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## Variability of epipelagic macrozooplankton/micronekton community structure in the NW Weddell Sea, Antarctica (1995–1996)

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**Abstract** Macrozooplankton/micronekton in the epipelagic zone (0–100 m) of the NW Weddell Sea were sampled with a 10 m<sup>2</sup> multiple opening-closing net environmental sampling system (MOCNESS) trawl during three cruises in 1995 and 1996. A total of 40 species were collected during all cruises. Community composition, as measured using Bray-Curtis analysis and multi-dimensional scaling, permitted separation into two groups: group 1 included samples collected during September–October 1995 and group 2 contained samples collected during April–May 1996 and November–December 1996. Zooplankton collections were dominated by *Thysanoessa macrura* in September–October 1995 (high pack-ice cover) and by both *Euphausia superba* and *Salpa thompsoni* in April–May 1996 (intermediate pack-ice cover) and November–December 1996 (open water). Copepods were not sampled quantitatively by the MOCNESS trawl and were not included in this analysis. Trends in measured parameters of community structure are discussed with respect to environmental characteristics during each sampling period.

### Introduction

The Southern Ocean includes some of the most productive waters on Earth and it supports abundant and diverse pelagic communities (e.g. Ainley et al. 1991; Lancraft et al. 1991; Siegel et al. 1992; Hopkins et al.

1993; Voronina et al. 1994). Perhaps the most prominent environmental feature in this region is the Antarctic seasonal pack ice, which covers up to 20 million km<sup>2</sup> during the austral winter and contracts to less than 4 million km<sup>2</sup> during the summer (Zwally et al. 1983). In the NW Weddell Sea region of the Southern Ocean, for example, surface waters are covered by ice for 6–9 months of the year (Parkinson 1992), following a general trend of maximum ice cover in September and minimum ice cover in February (Zwally et al. 1983). This seasonal ice is an important physical feature structuring pelagic communities in the Antarctic (Laws 1985; Eiken 1992).

Pack ice influences water column primary production, in part by contributing to decreased irradiance in surface waters and a deepened mixed layer due to thermohaline convection (Eicken 1992). However, sea ice itself is an important habitat that contributes significantly to Southern Ocean productivity (Spindler et al. 1990; Garrison and Buck 1991; Arrigo et al. 1998). The seasonal formation and contraction of pack ice in the Southern Ocean has a dramatic effect on the annual variability of primary production, including both water column primary producers (Garrison and Buck 1989; Bianchi et al. 1992; Tréguer and Jacques 1992) and ice-associated microbiota such as diatoms, dinoflagellates, and ciliates (Garrison and Buck 1989, 1991; Garrison 1991; Ackley and Sullivan 1994) that increase primary production in the surrounding surface waters (Smith and Nelson 1986; Smith and Sakshaug 1990; Gleitz and Kirst 1991). In turn, primary producers influence the distribution of grazers, including planktonic species such as krill (Marschall 1988; Bergström et al. 1990; Daly and Macaulay 1991; Lascara et al. 1999), mesopelagic fishes (Lancraft et al. 1991), and even apex predators such as seabirds (Ainley et al. 1991).

Over the past two decades, the increased capabilities of research vessels have allowed scientists to study Antarctic waters year-round in regions of high ice cover that were previously inaccessible by ship. Extensive studies using both trawling (Siegel et al. 1992; Kaufmann et al. 1995; Ross et al. 1996; Loeb et al. 1997;

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Burghart et al. 1999) and acoustic methods (Godlewska and Klusek 1987; Kaufmann et al. 1995; Lascara et al. 1999) have revealed that Antarctic open water environments support different levels of zooplankton density and biomass than ice-covered environments. In addition, behavior, vertical distribution, and life cycles of important zooplankton species, such as the krill *Euphausia superba*, have been linked in varying degrees to the presence or absence of seasonal pack ice (Marschall 1988; Ainley et al. 1991; Godlewska 1993; Loeb et al. 1997; Lascara et al. 1999). However, whether ice cover universally influences the formation of distinct zooplankton communities in Antarctic waters is not well understood (Hosie 1994; Chiba et al. 2001).

This study examined macrozooplankton and micronekton community dynamics in the epipelagic zone of the NW Weddell Sea over a complete daily cycle during three cruises in 1995 and 1996. The epipelagic zone is of particular interest because ice cover most directly influences the ecology of species that inhabit surface waters. The goals of this study were to address three questions: (1) How does ice cover affect the density and biomass of epipelagic macrozooplankton and micronekton?; (2) How does ice cover affect the spatial and temporal distribution of epipelagic macrozooplankton and micronekton?; (3) How does ice cover affect the composition and structure of epipelagic macrozooplankton and micronekton communities?

## Materials and methods

### Sample collection and processing

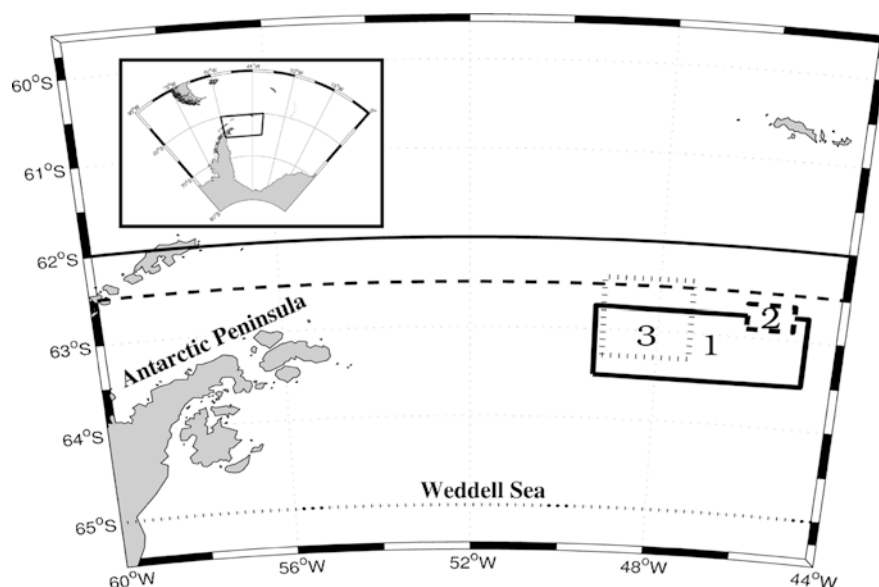
This study was conducted in the NW Weddell Sea between 62–64°S and 44–50°W (Fig. 1). Cruise dates were 26 September to 17 October 1995 (early to mid-spring) using the R.V.I.B. “Nathaniel B. Palmer” and 20 April to 5 May 1996 (mid- to late autumn) and

17 November to 6 December 1996 (late spring to early summer) using the R.V. “Polar Duke” (Fig. 1). The station locations in September–October 1995 spanned the largest geographic area and provided the southern, western, and eastern boundaries of the study site. The sampling location in April–May 1996 covered the smallest geographic area; station locations in November–December 1996 spanned an intermediate geographic area and delimited the northern margin of the study site.

Macrozooplankton and micronekton were collected with a six-net multiple opening-closing net environmental sampling system (MOCNESS) towed at an average ship speed of 2 knots. Each net had a 10 m<sup>2</sup> mouth opening with 4-mm circular mesh in the main body and a 505- $\mu$ m mesh cod end (Wiebe et al. 1982). Sampling periods lasted 1 h and covered one of two 50-m strata within the epipelagic zone, defined here as the region between the surface and 100 m depth. During September–October 1995 and November–December 1996, the sampling regime encompassed the entire 24-h diel cycle with two replicates at each time and depth (0–50 m and 50–100 m), yielding 96 discrete-depth samples from each cruise. During April–May 1996, the sampling regime included only one replicate at each time and depth, yielding 48 discrete-depth tows. The volume of water sampled during the 1-h sampling periods ranged from 22,274 to 46,832 m<sup>3</sup>. During September–October 1995, when ice cover was heaviest, some trawls were conducted within a large polynya, an area of open water surrounded by pack ice. The zooplankton community structure within such a polynya in the NW Weddell Sea was similar to that of communities under pack ice (Marschall 1988).

When possible, each trawl sample was sorted immediately after collection and displacement volume was measured for each taxon of fresh specimens. Pre-sorted specimens were preserved in 2% v/v glutaraldehyde in sea water (all gelatinous organisms) or 3.7% v/v formaldehyde in sea water buffered with borax (all other organisms). During November–December 1996, when sample sizes were very large, displacement volumes were measured for a subsample of dominant taxa. The remainder of the collection was left unsorted and preserved in formaldehyde for later laboratory analysis. Specimens were shipped to the laboratory and transferred to water to remove the formaldehyde prior to analysis. All macrozooplankton and micronekton were sorted, counted, identified to the lowest possible taxon, and weighed (preserved wet weight, uncorrected for preservation;  $\pm 0.01$  g). When the sample size was too large to realistically count every individual of a taxon, counts and weights of a subsample of individuals were used to estimate the total number of individuals in a sample. The total number of individuals then was calculated based on the biomass or displacement volume of the entire sample for a specific taxon. In the present

**Fig. 1** Chart of the NW Weddell Sea with the study area enlarged. The three boxes represent the sampling areas for each cruise: (1) September–October 1995; (2) April–May 1996; (3) November–December 1996. Lines delimit 50% ice cover and correspond to boxes outlined with the same pattern



study, total density or species density is defined as the number of individuals per unit volume sampled. For biomass and density comparisons among cruises, species biomass and density were standardized to no. 1,000 m<sup>-3</sup> water sampled.

Ctenophores other than *Calyropsis borchgrevinki* did not preserve well and were not recognizable in samples that were preserved unsorted; these ctenophores were not included in our analyses. The large medusa *Periphylla periphylla* was not included in biomass calculations for the same reason, but it was included in estimates of density and diversity. In all cases, copepods were a minor component of sample biomass and density and were not included in this study.

#### Statistical analyses

Community composition was expressed as the percentage of the total biomass or density composed of a single species. Species that comprised more than 5% of the total were reported as individual species; however, the following taxonomic groups may have contained more than one species: amphipods, cephalopods, chaetognaths, decapods, and scyphozoans. It was not possible to identify all individuals to species, and unidentified individuals were placed in the subcategory "sp." within major taxonomic groupings and were included as single taxa in compositional analyses. During the April–May 1996 cruise, five samples collected during the night, two at 0–50 m and three at 50–100 m, were eliminated from compositional analyses because preservation problems precluded identification or enumeration of species or individuals.

Cluster analysis, ordination, and statistical comparisons among sampling sites, depths, and times were performed on  $\log_{10}(x+1)$  transformed data using Statistica v. 5.5. Cluster analysis was based on unweighted pair group average linkage (UPGMA) for data pooled for time and depth of collection during each cruise. Multi-dimensional scaling (MDS) ordination was used on the same data matrix to provide a two-dimensional map of the sampling site similarities to complement the results of the cluster analysis. Within-cruise effects of depth for a given 1-h sampling period were compared using a Wilcoxon matched pairs test. Differences between times of collection (day or night) within a single depth stratum were compared using a Mann-Whitney U-test. A Kruskal-Wallis non-parametric ANOVA was used to test for differences in density and biomass among cruises at a given depth and time. If significance was established by the Kruskal-Wallis test, an a posteriori Mann-Whitney U-test was used to determine where statistical significance occurred among the samples.

## Results

### Environmental characteristics

Environmental parameters measured during each cruise are summarized in Table 1. The longest day length was 19 h and occurred during the late spring and early summer months of November–December 1996; the shortest day length was approximately 8.25 h and occurred during late fall in April–May 1996. The shortest day length did not co-occur with the heaviest ice cover.

**Table 1** Environmental characteristics of stations examined during the 1995 and 1996 cruises in the NW Weddell Sea

	Sep–Oct 1995	Apr–May 1996	Nov–Dec 1996
Time of sunrise (local)	0330–0430	0630–0715	0100–0200
Time of sunset (local)	1700–1800	1445–1530	2000–2100
Total ice cover	6/10–10/10	2/10–8/10	No pack; brash ice
Surface-water temperature (°C)	–1.8	–1.8	–1.5 to –1.8
Surface-water salinity (PSU)	33.8–34.3	33.6–33.7	34.3–34.4
Thermocline depth (m)	200–300	40–80	90–240

The heaviest ice cover was observed in September–October 1995, during mid-spring. No pack ice was present during November–December 1996, but occasional brash ice was observed.

The study site was located south of the Weddell-Scotia Confluence, an area of intense mesoscale mixing at least partially associated with the relatively shallow topography of the South Scotia Ridge (Deacon and Foster 1977; Gordon 1988). The intrusion of Scotia Sea water into the sampling region may have influenced data interpretation because the Scotia Sea zooplankton community appears to be distinct from the community in the Weddell Sea (Lancraft et al. 1989). However, based on hydrographic profiles of the Scotia Sea, Weddell Sea, and Weddell-Scotia Confluence (Lancraft et al. 1989; 1991), sampling took place within the Weddell Sea water mass during all three cruises (Fig. 2).

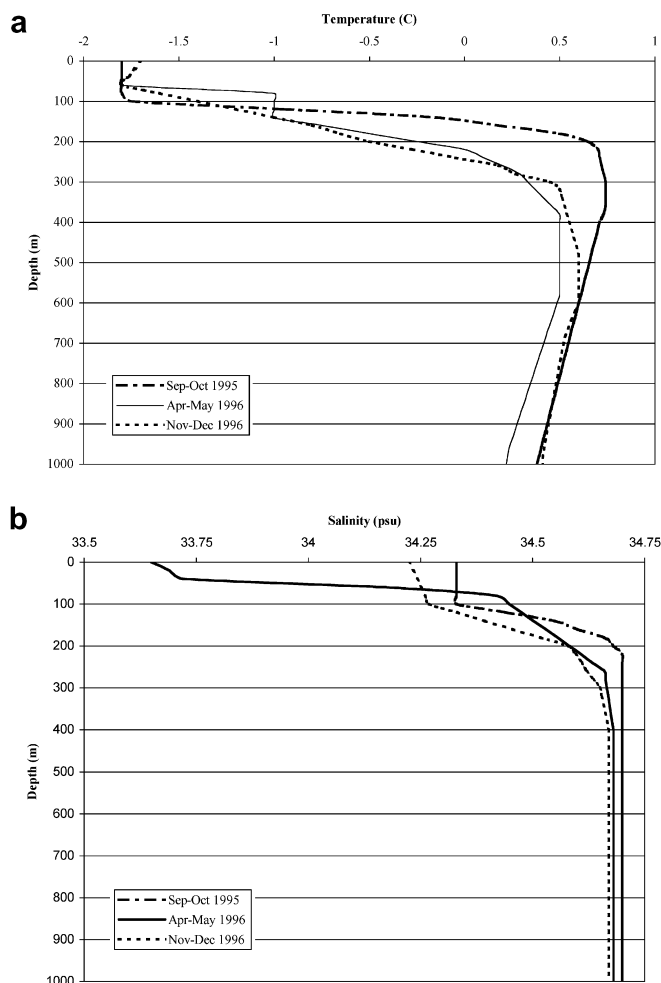
Surface currents in the NW Weddell Sea flow predominantly north-northeast with average speeds of 5–8 cm s<sup>-1</sup> (Foster 1984; Gordon 1988; Muench et al. 1992). During the winter, the pack ice exhibits drift patterns similar to those in surface currents, with daily mean drift rates of 12–24 cm s<sup>-1</sup> (Massom 1992). In our study, the surface layer was slightly colder at stations under the pack ice. The upper depth of the mixed layer ranged from 40–300 m among all cruises, which was within the vertical range of trawling during April–May 1996, but well below the sampling region in September–October 1995 and November–December 1996 (Fig. 2).

### Spatial distribution of density and biomass

A significant effect of depth (0–50 m or 50–100 m) on density was found within each cruise ( $P < 0.05$ ), with higher density samples collected at 50–100 m during September–October 1995 and at 0–50 m in April–May 1996 and November–December 1996 (Fig. 3a–c; Tables 2, 3, 4). As with density, sampling depth had a significant effect on biomass measurements within each cruise ( $P < 0.05$ ), with higher biomass at 50–100 m during September–October 1996 and 0–50 m during April–May 1996 and November–December 1996 (Fig. 3d–f; Tables 5, 6, 7).

### Temporal distribution of density and biomass

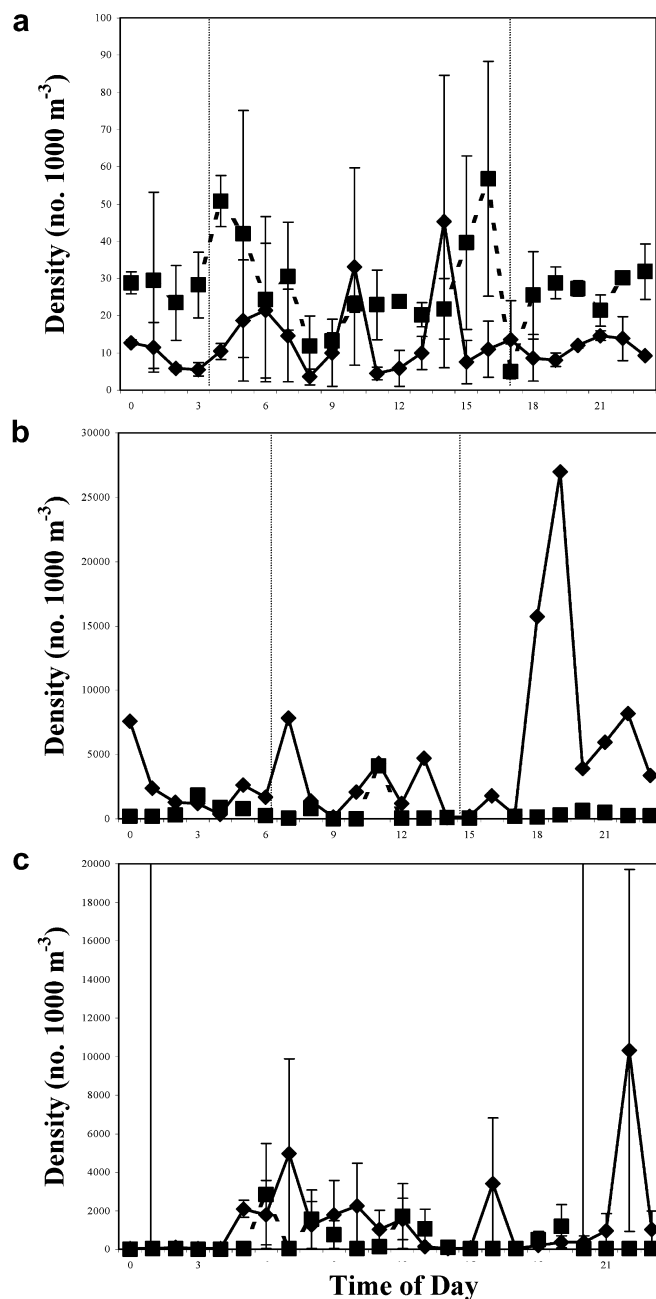
Within a single cruise, no significant effect of collection time (day or night) on density was found at either depth



**Fig. 2a,b** Representative hydrographic profiles from the area sampled during September–October 1995, April–May 1996, and November–December 1996. **a** Temperature, **b** Salinity

during September–October 1995 or November–December 1996 ( $P > 0.10$ ) (Tables 2, 4). However, in April–May 1996, density at 50–100 m was different between day and night ( $P = 0.019$ ), while time of sampling did not affect collections from 0–50 m ( $P = 0.161$ ) (Table 3). However, unlike density measurements, time of sampling significantly affected biomass measurements made in both depth strata during September–October 1995 and April–May 1996 ( $P < 0.05$ ), with higher biomass sampled during the night. Sampling time had no significant influence on collections made during November–December 1996 at either depth ( $P > 0.05$ ) (Tables 5, 6, 7).

When density was compared among cruises with respect to depth and time of collection, all samples were significantly different at 0–50 m during both day and night ( $P < 0.05$ ). At 50–100 m, samples collected during the day were not different between April–May 1996 and November–December 1996 ( $P = 0.273$ ), and samples collected during the night were not different between September–October 1995 and November–December 1996 ( $P = 0.237$ ) (Tables 2, 3, 4). All other comparisons



**Fig. 3a–c** Average (maximum/minimum) hourly density (no. 1,000  $\text{m}^{-3}$ ) and **d–f** biomass ( $\text{g } 1,000 \text{ m}^{-3}$ ) of macrozooplankton/micronekton collected in the NW Weddell Sea during **a, d** September–October 1995, **b, e** April–May 1996, and **c, f** November–December 1996. Data are presented for hourly time periods at each depth. Time of day indicates the beginning of each 1-h sample. Only one sample was collected for each depth and time during April–May 1996. Vertical lines denote average time of sunrise and sunset during each cruise. Note differences in y-axis scale among panels

were significantly different at the 50–100 m depth stratum ( $P < 0.05$ ). The same statistical tests using biomass data produced identical results (Tables 5, 6, 7). All tests were significant at the  $P < 0.05$  level, except the following: at 50–100 m during the day, April–May 1996 was not significantly different from November–December

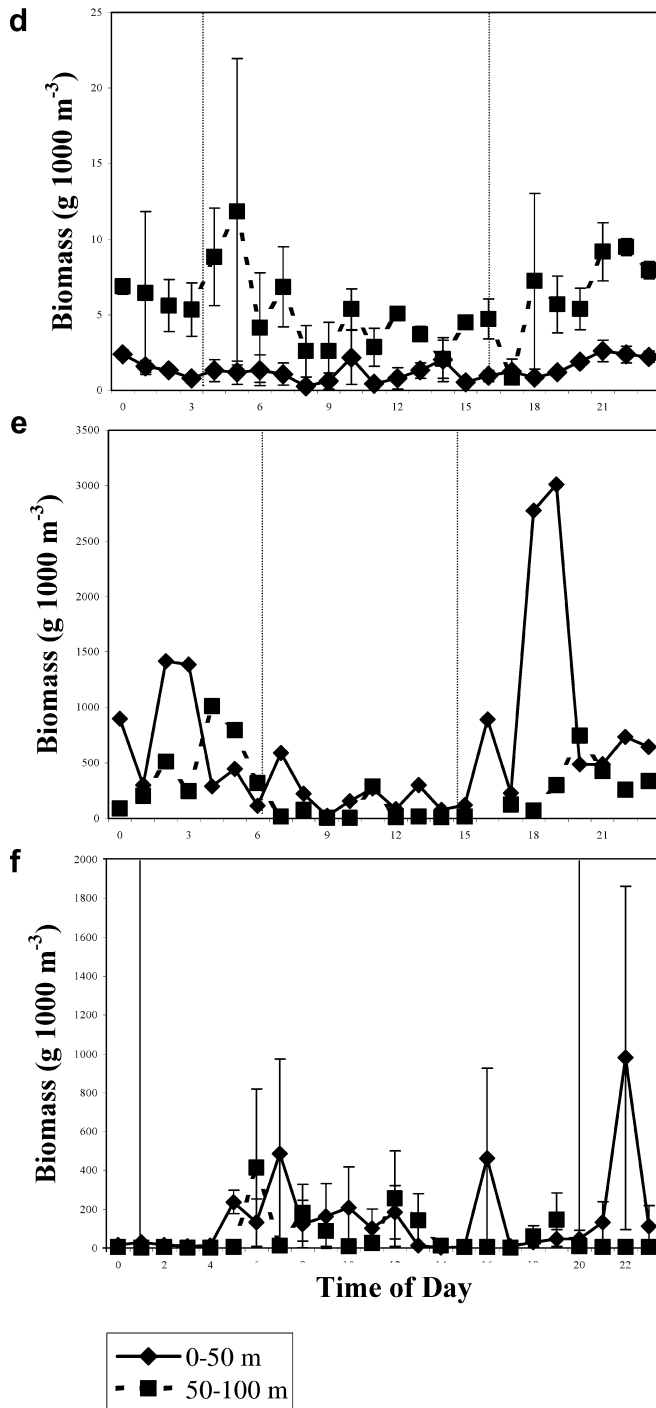


Fig. 3. a–c (Contd.)

1996 ( $P=0.165$ ), and at 50–100 m during the night, September–October 1995 was not significantly different from November–December 1996 ( $P=0.617$ ).

#### Taxonomic composition

A minimum of 40 species was collected during the present study (Tables 2, 3, 4, 5, 6, 7). Of these, 14 species

**Table 2** Mean density (no. 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during September–October 1995.  $n$  = Number of MOCNESS deployments on which density estimates were based

Species	0–50 m		50–100 m	
	Day ( $n=30$ )	Night ( $n=18$ )	Day ( $n=29$ )	Night ( $n=18$ )
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	—	—	—	—
<i>Diphyes antarctica</i>	0.452	0.457	7.094	7.311
<i>Periphylla periphylla</i>	—	—	—	0.008
Scyphozoa sp.	0.001	0.007	0.001	0.693
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	0.351	0.365	1.229	3.539
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	—	—	—	—
<b>Mollusca</b>				
Mollusc sp. A	—	—	—	—
<b>Gastropoda</b>				
Pteropod sp.	0.006	0.002	0.005	0.002
<i>Clio pyramidata</i>	0.221	0.865	0.548	0.255
<i>Clione antarctica</i>	0.141	0.166	0.178	0.260
<i>Limacina helicina</i>	—	—	—	—
<i>Spongiobranchaea australis</i>	0.021	0.066	0.053	0.021
Cephalopoda sp.	0.002	—	0.028	0.227
Nemertean sp.	—	—	—	—
<b>Polychaeta</b>				
Polychaete sp. A	0.007	0.044	0.118	0.028
Polychaete sp. B	—	0.008	0.005	0.007
<i>Tomopteris carpenteri</i>	0.002	0.125	0.005	0.027
<i>Vanadis antarctica</i>	0.069	0.094	0.236	0.109
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	0.025	0.403	—	0.355
<i>Euphausia superba</i>	0.014	1.984	0.014	4.140
<i>Thysanoessa macrura</i>	11.58	0.958	14.05	4.765
Decapoda sp.	0.018	0.124	0.010	0.221
<b>Amphipoda</b>				
Amphipod sp.	—	0.007	0.002	0.003
<b>Hyperiidea</b>				
<i>Cylopus lucasii</i>	0.018	0.469	0.051	0.470
<i>Hyperiella dilatata</i>	0.035	0.264	0.057	0.189
<i>Parathemisto gaudichaudii</i>	—	0.058	0.001	0.001
<i>Primno macropa</i>	0.037	0.019	0.040	0.024
<i>Vibilia antarctica</i>	<0.001	0.008	0.005	0.016
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	0.013	0.271	0.013	0.128
<i>Eusirus microps</i>	—	—	—	—
<i>Orchomene rossi</i>	—	—	—	0.002
Chaetognath sp.	1.573	2.526	3.709	4.432
<b>Tunicata</b>				
<i>Salpa</i> sp.	—	—	—	—
<i>Salpa thompsoni</i>	0.076	0.929	0.184	0.505
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	—	—	—	—
<i>Bathyrdraco joannae</i>	—	—	—	—
<i>Electrona antarctica</i>	—	—	—	—
<i>Notolepis coatsi</i>	0.001	0.002	0.002	0.002
<i>Pleuragramma antarcticum</i>	—	0.001	—	0.002
Mean total density	14.66	10.22	27.64	27.83
Standard error	(3.38)	(1.05)	(3.99)	(2.42)

comprised 10% or more of either total density or biomass during at least one time period. During September–October 1995, *Thysanoessa macrura*, *Diphyes antarctica*, *Salpa thompsoni*, chaetognaths and siphonophores other than *Diphyes* were the most

**Table 3** Mean density (no. 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during April–May 1996. *n* = Number of MOCNESS deployments on which density estimates were based

Species	0–50 m		50–100 m	
	Day ( <i>n</i> = 9)	Night ( <i>n</i> = 13)	Day ( <i>n</i> = 8)	Night ( <i>n</i> = 12)
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	0.327	1.552	2.067	1.486
<i>Diphyes antarctica</i>	0.860	0.775	12.24	16.34
<i>Periphylla periphylla</i>	–	–	–	–
Scyphozoa sp.	–	0.015	–	0.005
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	–	–	–	–
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	–	–	–	–
<b>Mollusca</b>				
Mollusc sp.	–	–	0.016	–
<b>Gastropoda</b>				
Pteropod sp.	–	–	–	–
<i>Clio pyramidata</i>	0.078	0.109	0.061	0.007
<i>Clione antarctica</i>	0.006	0.051	–	0.003
<i>Limacina helicina</i>	0.033	0.018	0.034	0.013
<i>Spongiobranchaea australis</i>	–	–	–	–
Cephalopoda sp.	–	–	–	0.005
Nemertean sp.	–	–	0.028	0.002
<b>Polychaeta</b>				
Polychaete sp. A	–	–	–	–
Polychaete sp. B	–	–	–	–
<i>Tomopteris carpenteri</i>	0.019	0.235	0.040	0.051
<i>Vanadis antarctica</i>	0.120	0.089	0.300	0.138
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	–	–	–	–
<i>Euphausia superba</i>	2331.4	5712.5	599.88	134.94
<i>Thysanoessa macrura</i>	11.76	1.251	27.19	17.52
Decapoda sp.	0.064	0.116	0.107	0.254
<b>Amphipoda</b>				
Amphipod sp.	–	–	–	–
<b>Hyperiid</b>				
<i>Cylopus lucasii</i>	0.347	1.087	0.058	0.836
<i>Hyperiella dilatata</i>	0.004	0.007	0.005	0.044
<i>Parathemisto gaudichaudii</i>	0.326	0.471	0.024	0.090
<i>Primno macropa</i>	0.013	0.007	0.008	0.002
<i>Vibilia antarctica</i>	0.021	0.020	0.008	0.031
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	–	0.002	–	–
<i>Eusirus microps</i>	–	–	–	–
<i>Orchomene rossi</i>	–	–	–	–
Chaetognath sp.	0.159	0.741	1.576	1.617
<b>Tunicata</b>				
<i>Salpa</i> sp.	1.977	0.161	0.012	0.75
<i>Salpa thompsoni</i>	98.09	494.2	11.60	229.1
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	0.003	0.007	0.016	0.028
<i>Bathyraco joannae</i>	–	–	–	–
<i>Electrona antarctica</i>	–	0.002	–	0.131
<i>Notolepis coatsi</i>	–	–	–	–
<i>Pleuragramma antarcticum</i>	–	–	–	–
Mean total density	2490.6	6213.5	655.33	403.33
Standard error	(938.1)	(2001)	(472.5)	(130.9)

prominent components of density and biomass at both sampling depths (Figs. 4, 5). At 0–50 m, *T. macrura* was dominant during the day and represented a greater proportion of the total density and biomass during the day than at night (Figs. 4, 5). In contrast to *T. macrura*, distributions of *D. antarctica*, *S. thompsoni*,

**Table 4** Mean density (no. 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during November–December 1996. *n* = Number of MOCNESS deployments on which density estimates were based

Species	0–50 m		50–100 m	
	Day ( <i>n</i> = 40)	Night ( <i>n</i> = 8)	Day ( <i>n</i> = 40)	Night ( <i>n</i> = 8)
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	0.004	0.003	0.211	0.208
<i>Diphyes antarctica</i>	1.897	0.117	5.930	7.687
<i>Periphylla periphylla</i>	–	0.013	–	0.016
Scyphozoa sp.	–	0.084	–	0.031
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	–	–	–	–
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	2.448	2.548	3.340	1.815
<b>Mollusca</b>				
Mollusc sp.	–	–	–	–
<b>Gastropoda</b>				
Pteropod sp.	–	–	–	–
<i>Clio pyramidata</i>	0.941	2.863	0.469	0.924
<i>Clione antarctica</i>	0.327	0.633	0.496	0.564
<i>Limacina helicina</i>	0.024	0.048	0.058	0.052
<i>Spongiobranchaea australis</i>	0.007	0.013	0.069	0.006
Cephalopoda sp.	0.013	0.007	0.062	0.023
Nemertean sp.	–	–	–	–
<b>Polychaeta</b>				
Polychaete sp. A	–	–	–	–
Polychaete sp. B	–	–	–	–
<i>Tomopteris carpenteri</i>	0.064	0.081	0.159	0.134
<i>Vanadis antarctica</i>	0.222	0.205	0.411	0.854
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	–	–	–	–
<i>Euphausia superba</i>	1101.3	2820.9	482.71	0.339
<i>Thysanoessa macrura</i>	9.067	4.889	2.959	3.289
Decapoda sp.	0.039	0.346	0.242	0.183
<b>Amphipoda</b>				
Amphipod sp.	–	–	<0.001	0.016
<b>Hyperiid</b>				
<i>Cylopus lucasii</i>	0.162	0.604	0.099	0.106
<i>Hyperiella dilatata</i>	0.071	0.137	0.062	0.210
<i>Parathemisto gaudichaudii</i>	–	–	–	–
<i>Primno macropa</i>	0.048	0.013	1.103	0.026
<i>Vibilia antarctica</i>	0.004	0.011	0.002	0.011
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	0.023	0.010	0.071	0.025
<i>Eusirus microps</i>	0.006	0.011	0.011	–
<i>Orchomene rossi</i>	–	–	–	–
Chaetognath sp.	0.965	0.721	2.010	3.422
<b>Tunicata</b>				
<i>Salpa</i> sp.	–	–	–	–
<i>Salpa thompsoni</i>	3.706	9.708	3.464	1.845
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	0.025	0.023	0.017	0.012
<i>Bathyraco joannae</i>	0.001	0.003	0.005	–
<i>Electrona antarctica</i>	–	–	–	–
<i>Notolepis coatsi</i>	–	–	–	–
<i>Pleuragramma antarcticum</i>	–	–	–	–
Mean total density	1121.3	2844.0	504.0	21.72
Standard error	(325.8)	(2266)	(113.1)	(3.63)

chaetognaths and siphonophores were patchy throughout the sampling regime. *D. antarctica* was a more prominent component of the epipelagic community in terms of both abundance and biomass at 50–100 m versus 0–50 m, but in general, spatial and temporal patterns of occurrence at 50–100 m were similar to those at 0–50 m.

**Table 5** Mean biomass (g 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during September–October 1995. *n* = Number of MOCNESS deployments on which biomass estimates were based

Species	0–50 m		50–100 m	
	Day ( <i>n</i> = 30)	Night ( <i>n</i> = 18)	Day ( <i>n</i> = 29)	Night ( <i>n</i> = 18)
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	–	–	–	–
<i>Diphyes antarctica</i>	0.166	0.167	3.193	2.926
<i>Periphylla periphylla</i>	–	–	–	–
Scyphozoa sp.	<0.001	0.114	0.021	–
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	0.104	0.096	0.425	1.267
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	–	–	–	–
<b>Mollusca</b>				
Mollusc sp. A	–	–	–	–
<b>Gastropoda</b>				
Pteropod sp.	<0.001	0.002	<0.001	0.002
<i>Clio pyramidata</i>	0.021	0.176	0.104	0.029
<i>Clione antarctica</i>	0.014	0.019	0.011	0.016
<i>Limacina helicina</i>	–	–	–	–
<i>Spongiobranchaea australis</i>	0.003	0.005	0.006	0.011
Cephalopoda sp.	0.002	–	0.002	<0.001
Nemertean sp.	–	–	–	–
<b>Polychaeta</b>				
Polychaete sp. A	0.008	0.036	0.020	0.057
Polychaete sp. B	–	<0.001	0.003	0.001
<i>Tomopteris carpenteri</i>	<0.001	0.026	0.003	0.013
<i>Vanadis antarctica</i>	0.042	0.048	0.098	0.043
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	<0.001	0.007	–	0.010
<i>Euphausia superba</i>	0.002	0.311	0.001	1.126
<i>Thysanoessa macrura</i>	0.523	0.057	0.675	0.262
Decapoda sp.	<0.001	0.009	0.004	0.016
<b>Amphipoda</b>				
Amphipod sp.	–	<0.001	<0.001	<0.001
<b>Hyperiid</b>				
<i>Cylopus lucasii</i>	0.003	0.091	0.008	0.081
<i>Hyperiella dilatata</i>	0.002	0.014	<0.001	0.012
<i>Parathemisto gaudichaudii</i>	–	0.006	<0.001	–
<i>Primno macropa</i>	0.003	0.002	0.005	0.005
<i>Vibilia antarctica</i>	<0.001	<0.001	<0.001	0.001
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	<0.001	0.013	0.002	0.010
<i>Eusirus microps</i>	–	–	–	–
<i>Orchomene rossi</i>	–	–	–	<0.001
Chaetognath sp.	0.151	0.423	0.284	0.415
<b>Tunicata</b>				
<i>Salpa</i> sp.	–	–	–	–
<i>Salpa thompsoni</i>	0.032	0.306	0.032	0.180
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	–	–	–	–
<i>Bathyraco joannae</i>	–	–	–	–
<i>Electrona antarctica</i>	–	–	–	–
<i>Notolepis coatsi</i>	<0.001	0.002	<0.001	<0.001
<i>Pleuragramma antarcticum</i>	–	0.001	–	0.001
Mean total biomass	1.074	1.931	4.896	6.493
Standard error	(0.18)	(0.18)	(0.85)	(0.61)

In contrast to September–October 1995, *Euphausia superba* and *S. thompsoni* were the overwhelming community dominants during April–May 1996 (Figs. 4, 5), especially at 0–50 m. *E. superba* appeared to be the density dominant at 0–50 m, while *S. thompsoni* accounted for a greater proportion of the biomass.

**Table 6** Mean biomass (g 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during April–May 1996. *n* = Number of MOCNESS deployments on which biomass estimates were based

Species	0–50 m		50–100 m	
	Day ( <i>n</i> = 9)	Night ( <i>n</i> = 13)	Day ( <i>n</i> = 8)	Night ( <i>n</i> = 12)
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	0.676	2.744	5.129	3.182
<i>Diphyes antarctica</i>	0.123	0.184	4.511	4.709
<i>Periphylla periphylla</i>	–	–	–	–
Scyphozoa sp.	–	0.017	–	<0.001
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	–	–	–	–
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	–	–	–	–
<b>Mollusca</b>				
Mollusc sp.	–	–	0.001	–
<b>Gastropoda</b>				
Pteropod sp.	–	–	–	–
<i>Clio pyramidata</i>	0.012	0.016	0.010	0.001
<i>Clione antarctica</i>	<0.001	0.003	–	<0.001
<i>Limacina helicina</i>	0.003	0.001	0.005	0.002
<i>Spongiobranchaea australis</i>	–	–	–	–
Cephalopoda sp.	–	–	–	0.001
Nemertean sp.	–	–	<0.001	<0.001
<b>Polychaeta</b>				
Polychaete sp. A	–	–	–	–
Polychaete sp. B	–	–	–	–
<i>Tomopteris carpenteri</i>	0.005	0.038	0.026	0.026
<i>Vanadis antarctica</i>	0.018	0.011	0.087	0.046
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	–	–	–	–
<i>Euphausia superba</i>	157.3	492.2	41.98	10.09
<i>Thysanoessa macrura</i>	0.489	0.065	1.525	0.568
Decapoda sp.	0.011	0.012	0.012	0.029
<b>Amphipoda</b>				
Amphipod sp.	–	–	–	–
<b>Hyperiid</b>				
<i>Cylopus lucasii</i>	0.013	0.114	0.003	0.057
<i>Hyperiella dilatata</i>	<0.001	0.002	0.004	<0.001
<i>Parathemisto gaudichaudii</i>	0.025	0.042	0.002	0.008
<i>Primno macropa</i>	<0.001	0.003	0.002	0.002
<i>Vibilia antarctica</i>	0.001	0.001	<0.001	0.002
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	–	0.002	–	–
<i>Eusirus microps</i>	–	–	–	–
<i>Orchomene rossi</i>	–	–	–	–
Chaetognath sp.	0.009	0.033	0.048	0.080
<b>Tunicata</b>				
<i>Salpa</i> sp.	1.286	0.017	0.002	0.146
<i>Salpa thompsoni</i>	45.79	375.1	2.154	258.7
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	<0.001	0.006	0.002	0.020
<i>Bathyraco joannae</i>	–	–	–	–
<i>Electrona antarctica</i>	–	0.004	–	0.265
<i>Notolepis coatsi</i>	–	–	–	–
<i>Pleuragramma antarcticum</i>	–	–	–	–
Mean total biomass	205.7	870.7	55.50	277.9
Standard error	(54.0)	(248)	(32.1)	(57.4)

Chaetognaths and unidentified siphonophores, both of which were conspicuous components of the epipelagic assemblage in September–October 1995, were virtually absent in April–May 1996. At 50–100 m the community was more diverse, with *D. antarctica*, *T. macrura*, and *Calyropsis borchgrevinki* contributing substantially to

**Table 7** Mean biomass (g 1,000 m<sup>-3</sup>) for individual species of macrozooplankton and micronekton collected in the NW Weddell Sea during November–December 1996. *n* = Number of MOCNESS deployments on which biomass estimates were based

Species	0–50 m		50–100 m	
	Day ( <i>n</i> = 40)	Night ( <i>n</i> = 8)	Day ( <i>n</i> = 40)	Night ( <i>n</i> = 8)
<b>Cnidaria</b>				
<i>Calyropsis borchgrevinki</i>	0.007	< 0.001	0.518	0.659
<i>Diphyes antarctica</i>	0.131	0.037	2.073	3.006
<i>Periphylla periphylla</i>	–	–	–	–
Scyphozoa sp.	–	0.137	–	0.538
Siphonophore sp. A ( <i>Dimophyes arctica</i> ?)	–	–	–	–
Siphonophore sp. B ( <i>Marrus antarcticus</i> ?)	0.473	0.416	0.508	0.232
<b>Mollusca</b>				
Mollusc sp.	–	–	–	–
<b>Gastropoda</b>				
Pteropod sp.	–	–	–	–
<i>Clio pyramidata</i>	0.087	0.176	0.036	0.039
<i>Clione antarctica</i>	0.009	0.017	0.012	0.016
<i>Limacina helicina</i>	0.001	0.008	0.040	0.028
<i>Spongiobranchaea australis</i>	0.002	0.001	0.001	< 0.001
Cephalopoda sp.	< 0.001	< 0.001	0.002	0.004
Nemertean sp.	–	–	–	–
<b>Polychaeta</b>				
Polychaete sp. A	–	–	–	–
Polychaete sp. B	–	–	–	–
<i>Tomopteris carpenteri</i>	0.004	0.034	0.026	0.050
<i>Vanadis antarctica</i>	0.035	0.021	0.078	0.152
<b>Euphausiacea</b>				
<i>Euphausia crystallorophias</i>	–	–	–	–
<i>Euphausia superba</i>	117.8	271.3	64.30	0.036
<i>Thysanoessa macrura</i>	0.304	0.215	0.131	0.179
Decapoda sp.	0.003	0.023	0.016	0.014
<b>Amphipoda</b>				
Amphipod sp.	–	–	< 0.001	0.003
<b>Hyperiidea</b>				
<i>Cylopus lucasii</i>	0.019	0.085	0.012	0.015
<i>Hyperiella dilatata</i>	0.017	0.003	0.002	0.031
<i>Parathemisto gaudichaudii</i>	–	–	–	–
<i>Primno macropa</i>	0.003	0.002	0.002	0.002
<i>Vibilia antarctica</i>	< 0.001	< 0.001	< 0.001	< 0.001
<b>Gammaridea</b>				
<i>Eusirus antarcticus</i>	0.004	0.005	0.021	0.006
<i>Eusirus microps</i>	< 0.001	–	0.004	–
<i>Orchomene rossi</i>	–	–	–	–
Chaetognatha sp.	0.082	0.111	0.132	0.250
<b>Tunicata</b>				
<i>Salpa</i> sp.	–	–	–	–
<i>Salpa thompsoni</i>	2.985	10.82	2.748	1.092
<b>Vertebrata (fish larvae)</b>				
Pisces sp.	0.004	0.003	0.005	0.005
<i>Bathyrdraco joannae</i>	0.001	0.002	0.002	–
<i>Electrona antarctica</i>	–	–	–	–
<i>Notolepis coatsi</i>	–	–	–	–
<i>Pleuragramma antarcticum</i>	–	–	–	–
Mean total biomass	121.9	283.4	70.67	6.359
Standard error	(35.1)	(213)	(15.7)	(1.29)

the daytime community. At night, *S. thompsoni* was dominant in terms of both density and biomass (Figs. 4d, 5d).

At both depths during November–December 1996, *E. superba* was the density and biomass dominant,

although it appeared to comprise a lower proportion of the total density and biomass during the 2–3 h preceding sunrise. At 0–50 m, *S. thompsoni* also was dominant just before dawn, but this trend was more obvious in biomass than in density, since *S. thompsoni* were larger on average than *E. superba*. *D. antarctica*, *T. macrura* and unidentified siphonophores also were present at 0–50 m, but the contribution of these species to the total community density and biomass was overshadowed by *E. superba*. At 50–100 m, the contribution of less abundant species such as *C. borchgrevinki*, *T. macrura*, chaetognaths, scyphozoans and siphonophores was more obvious. In addition, *E. superba* and *S. thompsoni* exhibited distinct diel patterns, with *E. superba* making up a greater proportion of the community during the day and *S. thompsoni* more abundant at night.

#### Cluster and ordination analysis

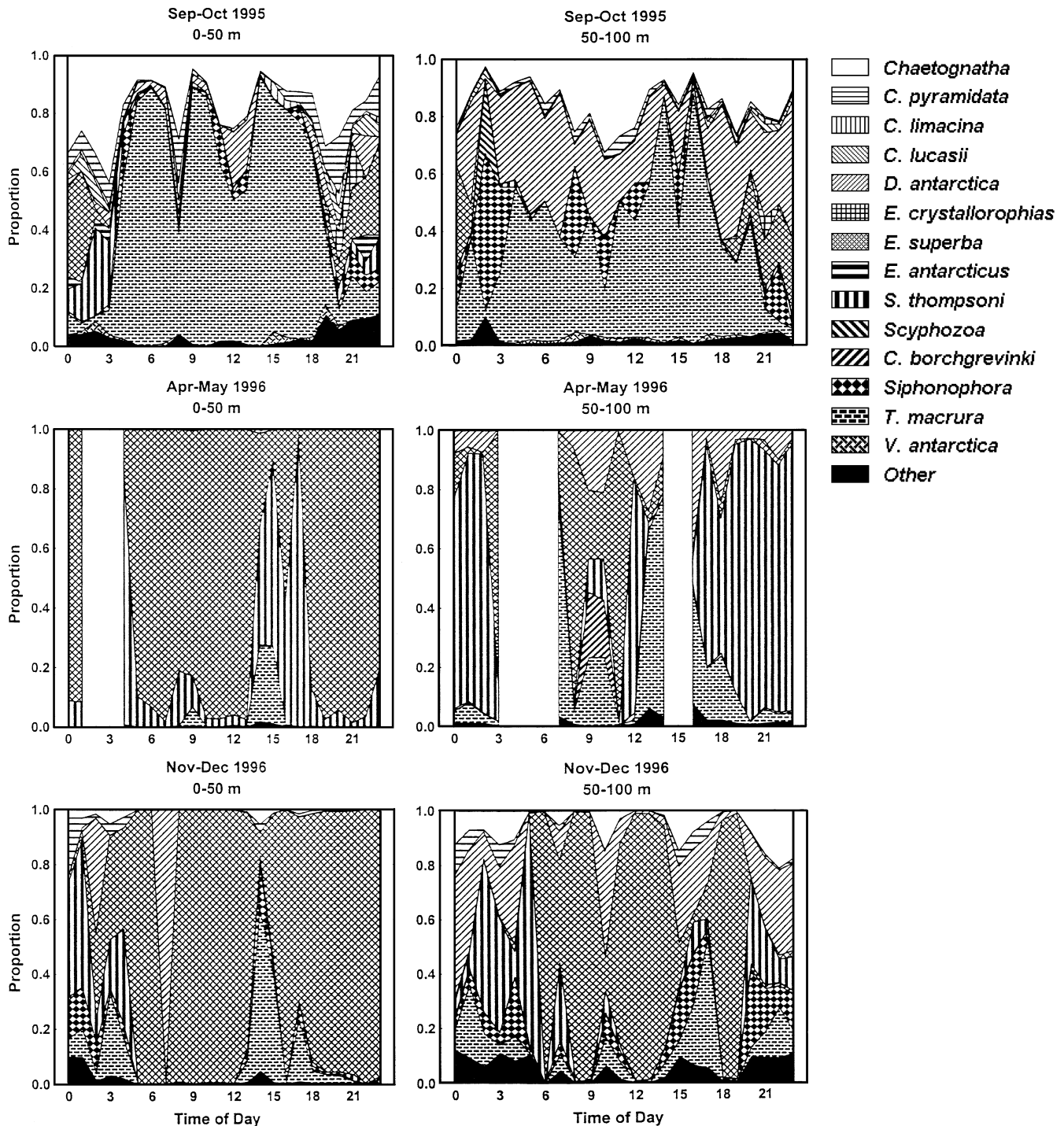
Two distinct cluster groups were defined at an arbitrary 78% dissimilarity, which showed differences between samples collected during September–October 1995 (group 1) and samples collected during both cruises in 1996 (group 2) (Fig. 6a). Group 2 was divided further into two subgroups at 69% dissimilarity. Group 2a comprised samples collected during April–May 1996 and group 2b comprised samples collected during November–December 1996. The MDS plot shows the same grouping as the dendrogram using the same dissimilarity index as the cluster analysis (Fig. 6b). Samples from September–October 1995 are clustered within a grouping defined by the dendrogram, and samples from April–May 1996 and November–December 1996 are indicated as subclusters of a single group. MDS was performed first in three dimensions, with a resulting stress of 0.056. This configuration then was used as the starting point for two-dimensional MDS, which converged to a stress of 0.090. These stress values were the lowest generated from 126 and 50 iterations on the three- and two-dimensional analyses, respectively. To examine whether *E. superba* was determining the groupings described above, *E. superba* was removed from the data set and the cluster and ordination analyses were performed again. Removing *E. superba* decreased the dissimilarity between subgroups 2a and 2b to 68%, but otherwise had no effect on the cluster or ordination results.

#### Discussion and conclusions

##### Depth distribution of density and biomass

Greater density and biomass was found deeper in the water column under heavy pack-ice cover in September–October 1995. In contrast, previous laboratory experiments (Hamner et al. 1983) and field observations (e.g. O'Brien 1987; Daly and Macaulay 1988; Marschall 1988) indicate that krill associate with the under-surface of pack ice. Brierley et al. (2002) used an autonomous underwater

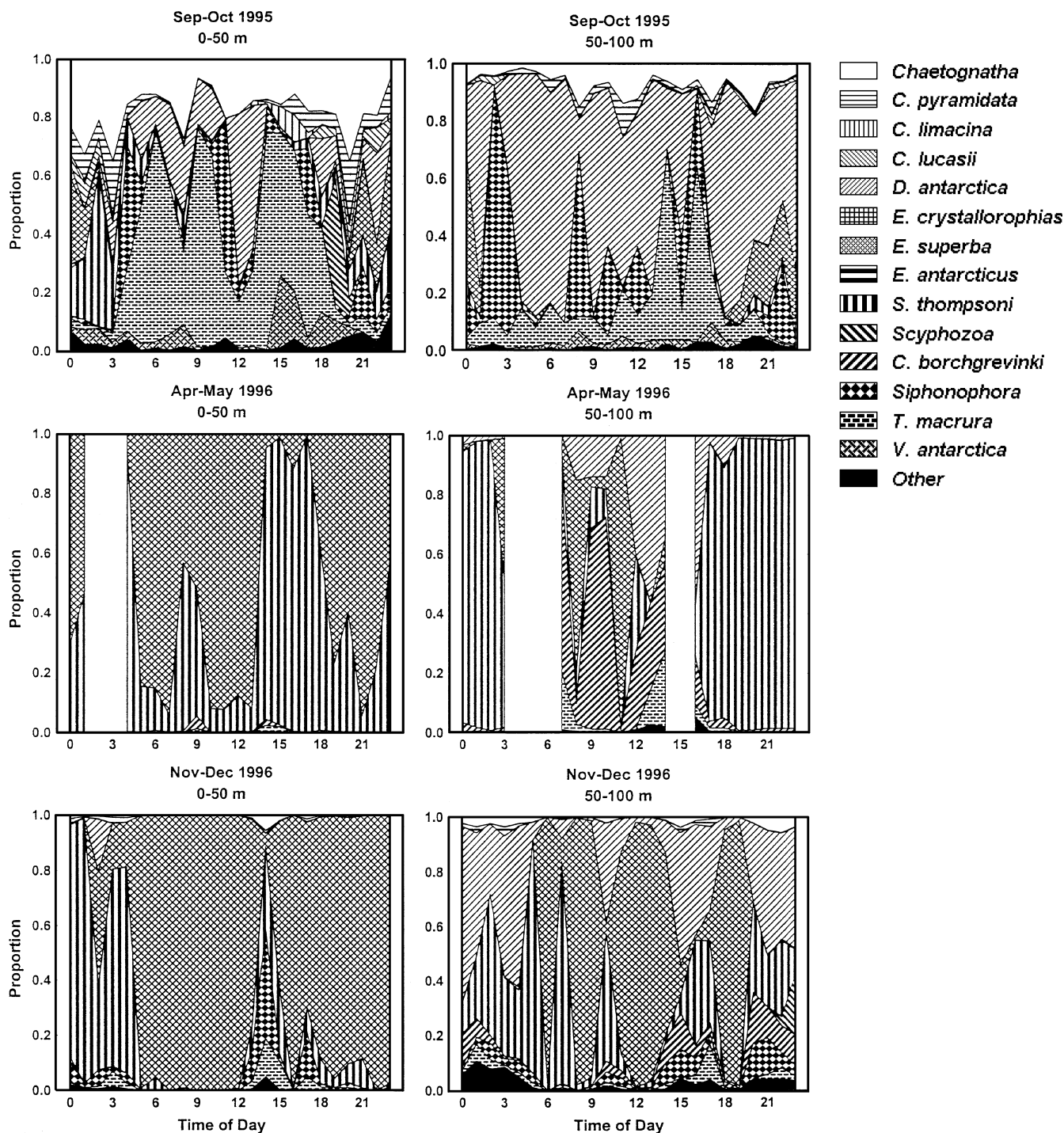




**Fig. 4** Hourly composition of the epipelagic community, based on densities of animals collected with the MOCNESS during 1995 and 1996. Areas represent proportions of the total community comprised by each species or group of species. *Top* September–October 1995, *centre* April–May 1996, *bottom* November–December 1996

vehicle to examine krill living under Weddell Sea ice and found krill densities under the ice that were five times greater than those in open water. Therefore, we might expect to find more animals near the surface, close to the pack ice, than deeper in the water column.

Net avoidance behavior due to visual or mechanical cues can lead to underestimates of zooplankton abundance, selective sampling of certain taxa or age classes, or misleading diel distribution patterns (e.g. Wiebe et al. 1982; Hamner et al. 1983; Hamner 1984; Everson and Bone 1986). Under ice, net avoidance likely increases because the physical process of breaking the pack ice with a ship probably leads to escape behaviors and underestimates of the pack-ice community (Hamner et al. 1983; Hamner 1984). We cannot rule out the possibility that our results might include sampling arti-



**Fig. 5** Hourly composition of the epipelagic community, based on biomass of animals collected with the MOCNESS during 1995 and 1996. Areas represents proportions of the total community comprised by each species or group of species during *top* September–October 1995, *centre* April–May 1996, *bottom* November–December 1996

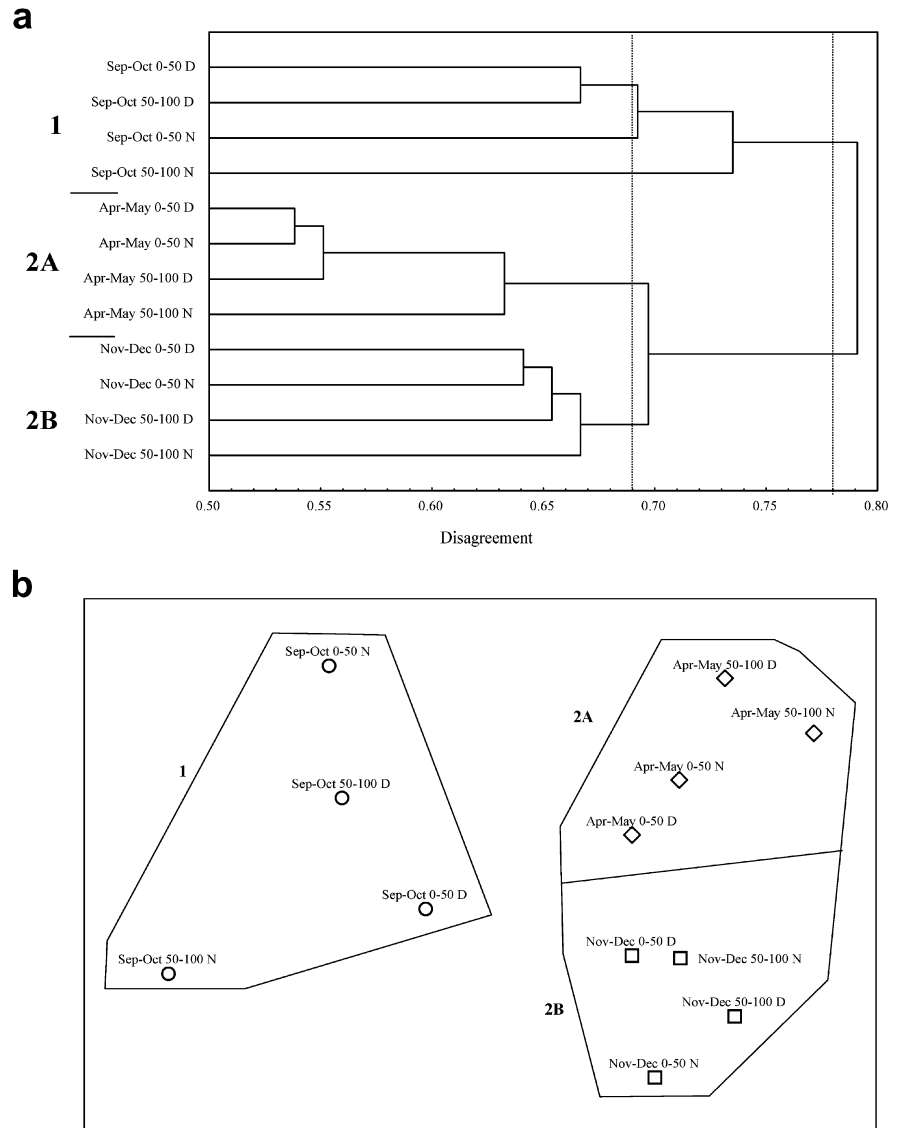
facts based on the method used to sample zooplankton under the pack ice.

Zooplankton biomass and density is likely to have been underestimated during April–May 1996 and November–December 1996 for the same reason. Both in

open water and in pack ice we would expect higher net avoidance at the surface, where more light may provide cues for a visual escape response and the mechanical cue of a pressure wave at the front of the ship may be more pronounced than at greater depths. However, because the density and biomass during April–May 1996 and November–December 1996 was higher at 0–50 m than at 50–100 m, net avoidance may not fully explain the distribution patterns observed.

During April–May 1996 and November–December 1996, *E. superba* was the dominant species sampled in

**Fig. 6 a** Cluster dendrogram of samples based on cruise, depth, and time of day. Three zooplankton community groups are apparent. *N* Night, *D* day. **b** Multi-dimensional scaling ordination of sampling stations with the three zooplankton community groups (Fig. 6a) superimposed



the 0–50 m depth stratum. *E. superba* often occurred in discrete aggregations (schools) near the surface that are characteristic of this species (Hamner et al. 1983; Hamner 1984; Miller et al. 1993; Lascara et al. 1999); these schools may provide protection from some types of predators (Hamner 1984). In addition, the aggregations are often larger in open water Godlewski (1993) and more prevalent during summer, under conditions of elevated food availability and high predation pressure (Daly and Macaulay 1991; Costa and Crocker 1996; Fraser and Trivelpiece 1996). Everson and Bone (1986) found that high-density swarms limit the ability of the krill to avoid a towed net. Therefore, the likelihood of sampling a large aggregation of krill, which would lead to high density and biomass estimates, would have been higher in surface waters during periods of open water in April–May 1996 and November–December 1996.

#### Diel distribution of density and biomass

During November–December 1996, no differences in total density and biomass between day and night were found at either depth stratum. However, clear differences in species composition were observed between day and night trawls during this time period (Figs. 4, 5), reflecting a change in the community structure, if not overall abundance. In contrast to November–December 1996, time of collection affected density during April–May 1996 at 50–100 m and biomass at both depths during September–October 1995 and April–May 1996. It is possible that a shift from large numbers of relatively small animals to an equivalent number of relatively large (higher biomass) animals led to the discrepancies between density and biomass measurements.

At both depths during September–October 1995, *T. macrura* accounted for a greater proportion of the

water column biomass during the day than at night, when *D. antarctica* and chaetognaths were the dominant taxa. While both *D. antarctica* and chaetognaths comprise a consistently patchy proportion of the biomass over the 24-h sampling regime, *T. macrura* in this study exhibited reverse diel vertical migration, with greater abundances in surface waters during the day than at night. Some studies have not reported diel vertical migration in *T. macrura* (e.g. Piatkowski 1985; Lancraft et al. 1989); however, greater clustering of *T. macrura* has been observed near the surface during the day than at night in the Atlantic sector of the Southern Ocean (Pakhomov et al. 1993; Maklygin and Pakhomov 1993). In addition, Nordhausen (1994) found strong diel vertical migration among adults and juveniles in the Gerlache Strait during the austral spring, and Lancraft et al. (1991) reported that *T. macrura* were distributed closer to the surface at night than during the day in pack ice.

During April–May 1996, *E. superba* and *S. thompsoni* dominated the water column density and biomass (Figs. 4, 5). The day and night differences in density at 50–100 m were likely the result of a shift from *E. superba* dominance during the day to *S. thompsoni* dominance at night (Fig. 4d, Table 3). In contrast to our results, previous studies using nets (e.g. Pavlov 1974; Nast 1979; Hopkins and Torres 1988) and acoustics (Arimoto et al. 1979; Tomo 1983; Godlewska and Klusek 1987) in open water provided strong evidence that *E. superba* is a vertically migrating animal. Although the forces driving vertical migration are not well understood, the additional evidence that krill aggregate into compact swarms during the day and disperse at night may explain why high-density *E. superba* samples were collected predominantly during the day (Everson 1983).

The shift in species dominance from *E. superba* during the day to *S. thompsoni* at night may explain the difference in biomass between day and night during April–May 1996 (Figs. 4, 5). While large samples of *E. superba* were collected during the day, *S. thompsoni* exhibited a diel vertical migration pattern at both depths. These data are supported by other studies that found salps below 100 m during the day and near the surface at night (e.g. Foxton 1966; Piatkowski 1985; Lancraft et al. 1989). As illustrated by the size discrepancy between the dominant species in September–October 1995, the biomass difference between *E. superba* and *S. thompsoni*, which is a much larger animal, likely accounted for the day-night biomass differences.

#### Among-cruise comparison of density and biomass

The total biomass and density of macrozooplankton and micronekton in the epipelagic zone was different among all cruises at 0–50 m. Biomass and density also were different among cruises at 50–100 m except during the

day between April–May 1996 and November–December 1996 and during the night between September–October 1995 and November–December 1996. In general, total density and biomass were lowest in areas of high ice cover (September–October 1995), highest in intermediate levels of ice cover (April–May 1996), and intermediate in open water (November–December 1996). These trends were influenced strongly by temporal variation in the abundance of krill, which exhibited similar temporal trends in density and biomass (Tables 2, 3, 4, 5, 6, 7).

While few studies have quantified total biomass and abundance of zooplankton at the same location during different times of the year, the results reported here support the findings of studies conducted synoptically at open water and ice-covered sites. For example, Siegel et al. (1992) measured higher zooplankton abundance and biomass at an open water site compared to an ice-covered site during October–November in the northern Weddell Sea.

Trawl-based differences in zooplankton density and biomass under pack ice compared to open water areas are supported by studies involving acoustics. Kaufmann et al. (1995) used moored upward-directed acoustic arrays to examine the abundance of zooplankton in open water and ice-covered sites and found that the abundance of acoustic targets was higher in open water than in pack ice. Trawling results from Kaufmann et al. (1995) provided additional support for these observations. However, a recent study using an autonomous underwater vehicle reported zooplankton densities five times higher in the marginal ice zone than in open water during austral summer (Brierley et al. 2002).

Although total density and biomass estimates for the upper 100 m of the water column in the NW Weddell Sea are likely to be conservative, the values are within the range of estimates reported for this area (Table 8). Published zooplankton density and biomass data for the Weddell Sea are on the order of 20–5,278 individuals  $1,000\text{ m}^{-3}$  and 3.5–465 g wet weight  $1,000\text{ m}^{-3}$ , respectively, encompassing studies that both did and did not include the quantitative collection of copepods (Table 8).

The density of numerically dominant species fluctuates within a season in the Antarctic Peninsula region, with the highest density of zooplankton in summer months. An acoustic study conducted by Lascara et al. (1999) found higher krill biomass in the Antarctic Peninsula region during austral spring and summer than during fall and winter. Oceanographic circulation, seasonal krill habitats, and changes in krill behavior, including horizontal and vertical migrations, may influence krill distributions and abundances at a single site over the course of 1 year (Heywood et al. 1985; Kawaguchi et al. 1986; Siegel 1988; Sprong and Schalk 1992; Gutt and Siegel 1994; Quetin et al. 1996; Lascara et al. 1999). Unfortunately, the influence of these processes on our current results is outside the scope of this study.

**Table 8** Literature values for Antarctic zooplankton collected within the Weddell Sea. Original data are presented in **bold**; conversion ratio DW:WW = 1:8 for copepod-dominated biomass and 1:5 for krill-dominated biomass (Hagen 1988)

Lat (°S)	Long (°W)	Conditions	Sampling Depth (m)	Net Mouth (m)	Mesh Size (µm)	Opening/Closing?	Oblique/Discrete	WW (g 1,000 m <sup>-3</sup> )	Abundance (n 1,000 m <sup>-3</sup> )	Dominant Taxa	Source
65–78	5–55	Pack ice	0–300	8	4500	Yes	Oblique	–	<b>490.7</b>	Chaetognaths	Boysen-Ennen and Platkowski (1988)
64–67	42–52	Open water	0–1,000	9	4000	Yes	Discrete	28.20	<b>20.12</b>	<i>Euphausia superba</i>	Lancraft et al. (1989)
66–78	30–60	Pack ice	0–300	8	4500	Yes	Oblique	<b>11.5</b>	–	Euphausiids	Boysen-Ennen et al. (1991)
57–62	34–50	Pack ice	0–1,000	1.8	4000	Yes	Discrete	22.89	<b>20.67</b>	<i>Euphausia superba</i>	Lancraft et al. (1991)
56–64	44–57	Open water	0–60	1 and 8	320 and 4,500	Yes	Discrete	<b>149.7</b>	<b>5278</b>	Copepods	Siegel et al. (1992)
56–64	44–57	Transitional	0–300	1 and 8	320 and 4,500	Yes	Discrete	<b>9.12</b>	<b>245.3</b>	Copepods	Siegel et al. (1992)
56–64	44–57	Pack ice	0–60	1 and 8	320 and 4,500	Yes	Discrete	<b>37.35</b>	<b>188.6</b>	Copepods	Siegel et al. (1992)
62–64	44–50	Open water	0–100	10	4000	Yes	Discrete	<b>104.7</b>	<b>915.7</b>	<i>Euphausia superba</i> <i>thompsoni</i>	Present study
62–64	44–50	Transitional	0–100	10	4000	Yes	Discrete	<b>465.5</b>	<b>2495.8</b>	<i>Euphausia superba</i> <i>thompsoni</i>	Present study
62–64	44–50	pack ice	0–100	10	4000	Yes	Discrete	<b>3.48</b>	<b>20.23</b>	<i>Thysanoessa macrura</i>	Present study

Because the time points for our study were more than 1 year apart, interannual variability in ice cover may have affected our measurements. Biomass has been observed to vary interannually in the region near the Antarctic Peninsula (e.g. Ross et al. 1996; Loeb et al. 1997; Siegel et al. 1998), with years of high *E. superba* biomass often following winters of high ice cover (e.g. Loeb et al. 1997; Siegel et al. 1998). This trend reflects the ability of *E. superba* larvae to overwinter under sea ice and take advantage of phytoplankton blooms in the spring (Loeb et al. 1997). During the winter of 1995, sea ice coverage and duration in the Antarctic Peninsula region were above average (Loeb et al. 1997). Siegel et al. (1998) found very high krill biomass in January 1996 following a winter of above-average ice cover; high ice coverage during the winter of 1995 also may explain the high *E. superba* biomass collected in the NW Weddell Sea in April–May 1996 during the present study. Less extensive ice coverage during the winter of 1996 may have accounted for the lower biomass collected during November–December 1996 than April–May 1996.

### Community composition

Previous studies have reported homogeneity in community composition between open water and pack ice sites in the Weddell Sea (Hopkins and Torres 1988; Siegel et al. 1992). However, in our study, two distinct zooplankton groups, defined at 78% dissimilarity, represented samples collected under different ice regimes (Fig. 3).

Group 1 included all four samples that were collected during September–October 1995, the ice-covered sampling period when *T. macrura* was dominant during the day and *E. crystallorophias* and the amphipod *Orchomene rossi*, both of which are ice-associated species (e.g. Boysen-Ennen et al. 1991; Kaufmann et al. 1995), were present (Figs. 4, 5; Tables 2, 3, 4, 5, 6, 7). Additionally, samples collected during the day in September–October 1995 were more similar to each other than to samples collected during the night. Group 2 included two subgroups, separable at the 67% dissimilarity level, in which *E. superba* and *S. thompsoni* were the dominant species. Group 2a included samples collected during April–May 1996 and group 2b included samples from November–December 1996. Unlike the groups from the September–October 1995 samples, subgroups within groups 2a and 2b were separated with respect to depth rather than time of collection.

The formation of these groups likely was due to the interaction of environmental and oceanographic parameters with the behavior and life history characteristics of the species that are present. For example, *T. macrura* comprised a greater portion of the total community in September–October 1995 than in April–May 1996 and November–December 1996, when large single species aggregations of *E. superba* and *S. thompsoni* were present. And, whereas Macaulay et al. (1985) observed small patches of krill, mostly *T. macrura*, near

the ice edge in the Weddell Sea, large aggregations of *E. superba* were more prevalent in areas of open water (Godlewski 1993). These krill swarms have been speculated to influence diversity of the zooplankton community by excluding other species from the area via competition (Hosie 1994), in turn influencing the overall zooplankton community composition and subsequent groupings.

## Conclusions

Differences in the density, biomass, and community composition of macrozooplankton/micronekton in the NW Weddell Sea were found among the three time periods that were sampled during this study: early to mid-spring (September–October 1995), mid- to late autumn (April–May 1996), and late spring to early summer (November–December 1996). While a number of measured environmental parameters varied among the three cruises, the most obvious variation occurred with ice cover, which ranged from 60% to 100% total cover in September–October 1995 to no ice cover during November–December 1996. Environmental conditions and sampling methods may have interacted with specific behaviors of dominant species to influence observed distribution patterns and community dynamics. Sampling time influenced not only the overall density and biomass sampled, but also the diel depth distribution of macrozooplankton/micronekton.

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