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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 ^{13}C to facilitate tracing in the harpacticoids. The biofilm on the *Fucus* was labeled through impregnation of the *Fucus* leaves in ^{13}C 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.

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 effects 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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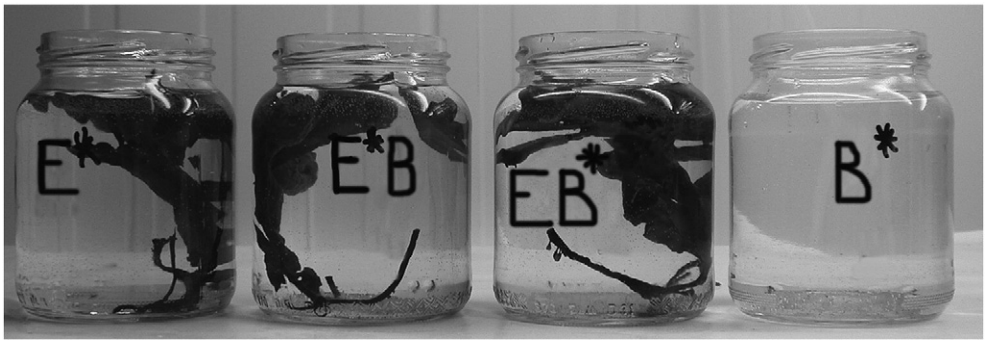

Fig. 1. The various applied treatments (from left to right): epiphytic labeled biofilm on *Fucus* (E*), labeled epiphytic biofilm and unlabeled benthic biofilm (E*B), unlabeled epiphytic biofilm and labeled benthic film (EB*), labeled benthic biofilm (B*). (* = ^{13}C labelled).

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: *Paramphiascella 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, *Paramphiascella 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 $NaH^{12}CO_3$ with $NaH^{13}CO_3$ when preparing the f2 medium. For this, 5 ml of a stock solution of 336 mg $NaH^{13}CO_3$ 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 (δ^{13}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 $NaH^{13}CO_3$ 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 δ^{13}C from −5‰ (before labeling) to 297‰ (at the start of the experiment) as was measured from small pieces (on average 2000 μg 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 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 homogenously 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}C/^{12}C ratios in the tissue of the harpacticoids, a minimum of 15 μg C per species was analysed corresponding to 8, 20 and 20 adults