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The effect of *Fucus vesiculosus* on the grazing of harpacticoid copepods on diatom biofilms

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ABSTRACT

The effect of *Fucus vesiculosus* on the functional traits of three harpacticoid copepod species (*Tigriopus brevicornis*, *Paramphiascella fulvofasciata* and *Microarthridion littorale*) was studied. These copepods are likely to be important grazers on biofilms consisting mainly of diatoms. Several microcosms were created using diatom cultures (*Navicula phyllepta* and *Seminavis robusta*) and vegetative thalli of *Fucus*, with the biofilm associated, collected from the field. The diatoms were enriched in the stable carbon ¹³C to facilitate tracing in the harpacticoids. The biofilm on the *Fucus* was labeled through impregnation of the *Fucus* leaves in ¹³C enriched seawater.

In all treatments a measurable uptake of diatoms was found for the three copepod species. All copepods showed a low uptake of labeled material when only *Fucus* thalli were available. The grazing on the benthic diatoms was negatively affected by the presence of the *Fucus* thalli in the case of *P. fulvofasciata*. One species, *T. brevicornis*, grazed efficiently both on sedimentary and epiphytic biofilms.

We hereby proved experimentally that benthic harpacticoid copepods are able to switch their food uptake under different habitat/food circumstances. This variety of food uptake is an illustration of the so-called 'niche complementarity effect' that lies at the basis of diverse communities.

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1. Introduction

Local biodiversity is strongly supported by niche complementarity among sympatric species (Bond and Chase, 2002). This model assumes that each species possesses certain traits that allow them to utilize available resources differently (Tilman et al., 1997; Loreau, 1998; Tilman, 1999). A clear niche differentiation thus results in the partitioning of resources by a high variety of species in order to avoid competition and maintain local diversity.

Although 'the niche complementarity effect' has often been discussed in recent biodiversity-ecosystem functioning studies (e.g. Duffy et al., 2001; Bond and Chase, 2002), an unambiguous understanding of whether and how the niche complementarity is accomplished between species is lacking. Especially in the marine environment, which is often regarded as a rather open and homogenous ecosystem, niche segregation is not always well understood. De Troch et al. (2003) demonstrated a clear niche separation among benthic harpacticoid copepods in the sediment of tropical seagrass beds, supporting a high species diversity in the community. Harpacticoid copepods are known as a diverse group of marine invertebrates occurring in a wide variety of habitats (Hicks and Coull,

1983; Huys and Boxshall, 1991). Based on their occurrence in marine habitats, the majority of free-living copepod species can be characterised as either benthic (occurring in the sediment) or epiphytic (found in close association with macroalgae, seagrasses). Both substrate preferences are often reflected in the habitus shape with benthic species being rather slender and vermiform while their epiphytic counterparts can be strongly flattened (dorsoventrally or laterally). Next to differences in habitus (see Remane, 1952 for more 'Lebensformtypen') and habitat preferences, one might expect different use of available resources (e.g. food). After all, the accessibility of these resources may be linked to the three-dimensional structure of the habitat.

Habitat structure is often a good predictor of the body size of associated organisms (e.g. Gee and Warwick, 1994) because of constraints imposed on organisms' access or movement (Hacker and Steneck, 1990; Yang, 2000). Nevertheless, the responses of organisms to habitat structure are not necessarily predictable from its architectural properties alone (Gutiérrez and Iribarne, 2004).

In this study, we tested whether the presence/absence of macroalgae affects the food uptake of harpacticoid copepods as grazers on biofilms. The primary producers were made available in the form of a diatom biofilm on the bottom of the experimental vessel (benthic biofilm) and/or on *Fucus vesiculosus* leaves (thalli) (epiphytic biofilm). As the community of harpacticoids are often highly diverse

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Fig. 1. The various applied treatments (from left to right): epiphytic labeled biofilm on *Fucus* (E*), labeled epiphytic biofilm and unlabeled benthic biofilm (E*B), unlabeled epiphytic biofilm and labeled benthic film (EB*), labeled benthic biofilm (B*). (* = ^{13}C labelled).

and well-adapted to their habitat, we assessed whether the uptake of diatoms by the grazers would change according to structural differences in the environment. This was tested for three harpacticoid copepod species: *Paraphysocella fulvofasciata*, *Microarthridion littorale* and *Tigriopus brevicornis*. This last species spends considerably more time in the water column (pers. observ.) as compared to the other two, benthic, species. We investigated whether there are species-specific responses in grazing activity due to the presence of *Fucus* thalli.

2. Materials and methods

2.1. Laboratory conditions and labeling technique

Three intertidal harpacticoid species common in temperate coastal systems were cultured in the laboratory: the epiphytic species *Tigriopus brevicornis* (family Harpacticidae, collected from *Fucus vesiculosus*, Audresselles, North of France) and two benthic species, *Paraphysocella fulvofasciata* (family Miraciidae (former family Diosaccidae), collected from German intertidal mudflats) and *Microarthridion littorale* (family Tachidiidae, collected from the Paulina intertidal flat, SW Netherlands). Stock cultures of these copepods were stored in glass beakers filled with 1 l of artificial seawater (c. 32 psu, Instant Ocean® salt, Aquarium Systems, France) and were regularly provided with a mixture of (unlabeled) diatoms and detrital matter.

Monoclonal cultures of two benthic diatom species, *Navicula phyllepta* and *Seminavis robusta*, were used in the present investigation. The clone of *Navicula* was established by isolating a single cell from a sample collected at Paulina, SW Netherlands (51°21'N, 3°43'E). The culture of *Seminavis* represented the F1 progeny which was obtained experimentally, after a cross of two natural clones (clone 75 and 88 in Chepurnov et al., 2002) sampled previously in Veerse Meer, SW Netherlands. The cultures were grown in f2 medium (seawater with additional nutrients and trace elements, see Guillard, 1975) and enriched with ^{13}C by replacing $\text{NaH}^{12}\text{CO}_3$ with $\text{NaH}^{13}\text{CO}_3$ when preparing the f2 medium. For this, 5 ml of a stock solution of 336 mg $\text{NaH}^{13}\text{CO}_3$ in 100 ml milliQ H_2O was added per 100 ml of the culture medium. These diatom cultures were inoculated into the labeled medium and then grown during 10 days before the start of the experiment in a 12 h/12 h light/dark regime. This enrichment resulted in isotope signatures ($\delta^{13}\text{C}$), for untreated and ^{13}C enriched cultures respectively, of -6% and 5361% for *N. phyllepta* and of -16% and 2846% for *S. robusta*. Afterwards, the labeled culture medium was gently washed away and replaced by artificial seawater prior to the experiments.

Fresh fragments of *Fucus vesiculosus* thalli (further referred to as *Fucus*) were collected on November 17, 2004 at low tide from different stations at the Paulina intertidal flat in the Westerschelde Estuary, SW Netherlands. In the laboratory, the thalli were impregnated in artificial

seawater (c. 32 psu) with $\text{NaH}^{13}\text{CO}_3$ added in the same concentration as for the diatom cultures (see above). The fragments of *Fucus* were kept under a constant light regime for 10 days (same conditions as for the diatoms) in order to incorporate ^{13}C into the biofilm on the thalli. This labeling technique resulted in an increase of $\delta^{13}\text{C}$ from -5% (before labeling) to 297% (at the start of the experiment) as was measured from small pieces (on average $2000\ \mu\text{g C}$) of *Fucus* thallus and its associated biofilm. The *Fucus* fragments were gently washed in artificial seawater before the transfer to the experimental units in order to remove the non-incorporated label.

Copepods were sorted from the original stock cultures, starved overnight and washed in artificial seawater (to remove all food and faecal pellet particles) prior to placing them in the experimental units.

The experiments were conducted in glass jars (height=8 cm, diameter=7 cm, effective bottom surface= $38.5\ \text{cm}^2$) filled with 300 ml of artificial seawater (c. 32 psu). Copepods, diatom cultures and experimental units were kept in the same climate room at 15 to 18 °C under a light regime of 12:12 h light/dark.

2.2. Experimental design

In order to test the effect of *Fucus* on the grazing activity of three harpacticoid copepods 4 treatments were used (Fig. 1): labeled biofilm on *Fucus* (= 'epiphytic' biofilm) (E*), labeled biofilm on the bottom of the jar (= 'benthic' biofilm) (B*), labeled epiphytic biofilm on *Fucus* + unlabeled benthic biofilm (E*B), unlabeled epiphytic biofilm + labeled benthic biofilm (EB*), (* = ^{13}C labeled).

To estimate the number of diatom cells, the cultures were homogeneously suspended by shaking and then 50 μl of the cell suspension was transferred into a 96-well plate. In an hour, after all the cells had settled to the bottom of the well, cell densities were counted under a Zeiss Axiovert 135 inverted microscope (Zeiss Gruppe, Jena, Germany); the values obtained allowed an estimate of the densities in the experimental units. In the treatments with labeled diatoms (EB* and B*) a total of 13 million diatom cells (10 million of *N. phyllepta* and 3 million of *S. robusta*) were offered as food. In the treatment with unlabeled diatoms (E*B) a total of 16 million diatom cells was offered, (15 million of *N. phyllepta* and one million of *S. robusta*). Both densities were far above levels of food limitation (De Troch et al., 2005a). Diatom cells were homogeneously spread over the bottom of the jar prior to transferring the copepods in the jar.

At the start of the experiment, triplicate samples for each copepod species were put in the freezer for natural isotopic signature measurements (T_0 values). They had not been feeding on the labeled diatoms but on a mixture of unlabeled food and as such they are typically depleted in the ^{13}C stable isotope.

In order to achieve more diversity in the experimental unit, each replicate consisted of one jar containing all three copepod species. To detect $^{13}\text{C}/^{12}\text{C}$ ratios in the tissue of the harpacticoids, a minimum of 15 $\mu\text{g C}$ per species was analysed corresponding to 8, 20 and 20 adults

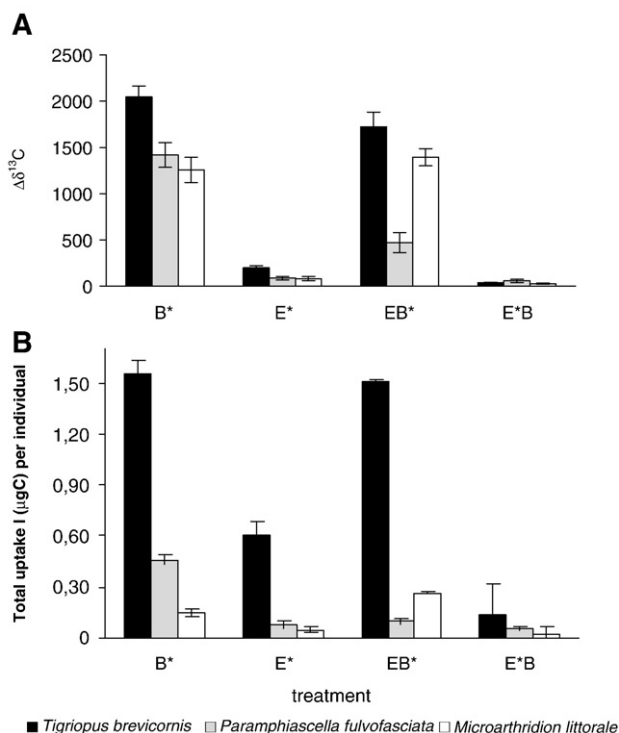


Fig. 2. Diatom uptake (mean±SE) by three harpacticoid copepods for the various treatments expressed as (A) $\Delta\delta^{13}C$ and (B) total uptake per individual relative to individual biomass.

of *Tigriopus brevicornis*, *Paramphiascella fulvofasciata* and *Microarthridion littorale* per replicate, respectively. Each treatment was replicated 5 times. As such, the complete experimental set-up consisted of 5×4 jars, placed randomly on one shelf in the climate room (Fig. 1).

2.3. Analytical technique and data treatment

The experiment lasted 4 days. Then all experimental vessels were immediately frozen at $-25^{\circ}C$. Afterwards, copepods were sorted manually, counted, washed several times in deionised water and transferred into tin capsules (8×5 mm, Elemental Microanalysis Limited) using a micro needle. The tin capsules containing the copepods and some water were desiccated at $60^{\circ}C$ for 12 h. Measurements of $\delta^{13}C$ values and copepod biomass (total carbon) were made using a continuous flow isotope ratio mass spectrometer (type Europa Integra) at the UC Davis Stable Isotope Facility (University of California, USA). The data are represented as $\Delta\delta^{13}C$ values, calculated as the difference between $\delta^{13}C$ values at the end of the experiment and the initial T_0 values (see before): $\Delta\delta = \delta_{\text{modified}} - \delta_{T0}$ values.

The obtained values of $\delta^{13}C$ were further standardised per individual copepod ($\mu g^{13}C$ per copepod) as recommended by Middelburg et al. (2000): incorporation of ^{13}C is reflected as excess (above background) ^{13}C , expressed as total uptake (I) in milligrams of ^{13}C per individual and calculated as the product of excess ^{13}C (E) and individual biomass (organic carbon). Excess ^{13}C is the difference between the fraction ^{13}C of the control (F_{control} , i.e. based on the natural signature of copepods that did not feed on labeled diatoms) and the sample (F_{sample}), where $F = \frac{^{13}C}{(^{13}C + ^{12}C)} = \frac{R}{R + 1}$. The carbon isotope ratio (R) was derived from the measured $\delta^{13}C$ values as $R = (\delta^{13}C / 1000 + 1) \times R_{VPDB}$ with $R_{VPDB} = 0.0112372$ as $\delta^{13}C$ is expressed relative to Vienna Pee Dee Belemnite (VPDB).

Since the offered food sources (benthic vs. epiphytic biofilm) had different initial $\delta^{13}C$ signatures (see before), the uptake per individual was further standardized taking into account the proportion of ^{13}C in

each food source. The amount of carbon that was taken up by copepods and expressed per copepod individual in the treatments was multiplied with a factor 18.5 and 69.4, for the treatments with labeled benthic biofilm and epiphytic *Fucus* biofilm, respectively. These correction factors were derived from the difference in the atomic percentage of ^{13}C in both food sources (i.e. on average 5.40% ^{13}C for the benthic biofilm and 1.44% ^{13}C for *Fucus*).

Differences in uptake among species×treatments were tested by means of 2-way analyses of variance (ANOVA) with Statistica 6.0 software (StatSoft Inc., 2001). A posteriori comparisons were carried out with the Tukey HSD test using 95% confidence limits. Prior to the ANOVA, the Cochran's C-test was used to check the assumption of homoscedasticity.

3. Results

All three harpacticoid species showed a measurable uptake of diatoms as their $\delta^{13}C$ values at the end of the experiment were far above their natural abundance values at the start of the experiment which were -14.5 , -8.1 , -17.5% for *Tigriopus brevicornis*, *Paramphiascella fulvofasciata* and *Microarthridion littorale*, respectively.

Overall, there was a highly significant difference in biofilm uptake (in terms of $\Delta\delta^{13}C$) among the species and between the various treatments (2-way ANOVA, species: $p < 0.001$, treatment: $p < 0.001$, interaction: $p < 0.001$; Fig. 2A). Over the various treatments, *T. brevicornis* showed a highly significant higher uptake of biofilm in comparison to *P. fulvofasciata* (Tukey post-hoc test, $p < 0.001$) and *M. littorale* (Tukey post-hoc test, $p < 0.001$). Although *P. fulvofasciata* and *M. littorale* differed also significantly from each other in terms of $\Delta\delta^{13}C$ (Tukey post-hoc test, $p < 0.05$). However, there was no significant difference in total uptake I per individual between *P. fulvofasciata* and *M. littorale* over all treatments (Tukey post-hoc test, Fig. 2B). The higher uptake by *T. brevicornis* was even more pronounced in terms of total uptake I ($\mu g C$ per individual, Fig. 2B).

Overall, all treatments were highly significantly different (Tukey post-hoc test, $p < 0.001$) from each other, except for the combination $E^* - E^*B$. For all copepod species, the use of the labeled biofilm on the *Fucus thalli* (epiphytic biofilm) was very low (see $\Delta\delta^{13}C$ values) and was not significantly different when unlabeled diatoms were present at the bottom (treatments E^* vs. E^*B).

Grazing on the benthic biofilm (expressed as $\Delta\delta^{13}C$ or total uptake/individual) in treatments B^* vs. EB^* was significantly lower in the presence of *Fucus* (EB^*) for *P. fulvofasciata* (Tukey post-hoc test, $p < 0.001$) but not significantly different for *T. brevicornis* and *M. littorale*.

4. Discussion

4.1. Species-specific effect of habitat structure on grazing of harpacticoid copepods

In the present study the habitat structure was experimentally modified by adding or removing *Fucus vesiculosus* thalli. In this way, the environment was enriched by bringing in an additional food source (i.e. the epiphytic biofilm and probably a small amount of detritus as well). Our results showed that the presence of *Fucus* had a significant negative effect on the benthic grazing of only one of our test organisms, the benthic copepod *Paramphiascella fulvofasciata*. Consequently, the increase in food availability and habitat complexity, by adding *Fucus* to the experimental unit, may have a negative impact on the energy transfer between benthic primary production and higher trophic levels which is normally ensured by these meiofaunal grazers. In addition, the *Fucus thalli* may have a certain grazing deterrence or may even cause a shift towards other food sources (e.g. bacterial biofilm).

The novelty in our results is the experimental demonstration of species-specific effect of the presence of *Fucus* on the grazing activity

of harpacticoids. Both *Paramphiascella fulvofasciata* and *Microarthridion littorale* were collected from sediment and are considered as benthic species but they respond in a different way to the environmental change i.e. the extra food source that was added. The lower uptake of diatoms from the benthic biofilm by *P. fulvofasciata* may indicate a partial shift to the epiphytic biofilm. However, a low total uptake per individual ($\mu\text{g C}$) was found for both species in the treatments with only labelled epiphytic biofilm.

Tigriopus brevicornis proved to be an efficient grazer on the epiphytic biofilm in this experimental set-up. However, in the presence of unlabeled benthic diatoms, its uptake resulted in a lower $\Delta\delta^{13}\text{C}$ suggesting a shift towards benthic diatoms. This can be due to the fact that the benthic biofilm was more easily accessible and consisted mainly of diatoms. Biofilms are typically an association of microalgae (predominantly diatoms and cyanobacteria), heterotrophic bacteria, sediment particles that aggregate by means of a matrix of mucilaginous extracellular polymers (EPS) at surfaces as e.g. sediment of intertidal sandflats, plant surfaces (Costerton et al., 1995, for review see Decho, 2000). The accessibility and palatability of a biofilm for meiofaunal grazers may largely depend on (1) the EPS matrix and (2) the cells in the biofilm. *T. brevicornis* was the most motile copepod in our experiment. It spends considerably more time in the water column than the other two benthic species (pers. observ.). Our results suggest that *T. brevicornis* is a flexible species in terms of feeding ecology since it makes use of the most favourable or most available food source.

Of course, we should be aware of the fact that the biofilm on the *Fucus* was not further characterized, nor was it quantified, nor were diatoms identified from it. So we might expect some differences in food quality and quantity between the benthic biofilm consisting mainly of diatoms vs. the epiphytic biofilm. The latter can potentially be considered as a more variable food source containing several different food items (see further) while the former is rather uniform. In addition, we observed that some faecal pellets of copepods in treatments with *Fucus* didn't contain any diatoms or empty frustules but consisted of rather unidentifiable, amorphous matter. As copepods were tested together in one jar and we collected some faecal pellets from the bottom, it was impossible to conclude whether all species used the same food source. A possible explanation is that the epiphytes' composition on the *Fucus* shifted from diatom-dominated to bacteria- and flagellates-dominated community during the labelling process (10 days). The lack of frustules in the faecal pellets may be explained by the absence of diatoms in the latter association.

However, Riera et al. (2004) illustrated the importance of benthic diatoms for primary consumers in the Westerschelde Estuary. They stated that although *Fucus* was abundant on the rocky substrate, neither the macrophyte nor its epiphytic flora contributed substantially to the diet of the primary consumers inhabiting these assemblages (Riera et al., 2004).

Apart from the accessibility of food, the lower uptake of epiphytic biofilms reported for all three harpacticoid species in the present study could be due to differences in enrichment levels. Taking into account these differential labelling, resulted into an even higher uptake by *T. brevicornis*. In spite of lower total uptake values for *P. fulvofasciata* after this standardisation, its switching behaviour remained clear. The real *Fucus* tissue is likely to show much lower signal than any surface biofilm since most of the cells would not have had time to be replaced while the opposite would happen with unicellular biofilm such as diatoms. To our knowledge, no other studies have tried to label the biofilm on algal material. Charles et al. (1996) used ^{14}C -formaldehyde-labelled detritus derived from 11 macrophytes. They crushed the macrophytes in a blender and stored them at $-20\text{ }^\circ\text{C}$. These detritus samples were labelled by adsorption of ^{14}C -formaldehyde following the protocol of Lopez and Crenshaw (1982) as modified by Charles (1994) to maximize labelling stability.

Next to differences in food quality (see before), the amount of edible material in both types of biofilms (benthic vs. epiphytic) can differ depending on the substrate (glass bottom vs. *Fucus* thalli) and

consequently influence food selectivity and uptake of the copepods. Unfortunately, the epiphytic biofilm was not quantified or qualified in this sense. Previous feeding experiments showed the highest feeding efficiency of harpacticoids on benthic biofilms in the absence of any sediment (De Troch et al., 2006).

4.2. Ecological implications for the functional position of harpacticoids as grazers

As grazers of primary production and food source for e.g. (juvenile) fishes harpacticoid copepods form an important link in the energy flux at the basis of marine food webs (e.g. Hicks and Coull, 1983; Sogard, 1984; Buffan-Dubau and Carman, 2000). In addition to important top-down control of these grazers by their main predators (Sarkaa, 1995), our study indicates the importance of bottom-up effects governed by the habitat and related resource availability. Macroalgae are known as precursors of an increase in habitat complexity (e.g. Warfe and Barmuta, 2004; McAbendroth et al., 2005) and their associated fauna is typically well-adapted to occur on leaves or thalli (e.g. Chemello and Milazzo, 2002; Fredriksen et al., 2005; Da Rocha et al., 2006). Our experiment suggests that copepods with good swimming capacities (here *Tigriopus brevicornis*) are also able to graze on benthic biofilms when available. The opposite case, in which sediment-bound copepod species are efficiently grazing on epiphytic biofilms, could be deduced from our experiment for *Paramphiascella fulvofasciata* but not for *Microarthridion littorale*.

The variety of feeding behaviour that was illustrated in this experiment, i.e. clear preference for benthic biofilm or a switching feeding behaviour, may lead to more efficient use of resources in a variable environment. Moreover, the presence of different feeding traits minimises competition for food and forms the basis of a diverse community. It is therefore a clear illustration of the so-called 'niche complementarity effect' (Duffy et al., 2001). Although the tested copepod species are all known as grazers on primary production (De Troch et al., 2005a), this high degree of complementarity also implies a low level of functional redundancy. Duffy et al. (2001) concluded that even superficially similar grazer species can differ in both sign and magnitude of impacts on ecosystem processes and they warned for the danger of assuming redundancy when assigning species to functional groups.

Moreover, this experiment illustrated that some grazer species might be very flexible and can easily switch their food preferences. This functional plasticity will depend on the food availability but also on the presence of other grazers.

In comparison to the environmental situation, our microcosms were designed quite uniformly as e.g. there was no sediment in the jars. Therefore, opportunities for niche partitioning were probably more limited than they are in the field. The conclusions on functional redundancy should be interpreted with care as species were examined together and not in a single species set-up. In this sense, our experimental set-up may be misleading since it has been reported that single species behave differently in the presence of other species. Duffy et al. (2001) reported that single grazer species showed stronger effects on the food source (e.g. epiphyte accumulation on eelgrass) than did several species together. Taking this into account, it can be expected that the food switching behaviour of e.g. *Paramphiascella fulvofasciata* may be the result of interaction with the other species and it remains uncertain whether the same pattern will be found in a single-species treatment. As such, the uptake that we measured may be influenced by interference. However, the experimental units were not crowded with a total of 48 individuals and interference between the species should be neglectable.

4.3. Importance of bottom-up effects for harpacticoid copepods

The presence of macrophytes (macroalgae, seagrasses) in coastal systems typically implies an increase in habitat complexity (e.g. Warfe and Barmuta, 2004; McAbendroth et al., 2005). In these diverse

ecosystems, harpacticoid copepods show a wide range of morphological adaptations to an epiphytic lifestyle (e.g. De Troch et al., 2001) e.g. prehensile legs, dorsoventrally flattened habitus. However, they use the plants merely as substrate, not as food source. This was illustrated e.g. by the use of plastic seagrass mimics in a colonisation experiment (De Troch et al., 2005b).

As epiphytic harpacticoids are largely dependent on this biofilm and its composition, any change in substrate structure may have major implications for the development of a biofilm and the grazers upon it. Several studies have illustrated the impact of e.g. nutrient enrichment on macroalgae with a switch from *Fucus vesiculosus* to filamentous algae (Duarte, 1995; Valiela et al., 1997 in Kraufvelin and Salovius, 2004). The latter ones are clearly opportunistic algae that are characterised by very fine, filiform thalli. As such, eutrophication might have major bottom-up effects on the food conditions of harpacticoid copepods. The flexibility in feeding traits of some harpacticoid copepods as illustrated in our experiment can be a way to cope with strong bottom-up effects of the habitat or to avoid competition.

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