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Some lower food web organisms in the nutrition of marine harpacticoid copepods: an experimental study

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ABSTRACT: Some lower food web organisms from the marine littoral environment were studied as food for harpacticoid copepods. In laboratory experiments, it could be shown that, among the ciliates, the slow-moving *Uronema* sp. was taken up while the fast-moving *Euplotes* sp. was not. *Asterionella glacialis*, a pennate diatom with spiny projections, was unsuitable as food. The centric diatom *Skeletonema costatum* was ingested by all harpacticoid species tested, including *Tisbe holothuriae, Paramphiascella vararensis, Amphiascoides debilis* and *Dactylopodia vulgaris*. All are epibenthic and phytal species occurring in the shallow waters of Helgoland (North Sea). The amount of ciliate and algal carbon taken up was less than that provided by bacteria under laboratory conditions. However, some diatom food may be essential for the development of *D. vulgaris*.

INTRODUCTION

Harpacticoid copepods (Crustacea, Copepoda) are important food items in the diet of many larval and juvenile fish (Kaczynski et al. 1973; Sibert et al. 1977; Hicks & Coull, 1983 and the literature cited therein; Morais & Bodiou, 1984). Harpacticoids may even constitute the main prey for young postmetamorphic flatfish (Hicks, 1984) and a small epibenthic fish, the spotted dragonet (Sogard, 1984). Methods for the mass cultivation of harpacticoids as food for fish larvae are presently being studied (Uhlig; unpubl. report). The ecology of harpacticoid copepods is thus of great interest and has been reviewed recently by Hicks & Coull (1983). This work includes a detailed section summarizing what is known about the trophic relations of harpacticoids. Meiobenthic forms ingest a wide variety of food including diatoms, phytoflagellates, bacteria, fungi and yeasts, blue-green algae, mucoid substances and ciliates. Some of this knowledge has been obtained by culturing individual harpacticoid species in the laboratory, or by observations made directly in situ or on gut contents. In many cases quantitative data are lacking.

It is the purpose of this paper to gain further insight into the nutritional requirements of marine harpacticoid copepods by means of feeding experiments with ciliates and algae, as a supplement to those performed with bacteria as food (Rieper, 1978). The species investigated were all isolated from the southern North Sea, are relatively abundant, and are easy to cultivate in the laboratory. The experiments described here were carried out under controlled laboratory conditions, in order to provide quantitative data on these organisms as related to the food web of coastal waters.

MATERIAL AND METHODS

The main criteria for the choice of the particular species investigated were their relative abundance, ecological relevance, availability (easy to isolate and maintain in culture) and suitability for feeding experiments (e.g. ciliates and algae small enough to be captured and ingested by harpacticoid copepods).

Habitats

Harpacticoid copepods

Tisbe holothuriae (Fam. Tisbidae): although commonly regarded as a phytal species, was, as the name implies, originally described as an intestinal parasite of the sea cucumber *Holothuria stellati* (Humes, 1957). *T. holothuriae* has been found in an outdoor swimming pool containing heated seawater (23 °C) (Uhlig & Noodt, 1966; *T. helgolandica* = *T. holothuriae*), as well as among brown algae in the rocky intertidal zone of Helgoland. The average length of an adult female is 930 µm.

Paramphiascella vararensis (Fam. Diosaccidae) has also been found in various biotopes, among red algae, mussels and coarse sand from Helgoland (Klie, 1949, 1950) as well as in sublittoral sediments, and in the seawater pipe system of the author's laboratory at Helgoland (Rieper, 1978). The average length of an adult female is 780 µm.

Amphiascoides debilis (Fam. Diosaccidae) was isolated from the sandy beach at List/Sylt, where it was found to prefer the surface of sediments (Mielke, 1976). *A. debilis* has also been located in the upper algae zone among laminarians at Helgoland (Klie, 1949, 1950). The average length of an adult female is ca 500 µm.

Dactylopodia vulgaris (Fam. Thalestridae) occurs mainly in the green and red algae zones and in tide pools (Lang, 1948; Klie, 1949). It was isolated from the rocky intertidal at Helgoland. The average length of an adult female is 540 µm.

Ciliates

Uronema sp. (probably indentical with *Uronema marinum* Dujardin, Fam. Uronematidae) was isolated from intertidal sediments at List/Sylt; it also occurs in the waters of the Helgoland rocky intertidal zone. The lag phase length of *Uronema* sp. is 20–30 µm.

Euplotes sp. (Fam. Euplotidae) was found as a persistent contaminant in laboratory cultures of *Tisbe*. *Euplotes* sp. bears resemblance to *E. moebiusi* Kahl. The length of cells in the lag phase is 30–35 µm. Although the genus *Euplotes* is considered benthic, some species of *Euplotes* and also *Uronema* occur in open coastal waters as well as in the mesopsammon and other biotopes (Hartwig, 1973).

Algae

Skeletonema costatum and *Asterionella glacialis* (Bacillariophyceae) are common representatives of centric and pennate diatoms, respectively, among the phytoplankton occurring in coastal waters (Drebes, 1974). Individual cells of *S. costatum* filaments have a diameter of 3–20 µm. *A. glacialis* cells have a basal diameter of 5 µm and an apical length of 50–100 µm; the cells are arranged in coiled filaments.

It is reasonable to assume that the organisms above may be found coexisting in the field, particularly during and immediately after the occurrence of plankton blooms.

Cultivation

For the most part, the methods of cultivation have been published in detail (Rieper, 1978; Rieper & Flotow, 1981), and will be described here in short form only.

Harpacticoid copepods: stock cultures of all species were maintained in seawater (ca 30 ‰ S) in small glass vessels at 15°–18 °C. Food consisted of dried mussel meat and a fish food mixture; *Dactylopodia vulgaris* received in addition a suspension of *Skeletonema costatum.*

Ciliate protozoans: *Uronema* sp. and *Euplotes* sp. were cultivated in small glass vessels with seawater and were fed loopfuls of live bacteria which were scraped directly from agar plates. The bacteria, *Vibrio* sp. (designated as List – 7 in Rieper & Flotow, 1981) were grown on standard yeast extract – peptone agar ZoBell 2216E.

Algae: *Skeletonema costatum* and *Asterionella glacialis* were grown in F/2 culture medium described in Guillard & Ryther (1962).

Feeding experiments

Experiments were carried out in covered glass dishes containing 30 ml seawater (ca 30 ‰ S). Parallel dishes were set up for each food tested, and each experiment was performed in duplicate. Fresh, healthy organisms were tested, and used only once in an experiment. The stock cultures of harpacticoids, ciliates and algae were not axenic, but the numbers of contaminating bacteria were too low to influence the feeding rates. Experiments were carried out at 18 °C (except with *D. vulgaris* at 15 °C) in incubators with a light:dark cycle of LD 12:12* (fluorescent lighting „warm white deluxe", 10–60 lux). Dishes were stirred gently for 2 min immediately before an aliquot was removed for counting. To determine the numbers of ciliates and algae, an aliquot of 1–2 ml was removed from each dish, fixed with Lugol's solution, filtered onto a 0.45 µm membrane filter, stained with erythrosin, and counted under a microscope at 160–400× magnification. Calculations were made from the average values obtained from 10–20 visual fields counted. For the algae, the total numbers of cells (filaments were of various lengths) were determined. Harpacticoid copepods were transferred with a Pasteur pipette and counted individually.

The method used for labelling the algae was based on that of Lampert (1974). A suspension of algae was incubated with ^{14}C-$NaHCO_3$ (Amersham Buchler, Braunschweig, FRG); the activity of the supension was 0.1 µCi ^{14}C ml^{-1}. After 16–17 h incubation, the algae were removed from the radioactive medium and resuspended in non-labelled seawater. Aliquots of this suspension were given to the harpacticoid copepods. At the end of an experiment, the activity in the harpacticoids was determined with a liquid scintillation counter (Betaszint 5000; Berthold & Frieseke). Further details are given in Rieper (1978).

The length of an experiment varied according to the food tested: 72 h with ciliates as food source, 24 h with labelled algae, and over 4 weeks with non-labelled algae (covering one life cycle of the harpacticoid species tested). Only late copepodite and adult ♂ and ♀ stages were used in all short-term feeding experiments with ciliates and

* A light:dark cycle of LD 15:9 (natural daylight conditions in the spring) was used for long-term feeding experiments with *Dactylopodia vulgaris* and algae.

labelled algae as food. The numbers of harpacticoids in each replicate dish ranged from 25–70 individuals. The long-term test series with *Dactylopodia vulgaris* was an exception: here the nauplii from one egg sac of a healthy gravid ♀ (usually 8 from one egg sac; in two cases 4 and 6 respectively) were used as initial test organisms in each replicate dish.

RESULTS

Figure 1 shows the uptake rate of the ciliate *Uronema* sp. by *Tisbe holothuriae* (1a) and *Paramphiascella vararensis* (1b) at 18 °C. The graphed values represent the averages of two replicate determinations in a test series using the given initial concentrations of

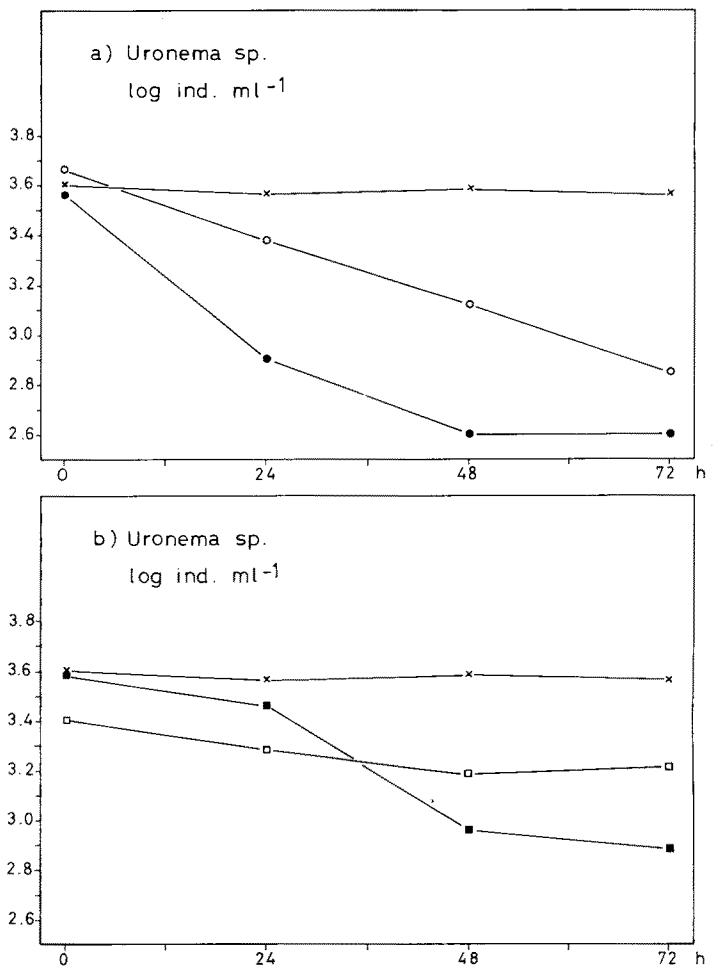

Fig. 1. Laboratory experiments with the ciliate *Uronema* sp. as food for the harpacticoid copepods *Tisbe holothuriae* (1a) and *Paramphiascella vararensis* (1b) at 18 °C. × ciliates without copepods (control); ○ ciliates + 25 *Tisbe;* ● ciliates + 50 *Tisbe;* □ ciliates + 35 *Paramphiascella;* ■ ciliates + 70 *Paramphiascella.* Points on graphs represent average values of 2 replicates, each replicate made with 25, 50, 35 and 70 copepods, respectively

ciliates (log ciliate individuals ml^{-1}) and harpacticoids (25 and 50 *T. holothuriae*, 35 and 70 *P. vararensis* for each separate replicate, respectively). In *T. holothuriae*, there was a strong decrease in the numbers of ciliates after 24 h already, and after 72 h a six to tenfold decrease. In *P. vararensis* the uptake of *Uronema* sp. was slower and not quite so pronounced. Nevertheless, compared to the controls without harpacticoids, there was a clear reduction in the numbers of ciliates present with both harpacticoid species. Considering the 72 h period as a whole, the uptake rates are as follows (ranges represent the average values for the two respective concentrations of harpacticoids, with the differences between the average and measured values): for *T. holothuriae*, 26.8 (0) to 65.3 (11.7) *Uronema* copepod^{-1} h^{-1}; for *P. vararensis*, 10.8 (6.0) to 18.2 (2.1) *Uronema* copepod^{-1} h^{-1}.

The results of feeding experiments with *T. holothuriae* and *P. vararensis* using the ciliate *Euplotes* sp. as the sole food source were negative. Neither of the harpacticoid species ingested *Euplotes* sp., although no other food was available. The question was posed as to whether *Euplotes* sp., generally considered benthic, would be more readily consumed if a substrate were present upon which the ciliates could settle. To answer this, pieces of dried mussel meat were given to *Tisbe* in addition to *Euplotes*. Although the ciliates concentrated around and upon the mussel meat particles, and thus would have been easier prey for the copepods, *Tisbe* ate the meat and ignored the ciliates.

Two species of algae were also used as food for the harpacticoid copepods, the diatoms *Skeletonema costatum* and *Asterionella glacialis*. The results of experiments in which the algae were labelled with ^{14}C are presented in Table 1. Among the harpacticoids, the highest uptake rate was found in *Tisbe holothuriae*, closely followed by that

Table 1. Uptake of ^{14}C-labelled algae by different harpacticoid species (18 °C). In all cases, 25 copepods were used in each replicate

Harpacticoid copepods	Algae	Initial concentration of algae (ml^{-1})	Average uptake algae cells cop.$^{-1}h^{-1}$ and deviation from mean	Average uptake µg C cop.$^{-1}d^{-1}$
Tisbe holothuriae	*Skeletonema costatum*	413,000	334.9 (0)	0.161
Paramphiascella vararensis	*Skeletonema costatum*	19,380	65.9 (9.4)	0.032
			94.5 (24.4)*	0.038*
		413,000	212.7 (100.8)	0.102
Amphiascoides debilis	*Skeletonema costatum*	413,000	50.3 (17.8)	0.024
Tisbe holothuriae	*Asterionella glacialis*	129,000	11.5 (1.8)	0.003
Paramphiascella vararensis	*Asterionella glacialis*	2,200	4.8 (0.6)	0.001
		4,500	4.8 (0.2)	0.001
		6,700	5.0 (1.3)	0.001
		28,700	11.5 (0.1)	0.003
			43.0 (2.4)*	0.007*
		129,000	20.6 (5.6)	0.005

* Values measured after 6 h; all others after 24 h

of *Paramphiascella vararensis*. The uptake of *Skeletonema* by *Amphiascoides debilis* was much lower. As a food source. *Skeletonema* proved far more attractive to the harpacticoids than *Asterionella*, even at a lower initial concentration (as in the case of *P. vararensis*), although the carbon content of the cells is similar: 2×10^{-5} µg for *Skeletonema* and 1×10^{-5} µg for *Asterionella* (Hagmeier, pers. comm.). The rates of carbon uptake in Table 1 are those measured for 24 h except where otherwise indicated. The uptake rates by *P. vararensis* were higher after the first 6 h, indicating that initial feeding took place at a more rapid rate than over the 24 h period as a whole. Two replicates were made for each test series, with 25 copepods for each replicate.

A long-term experiment with non-labelled *Skeletonema* was carried out with the harpacticoid species *Dactylopodia vulgaris*, to determine the effect of these algae on the growth rate. The results are shown in Table 2: 8 freshly-hatched nauplii were used

Table 2. Effect of various foods on the development of *Dactylopodia vulgaris* (15 °C): Mean values ± standard deviations; 8 freshly-hatched nauplii per replicate

Food	Number of replicates	Days from hatching of nauplii to first copepodite	Days from hatching of nauplii to first ♀ with egg sac	Days from hatching of nauplii to first hatching of new nauplii
Fish food and mussel meat	2	11.5	–	–
Fish food, mussel meat, *Skeletonema costatum*	4	7.8 ± 1.0	22.3 ± 4.8	24.8 ± 4.5
Skeletonema costatum (alone)	5	7.6 ± 0.5	23.2 ± 3.5	27.6 ± 2.5

initially per replicate. More rapid rates of growth were obtained when *Skeletonema* was offered as a supplement with fish food and mussel meat, than with the algae alone. *D. vulgaris* was unable to reproduce on a diet of dried fish food-mussel meat without the algae, under the experimental conditions given.

DISCUSSION

In previous investigations it was shown that the feeding rate of *Tisbe holothuriae* on *Uronema* sp. depends to some extent on the initial concentration of ciliate food (Rieper & Flotow, 1981). In the present study, the initial concentrations of *Uronema* sp. (2500–4600 ml^{-1}; Fig. 1) and *Euplotes* sp. (1000–5700 ml^{-1}; no uptake) were within a range where an increase in ciliate food would not have resulted in a substantially greater ingestion rate by the harpacticoids.

In the case of ^{14}C-labelled *Skeletonema costatum* (the uptake of *Asterionella glacialis* was too low to be considered here), a twentyfold increase in the initial algae concentration brought about only a threefold increase in the uptake by *Paramphiascella vararensis* (Table 1). Only one initial concentration of *Skeletonema* was used for *Tisbe holothuriae;* testing higher concentrations would have been unrealistic since one is not likely to encounter numbers of diatoms as high as 4×10^5 ml^{-1} or greater in the field. The large fluctuations in the algae uptake in some of the samples may be due to the difficulty of uniform labelling and inaccuracies in the method of counting cells on filters.

In order to compare the uptake of ciliates with that of the algae, the organic C content must be considered. Since the ciliate weights were not determined, those from the literature were employed in the calculations. For the given initial concentrations, ciliate uptake by the harpacticoids was approximately 27–65 *Uronema* cop. $^{-1}h^{-1}$ for *T. holothuriae* and 11–18 *Uronema* cop.$^{-1}h^{-1}$ for *P. vararensis* (Fig. 1; see text). If the dry weight of an individual *Uronema* sp. is 4×10^{-4} µg (Johannes, 1965) and 50 % of this is organic C (Gerlach, 1978), then the daily amount of ciliate C taken up was 0.13–0.31 µg C cop.$^{-1}d^{-1}$ by *T. holothuriae* and 0.05–0.09 µg C cop.$^{-1}d^{-1}$ by *P. vararensis*. These values are on the same order of magnitude as those found for *Skeletonema* (Table 1).

Even though previous feeding experiments using bacteria as food for harpacticoid copepods (Rieper, 1978) were performed under different conditions (dried bacteria particles vs. live ciliates and algae), the amounts of C uptake from these sources are compared in Table 3. It can be seen that the uptake of bacterial C per day is an order of

Table 3. Uptake of organic carbon by some harpacticoid copepods utilizing different food sources (ranges represent minimum and maximum values for the different kinds and initial concentrations of food organisms or copepods, respectively). Ciliate and algal uptake values calculated for organic C from results in Figure 1 and Table 1; for number of organisms and replicates, see text

Harpacticoid species	Bacterial uptake µg C cop.$^{-1}d^{-1}$ *	Ciliate uptake µg C cop.$^{-1}d^{-1}$	Algal uptake µg C cop.$^{-1}d^{-1}$
Tisbe holothuriae	1.03–1.71	0.13–0.31	0.16
Paramphiascella vararensis	1.53–3.54	0.05–0.09	0.03–0.10

* Rieper (1978)

magnitude higher than for ciliate or algal C. These results are compared to those of Brown & Sibert (1977) and Sibert et al. (1977) in which the feeding rate of harpacticoid copepods on different food sources was measured (Table 4). It can be seen that, in most cases, the uptake of bacterial C exceeded that derived from the algae. The algae here consisted of an enrichment containing "a wide variety of diatoms including some larger (> 200 µm) forms such as *Biddulphia* sp. and *Melosira* sp. as well as many small (≅ 20 µm) naviculoids" (Brown & Sibert, 1977).

Table 4. Uptake of organic carbon by some harpacticoid copepods utilizing different food sources (from Brown & Sibert, 1977), recalculated for a copepod with an average dry weight of 2.7 µg (Sibert et al., 1977)

Harpacticoid species	Bacterial uptake µg C cop.$^{-1}d^{-1}$	Algal uptake µg C cop.$^{-1}d^{-1}$
Tisbe furcata, Harpacticus uniremis	0.214	0.024
H. uniremis, H. spinulosus	0.266	0.025
Dactylopodia crassipes	0.292	0.324

CONCLUSION

It has been shown that whereas the ciliate *Uronema* sp. was ingested by both *Tisbe holothuriae* and *Paramphiascella vararensis, Euplotes* sp. was not. A reason may be that, due to the capability of rapid motion by *Euplotes,* these ciliates are not so easily captured or grazed upon as the relatively slow-moving *Uronema.* The rate of *Uronema* sp. ingested, compared to the daily C intake derived from other food sources such as bacteria (Rieper, 1978), suggests that ciliates do not play a major role in the nutrition of harpacticoid copepods, and probably only represent a dietary supplement. Other investigations have shown that some ciliates may be an important food source for planktonic

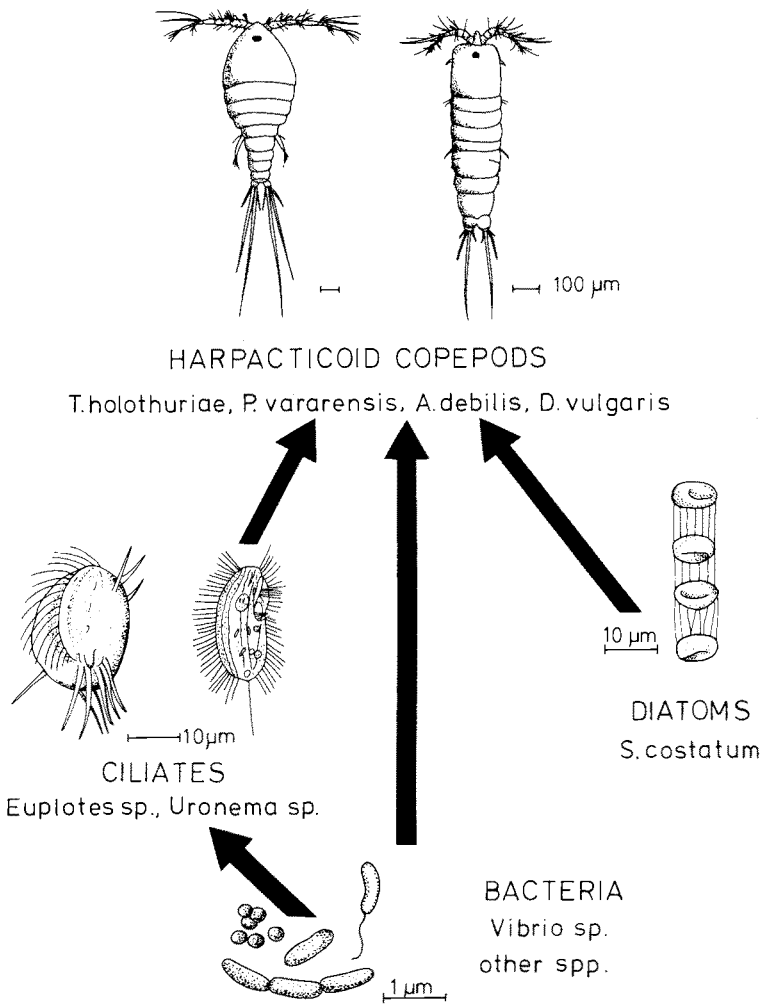

Fig. 2. Schematic representation of the role of some lower food web organisms in the nutrition of marine harpacticoid copepods

copepods such as *Eurytemora affinis* (Berk et al. 1977) and other zooplankton (Tezuka, 1974; Porter et al. 1979). Thus the role of the bacterivorous ciliates as links in the food web between bacteria and copepods requires further investigation.

The significance of diatoms in the nutrition of harpacticoid copepods has been well documented: Omori (1973) and Hicks & Coull (1983) compiled a list of literature references in which various foods for the cultivation and sustenance of harpacticoids in the laboratory were mentioned, and diatoms have often been used with success. In the studies described here, the uptake of the diatom *Asterionella glacialis* was negligible; the spiny projections on *A. glacialis* cells may cause these algae to be less attractive food items. Although short-term feeding experiments showed that *Skeletonema costatum* was ingested in relatively small amounts – as in the case of ciliates – compared to bacterial C, these algae were important in the development of *Dactylopodia vulgaris* (Table 2). Uhlig (unpubl. report) showed that cultures of *Tisbe holothuriae* fed with *S. costatum* exhibited a very high rate of naupliar production, exceeding that previously published with other food sources. This indicates that more long-term studies, as opposed to short-term observations, are needed before a general statement can be made on the role of algae as well as ciliates in the nutrition of harpacticoid copepods. The preliminary results with *D. vulgaris* reported here should also be supplemented with data on, for example, egg production, larval mortality and sex ratios, besides the length of developmental stages.

With the limitations of these laboratory studies in mind, a schematic representation of the role of some lower food web organisms as food for marine harpacticoids is given in Figure 2. Only the food organisms actually tested here are represented, and not the various other items which harpacticoids are known to ingest (phytoflagellates, fungi, mucoid substances, detritus, etc). Bacteria, which are consumed by many ciliates, are also directly ingested by some harpacticoid copepods. In contrast to *Euplotes* sp., *Uronema* sp. may form part of the diet of *Tisbe holothuriae* and *Paramphiascella vararensis*. The diatom *Skeletonema costatum* was ingested by all harpacticoid species tested and may be an important dietary supplement.

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