

Mesozooplankton beneath the summer sea ice in McMurdo Sound, Antarctica: abundance, species composition, and DMSP content

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Abstract The summer *Phaeocystis antarctica* bloom increases under-ice phytoplankton biomass in McMurdo Sound, Antarctica. The magnitude of mesozooplankton grazing on this bloom is unknown, and determines whether this production is available to the pelagic food web. We measured mesozooplankton abundance and body content of dimethylsulfoniopropionate (DMSP) during the McMurdo Sound austral summer (2006 and 2006–2007). Abundance varied from 20 to 4,500 ind. m⁻³ (biomass 0.02–274.0 mg C m⁻³), with peaks in mid-December and late-January/February. Abundance was higher but total zooplankton biomass lower in our study compared to previous reports. Copepods and the pteropod *Limacina helicina* dominated the zooplankton in both abundance and biomass. DMSP was detected in all zooplankton groups, with highest concentrations in copepod nauplii and *L. helicina* (95 and 54 nmol mg⁻¹ body C, respectively). Experiments suggested that *L. helicina* obtains DMSP by directly grazing on *P. antarctica*, which often accumulates to high biomass under the summer sea ice in McMurdo Sound.

Keywords Zooplankton · DMSP · Pteropod · Copepod · Sea ice

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Introduction

McMurdo Sound, Antarctica, marks a transition between the broad seasonally ice-free continental shelf of the Ross Sea and the waters under the Ross Ice Shelf. Parts of the Sound are covered by sea ice throughout the year, particularly in the near shore areas. At its annual maximum, sea ice covers 40% of the Southern Ocean, an area 50% greater than the entire Antarctic continent (Lizotte 2001). In the permanent ice zone of McMurdo Sound, the under-ice summer mesozooplankton community is often dominated by various copepods along with the pteropod *Limacina helicina* (Foster 1987; Knox et al. 1996; Seibel and Dierssen 2003). Annual maximum zooplankton abundance in near-shore fast ice environments occurs in the winter (Knox 2006), likely due to the contribution of copepodites of non-diapausing omnivorous copepod species (Deibel and Daly 2007). However, zooplankton abundances are also high during the austral spring and summer (November–February), when long daylight hours (up to 24 h) can result in high primary productivity.

During the austral summer, surface waters near Cape Armitage and the US McMurdo Station are dominated by relatively rapid alongshore (north–south) currents, with a slight mean southward flow (Barry and Dayton 1988). Consequently, the plankton community in this area is subject to a southward drift; and summertime increases in under ice phytoplankton biomass are in part due to advection of the Ross Sea plankton bloom to beneath the sea ice (Rivkin 1991). Thus, the phytoplankton community of McMurdo Sound is reflective of the community developing in the nearby ice-free areas of the Ross Sea, which is dominated by the haptophyte *Phaeocystis antarctica* (Arrigo et al. 1998; Goffart et al. 2000). Like the two temperate and northern members of the genus: *P. globosa* and

P. pouchetii, *P. antarctica* can exist as solitary cells or as large mucilaginous colonies (Lancelot et al. 1998).

Under-ice mesozooplankton represent an important link between phytoplankton and larger animals as in most marine food webs, and their grazing activities may exert a top-down control on the phytoplankton community. Reports of zooplankton grazing on *P. globosa* and *P. pouchetii* in the natural environment vary widely, and information for grazing on *P. antarctica* is very limited (Schoemann et al. 2005; Nejstgaard et al. 2007). Because *P. antarctica* constitutes a large fraction of the phytoplankton biomass and primary production in the southern Ross Sea (DiTullio and Smith 1996; Arrigo et al. 1999; Mathot et al. 2000), the extent to which this species is grazed relative to other food sources in the Ross Sea and McMurdo Sound represents a critically missing piece of information in our understanding of the region's ecology.

Based on immunochemical evidence, Haberman et al. (2002) found *P. antarctica* in the guts of Antarctic krill (*Euphausia superba*). Several other Antarctic copepod species have also been shown to ingest *P. antarctica* in the absence of alternative food sources (Nejstgaard et al. 2007). Zooplankton grazers are generally limited to food particle sizes that are much smaller than their body sizes (Hansen et al. 1997), which may explain the disparate ability of zooplankton to graze solitary cells vs. colonies of *Phaeocystis* spp. (Nejstgaard et al. 2007). In the Ross Sea, the pteropod *L. helicina* is abundant in the austral summers when extensive *P. antarctica* blooms occur in the region (Hopkins 1987; Pane et al. 2004). Unlike other zooplankton, *Limacina* spp. feed by extending a mucous web many times larger than their body size to entrain particles (Gilmer and Harbison 1991). Hence, *Limacina* spp. have been reported to ingest particles ranging from picoplankton (<2 μm) to particles of millimeters in size (Gilmer and Harbison 1991; Noji et al. 1997). This puts *Limacina* in the unique position of potentially being able to ingest a wide size range of the *Phaeocystis* population, from single cells to relatively large colonies.

During the austral summers of 2005–2006 and 2006–2007 we studied the zooplankton abundance and species composition under the sea ice in McMurdo Sound. In addition, we measured the dimethylsulfoniopropionate (DMSP) content of the zooplankton in situ. This was used to infer the trophic fate of *P. antarctica* because this species constitutes the primary source of DMSP in McMurdo Sound and Ross Sea water. For example, Gibson et al. (1990) reported extraordinarily high concentrations of dissolved dimethyl sulfide (DMS) in direct correlation with an Antarctic *Phaeocystis* bloom, presumably a result of cleavage of DMSP from *P. antarctica*. During their study (1987–1988 austral summer) dissolved DMS concentrations increased 1–2 orders of magnitude in direct correspondence with

increased *Phaeocystis* abundance. Similarly, DiTullio and Smith (1995) reported high DMS concentrations (>50 nM) in the southern Ross Sea exclusively in areas dominated by *P. antarctica* (as indicated by 19'-hexanoyloxyfucoxanthin pigment concentration). Because zooplankton are not known to synthesize DMSP de novo (Tang et al. 1999, 2000), the presence of DMSP in zooplankton bodies (DMSP_z) is indicative of either direct ingestion of phytoplankton DMSP (mainly from *P. antarctica*) or trophic transfer of phytoplankton-derived DMSP up the food web (e.g., Tang and Simo 2003).

Our goals were to quantify the abundance and taxonomic composition of the zooplankton present in the austral summer under the sea ice in McMurdo Sound. In addition, we measured DMSP_z to estimate the importance of *P. antarctica* to the planktonic food web of McMurdo Sound. Additional experiments were conducted to measure the grazing activities of the pteropod *L. helicina* on *P. antarctica* due to its abundance and unique feeding mode.

Methods

Zooplankton abundance, species composition, and DMSP content

Zooplankton samples were taken twice weekly between January and February 2006 (year 1) and weekly between December 2006 and January 2007 (year 2). All samples were taken from McMurdo Sound through a dive hole located approximately 50 m off of the southernmost tip of Ross Island (Cape Armitage). The water depth was approximately 25 m during year 1, and 16 m during year 2. The plankton community was sampled using a 200- μm mesh conical plankton net with a filtering cod-end. Tows were taken by dropping the net to just above the sea floor and slowly towing back to the surface. Tow contents were immediately preserved in a 4% formaldehyde solution. Subsamples (always >6% of the total) were taken with a Folsom plankton splitter and analyzed under a dissecting microscope. The number of zooplankton counted was always more than 200 individuals of each species except for extremely rare species. Animals were enumerated and identified to the lowest possible taxon. Additional tows were taken and the animals were returned to the lab where live individuals of the dominant species were immediately picked out, briefly rinsed with 0.2 μm filtered McMurdo Sound seawater to remove attached particles, and stored dry at -80°C . These samples were analyzed for body (gut and/or tissue) DMSP (DMSP_z) within 5 months of collection. DMSP_z values were normalized to body carbon values taken from the literature or estimated from published length-to-biomass regressions (Uye 1982; Ward and

Robins 1987; Donnelly et al. 1994; Fransz and Gonzalez 1997; Metz 1998; Yamaguchi et al. 2002). Carbon estimates were for the entire animals and specified developmental stages (Table 1), except in the case of *L. helicina* where the shells were not included.

Source of DMSP_z for *L. helicina*

Preliminary observations of large amount of DMSP_z in *L. helicina* supported the notion that this pteropod may ingest *P. antarctica* in situ. Therefore, an incubation experiment was run during the 2006–2007 season (year 2) to determine whether the pteropods rely on dietary intake to maintain their body DMSP content, and to quantify its grazing rate on *P. antarctica* in the absence of an alternative food source. Our preliminary experiment showed that small bottle (e.g., 2 L) restricted the swimming of this species and disrupted its feeding; therefore, large incubation bottles were used in combination with a slow plankton wheel rotation speed for this experiment. Pteropods were acclimated to initial DMSP replete food conditions (5–6 µg chl L⁻¹ of *P. antarctica*) for 24 h prior to the experiment. The acclimation of all animals to *P. antarctica* ensured that they had comparable DMSP_z at the beginning of the experiment. Triplicate 4 L bottles were set up for two treatments and the control. The *Phaeocystis* grazing treatment consisted of a pure culture of *P. antarctica* (CCMP 1871) added to 0.2 µm filtered seawater to an initial chlorophyll-*a* concentration representative of in situ values (5–6 µg L⁻¹). The chlorophyte *Dunaliella tertiolecta* was used for the non-DMSP food source treatment. *D. tertiolecta* is of similar size to single celled *Phaeocystis* but without appreciable DMSP content (Tang et al. 1999). A secondary control consisted of grazers in 4 L bottles of 0.2 µm filtered seawater without any phytoplankton (starvation treatment). Our expectation was that the pteropods consuming *P. antarctica* would maintain high DMSP_z, whereas the ones that fed on *D. tertiolecta* and those that were starved would show a decrease in DMSP_z.

Initial measurements of chlorophyll-*a* and total particulate DMSP (DMSP_p) were taken for each of the treatments and control. To begin the experiment five *L. helicina* individuals were added to each bottle (treatment and both controls). An additional three of the acclimated pteropods were collected and stored dry at -80°C for initial DMSP_z. The bottles were then incubated at 0°C for 5 days on a rotating plankton wheel (0.25 rpm) with continuous light (average 0.61 µmol m⁻² s⁻¹). At the end of the incubation, aliquots were collected from each bottle for measurements of final DMSP_p and chlorophyll-*a*. The pteropods were collected, verified as live or dead, and the live individuals stored at -80°C for measurement of final DMSP_z.

DMSP measurements

To measure both DMSP_p and DMSP_z, individual filters and frozen animals were hydrolyzed overnight in 1–2 ml of 1 N NaOH solution to convert DMSP to DMS. The samples were then analyzed by gas chromatography, using the purge and trap method (Kiene and Service 1991; Tang et al. 1999). Calibration was performed using standard DMS solution (Sigma co.).

Results

Zooplankton abundance, species composition, and DMSP content

In year 1 samples were taken only late in the summer (January–February). In year 2 sampling commenced earlier in the season (December) but was terminated at the end of January. Total zooplankton abundance in McMurdo Sound was always below 5,000 ind. m⁻³ (Fig. 1). During year 1, zooplankton abundances were already high by the time sampling commenced in mid January. Abundances then decreased in late January and into early February, and increased to their highest values (>4,000 ind. m⁻³) toward the end of the first week of February. During year 2, abundance first peaked in mid-December (1,600 ind. m⁻³) due to the appearance of a large number of small copepods. Abundances then decreased with each subsequent week through the rest of December and most of January, reaching values lower than 100 ind. m⁻³. A second period of relatively high abundances occurred in late January (300–1,500 ind. m⁻³), analogous to the second peak in early February of year 1. Given the large difference in sizes of the zooplankton species, abundance data were converted to carbon biomass for further comparison (Table 1). During the study, total zooplankton carbon biomass remained low until late January of year 1, when it increased due to an increase in abundance of pteropods (*L. helicina*) and large copepods (*Calanoides acutus*, *Metridia gerlachi*, and *Paraeuchaeta antarctica*). During year 2, this increase was less evident, although the highest biomass value for this year also occurred in the late summer (late January).

Numerically, copepods comprised nearly 100% of the zooplankton in many samples and over 50% in all samples (Fig. 1). In terms of carbon biomass, copepods were slightly less dominant, with other zooplankters (particularly pteropods) accounting for a substantial portion of the total carbon in many samples (Fig. 2). Six copepod species were observed to occur commonly in the samples (Table 1). These included the cyclopoid *Oithona similis* and the poecilostomatoid *Oncaea curvata*, which were ubiquitous in all samples. The calanoid *Ctenocalanus* sp. was found in all

Table 1 (a) Carbon conversion factors (published sources) for zooplankton taxa. Note: Value for *Limacina helicina* excludes the shell). (b) Abundance (ind. m⁻³) and carbon biomass (mg carbon m⁻³) data for zooplankton taxa on each sampling date

	<i>Oithona similis</i>	<i>Metridia gerlachi</i>	<i>Ctenocalanus</i> sp.	<i>Calanoides acutus</i>	<i>Oncaea curvata</i>	<i>Paraeuchaeta antarctica</i>	Copepod nauplii	<i>Limacina helicina</i>										
Carbon biomass (µg ind. ⁻¹)	2.1 (Fransz and Gonzalez 1997)	231.4 (Donnelly et al. 1994)	3.0 (Yamaguchi et al. 2002)	525 (Donnelly et al. 1994)	1.1 (Metz 1998)	4636.5 (Ward and Robins 1987)	0.2 (based on equation of Uye 1982)	140 (W.O. Smith unpublished data)										
Length (µm)	500	1,500	675	2,000	500	4,000–5,000	250	2,000										
(b)	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³	ind. m ⁻³										
7-Dec-06	1.6	2	0.3	157	0.5	0	0.0	61	0.1	0	0.0	0	0.0	0	0.0	0.0	6	0.8
16-Dec-06	741	1	0.3	679	2.0	0	0.0	161	0.2	0	0.0	26	0.0	0	0.0	0.0	5	0.7
21-Dec-06	436	3	0.6	304	0.9	0	0.0	124	0.1	0	0.0	27	0.0	0	0.0	0.0	1	0.2
29-Dec-06	469	0	0.0	133	0.4	0	0.0	91	0.1	0	0.0	31	0.0	0	0.0	0.0	4	0.6
3-Jan-07	246	0	0.0	28	0.1	0	0.0	33	0.0	0	0.0	1	0.0	0	0.0	0.0	0	0.0
11-Jan-07	130	1	0.2	17	0.1	0	0.0	82	0.1	0	0.0	14	0.0	0	0.0	0.0	0	0.0
17-Jan-07	17	0	0.0	9	0.0	0	0.0	12	0.0	0	0.0	19	0.0	0	0.0	0.0	9	0.3
18-Jan-06	411	22	5.1	5	0.0	69	36.1	114	0.1	0	0.0	615	0.1	0	0.0	0.1	142	12.3
21-Jan-06	637	5	1.1	5	0.0	67	35.4	30	0.0	0	0.0	324	0.1	0	0.0	0.1	119	14.9
25-Jan-06	627	3	0.8	11	0.0	90	47.3	80	0.1	2	10.8	440	0.1	0	0.0	0.1	123	16.1
25-Jan-07	6	0	0.0	2	0.0	0	0.0	9	0.0	0	0.0	4	0.0	0	0.0	0.0	0	0.0
28-Jan-06	334	9	2.0	0	0.0	14	7.2	12	0.0	3	12.4	155	0.0	0	0.0	0.0	56	5.0
31-Jan-07	75	0	0.0	48	0.1	0	0.0	27	0.0	0	0.0	40	0.0	0	0.0	0.0	134	5.0
2-Feb-06	354	1	0.2	17	0.1	61	32.0	58	0.1	3	15.5	239	0.0	0	0.0	0.0	52	5.8
5-Feb-06	2376	56	13.0	111	0.3	48	25.0	117	0.1	24	111.0	737	0.1	0	0.0	0.1	777	74.2
8-Feb-06	1328	0	0	230	0.68	149	78.23	248	0.28	0	0	332	0.06	0	0.0	0.06	1876	156.5

Fig. 1 Abundance of the three common groups of zooplankton (copepods and nauplii, the pteropod *Limacina helicina* and all other zooplankton taxa) during this study in McMurdo Sound. Samples from the first field season (2006) are denoted Y1, and samples from the second field season (2006–2007) are denoted Y2. Average range of literature reported abundances are shown for each corresponding week (data from Foster 1987 and Knox et al. 1996)

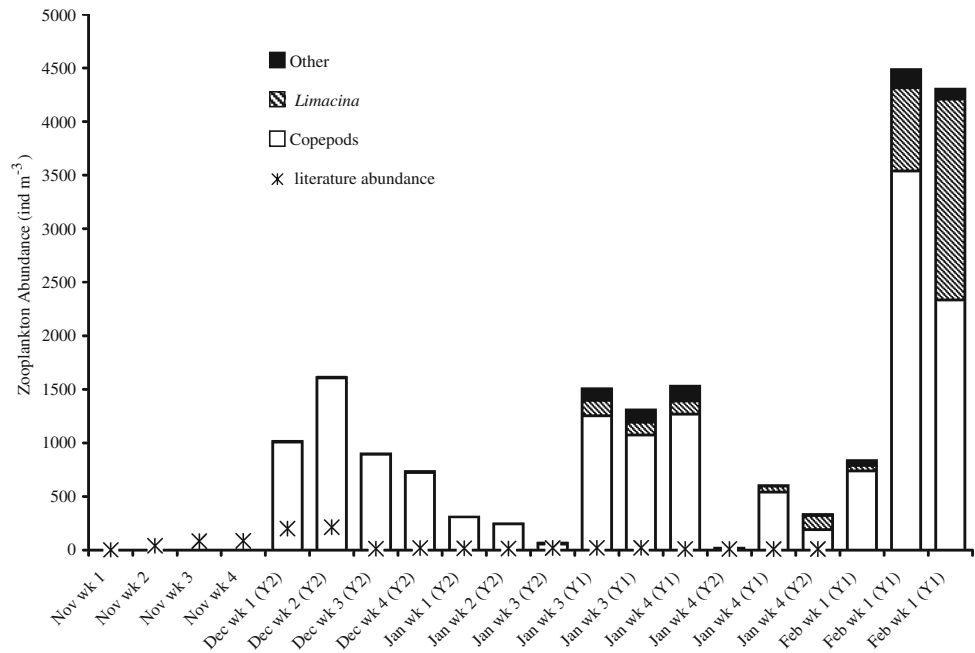
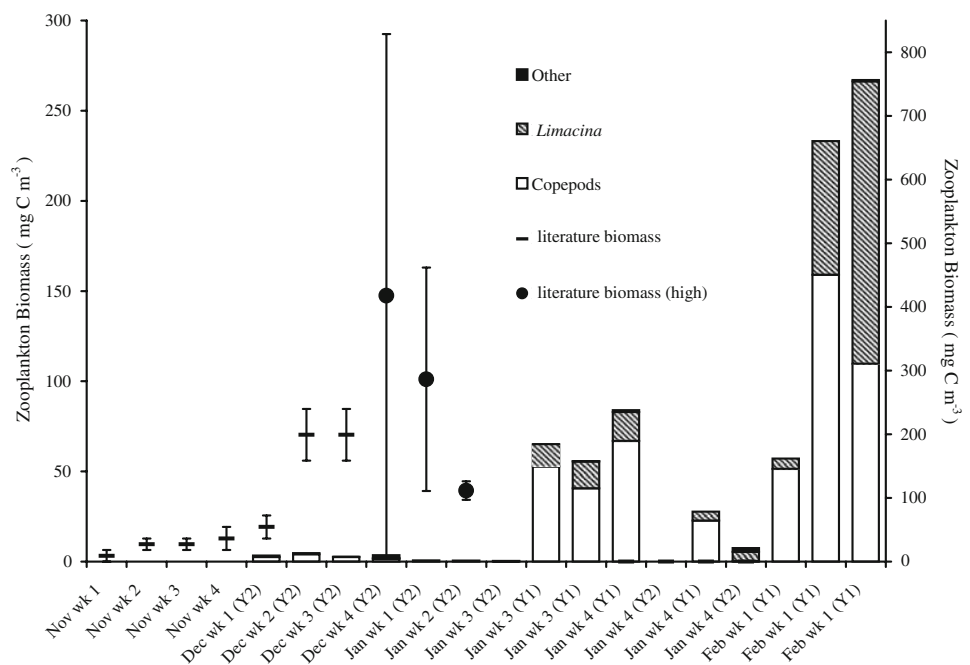


Fig. 2 Carbon biomass of the three common groups of zooplankton (copepods and nauplii, the pteropod *Limacina helicina* and all other zooplankton taxa) during this study in McMurdo Sound. Samples from the first field season (2006) are denoted Y1, and samples from the second field season (2006–2007) are denoted Y2. Average range of literature reported biomasses are shown for each corresponding week (data from Foster 1987 and Knox et al. 1996). Note: the literature data for carbon biomass on December week 4 through January week 2 (lit biomass high) are on the secondary Y-axis, due to their large magnitude in comparison to other values

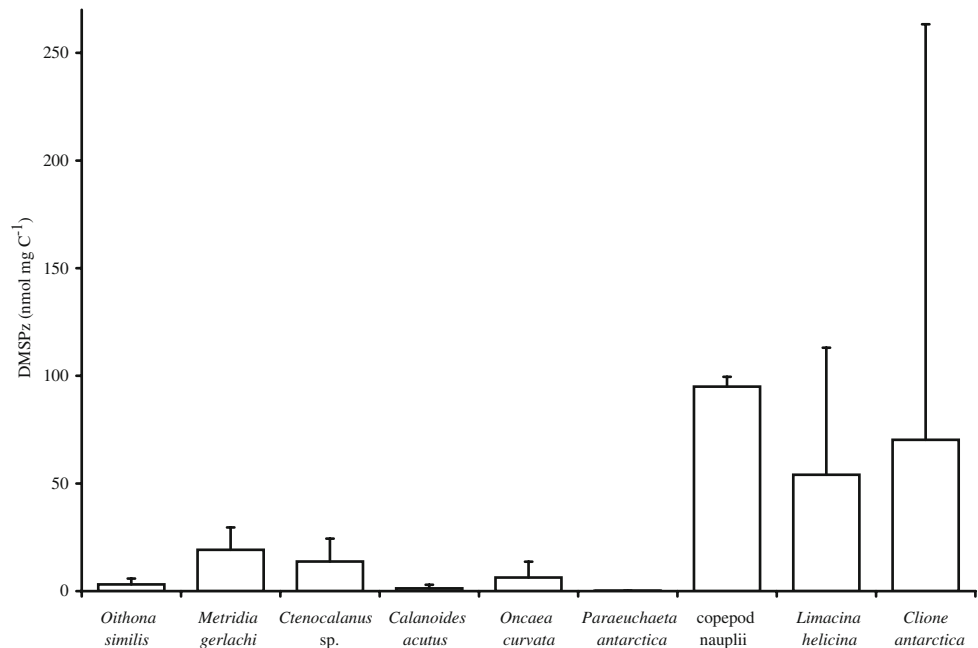


but one of 16 samples. The large calanoid *Metridia gerlachi* occurred in low abundances throughout the study. Another large calanoid species, *Calanoides acutus*, was relatively common in year 1, but not in year 2. The predatory copepod *Paraeuchaeta antarctica* commonly occurred in low abundances in the year 1, but was not found in year 2. Copepod nauplii were fairly abundant throughout the study, although more so in the late summer (Table 1). The pteropod *L. helicina* was a prominent member of the zooplankton community based on carbon biomass. During both years, *L. helicina* was present at low abundances (<50 ind.

m⁻³) from December to early January, and became more abundant in late January and early February (hundreds of individuals m⁻³). Another pteropod, the predatory *Clione antarctica*, remained extremely low in abundance and carbon biomass throughout the study.

All zooplankton groups collected from McMurdo Sound contained a detectable amount of DMSP_z (Fig. 3). The lowest mean value (<1 nmol DMSP mg⁻¹ body C) was for the predatory copepod *Paraeuchaeta antarctica*. DMSP_z values were also relatively low for all other adult copepods (1–20 nmol DMSP mg⁻¹ body C). Highest DMSP_z

Fig. 3 Body DMSP (DMSP_z) associated with zooplankton species collected during this study in McMurdo Sound. Error bars represent standard deviations among replicates



(>50 nmol DMSP mg⁻¹ body C) were observed for copepod nauplii and both of the pteropod species. The ecological significance of these findings is addressed in the discussion section.

Source of DMSP_z for *L. helicina*

For the incubation experiment, the very low chlorophyll-*a* concentrations (mean 0.03 μg L⁻¹ initial and 0.08 μg L⁻¹ final) measured in the starvation treatment confirmed that the treatment was virtually free of phytoplankton. Food concentrations in terms of chlorophyll-*a* were similar between the *Dunaliella* and *Phaeocystis* treatments (mean of 5.16 and 5.65 μg L⁻¹, respectively; no significant difference according to t-test). There was no detectable particulate DMSP (DMSP_p) in either the *Dunaliella* or starvation treatments; therefore, the only source of DMSP available to the grazers was *P. antarctica*. DMSP_p concentrations in the *Phaeocystis* treatment increased slightly during the incubation, as did chlorophyll-*a*. DMSP_z of the pteropods at the end of incubation were lower than initial pteropod DMSP_z in all three treatments (Fig. 4). According to ANOVA, there was a significant difference in final DMSP_z among the treatments ($P = 0.004$, $\alpha = 0.05$). Post-hoc pairwise comparisons (Fisher's individual error rate method) showed that final DMSP_z in the *Phaeocystis* treatment was significantly higher ($P < 0.05$, $\alpha = 0.05$) than in both the starvation and the *Dunaliella* treatments, but the latter two were not significantly different from each other. These results indicate that the pteropod was able to maintain significantly higher DMSP_z when feeding on *P. antarctica* than when feeding on *D. tertiolecta* or being starved.

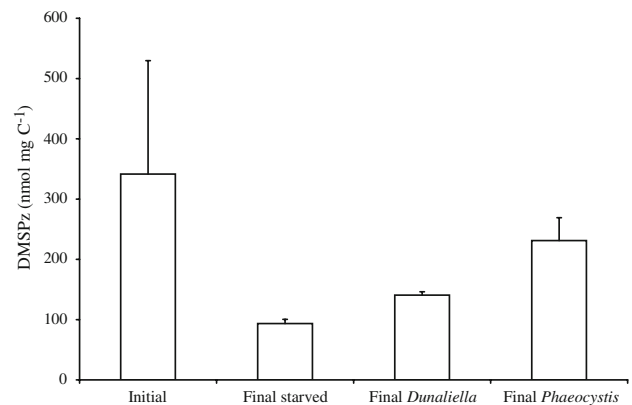


Fig. 4 Body DMSP (DMSP_z) associated with the pteropod *Limacina helicina* both prior to incubation (initial) and after a 5 day incubation period for each of three separate feeding treatments (finals). Error bars represent standard deviations among replicates. Note: Final starvation had only two replicates

Discussion

Zooplankton abundance, species composition, and DMSP content

The zooplankton community observed during this study was similar in species composition to previous reports for McMurdo Sound (Foster 1987; Hopkins 1987; Knox et al. 1996). Samples were usually dominated by the small copepods *Oithona similis*, *Oncaea curvata*, *Ctenocalanus sp.*, and copepod nauplii. However, these smaller copepods represented only a fraction of the total zooplankton biomass, excepting at times when they were the only zooplankton

present. Other common species included the pteropod *L. helicina*, as well as the large copepods *Paraeuchaeta antarctica*, *Calanoides acutus*, and *Metridia gerlachi*, cumulatively accounting for most of the zooplankton biomass when present. We know of no previous studies that have reported on the sub-ice zooplankton community in McMurdo Sound as late as February, and our study may be the first account of a secondary zooplankton peak occurring late in the summer. Abundances and biomasses seen during this second peak were comparable to those found in the open waters of Terra Nova Bay during January and February of 1995 (Pane et al. 2004).

A comparison of the total zooplankton abundance and biomass between this study and literature data for McMurdo Sound (Foster 1987; Knox et al. 1996) is shown in Figs. 1 and 2. The abundance and biomass of the dominant species both differed noticeably between this and the previous studies. The lower biomass in our study is likely due to the rarity of large bodied zooplankton in our samples. Unlike previous reports (Hicks 1974; Foster 1987, 1989; Hopkins 1987; Knox et al. 1996), we did not observe large numbers of macrozooplankton such as krill (*Euphausia crystallorophias*), amphipods, or as many large copepods. Our sampling station was relatively shallow (<30 m), and these larger zooplankton species tend to be found in the deeper (>50 m) parts of McMurdo Sound (Foster 1987, 1989), where migration to depth may provide protection from visual predators. On the other hand, the abundances of small copepods were often considerably higher in this study than previously reported. Foster (1987) found higher abundances of small copepods in the upper 100 m, in contrast to the majority of large zooplankters that were more abundant between 100 and 300 m depth. It is possible that shallow nearshore regions represent an ideal habitat for the smaller copepods in terms of both food availability and predator avoidance. Several of these smaller copepods (*Oithona similis* and *Oncaea curvata*) are known to be highly omnivorous and able to graze on a wide range of particles, including aggregates (González et al. 1994; Kattner et al. 2003). This opportunistic feeding behavior may allow them to capitalize on a variety of food particles that are present in the surface water or released from the bottom of the sea ice. In addition, the lower abundances of large, potentially predatory zooplankton in the surface water may present a lower predation risk for these small copepods.

The DMSP_z contents of zooplankton in this study (Fig. 3) are similar in magnitude to those found in previous studies. Kwint et al. (1996) reported a mean DMSP_z of around 90 nmol mg C⁻¹ for *Eurytemora affinis* (copepod) feeding on a high concentration of the diatom *Phaeodactylum tricoratum*. Tang et al. (1999) reported mean DMSP_z concentrations for Long Island Sound copepods ranging from less than 5 nmol mg C⁻¹ (*Acartia tonsa* and *Labido-*

cera sp.), to ca. 75 nmol mg C⁻¹ (*Centropages hamatus* and *Temora longicornis*). In addition to its potential use as an indicator of ingestion of a DMSP rich food source, DMSP is an important precursor to the climatically active gas DMS. Thus, McMurdo Sound copepods represent a pool through which phytoplankton DMSP may flow. Through grazing activities, copepods can influence the cycling and fate of this important precursor to the climatically active gas DMS, as described in multiple other studies (e.g., Dacey and Wakeham 1986; Kwint et al. 1996; Tang et al. 1999).

Zooplankton grazing inferred from in situ DMSP_z

DMSP_z data from field samples can be used to infer in situ zooplankton grazing on *P. antarctica* or other phytoplankton with a high cellular DMSP content. However, care is needed in the interpretation of the field DMSP_z data. Of the zooplankton species studied herein, the diets of three species have been relatively well characterized: *Clione antarctica*, *Calanoides acutus* and *Paraeuchaeta antarctica*. *C. antarctica* is known to feed almost exclusively on *L. helicina* (Whitehead et al. 2001). Accordingly, DMSP_z in *C. antarctica* indicates trophic transfer of DMSP through *L. helicina*, rather than direct ingestion of phytoplankton. The carbon-specific DMSP_z associated with *C. antarctica* was slightly higher than for its food (Fig. 3). This indicates that a substantial portion of this DMSP was likely retained in tissues. The feeding habits of *C. acutus* have also been well studied. Based independently on gut content analysis, mandibular morphology, and fatty acid composition, this Antarctic copepod has been described as almost exclusively herbivorous, feeding on relatively large phytoplankton cells such as diatoms (Hopkins 1987; Graeve et al. 1994; Michels and Schnack-Schiel 2005). This is consistent with the low carbon-specific DMSP_z found for *C. acutus* in our study, which suggests that this species does not obtain much of its dietary carbon from DMSP-rich particles, such as *P. antarctica*. Finally, the diet of *P. antarctica* consists mainly of other copepods (Michels and Schnack-Schiel 2005, and references therein). The virtual absence of DMSP_z in this copepod in this study suggests that its diet contained virtually no DMSP, and that trophic transfer of DMSP through copepod prey was negligible. Thus, *C. antarctica*, *C. acutus*, and *P. antarctica* provide a reference against which we can classify the other zooplankton species based on carbon-specific DMSP_z contents.

Among the remaining species studied, *Oithona similis*, *Oncaea curvata*, *Ctenocalanus* sp., and *Metridia gerlachi* contained intermediate levels of DMSP_z (Fig. 3). Small copepods such as *O. similis* and *O. curvata* are opportunistic omnivores, feeding on a variety of items from small phytoplankton and other zooplankton to aggregates and

fecal pellets (González et al. 1994; Kattner et al. 2003). Fatty acid analysis of these species from Antarctic samples also suggested an omnivorous diet (Kattner et al. 2003). Little is known about the diet of *Ctenocalanus* sp., although it has been suggested to be mainly herbivorous (Michels and Schnack-Schiel 2005, and references therein). Finally, *M. gerlachi* is omnivorous (Graeve et al. 1994; Michels and Schnack-Schiel 2005). These species all had intermediate levels of DMSP_z in our field samples, which could indicate that *P. antarctica* made up only a small portion of their diets. Alternatively, DMSP could be obtained through an intermediate of microzooplankton that have fed on *P. antarctica*, with a majority of the DMSP lost due to low transfer efficiency (44% as estimated by Tang and Simo 2003).

The two remaining zooplankton groups are *L. helicina* and small non-descript copepod nauplii. The carbon-specific DMSP_z of both was relatively high (Fig. 3), suggesting that their diets were composed of a DMSP-rich carbon source. While gut content analysis has indicated that large individuals of *L. helicina* can consume other zooplankton (Gilmer and Harbison 1991), lipid measurements show that the majority of this species' diet is composed of phytoplankton (Gannefors et al. 2005). By and large, *Limacina* spp. are thought to be mainly herbivorous (Perissinotto 1992; Seibel and Dierssen 2003; Bernard 2006), and feeding studies on this pteropod suggest that it ingests a large portion of nanoplankton sized particles (Gilmer 1974). Copepod nauplii have been reported to prefer relatively small and motile prey, due to their own small size and limited motility (Titelman and Kiørboe 2003; Ingerslev Henriksen et al. 2007). Accordingly, motile nanoflagellates would be good prey for both *L. helicina* and small copepod nauplii. In the Ross Sea surface waters near McMurdo Sound, *P. antarctica* single cells account for the majority of nanoflagellates (Fonda Umani et al. 2005). The observed high in situ carbon-specific DMSP_z, together with our lab incubation experiment with *L. helicina* (see below) and literature information on their feeding habits, suggest that *L. helicina* and small copepod nauplii are actively grazing on *P. antarctica* in McMurdo Sound.

Source of DMSP_z for *L. helicina*

The results of the *L. helicina* incubation experiment confirm that this grazer could maintain a DMSP_z content similar to field samples by feeding solely on *P. antarctica*, and that DMSP_z decreased upon starvation or feeding on a DMSP-poor food source. This strongly suggests that the DMSP associated with *L. helicina* in the field is derived from ingestion of *P. antarctica*.

Ingestion rate of *L. helicina* on *P. antarctica* can be estimated from the DMSP_z data obtained in the incubation experiment. Baseline DMSP_z, i.e., DMSP_z assimilated into

body tissues, is estimated as the mean DMSP_z in the *Dunaliella* treatment and the starvation treatment (Fig. 4), which amounts to 16.4 nmol DMSP ind.⁻¹ (117 nmol mg C⁻¹). DMSP_z above this baseline is assumed to be derived from *P. antarctica* in the animal's gut, which is 16 nmol DMSP ind.⁻¹. Assuming that the gut content of the animals is at equilibrium between ingestion and egestion, the DMSP ingestion rate can be calculated as gut DMSP_z divided by the gut passage time, which is 1.02 hours for Antarctic *Limacina* sp. (Perissinotto 1992). Because the DMSP was derived from *P. antarctica* in our incubation experiment, we use a DMSP:carbon ratio of 1.2 mmol g⁻¹ for *P. antarctica* (Stefels and van Leeuwe 1998) to calculate the carbon ingestion rate, which is 13.1 μg C ind.⁻¹ h⁻¹, equivalent to a daily ration of 225% of body carbon. Using the low-end respiration rate reported for *L. helicina* (Seibel and Dierssen 2003), this pteropod respire an estimated 6% of its body carbon per day. Even in the absence of an alternative food source, it appears that *L. helicina* could more than sustain its metabolic requirement by grazing on *P. antarctica* in situ.

Limacina helicina can account for a large portion (ca. 20% or greater) of zooplankton abundance and biomass in McMurdo Sound and the Ross Sea (Hopkins 1987; Pane et al. 2004). The increase in abundance of *L. helicina* between late January and February in this study overlaps with the period of high abundance of *P. antarctica* in the southern Ross Sea (Smith et al. 2003). Based on our in situ abundance data for *L. helicina*, and an estimated ingestion rate of 13.1 μg of *P. antarctica* C ind.⁻¹ h⁻¹ from our incubation experiment, grazing by *L. helicina* could remove *P. antarctica* by as much as 550 mg C m⁻³ day⁻¹ (mean 31 mg C m⁻³ day⁻¹) in the field. The water column primary productivity in the Southern Ross Sea between January and February is roughly 300–1,200 mg C m⁻³ day⁻¹ (Smith et al. 2000). The estimated grazing impact of *L. helicina* therefore corresponds to a substantial portion of this water column primary production (ca. 10–50% of primary production day⁻¹). In a study at Prince Edward Archipelago during April and May, Perissinotto (1992) estimated that *Limacina* sp. accounted for the highest in situ mesozooplankton grazing impact (2.6–19.0% of primary production day⁻¹). Our estimates of grazing impact are higher than those obtained in his study, likely due to differences in pteropod abundance. While the pteropods were of a comparable size in both cases (ca. 100 μg C ind.⁻¹; assuming a C:dry weight ratio of 0.5 for the data of Perissinotto), the abundances of *Limacina* sp. at Prince Edward (107–221 ind. m⁻³) were at the low end of those in our study (Table 1). Given the spatial and temporal overlapping in the occurrence of *P. antarctica* and *L. helicina*, this pteropod represents a potentially important top-down control of *P. antarctica* blooms in the Ross Sea. In the sub-ice

environment of McMurdo Sound, where light is much more limiting to phytoplankton growth, feeding by *L. helicina* could potentially remove all *P. antarctica* within the grazeable size range from the water. Considering the threat that ocean acidification presents to aragonite shelled organisms such as pteropods in the Southern Ocean (Orr et al. 2005), a decrease or disappearance of this species would result in a decrease in grazing pressure on *P. antarctica*. This in turn could affect the extent of *P. antarctica* blooms in the Southern Ocean, the vertical flux of *P. antarctica* carbon to the deep ocean, and even the dynamics of DMSP/DMS in the region.

Overall conclusions

The zooplankton community seen during this study is in agreement with other reports for McMurdo Sound. The community was numerically dominated by small copepods. However, larger copepods and pteropods, when present, composed the majority of the biomass. A secondary peak in zooplankton abundance and biomass in the late summer was observed for the first time in sub-ice environment of McMurdo Sound. DMSP_z measurements suggest that most of the zooplankton species in McMurdo Sound are a part of a *Phaeocystis*-based food web. In particular, the diets of *L. helicina* and copepod nauplii are likely to consist to a large extent of *P. antarctica*. Future research should concentrate on directly quantifying the effects of grazing by these two groups on *P. antarctica* in the Ross Sea and McMurdo Sound.

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