



## Antarctic mesozooplankton community structure during BROKE-West (30°E–80°E), January–February 2006

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### ARTICLE INFO

#### Article history:

Received 9 October 2008

Accepted 9 October 2008

Available online 24 November 2009

#### Keywords:

Zooplankton

Sea ice

Multivariate analyses

Environment

Species associations

### ABSTRACT

The distribution of mesozooplankton, based on the catch by a RMT1 net, in the upper 200 m of the South Western Indian Ocean sector (30°E–80°E) of the Southern Ocean was examined during the large-scale BROKE-West survey in summer 2006. Multivariate analyses revealed four groups of zooplankton that could be broadly linked to oceanographic features. The first group, occurring south of the southern boundary of the Antarctic Circumpolar Current (sbACC) and west of 40°E, was associated with waters from the eastern limb of the Weddell Gyre. The group was typified by moderate abundance (mean: 11,251 ind. 1000 m<sup>-3</sup>) and included foraminiferans, appendicularians and small copepods. Group 2 was composed of stations found in the deeper, warmer waters lying between the sbACC and the southern ACC front (sACCf), along with a few stations north of the sACCf. Sites in this group exhibited the highest mean zooplankton abundance (81,750 ind. 1000 m<sup>-3</sup>) and comprised large numbers of small copepods and appendicularians. Sites in group 3 fell south of the sbACC, were situated east of 50°E, and generally located near the Antarctic slope current (ASC), a strong and narrow jet of westward flowing water. Typical species for this group included *Euphausia crystallorophias*, *Fritillaria* spp. and *Metridia gerlachei*. Finally, group 4 represented neritic sites in the far southwestern corner of the survey region. Abundances were lowest (mean: 2588 ind. 1000 m<sup>-3</sup>) and the assemblage was dominated by *E. crystallorophias*, *Neogloboquadrina pachyderma* and *Fritillaria* spp. The four groups differed more by abundance than by composition. The suite of environmental variables that best correlated with patterns in the species data included chlorophyll *a* concentration, proximity to the ASC and length of time without an ice cover, all features which indicated that large scale oceanographic processes were underpinning the patterns in mesozooplankton distribution.

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### 1. Introduction

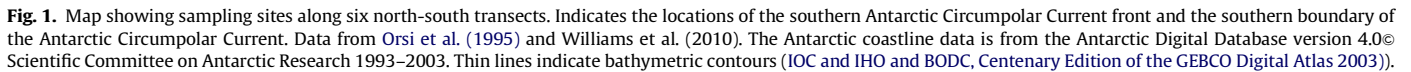
Zooplankton are abundant and important in the Southern Ocean. While many species have circum-Antarctic distributions, their biogeographical patterns are shaped by regional-scale features such as oceanographic fronts and currents, and the interactions of these with the dynamics of sea-ice growth and decay (Atkinson, 1998; Hunt and Hosie, 2005). At local scales, zooplankton distributions are further influenced by the responses of individual species to cycles in primary productivity, other trophic interactions, and their complex life history strategies. Determining which factors are significant drivers in structuring zooplankton communities is an important goal for predicting how climate-mediated changes will influence the Southern Ocean ecosystem. To meet this goal a combination of ecosystem-scale studies and smaller, process-based studies is required.

The number of synoptic surveys in Southern Ocean waters is increasing, though there have been fewer large-scale field surveys in the Indian sector of Antarctica than in the southwest Atlantic sector (Hosie, 1994a; Hosie and Cochran, 1994). BROKE-West (Baseline Research on Oceanography, Krill and the Environment–West) was designed to investigate the oceanography and ecology of an infrequently studied region of the Southern Ocean between 30°E–80°E, covering an area of more than 1 million km<sup>2</sup> that included the Cosmonaut and Cooperation Seas and Prydz Bay (Nicol et al., 2010). The BROKE-West survey complemented the original BROKE survey (80°E–150°E) carried out in 1996 (Nicol, 2000), with its final transect (Fig. 1) following the first transect of the original cruise. Notable features of BROKE-West are that it encompassed regions to the north and south of the southern Antarctic Circumpolar Current front (sACCf; Fig. 1), as well as repeatedly crossing the southern boundary of the Antarctic Circumpolar Current (sbACC; Fig. 1), thus providing the opportunity to examine biological patterns in relation to major water masses.

Previous studies in the region have included detailed oceanographic surveys by scientists from the USSR during the 1970s and 1980s (cited in Hunt et al., 2007), and cruises under the SIBEX 2,

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Many large-scale zooplankton surveys employ RMT1+8 nets, which provide good coverage of larger, faster species such as *Euphausia superba* (RMT8) and smaller, less mobile groups that traditionally characterise the mesozooplankton (RMT1). However, while both nets are usually deployed, often only the catches from the RMT8 are reported in the literature (e.g., [Hosie et al., 2000](#)). This can have the effect of under-representing the smaller components of zooplankton assemblages, such as copepods and larval krill ([Beaumont and Hosie, 1997](#)). In this study we examined in detail the composition of the RMT1 component of the zooplankton samples obtained during BROKE-West. Species composition, distribution and community structure are presented, along with univariate and multivariate analyses designed to explore relationships between species' biogeographical patterns and their physical environment.

### 2.1. Sampling

The RMT1 net had a mesh size of 315  $\mu\text{m}$  and a mouth area of 1  $\text{m}^2$ . The RMT8 net was equipped with a flowmeter, and the volume of seawater filtered by the RMT1 was calculated by dividing the volume filtered by the RMT8 by a factor of 9.42 (Ikeda et al., 1986). The catch from the RMT1 was preserved in 10% Steedman's solution (Steedman, 1976). A total of 50 stations was sampled for zooplankton. In the laboratory samples were split with a Folsom plankton splitter so that 500–1300 individuals

were counted per sample. Animals were identified to species level where possible, and, in the case of euphausiids and copepods, to sex and/or developmental stage. Total abundance is expressed as the number of individuals  $1000\text{ m}^{-3}$ . Biomass, expressed as  $\text{mg C m}^{-3}$ , was determined by multiplying the abundance of each species by its carbon content (K. Swadling, unpublished data) and summing the results.

Several environmental variables that could be used to explore zooplankton-environment relationships were measured during the cruise: (1) A Seabird SBE9 plus CTD (conductivity-temperature-depth) profiler was deployed at each sampling site. Temperature and salinity were measured at 2-m intervals down to 250 m, or to the station bottom in shallower regions (Williams et al., 2010). However, for the purposes of comparison with zooplankton abundances, the data were averaged as mean temperature and salinity over 200 m. (2) To determine the number of ice-free days at each station the mean sea ice concentration in a 50 km radius was calculated from daily data obtained via the Advanced Microwave Scanning Radiometer – Earth Observing System (AMSR-E) files. The ‘end of ice’ was defined as the mean ice concentration dropping below 10% (Williams et al., 2010). A negative value implies that a site was defined as ice free a number of days after it had been sampled. (3) Approximate distance (km) from each sampling station to the Antarctic Slope Current (ASC) was determined. (4) Water samples were collected with  $22 \times 10\text{-L}$  General Oceanics Niskin bottles mounted on a Seabird rosette, with six samples taken over 150 m; two of the six samples always included the surface and the depth of the chlorophyll maximum (Westwood et al., 2010). Chlorophyll *a* concentrations were determined using the HPLC method of Wright and van den Enden (2000), and integrated over 150 m for comparison to zooplankton distribution (Wright et al., 2010).

## 2.2. Analysis

All distribution maps of zooplankton abundance were produced using ArcGIS version 9.2. Multivariate analyses were performed using PRIMER version 6 (Plymouth, UK) and SPSS version 15 (Illinois, USA). The analyses progressed in a fashion similar to those outlined by Hosie (1994a,b) and Hosie et al. (1997), which were originally adapted from Field et al. (1982). Zooplankton abundances were fourth root transformed; this transformation is suitable for ecological data where there are many zeros and few large values (Quinn and Keough, 2002), and is recommended when using the Bray-Curtis index as a measure of (dis)similarity. To investigate associations between the zooplankton assemblages at the sampling stations (Q-mode analysis), a matrix of Bray-Curtis similarities (Bray and Curtis, 1957) was constructed for the 50 sites and subjected to cluster analysis using the unweighted pair group method with arithmetic linking (UPGMA). Relationships between the sampling stations were further explored using non-metric multidimensional scaling (NMDS), an ordination method that can summarise relationships into 2-dimensional space, facilitating comparison with station environmental data. ANOSIM (analysis of similarities) was used to test the null hypothesis that there was no significant difference in community composition between any groups identified with the cluster and NMDS analyses. SIMPER (similarity percentages) analysis was then applied to identify which species contributed to the top 50% of abundance for each group.

Station environmental data associated with each of the resultant groups were summarised and statistical differences between the means of the following variables were tested for using ANOVA: latitude, longitude, temperature, salinity, chloro-

phyll *a*, depth, ice free days, and distance to the ASC. When a significant difference between group means was identified, an unplanned post-hoc comparison of the means using the Ryan, Einot, Gabriel and Welsch procedure (REGW) was applied to distinguish which groups were statistically different. REGW is a conservative procedure that provides control over family-wise Type I error rates (Quinn and Keough, 2002). Relationships between the environmental variables and zooplankton community structure were investigated using BIOENV (PRIMER) to explore correlations between the similarity structure of the environmental variables and the similarity structure of the species matrix. Finally, correlations between axes 1 and 2 of the NMDS and the environmental variables were explored.

Common associations between zooplankton taxa (R-mode analysis) were also defined using cluster analysis, followed by NMDS. Prior to analysis the species by station matrix was reduced to a subset of common dominant species, based on the IndVal (Indicator Value) method designed to find indicator species and species assemblages that characterise groups of samples (Dufrêne and Legendre, 1997). Indicator values for each species were computed using IndVal 2.0, and the random reallocation procedure of sites among site groups was used to test the significance of the maximum IndVal calculated for each species. 499 permutations were used and significance was defined as  $p < 0.05$ . Relative abundance was combined with relative frequency of a species' occurrence in the various clusters. Each IndVal was calculated as:

$$\text{IndVal}_{ij} = A_{ij} * B_{ij} * 100 \quad (1)$$

Where  $A_{ij} = \text{Nindividuals}_{ij} / \text{Nindividuals}_i$  and  $B_{ij} = \text{Nsites}_{ij} / \text{Nsites}_j$

In the formula for  $A_{ij}$ , which is a measure of site specificity,  $\text{Nindividuals}_{ij}$  is the mean number of individuals in species *i* across sites of group *j*, while  $\text{Nindividuals}_i$  is the sum of the mean numbers of individuals of species *i* over all groups. In the formula for  $B_{ij}$ , a measure of group fidelity,  $\text{Nsites}_{ij}$  is the number of sites in cluster *j* where species *i* is present, while  $\text{Nsites}_j$  is the total number of sites in that cluster (Dufrêne and Legendre, 1997).

Generally species were included in the R-mode analysis if their IndVal in any one group was greater than 25%. This value meant that a species was present in more than 50% of the sites at greater than 50% abundance (Dufrêne and Legendre, 1997). IndVal analysis resulted in a subset of 29 species. The abundances of each species were standardised, then subjected to cluster analysis and NMDS to examine taxonomic associations. Finally, the subset of 29 indicator species ( $\sqrt{\text{ }}$ -transformed) was correlated with the matrix of environmental variables to assess species-environment relationships.

## 3. Results

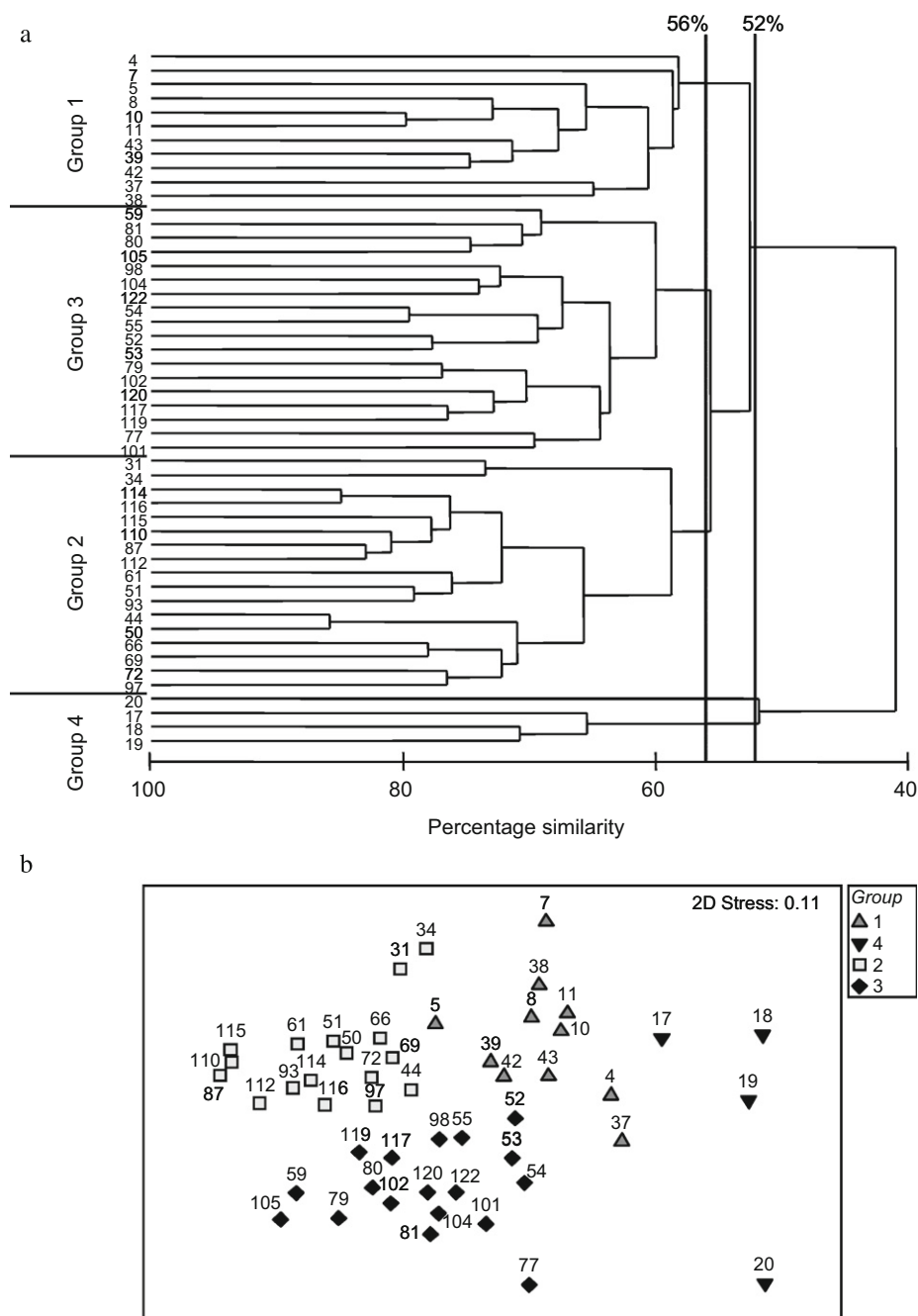
### 3.1. Oceanography

The oceanography of the BROKE-West survey region, highlighting the main features, definitions of the water masses and descriptions of vertical mixing and sea ice conditions, is discussed in detail by Williams et al. (2010). Five major oceanographic features influenced the survey region and these are briefly described here. In the north the sACC entered the survey grid at around  $60^\circ\text{E}$  and crossed the northern ends of transects 7, 9 and 11 (Fig. 1). This front is a sharp circumpolar jet in the eastward flowing ACC, which predominantly consists of Circumpolar Deep Water (CDW). Further south, the southern boundary (sb) of the ACC marked the southern extent of the circulation of warm ( $+1^\circ\text{C}$  to  $+2^\circ\text{C}$ ) CDW; the sbACC was closest to the coast on transect 7 (Fig. 1). The westward flowing ASC crossed all transects along the

upper continental shelf. The ASC, which lies to the south of the Antarctic Slope Front, is a strong and narrow jet of water that flows at speeds of up to  $25 \text{ cm s}^{-1}$  (Williams et al., 2010). Two large, anti-cyclonic gyres influenced the survey region: (1) the eastern limb of the Weddell Gyre that extended to approximately  $50^\circ\text{E}$  and returned clockwise with the ASC in the Cosmonaut Sea ( $30^\circ\text{E}$ – $60^\circ\text{E}$ ), and (2) the Prydz Bay Gyre in the Cooperation Sea ( $60^\circ\text{E}$ – $80^\circ\text{E}$ ), which had broad clockwise circulation that resulted from a branch of the sACCF moving southeastwards below the Kerguelen Plateau. Finally, transects 5 and 7 were associated with an area known as the Cosmonaut Polynya, an area thought to be formed through a divergence caused by the gyres either side, and at times a closer proximity of warm CDW to the surface (Williams et al., 2010).

### 3.2. Mesozooplankton

Forty-eight zooplankton taxa were identified from the 50 sites (Appendix 1). Cluster analysis (Fig. 2a.) identified four groups at 56% similarity. These groups are represented on the NMDS plot shown in Fig. 2b. Results from the ANOSIM indicated that the four groups were significantly different at  $\alpha < 0.05$ ; i.e. the distances (from the Bray-Curtis similarity matrix) between pairs of samples between groups were greater than the distances between samples within groups. Group 4 was most distinct from the other three groups, separating at 51% similarity, while group 1 separated from groups 2 and 3 at 54%. Note that although station 20 separated from stations 17, 18 and 19 at 52% similarity, the four stations were geographically close and have been grouped together to represent a single neritic cluster.

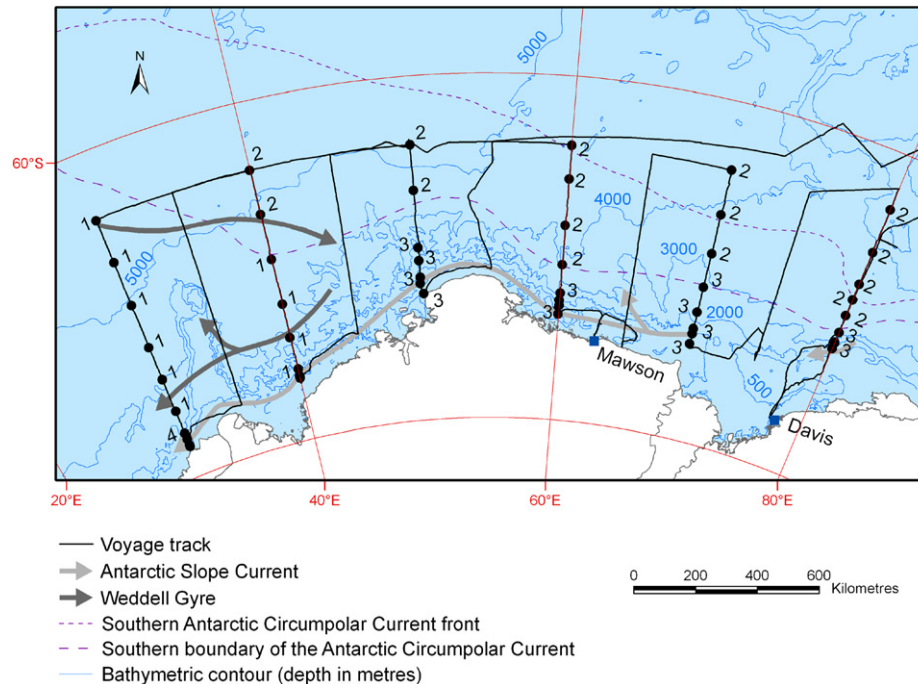


**Fig. 2.** (a) Dendrogram of cluster analysis comparing zooplankton species composition at each sampling site. Bray-Curtis similarity index with UPGMA linkage. (b) Ordination plot of sampling sites showing 4 groups as determined by cluster analysis (Bray-Curtis).



Fig. 3 represents a plot of each sampling station according to its group, while Table 1 summarises the environmental variables associated with the stations included in each group. Although many of the environmental variables showed considerable variation within a group (Table 1), ANOVA indicated that there were distinct differences between the means for the groups. Group 1 was represented by 12 stations that were positioned along transects 1 and 3, located in the Cosmonaut Sea. All twelve stations occurred south of the sbACC and corresponded to the outer eastern limb of the Weddell Gyre (Fig. 3). The region was characterised by deep (apart from 2 stations near the coast), cool water with moderate chlorophyll *a* standing stocks (Table 1). Group 2 comprised 16 stations, spread over transects 3 to 11,

which were associated with deeper, warmer waters that lay south of the sACC and north of the sbACC (Table 1). Group 2 stations were farthest from the ASC and had been ice free for the longest time; it is possible that some of the stations had been ice free for the entire year prior to sampling (Schwarz et al., 2010). Group 3, with 18 stations along transects 5 to 11, was located east of 50°E and was associated with shelf break/slope waters that lay south of the sbACC. These waters were shallower and cooler than those associated with groups 1 and 2 and had high chlorophyll *a* standing stocks (Table 1). The stations in group 3 had experienced quite variable lengths of ice coverage. Finally, group 4 represented a small cluster of four stations located in the farthest southwest part of the survey region. This neritic group was found over the



**Fig. 3.** Sample groupings, identified by numbers 1–4, as determined from cluster analysis and NMDS. Map indicates the locations of the eastern limb of the Weddell Gyre and the Antarctic Slope Current. Thin lines indicate bathymetric contours (IOC and IHO and BODC, Centenary Edition of the GEBCO Digital Atlas 2003)).

**Table 1**

Mean values for each environmental variable, shown with their ranges (minimum – maximum).

Number of stations	Group				$F_{\text{between groups}}$
	1 12	2 16	3 18	4 4	
Latitude, °S	66.08 <sub>a</sub> (68.20–62.01)	63.35 <sub>b</sub> (65.50–61.66)	66.16 <sub>a</sub> (67.18–65.00)	68.94 <sub>c</sub> (69.11–68.69)	27.76
Longitude, °E	35.00 <sub>a</sub> (30–40)	64.38 <sub>b</sub> (40–80)	64.45 <sub>b</sub> (50–80)	30.01 <sub>a</sub> (30)	28.54
Depth, m	3545 <sub>a</sub> (315–5075)	3964 <sub>a</sub> (2280–4880)	1535 <sub>b</sub> (175–3180)	1489 <sub>b</sub> (259–2950)	17.10
$T_{200 \text{ m}}$ , °C	–0.89 <sub>a</sub> (–1.67–0.57)	0.39 <sub>b</sub> (–0.21–0.88)	–1.32 <sub>c</sub> (–1.64–0.74)	–1.38 <sub>c</sub> (–1.55–1.21)	41.94
$S_{200 \text{ m}}$	34.23 <sub>a,b</sub> (34.04–34.42)	34.29 <sub>a</sub> (34.19–34.39)	34.19 <sub>b</sub> (33.93–34.32)	34.10 <sub>b</sub> (34.04–34.14)	6.37
Chl <sub>a</sub> <sub>150 m</sub> , mg m <sup>–2</sup>	47 <sub>a</sub> (33–77)	49 <sub>a</sub> (31–71)	87 <sub>b</sub> (34–236)	186 <sub>c</sub> (73–329)	11.01
ASC, km	276 <sub>a</sub> (8–775)	351 <sub>a</sub> (93–674)	20 <sub>b</sub> (40–145)	13 <sub>b</sub> (4–41)	15.00
Ice free days	18 <sub>a</sub> (–21–43)	70 <sub>b</sub> (49–101)	24 <sub>a</sub> (–8–72)	–24 <sub>c</sub> (–35–5)	33.17

Significant differences ( $p \leq 0.01$ ) were found between groups for each environmental variable, based on ANOVA; d.f.=3,46. Subscripts (a,b,c) denote which means were similar under the REGW post-hoc test.

shelf break/slope, had the coldest water temperatures, the lowest salinity (probably as a result of meltwater intrusion from the Antarctic plateau and melting sea ice), and exhibited the highest chlorophyll *a* concentrations (Table 1).

Table 2 shows the mean abundance of each species in each group that scored an IndVal of greater than 25%. The table also highlights the taxa that contributed to the top 50% of abundance in each group, as determined by SIMPER analysis. Groups 1, 2 and 3 all had high abundances of *Fritillaria* spp., *Oithona similis*, and *Microcalanus pygmaeus* ( $> 500$  ind.  $1000\text{ m}^{-3}$ ), although these three species only met the criteria to be designated as indicator species for group 2. Other taxa that contributed high abundances were *Neogloboquadrina pachyderma*, *Pelagobia longicirrata* and *Scolecithricella minor* to group 1, *Amalothrix* sp., *Rhincalanus gigas*, *Scolecithricella minor* and *Thysanoessa macrura* to group 2, and *Ctenocalanus citer*, *Metridia gerlachei*, *Oithona frigida* and *Scolecithricella minor* to group 3. Group 4 showed a slightly different profile, with the euphausiids *Thysanoessa macrura* and *Euphausia crystallorophias* contributing to the top 50% of abundance, along with *Calanoides acutus*, *Fritillaria* spp., *Microcalanus pygmaeus* and *Neogloboquadrina pachyderma*.

BIOENV analysis indicated that the suite of environmental variables that best correlated with patterns in the species distribution, as represented by the four groups, comprised chlorophyll *a* concentration, proximity to the ASC and the length of time that stations had been free from ice cover (*R*-statistic 0.488;  $p < 0.01$ ). Correlation analysis based on the first two axes of the NMDS revealed that dimension 1 was significantly correlated with latitude, longitude, temperature and ice-free days (Table 3).

**Table 2**  
Mean abundances ( $1000\text{ m}^{-3}$ ) for species with IndVal  $> 25\%$  in any one group.

	Group 1	Group 2	Group 3	Group 4
<i>Amalothrix</i> sp. (Am)	84	<b>1162*</b>	336	3
<i>Calanoides acutus</i> (Ca)	153	950	<b>348</b>	59*
<i>Calanus propinquus</i> (Cp)	51	<b>110</b>	70	7
<i>Calanus simillimus</i> (Cs)	3	<b>454</b>	0	0
<i>Clausocalanus brevipus</i> (Cb)	26	<b>466</b>	44	1
<i>Ctenocalanus citer</i> (Cc)	0	<b>1469</b>	<b>958*</b>	0
<i>Euchirella rostromagna</i> (Er)	11	84	<b>159</b>	0
<i>Eukrohnia hamata</i> (Eh)	47	<b>730</b>	63	0
<i>Euphausia crystallorophias</i> (Ec)	1	12	<b>958</b>	42*
<i>Fritillaria</i> sp. (Fr)	1870*	<b>17381*</b>	3158*	863*
<i>Haloptylus oxycephalus</i> (Ho)	<b>46</b>	<b>91</b>	5	4
<i>Limacina helicina antarctica</i> (Lha)	19	<b>2424</b>	31	5
<i>Metridia gerlachei</i> (Mg)	135	<b>673</b>	<b>616*</b>	18
<i>Microcalanus pygmaeus</i> (Mp)	906*	<b>6618*</b>	469	384*
<i>Neogloboquadrina pachyderma</i> (Np)	<b>1313*</b>	401	120	192*
<i>Oithona frigida</i> (Of)	114	<b>756</b>	<b>316*</b>	8
<i>Oithona similis</i> (Os)	1269*	<b>13112*</b>	2114*	12
<i>Oncaea antarctica</i> (Oa)	106	<b>326</b>	7	1
<i>Oncaea curvata</i> (Oc)	6	<b>632</b>	61	0
Ostracod (Ost)	140	<b>537</b>	<b>51</b>	0
<i>Paraeuchaeta antarctica</i> (Pa)	<b>83*</b>	65	<b>106</b>	44
<i>Pelagobia longicirrata</i> (Pl)	<b>89*</b>	354	<b>145</b>	0
<i>Racovitzanus antarcticus</i> (Ra)	33	<b>161</b>	4	0
<i>Rhincalanus gigas</i> (Rg)	153*	<b>676*</b>	36	5
<i>Rhynchonerella bongraini</i> (Rb)	21	<b>17</b>	4	1
<i>Sagitta gazellae</i> (Sg)	<b>79</b>	63	2	49
<i>Salpa thompsoni</i> (St)	19	3	3	<b>6</b>
<i>Scolecithricella minor</i> (Sm)	<b>335*</b>	2159*	903*	7
<i>Thysanoessa macrura</i> (Tm)	84	<b>469*</b>	60	69*
Total Mean Abundance	11251	81750	16446	2588
Minimum Abundance	4687	15968	2782	660
Maximum Abundance	29748	180161	48471	4236

Bold type indicates an IndVal of greater than 25% for that group.

\* Represents top 50% of species in each group according to SIMPER analysis. Mean total abundance for each group is shown below with the range (minimum and maximum).

Dimension 2 was negatively correlated with latitude, depth, temperature, salinity, chlorophyll *a* concentration and proximity to the ASC, and positively correlated with longitude.

The mean total abundance of animals in group 2 (81,750 ind.  $1000\text{ m}^{-3}$ ) was approximately 5 times greater than those of groups 1 and 3, and was an order of magnitude higher than the mean total abundance of group 4 (Table 2). Group 2 was also characterised by a large number of indicator taxa (20) compared to groups 1 (6) and 3 (9), while group 4 had only one indicator species, *Salpa thompsoni*. This species did not contribute to the top 50% of abundance for group 4 and highlights that while a species might have high abundance within a group it does not necessarily have value as an indicator species for that group.

Total zooplankton abundance across the survey region varied between 660 and 180,161 ind.  $1000\text{ m}^{-3}$  (Fig. 4a). Biomass, as  $\text{mg C m}^{-3}$ , was generally low, with mainly sites east of  $60^\circ\text{E}$  showing values higher than  $5\text{ mg C m}^{-3}$  (Fig. 4b). Overall, abundances tended to be higher in the east and above the sbACC, particularly on the eastern side of Prydz Bay. The dominant groups, accounting for between 24 and 100% (median: 98%) of total abundance, were euphausiids (3 species), copepods (27 species), pteropods (4 species), appendicularians (2 genera), chaetognaths (3 species), polychaetes (4 species) and 2 species of hyperiid amphipods. A foraminiferan, *Neogloboquadrina pachyderma*, represented between 14 and 74% of the abundance at the sites where they were present. Other locally dominant groups included ostracods and tintinnids. Finally, gammarid amphipods, siphonophores and fish larvae were present, although rarely in high abundances.

### 3.3. Species associations and distributions

Twenty-nine species were identified as having IndVal  $> 25\%$  and were included in the reverse, R-mode analysis of species (Fig. 5). Four clusters were separated at 30% similarity (Fig. 5a): (A) *Euphausia crystallorophias* showed a clear dissociation from the other species at 15%. (B) A second cluster that separated at 20% similarity comprised *Neogloboquadrina pachyderma*, *Rhynchonerella bongraini*, *Salpa thompsoni* and *Sagitta gazellae*. (C) A third cluster consisted of *Paraeuchaeta antarctica*, *Euchirella rostromagna* and ostracods. (D) The remaining 21 species clustered together in the largest group (Fig. 5b).

Correlations between the 29 indicator species and the environmental variables are shown in Table 3, and are listed according to their species associations as defined by the R-mode analysis. *Euphausia crystallorophias* was distributed over the continental shelf/slope (Fig. 6) close to the ASC, and was correlated with shallower depths, lower temperature and salinity, higher chlorophyll *a* concentration and longer duration of ice cover. Three of the 4 species that grouped in cluster B tended to be more abundant in the western sector of the survey grid (Fig. 6) and were correlated with longitude (Table 3); the fourth member, *Neogloboquadrina pachyderma*, was distributed throughout the sampling region (Fig. 6) and did not correlate significantly with any of the environmental variables measured. Members of the third cluster did not show consistent distributions, though they tended to be more numerous closer to the continent (Fig. 6). Ostracods did not correlate with any environmental variables, while *Euchirella rostromagna* was more abundant in the east and *Paraeuchaeta antarctica* generally preferred cooler waters (Table 3). In cluster D many species were positively correlated with ice free days; i.e. abundances increased with increasing length of exposure (Table 3). While most species were widespread across the survey region some were more locally distributed. *Calanus similillimus*, *Clausocalanus*

**Table 3**Correlations between indicator species ( $\sqrt{-}$ -transformed) and environmental variables.

	Latitude	Longitude	Depth	Temperature	Salinity	Chlorophyll <i>a</i>	Antarctic Slope Current	Ice free days
Axis 1	−0.595	−0.727		−0.458				−0.644
Axis 2	−0.384	0.391	−0.728	−0.476	−0.394	−0.468	−0.640	
Cluster A								
<i>Euphausia crystallorophias</i>			−0.411	−0.381	−0.363	0.461	−0.444	−0.415
Cluster B								
<i>Neogloboquadrina pachyderma</i>								
<i>Rhynchoneerella bongraini</i>		−0.433	0.437					
<i>Sagitta gazellae</i>		−0.437						
<i>Salpa thompsoni</i>		−0.463						
Cluster C								
<i>Euchirella rostromagna</i>		0.412						
<i>Paraeuchaeta antarctica</i>	−0.439			−0.424				
Ostracod								
Cluster D								
<i>Amallothrix</i> sp.	0.377	0.645						0.486
<i>Calanoides acutus</i>								
<i>Calanus propinquus</i>								
<i>Calanus simillimus</i>	0.299	0.555		0.375				0.504
<i>Clausocalanus brevipes</i>	0.423	0.430		0.427				0.548
<i>Ctenocalanus citer</i>		0.901						0.467
<i>Eukrohnia hamata</i>		0.499						0.353
<i>Fritillaria</i> sp.	0.570	0.397		0.561			0.389	0.494
<i>Haloptilus oxycephalus</i>			0.445					
<i>Limacina helicina antarctica</i>		0.450						0.407
<i>Metridia gerlachei</i>		0.524	−0.402				−0.398	
<i>Microcalanus pygmaeus</i>	0.566		0.506	0.644		−0.369	0.480	0.555
<i>Oithona frigida</i>		0.602						0.496
<i>Oithona similis</i>	0.753	0.575	0.371	0.549		−0.461	0.436	0.713
<i>Oncaea antarctica</i>	0.383		0.461		0.388		0.446	0.372
<i>Oncaea curvata</i>	0.461	0.569		0.402				0.563
<i>Pelagobia longicirrata</i>	0.374							0.414
<i>Racovitzanus antarcticus</i>			0.396	0.481				0.380
<i>Rhincalanus gigas</i>	0.665		0.678	0.683		−0.515	0.635	0.621
<i>Scolecithricella minor</i>		0.604						0.435
<i>Thysanoessa macrura</i>	0.432		0.402	0.499			0.365	0.530

Shows those correlations (*r*) that were significant at the  $p \leq 0.01$  level,  $n=50$  sampling sites. Species are listed according to species associations as defined by reverse cluster analysis and NMDS.

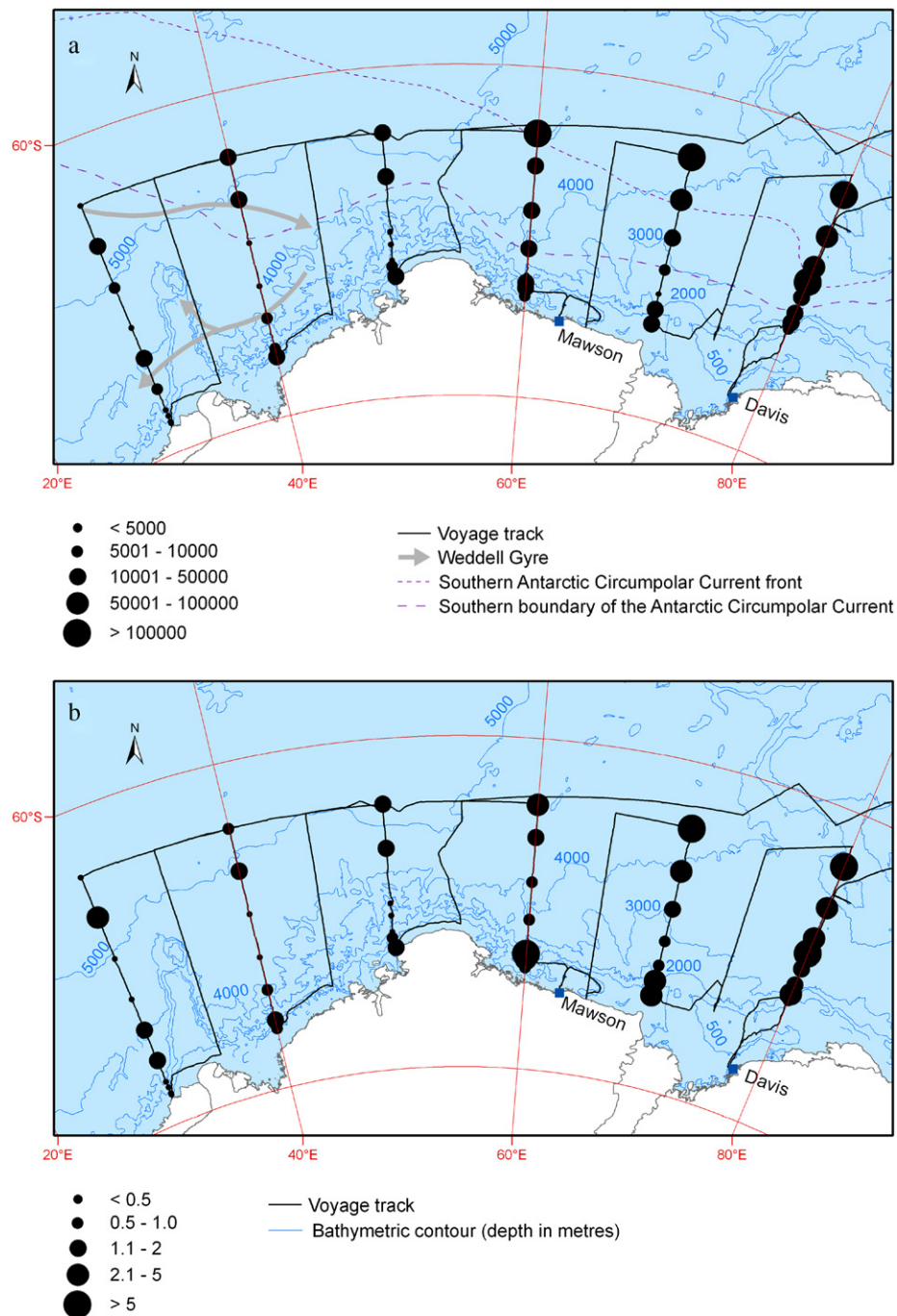
*brevipes*, *Ctenocalanus citer*, *Limacina helicina antarctica*, *Metridia gerlachei* and *Oncaea curvata* all showed strong correlations with longitude (Table 3) and were more abundant in waters east of 50°E (Fig. 6).

#### 4. Discussion

Forty-eight mesozooplankton taxa were identified from the RMT\_1 net deployed during the BROKE-West survey. The suite of species recorded during this study was typical of that found in the seasonal ice zone in eastern Antarctica (e.g., Hosie et al., 2000; Chiba et al., 2001; Hunt and Hosie, 2005), and was consistent with previous studies from the Ross Sea (Foster, 1987; Hopkins, 1987), the Antarctic Peninsula (Calbet et al., 2005) and the Weddell Sea (Boysen-Ennen and Piatkowski, 1988). Copepods generally comprised the dominant group, though appendicularians, foraminiferans and euphausiids were also abundant. Common copepod species included the small cyclopoids *Oithona* spp. and *Oncaea* spp., biomass-dominant calanoids such as *Rhincalanus gigas*, *Calanus propinquus*, *Calanoides acutus* and *Metridia gerlachei*, and the small calanoids *Scolecithricella minor*, *Microcalanus pygmaeus* and *Ctenocalanus citer*. Euphausiids identified included *Thysanoessa macrura*, *Euphausia crystallorophias* and *Euphausia superba*. Most developmental stages of *T. macrura* and *E. crystallorophias* were present in the RMT\_1 samples, while *E. superba* was represented mainly by furciliae and a few incidental adults. Due to the inability of the RMT\_1 net to sample adult *E. superba* quantitatively they have not been included in the present

analysis; for full accounts of the distributions of adult *E. superba* during BROKE-West consult Kawaguchi et al. (2010) and Jarvis et al. (2010). Species that were not captured during the present study, but which have been recorded previously in the Cosmonaut Sea, include the hyperiid amphipods *Cylopus* spp. and the fish *Pleurogramma antarcticum* (Hunt et al., 2007).

The distribution of the mesozooplankton assemblage varied considerably across the survey region, ranging from 660 to more than 180,000 individuals per 1000 m<sup>3</sup>. Abundances of the non-copepod fauna were similar to those observed in the Cosmonaut Sea (Hunt et al., 2007), and were substantially higher than those recorded during BROKE (80°E–150°E) from an RMT\_8 net (Hosie et al., 2000). It should be noted, however, that BROKE did not extend as far north as BROKE-West and so the high concentrations of zooplankton found north of the sACCF in BROKE-West were potentially not sampled during BROKE. It was determined previously that the RMT\_8 can underestimate abundance of common large copepods by between 5 (*Rhincalanus gigas*) and 118 (*Metridia gerlachei*) times (Beaumont and Hosie, 1997), and usually does not sample small copepods at all. Whether the RMT\_8 also undersampled other large mobile species such as *Thysanoessa macrura* and *Eukrohnia hamata* or whether they simply occurred in lower abundance during the BROKE survey is uncertain. Primary productivity was higher during BROKE-West than during BROKE (Westwood et al., 2010), possibly leading to higher secondary productivity. Whatever the case, it does highlight the important information about mesozooplankton abundance and distribution that is gained by examination of RMT\_1 samples in synoptic surveys. It should also be pointed out that the

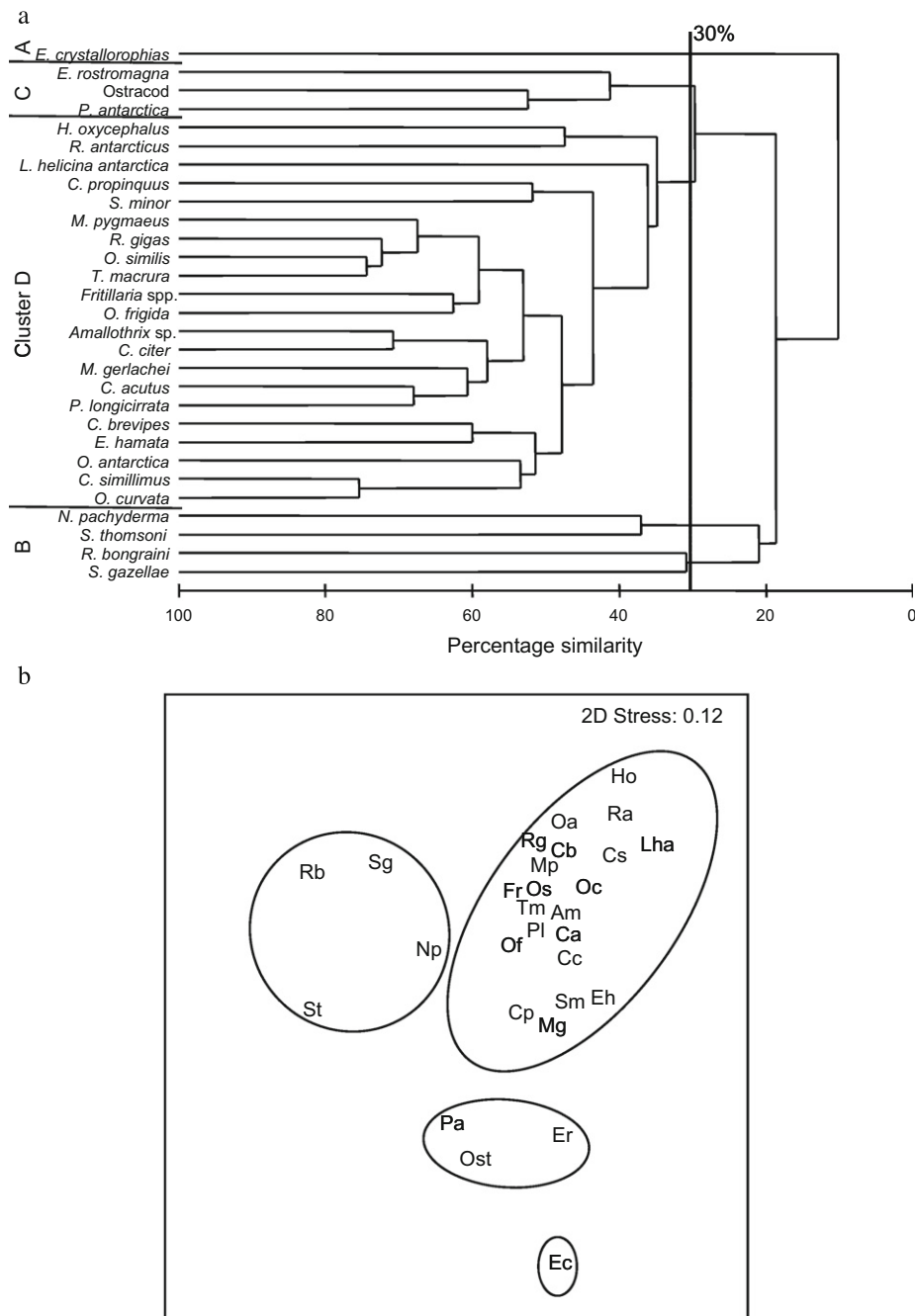


**Fig. 4.** (a) Total zooplankton abundance (ind.  $1000\text{ m}^{-3}$ ) at each sampling site. Thin lines indicate bathymetric contours (Centenary Edition of the GEBCO Digital Atlas, 2003). (b) Zooplankton biomass ( $\text{mg C m}^{-3}$ ) at each sampling site.

RMT\_1 itself likely undersampled many of the small copepods, as well as juvenile stages of larger ones. Mesozooplankton in the Southern Ocean are usually sampled with  $200\text{-}\mu\text{m}$ -mesh nets, although a more suitable size is  $100\text{-}\mu\text{m}$ -mesh, and both of these will still undersample juveniles stages of some cyclopoid species. In spite of this limitation RMT\_1 samples, which are collected coincidentally with RMT\_8 samples, do offer a means of advancing our knowledge about smaller pelagic species. While small copepods and appendicularians do not always contribute substantially to biomass, their roles as conduits of energy between primary production and higher trophic levels, as well as remineralisers of organic material in the upper ocean, warrant further investigation into their biogeography.

Four main mesozooplanktonic assemblages that could be broadly linked to major water masses were defined via multivariate analyses for the BROKE-West survey. Group 1 was largely associated with the edge of the Weddell Gyre that circulates clockwise into the Cosmonaut Sea and returns with the ASC. Group 2 was found in deeper waters north of the sbACC, including a few stations north of the sACCf, while Group 3 was located mainly in shelf slope/break waters south of the sbACC and east of  $50^\circ\text{E}$ . Finally Group 4 represented a neritic zone in the south-western corner of the survey grid. However, although the ordination analyses showed distinct separation between the groups the level of similarity was close to 50%. Therefore, while there was some zonation in the mesozooplankton assemblages





**Fig. 5.** Species associations. (a) Dendrogram of the inverse cluster analysis comparing species with IndVal > 25%. Bray-Curtis similarity index with UPGMA linkage. (b) NMDS inverse ordination plot comparing indicator species (IndVal > 25%). Cluster groups identified by cluster analysis at similarity of 30% are superimposed. Species abbreviations as in Table 2.

that probably related to major water masses, the zones were not as distinctive as those in past surveys; e.g. the BROKE survey revealed strong zonation between many of the biological groups at 120°E (Hosie et al., 2000). This is likely to result, at least in part, from the stronger oceanographic zonation observed during BROKE. A clear discontinuity in productivity was observed during BROKE at 115°E, which related to the sbACC and sea ice extending further north between 80 and 115°E than east of 115°E (Nicol et al., 2000). Hosie et al. (2000) found that the cooler, high chlorophyll *a* waters in the west supported copepods, chaetognaths and euphausiids, while the warmer, low primary productivity waters to the east were dominated by salps. Such distinct zonation in major currents, and, hence, in sea ice extent was not observed for the BROKE-West region (Nicol et al., 2010).

The list presented in Table 2 shows that groups 1, 2 and 3 comprised many of the same species, with mainly differences in the ratios of taxa, and higher abundances in the case of group 2, rather than significant changes in taxonomic composition accounting for differences between the groups. This is supported by the inverse ordination showing species relationships, in which the majority of the indicator taxa clustered together in a large group. Group 4 was characterised more by the absence of some species, than by the presence of a distinct faunal suite. The subtle changes between groups 1, 2 and 3 might reflect different water conditions, perhaps related to temperature or different regions of productivity.

The environmental variables measured during BROKE-West provided an opportunity to examine the patterns in

mesozooplankton distribution in relation to the physical environment. According to the BIOENV analysis the three environmental variables that best correlated with patterns in the mesozooplankton assemblages included chlorophyll *a* concentration, proximity to the ASC and length of time without an ice cover. Clearly the influence of these variables was to some extent geographical. Ice retreat proceeded from the northeast towards the southwest, with sites in the northeast experiencing significantly longer ice-free duration by the time they were sampled. Similarly, proximity to the ASC and chlorophyll *a* concentrations showed latitudinal gradients: maximum chlorophyll *a* concentrations were recorded south of the ASC jet, with minima found south of the SACCf (Williams et al., 2010).

While relationships between phytoplankton and zooplankton are rarely straightforward, the present study showed that in regions where zooplankton abundance was high chlorophyll *a* concentrations tended to be low, hinting at possible grazing effects. For example the highest integrated chlorophyll *a* concentrations were recorded along transects 5 and 7 near the ASC (Westwood et al., 2010), a region where zooplankton abundances were lower. However, it is sometimes more profitable to consider the taxonomic composition of phytoplankton in relation to zooplankton, rather than looking solely at biomass. A phytoplankton bloom dominated by *Phaeocystis* was observed along transect 1 (Westwood et al., 2010). Whether *Phaeocystis* was in its colonial or solitary phase could have influenced

both the composition and abundance of the zooplankton assemblage, as large copepods, including *Calanus* spp., can consume the colonies (Huntley et al., 1987), while small species tend to avoid both phases (Gasparini et al., 2000). As transect 1 tended to be dominated by smaller copepods the lack of an appropriate food source could have acted to keep numbers low. Alternatively top-down forces could have suppressed zooplankton abundance: *Sagitta gazallae*, a predator of copepods, was abundant along transects 1 and 2. While large scale physical features probably are the main structuring forces of zooplankton distributions, these are also underpinned by direct biological interactions.

Surprisingly, temperature was not a major variable in structuring the mesozooplankton community overall, although it did correlate significantly with the latitudinal distributions of several species, including cold water species such as *Euphausia crystallorophias* and *Paraeuchaeta antarctica*, and those that prefer warmer water such as *Thysanoessa macrura* and *Rhincalanus gigas*. Previous surveys in Prydz Bay and the BROKE survey have generally shown temperature to be a significant driver of north-south zonation, while salinity rarely correlated with zooplankton patterns (Hosie, 1994a; Hosie et al., 2000). In the present study neither salinity nor depth of the water column showed significant correlation with overall community structure, though depth was positively correlated with many of the species that were abundant in the deep oceanic waters associated with group 2.

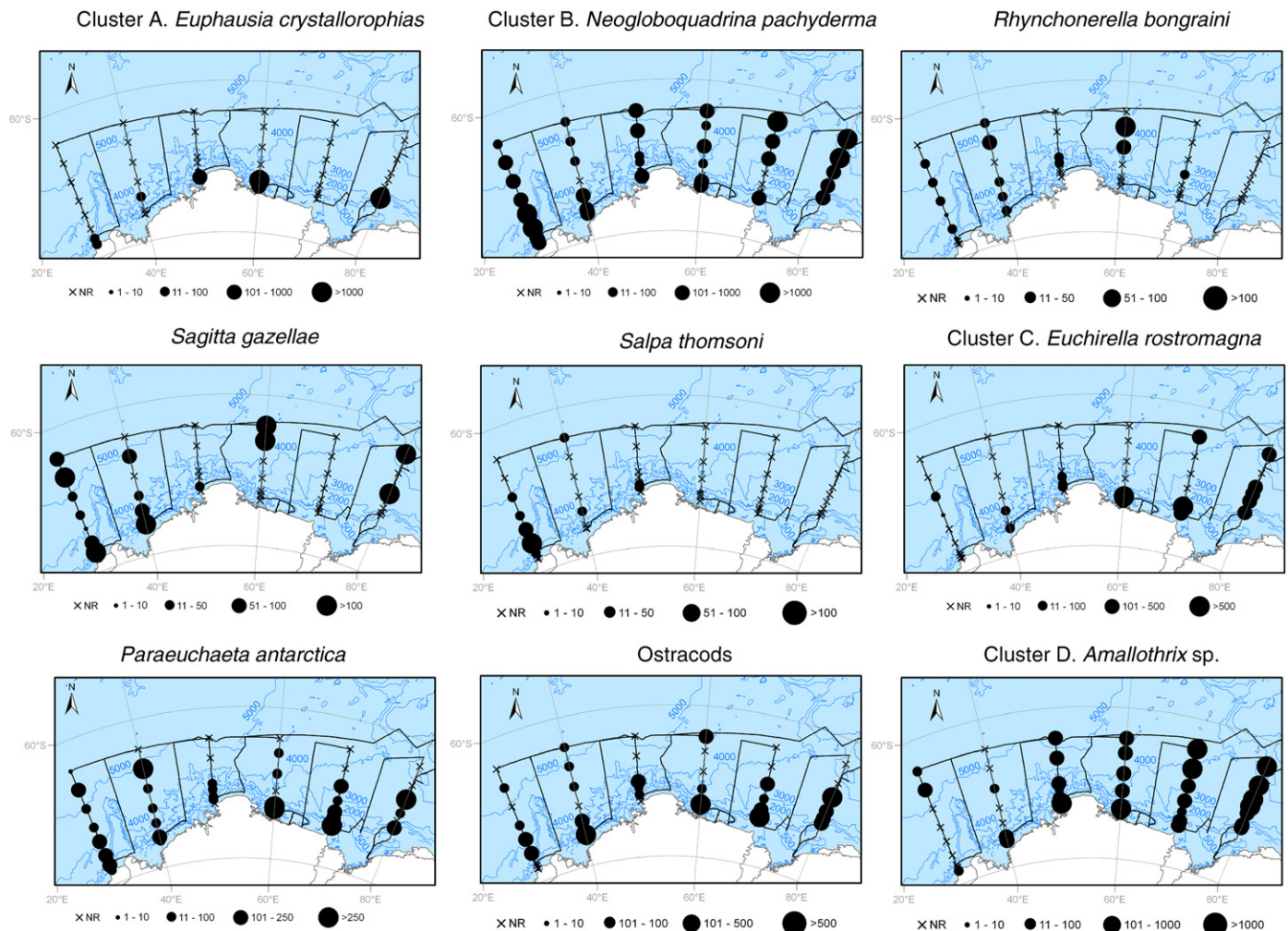


Fig. 6. Distribution plots for 29 indicator species across the BROKE-West survey region. Bubbles represent abundance as ind. 1000 m<sup>-3</sup>. Note that scales differ between species.

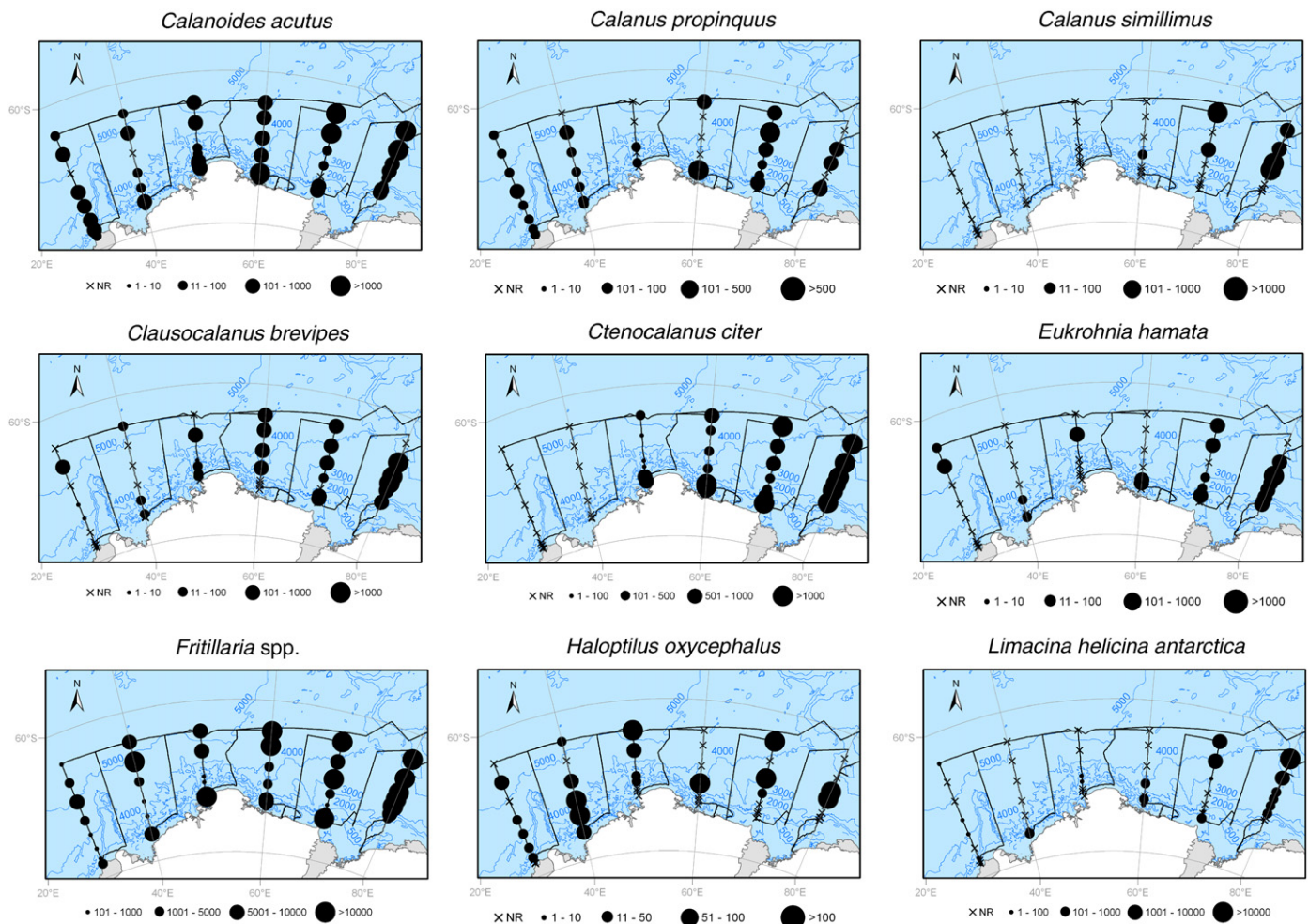


Fig. 6. (Continued)

The west-east zonation patterns observed in this study were probably driven by the two major gyral systems that penetrated the survey area: the eastern limb of the Weddell Gyre in the Cosmonaut Sea (transects 1 and 3) and the Prydz Bay Gyre in the Cooperation Sea (transects 9 and 11). Of the three oceanic assemblages (groups 1 to 3), the one associated with the Weddell Gyre exhibited the lowest mean abundance. Fewer species tended to have their main centres of distribution in that region and many were not found in the western sector at all. Many copepods complete their life cycles within gyres and so are bounded both by the amount of primary productivity and the number of predators that can enter the gyre. There was also an indication of separate, possibly self-sustaining populations of *Euphausia superba* in the two gyral systems (Kawaguchi et al., 2010), with the eastern population maturing earlier due to the earlier retreat of sea ice (Williams et al., 2010). The Weddell Gyre could have slowed the retreat of sea ice in the west (Williams et al., 2010), thus restricting primary production and, subsequently, zooplankton growth. At the same time the northeastern sector, situated over a site of deep upwelling and experiencing earlier sea ice retreat, might have previously experienced high primary productivity that subsequently influenced zooplankton growth. By the time the region was surveyed the high numbers of zooplankton along transect 11 were not reflected in the chlorophyll *a* concentrations (Westwood et al., 2010), but it is possible that the diatoms in that region had already passed their major growth period and had entered a period of senescence.

Zooplankton biomass will generally lag a week or two behind phytoplankton biomass.

Undoubtedly there was a temporal component to this survey that may also have influenced the observed patterns in zooplankton zonation. The survey cruise was conducted over a period of six weeks, providing time for species in the east to respond to increases in primary production. This is particularly true for shorter-generation organisms such as appendicularians and some of the small cyclopoid copepods. However, for larger calanoid copepods and euphausiids the increase is not so much in abundance but in growth; i.e. development to later stages. Several species did show substantial development through life stages across the survey period, including *Thysanoessa macrura*, *Rhincaalanus gigas*, *Scolecithricella minor* and *Paraeuchaeta antarctica* (K. Swadling, unpublished data). Given that some sites along a transect that were sampled within 24 hours showed quite different total abundances it is unlikely that sampling date was the sole driver of west-east zooplankton zonation. Furthermore, initial consideration of sampling date as an environmental variable showed that, while it clearly correlated strongly with longitude ( $r=0.99$ ), it did not correlate with the distributions of any individual species. For both of these reasons sampling date was not retained as an environmental variable in any analyses presented here.

Over the north-south gradient, the first major zone was the sACCF, which has been previously suggested to be an important ecological boundary, particularly in the southwest Atlantic. The



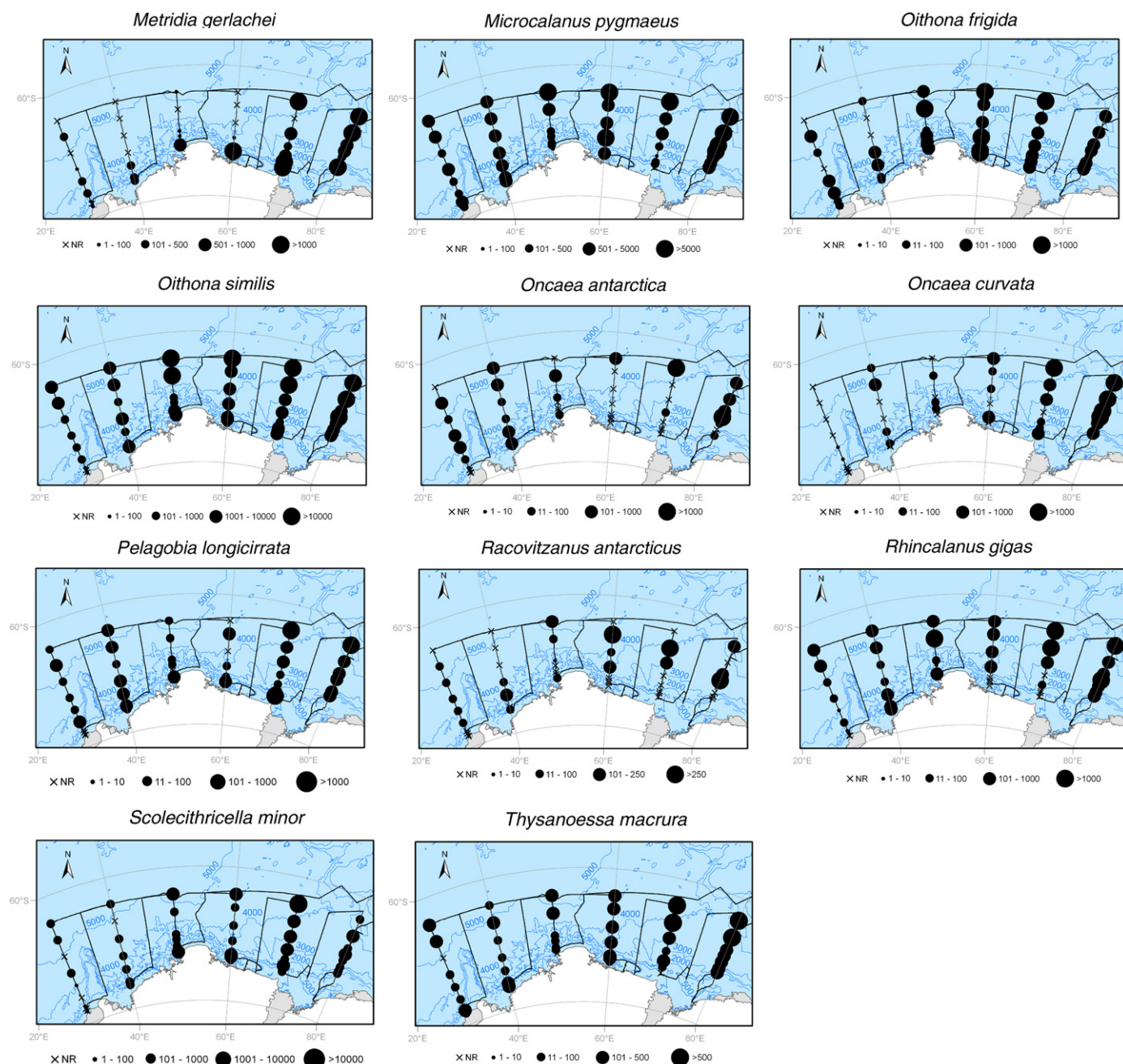


Fig. 6. (Continued)

sACCF entered the survey grid at transect 7 and warmer waters associated with this front supported higher abundances of zooplankton. Many small copepods, including the calanoids *Microcalanus pygmaeus*, *Ctenocalanus citer* and cyclopoids (*Oithona* spp. and *Oncaea* spp.) were abundant in these warmer waters, a phenomenon that had been recognised earlier (Chiba et al., 2001). Other abundant groups included appendicularians (mainly *Fritillaria* spp.) and the foraminiferen *Neogloboquadrina pachyderma*. South of the sACCF was a site of minimal chlorophyll *a* concentration (Williams et al., 2010), possibly contributing to the reduced zooplankton abundance observed for this area along transects 5 to 9. However, in the east abundances remained high between the sACCF and the sbACC. Transect 11 is where these fronts were closest together

and so the influence of the sACCF was probably still strong. The fast and westward flowing ASC appears to act as a physical barrier and could be a strong driver of biological zonation patterns. As mentioned previously it was a site of maximum chlorophyll *a* concentration. The ASC is believed to be generally too fast to allow krill (and hence other zooplankton) to aggregate (Williams et al., 2010). It was weakest on either side of the Amery Basin (Williams et al., 2010) and this might have led to an increase in zooplankton abundance at the bottom of transect 9.

Earlier assessments of north-south zonation patterns have indicated the presence of a neritic assemblage south of 67°S in Prydz Bay (Hosie, 1994a) that was dominated by *Euphausia crystallophias*, and Hunt et al. (2007) found a distinct division



between the neritic and oceanic communities that was consistent between years. In the present study groups 3 and 4 had high abundances of *E. crystallorophias*, a species that is restricted to continental shelf waters, and so groups 3 and 4 likely represented a neritic assemblage, while groups 1 and 2 comprised the oceanic assemblage. However, there is considerable fluidity in the ranges of most of the species that occupy the neritic and oceanic zones and in most cases they are responding to prior water mass history, rather than adhering to strict biogeographical boundaries. For example, in the first two years of the macrozooplankton surveys in the Cosmonaut Sea warmer waters from the ACC intruded further south, bringing more of the oceanic assemblage south into the neritic zone (Hunt et al., 2007). Similarly, in Prydz Bay it was found that the large scale movement of water masses was the strongest force behind the distribution of zooplankton communities and dictated how far south (or north) the communities penetrated each year (Hosie, 1994a). Therefore it is likely that if the present survey were to be repeated a similar suite of species would be found, but their distributional patterns would differ depending on a combination of physical factors including the retreat of sea ice, the southwards intrusion of the ACC and the

effects of the interactions of these on the patterns of primary productivity.

## Acknowledgments

We thank Guy Williams for access to sea ice data and temperature and salinity data, and Simon Wright for the chlorophyll *a* data. Marc Dufrêne provided some assistance with using IndVal. Maps were produced by David Smith at the Australian Antarctic Data Centre© Commonwealth of Australia. Thanks to Toby Jarvis for use of the Antarctic Slope Current and Weddell Gyre data to include in our plots.

## Appendix 1

Abundances (individuals 1000 m<sup>-3</sup>) of all taxa identified from the BROKE-West RMT 1 samples.

See Table A1.

Table A1

Station number	4	5	7	8	10	11	17	18	19	20
Latitude (°S)	62.01	63.33	64.68	66.00	67.00	68.00	68.69	68.88	69.06	69.11
Longitude (°E)	29.99	30.02	29.99	29.98	29.99	30.01	30.00	30.02	30.00	30.00
<i>Amallothrix</i> sp.	48.1	169.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	11.1
<i>Calanoides acutus</i>	16.0	620.9	0.0	370.2	262.5	202.7	144.2	60.7	15.9	16.6
<i>Calanus propinquus</i>	16.0	28.2	56.7	178.0	33.9	62.9	14.9	3.4	15.9	0.0
<i>Calanus simillimus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Candacia</i> sp.	40.1	141.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.8
<i>Clausocalanus brevipes</i>	0.0	197.6	0.0	7.1	8.5	0.0	0.0	0.0	0.0	3.7
<i>Clio pyramidata</i>	8.0	38.5	11.3	0.0	8.5	0.0	0.0	0.0	0.0	1.8
<i>Cione antarctica</i>	0.0	28.2	15.2	7.1	0.0	0.0	5.0	0.0	0.0	0.0
<i>Ctenocalanus citer</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eucalanus longiceps</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euchirella rostromagna</i>	0.0	0.0	11.3	7.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Eukrohnia hamata</i>	32.0	169.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euphausia crystallorophias</i>	0.0	0.0	0.0	0.0	0.0	0.0	44.7	10.1	47.8	66.5
<i>Euphausia superba</i>	0.0	0.0	0.0	0.0	0.0	21.0	19.9	20.2	0.0	1.8
<i>Fritillaria</i> sp.	592.9	3415.0	6253.5	1131.9	398.0	608.2	119.3	445.4	2771.1	116.4
<i>Haloptilus oxycephalus</i>	0.0	56.4	0.0	14.2	42.3	35.0	14.9	0.0	0.0	0.0
<i>Heterorhabdus austrinus</i>	0.0	141.1	0.0	7.1	0.0	21.0	0.0	0.0	0.0	0.0
<i>Heterostylites longicornis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hyperietta dilatata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Limacina helicina antarctica</i>	8.0	0.0	0.0	7.1	42.3	0.0	14.9	0.0	0.0	5.5
<i>Metridia gerlachei</i>	0.0	112.9	0.0	21.4	262.5	321.6	5.0	0.0	47.8	18.5
<i>Metridia lucens</i>	8.0	28.2	34.0	0.0	76.2	21.0	44.7	10.1	47.8	1.8
<i>Microcalanus pygmaeus</i>	1177.7	2427.2	283.7	569.5	270.9	433.4	924.6	263.2	223.0	127.5
Unidentified nauplii	0.0	56.4	113.5	42.7	25.4	125.8	14.9	60.7	8.0	0.0
<i>Neoglobobadrina pachyderma</i>	72.1	479.8	533.4	156.6	9068.3	4362.4	268.4	182.2	318.5	1.8
<i>Oikopleura</i> sp.	0.0	0.0	0.0	0.0	25.4	0.0	0.0	0.0	47.8	7.4
<i>Oithona frigida</i>	0.0	366.9	34.0	0.0	143.9	118.8	14.9	0.0	15.9	0.0
<i>Oithona similis</i>	1722.5	5616.5	805.8	832.9	414.9	587.2	29.8	0.0	0.0	16.6
<i>Oncaea antarctica</i>	0.0	451.6	11.3	199.3	262.5	28.0	5.0	0.0	0.0	0.0
<i>Oncaea curvata</i>	0.0	0.0	0.0	0.0	8.5	7.0	0.0	0.0	0.0	0.0
Ostracods	0.0	56.4	0.0	21.4	152.4	405.5	0.0	0.0	0.0	0.0
<i>Paraeuchaeta antarctica</i>	8.0	169.3	22.7	71.2	135.5	160.8	109.4	33.7	31.9	1.8
<i>Pelagobia longicirrata</i>	40.1	169.3	56.7	64.1	16.9	111.9	0.0	0.0	0.0	0.0
<i>Primno macropa</i>	48.1	141.1	34.0	49.8	33.9	0.0	0.0	10.1	15.9	0.0
<i>Racovitzanus antarcticus</i>	0.0	84.7	22.7	35.6	25.4	14.0	0.0	0.0	0.0	0.0
<i>Rhincalanus gigas</i>	344.5	705.6	56.7	42.7	8.5	35.0	9.9	10.1	0.0	0.0
<i>Rhynchoerella bongraini</i>	0.0	28.2	11.3	42.7	8.5	48.9	5.0	0.0	0.0	0.0
<i>Sagitta gazellae</i>	56.1	395.1	34.0	14.2	8.5	69.9	139.2	40.5	15.9	0.0
<i>Sagitta marri</i>	0.0	0.0	0.0	28.5	381.0	426.4	34.8	0.0	47.8	12.9
<i>Salpa thomsoni</i>	0.0	0.0	11.3	42.7	50.8	111.9	24.9	0.0	0.0	0.0
<i>Scolecithricella minor</i>	184.3	479.8	0.0	163.7	42.3	0.0	14.9	0.0	0.0	13.9
<i>Siphonophora nectophore</i>	16.0	56.4	11.3	14.2	33.9	7.0	0.0	10.1	0.0	1.8
Spinocalanidae	0.0	338.7	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stephos longipes</i>	8.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8
<i>Thysanoessa macrura</i>	168.2	254.0	0.0	71.2	25.4	90.9	94.4	111.4	55.7	14.8
Tintinnids	8.0	0.0	11.3	0.0	8.5	0.0	0.0	0.0	0.0	0.0
<i>Tomopteris</i> spp.	32.0	84.7	0.0	0.0	0.0	0.0	5.0	0.0	0.0	0.0

Table A1. (continued)

<i>Travisopsis levinsemi</i>	0.0	0.0	0.0	7.1	0.0	7.0	0.0	0.0	0.0
Station number	31	34	37	38	39	42	43	44	
Latitude (°S)	62.00	63.32	64.67	66.00	67.00	67.94	68.14	68.20	
Longitude (°E)	39.97	40.00	40.00	40.00	39.97	40.02	40.00	40.00	
<i>Amalothrix</i> sp.	0.0	0.0	21.2	0.0	0.0	249.3	154.4	368.6	
<i>Calanoides acutus</i>	47.3	180.1	0.0	27.4	66.1	187.0	45.4	36.9	
<i>Calanus propinquus</i>	0.0	120.1	63.7	27.4	39.7	83.1	18.2	0.0	
<i>Calanus simillimus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Candacia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Clausocalanus brevipes</i>	47.3	0.0	0.0	0.0	79.3	20.8	0.0	0.0	
<i>Clio pyramidata</i>	47.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Clione antarctica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Ctenocalanus citer</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Eucalanus longiceps</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Euchirella rostromagna</i>	0.0	0.0	0.0	0.0	79.3	0.0	0.0	36.9	
<i>Eukrohnia hamata</i>	0.0	0.0	0.0	0.0	39.7	0.0	27.2	36.9	
<i>Euphausia crystallorophias</i>	0.0	0.0	0.0	0.0	13.2	0.0	0.0	0.0	
<i>Euphausia superba</i>	0.0	0.0	31.9	0.0	52.9	10.4	0.0	0.0	
<i>Fritillaria</i> sp.	8354.1	14470.2	1051.7	192.1	899.2	124.7	299.7	7482.0	
<i>Haloptilus oxycephalus</i>	47.3	0.0	63.7	109.8	145.5	10.4	72.7	0.0	
<i>Heterorhabdus austrinus</i>	0.0	0.0	0.0	54.9	0.0	0.0	0.0	0.0	
<i>Heterostylites longicornis</i>	23.7	60.0	10.6	13.7	0.0	0.0	0.0	0.0	
<i>Hyperiella dilatata</i>	23.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Limacina helicina antarctica</i>	0.0	0.0	0.0	0.0	0.0	62.3	0.0	110.6	
<i>Metridia gerlachei</i>	0.0	0.0	0.0	0.0	145.5	457.1	0.0	294.9	
<i>Metridia lucens</i>	0.0	0.0	0.0	0.0	13.2	51.9	36.3	0.0	
<i>Microcalanus pygmaeus</i>	591.6	780.6	626.8	988.1	753.7	934.9	308.8	2100.9	
Unidentified nauplii	1065.0	1200.8	0.0	54.9	26.4	0.0	0.0	36.9	
<i>Neogloboquadrina pachyderma</i>	47.3	60.0	42.5	0.0	396.7	228.5	199.8	221.1	
<i>Oikopleura</i> sp.	118.3	60.0	0.0	0.0	26.4	20.8	0.0	0.0	
<i>Oithona frigida</i>	23.7	0.0	0.0	219.6	357.0	62.3	63.6	0.0	
<i>Oithona similis</i>	4472.9	7025.0	658.6	1180.3	806.6	311.6	199.8	2100.9	
<i>Oncaea antarctica</i>	331.3	300.2	10.6	41.2	119.0	114.3	36.3	0.0	
<i>Oncaea curvata</i>	94.7	120.1	0.0	0.0	13.2	41.6	0.0	0.0	
Ostracods	71.0	60.0	42.5	0.0	185.1	685.6	127.2	0.0	
<i>Paraeuchaeta antarctica</i>	0.0	420.3	31.9	68.6	66.1	197.4	36.3	36.9	
<i>Pelagobia longicirrata</i>	118.3	300.2	21.2	164.7	198.4	103.9	81.7	36.9	
<i>Primno macropa</i>	0.0	0.0	0.0	0.0	0.0	31.2	0.0	0.0	
<i>Racovitzanus antarcticus</i>	0.0	0.0	0.0	54.9	105.8	0.0	54.5	0.0	
<i>Rhincalanus gigas</i>	236.7	240.2	63.7	82.3	105.8	249.3	109.0	36.9	
<i>Rhynchoerella bongraini</i>	23.7	60.0	0.0	27.4	39.7	41.6	0.0	0.0	
<i>Sagitta gazellae</i>	0.0	60.0	0.0	13.7	66.1	238.9	45.4	0.0	
<i>Sagitta marri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
<i>Salpa thomsoni</i>	47.3	0.0	0.0	0.0	13.2	0.0	0.0	0.0	
<i>Scolecithricella minor</i>	142.0	0.0	435.6	247.0	343.8	550.6	690.3	884.6	
<i>Siphonophora nectophore</i>	23.7	0.0	31.9	0.0	0.0	0.0	0.0	0.0	
Spinocalanidae	0.0	0.0	0.0	0.0	13.2	0.0	0.0	0.0	
<i>Stephos longipes</i>	0.0	0.0	0.0	0.0	0.0	41.6	0.0	73.7	
<i>Thysanoessa macrura</i>	47.3	300.2	10.6	13.7	79.3	114.3	72.7	110.6	
Tintinnids	118.3	180.1	0.0	0.0	13.2	41.6	18.2	0.0	
<i>Tomopteris</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	45.4	0.0	
<i>Travisopsis levinsemi</i>	0.0	0.0	0.0	0.0	0.0	0.0	9.1	0.0	
Station number	50	51	52	53	54	55	59	61	
Latitude (°S)	62.00	63.33	65.00	65.38	65.87	66.04	66.34	62.02	
Longitude (°E)	50.01	50.00	50.00	49.99	49.99	49.96	50.16	60.00	

<i>Amalothrix</i> sp.	984.8	294.1	151.2	100.1	87.6	243.8	1012.7	972.7
<i>Calanoides acutus</i>	140.7	294.1	95.7	31.3	125.2	313.5	540.1	607.9
<i>Calanus propinquus</i>	0.0	0.0	15.1	0.0	6.3	34.8	0.0	486.3
<i>Calanus simillimus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Candacia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Clausocalanus brevipes</i>	0.0	784.2	10.1	12.5	31.3	69.7	0.0	607.9
<i>Clio pyramidata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Clione antarctica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ctenocalanus citer</i>	140.7	98.0	95.7	37.6	269.1	661.8	573.8	972.7
<i>Eucalanus longiceps</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euchirella rostromagna</i>	0.0	0.0	0.0	12.5	18.8	17.4	0.0	0.0
<i>Eukrohnia hamata</i>	0.0	196.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euphausia crystallorophias</i>	0.0	0.0	0.0	0.0	6.3	0.0	371.3	0.0
<i>Euphausia superba</i>	0.0	98.0	5.0	0.0	0.0	0.0	0.0	0.0
<i>Fritillaria</i> sp.	6049.4	6862.1	257.0	287.9	363.0	731.4	11004.2	57752.7
<i>Haloptilus oxycephalus</i>	140.7	98.0	30.2	12.5	0.0	0.0	0.0	0.0
<i>Heterorhabdus austrinus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Heterostylites longicornis</i>	0.0	0.0	15.1	0.0	31.3	52.2	0.0	0.0
<i>Hyperiella dilatata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Limacina helicina antarctica</i>	0.0	0.0	20.2	12.5	0.0	0.0	0.0	0.0

Table A1. (continued)

<i>Metridia gerlachei</i>	70.3	0.0	95.7	75.1	300.4	835.9	0.0	0.0
<i>Metridia lucens</i>	0.0	0.0	65.5	12.5	18.8	69.7	0.0	0.0
<i>Microcalanus pygmaeus</i>	6541.8	1372.4	181.4	169.0	137.7	383.1	67.5	13252.7
Unidentified nauplii	1688.2	1470.5	5.0	31.3	0.0	52.2	506.3	1580.6
<i>Neogloboquadrina pachyderma</i>	281.4	196.1	45.3	12.5	6.3	0.0	675.1	364.8
<i>Oikopleura</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Oithona frigida</i>	211.0	1372.4	85.7	150.2	144.0	348.3	472.6	2553.3
<i>Oithona similis</i>	18711.0	20978.4	191.5	638.4	632.2	1637.0	2767.9	23830.6
<i>Oncaea antarctica</i>	0.0	490.2	20.2	0.0	0.0	0.0	67.5	364.8
<i>Oncaea curvata</i>	0.0	98.0	0.0	12.5	43.8	0.0	0.0	121.6
Ostracods	0.0	0.0	131.0	68.9	18.8	0.0	0.0	121.6
<i>Paraeuchaeta antarctica</i>	0.0	0.0	50.4	12.5	18.8	34.8	0.0	0.0
<i>Pelagobia longicirrata</i>	70.3	98.0	20.2	56.3	0.0	0.0	202.5	0.0
<i>Primno macropa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Racovitzanus antarcticus</i>	211.0	98.0	10.1	0.0	0.0	0.0	67.5	0.0
<i>Rhincalanus gigas</i>	703.4	1078.3	95.7	6.3	37.6	104.5	0.0	243.2
<i>Rhynchoerella bongraini</i>	0.0	0.0	15.1	25.0	0.0	0.0	0.0	0.0
<i>Sagitta gazellae</i>	0.0	0.0	0.0	0.0	6.3	34.8	0.0	364.8
<i>Sagitta marri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Salpa thomsoni</i>	0.0	0.0	0.0	0.0	18.8	34.8	0.0	0.0
<i>Scolecithricella minor</i>	1195.8	294.1	146.1	350.5	206.6	383.1	2092.8	1459.0
<i>Siphonophora nectophore</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spinocalanidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stephos longipes</i>	0.0	0.0	0.0	0.0	0.0	0.0	67.5	0.0
<i>Thysanoessa macrura</i>	492.4	490.2	25.2	12.5	12.5	69.7	0.0	243.2
Tintinnids	211.0	98.0	0.0	0.0	6.3	34.8	0.0	364.8
<i>Tomopteris</i> spp.	140.7	0.0	10.1	0.0	0.0	0.0	67.5	0.0
<i>Travisioopsis levinsoni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Station number	66	69	72	77	79	80	81	87
Latitude (°S)	63.00	64.35	65.50	66.32	66.53	66.68	66.94	62.00
Longitude (°E)	60.01	59.99	60.01	60.01	59.98	60.00	59.97	70.00
<i>Amallothrix</i> sp.	260.2	275.3	548.5	17.1	890.5	1263.9	200.3	4815.0
<i>Calanoides acutus</i>	130.1	110.1	102.8	17.1	763.3	2317.1	267.0	4012.5
<i>Calanus propinquus</i>	0.0	0.0	0.0	42.8	508.9	0.0	0.0	267.5
<i>Calanus simillimus</i>	0.0	0.0	34.3	0.0	0.0	0.0	0.0	2006.2
<i>Candacia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Clausocalanus brevipes</i>	195.2	165.2	137.1	0.0	0.0	0.0	0.0	936.2
<i>Clio pyramidata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Clione antarctica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ctenocalanus citer</i>	195.2	468.0	240.0	124.1	2099.1	2580.4	984.6	6553.7
<i>Eucalanus longiceps</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	535.0
<i>Euchirella rostromagna</i>	0.0	0.0	0.0	72.8	445.3	684.6	133.5	401.2
<i>Eukrohnia hamata</i>	0.0	0.0	0.0	171.2	381.7	0.0	0.0	267.5
<i>Euphausia crystallorophias</i>	0.0	0.0	0.0	719.0	10559.3	316.0	166.9	0.0
<i>Euphausia superba</i>	0.0	0.0	34.3	0.0	0.0	0.0	0.0	0.0
<i>Fritillaria</i> sp.	15938.2	1706.9	2742.5	34.2	7251.6	7477.9	4572.5	14846.2
<i>Haloptilus oxycephalus</i>	0.0	0.0	102.8	0.0	0.0	0.0	0.0	267.5
<i>Heterorhabdus austrinus</i>	65.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Heterostylites longicornis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	133.7
<i>Hyperietta dilatata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Limacina helicina antarctica</i>	0.0	0.0	171.4	0.0	127.2	0.0	33.4	8560.0
<i>Metridia gerlachei</i>	0.0	0.0	68.6	34.2	1399.4	631.9	216.9	2273.7
<i>Metridia lucens</i>	65.1	0.0	102.8	0.0	381.7	0.0	0.0	0.0
<i>Microcalanus pygmaeus</i>	3317.8	2092.3	5347.8	34.2	381.7	947.9	33.4	8426.2
Unidentified nauplii	910.8	82.6	137.1	17.1	318.1	52.7	83.4	3343.7
<i>Neogloboquadrina pachyderma</i>	65.1	110.1	68.6	0.0	0.0	316.0	267.0	2273.7
<i>Oikopleura</i> sp.	0.0	55.1	137.1	0.0	0.0	316.0	0.0	0.0
<i>Oithona frigida</i>	780.6	357.9	1062.7	102.7	1145.0	1053.2	33.4	1471.2
<i>Oithona similis</i>	7155.9	1954.6	2468.2	205.4	5216.1	1895.8	567.4	27418.7
<i>Oncaea antarctica</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1203.7
<i>Oncaea curvata</i>	65.1	82.6	0.0	0.0	190.8	0.0	0.0	2675.0
Ostracods	0.0	0.0	68.6	119.8	508.9	105.3	33.4	0.0
<i>Paraeuchaeta antarctica</i>	65.1	55.1	0.0	55.6	445.3	263.3	33.4	0.0
<i>Pelagobia longicirrata</i>	130.1	0.0	68.6	17.1	0.0	316.0	0.0	1070.0
<i>Primno macropa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Racovitzanus antarcticus</i>	260.2	55.1	171.4	0.0	0.0	0.0	0.0	0.0
<i>Rhincalanus gigas</i>	325.3	165.2	274.2	0.0	0.0	0.0	0.0	1070.0
<i>Rhynchoerella bongraini</i>	130.1	55.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sagitta gazellae</i>	130.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sagitta marri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Salpa thomsoni</i>	0.0	0.0	0.0	4.3	0.0	0.0	0.0	0.0
<i>Scolecithricella minor</i>	390.3	247.8	959.9	171.2	3180.5	1158.6	200.3	17788.7
<i>Siphonophora nectophore</i>	0.0	0.0	0.0	34.2	0.0	0.0	0.0	0.0
Spinocalanidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stephos longipes</i>	0.0	0.0	0.0	0.0	0.0	0.0	33.4	0.0
<i>Thysanoessa macrura</i>	325.3	247.8	240.0	12.8	254.4	105.3	50.1	668.7

[illegible]



Table A1. (continued)

<i>Hyperietta dilatata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Limacina helicina antarctica</i>	2887.6	589.6	671.4	853.6	186.5	0.0	0.0	0.0
<i>Metridia gerlachei</i>	2475.1	589.6	671.4	142.3	217.6	1294.6	1152.3	215.2
<i>Metridia lucens</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Microcalanus pygmaeus</i>	17325.9	6780.6	12757.2	3319.5	994.7	3054.0	691.4	358.6
Unidentified nauplii	206.3	1031.8	2238.1	1659.7	341.9	298.8	115.2	71.7
<i>Neogloboquadrina pachyderma</i>	1031.3	147.4	0.0	189.7	0.0	132.8	184.4	71.7
<i>Oikopleura</i> sp.	0.0	0.0	895.2	0.0	0.0	0.0	0.0	0.0
<i>Oithona frigida</i>	825.0	884.4	671.4	94.8	248.7	265.6	92.2	143.5
<i>Oithona similis</i>	16294.6	7665.1	16338.2	5880.2	3916.8	3983.4	2074.1	3801.5
<i>Oncaea antarctica</i>	412.5	442.2	1342.9	94.8	0.0	0.0	0.0	17.9
<i>Oncaea curvata</i>	1031.3	1768.9	1119.1	474.2	0.0	298.8	161.3	0.0
Ostracods	0.0	589.6	0.0	284.5	497.4	265.6	138.3	0.0
<i>Paraeuchaeta antarctica</i>	0.0	294.8	0.0	47.4	0.0	0.0	0.0	233.1
<i>Pelagobia longicirrata</i>	618.8	294.8	447.6	0.0	155.4	132.8	115.2	71.7
<i>Primno macropa</i>	0.0	0.0	671.4	0.0	0.0	0.0	0.0	0.0
<i>Racovitzanus antarcticus</i>	0.0	147.4	447.6	0.0	0.0	0.0	0.0	0.0
<i>Rhincalanus gigas</i>	412.5	442.2	1790.5	474.2	248.7	132.8	0.0	0.0
<i>Rhynchoerella bongraini</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sagitta gazellae</i>	0.0	0.0	223.8	0.0	0.0	0.0	0.0	0.0
<i>Sagitta marri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Salpa thomsoni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Scolecithricella minor</i>	1650.1	442.2	1119.1	189.7	870.4	929.5	322.6	430.4
<i>Siphonophora</i> nectophore	0.0	0.0	223.8	0.0	0.0	0.0	46.1	0.0
Spinocalanidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Stephos longipes</i>	618.8	0.0	447.6	0.0	0.0	0.0	46.1	0.0
<i>Thysanoessa macrura</i>	618.8	442.2	447.6	426.8	124.3	132.8	46.1	0.0
Tintinnids	0.0	737.0	223.8	189.7	0.0	0.0	0.0	0.0
<i>Tomopteris</i> spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Travisopsis leviseni</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

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