



The seasonal cycle of the Lazarev Sea macrozooplankton community and a potential shift to top-down trophic control in winter

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ABSTRACT

Between 2004 and 2008, during the German Southern Ocean GLOBEC programme, four large scale bio-oceanographic surveys were conducted in the Lazarev Sea for the Lazarev Sea Krill Survey (LAKRIS). These surveys were completed in Autumn (April–May) 2004, Summer (December–January) 2005/06, Winter (July–August) 2006, and Summer (December–January) 2007/08. On each occasion macrozooplankton communities were sampled by RMT-8 in the upper 200 m of the water column. Chlorophyll *a* biomass averaged $\sim 1.5 \text{ mg m}^{-3}$ (max = 8.2 mg m^{-3}) in Summer 05/06, 0.88 mg m^{-3} (max = 2.77 mg m^{-3}) in Summer 07/08, 0.24 mg m^{-3} (max = 0.73 mg m^{-3}) in Autumn 04, and 0.042 mg m^{-3} (max = 0.1 mg m^{-3}) in Winter 06. Macrozooplankton densities did not differ significantly between seasons and were 53, 68, 59, and 48 ind. 1000 m^{-3} in Summer 05/06, Summer 07/08, Autumn, and Winter, respectively. Total macrozooplankton biomass, however, increased significantly from summer (0.88 and $0.97 \text{ g dry weight } 1000 \text{ m}^{-3}$ in Summer 05/06 and Summer 07/08, respectively) to Autumn 04 ($2.66 \text{ g dry weight } 1000 \text{ m}^{-3}$) and Winter 06 levels ($1.75 \text{ g dry weight } 1000 \text{ m}^{-3}$). This biomass increase was due to both an increased occurrence of *Euphausia superba* and fish and a shift to a larger size structure in the latter group. Siphonophores (predominantly *Diphyes antarctica*), chaetognaths (predominantly *Eukrohnia hamata* and *Sagitta gazellae*) and euphausiids (predominantly *Thysanoessa macrura* and *E. superba*) contributed $> 80\%$ to total densities in all four surveys. However, a strong and distinctive change in assemblage structure was observed between seasons. Key amongst these was a shift within the euphausiids from a dominance of *T. macrura* in summer to that of *E. superba* in autumn and winter; a winter decrease in *E. hamata*; an autumn and winter decrease in *Tomopteris* sp.; and a winter increase in the abundance of the grazers *Clio pyramidata sulcata* and *Ilhlea racovitzai*, hyperiids, and the myctophid fish *Electrona antarctica*. Carnivorous macrozooplankton formed the major trophic group in all seasons, contributing 44–60% to total macrozooplankton abundance and 39–58% to total macrozooplankton biomass in all four surveys. The combined predation pressure of carnivores and potential increased winter carnivory by *E. superba* and other omnivorous species, was expected to be high. In view of low winter primary production, we suggest that the epipelagic food web of the Lazarev Sea shifted from being bottom-up controlled in summer to top-down controlled in winter.

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1. Introduction

The Antarctic is a highly seasonal environment because of a pronounced annual cycle of solar radiation, and consequently heat and light (Murphy et al., 2007). The seasonal temperature cycle causes an average change in sea-ice extent from twenty million km^2 in winter to four million km^2 in summer (Gloersen and Campbell, 1991; Zwally et al., 2002). Although during the summer growth season phytoplankton production is controlled by iron and macronutrients, the seasonal cycle of light imposes a strong annual

primary production regime characterised by substantial reductions from summer to winter (Knox, 2006). This seasonal cycle of primary production is probably the most significant biological factor affecting the heterotrophic pelagic community.

Because of the logistical difficulties of sampling in heavy sea-ice cover, zooplankton data from winter are rare in the Southern Ocean and, as a consequence, so are data on the full seasonal cycles of biota. Of the seasonal studies that have been conducted the majority are species specific and have focussed on just a few taxa, including *Euphausia superba* and the large calanoid copepods *Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei*, and *Rhincalanus gigas*. These studies have considered the aspects of seasonal vertical distribution (Schnack-Schiel et al., 1998; Atkinson and Sinclair, 2000), life cycle (Atkinson, 1998; Nicol, 2006), and

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overwintering strategies (feeding and metabolic activity) (Frazer et al., 2002; Daly, 2004).

Seasonal data on zooplankton communities, in combination with species biological data, are essential for an understanding of the entire ecosystem's functioning, including trophic pathways and interactions (primary and secondary consumption), carbon flow and carbon cycling, factors affecting overwintering strategies, and the effect of winter processes on spring community structure (Cornejo-Denoso and Antezana, 2008). The trophic level (diet) of a species is a major determinant of the food available to it over the seasons and is a key driver of overwintering strategies. Accordingly, Torres et al. (1994) identified three types of overwintering strategy:

Type 1—Accumulate lipid reserves and diapause with reduced metabolic activity (herbivores).

Type 2—Reduced metabolism with opportunistic feeding (omnivores).

Type 3—Business as usual (carnivores).

In the absence of in situ metabolic and feeding data, knowledge of a species trophic level can therefore provide useful insights into its seasonal activity.

A review of the Southern Ocean/Antarctic literature found a small number of seasonal studies on macrozooplankton. Data from the Antarctic Peninsula region demonstrated, in general, that there was little seasonal variability in community structure and a dominance of *E. superba* in summer and that of *Salpa thompsoni* in autumn and winter, with other important species being the chaetognath *Eukrohnia hamata* and the euphausiid *Thysanoessa macrura* (Siegel and Piatkowski, 1990). In the Weddell Sea/Scotia Sea abundance was dominated by, in order of decreasing abundance, *E. superba*, *T. macrura*, the chaetognaths *Sagitta gazellae* and *E. hamata*, and *S. thompsoni*, while biomass was dominated by mesopelagic fish and *E. superba* (Hopkins et al., 1993; Lancraft et al., 1991—both in case of the same survey). In the Prydz Bay region the macrozooplankton community was similarly dominated by euphausiids and chaetognaths (Hosie and Stolp, 1989). It is significant that the latter study found an actively reproducing community in September/October that did not differ significantly from the summer community.

The Lazarev Sea is located to the east of the Weddell Sea, centred approximately on the Greenwich Meridian (Fig. 1), in the southern, westward flowing branch of the Weddell gyre. The region is seasonally ice covered with a maximum northern sea-ice extent of $\sim 56^\circ\text{S}$ Turner et al., 2004). A summer survey (January–February) conducted in 1990 found a macrozooplankton community that was numerically dominated by *E. hamata* and *T. macrura*, while biomass was dominated by the gelatinous taxa *S. thompsoni* and siphonophores (Pakhomov et al., 1994). Although elevated primary production was measured at the seasonal ice edge (60°S) in December–January 1997/98 (Froneman et al., 2004), mesozooplankton abundance was low in comparison to levels prevalent in

the Permanently Open Ocean Zone to the north (Pakhomov and Froneman, 2004a), with a correspondingly low grazing impact (Pakhomov and Froneman, 2004b).

The 1990 Lazarev Sea macrozooplankton survey indicated that the region was characterised by a low summer biomass of *E. superba*, although these data need to be viewed with some caution as they were collected with a small mouth area Bongo net, which is likely to have under sampled large active macrozooplankton (Pakhomov et al., 1994). Between 2004 and 2008, during the German Southern Ocean GLOBEC programme, four voyages were completed for the Lazarev Sea Krill Survey (LAKRIS). Using a large-mouth-area rectangular midwater trawl, the LAKRIS programme included two summer, one autumn, and one winter surveys (Fig. 1). To our knowledge these are the first detailed seasonal data on the macrozooplankton collected in this region of the Southern Ocean. In this paper we investigate the seasonal cycle of the macrozooplankton community, its size structure, and, based on species trophic level, discuss the implications for the food web structure of the Lazarev Sea ecosystem.

2. Methods

The LAKRIS surveys were conducted in Autumn 2004, Summer 2005/06, Winter 2006, and Summer 2007/08 (Table 1). Stations were organised in a regular grid made up of three to four meridional sections running between 60°S and 70°S and between 6°W and 3°E (Figs. 1 and 4). At each station vertical profiles of conductivity, temperature, and depth were collected with a Sea-Bird Electronics SBE 911 plus CTD, to a minimum depth of 1000 m. Total chlorophyll *a* was measured from discrete depths in the upper 200 m of the water column at each station. At least 300 ml of water was filtered through a 25 mm GF filter. The filter was then placed in a tube filled with 10 ml of 90% acetone and was pigment-extracted for at least 24 hours in a -20°C freezer. The supernatant was used to measure chlorophyll *a* with a Turner 700D fluorometer. We present near-surface chlorophyll *a* collected from 5, 10, 10, and 20 m in Summer 05/06, Summer 07/08, Autumn 04, and Winter 06, respectively.

Macrozooplankton samples were collected using an 8-m² Rectangular Midwater Trawl (RMT-8) mounted with a flowmeter for volume filtered determination. The RMT-8 was harnessed with a 4.5 mm mesh, although the last 1–2 m were 1.5 mm and the cod-end 0.85 mm (Clarke, 1969). Net tows were conducted at a speed of ~ 2.5 kn and were completed as double oblique hauls in the upper 200 m of the water column. Samples were preserved in a ~ 4 –5% buffered formaldehyde seawater solution and were returned to the laboratory for processing. Macrozooplankton were identified to the species level wherever possible. Rare species were identified and counted from the whole sample and common species were counted from sub-samples made using a Folsom splitter (McEwen et al., 1954). Copepods were not considered in the analysis as they are not quantitatively sampled, if at all, by the large mesh RMT-8. All macrozooplankton specimens were measured and placed into 5 mm size bins, starting at 2.5 mm. Macrozooplankton abundance was calculated as individuals 1000 m^{-3} and was entered into a sample by species matrix. Macrozooplankton biomass was calculated using

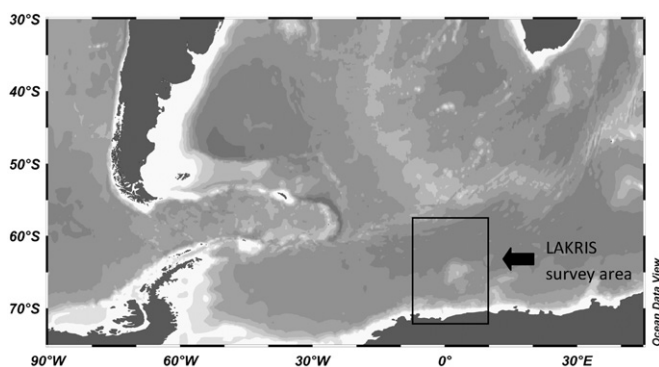


Fig. 1. Location of LAKRIS survey area in the Lazarev Sea.

Table 1

Sampling dates and number of RMT-8 macrozooplankton samples collected during each LAKRIS survey.

Voyage name	Season	Dates of sampling	No. of samples
ANT-XXI/4	Autumn	19–26 April 2004	26
ANT-XXIII/2	Summer	6 December–1 January 05/06	19
ANT-XXIII/4	Winter	26 June–12 August 2006	48
ANT-XXIV/2	Summer	21 December–21 January 07/08	50

known length weight relationships and was expressed as mg dry weight 1000 m^{-3} (Mizdalski, 1988; E. Pakhomov, unpublished data).

2.1. Analysis

Variation in Lazarev Sea macrozooplankton assemblage structure was investigated using multivariate methods. Species densities were $\log_{10}(x+1)$ transformed and the percentage similarity between stations, from all surveys, was calculated using the Bray–Curtis similarity index (Field et al., 1982). The similarity matrix was then subjected to a Q-type cluster analysis using the un-weighted pair group average sorting method (UPGMA). A two-dimensional ordination was produced using non-metric multidimensional scaling (NMDS) so as to confirm the station groupings generated by the cluster analysis. Subsequently, Simper analysis was used to identify the macrozooplankton taxa contributing to 90% of the within group similarity. All multivariate analyses were performed using PRIMER 5 (Clarke and Warwick, 2001). The contributions of latitude, longitude, 200 m integrated temperature, and chlorophyll biomass (from the depths described above) towards the structuring of the macrozooplankton community were tested by multiple regression using the first two dimensions of the NMDS ordination as the independent variables and the environmental measures as the dependent variables (Hosie and Cochran, 1994).

ANOVA was used to test for significant differences between seasons in $\log_{10}(x+1)$ total macrozooplankton abundance and biomass. Where significant differences were detected a Neumann–Keuls multiple-range test was used to investigate seasonal differences. Light was expected to have a significant effect on vertical zooplankton distributions. As light has a strong seasonality and as some macrozooplankton are known to undergo seasonal migrations, we investigated the interactive affects of light and season using a two-way factorial ANOVA. ANOVA was performed using Statistica 6.

Lastly, macrozooplankton were divided into four trophic groups: herbivores, omnivorous herbivores, omnivorous carnivores, and carnivores for comparison of the trophic structure of macrozooplankton assemblages between surveys. Omnivorous herbivores were defined as species that are predominantly herbivorous, but may supplement their diet with metazoan prey, while omnivorous carnivores feed predominantly on metazoans, but may supplement their diet with phytoplankton. Trophic groups were determined

from Hopkins et al. (1993), Hopkins (1987), Hopkins and Torres (1989), or otherwise based on the known trophic affinities of taxonomic groups. The trophic groups that macrozooplankton were assigned to are indicated in Appendix A.

3. Results

The largest part of the LAKRIS survey area is characterised by an inflow of water of circumpolar origin with the southern, westward setting branch of the Weddell Gyre. The Weddell Gyre centre line, the transition to the eastbound flow, was located to the north of the LAKRIS survey grid during all surveys except in Summer 07/08. The inflowing water mass of a circumpolar origin is termed Warm Deep Water (WDW), after the nomenclature of Carmack and Foster (1975), or Upper Circumpolar Deep Water (UCDW, Orsi et al., 1993), and it forms a temperature maximum layer between 200 and 400 m. The result of water mass advection is therefore most clearly revealed by the distribution of temperature at the depth of the temperature maximum.

The lowest temperatures in the temperature maximum layer were generally $\theta > 0.4\text{ }^{\circ}\text{C}$, which were hence well above $0.0\text{ }^{\circ}\text{C}$, indicating waters of the WDW (see Fig. 2 in Pakhomov et al., 2011). The temperature maximum descended very steeply at the Antarctic Slope Front (ASF), at $\sim 69^{\circ}\text{S}$, and disappeared to the south of that front. South of the ASF, the Coastal Current (CC) dominated and cold water of $\theta < -1\text{ }^{\circ}\text{C}$ extended down to below 500 m depth. The cold CC waters were clearly evident in the distribution of 200 m integrated temperature values (Fig. 4). The ASF appeared to be located further north in the summer surveys than it was in Autumn 04 and Winter 06. Apart from the westerly flowing CC, only one other persistent strong current was found in the LAKRIS area, a jet restricted to the northern topographic slope of Maud Rise. Mesoscale eddies forming in the lee of this sea mount propagated in a south/south-westerly direction. Integrated temperature (200 m) was similar across Summer 05/06, Summer 07/08, and Winter 06, generally ranging between -0.5 and $-1\text{ }^{\circ}\text{C}$ (Fig. 4). A region of relatively warm water (-0.5 to $0\text{ }^{\circ}\text{C}$) was evident along the Greenwich meridian at $\sim 66^{\circ}\text{S}$ in all three of the aforementioned surveys. In Autumn 04 this warmer water was pervasive between 66 and 68°S .

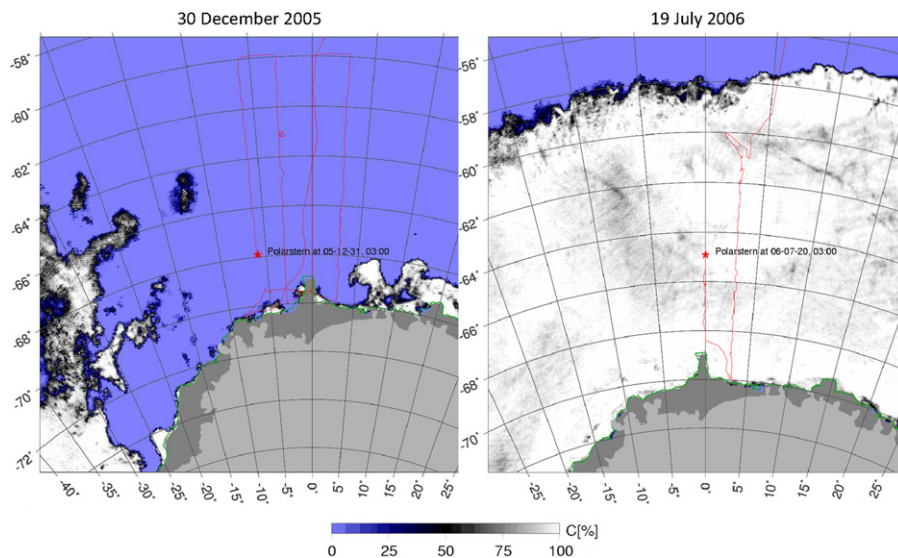


Fig. 2. Sea-ice concentrations in the eastern Weddell Sea during two of the LAKRIS surveys, Summer 05/06 and Winter 06. Sea Ice charts were computed by the Institute of Environmental Physics at the University of Bremen using the ARTIST Sea Ice algorithm (ASI) from the 89 GHz AMSR-E channels. The red line indicates the cruise track of R.V. *Polarstern* (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

The surface mixed layer depth ranged between 4 and 49 m in Summer 05/06 and between 4 and 44 m in Summer 07/08, whereas it ranged between 12 and 204 m in Autumn 04 and between 30 and 453 m in Winter 06. Substantial seasonal variation in sea-ice extent was observed in the LAKRIS study area (Fig. 2). It was almost ice-free in Summer 05/06 and Summer 07/08. Significant amounts of sea ice occurred south of 68°S in Autumn 04 and a substantial pack-ice cover was present throughout the entire area in Winter 06 (Fig. 2).

The LAKRIS study area lies between 60° and 70°S. The hours of daylight, calculated between sunrise and sunset, ranged between 18.4 hours during summer and 5.5 hours during winter at 60°S, and between 24 hours during austral summer and zero hours during winter at 70°S. As would be expected with surveys operated around the clock, the majority of summer samples (> 75%) were completed during daylight in summer (Fig. 3A). Conversely, in winter the majority of samples were collected in darkness (> 75%). Chlorophyll *a* biomass was highest in summer averaging ~1.5 mg m⁻³ and reaching up to 8.2 mg m⁻³ in Summer 05/06, and averaging 0.88 mg m⁻³ and reaching up to 2.77 mg m⁻³ in Summer 07/08 (Fig. 3B). Autumn chlorophyll *a* biomass averaged 0.24 mg m⁻³, with a maximum of 0.73 mg m⁻³, while the lowest chlorophyll *a* biomass was recorded in winter, averaging 0.042 mg m⁻³ with a maximum of 0.1 mg m⁻³.

Total macrozooplankton abundance showed no significant difference between seasons (ANOVA of log₁₀(x+1) transformed abundance) and were 53, 68, 59, and 48 ind. 1000 m⁻³ in Summer 05/06, Summer 07/08, Autumn 04, and Winter 06, respectively (Fig. 3C). Total macrozooplankton biomass, however, increased from summer to winter and differed significantly between seasons (ANOVA; *p* < 0.0001). Biomass levels were found to be 0.88 and 0.97 g dry weight 1000 m⁻³ in Summer 05/06 and Summer 07/08, respectively. Autumn 04 (2.66 g dry weight 1000 m⁻³) and Winter

06 levels (1.75 g dry weight 1000 m⁻³) were significantly higher than those recorded in summer (Fig. 3D).

Multivariate cluster analysis identified four macrozooplankton assemblages (Fig. 4), and this grouping was supported by the NMDS ordination (Fig. 5). Multiple regression analysis found no significant relationship between the first two dimensions of the NMDS ordination and latitude, longitude, or 200 m integrated temperature. This indicated that there was no consistent spatial pattern to macrozooplankton assemblage distribution or association of macrozooplankton changes with different water masses. However, both dimensions were significantly correlated with chlorophyll biomass (*F* = 11.80; *p* < 0.001).

Simper analysis demonstrated that there was a high degree of similarity in the dominant species between seasons (Fig. 5). Differences between clusters were largely determined by different abundance levels of a small suite of taxa, key amongst those being the siphonophore *Diphyes antarctica*, the euphausiids *T. macrura* and *E. superba*, and the chaetognaths *S. gazellae* and *E. hamata*. Cluster 1 was present in all surveys, particularly in the southern part of the survey area in Summer 07/08. Cluster 1 was characterised by relatively high densities of *Pyrostephos vanhoeffeni*, *Calyropsis borchgrevinki*, *Hyperietta dilatata*, and *T. macrura*, but low densities of most other taxa. Cluster 2 included the majority of Autumn 04 and Winter 06 samples. This cluster had the highest densities of *S. gazellae* (14.41 ind. 1000 m⁻³) and relatively high densities of *E. superba* (6.58 ind. 1000 m⁻³). *Clio sulcata*, *Notolepis coatsi*, *Cylopus lucasii*, and *Electrona antarctica* made a greater contribution to similarity within cluster 2 than to any other cluster. Cluster 3 comprised the majority of Summer 05/06 and Summer 07/08 samples, and was characterised by the highest densities of *T. macrura* (35.67 ind. 1000 m⁻³) and chaetognaths (*S. gazellae* and *E. hamata*). Cluster 4 comprised a small number of predominantly winter and autumn samples that had high densities of *E. superba* (118.02 ind. 1000 m⁻³) and *D. antarctica* (28.30 ind. 1000 m⁻³).

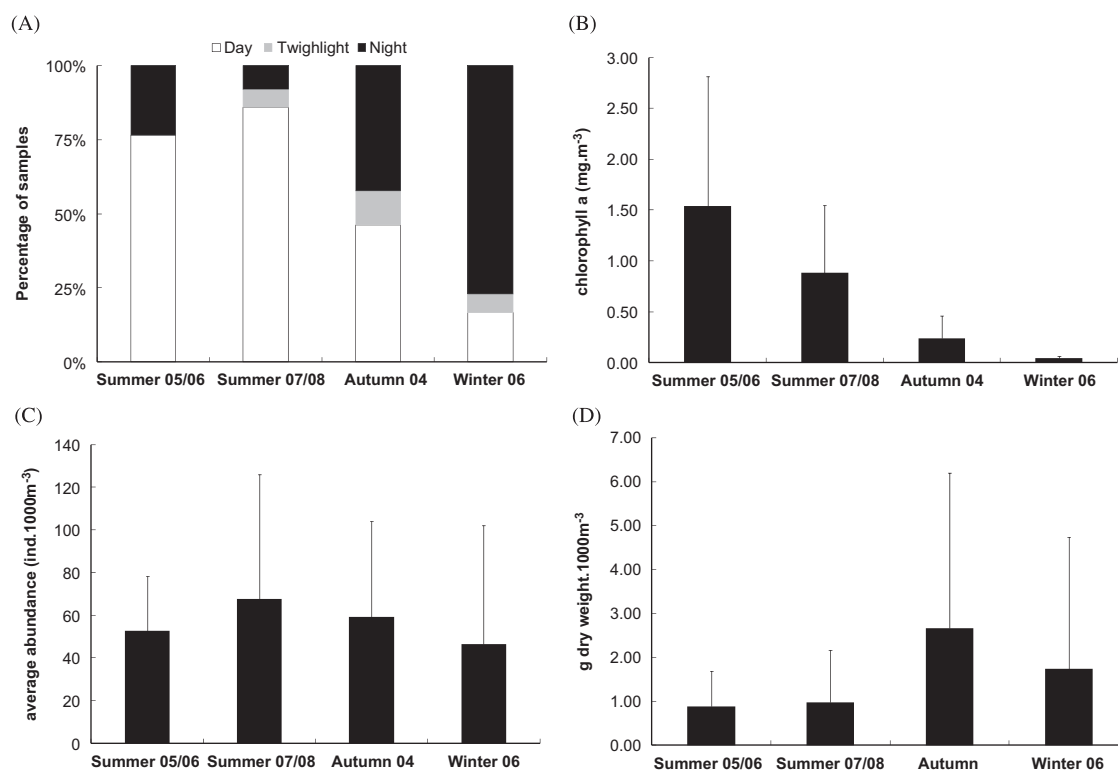


Fig. 3. (A) Percentage of samples collected in daylight, twilight, and at night; (B) surface chlorophyll *a* biomass (mg m⁻³); (C) average and standard deviations of macrozooplankton abundance (individuals 1000 m⁻³); and (D) average and standard deviations of macrozooplankton biomass (g dry weight 1000 m⁻³) for each of the four LAKRIS surveys. Samples for total chlorophyll *a* were collected from 10, 5, 20, and 10 m in Autumn 04, Summer 05/06, Winter 06, and Summer 07/08, respectively. Zooplankton were collected by double oblique tows to 200 m.

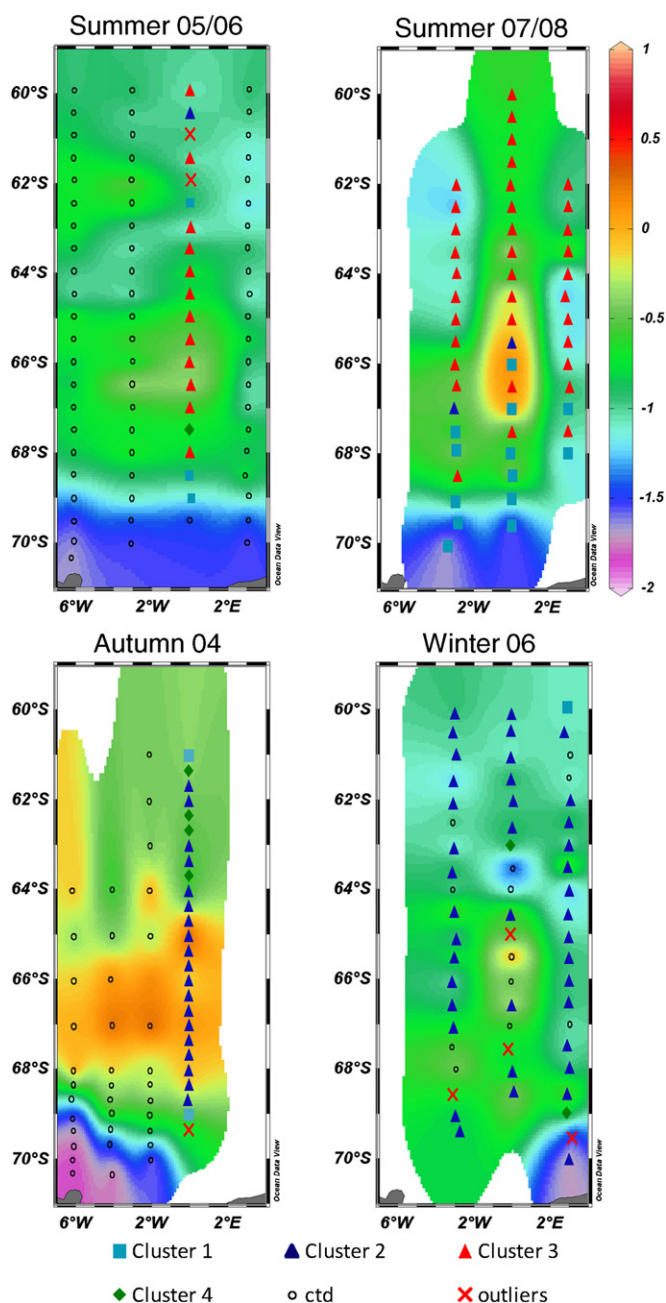


Fig. 4. The spatial distribution of sample clusters identified after cluster analysis of macrozooplankton samples. Stations where only physical parameters (no nets) were measured are indicated by open circles. The stations grid for each season is overlaid on contours of integrated temperature (°C) for the upper 200 m of the water column.

Of the macrozooplankton taxa contributing to 90% of the within group similarity only *C. lucasii*, *I. racovitzae*, and *N. coatsi* abundances were significantly ($p < 0.05$) affected by light (time of day), these species occurring at a higher abundance in night samples. The abundance of the euphausiids *E. superba* and *T. macrura*, the pteropod *Clione limacina antarctica*, and the polychaete *Tomopteris* sp. were significantly affected by season, with *T. macrura*, *C. limacina antarctica*, and *Tomopteris* sp. having significantly higher abundance in summer and *E. superba* having significantly higher abundance in autumn and winter. The abundance of the pteropod *Clio pyramidata sulcata* and the siphonophore *P. vanhoeffeni* both demonstrated a significant light/season interaction, the hyperiid *Primno macropa* a significant light and light/season interaction, while the fish

E. antarctica was significantly affected by light, season, and the season/light interaction.

Total siphonophore abundance ($15\text{--}20$ ind. 1000 m^{-3}) was similar between seasons (Fig. 6; Appendix A), contributing $\sim 33\%$ to total macrozooplankton abundance in Summer 05/06, Autumn 04, and Winter 06, and 24% in Summer 07/08. Siphonophores were dominated by the species *D. antarctica*, which was similarly abundant in all surveys, with a minor contribution from *P. vanhoeffeni* (Fig. 6).

Chaetognath abundance averaged ~ 11 ind. 1000 m^{-3} in Summer 05/06, Summer 07/08, and Autumn 04, with *E. hamata* and *S. gazellae* each contributing approximately half to total chaetognath numbers (Fig. 6). Chaetognaths proportionally contributed 22%, 16%, 20%, and 9% to total macrozooplankton abundance in Summer 05/06, Summer 07/08, Autumn 04, and Winter 06, respectively. Reduced abundance in winter (4.1 ind. 1000 m^{-3}) was largely due to the greatly reduced abundance of *E. hamata* (Fig. 6).

Total euphausiid abundance was similar in Summer 05/06, Autumn 04, and Winter 06, averaging $17\text{--}18$ ind. 1000 m^{-3} , and representing 33%, 32%, and 37% of the total macrozooplankton abundance in each season, respectively (Fig. 6). Abundance was twice as high in Summer 07/08, reaching 35 ind. 1000 m^{-3} and 52% of total macrozooplankton abundance. The seasonal contribution of species reflected the results of the community analysis (Figs. 4 and 5). Both summer surveys were dominated by *T. macrura*, and it was the increased abundance of this species that contributed to the high total euphausiids' abundance in Summer 07/08. *E. superba* abundance was low in both summer surveys; however, in autumn and winter it contributed the most to the total euphausiid abundance, while *T. macrura* was scarce. The two other euphausiid species that were collected, *E. frigida* and *E. crystallorophias*, were rare in all surveys.

Fish abundance was at its highest in autumn and winter (> 1 ind. 1000 m^{-3}) and at its lowest in summer. Although 11 species of fish were sampled, total abundance was dominated by *E. antarctica* and *N. coatsi* and it was the low summer abundance of these species that caused the reduction in total fish abundance levels (Fig. 6).

Pteropod abundance was at its highest in Summer 05/06 averaging 1.8 ind. 1000 m^{-3} , decreasing to ~ 1 ind. 1000 m^{-3} in Summer 07/08, Autumn 04, and Winter 06. The thecosome pteropod *C. pyramidata sulcata* was an important contributor to the total pteropod abundance during all seasons, but was particularly so in autumn and winter (Fig. 6). Summer 05/06 exhibited high abundances of *Limacina helicina antarctica* and *C. limacina antarctica*. *L. helicina antarctica* was almost absent in autumn and winter, while *C. limacina antarctica* occurred at low abundance. The relative contributions of pteropod species in Summer 07/08 was similar to that in Summer 05/06; however the abundances of *L. helicina antarctica*, *C. limacina antarctica*, and *C. pyramidata sulcata* were somewhat lower.

Salp (Thaliacea) abundance was lowest in the summer surveys, averaging ~ 0.5 ind. 1000 m^{-3} , and increasing to ~ 2 ind. 1000 m^{-3} in autumn and winter (Fig. 6). Abundance was dominated by *Ihleia racovitzae* in all seasons with the exception of autumn, where *S. thompsoni* made the largest contribution to the total salp abundance.

Polychaete abundance was highest in summer and declined through autumn and winter, mostly because of a decline in the abundance of *Tomopteris* sp. Summer 07/08 differed from all other seasons that were sampled in that it had a high abundance of the species *Rhynchonerella bongraini*.

Hyperiid were the most species rich macrozooplankton group (15 species). Average hyperiid abundance was at its highest in Autumn 04 and Winter 06, averaging ~ 2.5 ind. 1000 m^{-3} compared to the value of ~ 1 ind. 1000 m^{-3} in Summer 05/06 and that of 0.5 ind. 1000 m^{-3} in Summer 07/08 (Fig. 6). Low summer

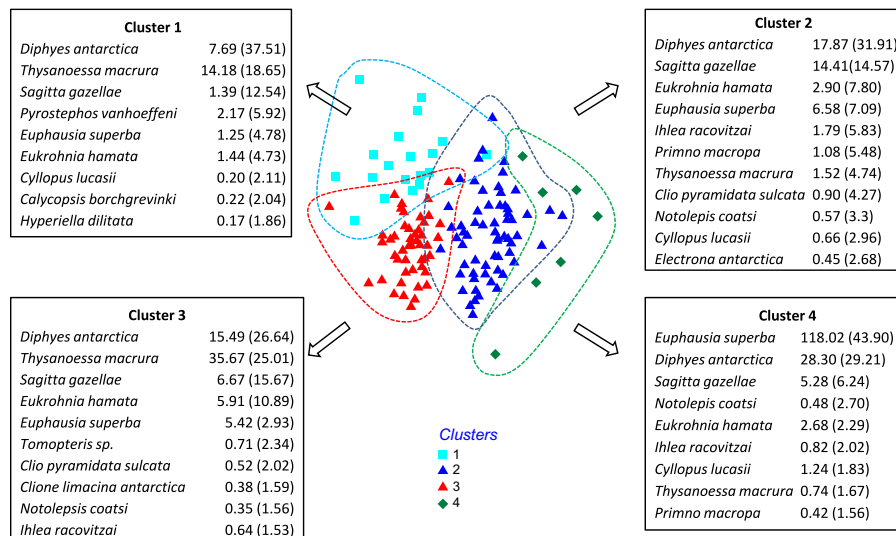


Fig. 5. Two-dimensional NMDS ordination (stress value=0.19) of macrozooplankton stations using the same similarity matrix as the cluster analysis. Stations are colour coded according to the four groupings identified by the cluster analysis. The species identified as contributing 90% to within cluster similarity are indicated for each cluster with individual species abundance (ind. 1000 m⁻³) and percentage contribution to similarity in parenthesis.

abundance was largely due to the low densities of *C. lucasii*, *Hyperoche capucinus* and *P. macropa*.

The size frequency distribution of the macrozooplankton community was similar between surveys (Fig. 7A). However, Autumn 04 and Winter 06 had a higher abundance of macrozooplankton larger than 27.5 mm, a feature also evident in the percentage contribution of macrozooplankton to abundance (Fig. 7B). The majority of macrozooplankton were in the size range 12.5–25 mm. Autumn 04 had a distinct abundance peak at 37.5 mm, primarily because of a large contribution of *E. superba* (Fig. 7B). In terms of biomass spectra, all surveys showed a similar distribution up to 27.5 mm. At sizes greater than 27.5 mm Summer 07/08 had the lowest biomass, followed by Summer 05/06. Autumn 04 and Winter 06 had a similar biomass contribution between sizes of 27.5 and 85 mm (Fig. 7C). There was greater variation in the percentage biomass contribution of size classes than in abundance; however the higher contribution of size classes larger than 27.5 mm was again evident in case of Autumn 04 and of Winter 06 (Fig. 7D).

Overall there was no substantial variation in the size structure of individual species' populations sampled by the RMT-8. The larger contribution of macrozooplankton of more than 32.5 mm length in Autumn 04 and Winter 06 was attributable to the larger sizes of the fish *E. antarctica* and *N. coatsi*, particularly in Autumn 04, as well as to the higher contribution of *E. superba* (Fig. 8). The *E. antarctica* that were caught in the summer surveys were predominantly larval stages. *E. superba* showed similar size frequency distributions in Summer 07/08, Autumn 04, and Winter 06, but had a strong bimodal distribution in Summer 05/06. *C. borchgrevinkii*, *D. antarctica*, and *S. gazellae* showed no seasonal change in size frequency distribution. *P. macropa*, *Tomopteris* sp., *T. macrura*, and *E. hamata* were slightly larger in Summer 05/06 than they were in other surveys, while *C. pyramidata sulcata* and *C. limacina antarctica*, *H. dilatata*, and *P. vanhoeffeni* were larger in Summer 07/08.

Carnivorous macrozooplankton contributed > 50% to accumulative abundance in Summer 05/06, in Autumn 04, and in Winter 06 (Fig. 9). In Summer 07/08 carnivores and omnivorous carnivores were equally abundant (44% and 46%, respectively), and the latter group were also relatively abundant in Summer 05/06 (30%). Carnivores comprised predominantly siphonophores and chaetognaths (Appendix A) while omnivorous carnivores comprised predominantly *T. macrura*. Entirely herbivorous macrozooplankton were

a consistently small component of the community, contributing between 3% and 7% to total abundance. Amongst omnivorous species a shift was observed from predominantly omnivores carnivores in summer to predominantly omnivorous herbivores in autumn and winter (Fig. 9). This largely reflected the shift within the euphausiids from being dominated by the omnivorous carnivore *T. macrura* in summer to being dominated by the omnivorous herbivore *E. superba* in winter.

A dramatic change in the contribution of trophic groups did not occur when biomass was considered. Carnivores remained the dominant group in Summer 05/06, in Autumn 04, and in Winter 06, contributing between 49 and 58% to total macrozooplankton biomass (Fig. 9). In Summer 07/08 omnivorous carnivores remained important, contributing 35% while carnivores contributed 39%. Omnivorous herbivores made a larger contribution to biomass than abundance because of the large dry weight of *E. superba*, particularly in Winter 06 when this group contributed 46% to total macrozooplankton biomass.

4. Discussion

The four LAKRIS surveys described a seasonal cycle in the Lazarev Sea that is typical of the high latitude of the Southern Ocean. The summer months were largely ice free. High irradiance levels and a surface mixed layer depth coincided with a phytoplankton biomass of up to 8.2 mg m⁻³, indicative of high summer primary production. By winter however, the Lazarev Sea had changed dramatically. Sea-ice had extended northwards across the entire survey area, irradiance decreased from 18 to 6 hours at 60°S, and the surface mixed layer deepened by an order of magnitude. The extremely low chlorophyll biomass (average=0.042 mg m⁻³) indicated that primary production had decreased substantially from summer levels.

4.1. Seasonal cycle of community structure

Multivariate analysis of Lazarev Sea net data showed that the macrozooplankton community was dominated by a small number of taxa. Most of these taxa were present in all seasons; nevertheless, a strong and distinctive seasonal change in assemblage structure

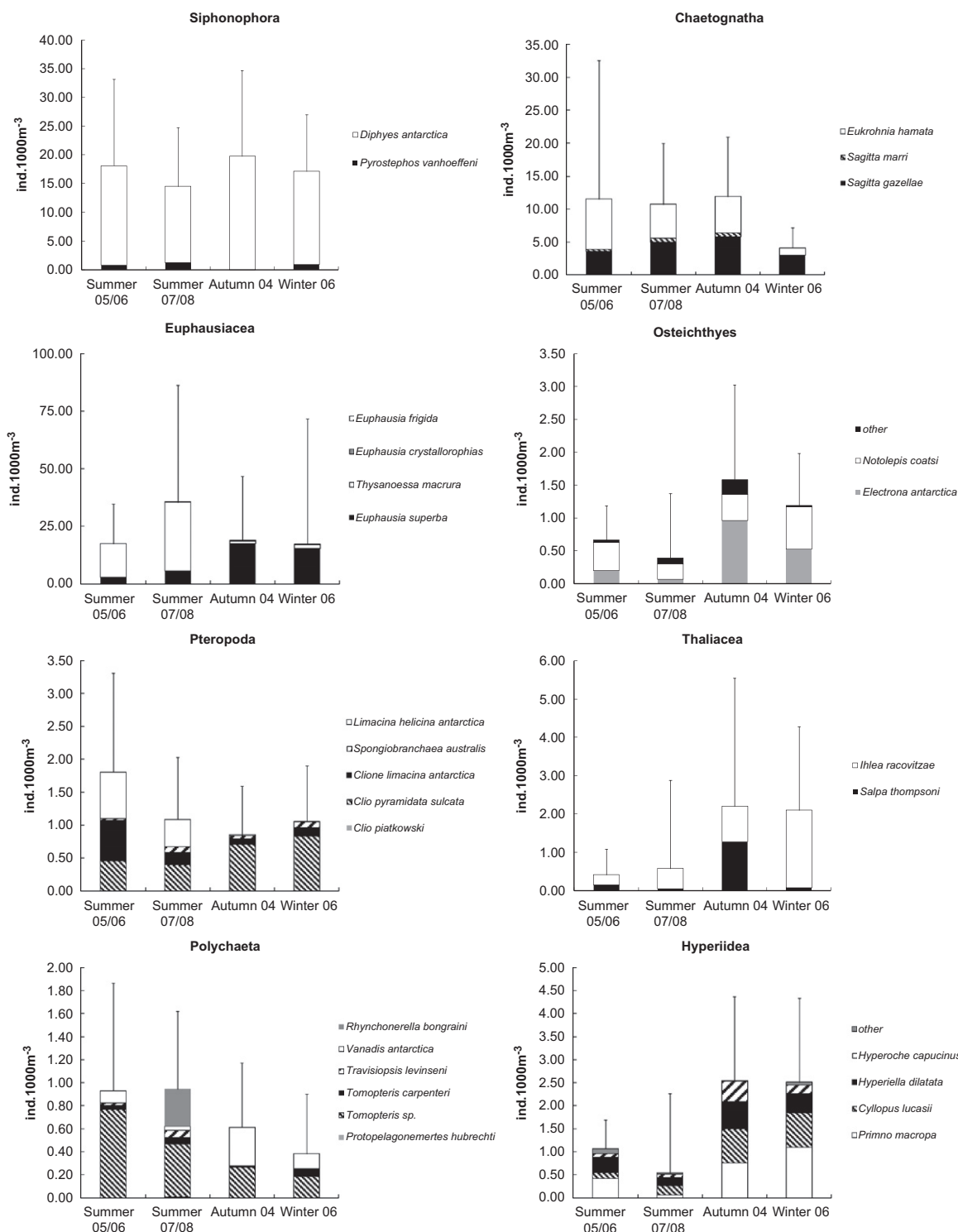


Fig. 6. Total abundance and standard deviations (ind. 1000 m⁻³) of major macrozooplankton groups for each survey, with the contribution of key species indicated.

was observed. Consistent spatial variation across the survey area did not appear to be a confounding factor in the seasonal shift of macrozooplankton assemblage structure and changes did not appear to be associated with changes in water mass structure. The dominant role of seasonality in the structuring of the macrozooplankton community was supported by the significant correlation of both dimensions of the NMDS ordination with chlorophyll biomass. The summer surveys were characterised by high densities of the euphausiid *T. macrura* and low densities of *E. superba*, while

the opposite pattern was observed in case of autumn and winter. Factorial ANOVA indicated that this seasonal shift was not due to higher net avoidance or diel migration in the daylight dominated summer months, but that it was in fact a real seasonal pattern. In the case of *T. macrura* low autumn and winter densities were suggestive of a seasonal migration to deeper layers. This was supported by preliminary results from mesopelagic tows conducted in the winter months that found *T. macrura* to be abundant below 500 m (Kruse et al., 2009). Summer dominance of *T. macrura*

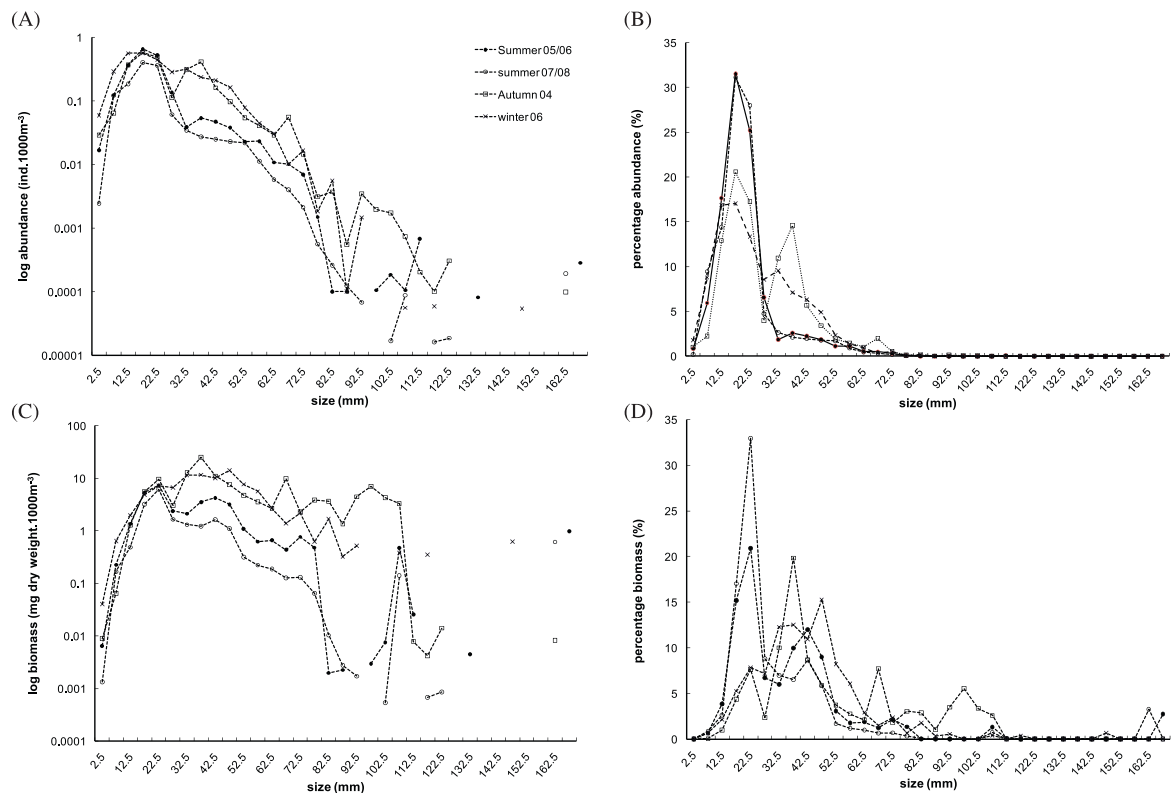


Fig. 7. (A) Log abundance (ind. 1000 m⁻³) distribution of macrozooplankton for 5 mm size bins; (B) percentage abundance contribution of 5 mm size bins to total macrozooplankton abundance; (C) Log biomass (mg dry weight 1000 m⁻³) distribution of macrozooplankton for 5 mm size bins; and (D) percentage biomass contribution of 5 mm size bins to total macrozooplankton biomass for each of the four LAKRIS surveys.

over *E. superba* in the Lazarev Sea was also demonstrated by Pakhomov et al. (1994), indicating that this may be a consistent feature of the region. Although the LAKRIS seasonal sampling took place over a number of years, Summer 05/06 and Winter 06 were sampled in the same year, and thus the increase in *E. superba* density from summer to winter was not an artefact of inter-annual variation, but was possibly related to advection or behavioural change, e.g. such as aggregation. Higher autumn and winter *E. superba* densities were indeed associated with the occurrence of dense patches (Cluster 4 of Figs. 4 and 5).

Euphausiids were not the only group that showed strong seasonal cycles. The chaetognath *E. hamata* was scarce in the epipelagic in winter, although it was highly abundant in summer and in autumn. As was the case with *T. macrura*, mesopelagic tows conducted in the winter months found *E. hamata* to be abundant below 500 m, indicating that it undergoes a seasonal migration (Kruse et al., 2009). The other dominant chaetognath species, *S. gazellae*, remained abundant in the epipelagic in all seasons.

The two dominant fish species, *E. antarctica* and *N. coatsi*, both showed variability related to diel migration, occurring at significantly higher densities in the epipelagic during dark hours. Day-time migration of fish species to below 200 m is well known in the case of Antarctic pelagic fish (Lancraft et al., 2004). Diel migration is therefore expected to have contributed to low summer densities; however, factorial ANOVA found that differences in *E. antarctica* abundance between surveys were also affected by season and the season/light interaction. This indicated a seasonal migration and/or increased residence time in the epipelagic during the winter months, which size data showed was associated with an increased abundance of fish that were larger than 27.5 mm in length. Analysis of size data for *N. coatsi* also found this species to be of a larger average size in autumn than that found in the summer months, though this was not the case in winter.

Pteropods were characterised by high summer abundance levels associated with high densities of the thecosome *L. helicina antarctica* and the gymnosome *C. limacina antarctica*. However, these two species were almost completely absent during autumn and winter, a seasonal occurrence consistent with other regions of the Southern Ocean (Hunt et al., 2008). *L. helicina antarctica* and *C. limacina antarctica* are intimately related as the latter is a monophagous predator of the former. It is possible that the autumn/winter decline was related to migration out of the epipelagic; however, at least in the case of *L. helicina antarctica*, it is possible that they were under sampled by the large mesh RMT-8 due to a population dominated by small juveniles (Hunt et al., 2008). The large thecosome species *C. pyramidata sulcata* was abundant in all surveys, despite its increasing abundance from summer to winter, and showed no clear pattern in population size structure. Factorial ANOVA showed that diel migration contributed to lower summer densities, but indicated that there was also a seasonal component to the winter increase in abundance. The gymnosome *Spongiobranchaea australis*, a monophagous predator of *C. pyramidata sulcata*, occurred in all seasons, thus reflecting its prey's availability.

Salps were largely dominated by *I. racovitzai*. This species had higher densities in winter than in summer, but Factorial ANOVA indicated that this was due to the enhanced diel migration in the summer months. *S. thompsoni* only occurred at high abundance in autumn. Amongst the polychaetes a reduction in total abundance was associated with a significant seasonal decline in the abundance of *Tomopteris* sp. The size structure data of this species indicated that this may have been driven by the under sampling of smaller autumn and winter specimens by the RMT-8. Finally, an important factor in the differentiation of summer from autumn and winter samples was the increase in abundance of all hyperiids, particularly *P. macropa* and *C. lucasii*, in the latter months. Factorial ANOVA indicated that in the

case of *C. lucasii* this was due to the enhanced diel migration in the summer months, while *P. macropa* abundance was affected by both diel migration in summer and a seasonal winter increase. No clear size related pattern was seen to drive this increase in abundance.

Overall, the community composition observed in the Lazarev Sea was similar to that of previous studies carried out in the Weddell/Scotia confluence (Lancraft et al., 1991), the Prydz Bay region (Hosie and Stolp, 1989) and the Antarctic Peninsula (Siegel and Piatkowski, 1990).

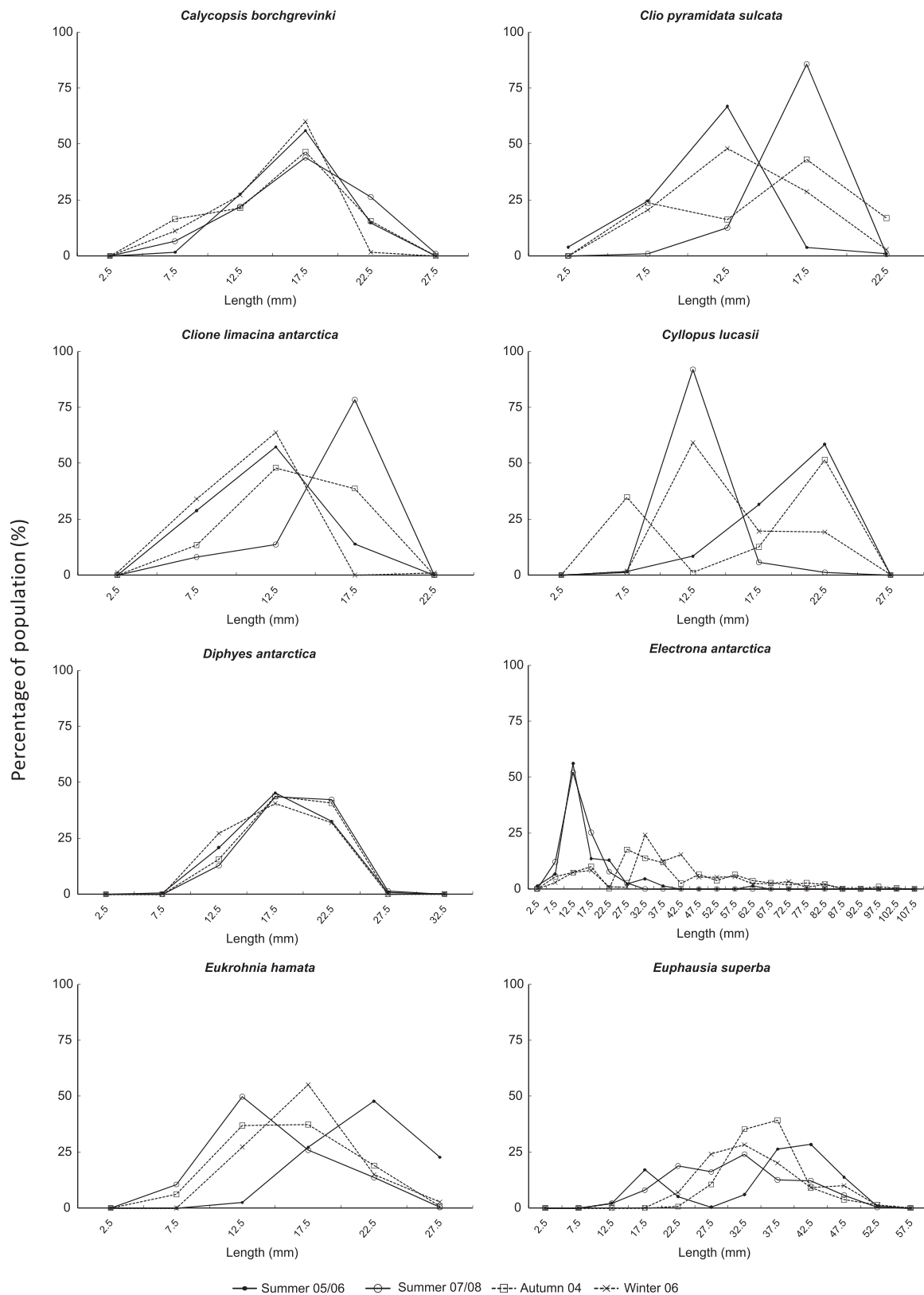


Fig. 8. The size structure of the populations of key macrozooplankton species, identified as those species contribution to the first 90% of within cluster similarity from the cluster analysis (Figs. 5 and 6).

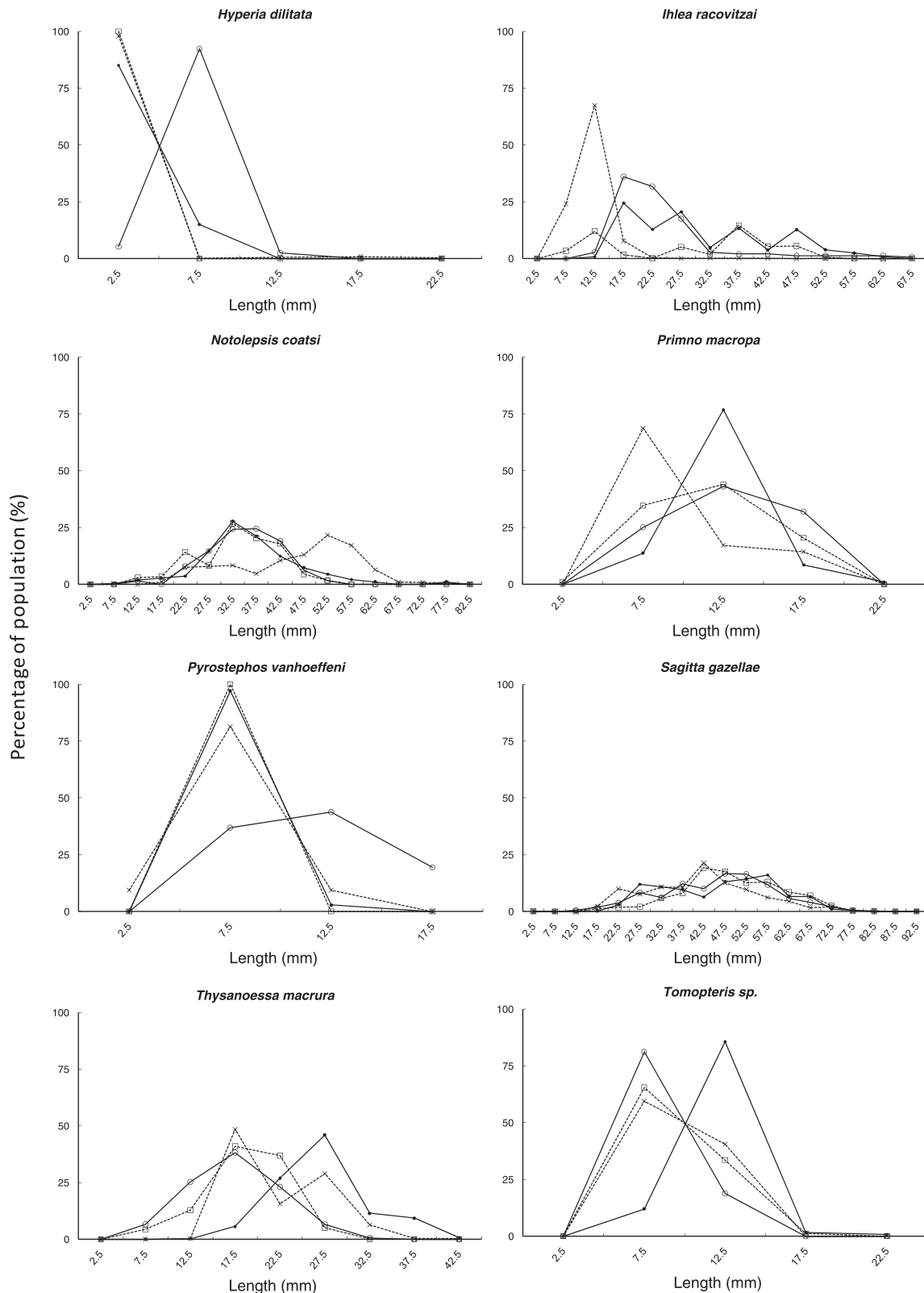


Fig. 8. (Continued)

However, in none of these other regions did siphonophores densities contribute > 10% to total macrozooplankton abundance. The minimum contribution of siphonophores to the Lazarev Sea macrozooplankton community during our study was 24% in Winter 06 and ~33% in Summer 05/06, in Summer 07/08, and in Autumn 04. Similarly high siphonophore contributions (up to 40%) in the Lazarev Sea were

observed by Pakhomov et al. (1994) in Summer 1990, suggesting that it may be a typical feature of this pelagic ecosystem and pointing to a regionally important trophic role of this carnivorous group.

In summary, against a background of high and consistent siphonophore abundance, the Lazarev Sea macrozooplankton community showed large seasonal changes. Key amongst these

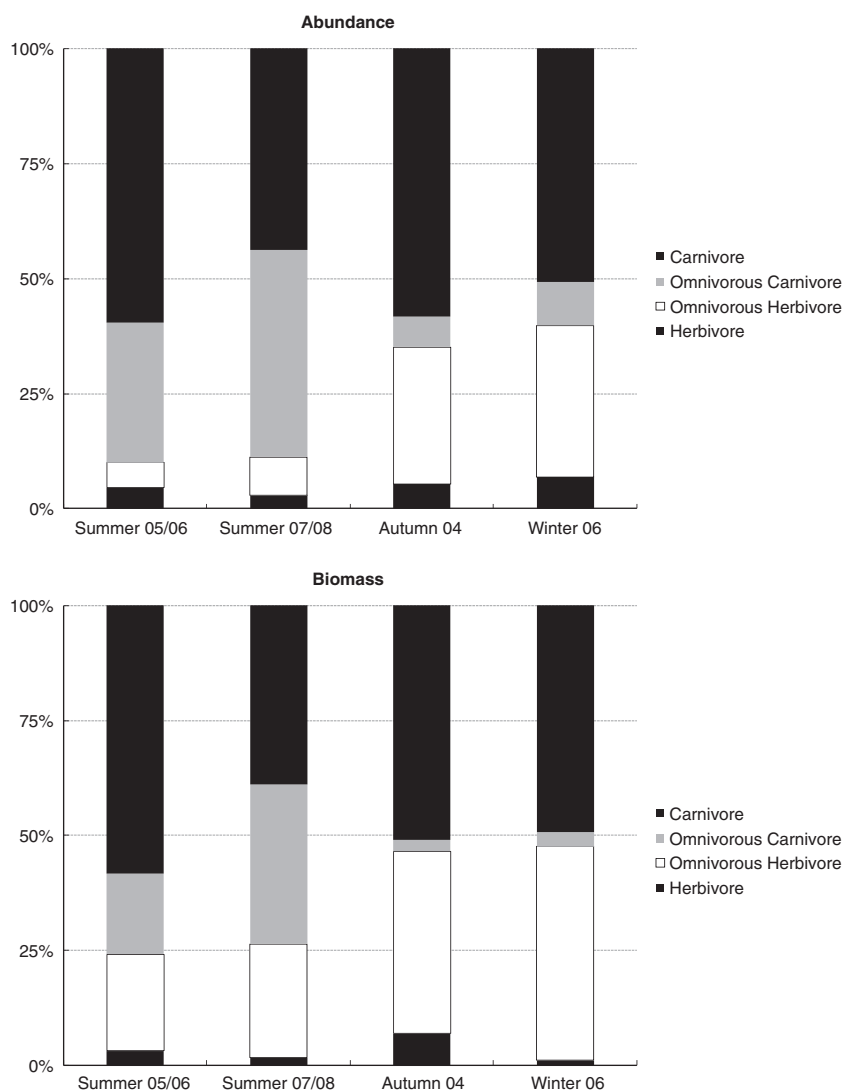


Fig. 9. Percentage contribution of the four major trophic groups of macrozooplankton: carnivores, omnivorous carnivores, omnivorous herbivores and herbivores. A full list of species comprising each group is presented in Appendix A.

included a shift within the highly abundant euphausiids from a dominance of *T. macrura* in summer to that of *E. superba* in autumn and winter; a winter decrease in *E. hamata*; an autumn and winter decrease in *Tomopteris* sp.; a winter increase in the abundances of the grazers *C. pyramidata sulcata* and *I. racovitzi*, hyperiids, and the myctophid fish *E. antarctica*. These abundance changes were probably driven by a combination of diel and seasonal migration, net avoidance, under sampling of small population fractions, and species' behavioural changes. Despite the seasonal shifts in zooplankton assemblage structure, total macrozooplankton abundance levels did not differ significantly between seasons. Biomass on the other hand increased substantially (> 45%) from summer to autumn and winter. This was associated with the increase in contribution of some biomass heavy species, particularly *E. superba*, as well as with the increased occurrence of pelagic fish > 30 mm in length.

4.2. Trophic ecology

Data on the winter behaviour and survival strategies of macrozooplankton species are largely confined to *E. superba*, with some disparate and sometimes contradictory data on other species.

E. superba has been shown to have reduced metabolic activity in winter, although feeding does occur (Torres et al., 1994; Lancraft et al., 1991). It is important to note that in the case of this species winter feeding marks a shift to omnivorous carnivory, with copepods constituting an important dietary component (Ju and Harvey, 2004). The chaetognath *E. hamata* has higher levels of esters and triacylglycerides than *S. gazellae* or *S. marri* suggesting an important role of lipids as an energy store for this species and possibly reduced winter activity (Hagen, 1988). However, Orseland (1995) found that the winter feeding rates for *E. hamata* were the same as those in summer, while Donnelly et al. (1994) found no differences in gut fullness between autumn and winter. Data collected during the LAKRIS surveys, provide further evidence of normal winter activity of *E. hamata*, with the observation of extended or continuous winter reproduction (Kruse et al., 2009). The fish *E. antarctica* and *Bathylagus antarcticus* were both reported to have less food in their gut in winter (Lancraft et al., 1991). *T. macrura* seems to maintain its lipid stores during the winter, using these for reproductive purposes in late winter/early spring (Hagen and Kattner, 1998), despite not reducing its metabolism (Torres et al., 2007). This indicates that the feeding activity of *T. macrura* is not reduced in winter when due to low chlorophyll *a* biomass this carnivorous omnivore may be primarily carnivorous.

Table A1

Average densities (individuals 1000 m⁻³) and biomass (mg dry weight 1000 m⁻³) of taxa collected during the four LAKRIS surveys.

Trophic group	Species/group	Summer 05/06		Summer 07/08		Autumn 04		Winter 06	
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Herbivore	<i>Clio piatkowski</i>			0.002	0.026			0.001	–
Herbivore	<i>Clio pyramidata sulcata</i>	0.455	1.179	0.392	4.883	0.703	8.540	0.834	9.055
Herbivore	<i>Doliolina intermedium</i>							0.005	0.010
Herbivore	<i>Ihleia racovitzai</i>	0.257	7.929	0.534	9.475	0.926	162.473	2.026	8.993
Herbivore	<i>Limacina helicina antarctica</i>	0.705	0.275	0.417	0.913	0.016	0.084	0.005	
Herbivore	<i>Protopelagonemertes hubrechtii</i>			0.006	0.061				
Herbivore	<i>Salpa thompsoni</i>	0.148	18.457	0.044	0.097	1.272	14.194	0.070	0.264
Herbivore	<i>Tomopteris</i> sp.	0.765	0.341	0.461	0.224	0.265	0.220	0.184	0.469
Herbivore	<i>Tomopteris carpenteri</i>	0.035	0.274	0.057	0.703	0.011	0.209	0.065	0.540
Herbivore	<i>Travisopsis levinseni</i>	0.022	0.037	0.061	0.055			0.001	0.012
Omnivorous Herbivore	<i>Euphausia superba</i>	2.850	185.735	5.622	240.319	17.460	1052.726	15.349	810.734
Omnivorous Herbivore	<i>Euphausia frigida</i>					0.141	0.748		
Carnivore	<i>Aegina citrea</i>			0.002	0.036				
Carnivore	<i>Alluroteuthis antarcticus</i>	0.024	1.252	0.010	0.538	0.005	0.110	0.002	0.638
Carnivore	<i>Beroe cucumis</i>				9.240	0.005	1.026	0.002	0.208
Carnivore	<i>Atolla wyvillei</i>			0.028	9.243	0.004	15.450	0.001	–
Carnivore	<i>Bathylagus antarcticus</i>	0.017	2.377	0.030	1.322	0.079	15.450	0.007	0.208
Carnivore	<i>Callianira</i> sp.					0.105	–	0.007	–
Carnivore	<i>Calycopsis borchgrevinki</i>	0.157	9.545	0.243	18.254	0.159	8.809	0.211	9.174
Carnivore	<i>Clione limacina antarctica</i>	0.617	5.590	0.184	2.741	0.084	1.091	0.120	0.884
Carnivore	Cranchiidae (larvae)			0.014	0.007				
Carnivore	Ctenophora	0.012	–	0.011	0.370				
Carnivore	<i>Desmonema</i> sp.	0.014	–						
Carnivore	<i>Dimophyes arctica</i>			2.756	3.481				
Carnivore	<i>Diphyes antarctica</i>	17.331	210.891	13.234	177.422	19.721	258.683	16.260	180.872
Carnivore	<i>Electrona antarctica</i>	0.197	4.497	0.064	0.390	0.957	541.624	0.524	195.938
Carnivore	<i>Eukrohnia hamata</i>	7.673	12.918	5.176	2.034	5.555	3.222	1.115	2.628
Carnivore	<i>Galiteuthis glacialis</i>					0.095	1.400	0.219	29.941
Carnivore	<i>Gymnoscopelus braueri</i>			0.002	7.178	0.043	31.335	0.001	6.621
Carnivore	<i>Gymnoscopelus nicholsi</i>					0.101	312.586		
Carnivore	<i>Halicera conica</i>					0.008	0.035		
Carnivore	Hydromedusae	0.073	0.218	0.043	0.153	0.006	0.007		
Carnivore	<i>Kondakovia longimana</i>			0.001	–				
Carnivore	Macrouridae spp.			0.001	0.013			0.003	1.132
Carnivore	<i>Mesonychoteuthis hamiltoni</i>	0.026	0.222			0.369	12.340	0.038	14.303
Carnivore	<i>Mitrocomella</i> sp.							0.022	–
Carnivore	<i>Moroteuthis robsoni</i>			0.002	1.614				
Carnivore	<i>Muraenolepididae</i> sp.							0.003	1.521
Carnivore	Neoteuthidae							0.004	0.802
Carnivore	<i>Notolepis coatsi</i>	0.424	137.330	0.234	63.164	0.402	99.060	0.641	322.539
Carnivore	<i>Notothenia kempii</i>							0.001	–
Carnivore	Osteichthyes larvae	0.019	68.577	0.021	–				
Carnivore	<i>Pandea rubra</i>					0.004	0.054	0.056	–
Carnivore	<i>Pegantia</i> sp.	0.006	0.084	0.001	0.020	0.010	0.106	0.038	0.056
Carnivore	<i>Periphylla periphylla</i>	0.020	24.652	0.013	32.120	0.006	–	0.010	0.248
Carnivore	<i>Pleurogramma antarcticum</i>			0.021	0.023			0.004	0.149

Table A1 (continued)

Trophic group	Species/group	Summer 05/06		Summer 07/08		Autumn 04		Winter 06	
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	Abundance	Biomass
Carnivore	<i>Pyrostephos vanhoeffeni</i>	0.748	3.165	1.231	6.761	0.024	0.099	0.863	9.629
Carnivore	<i>Racovitzia glacialis</i>			0.001	0.239				
Carnivore	<i>Rhynchonerella bongraini</i>			0.325	2.081				
Carnivore	<i>Sagitta gazellae</i>	3.568	33.519	4.946	44.697	5.757	61.625	2.938	78.836
Carnivore	<i>Sagitta marri</i>	0.261	0.029	0.582	0.032	0.592	0.044	0.048	0.021
Carnivore	Siphonophora							0.267	0.691
Carnivore	<i>Spongiobranchaea australis</i>	0.029	0.133	0.087	0.796	0.049	0.324	0.093	0.371
Carnivore	<i>Squid</i>	0.003	–						
Carnivore	<i>Vanadis antarctica</i>	0.107	1.851	0.036	0.786	0.334	5.964	0.133	2.426
Carnivore	<i>Vogtia serrata</i>			0.347	1.045				
Carnivore	<i>Zanclonia weldoni</i>							0.005	0.019
Omnivorous Carnivore	<i>Cyllopus lucasii</i>	0.127	3.863	0.201	1.850	0.736	22.828	0.750	9.980
Omnivorous Carnivore	<i>Cyllopus magellanicus</i>	0.002	0.008	0.001	–			0.006	–
Omnivorous Carnivore	<i>Cyllopus</i> spp.					0.017	0.009		
Omnivorous Carnivore	Decapod (caridean)	0.008	0.011	0.005	0.010	0.004	–	0.007	0.014
Omnivorous Carnivore	<i>Euchaetonema</i> sp.	0.010	–	0.022	–				
Omnivorous Carnivore	<i>Euphausia crystallorophias</i>			0.020	0.260	0.067	0.225	0.071	0.675
Omnivorous Carnivore	<i>Eusirus antarcticus</i>					0.002	0.041		
Omnivorous carnivore	<i>Eusirus/Eusirella</i> spp.			0.010	0.090				
Omnivorous Carnivore	<i>Hyperia antarctica</i>			0.008	0.024			0.013	0.006
Omnivorous Carnivore	<i>Hyperia macrocephala</i>	0.002	0.041	0.002	0.040	0.008	0.581	0.006	0.077
Omnivorous Carnivore	<i>Hyperia medusarum</i>							0.004	–
Omnivorous Carnivore	<i>Hyperia</i> sp.	0.008	–						
Omnivorous Carnivore	<i>Hyperiella dilitata</i>	0.341	0.281	0.184	0.697	0.588	0.186	0.413	0.676
Omnivorous Carnivore	<i>Hyperiella macronyx</i>	0.014	0.071	0.001	–	0.002	0.010	0.012	0.072
Omnivorous Carnivore	<i>Hyperoche capucinus</i>	0.067	0.536	0.070	0.611	0.445	5.626	0.191	2.449
Omnivorous Carnivore	<i>Hyperoche medusarum</i>	0.085	0.613	0.007	0.106			0.001	0.022
Omnivorous Carnivore	<i>Hyperoche</i> sp.	0.002	0.025						
Omnivorous Carnivore	<i>Lanceola</i> spec.							0.005	0.022
Omnivorous Carnivore	<i>Mysidacea</i> sp.	0.002	–		0.003				
Omnivorous Carnivore	<i>Nematocarcinus</i> sp.	0.289	7.393	0.161	5.225	0.164	1.756	0.181	3.554
Omnivorous Carnivore	<i>Orchomene</i> sp.							0.001	0.025
Omnivorous Carnivore	<i>Phippsiella nipoma</i>								
Omnivorous Carnivore	<i>Primno macropa</i>	0.417	2.886	0.055	0.552	0.760	5.591	1.089	7.224
Omnivorous Carnivore	<i>Russelia mirabilis</i>			0.001	0.015				
Omnivorous Carnivore	<i>Scina</i> sp.			0.001	0.002				
Omnivorous Carnivore	<i>Themisto gaudichaudii</i>							0.015	0.039
Omnivorous Carnivore	<i>Thysanoessa macrura</i>	14.623	139.858	29.712	328.859	1.092	32.419	1.597	32.502
Omnivorous Carnivore	<i>Vibilia antarctica</i>			0.002	0.015			0.004	0.130

There are indications of reduced metabolic activity in *C. lucasii* during winter (Torres et al., 1994), although this species does continue to feed (Lancraft et al., 1991).

In general, however, data on rate processes (e.g. metabolic activity, feeding rates, reproduction) are almost completely lacking in the case of most Southern Ocean macrozooplankton species at all times of the year. As highlighted in the introduction, three types of overwintering strategy have been postulated with regard to zooplankton, based on their trophic level (Torres et al., 1994): Type 1—diapause (herbivores); Type 2—reduced metabolism with opportunistic feeding (omnivores); and Type 3—business as usual (carnivores). If we assume a Type 3 strategy of business as usual in the case of carnivorous species during the winter months, ~50% of the macrozooplankton community (in terms of both abundance and biomass) in the Lazarev Sea would have remained actively feeding during this time. Coupled with the increased carnivory by omnivorous carnivores and omnivorous herbivores such as krill, winter predation pressure is expected to have been high and potentially higher than it was in summer. In view of the substantially reduced winter primary production in the Lazarev Sea (Winter 06 chlorophyll *a* biomass levels were < 3% of those recorded in Summer 07/08), we suggest that the pelagic system shifted from one of a bottom-up controlled in summer to top-down controlled in winter.

Mesozooplankton copepods would be expected to be the primary prey of carnivorous plankton. In the vicinity of South Georgia island copepods and total zooplankton biomass in winter in the upper 1000 m of the water column were 77% and 68% of summer levels, respectively (Atkinson and Ward, 1988). Although a proportion of the biomass was expected to be below 1000 m and factors such as population size structure and water mass change are expected to have contributed, the summer to winter difference indicated an important role of predation mortality. In Marguerite Bay, average mesozooplankton abundance and biomass decreased by 57% and 63%, respectively, from autumn to winter (Ashjian et al., 2004). Copepods contributed an average of 43% to total biomass and were a major component of the seasonal depletion, further indicating a substantial role of predation in winter copepod biomass reduction. RMT-1 net tows, sampling the mesozooplankton fraction of the pelagic, were collected in conjunction with RMT-8 data during the LAKRIS surveys and demonstrated that average copepod abundance actually increased in the survey area from 11 to 44 ind. m⁻³ between Summer 05/06 and Winter 06 (E. Pakhomov, unpublished data). However, these findings are consistent with the early winter peak in copepod abundance demonstrated by a high temporal resolution study, with sampling performed every 2–3 weeks between May and December, in the fast ice area near Syowa Station (Fukuchi et al., 1985). Sampling the entire water column (675 m), these data showed a peak in copepod abundance in June and a subsequent steady decline in their densities till December, concomitant with an increase in the densities of predatory species. The high copepod abundance levels observed in June/July in the Lazarev Sea would have provided a ready food source for carnivorous macrozooplankton. In addition, high copepod abundance would likely have contributed intense top-down grazing pressure on the already depleted phytoplankton standing stock, enhanced by the winter increase in abundance of some macrozooplankton grazers, e.g., *C. pyramidata sulcata* and *I. racovitzai*. The latter species was shown to be actively feeding during the winter months (van Harbou et al., submitted).

5. Conclusions

The Lazarev Sea macrozooplankton community showed a high degree of seasonal stability in terms of species composition, despite a distinct seasonal shift in species' contribution to abundance.

Despite the seasonal change in assemblage structure the macrozooplankton community was always dominated by carnivorous species, contributing 44–60% to total macrozooplankton abundance and 39–58% to total macrozooplankton biomass in all four surveys. This has significant implications for the functioning of the Lazarev Sea ecosystem. In view of the low winter primary production, it is probable that because of the impacts of macrozooplankton predation the Lazarev Sea shifted from being bottom-up controlled in Summer to top-down controlled and copepod fuelled in winter. Similarly predator dominated macrozooplankton communities have been observed in other parts of the Southern Ocean, indicating that such a trophic shift may be typical during the winter months. In order to quantify the seasonal role of macrozooplankton and winter-time carbon flow there is a need for data on metabolic and feeding rates. Such data are available for only a few macrozooplankton species, and they are urgently required in the case of previously ignored, yet significant and seasonally persistent, community components such as the siphonophore *D. antarctica* and chaetognaths. The former species was remarkably abundant in the Lazarev Sea, contributing up to 36% to total macrozooplankton densities.

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Appendix A

Table A1.

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