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Predation by *Oithona* spp. on protozooplankton in the Ross Sea, Antarctica

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Abstract

We investigated predation rates of small copepods, primarily species of *Oithona*, on microprotozooplankton and net growth rates of these prey at several locations in the Ross Sea, Antarctica, during an austral summer (January 1997; US JGOFS Process Study II). Ciliates, particularly non-loricate ciliates, contributed substantially to the carbon ration of *Oithona* spp., averaging 90% body C d^{-1}, while dinoflagellates were much less important (1% body C d^{-1}) despite the latter's higher abundances. We found no significant difference in net growth rates among non-loricate ciliates, tintinnid ciliates and dinoflagellates when zooplankton predators $>64\,\mu m$ were removed. The overall average growth rate for each protozoan taxon across the main transect line (76°30′S) was $0.1\,d^{-1}$ (rates ranged from -0.5 to $1.0\,d^{-1}$). Our findings also suggest that copepod predation has a minimal impact on the regulation of protozoan abundances. We estimated that predation by *Oithona* spp. could account for the removal of only 0.3–4.8% d^{-1} of ciliate standing stocks, and even less (<0.05–0.2% d^{-1}) of the dinoflagellates. Low mortality from predation may help explain the relatively abundant populations of microprotozooplankton in the Ross Sea despite their low average net growth rates.

1. Introduction

Feeding preferences of copepods for protozooplankton have not been carefully documented for Antarctic waters compared to other aquatic ecosystems (Sherr et al., 1986; Stoecker and Capuzzo, 1990; Sanders and Wickhan 1993). Indirect indices of

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feeding selectivity such as lipid biomarkers and stable isotope analysis have indicated that a number of Antarctic copepod species display opportunistic or omnivorous diets (Rau et al., 1991; Graeve et al., 1994). Atkinson (1995, 1996) directly investigated the feeding preferences of Antarctic copepods during an austral spring, and found motile prey, such as dinoflagellates and ciliates were preferred by the copepod genera *Oithona* and *Metridia* when compared to diatoms. The copepod genera *Rhincalanus* and *Calanoides* did not exhibit this preference, but motile prey items still comprised a considerable fraction (43%) of the carbon intake of these copepods (Atkinson, 1994). Smaller nanoplanktonic species of algae often dominate Antarctic plankton assemblages (Von Brokel, 1981; Hewes et al., 1985; Weber and El-Sayed, 1987). Therefore, it is probable that some energy transfer from primary producers to crustacean zooplankton occurs through an intermediary trophic level (e.g., ciliates and large heterotrophic flagellates). Given this scenario, it is also probable that protozooplankton populations are regulated by mesozooplankton predation in these waters (e.g., Atkinson, 1995).

Our initial studies in the Ross Sea indicated low rates of zooplankton grazing on phytoplankton (U.S. JGOFS Process I, November 1996; Caron et al., 2000), so we undertook a modest ancillary study to examine zooplankton predation on protozooplankton. These experiments were conducted in mid-late austral summer in the Ross Sea, Antarctica during the U.S. JGOFS Process Study II (January 1997). Specifically, we measured predation rates of small copepods, primarily species of the cyclopoid *Oithona*. We selected this genus for study because, at times, it can numerically dominate the metazoan zooplankton in the mixed layer of Antarctic waters (e.g., Metz, 1995; Fransz and Gonzalez, 1997; Swadling et al., 1997). Also, it has been shown in other environments that *Oithona* is highly dependent on protozooplankton to support growth (e.g., North Sea and temperate coastal waters; Nielsen and Sabatinai, 1996; Nakamura and Turner, 1997).

2. Materials and methods

Copepod predation experiments were conducted in conjunction with zooplankton herbivory studies (Caron et al., 2000). The sampling stations for our predation experiments and most protozoan population growth studies were located along an east–west transect line at 76°30′S (Stations Minke, "O" and Orca), and two additional protozoan growth rate studies were conducted near the Ross Ice Shelf (Station Emperor) and in the northern Ross Sea (Station Sei) (Table 1). In general, the water used in the predation and growth rate experiments was obtained from the same casts at water depths of 5 or 10 m (Table 1), depths that corresponded to $\sim 50\%$ incident light (Caron et al., 2000). We used a predator exclusion/addition approach and focused on protozooplankton prey $> 20\,\mu m$ because of the methodological difficulties of addressing grazing on smaller protozoa (i.e., "trophic cascade" effects on nanoplankton from changes in microplankton concentration).

Size-fractionated seawater (< 200 or $< 64\,\mu m$) was prepared using in-line filters to minimize bubbling. The purpose of this filtration was to remove all mesozooplankton

Table 1
Summary of protozoan growth rate (D) and copepod predation (C) experiments conducted at five stations in the Ross Sea. Information on controls for the predation experiments is also included; $< 200\,\mu m$ filtered seawater served as controls for larger copepods and $< 64\,\mu m$ filtered seawater for the nauplii experiments. For the nauplii predation experiments conducted at "O" 205, D2 incubations served as the control. For the C8 predation experiments (Orca 220), controls (both < 200 and $< 64\,\mu m$ filtered seawater) were placed in a walk-in incubator along with experimental bottles because of limited on-deck incubation space for the predation studies (see Section 2)

Station name/ no.	Station location	Sampling date	Sampling depth (m)	Chlorophyll a ($\mu g\,l^{-1}$)	Experiment	Zooplankton predators	Replicates	Incubation time (h)
Minke 201	76°30′S 169°E	13 Jan	10	2.0	C1	*Oithona*	3	40.3
						Metridia	3	25.6
						$<200\,\mu m$	3	37.3
					D1	$<64\,\mu m$	3	37.3
Minke 213		27 Jan	5	0.6	C6	*Oithona*	3	50.5
						$<200\,\mu m$	3	77.5
			5	0.5	D6	$<64\,\mu m$	3	77.5
"O" 205	76°30′S 176°E	16 Jan	10	5.8	C2	*Oithona*	3	38.8
						$<200\,\mu m$	3	42.7
						Nauplii	2	37.0
					D2	$<64\,\mu m$	3	42.7
"O" 217		30 Jan	5	3.6	D7	$<64\,\mu m$	3	74.0
Orca 220	76°30′S 178°W	1 Feb	5	0.8	C8	*Oithona*	3	65.5
						$<200\,\mu m$	2	65.5
						Nauplii	2	55.0
						$<64\,\mu m$	1	55.0
					D8	$<64\,\mu m$	3	76.3
Orca 208		19 Jan	5	2.0	D3	$<64\,\mu m$	3	37.9
Emperor 209	78°3′S 176°4′W	21 Jan	5	1.0	D4	$<64\,\mu m$	3	38.0
Sei 211	74°2′S 176°58′E	25 Jan	5	0.7	D5	$<64\,\mu m$	3	73.7

or larger microzooplankton (e.g., most copepod nauplii), that might prey on the larger protozoa. Predator exclusion allows an estimate of net protozoan population growth in the absence of targeted predators, and is necessary for more accurately estimating a predation coefficient for copepods (sensu Frost, 1972). Samples of the size-fractionated seawater were preserved in Lugol's iodine for microplankton counts (Sherr and Sherr, 1993; Stoecker et al., 1994).

Copepods were collected in slow, drift tows using ring nets (64, 200 or 500 μm mesh). Collection depths ranged from 5 to 30 m, with the exception of *Metridia* spp., which were collected at 200 m. Copepods were immediately sorted in a walk-in incubator ($\sim 0^{\circ}$C) using a dissecting microscope equipped with a fiber optic illuminator. Late-stage copepodites (CIV–CV) and adults (both male and female) were sorted to genus, while copepod nauplii were pooled, although many were identified as *Oithona* nauplii. Identifications of adult copepods were made according to Razouls (1994). Prior to final transfer to incubation bottles, experimental copepods were transferred three times into the size-fractionated seawater used for incubations and checked for swimming activity and morphological damage. These steps were taken in order to ensure that healthy copepods were employed and to dilute out other zooplankton from the concentrated zooplankton sample. Experimental and control bottles (acid-washed, 2 l polycarbonate for predation studies and 1.2 l for protozoan growth rate studies) contained either < 200 μm (for copepod predation experiments) or < 64 μm filtered seawater (for naupliar predation and protozoan growth rate experiments; Table 1). Copepod concentrations in experimental bottles ranged between 7.5 and 10 *Oithona* spp. l^{-1}, 22 and 25 nauplii l^{-1} and 5 *Metridia* spp. l^{-1}.

Incubations were carried out for at least 36 h but no longer than 78 h (Table 1), corresponding to herbivory studies. All protozoan growth rate experiments and most predation experiments were conducted in an on-deck incubator under natural light that was attenuated to $\sim 50\%$ of incident light using neutral screening. Due to limited on-deck incubation space, however, C8 experimental and control bottles were incubated in a walk-in incubator ($\sim 0^{\circ}$C) under 24 h indirect lighting from a fluorescent fixture.

Following incubation, water samples for microzooplankton preservation (as above) were obtained from all control and experimental bottles. Microplankton were enumerated in the laboratory using standard settling techniques (Utermohl, 1958). Abundances of ciliates and dinoflagellates (> 20 μm) were determined by examination of the settled samples (100 ml) using an inverted microscope, either a Zeiss IM 35 or Olympus CK 2. Microplankton biovolumes were determined from their linear dimensions and volume equations for appropriate geometric shapes, and these biovolumes were converted to carbon biomass using published conversion factors (i.e., Putt and Stoecker (1989) for non-loricate ciliates, Stoecker et al. (1994) for heterotrophic dinoflagellates, and Verity and Langdon (1984) for tintinnids).

Net growth rates of protozoan populations (d^{-1}) were calculated separately for the three taxa (i.e., non-loricate ciliates, tintinnid ciliates and dinoflagellates) from the > 64 μm predator exclusion experiments. Growth rate (μ) was calculated as $\ln C_1 - \ln C_0/t$, where t is incubation time (d), and C_0 and C_1 are protozoan concentrations (ml^{-1}) at the beginning and end of the experiment, respectively. Prior to

analysis of variance (BIOMSTAT 3.3), the data were tested for homogeneity of variances using Bartlett's test (BIOMSTAT 3.3; Sokal and Rohlf, 1981)

3. Results

Experiments were conducted from mid-January to early February in open waters of the Ross Sea polynya. This period coincided with the seasonal peak in chlorophyll concentration for this area, and by the end of the cruise, chlorophyll *a* concentrations were declining (Caron et al., 2000). Cells of the prymnesiophyte *Phaeocystis antarctica* dominated the phytoplankton community ($> 80\%$ of the nano/microplankton community) at most of the stations (Table 1) except for Minke 201 (15%) and Orca 208 (61%) where diatoms were in relatively high abundance (Dennett et al., unpublished).

There was significant variation (Table 2) in the net growth rates of the protozooplankton taxa among stations ($p < 0.0001$; two-way ANOVA) when zooplankton $> 64\,\mu m$ were excluded. These rates were highest at Station Minke, averaging 0.4, 0.6 and $0.2\,d^{-1}$ for non-loricate ciliates, tintinnid ciliates and dinoflagellates, respectively. We did not detect any significant differences in growth rates among the three taxa ($p = 0.570$). Along the main transect line (76°30′S) where growth rate experiments were conducted twice at each station during the cruise, the overall mean growth rate for each taxon approximated $0.1\,d^{-1}$. There also was no interaction effect of station and taxon ($p = 0.319$). The initial protozoan abundances in the $< 64\,\mu m$ seawater were reduced on average by 30% compared to whole seawater. But, it is unlikely that their growth rates were stimulated above natural levels because these communities do not appear to be resource-limited (Caron et al., 2000).

Table 2
Mean net growth rates (d^{-1} and range of values) of protozoan populations in $> 64\,\mu m$ predator exclusion experiments at five stations in the Ross Sea

Prey taxon	Non-loricate ciliates	Tintinnid ciliates	Dinoflagellates
Minke			
201	0.61 (0.51–0.69)	1.00 (0.91–0.99)	0.13 (0.02–0.27)
213	0.18 (0.15–0.24)	0.17 (0.10–0.25)	0.37 (0.35–0.38)
"O"			
205	0.03 (− 0.13–0.21)	− 0.34 (− 0.54– − 0.10)	− 0.28 (− 0.41– − 0.20)
217	− 0.34 (− 0.50– − 0.18)	− 0.19 (− 0.25– − 0.13)	0.04 (− 0.06–0.11)
Orca			
220	− 0.10 (− 0.14– − 0.06)	− 0.07 (− 0.17–0.04)	− 0.07 (− 0.19–0.01)
208	0.20 (0.10–0.30)	0.23 (0.15–0.30)	0.28 (0.25–0.30)
Emperor			
209	− 0.01 (− 0.28–0.25)	− 0.03 (− 0.17–0.23)	− 0.26 (− 0.41– − 0.08)
Sei			
211	0.01 (− 0.13–0.12)	0.07 (− 0.05–0.15)	0.09 (0.06–0.12)

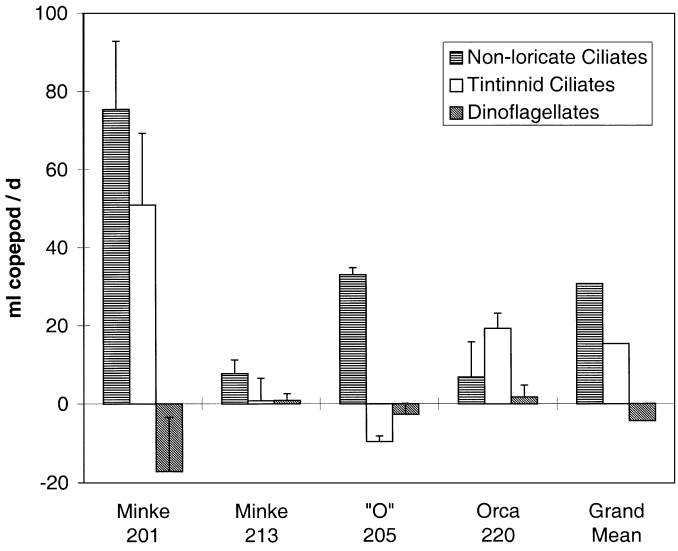

Fig. 1. Mean clearance rates (and upper range) of *Oithona* spp. on protozoa at three stations in the Ross Sea, Antarctica. Station locations are Minke 76°30′S, 169°E, "O" 76°30′S, 176°E, and Orca 76°30′S, 178°W.

Clearance and ingestion rates of copepods on non-loricate ciliates, tintinnids and dinoflagellates were calculated using the equations of Frost (1972). Experiments with *Oithona* spp. were conducted once at Stations "O" and Orca, and twice at Station Minke. Although there appeared to be variation in clearance rate among stations (Fig. 1), this variability was not significant ($p = 0.369$; two-way ANOVA; for the interaction term, $p = 0.204$). However, *Oithona* spp. did exhibit differential predation on the protozoa ($p = 0.034$), with the highest clearance rates observed for non-loricate ciliates, averaging 27.1 ml copepod^{-1} d^{-1} across the three stations. Feeding on dinoflagellates was mostly lower compared to ciliates; the highest clearance rate on this taxon was 1.7 ml copepod^{-1} d^{-1} at Station Orca. We did not detect any consistent reduction in initial protozoan concentrations in the $< 200\,\mu m$ filtered water compared to whole seawater.

Using Swadling et al.'s (1997; see Table 1 therein) measure of carbon content of *O. similis* (0.78 μg C copepod^{-1}), and our values of carbon content of protozoan cells (Table 3), we estimated that this copepod obtains on average 91% of its carbon ration (% body C d^{-1}) from these prey, with percentages ranging from 5 to 327% (both values were obtained at Minke; carbon rations were 8 and 26% at "O" and Orca, respectively). Among the three taxa, non-loricate ciliates contributed the most substantial fraction (average = 78% body C d^{-1}) to the copepod's carbon ration. The greater contribution of non-loricate ciliates compared to tintinnids (12% body C d^{-1}), in part, reflects the former's generally higher abundance (Table 3).

Metrida spp., calanoid copepods that are substantially larger than *Oithona* spp., had the highest clearance rate per copepod per day. The rates determined at Minke

Table 3
Average carbon content (ng C cell^{-1}) and abundance (no. ml^{-1}) of protozoan prey in whole seawater. The average carbon content was used to calculate daily carbon consumption by copepod predators. Abundance data were used to estimate the predation impact of copepods on standing stocks of these protozoan taxa

Prey taxon	Non-loricate ciliates		Tintinnid ciliates		Dinoflagellates	
	ng C	no.	ng C	no.	ng C	no.
Minke 201	2.54	9.6	2.04	2.1	2.28	27.0
Minke 213	1.96	9.3	2.07	0.8	2.22	21.7
"O" 205	1.11	6.6	2.05	0.3	1.89	35.7
Orca 220	4.55	0.3	2.02	1.6	2.92	6.1

Table 4
Mean clearance rates (ml individual^{-1} d^{-1}) (range) of copepod nauplii on protozoan prey at two stations in the Ross Sea

Prey taxon	Non-loricate ciliates	Tintinnid ciliates	Dinoflagellates
"O" 205	4.9 (−1.8–11.6)	10.8 (9.5–2.1)	4.8 (3.1–6.6)
Orca 220	6.0 (4.7–7.2)	2.3 (−2.2–6.3)	1.5 (0.03–2.9)

201 were 231.4 ml (range 219.3–241.4 ml), 197.2 ml (105.8–290.5 ml) and 3.1 ml copepod^{-1} d^{-1} (− 40.1 to 33.6 ml) for non-loricate ciliates, tintinnids and dinoflagellates, respectively. Protozoan consumption contributed 9–18% body C d^{-1}, depending on *Metridia* species (assuming a C mass of 45% of dry weight, *M. lucens* = 42 μg C and *M. gerlachei* = 82 μg C copepod^{-1}; dry weights reported by Atkinson, 1996 and 1995, respectively). As found for *Oithona* spp., non-loricate ciliates contributed the largest fraction to *Metridia's* carbon ration (8 and 16% body C d^{-1} for *M. gerlachei* and *M. lucens*, respectively). The dietary contribution from dinoflagellates was negligible (< 0.3% body C d^{-1}).

Copepod nauplii were also found to feed on protozooplankton (Table 4), ranging from a low mean clearance rate of 1.5 ml nauplius^{-1} d^{-1} (range 0.03–2.9 ml) on dinoflagellates (C8, Station Orca) to a high on non-loricate ciliates of 10.8 ml nauplius^{-1} d^{-1} (9.5–12.21 ml) (C2, Station "O"). These clearance rate values may be higher than in nature because, as noted above, the initial abundances of protozoa in < 64 μm filtered seawater were less than in whole seawater.

4. Discussion

4.1. Protozoa in copepod diets

The importance of protozooplankton in the diets of species of *Oithona* has been recognized in other environments. In the North Sea, for example, egg production by

O. similis was positively correlated with protozooplankton abundance but not with chlorophyll *a* concentration (Nielsen and Sabatini, 1996). Nakamura and Turner (1997) also concluded that this species is highly dependent on ciliates and heterotrophic dinoflagellates to support metabolism and egg production during the summer in a temperate environment (Massachusetts, USA). In their study, protozooplankton and copepod nauplii contributed on average 41% body $C\,d^{-1}$, with the former prey being more important (28% body $C\,d^{-1}$). Our average of 91% body $C\,d^{-1}$ contribution of protozoa to *Oithona's* diet is higher, but is largely due to the high value determined at Minke (327%; Minke 201). Removal of this value from the data gives a conservative average of 13% body $C\,d^{-1}$. During midsummer in the subantarctic, Atkinson (1996) found that *Oithona* spp. consume phytoplankton and this resource contributed up to 34% to their daily carbon ration. The author noted that this ration was below *Oithona's* respiratory requirement. Atkinson concluded that even if the carbon intake of *Oithona* spp. doubled from protozoan consumption (determined from Atkinson's predation experiments), this mixed diet would "still be insufficient to meet their estimated metabolic needs" (Atkinson, 1996, p. 94). Although our estimate of 91% daily carbon ration from protozoa is largely due to the high values obtained at one station, this average may not be unrealistic given that we noted many of the copepods were reproductive, thus requiring energy beyond that needed to meet metabolic demand.

Surprisingly, we found that dinoflagellates contributed little to copepod diets despite high ambient abundances of dinoflagellates. Clearance rates of *Oithona* spp. on dinoflagellates were mostly lower compared to ciliates, ranging from negative values to a high of $1.7\,ml\,copepod^{-1}\,d^{-1}$. This highest clearance rate estimate is similar to the lower value reported by Atkinson (1995) of $2.1\,ml\,copepod^{-1}\,d^{-1}$. The highest rate reported in that study was $7.5\,ml\,copepod^{-1}\,d^{-1}$ (for comparison, these rates were obtained by converting the author's reported clearance values, $ml\,mg^{-1}\,d^{-1}$, using weight estimates of individual copepods). Interestingly, a negative clearance rate on dinoflagellates occurred during the same experiment in which the highest clearance rates were found for ciliates (Minke 201), suggesting selective feeding by *Oithona* spp. on these taxa. This interpretation is supported by our finding that these copepods showed significant variation in clearance rates among taxa. We cannot say, however, if our lower values compared with Atkinson are due to differences in dinoflagellate composition which was not reported in Atkinson's works, nor did we enumerate many dinoflagellates beyond this taxonomic designation (Dennett et al., unpublished)

4.2. Potential impacts of copepod predation on food web structure

In the Ross Sea, Antarctica, the biological and physical factors controlling the population dynamics of protozooplankton remain largely unknown. In many aquatic environments, predation, particularly by copepods, can be an important mechanism regulating protozooplankton populations (e.g., subantarctic; Atkinson, 1996). This initial study in the Ross Sea does not suggest the same. Results from our predation studies and estimates of copepod concentrations in another part of the Southern

Ocean (60°S; Fransz and Gonzalez, 1995) suggest late-stage (CIV and CV) and adult *Oithona* spp. combined could remove on average only 0.3–1.2% d^{-1} of the standing stocks of ciliates, and even less ($< 0.05\%\, d^{-1}$) of the dinoflagellates. Franz and Gonzalez reported the abundance of *O. similis* as $\sim 100\, m^{-3}$ (CIV through adults) during January and 400 copepods m^{-3} in April, and we utilized the mean concentration of each protozoan taxon (Table 3) corresponding to stations where copepod predation studies were conducted. Recently, Urban-Rich et al. (1999) reported substantially higher concentrations of *Oithona* spp. in the Antarctic Polar Front Zone at 66°S (average for day/night = $1629\, m^{-3}$ at Mooring 5 at 66°S; US JGOFS Process II), suggesting that we may be underestimating the maximum predation impact of *Oithona* spp. by a factor of four (up to $4.8\%\, d^{-1}$ on ciliates and $< 0.2\%$ on dinoflagellates). However, Atkinson (1998) has pointed out that the abundances of *Oithona* spp. in the Polar Front Zone appear to be significantly higher than more southerly locations in the Southern Ocean.

It remains to be determined if the cumulative impact by all predaceous zooplankton could be important to protozoan population dynamics in the Ross Sea. Application of our naupliar predation rates and Fransz and Gonzalez's estimates of NIV–NVI abundances of *O. similis* (150–320 nauplii m^{-3}) indicates that these nauplii would remove an additional 0.2% of the ciliate stocks and *Metridia* spp. at a concentration of 10 copepods m^{-3} only remove another 0.4%.

Our herbivory experiments in the Ross Sea indicated low to negligible grazing pressure, despite the presence of relatively high abundances of microzooplankton (Caron et al., 2000). We speculated that these low rates of zooplankton grazing are explained primarily by low ambient water temperatures in this environment and not to unusually low abundances of microzooplankton grazers. The results presented here indicate that, while mesozooplankton predation on microzooplankton may constitute a significant source of nutrition for these metazoan predators, their grazing impact on protozooplankton appears to be modest. These low predation rates may account for the build-up of the sizable protozoan stocks in the Ross Sea. Given that these protozoa have substantially lower growth rates than in other environments (e.g., Stoecker et al., 1983), but have comparable biomass to some (see Caron et al., 2000, and references therein), the likely explanation is lower mortality. Further work in the Ross Sea may resolve the role of copepod predation in structuring microbial food webs, and the relative importance of herbivory and carnivory to copepod production.

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