

Food patch size, food concentration and grazing efficiency of the harpacticoid *Paramphiascella fulvofasciata* (Crustacea, Copepoda)

Marleen De Troch^{a,*}, Mateja Grego^b, Victor A. Chepurinov^c, Magda Vincx^a

^a Ghent University, Biology Department, Marine Biology Section, Campus Sterre, Krijgslaan 281 — S8, B-9000 Ghent, Belgium

^b National Institute of Biology, Marine Biology Station Piran, Fornace 41, SI-6330 Piran, Slovenia

^c Ghent University, Biology Department, Protistology and Aquatic Ecology, Campus Sterre, Krijgslaan 281 — S8, B-9000 Ghent, Belgium

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Abstract

Harpacticoid copepods are known as important grazers on primary producers. The underlying factors for their food selectivity and grazing efficiency are however far from well known. For instance, their patchy distribution in the marine environment is well documented but how meiofaunal organisms cope with the spatial distribution/accessibility of the available food resources is less clear.

In the present study a laboratory experiment was conducted to test the grazing efficiency of *Paramphiascella fulvofasciata* (Copepoda, Harpacticoida) on the epipelagic diatom *Seminavis robusta* applied in recipients of different area and in various concentrations. Diatoms were enriched in the stable isotope ¹³C in order to trace food uptake and copepods were left to graze for 4 days.

We found that the grazing efficiency of *P. fulvofasciata* was diatom concentration-dependent. A lower diatom uptake at lower diatom densities illustrated this clear functional response. On the contrary, there was no significant effect of the area *per se* where the copepods could graze upon. The lack of a significant effect of area is mainly due to the high variability in uptake that was recorded in some treatments. Although *P. fulvofasciata* is a very motile copepod, known as endobenthic and epibenthic species, it was able to concentrate on food uptake at the bottom of the experimental unit as there was no significant difference in uptake between treatments with different water heights in the units. In addition, it was found that a diatom concentration of about 140000 cells/cm² favours egg production of *P. fulvofasciata*.

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1. Introduction

The use of space by organisms and the spatial organisation of species communities have been subject to numerous studies (e.g. Jetz et al., 2004; Weitz and Levin, 2006). Spatial pattern, or the areal variation of species densities in their environment, is an important

component of community structure in ecosystems (Sandulli and Pickney, 1999). Reliable information on spatial patterns and their scale is crucial to determine appropriate sample sizes, to provide sound population estimates, and to study competitive interactions (Legendre and Fortin, 1989; Thrush, 1991; Hewitt et al., 1993; Legendre, 1993). Comparisons between spatial patterns of consumers and their potential food resources inform on trophic interactions and superimpose a more functional aspect to structural (spatial) analyses (e.g. Weitz and Levin, 2006).

* Corresponding author. Tel.: +32 9 264 85 20; fax: +32 9 264 85 98.
E-mail address: marleen.detroch@UGent.be (M. De Troch).

A typical patchiness at centimetre scales in the marine realm is reported for meiofaunal organisms and benthic microalgae (e.g. Admiraal, 1984; Fleeger and Decho, 1987; Reise, 1987). Both abiotic (e.g. hydrodynamics and sediment characteristics) and biotic factors (e.g. predation, competition, reproduction and disturbance) are known as underlying factors (see for review Fleeger and Decho, 1987). Several studies (e.g. Pickney and Sandulli, 1990; Sandulli and Pickney, 1999) documented the structuring role of unevenly distributed food resources to explain the corresponding patchy distribution of herbivorous meiofauna.

However, how meiofaunal organisms cope with the spatial distribution/accessibility of the available food resources is less clear. According to the ‘optimal foraging’ theory (Hughes, 1980), consumers are expected to select the food resources that maximize the net rate of energy intake. This depends on the amount of energy a certain food source yields and the energy that is required to search for the food and process it. Although bioenergetics receives increasing interest (e.g. Marquet et al., 2004; Tilman et al., 2004; Economo et al., 2005), several important questions remain open. E.g. How do herbivores modify their food choices according to changing circumstances? What is the functional relationship between feeding rate and food density (Hughes, 1980)? Does an individual use an area just sufficient to meet its metabolic requirements (Jetz et al., 2004)? In several studies of terrestrial habitats significant efforts have been made in an attempt to answer these and related questions. One important guiding principle which resulted from these research works proved to be the resource concentration hypothesis formulated by Root (1973). The hypothesis predicts that specialist herbivores should achieve higher densities in large patches. Several later studies revised the idea of Root (e.g. Hambäck and Englund, 2005) and pointed at the discrepancy between the hypothesis and field data due to e.g. variability in search mode and diet width (e.g. Bowman et al., 2002; Bukovinszky et al., 2005), density dependence (e.g. Doak, 2000), different processes in small and large patches (e.g. Matter, 1997). So far, marine studies lag far behind on this domain if compared with those of terrestrial habitats, and this is partly due to the open nature of marine ecosystems. However, in view of the patchy distribution of some groups of organisms (e.g. microalgae) which serve as food source for meiofauna, the area of food distribution is a significant factor which affects the feeding of grazers and deserves more attention.

In the present study, we tested experimentally how area, i.e. the surface area on which food is distributed,

affects the uptake of primary producers by a marine grazer. We used *Paraphysocella fulvofasciata*, a benthic harpacticoid copepod, as test grazer and *S. robusta*, a marine epipelagic diatom, as food. We let the copepod graze in several experimental units with different bottom areas. Larger units were set up to test whether more energy is spent in the search for food because of the greater area to cross, leaving less energy available for food uptake. In order to test the effect of food concentration *per se*, we diluted the diatom concentration but kept the grazing area constant in an additional experimental series. As such, we were able to test the grazing efficiency of *P. fulvofasciata* under different circumstances in terms of (1) size of the feeding ground and of (2) food concentration.

2. Materials and methods

2.1. Laboratory conditions and labelling technique

Laboratory stock cultures of the copepod species *P. fulvofasciata* [family Miraciidae (former family Diosaccidae), initially collected from a subtidal area of Helgoland, Germany] were maintained in 1 l glass beakers, with artificial seawater (c. 32 psu, Instant Ocean® salt, Aquarium Systems, France) (see also De Troch et al., 2005, 2006a,b). They were regularly provided with a mixture of benthic diatom cultures, composed of epipelagic pennate species *Navicula phyllepta*, *S. robusta* and *Cylindrotheca closterium*. Specimens of the copepod reaches up to 0.83 mm in size (body length) (De Troch et al., 2005).

Previously, cultures of the epipelagic pennate diatom *S. robusta* were already used successfully as food source for various harpacticoid copepods in laboratory experiments (e.g. De Troch et al., 2006a,b). In the present investigation, we used a monoclonal culture of this diatom species, which represented the F2 generation derived originally after a cross of two sexually compatible clones (mating system of *S. robusta* is heterothallic). The clones from which the lineage was started were isolated from a sample collected in November 2000 from the ‘Veerse Meer’, a brackish water lake in Zeeland, The Netherlands, and their principal life-cycle traits were studied in detail (Chepurnov et al., 2002). The clone involved in the current experimental work is referred to as F2-44 in the diatom culture collection of the Laboratory of Protistology and Aquatic Ecology, Ghent University, Belgium. By the time of setting the experiment, the cells were measured to be $42.9 \pm 1.34 \mu\text{m}$ ($n=20$) in length. The cultures were grown in an incubator at 18–20 °C with a 12:12-h light-dark

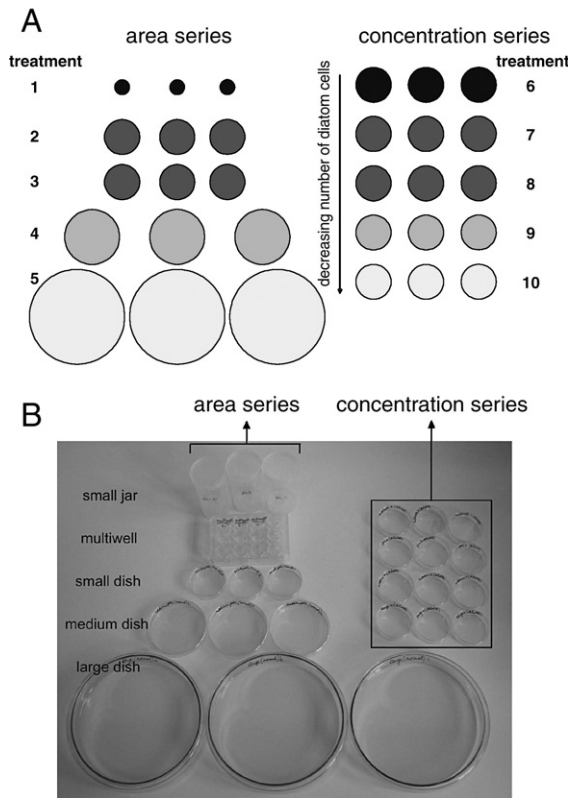


Fig. 1. (A) Experimental set-up with indication of the diatom concentration per vessel. The shading of the units is indicative for the diatom concentration in each treatment, presented from high (darker) to low (lighter) concentration. (B) Overview of the different experimental vessels before adding any diatoms or copepods.

period and $25\text{--}50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The culture medium was *f/2* (Guillard, 1975) which was based on filtered and sterilized seawater (32 psu) collected from the North Sea.

For labelling the diatom cells with the stable isotope ^{13}C , 5 ml of a solution with $\text{NaH}^{13}\text{CO}_3$ (336 mg in 100 ml milliQ H_2O) was added per 100 ml of the culture medium. Diatoms underwent multiple mitotic divisions to reach high densities of cells and high levels of labelling. This labelling technique resulted in an increase in $\delta^{13}\text{C}$ from -14.9 to 8847‰ . Prior to the feeding experiment, the labelled medium was replaced by artificial seawater. To estimate the density of diatom cells in the cultures, the cells were homogeneously suspended by shaking the bottles in which the cultures were grown and then $50 \mu\text{l}$ of the cell suspension was transferred into a well of a 96-well plate. In an hour, after all the cells confidently settled to the bottom of the well, their number was counted under a Zeiss Axiovert 135 inverted microscope (Zeiss

Gruppe, Jena, Germany) and the values obtained have allowed to estimate the densities in the experimental vessels.

Single specimens of copepods were picked up by micropipette from the original stock cultures and placed into Petri dishes containing artificial sea water where they were starved of food overnight. After starving, the copepods were transferred into the different experimental vessels (see experimental design).

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 per replicate corresponding to 20 adults of *P. fulvofasciata* in one experimental unit, independent of its size.

Both copepods and diatoms were kept and the experiments were performed at $17 \pm 1 \text{ °C}$ and under a 12:12 h light-dark regime.

2.2. Design of the experiment

2.2.1. Area series

In order to test the effect of the grazing area ('area' series), five various experimental units were selected, which differed in area of the bottom (Fig. 1B):

- (1) 12-well plate (polystyrene, diameter of well = 2.1 cm, surface area = 3.5 cm^2 , 4 ml) (treatment 1)
- (2) small Petri dish (polystyrene, diameter = 5.2 cm, surface area = 21.2 cm^2 , 20 ml) (treatment 2)
- (3) small jar (polystyrene, diameter = 5.2 cm, surface area = 21.2 cm^2 , 100 ml) (treatment 3)
- (4) medium Petri dish (polystyrene, diameter = 8.4 cm, surface area = 55.4 cm^2 , 55 ml) (treatment 4)

Table 1

Surface area and diatom cell numbers in the two experimental series

Treatment no.	Surface (cm^2)	Total number of diatom cells	Number of diatom cells per cm^2
<i>'Area' series</i>			
1	3.5	3,000,000	866,150
2	21.2	3,000,000	141,260
3	21.2	3,000,000	141,260
4	55.4	3,000,000	54,130
5	260.2	3,000,000	11,530
<i>'Concentration' series</i>			
6	21.2	18,394,558	866,150
7 ^a	21.2	3,000,000	141,260
8 ^a	21.2	3,000,000	141,260
9	21.2	1,149,660	54,130
10	21.2	244,898	11,530

^a Corresponds to treatment 2 in the 'area' series.

- (5) large Petri dish (glass, diameter=18.2 cm, surface area=260.2 cm², 260 ml) (treatment 5)

In four of the five experimental units, the column of water was 1 cm high and, in treatment 3, 5 cm. This treatment was added to test, in comparison with treatment 2 (identical area of the bottom), whether copepods would spend more time swimming in the water column rather than being associated with the bottom (and hence grazing less efficiently on the diatom biofilm).

A total of $3 \cdot 10^6$ of diatom cells per experimental unit (Table 1, 'area' series) were applied by means of a micropipette. It took c. 15 min before all the cells had settled to form a homogeneous layer over the bottom (De Troch and Chepurnov, pers. observ.). According to our previous experience (De Troch et al., 2005), the level of food supply provided can be considered as very saturated.

The constant number of cells in units of different sizes ('area' series, Table 1) resulted in different cell densities (Fig. 1A) which became proportionally lower while the surface area increased (Table 1, 'area' series).

2.2.2. Concentration series

In this set-up, area was kept constant and densities of diatom cells were identical to those of 'area' series. The area of small Petri dishes (diameter=5.2 cm, surface=21.2 cm², treatment 2) from the *area* series was set as a reference point (=1) (Fig. 1A). The number of diatom cells per surface unit was recalculated to the size of this reference (see relative concentrations in Fig. 1A) and total number of diatom cells per experimental unit is shown in Table 1 ('concentration' series). In that way treatment 6 of the 'concentration' series corresponds to treatment 1 of the 'area' series. Consequently treatment 7 ('concentration' series) corresponds exactly to the outcome of treatment 2 ('area' series) (same area, same concentration).

As we used an epipellic diatom which formed a biofilm on the bottom of the vessel, the concentration of diatom cells is independent of the water height. Therefore, the diatom concentration in treatment 3 (small jar) corresponds to the one in treatment 2 (small dish). In order to present a complete design, the counterpart of treatment 3 (small jar) in the concentration series, *i.e.* treatment 8, is included as well although it is similar to treatment 7 and thus also similar to treatment 2.

Diatom growth in the experimental containers was negligible as the feeding experiments were conducted in artificial seawater (without silica) and growth rate was

very low compared to the growth noted when kept in f/2 medium (De Troch, pers. observ.).

All treatments were triplicated (Fig. 1). Experimental units were placed at random on a shelf under the same controlled conditions as stated before. Prior to setting the experiment, 60 individuals of *P. fulvofasciata* were frozen to measure the natural ¹³C signals.

2.3. Analytic techniques and data treatment

After 96 h, the survival rate was estimated and the experiment was terminated by freezing of the experimental units. In a few days, the material was thawed and the copepods were manually sorted within 2 h after thawing to prevent or minimise leakage of label (see Mourelatos et al., 1992; Moens et al., 1999). Subsequently, the specimens were washed several times in deionised water and placed in tin capsules (8*5 mm, pressed, standard weight) by means of a needle. The material collected was desiccated in an oven at 60 °C for 12 h. Delta ¹³C values were measured using an isotope ratio mass spectrometer (type Europa Integra) at the UC Davis Stable Isotope Facility (University of California, USA).

Further standardisation towards the body size of copepods was done by recalculating the $\delta^{13}\text{C}$ values (following Middelburg et al., 2000) taking into account their individual biomass. For this, incorporation of ¹³C is reflected as excess (above background) ¹³C and expressed as total uptake (*I*) in milligrams of ¹³C per individual, calculated as the product of excess ¹³C (*E*) and individual biomass (organic carbon). Excess ¹³C is the difference between the fraction ¹³C of the control (F_{control}) and the sample (F_{sample}), where $F = {}^{13}\text{C}/({}^{13}\text{C} + {}^{12}\text{C}) = R/(R+1)$. The carbon isotope ratio (*R*) was derived from the measured $\delta^{13}\text{C}$ values as $R = (\delta^{13}\text{C}/1000 + 1) \times R_{\text{VPDB}}$, with $R_{\text{VPDB}} = 0.0112372$ as $\delta^{13}\text{C}$ is expressed relative to Vienna Pee Dee Belemnite (VPDB). This total uptake was further standardised and expressed per unit carbon of copepod.

Differences in uptake among the various treatments were tested by means of one-way and two-way analyses of variance (ANOVA) with Statistica software. *A posteriori* comparisons were carried out with the Tukey test using 95% confidence limits. Prior to the ANOVA, the Cochran's C-test was used to check the assumption of homoscedasticity.

3. Results

There was a 100% copepod survival rate in all units, even in the smallest experimental units (*i.e.* the

multiwell). *P. fulvofasciata* didn't suffer from possible increased salinity in these smaller units because of evaporation as the experiment last for only 4 days.

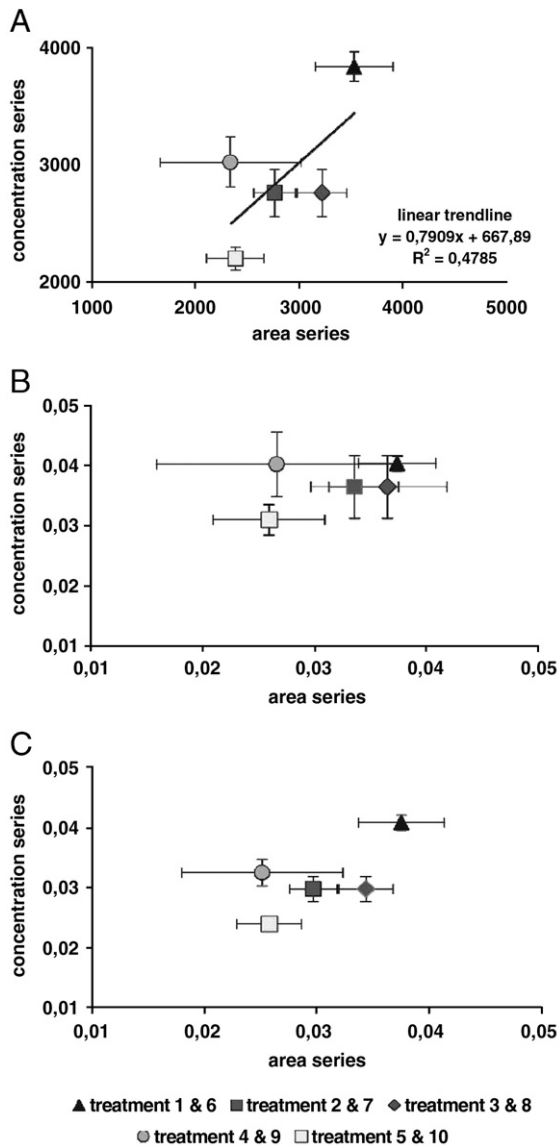


Fig. 2. Diatom uptake (mean±standard error) by *Paramphiascella fulvofasciata* for the different treatments expressed as (A) $\delta^{13}\text{C}$, (B) total uptake per individual relative to individual biomass, and (C) total uptake per unit carbon of copepod. The results of 'area' series were plotted on the x-axis vs. the results of the 'concentration' series plotted on the y-axis. The shading of the labels corresponds to the shading (concentration levels) of Fig. 1. The outcome of treatments 7 and 8 ('concentration' series) corresponds to the outcome of treatment 2 ('area' series) as the latter was set as reference for the 'concentration' series and has the same diatom concentrations as treatments 7 and 8. The other treatments of the 'concentration' series were conducted in the same recipient as treatment 2 ('area' series), though with different diatom concentrations.

Within the 'area' series, no significant differences in uptake of diatoms by copepods (expressed as $\delta^{13}\text{C}$, Fig. 2A) were reported between the various treatments (one-way ANOVA, $p=0.21$) mainly because of high variability in treatment 4. The enrichment level in treatment 1 was noted to be higher if compared with treatment 4 and 5 which were conducted in recipients of larger area. This difference, however, was illustrated to be statistically insignificant. There was no significant difference even between treatment 2 (small dish) and 3 (small jar) in which the water-column height above the diatom biofilm differed considerably, i.e. 1 cm and 5 cm, respectively. In terms of total uptake per individual (Fig. 2B), again no significant differences between the treatments were found. The values after standardisation per unit carbon of copepod (Fig. 2C) showed the same trend as the $\delta^{13}\text{C}$ values (Fig. 2A).

Within the 'concentration' series, however, each treatment was characterized by a distinctive level of enrichment ($\delta^{13}\text{C}$, Fig. 2A) and the differences reported proved to be statistically significant (one-way ANOVA, $p<0.001$). This outcome suggested a functional response of *P. fulvofasciata* on the different food concentrations. Treatment 6 was apparently the most distinguishable from the rest of treatments (Tukey *post-hoc*, $p<0.05$ for treatment 6–9, $p<0.001$ for treatment 6–10, $p<0.01$ for all other combinations). From all combinations, *P. fulvofasciata* was significantly more enriched in treatment 6 because of a higher uptake of labelled diatoms. Diatom uptake in treatment 10 (with the lowest diatom concentration) was the lowest but this difference was found to be statistically significant only in comparison with treatment 6 ($p<0.001$, see before) or with treatment 9 (Tukey HSD, $p<0.05$).

As in the area series, the standardisation towards unit carbon of copepod (Fig. 2C) yielded the same outcome as for the $\delta^{13}\text{C}$ values (Fig. 2A).

Comparison between the corresponding treatments of both series (area vs. concentration: treatment 1 vs. 6, 2 vs. 7, 3 vs. 8, 4 vs. 9, 5 vs. 10) showed no significant differences.

4. Discussion

Our results demonstrated that the grazing efficiency of *P. fulvofasciata* was diatom concentration-dependent. There was a clear functional response to the different concentrations with lower uptake at lower diatom densities. In terms of $\delta^{13}\text{C}$, the enrichment level in the lowest food concentration ($2200\pm 100\text{‰}$) was almost half of the uptake in the highest food concentration ($3850\pm 125\text{‰}$) although the diatom

density was 75 times higher in the latter treatment. However, in terms of total uptake per individual, the difference in uptake between lowest and highest concentration was not that pronounced with average values of 0.03 ± 0.002 and 0.04 ± 0.001 , respectively.

This outcome corresponds to a type I — functional response (*sensu* Holling, 1959) *i.e.* a linear relation between food density and food uptake. This assumes that the consumers require little or no search and handling time. For the concentrations applied in this experiment, there was no asymptote in the curve (type II — functional response, Holling, 1959). This lack of leveling off at the maximum food densities suggests that *P. fulvofasciata* is able to consume even more diatom cells when higher densities would be available. However, in this experimental set-up the available diatom cells were never finished at the end of the experiment (*i.e.* after 4 days).

From their field study, Montagna et al. (1995) found that an increase in microphytobenthos biomass resulted into increased grazing rates of meiofauna organisms. Especially harpacticoid copepods reacted positively to food increase. The same authors concluded that particularly harpacticoids have a dependent relationship with their autotrophic food resources in intertidal habitats and can regulate their behavior to maximize intake of food. Our data support these findings as *P. fulvofasciata* can maximize its uptake when food is highly concentrated.

These results follow the optimal foraging theory (Hughes, 1980) as the grazer maximizes the net energy intake by taking more food. In the current set-up, the grazer could not switch between food sources as there was only one diatom species available. As the area of the experimental unit was kept constant in the ‘concentration’ series, possible differences in energy spent to search the food should be minimal. This experiment showed that the extra energy spent to collect and process more food from a certain area counts little to the energy from the larger amount of food.

The effect of food density was evaluated here on a short term basis as we quantified food uptake but not in relation to time (feeding rate). Long-term effects of different food concentrations can be seen in growth, reproduction rate and population densities. As for the latter parameter, the consumers are supposed to become more abundant as food densities increase (numerical response, Holling, 1959). The present experiment didn’t last long enough to test for a possible numerical response. Actually, the number of individuals remained constant in the experimental units in view of the short duration of the experiment. However, we observed that

most of the females were gravid (*i.e.* carrying a double egg sac) in all and in two out of three replicates for treatment 2 and 3 of the ‘area’ series (corresponds to treatment 7 and 8 in the ‘concentration’ series), respectively. This suggest that the applied concentration of diatoms in these treatments (about 140 000 cells/cm²) favours egg production of this copepod species. Dahms (1986) found no seasonal effects on reproductive activity. However, if egg production is governed by food concentration (in this case diatoms) there may be a strong seasonal effect. Therefore, a specific reproduction experiment with different food levels could give support to these suggestions.

Contrary to our expectations, there was no significant effect of the area *per se* where the copepods could graze upon. The lack of a significant effect of area is mainly due to the high variability in uptake that was recorded for treatment 4. We expected more variability in treatment 3 because of the larger amount of water in this treatment and the probability to spend more time in the higher water column. The delta ¹³C signal however was not significantly different between treatments 2 and 3 whereby in treatment 2 the same bottom area was covered with diatoms but with a limited amount of water. This outcome supports the assumption of Jetz et al. (2004) that an individual uses an area just sufficient to meet its metabolic requirements in their calculations of required home range. In this experiment, *P. fulvofasciata* seems to be very efficient in the use of space (*e.g.* in the water column) although our test organism is a very motile copepod species.

Dahms (1987) was the first to report the species from the German Bight and offered the original material for our stock cultures. He collected the species in holdfasts of *Laminaria hyperborea* from a subtidal area of Helgoland. From his observations in the laboratory it could be deduced that it is an endobenthic as well as epibenthic species.

It was hardly possible to observe any aggregational response of these copepods to their food source as they were quickly moving around in the experimental units. Furthermore, the food was quite homogenous spread over the bottom of experimental units.

It is obvious that the outcome of this experiment is influenced by the applied concentration of diatom cells. The applied densities were far above food limitation (De Troch et al., 2005). It can be expected that this functional response will even be more pronounced in case of food limitation. At the end of the experiment, there was no food depletion in any of the treatments.

Despite the constraints of the experimental set-up, a clear functional response to food concentration of this

marine grazer was recorded. This can be the onset for future experiments to test the effect of this grazer on the diatoms and their physiological conditions.

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