

Feeding of *Oncaea curvata* (Poecilostomatoida, Copepoda)

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ABSTRACT: *Oncaea curvata* is one of the dominating copepod species of the Antarctic in terms of numbers, and in the vicinity of the shelf often also in terms of biomass. However, little is known about its role in the ecosystem. The experiments of this study show that *O. curvata* females prefer large, non-motile food particles such as aggregates or gelatinous *Phaeocystis* colonies. Up to 18% of their body carbon was ingested daily from a *Phaeocystis* cf. *pouchetii* culture at natural concentrations, and up to 35% from a *Phaeocystis* bloom, which consisted of gelatinous colonies with other flagellate species and diatoms. The highest ingestion rates of about 300% of their body carbon per day were measured when feeding on a *Phaeocystis* bloom at higher than ambient concentrations. Diatoms were an acceptable food as well. The daily carbon uptake amounted to 2–26% of *O. curvata*'s body carbon at natural chlorophyll *a* concentrations. Accordingly this species may have as much influence on phytoplankton stocks as calanoid copepods. In contrast to many other Oncaeidae, *O. curvata* females were not carnivorous and did not feed on motile food (copepods or flagellates).

KEY WORDS: Copepod · *Oncaea curvata* feeding · Antarctic

INTRODUCTION

Copepods of the genus *Oncaea* (Poecilostomatoida, Copepoda) occur worldwide in high abundances. They inhabit different habitats from the tropics to the polar regions and from shallow areas to the deep sea (e.g. Turner & Dagg 1983, Nishida 1985, Schnack et al. 1985, Böttger-Schnack 1990, Paffenhöfer 1993) and often dominate numerically. However, they have been grossly neglected in former investigations of plankton. There are few studies of the Oncaeidae, and they are often only mentioned together with Oithonidae as 'cyclopoid copepods'. This is partly due to the sampling, which has mainly been in the upper part of the water column, where other species are abundant as well, and partly due to the small size of these copepods. It is their small size and their high abundance that probably allocates them an important role in the food web of pelagic communities. The Oncaeidae are ideal food organisms for fish larvae (Kellerman 1987) and other planktonic predators such as the calanoid

copepod *Euchaeta* sp. (Øresland & Ward 1993) and chaetognaths (Øresland 1990). Small facultatively carnivorous or omnivorous organisms also use Oncaeidae as food (Metz & Schnack-Schiel 1995). Only a few investigations into the feeding habits of the genus *Oncaea* have been made. Hopkins & Torres (1988) found remains of diatoms in their guts and Turner (1986) concluded that *Oncaea* were omnivorous because of their fecal pellet contents. Wickstead (1962) suggested a raptorial feeding habit for *Oncaea*, either as predator or semiparasitic/ectoparasitic on larger zooplankton. Only Paffenhöfer (1993) has worked experimentally with *Oncaea*. His data suggest omnivorous feeding.

In Antarctic waters there are several species of Oncaeidae, but the dominant species is the endemic, epipelagic *Oncaea curvata*. This species is very abundant and often dominates in terms of numbers or even in terms of biomass, especially in the shelf region (Metz 1996). However, its role in the pelagic food web of that area is unknown. Therefore, the purpose of this study was to investigate the feeding habits of *O. curvata*, especially food preferences and the effect of different conditions on feeding rates.

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MATERIAL AND METHODS

During 2 expeditions with the RV 'Polarstern' to the southern Bellingshausen Sea, west of the Antarctic Peninsula (Fig. 1), in January to March 1994 and in April 1995, live animals for experiments were caught from the upper 500 m of the water column with a Bongo net. It had a mesh size of 100 μm and an opening of 60 cm diameter. *Oncaea curvata* females were sorted from the catch under a Wild M3 dissecting microscope as soon as possible, and transferred to 2 l jars with filtered seawater and algae from different cultures. The jars were sealed without air bubbles and rotated on a Ferris wheel at 0.5 rpm at 0°C and in dimmed light for at least 3 d to adjust the copepods to laboratory conditions before setting up the experiments. The slow rotation simulates microturbulence and prevents algae and copepods from sinking to the bottom of the jars. During the acclimation period the *O. curvata* females were fed with the respective food organisms of the following experiments.

During the first expedition, experiments to quantify herbivorous feeding were conducted with cultures of the diatom *Porosira pseudodenticulata* [culture from M. Baumann, Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI), Bermerhaven, Germany], which occurs mainly as single cells or 2-cell chains, and the flagellate *Prorocentrum redfieldii* (culture from M. Elbrächter, Biologische Anstalt Helgoland, Germany). In addition, 2 mixed cultures were grown

from *in situ* water samples for other experiments. The culture 'ice algae' was dominated by different pennate diatoms from the ice, and the culture 'Phaeocystis bloom' by gelatinous colonies of *Phaeocystis* sp. The latter culture contained large diatom species as well. During the second expedition in autumn cultures of *Phaeocystis* cf. *pouchetii* (from L. Medlin, AWI) were tested as food. The algae were reared in the lab at 0°C (for *P. pseudodenticulata*, 'ice algae', 'Phaeocystis bloom' and *P. cf. pouchetii*) or in an incubation refrigerator at 5°C (for *P. redfieldii*). At constant light they were cultivated to high densities in Drebes medium (for diatoms) or f/2 medium (for flagellates). To keep the algae growing, the cultures were diluted with new medium every 3 to 7 d.

For the feeding experiments with *Oncaea curvata*, 0.5 l jars were filled with algae suspension, 5 to 80 copepods were added, depending on the algae concentration, and the jars were sealed bubble free. These jars were incubated on the Ferris wheel under laboratory conditions for 24 h, thus avoiding effects of diurnal changes in feeding rates on the experiments. At the beginning and end of every experiment water samples were filtered onto GF/C filters, and chlorophyll *a* (chl *a*) was measured with a Turner fluorometer (Evans & O'Reilly 1983). During the first expedition the measurements were done immediately after the experiment on board ship. The samples from the second cruise were frozen at -20°C and measured 2 mo later, in the lab. The chl *a* concentrations in the experiments ranged between 0.1 and 25 $\mu\text{g l}^{-1}$, to cover the range of concentrations occurring in different habitats of Antarctica.

Carnivorous feeding of *Oncaea curvata* was tested with calanoid copepods during the summer expedition. Nauplii, copepodids and adults of *Calanus propinquus*, *Calanoides acutus*, *Rhincalanus gigas* and *Metridia gerlachei* were isolated from Bongo net hauls and reared in beakers with algae suspensions at 0°C. For the experiments *O. curvata* females were transferred into 200 ml dishes, which contained a known number of calanoid nauplii, juveniles or adults of the above mentioned species in filtered seawater (see Table 2). The number of animals at the beginning and end of the 24 hour experiments was recorded and the behaviour of the animals observed. During experiments with copepodids and adults the containers were also checked every 3 h and the animals counted. During the sorting of the hauls the behaviour of *O. curvata* relative to other animals was observed.

Mean food concentrations in the experiments, volume swept clear (VSC) and ingestion rates (*I*) were calculated according to the equations of Frost (1972). The ingestion rates are given in $\mu\text{g C female}^{-1} \text{d}^{-1}$. To convert chl *a* values to carbon, a factor of 40 was used

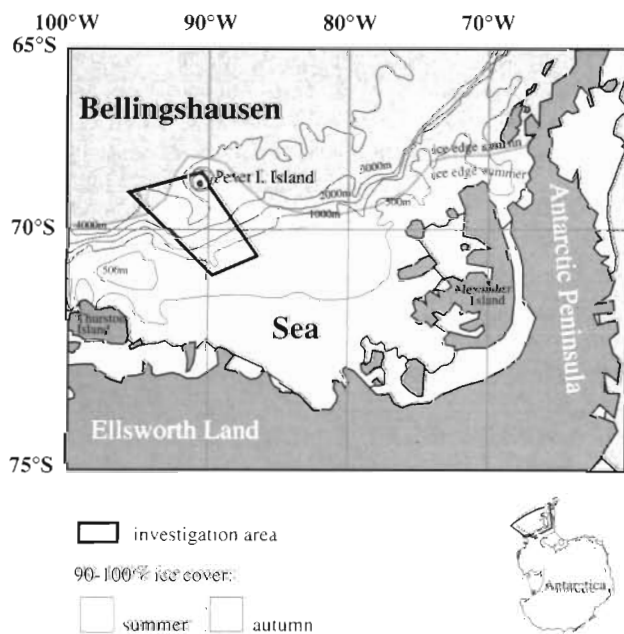


Fig. 1. Investigation area, southern Bellingshausen Sea

(Lenz 1974). VSC and I were plotted against the mean food concentration in the experimental jars. For ($0.5 \mu\text{g chl a l}^{-1}$)-classes mean VSC and I and their 'mean absolute deviation from the mean' (MA) was calculated according to the following equation:

$$\text{MA} = \sum |x_i - \bar{x}| n^{-1}$$

where x_i represents the datapoints, \bar{x} the mean and n the number of datapoints. The daily carbon uptake as a percentage of the body carbon of the females was calculated from the ingestion rates and the measured mean carbon content of the females.

During the autumn expedition 16 samples of *Oncaea curvata* females and 5 samples of *O. curvata* males were obtained for carbon analysis from Bongo net hauls at Stn 69 (8 April 1995) at $63^\circ 26.7' \text{S}$, south of the Polar Front, and Stn 104 (12 April 1995) at $69^\circ 24.6' \text{S}$. From the hauls, 7 to 10 *O. curvata* per sample were sorted, cleaned overnight in filtered seawater and then transferred to small silver capsules with fine forceps. These samples were frozen on board at -80°C . The carbon content was measured using the EasyQuant Carbon Analyzer EQ 92 of H.-J. Hirche (AWI). This instrument burns the carbon in the sample and measures the resulting CO_2 in a cuvette with a very sensitive double-beam infrared photometer. The carbon analyzer was calibrated with oxalic acid standards. The results (see Table 1) were converted into carbon content per individual (body carbon). The copepods for the feeding experiments originated from the area of Stn 104. Therefore, for the calculation of the feeding rates, only values from Stn 104 were used, because of extreme regional differences in the carbon content of this species. These were statistically proved by application of a t -test to the results of the carbon analysis.

RESULTS

Carbon measurements

The carbon contents of *Oncaea curvata* adults showed little variability within stations but were significantly different between stations (Table 1). According to statistical tests, the mean carbon contents of *O. curvata* females at Stn 69 are significantly ($p > 99.9\%$) lower than at Stn 104. The difference is not as pronounced in the males ($95\% < p < 99\%$). Stn 69 was far north of the investigation area, but south of the Polar Front, in an area with extremely low chl a concentrations in the water column ($< 0.01 \mu\text{g chl a l}^{-1}$). At the more southerly Stn 104, in the investigation area, the chl a content in the upper 50 m reached a maximum of $0.23 \mu\text{g chl a l}^{-1}$.

Table 1. *Oncaea curvata*. Carbon content ($\mu\text{g C ind.}^{-1}$) with mean (\bar{x}) and standard deviation (SD) of females and males (in parentheses: number of individuals per measured sample)

	Station 69		Station 104	
	Female	Male	Female	Male
	0.73 (10)	0.57 (20)	1.67 (10)	0.69 (20)
	0.96 (10)	0.51 (7)	1.53 (12)	0.74 (20)
	0.72 (10)		1.40 (10)	0.70 (20)
	0.89 (10)		1.66 (10)	
	0.61 (10)		1.70 (10)	
	0.45 (20)		1.48 (10)	
	0.76 (20)		1.45 (10)	
	0.65 (9)		1.49 (10)	
\bar{x}	0.72 (99)	0.54 (27)	1.55 (82)	0.71 (60)
SD	0.16	0.04	0.12	0.03

Herbivorous feeding

The diatom *Porosira pseudodenticulata* occurred normally as single cells of an average diameter of $18.5 \mu\text{m}$ or as short 2-cell chains. When *Oncaea curvata* females fed on this diatom, the clearance rate (VSC) decreased with increasing food concentration. The highest VSC measured was $33.4 \text{ ml female}^{-1} \text{ d}^{-1}$ (Fig. 2a). The ingestion rates (Table 2) increased with increasing food concentration up to $6.9 \mu\text{g chl a l}^{-1}$ (Fig. 2a). With higher chl a concentrations, I decreased again.

Using the culture of 'ice algae', which consisted mainly of pennate diatoms from the ice (*Fragillaria* sp. and others) as food, the mean VSC decreased more strongly with increasing food concentration (Fig. 2b) than with the monoculture described above. Especially at high chl a concentrations ($> 3 \mu\text{g chl a l}^{-1}$) it was clearly lower in this series of experiments. Exceptions are the 2 relatively high VSC of 3.3 and $1.7 \text{ ml female}^{-1} \text{ d}^{-1}$ at 12 and $16 \mu\text{g chl a l}^{-1}$. In these 2 experiments with high algae concentrations the algae began to clump, so

Table 2. *Oncaea curvata*. Herbivorous feeding on *Porosira pseudodenticulata*, ice algae, *Phaeocystis* cf. *pouchetii*, or a *Phaeocystis* bloom. Highest mean values of ingestion rates ($\mu\text{g C female}^{-1} \text{ d}^{-1}$) at natural food concentrations as encountered in the investigation area (I_{nat}) and maximum ingestion rates (I_{max}) are given. For each of these, daily carbon uptake ($I_{\%}$) in % of female carbon content per day at the respective food concentrations c ($\mu\text{g chl a l}^{-1}$) is shown

	I_{nat}			I_{max}		
	$I_{\%}$	c	$I_{\%}$	c	$I_{\%}$	c
<i>P. pseudodenticulata</i>	≤ 0.39	≤ 25	≤ 3.7	1.33	84	6.9
Ice algae	≤ 0.40	≤ 26	≤ 4.8			
<i>P. cf. pouchetii</i>	≤ 0.28	≤ 18	≤ 3.3	1.29	84	12.4
<i>Phaeocystis</i> bloom	≤ 0.54	≤ 35	≤ 2.8	4.66	301	18.5

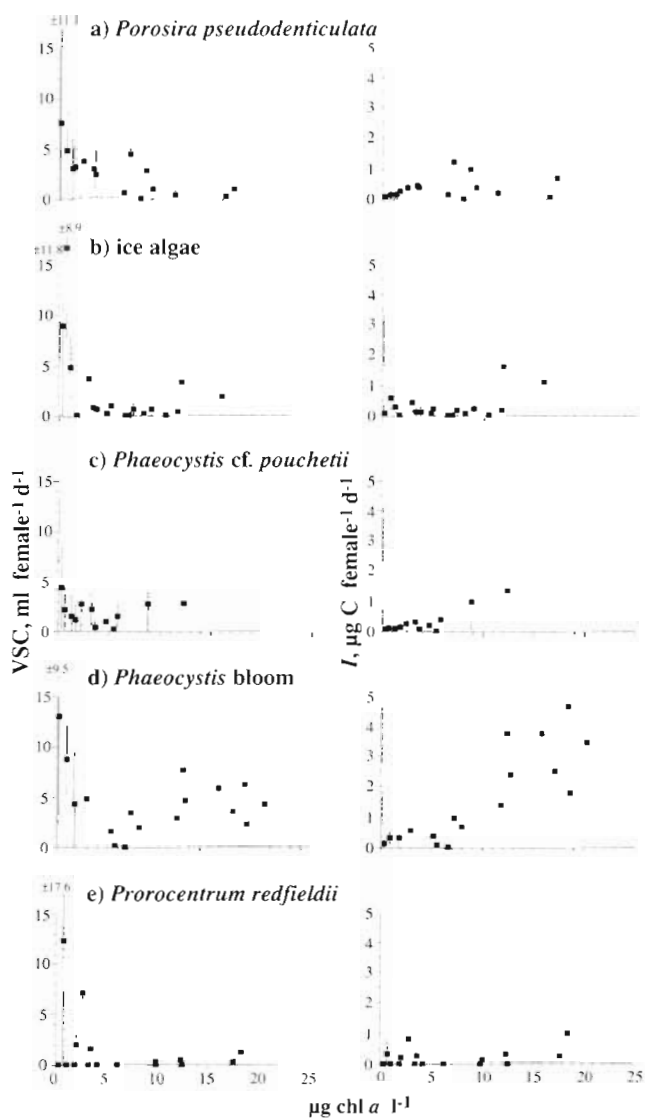


Fig. 2. *Oncaea curvata*. Clearance rates (volume swept clear, VSC) and ingestion rates (I) in relation to the concentration of algae in the experiments ($\mu\text{g chl } a \text{ l}^{-1}$). Shown are mean values over ($0.5 \mu\text{g chl } a \text{ l}^{-1}$)-classes \pm mean absolute deviation from the mean (MA)

that the food conditions were not comparable with the other experiments of this series. Aggregates of algae were found instead of single cells. The resulting I values of 1.58 and $1.08 \mu\text{g C female}^{-1} \text{ d}^{-1}$ equaled 102 and 70% of body carbon and were also clearly higher than the other results of experiments with 'ice algae' (Fig. 2b). Most ingestion rates at food concentrations between 0.5 and $3.0 \mu\text{g chl } a \text{ l}^{-1}$ were between 0.2 and $0.4 \mu\text{g C female}^{-1} \text{ d}^{-1}$ (13 to 26% of body carbon). At lower food concentrations the copepods generally took up less than 3% of their body carbon per day.

With the colony-forming *Phaeocystis cf. pouchetii* as food, only a slight decrease in VSC was found with

increasing concentration (Fig. 2c). The highest measured VSC was only $16.3 \text{ ml female}^{-1} \text{ d}^{-1}$ at $0.4 \mu\text{g chl } a \text{ l}^{-1}$. At food concentrations $>4 \mu\text{g chl } a \text{ l}^{-1}$, the values increased again. I increased with increasing food concentration (Fig. 2c) up to the highest investigated concentration of $12.4 \mu\text{g chl } a \text{ l}^{-1}$ (see also Table 2). At chlorophyll a concentrations as encountered in the investigation area, however, I was lower (Fig. 2c, Table 2).

The culture of *Phaeocystis* bloom consisted mainly of flagellates, mostly *Phaeocystis* sp. in the colony-forming state, and the rest mainly of large planktonic diatoms. On the surface of the gelatinous *Phaeocystis* colonies, diatoms and other flagellates, which were either trapped or had colonized the surface, were often found. *Oncaea curvata* females fed with this culture showed a minimum VSC at a food concentration of $6.6 \mu\text{g chl } a \text{ l}^{-1}$ (Fig. 2d). The highest measured VSC was $27.2 \text{ ml female}^{-1} \text{ d}^{-1}$ at $0.2 \mu\text{g chl } a \text{ l}^{-1}$ in the experiment, and the maximum VSC at high food concentrations was $7.7 \text{ ml female}^{-1} \text{ d}^{-1}$ (at $12.7 \mu\text{g chl } a \text{ l}^{-1}$). The I of *O. curvata* females increased with increasing food concentrations (Fig. 2d, Table 2). At the much lower chl a concentrations in the investigation area, I was considerably lower (Fig. 2d, Table 2).

Experiments with the flagellate *Prorocentrum redfieldii* showed that *Oncaea curvata* used this species only occasionally: 68% of all experiments of this series resulted in zero VSC and I ; non-zero data scattered strongly. However, even with this food a decrease of VSC with increasing food concentrations is noticeable (Fig. 2e). I showed no apparent trend (Fig. 2e).

Carnivorous feeding

Carnivorous feeding of *Oncaea curvata* was not observed in the experiments. The copepodite stages of the 4 tested calanoids with different feeding and swimming behaviour, which were offered as food, were all recovered after each experiment. Nauplii of calanoids were also not eaten by *O. curvata*. Slight decreases of 1 and 4% of the nauplii in 2 experiments are probably due to the handling of the specimens.

DISCUSSION

There is varied and partly contradictory information about feeding of Oncaeidae in the literature, and very little information concerning Antarctic species. It seems that the species of Oncaeidae differ in their preferred food and their feeding mode. Most of the investigated species, however, were able to use gelatinous food sources or soft-bodied animals as food, and proba-

bly prefer this type of food; the existence of such a preference is supported by the results of this study. Wickstead (1962) discussed the feeding habits of Oncaeidae and, based on their mouth parts and on behaviour studies with chaetognaths and other copepods, concluded that Oncaeidae live semi-parasitically and either graze particles from the surface of their host or penetrate the host body surface and feed on their body liquids. Kosikhina (1980) confirmed that *Oncaea mediterranea* and *O. venusta* preferentially eat chaetognaths (*Sagitta* sp.) and with this diet ingest 100 to 350% of their body weight daily. As Oncaeidae are important food organisms of chaetognaths (Hopkins 1985, Øresland 1990), predation on chaetognaths must involve a high risk for the Oncaeidae. It is therefore more likely that these Oncaeidae eat weakened or dead chaetognaths. *O. mediterranea* are also found in discarded houses of Larvaceae (Alldredge 1972, Ohtsuka et al. 1996), where they feed on the enriched plankton in the filters. This behaviour enables the species to feed on nanoplankton that they cannot otherwise use (Lampitt et al. 1993) and is equivalent to grazing on surfaces as described by Wickstead (1962).

Oncaea curvata females display this feeding mode in a preference for aggregates of algae or gelatinous *Phaeocystis* colonies as food, as the results of this study show. The highest ingestion rate from experiments with the *Phaeocystis* bloom was about 300% of body carbon per day. The large aggregates of the colonies are probably grazed, as was observed for appendicularian houses (Alldredge 1972). Possibly, aggregates from sinking algal and animal material as well as fecal pellets (González et al. 1994) are the main food of *O. curvata* females.

Lipid analyses support this assumption. *Oncaea curvata* stores mainly wax esters, and only short-chained fatty acids occur (C. Albers pers. comm.). The lipid composition with oleic acid strongly dominating the fatty acids is typical for detritus (Kattner et al. 1983) and detritus feeders.

This feeding strategy might offer an explanation for the comparatively high stock of this species in the East Wind Drift and especially in the shelf area of Antarctica. Eastwards—that is 'upstream' of the investigation area, in Marguerite Bay and in the area around Rønne Entrance—strongly developed *Phaeocystis* blooms were found in summer. They reached concentrations up to $5.8 \mu\text{g chl } a \text{ l}^{-1}$ (Stambler 1996), which was the highest chlorophyll concentration measured during the expedition. *Phaeocystis* blooms like this are typical for the summer situation in this area and might provide good food conditions for the *Oncaea curvata* population, which could be transported by the East Wind Drift to the area around Peter I. Island within 3 mo. As *Phaeocystis* sp. also grows under low light conditions, live cells are found

down to 100 m (Wassmann et al. 1990), where mainly juvenile *O. curvata* occur (Metz 1996). If juveniles also use the gelatinous *Phaeocystis* colonies, these blooms might help the copepods to develop rapidly. Although *Phaeocystis* colonies do not form aggregates (Riebesell 1993, Riebesell et al. 1995), fast sedimentation of these colonies was reported from the Barents Sea and the North Sea (Wassmann et al. 1990, Riebesell 1993). They degraded rapidly below the euphotic zone (Wassmann et al. 1990). Among other causes, feeding of zooplankton was mentioned. This study shows that *O. curvata* females, which occur mainly below the euphotic zone (>150 m) in very low phytoplankton concentrations, may profit from the dying and sinking *Phaeocystis* colonies, especially if they are already colonized by bacteria and diatoms (Wassmann et al. 1990).

Some Oncaeidae are obviously also capable of using other phytoplankton as food. Paffenhöfer (1993) found feeding rates of 33 to 114% of body carbon per day for *Oncaea mediterranea* with a diet of flagellates (*Rhodomonas* sp. as food for nauplii and young copepodites, and large *Gymnodinium* sp. as food for older copepodites and adults). A diet of diatoms, however, resulted in an increased mortality among the copepods. An investigation of gut contents of the Antarctic species *O. curvata* and *O. antarctica* (Hopkins 1985, 1987), in contrast, showed that feeding on diatoms occurred in nature, and in the experiments of this study *O. curvata* seemed to thrive on a purely herbivorous diet. *O. antarctica* guts also contained metazooplankton, which amounted to 20 to 40% of their diet (Hopkins 1987). This concurs with observations of S. B. Schiel & E. Mizdalski (pers. comm.) that *Oncaea* sp. (probably *O. antarctica*) attacked the larger calanoid copepod *Metridia gerlachei* and cut their abdomen or antennae off. Ohtsuka et al. (1996) also found that large Oncaeidae prey on zooplankton.

According to my investigations *Oncaea curvata*, unlike *O. antarctica*, feeds neither carnivorously nor semi-parasitically. All types of mobile food, such as animals or flagellates, are rejected by this species. In comparison with other Oncaeidae, *O. curvata* is a very slow, lethargic species which swims only seldom and only short distances. During the sorting of live animals from the catches, no attacks by *O. curvata* on other organisms were observed. However, *O. curvata* was twice found feeding on dead chaetognaths. Instead of feeding on copepods, as observed for other Oncaeidae (S. B. Schnack-Schiel & E. Mizdalski pers. comm.), *O. curvata* was preyed upon by the omnivorous calanoids *Metridia gerlachei* and *Calanus propinquus*, but not by the herbivorous *Calanoides acutus* and *Rhincalanus gigas* (Metz & Schnack-Schiel 1995).

Oncaea curvata can feed on diatoms, which supports the gut content analysis of Hopkins (1985, 1987). Feed-

ing on the strongly pulsed diatom blooms of the Southern Ocean might be advantageous for the Oncaeidae of that area. During these short periods lipids might be stored as energy reserves for times of food shortage or reproduction. For bloom situations, as occurred in the southern Bellingshausen Sea, daily ingestion rates of 18 to 35% of body carbon can be assumed for *O. curvata*, according to this study. Thus, *O. curvata* has a higher food turnover than the large calanoids. For *Metridia gerlachei*, for example, daily ingestion rates of 2.1 to 7.2% of body carbon were found (Lopez & Huntley 1995), for *Calanoides acutus* 5.6 to 27.0% and for *Rhincalanus gigas* 1.5 to 2.0% (Atkinson et al. 1992). Atkinson (1994) shows a relationship between the ingestion rate and the body mass of Antarctic copepods. Accordingly, the large calanoids have ingestion rates of <10% of body carbon per day and small copepods up to 120%. Females of *O. curvata*, with a dry weight of about 4 µg, would be expected to have ingestion rates of about 38% of body carbon per day, which concurs with the results of this study. According to Atkinson's (1994) relationship, juveniles should have higher ingestion rates. Several of *O. curvata*'s copepodite stages occur in the euphotic zone (Metz 1996) and the biomass of the population is as high or even higher than the population biomass of some dominant calanoids, especially on the Antarctic shelf. Therefore, the influence of *O. curvata* on the phytoplankton community should prove to be as important as the influence of calanoid species.

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