Effects of changing phytoplankton species composition on carbon and nitrogen uptake in benthic invertebrates

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Abstract

Pelagic primary production is the main input of organic energy for benthic production below the photic zone. In the Baltic Sea, spring phytoplankton blooms are dominated by diatoms that sink out rapidly and export nutritionally favorable matter to benthic secondary production, while the summer blooms have more variable sedimentation rates and nutritional profile. Changes in phytoplankton species composition and bloom dynamics, as a consequence of climate change and eutrophication are reducing high quality diatoms reaching the benthic fauna, while promoting cyanobacteria. Here, we test uptake and assimilation of changing phytoplankton composition for three common benthic invertebrates, a clam, an amphipod and a polychaete under varying degrees of spring-bloom associated diatoms (Skeletonema costatum) and summer-bloom associated cyanobacteria (Nodularia spumigena). The phytoplankton were labeled with stable isotopes (15N and 13C, respectively) in order to trace assimilation in consumers’ tissues. We found that all three macrofauna species fed on both diatoms and cyanobacteria. A linear pattern was found for all three species in assimilation of carbon and nitrogen from diatoms, with increasing assimilation associated with higher proportion of diatoms. There was no clear pattern found between proportion of cyanobacteria and assimilation of carbon and nitrogen for any of the species. This study shows that the investigated macrofaunal species display a selective feeding behavior with preference for spring-bloom associated diatoms. Thus, changes in phytoplankton bloom composition are likely affecting benthic species composition and production.

Phytoplankton production is the key organic energy input to aquatic ecosystems and constrains transfer of organic carbon and nutrients to support higher trophic levels of pelagic and benthic consumers (Falkowski 2012). Phytoplankton species composition and bloom dynamics are changing as a response to climate change and eutrophication, particularly in coastal areas that often experience high impact of human activities (Heiskanen et al. 2019). Effects of climate warming and eutrophication typically result in earlier onset of spring blooms, increasing pelagic turnover and favoring filamentous cyanobacterial blooms with increased magnitude and increased duration (Funke et al. 2014; Tamelander et al. 2017). These shifts in phytoplankton dynamic are affecting pelagic food webs (Winder and Sommer 2012) and are also expected to affect quantity and quality of organic carbon input to benthic organisms (Tamelander et al. 2017). Secondary benthic production below the euphotic zone is fueled by sedimentation of organic material from the water column, which is determined by seasonal phytoplankton succession and composition (Heiskanen and Kononen 1994; Tamelander et al. 2017). Diatom dominated spring blooms sink down rapidly, contributing to high export rates of nutritionally favorable matter to the benthic fauna (Höglander et al. 2004; Gustafsson et al. 2013), while sedimentation rates of summer-associated phytoplankton is more variable depending on species composition (Gustafsson et al. 2013). Consequently, climate warming and eutrophication is changing the magnitude and composition of organic material deposited to the seafloor. However, the response of benthic consumers to different types of organic material supply and how it affects their uptake rates are largely unknown (Basen et al. 2013).

Community composition in soft bottom habitats largely affects biogeochemical cycles, which can be substantially altered by benthic fauna (Norko et al. 2015). The amount of surface primary productivity and sedimentation is directly linked to the biomass of benthic macrofauna in the aphotic zone and promotes surface and subsurface deposit feeders (Rowe et al. 1974; Rosenberg 1995). In addition, there is a strong positive relationship between amount and quality of...
organic matter input and macrofaunal biomass (Johnson et al. 2007). Diatoms, being rich in essential fatty acids for example, have often been considered a high-quality food for benthic primary consumers, while cyanobacteria lack essential biomolecules, including fatty acids and amino acids (Basen et al. 2013; Galloway and Winder 2015) and are thus thought to be of lower quality food for benthic consumers (Nascimento et al. 2009). The presence of toxins in filamentous cyanobacteria such as *Nodularia spumigena* has further been shown to accumulate in invertebrate consumers and cause toxicity in higher trophic consumers (El-Shehawy and Gorokhova 2013). While the proportion of cyanobacteria deposition to the seafloor is unknown, it has been shown that cyanobacterial pigments are present in high abundances on bottom substrates (Josefson et al. 2012) and are being consumed by benthic macrofauna (Carlson et al. 2014) that may use up to 80% of the annual organic carbon sedimentation to the seafloor (Ehmsen et al. 2019). As benthic macrofauna prefer high-quality phytoplankton species (Sun et al. 2009), an increased sedimentation of cyanobacteria that is not consumed by the macrofauna makes more material available for bacterial breakdown, enhancing benthic bacterial production and thus oxygen depletion (Andersson et al. 2015). Consequently, organic matter input may not only affect benthic production and community composition but also biogeochemical cycles.

Seasonal cycles of pelagic primary production are strong in northern temperate seas in general and in the Baltic Sea in particular, where benthic deposit-feeding macrofauna living below the photic zone rely heavily on sedimentation of pelagic phytoplankton blooms (Griffiths et al. 2017; Tamelander et al. 2017). Here, the main portion of the spring bloom is dominated by diatoms, which utilize the excess nutrients that have built up during winter (Josefson and Hansen 2003). The spring bloom is considered to be the main input of high-quality food for benthic soft-bottom organisms (Lehtonen and Andersin 1998) as densities of zooplankton typically are low during this time of the year, resulting in large quantities of bloom-material reaching the bottom (Höglander et al. 2004). As spring transitions into summer, pelagic dissolved nitrogen is used up by primary producers, making large areas nitrogen-limited by mid-summer and giving nitrogen fixing cyanobacteria an advantage as dissolved phosphorous still is available (Reusch et al. 2018). Although the presence of diazotrophic, or nitrogen fixing, cyanobacteria in the Baltic Sea in general has been shown to occur for at least 7000 years (Bianchi et al. 2000), bloom size, duration and frequency has increased since the 1970s (Poutanen and Nikkilä 2001), especially for *N. spumigena* (Kahru and Elmgren 2014). While there is annual variability, the overall trend seems to be an increase in duration and magnitude of the summer cyanobacterial blooms and a decrease in the diatom dominated spring bloom duration and magnitude (Hjerne et al. 2019). In addition, warming of the Baltic Sea might cause a more rapid turnover of pelagic consumers and carbon cycling in the water column, causing an even further reduction in spring bloom material available for benthic fauna (Aberle et al. 2012).

The soft-bottom benthic macrofauna of the northern Baltic proper is dominated by the amphipods *Monoporeia affinis* and *Pontoporeia femorata*, the Baltic clam *Limecola balthica*, the invasive polychaetes *Marenzelleria* spp. and to some extent the predatory isopod *Saduria entomon* and priapulid *Halicypris spinulosus* (Gogina et al. 2016). These organisms are important oxygenators of sediments due to bioturbation and food for higher trophic level organisms (Bonsdorff and Blomqvist 1993; Elmgren and Hill 1997), while also facilitating benthic to pelagic coupling by increasing germination of phytoplankton resting stages (Carlson et al. 2008; Carlson et al. 2012). While hypoxia and anoxia in both the coastal zone and deeper waters have reduced macrofaunal communities substantially (Carstensen et al. 2014), the oxygenated areas have seen an increase in these species as an effect of increased primary production due to eutrophication (Elmgren et al. 2015). Several studies have shown that the common benthic macrofauna species consume both diatoms and cyanobacteria, but seem to grow less from the latter, probably due to toxins and less suitable fatty acids (Carlson et al. 2011; Carlson et al. 2012). Palatability and nutritional quality of cyanobacteria for sediment-dwelling amphipods, however, increases when processed through clams and released as biodeposition material largely due to predigestion and addition of essential lipids released by the clam (Basen et al. 2013). Currently there is a gap in the knowledge on how these species will consume and assimilate diatoms and cyanobacteria when presented with a choice of both. It is of utmost importance to disentangle whether there is any discrepancy in actively choosing for or against certain species of phytoplankton as their bloom dynamics are changing as a result of climate change.

To increase the understanding of the effect of changing phytoplankton species composition on benthic macrofauna production, we investigated uptake and assimilation of spring-bloom and summer-bloom associated phytoplankton species by macrofauna in an experimental mesocosm set-up. Three of the most abundant macrofauna species were kept in mesocosms with different proportions of diatom and filamentous cyanobacteria phytoplankton, labeled with stable isotopes to measure species specific rates of carbon and nitrogen assimilation. Our study reveals the general response of benthic consumers to changing primary producers and implications for benthic species composition and production under climate change.

**Materials and methods**

**Collection of sediment and animals**

Sediment was collected in September 2017 in the Northern Baltic Proper, Askö area (Hållsviken, 58°50′5842N, 17°31′3089E, Askö area) at a depth of 27 m with a Van Veen
grab and sieved under filtered running brackish water (6 PSU) through a 500 μm mesh in order to remove macrofauna. The sieved sediment was left to stand in dark and submerged in filtered brackish water with light aeration to facilitate even oxygenation, in a container at 5°C for 6 d to regain its compact structure. Animals were collected during the same time period in the same area, using a benthic sled and sieved out using brackish water and a 500 μm mesh. We selected three common benthic macrofaunal species for the experiment: the surface-feeding amphipod *M. affinis*, the facultative suspension and deposit-feeding clam *L. balthica* and the deposit-feeding polychaete *Marenzelleria* sp. Body length of *M. affinis* was 7–9 mm, of *Marenzelleria* sp. 20–35 mm and shell length of *L. balthica* was 10–13 mm. All three species were kept separately in individual holding containers in filtered brackish water (6 PSU) with light aeration at 5°C in darkness for 48 h before start of the experiment.

**Phytoplankton culturing and labeling with stable isotopes**

We used the cyanobacteria *N. spumigena* (strain K-1537, NIVA-CCA, Oslo, Norway) and the diatom *Skeletonema costatum* (strain LYS6 AAF, Department of Environmental Science and Analytical Chemistry, Stockholm University, Sweden) (hereafter referred to as cyanobacteria and diatoms, respectively) as primary producers. Individual cell lengths were approximately 6.5 μm for the diatoms and 59.5 μm for the cyanobacteria and both species formed long chains. These species were chosen as they are part of the spring bloom (diatom) and summer bloom (cyanobacteria) in coastal zones of the northern Baltic proper (Höglander et al. 2004; Kahru and Elmgren 2014). Both species were grown in f/2 media (Guillard 1975) with added micronutrients and peat extract, at salinities of 11 PSU (cyanobacteria) and 23 PSU (diatoms), with the diatoms receiving twice the amount of SiO4 as the cyanobacteria. Both species were grown in a climate-controlled room on a shaking table at 15°C in a 16:8 h day:night cycle under fluorescent tube lighting, receiving 3625 lux. For labeling with stable isotopes, each species was first pooled from several flask samples into a total volume of 10 liters with excess nutrient to maintain growth. Carbon (C) and nitrogen (N) in the nutrient media were replaced with Sigma Aldrich enriched 1³C (NaH¹³CO₃) for the cyanobacteria at 2.3 μmol L⁻¹ and 1⁵N (Na¹⁵NO₃) for the diatom at 882 μmol L⁻¹, 98% heavy isotope and incubated for 48 h. After incubation, both species were concentrated to 2 liters. To prevent phytoplankton cell rupture due to osmotic shock and to not alter the salinity of the mesocosms, both phytoplankton species were subjected to lowering of the salinity in a series of steps. The cyanobacteria were rinsed three times with 2 liters nutrient-free artificial sea water at a salinity of 6 PSU which was the salinity used in the mesocosms. The diatoms were rinsed and centrifuged in three steps, beginning with rinsing in 20 PSU nutrient-free artificial sea water, then centrifuged at 4700 rpm for 5 min, rinsed in 17 PSU nutrient-free artificial sea water and centrifuged at 4700 rpm for 9 min and finally rinsed in 15 PSU nutrient-free artificial seawater, following the method of Kotta and Olafsson (2003), and centrifuged at 700 rpm for 10 min. Both species were further concentrated down to a final volume of 1 liter and placed for 24 h in a climate-controlled room in which they had been cultured (temperature and light as mentioned above). Following the 24 h period, both concentrated cultures were placed in darkness at 10°C, to prevent deterioration, for 6 d before starting the experiment. In order to make the cyanobacteria sink, they were subjected to a pressure shock to break their gas vacuoles (Walsby 1972).

**Experimental set-up**

We filled 30 clear cylindrical plexiglass pipe mesocosms (25 cm high, 7.4 cm diameter) with 5 cm of sieved sediment as bottom substrate and filtered brackish water (6 PSU) and left to stand for 48 h with gentle aeration at 5°C in darkness until no sediment was suspended. Each mesocosm was covered by parafilm with small holes to facilitate light aeration via a thin nylon tube and to allow gas exchange and to prevent precipitation. 24 h before start of the experiment, five animals of each species were introduced to each of the 30 mesocosms, which represents an estimated average density in the northern Baltic proper (Gogina et al. 2016).

Shortly after collection of sediment and animals, the experiment was started by adding different phytoplankton mixtures to the mesocosms. Treatments were based on proportion of organic matter originating from the two cultured phytoplankton species, calculated as loss on ignition based on a carbon content of 40% for diatoms and 60% for cyanobacteria. Calculated amounts of organic matter added to the different treatments were based on sedimentation rates of 4 g of C m⁻² during spring bloom (Höglander et al. 2004) and 44.6 ± 4.0 g C m⁻² yr⁻¹ (Gustafsson et al. 2013), which corresponds to 0.017 g C for a mesocosm surface area of 0.004 m². Treatments were set to 100% diatoms (100Di), 80% diatoms and 20% cyanobacteria (80Di-20Cy), 50% diatoms and 50% cyanobacteria (50Di-50Cy), 20% diatoms and 80% cyanobacteria (20Di-80Cy), 100% cyanobacteria (100Cy) and control (CTRL) without any addition of phytoplankton. All treatments had five mesocosm replicates each (Table 1). Aeration was stopped prior to addition of phytoplankton in order to not disturb the sinking and turned back on 24 h later. For treatments with cyanobacteria, small amounts of filaments were detected floating in the water, which were removed with a syringe, mixed with 2 g of sediment and pipetted onto each individual replicate sediment surface to assure that no filaments remained floating in the water. In the two treatments without addition of cyanobacteria (100Di and CTRL), 2 g of sediment without any cyanobacteria was pipetted onto the surface of each individual replicate, in the same manner as for the others. Aeration was turned back on and no filaments were detected upon inspection or throughout the experiment. During the experiment, a day:night cycle of 15:9 h with fluorescent tubes covered by green plastic sheets and emitting very weak light was installed to simulate in situ conditions.
The experiment was terminated after 4 weeks. The water was siphoned out from each mesocosm, sediment surface samples were taken, homogenized and frozen at −80°C. All animals were sieved out with a 500 μm mesh and running filtered brackish water. Living and dead animals were noted and dead animals were rinsed in deionized water, placed in individual 2 mL cryo-vials and frozen at −80°C. All living animals were placed in replicate-specific beakers with aerated filtered brackish water at 5°C for 24 h to facilitate gut evacuation in order for any gut-remains to not influence stable isotope analysis. After 24 h, L. balthica were separated from their shell and all animals were rinsed in deionized water and frozen at −80°C.

Stable isotope analyses

One individual of both L. balthica and Marenzelleria sp. and two individuals of M. affinis from each individual mesocosm replicate were freeze dried at −120°C, ground into a fine powder and placed in tin capsules. Both phytoplankton species, labeled and unlabeled, were pipetted onto pre-combusted GF/F filters and dried at 60°C, then placed in tin capsules. Sediment from T0 and control treatment was freeze dried at −120°C, ground into a fine powder with mortar and pestle and placed in tin capsules. All material was analyzed for bulk stable isotope, nitrogen and carbon content (13C and 15N) at UC Davis Stable Isotope Facility, California using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd).

Statistical analyses and mixing model

All statistical analyses were done with R (R Core Team 2018). Treatment effects of labeled phytoplankton assimilation into the macrofauna species was analyzed with a linear model for δ13C and a generalized least squares model for δ15N to account for variance heterogeneity using the gls function in the package nlme (Pinheiro et al. 2019) and δ13C and δ15N values from macrofauna as response variables. The amount of assimilated C and N was calculated per individual (ind.−1) and per relative to body mass (only for C, mg−1; dry weight). For the latter, 10–14 M. affinis, 18–20 Marenzelleria sp. and 20 L. balthica individuals from each treatment were freeze-dried and weighed (see Table S1) and calculated by dividing individual assimilation by mean species weight per treatment. Proportional assimilation of absolute C and N into macrofauna from the two different phytoplankton sources was calculated in a two (100Di and 100Cy) and three (80Di-20Cy, 50Di-50Cy, and 20Di-80Cy) source mixing model with ISOerror version 1.04 (Phillips and Gregg 2001) and further analyzed for each element and species separately in an either linear model or generalized least squares model depending on homo- or heterogeneity of variances. Differences among treatments in total assimilation for each element and species, as well as C relative to body mass and species, were analyzed either in a linear model or in a generalized least squares model depending on homo- or heterogeneity of variances. Differences among treatments for the gls functions were calculated using the package piecewiseSEM (Lefcheck 2016). C:N ratio as an indicator of body condition was analyzed for each individual species in a linear model for each treatment against the control. Differences between species and treatments for all models were further analyzed with ANOVA.

Results

Survival of macrobenthic fauna was high throughout the experimental period with 98% survival for Marenzelleria sp. (mortality was 3 out of 150), 94.6% survival for M. affinis (mortality was 8 out of 150) and 100% survival for L. balthica. Mean body mass of L. balthica was 10.46 mg (dry weight), about three times the weight of both other species (p < 0.001), while no difference in body mass was found between M. affinis (mean body mass of 2.63 mg) and Marenzelleria sp. (mean body mass of 3.39 mg) (p = 0.84) considering all treatments. Isotope values, C and N content and C:N ratio of sediment and animals, unlabeled and labeled phytoplankton species before the start of the experiment can be found in Table 2.

Assimilation of labeled δ15N and δ13C

All macrobenthic species assimilated diatoms when available, as indicated by the increase in δ15N compared to the 100% cyanobacteria and control treatments (Fig. 1a). δ15N values increased linearly with higher diatom proportions in all

### Table 1. Total organic matter (OM) input and proportions of added phytoplankton to the different treatments based on loss on ignition (40% C from diatoms and 60% C from cyanobacteria). Total OM are based on calculations from Höglander et al. (2004) and Gustafsson et al. (2013).

| Treatment                        | ID  | Total OM input (g m⁻²) | % diatoms | % cyanobacteria |
|---------------------------------|-----|------------------------|-----------|-----------------|
| Control                         | CTRL | 0                      | 0         | 0               |
| 100% diatoms                    | 100Di | 1.76                   | 100       | 0               |
| 80% diatoms – 20% cyanobacteria | 80Di-20Cy | 1.82                   | 77        | 23              |
| 50% diatoms – 50% cyanobacteria | 50Di-50Cy | 1.93                   | 46        | 54              |
| 20% diatoms – 80% cyanobacteria | 20Di-80Cy | 2.03                   | 17        | 83              |
| 100% cyanobacteria              | 100Cy  | 2.10                   | 0         | 100             |


Cyanobacteria labeled 12.3±0.5 0.2±0.4 20.4±0.6 3.9±0.1 5.1±0.0

Diatoms labeled

Diatoms unlabeled

Marenzelleria sp.

M. af

L. balthica

−

−

−

−

treatment. Treatments are as in Table 1.

R

in a linear fashion in any benthic species, as suggested by
variable between treatments and species and did not change
(LM: slope = 61.82, p < 0.001, R^2 = 0.63), particularly in
treatments with more than 20% diatoms, and values are more than
double compared to L. balthica (LM: slope = 12.64, p < 0.009,
R^2 = 0.65) and Marenzelleria sp. (LM: slope = 14.66, p < 0.002,
R^2 = 0.73). The latter two species reached similar values of assimilated δ^{15}N across the treatments. For M. affinis, δ^{15}N dropped off quickly below 50% diatom proportions.

Compared to δ^{15}N, assimilation of cyanobacteria was more variable between treatments and species and did not change in a linear fashion in any benthic species, as suggested by δ^{13}C values (Fig. 1b) (LM for all species: slope < 0.59, p > 0.01, R^2 < 0.16). δ^{13}C values for M. affinis did not differ between treatments and the control (ANOVA: F_{5,54} = 1.59, p > 0.2), with the mean δ^{13}C value varying between −22 and −18.5. In the cyanobacteria treatment that had not received any ^{15}N-labeled material, the δ^{13}N value differed from the control with a mean δ^{13}N of 7.58, which is lower than the control (mean δ^{13}N value of 8.35, p < 0.01). L. balthica assimilated labeled cyanobacteria in all treatments where available (ANOVA: F_{5,24} = 3.64, p < 0.02), except in the 50–50 treatment (p > 0.2) (Fig. 1b). Marenzelleria sp. assimilated labeled cyanobacteria in treatments with 50% and higher cyanobacteria proportions (ANOVA: F_{5,24} = 3.74, p < 0.03), whereas values with 20% cyanobacteria were not significantly different from the control (p > 0.05) (Fig. 1b).

Assimilation of carbon and nitrogen amount from diatoms

Absolute amounts of C and N assimilation and C assimilation relative to body mass increased in a linear fashion with higher diatom proportions for all benthic species (Fig. 2a; Fig. S1a). Absolute assimilated C and N from diatoms was high for M. affinis across all treatments, ranging between 1.8 μg C (20Di-80Cy) to 9.6 μg C (100Di), and 0.4 μg N (20Di-80Cy) to 1.6 μg N (100Di) (LM: slope = 2.28, p < 0.001, R^2 = 0.98 and slope = 0.38, p < 0.001, R^2 = 0.96, respectively), and compared to the other two species was almost three times higher for C and two to four times higher for N. For L. balthica, absolute assimilation of C and N from diatoms followed almost the same linear pattern as for M. affinis (LM: slope = 0.63, p < 0.001, R^2 = 0.99 and slope = 0.16, p < 0.001, respectively) (Fig. 2a), showing a higher amount with increasing access to diatoms ranging between 0.6 μg C (20Di-80Cy) to 2.1 μg C (100Di) and 0.1 μg N (20Di-80Cy) to 0.6 μg N (100Di). Similarly, Marenzelleria sp. showed an increasing amount of C and N assimilation with increasing proportion of diatoms (LM: slope = 0.94, p < 0.001, R^2 = 0.99 and slope = 0.24, p < 0.001, R^2 = 0.99, respectively) (Fig. 2a), ranging between 0.6 μg C (20Di-80Cy) to 3.3 μg C (100Di) and 0.1 μg N (20Di-80Cy) to 0.7 μg N (100Di). Full model outputs can be found in Table S2a.

Similarly, assimilated C per mg body mass was high for M. affinis, ranging between 0.6 μg C mg^{-1} body mass (20Di-
80Cy) to 4.0 μg C mg⁻¹ body mass (100Di) (LM: slope = 0.82, p < 0.001, R² = 0.98) (Fig. S1a), and compared to the other two species at least three to four times higher across all treatments. For *L. balthica*, the assimilation of C per mg body mass followed almost the same linear pattern as for *M. affinis* (LM: slope = 0.07, p < 0.001, R² = 0.99) (Fig. S1a), showing a higher assimilation with increasing access to diatoms ranging between 0.06 μg C mg⁻¹ body mass (20Di-80Cy) to 0.25 μg C mg⁻¹ body mass (100Di). *Marenzelleria* sp. showed an increasing assimilation of C per mg body mass with increasing access to diatoms (LM: slope = 0.27, p < 0.001, R² = 0.99) (Fig. S1a), ranging between 0.14 μg C mg⁻¹ body mass (20Di-80Cy) to 0.96 μg C mg⁻¹ body mass (100Di). Full model outputs can be found in Table S3.

**Assimilation of carbon and nitrogen amount from cyanobacteria**

Assimilation of absolute C and N and C assimilation relative to body mass from cyanobacteria do not follow a clear pattern as seen for diatoms, for all benthic species, with increasing access across the treatments (Fig. 2b; Fig. S1b). Deviations from the linear pattern observed for diatoms are most prominent in *M. affinis* and *L. balthica* (80Di-20Cy vs. 50Di-50Cy) for absolute assimilation. For *Marenzelleria* sp. a somewhat linear pattern is observed, that levels off at 80% or more cyanobacteria. Absolute assimilated C and N for *M. affinis* ranged from 5.6 μg C (50Di-50Cy) to 32.1 μg C (100Cy) and 1.0 μg N (50Di-50Cy) to 5.6 μg N (100Cy) (ANOVA: F₄₀,₃₆ = 993.29, p < 0.001 and F₄₀,₃₆ = 646.11,
Assimilated C from diatoms (µg ind⁻¹) and N from diatoms (µg ind⁻¹) for the three macrobenthic species across all treatments.

For *L. balthica*, absolute amounts of assimilation varied from 17.2 µg C (50Di-50Cy) to 22.4 µg C (100Cy), and 3.6 µg N (50Di-50Cy) to 4.8 µg N (80Di-20Cy) (ANOVA: *F*₂₀,₁₆ = 59.21, *p* < 0.001 and *F*₂₀,₁₆ = 9.11, *p* < 0.001, respectively). Similar values were reached for *Marenzelleria* sp., ranging from 11.7 µg C (80Di-20Cy) to 20.7 µg C (20Di-80Cy), and 2.6 µg N (80Di-20Cy) to 4.8 µg N (20Di-80Cy) (ANOVA: *F*₂₀,₁₆ = 266.01, *p* < 0.001 and *F*₂₀,₁₆ = 112.66, *p* < 0.001, respectively). Full model outputs can be found in Table S2b.

Assimilation of C relative to body mass for *M. affinis* ranged from 1.82 µg C mg⁻¹ body mass (50Di-50Cy) to 12.91 µg C mg⁻¹ body mass (100Cy) (ANOVA: *F*₄₀,₃₆ = 981.09, *p* < 0.001) and for *L. balthica* from 1.43 µg C mg⁻¹ body mass (50Di-50Cy) to 2.37 µg C mg⁻¹ body mass (100Cy) (ANOVA: *F*₂₀,₁₆ = 128.96, *p* < 0.001) (Fig. S1b). Assimilation of C per mg body mass for *Marenzelleria* sp. increased in a linear fashion with higher cyanobacteria proportions, from 3.42 µg C mg⁻¹ body mass (80Di-20Cy) to 7.29 µg C mg⁻¹ body mass (100Cy) (LM: slope = 0.93, *p* < 0.001, *R*² = 0.98) (Fig. S1b). Full model outputs can be found in Table S3.

**Fig. 3.** Mean (± SE) assimilated carbon and nitrogen amount in µg ind⁻¹, from diatoms (a) and from cyanobacteria (b) for the three macrobenthic species across all treatments.

**Ratios of C:N in macrobenthic species**

Ratios of C:N for *L. balthica* ranged from 4.1 to 5.6 and for *Marenzelleria* sp. from 4.1 to 4.9, but did not differ from controls in any treatment (ANOVA: *F*₅,₂₄ = 0.74, *p* > 0.15 and *F*₅,₂₄ = 1.06, *p* > 0.27, respectively). For *M. affinis*, the C:N ratio ranged from 4.4 to 7.6 and was lower than the control in the 50Di-50Cy treatment (ANOVA: *F*₅,₅₄ = 1.36, *p* < 0.05), but did
Changing phytoplankton composition affects inverts

not differ from the control in any other treatment (data not shown).

**Discussion**

In this study, we offered two different phytoplankton species as food to three common species of macrofauna and find that incorporation or assimilation rates of organic matter vary between food types. In general, the clam *L. balthica*, the polychaete *Marenzelleria* sp. and the amphipod *M. affinis* can feed on both spring bloom associated diatoms and summer bloom associated cyanobacteria. However, assimilation of C and N from diatoms followed a linear pattern with increasing assimilation associated with higher proportion of diatoms available in all benthic species. No clear pattern was found between availability and assimilation of C and N from cyanobacteria although absolute amounts of assimilation were high. These findings indicate that diatoms are incorporated preferentially by benthic macrofauna when given a choice of food items.

Our results reveal a linear relationship in resource utilization and the amount offered of diatoms in diverse benthic species. Both absolute amounts of C and N assimilation and C per body mass from diatoms directly followed the amount of organic material from this resource. This supports findings from previous studies that emphasized the importance of sinking spring bloom diatoms as the major input of high-quality food (Lehtonen and Andersin 1998; Höglander et al. 2004; Hjerne et al. 2019). The increasing assimilation regarding both absolute values and per body mass with amount offered suggests that diatoms are a limiting food source and preferred food type that is actively selected for, as a similar pattern was not clearly found for cyanobacteria. The assimilation of absolute amount of as much as three to four times the amount C and N and about three times the amount per body mass from diatoms in the amphipod *M. affinis* (Fig. 2a; Fig. S1a) could possibly be attributed to active foraging of amphipods compared to the more sedentary and slow moving nature of the other two species. In comparison regarding absolute assimilated amounts, there is inconsistency in any linearity for *M. affinis*, a leveling-off for *Marenzelleria* sp. and in addition, the lack of a relationship between amount offered and assimilation for *L. balthica* for cyanobacteria (Fig. 2b). Assimilated C per body mass also has inconsistencies, although a linear relationship with amount offered exists for *Marenzelleria* sp. (Fig. S1b). It is likely that cyanobacteria are not actively selected for, compared to the diatoms and rather used as a complement to existing food. This confirms previous studies showing that cyanobacteria (e.g., *N. spumigena*) are consumed by the benthic macrofauna (Karlson et al. 2011, 2014). The absolute amounts of assimilated C and N from cyanobacteria varied greatly between treatments but were at a similar level in all benthic species. Assimilation of C per body mass from cyanobacteria varied, but not to the same extent and *L. balthica* assimilated low amounts compared to the two other species. This indicates that although actively consuming and assimilating cyanobacteria, as shown for meiofauna of the Baltic Sea (Nascimento et al. 2009), particularly *M. affinis* but also *L. balthica* and *Marenzelleria* sp. preferentially select diatoms over cyanobacteria.

Diverse studies show that essential biomolecules, such as fatty acids, amino acids, and vitamins are positively linked to consumer growth and health for a wide array of taxa, such as crustaceans, bivalves and fish (Winder et al. 2017; Ruess and Müller-Navarra 2019). While the duration of our experiment was too short to estimate growth rates in the consumers, differences in consumer production among the different food types are likely. High amounts of essential fatty and amino acids in diatoms and the lack of them in cyanobacteria (Galloway and Winder 2015) make diatoms a suitable constituent of nutritional intake, promoting growth. Cyanobacteria contribute to the diet of zooplankton during the summer in the Baltic Sea and increase storage lipids in some copepods, although many species seem to utilize cyanobacteria as a dietary supplement and not the staple of their food intake (Högfors et al. 2014). Similarly, benthic meiofauna consume cyanobacteria, but it does not contribute to their growth (Nascimento et al. 2009). Preference for food with higher nutritional value in our experiment confirms the findings of Sun et al. (2009) showing that the food with better nutritional profile was preferred by the clam *L. balthica*. We cannot however, rule out that particle size plays an important role in feeding preference, as cyanobacteria cell length was almost 10 times as long as the diatoms. Whether this affected feeding preference is unknown. In addition, the production of toxins is another factor for selection against *N. spumigena* as food in invertebrate consumers (Sellner et al. 1994). Access to single species food is an unlikely scenario for benthic animals inhabiting soft bottoms in nature, as a sudden influx of either diatoms or cyanobacteria would likely be mixed with other phytoplankton taxa and older material already present and animals could select either fresh newly deposited or old material (Elmgren 1978). Food limitation may arise once the old material has been exhausted and contains little to no nutrition and if the timing of new high-quality material influx is not met. If amounts of diatoms decrease and amounts of cyanobacteria increase, as shown by previous studies (Hjerne et al. 2019; Olofsson et al. 2019), this might affect all three species in the present study, especially *M. affinis* as they more strongly favor and select diatoms over cyanobacteria. Many invertebrates like bivalves, for example, can reduce their metabolism to extremely low levels as an adaptation to extreme conditions (Oeschger 1990). This has been observed for *L. balthica*, as individuals survived in sediment-free water with weak oxygenation at 5°C without food for more than 4 weeks (Hedberg pers. obs., Aug-Sept 2018), which corresponds to the duration of the experiment. Benthic macrofauna is thought to be well adapted to times with low nutritional input (Hill et al. 1992). They do, however, depend
on diatoms in spring and to some extent in the fall in order to grow, allocate resources to egg production and reproduction, and could starve if not finding adequate amounts of newly settled material (Eriksson Wiklund et al. 2008; Eriksson Wiklund and Andersson 2014).

Carbon and nitrogen assimilation

Mean assimilation of absolute C amounts for the duration of the experiment for *M. affinis* was at highest around 30 μg ind.\(^{-1}\) of cyanobacteria (treatment 100Cy) and close to 10 μg ind.\(^{-1}\) of diatoms (treatment 100Di). The amount of absolute assimilated amounts of C and N for *L. balthica* and *Marenzelleria* sp. throughout all treatments were similar for both diatoms and cyanobacteria, with highest amounts of 3 μg C ind.\(^{-1}\) and 0.6 μg N ind.\(^{-1}\), respectively, for diatoms and 20 μg C ind.\(^{-1}\) and 4.8 μg N ind.\(^{-1}\), respectively, for cyanobacteria, confirming the same finding of Karlson et al. (2011) that assimilation is similar for these two benthic species. Considering assimilation of C per body mass from diatoms, the patterns are similar to absolute C assimilation (per ind.) for all species and increased with higher diatom proportions (Fig. S1a and Fig. 2a). In contrast, Karlson et al. (2011) reported similar C assimilation for *L. balthica* and *M. affinis* when both species had similar body mass. The lower C assimilation of *L. balthica* in our study could be attributed to the age of the clams as the present study used only adult *L. balthica* individuals. However, Karlson et al. (2011) did not find as high assimilation of absolute amounts of C and N in *M. affinis* as in the present study. *M. affinis* assimilated on average more N (around 1 μg) compared to *L. balthica* and *Marenzelleria* sp. from both phytoplankton resources, suggesting that amphipods have high N requirements. The pattern of assimilation C per body mass for cyanobacteria is similar to that of absolute amounts of C, although more pronounced for *Marenzelleria* sp. with an increase in assimilation with higher cyanobacteria proportions.

The amount of assimilated C from the different phytoplankton sources, however, is not necessarily related to suitability as food in our study as the cyanobacteria had about five times as much C. In a study on the use of bacterial carbon by *M. affinis*, Goedkoop and Johnson (1994) estimated C requirements to be around 3.7 μg ind.\(^{-1}\) d\(^{-1}\), while bacterial C exceeded the requirement of *M. affinis*, no more than 6.3% bacterial C was utilized. Lehtonen (1996) showed that *M. affinis* primarily uses lipids as energy for most of the year, but in summer and during egg production switches to use more proteins as energy. This essentially means that meeting the C requirements with food depleted in lipids would not be a good strategy for this species. In a study by Aljetlawi and Leonardsson (2002), adult *M. affinis* were found to have a competitive advantage over young or juvenile individuals, when foraging for food items, due to faster handling times for instance. It is likely that the active foraging behavior of *M. affinis* in particular, but also that of *Marenzelleria* sp. gives these species an advantage over the clam *L. balthica*, as the amount of C from diatoms (and to some extent also C from cyanobacteria), which is shown in this study to actively be selected for, generally is higher in terms of absolute amounts and per body mass. Both *M. affinis* and *Marenzelleria* sp. are active foragers, which can explain the higher assimilation of C from both phytoplankton species compared to *L. balthica*.

Ratios of C:N of all animals and treatments did not indicate that they were subjected to inadequate food availability as solely surviving on stored resources should alter the C:N ratios (Post et al. 2007), which means that mesocosm sediment contained sufficient material for maintaining their body condition during the experiment. The absolute assimilated amount of C and N from cyanobacteria were about 3 (M. affinis) to 10 (*L. balthica*) times higher compared to assimilation from diatoms (Fig. 3). An explanation for this could be the difference between the C content based on loss on ignition (40% C for diatoms and 60% for cyanobacteria) for the experimental setup and actual measured C content after the experiment, which was only 6% C and 0.9% N in diatoms and moderate for cyanobacteria with 20% C and 3.9% N (Table 2). Although the measured C and N content in diatoms was unexpectedly low, this difference would suggest that the amount organic material offered as diatoms, was lower compared to cyanobacteria, which can explain the higher assimilation of cyanobacteria. While higher amounts of diatoms offered would increase actual amounts of assimilation, this is not expected to have an impact on the patterns observed (Figs. 1, 2; Fig. S1).

Effects on benthic species composition

In previous studies involving *M. affinis* and any or both of the other two species, *L. balthica* and *Marenzelleria* sp. showed that particularly *M. affinis* seem to suffer from competition for food (Kotta and Olafsson 2003; Karlson et al. 2008; Sun et al. 2009). *Marenzelleria* sp. tolerates lower oxygen levels (Schiedek 1997) and can make use of older organic material as food than *M. affinis* (Kotta and Olafsson 2003). Additionally, *Marenzelleria* sp. grows faster than *M. affinis* (Kotta and Olafsson 2003) and could possibly outcompete *M. affinis* if conditions deteriorate regarding anoxia and reduced spring-bloom duration and magnitude. The other amphipod species found in association with *M. affinis*, *P. femorata*, also feeds on similar food as *M. affinis*, but make use of older more decomposed material (Hill and Elmgren 1987), thus could perhaps replace *M. affinis* and take over the ecological role as an active subsurface forager, should *M. affinis* populations decline substantially. Whether it also could replace *M. affinis* as food for higher trophic levels is not known.

Differences in quality, quantity, and timing of organic matter supply to the seafloor likely affect interspecific competition and consequently benthic macrofauna composition (Eriksson Wiklund et al. 2008). Reduced input of high-quality diatoms may favor benthic species that can make use of older more
decomposed material, such as Marenzelleria sp. and P. femorata (Hill and Elmgren 1987; Karlson et al. 2011) and species that are adapted to low-nutritious food supply. Our study shows that the added diatoms were a nutritious addition highly favored by all species in general and the amphipod M. affinis in particular as both assimilation of $\delta^{13}C$ and C and N from diatoms was high. This suggests that growth and recruitment of M. affinis is likely strongly affected by reduced diatom and increased cyanobacteria input. In turn, this may explain the observed declines of this species in some regions of the Baltic Sea while in comparison, L. balthica and P. femorata abundances have increased throughout the Baltic Sea (HELCOM 2018), suggesting that they are less sensitive to the exact timing of certain phytoplankton blooms.

Implications for benthic production under climate change

Climate warming is expected to reduce pelagic primary production due to increased stratification, which is expected to reduce diatoms but will favor cyanobacteria in eutrophic systems. The Baltic Sea has already experienced a decline in spring diatom biomass and increase in cyanobacteria (Kahru and Elmgren 2014; Hjerne et al. 2019). Similarly, diatom-associated ice algae are expected to decline with climate warming in arctic systems with melting sea ice (Kohlbach et al. 2016). Our study suggests that reduced diatom deposition to the seafloor will likely negatively affect benthic primary consumers as diatoms are actively selected for by diverse benthic organisms. Shifting species composition and reduction in benthic macrofaunal production will have cascading effects on oxygenation of soft bottoms if key-species populations were to be reduced or replaced in certain areas. Active surface foragers such as M. affinis have the ability to release sediment bound pollutants recently deposited in the upper layers and the deep borrowing activities of Marenzelleria sp. have been shown to release similar amounts of older deposited deeper burrowed pollutants (Hedman et al. 2009). If benthic communities shift toward a higher proportion of Marenzelleria sp. and a declining proportion of M. affinis, this could have an effect on remobilization of pollutants. Given that benthic macrofauna process the majority of organic carbon deposition via ingestion and respiration, a decline in suitable food can lead to reduced reproduction, resulting in less oxygenation of soft bottoms, less food for higher trophic levels relying on them for food, and altered biogeochemical cycles.

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Conflict of interest

None declared.

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