



Phytoplankton community composition as a driver of annual autochthonous organic carbon dynamics in the northern coastal Baltic Sea

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ABSTRACT: Phytoplankton are the major primary producers in the pelagic system. They greatly influence biogeochemical cycles but little is known about the importance of shifting phytoplankton community composition for carbon dynamics. This study investigates the impact of seasonal changes in coastal phytoplankton communities on pelagic carbon fluxes. A field sampling campaign, covering an annual cycle in primary production, was conducted to assess the seasonal changes of phytoplankton communities and relevant organic carbon parameters in the coastal Baltic Sea. The monitoring frequency ranged from 1 to 3 wk, adapted to match the seasonal phytoplankton blooms. In addition, sediment traps were deployed to determine the particulate carbon and nutrient export to the seafloor in every season. We found that the phytoplankton biomass during the spring bloom was as high as $550 \mu\text{g C l}^{-1}$ and was dominated by diatom species (88% of total phytoplankton biomass). In comparison, the more species-rich summer bloom reached a combined maximum biomass of $236 \mu\text{g C l}^{-1}$. However, the highest export flux of particulate organic carbon was found in the middle of August ($561 \text{ mmol C m}^{-2} \text{ d}^{-1}$) and, not as expected, around the spring bloom in May ($226 \text{ mmol C m}^{-2} \text{ d}^{-1}$), suggesting a high potential for carbon recycling within the pelagic food web rather than being exported to the seafloor or advected laterally. Our study emphasizes the importance of keystone species and diversity for carbon transport processes in marine coastal ecosystems and highlights complex relationships between phytoplankton biomass production, community composition and carbon dynamics.

KEY WORDS: Organic carbon dynamics · Phytoplankton community composition · Phytoplankton bloom · Phytoplankton monitoring · Baltic Sea

1. INTRODUCTION

Phytoplankton is the basis of marine life and has a significant effect on climate due to its role in carbon cycling (Basu & Mackey 2018) and contribution to global atmospheric oxygen production (Behrenfeld et al. 2001). The growth of phytoplankton is strongly linked to the annual climatic cycle (Gasiūnaitė et al. 2005), and studies have shown that phytoplankton react quickly to changes in their environment (Mitra & Zaman 2015). The composition of phytoplankton communities, in terms of species diversity, relative

abundance and biomass, is recognized as a key driver of autochthonous organic carbon dynamics (Duarte & Cebrián 1996, Hjerne et al. 2019). Therefore, changes in phytoplankton community composition can have a strong impact on the carbon cycle, including direct effects on higher trophic levels and benthic communities, due to individual phytoplankton traits regulating carbon fluxes (Litchman et al. 2015, Griffiths et al. 2017).

There is considerable variability among phytoplankton species in their potential support of carbon export to the seafloor as a result of species-specific

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variation in the uptake of inorganic carbon (Beardall et al. 2009), the cellular carbon-to-volume relationship (Menden-Deuer & Lessard 2000), sinking velocity and turnover rates (Carstensen et al. 2015). Hence, phytoplankton community composition in the euphotic zone largely determines the quality and quantity of organic matter that sinks to depths where it can potentially be sequestered (Basu & Mackey 2018).

Fast-growing and bloom-forming diatoms typically promote carbon burial because of their large size, heavy silica shells and high sinking velocity (Carstensen et al. 2015). By contrast, picoplankton such as cyanobacteria likely contribute to the carbon efflux to the atmosphere because of their low sinking velocities and high turnover rates in the microbial loop (Basu & Mackey 2018). These 2 groups are dominant during different seasons. The spring bloom in the northern Baltic Sea is dominated by fast-growing diatoms (e.g. *Skeletonema* spp.) and dinoflagellates (e.g. *Peridiniella catenata*), while the summer bloom is dominated by filamentous cyanobacteria (e.g. *Planktothrix agardhii*) (Gasiūnaitė et al. 2005, Carstensen et al. 2015).

Phytoplankton community structure is of high importance for the biological carbon pump, which transports organic carbon produced by primary producers in the euphotic layer to the deep sea (Basu & Mackey 2018, Henson et al. 2021). Therefore, seasonal changes in phytoplankton community composition can be crucial in determining the role of phytoplankton in the pelagic carbon flow and its contribution to carbon fluxes (Spilling et al. 2018). However, the impact of phytoplankton and specific species compositions on carbon fluxes along with the resulting consequences for the carbon budget have not yet been sufficiently researched and are rarely considered in carbon-climate research (Finkel et al. 2010).

To address these knowledge gaps, the aims of this study were 2-fold: (1) to assess the impact of seasonal environmental changes and shifts in the phytoplankton community composition on the pelagic carbon cycle and (2) to quantify the main pelagic carbon flow driven by the phytoplankton community.

We expected that seasonal environmental changes affect nutrient availability, phytoplankton community composition and biodiversity, and, consequently, carbon transport. We hypothesised that season-specific phytoplankton community composition will lead to different amounts of carbon accumulating in the water column and sinking to the seafloor. In particular, the phytoplankton community in spring was expected to accumulate more carbon that sinks to the seafloor due to higher sinking velocities of the domi-

nant diatoms (Carstensen et al. 2015), while the summer bloom community was expected to have a lower carbon content and lower sinking velocities. This difference was expected to contribute to a faster carbon turnover in the microbial loop in summer and thereby lead to increased carbon outgassing to the atmosphere.

2. MATERIALS AND METHODS

To understand how phytoplankton biodiversity affects carbon dynamics in coastal ecosystems, we conducted a field monitoring campaign over an annual cycle in the coastal Baltic Sea. Between October 2021 and October 2022, we collected samples to analyse water chemistry, organic carbon quantity and characteristics as well as phytoplankton biomass and community composition. Sampling frequencies ranged from 1 wk during the bloom periods (April–May 2022 and July–August 2022) to 3 wk during the winter season (October 2021–February 2022 and September–October 2022). In the remaining time, samples were taken biweekly. In addition, every 3 mo, sediment traps were deployed to determine the amount and stoichiometric characteristics of the sinking organic matter.

2.1. Sampling area and procedure

Samples were taken in the north-western Gulf of Finland at the coastal area close to the Tvärminne Zoological Station. The sampling point presented in Fig. 1 is located north of Idgrund (59.8424° N, 23.2509° E), with a water depth of 4.6 m. This area is characterised by low salinity (from 4.5–6.6 PSU) and strong seasonal changes in water temperature (0.4–20.5°C). In addition, horizontal currents are rather weak at the sampling site and resuspension is not an issue due to the low organic matter content of the seafloor (T. Jilbert pers. comm.).

Surface water samples were taken for water chemistry analyses and phytoplankton using a 2 l Limnos-type water sampler. A Valeport mini CTD was used for a depth profile measuring temperature, salinity, conductivity and pressure. Additionally, sediment traps consisting of 2 tubes (1.8 l volume, 45 cm high, 7.2 cm inner diameter, 6.25:1 aspect ratio) were deployed for 24 h, 3 m below the surface in every season (13 Oct 2021, 8 Mar 2022, 11 May 2022, 23 Jun 2022, 17 Aug 2022). The sediment traps were retrieved by carefully decanting about two-thirds of the contents

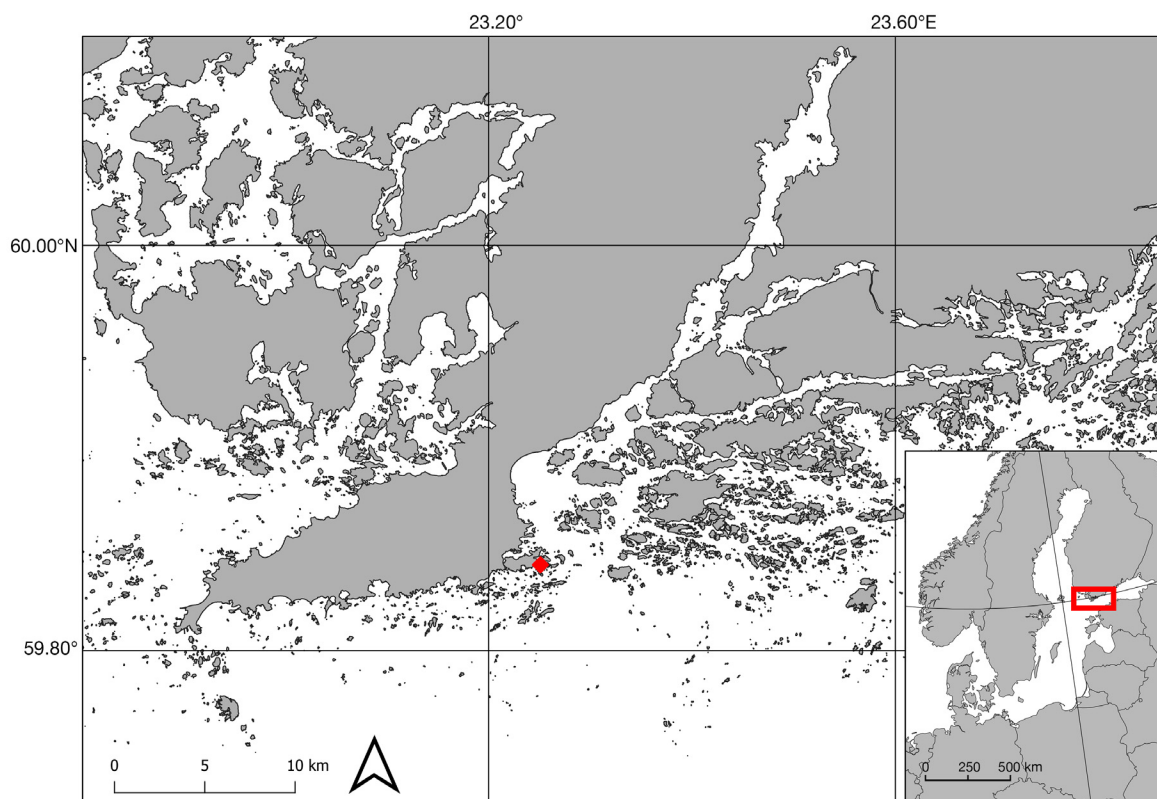


Fig. 1. Map showing the monitoring site. The coordinates of the sampling site are 59.8424° N, 23.2509° E

into a wide-mouth Nalgene bottle. The last third was thoroughly homogenised and transferred into the bottle to ensure that the whole water volume of the sediment trap (1.8 l) and all material that sank was collected for lab analysis. The contents of the bottle were mixed before the fractions for the various analyses were taken.

2.2. Water chemistry

All samples (water column and sediment trap samples) were analysed for total suspended matter (TSM), chlorophyll *a* (chl *a*), particulate organic phosphorus (POP), particulate organic carbon (POC), particulate organic nitrogen (PON), dissolved organic carbon (DOC), dissolved inorganic nitrogen (DIN, including NH_4 , NO_2 and $\text{NO}_3 + \text{NO}_2$), dissolved inorganic phosphorus (DIP), total phosphorus (TP), total nitrogen (TN) as well as chromophoric and fluorescence dissolved organic matter (CDOM and FDOM).

Samples for TP and TN analysis were taken directly from the water samples. The remaining water was filtered through acid-washed and combusted (450°C for

4 h) glass fibre filters (Whatman GF/F, 0.7 μm mesh size). The filters were used for TSM, chl *a*, POP, POC and PON analyses. For DIN, DIP, DOC, CDOM and FDOM analyses, the filtrate was used. DOC samples were fixed with 2 mol HCL before analysis. For TSM, water was filtered through a pre-weighed glass fibre filter dried for 12 h at 60°C and reweighed. The TSM was calculated by subtracting the weight of the clean filter from the filter weight containing the sample of organic matter. Total and dissolved nutrients were analysed using a continuous flow autoanalyser (AII) after Hansen & Koroleff (1999). DOC was analysed in 3 replicates following Cauwet (1999) using the Shimadzu TOC-V_{CHP} with ASI-V auto sampler (and TNM-1 Total Nitrogen detector for TDN). The mean value of the replicates was used; outliers were determined using Cook's distance and removed accordingly. POP was analysed following Koistinen et al. (2019). To estimate POC and PON, filters were dried at 60°C for 24 h and folded into tin caps to be analysed with the Vario micro cube by Elementar following DIN 38409-46:2012-12 (Hedges & Stern 1984). Chl *a* analysis was performed using a Varian fluorescence spectrofluorometer. Filters were submerged in ethanol in the dark for 24 h prior to analysis.

Analysis of CDOM was performed using a Shimadzu UV-2501PC spectrophotometer with a 1 cm quartz cuvette over a spectral range of 200–800 nm. As references for all samples, Millipore water was used and later subtracted as a blank from sample absorbance measurements. FDOM analysis was performed using a Varian fluorescence spectrofluorometer with a 1 cm cuvette. The excitation was set to 220 and the emission ranged from 280 to 600 nm. Processing of the excitation–emission matrices (EEMs) was done using the 'eemR' package for R software (Massicotte 2017). A blank sample of ultrapure water was subtracted from the EEMs, and the Rayleigh and Raman scattering bands were removed from the spectra after calibration. EEMs were calibrated by normalising to the area under the Raman water scatter peak (excitation wavelength of 350 nm) of an ultrapure water sample run in the same session as the samples and were corrected for inner filter effects with absorbance spectra (Murphy et al. 2010). For assessing the characteristics and the quality of the DOM pool, fluorescence peaks (Coble 1996) were calculated from the EEMs (peak T: protein-like).

2.3. Calculations for phytoplankton and carbon flux

Phytoplankton samples for microscopic analysis were fixed with acidified Lugol's iodine solution and counted following the Utermöhl technique (Utermöhl 1958). Due to the limited volume of the sediment traps, it was not possible to take phytoplankton samples for microscopic analysis. Cell biovolume was calculated using average cell sizes after Karlson et al. (2022) following approximation to geometric standards established by Hillebrand et al. (1999).

Phytoplankton community evenness was calculated using Pielou's Index (Pielou 1966), and carbon content was estimated based on species-specific cell biovolume following Olenina et al. (2006) and its annually updated annex (version 2023). In addition, phytoplankton carbon content (POC [Phyto]) was calculated from the chl *a* content following Jakobsen & Markager (2016) using values for estuaries. This was done to directly compare carbon quotas between the sediment traps and the water column even without the microscopic phytoplankton cell counts from the sediment traps.

The export fluxes in ($\text{mmol m}^{-2} \text{d}^{-1}$) were calculated from the POC, PON, POP and POC (Phyto) content in the sediment traps and corrected for the respective concentrations in the water column considering the

size of the traps and deployment time. The correction was achieved by subtracting the content of the water column from the content of the sediment traps.

3. RESULTS

3.1. Annual changes in environmental conditions

Temperature dynamics followed the typical annual cycle in boreal regions, with the highest temperatures in August and the lowest in February. Nutrients, organic carbon and chl *a* showed high variability throughout the year (Table 1). For example, TP concentrations in the water column ranged from 0.42–1.08 $\mu\text{mol l}^{-1}$ with a peak in February, while TN had a range of 10.9–27.9 $\mu\text{mol l}^{-1}$ with maximum values observed in September. The TN:TP ratio, on the other hand, showed a maximum in May and had a range of 18.3–42.7.

An increase in DIN concentrations was observed in the water column during winter (highest in February at 9.95 $\mu\text{mol l}^{-1}$; Table 1) and a rapid decrease was seen in spring (May: 0.31 $\mu\text{mol l}^{-1}$). DIP followed an annual pattern similar to DIN, decreasing at the beginning of spring and increasing at the end of summer and in the winter months. The same changes were observed for both DIN and DIP in the sediment traps (Fig. 2a,c). DOC in the water column slowly increased from October until August, and the sediment traps showed no pronounced differences in relation to the water column except in August, when higher DOC was detected in the water column than in the sediment traps (Fig. 3c).

As expected, POC concentrations in the water column increased with the spring bloom in March and decreased at the beginning of May. POC values were stable during the summer. PON slowly increased in the water column from April until September, and the POC:PON ratio varied 4-fold over the year in a range of 2–8. The sediment traps showed an increase in POC and PON sinking to the seafloor during the growing season. The highest amount of POC and PON in the sediment traps was found in August (POC: 168 $\mu\text{mol l}^{-1}$; PON: 38.9 $\mu\text{mol l}^{-1}$; Fig. 3a,b). In general, the POC:PON ratio was higher in the sediment traps than in the water column except in August (Fig. 3d).

The chl *a* concentration in the water column was low during the winter (0.3 $\mu\text{g l}^{-1}$) and increased rapidly in March and April (5.96 $\mu\text{g l}^{-1}$), indicating the spring phytoplankton bloom. Another increase was detected from the end of June (1.47 $\mu\text{g l}^{-1}$) until the end of October (4.9 $\mu\text{g l}^{-1}$). Corresponding maxi-

Table 1. Ranges (min. –max.) and mean values for water chemistry parameters measured in the water column and sediment traps. TSM: total suspended matter; TP: total phosphorus; TN: total nitrogen; DIP: dissolved inorganic phosphorus; DIN: dissolved inorganic nitrogen; DOC: dissolved organic carbon; POP: particulate organic phosphorus; POC: particulate organic carbon; PON: particulate organic nitrogen; POC (Phyto): phytoplankton carbon content

	Water column		Sediment trap		Month with highest value	
	Range	Mean	Range	Mean	Water column	Sediment trap
TSM (mg l^{-1})	0.65–4.20	1.61	2.90–12.0	7.80	Apr	Aug
TP ($\mu\text{mol l}^{-1}$)	0.42–1.08	0.81	0.85–1.64	1.22	Feb	Jun
TN ($\mu\text{mol l}^{-1}$)	10.9–27.9	21.3	21.9–32.9	26.3	Sep	Aug
TN:TP	18.3–42.7	27.7	17.8–26.6	22.3	May	Mar
DIP ($\mu\text{mol l}^{-1}$)	0.01–0.26	0.13	0.04–0.21	0.09	Feb	Mar
DIN ($\mu\text{mol l}^{-1}$)	0.31–9.95	4.01	1.93–9.14	3.92	Feb	Mar
DIN:DIP	5.72–90.9	33.6	24.2–64.5	46.9	May	Aug
DOC ($\mu\text{mol l}^{-1}$)	360–602	421	372–423	396	Aug	Jun
POP ($\mu\text{mol l}^{-1}$)	0.06–0.40	0.20	0.21–1.37	0.70	Apr	Aug
POC ($\mu\text{mol l}^{-1}$)	10.4–72.7	27.8	25.6–168	85.1	Apr	Aug
PON ($\mu\text{mol l}^{-1}$)	1.32–15.3	6.43	4.50–38.9	15.7	Aug	Aug
POC:PON	2.08–8.43	5.00	4.32–9.38	6.20	May	May
Chl a ($\mu\text{g l}^{-1}$)	0.32–5.96	2.01	0.77–9.29	3.89	Apr	Aug
POC (Phyto) ($\mu\text{mol l}^{-1}$)	0.75–13.2	4.53	1.76–20.4	8.63	Apr	Aug

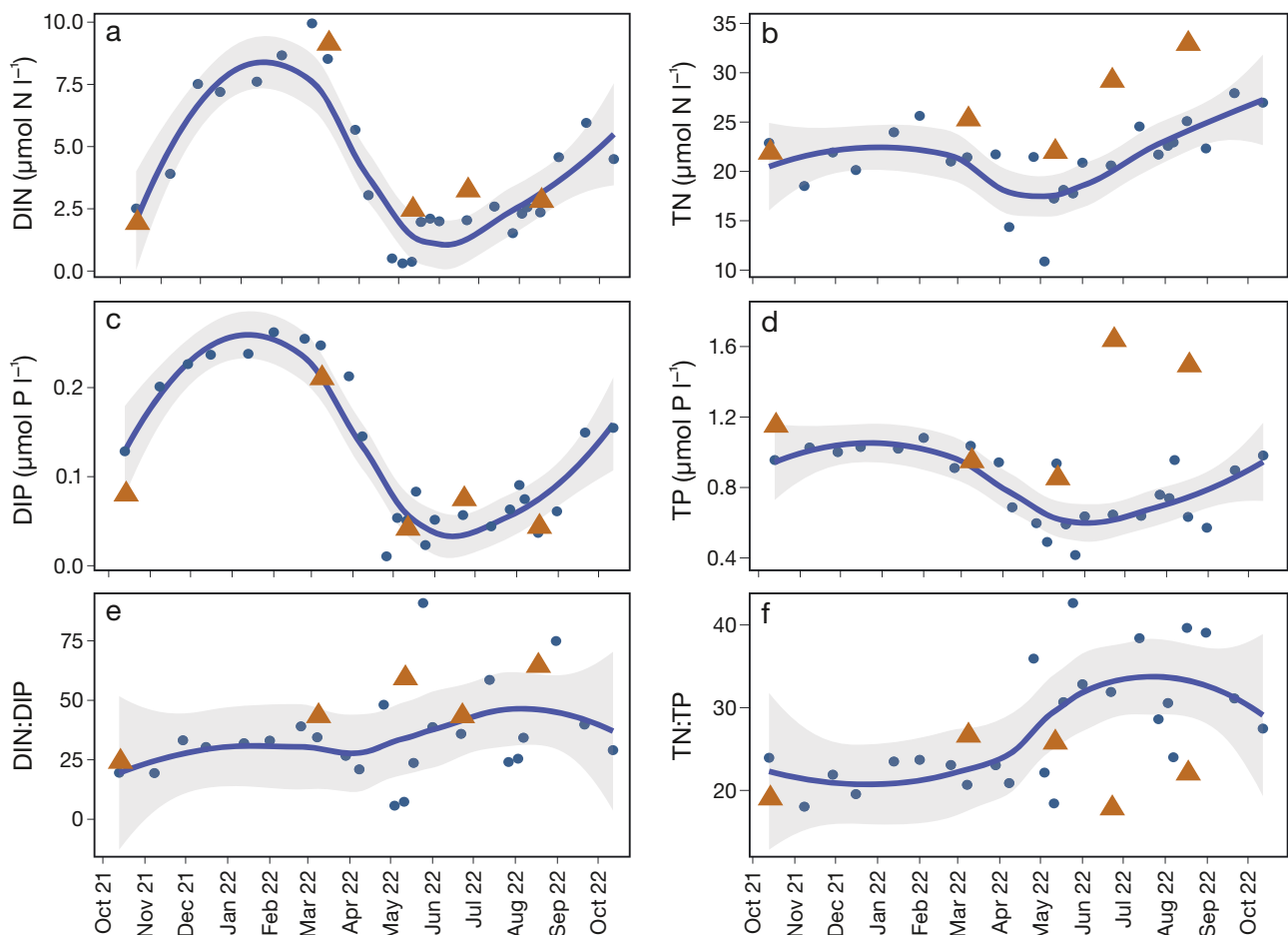


Fig. 2. Seasonal patterns at the monitoring site, showing (a) dissolved inorganic nitrogen (DIN), (b) total nitrogen (TN), (c) dissolved inorganic phosphorus (DIP), (d) total phosphorus (TP), (e) DIN:DIP ratio and (f) TN:TP ratio. Circles: values for the water column; triangles: values for the sediment traps; blue line: Loess smoother, used for visualisation; grey shading: 95% confidence interval

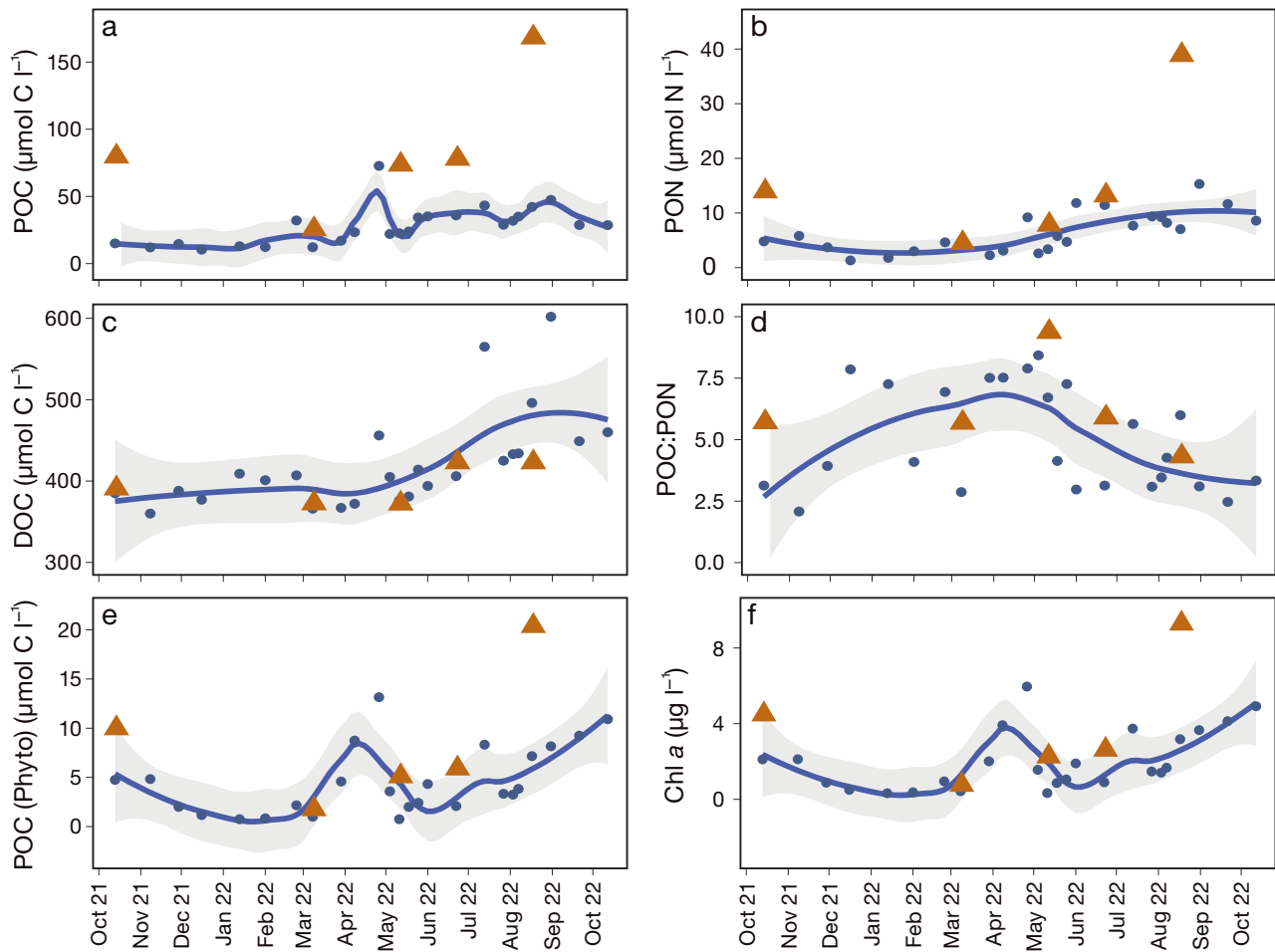


Fig. 3. Seasonal patterns for carbon-related parameters at the monitoring site, showing (a) particulate organic carbon (POC), (b) particulate organic nitrogen (PON), (c) dissolved organic carbon (DOC), (d) POC:PON ratio, (e) phytoplankton carbon content (POC [Phyto]) and (f) chlorophyll *a* (chl *a*). Graph components as in Fig. 2

mum concentrations of POC (Phyto) were $0.75 \mu\text{mol l}^{-1}$ in winter, $13.6 \mu\text{mol C l}^{-1}$ during the spring bloom in April and May, and $8.33 \mu\text{mol C l}^{-1}$ in June. In line with the results of POC and PON, the highest concentration of chl *a* in the sediment traps was measured in August (9.3 mg l^{-1}), with corresponding POC (Phyto) of $20.4 \mu\text{mol C l}^{-1}$ (Fig. 3). TSM in the water column increased and decreased in accordance with chl *a*. The sediment traps captured a steep increase in TSM from April to late August ($2.9\text{--}12.0 \mu\text{g l}^{-1}$; Table 1).

The DOM humification index (HIX), which indicates dead organic matter, and the DOM biological index (BIX), which indicates fresh organic matter, showed clear seasonal patterns (Fig. 4a,b) with higher HIX values in winter and higher BIX values in summer. Protein-like fluorescence (peak T), which suggests labile autochthonous production of DOM, decreased from October until February and increased from mid-March until mid-August (Fig. 4c).

3.2. Particle fluxes — annual shifts in export fluxes from the pelagic to the benthic system

A strong decrease in carbon flux to the seafloor was detected from October ($287 \text{ mmol C m}^{-2} \text{ d}^{-1}$) until March ($59 \text{ mmol C m}^{-2} \text{ d}^{-1}$). The carbon flux increased rapidly from March until May ($226 \text{ mmol C m}^{-2} \text{ d}^{-1}$), with a slight decrease in June ($187 \text{ mmol C m}^{-2} \text{ d}^{-1}$). The highest carbon flux to the seafloor was detected in the middle of August ($561 \text{ mmol C m}^{-2} \text{ d}^{-1}$; Fig. 5a). POC (Phyto) as a fraction of the total POC flux increased from March ($3.4 \text{ mmol m}^{-2} \text{ d}^{-1}$, 5.8% of total POC) until May ($19.7 \text{ mmol m}^{-2} \text{ d}^{-1}$, 8.6% of total POC). A slight decrease occurred in June ($17.3 \text{ mmol m}^{-2} \text{ d}^{-1}$, 9.2% of total POC), with another strong increase in August ($59.6 \text{ mmol m}^{-2} \text{ d}^{-1}$, 10.6% of total POC; Fig. 5c). The proportion of the POC (Phyto) fraction to the total POC flux increased steadily from March to August. There was a major increase in PON

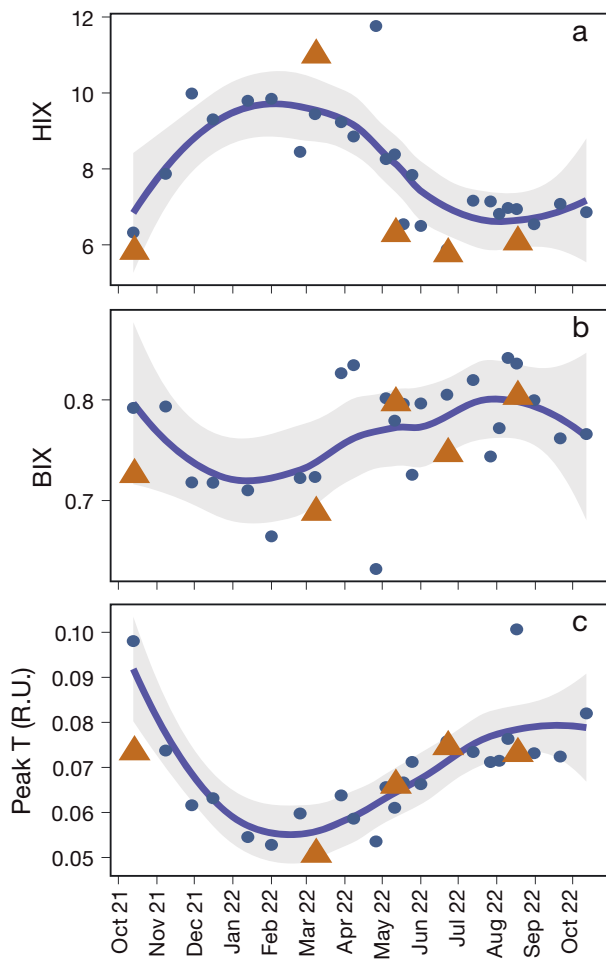


Fig. 4. Seasonal patterns of dissolved organic matter (DOM)-related parameters at the monitoring site, showing (a) DOM humification index (HIX), (b) DOM biological index (BIX) and (c) protein-like fluorescence (peak T, raman units). Graph components as in Fig. 2

export flux from March until August ($1.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$ and $144 \text{ mmol N m}^{-2} \text{ d}^{-1}$, respectively; Fig. 5b). The export flux of POP increased from March ($0.5 \text{ mmol P m}^{-2} \text{ d}^{-1}$) until August ($4.4 \text{ mmol m}^{-2} \text{ d}^{-1}$; Fig. 5d).

3.3. Ecology — seasonal shift in phytoplankton community

Strong seasonal patterns in phytoplankton community composition and diversity were detected during the 1 yr sampling period. Species richness increased from October until August (12–34, respectively; Fig. 6a). Pielou's evenness had the lowest values during the spring phytoplankton bloom in late April and early May (0.31) and the highest values in early August (0.9; Fig. 6b).

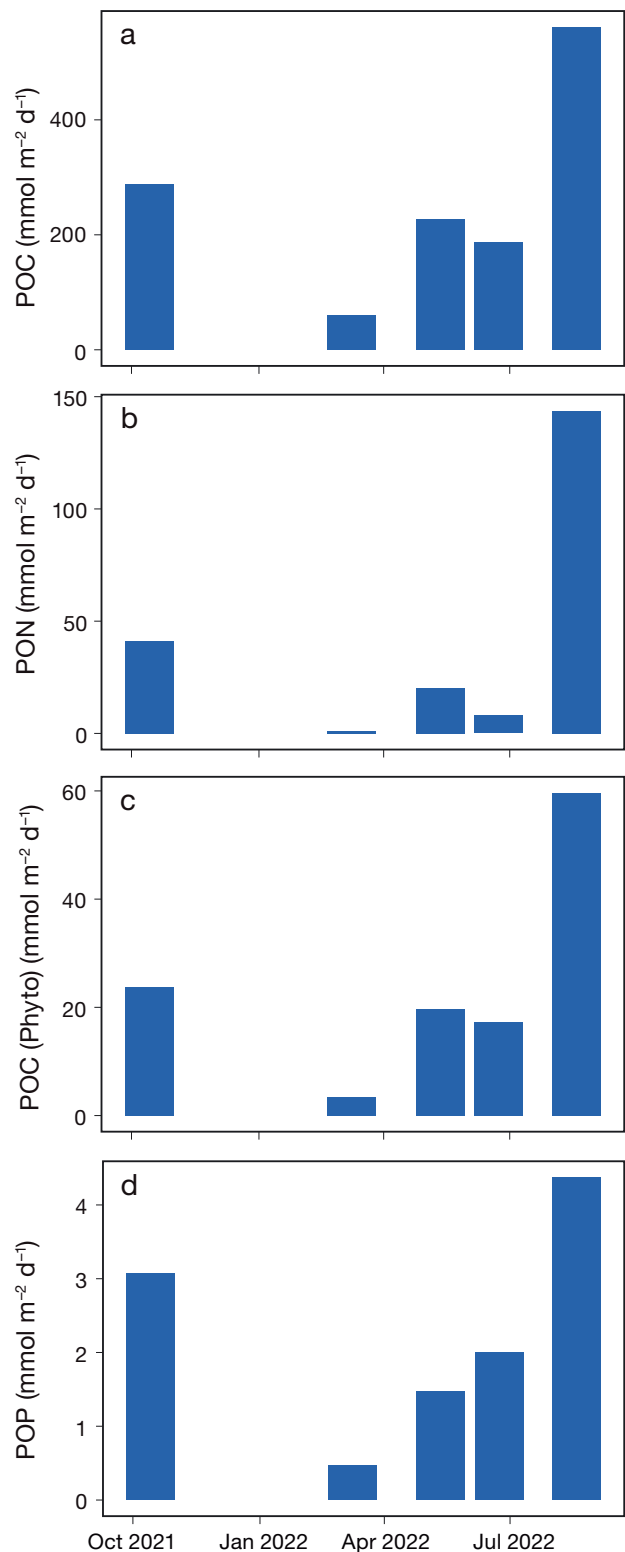


Fig. 5. Seasonal export fluxes to the seafloor calculated from the sediment traps, showing (a) particulate organic carbon (POC) flux, (b) particulate organic nitrogen (PON) flux, (c) phytoplankton carbon content (POC [Phyto]) flux and (d) particulate organic phosphorus (POP flux)

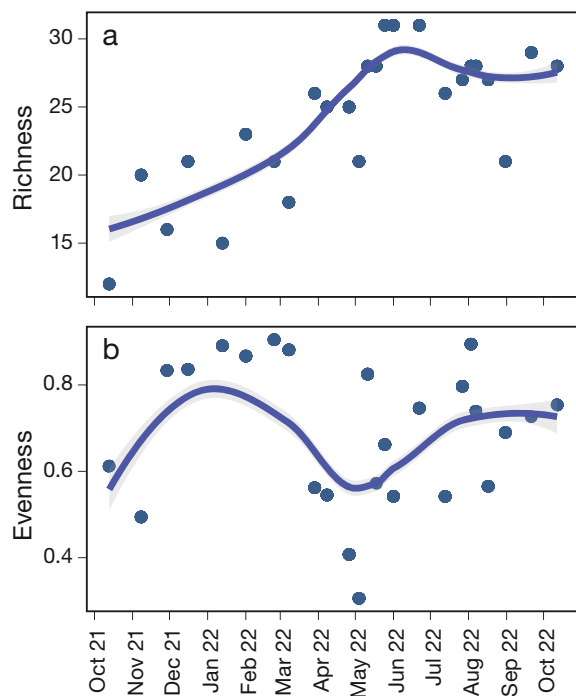


Fig. 6. Seasonal patterns of (a) species richness and (b) Pielou's evenness at the monitoring site. Circles: values for the water column; blue line: Loess smoother for visualisation; grey shading: 95% confidence interval

Ochrophyta (later referred to as diatoms) were dominant in winter and spring, contributing 90% of the cells to the total phytoplankton abundance (cells l^{-1}), with *Skeletonema* spp. as the dominant species. Chlorophyta were most abundant in August (34.5%), with *Tetraselmis* spp. and *Pyramimonas* spp. as the dominant species. Cyanobacteria were dominant in summer (July: 64.4%), with *Dolichospermum* spp., *Pesudana-baena* spp. and *Microcystis* spp. as the most abundant species. The contribution of Cryptophytes varied during the year, with proportional abundances between 27.5 and 0.4%, and *Plagioselmis prolunga* and *Teleaulax* spp. as dominant species. Haptophytes were most abundant in winter (14.5%), with *Chrysochromulina* spp. as the dominant species. Myzozoa (later referred to as dinoflagellates) were abundant in late spring and early summer (~30% of total abundance), with *Heterocapsa rotundata* and *Scropsiella* spp. as dominant species (Fig. 7).

During April and May, diatoms held 2 times more carbon ($486 \mu\text{g C l}^{-1}$) than all other phyla combined (Fig. 7). Among diatoms, the species contributing most to the carbon pool were *Skeletonema* spp. ($189 \mu\text{g C l}^{-1}$) and *Chaetoceros* spp. ($179 \mu\text{g C l}^{-1}$) in March. Dinoflagellates had the highest biomass at the end of April ($37 \mu\text{g C l}^{-1}$). Even though *Heterocapsa* spp. was

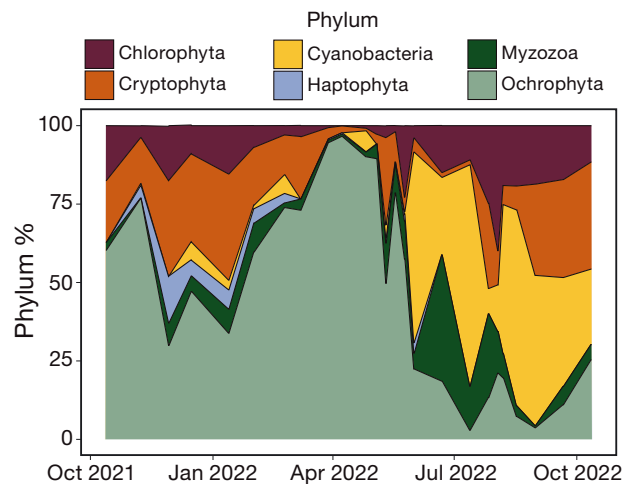


Fig. 7. Changes in proportional abundance of phytoplankton phyla during the span of 1 yr (Oct 2021 to Oct 2022)

the most abundant dinoflagellate during that time, *Peridiniella catenata* contributed the most carbon ($16 \mu\text{g C l}^{-1}$), followed by *Scropsiella* spp. ($12 \mu\text{g C l}^{-1}$). *Heterocapsa* spp. accounted only for $3 \mu\text{g C l}^{-1}$. Cyanobacteria ($31 \mu\text{g C l}^{-1}$), Chlorophyta ($28 \mu\text{g C l}^{-1}$), Cryptophyta ($6.3 \mu\text{g C l}^{-1}$) and Haptophyta ($0.2 \mu\text{g C l}^{-1}$) all had the highest biomass in June and July. The peak of Cyanobacteria biomass was reached in July, with *Dolichospermum* spp. accounting for $29 \mu\text{g C l}^{-1}$ carbon. Chlorophytes had the highest amount of biomass in July, with *Tetraselmis* spp. contributing the most to the carbon quota ($26 \mu\text{g C l}^{-1}$; Fig. 8).

4. DISCUSSION

4.1. Seasonal phytoplankton community succession

The phytoplankton community composition followed a typical successional pattern for the coastal Baltic Sea, from diatoms to dinoflagellates in spring and cyanobacteria in summer, according to their favourable environmental conditions (Sommer et al. 2012, HELCOM 2013, Hjerne et al. 2019, Elovaara et al. 2020, Griffiths et al. 2020). The first peak of phytoplankton biomass in spring was formed by 2 dominant genera, *Skeletonema* spp. and *Chaetoceros* spp. (34 and 32% of the total phytoplankton biomass, respectively), while the second peak in summer was characterized by high species richness and evenness.

The diatom-dominated spring bloom contained more than twice the carbon ($550 \mu\text{g C l}^{-1}$ total phytoplankton biomass, $486 \mu\text{g C l}^{-1}$ in diatom species)

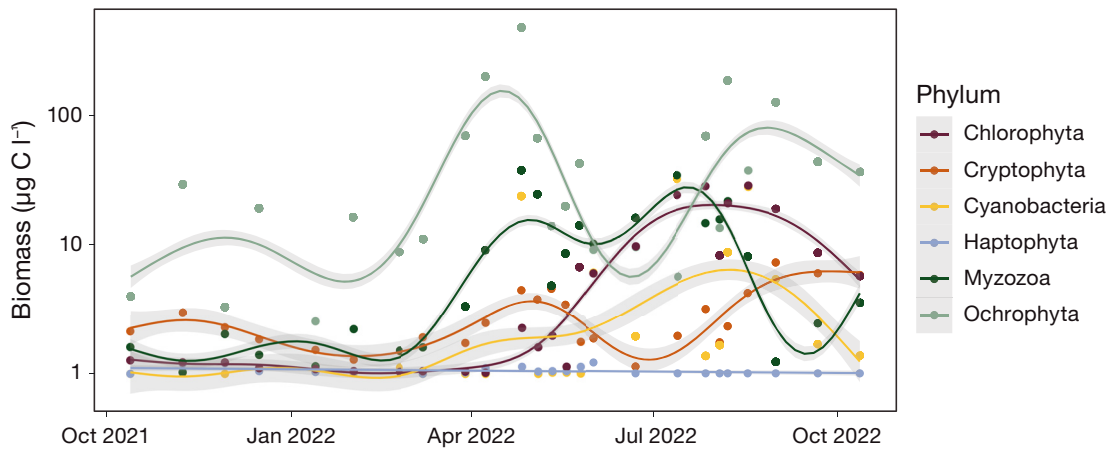


Fig. 8. Annual changes in phytoplankton carbon per phylum (Oct 2021 to Oct 2022). Lines: Loess smoother for visualisation; grey shading: 95% confidence intervals

compared to the peak of the summer phytoplankton biomass ($236 \mu\text{g C l}^{-1}$). Similar findings were reported for the Gulf of Riga by Klais et al. (2011), who suggested that the spring bloom contributes 40–60% to the annual carbon quota. Furthermore, even though cyanobacteria were the most abundant taxonomic group during the summer bloom, they contributed around the same amount to the total phytoplankton biomass ($31 \mu\text{g C l}^{-1}$, 13% of total summer phytoplankton biomass) as diatoms, dinoflagellates and chlorophytes (19 , 33 and $28 \mu\text{g C l}^{-1}$, respectively). This emphasises the importance of species-specific carbon content, while indicating that high species richness is crucial for the efficiency of carbon uptake by phytoplankton communities in summer (Kwiatkowski et al. 2018, Elovaara et al. 2020).

Our results suggest that the POC flux in spring relies on the specific carbon uptake and accumulation by the dominant diatom species, while the species richness of the whole phytoplankton community is more important for the primary production and POC flux in summer. This matches the expectations that a more diverse community utilises resources more efficiently (Ptacnik et al. 2008), often leading to higher biomass production (Cardinale et al. 2009, 2011). Even with specific species being more carbon-rich, it is the sum of all species contributing to the pelagic phytoplankton carbon pool in summer.

4.2. Organic matter characteristics

In the study area, high freshwater discharge from rivers with large inputs of associated allochthonous material is a common phenomenon in spring after the

snowmelt in the catchment area (Asmala et al. 2013, 2016). The dissolved inorganic nutrients (DIN, DIP) accumulating during that time were taken up by the rapid growth of phytoplankton in spring, resulting in an increase of PON concentrations in April and May and leading to an enhanced carbon stock (POC and POC [Phyto]) and a higher POC:PON ratio. Protein-like DOM (as indicated by Peak T) increased from winter–spring values of 0.05 to 0.07 raman units with increasing phytoplankton biomass, indicating production and rapid transformation of autochthonous DOM within the pelagic microbial food web (Asmala et al. 2018). The influence of the freshly produced organic matter was also apparent in the dynamics of the BIX, which is linked to autochthonous production (Murphy et al. 2008, Hugué et al. 2009). Conversely, high HIX values were observed during winter and early spring, when the allochthonous inputs are most pronounced.

The seasonal dynamic of the POC:PON ratio indicates that phytoplankton in spring were more carbon-rich, while phytoplankton in summer were richer in nitrogen. This is due to one of the key diazotrophs in summer at the sampling site, *Dolichospermum* spp. (>50%), an established N_2 -fixing cyanobacteria (Wasmund et al. 2001, Adam et al. 2016). Consequently, cyanobacteria species increased the amount of PON in the water column. Adam et al. (2016) found that parts of the fixed N_2 by *Dolichospermum* spp. are released as NH_4 into the water, which is assimilated efficiently by many phytoplankton species, increasing the primary productivity of the system and enhancing the N content of the phytoplankton cells and, consequently, the PON content (McCarthy et al. 1977, Gilbert et al. 2016). This increase in PON in the system is

reflected in the PON export fluxes measured here, which rose significantly over the phytoplankton growth period in our study.

The shift in resources from allochthonous to autochthonous sources has implications for higher trophic levels and the benthic–pelagic coupling processes, controlling the flow of inorganic nutrients and organic material (Griffiths et al. 2017). Higher nitrogen content in phytoplankton has the potential to increase the resource quality for pelagic and benthic consumers (Sterner & Elser 2002, Van De Waal et al. 2010, Mäkelin & Villnäs 2022), which are dependent on the organic matter subsidies from the pelagic realm. Hence, with higher nitrogen input into the benthic system, benthic primary production is enhanced during the summer phytoplankton bloom (Attard et al. 2019).

4.3. Carbon transport

Based on our data from the sediment traps, the total POC export and the proportional export of POC (Phyto) from the pelagic to the benthic system increased from May ($226 \text{ mmol C m}^{-2} \text{ d}^{-1}$, 8.6% of total POC export as POC [Phyto]) to August ($561 \text{ mmol C m}^{-2} \text{ d}^{-1}$, 10.6% of total POC export as POC [Phyto]), indicating that the highest amount of POC is transported to the seafloor for benthic consumption and potential sequestration at the end of the growing season — not, as we expected, in spring. Our results show an order of magnitude higher POC export compared to deeper sites in the open Baltic Sea (Cisternas-Novoa et al. 2019), indicating that site-specific characteristics and time of the year are important factors regulating POC flux from surface waters to the seafloor.

The highest respiration in various benthic habitats of the coastal Baltic Sea is typically between June and August (Attard et al. 2019). However, in August, benthic respiration on coastal bare sand habitats is $40 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Attard et al. 2019), which equals 7% of the carbon export from the pelagic system. This shows a strong mismatch in pelagic carbon export and benthic respiration, suggesting that the carbon sinking from the pelagic system in August is either permanently buried in the sediment or transported laterally to other areas where it is remineralised.

These counter-intuitive POC export results could be due to an increasing mesozooplankton community grazing on the phytoplankton caused by shifting phenology and composition of mesozooplankton communities with climate warming (Jansson et al. 2020). Long-term data showed that mesozooplankton

is emerging increasingly early in the year at the study site, especially in warmer years with little to no ice cover in winter (Forsblom et al. 2024). During the sampling period, there was little to no ice cover at the site and the ice disappeared 12–17 d earlier in the Gulf of Finland than usual (Finnish Meteorological Institute 2022). This suggests earlier mesozooplankton growth in the year of the study and, consequently, increased grazing. Similarly, shifting mesozooplankton community composition from copepods, which are characterised by the long ontogenetic development, towards smaller, fast-developing organisms like cladocerans and rotifers (Suikkanen et al. 2013, Vehmaa et al. 2018, HELCOM 2023) could shorten the time window between the phytoplankton bloom and zooplankton grazing.

An alternative explanation for the low POC export in spring would be outgassing to the atmosphere, although this scenario is rather unlikely. According to Asmala & Scheinin (2023) and continuous flux measurements at the study site (A. Vähä unpubl. data), the atmospheric fluxes of CO_2 and CH_4 in the study region were lowest in April and July ($-15.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and $0.628 \text{ mmol C m}^{-2} \text{ d}^{-1}$, respectively), reflecting the seasonal growth pattern of the spring phytoplankton community, which is dominated by fast-growing diatoms, leading to a higher net CO_2 influx and remineralization of pelagic OC. As the pelagic OC production is an order of magnitude higher than benthic respiration rates (Attard et al. 2019) or atmospheric fluxes (Asmala & Scheinin 2023) observed in the study area, our results suggest that the high amount of OC produced by phytoplankton is neither outgassed to the atmosphere nor sinking to the seafloor. Instead, it is likely mostly consumed, transformed and re-used in the pelagic system during spring, e.g. transported to higher trophic levels at this time of year, supporting the pelagic food web (Winder & Schindler 2004, Sommer et al. 2012, Hjerne et al. 2019, Asmala & Scheinin 2023). Thus, there is a high production of OC in spring, which accumulates in the pelagic system during the year (Schneider & Müller 2018).

Furthermore, the highest CO_2 and CH_4 flux values were observed in October ($94.8 \text{ mmol C m}^{-2} \text{ d}^{-1}$ and $7.93 \text{ mmol C m}^{-2} \text{ d}^{-1}$, respectively), indicating that the sea becomes oversaturated with carbonated greenhouse gases at the end of the growing season (Asmala & Scheinin 2023). The annual phytoplankton growth dynamic is reflected in these findings, highlighting the primary production during spring which shifts to respiration of the accumulated OC at the end of the growing season (Schneider & Müller 2018, Asmala & Scheinin 2023).

Our results highlight the complex relationships between phytoplankton biomass, community composition and carbon dynamics, with strong seasonal variations observed throughout the year. Our findings emphasise the critical role of keystone diatom species for carbon uptake and production in fuelling carbon turnover in the pelagic food web in spring and the importance of phytoplankton diversity for ecosystem productivity and carbon export in summer.

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