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LETTER

Variation in fatty acid content among benthic invertebrates in a seasonally driven system

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Scientific Significance Statement

Algae produce essential nutrients, such as fatty acids (FAs) that are transported to animals living on the seafloor and fish that feed on them. With varying algal species, it is expected that the FA content of animals is changing, but this has not been tested with seafloor animals. Contrary to this, we find low seasonal variation in FAs in seafloor animals in a system with nutritious spring bloom and summer algae with low essential FAs. But we find differences in FAs between benthic animals that vary with trophic levels. This suggests that seafloor animals have evolved mechanisms to adapt to low-quality food inputs and that species composition of seafloor animals is important for determining food quality for fish.

Abstract

At temperate latitudes where seasonal changing environmental conditions strongly affect the magnitude, duration and species composition of pelagic primary production, macrobenthic organisms living below the photic zone rely on the sedimentation of organic matter as their primary energy source. The succession from nutritious spring blooms to summer cyanobacteria is assumed to reduce food quality for benthic primary consumers and their fatty acid (FA) profiles. In contrast, we find low seasonal variability in FA content of five benthic macroinvertebrates spanning two trophic levels in the Baltic Sea, a system with high seasonal variation in phytoplankton species composition. However, levels of the major FA groups vary greatly between benthic species. The results suggest that benthic macroinvertebrates have evolved FA metabolism adapted to degraded sedimenting material. Moreover, our study shows that species composition of benthic macrofauna rather than seasonal changing conditions affect availability of essential nutrients to higher trophic levels.

Benthic animals living below the photic zone rely on the sedimentation of organic matter (OM) produced by phytoplankton as the primary energy source (Kortsch et al. 2015; Griffiths et al. 2017). Benthic macroinvertebrates

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Author Contribution Statement: PH and MW designed the study. PH and SA collected samples from the field. PH prepared samples for FA analysis. DL together with PH analyzed samples for FAs. PH and MW analyzed and visualized the data. PH and MW wrote the manuscript. All authors contributed to the written work in discussions and editing.

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Additional Supporting Information may be found in the online version of this article.

are themselves an important trophic vector and source of essential compounds produced by phytoplankton for fish, birds, and mammals (Benke and Huryn 2010). Benthic invertebrates often respond in biomolecule composition to inputs of sedimenting OM, which is, however, variable between species (Graf et al. 1982; Lehtonen and Andersin 1998; Lahdes et al. 2010). At temperate latitudes, seasonal changing environmental conditions strongly affect the magnitude, duration, and species composition of phytoplankton blooms (Lutz et al. 2007; Winder and Cloern 2010), and consequently sedimenting input for benthic animals. Spring blooms, largely composed of diatoms and dinoflagellates, are thought to be the major annual input of high-quality food, while summertime exports are more variable depending on species composition (Simis et al. 2017). Coastal ecosystems, including the Baltic Sea, are experiencing an increase in summer cyanobacteria due to eutrophication and climate warming, which is expected to decrease inputs of essential macromolecules and their availability for higher trophic levels (Lehtonen and Andersin 1998; Hjerne et al. 2019; Schmidt et al. 2020). However, little is known about dietary transfer of essential compounds in benthic consumers and how they respond to seasonally varying inputs of OM.

Phytoplankton are assumed to be the main producers of essential biomolecules, like amino acids and fatty acids (FAs) for consumers in general and benthic invertebrates residing in the nonphotic zone in particular (Petersen and Curtis 1980). FA composition varies between major phytoplankton taxa, with diatoms and dinoflagellates being rich in the essential polyunsaturated fatty acids (EFAs), including arachidonic acid (ARA, 20:4ω6), eicosapentaenoic acid (EPA, 20:5ω3), and docasahexaenoic acid (DHA, 22:6ω3), while cyanobacteria to a large extent are lacking these compounds (Galloway and Winder 2015). EFAs are generally not synthesized de novo by consumers and mainly assimilated from diet (Parrish 2008); however, there is increasing evidence for potential EFA synthesis in a wide variety of invertebrate animals (Kabeya et al. 2018). EFAs are important for fish nutrition and commonly linked to consumers' growth and fecundity (Brett and Müller-Navarra 1997). Consequently, shifts in phytoplankton species composition and particularly declines in nutritious spring blooms and increase in low-quality phytoplankton during summer periods is assumed to result in decreased EFAs at higher trophic levels, affecting ecosystem productivity (Taipale et al. 2016; Schmidt et al. 2020; Svedäng et al. 2022). Although EFA transfer pathways in aquatic environments are well documented within the pelagic food web (Brett and Müller-Navarra 1997; Arts et al. 2001), this field is largely understudied in benthic primary consumers (Monroig et al. 2013).

To address this gap, we study effects of seasonal changing phytoplankton species on FA quantity and composition of pelagic sedimenting OM and benthic macroinvertebrates. This study was performed in the Baltic Sea, where diatoms and dinoflagellates dominate the spring bloom and cyanobacteria the summer bloom (Fig. 1A). We explore this by analyzing seasonal FA content per dry weight, tracing of food sources' origin and partitioning of trophic levels using stable isotopes (SI) in OM and dominating benthic primary consumers.

Methods

Seston, sediment, and benthic animals were sampled at a coastal site in the north-western Baltic Proper (58°48′39.5″N, 17°36′25.1″E). The site was situated at 40 m depth with a bottom water salinity varying from 6 to 7 and temperature from 0.18°C to 6.84°C during our sampling occasions. Sampling was done in July, August, October, November 2018, and March, April 2019, representing summer, autumn, and spring bloom conditions. Seston was collected as a vertical integrated water sample from the surface to 20 m depth and was prefiltered through a 100-μm mesh, then filtered onto GF/F filters and frozen at −80°C. Sediment was sampled with a boxcorer, subsampled with plexiglass tubes, after which the upper sediment (ca 9 mm) was sliced off, homogenized, and frozen at −80°C. Animals were sampled with a benthic sled. We selected adult stages of common macrofauna species, including the surface and subsurface feeding amphipods, *Monoporeia affinis* and *Pontoporeia femorata*, respectively, the facultative suspension and deposit-feeding clam *Macoma balthica*, the deposit-feeding polychaete *Marenzelleria* spp. and the predatory priapulid worm *Halicryptus spinulosus* (referred hereafter to their genera). Animals were sieved from the sediment, placed in aerated filtered sea water for 24 h in order to facilitate gut evacuation, keeping *Halicryptus* separate. *Macoma* was separated from their shell and all animals were frozen at −80°C. For FA and SI analyses, samples were freeze-dried at −120°C (one replicate for seston and sediment, three for each species) and pulverized. Further details of sample collection, and FA and SI analyses are provided in the Supporting Information. FAs were grouped into major groups: Saturated FAs (SAFAs), monounsaturated FAs (MUFAs), polyunsaturated FAs (PUFAs, including EFAs and their precursors alpha-linolenic acid [ALA] and linoleic acid [LIN]), and bacterial FAs (BAFAs); a full list of individual FAs analyzed is provided in Supporting Information Table S1.

Differences of FA group and EFA content between species for the whole sampling period and within species over time were analyzed with permutational multivariate ANOVA (PERMANOVA) using the vegan (Oksanen et al. 2020) and pairwiseAdonis (Martinez Arbizu 2020) packages after testing for normality and variances. Nonmetric Multidimensional Scaling (NMDS) with Bray–Curtis dissimilarity distance was used to explore similarity of individual FAs among benthic species, seston, and sediment based on percentages over the whole sampling period. Individual differences within certain groups of FAs, for each species over time and between species

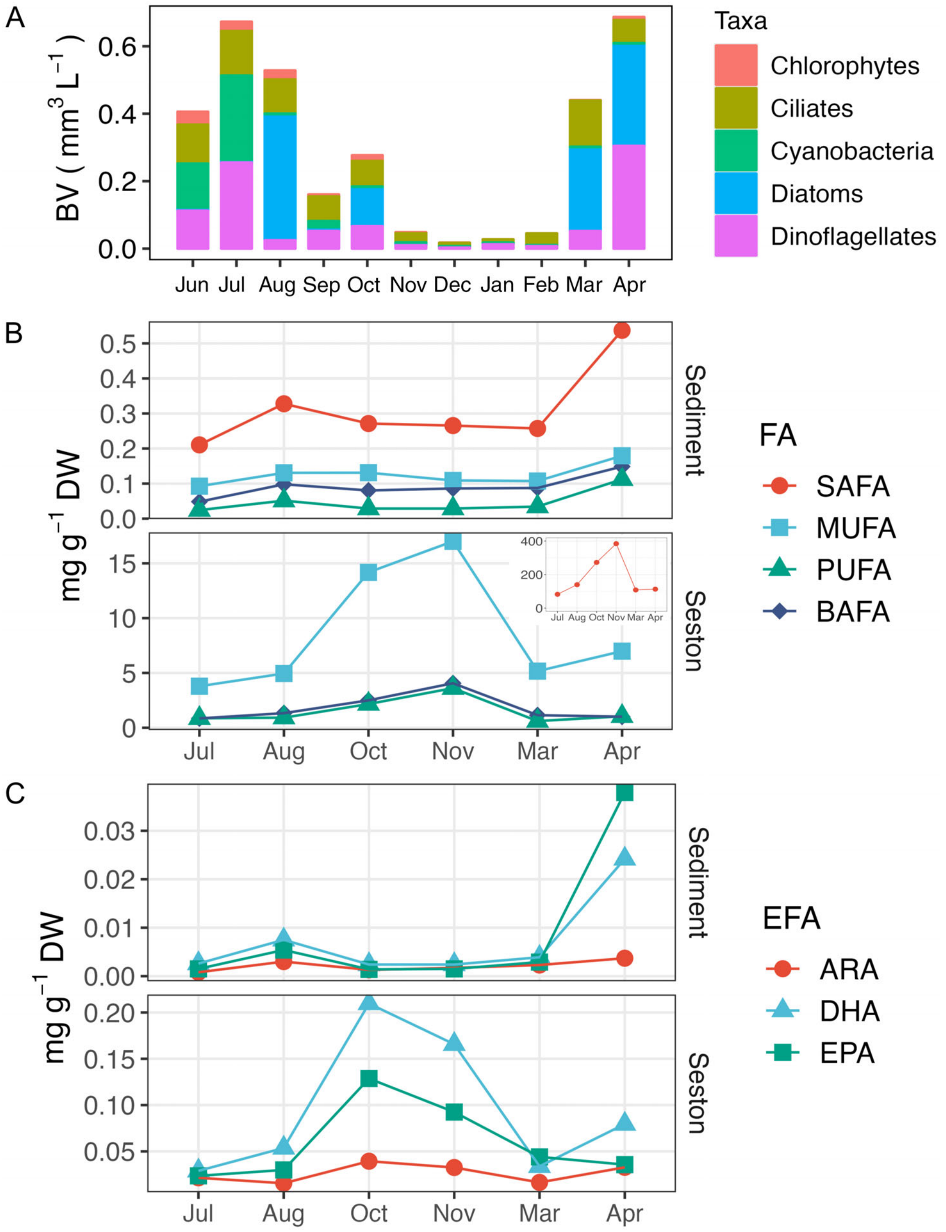

Fig. 1. Seasonal dynamics of phytoplankton as well as seston and sediment FA content in the Baltic Sea from July 2018 to April 2019. (**A**) Average monthly biovolume of major phytoplankton taxa. Note, ciliates constitute the mixotroph Mesodinium rubrum. X-axis abbreviations are month of the year. (**B**) Seston and sediment (upper 9 mm) content of major FA groups, including SAFAs, MUFAs, PUFAs, and BAFAs. SAFAs of seston is shown in the insert. (**C**) Seston and sediment EFAs, including ARA, DHA, and EPA. Data on plankton biovolume are available from the Swedish Meteorological and Hydrological Institute (SMHI) website (https://sharkweb.smhi.se/).

over time, SI data and C:N ratio were analyzed either with a one-way or two-way ANOVA in a generalized least squares model (gls) in the nmle package (Pinheiro et al. 2006). Relationships between major phytoplankton groups ($\text{mm}^3\ \text{L}^{-1}$) and individual FAs ($\text{mg g}^{-1}$) in seston, sediment and animals were investigated with multiple linear regression models, on log-transformed FA data to fulfill assumptions of linearity. All analyses were done using R (R Core Team, 2020).

Results

Seston contained high levels of SAFA, ranging from 80 to about 400 mg g^{-1} or more than 90% of total FA, with all major FA groups and EFA peaking in October and November (Fig. 1B,C; Supporting Information Fig. S1). Seston C:N ratio reached up to 34 during the spring bloom (March–April) and varied between 5 and 16 for the remaining months, while sediment C:N was around 7.8 (Supporting Information Fig. S2).

In comparison to seston, sediment contents of major FA groups and individual EFA were orders of magnitude lower, not exceeding 0.6 mg g^{-1} (Fig. 1B,C) and consisting mainly of the SAFA palmitic acid (16:0; Supporting Information Table S1). Sediment FA showed low seasonal variation, except for an increase of EPA and DHA in April (Fig. 1C).

Seasonal variation of major FA groups and individual EFAs in benthic species were unrelated to the succession in phytoplankton biomass of major taxa ($p > 0.05$) and showed generally low variation throughout the season, with two exceptions (Fig. 2; Supporting Information Fig. S1; Table S2). In *Marenzelleria*, total FAs differed between November (higher) and March (lower) at $p < 0.05$ (Fig. 2A; Supporting Information Table S3). *Monoporeia* had a slight increase of BAFAs in March before the spring bloom ($p < 0.05$) and a low C:N ratio of 5.7 in April (Fig. 2A; Supporting Information Table S4), while the ω3:ω6 ratio was low during the summer and increased after the autumn and spring bloom (Supporting Information Fig. S3; Table S5).

In contrast to low seasonal changes, we observed variation among the benthic animals. The amphipods *Monoporeia* (29.9 mg g^{-1}) and *Pontoporeia* (35.1 mg g^{-1}) and the polychaete *Marenzelleria* (30.8 mg g^{-1}) reached the highest total FA content averaged over the whole sampling period among all macroinvertebrates, which is largely due to high content of SAFAs and MUFAs in amphipods, and also PUFAs in *Marenzelleria* (Fig. 2A). In comparison, total FAs, SAFAs, and MUFAs were significantly lower for *Macoma* and *Halicryptus* ($p < 0.001$; Supporting Information Table S6). *Marenzelleria* had about two to three times as high levels of BAFAs than the other species ($p < 0.01$; Supporting Information Table S8), except for July and March (Fig. 2A; Supporting Information Table S8). BAFA values were similar for the amphipod species, except for a peak in March for *Monoporeia* ($p < 0.05$; Supporting Information Table S4), and low in *Halicryptus* and *Macoma*. *Marenzelleria* had a lower ω3:ω6 ratio (less than 1) than all other species throughout the sampling period ($p < 0.001$; Supporting Information Table S5), indicative of high amounts of the 20:2ω6 FA intake (Supporting Information Fig. S3; Table S1). In addition, *Marenzelleria* and *Halicryptus* had the lowest C:N ratio of about 5.2 with other species reaching up to 11.7 (Fig. 2A).

Marenzelleria reached the highest PUFA levels with an average of about 7.9 mg g^{-1} related to high EPA and DHA values, while PUFA contents of all other species were significantly lower and ranged between 0.6 and 1.9 mg g^{-1} throughout the sampling period ($p < 0.01$; Figs. 2, 3A; Supporting Information Table S7). DHA content in *Monoporeia* was significantly higher from November to April compared to August (Supporting Information Table S2). *Macoma* and *Halicryptus* had the lowest EFA content among the species and sediment contained minimal levels of EFAs (Fig. 3A).

The NMDS revealed separate clustering of sediment and seston from the animal species, being mostly associated with SAFAs (Fig. 3B). Between species, the two amphipods and the clam displayed similar patterns and were positively associated to ALA, SAFAs, and other FAs. Likewise, *Marenzelleria* and *Halicryptus* clustered, positively associated with PUFAs like LIN, ARA, EPA, and DHA.

Stable isotopes

Seston δ^{13}C and δ^{15}N varied throughout the sampling period (Supporting Information Fig. S4), while SI values of sediments did not change (Fig. 4). Among all benthic macroinvertebrates (with the exception of April), *Halicryptus* had the highest trophic position according to its δ^{15}N mean value of 11.02‰ ($p < 0.05$), followed by *Marenzelleria* with a mean of 9.32‰ ($p < 0.01$), while *Monoporeia*, *Pontoporeia*, and *Macoma* had similar δ^{15}N value ranging from 7.21‰ to 7.74‰ ($p > 0.1$; Fig. 4; Supporting Information Table S9). All benthic invertebrates had similar δ^{13}C values (−21.5) with higher values than sediment (−23.0) and seston (−26.5). *Monoporeia* was more negative in δ^{13}C in April compared to all other months ($p < 0.001$; Supporting Information Table S10).

Discussion

We find that the most dominant benthic invertebrates show low seasonal variation in FA content in a system with large variation in phytoplankton species composition of different nutritional quality. Although seston and sediment FA values partially reflect seasonal change in phytoplankton production and sedimentation, these subtle changes were only translated to a few benthic macrofauna. By measuring quantitative FA content per dry weight, we find that EFA contents of benthic macrofauna are orders of magnitude higher compared to seston and sediment, and vary across benthic species. These findings indicate that by rather converting dietary EFA, the FA content of benthic species is regulated by diverse mechanisms.

Seston FA content remained low during the spring and summer period but increased in autumn (October–November), likely related to a phytoplankton bloom, zooplankton activity through the production of fecal pellets and particle resuspension coupled to the break-down of the stratified water column (Tiselius et al. 2012). In comparison to seston, sediment FA content, C:N ratio, and isotopic signatures were stable throughout the sampling period, except in April when EPA and DHA increased slightly. This increase is most likely linked to the settling of the spring phytoplankton bloom. Manifold lower sediment content, mainly consisting of the SAFA palmitic acid (16:0) suggests breakdown of FAs during sedimentation and low nutritional value of sediment, in accordance to previous findings (Goedkoop et al. 2000). These data are in line with other studies, indicating that spring blooms contribute to the highest level of fresh OM sedimentation (Spilling et al. 2014). Subsequent blooms throughout the year are subjected to increased degradation, grazing by zooplankton and are generally lower in organic quantity and

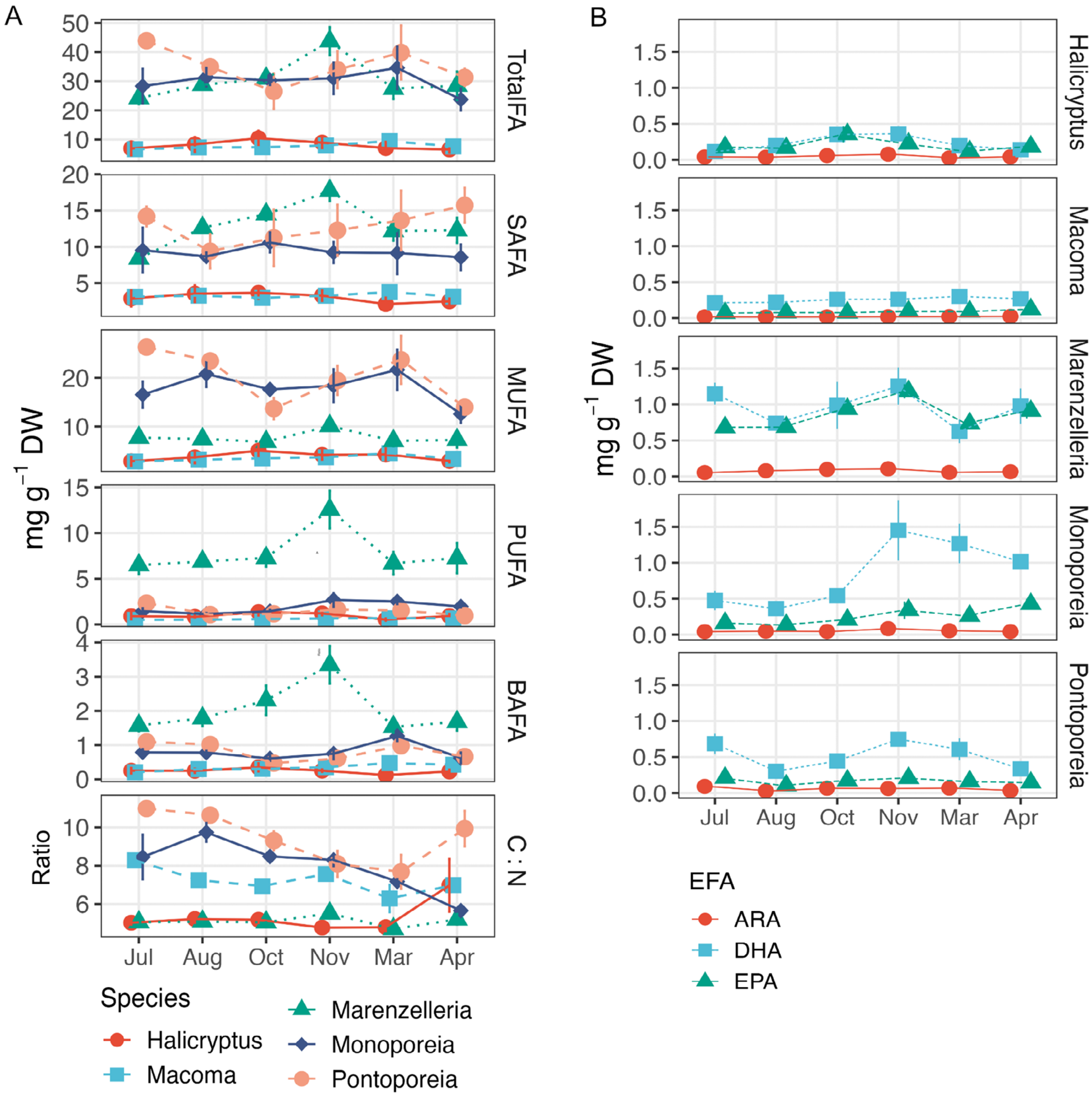

Fig. 2. Seasonal dynamics of FA content and C:N ratio of benthic macroinvertebrate species in the Baltic Sea from July 2018 to April 2019. (**A**) Total FA, major FA groups, and C:N ratio, and (**B**) EFAs. Error bars represent standard errors.

quality (Lovvorn et al. 2005; Tamelander et al. 2017; Rodil et al. 2020).

We find that the content of the major FA groups varies greatly between macroinvertebrate taxa but intraspecific variation over the season is low, with the exception of *Marenzelleria* and a spring-bloom related change in *Monoporeia*. The two amphipod species *Monoporeia* and *Pontoporeia* show similar FA content and cluster at trophic level two, indicating that they are primary consumers dependent on sedimenting organic material as food. The increase in EPA, ω3:ω6 ratio and more negative δ^{13}C for *Monoporeia* in April suggests rapid assimilation of spring-bloom material, which is supported by both field and experimental studies (Hill et al. 1992; Van de Bund et al. 2001; Dalsgaard et al. 2003; Lahdes et al. 2010). The lack of a phytoplankton-related FA signal in the amphipod *Pontoporeia* is likely related to its

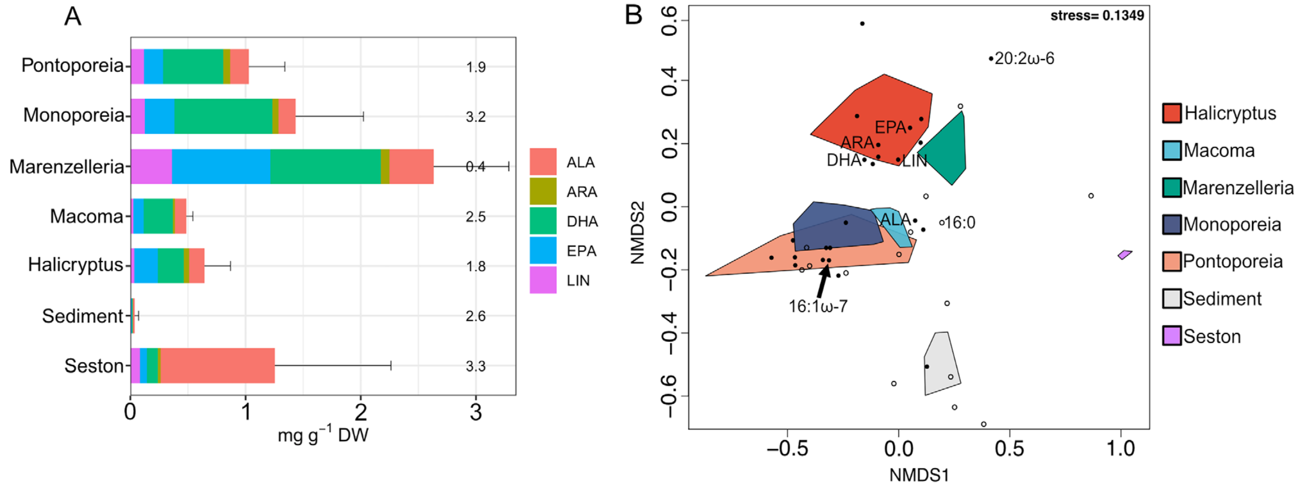

Fig. 3. (**A**) Seasonal averaged content of PUFAs (including EFAs and their precursors ALA and LIN). The number reports the ω3:ω6 PUFA ratio. (**B**) NMDS clustering of benthic macroinvertebrate species, sediment and seston based on the proportion of individual FAs over the whole sampling period. Polygons represent connections between the outermost scores in ordination of FAs in relation to each species, sediment and seston. Black points are individual FAs, with open points representing SAFAs; dominating FAs are labeled. The closer a species polygon is to a FA (point), the higher content of that particular FA is present in the species represented by the polygon.

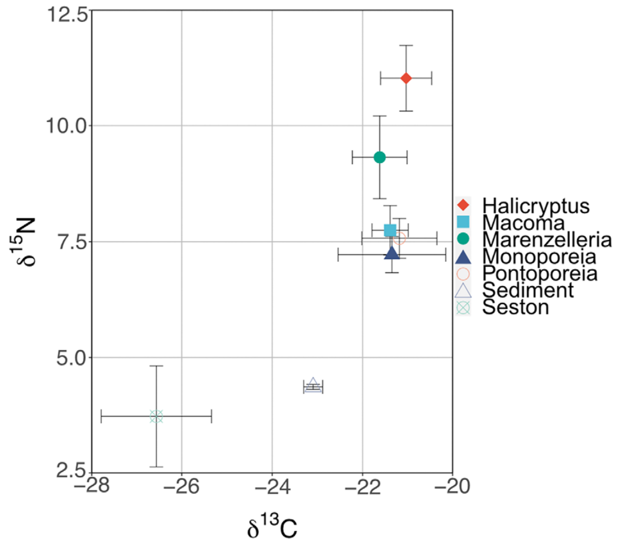

Fig. 4. Biplot of δ^{13}C and δ^{15}N SI values for benthic macroinvertebrates, seston, and sediment in the Baltic Sea from July 2018 to April 2019. Error bars represent standard deviations.

deeper foraging strategy compared to *Monoporeia*, which may cause a competitive disadvantage for freshly deposited OM for this species (Hill and Elmgren 1987).

Our results show for the first time that *Marenzelleria*, a wide-spread ploychaete in the Northern Hemisphere and a successful invasive species in the Baltic Sea has the highest EFA content among the studied species. In addition, its low C:N ratio, indicative of high nutritional value for predators is in line with previous studies (Karlson et al. 2015). High levels of EFA are surprising because *Marenzelleria* is adapted to forage in deeper sediment layers and likely has a higher tolerance for degraded and nutritionally poor food than other benthic macrofauna (Renz and Forster 2013). This is partially reflected in their comparably high levels of BAFAs and low ω3:ω6 ratios, indicating ingestion of high levels of FAs from terrestrial origin of low quality (Lau et al. 2014; Taipale et al. 2014). However, *Marenzelleria* was the only species showing a relationship with the diatom FA biomarker 16:1ω-7 (palmitoleic acid; Dalsgaard et al. 2003) when spring bloom had settled in April ($p < 0.01$; Supporting Information Table S11). In addition, linear mixed effects regression between the two precursors 18:3ω-3 (ALA) and 18:2ω-6 (LIN), and their EFA end-products DHA and ARA ($p < 0.001$; Supporting Information Table S12), respectively, indicate the possibility of this species to elongate and desaturate EFAs from precursors. This suggests that *Marenzelleria* not only consumes old degraded and fresh sedimenting organic material but also has the possibility to produce EFA de novo. These observations are supported by a taxonomically widespread survey, indicating that polychaetes and other marine invertebrates have active desaturase genes to elongate and introduce double bonds from corresponding precursors (Kabeya et al. 2020).

In addition, the relatively high δ^{15}N value and a DHA: EPA ratio of roughly 1 : 1 in *Marenzelleria* suggest an omnivorous feeding mode, which is contrary to the assumption of being a primary consumer (Dauer et al. 1981; Dauer 2000) and suggest possible trophic upgrading by the bacteria-based food chain that eventually provide EFA to *Marenzelleria*. High δ^{15}N values, however, may also result from material ingestion from deeper sediment subjected to anaerobic ammonium oxidation (anammox) that removes the lighter isotope (Brunner et al. 2013). *Marenzelleria* also showed a steady build-up of all major FA groups, including total FAs from summer toward late autumn (i.e., November), followed by a sharp drop for all FA groups between November and March, which is likely due to build-up of gametes, rich in FAs and spawning in late autumn (Bochert et al. 1997; Sikorski and Bick 2004; Kauppi et al. 2018). Overall, our findings strengthen previous experimental studies of *Marenzelleria's* competitive advantage compared to amphipods (Kotta and Ólafsson 2003) and its adaptation to seasonal fluctuations in fresh OM sedimentation.

Unlike *Marenzelleria*, the clam *Macoma* is low in FA content but nevertheless has a high C:N ratio, suggesting that this clam species has nutritional value for predators, including other lipid classes and glycogen (Graf et al. 1982; Wenne and Polak 1989). Low FA content in *Macoma* is in line with other studies showing that they accumulate low FA from primary production (Sun et al. 2009). This clam species has, however, an overall high ω3:ω6 ratio throughout the sampling period owing to relatively high levels of DHA, which is likely related to its ability to utilize EFAs from fresh pelagic OM (Lessin et al. 2019) and its selective assimilation of DHA. Surprisingly, the priapulid *Halicryptus* had similarly low levels of total FAs, including EFAs, despite its predatory feeding mode and expected FA increase with trophic level. Similar FA profiles in these two species are probably attributed to their tolerance for extended periods of hypoxia/anoxia conditions as anoxic metabolism uses glycogen as energy source in invertebrates, thus perhaps lowering the requirement for lipid reserves (Hochachka et al. 1973).

High interspecific variation in FA content of soft bottom benthic fauna as shown here is in line with observations for zooplankton and lake benthic macroinvertebrate species (Lau et al. 2012, 2021; Vesterinen et al. 2020). Similarly, the magnitude of seasonal fluctuations in FAs, especially EFAs are often taxa dependent among aquatic consumers (Goedkoop et al. 2000; Ravet et al. 2010; Lau et al. 2012). However, FA profiles of aquatic primary consumers may also be uncoupled to phytoplankton production, but rather vary with changing water temperature (McMeans et al. 2015; Lau et al. 2021), life history strategies related to reproduction, as shown for *Marenzelleria*, quality upgrading (Klein Breteler et al. 1999) or physiological FA regulation in anoxic environments, as assumed for *Macoma* and *Halicryptus*. The FA content of the benthic fauna investigated here did not respond to the spring inputs of OM. Although we can expect that sufficient time for settling of the spring bloom had passed (Rodil et al. 2020), making fresh OM available for the fauna as indicated by the increase in sediment EFAs in April. The lack of a response to spring bloom inputs is in contrast to previous studies, showing that total lipids, glycogen and FA percentages of some benthic animals respond to deposited spring OM, although the signal is usually short-lived (Graf et al. 1982; Lehtonen 1996; Lahdes et al. 2010). However, our study agrees with Jardine et al. (Jardine et al. 2020), emphasizing that metabolic transformation, integration, and biosynthesis of certain FAs could mask the immediate dietary intake. Stable FA content of zooplankton and benthic species over the season suggest that these taxa have internal mechanisms to synthesize EFAs when supply is low or depend on food resources with low seasonal variation in biochemical composition. Moreover, low variation in abiotic conditions characteristic of deep soft bottom environments (Janas et al. 2007) may cause low turnover rates of FAs, especially in benthic consumers with low somatic growth rates and low lipid metabolism at low temperature. This suggests that FA composition of benthic macrofauna and the transfer of EFAs from primary producers to consumers are affected by different mechanisms related to a multitude of drivers (Goedkoop et al. 2000; Ravet et al. 2010; Lau et al. 2012, 2021; McMeans et al. 2015). Our results indicate that benthic organisms from multiple trophic levels and feeding guilds have evolved strategies to adapt to the low nutritional value provided by sediment OM, including the capability to biosynthesize EFA (Kabeya et al. 2018).

Several ecosystems experience decline in fisheries production, which is often linked to reduced dietary conversion of EFAs related to increasing cyanobacteria (Schmidt et al. 2020). We find that phytoplankton species composition and the quality of fresh settling OM does not directly translate into essential biomolecule composition for benthic animals, which are an important link to higher trophic levels. Our findings contradict the assumption that spring bloom sedimentation enhances nutritional value of FAs in benthic consumers, while summer blooming cyanobacteria settling is of reduced qualitative value and that this might have consequences for higher trophic levels. This indicates that the transfer of essential biomolecules from primary producer to upper trophic levels is more complex and not directly related to the taxonomic composition and content of phytoplankton. However, long-term increase in cyanobacteria biomass and reduced input of spring bloom material may affect consumer fecundity and growth rates and consequently community composition by favoring species best adapted to low-quality OM, rather than changing the FA profile of consumers.

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