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Ross Sea deep-ocean and epipelagic microzooplankton during the summer-autumn transition period

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ABSTRACT: Microzooplankton populations are key participants in the transfer, recycling and export of carbon in epipelagic waters, but little is known about their role, abundance and diversity at depth, especially in the Antarctic region. We surveyed microzooplankton populations and their potential prey in the Ross Sea area from 66° S to 77° S during the New Zealand IPY-CAML survey, 12 February to 11 March 2008. Samples were taken throughout the available water column at depths between ~5 and 3400 m, allowing us to compare deeper, largely unknown, mesopelagic and bathypelagic waters with the traditionally studied epipelagic zone. Microzooplankton diversity and abundance were highest in the high chlorophyll *a*, diatom-dominated waters of the epipelagic zone, but occasionally, peaks did occur in the upper mesopelagic before populations declined with depth. Ciliates and dinoflagellates declined more rapidly than heterotrophic nanoflagellates, which led to the latter dominating at depth. Ciliate populations in epipelagic waters were correlated with bacteria, picophytoplankton and chlorophyll *a*, but these potential prey did not correlate well with heterotrophic nanoflagellates in deeper or low-biomass waters. Despite their rapid decline with depth, due to the large volume of deeper waters, the total integrated microzooplankton biomass exceeded that found in the epipelagic zone. This indicates that the deeper waters of the Ross Sea, at this time, contained a significant pool of microzooplankton biomass. These deeper populations are likely to aid in the recycling and remineralisation of sinking phytoplankton biomass traditionally thought to be exported to the ocean floor.

KEY WORDS: Microzooplankton · Protists · Mesopelagic · Bathypelagic · Epipelagic · Ross Sea

INTRODUCTION

A diverse assemblage of microzooplankton is known to inhabit the Ross Sea region and is dominated by heterotrophic protistan species, including substantial populations of ciliated protozoa, heterotrophic dinoflagellates and choanoflagellates (Garrison & Gowing 1993, Marchant & Murphy 1994, Garrison et al. 1996, Scott & Marchant 2005). In Southern Ocean waters, microbial food web processes centred around microzooplankton often dominate biological processes in the epipelagic zone, especially during post-bloom successional periods when phytoplankton biomass is low (Alder & Boltovskoy 1993, Garrison et al. 1996, Dennett et al. 2001). In the deeper waters of this region, however, beyond the epipelagic zone, little is known about the biomass or role of microzooplankton.

Microzooplankton through grazing are responsible for much of the transfer of smaller phytoplankton and bacteria through the food web (Burkill et al. 1995, Becquevort 1997, Klaas 1997, Fonda Umani et al.

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1998, Caron et al. 2000, Hall & Safi 2001, Landry et al. 2002). In both surface water and increasingly at depth, microzooplankton influence carbon transfer and export through their influence on food web processes (Caron et al. 2000, Tanaka 2009, Sohrin et al. 2010). In epipelagic waters, this may be achieved by uppressing phytoplankton population growth through grazing (Burkill et al. 1995, Timmermans et al. 2001) and by repackaging smaller phytoplankton biomass (Rivkin et al. 1999) for larger predators, both processes providing a path for the flux of carbon. Microzooplankton may even enhance carbon flux into deeper Southern Ocean waters by favouring the growth of larger, faster-sinking species (Hall & Safi 2001, Landry et al. 2002). Due to their substantial potential for carbon consumption, growth and turnover, microzooplankton are also important in nutrient cycling in both the epipelagic zone and deeper waters (Brzezinski et al. 2001, Fennel & Neumann 2003). More recent studies in some marine systems now suggest that the majority of particulate organic carbon thought to be exported may be remineralised with the aid of protist grazing and bacterial activity and hence may never reach the deep ocean (Buesseler & Boyd 2009, Tanaka 2009, Sohrin et al. 2010). This in turn has important implications, especially if similar processes occur in Southern Ocean waters, which are regarded as an important sink for atmospheric carbon.

Microzooplankton also serve as an important food source for larger predators, such as mesozooplankton, in the Ross Sea region (Caron et al. 1999, 2000, Lonsdale et al. 2000). Conversely, the impact of mesozooplankton grazing on microzooplankton biomass appears to be only modest due to the relatively low biomass of these larger predators reported in these waters (Lonsdale et al. 2000). Until now, little has been known about the abundance and potential role of these organisms in the deeper waters of the Ross Sea region.

The present study was undertaken following the spring-summer period when phytoplankton biomass peaks occur (Arrigo et al. 1998, Smith et al. 2000a,b, Dennett et al. 2001) but before the onset of the heterotrophic, low phytoplankton biomass period characteristic of autumn in the Ross Sea (Dennett et al. 2001). To date, studies in the Ross Sea region have not captured this transitional period and have been largely limited to the epipelagic zone (Vanucci & Bruni 1999, Caron et al. 2000, Dennett et al. 2001). The aim of the present study was to find out how microzooplankton populations in the Ross Sea vary during this transition period, both spatially and with depth. We also aimed to determine whether the amount of microzooplankton biomass at depth was sufficient to influence carbon export to the ocean floor through recycling processes. Finally, we investigated the relationship between microzooplankton and their potential prey and how this changes with depth.

MATERIALS AND METHODS

Field sampling

Samples were collected during the New Zealand International Polar Year (IPY) Census of Antarctic Marine Life (CAML) voyage to the Ross Sea on board the RV 'Tangaroa' (voyage 0802) between 12 February and 11 March 2008. At 19 sites, a Seabird (SBE-9 plus) conductivity, temperature and depth sensor (CTD) and rosette fitted with 24 Niskin bottles (10 l) was used to collect sample water and assess a variety of physical and biological variables (Table 1, Fig. 1).

Epipelagic, mesopelagic, bathypelagic and mixed layer depth

As light measurements were not taken during CTD casts, epipelagic (euphotic) zone depths were calculated using the method of Morel & Genitili (2004) (see also Morel et al. 2007) using ocean colour data from the Aqua-MODIS sensor (Table 2). Epipelagic depths were generated using 9 km spatial resolution data composited across the

Table 1. Sampling region, area, bottom depth and site number of sites surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

Region	Area	Depth (m)	Site numbers
South	Shelf	200–400	C1,
South	Shelf	400–600	C3, C4
South	Shelf	600–1200	C2
Central	Slope (west)	600–1200	C16, C26
Central	Slope (west)	1200–2000	C17, C27
Central	Slope (shallow)	400–600	C15, C25
Central	Deep slope	2000–2500	C18
North	Abyss	2800–3500	C30, C33, C35
North	Seamounts	400–3000	C24, C29, C31, C34

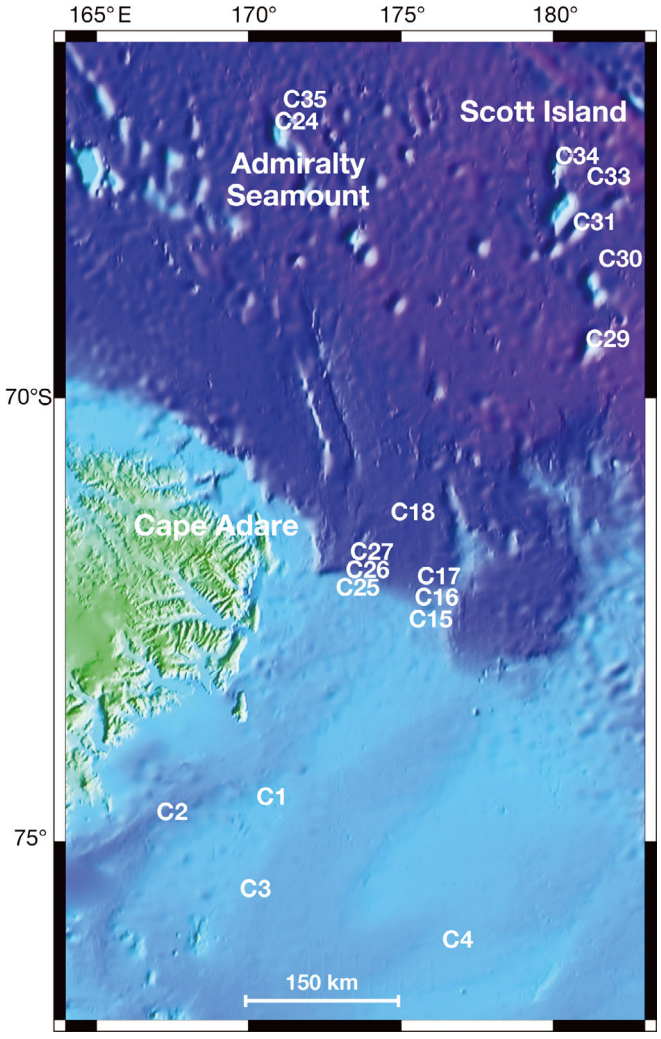

Fig. 1. Sampling sites surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

voyage time period with the NASA freeware 'SeaDAS'. Having identified epipelagic zone depths, we defined the mesopelagic zone as depths occurring between our calculated epipelagic zone depth and 1000 m. Depths >1000 m were considered to be bathypelagic. Mixed layer depths (MLD) were also calculated from CTD data collected during the voyage (Table 2) where data were available. When CTD data were not available, temperature and salinity profiles from Seabird Microcat devices deployed with other instruments were used to calculate the MLD. Where data were available from >1 source, an average was taken and used as the calculated MLD for these sites. Water masses were also categorised following Sokolov & Rintoul (2002, 2007).

Table 2. Epipelagic and mixed layer depths (m) at sites surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

Site number	Epipelagic zone depth	Mixed layer depth
C1	47	36
C2	36	30
C3	33	55
C4	36	55
C15	92	43
C16	83	43
C17	92	47
C18	86	72
C24	98	51
C25	97	28
C26	97	39
C27	72	48
C29	68	26
C30	69	39
C31	74	45
C33	80	48
C34	80	19
C35	118	35

CTD sampling

Water samples were collected at 9 to 15 discrete depths at each core site using 10 l Niskin bottles mounted on the CTD rosette (Fig. 1, Table 1). Dissolved nutrients (nitrate + nitrite, phosphate and silicate) were measured using an AlpKem nutrient analyser (Cowley et al. 1999). Chlorophyll *a* (chl *a*) was determined fluorometrically by filtering 500 to 1000 ml of seawater onto 25 mm Whatman glass fibre filters (GF/F). Filters were immediately frozen and analysed within 3 mo following the methods of Strickland & Parsons (1972) and using a Perkin-Elmer fluorometer. Discrete water samples were also collected for determination of ciliated protozoa, nauplii, nanoflagellates, bacteria, picophytoplankton and phytoplankton abundance and biomass.

Microzooplankton identification and enumeration

Ciliates and small mesozooplankton (miscellaneous non-ciliates) were identified and enumerated in samples using the sedimentation method with 250 ml to 2 l samples preserved with Lugol's iodine solution (1% final concentration). For enumeration, samples were left to settle for >48 h then counted and identified with an inverted microscope at 100× to 400× magnification. Ciliates and small mesozooplankton samples were identified to genus and/or

species level (Brandt 1906, Kofoid & Campbell 1929, 1939, Corliss 1961, Alder 1999, Scott & Marchant 2005). The dimensions of each taxon were measured, and the volume was estimated from approximated geometric shapes (spheres, cones or ellipsoids). Estimates of ciliate volume were then converted to carbon biomass using a factor of 0.19 pg C μm^{-3} (Putt & Stoecker 1989) and combined with abundances to give total biomass. Tintinnid ciliate volume was halved to compensate for lorica volume (Beers & Stewart 1967). Miscellaneous non-ciliates were estimated to be 0.2 µg C per individual, based on mean literature values of the most commonly observed species (N. Broekhuizen pers. comm.).

Subsamples for nanoflagellate counts were preserved in glutaraldehyde, filtered and stained with primulin following the methods described by Hall et al. (2004). Nanoflagellates were counted under UV excitation using a Leica compound microscope with autotrophic nanoflagellates (ANF) differentiated by chl *a* excitation (Hall et al. 2004). Where possible, given their preservation, all abundant organisms were identified to genus and/or species level (Chretiennot-Dinet et al. 1990, Patterson & Larson 1991, Throndsen 1993, Tomas 1997, Scott & Marchant 2005, Hoppenrath et al. 2009) or classed by size (<2 µm, 2 to 5 µm and 5 to 20 µm) and then counted. Cell carbon for ANF and heterotrophic nanoflagellates (HNF) was calculated from cell volumes using formulae representing geometric solids that approximated their shape (Rott 1981) and a conversion factor of 0.13 pg C μm^{-3} (Edler 1979).

Dinoflagellates

Smaller dinoflagellates <20 µm were identified and included in nanoflagellate counts for all depths. Larger (>20 µm) dinoflagellates were identified in Lugol-preserved samples to a depth of 100 m following the methods reported by Chang et al. (in press).

Picophytoplankton and bacteria

Picophytoplankton and bacterial samples were frozen in liquid nitrogen (Lebaron et al. 1998) and thawed immediately before counting by flow cytometry. For picophytoplankton analysis, we followed the methods of Hall et al. (1999), and for bacteria, we followed Safi et al. (2007). Cell carbon for eukaryotic picophytoplankton was determined by estimating the average spherical diameter and converted following Booth (1988) to yield a factor of 920 fg C $cell^{-1}$. For *Bacteria*, a conversion factor of 20 fg C $cell^{-1}$ for carbon content was used (Lee & Fuhrman 1987). *Archaea* have been reported to constitute significant fractions of Antarctic picoplankton assemblages (DeLong et al. 1994). These prokaryotes cannot be distinguished from bacteria with the flow cytometric method used; therefore, the terms bacterial abundance and bacterial biomass may include both *Bacteria* and *Archaea.*

Depth integration

All depth averages were calculated using the following equation:

$$I = \frac{\sum_{i=1}^{n-1} \Delta Z_{i,i+1} 0.5(B_i + B_{i+1})}{\sum_{i=1}^{n-1} \Delta Z_{i,i+1}} \quad (1)$$

where I denotes a sample level number (in increments from 1 at the sea-surface), B_i denotes the concentration (µg C l^{-1}) measured at this sample level, and $\Delta Z_{i,j+1}$ is the thickness (m) of the layer between sequential sampling depths. Depth-averaged concentrations are reported as µg C l^{-1}.

Statistical analysis

All statistical analysis of data was conducted using Microsoft Excel®. Data were compared by either Pearson's correlation analysis, analysis of variance or regression analysis.

RESULTS

The oceanographic environment and depth zones

All CTD casts were made south of the Polar Front in an area where surface waters were categorised as Antarctic Surface Water, being typically warm for the region (up to 2.0°C) and fresher (<34.5) than the deeper waters from which they were formed due to solar heating during summer and ice melt (Orsi & Wiederwohl 2009). Water mass characteristics showed some changes with depth, but the depth analysis of data presented in the present paper was based on the epipelagic zone (euphotic), mesopelagic and bathypelagic depths. The epipelagic zone was usually deeper than the MLD, except at shelf

Sites C3 and C4 (Table 2). Average epipelagic zone depth was lowest in shelf waters at 38 m, followed by seamounts at 80 m, with slope and abyss waters having similar average depths of 88 and 89 m, respectively.

Spatial and vertical variation in phytoplankton and nutrients

Late summer chl *a* concentrations were highest over the Ross Sea Shelf, reaching 1.3 mg m^{-3} (C4) in the strongly stratified surface waters and having an average of 0.7 mg m^{-3} in the epipelagic zone (Fig. 2). At the slope stations, chl *a* values reached a maximum of 0.5 mg m^{-3} and an average of 0.3 mg m^{-3} in the epipelagic zone. At both shelf and slope sites, chl *a* concentrations sharply decreased to almost 0 below 200 m. The seamount stations had similar average concentrations of chl *a*, with a maximum of 0.5 mg m^{-3} and an average of 0.3 mg m^{-3} in the epipelagic zone (Fig. 2). Abyss sites were more variable, with chl *a* detected to a depth of 250 to 300 m.

Late summer phytoplankton composition in the epipelagic zone of the Ross Sea was largely dominated by diatoms including *Chaetoceros*, *Asterionella*, *Melosira, Asteromphalus Dactyliosolen, Probosci* and *Fragilariosis* spp. (Chang et al. in press). There were 2 exceptions, with the prymnesiophyte *Phaeocystis* dominating biomass at shelf Site C4 (Chang et al. in press). Also, *Pyramimonas* sp. and dinoflagellates were abundant at Site C34 (Chang et al. in press).

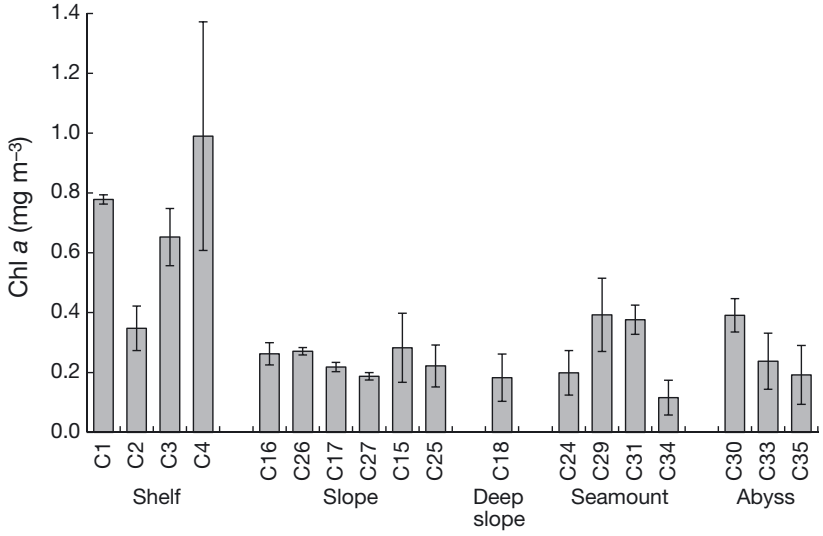

Fig. 2. Average chlorophyll *a* (mg m^{-3}) in epipelagic waters at sites grouped by area — shelf, slope, deep slope, seamount and abyss — surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008. Error bars are ±1 SD

Nitrate concentrations were never limiting, with values >0.65 µM throughout the survey. NH_4-N concentrations were highest around ~76° S in shelf waters and were statistically correlated with chl *a* ($r = 0.40$, $n = 196$, $p < 0.0001$).

Ciliate and small mesozooplankton composition

Ciliate composition in the epipelagic zone was usually dominated by large non-loricate ciliates (>20 µm), while at the high biomass shelf and selected seamount sites, tintinnids were also occasionally abundant (Table 3). Small oligotrichs (<20 µm) were more important in epipelagic waters at low biomass abyss and slope sites. In the deeper mesopelagic and bathypelagic waters, smaller oligotrichs increased in importance, while larger ciliate genera consistently declined. A number of genera were only reported in epipelagic waters, while in deeper waters, the tintinnids *Salpingella* spp. and *Amphorella* spp. often increased in importance (Table 3).

Spatially compositional differences in both oligotrich and tintinnid populations occurred. The oligotrich genus *Strobilidium* (>20 µm) and larger (>60 µm) unidentified round oligotrichs dominated in epipelagic waters at most sites and were especially important on the shelf (Table 4). Tintinnids also varied among areas, with *Cymatocylis, Laackmanniella* spp. and *Codonellopsis* spp. dominating at high biomass shelf and seamount sites (Table 3).

The small mesozooplankton (<200 µm, miscellaneous species) identified during ciliate counts were dominated by nauplii and showed no significant trends in composition with depth. Spatially, the highest diversity for this group was in the slope sites (Table 3), while biomass was again highest in shelf waters (Table 4) and lowest in slope and abyss sites. Proportionally small mesozooplankton declined at a lower rate with depth than ciliates in most areas (Table 4).

Heterotrophic nanoflagellate and heterotrophic dinoflagellate composition

Across our study areas and with depth, we found a wide range of HNF genera, a number of which we could not accu-

Table 3. Average ciliate depth-integrated (Eq. 1) biomass ranges reported as µg C l^{-1} for all sites grouped by area (shelf 200–1200 m; slope, separated into West slope 600–2000 m, central (shallow) slope 400–600 m and deep slope 2000–2500 m; seamount 400–3000 m; and abyss 2800–3500 m) surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008. nd: not detected; Y = observed, but ranges of biomass are not given for miscellaneous species

Ciliate Group/ Genera/Species	Shelf (C1–4)	West slope (C16–17, 26–27)	Central slope (C15, 25)	Deep slop (C18)	Seamount (C24, C29, C31, C32, C34)	Abyss (C30, C33, C35)
Oligotrichs						
Unid. Oligotrichia spp. <20 µm	2–5.3	2.8–3.6	1.5–3.6	1.1	1.4–5.8	1.6–2.7
Unid. Oligotrichia spp. >20 µm	0.8–2.1	0.4–0.5	0.3–0.5	0.2	0.2–1.2	0.2–0.5
Strombidium spp. >20 µm	0–0.4	0.1–0.2	0–0.6	nd	0–0.6	0.1–0.2
Strombidium spp. <20 µm	<0.1	nd	0–0.1	<0.1	0–<0.1	nd
Strobilidium spp. <20 µm	0.1–0.2	0.2–0.3	0.2–0.4	0.1	0.2–0.4	0.2–0.3
Strobilidium spp. >20 µm	2.2–5.9	1.4–1.5	0.4–1.3	0.4	0.5–3.6	0.8–1.2
Strobilidium spp. (curved)	0–<0.1	nd	0–0.1	nd	0–<0.1	nd
Lohmaniella spiralis	1.0–4.2	1.5–1.9	0.6–2.1	0.5	0.8–3.4	0.6–1.6
Mesodinium spp.	<0.1	nd	0<0.1	nd	nd	0–<0.1
Didinium spp.	0–0.4	nd	0.0.1	nd	0–0.7	0–0.6
Large spp. >60 µm round shape	2.8–13.4	0.4–7.8	0.6–2.5	0.7	0.7–5.1	1.0–2.3
Large spp. >60 µm cone shape	0.9–1.8	0.3–1.8	0.6–1.0	0.4	0.6–1.3	0.2–0.7
Laboea spp.	0.2–30	0.1–0.2	0–<0.1	<0.1	0.1	0–0.6
Laboea strobila	0.6–13.1	0.6–3.4	0.3–2.5	0.3	0–1.6	1.0–2.3
Tontonia spp.	0.1–0.3	0–<0.1	0–<0.1	<0.1	0–0.3	0–0.7
cf. *Kentrophyllum*?	0–30.7	0–0.1	0–0.1	nd	0–0.3	0–0.3
Tintinnids						
Amphorella spp.	0–3.9	0–0.2	0–0.8	<0.1	0.1–2.3	0.1–2.0
Amphorellopsis spp.	0–7.6	nd	nd	nd	nd	nd
Codonella spp.	0–0.1	nd	nd	nd	nd	nd
Codonellopsis cf. *gaussi*	0–5.8	0–<0.1	nd	nd	0.1–5.1	0.8–2.4
Codonellopsis cf. *gaussi* (small)	0–0.3	nd	0–0.1	nd	nd	nd
Coxliella spp.	0–<0.1	nd	nd	nd	nd	nd
Cymatocylis cf. *drygalskii*	1.3–31.9	1.7	0–1.9	0.4	0–8.7	nd
Cymatocylis cf. *vanhöffeni*	0–9.6	nd	nd	nd	nd	nd
cf. *Epiplocylis* spp.	nd	nd	nd	nd	nd	0–0.2
Favella spp.	0–0.1	nd	0–0.9	nd	0–0.9	nd
Laackmanniella cf. *naviculaefera*	0.3–8.1	0–0.1	0–0.2	nd	0–0.7	0.1–0.7
Parundella spp.	0–0.1	nd	nd	nd	nd	nd
Salpingella spp.	0–0.9	0–0.1	0–0.1	0.1	0–1.2	0–0.3
Tintinnus spp.	nd	0–<0.1	nd	nd	nd	nd
Cymatocylis cf. *convallaria*	nd	nd	nd	nd	0–0.4	0–0.6
cf. *Ormosella* spp.	nd	nd	nd	nd	0–0.1	nd
cf. *Steenstrupiella* spp.	nd	0–<0.1	nd	nd	nd	nd
Miscellaneous						
Copepoda: adults	Y	Y	Y	Y	nd	Y
Copepoda: copepodites	Y	Y	Y	nd	Y	Y
Nauplii	Y	Y	Y	Y	Y	Y
Appendicularians	Y	Y	Y	Y	Y	Y
Polychaete larvae	nd	Y	nd	nd	nd	nd

rately identify due to preservation and which had to be classed by size (Table 5). In epipelagic zone waters, <20 µm heterotrophic dinoflagellates, although rarely numerically dominant, often dominated HNF biomass due to their larger average size, especially when phytoplankton biomass was high. Heterotrophic <20 µm dinoflagellates were dominated by small non-thecate genera, including *Gymnodinium* spp., *Gyrodinium* spp. and some *Katodinium* spp., with *Oxytoxum* as the dominant thecate genus. In contrast, kinetoplastids, choanoflagellates and unidentified small genera dominated when biomass was low (especially at slope and abyss sites) and in the deeper mesopelagic and bathypelagic waters. Larger, >20 µm heterotrophic dinoflagellates were only important in epipelagic waters and contributed

Table 4. Depth-integrated ciliate (and miscellaneous non-ciliate) numbers and ciliate biomass across areas — shelf, slope, seamount and abyss — over epipelagic (33–118 m), mesopelagic (118–1000 m) and bathypelagic (>1000 m) depth ranges surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

	Miscellaneous non-ciliates (no. l^{-1})	Oligotrichs ≤20 µm (no. l^{-1})	Oligotrichs >20 µm (no. l^{-1})	Tintinnids (no. l^{-1})	Total ciliates (no. l^{-1})	Oligotrichs ≤20 µm (µg C l^{-1})	Oligotrichs >20 µm (µg C l^{-1})	Tintinnid biomass (µg C l^{-1})	Total ciliate biomass (µg C l^{-1})
Epipelagic									
Shelf	10	1472	858	251	2581	0.6	7.9	2.6	11.2
Slope	3	1198	210	27	1435	0.5	1.3	0.3	2.0
Seamount	4	1630	343	161	2133	0.8	2.0	1.4	4.2
Abyss	3	1061	201	145	1407	0.4	1.2	0.8	2.4
Mesopelagic									
Shelf	1.5	534	217	21	771	0.2	1.1	0.5	1.9
Slope	1.3	223	34	2	260	0.1	0.2	0.0	0.4
Seamount	1.4	177	31	6	215	0.1	0.2	0.1	0.3
Abyss	0.8	104	14	3	120	0.0	0.1	0.0	0.2
Bathypelagic									
Slope	0.0	69	2.3	0.1	71	0.03	0.02	0.00	0.05
Seamount	0.3	20	1.0	0.0	21	0.01	0.00	0.00	0.01
Abyss	0.1	16	0.8	0.1	16	0.01	0.00	0.00	0.01

most in shelf and abyss sites, while their contribution was lowest in the slope sites (Fig. 3). A rapid decline in all heterotrophic dinoflagellates with depth meant that they were rarely seen beyond 200 m. As depth increased and smaller non-dinoflagellate HNF genera became dominant, however, especially at depth, many could not be identified and were grouped only by size (Table 4).

Phytoplankton data for dinoflagellates as reported by Chang et al. (in press) indicate that the majority of dinoflagellates reported during this voyage were heterotrophic, contributing 95.4% of dinoflagellate cell carbon over the Ross Sea shelf area and 82 to 98% in the slope, abyss and seamount zones (Chang et al. in press).

Spatially in the epipelagic zone, we found our identified HNF genera changed their ratio of abundance rather than the absence or presence of new genera; however, in slope sites, the genus *Telonema* was absent and dinoflagellate diversity was at its lowest, while the choanoflagellate *Monosiga* was only observed at some abyss and seamount sites. At depth, the occurrence of smaller (<8 µm) unidentifiable mono and biflagellate cells increased.

Table 5. Heterotrophic nanoflagellates and autotrophic nanoflagellates observed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

Class/size class	Genus/species
Heterotrophic nanoflagellates (including dinoflagellates)	
Kinetoplastids	*Bodo* spp.
	Pseudobodo spp.
	cf. *Pleurostomum*
	Telonema sp.
	Leucocrytos marina (Braarud)
Choanoflagellatea	*Calliacantha natans* (Grøntved)
	Pleurasiga sp.
	Monosiga sp.
Dinophyceae	*Oxytoxum* spp.
	Gymnodinium spp.
	Gyrodinium spp.
	Katodinium sp.
<2 µm	Unidentified
2 to 5 µm	Unidentified
5 to 20 µm	Unidentified
Autotrophic nanoflagellates (including dinoflagellates)	
Prymnesiophyceae	*Phaeocystis antarctica* (Karst)
	Phaeocystis spp.
	Chrysochromulina spp.
Cryptophyceae	*Cryptomonas* spp.
	Plagioselmis sp.
Dinophyceae	*Oxytoxum* spp.
	Gymnodinium spp.
	Gyrodinium spp.
	Katodinium sp.
Prasinophyceae	*Pyramimonas* spp.
Pedinophyceae	*Micromonas* sp.
Euglenophyceae	*Eutreptiella* sp.
<2 µm	Unidentified
2 to 5 µm	Unidentified
5 to 20 µm	Unidentified

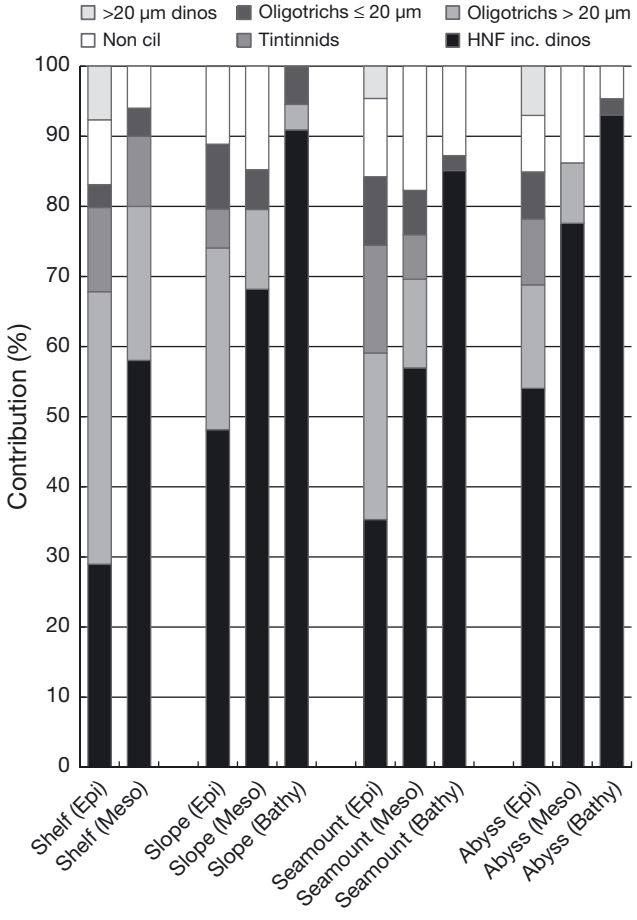

Fig. 3. Depth-integrated percentage contributions to total microzooplankton biomass of heterotrophic nanoflagellates (HNF) including heterotrophic dinoflagellates (dinos) < 20 µm, oligotrichs > 20 µm, tintinnids, oligotrichs ≤ 20 µm, non-ciliated miscellaneous species (Non cil) and heterotrophic dinoflagellates > 20 µm. Epipelagic, mesopelagic and bathypelagic waters in 4 areas — shelf, slope, seamount and abyss — were surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

ANF and autotrophic dinoflagellate composition

ANF diversity declined rapidly with depth, and the ANF identified by the presence of chloroplasts could not be distinguished from mixotrophs (autotrophs capable of grazing) in our study. ANF included representatives of Prymnesiophyceae, Cryptophyceae, Prasinophyceae, Pedinophyceae, Dinophyceae and Euglenophyceae (Table 5). The >20 µm autotrophic dinoflagellate biomass was very low, with on average 90% of dinoflagellate biomass being heterotrophic as reported by Chang et al. (in press). ANF including <20 µm autotrophic dinoflagellates contributed the most to larger phytoplankton biomass at Sites C18 (deep slope), C24 (seamount) and C33 (abyss).

Changes in microzooplankton biomass spatially and with depth

Ciliate biomass always peaked in the epipelagic or upper mesopelagic zone, with maxima between 20 and 150 m (usually ≥70 m) (Table 4). Ciliates declined most rapidly at shelf sites, falling below detection at between 250 m and 835 m. In contrast, at the deep abyss site C35, very low ciliate numbers were reported at 3385 m (Table 4). In the epipelagic zone, ciliate numbers (l^{-1}) were on average ~4-fold higher than in the mesopelagic zone and 200-fold higher than in the bathypelagic (Table 4).

Ciliate biomass also varied spatially (Table 4). Shelf sites had the highest ciliate biomass in epipelagic waters (Table 4), with maxima ranging between 6.5 µg C l^{-1} at C2 (20 m) and 41 µg C l^{-1} at C4 (20 m). Slope sites had the lowest average biomass (Table 4), with peaks at ~3 µg C l^{-1}, except C18, where the biomass maximum was only 0.9 µg C l^{-1}. The seamount sites peaked between 3.4 and 8.4 µg C l^{-1} between 20 and 70 m, while abyssal sites peaked between 3.9 and 4.7 µg C l^{-1} between 20 and 50 m (Table 4).

Spatially and with depth, HNF biomass was more variable than that of ciliates (Table 5). HNF overall declined at a much lower rate with depth than ciliates (Table 6), and at depths below the epipelagic zone, especially in the upper mesopelagic waters, the biomass and numbers of HNF remained relatively high at ~3 µg C l^{-1}, while even at depths of 400 m and below, biomass was between 0 and 1.0 µg C l^{-1} (with tens of cells ml^{-1} reported) (Table 6). In the epipelagic zone, HNF biomass was ~2-fold higher on average than in the mesopelagic zone and 6-fold higher than in the bathypelagic (Table 6).

Biomass was again highest on average at shelf sites, with maxima of 5.8 and 3.9 µg C l^{-1} at shelf Sites C3 (70 m) and C4 (250 m), respectively, while the highest variability occurred at slope sites, having both the highest biomass of 9.7 µg C l^{-1} at Site C17 (5 m) and a low biomass peak at Site C18 (50 m) of only 1.6 µg C l^{-1}. Low biomass seamount sites peaked at 4 µg C l^{-1} (100 m) at Site C24, while Site C34 peaked at only 1.3 µg C l^{-1} (10 m), the lowest of the study. Epipelagic abyssal waters were similar to slope sites on average (Table 6) but had a maximum of 8.92 µg C l^{-1} reported at Site C35 (5 m).

ANF rapidly dropped to near detection levels below 100 to 150 m in the seamount sites but were occasionally reported as deep as 1000 m in slope and abyssal sites.

Table 6. Depth-integrated (Eq. 1) heterotrophic nanoflagellate (HNF) and autotrophic nanoflagellate (ANF) numbers and biomass (including dinoflagellates) observed across each of 4 areas — shelf, slope, seamount and abyss — over epipelagic (33–118 m), mesopelagic (118–1000 m) and bathypelagic (>1000 m) depth ranges surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

	ANF (cells ml^{-1})	HNF (cells ml^{-1})	ANF (µg C l^{-1})	HNF (µg C l^{-1})
Epipelagic				
Shelf	667	464	3.6	4.6
Slope	412	373	1.5	2.6
Seamount	271	499	1.0	2.2
Abyss	271	351	1.5	3.5
Mesopelagic				
Shelf	492	277	2.0	2.9
Slope	82	153	0.3	1.2
Seamount	53	130	0.2	0.9
Slope	17	102	0.1	0.5
Bathypelagic				
Seamount	0	42	0.0	0.4
Slope	0	89	0.0	0.4
Abyss	0	51	0.0	0.9

Change in the contribution of different microzooplankton groups spatially and with depth

Ciliates were more important in the epipelagic zone and decreased in importance with depth (Fig. 3). In contrast, HNF clearly dominated in the mesopelagic and bathypelagic zones across all sites. Heterotrophic dinoflagellates were most important in the epipelagic zone, where both large (>20 µm) and small cells (incl. <20 µm HNF) made an important contribution. Small miscellaneous mesozooplankton did not change significantly in their contribution to total biomass with depth, with the exception of bathypelagic slope waters (Fig. 3). Spatially, in epipelagic waters, ciliates dominated microzooplankton biomass at shelf and seamount sites, whereas at abyssal and slope sites, HNF dominated (Fig. 3). There were 2 sites where the microzooplankton composition was inconsistent with our general observations. Slope site C15 had high ciliate biomass but low contributions from other microzooplankton. In contrast, Site C17 was distinct from all other sites as it had an unusually high HNF biomass in epipelagic waters.

Correlation analysis between microzooplankton and known prey populations

Across all sites, we found ciliate populations in the epipelagic zone were most significantly correlated (based on r-values) with chl *a* followed by bacterial populations, eukaryotic picophytoplankton (EPICO) and ANF. Small oligotrichs ≤20 µm were most highly correlated to EPICO, while large oligotrichs >20 µm and tintinnids were highly correlated with ANF (Table 7). Across all sites, HNF biomass was not significantly correlated with bacteria or EPICO but was correlated with small (≤20 µm) and large (>20 µm) oligotrich biomass (Table 7). When areas were analysed separately, HNF numbers were significantly correlated with EPICO and bacteria but only in shelf sites (Table 7).

Changes in the relationship between microzooplankton groups and bacteria with depth

The ratio of depth-integrated ciliate biomass, HNF populations and bacteria varied among our depth zones (Fig. 4). Total integrated HNF and ciliate biomass in mesopelagic waters exceeded the total biomass found in the epipelagic zone. In the bathypelagic, this remained true for HNF biomass, but total ciliate biomass was low. In these deeper zones, the total integrated bacterial biomass also steadily increased with depth (Fig. 4). The ratio of integrated bacterial biomass to integrated microzooplankton biomass increased from a low of 0.4 in the epipelagic zone to 0.7 in the mesopelagic to 1.8 in the bathypelagic zone, indicating a reduction in the prey to predator ratio with depth. To compare our relative

Table 7. Epipelagic zone correlation coefficients (r) between selected microzooplankton biomass (ANF: autotrophic nanoflagellates, HNF: heterotrophic nanoflagellates) and their potential prey biomass (µg C l^{-1}) for epipelagic biomasses surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008. $^{*}p < 0.05$, $^{**}p < 0.001$, ǂ: only significantly correlated at shelf sites, ns: not significant

	Eukaryotic pico-phytoplankton	Bacteria	ANF	Chl *a*
ANF	ns	0.47*	ns	0.76*
HNF	0.82^{**,ǂ}	0.57^{**,ǂ}	ns	ns
Misc. non-ciliates	0.36**	0.39**	0.47*	0.47*
Oligotrichs ≤20 µm	0.54**	0.38**	ns	ns
Oligotrichs >20 µm	0.45**	0.50**	0.31*	0.45*
Tintinnid biomass	0.49**	0.57**	0.66**	0.78**
Total ciliate biomass	0.53**	0.58**	0.50*	0.58*
Dinoflagellates >20 µm	0.45**	0.56**	ns	0.52**

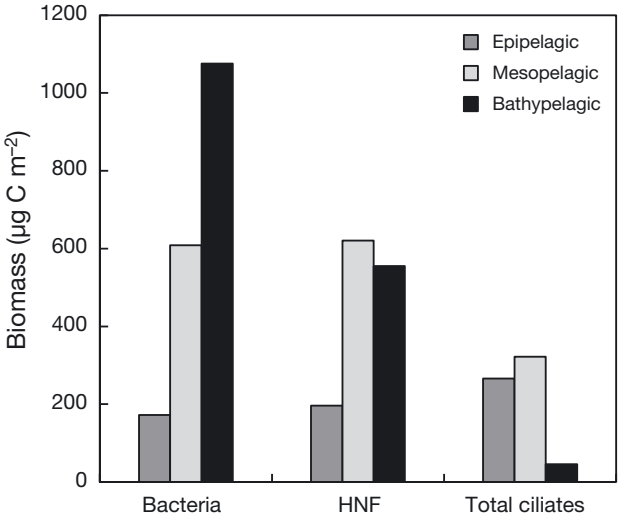

Fig. 4. Average total depth-integrated biomass for all sites of bacteria, HNF and ciliates in epipelagic, mesopelagic and bathypelagic zones surveyed during the NZ IPY-CAML voyage to the Ross Sea region, 12 February to 11 March 2008

rates of decline of these microbial food web components, we also examined the vertical attenuation rates of these populations across our entire study, as a linear regression slope of a log-log plot of biomass versus depth following the analysis method of Sohrin et al. (2010). The vertical attenuation rate of ciliate biomass was highest (linear slope), $y = -1.03$ ($R^2 = 0.68$), while that of HNF was much lower at $y = -0.36$ but more variable and less robust ($R^2 = 0.3$) although more similar to that of bacteria, $y = -0.33$ ($R^2 = 0.51$).

The integrated microzooplankton biomass found in deeper waters (Fig. 4) also exceeded that found in the epipelagic zone and consequently appears to be quantitatively significant in both mesopelagic and bathypelagic waters. Both ciliates and HNF increased in total biomass in the epipelagic, and while ciliates declined rapidly in the bathypelagic, bathypelagic HNF biomass still exceeded epipelagic biomass.

DISCUSSION

For the first time, the present study investigates changes in microzooplankton in the deeper mesopelagic and bathypelagic zones of the Ross Sea. The timing of this voyage in late summer (mid-February to mid-March) was also during the understudied period of transition between the autotrophic phytoplankton-dominated summer (November to February) and the heterotrophic grazer-dominated autumn (March to May) (Dennett et al. 2001). This, combined with the large depth range, variable topography and physical diversity among sampling areas, led to large variability in microbial assemblages.

Microzooplankton communities showed considerable variation both spatially and with depth (Tables 3 & 5), being dominated by a range of heterotrophic protistan species including ciliated protozoa, HNF and heterotrophic dinoflagellates. All genera that could be identified were consistent with those previously reported in this region (Garrison & Gowing 1993, Marchant & Murphy 1994, Garrison et al. 1996, Scott & Marchant 2005).

Microzooplankton and the microbial food web

To understand changes occurring in deeper waters, we needed to first understand the oceanographic environment and the microbial patterns and processes occurring in the productive epipelagic zone. Phytoplankton populations at the time of the present study were dominated by diatoms, with the flagellated *Phaeocystis antarctica* and *Pyramimonas* spp. dominating at only 2 of our 18 sampling sites. This predominance of diatoms, especially in higher biomass sites, indicated that autotrophic processes more typical of summer than of the heterotrophic autumn were still operating in most epipelagic waters (Dennett et al. 2001). The microzooplankton composition reflected this, with larger ciliates dominating in high-biomass, diatom-dominated epipelagic waters, where HNF assemblages were often dominated by small dinoflagellates. In contrast, in low biomass sites and in deeper waters, bacterivorous flagellates including choanoflagellates, kinetoplastids and unidentified small species became increasingly important (Garrison et al. 1996, Caron et al. 1999, Dennett et al. 2001). Beyond the epipelagic zone, at depth, it was also likely that many of these smaller HNF were associated with sinking aggregates rather than free living (Kiørboe et al. 2004).

Spatial variation among our different areas generally reflected the different oceanographic influences and topography. Abyssal sites were low in phytoplankton biomass (~0.3 mg m^{-3}), were HNF dominated with elevated quantities of >20 µm dinoflagellates and had deep epipelagic zones (down to 118 m) and deep mixed layers, all typical of Southern Ocean high nutrient, low chlorophyll waters (Hall & Safi 2001). In contrast, near-shore shelf sites were generally shallower, with shallow mixed layers (30 to 90 m), had relatively high phytoplankton biomass (up to 1.5 mg m^{-3}) and were dominated by larger ciliates

(although larger dinoflagellates were also elevated) in the epipelagic zone. Slope sites represented intermediate situations and were as such the most variable but were also the sites with the least >20 µm dinoflagellate biomass. The seamount sites, although influenced by shallower mixed layer depths and their proximity to land (e.g. Scott Island), were also highly variable due to the influence of surrounding waters and current flows.

Correlation analysis confirmed the general trends observed between microbial food web components in the epipelagic zone. Smaller ciliates (oligotrichs ≤20 µm) were most highly correlated with bacteria and EPICO, while larger ciliates (oligotrichs >20 µm and tintinnids) were more highly correlated with ANF and chl *a*. These results correspond to a size dependent grazing relationship for ciliates, as is widely reported elsewhere (Admiraal & Venekamp 1986, Weisse & Scheffel-Möser 1990, Foissner et al. 1991, Latasa et al. 1996, Landry et al. 2000). Larger heterotrophic dinoflagellates (>20 µm) were also correlated with chl *a*, EPICO and bacteria, indicating these factors are likely to be influencing food web structure in the epipelagic zone.

The relationship among HNF, bacteria and picophytoplankton was highly variable (Table 6). A lack of a consistent correlation between HNF and these prey populations is, however, not uncommon (Landry et al. 2000, Safi et al. 2007) and is affected by the successional phase being sampled, competition with other microzooplankton predators and predation upon HNF by other grazers.

In the epipelagic (and some upper mesopelagic waters) competition with mixotrophic phytoplankton (autotrophic dinoflagellates and ANF) and predation by large ciliates and heterotrophic dinoflagellates are both likely to have affected grazer relationships, with these populations being elevated in epipelagic waters (Jacobson & Anderson 1986, Strom & Buskey 1993, Verity et al. 1993). One example of where dinoflagellates and autotrophic flagellates were both proportionately high in biomass and were likely to have influenced the food web structure was seamount site C34: at this site, both ciliate size and biomass were low compared to phytoplankton biomass.

Deep water microzooplankton assemblages

In terms of composition, as alluded to earlier, we consistently observed an increase in the importance of HNF, especially kinetoplastids, choanoflagellate and small unidentified flagellates, in deeper mesopelagic and bathypelagic waters. In contrast, both small and large heterotrophic dinoflagellates declined rapidly with depth. We also observed that a number of the smaller flagellates, especially among the kinetoplastidae, appeared to be associated with (marine snow) aggregates, an observation consistent with other studies (Artolozaga et al. 2002, Kiørboe et al. 2004). Among the HNF genera, especially in bathypelagic waters, smaller unidentified species became increasingly important, as has also been reported elsewhere (Arndt et al. 2003, Not et al. 2007). Within ciliate populations, larger ciliates declined in importance, and bacterivorous oligotrichs <20 µm became increasingly dominant with depth. As larger ciliates declined with depth, so did carnivores, omnivores or species known to graze larger prey (Foissner et al. 1991, 1992, 1994). Similarly, the larger heterotrophic (and mixotrophic) dinoflagellates known to be capable of grazing larger prey also declined rapidly with depth. The loss of these populations was directly associated with the decline of phytoplankton prey, while smaller HNF and oligotrichs have a greater affinity for bacterial and detrital material and are known to colonise descending aggregates (Artolozaga et al. 2002, Kiørboe et al. 2004). Spatial changes in composition related to epipelagic waters only occurred in the upper mesopelagic zone; beyond these depths, due to the increasing importance of small unidentified HNF, we were unable to identify clear changes in terms of speciation.

Microzooplankton biomass and rates of decline with depth

Changes in microzooplankton groups with depth in other ocean environments are reported to be due to different microzooplankton populations declining at different rates (Tanaka & Rassoulzadegan 2002, Nagata et al. 2010, Sohrin et al. 2010). Lower rates of decline in HNF compared to other microzooplankton groups are common and led to this group being the most abundant in our deeper waters, as has been reported previously in the Mediterranean, Pacific and Atlantic oceans (Tanaka & Rassoulzadegan 2002, Nagata et al. 2010, Sohrin et al. 2010).

HNF, which had the slowest decline in numbers, ranged from below detection levels in the bathypelagic waters (<0.1 cells l^{-1}) to 127 000 cells l^{-1} at C18 at 1250 m. In comparison, Nagata et al. (2010) reported lower numbers in this zone of ca. 20 to 20 000 cells l^{-1}. Although we found that ciliates

declined more rapidly than HNF, they were still observed in the deeper mesopelagic and even in the upper bathypelagic zone, with a maximum value of 218 cells l^{-1} at 1500 m at site C18. These numbers were high compared to other studies, with Nagata et al. (2010) reporting ciliate abundances in bathypelagic waters ranging from below the detection limit (0.1 cells l^{-1}) to only 52 cells l^{-1}. The decline in heterotrophic dinoflagellates was fast compared to both HNF and ciliates, with this group being largely limited to the upper mesopelagic zone (100 to 250 m), as was reported in the Arabian Sea (Gowing et al. 2003).

We did find spatial differences in our rates of decline, but as with speciation these were largely limited to the epipelagic and upper mesopelagic waters and were linked to phytoplankton biomass. At the shallower shelf sites, which did not extend beyond the mesopelagic, all populations declined proportionately more rapidly with depth than in other areas, although these faster rates reflected the high surface biomass and shallow mixed layers, with absolute numbers on average higher at depth than reported in our other areas. In contrast, deep slope site C18 had consistently proportionately high numbers at depth, which did not reflect elevated surface concentrations. The higher numbers found at depth at this site may have been the result of higher export rates or export from a high surface population which existed prior to our arrival. At some sites, we also observed secondary peaks in HNF and ciliate numbers, usually in the upper mesopelagic but occasionally much deeper. In the upper mesopelagic, these may reflect an export zone where reduced competition allows HNF and occasionally ciliates to form a secondary peak. Ciliate populations also occasionally showed substantial peaks at substantial depths, which again appear linked to export events with other biological parameters also elevated at these depths (including POC and flagellates). Slope site C18 at 1500 m and seamount site C31 between 500 and 590 m are the best examples.

Our relatively high microzooplankton numbers (both ciliates and HNF) in deeper waters may also be linked to the timing of our voyage in late summer, following high summer phytoplankton biomasses (chl *a* concentrations up to ~15 mg m^{-3}) (Dennett et al. 2001). Some studies have suggested that although HNF can be described as a function of phytoplankton surface biomass, this may not incorporate export events, which will lead to higher abundances being observed at depth (Tanaka & Rassoulzadegan 2002, Arístegui et al. 2005). It is also likely that some of the nanoflagellates we observed at depth are themselves part of the export process, as flagellates are known to bloom in the Ross Sea during summer (DiTullio & Smith 1996, Arrigo et al. 1999).

Although biomass per unit volume is expected to be highest in epipelagic waters, it is also recognised that because deeper mesopelagic and bathypelagic waters represent larger volumes, the total biomass at depth could be significant and may even exceed that of the epipelagic zone (Nagata et al. 2010, Sohrin et al. 2010). When we integrated total microzooplankton biomass, the HNF biomass in the mesopelagic and bathypelagic exceeded that in the epipelagic zone, while ciliate biomass in the mesopelagic also exceeded that found in the epipelagic. The discovery of these large pools of biomass at depth indicates that HNF and ciliates are likely to play a significant role in the microbial loop at depth, both by grazing and repackaging carbon for larger zooplankton grazers. These processes will also aid in recycling of sinking carbon (detritus) for bacterial consumption through sloppy grazing and excretion.

The majority of prey available at depth, beyond the productive photic/epipelagic zone, is assumed to be either bacterial or detrital in nature. We focused on bacterial population changes at depth and compared their relative rate of decline to HNF, as these were the dominant populations in our deeper waters. Bacterial biomass increased proportionally to microzooplankton biomass with depth, a result consistent with previous reports in other deeper waters (Tanaka & Rassoulzadegan 2002, Sohrin et al. 2010), including the subarctic. Sohrin et al. (2010) reported an HNF attenuation rate 1.7-fold steeper than that of bacteria and suggested this could lead to an accumulation of bacteria at depth due to low grazing pressure. Our results were less conclusive, as our HNF attenuation rates were only 1.1-fold steeper than for bacteria, indicating a lower potential for accumulation in our system and a larger potential for grazing pressure on bacteria even at depth at the time of our study.

Further complicating the role of microzooplankton in mesopelagic and bathypelagic waters is predation by zooplankton, with reports that microzooplankton can represent up to 90% of the diet of some Ross Sea zooplankton (Lonsdale et al. 2000). This again has implications for the role of microzooplankton in carbon cycling at depth, as it has recently been suggested that zooplankton affect carbon export by transporting grazed organic matter across depth zones by diel vertical migration (Steinberg et al. 2008). Our results suggest that there is a significant population of microzooplankton at depth in the Ross

Sea, and if this population is being grazed by zooplankton, there is potential for significant carbon transport back into the epipelagic zone. Overall, our results indicate that microzooplankton at depth may play an important role in both converting biomass (allowing remineralisation processes to occur) and repackaging biomass in a form available for larger, deep-water consumers.

CONCLUSIONS

Microzooplankton composition and biomass varied both among sites and with depth but usually reflected their available potential prey. In high-biomass, epipelagic waters, large phytoplankton and ciliates (and occasionally dinoflagellates) dominated, while in deeper waters (or low phytoplankton-biomass epipelagic zones), bacteria and HNF dominated. Deep microzooplankton populations, although similar, were often higher in abundance than those reported in other waters, indicating for the first time that during this summer-autumn transition period, the Ross Sea has a large pool of deep microzooplankton biomass. In deeper HNF-dominated waters, we found, as has been reported elsewhere, that the total integrated microzooplankton biomass exceeded that of the epipelagic zone. Our findings suggest that microzooplankton biomass in the Ross Sea during the summer autumn transition period is important not only in the epipelagic zone, as traditionally observed, but also in mesopelagic and bathypelagic waters. This group of organisms has the potential to aid in recycling and remineralisation of sinking biomass traditionally thought to be exported to the ocean floor.

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