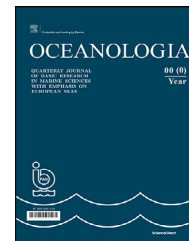




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ORIGINAL RESEARCH ARTICLE

Species-level associations of phytoplankton with environmental variability in the Neva Estuary (Baltic Sea)

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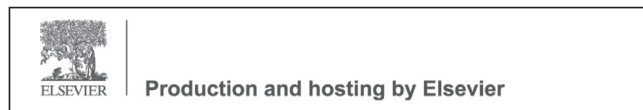
Gulf of Finland;
Species composition;
Eutrophication;
Harmful algae;
Long-term
observations;
Climate change

Abstract Changes in phytoplankton communities due to anthropogenic nutrient load and climate change often lead to eutrophication and harmful algal blooms that can affect biogeochemical cycling. However, little is known about the specific responses of various species to environmental variables. 17-year long data on the midsummer phytoplankton biomass in the Neva Estuary were analyzed to show the changes in the composition of phytoplankton in relation to water depth, transparency, salinity, temperature, concentrations of total phosphorus and chlorophyll *a*, and plankton primary production. One hundred seventy-four species and forms from eight taxonomic classes were found in phytoplankton. Fifteen species were potentially harmful. The most diverse and abundant groups were cyanobacteria, green algae and diatoms. Canonical Correspondence Analysis showed that the biomass of various species from each phytoplankton group correlated differently with environmental factors. However, within each group, there were some predominant trends in the correlative response to changes in environmental variables. The biomass of cyanobacteria was high in the middle and lower reaches of the estuary and, in general, positively correlated with water salinity. The biomass of most species of green algae and diatoms correlated negatively with it. These algae showed a positive trend in biomass in the upper and middle reaches of the estuary during the last decades that may be

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explained by changes in weather conditions. Taking into account that climate models predict future increases in precipitation and temperature in the northern Baltic, the future expansion of freshwater phytoplankton species in estuaries of the northern Baltic Sea is very likely.

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1. Introduction

Eutrophication and harmful algal blooms have been recognized as one of the major environmental problems of coastal areas around the world (Damar et al., 2020; Heisler et al., 2008; Holt et al., 2016; Kahru et al., 2020). This problem has been especially acute in recent years due to anthropogenic nutrient load and climate change, which may exacerbate the negative consequences of human activities (Behrenfeld et al., 2006; Doney et al., 2012; Golubkov and Alimov, 2010; Golubkov and Golubkov, 2020; Teutschbein et al., 2017). Improving our understanding of the factors that determine the development of algae in general and toxic species in particular requires determination and quantification of the physico-chemical environmental factors that create conditions for the accelerated growth and dominance of various groups and species of algae in the phytoplankton community (Stauffer et al., 2020). Such studies are important for understanding the patterns of formation of species diversity in plankton communities (Huisman and Weissing, 1999), for forecasting the direction of biogeochemical cycles and fish productivity (Boyce et al., 2010; Golubkov et al., 2020), and for predicting possible negative phenomena for humans, both on a regional and global scale (Dzierzbicka-Głowacka et al., 2011).

The Baltic Sea is highly susceptible to eutrophication caused by the influx of nutrients from densely populated and intensively cultivated catchment areas (Wasmund et al., 2011). The Neva Estuary, situated at the top of the Gulf of Finland, is one of the most eutrophic areas of the Baltic Sea (Golubkov and Alimov, 2010). The primary productivity and biomasses of autotrophic organisms in the estuary are high, mainly due to eutrophic effects of the large nutrient inflow from the Neva River, which is the major contributor of freshwater to the Baltic Sea (Golubkov, 2009; Golubkov et al., 2017). The Neva Estuary is characterized by a number of features that make it a convenient site for studying the relationships between physico-chemical factors and species composition and productivity of phytoplankton, which is important not only regionally, but also globally. It is a brackish-water, non-tidal and shallow water area, with vertical and horizontal gradients of salinity and temperature, concentrations of nutrients, and indicators of phytoplankton productivity. Plankton communities of the estuary include freshwater and marine species; eurytopic species also make up a significant proportion (Telesh et al., 2008).

Long-term data on seasonal dynamics of phytoplankton in the middle reach of the Neva Estuary show that since the late 1990s – early 2000s mean seasonal biomass of phytoplankton increased approximately twofold as compared with the 1980s (Nikulina, 2003). In addition, a significant increase in plankton primary production was observed in

the 2010s (Golubkov et al., 2017), and apparently this was due not only to the anthropogenic nutrient load, but also to changes in weather conditions in recent years because of the global warming, which manifests regionally in warm winters and cool rainy summer seasons (Golubkov and Golubkov, 2020).

Most regional climate models predict future increases in winter and summer air temperatures and precipitation in the northern Baltic regions (Meier et al., 2012; Teutschbein et al., 2017). Changes in weather conditions affect water temperatures and salinity, nutrient concentrations and plankton primary production (Friedland et al., 2012; Golubkov and Golubkov, 2020; Holt et al., 2016; Myakisheva, 1996). As a result, in addition to an increase in phytoplankton productivity, this leads to a change in the dominant groups in the phytoplankton community in various regions of the Baltic Sea (Jaanus et al., 2011; Klais et al., 2011; Nikulina, 2003; Wasmund et al., 2011), which affects biogeochemical cycling (Golubkov et al., 2020; Neumann and Schernewski, 2008; Spilling et al., 2018). In the Neva Estuary, diatoms (Bacillariophyceae) were the dominant group of phytoplankton until the late 1990s (Nikulina, 2003). Cyanobacteria were an important group only in late July and August. However, since the early 2000s, cyanobacteria biomass and the period of their predominance in plankton have increased significantly, which was accompanied by an increase in the total biomass of phytoplankton, as well as in its primary production and chlorophyll concentration (Golubkov et al., 2017; Nikulina, 2003). Later in the 2010s, the biomass of dinoflagellates also increased (Golubkov et al., 2019a). The same changes in the dominance of dinoflagellates and diatoms were observed in the Baltic Proper in the late 1980s and could be attributed to warming rather than to eutrophication (Wasmund, 2017). This leads to a regime shift because differences in the sinking of these two classes of phytoplankton affect ecosystem functioning and eutrophication feedback loops (Spilling et al., 2018; Wasmund et al., 2017). If diatoms are dominant, their rapid sinking reduces the food stock for zooplankton but delivers plenty of food to the zoobenthos. On the contrary, dinoflagellates sink slowly, mainly providing organic matter to pelagic consumers. To assess the environmental status of the Baltic Sea a pre-core indicator diatom/dinoflagellate index (Dia/Dino index) was developed (Wasmund et al., 2017).

The purpose of this study was to find statistical relationships between physical and chemical factors of the environment and indicators of phytoplankton productivity and biomass of various groups and species of phytoplankton in the Neva Estuary. Although statistical relationships do not reflect causality, they provide clues for finding the environmental conditions that regulate the development of

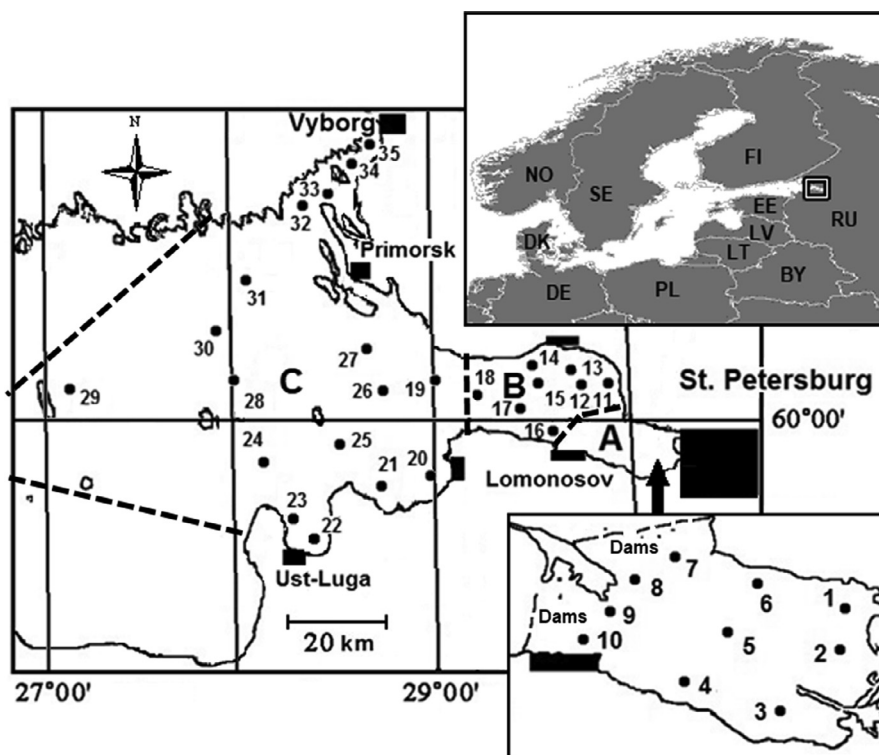


Figure 1 The Neva Estuary with an indication of sampling stations (A – the upper reach; B – the middle reach; C – the lower reach). The dotted line shows the boundaries between reaches. Two-letter country codes are given according to ISO 3166-1 alpha-2 (International Organization for Standardization (ISO) 2020).

algae and the dominance of certain groups and species in the phytoplankton community. This can help simulate conditions to predict the likelihood of abundant algal blooms in the future and forecast which groups of phytoplankton will dominate non-toxic green and diatoms, or potentially toxic cyanobacteria and dinoflagellates.

2. Material and methods

2.1. Study area

The Neva Estuary receives water from the Neva River, a relatively short canal (74 km) between Lake Ladoga and the Gulf of Finland, whose catchment area exceeds 280,000 km², and the water discharge averages 2,490 m³ s⁻¹ (78.6 km³ yr⁻¹), which is about a fifth of the total river discharge into the Baltic Sea.

Flood Protective Facility (Dams) separated the upper reach of the estuary from its lower reaches (Figure 1). It consists of eleven dams separated by broad water passages and ship gates in its southern and northern parts. The surface area of the upper reach (UR), is about 400 km², the salinity – 0.07–0.2 PSU. The depth of the UR is 1.6–5 m, the water residence time is 5.5 days. There is no temperature stratification in this reach of the estuary. High water turbidity (Secchi depth does not exceed 1.8 m) constrains the distribution of bottom vegetation in the UR. The middle reach (MR) of the Neva Estuary is brackish-water and located between Dams and a longitude of ca. 29°10'E (Figure 1). The salinity of surface waters in this part of the

estuary ranges from 0.5 to 3 PSU, and the depth – from 7 to 14 m in the eastern MR and up to 25 m in its western part. The water residence time is approximately 45 days. There is temperature stratification in the western part of the MR in summer: a warm water upper layer (UL) and a cold water deep layer (DL). The lower reach (LR) of the Neva Estuary located to the west of the ca. 29°10'E and to the east of the border of territorial waters of Russia (Figure 1). It has a depth up to 60 m, temperature stratification in summer and the salinity of UL up to 5.5 PSU. The water residence time is about 1500 days. The Neva Estuary is the recipient of discharges of treated and untreated wastewaters from St. Petersburg City, which is the largest megalopolis in the Baltic region with a population of more than 5 million citizens (Golubkov et al., 2019). A more detailed description of the estuary was given in previous publications (Golubkov et al., 2017; Golubkov and Golubkov, 2020; Telesh et al., 2008).

2.2. Sampling

Ten stations in the UR, eight stations in the MR and seventeen stations in the LR were sampled from 20th of July – to 5th of August 2003–2019. The number of stations varied in different years (Supplementary Table 1). Secchi depth (Sec), salinity (S) and temperature (T) were measured at each station. T and S were measured by the CTD90m 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 UR 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 phytoplankton species in the water column. These samples were composited and mixed to make up a pooled sample (10 l). Samples of total phosphorus and chlorophyll *a* (three replicates of water collection) were taken from these pooled samples.

In the LR of the estuary (Figure 1), integrated water samples were taken from the UL. Five water samples (2 l each) were taken from the UL: from the surface, the thermocline and from three equal depths between them. These samples were mixed to create a pooled sample (10 l). The samples for chlorophyll *a* and total phosphorus (three replicates of water collection) were taken from these pooled samples.

2.3. Sample analysis

Three hundred millilitres of water were filtered through 0.85 μm membrane filters (Millipore AAWP) to determine the chlorophyll *a* (C) concentration, which was followed by 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).

The primary production of plankton (PP) in the water column were measured by the oxygen method of light and dark bottles (Hall et al., 2007; Vernet and Smith, 2007). Since the depth of the UL practically coincided with the depth of euphotic zone in mid-summer 900 ml of water from the UL pooled samples from the MR, the LR and from the whole water column in the UR were used to determine PP. Three 100 ml light and three dark bottles were filled with the water from each sampling station and exposed in an aquarium on the ship's deck in shadow during 6 h at a surface water temperature to estimate PP. Three 100 ml bottles (control bottles) were filled with the water from each sampling station to determine the oxygen contents in water at the beginning of the experiment. The Winkler method was used to determine the oxygen contents in the control, the light and the dark bottles (Hall et al. 2007). The gross primary production under 1 m^2 of water surface was calculated according to Vollenweider (1969). The rate of plankton production was recalculated to organic carbon as recommended by Wetzel and Likens (2000) using a factor 0.43 mgC mlO^{-1} (Håkanson and Boulion, 2002). A more detailed description of the method and experimental design is given in Golubkov et al. (2017).

2.4. Phytoplankton assemblages

Phytoplankton (volume 0.3 l) was taken in one replicate of water collection from pooled samples and fixed with acid Lugol's solution. The phytoplankton taxa were identified and counted in sedimentation chambers (10–25 ml) with an inverted Hydro-Bios microscope. Phytoplankton biomass was calculated in the total volume of algal cells according to Olenina et al. (2006) and expressed in wet weight (WW) mg l^{-1} . Identification of phytoplankton 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 (2020).

2.5. Statistical analysis

The biomass for each of taxonomic classes was averaged for each station and was visualized using SURFER 8.0. Annual trends were estimated by averaging the biomass of each taxonomic class and were visualized using Microsoft Excell.

Canonical Correspondence Analysis (CCA) was used to assess the effect of environmental variables on phytoplankton groups and species in the Neva Estuary. S, T, Sec, TP, C and PP were used as environmental data sources. CCA was performed using R software (version 3.6.0; R Development Core Team, 2020; www.r-project.org/), R package 'vegan' (Oksanen et al., 2020) and visualised by R package 'ggplot2' (Wickham et al., 2020). We used only species that were found at least five times over the entire period of observation. The biomass of various species from the phytoplankton community was used as a biological data source. Prior to the CCA, each environmental variable was tested using the variance inflation factor (VIF). Function 'vif.cca' was used to give the variance inflation factors for each constraint and contrast in the constraints of the environmental variables. Variance inflation was a diagnostic tool to identify useless constraints. A common rule is that values over 10 indicate redundant constraints. If later constraints were complete linear combinations of conditions or previous constraints, they were completely removed from the estimation, and no biplot scores were calculated for these aliased constraints. A constrained model based on the length of the gradient calculated by CCA was built by function 'vare.cca'. It is based on Chi-squared distances and performs weighted linear mapping. Monte Carlo replacement tests (999 permutations) were carried out to determine the environmental factors that significantly explained the spatial distribution characteristics of the phytoplankton communities. R package 'ggplot2' was used to build CCA biplots. For better understanding the results of CCA we provided ordination diagram separately for eight taxonomical classes of algae.

In a CCA biplot, the arrows for environmental variables point in the general direction of maximum environmental change across the diagram with statistical significance ($p < 0.05$), and their lengths are approximately proportional to the rate of change in that direction. The correlation between biomasses of phytoplankton and environmental factors was examined based on the angle between arrows; an angle smaller than 90° indicates a positive correlation between the variables; the smaller the angle, the closer the positive correlation of the two variables. An angle between 90° and 180° suggests a negative correlation. Finally, there is no correlation between two variables when their angle is 90° . The projection of phytoplankton species biomass on the environmental variable vector is an approximation of the "optima" regarding that particular variable (ter Braak and Verdonschot, 1995).

3. Results

3.1. Environmental parameters

The environmental variables in the Neva Estuary during the study period are shown in Table 1. The shallowest sampling station 3 with a depth of 1.6 m was located in

Table 1 Environmental variables in the Neva Estuary during the study period.

Parameter	minimum	maximum	median	mean	SD
Water depth [m]	1.6	61.0	12.7	23.5	11.5
Depth of water layer above thermocline [m]	1.6	21.5	7.5	9.3	3.5
Salinity of water layer above thermocline [PSU]	0.05	5.55	1.80	2.73	1.04
Temperature of water layer above thermocline [°C]	16.2	26.2	19.8	20.0	2.12
Secchi depth [m]	0.3	4.3	1.6	2.0	0.7
Total phosphorus concentration in water layer above the thermocline [mg m ⁻³]	5.4	230.3	37.4	50.6	39.1
Chlorophyll <i>a</i> [mg m ⁻³]	0.88	127.65	14.5	17.50	17.25
Plankton primary production [gC m ⁻² d ⁻¹]	0.05	4.14	1.06	1.21	0.78

the upper reach of the estuary, and the deepest station 29 with a depth of 61 m was in the lower reach of the estuary (Table 1). The mean depth of UL was 9.3 m, but maximum depth was 21.5 m. The water temperature of UL varied within 10 degrees, from 16 to 26°C, averaging 20°C. The salinity of the water in this layer reached 5.5 PSU, averaging 2.7 PSU. Secchi depth varied from 0.2 m in the eastern part to more than 4 meters in the westernmost part of the estuary, with an average of 2 meters. The concentration of phosphorus averaged 50 mg m⁻³, the maximum TP (230 mg m⁻³) was at station 6 in 2017. The concentration of chlorophyll *a* varied from 0.8 to 127 mg m⁻³, and the primary production of plankton varied from 0.05 to 4.14 gC m⁻² d⁻¹ (Table 1). A detailed description of spatial and temporal pattern of environmental variables is given in Golubkov et al. (2017) and Golubkov and Golubkov (2020).

3.2. Phytoplankton assemblages: composition, trends and correlations with environmental variables

A total of 174 species and forms identified to genus from eight taxonomic classes were found in summer phytoplankton during the study period (Supplementary Table 2). The largest number of species (64) belonged to Chlorophyceae (Table 2), which accounted for 37% of the total species richness of phytoplankton. However, the biomass of green algae has been distributed across numerous species. It included many rare species (approximately 55%) that were found no more than 4 times at all stations during the study period. The most common species with the highest biomass in this class were *Monorahidium contortum* ((Thuret) Komárková-Legnerová 1969), *Mougeotia* sp. and *Mucidosphaerium pulchellum* ((H.C.Wood) C.Bock, Proschold & Krienitz 2011), which were observed 173, 119 and 81 times, respectively (Table 2). Green algae ranked second in the total phytoplankton biomass in the estuary. The highest biomasses were observed in its upper reach (Figure 2).

Cyanobacteria ranked second in species richness, but first in phytoplankton biomass (Table 2). Their biomass was particularly high in the middle and lower reaches of the estuary (Figure 2). The most common species with the highest biomass were *Dolichospermum flos-aquae* ((Brébisson ex Bornet & Flahault) P.Wacklin, L.Hoffmann & J.Komárek 2009), *Aphanizomenon flos-aquae* (Ralfs ex Bornet & Flahault 1886), *Limnothrix planctonica* ((Woloszynska) Meffert

1988) and *Planktothrix agardhii* ((Gomont) Anagnostidis & Komárek 1988) (Table 2).

Diatoms ranked third in species richness and biomass of phytoplankton (Table 2, Figure 2). As in green algae, their biomass was higher in the upper and middle reaches of the estuary (Figure 2). The most common species from this class were *Aulacoseira islandica* ((O.Müller) Simonsen 1979), *Skeletonema subsalsum* ((Cleve-Euler) Bethge 1928), *Tabellaria fenestrata* ((Lyngbye) Kützing 1844), *Skeletonema costatum* ((Greville) Cleve 1873) and *Pantocsekiella kuetzingiana* ((Thwaites) K.T.Kiss and E.Ács 2016) had the highest biomasses among these algae (Table 2).

These above-mentioned three classes together accounted for 76% of the total species richness and 74% of the total biomass of phytoplankton. Therefore, they can be considered dominant in the midsummer phytoplankton community in the Neva Estuary. The remaining five phytoplankton groups were not abundant, and their proportion in the total biomass was usually small. However, some species from these groups had a high biomass and frequency of occurrence. Chrysophyceae and Dinophyceae species accounted for 7% of the total species richness of phytoplankton (Table 2). The proportion of Dinophyceae in the total biomass of phytoplankton was about 5%, and the proportion of Chrysophyceae – only about 2%. Species from the Cryptophyceae and Euglenophyceae groups accounted for 4% each of the total species richness of phytoplankton (Table 2). However, despite the small number of species (Table 2), Cryptophyceae species accounted for 13% of the total phytoplankton biomass. Their biomass was rather high in the upper and middle reaches of the estuary (Figure 2). *Komma caudate* ((L.Geitler) D.R.A.Hill 1991) dominated this group. It occurred 174 times and was the most common species in the phytoplankton in the Neva Estuary (Table 2). Other abundant species of this group, *Cryptomonas erosa* (Ehrenberg 1832) and *Cryptomonas marssonii* (Skuja 1948), were also encountered often: 136 and 81 times, respectively (Table 2). Euglenophyceae comprised a much smaller fraction, only 2%, in the total biomass of phytoplankton. *Trachelomonas volvocina* ((Ehrenberg) Ehrenberg 1834) was most common in this group, and dominated in its biomass (Table 2). Xantophyceae had the least importance in the total species richness and biomass of the summer phytoplankton of the estuary. This group included only one species, *Tribonema affine* ((Kützing) G.S.West 1904), which was not common and had the highest biomass in the UR of the estuary (Table 2, Figure 2). In general, except

Table 2 The number of species, and the most common and dominant species in the biomass of phytoplankton in the Neva Estuary in 2003–2019.

Groups of phytoplankton	Number of species	Most common species (the number of occurrence)	Species predominant in biomass (min–average–median–max biomass per water area [WW g m ⁻³])
Cyanophyceae	37	<i>Dolichospermum flos-aquae</i> (128)	<i>Microcystis wesenbergii</i> (46.8–1335–230.2–11519)
		<i>Aphanizomenon flos-aquae</i> (117)	<i>Dolichospermum scheremetieviae</i> (70.1–902.9–410–3526)
		<i>Limnithrix planctonica</i> (111)	<i>Planktothrix agardhii</i> (0.7–784.2–237.0–8800)
Chlorophyceae	64	<i>Monorahidium contortum</i> (173)	<i>Mucidosphaerium pulchellum</i> (1.2–317.3–57.6–7833)
		<i>Mougeotia</i> sp. (119)	<i>Chlamidomonas</i> sp. (2.1–283.2–184.7–1319)
		<i>Mucidosphaerium pulchellum</i> (81)	<i>Sphaerocystis planctonica</i> (2.4–224.7–61.7–1393)
Bacillariophyceae	31	<i>Aulacoseira islandica</i> (112)	<i>Skeletonema costatum</i> (7.5–1465–146.4–6405)
		<i>Skeletonema subsalsum</i> (96)	<i>Pantocsekiella kuetzingiana</i> (0.8–546.4–67.2–16127)
		<i>Tabellaria fenestrata</i> (90)	<i>Lindavia glomerata</i> (0.5–313.6–145.1–3315.7)
Cryptophyceae	8	<i>Komma caudata</i> (174)	<i>Cryptomonas erosa</i> (0.5–498.8–180.8–4384)
		<i>Cryptomonas erosa</i> (136)	<i>Cryptomonas ovata</i> (1.3–426.9–126.2–7056)
		<i>Cryptomonas marssonii</i> (81)	<i>Cryptomonas marssonii</i> (1.0–410.6–213.1–2491)
Dinophyceae	13	<i>Apocalathium aciculiferum</i> (62)	<i>Peridinium cinctum</i> (18.7–610.9–304.8–2664)
		<i>Ceratium hirundinella</i> (56)	<i>Gymnodinium</i> sp. (5.2–352.6–47.6–2304)
		<i>Glenodinium</i> sp. (48)	<i>Ceratium hirundinella</i> (8.8–311.5–168.0–3200)
Euglenophyceae	7	<i>Trachelomonas volvocina</i> (46)	<i>Trachelomonas</i> sp. (16.5–395.8–139.4–2356)
		<i>Lepocinclis acus</i> (17)	<i>Trachelomonas volvocina</i> (4.0–293.4–198.3–2059.2)
Chrysophyceae	13	<i>Trachelomonas</i> sp. (11)	<i>Lepocinclis acus</i> (3.7–103.9–15.8–825)
		<i>Dinobryon divergens</i> (62)	<i>Uroglena</i> sp. (18.0–662.7–85.5–1749)
		<i>Mallomonas charkoviensis</i> (15)	<i>Dinobryon divergens</i> (1.2–111.1–38.6–1680)
Xanthophyceae	1	<i>Uroglena</i> sp. (13)	<i>Synura uvella</i> (2.1–113.2–64.3–514.6)
		<i>Tribonema affine</i> (32)	<i>Tribonema affine</i> (14.8)

Cyanobacteria, which had the highest biomass in the middle and low reaches of the Neva Estuary, other groups of phytoplankton had the highest biomass in its upper parts (Figure 2).

The biomasses of Chlorophyceae, Bacillariophyceae, Cryptophyceae and Dinophyceae showed statistically significant linear trends in the estuary in 2003–2019 (Figure 3B, C, D, E). Cyanophyceae did not show any trend at the same time (Figure 3A).

The CCA showed that the three dominant phytoplankton groups correlated differently with environmental factors. The eigenvalues of the first and second axes were 0.384 and 0.265 (Table 3). The correlations between the species biomass and the values of the environmental variables were high (0.897 and 0.859, respectively for the first and second axes). The first two axes explained 38% of species-environmental relation. Furthermore, the all axes explained 24% of the total species variance. Finally, the results of the Monte-Carlo permutation test (using the 999

permutations) showed that the analysis was statistically significant (Table 3).

The biomass of various species from each phytoplankton group correlated differently with environmental factors. However, within each group, there were some predominant trends in the correlative response to changes in environmental variables. As can be seen from the CCA biplots (Figure 4), species of diatoms and green algae are grouped in one part of the diagrams, and most of the cyanobacteria species are compactly grouped in the opposite part, separately from most species from the first two dominant phytoplankton classes. This means that the biomass of cyanobacteria was positively correlated with other one environmental factors than the biomasses of green algae and diatoms.

The biomass of most species of cyanobacteria, including dominant species, was positively correlated with salinity, depth and Secchi depth (Figure 4A). Only two species, *Coelosphaerium kuetzingianum* (Nägeli 1849) and *Oscillatoria* sp. negatively correlated with these environmental

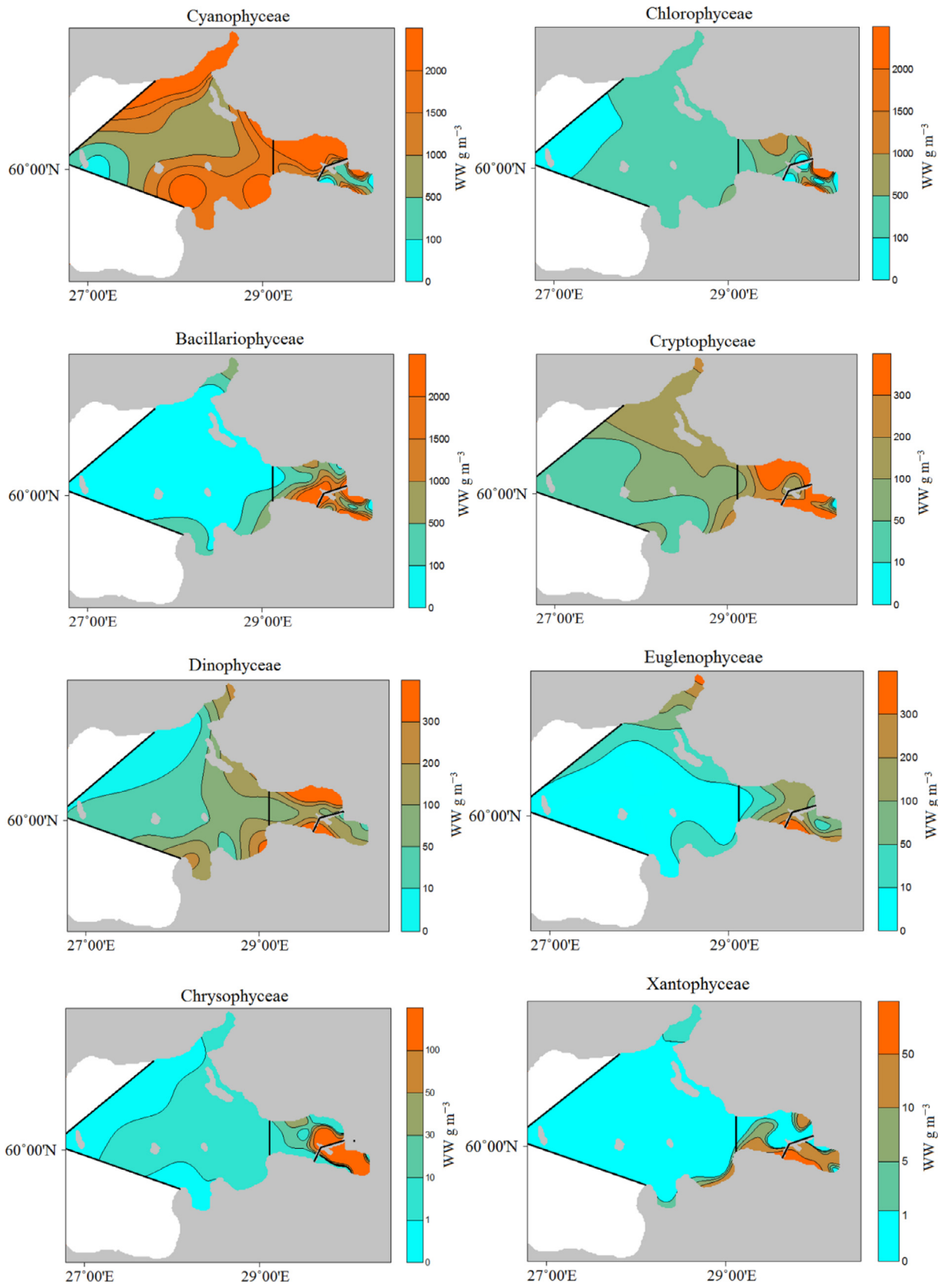


Figure 2 Distribution of the mean values of the biomass of phytoplankton taxonomic classes in the Neva Estuary in midsummer 2003–2019. The black line shows the boundaries between reaches.

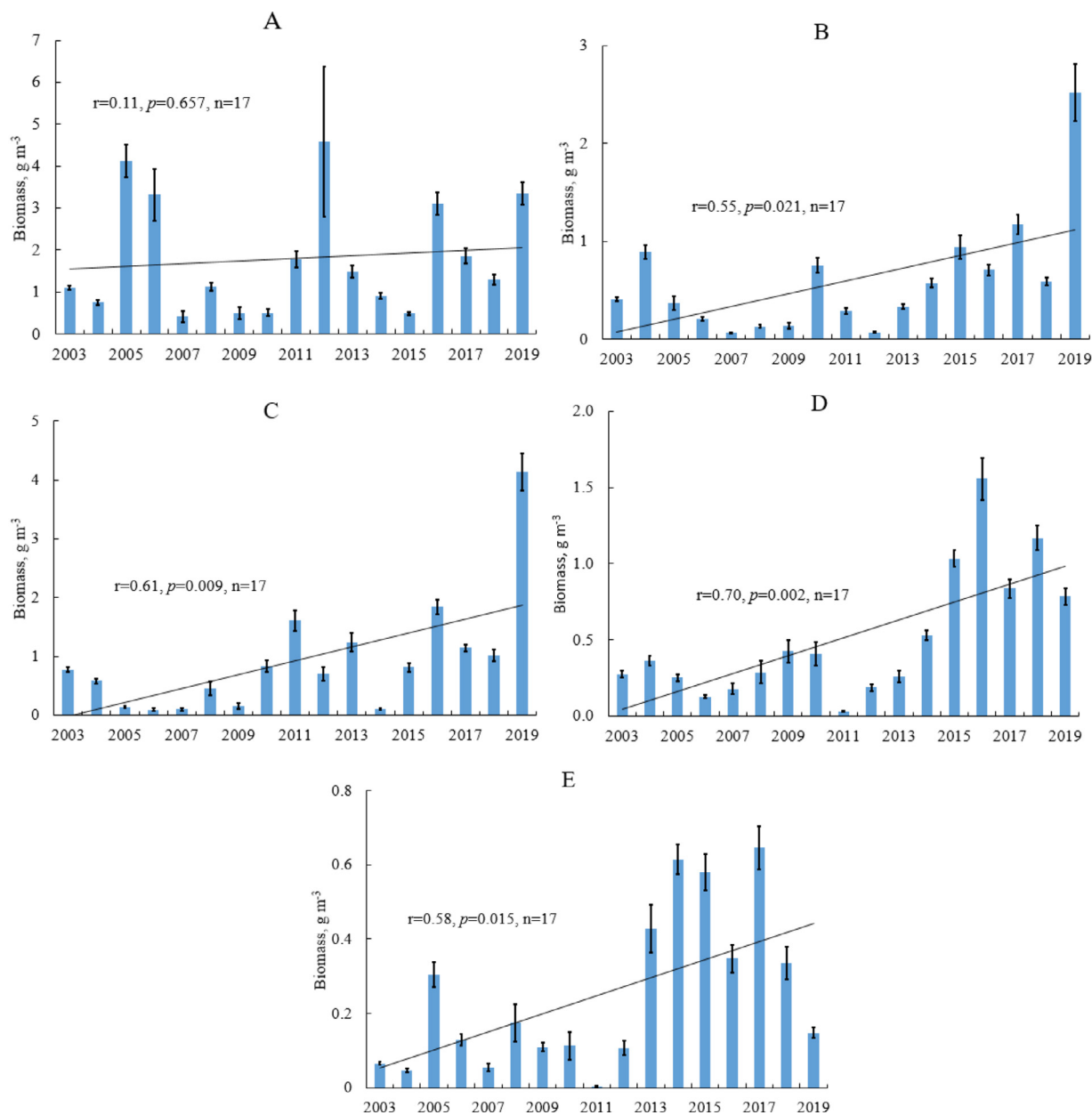


Figure 3 Mean biomass of Cyanophyceae (A), Chlorophyceae (B), Bacillariophyceae (C), Cryptophyceae (D), Dinophyceae (E) in the Neva Estuary in midsummer 2003–2019.

Table 3 Results of Canonical Correspondence Analysis.

Axes	1	2	3	4	Total
Eigenvalues	0.38	0.35	0.31	0.24	7.10
Canonical eigenvalues	0.38	0.26	0.19	0.15	1.70
F-ratio	9.41	6.48	2.61	2.47	
p-value	<0.001	<0.001	<0.001	0.019	
Species-environment correlations	0.90	0.86	0.77	0.70	
Cumulative % of explained variance of species data	5.4	9.1	11.8	13.9	24.0
Cumulative % of explained of species-environment relation	22.5	38.0	49.1	57.9	

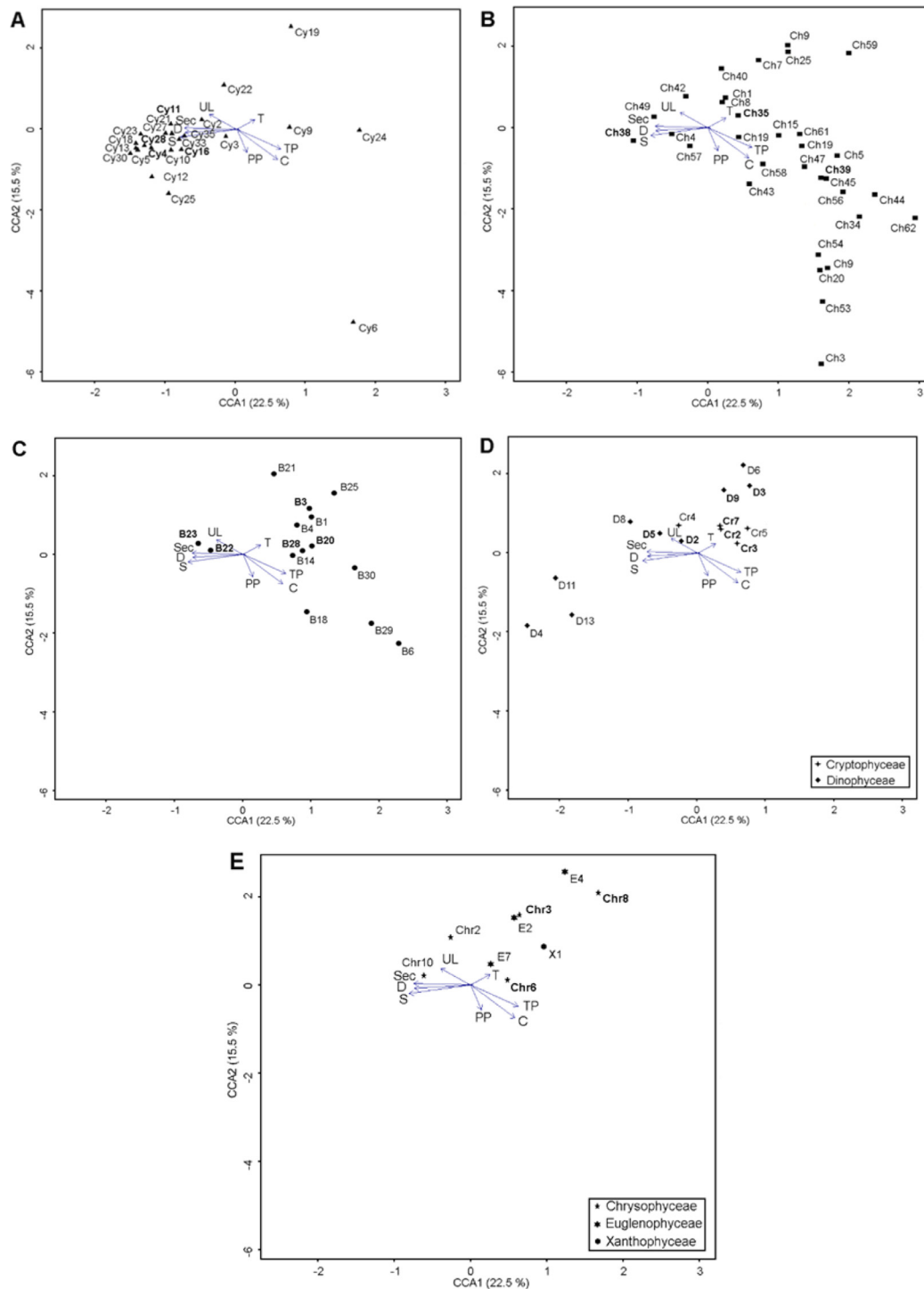


Figure 4 Canonical Correspondence Analysis biplots with Cyanophyceae (A); Chlorophyceae (B); Bacillariophyceae (C); Dinophyceae and Cryptophyceae (D); Chrysophyceae, Euglenophyceae and Xanthophyceae (E) species and environmental variables. Dominant species are highlighted in bold. Arrows represent statistical significance ($p < 0.05$) environmental variables (S – salinity [PSU]; T – temperature [$^{\circ}\text{C}$]; D – water depth [m]; UL – depth of layer above thermocline [m]; Sec – Secchi depth [m]; TP – concentration of total phosphorus [mg m^{-3}]; C – concentration of chlorophyll *a* [mg m^{-3}]; PP – plankton primary production [$\text{gC m}^{-2}\text{d}^{-1}$]). Codes of the phytoplankton taxa are given in Supplementary Table 2. The arrows for environmental variables point in the general direction of maximum environmental change across the diagram with statistical significance ($p < 0.05$), and their lengths are approximately proportional to the rate of change in that direction. The correlation between biomasses of phytoplankton and environmental factors was examined based on the angle between arrows; an angle smaller than 90° indicates a positive correlation between the variables; the smaller the angle, the closer the positive correlation of the two variables. An angle between 90° and 180° suggests a negative correlation. Finally, there is no correlation between two variables when their angle is 90° . The projection of phytoplankton species biomass on the environmental variable vector is an approximation of the “optima” regarding that particular variable (ter Braak and Verdonschot, 1995).

factors. Taking into account that *C. kutzingianum* was found 54 times (Table 2), this species can be considered common for freshwater and shallow parts of the estuary. One species of cyanobacteria, *Aphanocapsa reinboldii* ((Richter) Komárek & Anagnostidis 1995), was positively correlated with TP, C, and PP (Figure 4A). In addition, *Merismopedia tranquilla* ((Ehrenberg) Trevisan 1845) was the only species that positively correlated with water temperature.

In contrast to cyanobacteria, diatoms and green algae mostly negatively correlated with water salinity and Secchi depth, and dominated in the shallower parts of the estuary with less transparent waters (Figure 4B,C). However, although in many respects the distribution of biomass of the species from these two groups was similar, there were some differences. For instance, the biomass of most species of green algae, including the dominant *M. pulchellum*, negatively correlated with the depth of UL, and positively correlated with concentrations of TP and C, and PP (Figure 4A). The biomasses of only five species, one of which was the dominant *Mougeotia* sp., positively correlated with depth, salinity and Secchi depth. Another group of seven species, with a third dominant species, *M. contortum*, was also correlated with water temperature. In other words, most species of green algae preferred those parts of the estuary where salinity was low, but the concentration of chlorophyll and primary production were high.

As green algae, biomasses of most diatom species negatively correlated with water salinity, Secchi depth and water depth (Figure 4C). Only two species of Bacillariophyceae, *S. subsalsum* and *S. costatum*, positively correlated with D, S, Sec and UL. In contrast to green algae, only three species of diatoms, *Lindavia glomerata* ((H.Bachmann) Adesalu & Julius 2017), *Belonastrum beroliensis* ((Lemmermann) Round & Maidana 2001) and *Tabellaria flocculosa* ((Roth) Kützing 1844), positively correlated with concentration of TP and C (Figure 4C). The remaining diatoms did not show significant correlations with eutrophication indicators, but positively correlated with water temperature (Figure 4C).

Almost all species from the less abundant phytoplankton groups, with the exception of dinoflagellates, mainly had the same correlations with the studied environmental factors. For instance, biomasses of all dominant Cryptophyceae species positively correlated with temperature and negatively correlated with water salinity, water depth, and Secchi depth. At the same time, their biomasses were not correlated with the concentrations of total phosphorus and chlorophyll *a*, and the primary production of plankton (Figure 4D). Only *Komma caudate* negatively correlated with TP, C and PP and positively correlated with the UL depth (Figure 4D).

Biomass of autotrophic dinoflagellates showed more complex relationships with environmental variables compared to Cryptophyceae. Part of dinoflagellates negatively correlated with water salinity, depth and Secchi depth, but positively with water temperature (Figure 4D). For example, the biomasses of *Ceratium hirundinella* ((O.F.Müller) Dujardin 1841), *Peridinium cinctum* ((O.F.Müller) Ehrenberg 1832), and *Gymnodinium* sp. positively correlated with water temperature, and negatively with water salinity, the highest biomass of these species was found in the UR and the MR of the estuary. The biomass of the dominant *Apocalathium aciculiferum* ((Lemmermann) Craveiro,

Daugbjerg, Moestrup & Calado 2016) was positively related to the UL depth. However, the biomasses of some dinoflagellate species like cyanobacteria positively correlated with salinity, depth and Secchi depth of water, but negatively correlated with water temperature (Figure 4D). In more detail, the relationship of various dinoflagellates with environmental factors in the Neva Estuary is published in Golubkov et al. (2019a).

Species from Euglenophyceae, Xanthophyceae, and most Chrysophyceae have similar correlations with the studied environmental factors and did not show significant correlations with the concentration of total phosphorus and chlorophyll *a*, and the primary production of plankton (Figure 4E). *T. affine* (Xanthophyceae), *Lepocinclis acus* ((O.F.Müller) B.Marin & Melkonian 2003), *T. volvocina* and *Trachelomonas* sp. (Euglenophyceae) and three dominant species from Chrysophyceae (*D. divergens*, *M. charkoviensis* and *Mallomonas* sp.) positively correlated with water temperature and negatively with salinity, depth and Secchi depth (Figure 4E). Among other Chrysophyceae, *Chrysooccus rufescens* (Klebs 1892) was negatively correlated to phytoplankton productivity indicators, and *Mallomonas elegans* (Lemmermann 1904), unlike previous species, was positively correlated to salinity and other physical variables (Figure 4E).

4. Discussion

This study has explored and enhanced the knowledge on phytoplankton diversity and its correlation with environmental variables in the coastal waters of the easternmost Baltic Sea. In contrast to this region, the composition and biomass of phytoplankton in coastal and open waters in other parts of the Baltic are better studied (e.g., Gasiūnaitė et al., 2005; Jaanus et al., 2011; Olenina et al., 2006; Piwosza et al., 2018; Suikkanen et al., 2007; Wasmund et al., 2011, 2017). In the central Baltic, diatoms and autotrophic dinoflagellates dominate in spring and autumn phytoplankton whereas cyanobacteria dominate in the summer (Gasiūnaitė et al., 2005; Suikkanen et al., 2007; Wasmund et al., 2011). In Curonian Lagoon situated in the south-eastern part of the Baltic Sea, where salinity varies from 0 to 8 PSU, Cyanophyceae, Chlorophyceae and Bacillariophyceae are the main dominant classes in summer phytoplankton (Kreves et al., 2007). According to our results, cyanobacteria dominated the midsummer phytoplankton in the MR and LR of the Neva Estuary, whereas green algae dominated in the UR. Green algae is also common for summer phytoplankton of freshwater lakes at the watershed of the Neva Estuary (Golubkov et al., 2019b; Holopainen et al., 1996; Sharov et al., 2014), and in the coastal lakes of the southern Baltic Sea, where green algae preferred freshwaters (Obolowski et al., 2018). An analysis of our data showed that, overall, green algae dominated in more freshwaters and shallow coastal areas in the UR and the MR of the Neva Estuary (Figure 2), but some species, including the dominant *Mougeotia* sp., were abundant in the brackish parts of the estuary and showed a positive correlation with water salinity (Figure 4B). Similarly, green algae were most diverse in freshwaters and mixing zone of the Vistula River estuary (Gulf of Gdańsk). However,

species from Mamiellophyceae were characteristic groups for the brackish zone of this estuary and were found at salinities around 7 PSU (Piwożsa et al., 2018). In the Baltic Sea, periodic changes in the species composition of summer phytoplankton occur due to fluctuations in environmental factors. Analysis of long-term data showed a decrease in the proportion of green algae in the western, southern and central regions of the Baltic Sea in all seasons at the end of the 20th century (Wasmund et al., 2011). In the northern Baltic and the Gulf of Finland, on the contrary, the proportion of this group in the total biomass of phytoplankton increased from 1979 to 2003, which is apparently associated with a decrease in water salinity (Suikkanen et al., 2007). In the Neva Estuary, the biomass of green algae had statistically significant positive trend (Figure 3B).

In the Neva Estuary, many Chlorophyceae species correlated positively with total phosphorus concentration. In the most eutrophic waters, there were high biomass of *Tetrademus* sp., *Desmodesmus* sp. and *Ankistrodesmus* sp. (Figure 4 B). The same patterns were observed in Lake Ladoga, in which these species were found in its most eutrophic parts (Holopainen et al., 1996), and in the Bothnia Sea, the low saline part of the Baltic Sea (Kuosa et al., 2017).

Cyanobacteria were the dominant phytoplankton group in the MR and the LR of the Neva Estuary in 2003–2019 (Figure 2). They began to dominate phytoplankton in these parts of the estuary since the late 1990s (Nikulina, 2003). A similar increase in the significance of cyanobacteria in the summer phytoplankton was observed in the late 1990s and early 2000s in the western part of the Gulf of Finland and in different parts of the Gulf of Bothnian (Jaanus et al., 2011; Suikkanen et al., 2007). However, we did not find a continuation of this trend in the Neva Estuary in 2003–2019 (Figure 3A). Wasmund et al. (2011) showed that after the peak of 1979/1980, the proportion of cyanobacteria in the total biomass of phytoplankton in the southern Baltic even decreased, especially the proportion of *Aphanizomenon* sp. and *Nodularia spumigena* (Mertens ex Bornet & Flahault 1888).

The problem of summer cyanobacteria blooms that secrete toxins, which are dangerous to humans, is acute in the Central Baltic. Monitoring of this phenomenon by photographing the water surface from space showed that the concentration of chlorophyll in such places could be very high (Kahru et al., 2020). In the Neva Estuary, cyanobacteria blooms were also occasionally observed at some stations (Golubkov et al., 2017). According to information on species toxicity from Hallegraeff et al. (2003), thirteen species found in the estuary are harmful (Supplementary Table 2). *N. spumigena*, which produces a hepatotoxin, is the most toxic among them. Blooms of this species observed in the central Baltic Sea (Kahru et al., 2020). It was also found in the Neva Estuary, but was rare (Supplementary Table 2).

Some cyanobacteria species seem to enter the Neva Estuary from its catchment. For instance, the harmful *Microcystis wesenbergi* (Komárek) Komárek ex Komárek 2006, dominated among summer phytoplankton in the reservoir located on the northern coast of the estuary (Golubkov et al., 2019b). This species had highest biomass in the UR of the Neva Estuary. Other species, *A. flos-aqua* and *P. agardhii*, which are dominant in the Neva Estuary, are also

common in summer phytoplankton in the shallow mostly freshwater estuary, the Curonian Lagoon (Pilkaitytė, 2007) and in brackish-water Gulf of Riga (Purina et al., 2018).

Many authors believe that the development of cyanobacteria is mainly controlled by temperature, and the intensity of their development increases with increasing temperature (Gasiūnaitė et al., 2005; Obolewski et al., 2018). On the other hand, a recent study analyzing the influence of environmental factors on cyanobacteria blooms in the central part of the Baltic Sea showed that water temperature does not significantly affect the intensity of blooms in this area (Kahru et al., 2020). In our study, we also did not find such a positive correlation; on the contrary, the biomass of most species, including dominant ones, negatively correlated with water temperature (Figure 4A).

In the Neva Estuary, most species of cyanobacteria did not show correlations with phosphorus concentration and phytoplankton productivity. This suggests that the concentration of phosphorus for this group is not very important, which is also known from the literature. Kahru et al. (2020) concluded that the main factor affecting the intensity of cyanobacteria blooms is the ratio of nitrogen to phosphorus concentrations, which is consistent with earlier studies (Pliński and Jozwiak, 1999). In the Neva Estuary, phosphorus limits the development of phytoplankton in the UR, and further towards the western part of the Gulf of Finland, the role of nitrogen as a limiting element increases, and the role of phosphorus decreases (Ylöstalo et al., 2016). Thus, one of the reasons for the dominance of cyanobacteria in the MR and LR of the Neva Estuary may be the ability of many species to uptake atmospheric nitrogen, which gives them an advantage over other autotrophs under nitrogen-limited conditions.

Bacillariophyceae was also an important group of phytoplankton in the Neva Estuary in midsummer 2003–2019. Many species of diatoms, which were found in the estuary, were also common and predominated in freshwater bodies located in the estuary catchment. For example, the diatom *Aulacoseira muzzanensis* (F.Meister) Krammer 1991 dominated the summer phytoplankton in a reservoir located on the estuary coast (Golubkov et al., 2019b). *Aulacoseira* spp. and *Fragilaria crotonensis* (Kitton 1869), which negatively correlated with water salinity in the Neva Estuary (Figure 4C), were a common species for summer phytoplankton from Lake Ladoga and Lake Saimaa (Holopainen et al., 1996; Simola et al., 1993). Diatoms are also the main group of summer phytoplankton in Lake Onega, which is located in the northern part of the estuary catchment basin (Sharov et al., 2014). Only two species from the genus *Skeletonema* had a positive correlation with water salinity (Figure 4C), and had a high biomass in the MR and LR of the estuary. These species are common in phytoplankton in the central parts of the Baltic Sea (Wasmund et al., 2011) and in the Gulf of Finland (Suikkanen et al., 2007). Studies conducted in the western part of the Baltic Sea from 1997 to 2006, in the Gulf of Bothnia from 1988 to 2012, and in the Vistula lagoon at the end of 1980s and beginning of 2000s showed a general decrease in the biomass of diatoms (Henriksen, 2009; Kasperovičienė and Vaikutienė, 2007; Kuosa et al., 2017). A similar decrease in the role of diatoms in summer phytoplankton was observed in the Neva Estuary in the late 1990s (Nikulina, 2003). However, at present, we

have found a positive annual trend in biomass of Bacillariophyceae in the Neva Estuary (Figure 3C), due to an increase in biomass of freshwater species.

In recent years, intensification of harmful dinoflagellate blooms has been observed in regions across significant portions of the North Atlantic and in some regions within the North Pacific (Gobler et al., 2017). In the Baltic Sea, the role of autotrophic dinoflagellates in the spring season also has increased in last years, which in turn has affected the bacterioplankton community (Camarena-Gómez et al., 2018) and has led to a change in biogeochemical cycling (Spilling et al., 2018). In the summer seasons in 1970–2000 on the contrary, a decrease in the biomass of autotrophic dinoflagellates was observed in the southern part of the Baltic Sea, especially for the species *Gymnodinium* spp. and *Peridinium* spp. (Wasmund et al., 2011). Intensive development of *Gymnodinium* spp. was observed only in the summer of 1994, when the biomass of these species exceeded 1400 mg m⁻³. Low water temperatures in summer contribute to the development of dinoflagellates (Wasmund et al., 2011), so they often concentrate at a considerable depth (Gisselson et al., 2002). Our analysis showed similar results, as several marine species of dinoflagellates in the Neva Estuary had negative correlation with water temperature (Figure 4D). According to Hallegraeff et al. (2003), two species found in the estuary, *Phalacroma rotundatum* ((Claparède & Lachmann) Kofoid & J.R.Michener 1911) and *Prorocentrum lima* ((Ehrenberg) F.Stein 1878), are harmful. However, we did not record high biomass of these species in the Neva Estuary in midsummer 2003–2019 (Supplementary Table 2).

Cryptophyceae had a significant proportion in the phytoplankton biomass in the Neva Estuary. Although these algae were common throughout the estuary (Table 2), they had high biomasses in its freshwater part (Figure 2). This group of algae is an important component for the summer phytoplankton in Lake Ladoga, from which the Neva River flows. In the southern part of this lake, Cryptophyceae accounted for 30% of the total biomass of phytoplankton in July 2003 (Holopainen et al., 2006). A significant increase in the summer biomass of these algae in Baltic Proper in the summer of 1997 was associated with a decrease in salinity (Wasmund et al., 2011). This is consistent with our data.

Algae belonging to Chrysophyceae were also common in the Neva Estuary. In the Gulf of Finland and the northern Baltic Proper, an increase in the biomass of these algae was observed at the end of the 20th century (Suikkanen et al., 2007). In the Neva Estuary, all dominant species from this group positively correlated to water temperature (Figure 4E). Species of Euglenophyceae also positively correlated with water temperature and negatively with salinity in the Neva Estuary; the same correlations were observed in the central Baltic (Wasmund et al., 2011).

Most of the phytoplankton groups dominating in freshwater and slightly saline waters in the Neva Estuary showed a statistically significant trend towards an increase in their biomasses in the MR in 2003–2019, which may be associated with an increase in the amount of atmospheric precipitation in summer observed in the region in recent years. The amount of precipitation in July in the Saint Petersburg region increased from 53 mm in 2011 to 151 mm in 2016 (Golubkov and Golubkov, 2020). As a result, the

Neva River's run-off increased (Knuuttila et al., 2017); high concentrations of TP were measured in the UR of the Neva Estuary due to leaching of nutrients from the river catchment (Golubkov and Golubkov, 2020). This phenomenon is consistent with the results of model simulations, according to which an increase in the flow volume caused by an increase in net precipitation in the Baltic catchment area will stimulate nutrient loads from the land during the 21st century, especially in the northern regions (Meier et al., 2012). As was early shown, with an increase in the flow of the Neva River during rainy summers, the salinity of water in the MR of the Neva Estuary decreases (Myakisheva, 1996). Such environmental conditions should favor the development of freshwater species from various groups of phytoplankton. Taking into account that most regional climate models predict future increases in precipitation and temperature in the northern Baltic regions, the future expansion of the areas occupied by these freshwater phytoplankton species in the Neva Estuary and other estuaries of the Northern Baltic is very likely.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.oceano.2020.11.002.

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