



ORIGINAL RESEARCH ARTICLE

Effects of environmental variables on midsummer dinoflagellate community in the Neva Estuary (Baltic Sea)

Mikhail Golubkov^{*}, Vera Nikulina, Sergey Golubkov

Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia

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Summary Dinoflagellates account for most of the harmful phytoplankton species but relatively little is known about the specific responses of different species to environmental variables. 21 dinoflagellate species were recorded in the plankton of the Neva Estuary since the mid-19th century. 14-year long data of midsummer dinoflagellate biomass was statistically analyzed in the Neva Estuary to show the changes in dinoflagellate species in relation to environmental factors. Biomasses of *Dinophysis norvegica* (Clapared & Lachmann 1859), *Prorocentrum lima* ((Ehrenberg) F.Stein 1878) and *Peridinium aciculiferum* (Lemmermann 1900) had very similar positive relationships with salinity, temperature, phosphorus and suspended particulate organic matter concentrations while the biomass of the other common species *Peridinium cinctum* ((Müller) Ehrenberg 1832) and *Peridinium* sp. mostly showed quite opposite trends. Climate fluctuations leading to changes in the environmental variables could significantly affect the composition and productivity of the dinoflagellate community. Biomass of *Glenodinium* sp. and *Peridinium* sp. positively correlated with primary production and biomass and chlorophyll *a* concentration, but did not show a positive relationship with phosphorus. This may be due to the fact that these species in the conditions of the Neva Estuary, apparently, are more consumers than producers of organic matter, feeding on algae and cyanobacteria of phytoplankton. Therefore, to interpret the relationships between the dinoflagellate biomass and environmental variables one should take into account that the species of this group is characterized by mixotrophy and, consequently, their biomass may depend not only on the conditions of autotrophic, but also heterotrophic nutrition.

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^{*} Corresponding author at: Zoological Institute of Russian Academy of Sciences, 199034, Universitetskaya emb. 1, St. Petersburg, Russia. Tel.: +7 8123280311; fax: +7 8123282941.

E-mail address: golubkov_ms@mail.ru (M. Golubkov).

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1. Introduction

It is generally recognized that there have been more algal blooms, often of greater geographic extent and/or longer duration, with more toxic species observed, in the past decade than in previous decades (Heister et al., 2008). In fact, dinoflagellates account for about 75% of all harmful phytoplankton species (Smayda and Reynolds, 2003). They have often formed huge red tides, which have sometimes caused large-scale mortalities of fin-fish and shellfish and thus great losses to the aquaculture and tourist industries of many countries (Anderson et al., 2002; Heister et al., 2008; Zhou et al., 2017). This includes the proliferation of both spring and summer species (Jaanus et al., 2006; Klais et al., 2011; Smayda, 2002; Smayda and Reynolds, 2003; Smayda and Trainer, 2010). In the Baltic Sea the role of dinoflagellates in phytoplankton has increased everywhere from the northern to the southern regions (Golubkov et al., 2017; Jaanus et al., 2006; Klais et al., 2011; Kremp et al., 2008; Olli and Trunov, 2010; Wasmund and Uhlig, 2003).

Several reasons have been proposed to explain the observed prosperity of dinoflagellates. Eutrophication of coastal waters is the one of main reasons by which harmful algae appear to be increasing in extent and duration in many locations (Anderson et al., 2002; Heister et al., 2008; Price et al., 2017; Xiao et al., 2018). For instance, there is a definite dinoflagellate cyst which is considered as eutrophication signal along the estuaries of the NW Atlantic, thus confirming their value as indicators of water quality change and anthropogenic impact (Price et al., 2017).

The abundance of some species in the NW Atlantic region positively correlated to summer water temperatures (Price et al., 2017). Therefore, climate change may also contribute to their success. However, these changes are not so unambiguous. In the Gulf of Bothnia, the role of dinoflagellate in the phytoplankton community was higher in the colder period (Kuosa et al., 2017).

One of the most important features of dinoflagellates is their ability to become mixotrophic (uses both autotrophy and heterotrophy for growth). Many species are able to consume low molecular weight organic compounds, such as urea and amino acids, suspended organic matter, bacteria and other phytoplankton species (Hansen, 2011). Therefore, the proliferation of dinoflagellate can be associated with the increase in runoff of organic substances especially in coastal areas and with global warming. All climate projections predict an increase in average global humidity and so an increase in total rainfall. More locally, the mid-latitudes are predicted to become drier, while the wet regions, that is the tropics and polar and sub-polar regions, get wetter (Eggleton, 2018). Thus, the change in phytoplankton communities may be a result of proliferation of allochthonous organic matter-based food web (Kuosa et al., 2017), which is known to be important in northern parts of Europe (the Gulf of Bothnia) (Sandberg et al., 2004) and America (Gagnon, 2005). In some cases, the occurrence of red tides was associated with the introduction of alien species of dinoflagellates. For example, the invasion of *Prorocentrum minimum* (Pavillard) Schiller 1933) into the southern part of the Baltic Sea led to blooms in the area (Telesh et al., 2016). The prosperity of this species was facilitated by their resistance to changes in the salinity of coastal waters, which can also be caused by climate-induced changes in surface runoff (Skarlato et al., 2018).

In the Russian part of the eastern Gulf of Finland (Neva Estuary), studies of dinoflagellate began in the mid-19th century (Brandt, 1845) and continue to the present time. However, these data are poorly represented in international databases (e.g., HELCOM, 1996, 2004). Recent studies have shown that biomass of dinoflagellates has increased significantly over the past two decades. Before the late 1990s the dominant group of phytoplankton was diatoms (Bacillariophyta). In summer, the share of Dinophyta in total biomass did not exceed 3% (Nikulina, 2003). In 2000s their biomass considerably increased and in 2013–2014 this group of phytoplankton together with Cryptophyta became dominant and subdominant in midsummer phytoplankton in the upper and middle parts of the estuary respectively (Golubkov et al., 2017).

The mechanisms of bloom-species selection, and the causes of the shifts in phytoplankton community structure favoring flagellate taxa and their blooms, are major unresolved issues. Dinoflagellates have multiple life-form strategies consistent with their diverse habitat specializations. Indigenous phytoplankton communities are assembled from an extensive array of species of diverse size, shape and overlapping autecology, from which bloom species are selected (Smayda and Reynolds, 2003). However, the conditions, factors and mechanisms selecting for the genus, and species for bloom time windows remain poorly understood especially in variable coastal environments, and the outcome is thus highly unpredictable. Life-forms are selected primarily on specific habitat conditions like eutrophication and physical–chemical habitat templates. Identifying quantitative relationships between environmental variables and proliferation of certain algal species is very challenging and complex. Models of harmful algal blooms (HABs) need to include autecological characteristics of the HAB species (Glibert et al., 2010; Hense, 2010). Therefore, to predict future trends in assembly of dinoflagellate communities more information about specific habitat conditions for different species are needed.

The purpose of this study was to analyze, based on 14-year data, the effects of the environmental variables on biomass of different dinoflagellate species in the Neva Estuary. We analyzed environmental conditions such as water temperature, salinity, concentration of total phosphorus, primary production and mineralization of organic matter in order to relate them with dinoflagellate species composition and biomass in the upper, middle and lower parts of the Neva Estuary in midsummer. We tested a hypothesis that biomass of different species may be significantly correlated with these environmental variables. End of July–early August period was chosen for long-term observations because of maximum development of summer phytoplankton at this period in the Neva Estuary (Golubkov, 2009; Nikulina, 2003). The second task was to summarize the results of previous studies on the composition of the dinoflagellate community in the eastern Gulf of Finland.

2. Material and methods

2.1. Study site and sampling

The Neva Estuary receives water from the Neva River, a relatively short canal (74 km) between Lake Ladoga and

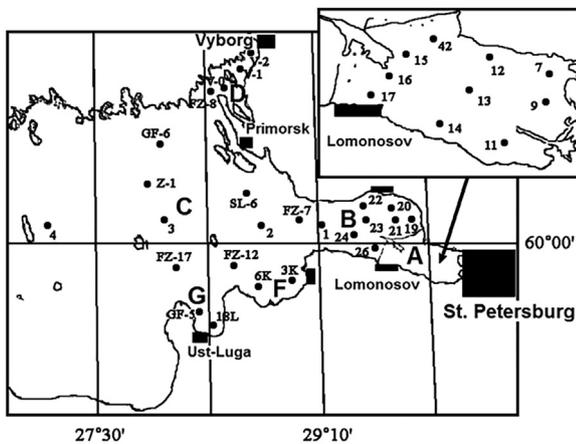


Figure 1 The Neva Estuary with indication of the sample stations (A – Neva Bay; B – Inner Estuary; C – Outer Estuary, D – Gulf of Vyborg; F – Koporskaya Bay; G – Luga Bay).

the Gulf of Finland. The catchment area of the Neva River exceeds 280,000 km², and its water discharge averages 2490 m s⁻¹ (78.6 km³ yr⁻¹). The Neva Estuary consists of three parts: the upper freshwater – Upper Estuary (Neva Bay), the brackish Middle (Inner) Estuary, and the Lower (Outer) Estuary. The surface area of the Neva Bay (Fig. 1) is about 400 km², the salinity – 0.07–0.2 PSU, with the exception of short-term surge events when brackish waters from the Middle estuary come to the Neva Bay and mix there with fresh waters. The depth of the bay is 3.5–5 m. At the end of 1980s, the Neva Bay was separated from the lower part of the estuary by the flood protection barrier (Dam). It has several sluices in its northern part and a broad ship lock in the southern part. There is no temperature stratification in this part of the estuary. Low water transparency, which does not exceed 1.8 m of Secchi depth in summer time, constrains the distribution of bottom vegetation in the bay. Dense reeds of 300–600 m width belt encircle its shallow coastal zone.

The Inner Estuary is a slightly brackish-water basin in the eastern Gulf of Finland and is located between the Dam and the longitude ca. 29°E. The salinity of surface waters in this part of the Neva Estuary ranges from 1 to 3 PSU and depth from 12 to 14 m in the eastern part and up to 30 m in its western part. There is temperature stratification in this part of the estuary: the warm water upper layer (epilimnion) and cold water deep layer (hypolimnion). The Outer Estuary is located to the west of the ca. 29°E and has a depth up to 50 m and salinity 3–7 PSU.

Ten stations in the Neva Bay and eight stations in the Inner Estuary, thirteen stations in the Outer Estuary and four stations in the Gulf of Vyborg (Fig. 1) were sampled from 20th of July to 5th of August 2003–2016. The number of stations varied in different years. Secchi depth (Sec), salinity and temperature were measured at each station. Temperature and salinity was measured by the CTD90 m probe (Sea&Sun Tech., Germany) every 20 cm from the surface to the bottom in the whole water column. Taking into account that according to these measurements the whole water column in the shallow Neva Bay was mixed, we collected five water samples (2 l each): from the surface, half a meter from the bottom and from three equal depths between them. Samples from different depths were taken in order to avoid errors

associated with the vertical distribution of different dinoflagellate species in the water column. These samples were mixed to make up an integrated sample (10 l). Samples of total phosphorus, chlorophyll *a*, suspended particulate matter and suspended particulate organic matter (three replicates) were taken from the integrated samples.

In the Inner and Outer Estuaries and in the Gulf of Vyborg, integrated water samples were taken from the two water layers: above (epilimnion) and below (hypolimnion) of the thermocline (the steepest slope of the temperature gradient from the surface to the bottom). Five water samples (2 l each) were taken from the epilimnion: from the surface, thermocline and from three equal depths between them. These samples were mixed to make up an integrated sample (10 l). Integrated water samples from hypolimnion were collected in the same way from thermocline to the bottom. Samples of chlorophyll *a* and total phosphorus (three replicates) were taken from the epilimnion integrated samples.

2.2. Sample analysis

Three hundred milliliters of water was filtered through 0.85 μm membrane filters (Millipore AAWP) for the determinations of chlorophyll *a* (C) concentration, followed by a 90% acetone extraction and spectrophotometric determination (Grasshoff et al., 1999). Total phosphorus (TP) was determined after acid hydrolysis with the molybdate blue method (Grasshoff et al., 1999). Suspended particulate matter (SPM) concentration was determined after filtration through Whatman GF/F filters with a gravimetric technique. Suspended particulate organic matter (SOM) was determined after filtration with Whatman GF/F filters (with the dichromate acid oxidation) (Grasshoff et al., 1999).

The primary production of plankton (PP) and the mineralization of organic matter (D) in water column were measured by means of the oxygen method of light and dark bottles (Hall et al., 2007; Vernet and Smith, 2007). Ratio (R) between PP and D under 1 m² was calculated as R = PP/D. The method of determination and design of experiments were described in details in the Golubkov et al. (2017).

2.3. Autotrophic dinoflagellate assemblages

Phytoplankton (volume 0.3 l) was taken in one replicate from epilimnion integrated samples and fixed with acid Lugol's solution. Since in shallow Neva Bay the whole water column was mixed, we collected only one integrated water sample from the whole column in the same way as in the Inner Estuary. The phytoplankton taxa were identified and counted in sedimentation chambers (10–25 ml) with an inverted Hydro-Bios microscope. Phytoplankton biomass was calculated in total volume of algal cells according to Olenina et al. (2006) and expressed in WW mg l⁻¹. Identification of dinoflagellate taxa was conducted according to Kiselev (1954), Pankov (1976) and Tikkanen (1986). Phytoplankton species have been listed in the modern nomenclature according to Guiry and Guiry (2018).

2.4. Statistical analysis

Statistical analyses were performed using the R software (version 3.4.0; R Development Core Team, 2017; www.

r-project.org/). Non-metric Multidimensional Scaling (NMDS) was used to analyse changes within the dinoflagellate communities by ordinating samples based on the dissimilarities of environmental conditions (function “metaMDS”, R package ‘vegan’, Oksanen et al., 2017). NMDS is an ordination technique that uses rank orders to collapse information from multiple dimensions, so they can be visualised and interpreted. The range of data values was so large that the data were square root transformed, and then submitted to Wisconsin double standardization, or species divided by their maxima, and stands standardized to equal totals. We used the Bray-Curtis dissimilarity as the distance metric in the NMDS. In the NMDS ordination space, the samples position themselves based on their taxon specific biomass. To overlaying environmental information onto ordination diagrams we use function “envfit” (R package “vegan”, Oksanen et al., 2017). The arrow points to the direction of most rapid change in the environmental variable. This is called the direction of the gradient. The length of the arrow is proportional to the correlation between ordination and environmental variable. This is called the strength of the gradient. We add the fitted vectors to an ordination using “plot” command and limit plotting to most significant variables with argument “p.max = 0.05”.

3. Results and discussion

3.1. Species composition and abundance of autotrophic dinoflagellates

A total of 134 phytoplankton midsummer samples were processed, and 9 dinoflagellates species were identified across the samples. Four dinoflagellates groups were identified only to genus (Table 1). Since the number of stations where phytoplankton samples were collected varied over the years, we did not analyze the interannual variability of the composition and biomass of the dinoflagellate community.

The most common species for the Neva Estuary were *Ceratium hirundinella* ((Müller) Dujardin 1841), *Peridinium*

aciculiferum and *Glenodinium* sp. These species were found in the samples 34–42 times; had high biomass and were distributed in all parts of the estuary, almost every year (Table 1). *C. hirundinella* was also common in plankton during the summers 1911–1912, 1914, 1920–1921 and 1923 (Kiselev, 1924; Vistlough, 1913, 1921) (Table 2), giving a maximum biomass in late July–early August. In summer 1930 it was found in the Outer Estuary in Koporskaya Bay (Kiselev, 1948). In addition, it was a subdominant species in the summer phytoplankton of the Neva Bay in 1982–1984, 2000 and 2002 (Lange, 2006; Nikulina, 1987). This dinoflagellate species was found throughout the Baltic Sea in areas with low salinity (HELCOM, 2004). *P. aciculiferum* was common in the Neva Estuary in 1982–1984 (Nikulina, 1987). But this species was not in the list of dinoflagellates found in the Baltic Sea published by HELCOM (2004). This may be due to the fact that it is mainly a freshwater species, which does not withstand a significant increase in water salinity (Craveiro et al., 2016). However, the water salinity in the Neva Estuary is rather low, and it was found in all its parts.

Peridinium cinctum, another freshwater species, which was found in the Neva Bay and the Inner estuary mainly in 2014–2016, had the highest biomass (Table 1). This species was also previously recorded in the Neva Estuary (Nikulina, 1987), Arkona Basin, Gulf of Riga and the western Gulf of Finland (HELCOM, 2004). *Gymnodinium* sp. reached to similar biomasses. *Gymnodinium simplex* ((Lohmann) Kofoid & Swezy 1921) was the rarest species of dinoflagellates in the Neva Estuary. We found this marine species, which occurred throughout the Baltic Sea (HELCOM, 2004), only once in the Outer Estuary station in 2014. *Amphidinium* spp., and *Dinophysis rotundata* (Clapared & Lachmann 1859) were also rare (Table 1).

21 taxa of dinoflagellate were noted in the Russian part of the Gulf of Finland since the mid-19th century (Table 2). The first data on phytoplankton of the Neva Estuary belong to Brandt, 1845 (Table 2). Working in the summer 1843 near the southern coast of the Neva Estuary, 40 km to the west of Lomonosov town, he found one species of dinoflagellates: *Prorocentrum micans* (Ehrenberg 1834). This marine species

Table 1 Species composition and biomass of dinoflagellates in midsummer 2003–2016 in the Neva Estuary.

Species	The number of occurrence	The year of occurrence	The station where species were found	Biomass [mg m ⁻³]
<i>Amphidinium</i> spp.	2	2003	6k, FZ-17	43.4–180.1
<i>Ceratium hirundinella</i>	42	2003, 2004, 2006, 2007, 2009, 2010, 2013–2016	Everywhere	17.6–1760.0
<i>Dinophysis norvegica</i>	9	2006–2008, 2014	16, 1, 2, 3, 4, 6k	5.0–124.3
<i>D. rotundata</i>	4	2003	18L, GF-5, z-1, FZ-17	12.3–49.3
<i>Glenodinium</i> sp.	34	2003–2006, 2008, 2010–2014, 2016	Every where	0.5–275.5
<i>Gymnodinium</i> sp.	13	2011, 2014, 2015	Neva Bay, Inner Estuary	5.2–2304
<i>Gymnodinium simplex</i>	1	2004	1	10.9
<i>Peridinium</i> sp.	9	2003, 2012, 2013,	Everywhere	13.4–544.5
<i>Peridinium aciculiferum</i>	36	2003–2006, 2008–2009, 2014–2016	Everywhere	1.6–977.3
<i>P. cinctum</i>	18	2004, 2014–2016	Neva Bay, Inner Estuary	18.7–2664
<i>Peridiniella catenata</i>	3	2005, 2010	Inner Estuary	49.5–85.5
<i>Proto-peridinium bipes</i>	9	2004–2007, 2009, 2014	Inner Estuary, Outer Estuary	8.3–832
<i>Prorocentrum lima</i>	7	2005–2006	1, 2, 4, GF-5, 3k, FZ-17,	1.0–411.5

Table 2 Species composition of dinoflagellates in the Neva Estuary in different years (according to Brandt, 1845; Kiselev, 1924, 1948; Lange, 2006; Nikulina, 1987; Shishkin et al., 1989; Tereshenkova, 2006; Vislouh, 1913, 1921 and own data).

Species	1843	1911–1912, 1914	1920–1921	1930–1937	1982–1984	1988	1997	1999–2002	2003–2016
	July–August			All seasons	August	All seasons	All seasons	August	July–August
<i>Amphidinium</i> sp.									+
<i>Ceratium hirundinella</i>	+		+	+	+			+	+
<i>C. longipes</i>				+					
<i>Dinophysis norvegica</i>									+
<i>D. ovum</i> var. <i>baltica</i>				+					
<i>D. rotundata</i>									+
<i>Diplopsalis lenticular</i>				+					
<i>Glenodinium</i> sp.					+			+	+
<i>Glenodinium paululum</i>								+	
<i>Gymnodinium</i> sp.					+			+	+
<i>Gymnodinium simplex</i>									+
<i>Peridinium</i> sp.								+	+
<i>Peridinium aciculiferum</i>					+				+
<i>P. cinctum</i>			+	+	+			+	+
<i>P. divergens</i> var. <i>oblongum</i>				+					
<i>P. inconspicuum</i>			+		+				
<i>Peridiniella catenata</i>				+		+	+		+
<i>Proto-peridinium bipes</i>				+	+				+
<i>P. granii</i>				+					
<i>Prorocentrum micans</i>	+								
<i>P. lima</i>									+

is capable of forming blooms but is usually considered as harmless. Recent incidents with *P. micans* involving shellfish mortality was attributed to oxygen depletion (Faust and Gullede, 2002). In our study we did not find this species.

Further studies of dinoflagellates were continued at the beginning of the 20th century (Kiselev, 1924; Vislouh, 1913, 1921). Ten species of photosynthetic dinoflagellate were found in phytoplankton in the outer part of the Neva Estuary in Koporskaya Bay and near Seskar Island in 1930: *Dinophysis ovum* var. *baltica* (Paulsen 1908), *P. cinctum*, *Diplopsalis lenticula* (Bergh 1881), *C. hirundinella*, *Ceratium longipes* ((Bailey) Gran 1902), *Peridinium divergens* var. *oblongum* (Aurivillius 1898), *Proto-peridinium granii* ((Ostenfeld) Balech 1974), *Proto-peridinium bipes* ((Paulsen) Balech 1974), *Proto-peridinium pyriforme* subsp. *breve* ((Paulsen) E. Balech 1988), *Peridiniella catenata* ((Levander) Balech 1977) (Kiselev, 1948). Although the author did not provide numerical values of biomass, he noted that *P. catenata* was on the fourth place in the biomass of phytoplankton in Koporskaya Bay. This cold-loving species, found throughout the Baltic Sea (HELCOM, 2004), was found in 2003–2016 only three times in the samples from the Inner Estuary (Table 1). However, in 1935–1937, 1988 and 1997 this species was a sub-dominant species in phytoplankton of brackish water part of the Neva Estuary (Kiselev, 1948; Shishkin et al., 1989; Tereshenkova, 2006) (Table 2). Moreover, the dinoflagellate spring blooms of the mid 1990s in the Baltic Sea were dominated by *P. catenata* (Wasmund et al., 2011). This contrasted with the previous decade, when HELCOM (1996) did not report *P. catenata* in the list of the five most important spring species in 1979–1983.

Among other species found in the estuary in 2003–2016, *D. norvegica* is a typical species for the Baltic Sea (HELCOM, 2004). *P. lima* is a marine species found in the Kattegat and the Belt Sea, Arkona Basin, preferring coastal waters in these areas (HELCOM, 2004). In the Neva Estuary *P. lima* had the lowest abundance, although in some years their biomass was significant (Table 1). Its presence in the Neva Estuary was somewhat unexpected, as it has not been previously found in this part of the Baltic Sea. In the Neva Estuary, it occurred in the most marine part in 2005–2006, and its biomass was higher at the stations with higher salinity. After 2006, this species was not found. Perhaps his appearance was associated with an inoculation with ballast water by sea vessels. The fact is, that the sea traffic in this area is quite active; several cargo ports are located along the coast of the estuary. However, the conditions for this species in the estuary are not particularly suitable and after 2006 it disappeared. This dinoflagellate is also interesting because it releases toxins, which are dangerous for humans (Lassus et al., 2016).

Amphydinium spp., *Dinophysis rotundata* (Clapared & Lachmann 1859) and *P. bipes* that rarely occurred in brackish water part of the Neva Estuary in 2003–2016 (Table 1) are marine species found throughout the Baltic Sea (HELCOM, 2004).

3.2. Relationships between environmental factors and dinoflagellate community structure

The NMDS method used in this study provides insights about the abundance and distribution of dinoflagellate taxa,

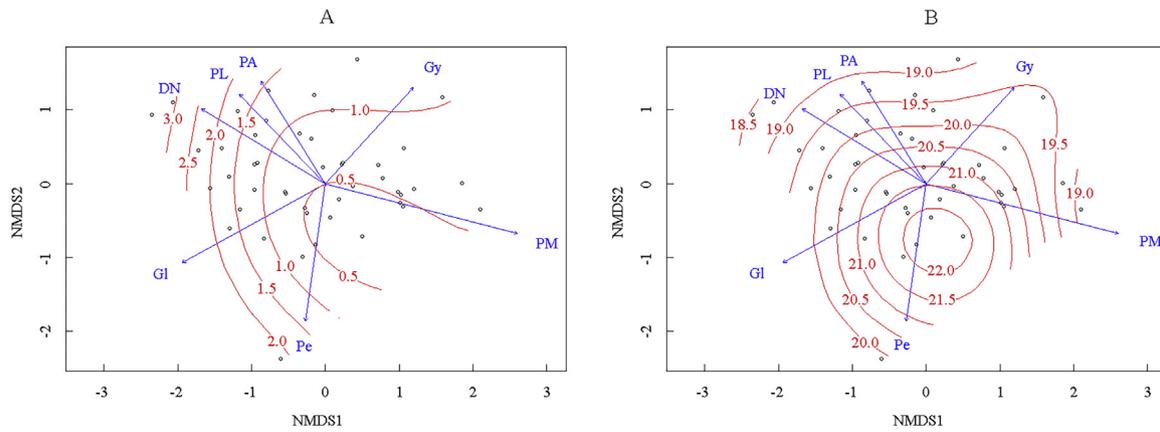


Figure 2 Dinoflagellates biomass vectors based on NMDS result and environmental variables in the Neva Estuary 2003–2016. Plot A: dinoflagellate biomass vectors and salinity (PSU), plot B: dinoflagellate biomass vectors and temperature (°C). DN – *Dinophysis norvegica*, PL – *Prorocentrum lima*, PA – *Peridinium aciculiferum*, PM – *Peridinium cinctum*, Pe – *Peridinium* sp., Gy – *Gymnodinium* sp., Gl – *Glenodinium* sp.

including some potentially toxic and bloom-forming species, along physiochemical gradients in an estuary under chronic anthropogenic nutrient enrichment. It enabled insight what environmental factors best explain dominant species composition and overall dinoflagellate assemblage structure and how they may be related to climate changes. We analyzed the factors influencing the composition of dinoflagellate community in the estuary and revealed species whose biomass significantly ($p < 0.05$) correlates with the studied environmental factors. These were 7 of 13 species that have been repeatedly encountered in the phytoplankton of the estuary and can be regarded as the most significant in the dinoflagellate community (Table 1). Biomasses of the other six species that were found in the estuary in different years did not show significant correlations with the studied factors. In most cases, this was explained by the fact that these were single findings (Table 1) and their number was insufficient for reliable correlations. Among these species, only *C. hirundinella* was found in all parts of the estuary at any studied environmental parameters.

Unidirectional vectors in a multidimensional space, for example, corresponding to the *D. norvegica*, *P. lima* and *P. aciculiferum* in Figs. 2–6, mean that changes in the biomass of these species, as a rule, are related similarly to the changes in some environmental factors. It is known that salinity and temperature are significant parameters influencing dinoflagellate assemblages in many regions (Price et al., 2017; Zonneveld et al., 2013).

In the Neva Estuary, the biomasses of *D. norvegica*, *P. aciculiferum* and *P. lima* were positively related to water salinity. These species showed higher biomasses with increasing water salinity (Fig. 2A). The marine species *D. norvegica* and *P. lima* were mainly found in the lower most marine part of the estuary. In contrast, *P. aciculiferum* was widely distributed throughout the estuary (Table 1), but higher biomass was in more saline waters. The oppositely directed *P. cinctum* vector means that this species reacted in the opposite way to the changes in the same environmental factors. The biomass of freshwater *P. cinctum* was higher in less saline waters (Fig. 2A). The transverse vectors of the *Peridinium* sp.,

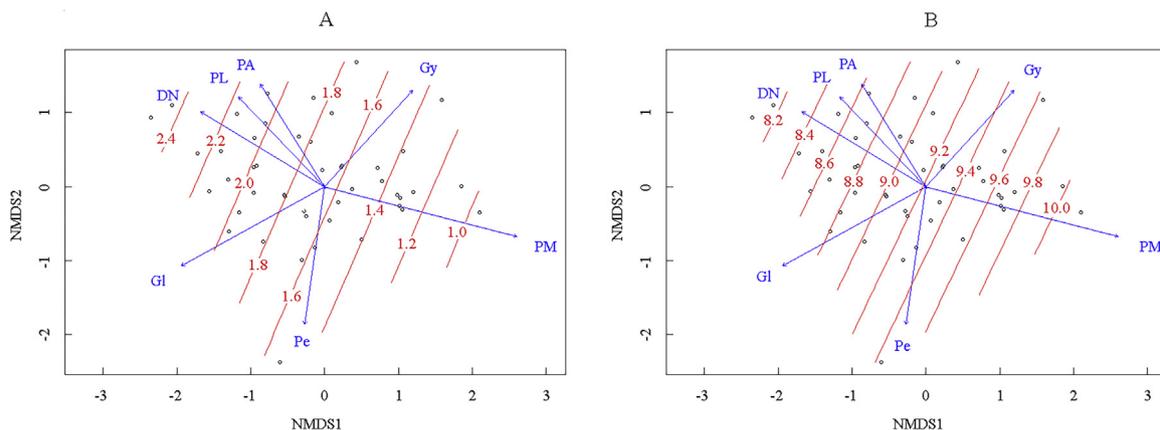


Figure 3 Dinoflagellates biomass vectors based on NMDS result and environmental variables in the Neva Estuary 2003–2016. Plot A: dinoflagellate biomass vectors and water transparency [m], plot B: dinoflagellate biomass vectors and concentrations of SPM [g m^{-3}]. DN – *Dinophysis norvegica*, PL – *Prorocentrum lima*, PA – *Peridinium aciculiferum*, PM – *Peridinium cinctum*, Pe – *Peridinium* sp., Gy – *Gymnodinium* sp., Gl – *Glenodinium* sp.

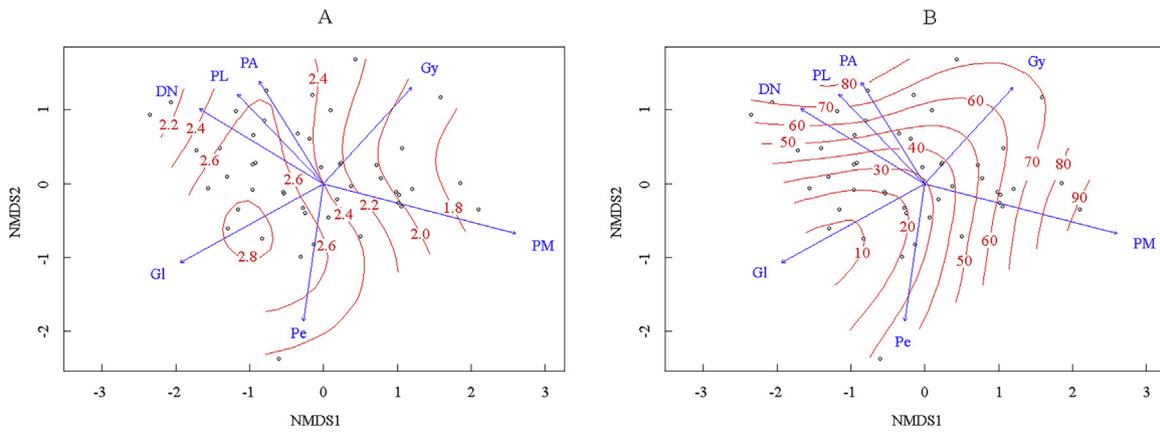


Figure 4 Dinoflagellates biomass vectors based on NMDS result and environmental variables in the Neva Estuary in 2003–2016. Plot A: dinoflagellate biomass vectors and the concentration of particulate organic matter [g m^{-3}], plot B: dinoflagellate biomass vectors and the concentration of total phosphorus [mg m^{-3}]. DN – *Dinophysis norvegica*, PL – *Prorocentrum lima*, PA – *Peridinium aciculiferum*, PM – *Peridinium cinctum*, Pe – *Peridinium* sp., Gy – *Gymnodinium* sp., Gl – *Glenodinium* sp.

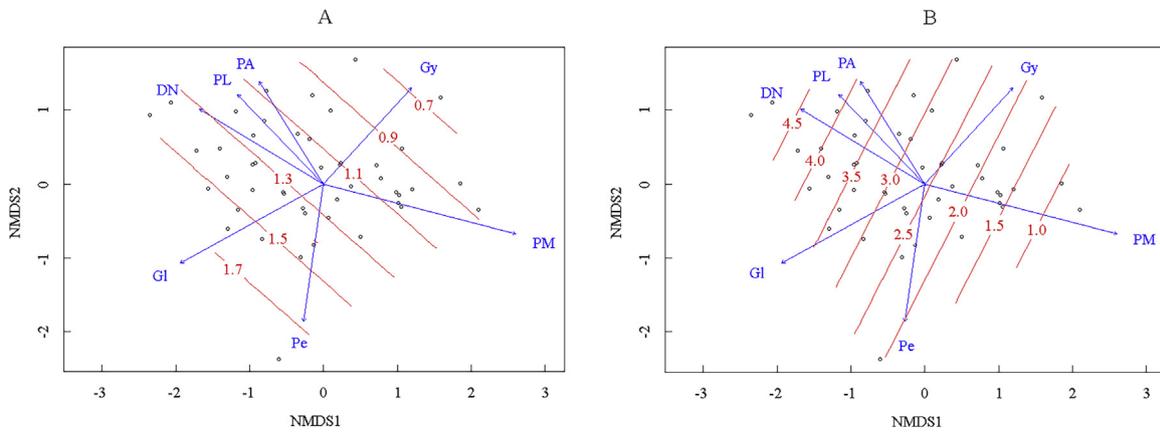


Figure 5 Dinoflagellates biomass vectors based on NMDS result and environmental variables in the Neva Estuary 2003–2016. Plot A: dinoflagellate biomass vectors and the rates of plankton primary production [$\text{gC m}^{-2} \text{day}^{-1}$], plot B: dinoflagellate biomass vectors and the rates of mineralization of organic matter [$\text{gC m}^{-2} \text{day}^{-1}$]. DN – *Dinophysis norvegica*, PL – *Prorocentrum lima*, PA – *Peridinium aciculiferum*, PM – *Peridinium cinctum*, Pe – *Peridinium* sp., Gy – *Gymnodinium* sp., Gl – *Glenodinium* sp.

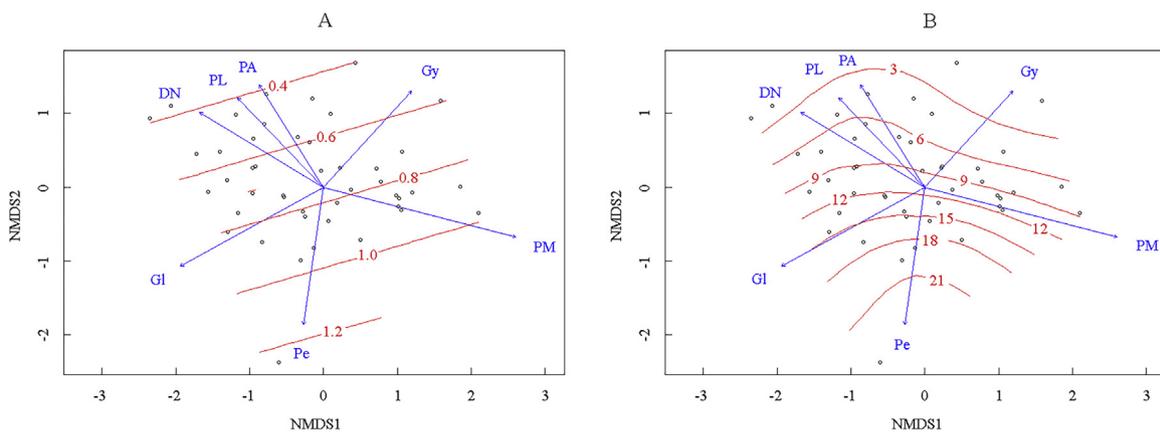


Figure 6 Dinoflagellates biomass vectors based on NMDS result and environmental variables in the Neva Estuary in 2003–2016. Plot A: dinoflagellate biomass vectors and PP/D ratio, plot B: dinoflagellate biomass vectors and chlorophyll a concentration [mg m^{-3}]. DN – *Dinophysis norvegica*, PL – *Prorocentrum lima*, PA – *Peridinium aciculiferum*, PM – *Peridinium cinctum*, Pe – *Peridinium* sp., Gy – *Gymnodinium* sp., Gl – *Glenodinium* sp.

Gymnodinium sp. and *Glenodinium* sp. mean that other, different from the first group, environmental factors significantly influenced their biomass, although these species preferred relatively salt waters. The biomass of these species did not show a significant correlation with water salinity, i.e., salinity was not a significant factor for them.

The temperature also had an effect on dinoflagellates in the Neva Estuary. Most species preferred relatively low temperatures. Only *Peridinium* sp. showed high biomass at the temperatures above 20°C. Biomasses of the other species were higher at lower temperatures (Fig. 2B). Similar result was obtained in the East China Sea, where two obvious peaks of dinoflagellate pigments were recorded at temperatures ~18°C and ~25°C (Xiao et al., 2018). Well-known late spring dinoflagellate blooms (*Gymnodinium* and *Prorocentrum* species) in the East China Sea occurred at the temperatures of ~18°C (Guo et al., 2014). In the Baltic Sea many dinoflagellates prefer low temperatures in summer perhaps due to nutrients coming up to surface by vertical mixing in cold weather and during cold water period. For example, the largest biomass of *D. norvegica* in the Baltic Sea was recorded at the thermocline boundary at about 12°C, as higher temperatures did not contribute to the growth of this species (Carpenter et al., 1995). Another closely related species, *D. rotundata*, also widespread in the Baltic Sea (HELCOM, 2004), was registered in 2003 at four stations in the south-western part of the estuary (Table 1) in the period of intensive upwelling of bottom cold waters in that area.

The negative reaction of most species of dinoflagellate in the Neva Estuary to the increase in summer water temperature may be partly explained by sharp domination in phytoplankton of toxin producing cyanobacteria in the years with high temperature (Nikulina and Gubelit, 2011). This should adversely affect other species of phytoplankton, including dinoflagellates (Carpenter et al., 1995; Codd and Poon, 1988; Sivonen et al., 1989). In recent years, a trend to lower water temperatures in summer was observed in St. Petersburg region caused by the predominance of cloudy and rainy weather (Golubkov and Golubkov, 2018) that might contribute to the development of dinoflagellate species.

Transparency of the water was important for photosynthetic dinoflagellates. The biomass of *P. cinctum* was higher in the waters with low transparency and high concentration of SPM (Fig. 3). The biomasses of *D. norvegica*, *P. aciculiferum* and *P. lima* were significantly higher in relatively transparent waters with low concentration of SPM. Water transparency and SPM concentrations did not have a significant effect on the biomasses of *Gymnodinium* sp., *Glenodinium* sp. and *Peridinium* sp. (Fig. 3).

The biomass of most species was lower at relatively high concentrations of SOM (Fig. 4A). High concentration of SOM especially negatively affected the biomass of *P. cinctum*. Only biomass of *Glenodinium* sp. was higher in the waters with high SOM concentration. The biomass of *Gymnodinium* sp. has not shown relationships with this environmental parameter (Fig. 4A). The reaction of various dinoflagellates to water transparency and the amounts of SPM and SOM was completely different. This is possibly explained by the ability of dinoflagellates to mixotrophic feeding. Practically all phototrophic dinoflagellates are suggested to be mixotrophic (Jeong et al., 2008). The mixotrophic and heterotrophic dinoflagellates are able to feed on diverse prey

items including bacteria, picoeukaryotes, nanoflagellates, diatoms, other dinoflagellates, heterotrophic protists, metazoans and probably organic particles due to their diverse feeding mechanisms (Burkholder et al., 2008; Hansen, 2011; Jeong et al., 2010). For instance, mixotrophy appears to be quite common among species of *Dinophysis*, *Prorocentrum* (Hansen, 2011; Jeong et al., 2010). Food uptake of some *Dinophysis* species may provide them with ~80% of their carbon needs at high prey concentrations (Riisgaard and Hansen, 2009).

The total phosphorus concentration positively influenced most dinoflagellate species in the Neva Estuary. The biomass of *D. norvegica*, *P. lima*, *P. aciculiferum*, *P. cinctum* and *Gymnodinium* sp. was higher in the waters with higher concentration of total phosphorus (Fig. 4B). This suggests that autotrophy was also important trophic mode for these species. For instance, there was a definite *Prorocentrum* cyst eutrophication signal in some estuaries of the North-Western Atlantic, thus confirming their value as indicators of water quality change and anthropogenic impact (Price et al., 2017). A negative relationship was observed only for *Glenodinium* sp. *Peridinium* sp. did not show any correlation with total phosphorus concentration (Fig. 4B).

The biomass of dinoflagellates was also related to the rate of plankton primary production. The biomass of *Glenodinium* sp. and *Peridinium* sp. were higher in the waters with high primary production, whereas *Gymnodinium* sp. was more abundant in the waters with lower primary production (Fig. 5A). Biomass of *D. norvegica*, *P. lima* and *P. aciculiferum* did not show relationships with primary production. At the same time, these species had a larger biomass in the waters with high rate of organic matter mineralization (Fig. 5B). This probably indicated that bacteria played an important role in the feeding of these species. Although the dinoflagellates may have difficulty in detecting and capturing tiny bacterium cells, some species fed on a single bacterium cell like filter/interception feeders; they generate feeding currents using the flagella (Jeong et al., 2008).

The ratio of primary production and mineralization of organic matter shows which processes prevail. The PP/D ratio above one indicates eutrophication of water area. The biomass of *Peridinium* sp. was significantly higher in the waters with high PP/D (Fig. 6A). On the contrary, the biomasses of *D. norvegica*, *P. aciculiferum* and *P. lima* were higher with the predominance of mineralization processes over primary production. Biomass of *Gymnodinium* sp., *Glenodinium* sp. showed no relation with this parameter.

A similar pattern was demonstrated by the relationship between the biomass of dinoflagellates and the concentration of chlorophyll *a*. The biomass of *Peridinium* sp. was higher in the waters with high chlorophyll *a* concentration, whereas the biomasses of *D. norvegica*, *P. aciculiferum* and *P. lima* were higher at the stations with lower concentrations of the pigment (Fig. 6B). Unlike SOM concentration (Fig. 4B), this parameter did not affect the biomasses of *P. cinctum* and *Glenodinium* sp. Consequently, their biomasses were influenced by the concentration of SOM, which was not related to algae.

Biomass of *Glenodinium* sp. and *Peridinium* sp. positively correlated with primary production, and biomass of *Peridinium* sp. also positively reacted to an increase in the concentration of chlorophyll *a* and the PP/D ratio

(Figs. 5A and 6). However, these species did not show a positive relationship with phosphorus (Fig. 4B). This may be due to the fact that *Glenodinium* sp. and *Peridinium* sp. in the conditions of the Neva Estuary, apparently, are more consumers than producers of organic matter, feeding on algae and cyanobacteria of phytoplankton. Therefore, they responded positively to the increase in biomass and productivity of other phytoplankton species.

The proliferation of dinoflagellate could be due to an increase in runoff of organic substances from the catchment area induced by climate change. Model simulations predict that the climate change in the Baltic Sea region will result in a strong increase in precipitation and river discharge which, in turn, will lead to an increase in nutrient load and runoff of particulate and dissolved organic matter from the catchment area (Friedland et al., 2012; Meier et al., 2012). In this case, the changing conditions will contribute to the development of species that react positively to the increase in suspended and dissolved organic matter and associated bacteria, as well as an increase in nutrient load.

4. Conclusions

Twenty one dinoflagellate species were noted in the plankton of the Russian part of the Gulf of Finland at different times since the mid-19th century. Thirteen distinct species were observed in the present investigation and nine of them could be identified to species level. The statistical analysis showed that different species of dinoflagellates differ in relation to changes in environmental factors. Biomasses of *D. norvegica*, *P. lima* and *P. aciculiferum* had very similar relationships with investigated environmental variables that included salinity, temperature, phosphorus and suspended particulate organic matter concentrations. The biomasses of the other common species, *P. cinctum* and *Peridinium* sp., showed quite opposite trends. Current climate fluctuations leading to changes in temperature, salinity, nutrient and organic matter runoff from the catchment area could significantly affect the composition and productivity of the dinoflagellate community. At the same time, when interpreting the results of the analysis, it should be taken into account that the species of this group is characterized by mixotrophy and, consequently, their biomass may depend not only on the conditions of autotrophic, but also heterotrophic nutrition.

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