Macrofauna Community Dynamics and Food Webs in the Canopy-forming Macroalgae and the Associated Detrital Subsidies

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Abstract

Dietary variability and the degradation and incorporation of macroalgae in key macroinvertebrate consumers were examined (1) in a monitoring field study including a natural attached canopy habitat and an adjacent habitat receiving natural accumulations of detritus, and (2) in a manipulative in situ experiment of macroalgal detritus at two different depths (3 and 6 m) in the archipelago of SW Finland. The monitoring field study, examining species-specific dietary responses across three sampling dates in natural macroalgal stands, showed that a pulse of drifting filamentous macroalgae shaped the dietary compositions of the abundant benthic macroinvertebrate consumers and that accumulations of drifting filamentous macroalgae were rapidly incorporated into the food web through epigrazers. The in situ field experiment simulating a natural accumulation event and the degradation process of *Fucus vesiculosus* during 60 days showed that algal decomposition progressed relatively slowly at both depths. Detectable increasing incorporation of *Fucus*-derived matter to epigrazers and detritivorous bivalves occurred after 2−3 weeks, while simultaneously the incorporation of filamentous algae decreased over time. Hence, the ecological role of decomposing *F. vesiculosus* might be more important in areas where the algal matter can accumulate for several months. The effect of depth influenced the food incorporation of typical epigrazers. The increasing depth from 3 to 6 m lowered the median proportion of *Fucus*-derived matter incorporated into the macrofauna community approximately by 10% points compared to the shallower depth of 3 m.

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Introduction

Canopy-forming kelp macroalgae are extensive underwater forests with global distribution, high biological activity, and a key role in supporting the economic and ecological value of coastal areas (Dayton 1985; Steneck et al. 2002; Gutiérrez et al. 2011; Steneck and Johnson 2013; Coleman and Wernberg 2017). Macroalgae are typical foundation species (sensu Dayton 1972) that modify the environmental conditions and provide shelter for a variety of associated organisms on rocky shorelines and shallow reefs (Wernberg et al. 2005; Christie et al. 2009; Coleman et al. 2007; Gutiérrez et al. 2011). Macroalgal forests also provide food for a variety of animals from inconspicuous invertebrates to fish and seabird species, shaping community dynamics and the trophic food web of coastal areas (Fredriksen 2003; Graham 2004; Norderhaug et al. 2005; Kahma et al. 2020, 2021).

Highly productive macroalgal forests generate large amounts of particulate detritus in the form of dislodged and

fragmented organic material often occurring as seasonal or pulsed events that provide a surplus of food input to adjacent environments (Krumhansl and Scheibling 2012; Renaud et al. 2015; Filbee-Dexter et al. 2018). Generally, direct feeding on macroalgae by grazing is considered a small fraction of the annual macroalgal production compared to the large fraction (> 80%) transferred to the detrital pool (Krumhansl and Scheibling 2012). Algal detritus is then either consumed by detritivores or decomposed and accumulated in deeper and colder depositional pools where it has the potential to be locked away in more long-term carbon pools (Krause-Jensen and Duarte 2016). Depositing drifting algae is a spatial subsidy that can play a major role in the flow of energy through coastal habitats, significantly influencing the dynamics of associated biota and food webs in many adjacent ecosystems (Vetter 1994; Norkko et al. 2000; Salovius et al. 2005; Renaud et al. 2015; Filbee-Dexter et al. 2018; Kahma et al. 2020). Several studies have focused on the ecological role of macroalgal accumulations on beaches, seagrass meadows, coral reefs, and deep subtidal areas (e.g., Norkko and Bonsdorff 1996a, b; Wernberg et al. 2006; Lastra et al. 2008; Krumhansl and Scheibling 2012; Renaud et al. 2015; Filbee-Dexter and Scheibling 2016; Filbee-Dexter et al. 2018). The potential role of macroalgal forests as blue carbon ecosystems (Krause-Jensen and Duarte 2016; Lovelock and Duarte 2019) has renewed the research interest in understanding the decomposition dynamics of macroalgae (see de Bettignies et al. 2020). The decomposition process generally improves the dietary palatability of macroalgae to associated primary consumer fauna by reducing the C/N ratio, increasing microbial colonization and causing loss of deterring phytochemicals of algal tissue (e.g. Duggins and Eckman 1997; Amsler 2001; Norderhaug et al. 2003; Jormalainen et al. 2005; Jormalainen and Ramsay 2009; Dethier et al. 2014; Pedersen et al. 2021).

In the Baltic Sea, the bladder-wrack *Fucus vesiculosus* (L., 1753) (hereafter *Fucus*) is a perennial macroalga that forms abundant monospecific forest-type beds within near-shore areas where it has a well-recognized community structuring role and a major contribution to carbon dynamics (e.g., Hällfors and Niemi 1981; Wikström and Kautsky 2007; Råberg and Kautsky 2007; Attard et al. 2019a, b; Kahma et al. 2020, 2021, Buck-Wiese et al. 2022). Associated with the *Fucus*-beds also other long-lived rhodophyte species thrive (e.g., *Furcellaria lumbricalis*, *Ceramium* spp.), and a diverse number of seasonally opportunistic green and brown algal species (e.g., *Cladophora* spp., *Pilayella littoralis*) play an important, but not fully understood role in the macrofauna community dynamics of these shallow rocky communities (Hällfors and Niemi 1981; Wikström and Kautsky 2007; Saarinen et al. 2018). These rocky macroalgal communities, comprised of a mix of perennial large species, such as *Fucus*, and many associated other

filamentous algal vegetation types co-occur in the Baltic Sea (Råberg and Kautsky 2007). However, the full range of different macrophyte species has not been taken into account to unravel the food web complexity of shallow coastal habitats in the Northern Baltic Sea until recently (Kahma et al. 2021).

The current global scenario of climate change, and the less favourable conditions for large perennial macroalgae, are causing significant declines in many kelp forests worldwide in favour of opportunistic algae (Coleman and Wernberg 2017; Filbee-Dexter and Wernberg 2018). Eutrophication affects coastal habitats globally through the increasing proliferation of seasonal blooms of ephemeral algae that inhibit the growth and survival of large macrophytes and associated communities (McGlathery et al. 2007; Cebrián et al. 2014; Wikström et al. 2016). Eutrophication can cause harm to benthic macrofauna (Norkko and Bonsdorff 1996a, b), but might also benefit some epigrazer species (Norkko et al. 2000; Salovius and Kraufvelin 2004; Rodil et al. 2021). While several studies in the Baltic Sea have focused on the fate and ecological impacts of macroalgal detritus comprised of ephemeral algae, which have proliferated due to eutrophication, our understanding of the fate of foundation species such as *Fucus* is lagging. Climate change, especially increasing temperatures, together with a strong legacy of eutrophication is predicted to alter the structure and functioning of the macroalgal bed ecosystems in the Baltic Sea (see Takolander et al. 2017). For example, *Fucus*-forests have already suffered major changes in the extent and depth distribution in the Baltic Sea since the 1940s (Kautsky et al. 1986; Torn et al. 2006). The consequences of such changes in the biodiversity and trophic food webs of coastal zones are far from understood.

Here, we studied the twofold ecological role of *Fucus* for benthic biodiversity and food supply in coastal areas of the Baltic Sea. Firstly, as perennial macrophyte biomass hosting abundant macrofauna community in the rocky macroalgal bed, and secondly, as a temporal resource subsidy in adjacent sedimentary depositional pools when it becomes to detritus. To examine these two roles, our study combines two parts: (1) a monitoring field study exploring the natural dynamics of *Fucus*-consumer relationships of a shallow macroalgal community (both in the attached canopy habitat and the adjacent natural accumulations of detritus) and (2) a manipulative field experiment (60 days) using experimentally replicated mesh-bags to mimic natural macroalgal depositions, their decomposition, and resource utilization by macrofaunal communities. In the first study, we compared the macrofauna community dynamics, and the dietary compositions (using a dual stable isotope approach, $\delta^{13}C$ and $\delta^{15}N$, and a Bayesian mixing model) of abundant epigrazer species in two habitats: a *Fucus*-bed and an adjacent shallow depositional pool at three different times. We hypothesize that the

decomposing *Fucus* matter from the depositional pool will incorporate faster into the associated comsumer macrofauna due to its better palatability. Detached macroalgal fragments can retain physiological and reproductive capabilities for up to several months (Frontier et al. 2021) and the rate of degradation depends on the characteristics of the algae and the environmental conditions, mainly related to depth, such as temperature and irradiance (Salovius and Bonsdorff 2004; Rothäusler et al. 2011a, b; Krumhansl and Scheibling 2012). Therefore, we set up a 2-month in situ experiment to examine the *Fucus*-associated macrofauna community and their dietary composition during the algal decay process at shallow (3 m) and deep (6 m) depositional sedimentary sites. We hypothesize that the dietary incorporation of detrital *Fucus* matter to associated consumer macrofauna will increase as the matter gradually decomposes over time, and that increasing depth might slow the decomposition process and thus the dietary incorporation of the detritus.

Materials and Methods

Study Area

The study took place at Spikarna, a small group of rocky outer islets enclosing a shallow lagoon in Hanko archipelago, SW Finland (Fig. 1). The maximum depth of the enclosed lagoon is approximately 3 m, while the depth rapidly increases to 10–20 m outside the islets. Although there are no noticeable tidal water movements in the Baltic Sea, the Spikarna islets are highly exposed to wave action. Outside the islets, a wave height of > 2 m is exceeded 10% of the time when the sea is not ice covered (Kahma 2021). Two different habitats can be observed in the lagoon. The Southern part of the lagoon (*Fucus* canopy habitat, "FC") is dominated by an abundant community of *Fucus* attached to the rocky seafloor (Fig. 1A). Instead, the Northern part of the lagoon (Detritus accumulation habitat, "DA") is characterized by a sandy seafloor, which frequently receives large

Fig. 1 Map and locations of the study sites: the canopy-forming *Fucus vesiculosus* canopy site (FC) and the algal detritus accumulation site (DA) from the temporal study, and the shallow (Sh, 3 m) and deep (De, 6 m) sites from the mesh-bag algal degradation experiment. Pictures taken from the FC (**A**), the DA (**B**), the set-up experiment on the last sampling day after 2 months (**C**) and at the starting (**D**) of the mesh-bag experiment
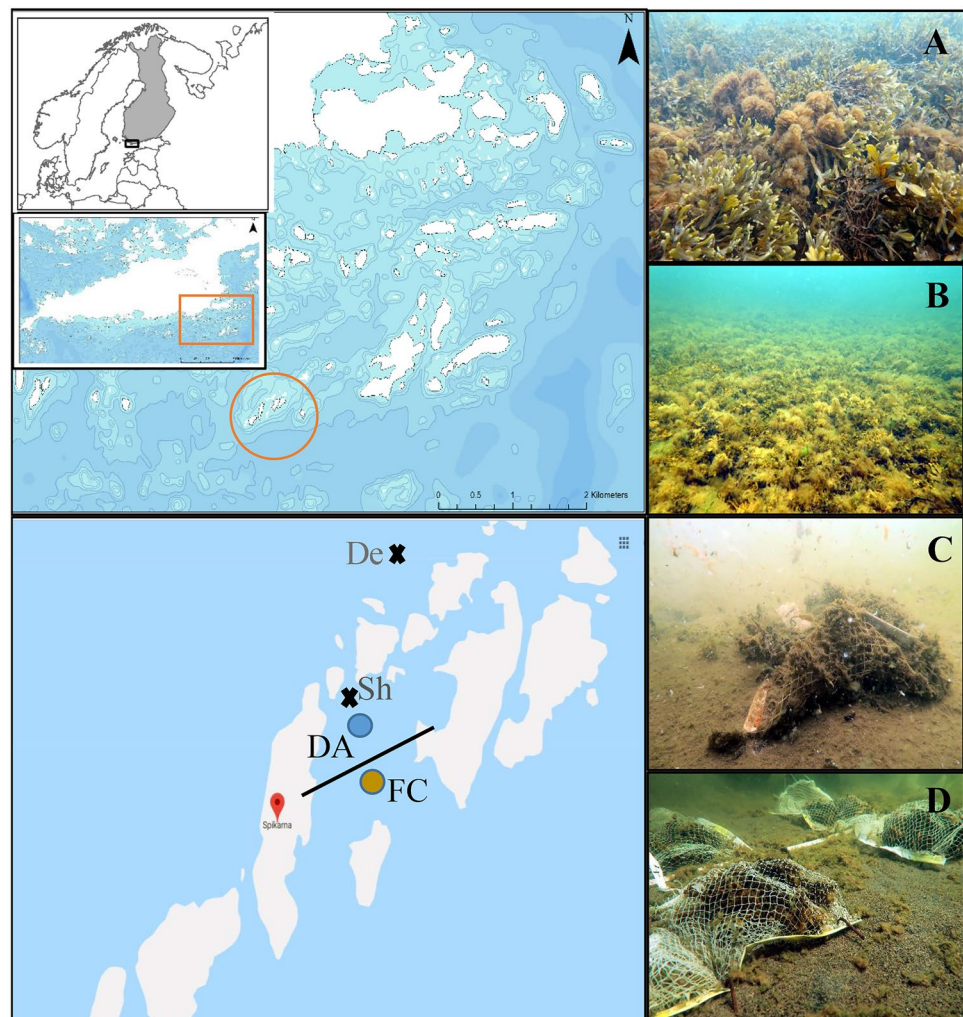
amounts of detached *Fucus* and other macroalgae from the Southern part of the lagoon, forming thick detritus mats covering the sandy seafloor (Fig. 1B).

Monitoring Field Study of the Natural Macrofauna Community Dynamics

To examine the natural variations of macrofauna communities and the isotopic and dietary compositions in the two different habitats of the lagoon (i.e. FC and DA), the habitats were sampled on three dates (i.e., June 2017, September 2017 and May 2018). Macrophyte material was hand-picked by SCUBA divers from both habitats of the lagoon. At the canopy habitat, eight *Fucus* individuals were removed from the hard substrate by a scraper into separate net bags. At the detritus accumulation habitat, the thickness of drifting macrophyte material was measured ($n=8$), and a rectangular frame (20×20 cm) or a circular frame (Ø 19 cm, to sample the thickest detritus layers) ($n=8$) was used to sample the area. All drifting macroalgal material and associated epifauna enclosed within the frames were then collected by hand into net bags. Finally, sediment under the accumulated algae was sampled by a hand corer (Ø 5 cm, 15 cm deep) to collect benthic macroinfauna, and with syringe samplers (Ø 3.5 cm) to collect surface (1 cm) sediment material for the analysis of isotopes.

Algal Decay Mesh-Bag Experiment at Two Different Depths

To study the decomposition process of the macroalgal detritus and the dietary compositional changes of the associated macrofauna consumers over time, we simulated drifting *Fucus* accumulations around the sedimentary area of the Spikarna lagoon (Fig. 1C, D) with an in situ mesh-bag experiment. Fresh *Fucus* individuals were collected by SCUBA divers from the rocky area of the lagoon (FC, Fig. 1). The individuals were washed by hand and the associated epifauna was removed. To start the decomposition process, *Fucus* individuals were stored in water in a dark cold room for 6 days. Approximately 300 g (± 100 g) of wet *Fucus* material was then weighted into net bags (mesh size 20 mm). In total, 40 bags were prepared. At the same time, the algal tissue (the topmost 2 cm of the apical thalli) was sampled from each bag for stable isotope analysis. At the start of the experiment, twenty bags were randomly placed in paired-row arrangements (Fig. 1C, D) at two different depths: (1) inside the sandy-bottom Northern area of the lagoon at a shallow depth of 3 m ("Sh", Fig. 1), and (2) the other twenty bags were placed outside the islets at a depth of 6 m ("De", Fig. 1). The mesh-bags were anchored to the sandy seafloor using metal pegs, separated from each other by half a meter, and left to decay for 2 (t_1), 6 (t_2), 21 (t_3)

and 62 (t_4) days. Five mesh-bags were randomly selected at each sampling day per depth. Variable amounts of detached ephemeral *Pilayella littoralis* (hereafter *Pilayella*) naturally settled on the bags over time, and all the colonizing algae and associated epifauna were collected from each bag for later analysis. The sediment under each mesh-bag was sampled by a hand corer (Ø 5 cm, 15 cm deep) to collect benthic infauna ($n=4$), and a syringe sampler (Ø 3.5 cm) was used for stable isotope sediment analysis ($n=4$). Simultaneously, control bare sediment samples were randomly taken around the mesh-bags on each sampling date for comparison. During the experiment, temperature and light intensity (lux) were measured with a HOBO data logger sensor at each depth (one per site).

Sample Preparation

The macrophytes were washed using deionized water and associated epifauna was removed. Samples of fresh macrophyte tissues were taken by a scalpel and stored in Eppendorf tubes. Macrophyte material was then dried and weighed to measure biomass. All the sediment collected with the corer was washed away through a sieve (1 mm) and all the macroinfauna individuals were picked by hand. Sediment samples were collected from the syringe samplers by slicing the topmost layer (< 1 cm) of the sediment core. The abundance of epifauna and infauna (individuals per m^2 for the detritus accumulation habitat, or per *Fucus* individual for the canopy habitat, or per mesh bag for the in situ experiment) was calculated, and the animals were then stored in autoclaved and filtered (Ø 0.2 μm) seawater overnight to empty gut contents. The animals were then killed by freezing and washed with deionized water. The shell lengths of bivalves and gastropods were measured, and the wet weight of all other macrofauna was measured by laboratory scales. The dry weights were then estimated by using conversion equations proposed by Rumohr et al. (1987). For stable isotope analysis, the macrophyte and animal samples were stored at -20 °C in Eppendorf tubes.

Stable Isotope Analyses

The macrophyte material and macrofauna were freeze-dried for 2 days and homogenized with a ball mill. Homogenized samples were weighed with a microbalance (accuracy 0.001 mg) into tin cups. The stable isotopic compositions of carbon and nitrogen were measured on a NC2500 elemental analyzer coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer at the Laboratory of Chronology, Finnish Museum of Natural History, Helsinki. The raw isotope data were normalised with a multi-point calibration using certified isotopic reference materials (USGS-40, USGS-41, IAEA-N1, IAEA-N2 for N, and USGS-40,

USGS-41, IAEA-CH7 and IAEA-CH6 for C). The mean measured raw $\delta^{13}C$ and $\delta^{15}N$ values, respectively, for calibration references were -26.2 and -4.5 for USGS-40, $+36.7$ and $+46.7$ for USGS-41, $+0.6$ for IAEA-N1, $+20.1$ for IAEA-N2, -31.8 for IAEA-CH7 and -10.5 for IAEA-CH6. Replicate analyses of quality control reference materials analysed alongside the unknowns indicate a 1σ internal precision of ≤ 0.10 for $\delta^{13}C$ and ≤ 0.15 ‰ for $\delta^{15}N$. The results are expressed in the δ-notation ($\delta^{13}C$ or $\delta^{15}N$ in ‰ $= R_{sample}/R_{standard} \times 1000$, 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.

Statistical Analyses and Mixing Models

The distribution of sedimentary, macroalgal, and macroinvertebrate variables was first visually examined by Draftsman and histogram plot routines, and a 4th-root transformation was applied to avoid skewness of some of the data. Non-parametric multivariate analyses of variance (PERMANOVA) were run to detect significant changes in the abundance of the macrofauna associated with macroalgae in both the canopy and the detritus habitats (unrestricted permutation of raw data, Type III SS). We calculated distance resemblance matrices using Euclidean dissimilarity measures (4999 permutations). We used habitat (i.e., canopy and detritus) as a fixed factor and date (i.e., Jun17, Sep1,7 and May18) as a random factor for the monitoring study. For the mesh-bag experiment, changes in the abundance of the macroinvertebrate species were also analysed with PERMANOVA using depth (i.e., 3 and 6 m) as a fixed factor and time (i.e., t_{1-4}) as a random factor. Analyses were performed using PRIMER7 (Clarke and Gorley 2015).

For both studies, we used a dual-isotope (CN) approach and the Bayesian MixSIAR package (Stock et al. 2018) for R software (R Development Core Team 2019) to estimate the relative importance of different types of food sources. For epigrazer taxa, we performed a comparison between two food sources: (1) abundant ephemeral algae (*Pilayella* and/or *Ceramium* sp., clustering close together in terms of their $\delta^{13}C$ and $\delta^{15}N$ signatures), and (2) *Fucus*. For suspension feeders and omnivores, we also included a combined food source of pelagic particulate organic matter and dissolved organic matter (POM/DOM) as a third potential food source (stable isotope data obtained from Kahma et al. 2020, where we concluded that the sampled POM was mainly of autochthonous origin). Our previous study reports great spatial variabilities of *F. vesiculosus* $\delta^{13}C$ and $\delta^{15}N$ signatures in the study area (Kahma et al. 2020 and Fig. 2). To calculate the MixSIAR models for the four abundant and mobile epigrazers (*Gammarus* sp., *Idotea balthica*, *Theodoxus fluviatilis*, *Lymnaea peregra*) of the monitoring study, we used raw stable isotope data
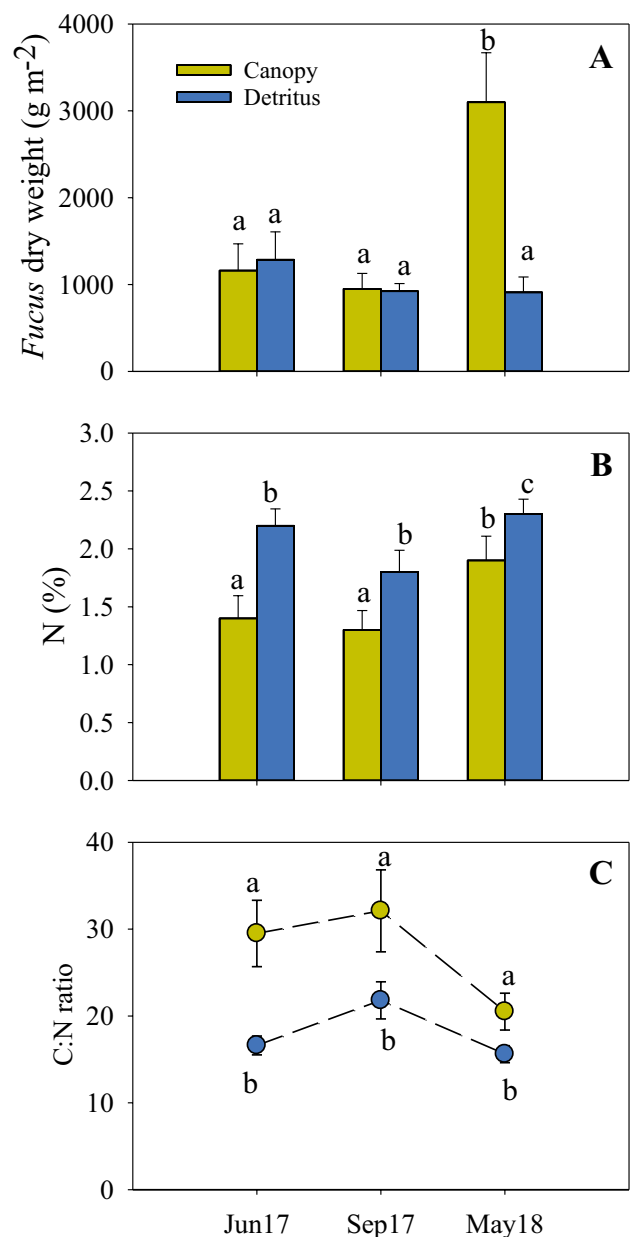

Fig. 2 Summary of the mean ($\pm$ SE) characteristics of *Fucus vesiculosus* across habitat sites (canopy vs detritus, fixed factor) and over time (June 2017, September 2017, May 2018; random factor) including algal dry weight (**A**), total nitrogen content (**B**) and C:N ratio (**C**). Different letters indicate significant differences across habitats (pairwise comparisons)

of the food sources from the whole period as a general estimate to take possible spatio-temporal source variability effect into account, i.e. single $\delta^{13}C$ and $\delta^{15}N$ observations of *Fucus* ($n=30$) and of *Pilayella* and *Ceramium* sp ($n=8$) were applied as an input data for the MixSIAR (Supplementary information Fig. S4). For the manipulated mesh bag experiment, mean ($\pm$SD) $\delta^{13}C$ and $\delta^{15}N$ values of all collected *Fucus* ($\delta^{13}C= -13.14\pm2.51$ ‰ and

$\delta^{15}N = 3.28 \pm 0.72$ ‰) and *Pilayella* ($\delta^{13}C = -20.1 \pm 1.4$ ‰ and $\delta^{15}N = 4.0 \pm 0.8$ ‰) samples were used as a general estimate for the MixSIAR (the $\delta^{13}C$ values of *F. vesiculosus* fell between approx. −12‰ to −16‰, and $\delta^{15}N$ values between 2‰ and 3.5‰ during the mesh-bag experiment, see the Supplementary information Table S5 for details). The mixing polygon fits were tested with the MixPolySim package by Smith et al. 2013.

For arthropod species (*Gammarus* sp., *Idotea balthica*, Chironomid larvae) and gastropods (*Theodoxus fluviatilis*, *Lymnaea peregra*), trophic enrichment factor (TEF) estimates (0.5 ± 0.13‰ for carbon and 2.3 ± 0.18‰ for nitrogen) based on a meta-analysis by McCutchan et al. (2003) were used in the absence of reported species-specific TEF values. For the facultative deposit/suspension-feeding clam *Macoma balthica*, traditional standard literature values of 0.8‰ for carbon and 3.4‰ for nitrogen (DeNiro and Epstein 1978; Fry 2006) were used, since according to Yokohama et al. (2005), the observed TEF values of infaunal clams were very close to them. For obligate suspension feeder *Mytilus trossulus*, previously reported TEF values of 2.2‰ (SD ± 0.44) for carbon and 3.8‰ (SD ± 0.76) for nitrogen were applied (Dubois et al. 2007). For *Hediste diversicolor*, reported species-specific values were applied, i.e. 1.57‰ (SD ± 2.28) for carbon and 5.01‰ (SD ± 1.24) for nitrogen (Kristensen et al. 2019). Two types of Mix-SIAR models were calculated for the consumer species: (1) models with species as a fixed variable and habitat/site as a random variable (both monitoring study and mesh-bag experiment), and for those species with a dataset big enough for the MixSIAR modelling requirements, we used (2) models with time as a continuous variable (mesh-bag experiment only).

Results

Monitoring Study on the Macrofauna Communities and Food Webs Associated with Macroalgae

A Description of the Canopy and Detritus Study Habitats

The abundance and height of *Fucus* individuals in the canopy-forming habitat were similar during our study, i.e. 40–47 cm and 17–18 fronds m^{-2} (Table 1). However, the depth of the accumulated algae covering the seafloor in the detritus habitat decreased significantly over time from 40 to 13 cm (Pseudo-$F_{2,21} = 18.62$; $p < 0.001$) (Table 1). A comparison between habitats showed that *Fucus* dry weight was significantly higher (Pseudo-$F_{2,42} = 4.47$; $p < 0.05$) in the canopy than in the detritus in May 2018, i.e. 3100 vs. 910 g m^{-2} (Table 1 and Fig. 2A). The total nitrogen (TN) content of the *Fucus* samples was significantly ($p < 0.05$) higher in the detrital than in the canopy habitats over time (Fig. 2B and Table S1). The C:N ratio was significantly ($p < 0.05$) lower (i.e., more decomposed) in the detritus habitat (Fig. 2C and Table S1). The $\delta^{13}C$ and $\delta^{15}C$ values of macrophyte and macrofauna species were quite constant across the sampling period, and the temporal variations within a species were approximately < 2.5‰ points (Table S4).

Macrofauna Community Dynamics

In total, eight macrofauna taxa were found associated with the canopy-forming *Fucus* (7) and the algal detritus (8) habitats (Table S2). In the detritus habitat, the temporal variability of the associated epifaunal community was more variable between the three sampling dates compared to the

Table 1 Summary of the main characteristics of *Fucus vesiculosus* (mean ± se) in the underwater canopy-forming habitat (rocky bed community) and depth of the algal accumulation in the sedimentary detrital pool habitat over one year (three sampling dates)

Characteristics	Canopy-forming habitat			Detritus habitat		
	June 2017	September 2017	May 2018	June 2017	September 2017	May 2018
Height (cm)	40.9(6.1)	46.7(10.0)	40.2(5.8)	-	-	-
Abundance (fronds m^{-2})	18(3)	17(3)	18(3)	-	-	-
Dry mass (g m^{-2})	1160.9(307.0)	949.9(178.4)	3099.4(569.7)	1285.3(321.2)	922.8(88.2)	909.3(177.1)
TC (%)	40.1(1.4)	38.5(1.4)	37.4(0.5)	36.5(0.5)	37.4(0.6)	35.1(0.4)
TN (%)	1.4(0.2)	1.3(0.2)	1.9(0.2)	2.2(0.1)	1.8(0.2)	2.3(0.1)
C/N	29.5(3.8)	32.1(4.7)	20.5(2.1)	16.6(1.1)	21.8(2.1)	15.6(1.0)
$^{13}\delta C$	−14.8(1.1)	−14.7(0.3)	−12.0(0.8)	−16.0(0.7)	−16.9(0.5)	−18.1(0.9)
$^{15}\delta N$	4.3(0.1)	5.3(0.2)	4.6(0.6)	5.6(0.2)	5.2(0.5)	5.4(0.3)
Depth algal accumulation (cm)[a]	-	-	-	40.4(6.0)	17.1(2.0)	12.8(0.8)
Temperature	11	14	9	11	14	9

[a]Mainly *F. vesiculosus* mixed with other species (see Table S4)

rocky *Fucus* canopy habitat, where the community was more stable (Fig. 3). Especially in Sep17, when the sampling was performed, an intensive accumulation of filamentous algal detritus (mainly *Ceramium tenuicorne*) was observed. As a response, high abundances of the epigrazers *L. peregra* and *Gammarus* sp. colonized the drifting detritus. The total macrofauna abundance was significantly higher in the detritus than in the canopy habitats only in Sep17 (Fig. 3A and Table 2). The community was dominated by a few species and their abundances were significantly different between habitats and over time (Fig. 3B and Table 2). For instance, *T. fluviatilis* was significantly more abundant in the canopy than in the detritus habitats on Sep17 and May18, *L. peregra* was more abundant in the detritus than in the canopy on Jun17 and Sep17, *Gammarus* sp. was more abundant in the canopy than in the detritus in May18, and *I. balthica* was significantly more abundant in the detritus in Jun17 and in the canopy in May18 (Fig. 3B and Table 2). The abundance of *M. trossulus* showed no significant differences (Table 2).

The Diet Compositions of the Main Epigrazer Macrofauna Species

The Bayesian MixSIAR diet models obtained from the stable isotope data (Table S4 and Fig. S3) showed variations for the main epigrazer species (i.e., *Gammarus* sp., *I. balthica*, *T. fluviatilis,* and *L. peregra*) in the two habitats across the sampling dates (Fig. 4). These variations differed between the habitat types. In the canopy site, the median dietary proportions of filamentous algae (*Pilayella* and *Ceramium* sp.) and *F. vesiculosus* fit within the 90% Bayesian credibility intervals across the sampling dates within each consumer species

(Fig. 4A), indicating non-significant differences between the dates. In contrast, larger dietary differences can be observed in September in comparison to the other sampling dates in the detritus site (Fig. 4B). Here, the median dietary proportion of filamentous algae was approx. 20–30% points higher than in June and May. In general, the amphipod *Gammarus* sp. tends to prefer filamentous algae (approx. 50–90% within the credibility interval of 90%) over *Fucus*, while the isopod *I. balthica* is less specialized in terms of algal preference (approx. 10–75% of filamentous algae and 25–90% of *Fucus* within the credibility intervals of 90%) and its diet was more variable over time in the detritus site. Of the gastropods, *L. peregra* highly prefers filamentous algae (approx. 55–95% within the credibility interval of 90%) over *Fucus*, but *T. fluviatilis* was less specialized (Fig. 4). When comparing the habitats, the median dietary proportions of *Fucus* are systematically approx. 5–10% points lower in the canopy habitat (Fig. 4A) than in the accumulation habitat (Fig. 4B) in June and May, and this observation concerns all species.

Mesh-Bag Degradation Experiment at Two Different Depths

Environmental Conditions at the Shallow and Deeper Sedimentary Sites

Water temperature was on average (mean ± se) similar between the shallow and deep (i.e., 14.6 °C ± 0.2) sites, ranging from 5.86 to 26.1 °C (shallow) and from 6.8 to 26.2 °C (deep) (Fig. S2). However, the mean temperature was higher in the shallow (11.5 °C ± 0.6) than in the deep (9.2 °C ± 0.2) sites during the first 10 days of the experiment
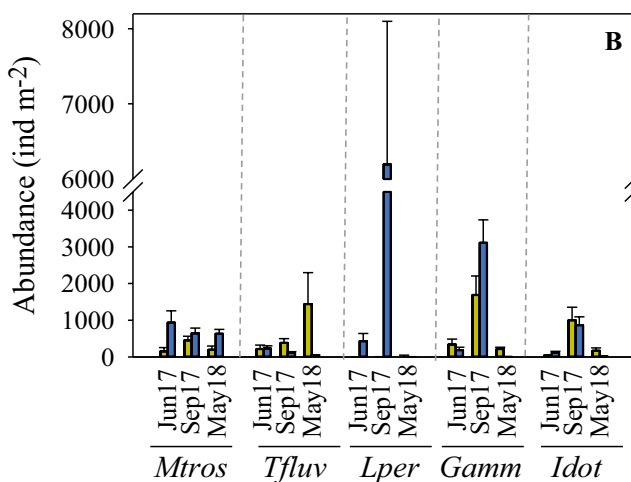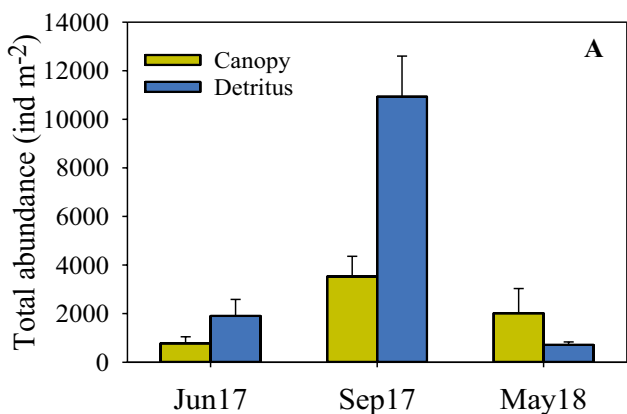

Fig. 3 Summary (mean ± SE) of the total macrofauna abundance and abundance of the dominant taxa (i.e. *Mytilus trossulus* (Mtros), *Theodoxus fluviatilis* (Tfluv), *Lymnaea peregra* (Lper), *Gammarus* sp. (Gamm), *Idotea* sp. (Idot) in the canopy and detritus sites over time

(June 2017, September 2017, and May 2018). See Table 2 for significant pairwise comparisons. For biomasses, see the supplementary information (Fig. S1)

Table 2 Results of PERMANOVA on the abundance (ind m^{-2}) of the macrofauna community (Fig. 3, total abundance and abundance of the main species: *Mytilus trossulus, Theodoxus fluviatilis, Lymnaea peregra, Gammarus* sp., and *Idotea* sp.) between habitat sites (canopy FC vs detritus DA; fixed factor) over three sampling dates (June 2017, September 2017, and May 2018; random factor). Significant interaction effects ($^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{+}$ $0.10 < p < 0.05$) were further investigated through pairwise comparisons

Source	df	Total		M. trossulus		T. fluviatilis		L. peregra		Gammarus sp.		Idotea sp.	
		MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F	MS	Pseudo-F
Habitat (Ha)	1	19.31	1.56	43.40	7.19	14.69	1.03	181.91	2.87	5.45	0.26	1.44	0.09
Date (Da)	2	60.91	23.40***	5.10	2.67^{+}	0.66	0.28	73.22	60.03***	83.10	42.15***	47.12	34.30***
HaxDa	2	12.40	4.76*	6.03	3.16^{+}	14.18	6.09**	63.33	51.92***	21.02	10.66***	16.75	12.30***
Res	42	2.60		1.91		2.33		1.22		1.97		1.36	
Total	47												
Pairwise comparisons													
HaxDa		Sep17:		n.s.		Sep17, May18:		Jun17, Sep17:		May18:		Jun17:	
		FC<DA				FC>DA		FC<DA		FC>DA		FC<DA	
												May18:	
												FC>DA	

(Fig. S2). Irradiance (i.e., light lux) was on average higher in the shallow site (1950 lx ± 135) compared to the deep site (30 lx ± 21), with maximum values of 26,178 lx in the shallow site and 3272.2 lux in the deep site (Fig. S2).

The C:N ratio of *Fucus* decreased significantly over time in both sites (Fig. 5A). This resulted from increasing total nitrogen contents of the algae (Table S6). However, there was a significant site × time interaction (Pseudo-F$_{1,3}$ = 2.57; $p < 0.05$). The C:N ratio was significantly lower in the deep than in the shallow sites at t$_2$ ($t = 2.04$; $p < 0.05$) (Fig. 5A). The C:N ratio decreased slightly faster in the deep site (t$_1$ vs t$_2$; $t = 3.59$; $p < 0.01$; slope = −4.87) compared to the shallow site (t$_2$ vs t$_3$; $t = 3.43$; $p < 0.05$; slope = −4.13) (Fig. 5A). The C:N ratio of *Pilayella* decreased significantly by the end of the experiment (Pseudo-F$_{1,3}$ = 21.98; $p < 0.001$) in both sites (Fig. 5B and Table S1).

Macrofauna Community Colonization and Succession

In total, nine macrofauna species were found associated with the mesh-bags in the shallow (5) and deep (9) sites (Table S5). Macroinfauna abundance was not significantly different between the controls and the sediment underneath the bags in any of the sites (Pseudo-F$_{1,64}$ = 4.38; $p = 0.132$). The colonization of the mesh-bags was very fast in both sites (Fig. 6). Over time, with increasing *Fucus* decay, there was a significant increase in the macrofauna abundance associated with the mesh-bags in both sites (Table 3). The average abundance was significantly higher in the deep (mean N > 180 individuals per bag) compared to the shallow (mean N > 20 individuals per bag) sites due to the abundance of *M. trossulus* (Fig. 6 and Table S5).

The colonization response was different between sites (Fig. 6B, C and Table 3). At the shallow site, the amphipod *Gammarus* sp. was the fastest and most abundant colonizer (mean N ranging from 17 to 29 individuals per bag between t$_1$ and t$_3$) of all the species, followed by *Idotea* sp. (mean N = 4 at t$_2$) and *M. balthica* (mean N < 7 at t$_3$) (Fig. 6B and Table 3, S5). In the deep site, the blue mussel *M. trossulus* was the most abundant species (mean N ranging from 57 to 344 individuals per bag between t$_1$-t$_3$), followed by *Gammarus* sp. (N > 50 at t$_3$), *T. fluviatilis* (N > 25 at t$_3$) and *Idotea* sp. (N > 12 at t$_2$) (Fig. 6C and Table 3, S5). In addition to epifauna, also the infaunal clam *M. balthica* (more abundant in the deep site) and polychaete *Hediste diversicolor* (only in the deep site) were present under the decomposing algae (Table S5). At the end of the experiment (t$_4$), some of the *Fucus* bags were also colonized by Chironomid larvae (Table S5).
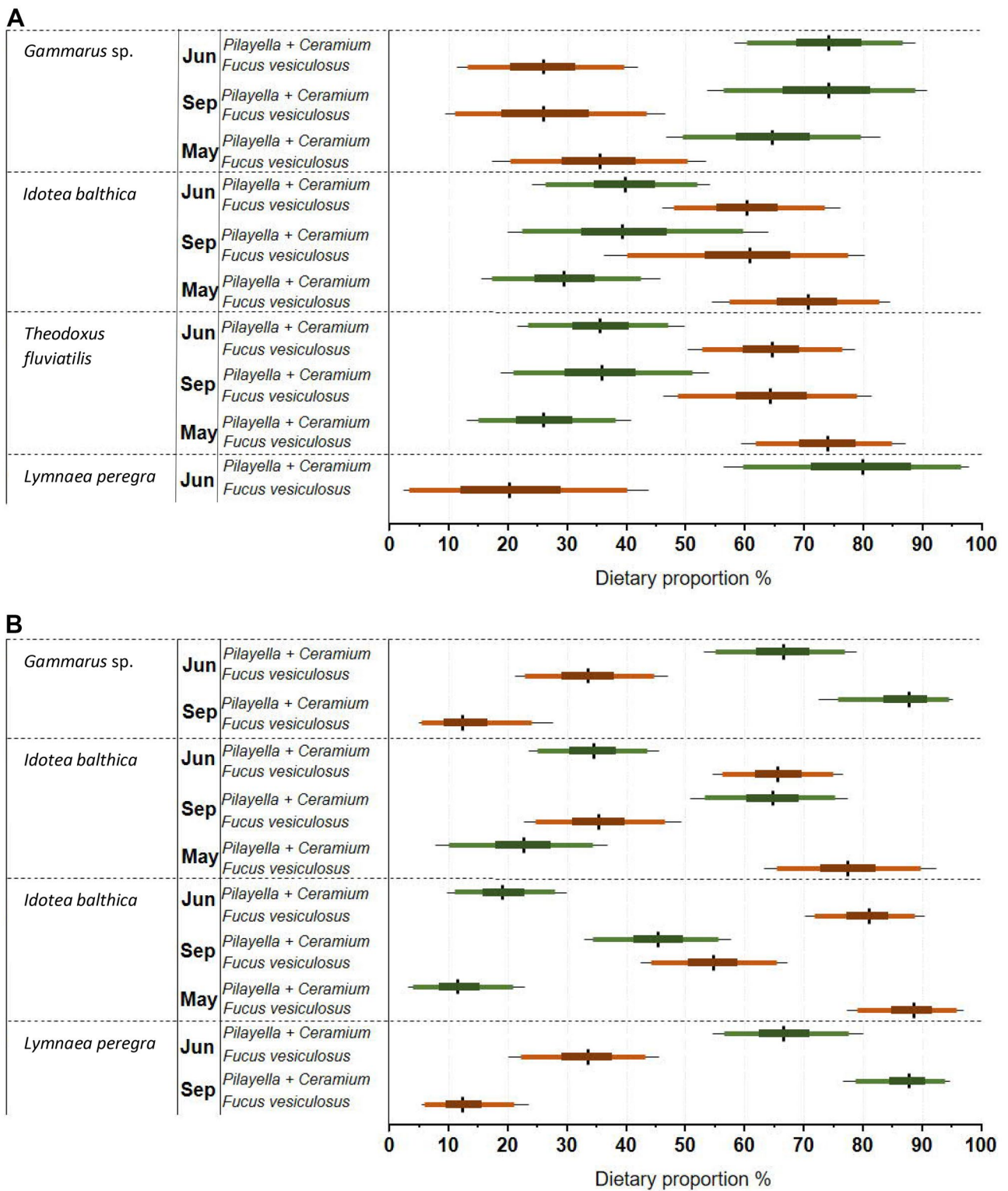
Fig. 4 Median proportions of *Fucus vesiculosus* (brown) and filamentous algae (*Pilayella littoralis* and *Ceramium* sp.; green) in the diet of four main epigrazer species (*Gammarus* sp., *Idotea balthica*, *Theodoxus fluviatilis* and *Lymnaea peregra*) in the canopy site (**A**) and detritus site (**B**) over time (June 2017, September 2017, and May 2018). Bayesian credibility intervals (50%, 90% and 95%) are presented
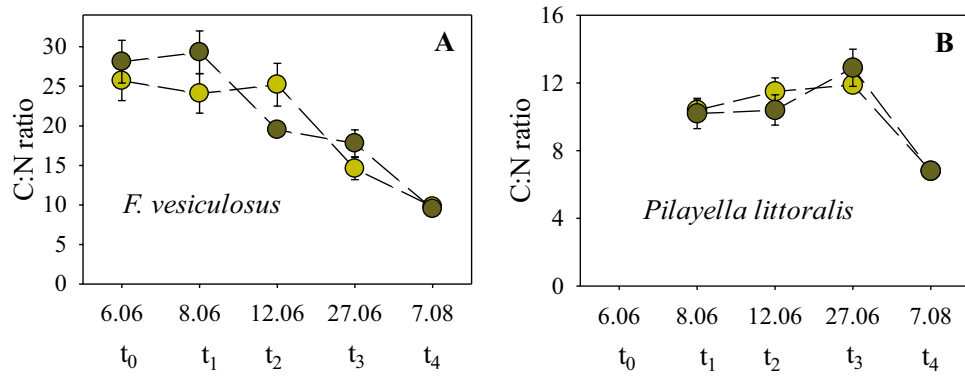
Fig. 5 Mean (±SE) of C/N ratios of *Fucus vesiculosus* (**A**) and *Pilayella littoralis* (**B**) over time (sampling dates, t1-t4; random factor) at the shallow ( ) and deep ( ) sites (fixed factor) in the field mesh-bag experiment. The ephemeral algae *P. littoralis* colonized quickly (t^1) the mesh-bags. Regression equations for *F. vesiculosus* at the shallow ($Y = 28.14–4.13X$; $p < 0.05$, $R^2_{adj} = 0.752$) and deep ($Y = 30.58–4.87X$; $p < 0.05$, $R^2_{adj} = 0.865$) sites. The C:N ratio values for fresh *F. vesiculosus* individuals are showed in t^0

Diet Composition Models for the Main Macrofauna Species

As a general observation, the average MixSIAR models for the whole mesh-bag experiment indicate that the median proportions of *Fucus* (i.e. the dietary contribution) were higher at the shallow (3 m) site inside the lagoon than at the deep (6 m) site outside the islets (Fig. S4). Correspondingly, the dietary contribution of *Pilayella* to the macrofaunal species was higher in the deep site than in the shallow site (Fig. S4). This difference is roughly between 10 and 40% points, depending on the consumer species in question (Fig. S4). The largest difference (~35% points) was observed for *I. balthica* with a 65% median dietary contribution of *Fucus* in the shallow site, but only 28% in the deep site. *Gammarus* sp. showed a higher preference for *P. littoralis*

(> 65%) in both sites (Fig. S4). The difference between sites with *T. fluviatilis* is of the same magnitude as that of *I. balthica* (~35% points), but with a preference for *Pilayella* in the shallow site (83%), and for *Fucus* in the deep site (52%). Another gastropod *L. peregra*, with observations only from the deep site, highly preferred *Pilayella* (> 95%).

The obligate suspension feeder bivalve *M. trossulus* showed a higher contribution of *Fucus* in the shallow site (18%) compared to the deep site (7%), but as an obligate suspension feeder, its diet mainly consisted of pelagic material (> 65%, pelagic POM/DOM) in both sites (Fig. S4). The facultative suspension-deposit feeder clam *M. balthica* shows equal dietary proportions (45%) of pelagic POM/DOM and *Pilayella* (which might also contain sedimentary MPB due to close δ^{13}C and δ^{15}N signals, Table S5), while the proportion of *Fucus* was
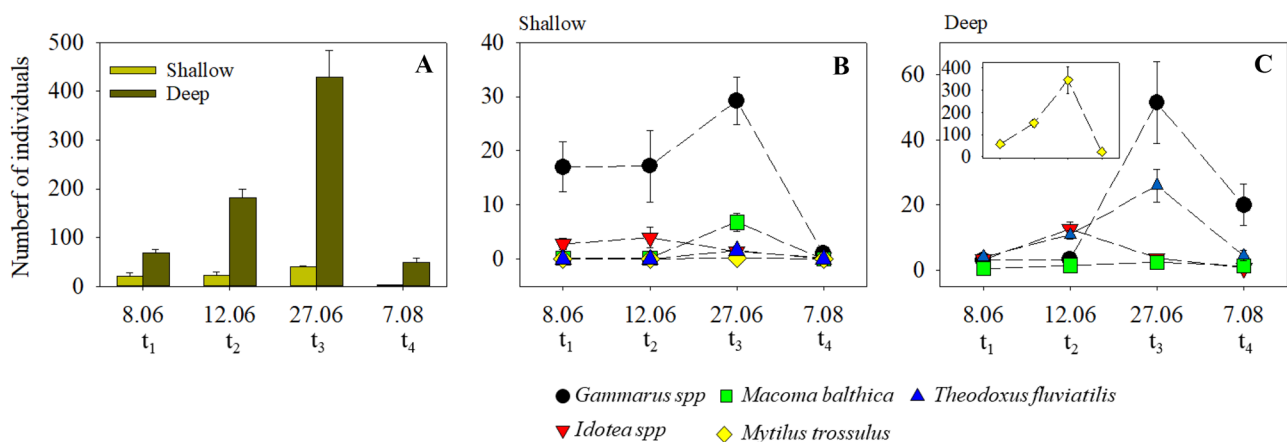

Fig. 6 The total number of macroinvertebrates (mean ± SE) in the shallow and deep sites (**A**) and the abundance of the dominant species in the shallow (**B**) and deep (**C**) sites per bag over time (sampling dates, t^1-t^4 2018) (Table S5). The number of individuals is a composite of the epifauna associated with the algae within the mesh bag and the macroinfauna (benthic core) living in the sediment under the bag. See Table 3 for significant pairwise comparisons. The first sampling date (t^1) occurred 2 days after the experimental set-up (from 06.06.2018 to 08.08.2018), and the last sampling date (t^4) occurred 64 days later (07.08.2018)

Table 3 Results of PERMANOVA on the abundance of the main macroinvertebrates found at two depth sites (Fig. 6, shallow vs deep, fixed factor) over four sampling dates (t_1-t_4; random factor). Permutations (4999) of residuals under unrestricted permutation of raw data (SS Type III, SS) were based on Euclidean distances. Significant effects ($^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^+$ $0.10 < p < 0.05$) were investigated through pairwise comparisons

		Source				
		Site (Si)	Date (Da)	SixDa	Residuals	
	df	1	3	3	32	Pairwise comparisons
Total abundance	MS	21.11	13.56	2.03	2.50	Shallow ≠ Deep (over time)
	Pseudo-F	31.2**	57.90***	8.66***		Shallow: $t_1 = t_2 = t_3 \neq t_4$; $t_1 \neq t_3$
						Deep: $t_1 = t_4 \neq t_3 \neq t_2$
Gammarus sp.	MS	0.05	2.32	2.44	0.22	Shallow ≠ Deep (t_1, t_2, t_4); Shallow = Deep (t_3)
	Pseudo-F	0.02	10.76***	11.31***		Shallow: $t_1 = t_2 = t_3 \neq t_4$
						Deep: $t_1 = t_2 \neq t_3 = t_4$
Idotea sp.	MS	2.20	2.03	0.29	0.21	
	Pseudo-F	7.72	9.64***	1.36		
Mytilus trossulus	MS	87.96	1.71	2.62	0.17	Shallow ≠ Deep (over time)
	Pseudo-F	33.63*	10.33***	15.80***		Shallow: $t_1 = t_2 = t_3 = t_4$
						Deep: $t_1 \neq t_2 \neq t_3 \neq t_4$
Theodoxus fluviatilis	MS	21.39	1.77	0.14	0.06	Shallow ≠ Deep (over time)
	Pseudo-F	158.2**	28.54***	2.18		
Macoma balthica	MS	0.47	3.00	0.58	0.19	Shallow = Deep (t_1, t_2, t_4); Shallow ≠ Deep (t_3)
	Pseudo-F	0.89	15.47***	3.01*		Shallow: $t_1 = t_2 = t_4 \neq t_3$
						Deep: $t_1 \neq t_3$

approx. 10% (Fig. S4). The polychaete *H. diversicolor* showed a diet composition characteristic of an omnivore with median proportions between 25 and 35% for all three food sources included (Fig. S4). Finally, the small dataset for the Chironomid larvae indicated negligible dietary differences between the sites (Fig. S4).

Across the 2-month mesh-bag experiment, the MixSIAR models using time as a continuous variable indicated an increasing trend of median dietary proportions of *Fucus* for all the observed consumer species and sites, while the incorporation of *Pilayella* decreases simultaneously (Figs. 7 and 8). This trend can be observed with both epigrazers in both depths (Fig. 7) and bivalves (Fig. 8), despite different feeding behaviours. For *Gammarus* sp., the incorporation of *Fucus* into its diet was notably faster in the shallow site than in the deep site (Fig. 7). In the deep site, *T. fluviatilis* showed a rapid dietary increase of *Fucus* at the end of the experiment (Fig. 8). The highest dietary contributor of the bivalves *M. trossulus* and *M. balthica* was pelagic POM/DOM, of which median dietary proportion shows a slightly increasing trend across the time (Fig. 8). The bivalves showed a slight increasing diet contribution of *Fucus* over time, while the proportion of *Pilayella* contributing to the diet of the bivalves decreased (Fig. 8).

Discussion

Variability of Fucus-Associated Macrofauna Communities in Natural Habitats

In the Baltic Sea, perennial macroalgae, like *Fucus*, compete with short-lived filamentous algae (Kiirikki and Lehvo 1997). In our study location, *Fucus* is the biomass dominant macrophyte producer, and similarly to larger kelps in oceanic systems (Pessarrodona et al. 2018; Pedersen et al. 2020), we observed large amounts of detached *Fucus* drifting to adjacent habitats, complemented by a seasonal export of filamentous algae (mainly *Ceramium tenuicorne*) in Sep17. The variable pulses of detrital food subsidy from the *Fucus*-canopy site can explain here the hypothesized inter-habitat differences and the more variable community structure of the associated macrofauna in the detritus accumulation site. It has also been previously reported (Saarinen et al. 2018) that *Ceramium* sp. hosts higher epifaunal abundances compared to other macroalgal species in the Baltic Sea. This is in line with our observation that in the detritus site in Sep17, high abundances of the epigrazers *L. peregra* and *Gammarus* sp. colonized the *Ceramium* detritus.
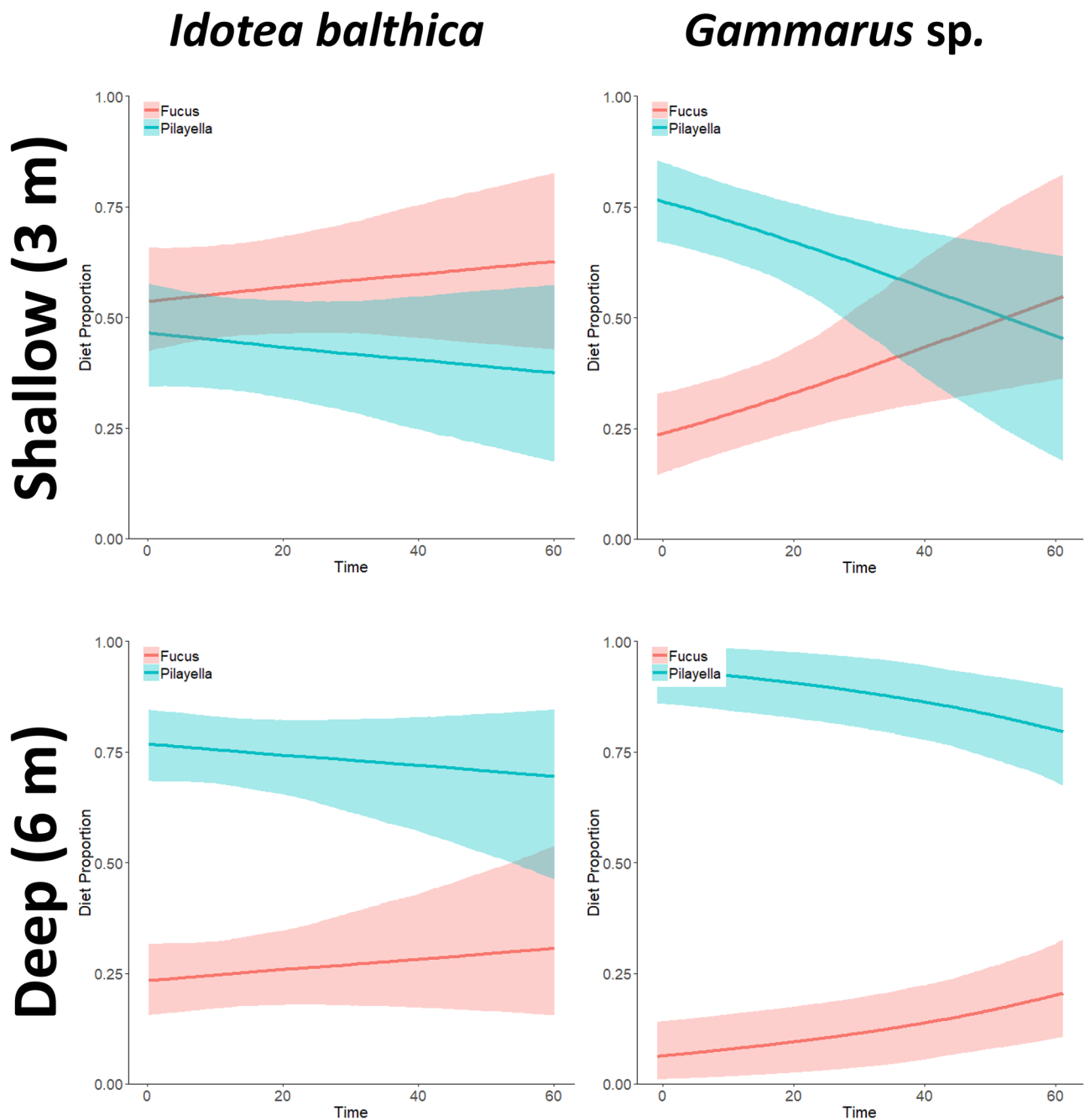
Idotea balthica

Gammarus sp.

Fig. 7 Bayesian continuous variable models showing the median dietary proportions of *Fucus vesiculosus* (red) and *Pilayella littoralis* (blue) in the diets of epigrazer arthropods *I. balthica* and *Gammarus* sp. as a nonlinear function of the 2-month incubation time in the shallow (3 m) and deep (6 m) sites. The colored fades indicate the Bayesian 95% credibility intervals

Macrofauna Feeding Preferences and Macroalgal Dietary Contribution in Natural Habitats

The general interspecific differences in the MixSIAR dietary models for the main epigrazer species reflect the variability of the species-specific feeding preferences in the two habitats. Previous studies in the Baltic Sea have reported that *Gammarus* spp., *I. balthica* and *L. peregra* prefer filamentous algae over *Fucus* (Jormalainen et al. 2001; Goecker and Kåll 2003; Kahma et al. 2021), while *T. fluviatilis* can consume both micro- and macroalgae (Råberg and Kautsky 2007; Korpinen et al. 2008). Our MixSIAR models indicated that *L. peregra* and *Gammarus* sp. highly prefer filamentous algae in both habitats. The dietary preference of *T. fluviatilis* for *F. vesiculosus* is similar to our previous observations from the same area (Kahma et al.
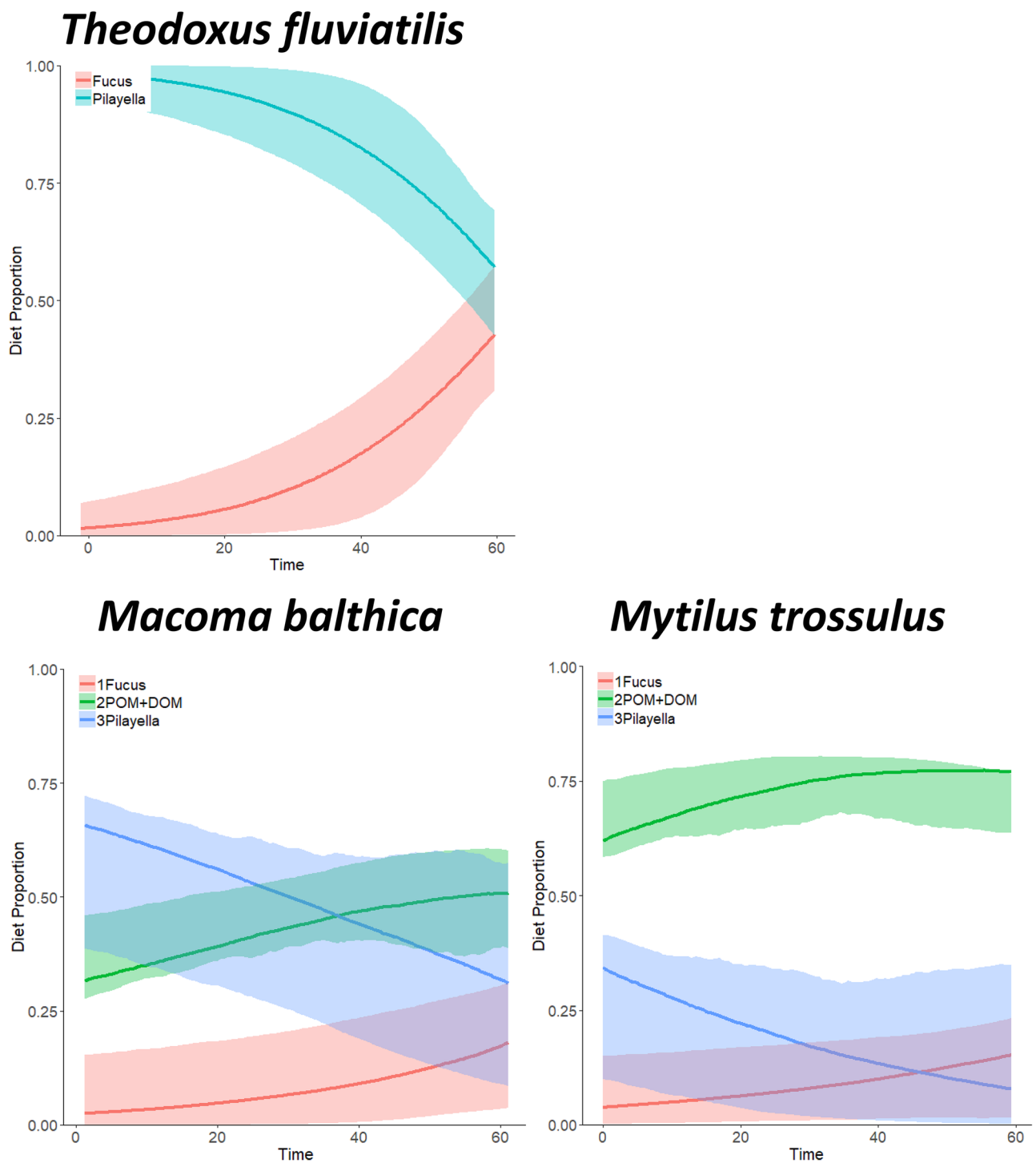
Fig. 8 Bayesian continuous variable models showing the median dietary proportions of *Fucus vesiculosus* (red), *Pilayella littoralis* (blue) and pelagic POM/DOM (green) in the diets of *T. fluviatilis*, *M. bal-thica* and *M. trossulus* as a nonlinear function of the 2-month incubation time in the deep (6 m) site. The colored fades indicate the Bayesian 95% credibility intervals

2021), but it should be mentioned that we did not sample epiphytic microalgae as a potential food source (Råberg and Kautsky 2007).

The observed greater dietary variations over time in the detritus accumulation habitat might likely result from larger variability of the food sources available over time. The

results might indicate that seasonal accumulations of filamentous algae can be rapidly incorporated into the associated food webs through epigrazers. However, another explanation here could be that in Sep17, the epigrazer community was probably more dominated by juvenile individuals, preferring palatable filamentous algae over *F. vesiculosus*.

Although the diets of the epigrazer fauna were variable over time in both sites, our models consistently indicate slightly (< 10% points) higher median dietary contributions of *Fucus* in the detritus site in June and May, compared to their diets in the *Fucus*-canopy site. As hypothesized, this observation is likely related to the better palatability of the partly decomposing algae compared to fresh canopies. The lower C/N ratio and higher total nitrogen content of decomposed macroalgae increases its nutritional value and palatability (Cruz-Rivera and Hay 2000; Norderhaug et al. 2003; Pedersen et al. 2021), which was observed with *Fucus* in the detritus site and explains these results (Fig. 2B, C and Table S1). Although grazer species are mobile and can feed on both fresh and degrading material, the palatability of detached and degrading *Fucus* is presumably better due to the loss of phytochemicals acting as deterrents (Amsler 2001; Norderhaug et al. 2003; Jormalainen and Ramsay 2009; Rodil et al. 2015; Pedersen et al. 2021) reducing assimilation efficiency of fresh algal tissue (Jormalainen et al. 2005). This likely explains our observation that grazer individuals colonizing the drifting and degrading *Fucus* material tend to show higher incorporation of *Fucus* compared to individuals associated with *Fucus* canopies.

Mesh-Bag Field Experiment

Fucus vesiculosus Degradation and Macrofauna Colonization Response

The decreasing C/N ratio of *Fucus* during the mesh-bag experiment (Fig. 5A) indicates that the degradation process of *Fucus* started immediately and continued through the controlled experiment simulating the natural algal degradation process (e.g. Rice and Tenore 1981; Krumhansl and Scheibling 2012; Dethier et al. 2014; Bettignies et al. 2020). Increasing total nitrogen content over time might have indicated here a microbial colonization and increasing nutritional value (Duggins and Eckman 1997; Norderhaug et al. 2003). Although we did not include ephemeral *Pilayella* in the experiment, a continuous export of detached fresh *Pilayella* colonized the mesh-bags during the experiment, except for the last sampling date, when the C/N ratio decreased dramatically indicating a high degradation process of this opportunistic species (Fig. 5B). It is likely that different environmental factors (i.e. temperature, light, exposure to currents) characterizing the contrasting shallow and deep sites have affected the colonization. The proximity of the *Fucus*-canopy habitat to the shallow site inside the lagoon can also explain the faster colonization of the mobile amphipod *Gammarus* sp. in the mesh-bags from the shallow site. The typically sessile blue mussel *M. trossulus*, which colonized the algae in great numbers in the deep site, was most likely transported via currents.

Dietary Differences Between Macrofauna Species at Different Depths

The dietary proportions of *Fucus* in *Gammarus* sp. and *I. balthica* were higher inside the shallow lagoon than in the deep site, which might be related to the proximity of fresh *Fucus* canopy habitat, since the C/N ratios (Fig. 5A) indicated only small differences in decomposition processes between the sites. The lower photosyntetic activity of *Fucus* has been reported to increase the grazing activity of *Gammarus* sp. and *I. balthica* (Kotta et al. 2006), but our results from the deeper site with lower light conditions (Fig. S2) are contrasting. In the shallow site, their diets were close to the monitoring study (Fig. 4). The contrasting observation that *I. balthica* showed a high (> 70%) preference over *Pilayella* in the deep site, in contrast to the shallow site, where the proportion of *Fucus* was the highest, seems to be in line with previous studies in the Baltic Sea. According to Jormalainen et al. (2001), *I. balthica* shows a variable feeding behaviour on different macroalgae species, and its dietary preferences do not necessarily depend on the phytochemical contents of its food. The resulting loss of deterring phytochemicals due to degradation might explain *I. balthica* preference for *Fucus* in the shallow site compared to the deep site (e.g. Jormalainen and Ramsay 2009; Rothäuser et al. 2017), but on the other hand, the C/N ratios (Fig. 5A) do not necessarily support this. Measuring the contents of deterring phytochemicals would have provided more information in this case.

Similar to the monitoring study (Fig. 4), the gastropod *L. peregra* preferred *Pilayella* in the controlled experiment (Fig. 7). The gastropod *T. fluviatilis* showed high (35% points) dietary differences between sites, but it should be noted here that the dataset from the shallow site is too small for reliable conclusions (only one observation occasion at t₃). The bivalves *M. trossulus* and *M. balthica* showed quite similar dietary proportions as our previous studies from the area report (Kahma et al. 2020, 2021), but the higher (15–20%) *Fucus* proportion of *M. trossulus* in the shallow habitat might indicate the proximity of the productive *Fucus*-canopy habitat with a large detrital carbon export potential (Attard et al. 2019a).

Food Incorporation Over Time

In general, ephemeral algae show faster degradation rates compared to large perennial macroalgae (Rice and Tenore 1981; Dethier et al. 2014; Conover et al. 2016; Bettignies et al. 2020). In our mesh-bag experiment, *Fucus* degraded constantly over time (i.e. decreasing C/N ratio, Fig. 5A). The ephemeral algae *Pilayella* instead, seemed to be freshly settled for most of the time, although at the end of the experiment, its C/N ratio showed signals of degradation (Fig. 5B). In our experiment, the increasing incorporation of *Fucus* to the diets of the consumer fauna during the experiment mirrored the gradual degradation of the algae (Figs. 7 and 8).

We have comparative MixSIAR models between the two different depths only for *Gammarus* sp. and *I. balthica* due to the lack of enough replicates (Fig. 7). The amphipod *Gammarus* sp. seemed to greatly benefit from decomposing *Fucus* in the shallow site since the median dietary proportions of the two algae species overlapped and switched at the end of the experiment. Similar observations have been reported by Norderhaug et al. (2003) with decomposing oceanic kelp (*Laminaria*). For the isopod *I. balthica*, the consumption of *Fucus* matter showed increasing trends over time in both sites, but the slopes were more similar between the sites than those of *Gammarus* sp. Although the C/N ratios of *Fucus* showed only slight differences between depths (Fig. 5A), the changes in median dietary proportion for both species over time were a bit steeper in the shallow (3 m) than in the deep (6 m) sites (Fig. 7). These differences might be explained by the higher C/N ratio of *Fucus* in the deep site at the beginning of the experiment, as well as by the lack of fresh *Fucus* canopies nearby. In the deep site, the rapid dietary switch to *Fucus* with gastropod *T. fluviatilis* (Fig. 8) likely relates to its specific functional anatomy and physiology (e.g. lack of cellulase, see Neumann 1961), since at the end of the experiment, *Fucus* was softened (Fig. 1C) and become potentially more palatable for *T. fluviatilis*.

With the bivalves *M. trossulus* and *M. balthica*, the temporal trends of the different food source proportions across the experimental period (Fig. 8) indicated ingestion of some fine-sized detrital *Fucus* matter from the water column (Duggins and Eckman 1997; Maloy et al. 2013; Navarro et al. 2016), especially when *Fucus* had degraded significantly by the end of the experiment and became more palatable due to high nitrogen content and loss of polyphenolic compounds (Duggins and Eckman 1997; Pedersen et al. 2021). However, the diet proportion differences show their specific feeding behaviour. As an obligate suspension feeder, *M. trossulus* is highly dependent on the pelagic component, while *M.balthica* can switch its feeding mode to deposit feeding (Ólafsson 1986). It should be noted here that the food source *Pilayella* might include sedimentary organic matter as well since their δ^{13}C and δ^{15}N values were overlapping (Table S6).

Conclusions and limitations

Degradation of *F. vesiculosus* increased its dietary incorporation to associated consumer fauna, but a degradation process of at least several weeks is required before the incorporation starts to show changes in natural environments. Thus, the ecological significance of *Fucus*-derived food subsidy might be especially important in deeper accumulation areas allowing the detached algae decay for periods of several months (Filbee-Dexter and Scheibling 2016). However, also in shallow and warmer coastal areas of the Baltic Sea, where the degradation of large-sized *F. vesiculosus* occurs at faster speeds compared to deep offshore areas, its ecological importance as a food subsidy could be higher. In our field experiment, the two depth levels (3 m vs. 6 m) were relatively shallow, and further studies at greater depths (> 30 m in the Baltic Sea) would be necessary to understand the food web incorporation and sedimentary burial of *Fucus*-derived detrital matter and evaluate its potential role in marine carbon sequestration and the global carbon budget in the Baltic Sea (Buck-Wiese et al. 2022).

Despite using the best possible TEF approximations available (see the "Statistical analyses and mixing models" section), our Bayesian mixing models might include some uncertainties resulting from the determination of TEF values of the consumer fauna (Bond and Diamond 2011). Several possibilities for determining the TEF values have been proposed (e.g. McCutchan et al. 2003; Nadon and Himmelmann 2006; Caut et al. 2009; Phillips et al. 2014), underlining the need of futher research on this topic.

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