

# Interactions between two closely related phytal harpacticoid copepods, asymmetric positive and negative effects

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Received 18 April 2006; received in revised form 10 September 2006; accepted 10 October 2006

## Abstract

Competition for food is generally thought to exert a strong evolutionary pressure, driving trophic niche separation, either by specialization and/or by widening the choice of potential food resources. Harpacticoid copepods are common inhabitants of phytal assemblages, where several closely related species of the so-called phytal dwelling families often co-occur. However, direct competition among phytal harpacticoids has been thought to be unlikely, due to the abundant and continuously available food supplies. We conducted a series of field and laboratory studies to assess the role of competition in the abundance distribution of two closely related harpacticoid species, *Mesochra rapiens* and *M. aestuari*. We found that the abundance of both species co-varied on several seaweed species in the northern Baltic Sea, during a 3-month period. Stable isotope ratios in the green alga *Cladophora glomerata* field samples indicated different resource utilization of the two species, both in fresh and deteriorated *C. glomerata*, and in drifting algae. We tested in the laboratory if resource utilization was different between the species in sympatry and allopatry. We used enriched stable carbon isotope ratios (<sup>13</sup>C/<sup>12</sup>C) of the diatom *Phaeodactylum tricorutum* to trace the uptake in both species. Results from these experiments showed a much higher assimilation by *M. aestuari* in sympatry with *M. rapiens*, while the latter species showed a higher assimilation in allopatry. Our results show that while there is no apparent competition for resources between these two species in the field, there seems to be an asymmetric reaction when in sympatry and provided one single resource in the laboratory. We suggest that *M. rapiens* may facilitate assimilation by *M. aestuari* and discuss the mechanisms by which this may take place.

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**Keywords:** Competition; Facilitation; Faecal pellets; Harpacticoids; Indirect effects; *M. aestuari*; *M. rapiens*

## 1. Introduction

Interactions between species have been suggested to play a major role in shaping ecological and evolutionary

patterns through their concomitant direct and indirect effects (Tauber and Tauber, 1989; Menge, 1995; McPeck, 1996; Liess and Hillebrand, 2004). Negative effects, whether direct or indirect, are considered to be responsible of character shifts and behaviours favouring reduced co-existence or the minimization of their consequences (Darwin, 1859; Rosenzweig, 1987; Bertness and Leonard, 1997). On the other hand, theory postulates that positive effects favour the evolution of traits increasing sympatry between species involved in

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the interaction or others that effectively maximize the effect (Wootton, 1994; Bertness et al., 1999). The extent to which some of these interactions have a bearing in the ecology and evolution of natural communities remains uncertain, mainly due to the methodological difficulties involved in determining their existence and strength. Despite these conjectures, it is now an accepted idea that interspecific competition may at least explain patterns of habitat selection, niche overlap, and the co-evolution of interacting species (Rosenzweig, 1987; Iken et al., 2001; Schluter, 2001). On the other hand, habitat heterogeneity is thought to stabilize competitive interactions, enhancing co-existence of putative competitors which are not forced into a marked niche differentiation due to the high availability and variability of resources provided (Heck and Wetstone, 1977; Rosenzweig, 1981; Bonesi and Macdonald, 2004).

In marine phytal environments, competition has traditionally been considered unlikely due to this heterogeneity, and the capability of animals associated with the plants to vary in resource use and feeding strategy, being able to shift from preferred to less preferred items in situations of food shortage (Heck and Orth, 1980; Hicks, 1985; Dean and Connell, 1987; Pavia et al., 1999). Nevertheless, some authors (e.g., Edgar, 1990), have suggested that little previous evidence for competition in phytal habitats may be explained by the fact that studies have generally concentrated on interference competition rather than exploitative competition. Diffused exploitative competition may perhaps be unusually prevalent amongst motile epifaunal assemblages due to their rapid turnover rates and their ability to capitalize on available excess food resources (Dean and Connell, 1987).

Harpacticoid copepods are often the numerically dominant and most diverse invertebrate taxa within phytal communities (Hicks, 1985). They are generally very motile, reproduce rapidly, feed on a variety of resources, and some are morphologically adapted to live in the phytal (see Hicks and Coull, 1983 for a review). A common “phytal harpacticoid fauna” has been found to occur in similar habitats world-wide (Hicks and Coull, 1983; Hicks, 1985), often including several con-generic species which co-exist over space and time within specific algal habitats. Direct competition among phytal harpacticoids has been considered unlikely because of the aforementioned abundant and continuously available food supplies (Hicks, 1977a, 1979), and because in general, co-existing harpacticoids have been found to forage at different spatial levels, effectively partitioning food resources and minimizing competitive interactions (Hicks, 1977a; Marcotte, 1977; Vanden Berghe and

Bergmans, 1981; Ustach, 1982; Pace and Carman, 1996). Competition has however been suggested to be a primary force leading to the diversification and ecological distribution of some harpacticoids, and episodes of past or present competitive interactions, responsible for shifts in behaviour, habitat displacement or trophic specialization currently being observed in harpacticoid communities (Marcotte, 1977). In the phytal, where a “specialized” harpacticoid fauna has seemingly evolved, species interactions are likely to have had an important bearing on speciation processes. Yet, competition between harpacticoids as such has been investigated rarely and actual studies on species interactions remain scarce (Hicks, 1977b; Ivester and Coull, 1977; Fleegeer and Gee, 1986; Chandler and Fleegeer, 1987), rendering theoretical conclusions and generalizations on the subject, rather speculative and in need of further validation.

We conducted a series of field and laboratory studies to assess the role of competition in the abundance distribution of two closely related phytal harpacticoid species, *Mesochra rapiens* and *M. aestuari*. The aim of our study was three-fold:

- 1) To examine abundance patterns of these two species in the field, for which we sampled several algal assemblages during a 3-month period.
- 2) To assess patterns of resource use by both species in the field, for which we sampled 3 different stages in the degradation of *Cladophora glomerata* (L.) Kütz (fresh attached, deteriorated attached and deteriorated drifting) and investigated resource utilization of the harpacticoids by means of stable isotope analyses.
- 3) To evaluate whether competition between these two species would take place when isolated from their natural environment and provided one unique food resource (i.e.: under habitat homogeneity and resource limitation). We hypothesized that if competition for that resource were occurring, assimilation would be lower in sympatry than in allopatry, the competitively dominant species showing greater efficiency than the other one, and conducted a laboratory experiment in order to evaluate it.

## 2. Materials and methods

### 2.1. Sampling and processing

We collected samples of *C. glomerata* (Chlorophyceae), *Ceramium tenuicorne* (Kützting) Wærn (Rhodophyceae), *Fucus vesiculosus* L. (Phaeophyceae) and

drifting algal mats on a monthly basis over a 3-month period (early July–late September 2002). Samples were collected at Hinderbengtsviken (hereafter HBV, 60°09' 53"N, 20°32'05"E, Åland islands, Finland). HBV is a shallow bay where the three abovementioned algal species dominate the algal belts occurring on the rocky areas. On each sampling occasion, 100 cm<sup>2</sup> algal areas of *C. glomerata* and *C. tenuicorne* growing on the rocks were randomly chosen, scraped off with a paint-scraper and placed in plastic bags. *F. vesiculosus* samples were collected by covering individuals with a plastic bag and detaching them wholly (including the holdfast) from the rock. Drifting algal mats (which consisted mainly of *C. glomerata* and *C. tenuicorne*) were sampled by sweeping the beds with a push net, and taking approximately equal samples from the swept bulk by hand. Samples were replicated three times.

In the laboratory, samples were either processed immediately or frozen until subsequent faunal extraction. The whole content of the bag was rinsed thoroughly under running fresh water through a series of 500–125–63 µm sieves. Animals retained on the 63 and 125 µm sieves were preserved in 4% hexamine-buffered formalin with rose-bengal until taxonomic study. Following animal extraction, wet and dry (60 °C for 48 h in a drying oven) weight of the algae were determined. Copepods were sorted under a stereomicroscope at 20–60 × magnification and identified to the lowest taxonomic level possible.

In 2003, samples were taken at a different location also in the Åland islands (Äppelö, 60°17'N, 19°49'E), on a single occasion, and only from *C. glomerata* and drifting algal mats (consisting, this time, essentially of *C. glomerata*). Two types of *C. glomerata* were sampled, one green and healthy looking and the other brownish, showing clear signs of decay. Four replicate samples of each type were taken by hand, each from an area covering approximately 0.5 m<sup>2</sup>. Drift algal samples were collected as mentioned above, with the aid of a push net. All samples were taken immediately to the laboratory and processed directly, as indicated above. On this occasion however, both the macro (>500 µm) and meiofauna (<500 µm) fractions were directly frozen once extracted until further sorting, taxonomic identification and processing for stable isotope analyses.

Animals for the experiments were collected at different sites of the Baltic Sea in Finland and Sweden: the Åland archipelago, coastal areas near Turku (60°27'N, 22°17'E) and Stockholm (59°23'N, 18°00'E). Algae were scraped off from the rocks and rinsed thoroughly in sea-water on the shore. Water was

then sieved through a 63 µm mesh size sieve and animals collected in containers for subsequent sorting in the laboratory. There, harpacticoid copepods were isolated from the samples and putative species separated for bulk culturing under laboratory conditions. Ovigerous females of *M. rapiens* and *M. aestuari* were then isolated and cultured independently in order to obtain pure cultures of each species. All cultures were fed with the diatom *Phaeodactylum tricorutum* Bohlin. We used this diatom since it is easily cultured and labelled in the laboratory and has proven to be a good food resource to maintain cultures of various species of harpacticoids.

## 2.2. Competition experiment

To examine whether competition for a single resource occurs between *M. rapiens* and *M. aestuari* we conducted a laboratory experiment in which both species were placed in sympatry and allopatry, and provided with different resource levels. We used three food levels (*P. tricorutum* labelled with bicarbonate enriched in <sup>13</sup>C): low ( $1.3 \times 10^5$  cells), medium ( $6.5 \times 10^5$  cells) and high ( $6.5 \times 10^6$  cells). Three replicate Petri plates (5 cm ø) containing 80 specimens of *M. aestuari* were fed at each of these levels. Low densities of *M. rapiens* in the bulk cultures at the time of initiation of the experiment allowed for allopatry analyses only at the medium resource level (also, three replicates with 80 specimens each). Additionally, 3 plates with 40 individuals of each species were prepared and fed at the three different food levels. After five days, all copepods were killed by freezing (–20 °C) and preserved frozen until sorting and processing for stable isotope analyses. Control samples consisted of three replicates of 40 individuals of each species extracted directly from the bulk cultures.

## 2.3. Stable isotope analyses

Animals in the samples or in the frozen plates were allowed to thaw and identified, counted and picked out under a stereomicroscope, placed in tin capsules containing 6 psu MilliQ water, and dried at 60 °C for 24 h. Using continuous flow, the samples were introduced into an isotope ratio mass spectrometer for isotopic analysis.  $\delta^{13}\text{C}$  values were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (vPDB) standards according to the formula:  $\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}}) - 1 \times 10^3$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$ . Analyses were performed by the UC Davis Stable Isotope Facility.

Table 1  
Copepods associated with the different algae over time

		Calanoids	Copepodites	Cyclopoids	Ectinosom.	<i>Halectinosoma curticorne</i>	<i>Itunella muelleri</i>	<i>Mesochra aestuاري</i>	<i>Mesochra rapiens</i>	<i>Mesochra copepodites</i>	<i>Nitokra spinipes</i>	<i>Pseudobradya sp.</i>	<i>Tachidius discipes</i>	Total
<i>C. glomerata</i>	E. July		1±0.4			3±0			4±0.5		4±1			3±1
	L. July	0.8±0							6±4		2±0			4±2
	August	5±5	17±0					18±17	41±43	4±0	11±8		2±0	21±30
	September	4±2	8±6				3±0	95±112	198±260	19±3	88±0		2±1	91±159
	Total	4±4	7±7			3±0	3±0	66±95	51±84	15±8	21±37		2±1	46±110
Drift algae	E. J.	22±16								1±0			1±0	13±16
	L. J.	195±259				0.02±0	0.1±0.1	0.6±0.6	0.07±0	0.6±0.5			0.5±0.6	16±75
	A	3±0.1	1±1	0.7±0.8		0.06±0	2±0.3	1±0.3	0.6±0.5	0.7±0			0.1±0	1±1
	S	0.08±0				0.3±0		0.1±0		0.1±0				0.1±0.1
	T	58±130	0.7±1	0.7±1		0.1±0.1	1.7±1	0.9±0.6	0.6±0.5	0.6±0.4			0.5±0.6	8±47
<i>F. vesiculosus</i>	E. J.	0.09±0.16	14±9	0.09±0.16		0.6±0.6	0.9±0.9	25±13			21±15		0.4±0.5	63±26
	L.J		10±4			0.09±0.15	2±1	3±3	41±39		50±44		0.1±0.2	107±90
	A	0.4±0.3	3±3	0.04±0.06				4±5	4±5		0.04±0.06		0.2±0.1	12±13
	S	0.8±0.6	0.2±0.4			0.1±0.2		0.2±0.2			0.09±0.1			1±1
	T	0.2±0.4	7±6	0.04±0.08		0.05±0.11	0.6±0.9	2±3	19±22		19±26		0.2±0.3	48±53
<i>C. tenuicorne</i>	E. J.		6±6				1±0	1±0	2±0		7±3		0.8±0	5±4
	L. J.		126±0		12±0	30±0.2		31±10	382±125	123±131	83±69	36±0	134±94	140±155
	A							7±0	62±54	4±0	19±10			30±38
	S	2±0.1						13±9	21±5	8±7	1±0.6	1±0	2±0	12±9
	T	2±0.1	36±60		12±0	30±0.3	1±0	20±13	170±188	53±92	30±44	24±20	114±99	71±120
Total	20±77	7±24	0.3±0.6	12±0	19±15	0.6±0.7	25±56	77±155	25±58	14±31	24±20	43±81	33±90	

Values represent mean±SD of abundance per gram of dry weight algae in all cases except that of *F. vesiculosus*, where values are given per 10 g dry weight algae. E., early; L., late; A, August; J, July; S, September, T, total.

Table 2

Summary of results from one-way ANOVA investigating differences in the mean abundance of *M. aestuari* and *M. rapiens* between the three *Cladophora* stages in 2003

	Deteriorated	Drifting
<i>M. aestuari</i>		
Fresh	***	**
Drift	n.s.	
<i>M. rapiens</i>		
Fresh	***	**
Drift	n.s.	

n.s. = non-significant; \*\*= $p < 0.01$ ; \*\*\*= $p < 0.001$  in post-hoc Tukey tests.

2.4. Statistical analyses

2.4.1. *M. rapiens*–*M. aestuari* abundance patterns

We examined whether variations in the abundance of both species followed similar patterns at HBV using correlation analyses. We considered mean abundance of each species per gram of dry weight algae and run correlations for each of the algal types pooling data from all sampling dates together, and for each of the sampling dates pooling data from all algal species. Pearson Product Moment or Spearman correlation analyses were used depending on compliance of the log-transformed data with parametric assumptions of normality and homoscedasticity.

To analyse whether there were significant differences in the abundance of *M. aestuari* and *M. rapiens* in the different algal assemblages sampled at HBV and ÄÖ, and in the relative abundance of both species over time at HBV, we performed a Student *t*-test or its non-parametric counterpart, the Mann–Whitney *U* test on

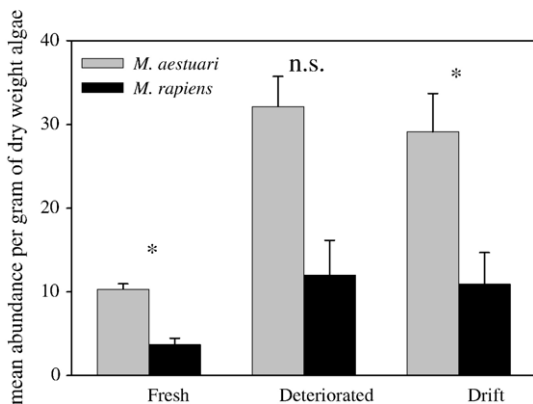


Fig. 1. *M. aestuari* and *M. rapiens* average ( $\pm 1SE$ ) abundance in the different *C. glomerata* deterioration stages and drifting algae at Äppelö, in 2003. The results of the Student *t* and Mann–Whitney *U* tests are indicated by n.s. = non-significant and \*= $p < 0.05$ .

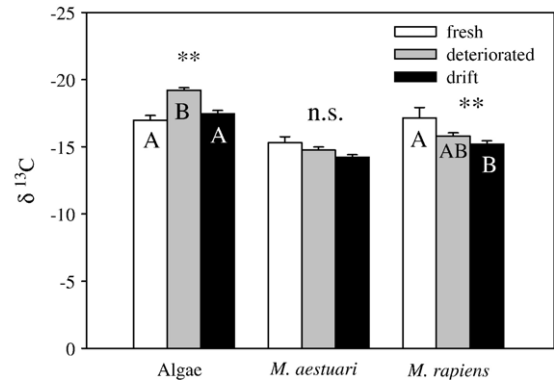


Fig. 2. Average ( $\pm 1SE$ ) stable carbon isotope ratios in fresh, deteriorated and drift *Cladophora glomerata* and in the two copepod species from the respective algal types. The results of ANOVA are indicated by n.s. = not significant and \*\*= $p < 0.01$ . Columns with common letter codes indicate no significant difference according to Tukey test.

ranks, based on the previously mentioned parametric assumptions, for each of the algal types under analysis at each site and for each of the sampling times, at HBV. Again, all analyses were conducted on log-transformed data (indiv. per gram of dry weight algae) by pooling all the samples of each algal species from all sampling dates ( $N_{C. glomerata} = 11; N_{C. tenuicorne} = 12, N_{Fucus} = 12; N_{Drift} = 9$ ) or vice versa ( $N_{early July} = 12; N_{late July} = 12; N_{August} = 12; N_{September} = 11$ ) at HBV, and for each of the 3 algal types at ÄÖ ( $N_{fresh} = 4; N_{deteriorated} = 4; N_{drift} = 4$ ). Due to the high number of comparisons involved in these analyses we performed the Bonferroni sequential correction to prevent Type I error.

Table 3

Summary of one-way ANOVA within species results for the competition experiment

	Sym. low	Sym. med.	Sym. high	Allo. low	Allo. med.	Allo. high
<i>M. aestuari</i> (one-way ANOVA, $F = 211, 829; p < 0.001$ )						
Control	n.s.	*	***	n.s.	n.s.	**
S. low		*	***	n.s.	n.s.	**
S. med			***	**	n.s.	n.s.
S. high				***	***	***
A. low					n.s.	**
A. med						n.s.
<i>M. rapiens</i> (one-way ANOVA, $F = 72, 248; p < 0.001$ )						
Control	n.s.	n.s.	***		***	
S. low		n.s.	***		***	
S. med			***		***	
S. high					n.s.	

n.s. = non-significant, \*= $p < 0.05$ , \*\*= $p < 0.01$ , \*\*\*= $p < 0.001$ , in Tukey post-hoc comparisons, respectively. Sym. and s. = sympatry; allo. and a. = allopatry; low, med., high, low, medium and high food levels respectively.

Differences in the abundance of both species among the three *C. glomerata* algal stages were examined by means of a one-way ANOVA, using Tukey's as post-hoc test.

#### 2.4.2. Stable isotope analyses in *C. glomerata*, and competition experiment

Differences in  $\delta^{13}\text{C}$  values among treatments were analysed by means of one-way ANOVA or Student *t*-tests on log-transformed data, after checking that data complied with homoscedasticity and normality. Post-hoc differences were examined using Tukey's test.

### 3. Results

#### 3.1. *M. rapiens*–*M. aestuari* abundance patterns

At HBV *M. rapiens* and *M. aestuari* were the dominant copepods throughout the sampling season and in all the sampled algal types except drifting algae, where calanoid copepods amounted to 82% of total abundance (Table 1). Both species abundance co-varied in *C. glomerata* (Pearson  $r^2=0.83$ ;  $p<0.001$ ) and *C. tenuicorne* (Spearman  $R=0.745$ ;  $p<0.01$ ), while no relationship was found between their abundance in drifting algae or *F. vesiculosus* (for both,  $p>0.05$ ). Over time, their abundance was highly correlated in late July (Pearson  $r^2=0.92$ ,  $p<0.001$ ) and September (Pearson  $r^2=0.84$ ,  $p<0.001$ ) when the abundance of both species was higher (Table 1), while no relationship occurred in early July or August ( $p>0.05$ ).

The abundance of both species was not significantly different in any of the algal types under analyses ( $p>0.05$ ), grouping all sampling times together. Over time, the abundance of both species experienced more or less the same peaks in all algal types (Table 1). No

significant differences in the abundance of these two species were found at any sampling time, considering all algal types together ( $p>0.05$ ).

In *C. glomerata* samples from 2003, *M. aestuari* was significantly more abundant than *M. rapiens* in both fresh (Student *t*-test,  $p<0.05$ ) and drifting algae (Mann–Whitney *U* test,  $p<0.05$ ), but not in the deteriorated algal samples ( $p>0.05$ ). Both species were significantly more abundant in the deteriorated and drifting samples than in fresh *C. glomerata* (Table 2, Fig. 1).

#### 3.2. Stable isotope analyses in *C. glomerata*

Results on stable isotope analyses indicated the  $\delta^{13}\text{C}$  signals of both *Mesochra* species, were close to that of the algae in fresh *C. glomerata* samples, but differed notably from the signals in deteriorating and drifting algae (Fig. 2). While no significant differences were found between both species  $\delta^{13}\text{C}$  values in fresh *C. glomerata* ( $p>0.05$ ), *M. rapiens* showed a significantly lower signal than *M. aestuari* in both deteriorated (Student *t*-test,  $p<0.01$ ) and drifting algal samples (Student *t*-test,  $p<0.01$ ). Even if both species showed a similar trend, higher signals being registered with progressive deterioration of the algae, *M. aestuari* showed no significant differences in  $\delta^{13}\text{C}$  values between the different algal types, while *M. rapiens*  $\delta^{13}\text{C}$  signal differed significantly between fresh and drift algae (Fig. 2).

#### 3.3. Competition experiment

Both harpacticoid species thrived under the experimental conditions. However, behavioural differences were observed between them. While *M. aestuari* displayed less activity and a tendency to lie on the bottom of the Petri plates, only performing short excursions every now and then and avoiding contact with other animals, *M. rapiens* showed high activity and moved rapidly all over the Petri plates. As regards the stable isotope values, *M. aestuari* showed significant higher assimilation in the company of *M. rapiens* at high food levels than at any food level in allopatry (Table 3), while *M. rapiens*' assimilation was significantly higher in the absence of *M. aestuari*, at medium and low levels (Table 3; Fig. 3). When we compared assimilation values between species cultured in sympatry, the dependent samples *t*-test revealed a significantly higher carbon signal for *M. aestuari* only at medium food levels ( $p<0.05$ ), while no differences between species were detected at low or high food levels ( $p>0.05$ ).

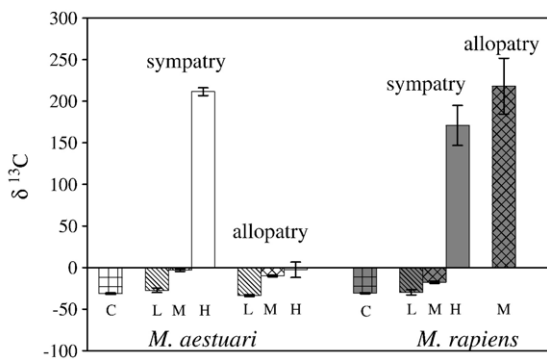


Fig. 3. Average ( $\pm 1$  SE) stable carbon isotope ratios in the two copepod species in allopatry and sympatry at 3 resource levels (L: low, M: medium, H: high). C indicates initial stable isotope ratios in the copepods.

#### 4. Discussion

The apparent variety of resources used by *Mesochra aestuari* and *M. rapiens* in the field is in agreement with the general belief that phytal harpacticoids effectively partition resources and feed on a variety of them, allowing for co-existence of even closely related species in the same habitats (Marcotte, 1977; Nilsson, 1987; Steinarsdóttir et al., 2003; Arroyo et al., 2006). Differences in carbon signatures detected through the stable isotope analyses, together with data on other harpacticoid species collected from the same habitats showing a general high variation in resource use (Aarnio et al., unpublished), support these data and the extended view that harpacticoids tend to be selective in their food choice (e.g. Lee et al., 1977; Vanden Bergh and Bergmans, 1981; Rieper, 1982; Carman and Thistle, 1985; Buffan-Dubau and Carman, 2000). The carbon isotopic ratio in *M. aestuari* was similar in the three stages of *C. glomerata* while there was a significant difference among habitats in *M. rapiens*. This may indicate that while *M. rapiens* used a wider variety of resources within the different *C. glomerata* stages, *M. aestuari* was more confined to a single food type which it exploited regardless of the state of deterioration of *C. glomerata* or of whether the algae were extant or part of a drifting algal mat. On the other hand, it may also reflect different residential times of the two species between them and among the different algal types. Harpacticoid copepods and phytal meiofauna in general have been found to frequently enter and leave phytal assemblages (Hicks, 1985), and the different isotope abundances found may just be an indication of this trend. In this sense, both *Mesochra* species could be feeding differentially on resources other than the algae (i.e.: phytoplankton, macrophyte detritus, benthic microalgae), which would in itself account for variation in isotopic values.

These results must hence be interpreted with caution and do not allow for greater speculation regarding feeding relationships, or competition between these two species.

On the contrary, results from our experiments clearly show that at least in laboratory conditions, and when provided a unique resource, an asymmetric relationship between the two species takes place. The most striking part of these results is the fact that *M. aestuari*'s assimilation was higher when both species were together than when it was kept alone at similar food levels. This suggests that *M. rapiens*, while being negatively affected by the presence of *M. aestuari*, must have exerted some beneficial indirect effect on the latter species resource assimilation.

Facilitation between harpacticoid species was already suggested by Chandler and Fleeger (1987), who found

that certain sympatric species seemed to be attracted to the tubes and mucous secretions of *Pseudostenhelia wellsi* Coull and Fleeger. They speculated that *P. wellsi* might “garden” microflora in their tubes, as was discussed by them in a previous contribution (Chandler and Fleeger, 1984), and this rich environment may act as an attractant for the other species. Harpacticoid copepods have also been found to readily utilize the microbial film associated with their own (Hicks and Grahame, 1979) or diatom (Decho and Fleeger, 1988; Souza-Santos et al., 1999) mucous secretions. We have no evidence that *M. rapiens* produces any abundant mucous secretion that may enhance microbial proliferation, but the diatoms offered to them as food could have provided the necessary substrate for them to “garden” a rich microbial film, a possible source being the microbial fauna associated with their faecal pellets. Reworking of original food resources by gut processing and the additional nutritional value supplied by associated microbes, has been found to render faeces as a thrifty alternative in times of food shortage, and an important food item for larval or juvenile stages of same or different species which are unable to consume bigger or more difficult-to-assimilate food items (McBrayer, 1973; Mac Lachlan et al., 1979; Green et al., 1992). Consumption of faecal pellets by harpacticoids has been described (Feller, 1980), although the extent to which it is a common trait or just an alternative in times of food shortage remains questionable (see Hicks and Coull, 1983), mainly due to their low nutritional value compared to other food resources. However, De Troch et al. (2005) found higher assimilation rates when feeding *Nitokra spinipes* Boeck with its own faecal pellets rather than with diatoms alone, and suggested that enrichment via bacterial consumption was enhancing the assimilation of carbon by this species. Moreover, several authors have described dissemination of microbes and fungi via other invertebrates' faecal pellets and stimulation of their growth in the dispersers own produced mucous trails or abraded surfaces (Cayrol and Dreyfus, 1975; Riemann and Helmke, 2002; Silliman and Newell, 2003). We have often observed harpacticoids swimming among their own “faecal mounds” and carrying considerable amounts of faecal material entangled within their furcae while swimming.

Another possible way in which *M. rapiens* may have “assisted” *M. aestuari*'s feeding is by a mechanical “opening diatom” process. It could be that *M. rapiens* is more effective in breaking up diatoms than *M. aestuari*. If this is the case, then the latter may have benefited from organic matter being released from the diatoms that *M. rapiens* broke while feeding.

Our results reveal an asymmetric relationship between two closely related harpacticoid species in the

laboratory. While one has a negative effect on the other, this one has an indirect positive effect on the first one, possibly through resource amelioration via microbial gardening. The extent to which this indirect effect occurs also in nature and may be determinant for their co-occurrence in phytal habitats or just an “added value” of the species interactions is uncertain, as is the degree to which these two species (and their feeding strategies) have co-evolved in these habitats.

## Acknowledgments

We thank Husö Biologiska Station for providing the facilities and sampling equipment. M. Ekblad sorted the copepods from HBV and helped in the field, and N. Isaksson sorted and identified the copepods associated with *F. vesiculosus*. We also thank E. Bonsdorff for his support of this study (project IMAGINE under the BIREME-program of the Academy of Finland; contract # 202389) and an anonymous referee for constructive criticism. This study was supported by a European Community Marie Curie fellowship (EVK-CT-2002-50019) to the first author. [SS]

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