Food-web comparisons between two shallow vegetated habitat types in the Baltic Sea

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Abstract:	Coastal vegetated habitats maintain highly diverse communities, where the contribution of macrophyte production is significant for macroinvertebrate primary consumers. In the brackish-waters of the Baltic Sea, the taxonomical diversity of different macrophytes includes both marine and limnic species. To study the basal food-web differences of two key vegetated habitat types, either dominated by a perennial brown macroalgae (Fucus vesiculosus) or by angiosperm plants, 13 C and 15 N compositions of different primary producers and macroinvertebrate consumers were examined, and their diets were estimated by Bayesian mixing models. Carbon isotope diversity of primary producers was high especially in the hard-bottom Fucus -dominated habitats, which was also reflected in a larger consumer isotope niche. However, consumer isotope niche among sites was similar within the same habitat type. Our models indicated that the perennial macrophyte dietary median contribution was about 25% for deposit feeders and omnivores in both habitat types, while epigrazers preferred filamentous algae (30−60%). The niche positions of the abundant clams L. balthica, M. arenaria and C. glaucum differed between the two habitats, but they showed only small (<10% units) differences in their macrophyte dietary contributions. The isotopic compositions of the dominating primary producer assemblage reflected significantly in the isotope niche structure of the associated primary consumers.
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Highlights

- Shallow coastal vegetated habitats are completely different food environments in terms of the primary macrophyte sources they provide.
- The isotope niche sizes of the macrovegetation assemblage and associated primary consumers were bigger in *Fucus*-dominated hard-bottom habitats than in angiosperm-dominated soft-bottom habitats.
- The effect of spatial differences on the isotope niche structure was smaller than the effect of the dominating macrovegetation.
- Regardless of the dominating macrovegetation, our results indicated only small dietary differences of the infaunal clams (*C. glaucum*, *M. arenaria*, *L. balthica*) present in the adjacent soft bottom communities of the both habitat types.
- Perennial macrophyte dietary contribution was about < 25 % in omnivores and deposit feeders, while epigrazers preferred filamentous algae with a contribution of about 30–60 %.

Food-web comparisons between two shallow vegetated habitat types in the Baltic Sea

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Abstract

Coastal vegetated habitats maintain highly diverse communities, where the contribution of macrophyte production is significant for macroinvertebrate primary consumers. In the brackish-waters of the Baltic Sea, the taxonomical diversity of different macrophytes includes both marine and limnic species. To study the basal food-web differences of two key vegetated habitat types, either dominated by a perennial brown macroalgae (*Fucus vesiculosus*) or by angiosperm plants, ^{13}C and ^{15}N compositions of different primary producers and macroinvertebrate consumers were examined, and their diets were estimated by Bayesian mixing models. Carbon isotope diversity of primary producers was high especially in the hard-bottom *Fucus*-dominated habitats, which was also reflected in a larger consumer isotope niche. However, consumer isotope niche among sites was similar within the same habitat type. Our models indicated that the perennial macrophyte dietary median contribution was about 25 % for deposit feeders and omnivores in both habitat types, while epigrazers preferred filamentous algae (30−60 %). The niche positions of the abundant clams *L. balthica, M. arenaria* and *C. glaucum* differed between the two habitats, but they showed only small (<10 % units) differences in their macrophyte dietary contributions. The isotopic compositions of the dominating primary producer assemblage reflected significantly in the isotope niche structure of the associated primary consumers.

1. Introduction

Some of the most productive, abundant, species-rich and ecologically valuable marine communities can be found in coastal vegetated habitats such as tidal marshes, mangroves, seagrass meadows and macroalgal underwater forests (Dayton 1985, Duffy 2006, Gutiérrez et al. 2011, Seitz et al. 2014). Despite being confined to a narrow area around the shoreline of the oceans, coastal vegetated habitats have been estimated to support 1−10 % of the global marine net primary production (Duarte 2017). Macroalgae and seagrasses are typical foundation species, which can modify the physical environment around them, benefitting biodiversity and providing ecosystem services in coastal areas (Rönnbäck et al. 2007, Gutiérrez et al. 2011). As food sources, large macrophytes can be of great local importance (Renaud et al. 2015; Kahma et al. 2020), in addition to particulate organic matter, POM (mainly phytoplankton) and dissolved organic matter (DOM) (e.g. Bouillon et al. 2011; Hyndes et al. 2014). The ecosystem-level role of macroalgal carbon fixation is increasingly recognized. Some recent studies show the great magnitude of carbon export capacity of vegetated coastal ecosystems to offshore areas (Krause-Jensen and Duarte 2016, Kokubu et al. 2019, Watanabe et al 2020), and highlight their role as potentially important carbon sinks (e.g. Fourqueran et al. 2012, Duarte et al. 2013, Trevathan-Tackett et al. 2015, Cragg et al. 2020). However, coastal habitats are exceedingly impacted environments (Stanners and Bourdeau 1995, Lotze et al. 2006), and habitat loss and degradation of these ecosystems has raised growing concerns regarding the ecological and economic consequences (Stanners and Bourdeau 1995, Pendleton et al. 2013, Siikamäki et al. 2013).

The Baltic Sea exhibits a large taxonomical variety of primary producers, not only of marine but also of limnic origin, and thus a high diversity of macrophyte food sources (Hällfors and Niemi 1981). The macrophyte community is highly diverse and its structure and production change across environmental gradients (Gustafsson and Norkko 2019). The seafloor substrate (and salinity gradient) structuring the dominating vegetation type affects both taxonomical diversity and the traits of associated macrofauna, creating distinct habitat types in the coastal zone (Henseler et al. 2019). Hard rocky bottom habitats are dominated by the canopy-forming perennial macroalgae *Fucus vesiculosus* (L.) and many opportunistic ephemeral macroalgae, for example *Cladophora glomerata* (L.), *Pylaiella littoralis* (L.) and *Ceramium tenuicorne* ([Kützin]) Waern) (Hällfors et al. 1975, Hällfors and Niemi 1981, Kiirikki and Lehvo 1997). In these habitats, small crustaceans such as *Idotea balthica* (Pallas) and

Gammarus spp. (Fabricius), the bivalve *Mytilus trossulus* (Gould) and gastropods *Theodoxus fluviatilis* (L.) and *Peringia ulvae* (Pennant 1777) are typical macrofauna species (Lassig and Leppäkoski 1981). Soft-bottom shallow areas provide a habitat for a large assemblage of angiosperm species, such as marine *Zostera marina* (L.) and limnic *Potamogeton* spp. (L.), *Myriophyllum spicatum* (L.) (Hällfors et al. 1975, Hällfors and Niemi 1981, Boström et al. 2014). In soft-sediment areas, the benthic clam *Limecola* (*Macoma) balthica* (L.) is one of the key marine macrofauna species, and other typical invertebrate species include different gastropod species, polychaetes and insect larvae (Lassig and Leppäkoski 1981, Kautsky & Kautsky 2000, Gammal et al. 2019, Rodil et al. 2020a). In the Baltic Sea, eutrophication has resulted in a systematic decrease of macrophyte beds and the rise of a turbid-water system dominated by pelagic primary production and ephemeral algae (Leppäkoski et al. 1999, Gustafsson and Boström 2014, Takolander et al. 2017) with likely consequences for carbon storage and food-web interactions in coastal habitats. Hence, we need to understand the importance of different macrophytes as potential food sources for primary consumers in coastal food webs.

The ecology and food webs of macroalgal beds and seagrass meadows have been studied worldwide (e.g. Dayton 1985, Duffy 2006, Gutiérrez et al. 2011). However, there are few coastal food web studies considering a wide taxonomic range of potential primary producers (Hansen et al. 2012). This is particularly the case in the Baltic Sea, where most of the studies are based on monospecific seagrass habitats such as *Zostera marina* meadows (e.g. Jaschinski et al. 2008, Jephson et al. 2008, Mittelmayr et al. 2014, Mittelmayr et al. 2015, Thormar et al. 2016, Jankowska et al. 2018), and there are only few studies focusing on macroalgae (e.g. *Fucus vesiculosus*) as a potential food source (e.g. Wiedemeyer & Schwamborn 1996, Nordström et al. 2016, Kahma et al. 2020). Angiosperm plants, which tend to have high lignocellulose contents, are difficult to digest for many aquatic herbivores (e.g. Mattila 2014 et al., Cragg et al. 2020). While there are reports of isopod grazers, such as *I. balthica* feeding on *Z. marina* (Mattila et al. 2014), a recent study from the Southern Baltic Sea concluded that benthic invertebrates did not consume vascular plants, but rather fed on suspended particulate organic matter, phytoplankton and detrital matter (Ziółkowska et al. 2018). *Fucus vesiculosus* has been suggested recently as a key benthic energy source in coastal habitats of the Baltic Sea with a large detrital carbon export potential (Attard et al. 2019a,b; Kahma et al. 2020).

However, there is a lack of studies simultaneously evaluating the proportions of macroalgae and angiosperm as food sources for the macrobenthic associated coastal communities.

In a previous study (Kahma et al. 2020), we examined the seascape spatial variability of the main potential food sources for three key benthic consumers, focusing mainly on offshore areas and depth gradients. Our models for the shallowest habitats suggested relatively high macroalgae (*F. vesiculosus*) dietary proportions (Kahma et al. 2020). However, since the taxonomical diversity of different macrophytes is high in the shallow areas, and the dominating macrophyte assemblage varies spatially, a separate in-depth study in shallow vegetated habitats is necessary to examine possible differences in the macrophyte-derived subsidy to the basal food webs. Here, we performed a spatial comparison between two dominant coastal habitat types from the Baltic Sea: hard-bottom habitats dominated by macroalgae (mainly *F. vesiculosus* and different species of ephemeral filamentous algae), and soft-bottom habitats dominated by angiosperm vascular plants. The aims of this study were (1) to describe and compare the basal food web in typical coastal vegetated habitats of the Baltic Sea by using a dual stable isotope (^{13}C and ^{15}N) approach, and (2) to determine dietary contributions of the main primary food sources (i.e., *F. vesiculosus*, angiosperm plants, filamentous algae, sestonic matter) to key invertebrate primary consumer species, either directly grazing or feeding on sedimentary detritus including macrophyte-originated matter. We expect that the dominating macrovegetation type will influence the associated benthic food webs from the angiosperm and macroalgal dominated habitats. We used Bayesian isotope niche analysis (SIBER) to describe the potential differences in community wide trophic niches between habitats, and in population niche sizes for species that occurred in both habitats. Finally, Bayesian mixing models (MixSIAR) were used to estimate the relative importance of different types of food sources among macroinvertebrate species.

2. Materials and methods

2.1. Sampling area

The Storfjärden bay on the eastern side of Hanko peninsula in Southwestern Finland covers an area of about 30 km^2 (**Fig. 1**). The northern part of the bay is influenced by riverine input, whilst the southern

part borders to the open sea, thus more exposed to physical and biological influences of the marine environment. The maximum depth of the bay is approximately 40 meters. The shore types include both rocky and sedimentary habitats. At a large spatial scale, *F. vesiculosus* communities, *Z. marina* seagrass meadows and mixed angiosperm macrophyte beds, are the main primary benthic producer habitats at the study area. In the study area, we chose three sampling sites (A, B, C) where soft-bottom (1) and hard-bottom (2) habitats were closely located within each site (i.e. A1-2, B1-2, and C1-2) (**Fig. 1**). These sampling sites were common with our previous study (Kahma et al. 2020). The distance between the northernmost (A) and southernmost sampling location (C) was approximately 3.5 kilometers (Fig. 1). In addition, we included for this study our previously published data, where five different pelagic sampling locations (W1-W5) were chosen for the analysis of particulate and dissolved organic matter (POM and DOM) in the water column (for more details on the sampling sites, see Kahma et al. 2020).

FIGURE 1

2.2. Sampling

Different species of macrophyte primary producers, macrobenthic consumers (infauna and epifauna), and sediment (a heterogenous food source representing a mix of e.g. microphytobenthos, partly decomposed organic matter and microbes) were sampled from the sampling locations (**Table 1**). We generally aimed to collect 4–5 samples of each primary producer and consumer species, and three replicates from the surface sediment samples. We collected 15 *L. balthica* (which is the most abundant macroinfauna species) individuals from location B1 and 16 individuals from location B2 to improve model estimates of the dominant food sources in the dominant species.

TABLE 1

Samples were collected by SCUBA diving from the shallow (~ 2m) sampling locations from June 26 to July 6, 2017 (Table 1). Dominating macrophyte species at the sampling locations were targeted, and samples of each species present, with its associated macrofauna, were randomly picked by hand from their growing sites into a net-bag (e.g. Rodil et al. 2020a). In the lab, all the macrophyte samples were washed by hand with deionized water to remove associated epifauna and identified. All the associated epifauna was listed. On soft sediments, macroinfauna was sampled using a benthic corer

(diam. 10 cm, 15 cm depth). In the hard bottom habitats with no soft seafloor present (A1, B1, C1), we sampled the immediately adjacent (< 3 m of vertical distance) soft sediment a few meters deeper, as potential direct recipients of the organic matter (i.e. macroalgal detritus) export from the hard substrate habitat above (~5 m, Table 1). The sediment cores were sieved (mesh size 1 mm), and all the infauna (e.g. *L. balthica*, *Marenzelleria* spp., *Hediste diversicolor*) was manually collected. All epifaunal and infaunal animals retained were then left into autoclaved and filtered (Ø 0.2 µm) seawater over night to empty gut contents, then washed with deionized water and stored at -20 °C. All the bivalve and gastropod individuals were removed from their shells before washing and storing the samples. Macrophyte samples were washed with deionized water, and plant material was cut from different random parts of the plant individual, and then stored into Eppendorf tubes at -20 °C. For sediment sampling, we took 3 replicates per site with a 100 ml syringe sampler from the topmost layer (< 1−2 cm) and samples were stored at -20 °C.

Particulate organic matter (POM, representing mainly phytoplankton, terrestrial runoff matter and other detrital matter in the area) and dissolved organic matter (DOM, representing a fraction of < 0.2 µm) were collected (4-5th June 2017) from the water column (R/V Electra) from five pelagic locations (i.e. W1, W2, W3, W4 and W5) at a depth of 5 meters below the water surface with a Niskin bottle sampler (Table 1). POM was extracted on GF/F glass fiber filters (pore size Ø 0.2 µm) by using a vacuum pump. For DOM analysis, the filtered water was acidified to pH 2 with HCl and passed through Agilent Bond Elut-PPL cartridges 1 g, 6 ml in bed size (Dittmar et al. 2008). The samples were stored at -18 °C for further analysis.

In this study, we have used some previously published stable isotope data (see Kahma et al. 2020). For the food sources of our mixing model study, we used the ^{13}C and ^{15}N data of *F. vesiculosus*, water POM and DOM and sedimentary matter. We also present the previously published ^{13}C and ^{15}N data of *M. trossulus* and *Marenzelleria spp.*

2.3. Stable isotope analysis

For *L. balthica*, due to small size of the animals, 1 to 3 individuals were pooled as one sample to obtain enough sample material for the stable isotope analysis, and to improve sample

representativeness by creating an integrated population estimate of natural isotopic composition; similarly, for *T. fluviatilis* 3 to 10 individuals, and for *C. volutator* 5 individuals were pooled as one sample. Other macrofauna samples were analyzed individually. Macrophyte and animal samples were frozen, freeze-dried for 2 days and homogenized with a ball mill. Homogenized samples were weighed with a microbalance (accuracy of 0.001 mg) into tin or silver cups (0.5–2.0 mg depending on the carbon and nitrogen concentrations of the samples).

Sediment samples were freeze-dried for 2 days and weighed with a microbalance (accuracy of 0.001 mg) into silver cups (20–30 mg). To remove possible carbonates for organic $\delta^{13}C$ analysis, 2 M HCl was added into silver cups (approximately 3−5 drops to cover the sample with acid), and the cups with the samples were placed at 60 °C for 12 hours to evaporate the acid (Jacob et al. 2005). For $\delta^{15}N$ analysis, replicates without the acidification procedure were prepared from each sediment sample.

We analyzed all samples for stable isotope values of carbon and nitrogen (hereafter noted $\delta^{13}C$ and $\delta^{15}N$). The samples were combusted with a Carlo Erba NC2500 analyzer connected via a split interface to reduce the gas volume to a Thermo Delta V advantage mass spectrometer at Stockholm University, Department of Geological Sciences. The results are expressed in the δ-notation ($\delta^{13}C$ or $\delta^{15}N$ ‰ = $R_{sample}/R_{standard}$ x 1000, where R refers to the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ of the sample or standard) *vs.* Vienna Pee Dee Belemnite (VPDB) for carbon and *vs.* AIR for nitrogen. The long-term reproducibility/error in analysis was shown from some 20 years of measurements to be lower than ±0.15 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Standards used for calibration of the reference gases during the measurement period of the samples in this study were for CO_2, IAEA–CO–1 ($\delta^{13}C$ = +2.49 ‰, measured to +2.39 ± 0.14 ‰) and an in-house acetanilide standard ($\delta^{13}C$ = −27.07 ‰, measured to −27.13 ± 0.1 3‰) and for N_2, IAEA-N-1 ($\delta^{15}N$ = +0.43 ‰, measured to +0.51 ± 0.07) and IAEA–NO–3 ($\delta^{15}N$ = +4.72 ‰, measured to +4.69 ± 0.04 ‰). The carbon and nitrogen content (expressed as % of dry mass) were determined at the same time as the isotope ratios, and the relative error was < 1 % for both measurements.

2.4. Data analysis and statistics

We calculated the isotopic niche size (*sensu* Hutchinson niche concept, Newsome et al 2007) (1) for the macrophytes and for the consumers from each habitat, (2) the consumer community niche for each site within the two habitat types, and (3) the population niche for the "shared" species found in the soft bottom in the proximity of the two habitat types (the infaunal clams *C. glaucum*, L*. balthica* and *M. arenaria*) ignoring site separation. For all the species, the Bayesian standard ellipse area describing the isotope niche (SEA_B, i.e. the δ space area or distance between individuals in a $\delta^{13}C-\delta^{15}N$ biplot) was calculated using a Bayesian approach (SIBER package, version 2.1.5, Jackson et al. 2011). However, for *L. balthica*, *T. fluviatilis* and *C. volutator*, the calculation was estimated based on pooled isotope replicates (in order to obtain enough sample material, see section 2.3) per species for each site and habitat, for a proxy for a population niche. The Bayesian estimates for niche overlap (Bayesian Overlap function) between the ellipses were calculated from the overlap of the maximum likelihood fitted standard ellipses and expressed as the proportion of the sum of the non-overlapping areas to the sum of the full areas of the ellipses (value ranging from 0 when the ellipses are completely distinct, to 1 when the ellipses are completely coincidental). All metrics were measured according to the standard settings of the SIBER package (e.g. ellipses set to 40% of the data, Jackson et al. 2011).

To assess the proportions of different macrophyte sources in the diets of invertebrates, dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) Bayesian mixing modelling was performed with the MixSIAR package (Stock et al. 2018) for R software (R Development Core Team 2019). We selected three grazer species (epifaunal *Gammarus* spp., *Theodoxus fluviatilis* and larvae of Trichoptera), two obligate suspension feeder species (*Cerastoderma glaucum* and *Mya arenaria*), two facultative suspension-deposit feeders (*L. balthica* and *Corophium volutator*) and one omnivore (*Hediste diversicolor*) for the mixing model analysis and performed one model per species (**Fig. 2**). In the macrophyte source selection for the consumers, we based our decision on three factors: 1) isotopic difference between food sources to ensure a feasible source distinction in the modelling, 2) habitat of the consumer in question (i.e. *F. vesiculosus* or an angiosperm dominance), and 3) preferred feeding mode of the consumer. Because of the great diversity of different potential food sources, several food sources had to be combined to

avoid overlapping isotopic signals, resulting to fewer food groups as potential food sources. For the MixSIAR models, the mean $\delta^{13}C$ and $\delta^{15}N$ values of each combined food source was approximated by calculating the middle point of maximum and minimum values of standard deviations of individual food sources within the group. Then, the standard deviation was determined by using the entire standard deviation range of the included sources within the group (**Fig. 3**, rectangles A and B, see the section 3.1 in the Result for more details). The consumer animal species were classified into four functional groups according to their feeding modes (grazers, deposit-feeders, suspension-feeders and omnivores). Then, a combination of 2−4 different potential food sources was used, based on previously reported suggestions about their typical dietary preferences (e.g. Skoog 1978, Stuart et al. 1985, Strasser 1999, Jormalainen et al. 2001, Goecker and Kåll 2003, Råberg and Kautsky 2007, Sarà 2007, Aberson et al. 2016, Nordström et al. 2016, Jankowska et al. 2018, Ziółkowska et al. 2018). For herbivorous epigrazers (*Gammarus* sp., *I. balthica, T. fluviatilis,* Trichoptera larvae) we used two food sources: perennial *F. vesiculosus* and a combined source including all the ephemeral filamentous algal species examined (e.g. *Pylaiella littoralis and Cladophora glomerata,* see **Fig. 3,** rectangle A). For bivalves (*L. arenaria* and *C. glaucum*, *L. balthica*), three or four food sources were used, depending on the habitat type. Although we could consider that the pelagic matter (a combined food source including POM and DOM) would probably dominate the diet of bivalves (especially obligate suspension feeders *M. arenaria* and *C. glaucum*), we assumed that also some fine-sized fraction of macrophyte-derived detrital matter could be utilized by these consumers (Maloy et al. 2013, Navarro et al. 2016). Based on the SIBER analysis results indicating dissimilarities in stable isotope compositions and niches of the potential macrophyte source (**Fig. 4A**), we decided to use a different combination of potential macrophyte food sources for bivalves *M. arenaria*, *C. glaucum* and *L. balthica* in the two different habitat types (see 3.3). In hard bottom *Fucus*- dominated habitats, we used the most abundant and productive macroalgae *Fucus vesiculosus* as a perennial macrophyte food source. For the soft sediment habitats, we used two abundant angiosperms *Zostera marina* and *Potamogeton pectinatus* (*Stuckenia pectinata*) as perennial food sources. In addition, a combined food source including sedimentary matter and the most abundant ephemeral algae *P. littoralis* was used for the bivalves, because of their overlapping $\delta^{13}C$ and $\delta^{15}N$ values. For omnivorous *H. diversicolor*, three food sources were used: a combined source consisting of all perennial macrophytes (**Fig. 3**, rectangle B), a combined source including sedimentary matter and ephemeral algae *P.*

littoralis, and a combined source including seston POM/DOM. For the detrivorous facultative suspension-deposit feeder amphipod *C. volutator*, two food sources were used, i.e. perennial macrophytes (**Fig. 3**, rectangle B), and a combined source of sedimentary matter plus *P. littoralis* (**Fig. 3**).

For arthropods (i.e. *Corophium volutator*, *Gammarus* sp., *Idotea balthica,* Trichoptera larvae) gastropod *Theodoxus fluviatilis* and facultative deposit/suspension feeding clam *Limecola* (*Macoma) balthica*, standard trophic enrichment factors (TEF) of 0.8 ‰ for carbon and 3.4 ‰ for nitrogen were used in the absence of reported species-specific TEF values (DeNiro and Epstein 1978, Fry 2006, Yokohama et al. 2005). For obligate suspension feeder *Mya arenaria*, recently reported species-specific TEF values were applied, i.e. 1.9 ‰ (SD ±3.2) for carbon and 4.4 ‰ (SD ±0.91) for nitrogen (Kristensen et al. 2019). These values were applied also for the obligate suspension feeder *Cerastoderma glaucum*, in the absence of species-specific values. For the omnivorous *Hediste diversicolor*, reported species-specific values were also applied, i.e. 1.57 ‰ (SD ±2.28) for carbon and 5.01 ‰ (SD ±1.24) for nitrogen (Kristensen et al. 2019). For a comparison, we also calculated separate models with the C/N normalization equation ($\Delta\delta^{13}C = -3.32 + 0.99 \times C{:}N$) proposed by Post et al. (2007) that was applied for the consumer $\delta^{13}C$ values to reduce species-specific differences in lipid content, which could bias the $\delta^{13}C$ interpretation.

3. Results

3.1. Isotope composition of potential food sources

In total, 15 different macrophyte species from four phyla (Chlorophyta, Rhodophyta, Phaeophyta and Tracheophyta) were identified (Table 2). The dataset spans 18 different potential food sources in total, including macrophytes, sediment, seston particulate organic matter (POM) and dissolved organic matter (DOM) (**Table 2**). The stable isotopic composition of the potential food sources showed high variations between different species. The total variation range of carbon $\delta^{13}C$ values of food sources fell between mean values of approx. -36 ‰ and -10 ‰ (**Fig. 2, Table 2**).

TABLE 2

FIGURE 2

The isotope data (overall mean) indicates that the isotopic compositions of macrophyte primary producers can be divided into two separate functional groups: (1) Large-sized macrophytes (either macroalgae or angiosperms), and (2) opportunistic filamentous algae, of which the former is more ^{13}C enriched and the latter more depleted (**Fig. 3,** rectangles A and B). Within these two groups, the isotopic compositions of several species tend to overlap with each other, making accurate food source partitioning difficult. The most ^{13}C enriched (i.e., > -12 ‰) values were found within a group of three angiosperm species (*Z. marina*, *Ranunculus baudotii*, and *Potamogeton pectinatus*). Other angiosperms (*Potamogeton perfoliatus*, *Myriophyllum spicatum* and *Ceratophyllum demersum*) were more ^{13}C depleted (ranging from -15 ‰ to -16.5 ‰), but appeared on the ^{13}C enriched side of the examined macrophyte sources (**Fig. 3**). The $\delta^{13}C$ value of *Fucus vesiculosus* (15.8 ‰) was within the variation range of the examined angiosperms, and so was that of *Chorda filum*, a brown macroalgal species (**Figs. 2-3, Table 2)**.

FIGURE 3

Small-sized macroalgae species (i.e. *Cladophora glomerata*, *Ulva* sp., *Ceramium tenuicorne*, *Polysiphonia sp*, *Pylaiella littoralis*) were more ^{13}C depleted than angiosperms and *F. vesiculosus*, falling roughly between -25 ‰ and -21 ‰ (**Fig. 3**). A highly ^{13}C depleted value (-36.2 ‰) was detected for *Phyllophora* sp., a small-sized red algae species growing several meters below the *F. vesiculosus* belt (**Fig. 3**). The two other red algae species, *C. tenuicorne* and *Polysiphonia* sp., clustered close to the opportunistic algal species *C. glomerata*, *Ulva* sp. and *P. littoralis*. The pelagic component (i.e. seston POM and DOM) was on the ^{13}C depleted side of the examined food sources (**Table 2, Fig. 3**). POM (-27.6 ‰) was slightly more ^{13}C enriched than DOM (-26.9 ‰). The $\delta^{13}C$ value (-22.3 ‰) of sedimentary carbon (representing mainly mixed decomposed matter of sestonic and macrophyte origin and probably some microphytobenthos) overlapped with opportunistic filamentous algae, and fell roughly in the middle of the overall variation range between DOM/POM and the most ^{13}C enriched macrophytes (**Fig. 3, Table 2**).

The total variation range of nitrogen $\delta^{15}N$ values was between mean values of 1.6 ‰ and 7.6 ‰, while the most depleted value was found from seston DOM and the most ^{15}N enriched values were

found from a group of three angiosperm species (i.e. *Ranunculus baudotii*, *Ceratophyllum demersum* and *Z. marina*) (**Fig. 3, Table 2**). We note in particular that the $\delta^{15}N$ difference between the most ^{15}N depleted species (i.e. *C. filum*) and the most enriched one (i.e. *R. baudotii*) was 3.8 ‰ units, i.e. roughly the value often estimated for a single trophic enrichment (Fig. 3, Table 2). The $\delta^{15}N$ value of sedimentary matter (5.15 ‰) was very close to the calculated mean baseline $\delta^{15}N$ value of all primary producers (i.e. macrophytes) and POM (**Fig. 3, Table 2**).

3.2. Isotope composition of primary consumers

In general, the carbon isotope composition of the 11 animal species collected fell roughly between $\delta^{13}C$ values of -16 ‰ and -25‰, a narrower range than the food source range (**Fig. 2, Table 2**). The grazer species *Gammarus* spp., *Idotea balthica* and *Theodoxus fluviatilis* were more ^{13}C enriched (-16.7 ‰ to -19.3 ‰) than the bivalves *M. trossulus*, *C. glaucum*, *M. arenaria*, *L. balthica* (-21.6 ‰ to -24.5 ‰). The obligate suspension feeders *M. trossulus*, *C. glaucum* and *M. arenaria* were more ^{13}C depleted than the facultative deposit/suspension feeder l. *balthica*. *Mytilus trossulus* and *C. glaucum* clustered tightly together in terms of both $\delta^{13}C$ and $\delta^{15}N$, while *M. arenaria* was between them and *L. balthica* (Fig. 3). The mean $\delta^{15}N$ composition of all consumers seemed generally to be above the maximum $\delta^{15}N$ values of potential food sources, with the exception of the most ^{15}N enriched (7.6 ‰) angiosperm *R. baudotii* (**Fig. 3, Table 2**).

3.3. Isotope niche analysis of the macrobenthic communities

The carbon and nitrogen isotope values of a specific consumer and its potential food sources (when present in both habitats) differed between the two habitat types (**Table 3, Fig. S1**). Generally, these differences were less than 2 ‰ units in terms of both $\delta^{13}C$ and $\delta^{15}N$, and partly within the standard deviation ranges (**Table 3**). For instance, the facultative deposit-suspension feeder L*. balthica* was more ^{13}C depleted (-22.5 ‰) in the *Fucus* dominated habitat than in the angiosperm habitat (-20.6 ‰) but the obligate suspension feeders *C. glaucum* and *M. arenaria* did not show large differences between habitats (**Table 3**).

TABLE 3

The isotope niche analysis (SIBER) of the macrophytes and macroinvertebrates showed in both cases a larger niche size in the *Fucus* dominated habitat than in the angiosperm dominated habitat (**Figs 4A and B and 5 A and B**). The overlap in niche size between habitats was ca. 25% for both the macrophyte and the consumer communities (**Fig. 4A–B, 5A–B**). The different community sites were comparable in terms of isotope niche size within each habitat (overlap among sites ranging 21 to 60% for the *Fucus* habitat, 17 to 46% for the Angiosperm habitat; **Fig. 4C-D, Fig. 5C-D**). Complete overlap among sites within habitats was not expected due to the physical distance of the sites from each other (approx. 3.5 km from N to S, **Fig. 1**). At the population level, the isotope niche size of three infaunal clam species (*L. balthica, C. glaucum, M. arenaria*) found in both habitat types differed for the values for *Mya* **(Fig. 5E-F)***.* The niche position and size of C*. glaucum*, unlike the others, did not differ between the habitat types (**Fig. 4E and F**). The standard ellipse area of *Limecola* overlapped with *Mya* in the *Fucus* habitat (42%), and *Mya* overlapped with *Cerastoderma* in the angiosperm habitat (15%) ;(**Fig. 4E-F, Fig. 5E-F**).

FIGURE 4

FIGURE 5

3.4. MixSIAR dietary models for the benthic consumers

The MixSIAR models for the grazer species *Idotea balthica* and *Theodoxus fluviatilis,* all collected from *Fucus* dominated habitats, indicated that *F. vesiculosus* generally constituted a major part of their diet (medians 61 and 71 %), while filamentous opportunistic algae (**Fig. 3**, rectangle A) were more important for *Gammarus* spp. (median 63 %) (**Fig. 6**, **Table S1**). For Trichoptera larvae, the model suggests preference of ephemeral algae over *F. vesiculosus* (65 % and 35 %, respectively) (**Fig. 6**, **Table S1**).

The pelagic component, i.e. seston POM and DOM together, constituted the main dietary part of obligate suspension feeder bivalves , such as *C. glaucum* (medians 85–92 %) and *M. arenaria* (63–82 %) in the proximity of vegetated habitats (**Fig. 6, Table S1**). A comparison between the different habitat types indicated that macrophytes constituted quite low (< 8.3 %) median proportions of their diet (**Fig. 6**, **Table S1**). If we look at the median dietary reliance on the dominating macrophyte species, the differences between habitat types were low (ca. 2 % units) for these two bivalves (**Fig. 6,**

Table S1). At the same time, the model suggests a slightly lower median reliance (19 % units for *M. arenaria*, 7 % units for *C. glaucum*) on *Pylaiella littoralis* and sedimentary matter in angiosperm dominated habitats than in *Fucus* habitats. The models suggest that the small contributions of angiosperms *Z. marina* and *P. pectinatus* are equal. This observation is similar with both *M. arenaria* and *C. glaucum* (**Fig. 6**, **Table S1**).

The model suggests that the facultative suspension/deposit-feeding clam *Limecola* (*Macoma) balthica* fed mainly on a combined food source consisting of sedimentary matter (detritus and MPB) and ephemeral algae, with strongly overlapping contributions (95 % CI 7−78 and 10−83) in the two different habitats (**Fig. 6, Table S1**). In hard bottom *Fucus* dominated habitats, the median contribution of *F. vesiculosus* was 8 % (95 % CI 1−31) (**Fig. 6, Table S1**) and in soft bottom angiosperm habitats the median contributions on angiosperm plants (*Z. marina* and *P. pectinatus*) were 12 % (95 % CI 0−28) and 11 % (95 % CI 0−23), respectively.

The model for the omnivorous polychaete *Hediste diversicolor* suggests that its diet derived mainly from a combined food source of surface sedimentary matter and ephemeral algae *P. littoralis* (median 56 %) (**Fig. 6, Table S1**). Large macrophytes (**Fig. 3**, rectangle B) were also important (24 %), but there was a high level of uncertainty (95 % CI 6–45 %). The model suggests 21 % median contribution on pelagic matter (POM and DOM). According to the model for a single observation point (i.e. a pooled sample of approx. 5 individuals), the deposit-feeding amphipod *Corophium volutator* fed mainly on a combined food source of surface sedimentary matter and *P. littoralis* (median 86 %), while perennial macrophytes were a less important food source (14 %) (**Fig. 6**, **Table S1**).

Applying the C/N lipid normalization (Post et al. 2007) for the consumer $\delta^{13}C$ values increased the dietary proportions of ^{13}C enriched food sources (i.e. large macrophytes) at the expense of ^{13}C depleted sources (i.e. what?). This increasing effect can be roughly 10−30 % units depending on the consumer species in question. These models are presented in the supplementary material (**Fig. S2, Table S2**).

FIGURE 6

4. Discussion

4.1. Stable isotope composition and isotope niches across habitats

To our knowledge, the isotope compositions of some macroalgal species (such as *Phyllophora* sp., *Ceramium tenuicorne*, *Furcellaria lumbricalis*, *Chorda filum*) have not been examined before in the Baltic Sea. With only one exception (*Phyllophora* sp.), all our marine macrophyte species fell within the $\delta^{13}C$ range of between -30 ‰ and -10 ‰, which is typical for most marine macrophytes (Raven et al. 2002). Highly depleted $\delta^{13}C$ (< -30 ‰) of red algae species in the class Florideophyceae have been reported previously (Raven et al. 2002, Fredriksen 2003, Paar et al. 2019), and our observation of *Phyllophora* agrees well with those studies. In terms of spatial variability, previous studies reported that the $\delta^{13}C$ values of the same macroalgae or angiosperm species can vary typically a few ‰ units between different sites (Osmond et al. 1981, Raven et al. 2002). This spatial variability means that primary producer species should be sampled from a large spatial area to obtain reliable results in mixing model studies, or approximated large variances should be added for mixing modelling input data, as in our study. Our results indicate that the differences in the stable isotope diversity of the primary producers and consumers were higher between habitats than between the sites within each habitat type (Figure 4).

The isotope niches of both primary producers and benthic consumers were larger in the *Fucus* habitats than in the angiosperm habitat (**Fig. 4A–B**), which is related to the different species assemblages in the two habitats and to the higher species-specific $\delta^{13}C$ and $\delta^{15}N$ variations in the *Fucus* habitats. The niche sizes and positions among sites within the same habitat type were similar (**Fig. 4C–D)**, and differences are likely related to site-specific environmental variability, like exposure and salinity gradients influencing isotope baselines (e.g. Hansen et al. 2012, Lange et al. 2018). The slightly larger niche of *L. balthica* in the soft sediments adjacent to the *Fucus*-dominated habitats (**Fig. 4E–F**) indicates a larger isotopic diversity of the food sources (e.g. perennial and ephemeral macroalgae and phytoplankton) compared to the soft sediment angiosperm habitats, and it could relate to the high carbon export potential of the *Fucus* habitat (Attard et al. 2019a,b). In the angiosperm habitats, *L. balthica* could be more dependent on a limited pool of local and nearby food

sources with a more similar isotopic composition dominated by aquatic plant species. The largest niche size for *M. arenaria* in the angiosperm habitats (**Fig. 5F**) is likely related to the high variability of the data obtained due to the small number of replicates.

In general, the isotope compositions of the consumer macrofauna are expected to differ between habitats since they can feed on different primary producers, although some differences can also be caused by physiological isotope fractionation effects. For instance, Hansen et al. (2012) reported a correlation between $\delta^{13}C$ values of invertebrate primary consumers and macrophyte taxa present within a habitat (shallow macrophyte-dominated bays). Although the species-specific feeding preference has been reported as the most important factor determining the $\delta^{13}C$ and $\delta^{15}N$ values in grazers, the variable macrophyte isotopic composition (resulting from different dominant macrophyte taxa at different sites) will affect the isotopic values of consumers with unselective feeding strategy (Nordström et al. 2016). For instance, the facultative deposit-suspension feeder *L. balthica* showed $\delta^{13}C$ differences between the two habitat types (**Fig. 4E–F**, **Table 4**). Another possible explanation for this observation is the effect of habitat exposure (i.e. wave action and currents) on the dominant feeding mode, i.e. a more exposed habitat with a coarse seafloor substrate may result in shifting from deposit- to suspension-feeding (Ólafsson 1986, Nordström et al 2010). The latter could be supported by the observation that obligate suspension feeders *M. arenaria* and *C. glaucum* did not show such $\delta^{13}C$ differences between the habitats. This likely indicates that due to their fixed feeding mode (and the availability of pelagic POM over the year), the contribution of macrophyte-derived detrital matter is lower in their diet than the POM/DOM component (see Kristensen et al. 2019, Kahma et al. 2020).

4.2. Dietary composition of the macrofauna community: epigrazers, suspension/deposit feeders and others

Of the typical epifaunal grazers in *Fucus* dominated habitats, *Idotea spp.* and *T. fluviatilis* fed mainly on perennial *F. vesiculosus*. However, the model indicated that the dietary role of ephemeral algae (e.g. *P. littoralis*, *C. glomerata, Ceramium* sp.) was present in their diet, and ephemeral algae was the major food source of amphipod *Gammarus spp*. A previous study on *I. balthica* reported that its food

consumption rate on *F. vesiculosus* was 2−10 fold lower in comparison to different common ephemeral algae species in the Baltic Sea (Jormalainen et al. 2001). Our mixing model results indicating approximately 50−70 % dietary proportions of *F. vesiculosus*, suggests somewhat greater feeding on ephemeral algae. However, another feeding study reported that both *I. balthica* and *Gammarus* sp. prefer feeding on filamentous algae (*C. glomerata* and *Ulva intestinalis*) over *F. vesiculosus* (Goecker and Kåll 2003). In contrast, our mixing model results suggest that *F. vesiculosus* dominated only the diet of *I. balthica*, while filamentous algae (including *C. glomerata*) contributed more to the diet of *Gammarus* spp. (63 %). Similarly, the gastropod *T. fluviatilis* can consume macroalgae and epiphytic microalgae (Råberg and Kautsky 2007), and it has been reported to feed on smaller germlings of *F. vesiculosus* (< 1 mm, Malm et al. 1999). Our results indicate a high dietary proportions of *F. vesiculosus* (~70 %), but it should be mentioned here that our sampling did not include epiphytic microalgae growing on *F. vesiculosus*, which could also be grazed by *T. fluviatilis* (Skoog 1978). Of the herbivorous Trichoptera larvae, previous studies focusing on the gut contents reported both *F. vesiculosus* and filamentous algae in their diet, in approximately equal proportions (Haage 1970, Haage 1971). Our small dataset consisting of two observations showed quite similar results, suggesting a higher proportion of filamentous algae over *F. vesiculosus*.

The obligate suspension-feeding bivalves (*M. arenaria* and *C. glaucum*) mainly consumed pelagic matter (POM/DOM), while the dietary role of sedimentary matter and the ephemeral algae (a combined food source) was not significant. The facultative suspension/deposit feeder *L. balthica* suggested somewhat (~5−10 % units) higher median proportions of perennial macrophytes in its diet than the obligate suspension feeders. Similarly, a recent biomarker mixing model study suggested approx. 50 % contribution of sestonic suspended matter in the vegetated habitats examined (Jankowska et al. 2018). Our results on the three bivalve species suggest that although macrophytes may contribute to their diets (depending on the feeding modes), it is likely that the locally dominating perennial macrophyte species composition *per se* (i.e. either *F. vesiculosus* or an angiosperm) does not have a large influence on the dietary contribution of L*. balthica*, *M. arenaria* and *C. glaucum*. Instead, the macrophyte dietary contributions of the bivalves are quite similar between the habitat types, with no significant differences. Our previous triple-isotope study (Kahma et al. 2020) on

another common obligate suspension feeder bivalve *M. trossulus* suggested very similar dietary proportions as our new dual-isotope models for *M. arenaria* and *C. glaucum*. For *L. balthica*, our previous triple-isotope (C N S) model with a smaller dataset (n = 24) suggested higher (means between 13−49 %) proportions of macrophyte-derived matter than our new dual-isotope model with a larger dataset (n = 47) at the same sampling locations. However, the uncertainty ranges of the dual-isotope models are higher. In general, we suggest higher dietary proportions of macrophyte-derived matter for *L. balthica* compared to *C. glaucum* and *M. arenaria*. It is likely that this is related to the facultative ability of *L. balthica* to feed on freshly deposited detrital matter (Ólafsson 1986), while the obligate suspension feeders can feed only on very fine-sized fraction available in the water column, where the proportion of macrophyte detritus is after all small in comparison to the phytoplankton fraction.

Within our study sites, we observed a diverse mixture of different angiosperm species instead of a monospecific seagrass meadow, and *P. pectinatus* was among the dominating species. Hence, the limnic *P. pectinatus* probably is a more important local macrophyte detrital carbon source than the marine species *Z. marina* in the examined brackish-water habitats. Our mixing models, on the other hand, suggest equal dietary proportions of *P. pectinatus* and *Z. marina* for the bivalves. A more reliable distinction between *Z. marina* and *P. pectinatus* would require an estimate of biomasses or production rates as informative priors for the MixSIAR models. Our model assumes that they are equal, and thus the sum of these two food source proportions is probably more reliable in this case.

Our MixSIAR model results for *H. diversicolor* suggesting quite high (95 % CI of 6−45 %) reliance on perennial macrophytes are quite similar to a recent mixing model study in English estuaries (Aberson et al. 2016). Similarly, our single-observation MixSIAR model for *C. volutator* gives support to older studies (Stuart et al. 1985, Gerdol and Hughes 1994, Créach 1997) reporting preferred feeding on benthic microphytobenthos, but also some feeding on plant detritus. Bigger datasets for *H. diversicolor* and *C. volutator* are needed to obtain more accurate results.

4.3. Limitations and further studies

Typically, MixSIAR models contain uncertainties, mainly related to TEF values, multi-source mixing issues and possible spatio-temporal variations in the isotopic compositions. For instance, we have applied the same TEF values proposed by Kristensen et al. (2019) for *M. arenaria* and *C. glaucum*. It is possible that the TEF values of *C. glaucum* differ from those of *M. arenaria,* which would affect the MixSIAR model outputs. Hence, it is possible that the ^{13}C and ^{15}N enrichment of *M. arenaria* in comparison to *C. glaucum* and *M. trossulus* (**Fig. 3**) will result from higher physiological fractionation rather than dietary differences. For example, TEF values of 2.2 ‰ for carbon and 3.8 ‰ for nitrogen have previously been measured for *M. edulis* (Dubois et al. 2007), instead of the values that Kristensen et al. (2019) have reported for *M. arenaria* (i.e. 1.9 ‰ for carbon and 4.4 ‰ for nitrogen). Although our models suggest that the differences in the median dietary proportions between these two species can be 10−20 % units with some of the food sources we considered (**Fig. 6**), they should be interpreted with great caution. We emphasize the importance of further studies on species-specific TEF values for aquatic invertebrates if more accurate mixing models are to be obtained in the future (see also Bond and Diamond 2011).

To improve model reliability, the relative differences between consumers biomass and primary production rates of perennial and ephemeral macrophyte taxa should be assessed and used as informative priors for reliable mixing models. In addition, multiple (triple or even quadruple) isotope approaches and probably fatty acid biomarkers are necessary to resolve complex mixing problems caused by the high isotopic variabilities and large numbers of potential sources with overlapping $\delta^{13}C$ and $\delta^{15}N$ values, such as occur in coastal systems (e.g. Leduc et al. 2009, Jankowska et al. 2018). In the absence of such information, only the most productive and abundant macrophyte species at the study area can be used as the potential main food sources, assuming that the grazers naturally feed mainly on the most abundant ones. The effect of tissue lipid content on the consumer $\delta^{13}C$ values (see Post et al. 2007) might cause a dietary underestimation of ^{13}C enriched food sources (perennial macrophytes) by 10−30 % units. Some controversy has been reported on this issue, as well as on the reliability of using C/N ratios as proxies for lipid concentrations (Lehtonen 1996, Ricca et al. 2007, Patterson and Charmichael 2016). Spatial and temporal scales are factors of concern in food web

studies (Nordström et al. 2009, 2010), since the main macrophyte species differ in abundance and production with depth, salinity and season. For further studies, the temporal succession of macrophytes and possible temporal variabilities in isotopic compositions are other important factors to consider.

5. Conclusions

The isotope niche size and shape of the dominating primary producer assemblage mirrored in the associated primary consumer community, and the largest isotope niche was found in the *Fucus*-dominated habitats. Sites within a habitat type showed small differences in niches (overlapping niches), indicating that the dominating macrovegetation type is more important for the isotopic composition of the consumers than spatial differences. We found small dietary differences among the infaunal bivalve consumers (*C. glaucum*, *M. arenaria*, *L. balthica*) from the adjacent soft bottom communities. However, the dominating feeding mode of *L. balthica* can change depending on the habitat type and dominating food source. Since the isotope composition and niches of a habitat depends on the dominating primary producer assemblage, different habitat types must be carefully examined to construct comprehensive food web models across coastal ecosystems.

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References

Aberson, M.J.R.; Bolam, S.G.; Hughes, R.G. 2016. The effect of sewage pollution on the feeding behaviour and diet of *Hediste* (*Nereis diversicolor* (O.F. Müller, 1776)) in three estuaries in south-east England, with implications for saltmarsh erosion. Marine Pollution Bulletin 105: 150−160.

Attard, K.M.; Rodil, I.F.; Berg, P.; Norkko, J.; Norkko, A.; Glud, R.N. 2019a. Seasonal metabolism and carbon export potential of a key coastal habitat: The perennial canopy-forming macroalga *Fucus vesiculosus*. Limnology and Oceanography. 64: 149–164.

Attard, K.M.; Rodil, I.F.; Glud, R.; Berg, P.; Norkko, J.; Norkko, A. 2019b. Seasonal ecosystem metabolism across shallow benthic habitats measured by aquatic eddy covariance. Limnology and Oceanography Letters 4(3): 79–86.

Bond, A.L.; Diamond, A.W. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21(4): 1017–1023.

Boström, C. et al. 2014. Distribution, structure and function of Nordic eelgrass (*Zostera marina*) ecosystems: implications for coastal management and conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 24(3): 410–434.

Bouillon S., Connolly, R.M., Gillikin, D.P. 2011. Use of stable isotopes to understand food webs and ecosystem functioning in Estuaries. In: Wolanski E. & McLusky D.S. (eds.) Treaties on Estuarine and Coastal Science, Vol. 7, pp. 143–173. Waltham Academic Press.

Cragg, S.M.; Friess, D.A.; Gillis, L.G.; Trevathan-Tackett, S.M.; Terrett, O.M.; Watts, J.E.M.; Distel, D.L.; Dupree, P. 2020. Vascular Plants Are Globally Significant Contributors to Marine Carbon Fluxes and Sinks. Annual Review of Marine Science 12(1): 469−497.

Créach, V.; Schricke, M.T.; Bertru, G.; Marriotti, A. 1997. Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna. Estuarine, Coastal and Shelf Science 44: 599–611

Dayton, P.K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16: 215–245.

DeNiro M.J.; Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochima Acta 42:495–506.

Dittmar T.; Koch B.; Hertkorn N.; Kattner G. 2008. A simple and efficient method for the solid-phase extraction of dissolved organic matter (SPE-DOM) from seawater. Limnol. Oceangr. Methods 6(6): 230–235.

Duarte, C.M. 2017. Reviews and syntheses: Hidden forests, the role of vegetatedcoastal habitats in the ocean carbon budget. Biogeosciences 14: 301−310.

Duarte, C.M.; Losada, I.J.; Hendriks, I.E.; Mazarrasa, I.; Marbà, N. 2013. The role of coastal plant communities for climate change mitigation and adaptation. Nature Climate Change 3 (11): 961–968.

Dubois, S.; Blin, J-L.; Bouchaud, B.; Lefebvre, S. 2007. Isotope trophic-step fractionation of suspension-feeding species: Implications for food partitioning in coastal ecosystems. Journal of Experimental Marine Biology and Ecology 351(1–2): 121–128.

Duffy, J.E. 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology Progress Series 311: 233–250.

Fourquerean, J.W.; Duarte, C.; Kennedy, H.; Marba, N. 2012. Seagrass ecosystems as a significant global carbon stock. Nature Geoscience 5(7): 505–509.

Fredriksen, S. 2003. Food web studies in a Norwegian kelp forest based on stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis. Marine Ecology Progress Series 260: 71–81.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33(5): 1182–1190.

Fry, B., 2006. Stable Isotope Ecology. Springer, USA.

Galván, K.; Fleeger, J.W.; Fry, B. 2008. Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna Mar. Ecol. Prog. Ser. 359: 37-49

Gammal, J.; Järnström, M.; Bernard, G.; Norkko, J.; Norkko, A. 2019. Environmental Context Mediates Biodiversity–Ecosystem Functioning Relationships in Coastal Soft-sediment Habitats. Ecosystems 22: 137−151.

Gerdol, V.; Hughes, R.G. 1994. Feeding behaviour and diet of *Corophium volutator* in an estuary in southeastern England. Mar. Ecol. Prog. Ser. 114: 103−108.

Goecker, M.E.; Kåll, S.E. 2003. Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. J Sea Res 50: 309–314.

Gustafsson, C.; Norkko, A. 2019. Quantifying the importance of functional traits for primary production in aquatic plant communities. Journal of Ecology 107(1): 154−166.

Gutiérrez, J.L. et al. 2011. Physical Ecosystem Engineers and the Functioning of Estuaries and Coasts. In: Wolanski, E. and McLusky, D (ed.): Treatise on Estuarine and Coastal Science vol. 7. Pp 53−81. ISBN 978-0-08-087885-0. Waltham Academic Press.

Gustafsson, C.; Boström, C. 2014. Algal mats reduce eelgrass (*Zostera marina* L.) growth in mixed and monospecific meadows. Journal of Experimental Marine Biology and Ecology 461: 85–92.

Haage, P. 1970. On the Feeding Habits of Two Baltic Species of Caddis Larvae (Trichoptera). Insect Systematics & Evolution 1(4): 282–290.

Haage, P. 1971. A study of the feeding habits of larvae of L*imnephilus marmoratus* curtis (trichoptera) living in the *Fucus*-belt of the northern part of the Baltic. Hydrobiologia 37: 253–265.

Hansen, J.P.; Wikström, S.A.; Kautsky, L. 2012. Taxon composition and food-web structure in a morphometric gradient of Baltic sea land-uplift bays. Boreal environmental research 17: 1−20.

Hällfors, G.; Lappalainen, A.; Kangas, P. 1975. Littoral Benthos of the Northern Baltic Sea. III. Macrobenthos of the Hydrolittoral Belt of Filamentous Algae on rocky shores in Tvärminne. Internationale Revue der gesamten Hydrobiologie und Hydrographie 60(3): 313–333.

Hällfors, G.; Niemi, Å. Vegetation and primary production. In: Voipio, A. (Ed.). 1981. The Baltic Sea. Elsevier Oceanography Series, vol. 30, Pp. 220–238. ISBN 0-444-41884-9.

Henseler, C.; Nordström, M. C.; Törnroos, A.; Snickars, M.; Pecuchet, L.; Lindegren, M.; Bonsdorff, E. 2019. Coastal habitats and their importance for the diversity of benthic communities: A species- and trait-based approach. Estuarine, Coastal and Shelf Science 226 (2019) 106272.

Herlevi, H.; Aarnio, K.; Puntila, R.; Bonsdorff, E. 2018. The food web positioning and trophic niche of the non-indigenous round goby-a comparison between two Baltic Sea populations. Hydrobiologia 822(1): 1−18.

Hobson, K.A.; Welch, H.E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine ecology progress series 84: 9–18.

Hyndes, G. A. et al. 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biological Reviews 89: 232–251.

Jacob, U.; Mintenbeck, K.; Brey, T.; Knust, R.; Beyer, K. 2005. Stable isotope food web studies: a case for standardized sample treatment. Mar Ecol Prog Ser 287: 251−253.

Jackson, A.; Inger, R.; Parnell, A.C.; Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80: 595−602.

Jankowska, E.; De Torch, M.; Loïc, N.M.; Lepoint, G.; Wlodarska-Kowalczuk, M. 2018. Modification of benthic food web structure by recovering seagrass meadows, as revealed by trophic markers and mixing models. Ecological Indicators 90: 28–37.

Jaschinski, S.; Brepohl, D.C.; Sommer, U. 2008. Carbon sources and trophic structure in an eelgrass *Zostera marina* bed, based on stable isotope and fatty acid analyses. Marine ecology progress series 358: 103–114.

Jephson, T.; Nyström, P.; Moksnes, P-O.; Baden, S.P. 2008. Trophic interactions in Zostera marina beds along the Swedish coast. Marine ecology progress series 369: 63–76.

Jormalainen, V.; Honkanen, Y.; Heikkilä, N. 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Marine ecology progress series 220: 219−230.

Kahma, T.I.; Karlson, A.M.L.; Sun, X.; Mörth, C-M.; Humborg, C.; Norkko, A.; Rodil, I.F. 2020. Macroalgae fuels coastal soft-sediment macrofauna: a triple-isotope approach across spatial scales. Marine Environmental Research 162: 105163

Kautsky, L., Kautsky, H. 1989. Algal diversity and dominance along gradients of stress and disturbance in marine environments. Vegetation 83: 259–267.

Kautsky, L.; Kautsky, N. 2000. Baltic Sea, including Bothnian Sea and Bothnian Bay. In: Sheppard, C.R.C. (ed) Seas at the millenium: an environmental evaluation. Elsevier Science Ltd. Chapter 8. 1–14.

Krause-Jensen, D.; Duarte, C.M. 2016. Substantial role of macroalgae in marine carbon sequestration. Nature Geoscience 9: 732–742.

Kiirikki, M.; Lehvo, A. 1997. Life strategies of filamentous algae in the Northern Baltic Proper. Sarsia 82: 259−267.

Kristensen, E.; Quitana, C.O.; Valdemarsen, T. 2019. Stable C and N Isotope Composition of Primary Producers and Consumers Along an Estuarine Salinity Gradient: Tracing Mixing Patterns and Trophic Discrimination. Estuaries and Coasts 42: 144–156.

Kokubu, Y.; Rothäuser, E.; Filippi, J-B.; Durieux, E.D.H.; Komatsu, T. 2019. Revealing the deposition of macrophytes transported offshore: Evidence of their long-distance dispersal and seasonal aggregation to the deep sea. Scientific Reports 9: 4331

Lange, G.; Haynert, K.; Dinter, T.; Scheu, S.; Kröncke, I. 2018. Adaptation of benthic invertebrates to food sources along marine-terrestrial boundaries as indicated by carbon and nitrogen stable isotopes. Journal of Sea Research 131: 12-21.

Lassig, J., Leppäkoski, E., 1981. Benthic fauna of the Baltic Sea. In: Voipio, A. (Ed.), The Baltic Sea. Elsevier Oceanography Series, vol. 30, pp. 254–265. ISBN 0-444-41884-9.

Leduc, D.; Probert, P.K.; Duncan, A. 2009. A multi-method approach for identifying meiofaunal trophic connections. Marine Ecology Progress Series 383: 95−111.

Lehtonen, K.K. 1996. Ecophysiology of the benthic amphipod *Monoporeia affinis* in an open-sea area of the northern Baltic Sea: seasonal variations in body composition, with bioenergetic considerations. Marine Ecology Progress Series 143: 87−98.

Leppäkoski, E.; Helminen, H.; Hänninen, J.; Tallqvist, M. 1999. Aquatic biodiversity under anthropogenic stress: an insight from the Archipelago Sea (SW Finland). Biodiversity and Conservation 8: 55−70.

Lotze, H.K.; Lenihan, H.S.; Bourque, B.J.; Bradbury, R.H.; Cooke, R.G.; Kay, M.C.; Kidwell, S.M.; Kirby, M.X.; Peterson, C.H.; Jackson, J.B.C. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312(5781): 1806−1809.

Malm, T.; Engkvist, R.; Kautsky, L. 1999. Grazing effects of two freshwater snails on juvenile *Fucus vesiculosus* in the Baltic Sea. Mar Ecol Prog Ser 188: 63–71.

Maloy, A.P., Nelle, P., Culloty, S.C., Slater, J.W., Harrod, C., 2013. Identifying trophic variation in a marine suspension feeder: DNA- and stable isotope-based dietary analysis in *Mytilus* spp. Mar. Biol. 160, 479–490.

Mattila, J.M.; Zimmer, M.; Vesakoski, O.; Jormalainen, V. 2014. Habitat-specific gut microbiota of the marine herbivore *Idotea balthica* (Isopoda). Journal of Experimental Marine Biology and Ecology 455: 22−28.

Mittelmayr, A.; Hansen, T.; Sommer, U. 2014. Simultaneous analysis of d13C, d15N and d34S ratios uncovers food web relationships and the trophic importance of epiphytes in an eelgrass *Zostera marina* community. Marine Ecology Progress Series 497: 93–103.

Mittelmayr, A.; Fox, S.E.; Sommer, U. 2015. Temporal variation in stable isotope composition ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) of a temperate Zostera marina food web. Marine Ecology Progress Series 505: 95–105.

Navarro, E.; Méndez, S.; Urrutia, M.B.; Arambalza, U.; Ibarrola, I. 2016. Digestive selection underlies differential utilization of phytoplankton and sedimentary organics by infaunal bivalves: experiments with cockles (*Cerastoderma edule*) using cross-labelled mixed diets. Marine Environmental Research 120: 111−121.

Newsome, S.D.; Martinez del Rio, C.; Bearhop, S.; Phillips, D.L. 2007. A niche for isotopic ecology. Front Ecol Environ 5(8): 429–436.

Nordström, M.C.; Aarnio, K.; Bonsdorff, E. 2009. Temporal variability of a benthic food web: patterns and processes in a low-diversity system. Marine Ecology Progress Series 378: 13−26.

Nordström, M.C.; Linblad, P.; Aarnio, K.; Bonsdorff, E. 2010. A neighbour is a neighbour? Consumer diversity, trophic function, and spatial variability in benthic food webs. Journal of Experimental Marine Biology and Ecology 391: 101−111.

Nordström, M.C.; Aarnio, K.; Bonsdorff, E. 2016. Mesograzer identity, not host algae, determines consumer stable isotope ratios. Marine Biology Research 12(2): 186–192.

Ólafsson, E.B. 1986. Density dependence in suspension-feeding and deposit-feeding populations of bivalve *Macoma balthica*: A field experiment. Journal of Animal Ecology 55: 517−526.

Osmond, C. B.; Valaane, N.; Haslam, S. M.; Uotila, P. and Roksandic, Z. 1981. Comparisons of $\delta^{13}C$ values in leaves of aquatic macrophytes from different habitats in Britain and Finland; some implications for photosynthetic processes in aquatic plants. Oecologia 50(1): 117-124.

Paar, M.; Lebreton, B.; Graeve, M.; Greenacre, M.; Asmus, R., Asmus, H. 2019. Food sources of macrozoobenthos in an Arctic kelpbelt: trophic relationships revealed by stable isotope and fatty acid analyses. Marine Ecology Progress Series 615: 31−49.

Patterson, H.K.; Carmichael, R.H. 2016. The effect of lipid extraction on carbon and nitrogen stable isotope ratios in oyster tissues: Implications for glycogen-rich species. Rapid Communications in Mass Spectrometry 30(24): 2594−2600.

Pendleton, L. et al. 2012. Estimating Global ‘‘Blue Carbon’’ Emissions from Conversion and Degradation of Vegetated Coastal Ecosystems. Plos ONE 7(9): e43542

Pekkari, S. 1956. Notes on aquatic vegetation (the north-east corner). Acta Phytogeogr. Suec. 50: 209−214.

Post, D.M. et al. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152(1): 179–189.

Råberg, S.; Kautsky, L. 2007. Consumers affect prey biomass and diversity through resource partitioning. Ecology 88: 2468–2473.

Raven, J.A.; Johnston, A.M.; Kübler, J.E.; Korb, R.; McInroy, S.G.; Handley, L.L.; Scrimgeour, C.M.; Walker, D.I.; Beardall, J.; Vanderklift, M.; Fredriksen, S.; Dunton, K.H. 2002. Mechanistic interpretation of carbon isotope discrimination by marine macroalgae and seagrasses. Functional Plant Biology 29: 355−378.

Renaud, P.E., Løkken, T.S., Jørgensen, L.:; Jørgen, B.; Johnson, B.J. 2015. Macroalgal detritus and food-web subsidies along an Arctic fjord depth-gradient. Frontiers in Marine Science 2(31).

Ricca, M.A.; Miles, A.K.; Anthony, R.G.; Deng, X.; Hung, S.S.O. 2007. Effect of lipid extraction on analyses of stable carbon and stable nitrogen isotopes in coastal organisms of the Aleutian archipelago. Canadian Journal of Zoology 85(1): 40−48.

Rodil, I.F.; Attard, K.M.; Norkko, J.; Glud, R.N.; Norkko, A. 2020a. Estimating Respiration Ratesand Secondary Production of Macrobenthic Communities Across Coastal Habitatswith Contrasting Structural Biodiversity. Ecosystems 23: 630−647.

Rodil, I.F.; Lucena-Moya P.; Tamelander, T., Norkko, J.;, Norkko, A. 2020b. Seasonal Variability in Benthic–Pelagic Coupling: Quantifying Organic Matter Inputs to the Seafloor and Benthic Macrofauna Using a Multi-Marker Approach. Frontiers in Marine Science 7: 404.

Rönnbäck, P.; Kautsky, N.; Pihl, L.; Troell, M.; Söderqvist, T.; Wennhage, H. 2007. Ecosystem Goods and Services from Swedish Coastal Habitats: Identification, Valuation, and Implications of Ecosystem Shifts. Ambio 36(7): 534–577.

Sarà, G. 2007. Sedimentary and particulate organic matter: mixed sources for cockle *Cerastoderma glaucum* in a shallow pond, Western Mediterranean. Aquatic Living Resources 20: 271–277.

Scaps, P. 2002. A review of the biology, ecology and potential use of the common ragworm *Hediste diversicolor* (O.F. Müller) (Annelida: Polychaeta). Hydrobiologia 470: 203–218.

Seitz, R.D.; Wennhage, H.; Bergström, U.; Lipcius, R.N.; Ysebaert, T. 2014. Ecological value of coastal habitats for commerciallyand ecologically important species. ICES Journal of Marine Science 71(3): 648–665.

Siikamäki, J.; Sanchirico, J.N.; Jardine, S.; McLaughlin, D.; Morris, D. 2013. Blue Carbon: Coastal Ecosystems, Their Carbon Storage, and Potential for Reducing Emissions. Environment: Science and Policy for Sustainable Development 55: 14–29.

Skoog, G. 1978. Influence of Natural Food Items on Growth and Egg Production in Brackish Water Populations of *Lymnea peregra* and *Theodoxus fluviatilis* (Mollusca). Oikos 31: 340−348.

Stanners, D.; Bourdeau, P (eds.). 1995. Europe's environment: the Dobris assessment. Chapter 35: Coastal zone threats and management. Office for Official Publications of the European Communities, Luxembourg. ISBN 92-826-5409-5.

Stock, B.C.; Jackson, A.L.; Ward, E.J.; Parnell, A.C.; Phillips, D.L.; Semmens, B.X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6: e5096; DOI 10.7717/peerj.5096

Strasser, M. 1999. *Mya arenaria* − an ancient invader of the North Sea coast. Helgoländer Meeresuntersuchungen 52: 309−324.

Stuart, V.; Head, E.J.H.; Mann, K.H. 1985. Seasonal changes in the digestive enzyme levels of the amphipod *Corophium volutator* (Pallas) in relation to diet. Journal of Experimental Marine Biology and Ecology 88(3): 243−256.

Takolander, A.; Cabeza, M.; Leskinen, E. 2017. Climate change can cause complex responses in Baltic Sea macroalgae: A systematic review. Journal of Sea Research 123: 16−29.

Thormar, J.; Hasler-Sheetal, H.; Baden, S.; Boström, C.; Kuhlmann Clausen, K.; Krause-Jensen, D.; Olesen, B.; Ribergaard Rasmussen, J.; Svensson, C.J.; Holmer, M. 2016. Eelgrass (*Zostera marina*) Food Web Structure in Different Environmental Settings. PLoS ONE 11(1): e0146479.

Torn, K.; Krause-Jensen, D.; Martin, G. 2006. Present and past depth distribution of bladderwrack (*Fucus vesiculosus*) in the Baltic Sea. Aquatic Botany 84: 53−62.

Trevathan-Tackett, S.M.; Kelleway, J.; Macreadie, P.I.; Beardall J.; Ralph, P.; Bellgrove A. 2015. Comparison of marine macrophytes for their contributions to blue carbon sequestration. Ecology 96:3043–3057.

Watanabe, K.; Yoshida, G.; Umezawa, Y.; Moki, H.; Kuwae, T. 2020. Macroalgal metabolism and lateral carbon flows can create significant carbon sinks. Biogeosciences 17: 2425–2440.

Wiedemeyer, W.L.; Schwamborn, R. 1996. Detritus derived from eelgrass and macroalgae as potential carbon source for *Mytilus edulis* in Kiel Fjord, Germany: a preliminary carbon isotopic study. Helgoländer Meeresunters. 50: 409–413.

Wikström, S.A.; Kautsky, L. 2007. Structure and diversity of invertebrate communities in the presence and absence of canopy-forming *Fucus vesiculosus* in the Baltic Sea. Estuarine, Coastal and Shelf Science 72:168–76.

Yokoyama, H.; Tamaki, A.; Harada, K.; Shimoda, K.; Koyama, K.; Ishihi, Y. 2005. Variability of diet-tissue isotopic fractionation in estuarine macrobenthos. Marine Ecology Progress Series 296: 115–128.

Ziółkowska, M.; Sokołowski A.; Richard, P. 2018. Spatial and temporal variability of organic matter sources and food web structure across benthic habitats in a low diversity system (southern Baltic Sea). Journal of Sea Research 141: 47–60.

Figures captions

Fig. 1. The study area in Hanko peninsula and the sampling locations (A1−C2). Number 1 indicates a soft-bottom habitat dominated by angiosperm plants, while 2 indicates a hard-bottom habitat dominated by *F. vesiculosus*.

Fig. 2. Mean (±SD) $\delta^{13}C$ compositions of different food sources (macrophytes, seston POM and DOM, sedimentary organic matter) and consumer macrofauna classified into four types of feeding strategies. The data of *M. trossulus*, *Marenzelleria* spp.*, F. vesiculosus*, POM and DOM have been previously published in Kahma et al. 2020.

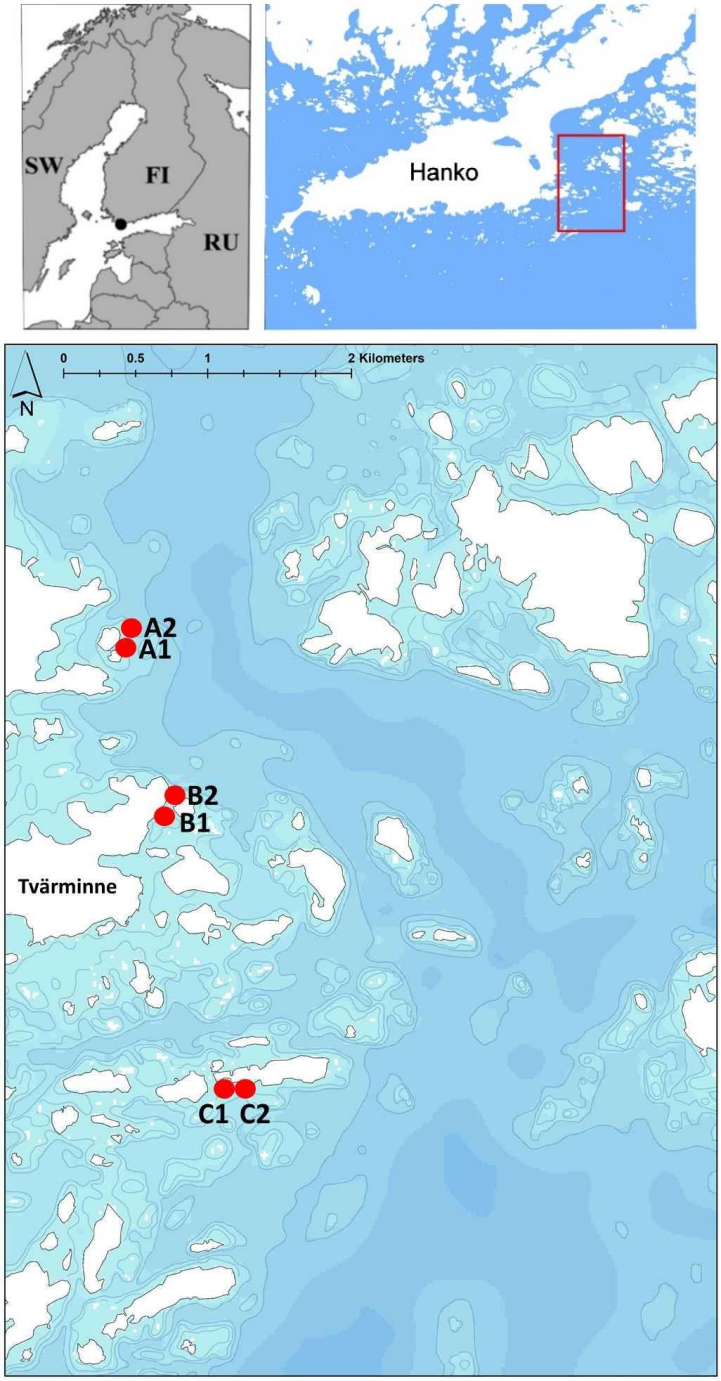
Fig. 3. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ signatures of food sources and consumers of the whole study area. Rectangles show the variation range (±SD) of ephemeral algae (A) and perennial macrophytes (B). The data of M. trossulus, Marenzelleria spp., F. vesiculosus, POM and DOM have been published in Kahma et al. 2020. For mean values in the two different habitat types, see supplementary material (Fig. S1).

Fig. 4. Maximum-likelihood fitted standard ellipses showing macrophytes (A) and consumer fauna (B) between the two habitat types, consumer animal community between the three sampling locations in Fucus-dominated (C) and angiosperm-dominated habitats (D), and infaunal clam community in Fucus-influenced (E) and angiosperm-dominated benthic habitats (F). Bayesian estimates are presented in Fig. 5.

Fig. 5. Bayesian estimates for the SIBER ellipse areas presented in Fig.4, with credibility intervals of 50 %, 90 % and 95 %. Estimates for ellipse overlapping areas are also presented.

Fig. 6. Median dietary compositions of different consumer animals with Bayesian credibility intervals (50 %, 90 % and 95 %). Means are presented in Table S1.

Figure 1. The study area in Hanko peninsula and the sampling locations (A1−C2). Number 1 indicates a soft-bottom habitat dominated by angiosperm plants, while 2 indicates a hard-bottom habitat dominated by *F. vesiculosus*.



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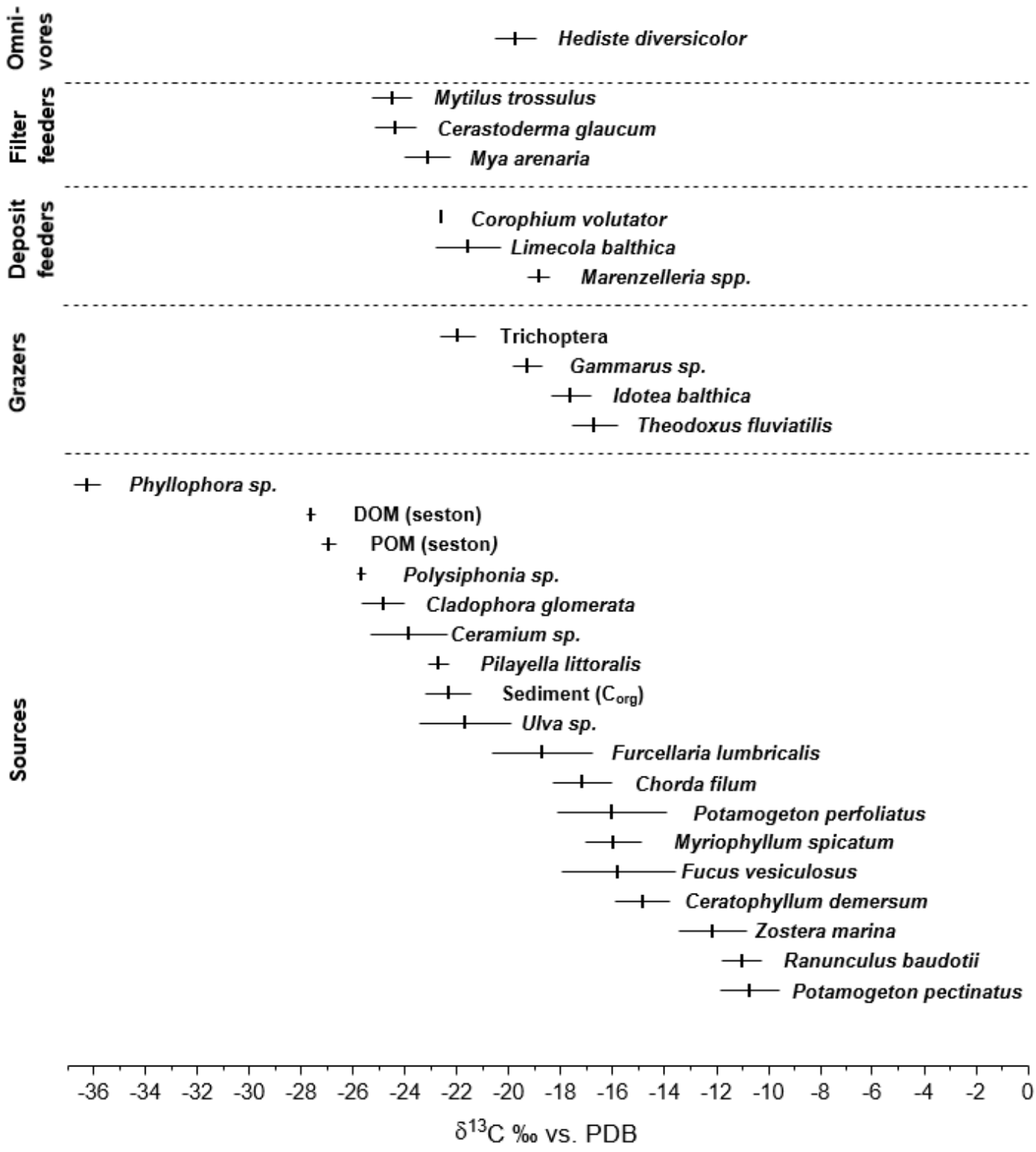

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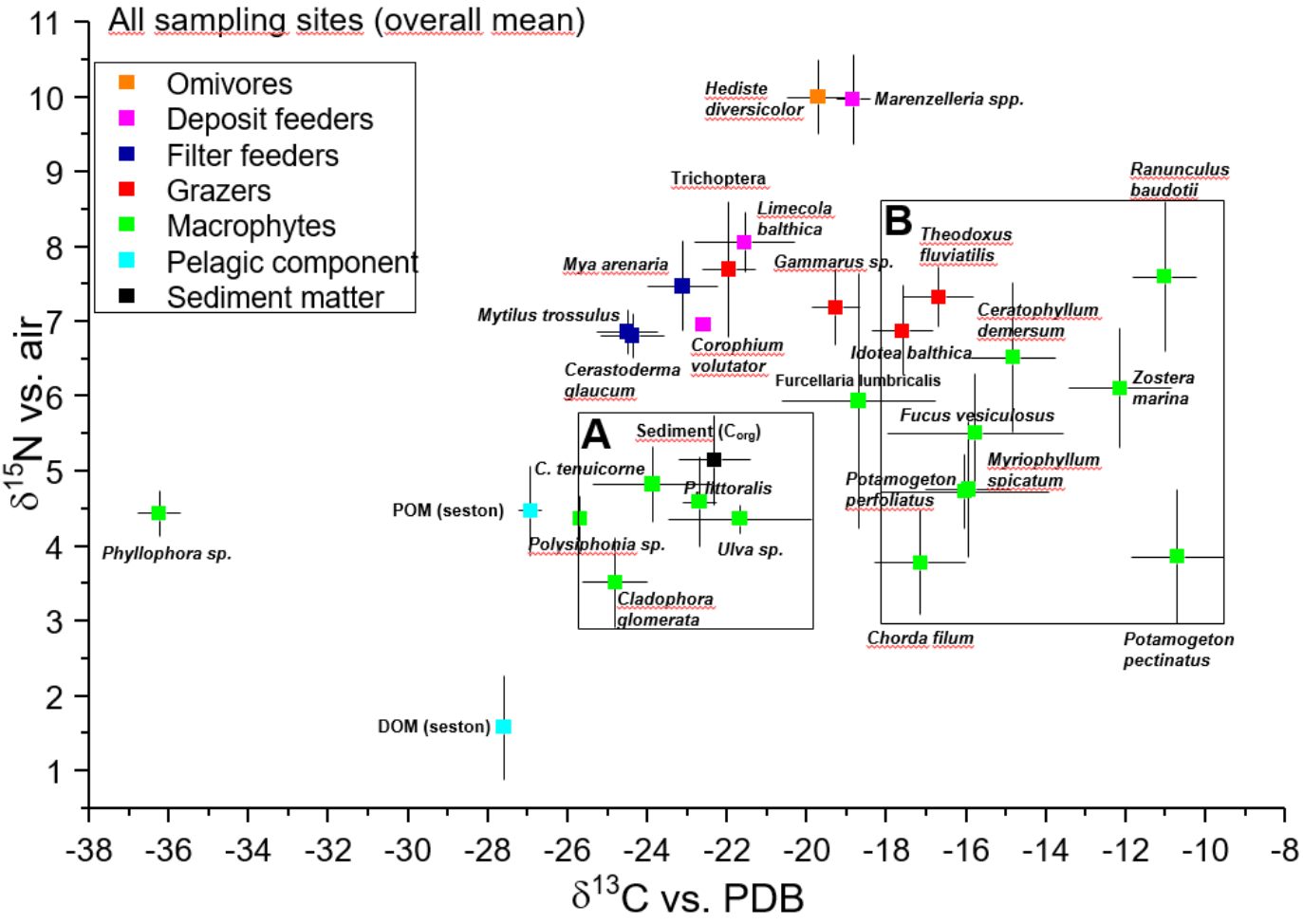

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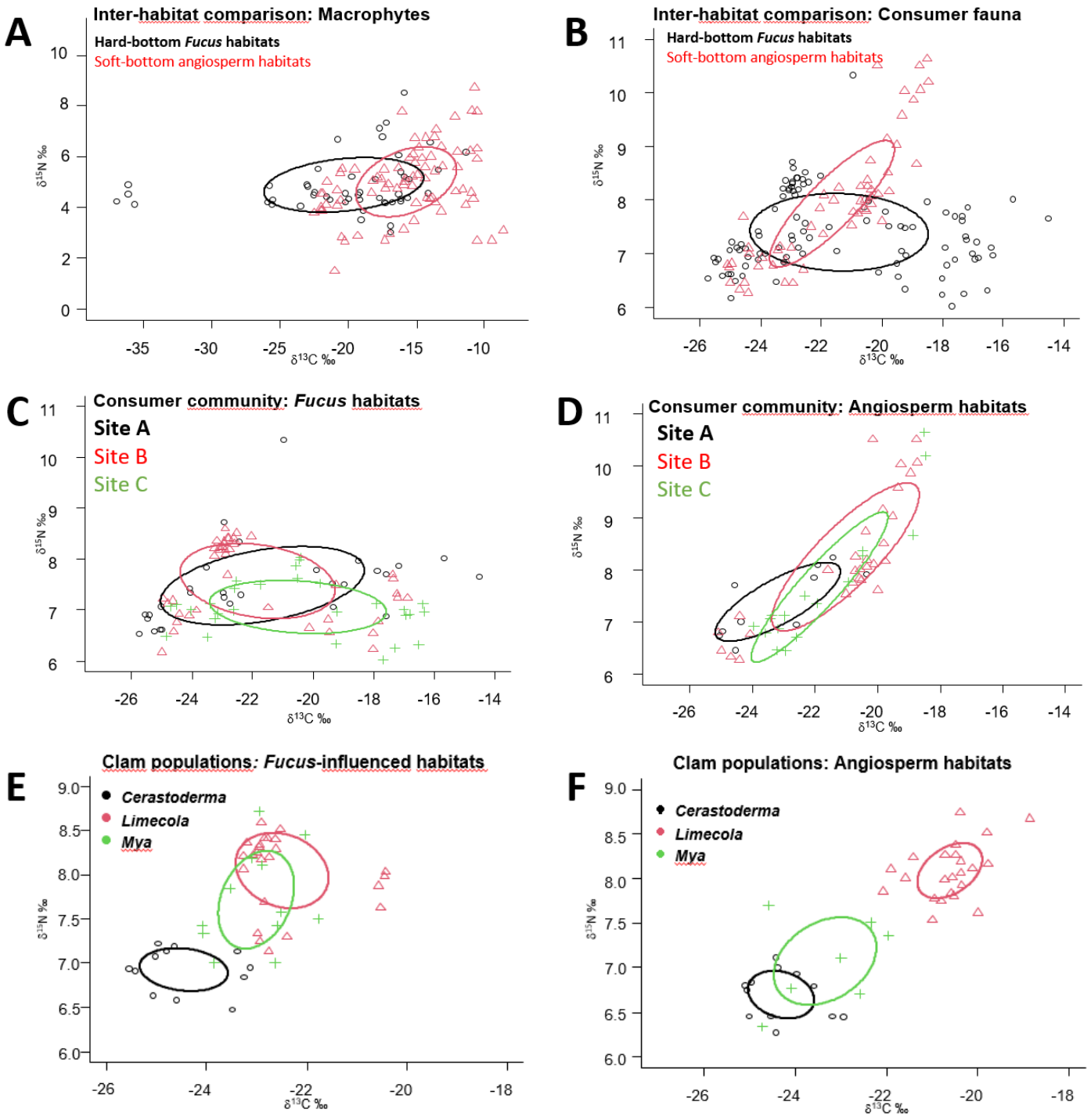

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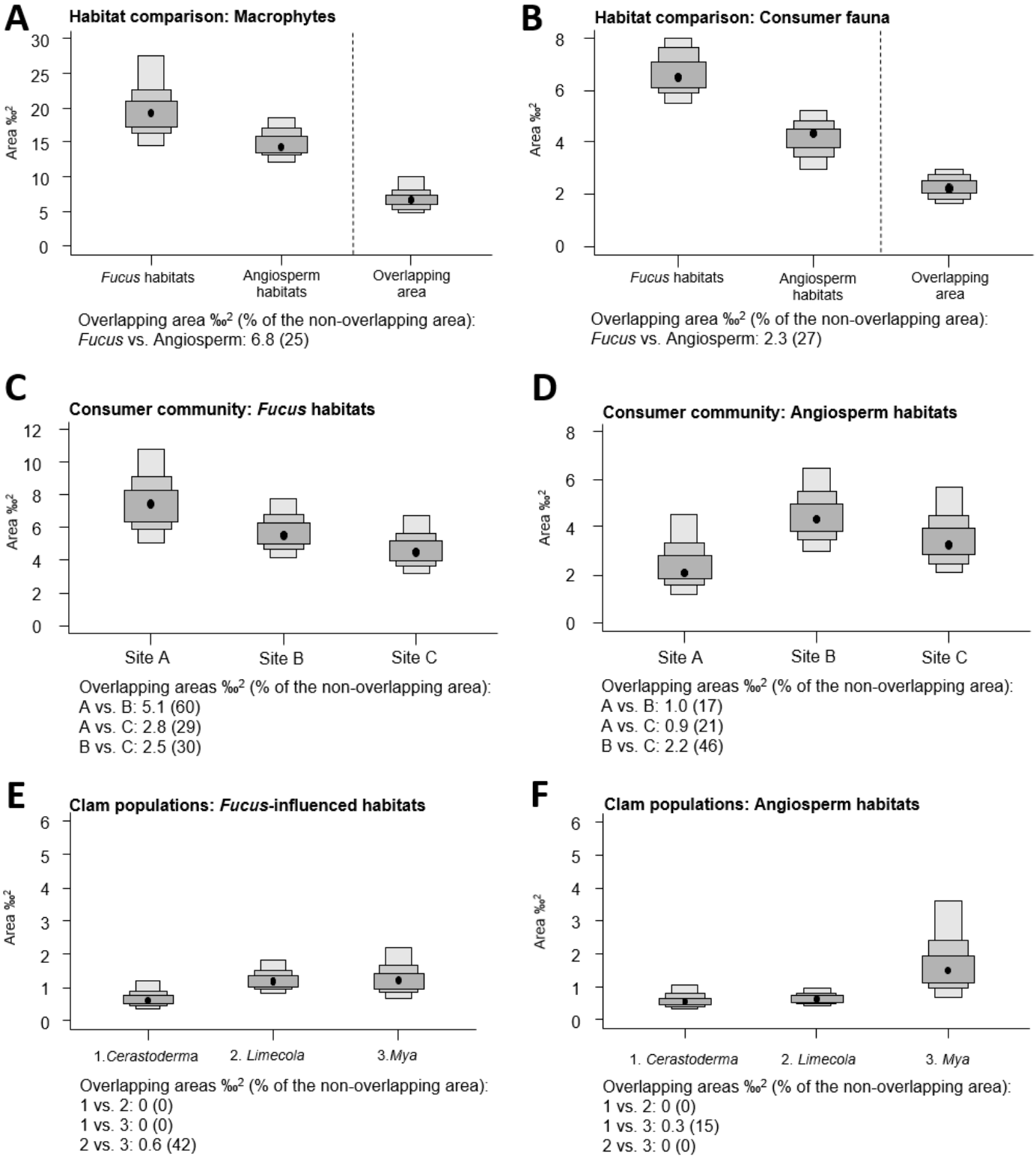

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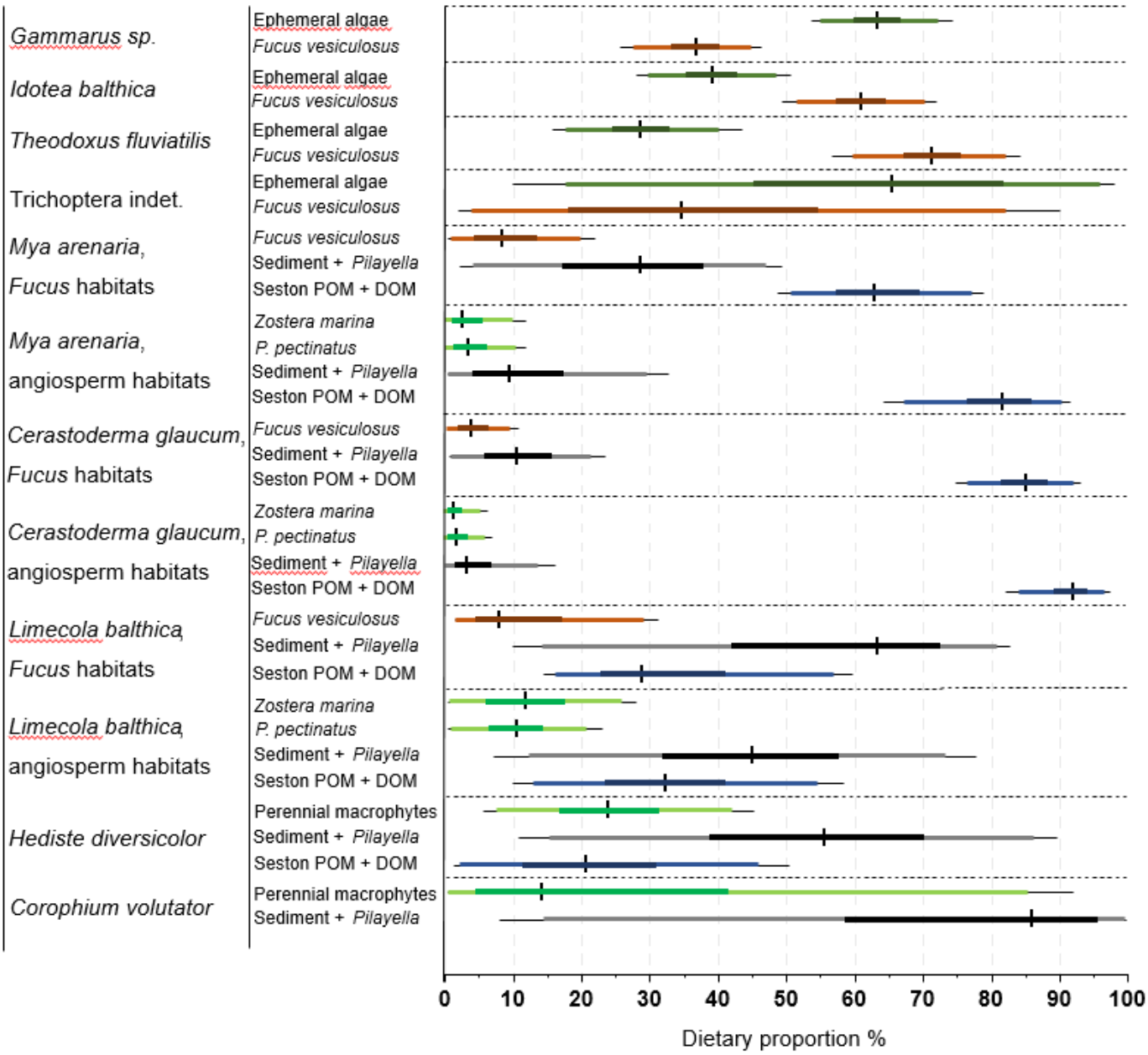

Table 1. Sampling locations. Locations A−C are shallow vegetated habitats, and W1−W5 are offshore locations for water sampling only.

Code	Date (2017)	Seafloor substrate	Dominating vegetation	Latitude (°N)	Longitude (°E)	Depth (m)
A1	5–6 July	Rocky + Soft bottom	*Fucus vesiculosus*	59.86040	23.24610	2.0–5.0
A2	28 June	Soft bottom	Angiosperms	59.85945	23.24598	2.0–3.5
B1	5–6 July	Rocky + Soft bottom	*Fucus vesiculosus*	59.85038	23.25263	1.5–5.0
B2	28 June	Soft bottom	Angiosperms	59.84895	23.25205	1.5–3.5
C1	5–6 July	Rocky + Soft bottom	*Fucus vesiculosus*	59.83227	23.26172	2.0–5.0
C2	28 June	Soft bottom	Angiosperms	59.83242	23.26520	2.0–3.5
W1	4–5 June	*(Pelagic)*	–	59.86200	23.25615	39.5
W2	4–5 June	*(Pelagic)*	–	59.84300	23.28035	37.0
W3	4–5 June	*(Pelagic)*	–	59.83185	23.29566	45.0
W4	4–5 June	*(Pelagic)*	–	59.85520	23.26455	39.0
W5	4–5 June	*(Pelagic)*	–	59.85360	23.26313	22.0

Table 2. Overall mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values and relative trophic levels (RTL) of all the examined food sources and fauna consumers. The values for *F. vesiculosus*, *M. trossulus*, *Marenzelleria* spp., POM and DOM have been previously published (Kahma et al. 2020).

Species	n	$\delta^{13}C$ ‰	SD ±	$\delta^{15}N$ ‰	SD ±
Chlorophyta					
Cladophora glomerata (L.)	16	-24.8	0.8	3.52	0.6
Ulva sp. (L.)	4	-21.7	1.8	4.36	0.2
Rhodophyta					
Ceramium sp. (Blume)	15	-23.9	1.5	4.83	0.5
Furcellaria lumbricalis (Huds.) Lamoroux	8	-18.7	1.9	5.94	1.7
Phyllophora sp. (Nägeli)	4	-36.2	0.5	4.44	0.3
Polysiphonia sp. (Greville)	4	-25.7	0.2	4.37	0.3
Phaeophyta					
Chorda filum (L.)	16	-17.2	1.1	3.78	0.7
Fucus vesiculosus (L.)	29	-15.8	2.2	5.51	0.8
Pylaiella littoralis[1] (L.)	20	-21.6	0.8	4.21	1.0
Tracheophyta					
Ceratophyllum demersum (L.)	4	-14.8	1.1	6.52	1.0
Myriophyllum spicatum (L.)	4	-16.0	1.1	4.76	0.9
Potamogeton pectinatus (L.) Böerner	8	-10.7	1.2	3.86	0.9
Potamogeton perfoliatus (L.)	12	-16.0	2.1	4.76	0.5
Ranunculus baudotii (Godr.)	4	-11.0	0.8	7.60	1.0
Zostera marina (L.)	8	-12.1	1.3	6.11	0.8
Sediment[2]	16	-22.3	0.9	5.15	0.6
Seston POM	5	-27.6	0.2	4.47	0.6
Seston DOM	4	-26.9	0.3	1.58	0.7
Crustacea					
Corophium volutator (Pallas)	1	-22.6	–	6.96	–
Gammarus sp. (Fabricius)	12	-19.3	0.6	7.19	0.5
Idotea balthica (Pallas)	12	-17.6	0.8	6.88	0.6
Gastropoda					
Theodoxus fluviatilis (L.)	11	-16.7	0.9	7.33	0.4
Bivalvia					
Cerastoderma glaucum (Bruguière)	24	-24.4	0.8	6.81	0.3
Limecola balthica (L.)	47	-21.6	1.3	8.06	0.4
Mya arenaria (L.)	20	-23.1	0.9	7.47	0.6
Mytilus trossulus[3] (Gould)	16	-24.5	0.8	6.86	0.3
Polychaeta					
Hediste diversicolor (Müller)	6	-19.7	0.8	10.0	0.5
Marenzelleria spp. (Mesnil)	5	-18.8	0.4	9.97	0.6
Insecta					
Trichoptera indet.	2	-22.0	0.7	7.70	0.9

1) *Includes also partly decomposed algae.*
2) *Organic carbon $\delta^{13}C$.*
3) *n = 15 for carbon analysis.*

Table 3. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of the food sources and fauna consumers for the different habitat types (3 sites per habitat, see Figure 1).

Species	*Fucus* habitats			Angiosperm habitats		
	n	Mean $\delta^{13}C$ ‰ ± SD	Mean $\delta^{15}N$ ‰ ± SD	n	Mean $\delta^{13}C$ ‰ ± SD	Mean $\delta^{15}N$ ‰ ± SD
Chlorophyta						
Cladophora glomerata	12	-25.2 ± 0.6	3.26 ± 0.4	4	-23.7 ± 0.3	4.29 ± 0.2
Ulva sp.	4	-21.7 ± 1.8	4.36 ± 0.2	–	–	–
Rhodophyta						
Ceramium sp.	11	-24.4 ± 1.4	4.88 ± 0.6	4	-22.4 ± 0.2	4.70 ± 0.4
Furcellaria lumbricalis	8	-18.7 ± 1.9	5.94 ± 1.7	–	–	–
Phyllophora sp.	4	-36.2 ± 0.5	4.44 ± 0.3	–	–	–
Polysiphonia sp.	4	-25.7 ± 0.2	4.37 ± 0.3	–	–	–
Phaeophyta						
Chorda filum	12	-17.1 ± 1.1	4.07 ± 0.6	4	-17.4 ± 1.4	2.91 ± 0.2
Fucus vesiculosus	13	-16.5 ± 2.9	5.35 ± 0.8	16	-15.2 ± 1.2	5.64 ± 0.9
Pilayella littoralis	4	-22.7 ± 0.4	4.9 ± 0.4	16[1]	-21.3 ± 0.7	4.03 ± 1.0
Tracheophyta						
Ceratophyllum demersum		–	–	4	-14.8 ± 1.1	6.52 ± 1.0
Myriophyllum spicatum		–	–	4	-16.0 ± 1.1	4.76 ± 0.9
Potamogeton pectinatus		–	–	8	-10.7 ± 1.2	3.86 ± 0.9
Potamogeton perfoliatus		–	–	12	-16.0 ± 2.1	4.76 ± 0.5
Ranunculus baudotii		–	–	4	-11.0 ± 0.8	7.60 ± 1.0
Zostera marina		–	–	8	-12.1 ± 1.3	6.11 ± 0.8
Sediment[2]	8	-22.86 ± 0.3	4.96 ± 4.9	8	-21.43 ± 0.8	5.27 ± 0.7
Crustacea						
Corophium volutator	–	–	–	1	-22.6	6.96
Gammarus sp.	12	-19.3 ± 0.6	7.19 ± 0.5	–	–	–
Idotea balthica	12	-17.6 ± 0.8	6.88 ± 0.8	–	–	–
Gastropoda						
Theodoxus fluviatilis	11	-16.7 ± 0.9	7.33 ± 0.9	–	–	–
Bivalvia						
Cerastoderma glaucum	12	-24.5 ± 0.9	6.92 ± 0.9	12	-24.3 ± 0.7	6.69 ± 0.3
Limecola balthica	24	-22.5 ± 0.9	8.04 ± 0.9	23	-20.6 ± 0.7	8.08 ± 0.3
Mya arenaria	12	-23.0 ± 0.8	7.71 ± 0.8	7	-23.3 ± 1.1	7.07 ± 0.5
Mytilus trossulus	12	-24.8 ± 0.5	6.76 ± 0.5	4[3]	-22.5 ± 1.7	7.18 ± 0.3
Polychaeta						
Hediste diversicolor	1	-21.0	10.3	6	-19.5 ± 0.5	9.96 ± 0.6
Marenzelleria spp.	–	–	–	5	-18.8 ± 0.8	10.0 ± 0.5
Insecta						
Trichoptera indet.	2	-22.0 ± 0.7	7.70 ± 0.7	–	–	–

1) *Includes also partly decomposed algae*
2) *Organic carbon $\delta^{13}C$.*
3) n = 3 for carbon analysis.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: