

Seawater browning alters community composition and reduces nutritional quality of plankton in a subarctic marine ecosystem

Tharindu Bandara, Sonia Brugel, Agneta Andersson, and Danny Chun Pong Lau

Abstract: Inflows of coloured terrestrial organic matter cause seawater browning and reduced phytoplankton production in subarctic coastal ecosystems, potentially deteriorating the nutritional quality of marine food webs. We analyzed the fatty-acid (FA) compositions of seston and the zooplankton taxa *Eurytemora affinis* and cladocerans at three locations of the northern Baltic Sea. At the coastal and northerly locations, salinity and phosphorus concentrations were low, while concentrations of humic substances (i.e., terrestrial organic matter) were high. The southerly location showed the opposite trend. The ratio between alga-specific ω 3 polyunsaturated FA and terrigenous monounsaturated FA (MUFA) in *Eurytemora* decreased from south to north, as did the ratio between the alga-specific docosahexaenoic acid (DHA) and terrigenous MUFA in cladocerans. With increasing humic substances, the biomass of DHA-rich phytoplankton decreased and the zooplankton MUFA content increased. Our results indicate that coloured terrestrial organic matter alters the phytoplankton composition, consequently affecting the zooplankton nutritional quality.

Résumé : Les influx de matière organique terrestre causent le brunissement de l'eau de mer et réduisent la production du phytoplancton dans les écosystèmes côtiers subarctiques, ce qui peut se traduire par une détérioration de la qualité nutritionnelle des réseaux trophiques marins. Nous avons analysé la composition d'acides gras du seston, du taxon de zooplancton *Eurytemora affinis* et de cladocères dans trois sites de la mer Baltique septentrionale. Dans les sites côtier et nordique, la salinité et les concentrations de phosphore étaient faibles, alors que les concentrations de substances humiques (c.-à-d. matière organique terrestre) étaient élevées. Le site plus au sud présentait des tendances inverses. Le rapport des acides gras polyinsaturés ω 3 spécifiques aux algues et des acides gras monoinsaturés (AGMI) terrigènes chez *Eurytemora* diminuait du sud au nord, tout comme le rapport de l'acide docosahexanoïque (ADH) spécifique aux algues et des AGMI chez les cladocères. Plus l'abondance de substances humiques était élevée, plus la biomasse de phytoplancton riche en ADH était faible et plus le contenu en AGMI du zooplancton était important. Nos résultats indiquent que de la matière organique terrestre colorée modifie la composition du phytoplancton et a par conséquent une incidence sur la qualité nutritionnelle du zooplancton. [Traduit par la Rédaction]

1. Introduction

Inputs of coloured terrestrial organic matter to subarctic marine environment, such as the northern Baltic Sea, cause browning of seawater, which enhances light attenuation and reduces phytoplankton production (Andersson et al. 2015, 2018). Browning is expected to intensify in the northern Baltic Sea in the next coming 100 years, due to ongoing widespread declines in atmospheric acid deposition combined with climate change-induced increases in catchment vegetation and precipitation in the northern landscape that result in increased inflows of coloured terrestrial organic matter to the coastal systems (Roulet and Moore 2006; Larsen et al. 2011; de Wit et al. 2016; Roberge et al. 2020). Over the last decades, terrestrially derived total organic carbon has significantly increased in the northern Baltic Sea (in the Bothnian Bay and Quark; Fleming-Lehtinen et al. 2015). Similarly, a period with higher precipitation and freshwater inflow to the northern Baltic

Sea (Gulf of Bothnia) was shown to result in reduced primary production, which further affected the benthic fauna negatively (Wikner and Andersson 2012; Eriksson-Wiklund and Andersson 2014). Inputs of terrestrial organic matter may indirectly favor the development of cyanobacteria, for example via co-transported nutrients (Stolte et al. 2006), but both terrestrial organic matter and cyanobacteria are of low food quality for zooplankton (Guschina and Harwood 2009; Berggren et al. 2018; Senar et al. 2019). Browning can also promote the production of heterotrophic bacteria instead of phytoplankton, thereby enhancing the bacterial trophic pathway (bacteria–ciliates – heterotrophic flagellates – zooplankton; Wikner and Andersson 2012). However, there is evidence that this bacterial trophic pathway does not favor zooplankton growth and reproduction, as it is dominated by components that have poorer food quality than phytoplankton (Taipale et al. 2014). It is expected that increased browning will negatively affect the trophic support

Received 10 May 2021. Accepted 23 January 2022.

T. Bandara. Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden; Department of Animal Science, Faculty of Animal Science and Export Agriculture, Uva Wellasa University, Passara Road, 90000 Badulla, Sri Lanka.

S. Brugel and A. Andersson. Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden; Umeå Marine Sciences Centre, Umeå University, 90571 Hörnefors, Sweden.

D.C.P. Lau. Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden; Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, 75007 Uppsala, Sweden.

Corresponding author: Tharindu Bandara (email: tharindu.bandara@umu.se).

© 2022 The Author(s). This work is licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/) (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

of phytoplankton for the higher trophic levels (Andersson et al. 2015; Degerman et al. 2018). However, it is still poorly known whether browning will also lead to changes in the marine food-web quality, such as in the fatty-acid (FA) composition of phytoplankton and zooplankton.

The nutritional quality of prey organisms can be defined by their tissue content of polyunsaturated fatty acids (PUFA) in the omega-3 and omega-6 families (Brett and Müller-Navarra 1997; Müller-Navarra et al. 2004). Long-chain PUFA that contain ≥ 20 carbon atoms, such as eicosapentaenoic acid (EPA, 20:5 ω 3) and docosahexaenoic acid (DHA, 22:6 ω 3), are particularly required for physiological functions in animals (Gladyshev et al. 2013). These long-chain PUFA are mainly biosynthesized de novo by algae (Napolitano 1999), although recent research suggests that a wide range of invertebrate taxa possess the genes for potential PUFA synthesis via elongation and desaturation of precursor FA (Kabeya et al. 2018). Consumers thus mainly obtain PUFA from the diet. For pelagic herbivores such as copepods, DHA is necessary for active overwintering, nervous system development (Persson and Vrede 2006), and successful egg hatching (Arendt et al. 2005). In comparison to copepods, cladocerans have higher EPA content as an adaptation for higher reproductive success and somatic growth (Smyntek et al. 2008). Aquatic predators such as fish depend on long-chain PUFA for growth, reproductive success, regulation of ion balance, and immune functions (Glencross 2009). The availability of long-chain PUFA in prey organisms has been shown to affect the efficiency of the trophic transfer and the quality and health of consumers (Müller-Navarra et al. 2000; Brett et al. 2006; Arts and Kohler 2009). Long-chain PUFA thus can be used as quantifiers of food-web quality (Brett and Müller-Navarra 1997).

The diet of crustacean zooplankton (i.e., seston) comprises phytoplankton, terrestrial organic matter, and bacteria, which differ in their FA composition (Napolitano 1999). The FA composition of phytoplankton is taxon-specific (Galloway and Winder 2015). Changes of the phytoplankton community composition, therefore, will also lead to changes in basal PUFA production and availability. Phytoplankton such as diatoms, dinoflagellates, and cryptophytes can effectively produce long-chain PUFA, while other phytoplankton such as cyanobacteria and chlorophytes are devoid of long-chain PUFA (Taipale et al. 2016). Diatoms are rich in EPA, while dinoflagellates contain high DHA content (Mishra 2015). Phytoplankton are generally devoid of long-chain saturated FA (LongSAFA; i.e., with ≥ 20 carbon) and have a low content of monounsaturated FA (MUFA). In contrast, both LongSAFA and MUFA are relatively abundant in terrestrial organic matter (Napolitano 1999; Hiltunen et al. 2019). Compared to PUFA, LongSAFA and MUFA have a lower nutritional value and may not be efficiently assimilated by zooplankton. Lower retention of LongSAFA in zooplankton can also be due to preferential excretion (Hiltunen et al. 2015), rapid oxidation (Schulz 2002), or conversion to other FA (Lichti et al. 2017). Increased browning may promote the development of cyanobacteria and bacteria that lack long-chain PUFA, which may reduce the overall nutritional quality of seston (Taipale et al. 2016, 2018). Reduced seston quality will in turn cause decreases in long-chain PUFA content of zooplankton (Hiltunen et al. 2015; Taipale et al. 2016, 2018; Lau et al. 2021). This may consequently lower the marine energy transfer efficiency, but the negative impacts of browning are yet to be verified.

The Baltic Sea is a high-latitude, semi-enclosed, brackish water ecosystem, characterized by strong environmental and ecological gradients. The length of the productive season, water temperature, salinity, phosphorus concentration, and primary production in the Baltic Sea increase from the north to the south (Andersson et al. 1996, 2015). The limiting nutrient changes from phosphorus to nitrogen along the north-south and the coastal-offshore gradients (Granéli et al. 1990; Andersson et al. 1996; Tamminen and Andersen 2007). The influx of freshwater and terrestrial organic matter further enhances the gradients in salinity, humic substances, and dissolved organic carbon (DOC) concentration (Hoikkala

et al. 2015). Increased browning in the coastal and northern regions of the Baltic Sea potentially alters the phytoplankton assemblages (Paczkowska et al. 2017). Changes of phytoplankton community composition and biomass along the environmental gradients are likely to affect the food-web quality and dynamics of the Baltic Sea (Andersson et al. 2015; Kniebusch et al. 2019).

In this study, we quantified the community composition of phytoplankton and the FA compositions of seston and crustacean herbivorous mesozooplankton ($>200 \mu\text{m}$) at three sampling sites from north to south of the northern Baltic Sea, aiming to elucidate the impacts of inflows of terrestrial organic matter and nutrients on the nutritional quality of the planktonic food chains. We selected common herbivorous mesozooplankton taxa (i.e., copepods and cladocerans) due to their differences in PUFA requirement (Dalsgaard et al. 2003) and their wide distribution in the Baltic Sea (Telesh et al. 2009, Karlsson and Winder 2020). The coastal and northern regions of the northern Baltic Sea are known to receive more humic substances from freshwater inflows than do the offshore regions (Andersson et al. 2015). Increases in humic substances concentration can negatively impact the phytoplankton production by increasing light limitation (Paczkowska et al. 2017) and can directly affect the seston FA composition as terrestrial organic matter lacks long-chain PUFA (Napolitano 1999). We expected that (i) seston at the southerly clear-water offshore station has higher biomass of PUFA-rich phytoplankton taxa, and therefore has higher DHA, EPA, and overall PUFA content than do its coastal and northerly counterparts, and (ii) PUFA concentration of herbivorous zooplankton follows the spatial PUFA pattern of phytoplankton (i.e., higher in the southern offshore region), as FA composition of zooplankton strongly reflects that of their diet (Brett et al. 2006).

2. Materials and methods

2.1. Sampling

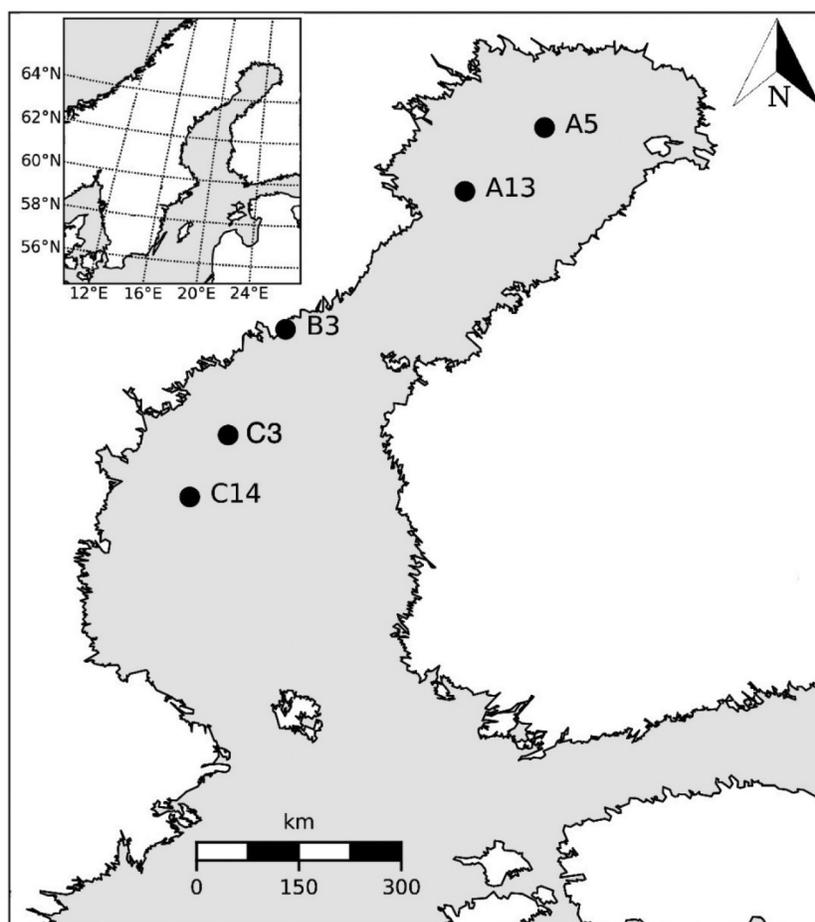
Seston and zooplankton samples for FA analysis were collected in the northern Baltic Sea, in the framework of sampling campaigns of the Swedish National Marine Monitoring program. Three stations (A5, B3, and C14) were sampled in August–September 2017. Station A5 (65°10'N, 23°14'E, depth 90 m) is located in the Bothnian Bay, while stations B3 (63°30'N, 19°49'E, depth 25 m) and C14 (62°06'N, 18°33'E, depth 85 m) are located in the Bothnian Sea. Stations A5 and C14 are offshore stations and station B3 is a coastal station (Fig. 1). The sampling sites thus represent the north-south gradient.

Water was sampled with an integrated hose from 0 to 10 m depth to collect samples for analysis of seston FA composition. 300 mL of the collected water was filtered onto precombusted (5 hours at 450 °C) GF/F filters (25 mm diameter). The filters were frozen at -20 °C and later freeze-dried before FA extraction.

At each sampling station, four vertical net hauls (WP2 plankton net, 90 μm mesh size) were deployed for zooplankton collection. The zooplankton collected were starved overnight in filtered (0.2 μm) natural seawater at 4 °C in dark to empty the gut content. Afterward, the mesozooplankton were sorted according to taxa: *Eurytemora affinis* (Copepoda: Temoridae) (hereinafter *Eurytemora*) and cladocerans (mostly *Bosmina coregoni maritima* (Phyllopoa: Bosminidae)). These taxa were selected to represent the herbivorous food chain from phytoplankton to higher trophic level (i.e., fish). At the sampling stations, major mesozooplankton taxa were cladocerans (predominantly herbivorous), *Eurytemora* (predominantly herbivorous), *Limnocalanus macrurus* (omnivorous) and *Acartia bifilosa* (omnivorous, rare at station A13). We focused on herbivorous mesozooplankton in this study, thus only *Eurytemora* and cladocerans were sorted. The sorted zooplankton samples were frozen at -20 °C and later freeze-dried before FA extraction.

To elucidate how phytoplankton assemblages and FA composition of seston and zooplankton changed along the environmental

Fig. 1. Sampling locations in the northern Baltic Sea. Map created with basemap 1.2.2 using python 3.7.



gradients, we obtained data of environmental variables as well as phytoplankton and zooplankton community compositions and biomass at the sampling sites. These variables were monthly measured by the Swedish National Marine Monitoring program following the HELCOM guidelines (2017) from January to October 2017. The environmental variables were (all averaged from surface to 10 m depth): salinity, DOC, humic substances, total phosphorus (P), and total nitrogen (N) concentrations. We used the combination of DOC and humic substances concentrations to assess the degree of seawater browning, as browning has been shown to be positively associated with DOC in the northern Baltic Sea (Harvey et al. 2015). DOC is a measure of coloured and noncoloured dissolved organic carbon, while humic substances are a measure of dissolved and particulate coloured matter. The phytoplankton data were collected from depth-integrated (surface to 10 m depth) water samples. Mesozooplankton for community composition and biomass measurements were sampled from whole water column using the method described above. All of these data are available at <https://sharkweb.smhi.se/>.

Since zooplankton accumulate seston FA during the active growth season, we used monthly phytoplankton data of the sampling stations from July–September 2017. For logistic reasons, seston and zooplankton samples for FA analyses had to be collected from stations A5 and C14; however, as phytoplankton were not regularly monitored at A5 and C14 stations, we also used the phytoplankton data from other nearby stations located in the same basins (A13 at 64°43'N, 22°04'E and C3 at 62°39'N, 18°57'E) in July–September 2017. Data from September 2017 showed that the phytoplankton composition was relatively similar at A5 and A13

and at C3 and C14. Thus, we assumed that A13 and C3 stations represent the A5 and C14 stations, respectively.

2.2. Fatty acid analyses

Methods for FA analyses of zooplankton and seston are reported in Bergström et al. (2020), which were modified from the method in Lau et al. (2012). Approximately 5 mg of homogenized freeze-dried sample of the presorted zooplankton taxa (i.e., *Eurytemora affinis* and cladocerans) were measured into a microcentrifuge tube, added with 20 μL internal standard D₂₉-pentadecanoic acid (120 $\text{ng}\cdot\mu\text{L}^{-1}$; C/D/N isotopes, Essex, UK) and 400 μL 3:2 (v:v) hexane–isopropanol solution to extract the FA. The solution was vortexed. Two metal beads were added and the mixture was shaken in a mixer mill (Mixer Mill MM400, Retsch GmbH, Haan, Germany) at a frequency of 30 s^{-1} for 120 s. The metal beads were removed and 111 μL of 6.67% Na_2SO_4 was added. Samples were kept in dark at 4 °C for 30 min and then centrifuged at 18845g at 4 °C for 5 min. 150 μL of the top organic phase was transferred to a 1.5 mL vial and then dried at 0 bar for 2 hours in an evaporator (miVac Quattro Concentrator, Genevac, Ipswich, England).

The dried extract was added with 60 μL hexane and 60 μL internal standard D33-methyl heptadecanoate (10 $\text{ng}\cdot\mu\text{L}^{-1}$; Sigma–Aldrich Sweden AB, Stockholm, Sweden), and vortexed. For methylation, 60 μL of the sample was transferred to a new vial, added with 200 μL of 1:17:83 (v:v:v) trimethylsilyldiazomethane:isopropanol:dichloromethane, and vortexed. The vial was then uncapped, and the methylation continued for at least 16 h at room temperature until the solution was dried. The resultant FA methyl esters were

dissolved in 60 μL heptane containing internal standards tridecane and octacosane ($10 \text{ ng}\cdot\mu\text{L}^{-1}$ each) and vortexed. Concentrations of the FA methyl esters were quantified using a gas chromatography-mass spectrometry (7890 A GC, Agilent Technologies, California, United States; Pegasus High Throughput TOF-MS, Michigan, United States) with a DB-5 capillary column (length 30 m, internal diameter 250 μm , film thickness 0.25 μm ; Agilent Technologies). Individual FA were identified by using the Supelco 37 Component FAME Mix (Sigma-Aldrich Sweden AB, Stockholm, Sweden) and the Bacterial Acid Methyl Ester BAME Mix (Sigma-Aldrich Sweden AB). Splitless injection of 1 μL was used for each sample. Concentrations of individual FA are reported as percentages (%) of total FA in the sample.

2.3. Statistical analyses

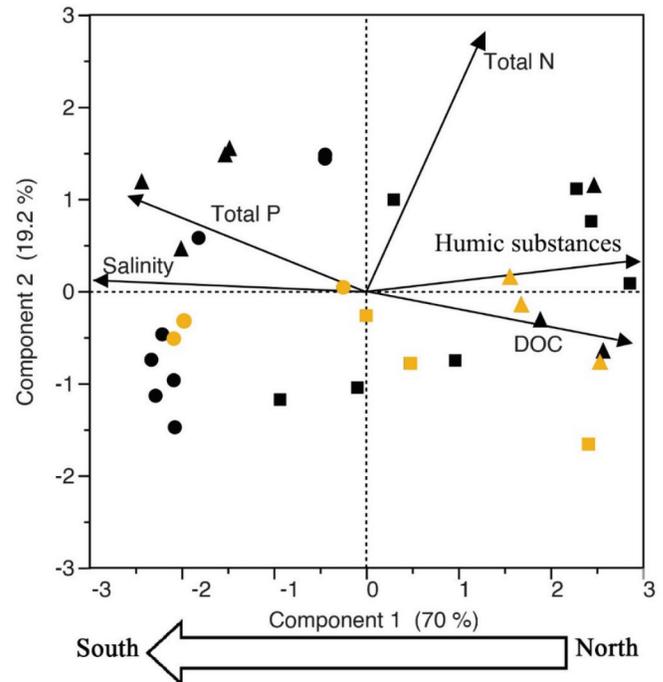
The seston and zooplankton FA were classified into major FA groups: long-chain saturated FA (LongSAFA), short-saturated FA (ShortSAFA), monounsaturated FA (MUFA), polyunsaturated FA (PUFA). The FA data were logit-transformed to meet the assumptions of normality and homoscedasticity for subsequent statistical analyses. Seston MUFA and LongSAFA are largely sourced from terrestrial organic matter (Napolitano 1999). This is also supported by oleic acid (18:1 ω 9c) constituting >76% of the MUFA in seston in our study, and oleic acid is much more abundant in plants than in algae (Napolitano 1999). Our preliminary analysis showed a strong positive linear relationship between seston MUFA and LongSAFA (linear regression: $F_{[2,6]} = 9.3$, $R^2 = 0.70$, $p < 0.03$); thus, only MUFA were used to represent the FA of terrestrial origin in seston and zooplankton. We then calculated the ratios between different alga-specific FA and MUFA (i.e., DHA:MUFA, EPA:MUFA, and ω 3 PUFA:MUFA) as indicators of the relative contributions of algae and terrestrial organic matter in the plankton. The higher ratios indicate the better nutritional quality of the plankton. For both seston and zooplankton, we used one-way ANOVA and post hoc Tukey's HSD test to compare the differences of major FA and FA ratios among the locations.

We used principal component analysis (PCA) to examine the spatial and temporal patterns of the environmental variables measured from January to October 2017 at A5, B3, and C14 stations. All these variables were log₁₀-transformed and standardized before the PCA. Scores of the sampling stations on the first and second principal components (i.e., PC1 and PC2) were extracted after the PCA. We considered that environmental conditions in July–September were the most relevant and had the strongest influence on seston and zooplankton, which were collected in August–September. Thus, only the summer scores (July–September) were selected and averaged by station.

Owing to the small sample size and variable distribution, the relationships between pairs of variables were mostly evaluated using Spearman's rank correlation; however, linear regression was also used when meeting assumptions. The averaged PCA summer scores (PC1_{summer} and PC2_{summer}) were used as the independent variables in the Spearman's rank correlations with the FA responses (DHA, DHA:MUFA, EPA:PUFA, ω 3 PUFA:MUFA ratios) of seston and zooplankton, as we intended to identify the environmental conditions that best described the changes in seston and zooplankton FA.

We classified chrysophytes, cryptophytes, dinoflagellates, and euglenophytes as DHA-rich phytoplankton taxa and diatoms as an EPA-rich taxon, according to Brett and Müller-Navarra (1997) and Taipale et al. (2016) (ca. 2%–5% of dry weight). Then we used Spearman's rank correlation to test whether the total biomass of DHA-rich phytoplankton taxa (PhytoBiomass_{DHA-rich}) changed with the environmental conditions represented by PC1_{summer} and PC2_{summer}. The influence of PhytoBiomass_{DHA-rich} and humic substances concentration on zooplankton (DHA:MUFA) ratio was tested using linear regression.

Fig. 2. Principal component analysis of environmental variables in the northern Baltic Sea stations in January–October 2017. Symbols represent measurements in individual months: triangles — A5 station, squares — B3 station, circles — C14 station. Yellow symbols are measurements in summer (i.e., July–September). DOC, dissolved organic carbon concentration; Total P and Total N, concentrations of total phosphorus and nitrogen, respectively.



All statistical tests were performed using JMP Pro software version 14.0. Significance of the tests was determined at $p < 0.05$, and all values are reported as mean \pm SD.

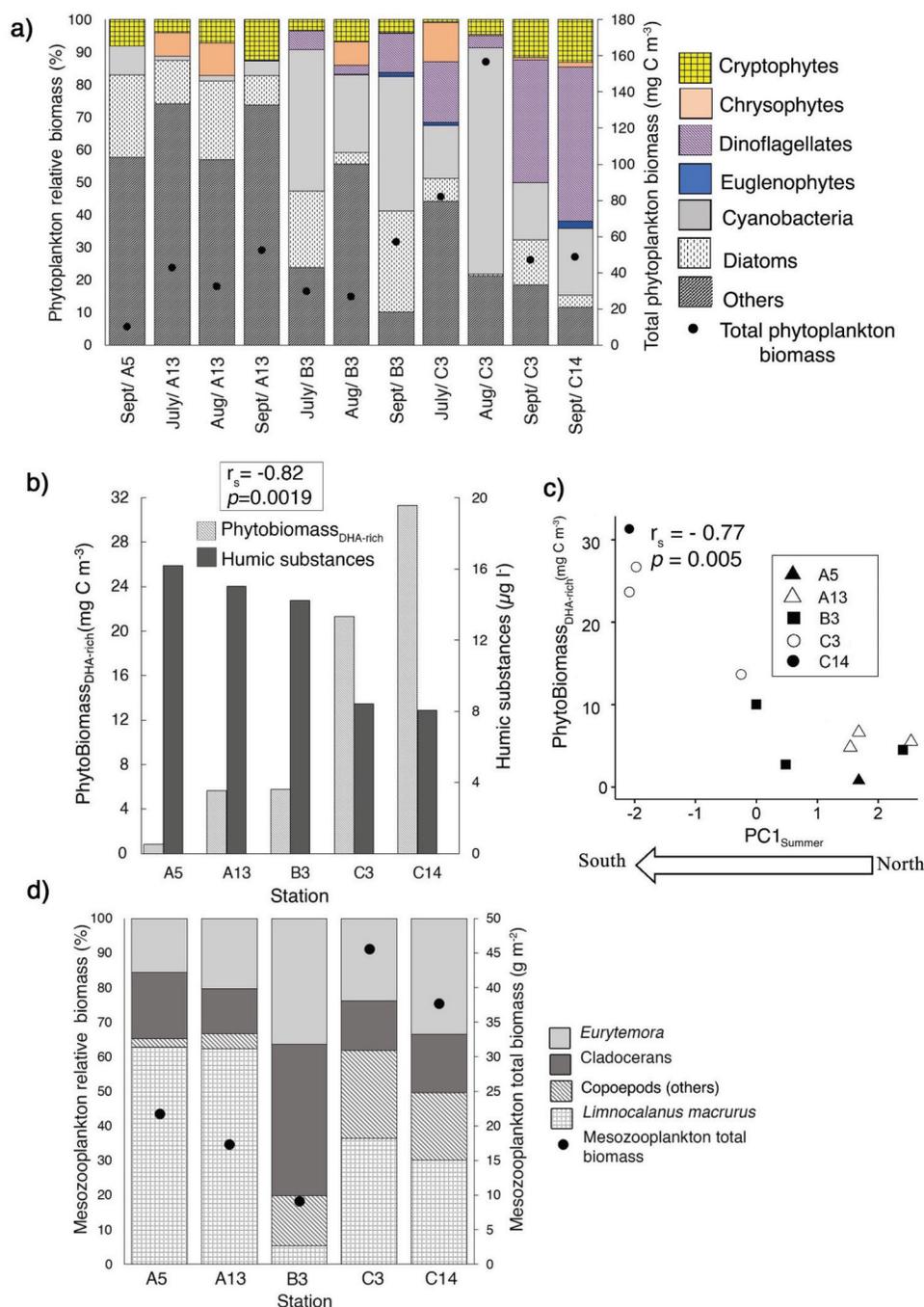
3. Results

The PCA of environmental data in 2017 showed that the first component (PC1) accounted for 70% of the total variance and was strongly correlated with salinity, total P, humic substances and DOC concentrations, while the second component (PC2) explained 19.2% of the total variance and was correlated with total N concentration (Fig. 2). The PC1 indicated the north–south gradient (A5–C14), which was clearly influenced by browning (i.e., DOC and humic substances) as well as salinity and total P (Fig. 2). Among the three sampling stations, salinity ranged between 2.4–5.3 psu, total N between 0.21–0.30 $\text{mg}\cdot\text{L}^{-1}$, total P between 0.004–0.02 $\text{mg}\cdot\text{L}^{-1}$, DOC between 3.83–4.93 $\text{mg}\cdot\text{L}^{-1}$, and humic substances between 8.0–19.9 $\mu\text{g}\cdot\text{L}^{-1}$. The environmental conditions differed between northern and southern stations. Compared to other stations, higher salinity and total P concentration were found at the southern station (C14). In contrast, the coastal (B3) and the northern regions (A5) overlapped and had higher concentrations of humic substances and DOC (Fig. 2, Fig. 3b). On average, the humic substances concentrations at the coastal and northern stations were approximately two times higher than that of the southern station (Fig. 3b).

3.1. Community composition of phytoplankton and zooplankton

Among all five stations, the lowest total phytoplankton biomass was recorded at the northernmost station A5 and the highest was observed at C3, the southern station (Fig. 3a). The cyanobacteria biomass at C3 peaked in August, while at A13 and B3 the peaks were observed in September (Fig. 3a). The EPA-rich diatoms were

Fig. 3. (a) Phytoplankton relative biomass (%) and total phytoplankton biomass. Cryptophytes, chrysophytes, dinoflagellates, and euglenophytes are classified as DHA-rich phytoplankton taxa, as per Brett and Müller-Navarra (1997) and Taipale et al. (2016). (b) Biomass of DHA-rich phytoplankton (PhytoBiomass_{DHA-rich}) and humic substances concentration at the sampling stations, and their Spearman's rank correlation. (c) Spearman's rank correlation between DHA-rich phytoplankton biomass (PhytoBiomass_{DHA-rich}) (mg C·m⁻³) and PC1_{Summer}. (d) Relative biomass (%) and total biomass of mesozooplankton at the sampling stations.



found at all stations in varying proportion from July–September. However, the highest diatom biomass was observed at B3 station in September (Fig. 3a). In July–September, the proportion of PhytoBiomass_{DHA-rich} in total phytoplankton biomass increased from north to south (i.e., from 8% at station A13 to 64% at station C14; Fig. 3a). At A13 station, chrysophytes were the most abundant group among the DHA-rich phytoplankton taxa in July and August, while cryptophytes became more dominant in September. At B3 station, dinoflagellates dominated the DHA-rich phytoplankton

taxa in July and September, but chrysophytes dominated in August. At C3 station, dinoflagellates dominated the DHA-rich phytoplankton taxa in July and September, while cryptophytes dominated in August. Relatively similar phytoplankton biomass distribution was observed between C3 and C14 and between A5 and A13 (e.g., at both C3 and C14 stations in September, the phytoplankton biomass was dominated by dinoflagellates and relatively similar biomass was observed for cyanobacteria, cryptophytes, and diatoms; Fig. 3a). Across the north–south gradient, the PhytoBiomass_{DHA-rich} increased when

Fig. 4. Spearman's rank correlation between PC2_{summer} and (a) logit-transformed DHA concentrations, (b) DHA:MUFA ratios, and (c) ω3 PUFA:MUFA ratios of seston at the sampling stations.

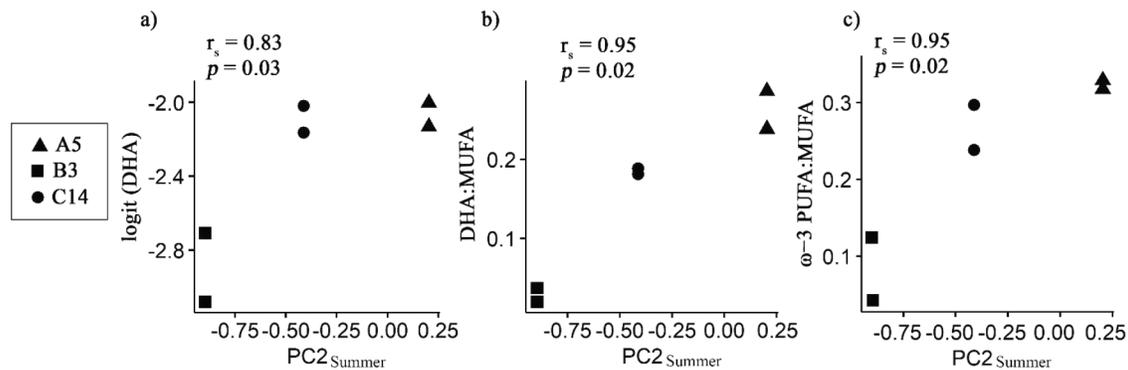
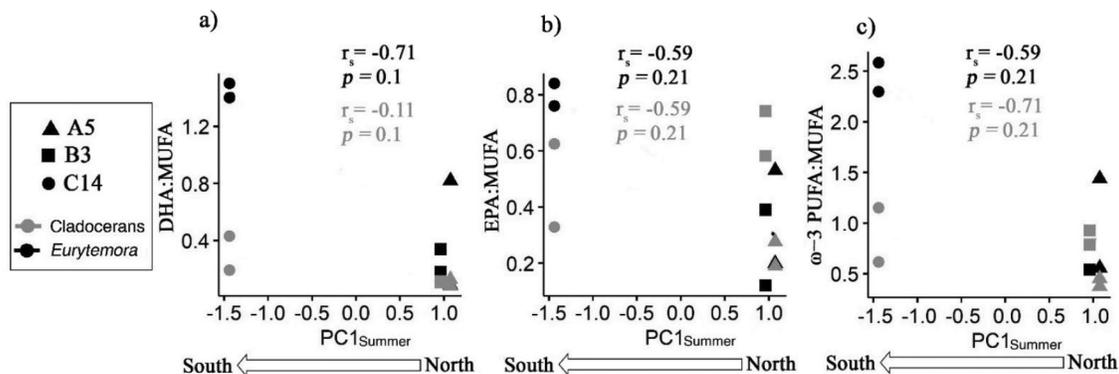


Fig. 5. Spearman's rank correlation between PC1_{summer} and (a) DHA:MUFA, (b) EPA:MUFA, and (c) ω3 PUFA:MUFA ratios of *Eurytemora* and cladocerans at the sampling stations.



the DOC and humic substances concentrations decreased, and there was a negative relationship between humic substances concentration and PhytoBiomass_{DHA-rich} ($r_s = -0.82$; $p < 0.05$; Figs. 3b, 3c).

The total mesozooplankton biomass increased from the north (A13) to the south (C3), as well as the relative and absolute biomass of herbivorous mesozooplankton taxa (i.e., cladocerans and *Eurytemora*; from ~35% at A13 to 50% at C14; Fig. 3d). Cladocerans were the dominant herbivorous taxa at the coastal station (B3), while *Eurytemora* was the dominant herbivorous taxa at A13 and C14 stations.

3.2. Fatty acids of seston and zooplankton

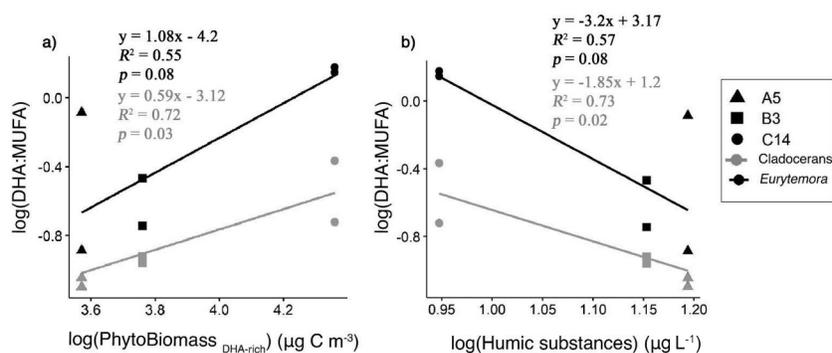
We identified in total 22 FA in the seston samples and 32 FA in the zooplankton samples. Saturated FA (SAFA) accounted for ~89% of total FA of seston. In seston, the relative concentration of PUFA was 6%–7% and that of MUFA was 3%–5% (Table A1). The relative concentration of DHA was about 2 times higher than that of EPA in seston. In both *Eurytemora* and cladocerans, the relative SAFA concentrations ranged from 36%–48%. The relative PUFA concentration of *Eurytemora* was slightly higher (24%–37%) than that of cladocerans (21%–30%). In both *Eurytemora* and cladocerans, the concentrations of ω3 PUFA were higher than those of ω6 PUFA. The relative MUFA concentration in cladocerans (28%–38%) was higher than that of *Eurytemora* (12%–24%). *Eurytemora* was richer in DHA (6%–18%) compared to cladocerans (3%–8%). In contrast, cladocerans were richer in EPA (9%–18%) than was *Eurytemora* (6%–10%). These differences were possibly caused by different DHA and EPA requirements between copepods and cladocerans (Brett et al. 2009), and (or) their different feeding strategies and diet (Dalsgaard et al. 2003). The ω3:ω6 ratio of seston was <1, while that of the zooplankton was >1.

We used DHA:MUFA, EPA:MUFA, and ω3 PUFA:MUFA ratios to indicate the relative contributions of algae compared to that of terrestrial organic matter in both seston and zooplankton, since DHA, EPA, and ω3 PUFA are much richer in algae. Relative concentrations of DHA, and the DHA:MUFA and ω3 PUFA:MUFA ratios in seston differed among stations ($p < 0.05$), where the lowest values were observed at B3 station (Table A2). Seston DHA and DHA:MUFA and ω3 PUFA:MUFA ratios were positively correlated with PC2_{summer} (Fig. 4). In cladocerans, the DHA:MUFA and ω3 PUFA:MUFA ratios and the relative PUFA concentrations did not differ among stations (Table A3), but higher values were recorded at the southern station (C14). The ω3 PUFA:MUFA and DHA:MUFA in *Eurytemora* differed among stations and were higher at the southern station (C14) (Table A4; Figs. 5a, 5c). The DHA:MUFA, EPA:MUFA, and ω3 PUFA:MUFA ratios of both *Eurytemora* and cladocerans were not correlated with PC1_{summer} (Fig. 5). However, the DHA:MUFA ratios of both *Eurytemora* and cladocerans were positively correlated to PhytoBiomass_{DHA-rich} and negatively correlated with humic substances concentrations (Figs. 6a, 6b). These results suggest the direct (terrestrial organic matter as a food source) and indirect negative effects (via impacts on PhytoBiomass_{DHA-rich}) of increasing terrestrial organic matter on the nutritional quality of zooplankton.

4. Discussion

Our results showed that the north–south gradients in humic substances, DOC, and nutrients in the northern Baltic Sea are reflected in the phytoplankton biomass and community composition, which in turn influences the zooplankton quality. In contrast to our first prediction, the southerly station had low seston

Fig. 6. Relationships of DHA:MUFA ratio of *Eurytemora* and cladocerans with (a) PhytoBiomass_{DHA-rich} ($\mu\text{g C}\cdot\text{m}^{-3}$) and (b) humic substances concentration ($\mu\text{g}\cdot\text{L}^{-1}$). Data are log₁₀-transformed.



quality as manifested by the low PUFA:MUFA ratios. Although the total biomass of DHA-rich phytoplankton taxa was high at the southerly station, the low PUFA:MUFA ratio in seston might be attributed to the relatively high cyanobacterial biomass (Fig. 3a). Cyanobacteria also contain MUFA, although with lower amounts as compared to the terrestrial organic matter (Vargas et al. 1998; Napolitano 1999; Bauersachs et al. 2017). *Eurytemora* and cladocerans FA quality (i.e., DHA:MUFA and ω 3 PUFA:MUFA) was higher at the southern station than at the northern or the coastal stations, supporting our second prediction. The higher zooplankton FA quality was likely linked to the greater biomass of DHA-rich phytoplankton taxa at the southern station. Based on these multiple lines of evidence, we infer that the DHA:MUFA ratio is a potential indicator for quality changes in zooplankton in response to environmental alterations and that ongoing browning will further reduce the pelagic food-web quality in northern marine ecosystems.

4.1. Seston fatty-acid composition and quality

In the coastal region, the low DHA content and FA ratios (DHA:MUFA, ω 3 PUFA:MUFA, and ω 3: ω 6) in seston could be attributed to the high concentrations of humic substances and high relative biomass of cyanobacteria (Figs. 3a, 3b). The relative biomass of cyanobacteria showed a negative correlation with PC_{2summer} (Fig. A1), which was positively associated with total N (Fig. 2). The coastal station had the lowest total N that may benefit the development of nitrogen-fixing cyanobacteria. The station with the lowest relative biomass of cyanobacteria (A5) had the highest seston DHA and DHA:MUFA and ω 3 PUFA:MUFA ratios. All these results suggest the negative effects of cyanobacteria on overall seston quality. Our results are in line with previous studies that showed the association of lower seston nutritional quality with increased cyanobacteria dominance in seston (Senar et al. 2019; Schmidt et al. 2020). The relative concentrations of DHA, EPA, and overall PUFA of seston in our study were lower than those of seston in northern lakes with DOC concentrations ranging from 2–10 $\text{mg}\cdot\text{L}^{-1}$ (Strandberg et al. 2015; Lau et al. 2021). The seston composition of the boreal lakes reported in Strandberg et al. (2015) largely consisted of PUFA-rich cryptophytes and diatoms and to a modest extent of cyanobacteria. In contrast to Strandberg et al. (2015), the seston in our study consisted of relatively smaller proportions of PUFA-rich phytoplankton and larger proportions of cyanobacteria, which may explain the lower nutritional FA quality of seston observed in our study.

Over the years, changes of global climatic conditions have increased the occurrence of cyanobacteria in aquatic ecosystems. In northern nutrient-poor lakes, the presence of cyanobacteria is favored by changes in climate (i.e., increased temperature and variations in precipitation; Freeman et al. 2020), while in the Baltic Sea, the increase of cyanobacterial blooms is also attributed

to other anthropogenic stressors (Stal et al. 2003). Many cyanobacterial species have advantageous traits to thrive in freshwater and marine ecosystems (Freeman et al. 2020). For example, cyanobacteria can efficiently photosynthesize under low light conditions owing to their accessory pigment composition, and they can also access nutrients by using various buoyancy regulation mechanisms (Ganf and Oliver 1982). Some cyanobacteria can also utilize nutrients from terrestrial organic matter, which gives them a competitive advantage over other photoautotrophs (Benavides et al. 2017). However, cyanobacteria affect the seston FA composition as they are devoid of PUFA, and they are poor-quality dietary resources that have a negative impact on growth and reproduction of zooplankton (Taipale et al. 2014). A recent study found that the increasing biomass of the picocyanobacterium *Synechococcus* sp. has contributed to ~50% reduction of summer copepod abundance on the Northeast Atlantic shelves (Schmidt et al. 2020). Increased *Synechococcus* sp. biomass also promotes the bacterial trophic pathway (*Synechococcus*-flagellates-ciliates-copepods-fish) that is relatively energy inefficient due to the higher numbers of trophic levels and the lower-quality primary producers (Schmidt et al. 2020). Therefore, increasing biomass of cyanobacteria may lower seston FA quality and trophic transfer efficiency in pelagic food webs.

Our results are in line with earlier studies that showed that the phytoplankton community in the northern Baltic Sea is associated with changes in concentrations of nutrients and humic substances (Andersson et al. 1996; Paczkowska et al. 2017). The southern station, where the humic substances concentration was the lowest, had the highest DHA-rich phytoplankton biomass. In contrast, a higher concentration of humic substances was associated with a decrease in the biomass of DHA-rich phytoplankton at the northern and the coastal stations, despite distinct nutrient availability. Previous studies have also reported that browning in boreal lakes has altered phytoplankton biomass and thereby reduced the PUFA availability in seston (Strandberg et al. 2015; Taipale et al. 2016; but see Hiltunen et al. 2015; Lau et al. 2021). The negative impacts of browning on phytoplankton composition, biomass, and distribution will lower the overall seston FA quality.

In addition to phytoplankton, heterotrophic flagellates and ciliates may also be important seston components (Strandberg et al. 2020), but they were not assessed in our study. Yet, it is unlikely that these organisms alone had provided sufficient amounts of PUFA for zooplankton even in the browner water conditions, due to the inefficient energy transfer via the bacterial trophic pathway (Hiltunen et al. 2017). Since phytoplankton are the major contributor to the seston PUFA (Strandberg et al. 2020; Hessen and Leu, 2006), it is reasonable that changes in their composition had led to variation in seston FA quality in our study.

4.2. Zooplankton fatty-acid composition and quality

The DHA:MUFA ratios of cladocerans and *Eurytemora* were positively associated with PhytoBiomass_{DHA-rich}, and both of these were higher at the clear-water southern station. This suggests that increasing biomass of DHA-rich phytoplankton had resulted in their greater trophic support and DHA transfer to zooplankton. Moreover, the other FA ratios of *Eurytemora* (i.e., EPA:MUFA and ω 3 PUFA:MUFA) followed the same pattern. Although the FA composition of zooplankton is related to multiple factors, including their phylogeny, feeding strategy, and trophic position (Dalsgaard et al. 2003; Persson and Vrede 2006), the PUFA composition of calanoid copepods can be mostly dependent on their diet (Dalsgaard et al. 2003). As the dietary requirement of DHA is higher in copepods than in cladocerans, *Eurytemora* may selectively feed on the DHA-rich phytoplankton taxa despite that the biomass of these taxa was low in the coastal and northern regions in our study (Brett et al. 2009). But at the southern station, the dietary DHA availability increased due to the higher PhytoBiomass_{DHA-rich} (e.g., dinoflagellates), thus the DHA concentrations in *Eurytemora* also remarkably increased. Cladocerans are nonselective feeders of both allochthonous (terrestrial) and autochthonous resources (algae) (DeMott 1986), and deemed to be less dependent on phytoplankton compared to copepods (Berggren et al. 2015). However, the DHA:MUFA ratio of cladocerans followed the same pattern as that of *Eurytemora* in our study. This result suggests that cladocerans also depend on phytoplankton DHA in the northern Baltic Sea, probably due to the fact that DHA is crucial for maintaining membrane functions and fluidity particularly in cold environments (Arts and Kohler 2009). Anyhow, we found higher absolute biomass of both *Eurytemora* and cladocerans at the southern station. This probably reflects that the trophic transfer from seston to zooplankton was enhanced by the high PhytoBiomass_{DHA-rich}.

In agreement with Ravet et al. (2010), we found higher DHA, EPA, and ω 3 PUFA concentrations in both *Eurytemora* and cladocerans than in seston. The ω 3: ω 6 FA ratios in both *Eurytemora* and cladocerans at all stations were greater than 1, while those in seston were below 1. Previous studies have also reported similar results in boreal lakes with different DOC concentrations (Lau et al. 2012; Hiltunen et al. 2015; Taipale et al. 2015; Hixson and Arts 2016). Also, relatively high SAFA concentrations were observed in both *Eurytemora* and cladocerans in our study. But the fractions of LongSAFA were much lower (~12-fold) than those of ShortSAFA in both zooplankton taxa. This reflects that LongSAFA, which are sourced from terrestrial organic matter, were either not efficiently accumulated or preferentially metabolized by zooplankton. Based on the FA results and ω 3: ω 6 FA ratios, we conjecture that zooplankton in the northern Baltic Sea generally received greater trophic support from phytoplankton than from terrestrial organic matter.

Our results indicate that the coloured terrestrial organic matter along with nutrients shape the phytoplankton community and thereby affects the FA composition of both seston and zooplankton in the northern Baltic Sea. To our knowledge, this is the first field study to show that increasing terrestrial organic matter, as reflected by higher DOC and humic substances concentrations, will affect the marine pelagic food-web quality. Our findings are in line with previous studies in boreal lakes where increased terrestrial organic matter concentrations have been found to impair the quality of both seston and zooplankton by reducing their PUFA content (Poste et al. 2019; but see Hiltunen et al. 2015; Lau et al. 2021). Increased inputs of coloured terrestrial organic matter in boreal lakes are also known to reduce the pelagic food-web efficiency and the nutritional quality of higher trophic levels (i.e., fish; Taipale et al. 2016). The northern Baltic Sea has high freshwater inputs and low salinity, similar to the conditions of oligotrophic freshwater ecosystems (Bonaglia et al. 2017). Therefore, reductions in PUFA availability in plankton caused by browning are expected to have strong repercussions for the northern Baltic Sea food webs.

5. Conclusion

We found that the phytoplankton community shifted toward greater proportions of DHA-rich taxa along the decreasing gradient in DOC and humic substances concentrations from north to south of the northern Baltic Sea. The northern and coastal regions had lower biomass of DHA-rich phytoplankton (i.e., dinoflagellates, cryptophytes). Consequently, the browner water in these regions resulted in lower DHA content and DHA:MUFA ratios in zooplankton, especially *Eurytemora*, as compared to those in the southern region. The DHA:MUFA ratio of zooplankton is a potential bioindicator for browning in the Baltic Sea. Increasing inputs of terrestrial organic matter in northerly coastal areas are expected to reduce the PUFA availability in seston and zooplankton, consequently impairing the overall pelagic food-web quality.

Competing interests

The authors declare there are no competing interests.

Acknowledgements

We thank Anne van Woerkom, Alberto Zannella, and the staff at the Umeå Marine Sciences Centre for help in sampling and the Swedish National Environmental Program for collecting the environmental data. We also thank Franziska Frank and the Swedish Metabolomics Centre for assistance in FA analysis. This project was financed by the Swedish research council FORMAS (FR-2019/0007) and by the Swedish research environment EcoChange. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

- Andersson, A., Hajdu, S., Haecky, P., Kuparinen, J., and Wikner, J. 1996. Succession and growth limitation of phytoplankton in the Gulf of Bothnia (Baltic Sea). *Mar. Biol.* **126**: 791–801. doi:10.1007/BF00351346.
- Andersson, A., Meier, H.E.M., Ripszam, M., Rowe, O., Wikner, J., Haglund, P., et al. 2015. Projected future climate change and Baltic Sea ecosystem management. *Ambio*, **44**: 345–356. doi:10.1007/s13280-015-0654-8. PMID:26022318.
- Andersson, A., Brugel, S., Paczkowska, J., Rowe, O.F., Figueroa, D., Kratzer, S., and Legrand, C. 2018. Influence of allochthonous dissolved organic matter on pelagic basal production in a northerly estuary. *Estuar. Coast. Shelf Sci.* **204**: 225–235. doi:10.1016/j.ecss.2018.02.032.
- Arendt, K.E., Jónasdóttir, S.H., Hansen, P.J., and Gärtner, S. 2005. Effects of dietary fatty acids on the reproductive success of the calanoid copepod *Temora longicornis*. *Mar. Biol.* **146**: 513–530. doi:10.1007/s00227-004-1457-9.
- Arts, M.T., and Kohler, C.C. 2009. Health and condition in fish: the influence of lipids on membrane competency and immune response. In *Lipids in aquatic ecosystems*. Edited by M. Kainz, M.T. Brett, and M.T. Arts. Springer, New York. pp 237–256.
- Bauersachs, T., Talbot, H.M., Sidgwick, F., Sivonen, K., and Schwark, L. 2017. Lipid biomarker signatures as tracers for harmful cyanobacterial blooms in the Baltic Sea. *PLoS ONE*, **12**: e0186360. doi:10.1371/journal.pone.0186360. PMID:29036222.
- Benavides, M., Berthelot, H., Duhamel, S., Raimbault, P., and Bonnet, S. 2017. Dissolved organic matter uptake by *Trichodesmium* in the Southwest Pacific. *Sci. Rep.* **7**: 41315. doi:10.1038/srep41315. PMID:28117432.
- Berggren, M., Bergström, A.-K., and Karlsson, J. 2015. Intraspecific autochthonous and allochthonous resource use by zooplankton in a humic lake during the transitions between winter, summer and fall. *PLoS ONE*, **10**: e0120575. doi:10.1371/journal.pone.0120575. PMID:25764501.
- Berggren, M., Bengtson, P., Soares, A.R.A., and Karlsson, J. 2018. Terrestrial support of zooplankton biomass in northern rivers. *Limnol. Oceanogr.* **63**: 2479–2492. doi:10.1002/lno.10954.
- Bergström, A.-K., Jonsson, A., Isles, P.D.F., Creed, I.F., and Lau, D.C.P. 2020. Changes in nutritional quality and nutrient limitation regimes of phytoplankton in response to declining N deposition in mountain lakes. *Aquat. Sci.* **82**: 31. doi:10.1007/s00027-020-0697-1.
- Bonaglia, S., Hylén, A., Rattray, J.E., Kononets, M.Y., Ekeröth, N., Roos, P., et al. 2017. The fate of fixed nitrogen in marine sediments with low organic loading: an in situ study. *Biogeosciences*, **14**: 285–300. doi:10.5194/bg-14-285-2017.
- Brett, M.T., and Müller-Navarra, D. 1997. The role of highly unsaturated fatty acids in aquatic food web processes. *Freshw. Biol.* **38**: 483–499. doi:10.1046/j.1365-2427.1997.00220.x.
- Brett, M.T., Müller-Navarra, D.C., Ballantyne, A.P., Ravet, J.L., and Goldman, C.R. 2006. *Daphnia* fatty acid composition reflects that of their diet. *Limnol. Oceanogr.* **51**: 2428–2437. doi:10.4319/lno.2006.51.5.2428.

- Brett, M.T., Müller-Navarra, D.C., and Persson, J. 2009. Crustacean zooplankton fatty acid composition. In *Lipids in aquatic ecosystems*. Edited by M. Kainz, M.T. Brett, and M.T. Arts. Springer, New York. pp. 115–146.
- Dalsgaard, J., St John, M., Kattner, G., Müller-Navarra, D., and Hagen, W. 2003. Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.* **46**: 225–340. doi:10.1016/S0065-2881(03)46005-7. PMID:14601414.
- Degerman, R., Lefebvre, R., Byström, P., Bämstedt, U., Larsson, S., and Andersson, A. 2018. Food web interactions determine energy transfer efficiency and top consumer responses to inputs of dissolved organic carbon. *Hydrobiologia*, **805**: 131–146. doi:10.1007/s10750-017-3298-9.
- Demott, W.R. 1986. The role of taste in food selection by freshwater zooplankton. *Oecologia*, **69**: 334–340. doi:10.1007/BF00377053. PMID:28311333.
- De Wit, H.A., Valinia, S., Weyhenmeyer, G.A., Fütter, M.N., Kortelainen, P., Austnes, K., et al. 2016. Current browning of surface waters will be further promoted by wetter climate. *Environ. Sci. Technol. Lett.* **3**: 430–435. doi:10.1021/acs.estlett.6b00396.
- Eriksson-Wiklund, A.K., and Andersson, A. 2014. Benthic competition and population dynamics of *Monoporeia affinis* and *Marenzelleria* sp. in the northern Baltic Sea. *Estuar. Coast. Shelf Sci.* **144**: 46–53. doi:10.1016/j.ecss.2014.04.008.
- Fleming-Lehtinen, V., Räsänen, A., Kortelainen, P., Kauppi, P., and Thomas, D.N. 2015. Organic carbon concentration in the northern coastal Baltic Sea between 1975 and 2011. *Estuar. Coasts*, **38**: 466–481. doi:10.1007/s12237-014-9829-y.
- Freeman, E.C., Creed, I.F., Jones, B., and Bergström, A.-K. 2020. Global changes may be promoting a rise in select cyanobacteria in nutrient-poor northern lakes. *Global Change Biol.* **26**: 4966–4987. doi:10.1111/gcb.15189. PMID:32445590.
- Galloway, A.W.E., and Winder, M. 2015. Partitioning the relative importance of phylogeny and environmental conditions on phytoplankton fatty acids. *PLoS ONE*, **10**: e0130053. doi:10.1371/journal.pone.0130053. PMID:26076015.
- Ganf, G.G., and Oliver, R.L. 1982. Vertical separation of light and nutrients as a factor causing replacement of green algae by blue-green algae in the plankton of a stratified lake. *J. Ecol.* **70**: 829–844. doi:10.2307/2260107.
- Gladyshev, M.I., Sushchik, N.N., and Makhutova, O.N. 2013. Production of EPA and DHA in aquatic ecosystems and their transfer to the land. *Prostaglandins Other Lipid Mediat.* **107**: 117–126. doi:10.1016/j.prostaglandins.2013.03.002. PMID:23500063.
- Glencross, B.D. 2009. Exploring the nutritional demand for essential fatty acids by aquaculture species. *Rev. Aquacult.* **1**: 71–124. doi:10.1111/j.1753-5131.2009.01006.x.
- Granéli, E., Kerstin, W., Larsson, U., Granéli, W., and Elmgren, R. 1990. Nutrient limitation of primary production in the Baltic Sea area. *Ambio*, **19**: 142–151.
- Guschina, I.A., and Harwood, J.L. 2009. Algal lipids and effect of the environment on their biochemistry. In *Lipids in aquatic ecosystems*. Edited by M. Kainz, M.T. Brett, and M.T. Arts. Springer, New York.
- Harvey, E.T., Kratzer, S., and Andersson, A. 2015. Relationships between colored dissolved organic matter and dissolved organic carbon in different coastal gradients of the Baltic Sea. *Ambio*, **44**: 392–401. doi:10.1007/s13280-015-0658-4. PMID:26022322.
- Hessen, D.O., and Leu, E.V.A. 2006. Trophic transfer and trophic modification of fatty acids in high Arctic lakes. *Freshw. Biol.* **51**: 1987–1998. doi:10.1111/j.1365-2427.2006.01619.x.
- Hiltunen, M., Strandberg, U., Taipale, S.J., and Kankaala, P. 2015. Taxonomic identity and phytoplankton diet affect fatty acid composition of zooplankton in large lakes with differing dissolved organic carbon concentration. *Limnol. Oceanogr.* **60**: 303–317. doi:10.1002/lno.10028.
- Hiltunen, M., Honkanen, M., Taipale, S., Strandberg, U., and Kankaala, P. 2017. Trophic upgrading via the microbial food web may link terrestrial dissolved organic matter to *Daphnia*. *J. Plankton Res.* **39**: 861–869. doi:10.1093/plankt/fbx050.
- Hiltunen, M., Peltomaa, E., Brett, M.T., Aalto, S.L., Strandberg, U., Oudenampsen, J., et al. 2019. Terrestrial organic matter quantity or decomposition state does not compensate for its poor nutritional quality for *Daphnia*. *Freshw. Biol.* **64**: 1769–1786. doi:10.1111/fwb.13368.
- Hixson, S.M., and Arts, M.T. 2016. Climate warming is predicted to reduce omega-3, long-chain, polyunsaturated fatty acid production in phytoplankton. *Global Change Biol.* **22**: 2744–2755. doi:10.1111/gcb.13295. PMID:27070119.
- Hoikkala, L., Kortelainen, P., Soinne, H., and Kuosa, H. 2015. Dissolved organic matter in the Baltic Sea. *J. Mar. Syst.* **142**: 47–61. doi:10.1016/j.jmarsys.2014.10.005.
- Kabeya, N., Fonseca, M.M., Ferrier, D.E.K., Navarro, J.C., Bay, L.K., Francis, D.S., et al. 2018. Genes for de novo biosynthesis of omega-3 polyunsaturated fatty acids are widespread in animals. *Sci. Adv.* **4**: aar6849. doi:10.1126/sciadv.aar6849. PMID:29732410.
- Karlsson, K., and Winder, M. 2020. Adaptation potential of the copepod *Eurytemora affinis* to a future warmer Baltic Sea. *Ecol. Evol.* **10**: 5135–5151. doi:10.1002/ece3.6267. PMID:32551088.
- Kniebusch, M., Meier, H.E.M., and Radtke, H. 2019. Changing salinity gradients in the Baltic Sea as a consequence of altered freshwater budgets. *Geophys. Res. Lett.* **46**: 9739–9747. doi:10.1029/2019GL083902.
- Larsen, S., Andersen, T.O.M., and Hessen, D.O. 2011. Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biol.* **17**(2): 1186–1192. doi:10.1111/j.1365-2486.2010.02257.x.
- Lau, D.C., Vrede, T., Pickova, J., and Goedkoop, W. 2012. Fatty acid composition of consumers in boreal lakes — variation across species, space and time. *Freshw. Biol.* **57**: 24–38. doi:10.1111/j.1365-2427.2011.02690.x.
- Lau, D.C.P., Jonsson, A., Isles, P.D.F., Creed, I.F., and Bergström, A. 2021. Lowered nutritional quality of plankton caused by global environmental changes. *Global Change Biol.* **27**: 6294–6306. doi:10.1111/gcb.15887. PMID:34520606.
- Lichti, D.A., Rinchar, J., and Kimmel, D.G. 2017. Changes in zooplankton community, and seston and zooplankton fatty acid profiles at the freshwater/saltwater interface of the Chowan River, North Carolina. *PeerJ*. **5**: e3667. doi:10.7717/peerj.3667. PMID:28828262.
- Mishra, G. 2015. Polyunsaturated fatty acids from algae. In *The algae world*. Edited by D. Sahoo and J. Seckbach. Springer, Dordrecht, the Netherlands. pp. 467–481.
- Müller-Navarra, D.C., Brett, M.T., Liston, A.M., and Goldman, C.R. 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature*, **403**: 74–77. doi:10.1038/47469. PMID:10638754.
- Müller-Navarra, D.C., Brett, M.T., Park, S., Chandra, S., Ballantyne, A.P., Zorita, E., and Goldman, C.R. 2004. Unsaturated fatty acid content in seston and trophic-dynamic coupling in lakes. *Nature*, **427**: 69–72. doi:10.1038/nature02210. PMID:14702086.
- Napolitano, G.E. 1999. Fatty acids as trophic and chemical markers in freshwater ecosystems. In *Lipids in freshwater ecosystems*. Edited by M.T. Arts and B.C. Wainman. Springer, New York. pp. 21–44.
- Paczkowska, J., Rowe, O., Schlüter, L., Legrand, C., Karlson, B., and Andersson, A. 2017. Allochthonous matter: an important factor shaping the phytoplankton community in the Baltic Sea. *J. Plankton Res.* **39**: 23–34. doi:10.1093/plankt/fbw081. PMID:28566797.
- Persson, J., and Vrede, T. 2006. Polyunsaturated fatty acids in zooplankton: variation due to taxonomy and trophic position. *Freshw. Biol.* **51**: 887–900. doi:10.1111/j.1365-2427.2006.01540.x.
- Poste, A.E., Hoel, C.S., Andersen, T., Arts, M.T., Færøvig, P.-J., and Borgå, K. 2019. Terrestrial organic matter increases zooplankton methylmercury accumulation in a brown-water boreal lake. *Sci. Total Environ.* **674**: 9–18. doi:10.1016/j.scitotenv.2019.03.446. PMID:31003089.
- Ravet, J.L., Brett, M.T., and Arhonditsis, G.B. 2010. The effects of seston lipids on zooplankton fatty acid composition in Lake Washington, Washington, USA. *Ecology*, **91**: 180–190. doi:10.1890/08-2037.1. PMID:20380207.
- Roberge, J.M., Fries, C., Nomark, E., Måråld, E., Sténs, A., Sonesson, J., et al. 2020. Forest management in Sweden: Current practice and historical background. Skogsstyrelsen, Sweden. Available from <https://www.skogsstyrelsen.se/globalassets/om-oss/rapporter/rapporter-2021/202020192018/rapport-2020-4-forest-management-in-sweden.pdf>.
- Roulet, N., and Moore, T.R. 2006. Browning the waters. *Nature*, **444**: 283–284. doi:10.1038/444283a. PMID:17108948.
- Schmidt, K., Birchill, A.J., Atkinson, A., Brewin, R.J.W., Clark, J.R., Hickman, A.E., et al. 2020. Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. *Global Change Biol.* **26**: 5574–5587. doi:10.1111/gcb.15161. PMID:32506810.
- Schulz, H. 2002. Oxidation of fatty acids in eukaryotes. In *New comprehensive biochemistry*. Edited by D.E. Vance and J.E. Vance. Elsevier, Amsterdam. pp. 127–150.
- Senar, O.E., Creed, I.F., Strandberg, U., and Arts, M.T. 2019. Browning reduces the availability—but not the transfer—of essential fatty acids in temperate lakes. *Freshw. Biol.* **64**: 2107–2119. doi:10.1111/fwb.13399.
- Smyntek, P.M., Teece, M.A., Schulz, K.L., and Storch, A.J. 2008. Taxonomic differences in the essential fatty acid composition of groups of freshwater zooplankton relate to reproductive demands and generation time. *Freshw. Biol.* **53**: 1768–1782. doi:10.1111/j.1365-2427.2008.02001.x.
- Stal, L.J., Albertano, P., Bergman, B., Bröckel, K.V., Gallon, J.R., Hayes, P.K., et al. 2003. BASIC: Baltic Sea cyanobacteria. An investigation of the structure and dynamics of water blooms of cyanobacteria in the Baltic Sea—responses to a changing environment. *Cont. Shelf Res.* **23**: 1695–1714. doi:10.1016/j.csr.2003.06.001.
- Stolte, W., Balode, M., Carlsson, P., Grzebyk, D., Janson, S., Lips, I., et al. 2006. Stimulation of nitrogen-fixing cyanobacteria in a Baltic Sea plankton community by land-derived organic matter or iron addition. *Mar. Ecol. Prog. Ser.* **327**: 71–82. doi:10.3354/meps327071.
- Strandberg, U., Hiltunen, M., Jelkänen, E., Taipale, S.J., Kainz, M.J., Brett, M.T., and Kankaala, P. 2015. Selective transfer of polyunsaturated fatty acids from phytoplankton to planktivorous fish in large boreal lakes. *Sci. Total Environ.* **536**: 858–865. doi:10.1016/j.scitotenv.2015.07.010. PMID:26282609.
- Strandberg, U., Hiltunen, M., Rissanen, N., Taipale, S., Akkanen, J., and Kankaala, P. 2020. Increasing concentration of polyunsaturated fatty acids in browning boreal lakes is driven by nuisance alga *Gonyostomum*. *Ecosphere*, **11**: e03189. doi:10.1002/eecs2.3189.
- Taipale, S.J., Brett, M.T., Hahn, M.W., Martin-Creuzburg, D., Yeung, S., Hiltunen, M., et al. 2014. Differing *Daphnia magna* assimilation efficiencies for terrestrial, bacterial, and algal carbon and fatty acids. *Ecology*, **95**(2): 563–576. doi:10.1890/13-0650.1. PMID:24669748.
- Taipale, S.J., Kainz, M.J., and Brett, M.T. 2015. A low ω₃:ω₆ ratio in *Daphnia* indicates terrestrial resource utilization and poor nutritional condition. *J. Plankton Res.* **37**: 596–610. doi:10.1093/plankt/fbv015.
- Taipale, S.J., Vuorio, K., Strandberg, U., Kahilainen, K.K., Järvinen, M., Hiltunen, M., et al. 2016. Lake eutrophication and brownification downgrade availability and transfer of essential fatty acids for human consumption. *Environ. Int.* **96**: 156–166. doi:10.1016/j.envint.2016.08.018. PMID:27685803.
- Taipale, S.J., Kahilainen, K.K., Holtgrieve, G.W., and Peltomaa, E.T. 2018. Simulated eutrophication and browning alters zooplankton nutritional

quality and determines juvenile fish growth and survival. *Ecol. Evol.* **8**: 2671–2687. doi:10.1002/ece3.3832. PMID:29531685.

Tamminen, T., and Andersen, T. 2007. Seasonal phytoplankton nutrient limitation patterns as revealed by bioassays over Baltic Sea gradients of salinity and eutrophication. *Mar. Ecol. Prog. Ser.* **340**: 121–138. doi:10.3354/meps340121.

Telesh, I., Postel, L., Heerkloss, R., Mironova, E., and Skarlato, S. 2009. Zooplankton of the open Baltic Sea: extended atlas. *Meereswiss. Ber.* **76**, 1–290.

Vargas, M.A., Rodriguez, H., Moreno, J., Olivares, H., Campo, J.A.D., Rivas, J., and Guerrero, M.G. 1998. Biochemical composition and fatty acid content of

filamentous nitrogen-fixing cyanobacteria. *J. Phycol.* **34**: 812–817. doi:10.1046/j.1529-8817.1998.340812.x.

Wikner, J., and Andersson, A. 2012. Increased freshwater discharge shifts the trophic balance in the coastal zone of the northern Baltic Sea. *Global Change Biol.* **18**: 2509–2519. doi:10.1111/j.1365-2486.2012.02718.x.

Appendix A

Figure A1 and Tables A2–A4 appear on the following pages.

Table A1. Concentrations of individual fatty acids (FA) (% of total FA; mean \pm SD) in seston and zooplankton at the sampling stations.

Station	Cladocerans			<i>Eurytemora</i>			Seston		
	A5	B3	C14	A5	B3	C14	A5	B3	C14
Total FA	0.62 \pm 0.38	0.26 \pm 0.06	0.31 \pm 0.06	1.00 \pm 0.77	0.35 \pm 0.09	0.57 \pm 0.07	0.08 \pm 0.03	0.07 \pm 0.05	0.03 \pm 0.01
SAFA	36.00 \pm 0.34	37.17 \pm 6.87	37.38 \pm 2.99	42.08 \pm 2.39	46.53 \pm 0.97	47.72 \pm 3.46	89.53 \pm 0.87	89.11 \pm 0.31	89.43 \pm 0.72
ShortSAFA	30.90 \pm 2.24	32.19 \pm 7.51	32.28 \pm 2.85	34.18 \pm 0.45	37.21 \pm 4.26	41.20 \pm 4.17	88.78 \pm 0.97	88.03 \pm 0.40	88.57 \pm 0.85
11:0	—	—	—	—	—	—	3.43 \pm 0.95	4.00 \pm 0.48	2.54 \pm 0.41
12:0	—	—	—	—	—	—	1.50 \pm 0.81	1.89 \pm 0.12	1.11 \pm 0.22
13:0	2.25 \pm 0.53	0.69 \pm 0.23	1.37 \pm 0.62	1.08 \pm 0.12	0.85 \pm 0.17	0.63 \pm 0.24	0.83 \pm 0.35	1.03 \pm 0.10	0.60 \pm 0.07
14:0	4.70 \pm 1.61	1.86 \pm 0.34	3.00 \pm 0.39	1.99 \pm 0.73	1.29 \pm 0.41	2.84 \pm 0.12	2.64 \pm 0.53	4.23 \pm 0.29	3.04 \pm 0.02
15:0	4.12 \pm 0.22	4.42 \pm 1.01	5.01 \pm 0.75	15.90 \pm 6.72	21.26 \pm 2.04	7.65 \pm 1.17	0.63 \pm 0.12	1.08 \pm 0.14	0.59 \pm 0.07
16:0	14.16 \pm 3.01	8.00 \pm 10.38	12.64 \pm 0.85	10.31 \pm 5.44	7.57 \pm 0.93	22.80 \pm 2.98	22.00 \pm 3.67	32.22 \pm 1.63	29.97 \pm 1.76
17:0	3.04 \pm 0.24	7.13 \pm 0.17	3.62 \pm 0.35	2.30 \pm 0.67	3.16 \pm 1.93	4.76 \pm 0.24	46.33 \pm 3.38	32.69 \pm 1.83	38.78 \pm 1.54
18:0	2.63 \pm 2.93	10.09 \pm 1.80	6.64 \pm 1.39	2.61 \pm 0.45	3.08 \pm 1.22	2.52 \pm 0.59	11.42 \pm 3.46	10.90 \pm 0.34	11.94 \pm 0.31
LongSAFA	5.10 \pm 1.90	4.98 \pm 0.64	5.10 \pm 0.14	7.90 \pm 2.84	9.32 \pm 3.29	6.52 \pm 0.72	0.75 \pm 0.10	1.08 \pm 0.09	0.87 \pm 0.13
20:0	1.08 \pm 0.74	0.75 \pm 0.56	0.80 \pm 0.28	0.83 \pm 0.47	3.22 \pm 2.11	1.39 \pm 0.21	0.16 \pm 0.06	0.29 \pm 0.02	0.22 \pm 0.05
21:0	0.82 \pm 0.05	1.01 \pm 0.53	0.69 \pm 0.29	2.32 \pm 1.03	2.03 \pm 2.04	1.16 \pm 0.05	0.09 \pm 0.04	0.10 \pm 0.01	0.08 \pm 0.02
22:0	0.94 \pm 0.16	1.05 \pm 0.13	1.37 \pm 0.34	1.74 \pm 0.56	1.35 \pm 0.07	1.77 \pm 0.10	0.20 \pm 0.02	0.22 \pm 0.01	0.19 \pm 0.01
23:0	1.33 \pm 0.47	1.29 \pm 0.35	1.30 \pm 0.94	2.29 \pm 0.45	2.22 \pm 1.04	1.99 \pm 0.50	0.10 \pm 0.01	0.15 \pm 0.09	0.12 \pm 0.07
24:0	0.93 \pm 0.47	0.88 \pm 0.20	0.94 \pm 0.11	0.72 \pm 0.32	0.49 \pm 0.26	0.21 \pm 0.04	0.20 \pm 0.03	0.31 \pm 0.01	0.27 \pm 0.01
MUFA	37.85 \pm 2.99	27.88 \pm 4.12	28.07 \pm 3.60	22.47 \pm 5.69	23.81 \pm 3.60	11.87 \pm 1.60	3.25 \pm 0.25	4.78 \pm 0.73	4.38 \pm 0.88
14:1 ω 5	1.16 \pm 0.29	0.97 \pm 0.27	1.37 \pm 1.15	1.39 \pm 0.02	2.19 \pm 0.53	1.13 \pm 0.74	—	—	—
15:1 ω 5	0.62 \pm 0.11	0.77 \pm 0.28	0.80 \pm 0.01	1.69 \pm 1.64	1.26 \pm 0.51	0.60 \pm 0.04	—	—	—
16:1 ω 7	22.78 \pm 2.43	6.10 \pm 3.32	6.05 \pm 1.32	7.55 \pm 2.55	3.18 \pm 0.61	1.55 \pm 0.37	—	—	—
17:1 ω 7	3.74 \pm 1.97	5.24 \pm 2.84	4.92 \pm 0.70	1.69 \pm 0.52	1.75 \pm 0.81	0.42 \pm 0.20	—	—	—
18:1 ω 9c	4.64 \pm 1.78	9.85 \pm 1.33	6.99 \pm 3.84	1.36 \pm 0.61	1.83 \pm 1.04	1.84 \pm 0.34	2.47 \pm 0.15	4.00 \pm 0.68	3.89 \pm 0.56
18:1 ω 9t	—	—	—	—	—	—	0.78 \pm 0.10	0.78 \pm 0.05	0.48 \pm 0.33
20:1 ω 9	3.03 \pm 0.70	3.06 \pm 2.04	4.32 \pm 1.04	2.85 \pm 0.85	1.27 \pm 0.28	2.17 \pm 0.35	—	—	—
22:1 ω 9	0.70 \pm 0.18	0.50 \pm 0.19	1.73 \pm 0.84	0.77 \pm 0.45	1.54 \pm 0.45	0.48 \pm 0.05	—	—	—
24:1 ω 9	1.18 \pm 0.62	1.39 \pm 0.50	1.89 \pm 0.10	5.17 \pm 0.26	10.79 \pm 2.56	3.68 \pm 0.40	—	—	—
BAFA	5.05 \pm 1.17	4.82 \pm 0.54	4.41 \pm 0.28	4.45 \pm 1.28	5.29 \pm 0.23	3.30 \pm 0.02	—	—	—
iso15:0	1.27 \pm 0.66	0.73 \pm 0.27	1.38 \pm 0.17	1.25 \pm 1.12	1.31 \pm 0.79	1.52 \pm 0.07	—	—	—
anteiso15:0	0.65 \pm 0.14	0.63 \pm 0.33	0.75 \pm 0.34	0.29 \pm 0.06	0.83 \pm 0.71	0.33 \pm 0.11	—	—	—
iso16:0	1.31 \pm 0.10	1.75 \pm 0.42	1.24 \pm 0.17	0.86 \pm 0.07	1.14 \pm 0.15	0.24 \pm 0.14	—	—	—
iso17:0	1.09 \pm 0.96	1.18 \pm 0.71	0.44 \pm 0.18	0.38 \pm 0.14	0.30 \pm 0.09	0.70 \pm 0.02	—	—	—
19:0	0.69 \pm 0.42	0.50 \pm 0.21	0.58 \pm 0.10	1.65 \pm 0.13	1.69 \pm 0.02	0.48 \pm 0.03	—	—	—
PUFA	21.11 \pm 1.49	30.13 \pm 2.21	30.13 \pm 6.31	31.00 \pm 9.36	24.37 \pm 2.40	37.11 \pm 1.83	7.22 \pm 1.12	6.11 \pm 0.42	6.39 \pm 0.16
ω 3	15.56 \pm 0.84	23.72 \pm 0.76	24.05 \pm 7.44	21.83 \pm 8.96	17.41 \pm 3.45	30.42 \pm 1.98	1.05 \pm 0.11	0.42 \pm 0.33	1.19 \pm 0.42
18:3 ω 3	1.21 \pm 1.13	0.80 \pm 0.25	0.65 \pm 0.12	2.52 \pm 3.12	2.61 \pm 1.66	0.91 \pm 0.01	—	—	—
20:5 ω 3 (EPA)	8.74 \pm 1.60	18.22 \pm 0.40	12.99 \pm 4.16	7.96 \pm 3.52	6.12 \pm 3.84	9.98 \pm 0.76	0.19 \pm 0.07	0.28 \pm 0.25	0.38 \pm 0.23
20:3 ω 3	1.65 \pm 0.48	1.63 \pm 0.65	1.98 \pm 0.22	2.06 \pm 0.90	2.28 \pm 0.60	1.44 \pm 0.61	—	—	—
22:6 ω 3 (DHA)	3.96 \pm 0.86	3.07 \pm 0.26	8.43 \pm 3.62	9.29 \pm 9.47	6.40 \pm 1.86	18.10 \pm 1.82	0.86 \pm 0.18	0.14 \pm 0.08	0.81 \pm 0.19
ω 6	5.55 \pm 0.64	6.41 \pm 1.45	6.08 \pm 1.14	9.16 \pm 0.40	6.97 \pm 1.05	6.69 \pm 0.15	6.16 \pm 1.23	5.69 \pm 0.75	5.20 \pm 0.58
18:2 ω 6c	0.96 \pm 0.09	1.29 \pm 0.63	0.59 \pm 0.17	2.62 \pm 1.40	2.25 \pm 1.25	0.93 \pm 0.52	0.83 \pm 0.29	1.41 \pm 0.04	1.28 \pm 0.11
18:2 ω 6c	—	—	—	—	—	—	0.81 \pm 0.04	0.92 \pm 0.10	0.67 \pm 0.01
20:3 ω 6	—	—	—	—	—	—	3.59 \pm 0.76	2.48 \pm 0.38	2.30 \pm 0.36
20:4 ω 6	1.86 \pm 0.87	2.56 \pm 0.07	1.45 \pm 0.40	0.79 \pm 0.32	1.74 \pm 0.20	0.54 \pm 0.09	—	—	—
20:2 ω 6	2.08 \pm 0.01	1.78 \pm 0.63	2.50 \pm 0.13	3.83 \pm 2.96	1.63 \pm 0.34	4.40 \pm 0.68	0.19 \pm 0.15	0.11 \pm 0.04	0.08 \pm 0.02
22:2 ω 6	0.65 \pm 0.15	0.78 \pm 0.26	1.54 \pm 0.78	1.92 \pm 0.84	1.35 \pm 0.06	0.81 \pm 0.41	0.74 \pm 0.02	0.77 \pm 0.27	0.67 \pm 0.15
ω 3: ω 6	2.81 \pm 0.17	3.78 \pm 0.74	4.14 \pm 2.00	2.36 \pm 0.88	2.57 \pm 0.88	4.55 \pm 0.40	0.18 \pm 0.05	0.08 \pm 0.07	0.24 \pm 0.11

Note: In zooplankton, 18:1 ω 9t co-eluted with 18:1 ω 9c and is grouped in 18:1 ω 9c. Units of total FA are mg FA·g⁻¹ C for seston and mg FA·g⁻¹ dry mass for zooplankton. The FA groups are boldfaced. DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid; SAFA, total saturated FA; ShortSAFA and LongSAFA, total short (<20 C) and long-chain (\geq 20 C) SAFA, respectively; MUFA, total monounsaturated FA; BAFA, total bacterial FA; PUFA, total polyunsaturated FA; ω 3 and ω 6, total ω 3 and ω 6 PUFA, respectively; ω 3: ω 6, ω 3 to ω 6 FA ratio.

Table A2. Results of one-way ANOVA and post hoc Tukey comparisons of individual FA and FA ratios of seston at A5, B3, and C14 stations.

FA	$F_{[2,3]}$	p	Tukey HSD comparisons
Logit (EPA)	0.34	0.74	NA
Logit (DHA)	15.05	0.03	A5 = C14 > B3
Logit (18:2 ω 6c)	3.97	0.14	NA
Logit (18:1 ω 9c)	7.95	0.06	NA
Logit (MUFA)	3.30	0.17	NA
Logit (ω 3 PUFA)	2.84	0.20	NA
Logit (ω 6 PUFA)	0.89	0.50	NA
Logit (PUFA)	1.62	0.33	NA
Logit (ShortSAFA)	0.48	0.66	NA
Logit (LongSAFA)	3.88	0.15	NA
ω 3 PUFA: ω 6 PUFA	2.10	0.27	NA
ω 3 PUFA:LongSAFA	7.77	0.07	NA
ω3 PUFA:MUFA	18.88	0.02	A5 = C14 > B3
PUFA:LongSAFA	8.87	0.05	A5 \geq C14 \geq B3
PUFA:MUFA	3.33	0.17	NA
EPA:LongSAFA	0.64	0.59	NA
DHA:LongSAFA	10.76	0.04	A5 \geq C14 \geq B3
EPA:MUFA	0.32	0.75	NA
DHA:MUFA	64.03	<0.01	A5 = C14 \geq B3

Note: Except for the ratios, FA data (% of total FA) were logit-transformed. p values smaller than 0.05 are boldfaced. See Table A1 for FA abbreviations.

Table A3. Results of one-way ANOVA and post hoc Tukey comparisons of individual FA and FA ratios of cladocerans at A5, B3, and C14 stations.

FA	$F_{[2,3]}$	p	Tukey HSD comparisons
Logit (EPA)	6.01	0.08	NA
Logit (DHA)	5.78	0.09	NA
Logit (18:2 ω 6c)	2.40	0.23	NA
Logit (18:1 ω 9c)	1.84	0.30	NA
Logit (MUFA)	4.50	0.12	NA
Logit (ω 3 PUFA)	3.09	0.18	NA
Logit (ω 6 PUFA)	0.27	0.77	NA
Logit (PUFA)	4.08	0.13	NA
Logit (ShortSAFA)	0.04	0.95	NA
Logit (LongSAFA)	0.01	0.98	NA
ω 3 PUFA: ω 6 PUFA	0.61	0.59	NA
ω 3 PUFA:LongSAFA	0.89	0.49	NA
ω 3 PUFA:MUFA	2.66	0.21	NA
PUFA:LongSAFA	0.75	0.54	NA
PUFA:MUFA	3.80	0.14	NA
EPA:LongSAFA	2.29	0.24	NA
DHA:LongSAFA	2.18	0.25	NA
EPA:MUFA	4.62	0.12	NA
DHA:MUFA	2.66	0.21	NA

Note: Except for the ratios, FA data (% of total FA) were logit-transformed. See Table A1 for FA abbreviations.

Table A4. Results of one-way ANOVA and post hoc Tukey comparisons of individual FA and FA ratios of *Eurytemora* at A5, B3, and C14 stations.

FA	$F_{[2,3]}$	p	Tukey HSD comparisons
Logit (EPA)	0.73	0.54	NA
Logit (DHA)	1.25	0.40	NA
Logit (18:2 ω 6c)	1.96	0.28	NA
Logit (18:1 ω 9c)	0.3	0.76	NA
Logit (MUFA)	7.89	0.06	NA
Logit (ω 3 PUFA)	2.13	0.26	NA
Logit (ω 6 PUFA)	1.63	0.33	NA
Logit (PUFA)	0.25	2.21	NA
Logit (ShortSAFA)	2.9	0.19	NA
Logit (LongSAFA)	0.67	0.57	NA
ω3 PUFA:ω6 PUFA	18.42	0.02	B3 = C14 > A5
ω 3 PUFA:LongSAFA	1.02	0.40	NA
ω3 PUFA:MUFA	10.58	0.04	C14 > A5 \geq B3
PUFA:LongSAFA	1.32	0.38	NA
PUFA:MUFA	9.57	0.04	NA
EPA:LongSAFA	0.08	0.92	NA
DHA:LongSAFA	11.27	0.39	NA
EPA:MUFA	5.29	0.10	NA
DHA:MUFA	8.59	0.05	NA

Note: Except for the ratios, FA data (% of total FA) were logit-transformed. p values smaller than 0.05 are boldfaced. See Table A1 for FA abbreviations.

Fig. A1. Spearman's rank correlation between relative cyanobacterial biomass (%; averages of monthly measurements in July–September 2017) and PC2_{summer} at the sampling locations.

