>Microphytoplankton abundance</i>	-	-	0,30	-	-	0,74	-
<i>Cyanobacteria</i>	0,48	0,41	-	-	-	-	0,88
<i>Dolichospermum</i>	0,75	0,52	-	-	-	-	-
<i>Merismopedia</i>	0,64	0,53	-	-	-	-	0,72
<i>Chlorophyta</i>	0,39	0,65	-	-	-	-	-
<i>Monoraphidium</i>	-	-	-	0,52	-	-	-
<i>Bacillariophyta</i>	-	-	0,28	-	-	-	-
<i>Cyclotella</i>	-	-	0,30	-	-	-	-
<i>Chrysochromulina</i>	-	-	0,28	-	-	-	-

* negative relationship between parameters (downward slope). Not marked coefficient of determination correspond to positive relationship between parameters and upward slope.

The appearance of another vortex dipole was recorded at Cape Taran in the period from August 7 to August 9, 2018, 12 days before the start of our research. The mushroom-like eddy was clearly visible on the satellite image only one day (Figure 9). Fortunately, hydrophysical soundings were carried out in the region of this dipole, and the currents were studied using an Acoustic Doppler Current Profiler (ADCP) and a complex of Lagrangian drifters. Results of these studies are given in details in Krayushkin *et al.* (2018).

Discussion

Driving forces of phytoplankton blooms along the western coast of the Sambia Peninsula

Cyanobacterial blooms are a typical midsummer phenomenon in the Baltic Sea. However, in 2018, due to the abnormally warm weather in August, they occurred at an unusual time (Lange 2017; Kudryavtseva *et al.* 2019; Hydrochemistry 1994; Springer 2008).

According to the established opinion, the accumulation of diazotrophic cyanobacteria at the western coast of the Sambia Peninsula was stimulated by calm weather and extremely weak currents in the coastal area. We found very interesting the following question: what is the reason for the "success" of *Dolichospermum* spp. in this place, because the Baltic Sea blooms are also formed by two other diazotrophic cyanobacteria – *Aphanizomenon* spp. (A. Morren ex Bornet & Flahault, 1888) and *Nodularia spumigena* (Mertens ex Bornet & Flahault, 1888)? The answer to this question may be related to the chemical properties of marine waters. The genus *Dolichospermum* consumes dissolved organic phosphorus and dissolved mineral phosphorus in approximately equal amounts, whereas *Aphanizomenon* spp. uses predominantly organic phosphorus and *N. spumigena* – predominantly mineral phosphorus (Schoffelen *et al.* 2015). In our study, *Aphanizomenon* spp. abundance varied simultaneously with *Dolichospermum* spp. abundance, but

nowhere reached bloom levels of *N. spumigena*, which inhabits the more saline waters of the open sea, was not found in the samples at all (Stal 2003; HELCOM 2009). Thus, dissolved organic phosphorus concentration was probably not a key factor in the development of this bloom.

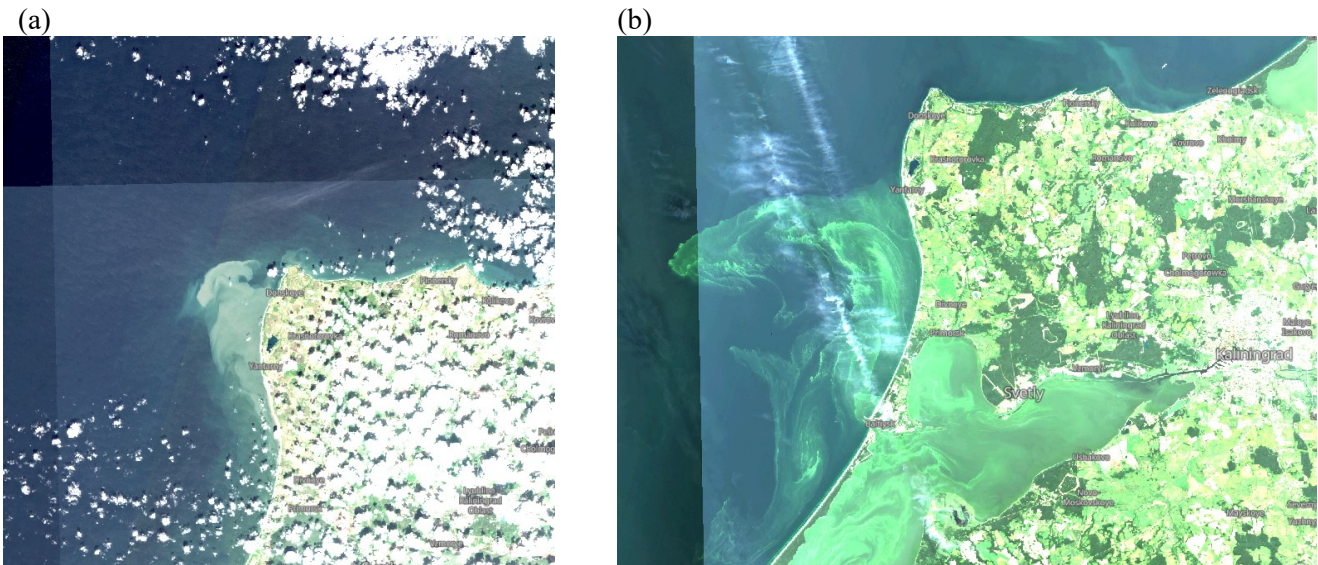


Figure 8. Fragments of optical satellite images derived from OLCI Sentinel-2 on May 3, 2019 (a) and August 28, 2022 (b).

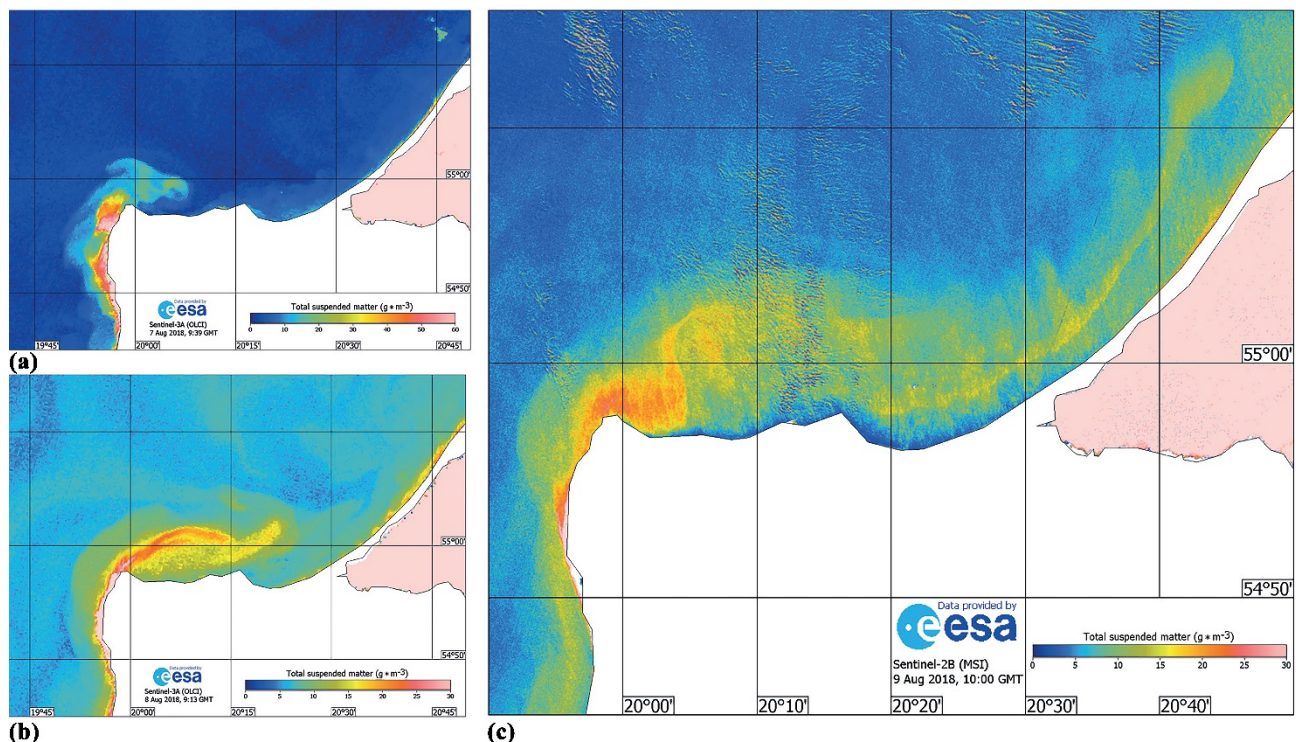


Figure 9. Dipole eddy evolution from August 7 to August 9, 2018 in the suspended matter field from OLCI Sentinel-3A data for August 7 (a) and August 8, 2018 (b) and MSI Sentinel-2B data for August 9, 2018 (c) according Krayushkin *et al.* (2018).

The reason for mass development of *Dolichospermum* spp. could be a local increase in mineral phosphorus concentration. We suggest that additional concentrations of reactive mineral phosphorus may be contained in amber mining waste discharged to the sea from the Yantarny Plant. Increased bioavailability of phosphorus inputs from the coast may be linked to prolonged water retention time near the coast (Delaney 1998; de Figueiredo *et al.* 2022). The bloom started after drenching rains when the water may wash

additional nutrients from the land and quarry (Krayushkin *et al.* 2018; Kostianoy *et al.* 2019). Moreover, wastewater discharged into the sea, even under normal conditions, may contain elevated concentrations of iron, N₂-fixing organisms needs are higher than others (Deutsch *et al.* 2007).

Cyanobacterial bloom in the Baltic Canal plume was induced by other reasons and could result from a consequence of mixing of different water types, which usually increase the intensity of biogeochemical processes in estuaries (Wasmund *et al.* 1999, 2001; Welgat *et al.* 2013, Zdun *et al.* 2021). However, due to the weak salinity gradients near the Canal entrance (Lavrova *et al.* 2017; Cubarenko *et al.* 2017; Nazirova & Krayushkin 2021) and the high species diversity of cyanobacteria which are typical species of the Vistula Lagoon ecosystem, the observed bloom could partly be a continuation of the phytoplankton bloom in the entrance to the Baltic Canal from the Vistula Lagoon's side. In the lagoon, a high level of PP is maintained throughout the summer due to a better water warming and a greater amount of nutrients (Renk *et al.* 2001; Alexandrov 2010). In addition to flushing from land, muddy sediments and bird colonies may be potential sources of nutrients for the central and coastal areas (Hesse *et al.* 2015; Vaičiūtė *et al.* 2021).

More recently, a decrease in the annual average concentration of Chl *a* during last 20 years was shown against the background of an increase in the concentration of zeaxanthin (the main cyanobacteria carotenoid) in the southern Baltic Sea (Stoń-Egiert & Ostrowska 2022). This may indicate that cyanobacteria are successfully thriving despite the possible downward trend in total phytoplankton biomass and primary productivity under current conditions (Zdun *et al.* 2021; Ostrowska *et al.* 2022). Studies of the mechanisms driving cyanobacteria blooms in both coastal and open marine areas are still relevant. In lagoons of the southeastern Baltic Sea, an extension of the cyanobacteria bloom period by more than 35 years was clearly detected (Vaičiūtė *et al.* 2021). It appears that climate warming in the Baltic Sea contributes to the dominance of cyanobacteria due to their competitive properties compared to other phytoplankton species and heat flux (Carey *et al.* 2012; Beltran-Pereza & Wanieka 2021). However, it is important to realize that environmental factors may only explain about 45% of the interannual variability in cyanobacterial biomass, because variability in bloom periods is also significantly influenced by biological interactions (Kahru *et al.* 2020).

Phytoplankton species changes in eddy impact area

Owing to the increase in velocity and change of water current direction in the place of eddy dipole formation near the western coast of the Sambia Peninsula, the bloom of *Dolichospermum flos-aquae* quickly decayed, and the abundance of representatives of *Chrysochromulina* increased. The maximum development of these haptophytes usually occur in spring at the end of diatom and dinoflagellate blooms, under conditions of relatively high underwater irradiance and maximum annual insolation (Nielsen *et al.* 1990; Hansen *et al.* 1995; Kudryavtseva *et al.* 2019). A reliable positive relationship of *Chrysochromulina* abundance with nitrogen excess has been proved (Dahl *et al.* 2005), which during the period of our study may be a consequence of intensive nitrogen fixation by diazotrophic *Dolichospermum flos-aquae*. Thus, representatives of *Chrysochromulina* naturally prevailed in a relatively warm eddy dipole current, in an environment with a high concentration of dissolved ammonium nitrogen and enhanced light conditions due to dilution of the number of cyanobacterial colonies.

Haptophytes are indicators of elevated concentrations of organic matter. This could be observed at Cape Taran, where their abundance increased in the relatively cold waters, which apparently came to the coast as a compensation for the outflow of warm water from the coast. Furthermore, haptophytes can ingest bacterial cells in acute nutrient deficiencies. *Teleaulax amphioxeia* has been found predominantly in haploid form along the western coast, as a sign of nutrient starvation (Altenburger *et al.* 2020). Our results correspond to previously obtained data on the intensive development of *Teleaulax*, *K. caudata* during periods of algae populations collapse, which form annual maximums of phytoplankton biomass in the study area - typically in the second half of summer and in the late autumn and winter seasons (Lange 2017; Kudryavtseva *et al.* 2019).

There was no intensive accumulation of cyanobacteria biomass detected at the mouth of the warm flow of A2 eddy near Cape Gvardeysky as it was found along the western coast of the Sambia Peninsula. The reason for that could partly be the longer existence of eddies near the northern coast of the Peninsula and the Curonian Spit. It was seen by a noticeable decrease in the concentration of Chl *a* on the second day of studies near Cape Gvardeysky, a decrease in the number of mobile phytoplankton species in A2 and A3 eddies, and comparatively low phytoplankton P^B values. The appearance of *C. granii* and *P. catenata* cells in

the growth stage and other species typical for autumn in the northeastern part of the study area confirmed that the shift of phytoplankton species composition developed precisely due to the existence of eddies. High abundance of *C. choctawhatcheana* was detected, being typical for a marine, relatively oligotrophic environment (Burić *et al.* 2007). The maximum development of this species was also observed as part of the marine boreal complex of species of the Baltic Sea, which form spring and autumn peaks of phytoplankton biomass.

Possible causes of succession: changes in phytoplankton growth rate within eddies or conservative mixing?

The relationship of phytoplankton photosynthesis with light conditions in the water column, the concentration of mineral forms of nutrients, and water temperature (parameters which reflect a direct response of phytoplankton to changes in habitat conditions) was not established during mathematical data processing due to a low variability of the measured values (Behrenfeld & Falkowski 1997; Kudryavtseva *et al.* 2022). However, the change in species composition in relatively warm and cold waters indicated conservative mixing under conditions of the rapid formation and displacement of the eddy dipole (i.e. actually reflect the distribution of phytoplankton in space), while P^B values reflected the instant response of phytoplankton to the current condition. We observed that the change in the dominant phytoplankton groups off the northern coast of Sambia Peninsula was no more than 5 days after a storm-related wind increase in August, 2008 (Kudryavtseva *et al.* 2019). Previously, it has been also shown that the change of community can occur within 2–3 days after storm events (Cote & Platt 1983).

Recently, numerical models have revealed a plenty of cold submesoscale filaments in the central Baltic Sea, characterized by sharp lateral buoyancy gradients, high vertical velocities, and strong convergence, favoring the preservation of a stratified layer even during autumn storms (Chrysagi *et al.* 2021). These results are well consistent with our data on the dominance of shade-adapted phytoplankton in cold jets – diatoms and haptophytes, often living at the boundary of the euphotic zone (Kudryavtseva *et al.* 2023). The data obtained from the Bornholm Basin have been confirmed that eddies can act in two ways: serve as containers transporting water and everything contained in it; and as fluid dynamic niches that promote the growth of specific phytoplankton groups (Fennel 2001; Vortmeyer-Kley *et al.* 2019). Based on the results of the present and previous studies, we assume the latter scenario in the study area.

Appearance of eddies may perform a manifestation of changes in circulation processes in the coastal zone according to interannual changes in the conditions of growth and development of phytoplankton. Similar to other physical factors, such as storm mixing or upwelling, which frequency increases during certain periods of the year (Lehmann *et al.* 2012), eddies can be one of the factors contributing to the successional change of phytoplankton species in the study area. There is a difference in phenologically homogeneous processes between the southern and northern regions of the Baltic Sea due to its significant elongation in the latitudinal direction. The outbreak of phytoplankton bloom development sweeps from south to north in a wave in spring, while the biological autumn and winter may start earlier in the northern areas. Thus, we observed the increase in phytoplankton composition of the autumn complex representatives in the Baltic Sea.

Conclusion

Studies in the southeastern Baltic Sea represented a snapshot of the coastal area ecosystem at the end of an abnormally warm summer of 2018, that showed the successional change of phytoplankton species along the southeastern coast of the Baltic Sea in a direction corresponding to the mean south-to-north quasi permanent water current (Elken & Mathaus 2008). The obvious reason for the observed succession could be the appearance of submesoscale eddies near the western coast of the Sambia Peninsula and Cape Taran. These eddies trap waters with different physical and chemical properties, and specific non-typical taxonomic composition of phytoplankton. An intermediate stage in the change of these communities was a period of increasing role of mobile species of phytoplankton (cryptophytes, haptophytes, and euglenales) associated with relatively cold waters captured by eddies near the boundary of the euphotic zone where they inhabit.

The trapping of cyanobacterial colonies by eddies resulted in the improved environmental condition during *Dolichospermum flos-aquae* bloom situation (a potentially harmful) along the coast of the Sambia Peninsula, as its photosynthesis was inhibited in the eddy current and its biomass was carried out of the coastal area and dispersed offshore. This highlights the important role of eddies in the coastal self-

purification. However, processes acting in the opposite direction, including light conditions deterioration (increased K_d), resuspension of fine sediments (increased water turbidity), and increased dissolved organic matter concentration (high bacteria and cryptophyte abundance) in the relatively cold waters, pumped by eddies from deeper layers.

The patterns found in this study are characteristic of cyanobacteria bloom situations at the end of abnormally warm summer and are not strictly true for other periods when additional studies are required. Nevertheless, the sharp reversal of the coastline, which determines the variability of the hydrometeorological conditions at Cape Taran, suggests that changes in plankton communities, vegetating in the coastal area, should often occur there.

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