



FEATURE ARTICLE

Krill larvae, copepods and the microbial food web: interactions during the Antarctic fall

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ABSTRACT: Experiments were run in the Antarctic Bellinghousen Sea during the austral fall to ascertain the interactive effects of krill larvae (furcilia) and copepods on the microbial food web. A cross-classified design with addition of the small cyclopoid copepod *Oithona similis* and either the furcilia larvae of *Euphausia superba* or the calanoid copepod *Metridia gerlachei* to the natural planktonic community was used, as well as a single experiment with varying densities of *O. similis*. The experiments showed furcilia to have much higher grazing rates on copepods and ciliates than on algae, with positive selection for ciliates that was not influenced by the presence or absence of *O. similis*. *M. gerlachei* had a grazing impact on ciliates that was much less than that of furcilia larvae, but due to a high taxonomic resolution of the ciliate community it could be shown that there were groups of grazing-vulnerable and -resistant forms. Contrary to expectations, *O. similis* had very low grazing rates on both ciliates and algae, but here too grazing-vulnerable and -resistant groups of ciliates could be distinguished. Neither the very strong impact of furcilia on ciliates, copepods and algae nor the more moderate impact of *M. gerlachei* cascaded down to heterotrophic and phototrophic nanoplankton or to bacteria. At least at the time of our experiments, ciliates were tightly bound to the 'classic' aquatic food web, but do not serve to transmit a trophic cascade from the classic and microbial food webs.

KEY WORDS: Ciliate · Grazing · Antarctica · Copepod · Krill · Furcilia · Trophic cascade

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Experiments conducted in the Bellinghousen Sea (Antarctica) during the austral autumn show that krill larvae (*Euphausia superba* furcilia, top) have much higher grazing rates on copepods (*Metridia gerlachei*, lower left; *Oithona similis*, lower right) and ciliates than on algae. Trophic levels beneath ciliates did not respond to the addition of furcilia, suggesting that top-down control of the microbial food web is minimal during the Antarctic autumn.

Photo: Stephen Wickham

INTRODUCTION

That microbial food webs play an integral role in aquatic systems has over the last 20 yr developed into a paradigm. In Antarctic waters, the microbial food web takes on particular importance in that the growing season of autotrophs is short, and for much of the year the system is net heterotrophic, with bacterial secondary production exceeding primary production (Rivkin 1991). In the Antarctic autumn and winter, heterotrophic protozoan biomass can match or exceed

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phytoplankton biomass (Garrison et al. 1993), making protozoans a potentially important food source for meso- and macroplankton. Copepods have long been known to feed on ciliates and, to a lesser extent, flagellates, with these protists often making up a substantial proportion of copepods' diets (Sanders & Wickham 1993). Preying on ciliates or other heterotrophic protozoans could give copepods which continue to feed during winter the possibility to continue to meet their metabolic demands without entering diapause.

The euphausiid *Euphasia superba* (hereafter referred to as 'krill') has long been known as a keystone herbivore in the Southern Ocean and has in recent years become acknowledged as a predator of copepods and ciliates (Price et al. 1988, Froneman et al. 1996, Atkinson & Snýder 1997, Perissinotto et al. 2000). This gives krill the opportunity to access heterotrophic food sources, which have been shown to contribute on average 79% (and at times nearly 100%) to krill gut contents (Perissinotto et al. 2000). Ciliates, particularly the oligotrichs (sensu lato) that are often the dominant planktonic ciliate group, graze mainly the nano- and picoplanktonic size classes not otherwise available to krill (Jonsson 1986, Kivi & Setälä 1995). Thus, krill grazing directly on ciliates would lead to a more efficient biomass transfer from lower to higher trophic levels than if copepods were a necessary intermediate step.

Considerably less is known of the feeding preferences of the furcilia larval stage of krill (hereafter simply 'furcilia'). Omnivorous feeding has been shown, with both ciliates and copepods found in the diet, and has been hypothesized as an over-wintering strategy for furcilia (Daly 1990, Meyer et al. 2002, Daly 2004, Pakhomov et al. 2004). When both copepods and ciliates are abundant, it is not clear whether larval or adult krill show any preference for one group over the other, or have a switching strategy dependent on the relative abundance of different prey groups. Understanding feeding preferences of furcilia is critical not only for understanding krill ecology or the importance of omnivory in aquatic food webs, but also for understanding the impacts of higher trophic levels on the microbial food web. If the copepod-ciliate link is the main path through which microbial production leaves the microbial food web, and krill graze much more on copepods than on ciliates, then high krill abundance will result in a microbial food web that is a biomass sink. On the other hand, if krill are effective ciliate grazers, then microbial production will move more efficiently into higher trophic levels than if an intermediate, copepod trophic level is necessary.

In order to better understand these phenomena, factorial experiments manipulating the presence or absence of furcilia and copepods in natural plankton communities were carried out. With this design, the

separate and combined predatory impacts of furcilia and copepods on ciliates and the rest of the microbial food web could be compared. If furcilia and copepods act independently, then their combined predatory impact should be the sum of their impacts when assessed alone. However, if furcilia prey on copepods that would otherwise consume ciliates, or if furcilia prey on ciliates only when copepods are absent, then the combined predatory impact of furcilia and copepods would be less than the sum of their separate impacts.

As a copepod that could potentially serve as both furcilia prey and a ciliate predator, the cyclopoid *Oithona similis* (hereafter '*Oithona*') was chosen. *Oithona* is often the most abundant copepod in Antarctic waters (Fransz & Gonzalez 1995), and has been shown to be an effective predator on ciliates (Atkinson 1996, Nakamura & Turner 1997). Moreover, freshwater research has established that cyclopoids are selective predators on ciliates, with the potential to alter the composition of the ciliate community (Wickham 1995). Experiments with *Oithona* and the calanoid copepod *Metridia gerlachei* (hereafter '*Metridia*') were conducted to provide a comparison with furcilia. *Metridia* continues to feed during winter and is known to prey on ciliates as well as other copepods (Atkinson 1996, 1998, Pasternak & Schnack-Schiel 2001). In addition, a grazing experiment with *Oithona* alone was conducted, in order to ascertain its impact on ciliates and the rest of the microbial food web independent of the presence of any other metazoan. Experiments were designed to run long enough to observe, if present, a trophic cascade from furcilia or copepods to ciliates and subsequently the rest of the microbial food web. The work was conducted in the Antarctic Bellinghousen Sea during the austral autumn, a time when heterotrophic prey should be becoming relatively more important.

MATERIALS AND METHODS

Experiments were conducted as part of Cruise ANT XVIII/5b conducted by RV 'Polarstern' in the Bellinghousen Sea, west of the Antarctic peninsula, between 67 and 72° S and from 13 April to 7 May 2001, during the Antarctic fall. Copepods and furcilia were captured with 300 µm-mesh Bongo nets with a 5 l closed cod end, and held in 100 µm-filtered seawater at -1°C for a minimum of 24 h to ensure that experimental animals were in good condition. Experiments were run in 2.7 l clear polycarbonate bottles, incubated on deck in 500 l tanks with transparent plastic covers that reduced incident photosynthetically active radiation (PAR) by approximately 10%. The bottles were free to move in the tanks, allowing the natural motion of the ship to

keep particles in the bottles in suspension. Seawater was pumped through the tanks to maintain a constant, near *in situ* temperature. Incubation water was warmed slightly as it passed through the ship, but remained between -0.9 and 2.4°C . The water for the experiments was collected in 12 l Niskin bottles from 10 m or 20 m water depth. Water was drawn off immediately, filtered through a $100\ \mu\text{m}$ mesh to remove most mesozooplankton, and stored until use in 24 l polycarbonate carboys under low light at -1°C . The copepods and furcilia used in the experiments were picked individually under a dissecting microscope with a large-bore pipette, and added to the experimental bottle along with a small volume (ca. 20 ml) of filtered water. There were either 4 (furcilia-*Oithona* and *Metridia*-*Oithona* experiments) or 3 (*Oithona* experiment) replicates per treatment combination.

A total of 4 experiments were carried out. Two experiments used a cross-classified design to examine the direct and indirect effects of furcilia and *Oithona*. The treatment combinations were furcilia alone ($2.9\ \text{ind. l}^{-1}$), *Oithona* alone (first experiment: $15\ \text{ind. l}^{-1}$; second experiment: $20\ \text{ind. l}^{-1}$), both furcilia and *Oithona* together, or both absent. These experiments were run for 64 and 66 h, respectively. The furcilia used in the first experiment were third-stage larvae (FIII), while those in the second experiment were a combination of third- and fourth-stage larvae (FIII and FIV). A third experiment was similar to the furcilia-*Oithona* experiments in purpose and design, but in place of furcilia, the calanoid copepod *Metridia ger-*

lachei ($2.9\ \text{ind. l}^{-1}$) was used. This experiment was of 70 h duration. The fourth experiment was designed to measure the impact of *Oithona* on microbial food webs, had as treatments either 0, 4, 8, 16 or $32\ \text{ind. l}^{-1}$. The *Oithona* used in this and other experiments were late-stage copepodites and adults without egg sacs. The fourth experiment was run for 48 h. Dates, locations, durations and experimental designs are summarized in Table 1, and the initial concentrations of the organisms examined in the experiments are given in Table 2.

At the beginning and end of the experiments, samples were taken for zooplankton (1100 ml), chlorophyll *a* (chl *a*) (500 ml), ciliates and dinoflagellates (1000 ml), phototrophic and heterotrophic organisms (predominantly flagellates) in the nanoplankton size class (PNAN and HNAN, respectively) and bacteria (together 100 ml). In all but the *Oithona* grazing experiment (see below), bacterial and flagellate samples were also taken at the mid-point of the experiments. Bacteria and flagellates were fixed in 2% formaldehyde, ciliates and dinoflagellates in 5% Bouin's solution, and zooplankton in 5% buffered formaldehyde (all final concentrations). Chl *a* samples were filtered onto GF/F filters, frozen, and later analyzed fluorometrically after ethanol extraction. Bacteria and flagellates were filtered onto $0.2\ \mu\text{m}$ pore-size black polycarbonate filters and stained with DAPI within a few days of the samples being taken, and then frozen until counted under an epifluorescence microscope (Porter & Feig 1980). Phototrophs were

Table 1. Date, location and design of experiments

Expt	Date (2001)	Location	Duration (h)	Manipulation
Furcilia- <i>Oithona</i> I	22 Apr	$71^{\circ}\text{S}, 85^{\circ}\text{W}$	64	Krill larvae presence/absence ($2.9\ \text{ind. l}^{-1}$) cross-classified with <i>Oithona</i> presence/absence ($15\ \text{ind. l}^{-1}$)
Furcilia- <i>Oithona</i> II	1 May	$67^{\circ}\text{S}, 68^{\circ}\text{W}$	66	Krill larvae presence/absence ($2.9\ \text{ind. l}^{-1}$) cross-classified with <i>Oithona</i> presence/absence ($20\ \text{ind. l}^{-1}$)
<i>Metridia</i> - <i>Oithona</i>	26 Apr	$67^{\circ}\text{S}, 68^{\circ}\text{W}$	70	<i>Metridia</i> presence/absence ($2.9\ \text{ind. l}^{-1}$) cross-classified with <i>Oithona</i> presence/absence ($20\ \text{ind. l}^{-1}$)
<i>Oithona</i> grazing	19 Apr	$67^{\circ}\text{S}, 69^{\circ}\text{W}$	48	0, 4, 8, 16, $32\ \text{ind. l}^{-1}$

Table 2. Initial concentrations of chl *a*, phototrophic and heterotrophic nanoplankton (PNAN and HNAN), bacteria, dinoflagellates and ciliates. Values are means of 3 replicates $\pm 1\ \text{SD}$

Expt	Chl <i>a</i> ($\mu\text{g l}^{-1}$)	PNAN ml^{-1} ($\times 10^3$)	HNAN ml^{-1} ($\times 10^3$)	Bacteria ml^{-1} ($\times 10^6$)	Dinoflagellates ml^{-1}	Ciliates ml^{-1}
Furcilia- <i>Oithona</i> I	0.155 ± 0.022	1.63 ± 0.32	0.27 ± 0.05	0.798 ± 0.091	0.21 ± 0.09	0.94 ± 0.10
Furcilia- <i>Oithona</i> II	0.401 ± 0.026	1.23 ± 0.77	0.28 ± 0.05	0.371 ± 0.057	0.10 ± 0.01	0.70 ± 0.08
<i>Metridia</i> - <i>Oithona</i>	0.139 ± 0.021	0.32 ± 0.09	0.25 ± 0.16	0.341 ± 0.100	0.27 ± 0.07	1.28 ± 0.30
<i>Oithona</i> grazing	0.347 ± 0.055	1.62 ± 0.37	0.60 ± 0.26	0.664 ± 0.025	0.13 ± 0.01	0.74 ± 0.27

distinguished from heterotrophs by their autofluorescence under blue light.

Ciliate/dinoflagellate samples were concentrated by first settling 1 l for 1 wk in graduated cylinders, then by removing the upper 900 ml of sample water. Between 5 and 50 ml of the concentrated sample was then settled again and counted in an inverted microscope. To aid identification, additional ciliate sub-samples were silver-stained using the quantitative protargol stain (QPS) technique, which usually allows identification to genus or species (Montagnes & Lynn 1987, Skibbe 1994). Ciliates were identified according to Kahl (1930–1935), Lynn & Montagnes (1988a,b), Lynn & Small (2000), Montagnes & Lynn (1991), Montagnes et al. (1988) and Petz et al. (1995). Zooplankton samples were counted and measured under a dissecting microscope. *Oithona* and *Metridia* lengths were converted to biomass using the equations of Sabatini & Kiørboe (1994) and Fransz & Gonzalez (1997). All surviving furcilia were picked out separately, fixed in 5% formaldehyde, and measured under a dissecting microscope. Furcilia size was converted to biomass using the equation of Pakhomov et al. (2004).

Data from the *Oithona* experiment were analyzed using linear regression, while factorial ANOVA was used for the other three experiments. Because there were 2 time-points for bacteria and flagellates in the furcilia-*Oithona* and *Metridia*-*Oithona* experiments, repeated measures ANOVA was used to analyze those data. In order to group the various ciliate taxa and morphotypes into similarly responding groups, disjoint (non-hierarchical) cluster analysis was used, using only species that made up at least 2% of total ciliate abundance. All analyses were conducted using SAS version 6.12 (SAS Institute 1989).

Clearance rates were calculated in order to estimate the per-predator impact on the prey population. In the *Oithona* experiment, this was done by calculating the per-day net ciliate or chl *a* exponential growth rates from beginning to end of the experiment. These growth rates were then regressed against ind. ml⁻¹, and the slope of the regression was clearance rate, with units of ml ind.⁻¹ d⁻¹ (Lehman & Sandgren 1985). For the furcilia-*Oithona* and *Metridia*-*Oithona* experiments, clearance rates (*F*) were calculated as:

$$F = \ln(N_{\text{control}} \times N_{\text{grazer}}^{-1}) \times \text{grazer}^{-1} \times \text{duration}^{-1}$$

N_{grazer} and N_{control} are the end prey abundances in treatments with and without the grazer, 'grazer' is the furcilia or *Metridia* abundance, and 'duration' is the experiment duration. This equation is equivalent to Frost's (1972) calculation of grazing rates, assuming the same initial prey abundance in treatments with and without predators. From the clearance rates, predator selectivity for the different prey types was

calculated as Chesson's α and converted to electivity in order to scale selection from -1 to 1, where 0 is no selection (Chesson 1983). Dinoflagellate abundance was too low (initial abundance 0.10 to 0.27 cells ml⁻¹, Table 2) to calculate grazing rates with any confidence. As a result, although dinoflagellate abundance data is shown, grazing and selectivity estimates do not include dinoflagellates.

RESULTS

Furcilia-*Oithona* experiments

Experimental conditions

The 2 furcilia-*Oithona* experiments were started 9 d apart but under considerably different conditions. In the first experiment, the initial chl *a* concentration was less than half, but bacterial numbers twice those found at the beginning of the second experiment (Table 2). Initial total ciliate abundance was 0.94 and 0.70 cells ml⁻¹ in the first and second experiments, respectively, and water temperature averaged -0.1°C (first experiment) and 1.7°C (second experiment). In the first experiment, FIII furcilia of mean size 6.35 mm and biomass 241 µg C l⁻¹ were used. In the second experiment, mean furcilia size was 8.52 mm (FIII and FIV larvae) and the biomass was 3 times higher (740 µg C l⁻¹). Survival of furcilia in the experiments was good: in all but one of the bottles, at least 7 of the 8 added furcilia (2.9 ind. l⁻¹) were recovered alive. Mean *Oithona* size was the same in the two experiments (0.75 mm; *t*-test: *p* = 0.23), and did not change due to the presence or absence of furcilia (*t*-test: *p* > 0.15). Despite the larger number of *Oithona* used in the second experiment (20 ind. l⁻¹ vs. 15 ind. l⁻¹ in the first experiment), the end biomass in the two experiments in treatments without krill was the same (25.5 µg C l⁻¹; *p* = 0.62), due to differences in copepod survival between the 2 experiments (97 and 82% survival in treatments without furcilia in the first and second experiment, respectively; Fig. 1A,B).

Grazing impact on *Oithona*, algae and ciliates

While furcilia had a considerable impact on total algal biomass, their suppression of copepods, ciliates and dinoflagellates was much greater. Presence of furcilia reduced end chl *a* concentrations by approximately 40% in the first, and 80% in the second experiment, both significant declines (*p* < 0.001; Fig. 1C,D). In both experiments, there were marginally higher chl *a* concentrations in treatments with *Oithona* than in

those without, but these differences were not significant ($p > 0.05$). Furcilia impact on copepods was much larger than that on chl *a*: in treatments with both krill and copepods, copepod end abundance was 8 and 5% of that in treatments without krill in the first and second experiments, respectively (Fig. 1C,D). The impact of furcilia on ciliates was even larger than that on copepods. At the end of both experiments, treatments with krill had less than 1% of the ciliate abundance of treatments without krill (Fig. 1E,F). *Oithona* had a somewhat different impact on ciliates, dependent on the experiment. In the first experiment, there was a marginal copepod main effect and a marginal krill \times cope-

pod interaction ($p = 0.082$ and $p = 0.086$, respectively), resulting from a trend towards higher ciliate abundance in treatments with copepods compared to those without, particularly when furcilia were not present (copepods present vs. copepods absent for treatments without furcilia: $p = 0.021$ in an unprotected *t*-test). In the second furcilia-*Oithona* experiment, which had higher initial copepod abundance, this trend was not seen (copepod main effect and copepod \times krill interaction: $p > 0.60$) (Fig. 1). The response of dinoflagellates to the experimental manipulations was similar to that of the ciliates. (Fig. 1G,H, Table 3).

Because furcilia reduced *Oithona* and ciliate abundances to such a great degree, the calculated grazing rates on *Oithona* and ciliates are certainly underestimates. Nevertheless, they provide an indication of the potential impact of furcilia on ciliates and small copepods. In the first experiment, the grazing rate of furcilia on *Oithona* was 5 times the grazing rate on algae, and the grazing rate on ciliates was almost 10 times higher than that on algae (Table 4). In the second experiment, with larger furcilia, grazing on algae was almost 3 times higher than that in the first experiment, but grazing on *Oithona* was roughly similar, and grazing on ciliates lower, than in the first experiment. As would be expected from the observed grazing rates, furcilia had strong positive electivities for ciliates, particularly in the first experiment (Table 4). Electivity for algae was always negative, whereas electivity for copepods was neutral in both experiments.

The ciliate community in our experiments was analyzed with a high taxonomic resolution. We could differentiate 28 different species and/or morphotypes, 11 of which made up at least 2% of total abundance. These were largely oligotrichs, such as *Strombidium acutum*, *Strombidium neptuni*, *Strombidium conicum*, *Leegaardiella ovalis* and *Lohmanniella oviformis*. The massive grazing impact of furcilia precluded any division between grazing-vulnerable or grazing-resistant groups — all ciliate taxa were reduced to near zero abundance. In addition, no differences in their vulnerability to copepod grazing could be found, even when bottles that contained furcilia were excluded. Once these samples were excluded, there was limited statistical power remaining with which to discern differences.

Grazing impact on nanoplankton and bacteria

In stark contrast to the effect of furcilia on copepods, chl *a* and ciliates, no significant or even near-significant effects on bacteria, HNAN or PNAN were found in either experiment (Fig. 2, Table 2). There

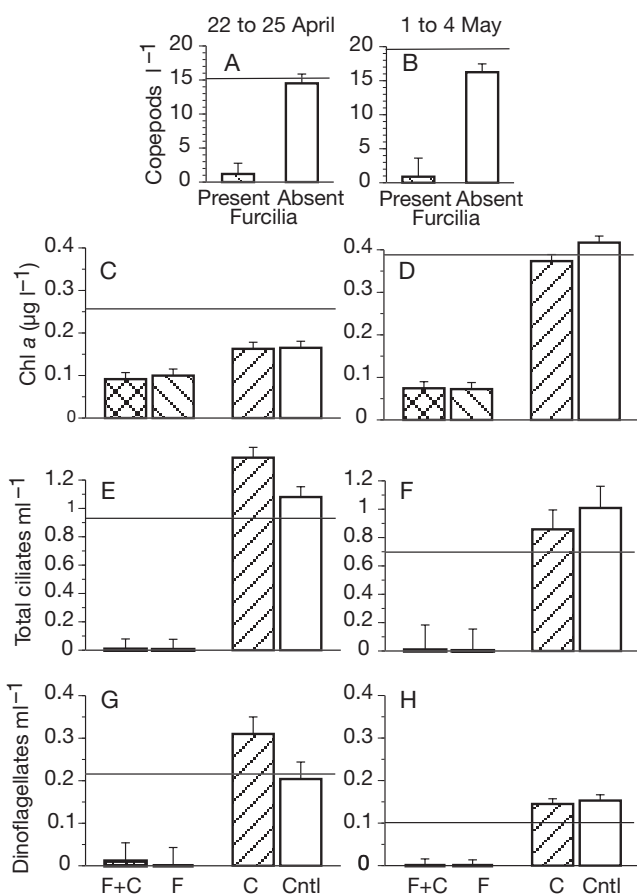


Fig. 1. Furcilia-*Oithona* experiments. Mean (A,B) copepod abundance, (C,D) chl *a* concentration, (E,F) total ciliate abundance, and (G,H) total dinoflagellate abundance. Left panels (A,C,E,G): first experiment (22 to 25 April 2001, initial *Oithona* abundance 15 ind. l⁻¹, FIII furcilia abundance 2.9 ind. l⁻¹). Right panels (B,D,F,H): second experiment (1 to 4 May 2001, initial *Oithona* abundance 20 ind. l⁻¹, FIII and FIV furcilia abundance 2.9 ind. l⁻¹). As a result of differences in furcilia stages, initial furcilia biomass in the second experiment was 3-fold that in the first experiment. F+C: treatments with both furcilia and copepods; F: furcilia alone; C: copepods alone; Cntl: control treatments without furcilia or copepods; horizontal lines: initial abundance; error bars: 1 SE

Table 3. *F*- and *p*-values from ANOVA of the furcilia-*Oithona* experiments. Bacteria, HNAN and PNAN (heterotrophic and phototrophic nanoplankton, respectively) were sampled twice during experiments and data analyzed in a repeated measures ANOVA. Chl *a* and ciliate abundance were measured only at the end of experiments and were analyzed with 2-way factorial ANOVA. 'Furcilia' is the furcilia presence/absence treatment, '*Oithona*' is the *Oithona* presence/absence treatment. For both between- and within-time effects, *df* = 1,12

Response variable		Treatment						
		Furcilia	<i>Oithona</i>	Furcilia × <i>Oithona</i>	Time	Time × Furcilia	Time × <i>Oithona</i>	Time × Furcilia × <i>Oithona</i>
Expt 1								
Chl <i>a</i>	<i>F</i>	26.2	0.16	0.05				
	<i>p</i>	<0.001	0.696	0.828				
Dinoflagellates	<i>F</i>	33.70	1.84	1.21				
	<i>p</i>	<0.001	0.208	0.300				
Ciliates	<i>F</i>	271	3.62	3.50				
	<i>p</i>	<0.001	0.082	0.086				
Bacteria	<i>F</i>	0.01	<0.01	0.90	4.17	0.03	0.18	2.58
	<i>p</i>	0.942	0.952	0.362	0.064	0.864	0.681	0.134
HNAN	<i>F</i>	0.10	0.21	1.58	35.0	1.31	0.44	5.72
	<i>p</i>	0.752	0.657	0.233	<0.001	0.274	0.518	0.034
PNAN	<i>F</i>	0.09	0.84	0.01	6.79	0.56	1.90	0.01
	<i>p</i>	0.774	0.379	0.916	0.023	0.467	0.193	0.934
Expt 2								
Chl <i>a</i>	<i>F</i>	334	1.39	1.67				
	<i>p</i>	<0.001	0.646	0.193				
Dinoflagellates	<i>F</i>	115.1	0.076	0.076				
	<i>p</i>	<0.001	0.787	0.787				
Ciliates	<i>F</i>	35.7	0.22	0.25				
	<i>p</i>	<0.001	0.607	0.574				
Bacteria	<i>F</i>	0.56	0.99	2.13	15.93	0.05	3.43	<0.01
	<i>p</i>	0.470	0.339	0.170	0.002	0.827	0.089	0.991
HNAN	<i>F</i>	0.20	0.66	1.74	<0.01	2.59	0.43	0.66
	<i>p</i>	0.665	0.431	0.212	0.993	0.134	0.527	0.433
PNAN	<i>F</i>	0.66	2.85	1.13	41.55	0.09	2.34	0.14
	<i>p</i>	0.432	0.117	0.308	<0.001	0.774	0.152	0.717

Table 4. Clearance rates and electivities of furcilia larvae, *Oithona* and *Metridia*. Clearance rate is scaled to predator abundance (ml ind.⁻¹ d⁻¹, ± 1 SE). Grazing rates given only when they differed significantly from 0. In the second furcilia-*Oithona* experiment, *Oithona* was present at the end of only 1 treatment; therefore, no SD could be calculated. Electivity was calculated from Chesson's α , scaled so that 0 is neutral selection (grazing in proportion to relative abundance in the environment). For the group of grazing-vulnerable ciliates, electivity was calculated with ciliates split into grazing-vulnerable and -resistant groups

Expt	Clearance rate				Electivity			
	Chl <i>a</i>	<i>Oithona</i>	Total ciliates	Vulnerable ciliates	Chl <i>a</i>	<i>Oithona</i>	Total ciliates	Vulnerable ciliates
Furcilia- <i>Oithona</i> I	78.5 ± 11	383 ± 24	768 ± 61	–	–0.78	0.03	0.71	–
Furcilia- <i>Oithona</i> II	215 ± 13	354	624 ± 45	–	–0.48	–0.04	0.48	–
<i>Metridia</i> - <i>Oithona</i>	–	202 ± 48	139 ± 26	325 ± 50	–1	0.56	0.05	0.52
<i>Oithona</i> grazing	–	–	–	9.67 ± 3.2	–1.0	–	–	1.0

were also no time-dependent interactions (except for 1 time × krill × copepod interaction for HNAN in the first experiment), indicating that the duration of the experiments did not affect their outcome. In the 1 significant time-dependent effect, HNAN abundance was higher in treatments with furcilia or copepods than in

the control treatments, but this effect was only seen at the end of the first experiment (Fig. 2C). PNAN increased between the first and second sampling occasions in both experiments (Fig. 2E,F), a trend also observed for the HNAN of the first experiment (Fig. 2C).

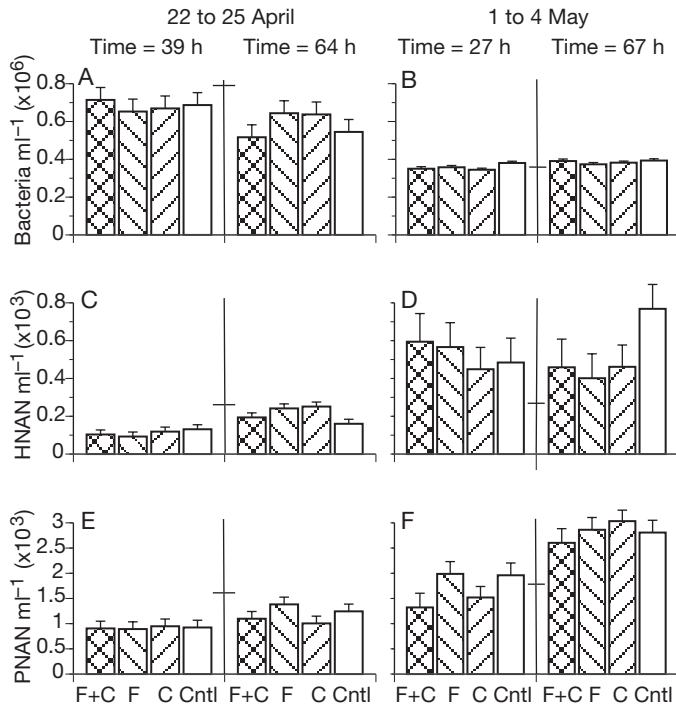


Fig. 2. Furcilia-*Oithona* experiments. Mean abundance of (A,B) bacteria, (C,D) heterotrophic nanoplankton (HNAN) and (E,F) phototrophic nanoplankton (PNAN). Left panels (A,C,E): first experiment (22 to 25 April 2001). Right panels (B,D,F): second experiment (1 to 4 May 2001). Initial abundance (horizontal lines), mid-point abundance (39 or 27 h) and end abundance (64 or 67 h) shown. Copepod and furcilia treatment abbreviations as in Fig. 1. Error bars: 1 SE

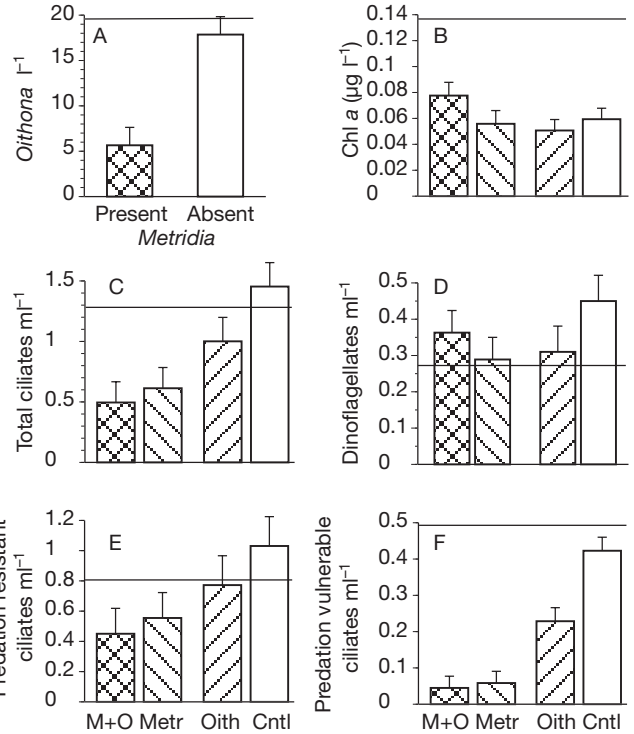


Fig. 3. *Metridia-Oithona* experiment. Mean (A) end copepod abundance, (B) chl *a* concentration, (C) total ciliates, (D) dinoflagellates, (E) grazing-resistant ciliates and (F) grazing-vulnerable ciliates. M+O: treatments with both *Metridia* and *Oithona*; Metr: *Metridia* alone; Oith: *Oithona* alone; Cntl: Control treatments without *Metridia* or *Oithona*; horizontal lines: initial abundance; error bars: 1 SE

Table 5. *F*- and *p*-values from ANOVA of the *Metridia-Oithona* experiment. Bacteria, HNAN and PNAN (heterotrophic and phototrophic nanoplankton, respectively) were sampled twice during experiments and data analyzed in a repeated-measures ANOVA. Chl *a* and ciliate abundance were measured only at the end of experiments and were analyzed with 2-way factorial ANOVA. For both between- and within-time effects, *df* = 1,12

Response variable		Treatment						
		<i>Metridia</i>	<i>Oithona</i>	<i>Metridia</i> × <i>Oithona</i>	Time	Time × <i>Metridia</i>	Time × <i>Oithona</i>	Time × <i>Metridia</i> × <i>Oithona</i>
Chl <i>a</i>	<i>F</i>	1.49	0.47	2.54				
	<i>p</i>	0.250	0.510	0.142				
Dinoflagellates	<i>F</i>	0.60	0.23	2.41				
	<i>p</i>	0.457	0.642	0.155				
Total ciliates	<i>F</i>	13.22	2.37	0.82				
	<i>p</i>	0.005	0.154	0.387				
Vulnerable ciliates	<i>F</i>	61.70	8.85	6.70				
	<i>p</i>	<0.001	0.014	0.027				
Resistant ciliates	<i>F</i>	4.83	1.00	0.18				
	<i>p</i>	0.053	0.341	0.698				
Bacteria	<i>F</i>	0.95	2.93	2.69	20.16	0.04	2.03	0.41
	<i>p</i>	0.352	0.118	0.132	0.001	0.847	0.185	0.535
HNAN	<i>F</i>	1.22	0.57	0.16	0.59	1.61	0.05	0.80
	<i>p</i>	0.296	0.469	0.696	0.459	0.233	0.831	0.393
PNAN	<i>F</i>	2.50	0.27	0.02	3.78	0.16	0.04	0.03
	<i>p</i>	0.145	0.614	0.884	0.080	0.700	0.838	0.874

Metridia-Oithona experiment

Experimental conditions

The *Metridia-Oithona* experiment had the lowest initial chl *a*, PNAN and HNAN concentrations, but the highest ciliate abundance of the 4 experiments (Table 2). Mean temperature during the experiment was 0.95°C. Both *Metridia* and *Oithona* survival was good. With the exception of 1 bottle (which was excluded from the analysis), 75 % of the *Metridia* and, in treatments without *Metridia*, 90 % of the *Oithona* were recovered at the end of the experiment. Mean length of *Metridia* was 2.98 mm, and total *Metridia* biomass at the end of the experiment was 376 $\mu\text{g C l}^{-1}$. *Oithona* biomass was 43 $\mu\text{g C l}^{-1}$ in treatments without *Metridia*.

Grazing impact on *Oithona*, algae and ciliates

The presence of *Metridia* reduced the abundance of *Oithona* by approximately two-thirds ($p = 0.01$; Fig. 3A), but did not alter *Oithona* mean size ($p > 0.1$). Although chl *a* declined over the course of the experiment, this was independent of the *Metridia* and *Oithona* treatments (Fig. 3B, Table 5). A total of 34 ciliate species were found, but only 10 species were abundant enough to contribute to at least 2 % of total abundance in any one treatment. Total ciliate and dinoflagellate abundance in the control treatments increased moderately over the course of the experiment. In *Metridia* treatments, ciliate abundance was reduced to approximately one-third of the control values (Fig. 3C, Table 5). Neither the apparent decline in ciliate abundance in the presence of *Oithona* nor the *Metridia-Oithona* interaction was significant. Dinoflagellate abundance was low and did not respond to either the *Metridia* or *Oithona* manipulations (Fig. 3D, Table 5). The cluster analysis (using species comprising $\leq 2\%$ total abundance in any treatment) separated ciliates into groups either relatively resistant or vulnerable to grazing. The grazing-resistant group made up two-thirds of total ciliate abundance and consisted of 10 species: 5 oligotrichs (*sensu lato*), 2 prostome species, the haptorids *Lacrymaria* sp. and *Mesodinium pupula*, the phylopharynid *Gymnozoum vivparum* and a peritrich. There was a non-significant trend towards lower ciliate abundance in treatments where *Metridia* were present, and no significant reduction due to the presence of *Oithona* (Fig. 3E, Table 5). The grazing-vulnerable group was made up of *Lohmaniella oviformis*, 3 other oligotrich species 20 to 45 μm in length, and a large *Lacrymaria* sp. that was 145 μm in length. These ciliates were strongly suppressed by *Metridia*, with an end abundance of only ca. 15 % of

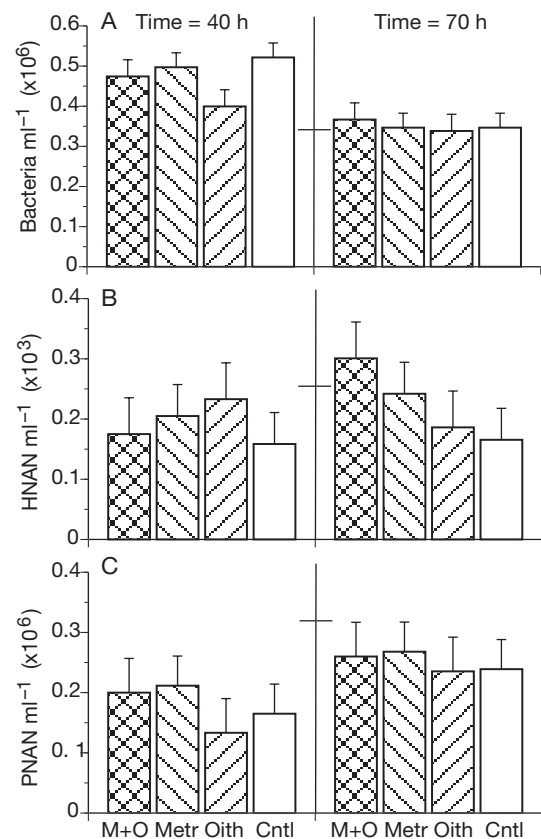


Fig. 4. *Metridia-Oithona* experiment. Mean abundance of (A) bacteria, (B) heterotrophic nanoplankton (HNAN) and (C) phototrophic nanoplankton (PNAN). Initial abundance (horizontal lines), mid-point abundance (40 h), and end abundance (70 h) shown. *Metridia* and *Oithona* treatment abbreviations as in Fig. 3. Error bars: 1 SE

the ciliate abundance in treatments without *Metridia*. The effect of *Oithona* on ciliates was more moderate, but also reduced grazing-vulnerable ciliate abundance by approximately 40 %. There was also an interaction between the effects of *Metridia* and *Oithona*, with the *Oithona* effect (along with much of the *Oithona*) disappearing in the presence of *Metridia* (Fig. 3F).

Grazing impact on nanoplankton and bacteria

As in the furcilia-*Oithona* experiments, manipulations at higher trophic levels did not affect flagellates or bacteria. HNAN, PNAN and bacteria were all unaffected by the presence/absence of *Metridia* and *Oithona* (Fig. 4, Table 5). Time-dependent effects were mostly absent, and only bacterial abundance varied between the 2 sampling occasions. End abundances of bacteria, HNAN and PNAN were similar to the initial abundances (Fig. 4).

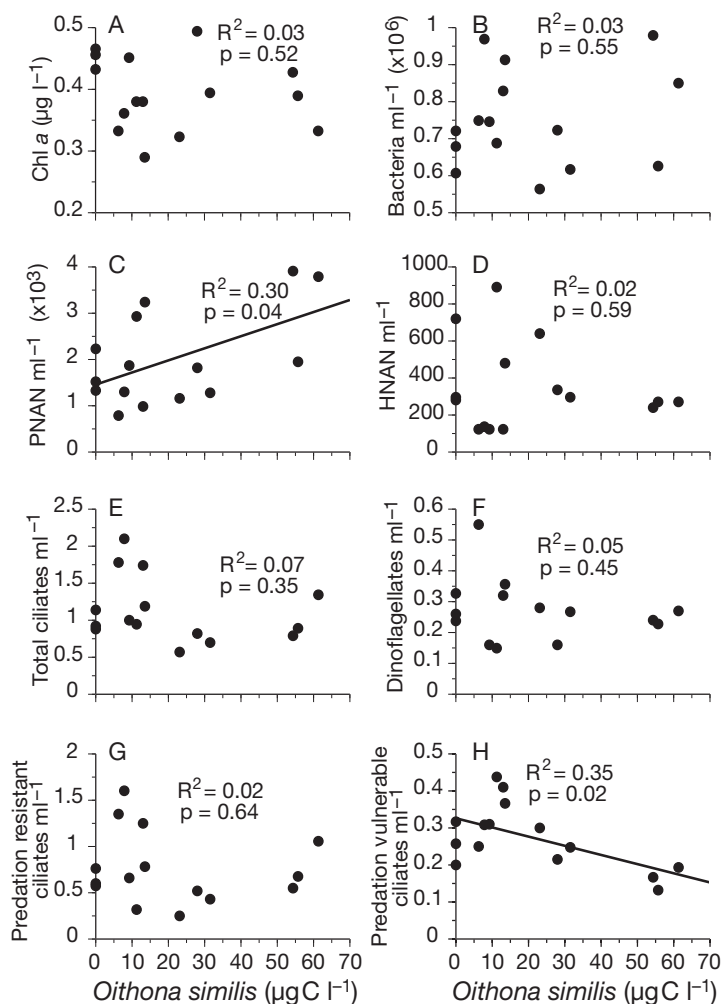


Fig. 5. *Oithona* grazing experiment. End values for (A) chl *a* concentration, and abundances of (B) bacteria, (C) phototrophic nanoplankton (PNAN), (D) heterotrophic nanoplankton (HNAN), (E) total ciliates, (F) dinoflagellates, (G) grazing-resistant ciliates and (H) grazing-vulnerable ciliates. Regression lines given only when slope differed significantly from zero

Oithona experiment

Experimental conditions

This experiment was run with water from 10 m depth from a shelf station (Table 1), with an average incubation water temperature of 1.1°C. Initial chl *a* concentration was 0.35 µg l⁻¹, and flagellate, bacterial and ciliate abundances were proportionately low (Table 2). Copepod survival was good, with no difference in copepod biomass from beginning to end of the experiment ($p = 0.11$). *Oithona* biomass in treatments with copepods ranged from 7.8 µg C l⁻¹ in the 4 ind. l⁻¹ treatment to 57 µg C l⁻¹ in the 32 ind. l⁻¹ treatment (mean size: 0.79 mm).

Grazing impact on the plankton community

The effect of *Oithona* on the plankton community was weaker than that recorded for furcilia and *Metridia*. Mean chl *a* concentration at the end of the experiment was 0.39 µg l⁻¹, with no relationship observed between chl *a* and end copepod biomass ($R^2 = 0.03$, $p = 0.56$; Fig. 5A). Mean bacterial and HNAN abundances at the end of the experiment were 0.75×10^6 and 2.01×10^3 cells ml⁻¹, respectively. Similar to chl *a*, there was no significant regression with copepod biomass ($p > 0.50$; Fig. 5B,D). However, a weak positive relationship between copepod biomass and PNAN abundance was present ($R^2 = 0.30$, $p = 0.036$). In the absence of copepods PNAN abundance was 1.46×10^3 cells ml⁻¹, increasing by approximately 100% in the treatment containing the highest concentration of copepods (Fig. 5C).

A total of 33 ciliate species were found in samples at the end of the experiment, 12 of these contributing at least 2% to total abundance. These were mostly oligotrichs (*sensu lato*), with 2 litostome and 1 protostome species. Final mean ciliate abundance in treatments without *Oithona* was 0.98 cells ml⁻¹, a non-significant increase ($p = 0.24$) from the initial abundance of 0.74 cells ml⁻¹. Total ciliate abundance did not vary with *Oithona* biomass ($p = 0.35$; Fig. 5E). However, the cluster analysis split the ciliates into 2 groups: one of which made up approximately two-thirds of the total ciliate abundance and was grazing-resistant (regression against copepod biomass: $p = 0.64$), and a grazing-vulnerable group that did decline with increasing copepod biomass ($R^2 = 0.35$, $p = 0.02$; Fig. 5G,H). The grazing-vulnerable group consisted of 2 small oligotrichs *Lohmanniella oviiformis* and *Cyrtostrombidium* sp., and the litostome *Mesodinium pupula*, all approximately 20 µm in diameter. Among the grazing-vulnerable group, the end ciliate abundance at the highest copepod density (32 ind. l⁻¹, 57 µg C l⁻¹) was reduced to ca. 55% of that in the copepod-free treatments (Fig. 5H). The response of total dinoflagellate abundance was similar to that of total ciliates, in that there was no significant decline with increasing *Oithona* abundance (Fig. 5F). However, dinoflagellate abundance was too low to distinguish between potentially grazing-vulnerable or grazing-resistant groups (initial abundance: 0.13 cells ml⁻¹).

Clearance rates were only calculated for the grazing-vulnerable ciliates, as these were the only group to significantly decline with increasing *Oithona* abundance. This produced a grazing rate of 9.67 ml ind.⁻¹ d⁻¹ ($R^2 = 0.42$, $p = 0.009$). Because there was no significant grazing on algal chl *a*, the electivity of *Oithona* was +1 for vulnerable ciliates and -1 for chl *a* (Table 4).

DISCUSSION

These experiments demonstrated that heterotrophic food sources make up a substantial proportion of the diet of furcilia, with strong positive selection for ciliates over algae. Grazing vulnerability of the ciliates was only species-specific when copepods, not furcilia, were the predators. There was a large range of impacts on ciliates, from minimal, selective predation by *Oithona*, through moderate selective predation by *Metridia*, to massive and unselective predation by furcilia. Despite this broad spectrum of predation pressures, in only one case (PNAN in the *Oithona* experiment) was there any response in the trophic levels beneath ciliates. There was no interaction between the grazing effects of *Oithona* and furcilia, due to the large direct grazing impact of furcilia on ciliates. In contrast, *Metridia* grazing on *Oithona* reduced grazing pressure on grazing-vulnerable ciliates. The impact of *Oithona* was minimal, but some selectivity among ciliate prey could be shown.

Grazing impact of krill larvae and copepods, importance of ciliate community composition

Both adult and larval krill are known herbivores, as demonstrated by the furcilia in these experiments. The differences in end chl *a* concentrations between treatments with and without furcilia resulted in grazing rates within the range previously observed for FIII larvae grazing on a mixed algal community at a similar time of year (Table 4; Meyer et al. 2002). However, it is also known that adult krill are not pure herbivores, and that heterotrophic food sources may make up a substantial proportion of krill's diet (Granéli et al. 1993, Atkinson & Snýder 1997, Perissinotto et al. 2000). There has been considerably less research carried out on larval krill, but here too, grazing on heterotrophs has been shown. Both Quetin et al. (1994) and Meyer et al. (2002) showed furcilia to be capable of grazing heterotrophs, but concluded that they were primarily herbivorous, and Meyer et al. (2002) found FIII larvae to be unselective. In contrast, the FIII–FIV larvae used in our experiments exhibited strong positive selection for ciliates. The presence or absence of *Oithona* did not affect the impact of furcilia on ciliates, indicating that, at least with the intense grazing pressure seen in our experiments, furcilia did not switch to or from ciliates depending on the availability of copepod prey.

Metridia also showed a clear preference for heterotrophic over phototrophic prey, with positive selection for *Oithona* and a subset of the ciliate community over algae. The significant interaction between the effects of *Metridia* and *Oithona* on grazing-vulnerable ciliates

implies that *Metridia* switched between ciliate and cyclopoid prey, with a greater reduction in grazing-vulnerable ciliate abundance when *Oithona* was absent than when it was present (Fig. 3). However, at least part of this interaction was due to grazing-vulnerable ciliates also being vulnerable to *Oithona* predation. This was reduced in the presence of *Metridia*, because *Metridia* also consumed *Oithona*.

A possible reason why selective feeding by furcilia was seen in these experiments, but not in those of previous research (Atkinson & Snýder 1997, Meyer et al. 2002), is that ciliates were relatively more abundant in our experiments. The range of chl *a* concentrations at the start of our experiments was similar to that in previous studies involving furcilia and ciliates, but ciliate abundance was higher. Ciliates comprised between 0.3 and 7.6% of total particulate organic matter in Meyer et al.'s (2002) study, whereas ciliate carbon represented approximately 10% of algal carbon (admittedly a subset of total POC) at the beginning of the furcilia-*Oithona* and *Oithona* grazing experiments (and 45% of algal carbon in the *Metridia*-*Oithona* experiment). Thus, there may be a threshold minimum algal concentration or relative ciliate abundance that determines whether furcilia feed selectively. The low algal and high ciliate abundance seen in our experiments represent conditions likely to be a common feature of the Antarctic fall. The peak in ciliate biomass is broader than that for chl *a*, extending until the end of May (Leakey et al. 1994).

The magnitude of the impact of furcilia on ciliates and *Oithona* is emphasized by the fact that the clearance rates measured in our experiments are clearly underestimates. Furcilia entirely depleted ciliate and copepod prey in several of the bottles, and drove the abundance in the remainder to near zero. As a result, the same amount of grazing could have been measured in an experiment of shorter duration. The duration and predator densities used in our experiments were chosen as an estimate of what would be sufficient to see a difference not only in the prey, but also in lower trophic levels, should a trophic cascade be operating. In terms of assessing the grazing impact on algae, we achieved our aims. However, if the duration of experiments had been shorter, or fewer furcilia per bottle were used, then the calculated grazing rates on ciliates and *Oithona* would have been higher and the positive selection of these prey organisms over algae would have been even greater. Neither the *Metridia* nor the *Oithona* experiments showed such extreme declines in prey densities; therefore, the grazing rates measured in these experiments are not likely to be underestimates.

The limited impact of *Oithona* on ciliates was unexpected, as it has been shown to be an effective cili-

ate predator and to positively select for ciliates over similar-sized diatoms or dinoflagellates (Atkinson 1996, Nakamura & Turner 1997, Lonsdale et al. 2000). *Oithona* is also known to reproduce in the Antarctic fall, implying a need to feed during the time of our study (Fransz & Gonzalez 1995). The condition of the copepods at the beginning of the experiments was good: both individuals with fat globules and females with egg masses were observed. Copepod survival in the experiments was also good, making experimental artifacts an unlikely explanation. In contrast to most other studies, we investigated the ciliate community with a high enough taxonomic resolution to discern grazing effects on individual taxa. The rate we measured for *Oithona*'s grazing on vulnerable ciliates (Table 5) was similar to that measured previously for total ciliates by both Atkinson (1996) and Nakamura & Turner (1997), but only a third of that measured by Lonsdale et al. (2000). In our experiment, the grazing-vulnerable ciliates were small (maximum dimension $\leq 21 \mu\text{m}$), and larger ciliates common in our experiments such as *Strombidium acutum* and *Leegaardiella ovalis* were not grazed, running counter to a previously reported trend of increasing vulnerability with increasing size (Nakamura & Turner 1997). Nevertheless, the group of grazing-vulnerable ciliates were close in size to those that Atkinson (1996) found to be preferred prey of *Oithona*. The small size of the grazing-vulnerable ciliates and the low grazing rates by *Oithona* led to an estimated ingestion rate that is approximately 1% of *Oithona* body carbon per day. This is not only well beneath their metabolic needs, but also much less than that found by Lonsdale et al. (2000), who observed that summer populations of *Oithona* spp. in the Ross Sea ingested on average 90% of their body carbon per day. In 3 of the 4 experiments in Lonsdale et al.'s (2000) study, ciliate abundance was almost an order of magnitude higher than in ours. Why *Oithona* restricted itself to a small subset of the available prey in our study is not clear.

Connection between the classic and microbial food web

During winter and early spring, Antarctic waters are net heterotrophic, with bacterial biomass and secondary production exceeding algal biomass and primary production (Rivkin 1991). Grazing on ciliates is then a possible route to channel microbial production to krill at times when primary production is minimal. In our experiments, however, ciliates did not serve as a part of a trophic cascade by transferring changes from higher trophic levels to the microbial food web. An unintended outcome of furcilia driving ciliate abun-

dance so low was that an entire trophic level—which supposedly links the microbial and classic food webs—was eliminated. If ciliates were exerting top-down control on flagellates or bacteria, then ciliate removal could be expected to result in an increase at the next, lower trophic level. Quite unequivocally, this did not occur (Figs. 1 & 2, Table 3).

Within-treatment variation was low, suggesting that there was power enough to detect real differences, had they been present. There was considerable variation in initial conditions (Table 2), suggesting that the lack of a trophic cascade from higher trophic levels to the microbial food web could be a general phenomena for the time of year within which experiments were carried out. Supporting this conclusion, recent work in the Bellinghausen Sea found bacterivory to be only slightly reduced when microzooplankton were removed (thus supposedly releasing bacterivorous HNAN from predation pressure), and the presence or absence of microzooplankton had little impact on either HNAN or bacterial abundance (Vaque et al. 2004). Top-down control of Antarctic microbial communities has been previously demonstrated, but this was during summer, with a microzooplankton community dominated by dinoflagellates that were largely absent from our experiments (Kuparinen & Bjørnsen 1992). A likely reason for the lack of top-down control in our experiments is that flagellates and bacteria were so resource-limited that they could not grow faster when grazers were removed. Resource limitation of bacteria in the Southern Ocean has been found even during the spring bloom and austral summer, and was cited as the reason why bacterial and primary production were uncoupled in the Gerlache Strait during spring, despite remarkably low (≤ 100) bacteria:HNAN ratios (Bird & Karl 1999). Whether this is also the case during the austral autumn is unclear, due to a lack of data. The results of our experiments indicate that although ciliates may transfer microbial biomass to higher trophic levels, changes in higher trophic levels do not necessarily transfer down to the microbial food web.

Part of the explanation as to why the removal of ciliates did not change HNAN, PNAN or bacterial abundance is that ciliates do not occupy a single trophic level. The species present in our experiments could graze on both HNAN and their bacterial prey, an argument also used by Vaque et al. (2004) to account for the lack of a measurable trophic cascade in their study. In addition, predacious species such as *Lacrymaria* sp. and *Litonotus* sp. were common in our experiments. Thus, when furcilia grazed down ciliate abundance, they simultaneously removed predators on ciliates, HNAN and bacteria. When complex ciliate communities are present, it is clearly overly simplistic to expect a trophic cascade to be easily observed.

While ciliates may have not been effective in channelling microbial production to copepods and krill, they provided indirect means of accessing algal production that would not have been otherwise available. It has been suggested that microzooplankton are generally the major grazers of phytoplankton in the ocean, and that in polar regions they consume on average 60% of primary production and 20% of algal standing stock per day (Calbet & Landry 2004). These rates are clearly dependent on season as well as on the composition of the algal and microzooplankton community. Antarctic microzooplankton, dominated by ciliates and dinoflagellates, can graze in excess of 100% of algal production in the marginal ice zone during late spring and early summer (Burkill et al. 1995). However, Froneman & Perissinotto (1996), working in late summer, found that microzooplankton grazed only 8 to 33% of primary production as algae were dominated by net plankton, and Caron et al. (2000) found minimal microzooplankton herbivory at 4 different times of year. The naked oligotrichs (*sensu lato*) that dominated the ciliate community during our experiments are largely grazers in the nanoplankton size range, with the smaller species capable of grazing smaller nanoplankton and the larger picoplankton size classes (Jonsson 1986, Kivi & Setälä 1995). These algal size classes are beneath the size range that can be effectively grazed by krill. But by grazing ciliates, krill would have access to at least part of the production from these size classes. However, whether ciliates are for furcilia primarily a method to access algal production from size classes too small to graze directly, or under different circumstances and times of year a route to microbial production, remains to be demonstrated.

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