Journal of Experimental Marine Biology and Ecology 345 (2007) 119–128

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Effects of food diversity on diatom selection by harpacticoid copepods

Marisa Wyckmans [a], Victor A. Chepurnov [b], Ann Vanreusel [a], Marleen De Troch [a,*]

[a] *Ghent University, Biology Department, Marine Biology Section, Campus Sterre, Krijgslaan 281-S8, B-9000 Gent, Belgium*
[b] *Ghent University, Biology Department, Protistology and Aquatic Ecology, Campus Sterre, Krijgslaan 281-S8, B-9000 Gent, Belgium*

Received 13 October 2006; received in revised form 14 February 2007; accepted 15 February 2007

Abstract

The diversity of species assemblages which occupy a basal position in the trophic pyramid (typically unicellular algae in aquatic environments) is known to influence the interaction with organisms of higher trophic levels. A laboratory feeding experiment was conducted with cultures of three benthic diatom species (*Navicula phyllepta*, *Grammatophora marina* and *Cylindrotheca closterium*) as primary producers and three harpacticoid copepod species (*Harpacticus obscurus*, *Paramphiascella fulvofasciata* and *Tigriopus brevicornis*) as grazers to evaluate the effects of food diversity (and concomitant food availability) on grazing selectivity. This kind of selectivity experiments is singular for benthic harpacticoid copepods as so far, information on food selection of harpacticoids is scarce.

Uptake of a unispecific food source by a single copepod species decreased as food diversity (and concomitant overall food concentration) increased. All three consumers reacted similarly to changing food diversity, but exhibited strong species-specific responses to food identity i.e. which diatom was added was crucial. Irrespective of level of food diversity, *H. obscurus* took up high amounts of *G. marina*, whereas both *P. fulvofasciata* and *T. brevicornis* preferred *C. closterium* when given the choice between different diatoms. As for zooplanktonic taxa, this experiment showed that in lower benthic marine food webs both prey organisms (primary producers) and grazers play a very specific role. Diversity of food and its identity are of critical importance at the base of the trophic pyramid, influencing trophic transfer from primary producers over grazers to higher trophic levels.

Keywords: Diatoms; Food choice; Food diversity; Food identity; Harpacticoid copepods

1. Introduction

Benthic meiofauna constitutes an important component of marine benthic food webs, both as producers (Gee, 1989) and consumers (Montagna, 1995). Harpacticoid copepods (Crustacea) are an important part of this meiobenthos throughout the world and are known to feed on a wide variety of food sources (see Hicks and Coull, 1983 for review). Although harpacticoids are rarely the dominant taxon in marine sediments, they are known to be the primary food source for bottom or phytal feeding juvenile and small fish. As harpacticooids are important grazers on primary production, they represent an important link between microalgal primary production and higher trophic levels (e.g. Coull, 1990; De Troch et al., 1998; Turner, 2004; Andersen et al., 2005).

In general, many factors interact to determine patterns of prey use by predators, but two are fundamental

* Corresponding author. Tel.: +32 9 2648520; fax: +32 9 2648598.
E-mail address: marleen.detroch@ugent.be (M. De Troch).

0022-0981/$ - see front matter
doi:10.1016/j.jembe.2007.02.002

(Wainwright, 1994). First, an environmental factor, only food items that are physically available can be eaten. The second factor is the consumer's effectiveness, since only food items that the consumer is able to locate, capture, handle and digest can be included in the diet (Wainwright, 1994). When searching for food, predators (including herbivores) may encounter a variety of prey items, differing in size, digestibility, accessibility and so on. Each encountered prey item will have a certain 'prey value', dependent on the assimilated energy yield and the energy spent while searching for and handling the prey item (Hughes, 1980). According to the optimal foraging theory, a consumer is assumed to choose the diet which maximizes net energy intake (Charnov, 1976; Hughes, 1980). Furthermore, it has been shown that predators (invertebrate mesograzers e.g. amphipods, isopods, gastropods) may feed at random when prey are in short supply, but may become selective when certain prey are abundant (e.g. Stephens and Krebs, 1986; Cruz-Rivera and Hay, 2000: amphipods; Aberle et al., 2005: isopod and gastropod). For meiofaunal grazers, however, food selectivity is far from well known.

As harpacticoids consume a wide variety of food sources, the question rises whether they feed at random, ingesting food particles as these are encountered, or whether they select specific food items to meet energetic requirements (nutritional quality of the food) or because certain food items are easier to access (food morphology, size). So far, studies on copepod feeding strategies have mainly focused on pelagic systems (e.g. DeMott, 1989; Irigoien et al., 2000; Sommer et al., 2000; Tackx et al., 2003). It has been shown for pelagic copepods (mainly Calanoida) that food selection not only depends on food particle size (Sommer et al., 2000), but that they can discriminate between similar-sized food particles because of chemical properties ('taste', DeMott, 1988).

For harpacticoids, choice of a particular food resource was first demonstrated convincingly by Vanden Berghe and Bergmans (1981). They found *Tisbe furcata* to have a clear preference for bacteria while two sibling species showed a generalized or indiscriminate selectivity. Several later studies have supported these findings, showing a great variability in food selection by harpacticoid copepods (e.g. Rieper, 1982; Carman and Thistle, 1985; Decho, 1986; Pace and Carman, 1996; Buffan-Dubau and Carman, 2000). Recently a few studies have addressed the importance of food particle size (De Troch et al., 2006) and food concentration (De Troch et al., 2007) on food selectivity in harpacticoid copepod species. So far, these aspects of food selectivity have only been tested by using strains of a single diatom species.

In the present study, the effect of food diversity on diatom selection (rather than total uptake) by harpacticoid copepods was investigated by means of prelabeled diatoms. *Harpacticus obscurus*, *Paramphiascella fulvofasciata* and *Tigriopus brevicornis* were fed on diets composed of three different diatom species that were selected in view of their different size and shape. The diatoms used here (*Navicula phyllepta*, *Grammatophora marina* and *Cylindrotheca closterium*) may therefore also have a different 'prey value'. Special attention was drawn to the effect of increasing food diversity on the uptake of *N. phyllepta* as this diatom has been shown to be a good food resource for harpacticoids (e.g. Sellner, 1976; Nilsson, 1987). This study aimed to test how harpacticoids react in an environment with different food sources or the other way around, an environment impoverished in food choice. Prey switching behavior (i.e. changes in prey selection according to the availability of alternative prey) has been demonstrated for the planktonic copepod *Acartia tonsa* (Kiorboe et al., 1996) and a variety of other grazers (Cruz-Rivera and Hay, 2000; Goecker and Kåll, 2003; Aberle et al., 2005). All these studies however, are restricted to only one level of food diversity and information on benthic copepods is still lacking.

Here, the effect of food diversity *per se* was tested. Therefore, experiments with different levels of food diversity (i.e. 1-diatom, 2-diatoms and 3-diatoms treatments) were designed to test whether copepods select other diatoms or switch diet when offered the choice between one, two or three different foods. Furthermore, the effect of diatom identity on food selection within each diversity level was evaluated.

2. Materials and methods

The effect of food diversity on food choice was investigated by feeding copepods with different combinations of diatoms. In each combination one diatom species was labeled with the stable isotope ^{13}C (see further) to trace the uptake of this particular diatom and to measure food selectivity (uptake of a particular food source) rather than total food uptake. Grouping the treatments that have the same labeled diatom allowed to evaluate diversity effects on the uptake of this diatom. In addition, treatments were grouped according to their level of food diversity (i.e. 1-diatom, 2-diatoms and 3-diatoms treatments) to test for identity effects on diatom uptake.

Clonal cultures of three pennate benthic diatom species (*N. phyllepta*, *G. marina* and *C. closterium*) were isolated from the North Sea and grown in f/2 medium