Observations on carnivorous feeding in Antarctic calanoid copepods

Cornelia Metz*, Sigrid B. Schnack-Schiel

Alfred-Wegener-Institut für Polar- und Meeresforschung, Postfach 12 01 61, D-27515 Bremerhaven, Germany

ABSTRACT: Feeding experiments were carried out on board RV 'Polarstern' in February 1994 in the Bellingshausen Sea, Antarctica, to investigate carnivorous feeding in dominant large calanoid copepods. Adult females of the winter diapause species *Calanoides acutus* and *Rhincalanus gigas* did not feed on females of the poecilostomatoid copepod *Oncaea curvata*. In contrast, adult *Calanus propinquus* and *Metridia gerlachei* females, which remain active during winter, fed on *O. curvata* females. However, no feeding on *O. curvata* females by juvenile *M. gerlachei* was observed. Additional food sources, such as detritus and small protozooplankton, are suggested, because the amount of animal prey ingested is not sufficient to meet the energy demands of the investigated species.

KEY WORDS: Copepod · Carnivorous feeding · Antarctic

INTRODUCTION

Temperate and polar seas are characterised by a distinct seasonal pattern of primary production, with a corresponding food limitation for herbivorous zooplankton. The life cycles of zooplankton are affected by the scarcity of food during winter months. Low standing phytoplankton stocks probably mean that herbivorous zooplankton are unable to meet metabolic demands solely on an algal diet, and presumably eat other food such as proto- and metazooplankton (Parsons & LeBrasseur 1970). Some copepod species are known to reduce their metabolic activities, overwintering in a dormant state (Smith & Schnack-Schiel 1990, Conover & Huntley 1991). Laboratory studies have shown that herbivorous *Calanus* species and *Rhincalanus nasutus* can ingest copepod eggs, copepod nauplii, barnacles and the brine shrimp *Artemia* (Conover 1966, Mullin & Brooks 1967, Corner et al. 1974, 1976, Landry 1981). These species can switch to animal prey, and it is possible that they survive periods of low phytoplankton stocks by feeding carnivorously.

In the Southern Ocean 4 calanoid copepods dominate the zooplankton biomass in many regions: *Cala-*

noides acutus, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei* (Hopkins 1985a, 1987, Hopkins & Torres 1988, Boysen-Ennen et al. 1991, Hopkins et al. 1993a, b). Gut content analyses indicate that all 4 species are predominantly small-particle grazers feeding on phytoplankton and protozoans (Hopkins 1985b, 1987, Hopkins & Torres 1989, Hopkins et al. 1993a, b). On the other hand, different life strategies in response to the distinct seasonality of phytoplankton stocks have been suggested (Schnack-Schiel & Hagen 1995). The herbivorous *C. acutus* is a strong ontogenetic seasonal migrant which overwinters in a resting stage at depth. It accumulates large lipid stores containing wax esters (Marin 1988, Atkinson 1991, Schnack-Schiel et al. 1991, Bathmann et al. 1993, Hagen et al. 1993, Schnack-Schiel & Hagen 1995). Part of the *C. propinquus* population remains active during winter in the upper water layers, the rest migrating to deeper waters (Marin 1988, Bathmann et al. 1993, Hopkins et al. 1993a). *C. propinquus* stores lipids in form of triacylglycerols, indicating a more opportunistic feeding mode (Schnack-Schiel et al. 1991, Hagen et al. 1993). Information about *R. gigas* is less clear: Hopkins et al. (1993b) described *R. gigas* as exclusively herbivorous, although deviating lipid compositions led Graeve et al. (1994) to suggest that *R. gigas* is not purely a herbivore. Gut content analyses suggest

Table 1 Mean copepod lengths and carbon contents. Carbon values are estimated from dry weights given in the literature (see 'Methods')

Species	Total length (mm)	Carbon content (µg)
Calanoides acutus female	4.9	275
Calanus propinquus female	5.1	490
Rhincalanus gigas female	7.8	405
Metridia gerlachei female	3.7	130
M. gerlachei CIII–CV	1.7	20
Oncaea curvata female	0.65	5
Oncaea parila female	0.67	5

active feeding of *R. gigas* in May (Marin & Schnack-Schiel 1993), but not in June to August (Hopkins et al. 1993b). *R. gigas* underwent winter diapause in the mesopelagic zone in the southern Scotia Sea (Hopkins et al. 1993a). Feeding experiments and analyses of lipid and fatty acid/alcohol compositions indicate that *M. gerlachei* is an omnivorous species (Huntley & Escritor 1992, Graeve et al. 1994). Hopkins et al. (1993a) found food in the guts of *M. gerlachei* in winter. This in conjunction with the low carbon:nitrogen ratios (Schnack 1985, Atkinson & Shreeve 1995) and the moderate lipid reserves (Schnack-Schiel & Hagen 1995) also indicates that *M. gerlachei* remains active during winter.

Small copepods of the families Oithonidae and Oncaeidae numerically dominate in the Southern Ocean throughout the year (Hopkins 1985a, Schnack et al. 1985a, Fransz 1988, Hopkins & Torres 1988, Conover & Huntley 1991, Schnack-Schiel unpubl.). The dominant species *Oncaea curvata* was therefore used as representative motile prey. However, during winter females are dispersed throughout the water column, whereas in summer they are concentrated between 300 m and the surface (Metz 1995). The aim of this study was to determine whether the 4 dominant Antarctic calanoid copepods can switch to carnivory and prey on

O. curvata, thereby taking advantage of the high number of this species in the water column during winter when phytoplankton is scarce.

METHODS

Feeding experiments were conducted on board RV 'Polarstern' during February 1994 in the central Bellingshausen Sea, Antarctica. Copepods were collected at several stations with a Bongo net of 100 µm mesh size hauled vertically in the upper 500 m. They were acclimated to experimental conditions for several days. All experiments were run at 0°C in continuous dim light. The experimental glass dishes contained 200 ml seawater (0.2 µm filtered), and 15 females of *Oncaea curvata* or, in one experiment, *Oncaea parila* (see Table 2). Into these dishes 5 to 10 females of *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas* and *Metridia gerlachei*, or copepodite stages III to V of *M. gerlachei* were transferred, respectively. The experiments were run with 2 to 3 replicates. The number of *Oncaea* spp. was checked every 3 h over a period of 24 h and the behaviour of the different species was observed. To calculate the carbon content of the species (Table 1), and carbon uptake in % of body carbon (Table 2), the copepod dry weight values published by Mizdalski (1988), Conover & Huntley (1991) and Huntley & Escritor (1992) were used. A body carbon content of 45 % was assumed (Conover & Huntley 1991).

RESULTS AND DISCUSSION

Calanoides acutus and *Rhincalanus gigas* females as well as juvenile *Metridia gerlachei* did not feed on *Oncaea* spp., and no reaction towards the copepod prey was observed. In contrast, *Calanus propinquus* and *M. gerlachei* females fed on *Oncaea* spp., the number of which decreased continuously over time (Fig. 1). All 4 species were trophically active. This was proved by grazing experiments, carried out at the same time with natural phytoplankton suspensions as food (Schnack-Schiel unpubl.). Hopkins et al. (1993b) also described *C. acutus* and *R. gigas* as being purely herbivorous, whereas *C. propinquus* and *M. gerlachei* guts contained phytoplankton, proto- and metazooplankton in all seasons (Hopkins 1985b, 1987, Hopkins & Torres 1988, Hopkins et al. 1993a, b). Interestingly the latter species had a significantly larger zooplankton component in their diet in the

Table 2. Summary of predation experiments. Experimental set up, ingestion rates I_n (n_{Oncaea} ingested copepod^{-1} d^{-1}) and I_C (µg C$_{Oncaea}$ ingested copepod^{-1} d^{-1}) and carbon uptake (% of body carbon d^{-1})

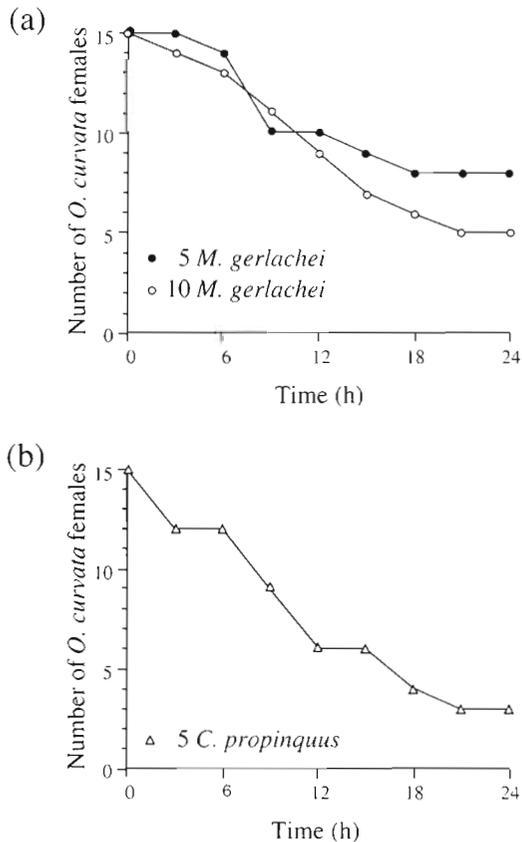| Predator species	n dish^{-1}	Prey species	I_n	I_C	C uptake
Calanus propinquus	5	*Oncaea curvata*	2.4	12.0	2.5
females	5	females	2.7	13.3	2.7
Metridia gerlachei	5	*O. curvata*	1.4	7.0	5.4
females	10	females	1.2	6.0	4.6
	10		1.0	5.0	3.9
	8	*Oncaea parila* females	1.3	6.7	5.1

Fig. 1. Time course of example feeding experiments. Graphs show decrease of the number of *Oncaea curvata* over time in experimental dishes containing (a) *Metridia gerlachei* females or (b) *Calanus propinquus* females

Fig. 2. Sketch of the feeding behaviours of (a) *Metridia gerlachei* and (b) *Calanus propinquus* catching *Oncaea curvata* (marked with a circle)

pack ice compared to open waters (Hopkins et al. 1993a). Additionally, crustacean remains, in addition to phytoplankton, have been found in the faecal pellets of *C. propinquus* in the pack ice (Atkinson & Shreeve 1995). *C. propinquus* and *M. gerlachei* actively selected motile food (ciliates and flagellates), in contrast to *C. acutus* and *R. gigas* which were unselective feeders (cited in Atkinson & Shreeve 1995).

The behaviour of *Metridia gerlachei* and *Calanus propinquus* females detecting and responding to copepod prey was remarkably different. *M. gerlachei* swam steadily, detecting their prey at a distance of about 1 mm. After the encounter they always displayed a complex behaviour (Fig. 2a): They stopped 1 to 2 body lengths behind the *Oncaea* spp., turned around and passed it again. This was repeated 1 or 2 more times, and the prey was then grabbed. It seemed that this facilitated the precise locating of the *Oncaea* spp. Once it was detected it never escaped. *C. propinquus* grabbed their prey the first time they passed it (Fig. 2b). In contrast to *M. gerlachei*, *C. propinquus* occasionally missed the *Oncaea* spp. or lost them
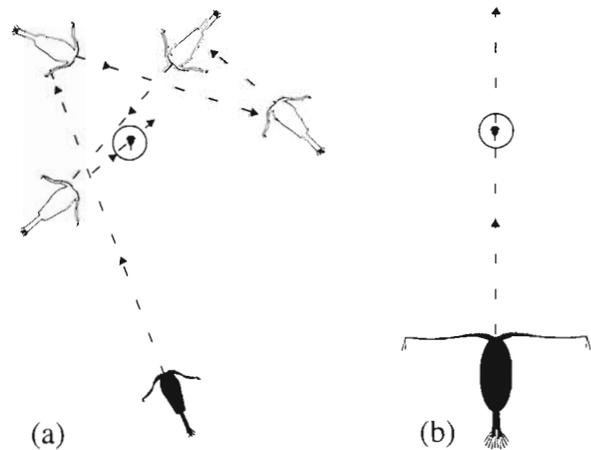
shortly after the attack. Their behaviour resembled that of *Calanus hyperboreus* described by Conover (1966). The feeding behaviour of *C. hyperboreus* depended on whether the prey was actively swimming or not: a moving nauplius was apparently sensed by *C. hyperboreus* at a few millimeters, whereas large non-motile food particles were only detected and captured if contact was made by the feeding appendages. Typically, *Oncaea curvata* remained stationary for long periods of time, jumping seldom even when a predator was very close. This might be a strategy to avoid hydrodynamic disturbances which could be sensed by predators (Paffenhöfer 1988). Therefore, *C. propinquus* responded to *O. curvata* females as *C. hyperboreus* did to non-motile food particles. The behaviour of *Metridia gerlachei*, however, indicated that this species was able to sense floating prey from a distance.

Few remains such as *Oncaea* spp. legs or abdomens were found, and there was no evidence of the calanoids sucking out the contents of large prey as described by Cushing (1955). As so few of the captured *Oncaea* spp. were only partly consumed, it is most likely that calanoids chew their larger prey and retain and ingest all pieces. This was occasionally observed in *Metridia gerlachei* during the experiments.

Daily rations depend on the size of grazers and on the size, shape and concentration of the food supply (Parsons et al. 1969, Paffenhöfer 1971, Schnack 1983b, Atkinson 1994). In the Southern Ocean most daily ration values of large calanoid species range between <1 and 20% of their body carbon when feeding on natural occurring phytoplankton concentrations of 0.1 to 2 µg chl a l^{-1} (Schnack 1985, Atkinson et al. 1992, Bathmann et al. 1993, Drits et al. 1993, Atkinson 1994). Feeding rates in the experiments with *Oncaea* spp.

females were also in this range. Calanus propinquus ingested 12 to 13 µg C copepod^{-1} d^{-1} and Metridia gerlachei 5 to 7 µg C copepod^{-1} d^{-1}, which is a daily ration of 2 to 3% and 4 to 5% body weight for C. propinquus and M. gerlachei respectively (Table 2). These values are at the lower limits to meet metabolic requirements (Huntley et al. 1991). The carnivorous feeding rates were low compared with grazing on natural phytoplankton (0.3 to 1.4 µg chl a l^{-1}) during the investigation period, which was in the range of 1.2 to 8% body weight for C. propinquus and 4 to 10.4% for M. gerlachei (Schnack-Schiel unpubl.). The daily rates of Oncaea curvata ingestion will be even lower in situ since our initial experimental concentration of 75×10^3 O. curvata females m^{-3} was higher than the concentrations of 2 to 50 females m^{-3} in the Bellingshausen Sea during summer (Metz unpubl.). During winter the concentrations will be even lower. However, it should be considered that this species was used only as an example of animal prey, and other organisms in the same size range, such as large nauplii, different copepodite stages of Oncaeidae, Oithonidae and smaller Calanoida, are probably also preyed upon.

In the eastern Weddell Sea, maximum concentrations of Oncaea spp., Oithona spp. and copepod nauplii combined (300 to 800 ind. m^{-3}) occurred in midwater layers during winter (August to November), while during summer/autumn, 1000 to 7500 ind. m^{-3} were found in the upper 100 m (Schnack-Schiel unpubl.). As the annual migration of Antarctic Oncaeidae and Oithonidae (Metz 1995, Schnack-Schiel unpubl.) is in a similar depth range as the migration of Calanus propinquus and Metridia gerlachei (Schnack-Schiel & Hagen 1995), the stock of Oncaeidae, and probably also Oithonidae, is a food source, in addition to phytoplankton, available to C. propinquus and M. gerlachei. This resource becomes more important during winter when phytoplankton is virtually absent in the water column. However, C. propinquus, which stays partly in the surface layer in winter (Marin 1988, Bathmann et al. 1993, Schnack-Schiel & Hagen 1995), might also graze ice-algae on the ice undersurfaces or which are released into the water C. propinquus frequently had full and green guts, despite the paucity of chlorophyll in the water (Atkinson & Shreeve 1995). M. gerlachei is a typical mid-water species never occurring in maximum concentrations at the surface (Hopkins & Torres 1988, Huntley & Escritor 1992, Schnack-Schiel & Hagen 1995) where high phytoplankton concentrations exist in summer. Therefore phytoplankton is probably not the only food resource. On the other hand, although this species lives mainly below the productive upper layers, it migrates into shallower water layers during night for feeding (Lopez & Huntley 1995). Additionally, M. gerlachei appears to be able to

grow on a pure phytoplankton diet (Schnack 1983a, 1985, Schnack et al. 1985b, Huntley & Escritor 1992). This information indicates that carnivorous feeding is not vital for this species, but might be very important during winter when phytoplankton is extremely scarce. We did not observe feeding on Oncaea spp. females by juvenile M. gerlachei. These developmental stages occur, as the adults, in maximum abundances in midwater-layers and account for 75 and 99% of the M. gerlachei population in the eastern Weddell Sea during winter (Schnack-Schiel & Hagen 1995). The lipid content of copepodite stages CIV and CV expressed as % of dry weight was about twice as high as that of female M. gerlachei in October/November in the eastern Weddell Sea (Schnack-Schiel & Hagen 1995). This could indicate that juvenile stages rely more on lipid reserves than females, although detritus and small heterotrophic microorganisms might be other sources of food. In the Ross Sea, Antarctica in summer young M. gerlachei guts contained tintinnids, peridian dinoflagellates and diatoms, while adult females had eaten additional metazoans, e.g. Oithona spp. and Oncaea spp. (Hopkins 1987). In winter, small flagellates, dinoflagellates and ciliates dominated the protist community in the Weddell Sea (Scharek 1991). These organisms, besides metazoans such as Oncaeidae and Oithonidae, may also contribute to the diet of calanoid copepods.

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