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ORIGINAL PAPER

Mesozooplankton distribution patterns and grazing impacts of copepods and *Euphausia crystallorophias* in the Amundsen Sea, West Antarctica, during austral summer

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Abstract The rapid melting of glaciers as well as the loss of sea ice in the Amundsen Sea makes it an ideal environmental setting for the investigation of the impacts of climate change in the Antarctic on the distribution and production of mesozooplankton. We examined the latitudinal distribution of mesozooplankton and their grazing impacts on phytoplankton in the Amundsen Sea during the early austral summer from December 27, 2010 to January 13, 2011. Mesozooplankton followed a latitudinal distribution in relation to hydrographic and environmental features, with copepods dominating in the oceanic area and euphausiids dominating in the polynya. Greater *Euphausia crystallorophias* biomass in the polynya was associated with lower salinity and higher food concentration (chlorophyll *a*, choanoflagellates, and heterotrophic dinoflagellates). The grazing impact of three copepods (*Rhincalanus gigas*, *Calanoides acutus*, and *Metridia gerlachei*) on phytoplankton was low, with the consumption of 3 % of phytoplankton standing stock and about 4 % of daily primary production. Estimated daily carbon rations for each of the three copepods were also relatively low (<10 %), barely enough to cover metabolic demands. This suggests that copepods may rely on food other than phytoplankton and that much of the primary production is channeled through microzooplankton. Daily carbon rations for *E. crystallorophias* were high (up to 49 %) with the grazing impact accounting for 17 % of the phytoplankton biomass and 84 % of primary production. The presence of *E. crystallorophias* appears to be a critical factor regulating phytoplankton blooms and determining the fate of fixed carbon in the coastal polynyas of the Amundsen Sea.

Keywords Copepods · *Euphausia crystallorophias* · Polynya · Grazing impacts · Amundsen Sea

Introduction

A significant proportion of the primary production in the Southern Ocean is consumed by mesozooplankton, a numerically important group that plays a major role in Antarctic food webs (Ross et al. 2008; Swadling et al. 2010; Ducklow et al. 2012; Murphy et al. 2012). Grazing by mesozooplankton, especially copepods and euphausiids, is a key factor controlling the composition and dynamics of phytoplankton communities in the Southern Ocean (Pakhomov and Perissinotto 1997; Li et al. 2001; Pasternak and Schnack-Schiel 2001; Daly and Zimmerman 2004; Pakhomov and Froneman 2004; Tanimura et al. 2008). Mesozooplankton grazing may also control the composition and development of phytoplankton blooms (Dubischar and Bathmann 1997; Hernández-León et al. 2000; Pakhomov and Froneman 2004).

The consumption of primary production by mesozooplankton is linked to species distribution and growth, which in the Southern Ocean are governed by temperature, seasonal and permanent sea ice cover, and environmental variability (Atkinson 1998; Bathmann et al. 2000;

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Pinkerton et al. 2010). Numerous studies have documented mesozooplankton distribution in different locations in the Southern Ocean, including the marginal ice zone, the waters around oceanic islands, the Atlantic and Indian Ocean sectors, the Antarctic Peninsula, and in the vicinity of major oceanic fronts (the Sub-Antarctic Front and the Antarctic Polar Front) (Atkinson and Peck 1988; Bathmann et al. 1993; Hopkins et al. 1993; Atkinson et al. 1996; Pakhomov et al. 2000; Hunt and Hosie 2005; Fielding et al. 2007; Swadling et al. 2010; Ducklow et al. 2012). The distribution of mesozooplankton is generally determined by oceanographic fronts and currents and the associated dynamics of sea ice. At local scales, for example, in coastal polynyas or the marginal ice zone, mesozooplankton distribution is influenced more by the responses of major species to cycles in primary productivity, trophic interactions, and complex life strategies (Donnelly et al. 2006; Murphy et al. 2012). Mesoscale patches of high chlorophyll *a* (Chl *a*) concentration and extended periods of productivity often occur in frontal regions, coastal/neritic waters, the marginal ice zone, and polynyas (Smith and Gordon 1997; Moore and Abbott 2000; Arrigo and van Dijken 2003).

Polynyas are recurring areas of seasonally open water surrounded by sea ice and are an important part of the Antarctic marine system. Coastal polynyas are particularly common in the seas surrounding the Antarctic continent during late winter and early spring (Jacobs and Comiso 1989; Deibel and Daly 2007; Massom and Stammerjohn 2010). In spring, the diminishing sea ice cover allows light to penetrate into the surface layer of the ocean, triggering early microalgal blooms that form the basis of the marine food chain. Therefore, polynyas are likely to be habitats where early intense production of planktonic herbivores can translate into the transfer of organic matter fixed by planktonic microalgae (Deibel and Daly 2007).

A number of coastal polynyas exist in the Amundsen Sea. The Amundsen Sea is one of the most productive areas in the Southern Ocean (Arrigo et al. 2012; Fragoso and Smith 2012), and extensive phytoplankton blooms have been observed near the coast using satellite-based ocean color sensors (Smith and Comiso 2008; Arrigo et al. 2012). Primary production in the Amundsen Sea reaches 160 g C m^{-2} $year^{-1}$, and Chl *a* concentrations are >10 μg l^{-1} (Arrigo and van Dijken 2003). The high productivity in this region is mostly attributed to two polynyas, the Amundsen Polynya and the Pine Island Polynya (Arrigo et al. 2012). High rates of warming have been reported for the Amundsen Sea (Massom and Stammerjohn 2010; Schoof 2010) and the rapid retreat of sea ice in the area has been the focus of a number of studies (Jacobs and Comiso 1997; Arrigo et al. 2012). There has also been obvious melting of the Pine Island Glacier (Jenkins et al. 2010; Jacobs et al. 2011), thought to be driven by the intrusion of relatively warm Circumpolar Deep Water (CDW) along deeper shelf troughs leading to the basal ablation of floating ice (Walker et al. 2007; Wåhlin et al. 2010). Sea ice influences mesozooplankton distribution and production, and the rapid melting of glaciers and loss of sea ice will result in a change in habitat conditions that may force substantial changes in mesozooplankton. To predict the impact of these changes on the ecosystem, it is important to understand the dynamics of the mesozooplankton community. However, to date, few studies have been published on the distribution and grazing impacts of mesozooplankton in the Amundsen Sea.

The primary objectives of this study were to describe the mesozooplankton community in the Amundsen Sea and to investigate the linkages between major environmental factors (seawater temperature, salinity, and Chl *a* concentration), protozoa, and the mesozooplankton community in the polynya and non-polynya areas. We also examined the grazing impacts of major copepods and *Euphausia crystallorophias* on the phytoplankton biomass in the polynya and non-polynya areas. This study presents the first detailed description of mesozooplankton communities and their grazing impacts in the Amundsen Sea during the early austral summer.

Materials and methods

Study area and hydrography

The Amundsen Sea is the part of the Southern Ocean located off Marie Byrd Land between 100° and 135°W (Fragoso and Smith 2012). It is historically known as a region with a relatively narrow continental shelf and a number of coastal polynyas located adjacent to large ice shelves. Sea ice extent in the Amundsen Sea has been decreasing over the last few decades (Arrigo and van Dijken 2003; Arrigo et al. 2012).

A multi-disciplinary survey was conducted on board the Korean icebreaker RV Araon in the Amundsen Sea between 64° and 74°S during the early austral summer from December 27, 2010 to January 13, 2011 (Fig. 1). Vertical profiles of seawater temperature and salinity were obtained using a CTD-Rosette system (SBE-911 plus, SeaBird Electronics) from the surface to a depth of 200 m at each sampling station. For Chl *a* concentration analysis, water samples were collected at each station at 6–8 depths (5, 10, 20, 40, 60, 80, 100, and 150 m). These samples were then fractionated into three size categories [total plankton, nanoplankton (<20 μm), and picoplankton (<5 μm)], by passing the water sample sequentially through 20- and 5-μm polycarbonate membrane filters (47 mm diameter) and Whatman GF/F filters (47 mm diameter) to obtain size-

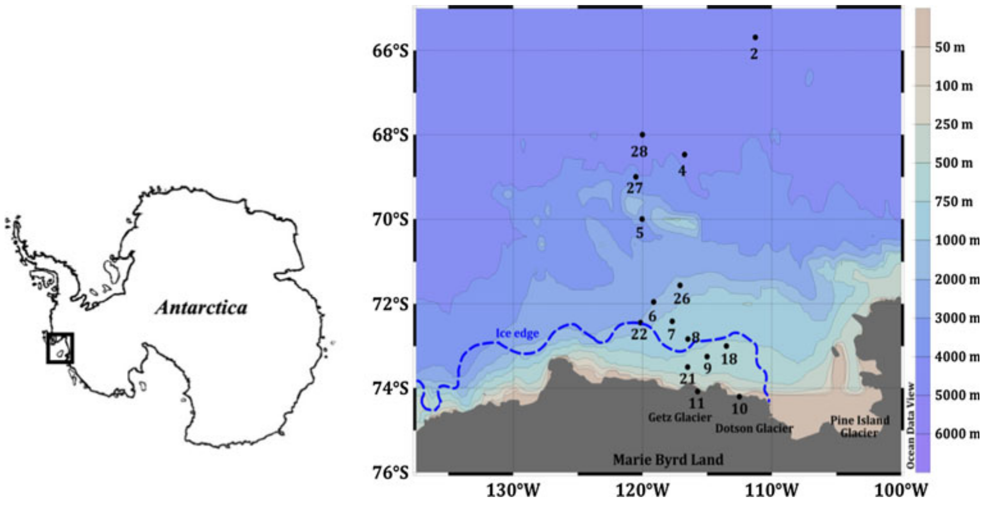

Fig. 1 Map of sampling sites in the Amundsen Sea. The *blue dashed line* indicates sea ice concentrations of approximately 10 %. (Color figure online)

fractionated samples of 200–1,000 ml. Concentrations of Chl *a* were measured on board using a Turner Designs Trilogy fluorometer, after extraction with 90 % aqueous acetone (Parsons et al. 1984).

Field sampling and analysis of protozoa and mesozooplankton

The samples for protozoa were collected from the surface water using a Rosette sampler. Water samples of 500 ml for choanoflagellates (CNF) and heterotrophic dinoflagellates (HDF) were preserved with glutaraldehyde (1 % final concentration) and stored at 4 °C before staining and filtration. Subsamples of 50 ml for CNF and 300 ml for HDF were filtered onto black 0.8-μm and 8-μm Nucleopore filters, respectively, and stained with proflavin (0.33 %) and 4′-6-diamidino-2-phenylindole (DAPI; 50 μg ml^{-1} final concentration). The samples were examined under an epifluorescence microscope (Nikon type 104) at 300–1,000× magnification. Heterotrophic dinoflagellates were examined under both UV and blue excitation wavelengths to distinguish autofluorescence of chlorophyll and other pigments, with at least 50 fields counted. Samples for ciliates were prepared by adding acid Lugol's iodine (5 % final concentration) into 250 ml of seawater and were stored in the dark until analysis. Subsamples of 50–100 ml preserved in Lugol's solution were concentrated in sedimentation chambers for ≥48 h, and the extract was examined with an inverted microscope (Olympus IX 70) at 100–200× magnification.

The carbon biomass of protozoa was estimated using cell volume to carbon biomass conversions. The factors and equations used to convert cell volume to carbon biomass were as follows: 220 fg C m^{-3} for CNF (Børsheim and Bratbak 1987), 0.19 μg C μm^{-3} for naked ciliates (Putt and Stoecker 1989), carbon (pg) = 44.5 + 0.053 × lorica volume (μm^3) for loricate ciliates (Verity and Lagdon 1984), and carbon (pg) = 0.216 × (volume, $\mu\text{m}^3)^{0.939}$ for HDF (Menden-Deuer and Lessard 2000).

Mesozooplankton samples were collected with a Bongo net (mesh apertures 330 and 505 μm) at 15 selected stations. The net was towed twice vertically or obliquely within the upper 200 m of the water column. Tow speed and duration were about 1.5–2 knots and 15–20 min, respectively. Samples from the first tows were immediately fixed and preserved with buffered formaldehyde (pH 8, final concentration ~5 %) for quantitative analyses. Mesozooplankton abundance and biomass were analyzed from samples obtained from the first tow with the 330-μm mesh net. Subsampling was carried out using a Folsom plankton splitter, and mesozooplankton were examined to the lowest taxonomic level possible under a dissecting microscope using a Bogorov tray. Abundance was expressed in terms of individual numbers per cubic meter (ind. m^{-3}) using volume filtered by the net, obtained from the revolution counts of a flow meter attached to the net.

Healthy individuals from the samples obtained during the second tows of both 330- and 505-μm nets were transferred to 10-l polycarbonate carboys filled with natural seawater. The animals were immediately transferred into 20-ml vials containing filtered seawater, which were frozen at −80 °C for later gut content analysis (Båmstedt et al. 2000).

Gut pigment contents and ingestion rates of copepods and *E. crystallorophias*

For gut content analyses, we chose a euphausiid, the dominant mesozooplankton in the polynya, and three numerically dominant copepods with different life cycle strategies as defined by Atkinson (1998): (1) *Metridia* *gerlachei* exhibiting an omnivorous/detritivorous diet, (2) *Calanoides acutus* behaving as an herbivore during summer, and (3) *Rhincalanus gigas* thought to have an intermediate strategy between (1) and (2).

Adult females of the four species (*R. gigas*, *C. acutus*, *M. gerlachei*, and *E. crystallorophias*) were sorted from the frozen samples as rapidly as possible in the laboratory. Three replicate samples of about 15–20 individuals for copepods (*R. gigas*, *C. acutus*, and *M. gerlachei*) and 1–2 individuals for *E. crystallorophias* were used for gut fluorescence analyses. Gut contents from the animals were extracted in centrifuge tubes containing 8 ml of 90 % acetone stored at 4 °C in the dark for 24 h. The fluorescence of the extract was measured using a Turner Designs Trilogy fluorometer before and after acidification with 2–3 drops of 10 % HCl. The Chl *a* and phaeopigment contents of each copepod species were calculated following the method described by Strickland and Parsons (1972). The gut pigment contents were determined by directly summing these two values and were expressed as ng Chl *a* eq. ind.$^{-1}$ (Dam and Peterson 1988; Head and Harris 1992). Grazing rates (ng Chl *a* eq. ind.$^{-1}$ day^{-1}) were calculated as the product of gut pigment content and the inverse of gut passage time (gut evacuation rate). We adopted the gut evacuation rate constant (k^{-1}) of 0.68 h and 0.77 h for *R. gigas* and *C. acutus*, respectively (Tirelli and Mayzaud 1999), 0.39 h for *C. acutus* copepodite V (Atkinson et al. 1992), 0.68 h for *M. gerlachei* (Li et al. 2001), and 0.44 h for *E. crystallorophias* (Pakhomov and Perissinotto 1996). The daily carbon ration (% body C day^{-1}) was calculated using the equation developed by Atkinson (1996). For the calculation, the carbon:chlorophyll ratio (C:Chl *a*) was assumed to be 50, and the carbon weights of the copepods were assumed to be 45 % of dry mass (Atkinson 1996). The in situ grazing impacts of adult females were calculated by multiplying individual ingestion rates with the corresponding species abundances and were expressed as the percentage of depth-integrated daily primary production.

Statistical analyses

Pearson's correlation analysis and *t* tests were performed to examine the relationships among the parameters of mesozooplankton abundance, biomass, and grazing rate, and seawater temperature, salinity, Chl *a* concentration, and protozoan carbon biomass. Statistical analyses were conducted using the SAS version 9.1.3 software package (SAS Institute Inc. 2005). Non-metric multidimensional scaling (NMDS), an ordination method based on the rank of order, was performed on the species abundance data to investigate the similarity among the sampling sites and to identify the environmental factors influencing the spatial pattern of the mesozooplankton community. Square-root transformation followed by Wisconsin double standardization was performed on the mesozooplankton abundance data, and Bray-Curtis dissimilarities were calculated (Oksanen 2008). NMDS analyses were performed using R, an object-oriented open-source program (R Development Core Team 2006).

Results

Hydrography and trophic conditions

Antarctic Surface Water (AASW) occupied the surface layer to the temperature minimum layer at about 80 m in the oceanic areas (St. 2, 4, 5, 27, and 28), and the layer below that was influenced by Circumpolar Deep Water (CDW) (Fig. 2a). The oceanic area was dominated by relatively warm water (−1.7 to 1.9 °C, mean = −0.5 °C). A colder water mass (−1.8 to −1.1 °C) extended from surface to 200 m in the transitional areas (St. 6, 7, 8, 22, and 26) (Fig. 2c). In the polynya (St. 9, 10, 11, 18, and 21), seawater temperatures decreased with depth but the temperature in the surface layer was higher than the surface temperature in both oceanic and transitional areas (Fig. 2e). Salinity was largely determined by melt from sea ice, resulting in regional differences. At all stations, salinity increased with water depth (Fig. 2b, d, f), but there was a pronounced halocline layer between 10 and 30 m in the transitional area, with little vertical change below the halocline (Fig. 2d). The vertical structure of temperature and salinity indicates the intrusion of relatively warm CDW along deeper shelf troughs (Fig. 2a, d), consistent with the findings of previous studies in the region (Walker et al. 2007; Wåhlin et al. 2010; Fragoso and Smith 2012).

Chl *a* concentrations varied across the stations with higher Chl *a* concentrations of all size fractions (total, nano, and pico) observed in the polynya (Fig. 3a). The highest Chl *a* concentration (total = 5.4 μg l^{-1}, nano = 3.8 μg l^{-1}, pico = 1.6 μg l^{-1}) was observed at St. 9 in the polynya area. The contribution of picophytoplankton to total Chl *a* concentration was greatest in low phytoplankton biomass waters, reaching as high as 70 %, but rapidly decreasing to <40 % when the total Chl *a* concentration was >1 μg l^{-1} (Fig. 3b). In the transitional area, Chl *a* concentration increased toward the inner part of the continental slope.

Based on sea ice concentration (Fig. 1) and multidimensional analysis of environmental factors (seawater temperature, salinity, and Chl *a* concentration), sampling stations were classified into three groups: polynya (St. 9, 10, 11, 18, and 21), transitional (St. 6, 7, 8, 22, and 26), and oceanic (St. 2, 4, 5, 27, and 28). The oceanic area was defined by relatively warm (−1.7 to 1.9 °C, mean = −0.5 °C) and salty

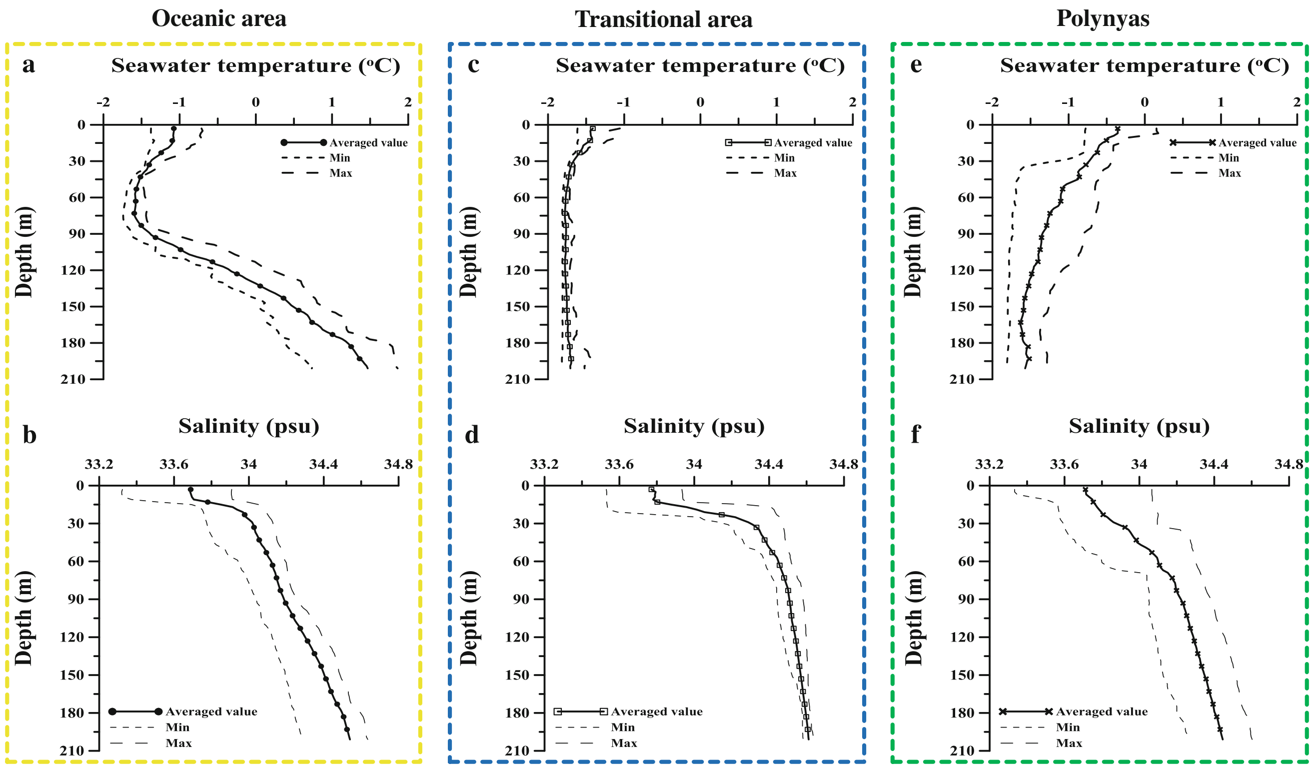

Fig. 2 Vertical profiles of seawater temperature and salinity in the upper 200 m of the water column for **a**, **b** oceanic area (St. 2, 4, 5, 27, and 28), **c**, **d** transitional area (St. 6, 7, 8 22, and 26), **e**, **f** polynyas (St. 9, 10, 11, 18, and 21)

(33.0–34.6, mean = 34.1) water, and low Chl *a* concentrations (0.18–0.24 μg l^{-1}, mean = 0.21 μg l^{-1}). The transitional area was defined by cold water (−1.8 to −1.1 °C, mean = −1.7 °C), intermediate salinities (33.6–34.1, mean = 34.0), and intermediate Chl *a* concentrations (0.24–1.89 μg l^{-1}, mean = 0.70 μg l^{-1}). The polynya area was defined by intermediate seawater temperatures (−1.8 to 0.2 °C, mean = −1.3 °C), intermediate salinities (33.7–34.1, mean = 34.0), and high Chl *a* concentrations (1.62–5.39 μg l^{-1}, mean = 3.56 μg l^{-1}).

Total protozoan biomass displayed a latitudinal variation with a decreasing trend toward the oceanic area, similar to that of phytoplankton, but the latitudinal patterns were different among various protozoan groups. The biomass of ciliates was similar between the polynya (9.4 ± 6.2 μg C l^{-1}) and non-polynya areas (transitional and oceanic areas, 9.5 ± 11.3 μg C l^{-1}; *t* test, $p > 0.05$), with the highest ciliate biomass observed at St. 6 and 7, in the transitional area between the polynya and oceanic area (Fig. 4a). However, biomasses of both HDF and CNF were greatest in the polynya (*t* test, $p < 0.05$; Fig. 4b, c). The HDF biomass was highest at St. 18, off the coastal zone, with a very low value in coastal waters, whereas the biomass of CNF was highest at St. 9 in the inner waters of the polynya area and declined sharply over the continental slope (Fig. 4c). The biomass was dominated by HDF in polynya and non-polynya areas, accounting for 71.0 and 64.3 %, respectively, of the total protozoan biomass, followed by CNF, which accounted for 11.5 and 5.0 %, respectively.

Mesozooplankton community

We used a 330-μm mesh net for mesozooplankton sampling; therefore, small mesozooplankton (e.g., *Oithona* and the copepodites and nauplii of large copepods) would have been under-sampled. Relatively large mesozooplankton are better represented, and this is inherent within our subsequent analyses.

A total of 32 mesozooplanktonic taxa were identified, including 19 copepod species (Table 1). Copepods accounted for 56 % of total mesozooplankton abundance, followed by *E. crystallorophias* (19 %), consisting mostly of juveniles. Chaetognaths (*Sagitta* spp.) and the tunicates (*Oikopleura* spp.) represented 4 and 5 % of total mesozooplankton abundance, respectively.

Latitudinal distribution patterns for mesozooplankton across the sampling zones (polynya, transitional, and oceanic) were apparent (Fig. 5). *Oithona* spp., *Drepanopus* spp., *R. gigas*, *Calanus propinquus*, *Scolecithricella minor*, and a crustacean nauplius, known to be herbivorous and/or omnivorous (Atkinson 1998), were found mainly in the

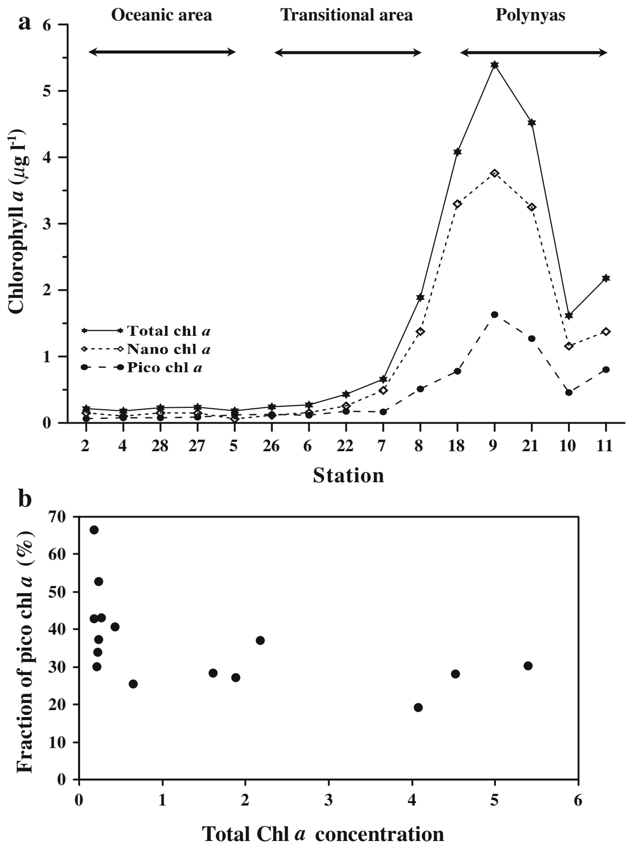

Fig. 3 Spatial distribution of **a** depth-averaged size-fractionated Chl *a* concentration and **b** contribution of picophytoplankton to total Chl *a* concentration

oceanic area. *M. gerlachei*, *Paraeuchaeta antarctica*, *Oncaea antarctica*, Hydrozoa, and *Oikopleura* spp. were more abundant in the transitional area. Copepods belonging to this group are known to be carnivorous and/or omnivorous (Atkinson 1998). The abundance of each major mesozooplankton taxon (>1 % of total mesozooplankton abundance) was significantly different (*t* test, $p < 0.05$ for all analyses) between polynya and non-polynya areas except for *C. acutus*, *P. antarctica*, and *E. crystallorophias*.

Euphausia crystallorophias, including the early life stages (eggs and nauplii), were most abundant in the polynya area (*t* test, $p < 0.05$; Fig. 6). The highest density of larvae (27 ind. m^{-3}) was found at St. 10, in the innermost part of the polynya. The abundance of adult *E. crystallorophias* ranged from 0.1 to 1.6 ind. m^{-3} and showed no significant spatial difference, but the furcilia stage of *E. crystallorophias* was found only at St. 2 and 8.

The distribution of the biomass of seven copepods followed the spatial patterns of abundance (Fig. 5) with greater biomass recorded in the non-polynya areas (*t* test, $p < 0.05$; e.g., *Oithona* spp., *Drepanopus* spp., *R. gigas*, *C. propinquus*, *M. gerlachei*, and *O. antarctica*; Fig. 7). However, the total biomass of major crustacean species was higher in the polynya area (30.4 ± 25.6 mg m^{-3}) than in transitional and oceanic areas (8.1 ± 5.9 mg m^{-3}, *t* test, $p < 0.01$) (Table 2), because *E. crystallorophias* accounted

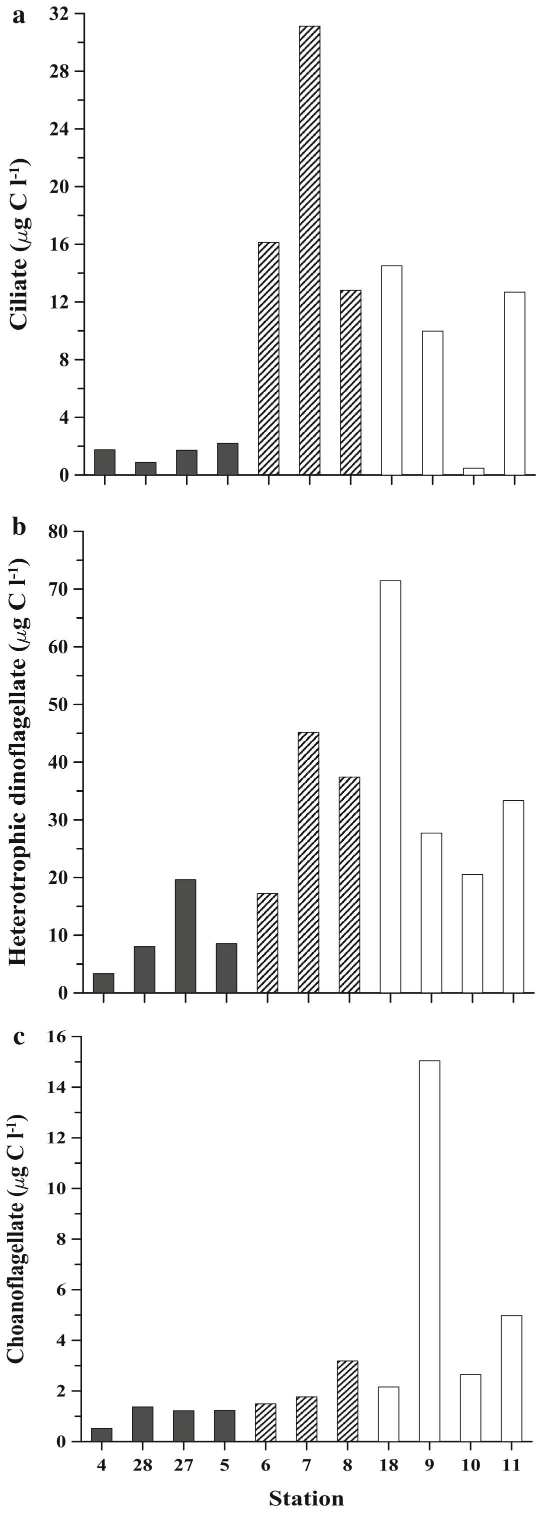

Fig. 4 Latitudinal distribution of protozoan biomasses. The *different bars* represent the three areas: polynya (*empty*), transitional (*shaded*), and oceanic (*filled*)

Table 1 Abundance (ind. m^{-3}) and composition (Com, %) of mesozooplankton at sample stations in the Amundsen Sea

Taxon	Station															Com (%)
	2	4	28	27	5	26	6	22	7	8	18	9	21	10	11	
C. acutus	28	1	1	1	6	7	5	13	9	7	2	11	9	5	12	19
R. gigas	3	2	1	1	1	<1				<1						1
C. propinquus		<1	<1	2	2	<1	<1	<1	<1				<1			1
Calanus simillimus	1		<1											<1		<1
M. gerlachei		2	1	1	6	9	3	7	5	2	1	2	3	1	1	7
Oithona spp. (mainly *similis*)	68	5	8	7	2	2	2	1	1	<1	<1	<1	<1	<1		15
P. antarctica	<1	1	2	2	3	6		6	5	4	<1	4	<1	3	1	6
O. antarctica	<1	1	<1	1	2	6	3	2	<1		<1					3
Racovitzanus antarcticus					<1	<1		<1								<1
Haloptilus oxycephalus		<1	<1	<1	<1		<1									<1
Heterohabdus austrinus					<1											<1
Paralabidocera antarctica	<1		<1	<1												<1
Drepanopus spp.	6	1	1	2	2	2	1	1	1	<1	<1	<1	<1	1	<1	3
Stephos longipes			<1	<1		<1	<1		<1							<1
S. minor	1	<1	<1	1	1			<1			<1					1
Microcalanus pygmaeus		<1	<1	<1	<1	<1	<1	<1	<1					<1		<1
C. laticeps	1			<1												<1
Scaphocalanus antarctica				<1												<1
Eucalanus longiceps																<1
Crustacean nauplii	42	<1	<1	<1	<1			<1	<1		<1	<1	<1			7
Euphausiids	8	1	2	4	1	4	1	1	2	18	12	18	3	27	15	19
Amphipoda	<1				<1	<1	<1	<1		<1			<1		<1	<1
Dcapoda larvae														<1		<1
Cirripedia larvae							<1		<1					<1		<1
Ostracoda		<1		<1	<1	1		1	<1	<1	1	<1	<1	1	1	1
Sagitta spp.	8	3	6	4	2	2	<1	1	<1		<1			<1		4
Polychaeta larvae	1	<1	1	<1	<1	1	<1	1	<1	1	<1		<1	<1	<1	1
Hydrozoa	<1	<1	<1	<1	<1	1	3	3	5	3	1	2	1	2	1	4
Gastropoda larvae		<1		<1	<1			<1	<1		<1	<1			<1	<1
Oikopleura spp.	2	1		<1	1	11	1	12	1							5
Fish larvae		<1		<1		<1			<1				<1		<1	<1
Foraminifera	2	1	6	1	<1	3	<1	1	<1	<1	<1		<1		<1	2
Total	173	20	30	29	30	55	21	51	29	36	18	37	17	41	33	100

for 91 % of the total crustacean biomass in the polynya area. With euphausiids excluded, the biomass was not significantly different between the polynya and non-polynya areas (*t* test, $p > 0.05$).

The combined biomass of the four major taxa (*R. gigas*, *C. acutus*, *M. gerlachei*, and euphausiids) that made up 99 % of the total biomass of major crustacean species was positively correlated with the Chl *a* concentration of the pico-sized fraction ($r = 0.53$, $p < 0.05$), but not with the total Chl *a* concentration or the Chl *a* concentration of the nano-sized fraction. The biomass of the copepod *C. acutus* was positively correlated with CNF ($r = 0.65$, $p < 0.05$) and the Chl *a* concentration of the pico-sized fraction ($r = 0.55$, $p < 0.05$), but not with other protozoan biomasses.

The NMDS analysis effectively characterized the spatial differences in the mesozooplankton community and the environmental parameters contributing to the heterogeneity (Fig. 8). The polynya area was clearly distinguished from the non-polynya areas (transitional and oceanic) along dimension 1, with the continental shelf stations positioned between the oceanic area and the polynya. NMDS revealed two distinctly clustered groups of mesozooplankton taxa (Fig. 8). The mesozooplankton occupying the right of the NMDS plot corresponding to the polynya included *E. crystallorophias*, *P. antarctica*, *C. acutus*, Hydrozoa, and

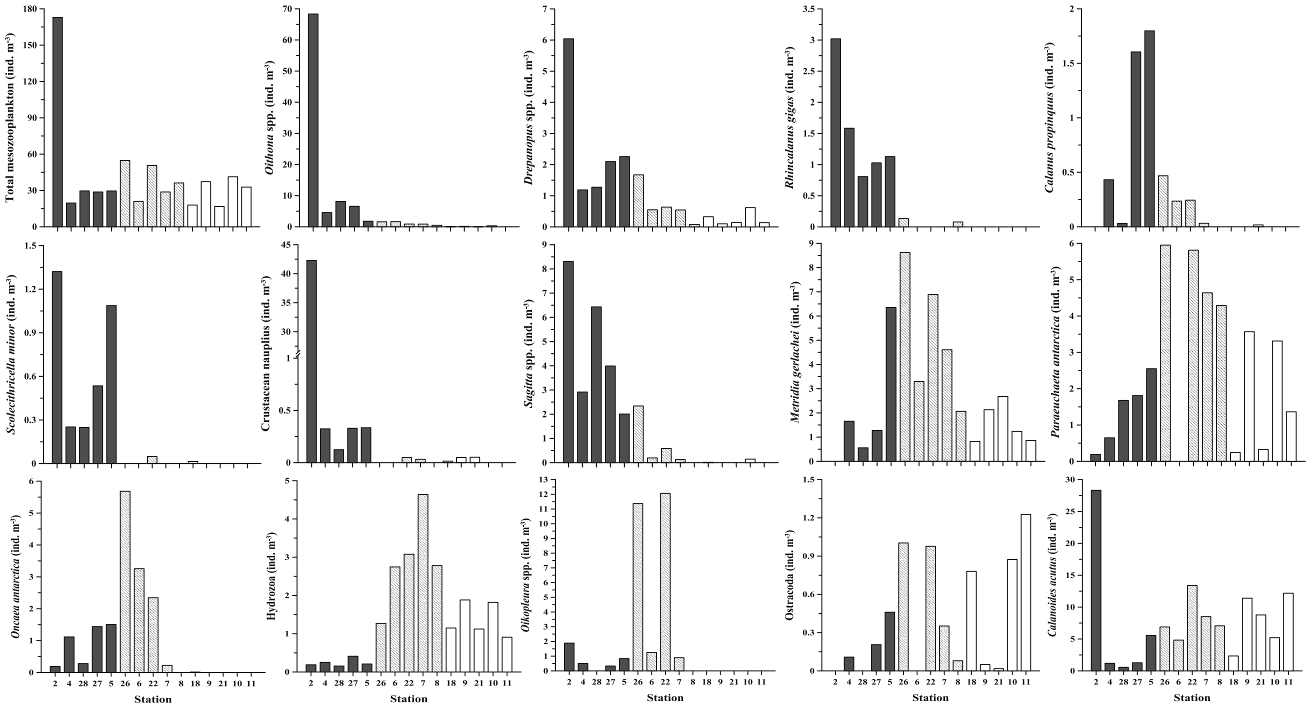

Fig. 5 Latitudinal distribution of mesozooplankton abundance. The *different bars* represent the three areas: polynya (*empty*), transitional (*shaded*), and oceanic (*filled*)

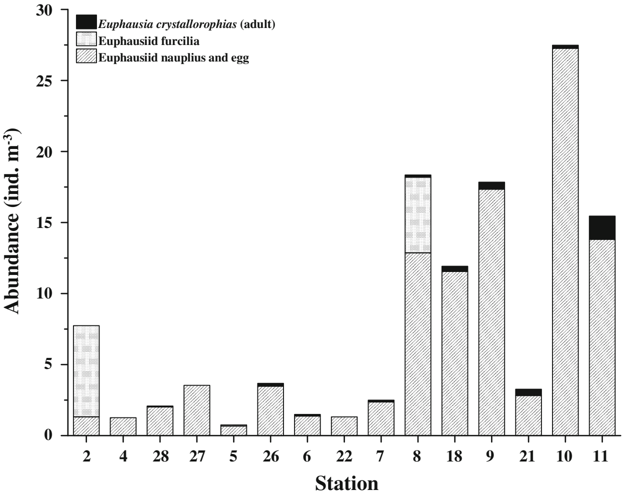

Fig. 6 Latitudinal distribution of *E. crystallorophias* abundance

Ostracoda, the taxa that were found to be more abundant in the polynya area. The taxa occupying the upper left of the NMDS plot were those found to be more abundant in the non-polynya areas, including *R. gigas*, *Oithona* spp., *Clausocalanus laticeps*, *S. minor*, and *Sagitta* spp. Of all parameters included in the analysis, only total Chl *a* concentration, CNF biomass, HDF biomass, and salinity were significantly correlated with the NMDS dimensions. The NMDS configuration shown in Fig. 8 illustrates the relationship between water types (polynya vs. non-polynya) and associated environmental parameters. The polynya stations were associated with lower salinity and higher food concentration. Our preliminary correlation analysis indicated that water temperature might be a contributing factor; however, this was not picked up by the NMDS, probably as a result of the narrow range of ambient temperatures in our study.

Grazing rates and daily carbon rations of copepods and *E. crystallorophias*

Gut pigment contents and grazing rates of *R. gigas* ranged from 0.6–2.0 ng Chl *a* eq. ind.$^{-1}$ (mean = 1.1 ± 0.6) and from 19.9–69.5 ng Chl *a* eq. ind.$^{-1}$ day^{-1} (mean = 38.0 ± 22.1), respectively (Fig. 9a). The values at St. 26 and 27 were approximately two times higher than values at other stations. Gut pigment contents of *C. acutus* and *C. acutus* copepodite V were similar within the non-polynya area, but the value for *C. acutus* copepodite V was significantly higher than that for *C. acutus* in the polynya area (*t* test, $p < 0.01$). The grazing rate of *C. acutus* copepodite V was higher than that for *C. acutus* at all experimental stations (Fig. 9b). Gut pigment contents and grazing rates of *M. gerlachei* were between 0.5–5.5 ng Chl *a* eq. ind.$^{-1}$ and 16.5–194.8 ng Chl *a* eq. ind.$^{-1}$ day^{-1}, respectively. The highest values were recorded at St. 7 (Fig. 9c). Gut pigment contents and grazing rates of *E. crystallorophias* varied from 4.8 to 141.5 ng Chl *a* eq. ind.$^{-1}$, and from 259.3 to 7,640.4 ng Chl *a* eq. ind.$^{-1}$ day^{-1}, respectively, with highest values recorded at St. 10 (Fig. 9d). Correlation

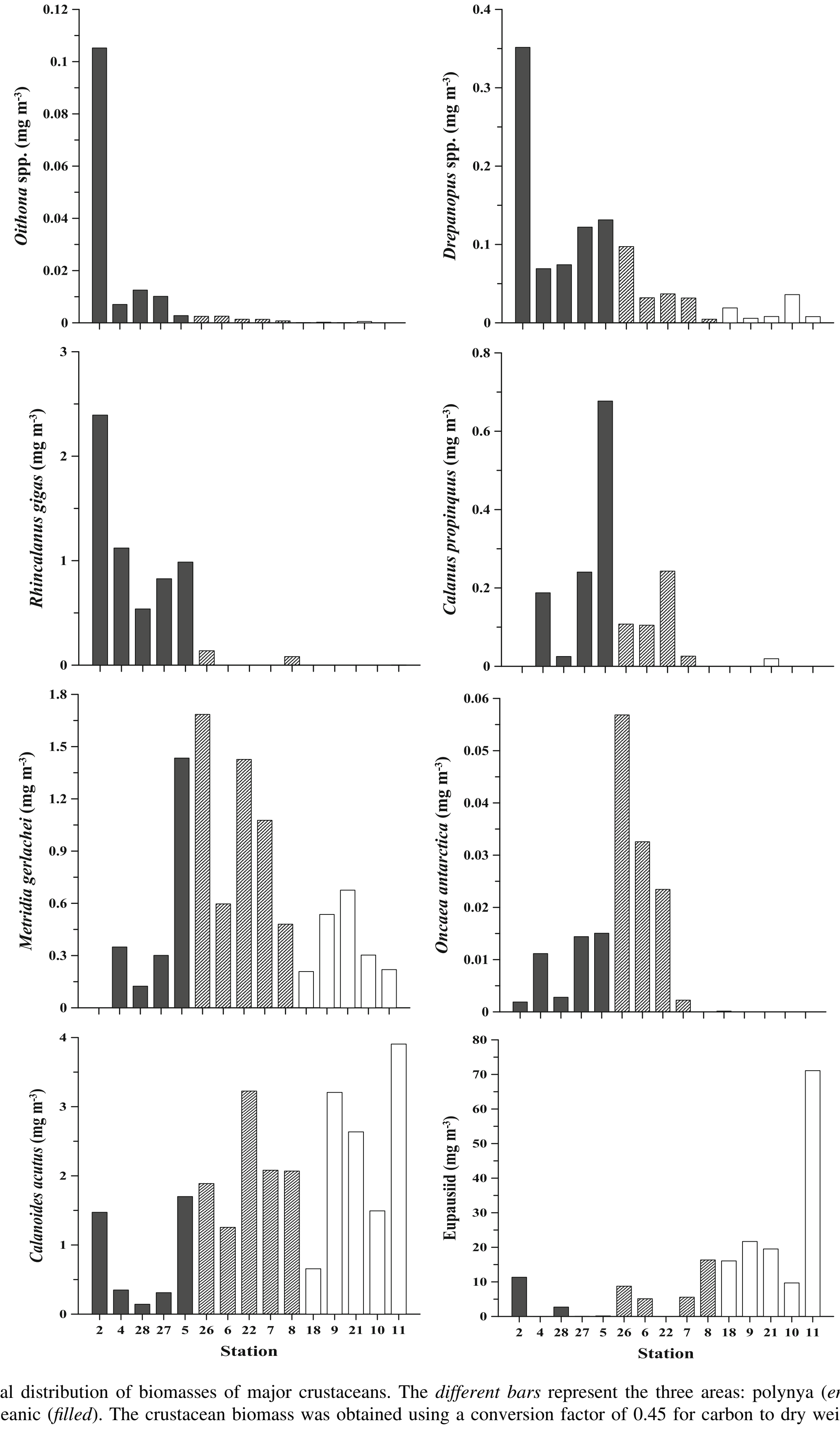

Fig. 7 Latitudinal distribution of biomasses of major crustaceans. The *different bars* represent the three areas: polynya (*empty*), transitional (*shaded*), and oceanic (*filled*). The crustacean biomass was obtained using a conversion factor of 0.45 for carbon to dry weight

Table 2 Comparison of relative contributions (%) of major crustacean biomasses (mg m^{-3}) between polynya and non-polynya areas in the Amundsen Sea

Taxon	Polynya		Non-polynya	
	Mean	SD	Mean	SD
C. acutus	2.38	1.31	1.45	0.97
R. gigas			0.87	0.78
C. propinquus	0.02		0.20	0.21
M. gerlachei	0.39	0.21	0.83	0.58
Oithona spp.	<0.01	<0.01	0.01	0.03
O. antarctica	<0.01		0.02	0.02
Drepanopus spp.	0.02	0.01	0.10	0.10
Euphausiids	27.61	24.73	5.01	5.64
Total	30.40	25.63	8.10	5.89

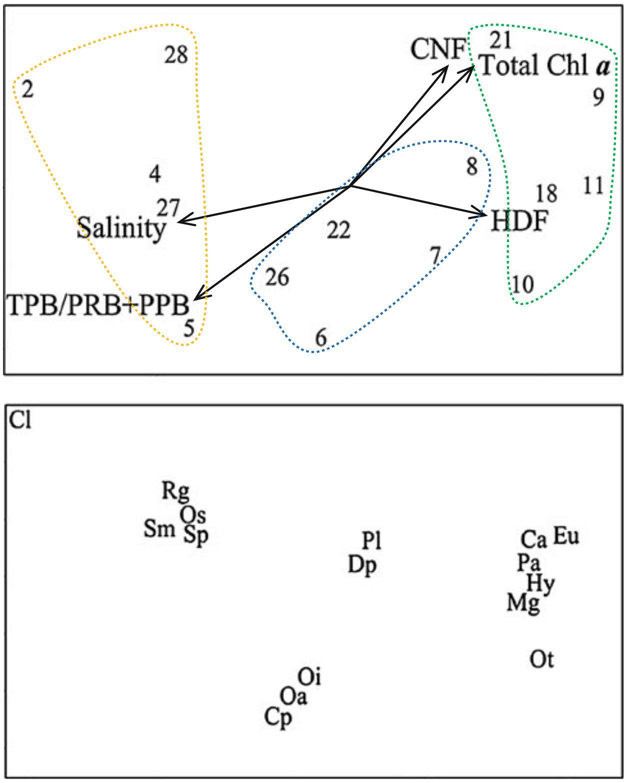

Fig. 8 Non-metric multidimensional scaling (NMDS) analysis of the 13 major taxa and sites related to environmental parameters contributing to the heterogeneity. *HDF* Heterotrophic dinoflagellate, *TPB* total protozoan biomass, *PRB* protozoan biomass, *PPB* phytoplankton biomass (*Cl C. laticeps*, *Rg R. gigas*, *Os Oithona* spp., *Sm S. minor*, *Sp Sagitta* spp., *Pl* Polychaeta larvae, *Dp Drepanopus* spp., *Oi Oikopleura* spp., *Oa O. antarctica*, *Cp C. propinquus*, *Eu* Euphausiids, *Ca C. acutus*, *Pa P. antarctica*, *Hy* Hydrozoa, *Mg M. gerlachei*, *Ot* Ostracoda). *Yellow dashed line* oceanic area, *blue dashed line* transitional area, *green dash line* polynya. Stress value = 0.08. (Color figure online)

analysis revealed that of the environmental factors (seawater temperature, salinity and Chl *a* concentration), estimated grazing rates of *C. acutus* and *C.acutus* copepodite V were significantly related to Chl *a* concentration (Table 3). No significant relationship was detected for any of the other copepods for any of the environmental parameters.

Daily carbon rations as a percentage of the total carbon mass of the organism and grazing impact by three copepods and *E. crystallorophias* on phytoplankton are summarized in Table 4. *R. gigas* had the lowest daily carbon ration as a percentage of the carbon mass of the organism, and *C. acutus* copepodite V had a higher daily carbon ration as a percentage of the carbon mass of the organism than the adult females. The value of the daily carbon ration for *E. crystallorophias* was highly variable but higher than the value for the copepods. Daily grazing impact with respect to primary production was calculated based on daily phytoplankton primary production rates at the stations (St. 2, 4, 5, 9, 18, and 27) where production rates varied between 8.7 and 2,277.4 mg C m^{-2} day^{-1} (Lee et al. 2012). The daily grazing impact of the three copepods was highest at St. 27 in the oceanic area. A very high value for the grazing impact of *E. crystallorophias* (>100 % of daily primary production) was observed at St. 10 in the polynya area, probably related to a combination of relatively lower productivity of phytoplankton and a higher grazing rate.

Discussion

Distribution patterns of copepods and euphausiids in relation to environmental factors

The high phytoplankton, protozoa, and major crustacean biomasses found in the polynya area in this study highlight the importance of polynyas in the Amundsen Sea ecosystem. Our results are consistent with previous studies that also found that the highest productivity occurred in coastal polynyas and other coastal zones in the Southern Ocean (Arrigo and van Dijken 2003; Smith and Comiso 2008; Arrigo et al. 2012). The range of phytoplankton productivity found in our study was comparable to that found in the Ross Sea (Lee et al. 2012), the area with the highest productivity among all polynyas in the Southern Ocean (Smith and Gordon 1997). Our results for mesozooplankton abundance (range 17–173 ind. m^{-3}, mean = 41 ± 38 ind. m^{-3}) and biomass (range 1.9–75.2 mg m^{-3}, mean = 15.5 ± 18.1 mg m^{-3}) were also similar to the levels (2.1–212 ind. m^{-3}, 1.2–91.5 mg m^{-3}) observed along a transect between the Antarctic continent and Cape Town in the Atlantic sector of the Southern Ocean using an identical mesh size (Pakhomov et al. 2000). The mesozooplankton biomass in our study area was higher than the 1–12 mg m^{-3} found in the Weddell Sea, the Ross Sea, and the Prydz Bay region of the Southern Ocean (Hosie et al. 1988; Boysen-Ennen et al. 1991; Pakhomov and

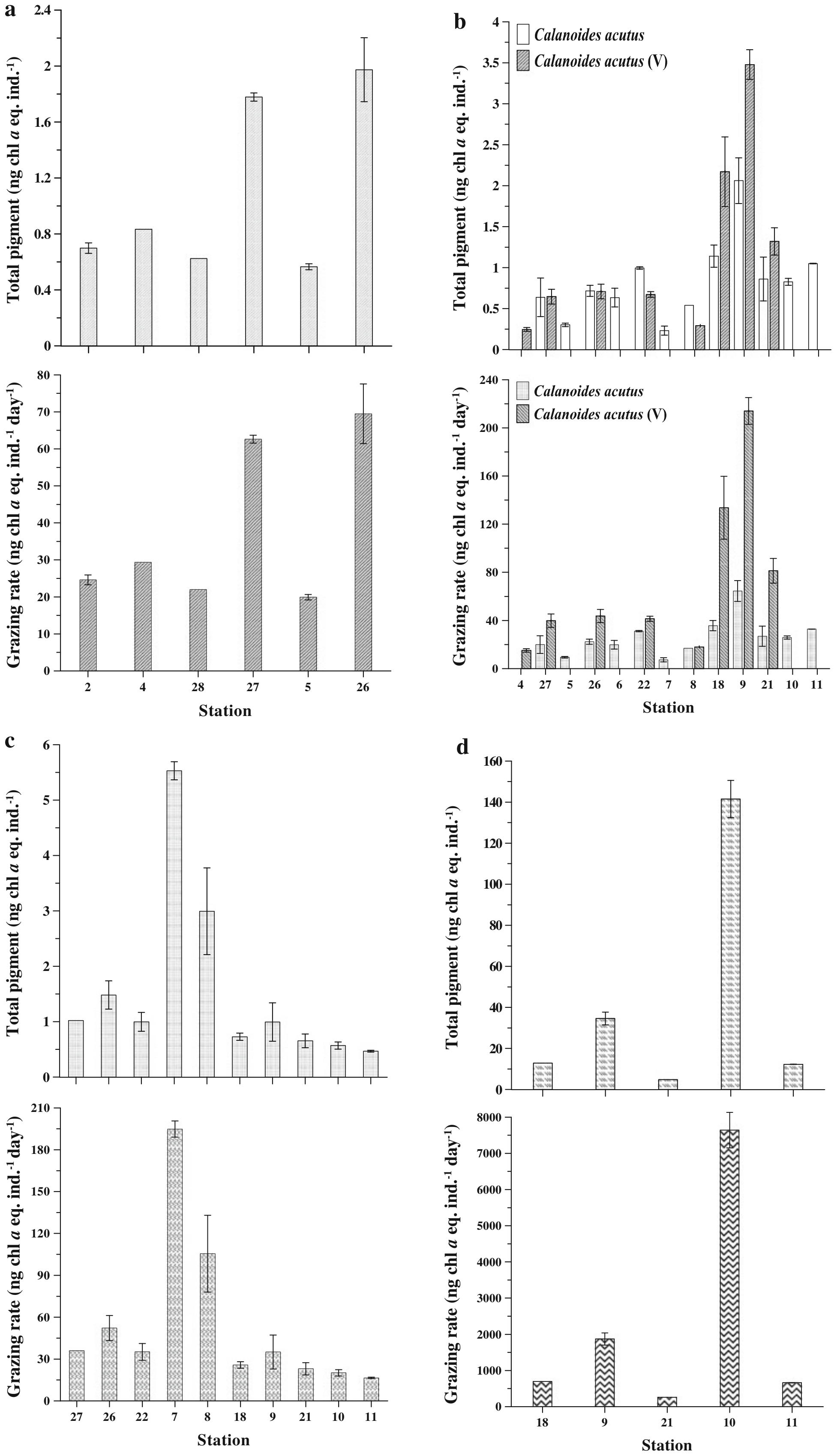

Fig. 9 Spatial distribution of gut pigment content and grazing rate of three copepods and *E. crystallorophias* **a** *R. gigas*, **b** *C. acutus* and *C. acutus* V, **c** *M. gerlachei*, **d** *E. crystallorophias*. *Vertical bars* indicate standard deviations and the absence of *vertical bars* indicates lack of replicate measurements

Perissinotto 1996). The biomass of adult *E. crystallorophias,* when it occurred in high densities close to the ice shelf of the Ross Sea (Sala et al. 2002), was higher (0.1–474 mg m^{-3}) than our values. Mesozooplankton abundance was generally low, but comparable to abundance reported in previous studies of different parts of the Southern Ocean (Table 1; Fig. 5; Hosie et al. 2000; Ward et al. 2004; Hunt and Hosie 2006; Swadling et al. 2010; Takahashi et al. 2010). Pakhomov et al. (1998) reported that swarms of *E. crystallorophias* were not observed in the Lazarev Sea, but the presence of high numbers in their Bongo net samples suggests *E. crystallorophias* was abundant during the austral spring.

Table 3 Correlation coefficients (*r*) between the grazing rates (ng Chl *a* eq. $ind.^{-1}$ day^{-1}) of three copepods and *E. crystallorophias*, and size-fractionated Chl *a* concentration in the Amundsen Sea

Species	Correlation coefficients (r)		
	Total chl *a* (μg l^{-1})	Nano chl *a* (μg l^{-1})	Pico chl *a* (μg l^{-1})
C. acutus	0.75*	0.72*	0.79*
C. acutus V	0.85*	0.83*	0.84*
R. gigas			
M. gerlachei			
E. crystallorophias			

Empty cells indicate no significant correlation

* Significance at $p < 0.01$

Some copepods were more abundant in the oceanic or transitional waters (Fig. 5 and 7). A zonal distribution of distinct mesozooplankton assemblages is a well-reported feature in the Southern Ocean. In our study, the oceanic species *R. gigas*, *Oithona* spp., *Drepanopus* spp., *M. gerlachei*, *C. propinquus,* and *O. antarctica* were common in open water and over the continental slope but not inside the polynya (Bathmann et al. 1993; Hosie 1994; Hosie et al. 2000; Carli et al. 2000). *Oithona* spp. were also relatively rare near the Amundsen Sea continental shelf, but were more abundant in open water toward the northern part of the Southern Ocean (Atkinson 1998; Ward et al. 2004; Hunt and Hosie 2005).

Mesozooplankton assemblages have been broadly associated with different water masses exposed to different sea ice influences in the Southern Ocean (Ducklow et al. 2012). The well-defined spatial pattern of seawater temperature, decreasing from an average of −1.3 °C at 200 m in the polynya area to an average of −1.7 °C at 200 m in the transitional area, and then increasing again to an average of −0.5 °C at 200 m in the oceanic area, suggests an alternation of distinctive water masses. The transitional area was packed with ice floes; therefore, the surface seawater temperature in this area was lower than that in the open ocean or polynya (Fig. 2c). The ice-free open water community is dominated by copepods and characterized by the mixture of Antarctic species (Pakhomov and Perissinotto 1997; Hosie et al. 2000; Pakhomov et al. 2000). Although differences in water temperature were relatively small among our sampling locations, a latitudinal pattern in

Table 4 The daily carbon ration (% total body C day^{-1}) and grazing impact (%) on daily phytoplankton primary production rate (mg C m^{-2} day^{-1}) for *R. gigas* (Rg), *C. acutus* (Ca), *C. acutus* copepodite V (CaV), *M. gerlachei* (Mg), and *E. crystallorophias* (Ec)

Station	Daily carbon ration					Grazing impact					Primary production
	Rg	Ca	CaV	Mg	Ec	Rg	Ca	CaV	Mg	Ec	
2	0.1					0.8					121.2
4	0.1		0.7			0.7		0.2			23.6
28	0.1										
27	0.3	0.3	1.7	0.9		8.9	0.7	1.6	1.6		8.7
5	0.1	0.2				1.0	0.5				38.5
26	0.3	0.4	1.9	1.3							
6		0.3									
22		0.5	1.8	0.9							
7		0.1		4.7							
8		0.3	0.8	2.6							
18		0.6	5.8	0.6	4.4		0.01	0.1	0.005	5.8	2,037.7
9		1.1	9.3	0.9	11.9		0.1	0.5	0.01	18.8	2,277.4
21		0.5	3.5	0.6	1.7						
10		0.4		0.5	48.8		0.1		0.03	227.2	340.0
11		0.6		0.4	4.2						

Empty cells indicate no data are available the mesozooplankton distribution was evident in relation to open water, the continental slope, and the polynya.

Biological factors also play a major role in the distribution of mesozooplankton. The grazing rates of *C. acutus* and *C. acutus* copepodite V were positively correlated with Chl *a* concentration (Table 3). The feeding pattern of this species is characterized by a short feeding period closely associated with phytoplankton blooms (Pasternak and Schnack-Schiel 2001). Atkinson (1998) reported that the appearance of the copepodite V cohort might coincide with the summer period of high Chl *a* concentration. The growing season for this species therefore appears to be more closely linked to the high primary production season than for other species.

Euphausiids (mainly *E. crystallorophias* with larval forms) were more abundant in the polynya area and were positively correlated with Chl *a* concentration and CNF biomass (Fig. 8). This finding agrees with previous studies in the western and central Indian sector (30–85°E) and the Prydz Bay area (80–150°E) of the Southern Ocean (Hosie 1994; Pakhomov and Perissinotto 1996; Hosie et al. 2000; Swadling et al. 2010). *E. crystallorophias* is generally considered to be a neritic species and is therefore an indicator species for a zone of cold continental shelf water (Smith and Schnack-Schiel 1990; Hosie 1994; Ducklow et al. 2012). Hosie et al. (2000) reported that this species dominated the neritic zone in Prydz Bay off East Antarctica. Polynya-related distributions of *E. crystallorophias* have been identified in the Ross Sea where this species generally increased in abundance in association with ice-covered areas (Azzali et al. 2006; Guglielmo et al. 2009). *E. crystallorophias* has been reported in large concentrations over the continental shelf, where they were found mostly in juvenile forms in the Ross Sea (Azzali and Kalinowski 2000; Azzali et al. 2000) and directly associated with ice floes (Falk-Petersen et al. 1999). Earlier studies have shown that maximum densities are found in some regions with permanent polynyas (Pakhomov and Perissinotto 1996; Guglielmo et al. 2009). Ross et al. (2008) found no long-term trends for *E. crystallorophias* in their 12-year time series study, but distribution and abundance were temporally and spatially correlated with the day of ice retreat. This suggests that the development stage of a polynya and associated food concentration producing an oasis effect are important factors for determining the spatial variability in the growth and abundance of *E. crystallorophias*.

Grazing impact on phytoplankton biomass

The gut fluorescence method has been widely used to estimate in situ grazing rates of herbivorous mesozooplankton in the Southern Ocean and elsewhere (Mackas and Bohrer 1976; Atkinson et al. 1992; Pakhomov and Perissinotto 1996; Dubischar and Bathmann 1997; Tirelli and Mayzaud 1999; Li et al. 2001; Urban-Rich et al. 2001; Mayzaud et al. 2002). This is a useful method despite some shortcomings including the variable degradation of Chl *a* into non-fluorescent substances during ingestion (Head and Harris 1992; Perissinotto and Pakhomov 1996; Perissinotto et al. 1997). The estimated grazing rate can be affected by the gut evacuation rate that changes with water temperature and food concentration. The gut evacuation rates adopted in this study were taken from environments with comparable ranges of water temperature and food concentration; therefore, the estimates of grazing rates in this study are likely to fall within realistic ranges. The estimated gut pigment contents (grazing rates) of the three copepods in our study were slightly lower than the results obtained in previous studies in the Southern Ocean (Atkinson et al. 1992; Pakhomov and Perissinotto 1996; Dubischar and Bathmann 1997; Tirelli and Mayzaud 1999; Hernández-León et al. 2000; Li et al. 2001; Pakhomov and Froneman 2004). The grazing impact of copepod groups (*R. gigas* + *C. acutus* + *M. gerlachei*) on phytoplankton was low in our study. The copepods consumed 3 % of phytoplankton standing stocks and about 4 % of primary production, consistent with the results (1–13 %) for other studies that used similar methods (Swadling et al. 1997; Li et al. 2001; Cabal et al. 2002; Pakhomov and Froneman 2004; Calbet et al. 2006; Atkinson et al. 2012). Our estimated daily carbon rations as a percentage of the carbon mass for the three copepods were also relatively low (<10 %), barely enough to meet metabolic demands, and lower than some values previously reported for the Southern Ocean, which ranged from 2 to 16 % (Hernández-León et al. 2000; Li et al. 2001; Cabal et al. 2002; Pakhomov and Froneman 2004).

The low grazing impacts in waters dominated by copepods in this study suggests that these copepods may employ selective feeding mechanisms to supplement insufficient nutrition. Calbet et al. (2006) reported that *C. acutus* is commonly considered to be a herbivore (Atkinson 1995; Atkinson and Shreeve 1995; Atkinson et al. 1996), while Calbet et al. (2006) reported that *C. acutus* displayed high clearance rates, preferring large motile organisms such as ciliates and dinoflagellates, although the species did obtain most of its daily food intake from autotrophs. There was no obvious correlation of mesozooplankton grazing rates with phytoplankton biomass. Together with the increased importance of protozoan biomass in waters with a low phytoplankton biomass (Fig. 3 and 4), this suggests that protozoans might form a substantial portion of the food source for mesozooplankton.

In polynyas, *E. crystallorophias* can exert a significant grazing impact on phytoplankton with dense schools, consuming between 13 and 96 % of daily primary production (Pakhomov and Perissinotto 1996). In this study, the daily carbon ration as a percentage of the carbon mass of *E. crystallorophias* was high (up to 49 %), and the grazing impact of *E. crystallorophias* was higher than the impact of copepods, accounting for 17 % of phytoplankton biomass and 84 % of daily primary production. Grazing impact studies in the Southern Ocean suggest that more than 50 % of daily primary production is grazed when dense salp and euphausiid swarms are dominant (Atkinson 1995; Dubischar and Bathmann 1997; Li et al. 2001), and Pakhomov and Perissinotto (1996) reported that the grazing impact could be up to 95 % of daily primary production where dense swarms occur, especially in polynyas. In spring and summer, coastal polynyas have relatively high phytoplankton stocks and productivities compared with the surrounding environment (Jacobs and Comiso 1989; Comiso et al. 1990; Sullivan et al. 1993; Arrigo and van Dijken 2003; Arrigo and Alderkamp 2012). *E. crystallorophias* larvae are usually concentrated in surface waters during phytoplankton blooms and are known to consume a substantial portion of neritic phytoplankton stock (Kittel and Ligowski 1980; Pakhomov and Perissinotto 1996; Pakhomov et al. 1998). Therefore, the high grazing rate of *E. crystallorophias* may represent one of the most important factors controlling phytoplankton blooms in coastal polynyas in the Amundsen Sea.

Conclusion

The mesozooplankton biomass was dominated by *E. crystallorophias* in the polynya waters of the Amundsen Sea during summer, but by copepods in waters outside the polynya. Greater mesozooplankton biomass in the polynya was associated with lower salinity and higher food concentration. The impact of copepod grazing on phytoplankton in the non-polynya waters was low, with copepods consuming only 3 % of phytoplankton standing stocks and about 4 % of primary production. The copepods may have relied on food sources other than phytoplankton. This suggests that much of the primary production is channeled through microzooplankton. In polynya waters, *E. crystallorophias* consumed 17 % of phytoplankton biomass and 84 % of daily primary production and are therefore likely to play a major role in governing phytoplankton blooms and the fate of fixed carbon in the coastal polynyas of the Amundsen Sea. This implies that a substantial portion of the primary production can be sequestered below the euphotic zone by a grazing-dominated trophic pathway.

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