



## Summertime grazing impact of the dominant macrozooplankton off the Western Antarctic Peninsula

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### ABSTRACT

The Western Antarctic Peninsula (WAP) is a region of rapid climate change that is altering plankton community structure. To investigate how these changes may impact carbon and energy transfer in the pelagic food web, grazing rates of the five dominant macrozooplankton species (euphausiids *Euphausia superba*, *Euphausia crystallophias*, and *Thysanøessa macrura*; the pteropod *Limacina helicina*, and the salp *Salpa thompsoni*) in the WAP were measured in January 2009 and 2010 as part of the Palmer Antarctica Long-Term Ecological Research (LTER) study. Measurements were made across the coastal-shelf-offshore and north-south gradients of the LTER survey grid. Highest grazing rates occurred offshore in both years, and in the south during 2009 and north during 2010, all associated with the presence of large localized salp blooms. During both years, *E. superba* was the major grazer at the coast, while *S. thompsoni* dominated grazing offshore. *L. helicina* was an important grazer throughout the study area during both years, but especially so over the shelf during 2009. During 2009, there was little difference in the relative importance of the macrozooplankton grazers along the north-south gradient. The presence of a salp bloom in the north during 2010, though, resulted in a distinct shift in the relative importance of major grazers from the euphausiids and *L. helicina* in the south to salps in the north. Grazing impact was low in coastal waters ( $\leq 0.3\%$  of phytoplankton standing stock and  $\leq 0.6\%$  of primary productivity). In contrast, in the offshore waters, where salp blooms were observed, grazing impacts of up to 30% of standing stock and 169% of primary productivity were recorded. If *S. thompsoni* and *L. helicina* continue to expand their ranges and increase in abundance, the associated shift in the food web dynamics of the WAP will alter the regional flow of carbon through the WAP food webs and the export of carbon to depth.

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### 1. Introduction

Climate change can alter the structure of zooplankton communities which will change energy and carbon flux within planktonic food webs (Richardson, 2008). The Western Antarctic Peninsula (WAP) has experienced one of the world's most rapid warming with an increase in winter atmosphere temperatures of  $\sim 1$  °C per decade over the last 60 years (Vaughan et al., 2003). The rise in temperature is being accompanied by a warming ocean (Martinson et al., 2008; Meredith et al., 2008) and declines in both the perennial and seasonal sea ice extent and duration (Ducklow et al., in press, 2007; Martinson et al., 2008; Stammerjohn et al., 2008a,b). These changes are transforming the northern WAP into a sub-polar ecosystem characterized by a warmer, moist, maritime climate instead of a cold and dry polar climate regime (Ducklow et al., in press, 2007).

Shifts in the physics of the WAP are accompanied by significant changes in plankton communities (Ducklow et al., in press, 2007; Montes-Hugo et al., 2008; Ross et al., 2008). During the retreat of sea ice in the spring months, the water column typically becomes stratified and an increase in nutrients and light availability promotes the formation of diatom blooms (Smith et al., 2008). However, increased wind forcing and cloud cover in the northern region of the WAP have resulted in a dramatic decline in the biomass of phytoplankton (measured as chlorophyll-*a* derived from satellites) in the austral summer months over the last thirty years (Montes-Hugo et al., 2009). In contrast, in the southern region of the WAP where there has been an increase in open water associated with shifts in the distribution of sea ice, phytoplankton biomass has increased (Montes-Hugo et al., 2009).

Changes in phytoplankton are mirrored by shifts in zooplankton. Ross et al. (2008) found that salps (*Salpa thompsoni*) are increasing in abundance in the northern WAP shelf region. Salps are considered to be an oceanic species, typically avoiding the ice covered regions of the high Antarctic, while favoring the open

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waters of the sub-Antarctic (Foxton, 1966). The trend of *S. thompsoni* expansion into higher latitudes has now been observed for much of the Southern Ocean (Atkinson et al., 2004; Chiba et al., 1998; Loeb et al., 1997; Pakhomov et al., 2002a). The pteropod, *Limacina helicina*, is also becoming increasingly prevalent in the shelf waters of the northern and mid WAP as well as over the slope in the southern WAP (Ross et al., 2008). In contrast, the Antarctic krill, *Euphausia superba*, is becoming less abundant throughout the Southern Ocean (Atkinson et al., 2004; Loeb et al., 1997). In the WAP, while the trend of declining *E. superba* abundance is less clear, Ross et al. (2008) note a distinct consistent decline in abundance at localized regions of the northern coastal WAP. The ice krill, *Euphausia crystallophias*, favor coastal waters in areas with lingering summer sea ice. While ice krill were historically found throughout the coastal waters of the WAP (Ross et al., 2008) and, at times the inner shelf, they are now limited to the southern coastal region, where summer sea ice persists (Steinberg et al., unpublished data).

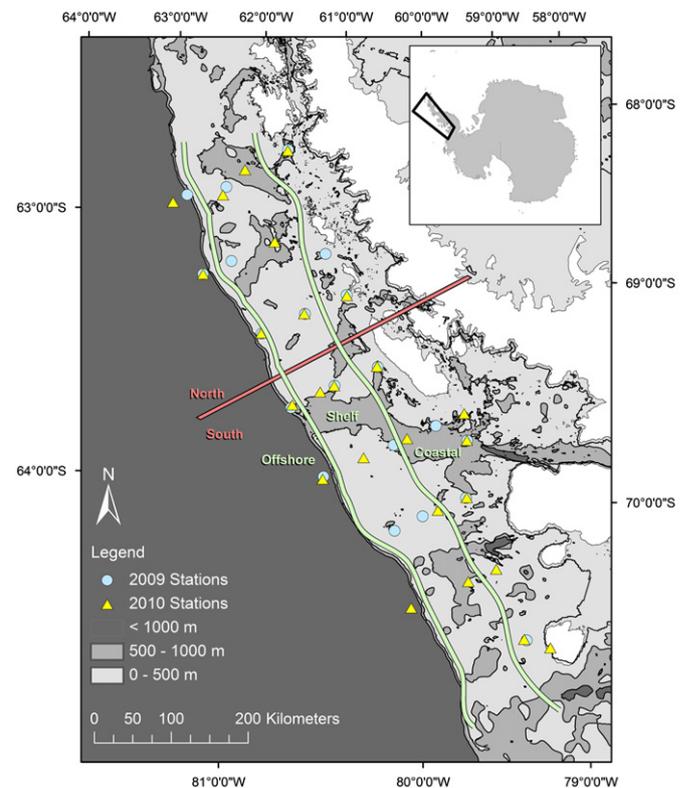
These shifts in plankton community structure are likely to have significant impacts on trophic energy transfer and food web dynamics of the WAP pelagic ecosystem. Euphausiids (krill) are important grazers of phytoplankton in the Antarctic ecosystem and form dense swarms that are capable of exerting considerable pressure on phytoplankton standing stocks (Froneman et al., 2000; Pakhomov and Froneman, 2004; Pakhomov and Perissinotto, 1996; Pakhomov et al., 1998; Perissinotto et al., 1997). Krill have feeding appendages and mouth parts that are adapted to selectively filter out particle sizes  $> 10 \mu\text{m}$  (McClatchie and Boyd, 1983). Salps, on the other hand, are non-selective filter feeders that trap food particles ranging in size from 1 to 1000  $\mu\text{m}$  in diameter (Fortier et al., 1994; Madin, 1974; Pakhomov et al., 2002a). With filtration rates that far exceed other zooplankton grazers (Pakhomov et al., 2002a) and the ability to rapidly multiply through asexual budding to form dense swarms (Aldredge and Madin, 1982; Heron and Benham, 1984), salps may be a major competitor with Antarctic krill for food (Loeb et al., 1997; Pakhomov et al., 2002a). The thecosome pteropod, *L. helicina*, is a particle feeder that deploys an external mucous net that is suspended in the water column, ensnaring food particles (typically  $< 5 \mu\text{m}$  in diameter) as the animal slowly sinks (Gilmer, 1974; Lalli and Gilmer, 1989). This is another rapid means of filtration and, as such, pteropods have relatively high ingestion rates (Bernard and Froneman, 2009; Hunt et al., 2008).

Understanding how phytoplankton carbon is divided between the major consumers is important to improving our understanding of carbon flows through the pelagic ecosystem. Thus, the primary objective of the present study is to examine the relative importance of the dominant macrozooplankton species as grazers of phytoplankton populations in the WAP. We compare macrozooplankton grazing rates along (i) the north–south gradient of the WAP, representing the climate gradient; (ii) the coastal–shelf–offshore gradient, which typically separates neritic from oceanic waters.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in January of 2009 and 2010 aboard the A.S.R.V. *Laurence M. Gould*. A series of stations were occupied along the standard Palmer Antarctica LTER grid (Waters and Smith, 1992) covering 41,000 square nautical miles off the Western Antarctic Peninsula (Fig. 1 and Table 1). During both surveys, the stations occupied were spread across two gradients, defined as (1) the coastal–shelf–offshore gradient, and (2) the north–south gradient. The coastal–shelf–offshore gradient is based



**Fig. 1.** Stations occupied during January 2009 and 2010 off the Western Antarctic Peninsula. Study region, highlighted by box, in relation to Antarctic continent (inset). The study area is divided across two gradients for comparative analyses in this study; the north–south gradient is separated by the orange line, and the coastal–shelf–offshore gradient is marked by two green lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

on that defined by Martinson et al. (2008) and is highlighted in Fig. 1 (see also Table 1). For the north–south gradient, the grid lines north of, and including, the 300 line are considered as *north*, while those south of, and including, the 200 line are considered as *south* (Fig. 1 and Table 1). The demarcation between north and south was based on a distinct change in penguin diet and consequently zooplankton community structure (W. Fraser, pers. comm.).

### 2.2. Macrozooplankton sampling

Macrozooplankton were collected using a 2 m-square frame Metro net (700  $\mu\text{m}$  mesh), towed obliquely to depths of approximately 120 m (Ross et al., 2008). Net depth was determined real time with a depth sensor attached to the bottom of the conducting hydro wire and confirmed with a Vemco Minilog Temperature–Depth Recorder. The net was fitted with a General Oceanics flow meter to calculate volume filtered. The whole catch, or a subsample of the catch (depending on the density of macrozooplankton in the tow), was sorted by taxon and abundance, and total biovolume of each species was subsequently determined. Only the five dominant macrozooplankton species (which comprised on average 97% of the total tow biovolume; see also Ross et al., 2008) are considered here: the euphausiids *E. superba* (adults and juveniles), *Thysanöessa macrura*, and *E. crystallophias*; the tunicate *S. thompsoni* (sorted by  $< 50 \text{ mm}$ ,  $50\text{--}70 \text{ mm}$ , and  $> 70 \text{ mm}$  total body lengths; aggregate form only, as the solitary form was scarce during both surveys); and the thecosome pteropod *L. helicina*. Animal length was recorded for *S. thompsoni* (Total and Body Lengths, according to

**Table 1**

Details of stations occupied during January 2009 and January 2010. C/S/O=coastal/shelf/offshore. N/S=north/south. 'Grid' is the Palmer LTER station identification (Waters and Smith, 1992). Stations occupied are stations at which macrozooplankton tows were conducted and analyzed for abundance and biomass. Gut fluorescence denotes stations at which animals were collected for pigment extraction to determine gut fluorescence. GER denotes stations at which gut evacuation rate experiments were conducted. Additional gut evacuation rate experiments were conducted during Jan 2011 at Palmer LTER grid station 221. –019 (67.764°S; 69.275°W) and in the vicinity of Avian Island (67.767°S; 68.900°W).

Grid	Latitude (S)	Longitude (W)	C/S/O	N/S	Stations occupied		Gut fluorescence		GERs
					January 2009	January 2010	January 2009	January 2010	January 2010
600.040	–64.933	–64.400	C	N	✓	✓			
600.100	–64.575	–65.341	S	N		✓		✓	
600.180	–64.089	–66.558	O	N	✓		✓		
600.200	–63.966	–66.856	O	N		✓		✓	
590.130	–64.460	–65.943	S	N	✓		✓		
585.135	–64.463	–66.090	S	N		✓	✓		✓
500.100	–65.234	–66.776	S	N		✓		✓	
500.160	–64.861	–67.695	S	N	✓				
500.200	–64.610	–68.293	O	N	✓		✓		
460.040	–65.864	–66.424	C	N	✓		✓		
400.040	–66.254	–67.337	C	N	✓		✓		
400.100	–65.878	–68.283	S	N	✓		✓		
400.160	–65.496	–69.202	O	N	✓		✓		
300.040	–66.891	–68.921	C	S	✓		✓		
300.100	–66.505	–69.867	S	S	✓				
300.120	–66.375	–70.175	S	S		✓		✓	
300.160	–66.114	–70.783	O	S	✓		✓		
200.–040	–68.030	–69.285	C	S		✓			
200.000	–67.772	–69.944	C	S	✓				
200.040	–67.511	–70.590	C	S		✓			
200.060	–67.380	–70.907	S	S	✓				
200.100	–67.115	–71.531	S	S		✓			
200.160	–66.714	–72.442	O	S	✓		✓		
167.–033	–68.190	–69.973	C	S	✓		✓		✓
100.000	–68.380	–71.705	C	S	✓		✓		
100.040	–68.112	–72.346	S	S		✓		✓	✓
100.060	–67.977	–72.661	S	S	✓				
100.100	–67.706	–73.280	S	S	✓		✓		
000.000	–68.967	–73.561	C	S		✓			
000.040	–68.693	–74.195	S	S		✓		✓	
000.120	–68.137	–75.418	O	S		✓			
–100.000	–69.533	–75.516	C	S	✓		✓		✓
–122.–023	–69.816	–75.595	C	S		✓		✓	✓

Foxton, 1966), and *E. superba* (Standard 1, according to Mauchline, 1970). Abundances ( $\text{ind. m}^{-2}$ ) and biovolume ( $\text{ml m}^{-2}$ ) were integrated over the depth of the tow and standardized to 120 m. Note that large calanoid copepods were present in some tows, but always constituted <10% of total tow biomass, thus are not included in the scope of this study. Relative contributions of each species to total abundance and biovolume were calculated for each station and then averaged for each region.

### 2.3. Determination of grazing rates and community grazing impact

Grazing rates were estimated for each of the five abundant macrozooplankton species using the gut fluorescence technique as described by Båmstedt et al. (2000). However, following the recommendations of Conover et al. (1986) we did not multiply phaeopigment concentrations by 1.51, as these values are already expressed as chlorophyll weight equivalents in standard fluorometric calculations and the conversion is not necessary. A recent study by Durbin and Campbell (2007) suggests that the gut pigment degradation value, traditionally used in ingestion rate equations (e.g. Båmstedt et al., 2000), is taken into account in gut evacuation rate experiments and is therefore is not required as a separate value to determine ingestion rates. We have therefore omitted the gut pigment degradation component of the gut fluorescence technique. The use of the gut fluorescence technique following both adaptations described above has recently been used to quantify grazing in the coastal upwelling system off Southern California (see Landry et al., 2009). Ingestion rates were thus calculated as:  $I = G \times k$ ;

where  $I$  is ingestion rate [ $\text{ng (chl-}a \text{ equivalent) ind.}^{-1} \text{ day}^{-1}$ ],  $G$  is instantaneous gut pigment content after background fluorescence is subtracted [ $\text{ng (chl-}a \text{ equivalent) ind.}^{-1}$ ], and  $k$  is daily gut evacuation rate ( $\text{day}^{-1}$ ). Background fluorescence was measured from animals starved for at least 24 h in 0.2  $\mu\text{m}$  filtered seawater plus added charcoal powder (see below).

Macrozooplankton samples used to determine instantaneous gut pigment content were collected at stations throughout the study area using the same 2 m Metro net. Individuals were immediately removed from the tow, their lengths recorded, and frozen at  $-80^\circ\text{C}$ . Gut pigment contents were determined fluorometrically for each individual before and after acidification with a Turner Designs TD700 Fluorometer. Whole animals were used for gut pigment measurements. Sample size for gut pigment analysis for each species ranged from a single individual to over 60 individuals for a given station, and at least one gut evacuation rate experiment was conducted for each species.

For gut evacuation rate experiments, freshly caught, actively swimming individuals were placed into a 20 L bucket containing particle-free seawater (gravity filtered through 0.2  $\mu\text{m}$ ) and non-fluorescent charcoal powder (at concentrations similar to typical particle concentrations for the region). Seawater in the bucket was kept within  $\pm 0.5^\circ\text{C}$  of in situ water temperature by placing buckets in a large flow-through aquarium tank supplied with pumped seawater or in a cold aquarium room for the duration of the experiments. Sub-samples of between three and five individuals were removed at set intervals over a period of two hours, with the first sub-sample immediately removed at the start of the

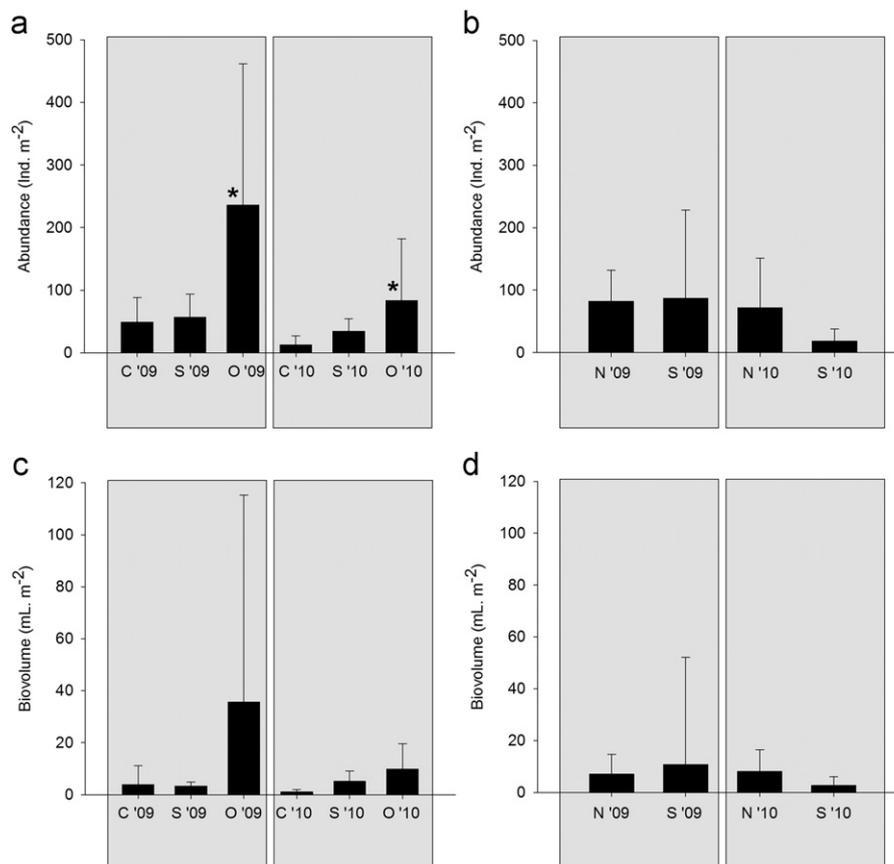
experiment. Individuals were quickly measured (Standard 1 length for euphausiids, Total Length for salps and shell diameter for pteropods) and frozen at  $-80^{\circ}\text{C}$ . Gut pigment concentrations were determined fluorometrically as described above. Gut evacuation rates ( $k$ , per hour) were then calculated as the slope of the exponential regression of gut pigments over time. Although experiments typically ran for 2 h, when calculating gut evacuation rates for *E. superba* and *E. crystallophias* we used data from the first 40 minutes only. This approach was based on recommendations by Clarke et al. (1988) who found that fecal pellet egestion by *E. superba* occurs within the first 30 to 40 minutes, after which gut clearance stops almost completely. Although we conducted a gut evacuation experiment for *T. macrura*, the individuals were generally not in good condition, thus we applied an average gut evacuation rate from the literature of  $0.53\text{ h}^{-1}$  (Froneman et al., 2000; Pakhomov and Froneman, 2004). For *S. thompsoni* and *L. helicina* we used data from the full two hours to calculate gut evacuation rates. Gut passage time (number of hours for a single gut evacuation) was calculated as  $1/k$ . Hourly gut evacuation rates were then converted to daily rates by dividing 24 h by the gut passage time. This value of  $k$  ( $\text{day}^{-1}$ ) was used in the equation to calculate ingestion  $I$ , described above. Additional gut evacuation rate experiments were conducted during a cruise in January 2011 to the same region (see Table 1).

Community grazing rates [ $\mu\text{g}$  (Chl-*a* equiv.)  $\text{m}^{-2}\text{ day}^{-1}$ ] were calculated for each species as the product of ingestion rate [ $\mu\text{g}$  (Chl-*a* equivalent)  $\text{ind.}^{-1}\text{ day}^{-1}$ ] and abundance ( $\text{Ind. m}^{-2}$ ) at each station. For stations where ingestion rates were not calculated, average values from the same region of the survey grid (for example, Northern Coastal) were used. Values for community grazing rates in

Chl-*a* equivalents were converted to carbon using an average Carbon: Chl-*a* ratio of 63:1 that was calculated from particulate organic carbon and Chl-*a* data collected during both years. The Carbon: Chl-*a* ratio was determined following the method used by Ducklow et al. (1993). Relative contributions (%) of each species to total grazing rates were first calculated for each station and then averaged for each region.

Grazing impact was estimated separately for each species as a percentage of phytoplankton standing stock and primary productivity consumed per day, and then summed for all five species to calculate community grazing impact. Both phytoplankton biomass and primary productivity were determined at selected depths and integrated over the top 100 m of the water column. Phytoplankton standing stock or biomass ( $\text{mg m}^{-2}$ ) was determined fluorometrically according to the methods described in the JGOFS Protocols (1994). Seawater samples at selected depths were gently filtered through Whatman GF/F filters, and chlorophyll-*a* (Chl-*a*) concentrations calculated by fluorescence recorded before and after acidification. Primary productivity ( $\text{mg C m}^{-2}\text{ day}^{-1}$ ) was determined using the  $^{14}\text{C}$  technique (JGOFS Protocols, 1994).

Average daily rations, expressed as a percentage of body carbon consumed per day, were estimated for each species at stations where gut pigment content samples were collected. For *E. superba* and large and medium *S. thompsoni*, body carbon was measured for a single individual per sample; while for *T. macrura*, *L. helicina*, and small *S. thompsoni*, body carbon was measured for up to ten individuals per sample. Shells were removed for *L. helicina*. Body carbon was determined using a high-temperature combustion technique in a Costech ECS 4010 CHNSO Analyzer. Length-specific



**Fig. 2.** Combined abundance (a,b;  $\text{Ind. m}^{-2}$ ) and biovolume (c,d;  $\text{mL. m}^{-2}$ ) of the dominant macrozooplankton, *Euphausia superba*, *E. crystallophias*, *Thysanöessa macrura*, *Limacina helicina* and *Salpa thompsoni*, across the coastal (C)–shelf (S)–offshore (O) (a,c) and the north (N)–south (S) (b,d) gradients of the WAP, during January of 2009 ('09) and 2010 ('10). See Section 2 for regional definitions. Values are means with standard deviation as error bars. \* denotes significance, where  $p < 0.05$ .

body carbon was estimated using length: dry weight and dry weight: body carbon regressions determined for each species pooled from samples collected during both years.

#### 2.4. Statistical analysis

Data were rank transformed to meet normality and equal variance assumptions. Three-way ANOVAs were used to compare values across the north–south and coastal–shelf–offshore gradients and between years. Only those ANOVA results for which comparisons were statistically significant ( $p < 0.05$ ) are described in Section 3, unless otherwise noted.

### 3. Results

#### 3.1. Distribution patterns of the dominant macrozooplankton

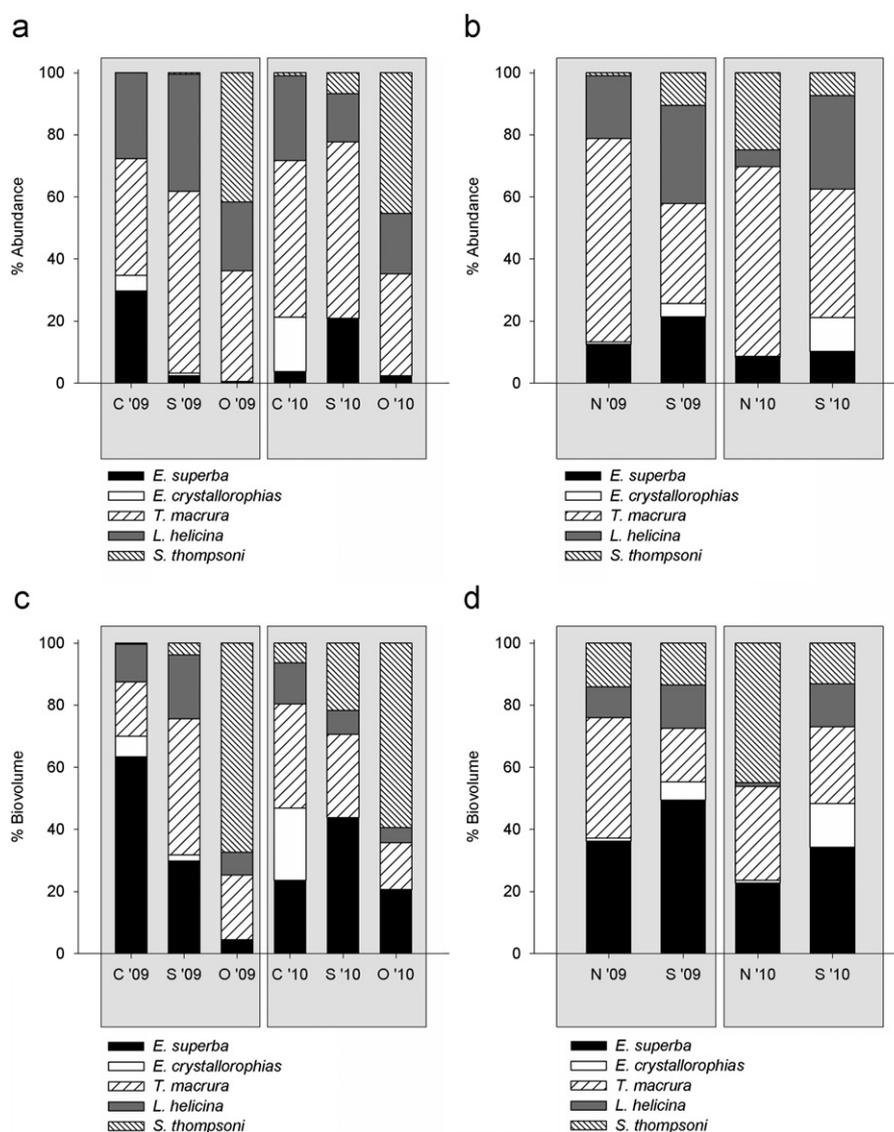
During both years, total abundance and biovolume of the five dominant species were highest offshore (Fig. 2a and c). Total abundance and biovolume were significantly higher in the north

(69 ind.  $m^{-2}$  and 12 mL  $m^{-2}$ , respectively) than in the south (17 ind.  $m^{-2}$  and 3 mL  $m^{-2}$ , respectively) during 2010, but there was no difference along the north–south gradient in 2009 (Fig. 2b and d). Overall, the total abundance was significantly higher in 2009 (80 ind.  $m^{-2}$ ) than in 2010 (35 ind.  $m^{-2}$ , Fig. 2a and b), but there was no significant difference in total biovolume between years due to high biomass variability. The most abundant species throughout the study was the euphausiid, *T. macrura* (~44% of total abundance), followed by *L. helicina* (~26% of total abundance, Fig. 3a and b; Table 2). Due to its larger size and relatively high abundance, the species with the highest biovolume overall was *E. superba* (~40% of total biovolume, Fig. 3c and d; Table 2). However, occurring in blooms, *S. thompsoni* dominated both in abundance (up to 93% of the total) and biovolume (up to 98% of the total) offshore during both years and in the north during 2010 (Fig. 3a–d; Table 2).

#### 3.2. Macrozooplankton grazing

##### 3.2.1. Individual ingestion rates

Hourly gut evacuation rates and daily individual ingestion rates are shown in Tables 3 and 4. Salps had the highest daily individual



**Fig. 3.** Relative contribution of the dominant macrozooplankton, *Euphausia superba*, *E. crystallorophias*, *Thysanøessa macrura*, *Limacina helicina* and *Salpa thompsoni*, to their total combined abundances (a,b; %) and biovolume (c,d; %) across the coastal (C)–shelf (S)–offshore (O) (a,c) and the north (N)–south (S) (b,d) gradients of the WAP, during January of 2009 ('09) and 2010 ('10). Refer to Section 2 for regional definitions.

**Table 2**  
Abundances (A; Ind. m<sup>-2</sup>) and biovolume (B; mL m<sup>-2</sup>) of the dominant macrozooplankton, *Euphausia superba* (Es), *E. crystallorophias* (Ec), *Thysanöessa macrura* (Tm), *Limacina helicina* (Lh), and *Salpa thompsoni* (St) across the coastal–shelf–offshore and north–south gradients of the WAP, in January of 2009 and 2010. See Section 2 for regional definitions. Values are means integrated over the top 120 m of the water column, with standard deviation in parentheses.

		Es		Ec		Tm		Lh		St	
		A	B	A	B	A	B	A	B	A	B
January 2009	Coastal	8.9(12.6)	9.4(9.1)	1.2(1.3)	0.2(0.2)	20.0(22.6)	0.8(0.5)	9.7(18.1)	0.6(1.2)	0.01(0.02)	0.02(0.04)
	Shelf	0.8(1.1)	0.9(1.0)	0.4(0.7)	0.1(0.1)	27.4(14.7)	1.1(0.6)	18.6(14.3)	0.6(0.4)	0.3(0.5)	0.5(1.2)
	Offshore	0.7(0.8)	0.8(0.9)	0.01(0.01)	0.002(0.005)	43.0(46.0)	2.5(1.6)	28.5(19.1)	1.1(0.5)	171.2(249.0)	45.6(93.4)
	North	6.7(14.2)	3.7(7.7)	0.5(1.1)	0.1(0.2)	49.6(34.4)	1.9(1.4)	17.7(20.1)	0.6(0.6)	1.3(2.9)	1.6(3.3)
	South	5.5(9.4)	4.7(6.8)	1.0(1.2)	0.1(0.2)	17.0(19.3)	0.9(0.6)	14.0(18.6)	0.8(1.0)	44.0(142.1)	19.8(63.9)
January 2010	Coastal	0.4(0.7)	0.3(0.4)	1.5(3.0)	0.3(0.6)	9.1(14.5)	0.4(0.5)	1.2(1.2)	0.1(0.1)	0.1(0.3)	0.1(0.2)
	Shelf	5.1(7.2)	2.9(3.6)	0.01(0.01)	0.3(0.8)	17.2(13.4)	0.5(0.5)	3.8(3.5)	0.1(0.1)	3.2(7.7)	1.4(2.6)
	Offshore	0.9(0.8)	1.1(1.0)	0	0	13.7(17.4)	0.5(0.4)	7.4(7.2)	0.1(0.1)	60.8(103.0)	8.1(9.9)
	North	3.1(6.6)	1.2(1.0)	0.1(0.2)	0.3(0.8)	24.3(16.6)	0.8(0.6)	3.3(2.8)	0.1(0.1)	37.8(87.7)	5.8(8.7)
	South	1.7(3.4)	1.5(3.0)	0.9(2.5)	0.2(0.5)	6.9(8.9)	0.3(0.3)	3.8(5.5)	0.1(0.1)	3.4(9.5)	0.6(1.6)

**Table 3**  
Results from gut evacuation rate experiments for the dominant macrozooplankton species: *Euphausia superba*, *E. crystallorophias*, *Thysanöessa macrura*, *Limacina helicina*, and *Salpa thompsoni*. Exponential regressions provided the best fit according to R<sup>2</sup> values. ‘Grid station’ is the Palmer LTER station identification (Waters and Smith, 1992).

Species	Hourly gut evacuation rate <sup>a</sup> (k <sub>hour</sub> , h <sup>-1</sup> )	Gut passage time (1/k, h)	Seawater temperature (°C)	Survey year (grid station)
<i>E. superba</i> (adults)	0.979 (R <sup>2</sup> =0.282; p=0.05)	1.0	-0.4	January 2010 (100.040)
	1.439 (R <sup>2</sup> =0.112; p=0.24)	0.7	0.8	January 2010 (167.-033)
<i>E. superba</i> (juveniles)	1.122 (R <sup>2</sup> =0.258; p=0.05)	0.9	0.8	January 2010 (167.-033)
	1.896 (R <sup>2</sup> =0.213; p<0.05)	0.5	0.2	January 2011 (221.-019)
	1.418 (R <sup>2</sup> =0.212; p<0.05)	0.7	0.2	January 2011 (221.-019)
<i>E. crystallorophias</i>	1.246 (R <sup>2</sup> =0.241; p=0.06)	0.8	-0.95	January 2010 (-122.-023)
	1.005 (R <sup>2</sup> =0.473; p<0.05)	1.0	-0.8	January 2010 (-100.000)
<i>T. macrura</i> <sup>b</sup>	0.53	1.9		
<i>L. helicina</i>	0.324 (R <sup>2</sup> =0.091; p<0.05)	3.1	0.5	January 2011 (Avian Is.)
<i>S. thompsoni</i> <sup>a</sup>	1.091 (R <sup>2</sup> =0.133; p=0.24)	0.9	0.75	January 2010 (585.135)
	0.232 (R <sup>2</sup> =0.253; p<0.05)	4.3	0.7	January 2010 (585.135)

<sup>a</sup> Hourly gut evacuation rates for *S. thompsoni* were estimated from small individuals, the most abundant size class.

<sup>b</sup> See Table 6; values for *T. macrura* were obtained from the average in the literature.

**Table 4**  
Average daily individual ingestion rates [ $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup>] of the dominant macrozooplankton, *Euphausia superba* (Es, Adults; Es, Juveniles), *E. crystallorophias* (Ec), *Thysanöessa macrura* (Tm), *Limacina helicina* (Lh) and *Salpa thompsoni* (St, Small; St, Medium; and St, Large) across the coastal–shelf–offshore and north–south gradients of the WAP, during January of 2009 and 2010. See Section 2 for regional definitions. Small = < 50 mm; medium = 50–70 mm; large = > 70 mm. Values are means.

		Average daily individual ingestion rates ( $\mu\text{g}$ (Chl- <i>a</i> equiv.) ind. <sup>-1</sup> day <sup>-1</sup> )							
		Es, adult	Es, juvenile	Ec	Tm	Lh	St, small	St, medium	St, large
January 2009	Coastal	5.23	6.01	1.34	0.02				
	Shelf	2.59	3.72		0.05	1.36	7.90	27.57	24.63
	Offshore	8.95			0.02	0.92	20.71	43.20	33.64
	North	3.26	3.70	1.94	0.07	1.18	8.28	27.28	27.75
	South	5.92	6.62	1.28	0.01		27.40	43.78	63.56
January 2010	Coastal	8.56	5.69	1.39	0.16	1.38	10.99	68.87	
	Shelf	4.73	3.15		0.09	1.86	16.36	99.67	198.39
	Offshore	3.77	1.37				13.80	98.62	240.40
	North	3.66	3.94	1.43	0.11	1.54	14.07	96.00	214.14
	South	7.35	4.24	1.38	0.11	1.54	16.11	82.87	

ingestion rates overall, with medium and large-sized salps showing significantly higher individual ingestion rates [up to 100  $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup> and 240  $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup>, respectively] than small salps (Table 4). *E. superba* had the highest recorded individual ingestion rates of the three euphausiids [up to 8.95  $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup>], and the second highest ingestion rate of the five species investigated (Table 4). Ingestion rates of *L. helicina* and *E. crystallorophias* were significantly higher [up to 1.86  $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup> and 1.94  $\mu\text{g}$  (Chl-*a*

equiv.) ind.<sup>-1</sup> day<sup>-1</sup>, respectively] than those of *T. macrura* but were lower than those of *E. superba* (Table 4). Lowest ingestion rates were observed for *T. macrura* [0.01–0.12  $\mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup>].

### 3.2.2. Daily rations

The proportion of body carbon consumed daily in the form of phytoplankton was generally low across all regions for euphausiids, (0–4% for *E. superba*; 0–2% for *E. crystallorophias*; and

**Table 5**  
Taxon-specific and total community grazing rates of the dominant macrozooplankton (*Es-Euphausia superba*, *Ec-E. crystallorophias*, *Tm-Thysanoessa macrura*, *Lh-Limacina helicina* and *St-Salpa thompsoni*) across the coastal–shelf–offshore and the north–south gradients of the WAP, during January of 2009 and 2010. See Section 2 for regional definitions. Phytoplankton standing stock (Int. SS) and primary productivity (Int. PP) are integrated over the top 100 m of the water column. Values are means with standard deviation in parentheses. Total grazing impact is presented as a percentage of phytoplankton standing stock (% SS) and primary productivity (% PP) consumed per day. Values are means with standard deviation in parentheses.

	Grazing rates						Total carbon (mg C m <sup>-2</sup> day <sup>-1</sup> )	Int. SS (mg Chl- <i>a</i> m <sup>-2</sup> )	Int. PP (g C m <sup>-2</sup> day <sup>-1</sup> )	Grazing impact	
	Species-specific grazing rates (μg(Chl- <i>a</i> equiv.) m <sup>-2</sup> day <sup>-1</sup> )									% SS	% PP
	Es	Ec	Tm	Lh	St						
Coastal	49.2 (68.2)	1.7 (1.8)	1.3 (2.5)	11.0 (20.6)	0.1 (0.2)	0.1 (0.01)	56.3 (12.6)	1.08 (0.4)	0.1 (0.1)	0.5 (0.6)	
Shelf	2.1 (2.5)	0.7 (1.1)	1.0 (1.4)	23.0 (16.8)	4.9 (8.4)	0.03 (0.02)	38.4 (17.2)	1.0 (0.5)	0.1 (0.1)	0.3 (0.3)	
Offshore	7.2 (8.5)	0.01 (0.02)	1.4 (1.7)	28.8 (17.8)	4702.9 (6906.0)	4.7 (6.9)	29.9 (18.2)	0.4 (0.2)	30.2 (44.4)	168.8 (248.3)	
North	24.4 (51.5)	0.9 (2.1)	3.8 (2.9)	18.7 (19.3)	13.7 (28.3)	0.01 (0.1)	44.8 (16.1)	1.1 (0.5)	0.2 (0.2)	0.6 (0.6)	
South	35.3 (60.6)	1.3 (1.5)	0.3 (0.4)	15.9 (21.1)	1215.5 (3927.6)	1.3 (3.9)	49.0 (19.0)	0.9 (0.5)	7.9 (25.2)	45.7 (143.5)	
Coastal	2.5 (3.7)	2.1 (4.1)	1.3 (2.9)	1.7 (1.7)	3.0 (7.4)	0.01 (0.01)	161.2 (175.3)	8.7 (8.8)	0.02 (0.03)	0.02 (0.02)	
Shelf	21.3 (27.7)	0.01 (0.02)	0.8 (1.0)	8.1 (9.3)	145.2 (361.8)	0.2 (0.4)	82.8 (19.4)	6.7 (3.6)	0.3 (0.7)	0.4 (0.9)	
Offshore	2.9 (3.2)	0	1.6 (2.0)	12.4 (12.2)	3067.0 (5734.3)	3.1 (5.7)	91.6 (50.7)	2.5 (1.3)	5.1 (9.4)	21.0 (46.9)	
North	11.3 (22.7)	0.1 (0.3)	2.9 (2.8)	5.1 (4.6)	2017.9 (4797.5)	2.0 (4.8)	72.6 (44.4)	3.7 (2.3)	3.4 (7.8)	14.0 (38.5)	
South	8.2 (16.6)	1.3 (3.4)	0.2 (0.4)	7.4 (10.7)	98.7 (277.9)	0.1 (0.3)	140.8 (137.6)	8.0 (7.1)	0.2 (0.6)	0.2 (0.6)	

0–0.6% for *T. macrura*). The daily rations of *L. helicina* were greater than those of the euphausiids, ranging from 1% to 27%. *S. thompsoni*, on the other hand, consumed relatively high proportions of their body carbon as phytoplankton. Daily rations of small salps (<50 mm total length) were highest with an average of 97%. Medium and large sized salps (50–70 mm and >70 mm total length, respectively) consumed 70 and 19% of their body carbon per day, respectively.

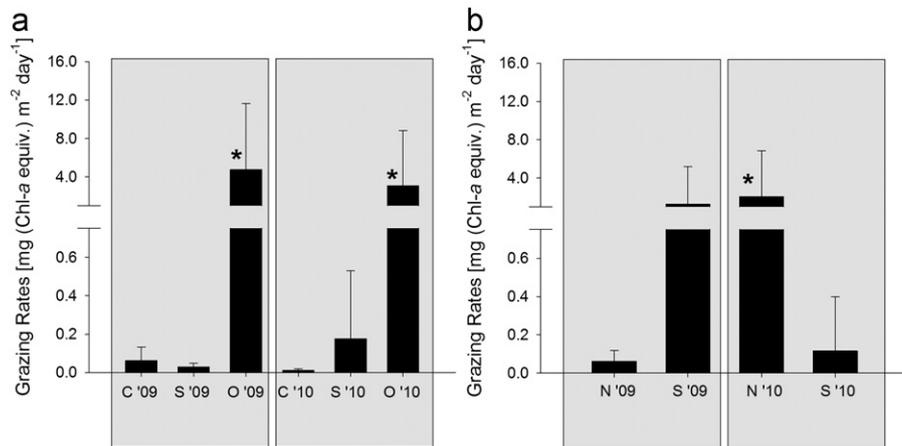
### 3.2.3. Community grazing rates and grazing impact:

Community grazing rates were significantly higher offshore than at the coast during both years (Table 5; Fig. 4a) and in the north compared with the south during 2010 (Table 5; Fig. 4b). We also observed elevated community grazing rates in the south during 2009 (Table 5; Fig. 4b), but these were not statistically significant. Increased community grazing rates appear to be coincident with the presence of salp blooms (Table 2; Fig. 3a and b). Major grazers at the coast and over the shelf were *E. superba* and *L. helicina*, while offshore total grazing was dominated by *S. thompsoni* (Fig. 5a). There was less distinction between the species along the north–south gradient during 2009; *E. superba* and *L. helicina* represented the major grazers in both the north and south (Fig. 5b). It is notable that at a single station in the south, where a large salp bloom occurred, *S. thompsoni* dominated total grazing impact (contributing to 100% of the total). On the other hand, during 2010, *S. thompsoni* was the dominant grazer in the north, while *E. superba* and *L. helicina* were the primary grazers in the south (Fig. 5b). Grazing impact of the dominant macrozooplankton species was typically low in areas where salp blooms did not occur—≤0.3% of the phytoplankton standing stock and ≤0.6% of primary productivity per day (Table 5). However, where salp blooms occurred, grazing impact was considerably higher and in some regions even exceeded primary production (e.g. offshore in 2009; Table 5).

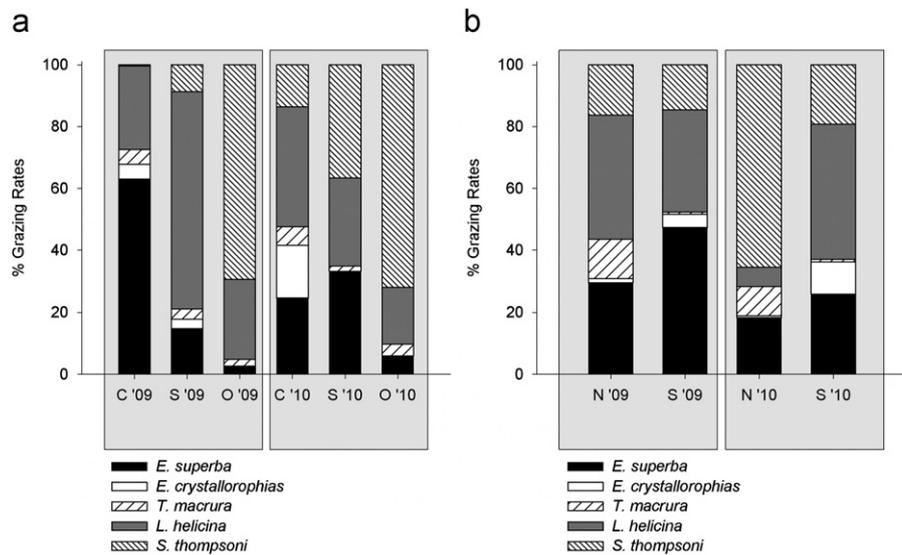
## 4. Discussion

### 4.1. Distribution patterns

We found that *S. thompsoni*, a species that is becoming increasingly abundant in the high Antarctic (Atkinson et al., 2004; Kawaguchi et al., 2004; Loeb et al., 1997; Pakhomov et al., 2006, 2002a), occurred throughout the study area, often at bloom densities (up to 650 ind. m<sup>-2</sup>) primarily offshore in the north, but also in the south. *L. helicina*, considered to be more of a shelf species, was observed in high densities right up to the coast during both years. In addition, *E. superba* and *E. crystallorophias*, both true Antarctic species, were relatively less abundant and appeared to be concentrated largely in the coastal waters of the WAP, which is consistent with previous studies (Atkinson et al., 2004; Loeb et al., 1997; Pakhomov et al., 2002a). Throughout much of the high Antarctic, the spatial distributions of *S. thompsoni* and *E. superba* tend not to overlap, with both species being limited in distribution by the presence of sea ice, the former avoiding it, and the latter requiring it (Pakhomov et al., 2002a). During our study, however, we found that *S. thompsoni* and *E. superba* co-occurred at some stations, possibly as a result of the intrusion of warmer Upper Circumpolar Deep Water (Pakhomov et al., 2002a). A number of studies suggest that salps may out-compete krill for food resources (Le Fèvre et al., 1998; Loeb et al., 1997); thus their increasing abundance and range expansion into regions where they overlap with *E. superba* may have negative implications for the krill in the area. Similarly, the broadening range of *L. helicina* may result in competition for food



**Fig. 4.** Combined community grazing rates of the dominant macrozooplankton, *Euphausia superba*, *E. crystallorophias*, *Thysanöessa macrura*, *Limacina helicina* and *Salpa thompsoni*, across the (a) coastal (C)–shelf (S)–offshore (O) and (b) north (N)–south (S) gradients of the WAP, during January of 2009 ('09) and 2010 ('10). See Section 2 for regional definitions. Values are means with standard deviation as error bars. \* denotes significance, where  $p < 0.05$ .



**Fig. 5.** Relative contribution of the dominant macrozooplankton, *Euphausia superba*, *E. crystallorophias*, *Thysanöessa macrura*, *Limacina helicina* and *Salpa thompsoni*, to community grazing rates across the (a) coastal (C)–shelf (S)–offshore (O) and (b) north (N)–south (S) gradients of the WAP, during January of 2009 ('09) and 2010 ('10). See Section 2 for regional definitions.

resources with krill, although this may not be as severe since *L. helicina* has a lower ingestion rate than *E. superba* (see below).

#### 4.2. Taxon-specific grazing rates

##### 4.2.1. Gut evacuation rates

There are a number of factors that can affect grazing rates as estimated using the gut fluorescence technique (see for example Conover et al., 1986; Dam and Peterson, 1988; Durbin and Campbell, 2007; Perissinotto and Pakhomov, 1996). For example, gut evacuation rate ( $k$ ) for a particular species can be influenced by seawater temperature, phytoplankton biomass, and phytoplankton size structure (Atkinson, 1995, 1996; Atkinson et al., 1996; Dam and Peterson, 1988; Perissinotto and Pakhomov, 1996) and thus may vary substantially for a given species. Moreover, the time period used to calculate gut clearance may have a substantial affect on the estimation of  $k$ . Following the recommendations of Clarke et al. (1988; see 'Materials and methods') resulted in values for  $k$  of  $1.34 \text{ h}^{-1}$  and  $1.13 \text{ h}^{-1}$  for *E. superba* (average for adults and juveniles) and *E. crystallorophias*, respectively. These estimates of  $k$  for *E. superba* are considerably higher

than values for  $k$  of  $0.53 \text{ h}^{-1}$  and  $0.62 \text{ h}^{-1}$  calculated over the full 2 h. period in our study and those found in the literature for *E. superba* also using at least a 2 h cut off (see Table 6). Thus, it is probable that previously reported ingestion rates for *E. superba* using the gut fluorescence method are underestimates.

Our gut evacuation rate estimate for *L. helicina*,  $0.33 \text{ h}^{-1}$ , was similar to previous reports,  $0.25$ – $0.33 \text{ h}^{-1}$  (Hunt et al., 2008; Pakhomov and Froneman, 2004; Pakhomov et al., 2002b) and is one of only a few available in the literature. During our study, *S. thompsoni* had a relatively wide range of gut evacuation rates ( $0.2$ – $1 \text{ h}^{-1}$ ), with an average value of  $0.7 \text{ h}^{-1}$ . This range is typical for the species (see Table 6); Pakhomov and Froneman (2004) found gut evacuation rates for small *S. thompsoni* ( $< 50 \text{ mm}$ ) that ranged from  $0.3$ – $1 \text{ h}^{-1}$ , and in a more recent study, von Harbou et al. (2011) reported values that ranged from  $0.1$ – $0.8 \text{ h}^{-1}$  (for small  $15 \text{ mm}$  and  $25 \text{ mm}$  *S. thompsoni*). Although we were unable to estimate the gut evacuation rates for medium and large-sized salps during our study, results of previous studies suggest that medium-sized salps ( $50$ – $70 \text{ mm}$ ) have gut evacuation rates within the range of those for small salps (Table 6). Thus, our assumption that medium-sized *S. thompsoni* had similar gut

**Table 6**

Literature values of gut evacuation and daily individual ingestion rates for the dominant macrozooplankton, *Euphausia superba* (adults and juveniles), *E. crystallorophias*, *Thysanessa macrura*, *Limacina helicina* and *Salpa thompsoni* (small, medium, and large) in various regions of the Southern Ocean. Values presented were estimated using the gut fluorescence technique. Values obtained during the present study are included for comparison (bold rows).

Taxon	$k$ ( $\text{h}^{-1}$ )	Ingestion rates [ $\mu\text{g}$ equiv. ind. $^{-1}$ day $^{-1}$ ] (Chl- <i>a</i> )	Region
Reference			
<b><i>E. superba</i>, adults</b>	<b>1–1.4</b>	<b>2.6–9</b>	<b>Western Antarctic Peninsula</b>
<b><i>E. superba</i>, juveniles</b>	<b>1.1–1.9</b>	<b>1.4–6.6</b>	<b>Western Antarctic Peninsula</b>
<i>E. superba</i> , adults	0.1–0.4	0.04–3.6	Winter Ice Edge of the Lazarev Sea; South Georgia
<i>E. superba</i> , juveniles	0.5	0.5–0.6	Winter Ice Edge of the Lazarev Sea
<b><i>E. crystallorophias</i></b>	<b>1–1.3</b>	<b>1.3–1.9</b>	<b>Western Antarctic Peninsula</b>
<i>E. crystallorophias</i>	2.3	1–11	Marginal Ice Zone of the Lazarev, Cosmonaut, and Cooperation Seas
<b><i>T. macrura</i></b>	<b>0.5</b>	<b>0.01–0.2</b>	<b>Western Antarctic Peninsula</b>
<i>T. macrura</i>	0.2–0.9	0.08–0.7	Winter Ice Edge and Spring Ice Edge of the Lazarev Sea
<b><i>L. helicina</i></b>	<b>0.3</b>	<b>0.9–2</b>	<b>Western Antarctic Peninsula</b>
<i>L. helicina</i>	0.2–0.3	2–6	Spring Ice Edge of the Lazarev Sea
<b><i>S. thompsoni</i>, small (&lt; 50 mm)</b>		<b>8–27</b>	<b>Western Antarctic Peninsula</b>
<b><i>S. thompsoni</i>, medium (50–70 mm)</b>		<b>27–100</b>	<b>Western Antarctic Peninsula</b>
<b><i>S. thompsoni</i>, large (&gt; 70 mm)</b>		<b>25–240</b>	<b>Western Antarctic Peninsula</b>
<i>S. thompsoni</i> , small (< 50 mm)	0.1–1.0	0.7–140	Antarctic Polar Front of the South Atlantic; Lazarev Sea; Western Antarctic Peninsula
<i>S. thompsoni</i> , medium (50–70 mm)	0.3	37–51	Antarctic Polar Front of the South Atlantic; Spring Ice Edge of the Lazarev Sea
<i>S. thompsoni</i> , large (> 70 mm)		125	Antarctic Polar Front of the South Atlantic
<i>S. thompsoni</i> , size not specified	0.2	0.2–160	Lazarev Sea

<sup>a</sup> Pakhomov and Froneman (2004).

<sup>b</sup> Pakhomov et al. (1997).

<sup>c</sup> Perissinotto and Pakhomov (1996).

<sup>d</sup> Froneman et al. (2000).

<sup>e</sup> Pakhomov and Perissinotto (1996).

<sup>f</sup> Pakhomov et al. (2002b).

<sup>g</sup> Hunt et al. (2008).

<sup>h</sup> Dubischar and Bathmann (1997).

<sup>i</sup> Pakhomov et al. (2006).

<sup>j</sup> von Harbou et al. (2011).

<sup>k</sup> Perissinotto and Pakhomov (1998a,b).

evacuation rates as small individuals is within reason. As far as we are aware, there are no values for  $k$  for large *S. thompsoni* (> 70 mm) in the literature. However, as large *S. thompsoni* constituted on average 1% of total *S. thompsoni* biomass during our study, any potential error in applying  $k$  from small salps to calculate large salp grazing rates would be negligible.

#### 4.2.2. Daily ingestion rates

Average daily ingestion rates for *E. superba* were higher than those reported in the literature (see Table 6), which was expected with higher calculated gut evacuation rates. Despite this, contribution of phytoplankton to their diet was low (mean daily rations of 0.3% body C for adults and 0.5% body C for juveniles; maximum daily rations of 3% for adults and 4% for juveniles). In a recent study, Meyer et al. (2010), present linear relationships between daily rations of Antarctic krill and food availability (phytoplankton biomass). We applied their regression equation for late spring to our phytoplankton biomass data, and predicted mean daily rations of 0.4% (maximum of 4%) for *E. superba*, which corresponds with our own estimated values of daily ration. According to Holm-Hansen and Huntley (1984) the minimum carbon uptake (MCU;  $\mu\text{g C ind.}^{-1} \text{h}^{-1}$ ) required for *E. superba* to meet metabolic demands can be estimated as:  $\text{MCU} = 0.452W^{0.975}$ ; where  $W$  is the dry weight (mg) of an individual krill. In our study, the average dry weight of an adult *E. superba* was 256 mg (47 mm in length), which corresponds to an MCU of 2.4 mg C ind. $^{-1}$  day $^{-1}$ . Similarly, the MCU for juvenile *E. superba* (mean dry weight 102 mg) is 0.98 mg C ind. $^{-1}$  day $^{-1}$ . MCU estimated in this manner equates to a daily loss of  $\sim 1\%$  of body carbon through metabolic processes, which is similar to that reported by Ikeda and Bruce (1986). Throughout the study, the

fraction of MCU consumed as phytoplankton was variable, ranging from < 1% to > 100% for both adults and juveniles. Typically, the fraction of MCU consumed as phytoplankton was greater for juveniles than for adults, suggesting that the adults were more carnivorous. In a study looking at the diet *E. superba* during early winter in the Lazarev Sea, Atkinson et al. (2002) found that adults tended to be more carnivorous than juveniles when phytoplankton concentrations were low. The contribution of phytoplankton to MCU was greatest at the coast in the south and lowest offshore in the north ( $p < 0.05$ ), which suggests that there was a regional difference in the diet of *E. superba*. The phytoplankton community structure of the northern WAP has changed over the last decade, with a shift from a diatom-dominated system in the spring and summer to one dominated by smaller phytoplankton cells, while the southern WAP remains diatom-dominated (Montes-Hugo et al., 2010). *E. superba* typically prefer diatoms over small phytoplankton, and in environments where small phytoplankton dominate, Antarctic krill may shift their diet to preferentially prey upon microzooplankton and copepods (Atkinson and Snýder, 1997; Atkinson et al., 1999; Price et al., 1988; Schmidt et al., 2006). In an analysis of WAP phytoplankton community structure in 2009 using high performance liquid chromatography (O.M.E. Schofield unpublished data), we found diatoms accounted for 33% of the total chlorophyll in the southern coastal region, where total phytoplankton biomass was high. Correspondingly, *E. superba* were largely herbivorous (i.e. high contribution of phytoplankton to MCU) in the south. Conversely, in the northern offshore waters where phytoplankton biomass was low and made up largely of a mixed flagellate and haptophyte community, diatoms accounted for < 10% of the total chlorophyll, and *E. superba* appeared more carnivorous (i.e. low contribution of phytoplankton to MCU), thus feeding on alternate sources of carbon

(Atkinson and Snjyder, 1997; Perissinotto et al., 2000; Price et al., 1988; Schmidt et al., 2006).

Our results for ingestion rates of *E. superba* are within the wide range of those reported in the literature ( $0.4\text{--}358 \mu\text{g}$  (Chl-*a* equiv.) ind.<sup>-1</sup> day<sup>-1</sup>), determined from either the gut fluorescence technique (see Table 6) or other methods; including in vitro feeding experiments, energy budget calculations, model estimations and radiocarbon techniques (Pakhomov et al., 2002a, and references therein). Price et al. (1988) conducted feeding experiments on Antarctic krill that used rates of particle removal in incubation containers to estimate clearance rates and consequently ingestion rates. They plotted ingestion rate against initial chlorophyll concentration resulting in the relationship:  $y = -0.30 + 0.45$  ( $r^2 = 0.98$ ) (Price et al., 1988).

We applied this equation to our own chlorophyll data to calculate ingestion rates for *E. superba* at each station and compared to ingestion rates we obtained using the gut fluorescence technique. There was no significant difference between the two sets of data (Mann-Whitney Rank Sum Test,  $p = 0.612$ ), indicating the two estimates of grazing rates are comparable.

The individual ingestion rates of *E. crystallorophias* and *T. macrura* were at the lower end of the range reported in previous studies (Table 6). Daily rations for these species were also low and it is likely that both were feeding primarily on alternate sources of carbon. The diet of *E. crystallorophias* varies from one that is more carnivorous during early spring to one that is truly omnivorous at the onset of the spring phytoplankton bloom (Pakhomov et al., 1998). As the spring bloom had only just been initiated in the southern coastal WAP during our study, *E. crystallorophias* may still have been feeding more carnivorously. The individual ingestion rates of *L. helicina* were approximately 50% lower than those reported in previous studies (Table 6). However, we did not incorporate gut pigment destruction in our calculation of ingestion rates (see Section 2 for details); taking this into account, we would expect our values to be approximately 50% lower than those reported in the literature (Pakhomov and Froneman, 2004; Perissinotto, 1992). Daily rations of *L. helicina* ranged from 1% to 27%, which suggests that these pteropods are primarily herbivorous, but at times may have been consuming alternative carbon sources. We found no previous reports of *L. helicina* daily rations or energy requirements, but gut content analyses of *L. helicina* indicate that they consume protozoans in addition to phytoplankton (Gilmer, 1974).

Average daily individual ingestion rates of *S. thompsoni* varied considerably both within and between surveys, but were within the spectrum of previously reported values (Table 6) and were higher than the individual ingestion rates of the other dominant macrozooplankton species. *S. thompsoni* is considered to be an important grazer of phytoplankton in the Southern Ocean (Dubischar and Bathmann, 1997; Perissinotto and Pakhomov, 1998a,b) and may present considerable competition to other zooplankton grazers, such as euphausiids (see for example Pakhomov et al., 2002a; Siegel and Loeb, 1995). We found that small and medium sized salps were able to consume up to 119% and 86% of their body carbon in the form of phytoplankton per day, respectively. These values are similar to those observed in the Lazarev Sea during summer (von Harbou et al., 2011). The daily rations of large salps were lower (15%). Since salps are non-selective filter feeders, it is possible that the larger individuals were consuming other sources of carbon (microzooplankton and small copepods) in addition to phytoplankton, thereby reducing the relative contribution of phytoplankton to their carbon uptake (Pakhomov et al., 2006; von Harbou et al., 2011).

#### 4.3. Community grazing rates

Total community grazing rates were greatest in the offshore waters, where *S. thompsoni* occurred in dense blooms. At those

stations, grazing impact on phytoplankton standing stock and primary productivity was substantial, suggesting that salps may have been able to control the phytoplankton stocks; indeed this has been reported in other parts of the Southern Ocean (Perissinotto and Pakhomov, 1998b). Across the coastal-shelf-offshore gradient, we observed a shift in the major grazers, from salps offshore, to *L. helicina* over the shelf and *E. superba* at the coast. There was less of a distinct difference along the north-south gradient. Total grazing rates were significantly higher in the north in 2010, and were elevated in the south during 2009, though the latter was not significant. While salps contributed the most to the community grazing rates in the north during 2010, *E. superba* and *L. helicina* were responsible for much of the overall community grazing in the south during 2009. However, the high grazing rates in the south in 2009 (Fig. 4b) were mostly attributable to a single station with a large salp bloom (Fig. 6).

With the exception of regions where salp blooms occurred (see below), the combined community grazing impacts on the phytoplankton standing stock (<0.3%) and productivity (<0.6%) in the WAP were low compared to 0.6–1.3% (standing stock) and 3.3–15% (primary productivity) reported from previous investigations (Pakhomov and Froneman, 2004; Pakhomov et al., 2002b). In contrast to our study, those investigations included the grazing impact of copepods and focused primarily on mesozooplankton grazing. The possible underestimation of total macrozooplankton grazing impact for our study as a result of excluding large copepods should be taken into account. However, we expect that this underestimation is minor for macrozooplankton, since during our study copepods accounted for an average of 5% of total macrozooplankton biovolume. Mesozooplankton, such as smaller copepods that can have a high grazing impact relative to their contribution to biomass (Bernard and Froneman, 2005), as well as microzooplankton, community grazing impact will be a focus of our future studies in the WAP.

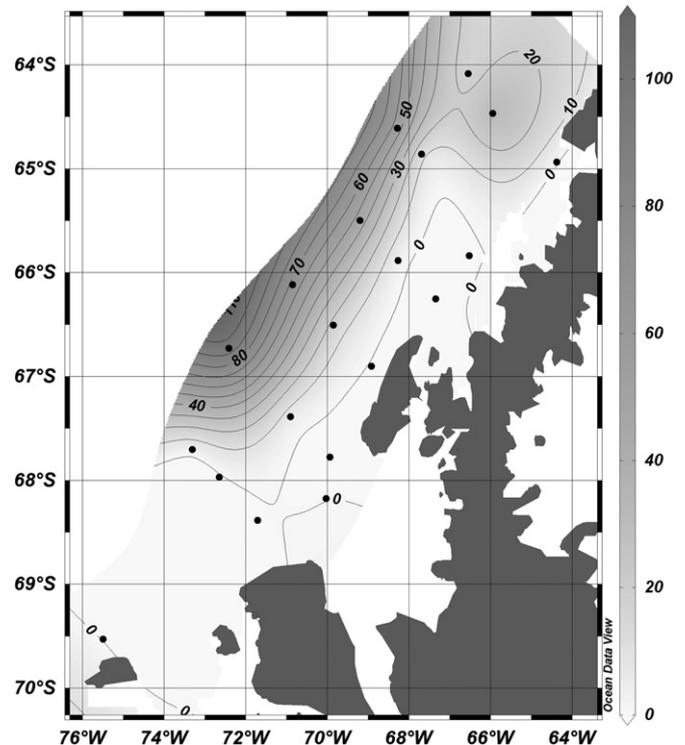


Fig. 6. Relative contribution (%) of *Salpa thompsoni* to total grazing rates during January 2009. Stations occupied during 2009 are represented by solid circles.

The presence of *S. thompsoni* at bloom densities resulted in a substantial increase in grazing impact (up to 30% of the phytoplankton standing stock and 169% of the primary productivity) in the southern offshore waters during 2009 and the northern offshore waters during 2010. A marked increase in grazing impact in the presence of salps has been observed in other parts of the Southern Ocean, such as the Lazarev Sea, where total grazing impact increased from < 1 to 16% of phytoplankton standing stock and from 5 to 50% of primary productivity due to salps (Pakhomov and Froneman, 2004; Pakhomov et al., 2002b). We note that salp blooms typically occurred in regions of lower primary productivity, which might explain the elevated grazing impact in those regions. There are two possible reasons for the negative correlation between salp densities and phytoplankton biomass: the first is that regions of low phytoplankton biomass may be more favorable for salps that can clog their mucous feeding apparatus in the presence of dense phytoplankton blooms (Alldredge and Madin, 1982); the second is that grazing pressure by salps may have been sufficient to control phytoplankton productivity by suppressing the standing stock.

While phytoplankton standing stocks and primary production during January 2009 (values recorded at stations ranged from 16–107 mg Chl-*a* m<sup>-2</sup> and 0.2–2 g C m<sup>-2</sup> day<sup>-1</sup>, respectively) fell within the range of what has been historically recorded for the WAP during past LTER surveys (Vernet et al., 2008), both were significantly higher during January 2010 ( $p < 0.05$ ; range = 25–614 mg Chl-*a* m<sup>-2</sup> and 1–28 g C m<sup>-2</sup> day<sup>-1</sup>, respectively). The duration of the winter sea ice season of the preceding year (i.e., winter of 2009) was long, with a late sea ice retreat (S. Stammerjohn, pers. comm.). It is thus likely that we sampled the early season phytoplankton bloom in 2010. Abundances of the dominant macrozooplankton were lower during 2010; thus we posit that the zooplankton community had not yet had sufficient time to respond to the phytoplankton bloom that year, and the relatively lower community grazing impact in 2010 was a result of low ratio of zooplankton biomass (and subsequently grazing) to phytoplankton standing stocks and productivity.

## 5. Conclusion

Long-term data indicate that the WAP is warming rapidly—ocean heat content over the shelf and coastal waters has risen, and sea ice duration has declined, and plankton communities are changing as a result (Ducklow et al., in press). As has become evident throughout the high Antarctic, salp densities are increasing and their distribution ranges are expanding, while that of Antarctic krill is decreasing (Atkinson et al., 2004; Loeb et al., 1997; Pakhomov et al., 2002a). We found that salps, with their high ingestion rates, were capable of significantly changing the macrozooplankton community grazing impact, and potentially controlling primary productivity by suppressing phytoplankton standing stocks. This finding has substantial ramifications; in an increasingly warmer WAP, we predict that salps could become key grazers and represent major competition for Antarctic krill. We note, though, that there were differences in community structure and grazing impact between the two years; the causes of this inter annual variability still need to be fully understood. Sea ice, a major driver of macrozooplankton community structure in Antarctica (Atkinson et al., 2004; Loeb et al., 1997), shows substantial variability between years in the WAP (Stammerjohn et al., 2008a). Elevated abundances of *S. thompsoni* during January 2009 could have been due to the particularly short sea ice season of winter 2008, which was followed by an early and rapid sea ice retreat (S. Stammerjohn, pers. comm.). *E. superba* densities are also closely correlated with sea ice, and the impacts of a particular ice season will influence krill larval recruitment the following season (Siegel and Loeb, 1995). Antarctic krill densities fluctuate from year to year

(Siegel and Loeb, 1995); during high density years we still expect krill to be important grazers, as they were at the coast during 2009. We also found that *L. helicina* contributed significantly to total grazing in some regions, particularly over the shelf. While this is not necessarily surprising considering recent publications highlighting the role of thecosome pteropods as grazers in the Southern Ocean (Bernard and Froneman, 2009; Hunt et al., 2008), *L. helicina* has historically not been considered as an important grazer in the WAP. Our results highlight the key role that this species plays in the pelagic food web of the WAP; this has important implications as *L. helicina* is likely to be strongly affected by ocean acidification (Orr et al., 2005).

Finally, changes in grazing and thus energy transfer in the WAP plankton food web, such as more energy funneling through gelatinous salps but away from more nutritious krill, may ultimately result in decline or range changes of higher trophic level predators (penguins, seals, and whales).

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