

Interannual variability of zooplankton in the Dumont d'Urville sea (139°E – 146°E), east Antarctica, 2004–2008

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Abstract

Spatial and temporal variability of zooplankton was studied during five summers (2004–2008) in the Dumont d'Urville Sea, east Antarctica. The species recorded, based on the catch of a 500 μm -mesh Bongo net, were typical of southern continental shelf communities in Antarctica, including *Euphausia crystallorophias*, polychaetes, pteropods and biomass-dominant copepods. There was a strong degree of temporal variation in abundance, possibly related to the thickness and extent of the sea ice cover during each spring prior to the surveys. Total mean abundance was highly variable between years, with a minimum of 961 ind. 1000 m^{-3} in 2004 (range 65–3407 ind. 1000 m^{-3}) and a maximum of 15,627 ind. 1000 m^{-3} in 2005 (range 5109–33,869 ind. 1000 m^{-3}). Spatially, within each year, abundances were also variable, and there were no uniform patterns in abundance from year to year. Water column physical characteristics (temperature and salinity) were relatively constant and did not contribute substantially to variation between the years. It is likely that variation in zooplankton distribution was largely related to a combination of localised features, such as the thickness and extent of sea ice cover, the position and extent of the Mertz Polynya, local wind conditions and bathymetric features. © 2011 Elsevier B.V. and NiPR. All rights reserved.

Keywords: Salinity; Temperature; Sea ice; Zooplankton-environment relationships; Mertz glacier

1. Introduction

Zooplankton that live at high latitudes are influenced by seasonal cycles in primary productivity, which are, in turn, driven by the light regime, strength and position of major oceanographic currents and the

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growth and decay of sea ice. There is evidence in the Southern Ocean that the West Antarctic Peninsula (WAP) is showing rapid regional warming (Anisimov et al., 2007), and, while the East Antarctic Ice Sheet has appeared to be more stable than the WAP, there is now concern that East Antarctica is more vulnerable to

rising temperatures than previously believed (Fox, 2010). Possible responses by algal communities to warming include shifts from large cells to small cells (Montes-Hugo et al., 2009), and decreases in phytoplankton biomass. The consequences of these physical and biological changes on the grazer

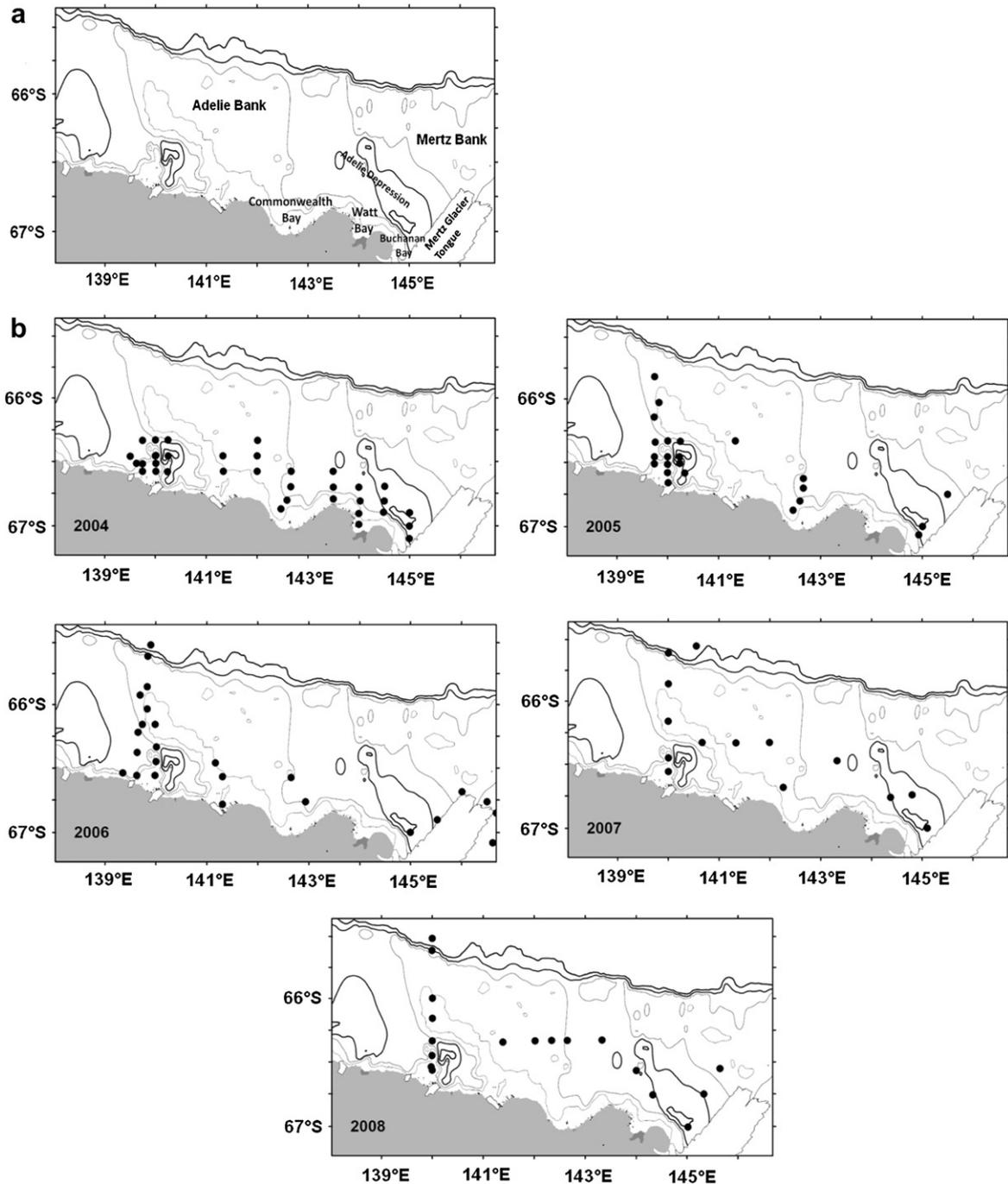


Fig. 1. Sampling region. (a) shows main locations mentioned in text. (b) shows positions of the sampling stations for the five ICO²TA surveys from 2004 to 2008.

communities are not well understood, but there are likely to be negative impacts on those species that can't graze efficiently on small cells (e.g. euphausiids), or that require predictable sea ice for reproduction and spawning (e.g. some copepods). Conversely, organisms that can graze efficiently on small cells or when phytoplankton biomass is low (e.g. salps) should be favoured by such shifts in the algal communities (Schofield et al., 2010). Any alterations to plankton dynamics will have ramifications further up the food chain. To assess how changes in the environment affect plankton communities it is necessary to examine patterns of distribution and abundance over several years and relate these patterns to biotic and abiotic drivers.

Since 2004, the ICO²TA (Integrated Coastal Ocean Observations in Terre Adélie) program, supported by the Institut Paul-Emile-Victor (IPEV), has conducted plankton surveys in the Dumont d'Urville Sea region between 139°E and 146°E, from Terre Adélie to the Mertz Glacier Tongue (MGT). Further, in 2008 the CEAMARC (Collaborative East Antarctic Marine Census) surveyed the Dumont d'Urville Sea as a contribution to the Census of Antarctic Marine Life. The Dumont d'Urville Sea is a dynamic region that is undergoing substantial change. It is dominated by the Mertz Glacier Polynya on its eastern side (~67°S, 145°E), which acts as a seasonally recurrent ice

factory. Three distinct zones have been described for the Dumont d'Urville Sea, based on hydrology and phytoplankton distribution in the summer of 2004 (Beans et al., 2008). Zone 1, defined as the Astrolabe Glacier zone, was characterised by mixed waters with high nutrient concentrations and was dominated by large diatoms such as *Corethron pennatum* and *Rhizosolenia* spp. Zone 3 was closest to the Mertz Glacier and exhibited stratified water containing low nutrient concentrations and was characterised by low diatom diversity, with *Fragilariopsis* spp. being most common. Zone 2 was located between Zones 1 and 3 and, not surprisingly, exhibited intermediate characteristics such as relatively mixed waters, moderate nutrient concentrations and a diatom assemblage featuring low diversity, predominantly *Chaetoceros criophilus*. As these zones were only described for the summer of 2004 it is not yet clear whether they are robust from year to year.

There have been a few studies of zooplankton distribution on the continental shelf between 139°E and 146°E (Hosie et al., 2000; Chiba et al., 2001), although the focus has generally been further offshore or near the shelf break where *Euphausia superba* dominates (e.g. Nicol et al., 2000; Hosie et al., 2000). In a repeated transect along ~64°S and located between 90°E and 160°E, two zooplankton communities were separated based on differences between water

Table 1

Mean values for each environmental variable, shown with their ranges (minimum – maximum) for stations sampled within each year. Significant differences between years ($P \leq 0.01$) are denoted by **, based on ANOVA; d.f. = 4,109. Subscripts (a,b,c) denote which means were similar under the REGW post-hoc test.

Year	2004	2005	2006	2007	2008	F _{between groups}
Sampling dates	19/1/04–28/1/04	10/1/05–19/1/05	9/1/06–18/1/06	24/1/07–1/2/07	10/1/08–18/1/08	
Number of stations	38	23	25	15	18	
Sea ice retreat ^a	15/11/03–27/11/03	9/11/04–24/11/04	2/11/05–20/11/05	2/11/06–19/11/06	6/11/07–04/12/07	
Latitude, °S	66.62 (67.10–66.33)	66.52 (67.06–65.82)	66.43 (67.08–65.52)	66.35 (67.00–65.55)	66.35 (67.01–65.52)	0.016
Longitude, °E	141.94 (139.00–145.00)	141.16 (139.74–145.50)	141.71 (139.35–146.68)	141.63 (139.99–145.10)	141.85 (139.98–145.33)	0.905
Depth, m	559 (128–995)	580 (192–1080)	473 (162–1284)	604 (163–1165)	553 (165–1599)	0.613
T _{0–100 m} , °C	–0.58 _a (–1.59–0.15)	–1.00 _{b,c} (–1.75 to –0.20)	–1.06 _b (–1.88–0.51)	–0.80 _c (–1.62–0.09)	–1.04 _b (–1.73–1.06)	12.89**
T _{100–200 m} , °C	–1.02 _{a,b} (–1.77 to –0.28)	–1.25 _{a,b} (–1.87 to –0.59)	–1.28 _{a,b} (–1.90 to –0.52)	–1.32 _b (–1.82 to –0.65)	–1.46 _b (–1.91 to –0.13)	4.19**
S _{0–100 m}	34.19 (33.31–35.09)	34.25 (33.24–34.37)	34.29 (33.85–34.45)	34.25 (34.70–34.44)	34.31 (33.59–34.93)	2.18
S _{100–200 m}	34.36 _a (34.10–34.78)	34.35 _a (34.20–34.50)	34.38 _a (34.19–34.52)	34.42 _b (34.32–34.52)	34.42 _b (33.69–35.03)	9.79**
Chl _a _{25 m} , µg m ^{–2}	639 _a (265–1474)	1325 _b (483–3150)	361 _c (116–748)	757 _a (201–1278)	712 _a (28–1612)	14.99**

^a Based on analysis by Martina Smith (15/6/10).

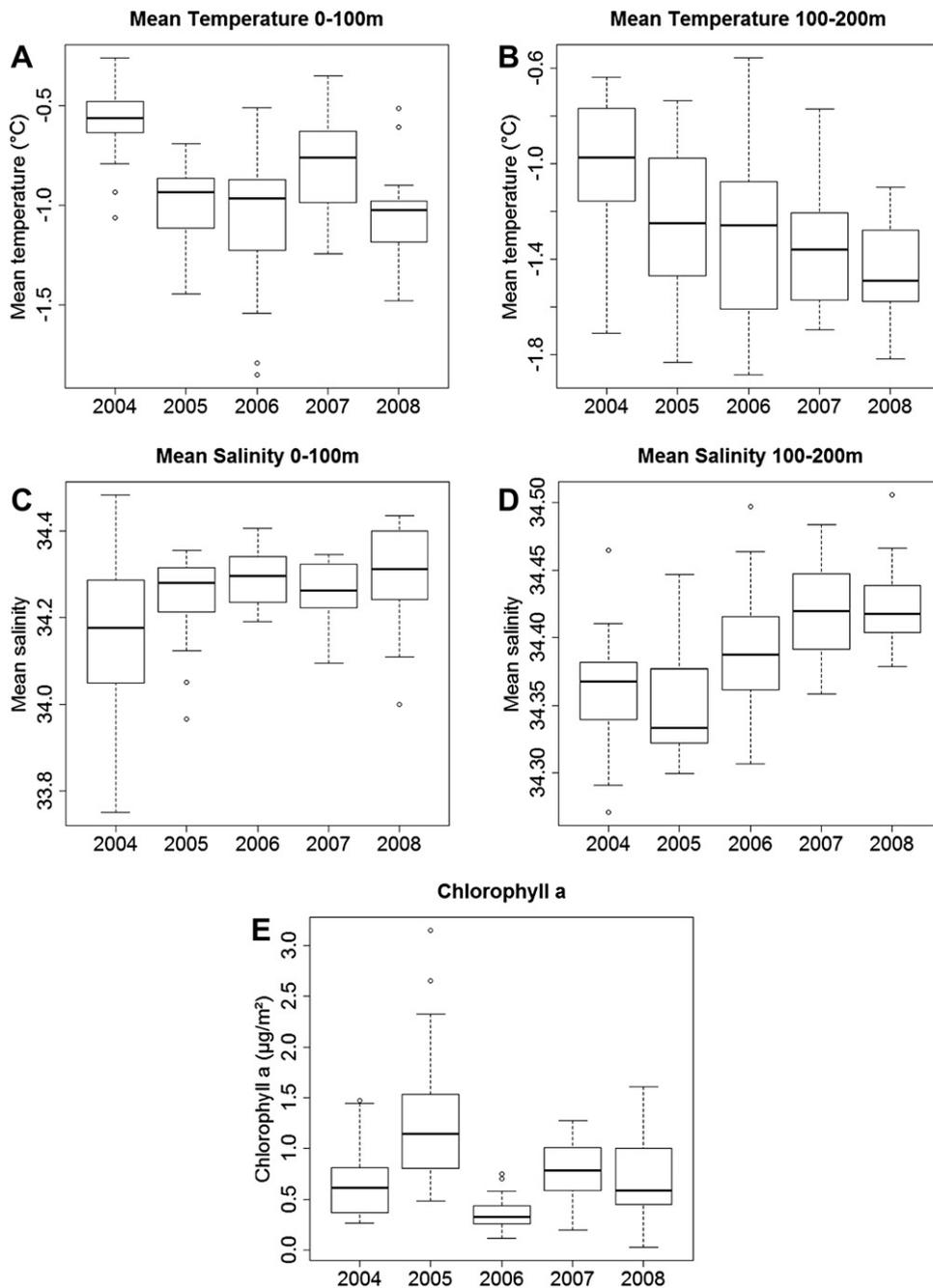


Fig. 2. Boxplots of (A) mean temperature 0–100 m and (B) 100–200 m (°C), (C) mean salinity 0–100 m and (D) 100–200 m, and (E) chlorophyll *a* concentration integrated to 25 m ($\mu\text{g m}^{-2}$) from 2004 to 2008. Boxplots have ends at the quartiles, the vertical line in the middle is the median. Bars are drawn to the farthest points that are not outliers. Dots represent every point more than $3/2$ times the interquartile range from the end of a box.

temperatures, silicate concentrations and chlorophyll *a* concentrations (Chiba et al., 2001). The two ‘communities’ occurred at the same latitude and indicated the presence of sporadic warm water intrusions from the north. The warmer waters were always dominated by small copepods and non-copepod

herbivores. Hosie et al. (2000) also found that temperature was a major determining feature that distinguished communities in the region between 80 and 150°E, with east of 120°E dominated by *Salpa thompsoni* in the oceanic realm and by *Euphausia crystallorophias* in the neritic zone.

The surveys that were undertaken as part of the present study enable an excellent opportunity to examine interannual variation in baseline distribution and abundance of zooplanktonic communities over five summers. This meso-scale study will complement the larger scale studies previously undertaken in the region (Hosie et al., 2000; Chiba et al., 2001) by focussing on localised drivers of zooplankton distribution. It will also provide the opportunity to test if the three zones that were based on phytoplankton and water column characteristics (Beans et al., 2008) are (i) evident at the zooplankton level and (ii) stable over time. This information will facilitate the development of sampling strategies designed to monitor any future changes in community structure.

2. Materials and methods

2.1. Study region

The entire region sampled during the 2004 to 2008 surveys was south of the continental slope and was under the influence of the westward flowing Antarctic Coastal Current. The region covered the area from 139°E to the western side of the Mertz Glacier at 145°E (Fig. 1a). The Mertz Glacier is one of the largest in the region, with smaller glaciers such as the Astrolabe and Zélée also present in the western sector. Three large bays are situated along the coastline: Commonwealth Bay, Watt Bay and Buchanan Bay. The region is characterised by strong katabatic winds that influence surface water currents (Wendler et al., 1997), and water mass characteristics depend on advection linked to wind and ice cover, and bathymetry. A long plateau of about 200 m depth is located between the Astrolabe Glacier and Commonwealth Bay. Deep areas (500–1000 m) are observed offshore from Dumont d'Urville and Port Martin, though the largest and deepest part of the shelf is located between Watt Bay and the Mertz Glacier; this is the Adélie Depression (from 142°E to 146°E), which has a depth of at least 1200 m (Williams and Bindoff, 2003). The Adélie Depression is an area of dense water formation where high salinity shelf waters accumulate in winter from brine rejected during sea ice formation. A cyclonic gyre transports water with the depression (Williams and Bindoff, 2003), which is an important source of deep water known as Adélie Land Bottom Water (Gordon and Tchernia, 1972).

During the period from April to October the region is covered by pack ice (80–100% sea ice concentration (SIC)) for approximately 27–29 weeks. Open water

(0–10% SIC) dominates in the region for approximately 14–16 weeks annually within the period from November to March. The transition between pack ice and open water phases (both retreat and growth of sea ice) lasts approximately 8–10 weeks in total each year. The spatial characteristics of sea ice during the transition periods are dynamic and variable from year to year. However, generally the November transition, or breakout, period follows a southeast to northwest trajectory from the Mertz Glacier Polynya. A qualitative assessment of the duration of the breakout periods was done by looking at daily satellite remotely sensed SIC maps. The end date of the breakout period was determined by observing the day when high concentrations of sea ice cease to cut the continental shelf zone off from the ocean north of the shelf. The beginning date of the breakout period was defined as the day when this annual final retreat began; when both the concentration and cover of sea ice began to substantially reduce within the month of November. The surveys presented in this study were all conducted throughout the open water period.

2.2. Sampling strategy

The ICO²TA surveys were carried out during each summer from 2004 to 2008, between January 9 and February 1, aboard the RV *l'Astrolabe*. We sampled a total of 117 stations over the continental shelf between 139°E and 145°E and 65°30'S and 67°S (Table 1; Fig. 1b). For the 2004 to 06 surveys the westernmost sampling stations were defined in relation to movement patterns of foraging Adélie Penguins, as determined by their satellite (Argo) positions. In 2005, 2006 the penguins were feeding primarily on *E. superba* and so travelled further north than in 2004, when poor *E. superba* stocks confined the penguins to feeding closer to the coast on *E. crystallophilas* and *Thysanoessa macrura* (C. Bost, personal communication). Subsequent to the penguin-related sampling stations, the surveys proceeded on a west to east direction, with individual stations determined primarily by weather conditions and logistical constraints. In 2007, 2008, although fewer in number, the stations were chosen to reflect the basic north-south and west-east transects from earlier years.

At each station, a CTD (Seabird SB25 in 2004, 2007 and 2008; FSI in 2005 and 2006) was used to record temperature and salinity down to 200 m. For the purposes of this study, where zooplankton samples were integrated over 200 m, we have used mean temperature and salinity for the 0–100 m and

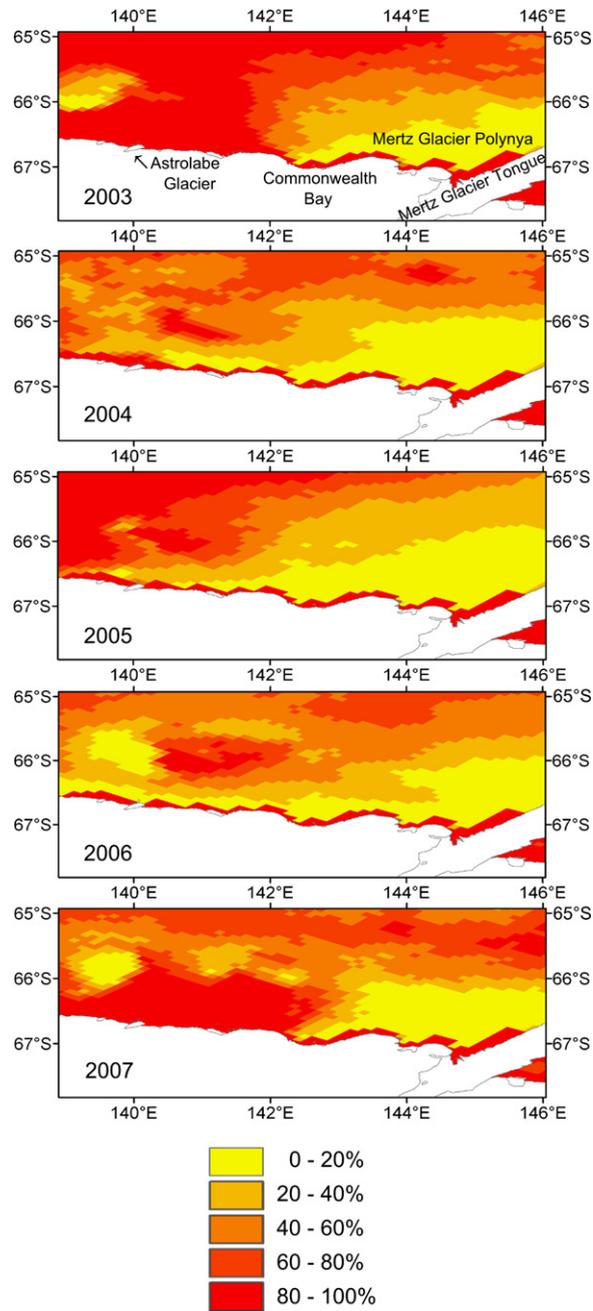


Fig. 3. Mean sea ice concentration for November each year (AMSR-E).

100–200 m intervals because the average thermocline depth each year generally ranged between 90 and 120 m. Seawater samples were taken with Niskin bottles. For photosynthetic pigments, seawater was filtered through 47-mm GF/F filters and then frozen. Pigments were extracted and analysed by HPLC (Williams and Claustre, 1991; Zapata et al., 2000). To compare zooplankton distribution with chlorophyll

a we have used the integrated chlorophyll concentrations over the top 25 m, the depth of the chlorophyll maximum.

Annual average SIC for the November sea ice breakout periods in the Dumont d'Urville Sea were derived from daily 6.25 km resolution SIC data obtained via the Advanced Microwave Scanning Radiometer – Earth Observing System (AMSR-E)

files. The ArcGIS (ESRI) *Single Output Map Algebra* tool was used on the AMSR-E data to calculate the November SIC averages.

Macrozooplankton were collected by oblique tows of a double-framed Bongo net fitted with 500 μm mesh, and mouth diameter of 63 cm. Tows were carried out at a speed of 2 knots from the surface to a depth of 200 m or near the seabed for shallower depths. The volume of water filtered by each net was measured with a flowmeter and used to calculate zooplankton abundances. Samples were fixed immediately on board with 5% buffered formaldehyde in seawater. Concentrated samples were split using a *Motoda (1959)* box where necessary. Counting proceeded until approximately one hundred individuals of a taxonomic group had been observed (*Gibbons, 1999*). Abundances are expressed as number of individuals per 1000 m^{-3} . Sorting and identification were carried

Table 2

List of zooplankton sampled. Abundances (ind. 1000 m^{-3}) are the means for all stations sampled each year. **BOLD** represents an IndVal of greater than 25% for that group. *denotes those species that contributed to the top 50% of abundance for a year (by SIMPER analysis).

	2004	2005	2006	2007	2008
Alciopidae	1	6	0	7	0
Amphipoda	6	0	11	2	12
Ascidia	1	16	0	0	0
<i>Calanoides acutus</i>	20	208	92	43	175
<i>Calanus propinquus</i>	146*	1166*	156*	508	182*
<i>Dimophyes</i> sp.	0	0	0	0	2
<i>Diphyes</i> sp.	0	2	1	3	2
<i>Euphausia crystallorophias</i>	144*	10819*	990*	1761*	1411*
<i>Euphausia superba</i>	0	0	1	0	3
Gastropoda	0	0	0	0	4
<i>Clione</i> sp.	5	2	6	12	1
<i>Haloptilus oxycephalus</i>	0	3	0	6	0
<i>Lensia</i> sp.	0	0	0	0	2
<i>Limacina helicina</i>	29	76	102*	20	49
Lopadorhynchidae	188	1092*	20	1829*	385
Medusa	1	16	3	45	7
<i>Metridia gerlachei</i>	112	992	365	756	230
Ostracoda	2	27	6	67	27
<i>Paraeuchaeta antarctica</i>	43	233	21	367	50
Polychaeta	227*	446*	254	573*	507*
<i>Rhincalanus gigas</i>	4	57	7	30	0
<i>Sagitta</i> sp.	0	3	5	3	3
<i>Salpa thompsoni</i>	0	0	0	34	0
<i>Sapphirina</i> sp.	3	0	0	0	0
Siphonophora	3	0	2	6	9
<i>Thysanoessa macrura</i>	14	437	123*	331*	95*
<i>Tomopteris</i> sp.	10	25	3	95	31
Total mean abundance	961	15627	2169	6499	3189
Minimum abundance	65	5109	80	1181	138
Maximum abundance	3407	33869	9013	15329	9165

out with a stereomicroscope (magnification: 10 \times), with the occasional use of a compound microscope (magnification: 50 \times – 400 \times) to aid in identification. Each individual was identified to species level where possible (e.g. for the majority of the copepods), or to a higher taxonomic level when necessary. Organisms such as *Oithona similis*, *Oncaea curvata* and *Fritillaria* spp. were present in the samples but due to their very small size they would have been substantially under-sampled by the plankton net. Therefore, these species were not included in any analyses presented in this paper.

2.3. Data analysis

Multivariate analyses were performed using PRIMER version 6 (Plymouth, UK) and SPSS version 18 (Illinois, USA). To investigate associations between the zooplankton assemblages at the sampling stations (Q-mode analysis), 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. A matrix of Bray–Curtis similarities (*Bray and Curtis, 1957*) was constructed for all sites and subjected to canonical analysis of principal coordinates (CAP), a constrained ordination method which finds the axes that best discriminate between groups; i.e. between the five sampling years. ANOSIM (analysis of similarities) was used to test the null hypothesis that there was no significant difference in community composition between the years. SIMPER (similarity percentages) analysis was then

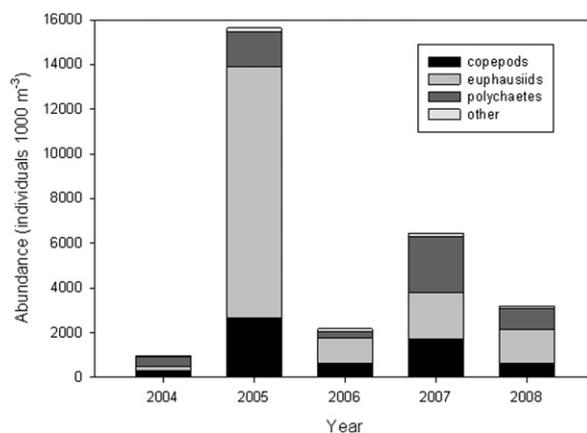


Fig. 4. Zooplankton total mean abundances (ind. 1000 m^{-3}) from 2004 to 2008, showing proportions represented by euphausiids, copepods and polychaetes.

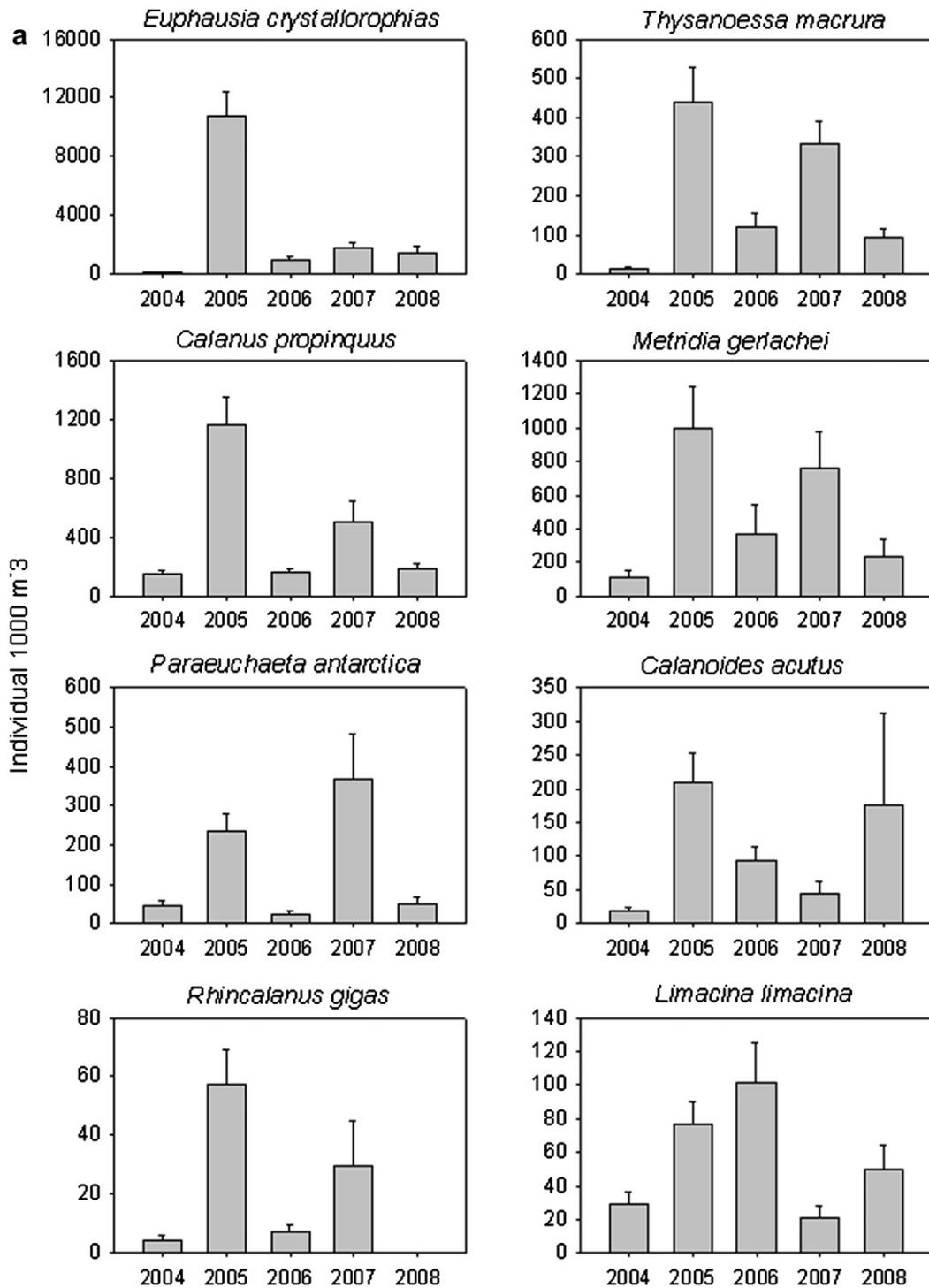


Fig. 5. Mean abundance (ind. 1000m⁻³) and standard errors of the dominant zooplankton taxa collected each summer, 2004–2008.

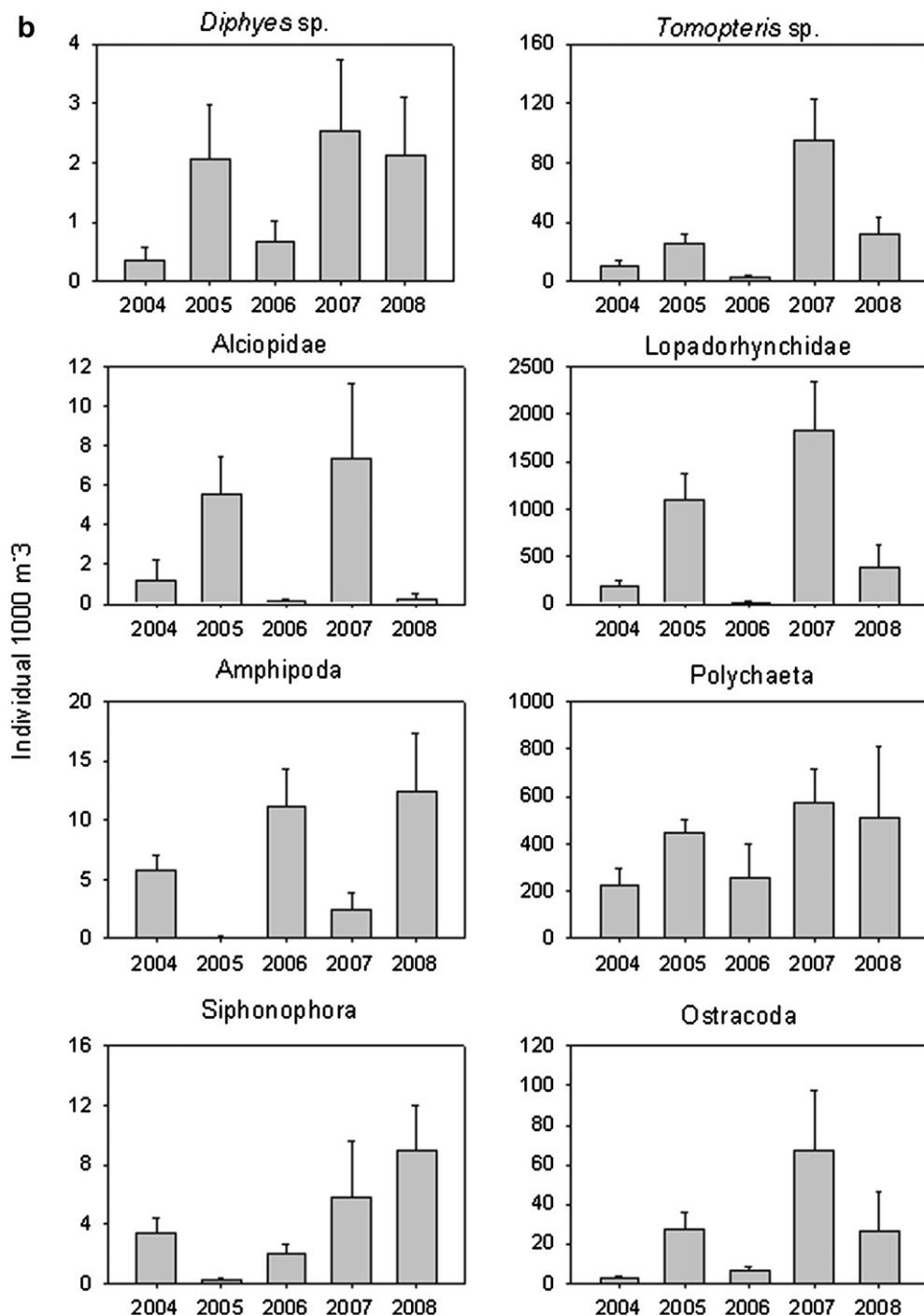


Fig. 5. (continued)

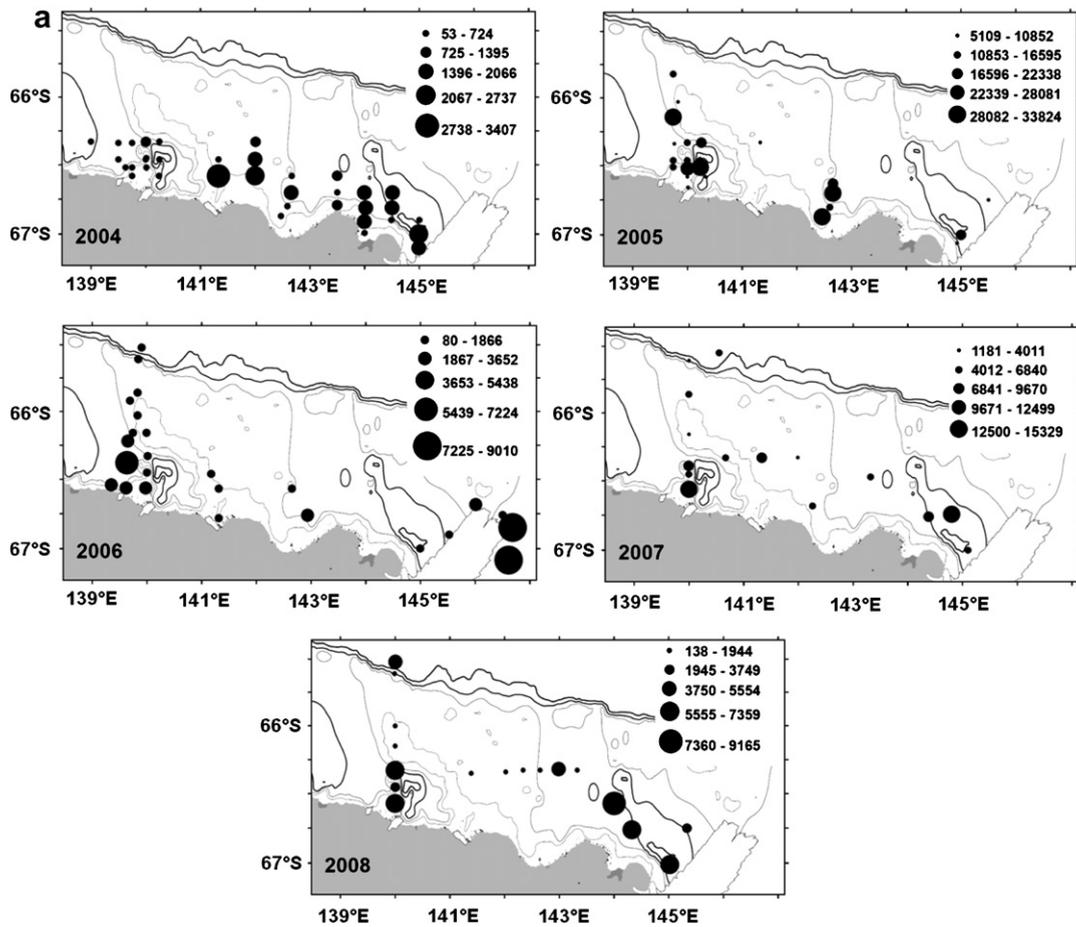


Fig. 6. (a) Abundances (ind. 1000 m⁻³) of the main taxa collected across the sampling region during each summer, 2004–2008. (b) relative proportions of the six dominant taxa sampled 2004–2008. Cal_pro = *Calanus propinquus*; Eup_cry = *Euphausia crystallorophias*; Lim = *Limacina helicina*; Lop = Lopadorhynchidae; Pol = Polychaeta; Thy_mac = *Thysanoessa macrura*.

applied to identify which species contributed to the top 50% of abundance of each group.

Station environmental data associated with each of the years were summarised and statistical differences between the means of the following variables were tested for using ANOVA: latitude, longitude, depth, chlorophyll *a*, mean temperature between 0 and 100 m (T_{0-100}), and between 100 and 200 m ($T_{100-200}$), and mean salinity between 0 and 100 m (S_{0-100}) and between 100 and 200 m ($S_{100-200}$). When a significant difference between year means was identified, an unplanned post-hoc comparison of the means using the Ryan, Einot, Gabriel and Welsch procedure (REGW) was applied to distinguish those years that were statistically different. 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.

Common associations between zooplankton taxa (R-mode analysis) were defined using cluster analysis, followed by non-metric multidimensional scaling (NMDS). Prior to analysis the species by station matrix was reduced to a subset of 16 taxa that was common to all five years. Indicator values (IndVal) (Dufrene and Legendre, 1997) were computed to determine indicator species and species assemblages that characterised groups of samples (IndVal 2.0). The random reallocation procedure of sites among years 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 years. Each IndVal was calculated as:

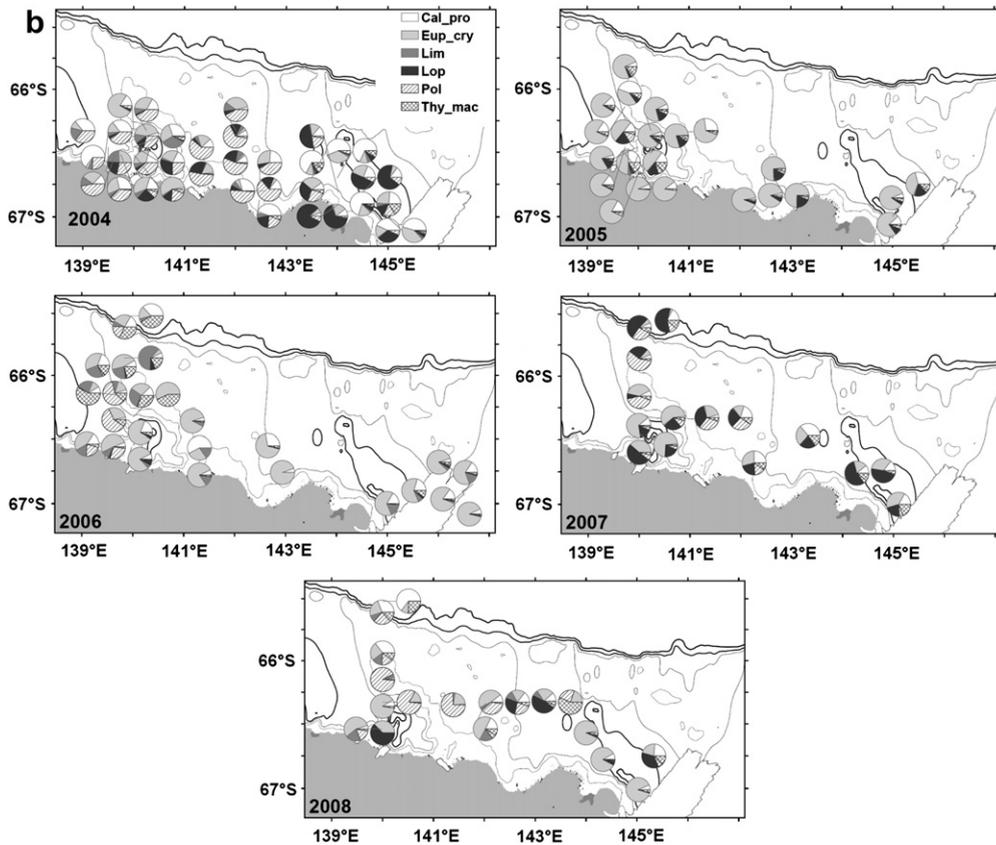


Fig. 6. (continued)

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

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

A_{ij} is a measure of site specificity, where Nindividuals_{ij} is the mean number of individuals in species i across sites of group j , while Nindividuals_i is the sum of the mean numbers of individuals of species i over all groups. B_{ij} is a measure of group fidelity, where Nsites_{ij} is the number of sites in cluster j where species i is present, while Nsites_j is the total number of sites in that cluster (Duf rene and Legendre, 1997).

3. Results

3.1. Environmental features

Table 1 presents means and ranges for the environmental variables measured during the plankton surveys, and box plots summarising temperature, salinity and chlorophyll a concentrations for each year are shown in Fig. 2. ANOVA revealed significant differences in

$T_{0-100\text{ m}}$ and $T_{100-200\text{ m}}$ between years (Table 1). 2004 was significantly warmer over the top 100 m, while 2005, 2006 and 2008 were cooler (Fig. 2A). Mean water temperatures between 100 m and 200 m were significantly different and showed a gradual cooling trend between 2004 and 2008 (Fig. 2B). Salinity in the upper 100 m did not vary between or within years, except in 2004 when there was large variation across the survey area (Fig. 2C). Deeper waters between 100 and 200 m were saltier in 2007 and 2008 (Table 1, Fig. 2D). Chlorophyll a concentrations were highest in 2005, reaching a mean concentration of $1325\ \mu\text{g m}^{-2}$ (Table 1; Fig. 2E). Mean chlorophyll a concentrations were similar during 2004, 2007 and 2008, ranging between $639\ \mu\text{g m}^{-2}$ and $757\ \mu\text{g m}^{-2}$, although the overall range was between 28 and $1612\ \mu\text{g m}^{-2}$. Overall, 2006 experienced the lowest mean concentration ($361\ \mu\text{g m}^{-2}$), however, concentrations in that year ranged between 116 and $748\ \mu\text{g m}^{-2}$.

Table 1 shows that the dates of the breakout period for each year of the study occurred prior to the January sampling survey. The breakout period ranged in duration from 12 days (in November 2003) to 28 days (throughout November and extending into December

2007). For the years 2004, 2005 and 2006 the breakout period lasted 16–18 days. The beginning date of the breakout period ranged from as early as November 2 in 2006 and 2007 to November 15 in 2003. Breakout in 2004 began on November 9, and in 2007 it began on November 6. The years 2005 and 2006 had the most similar breakout timing, with both beginning on

November 2 and ending on November 19–20. The years 2003 and 2004 were also relatively similar; the breakout period started about the middle of November and ended November 24–27. 2007 was different again, with a long breakout period characterised by an early November start and extending through to an early December finish.

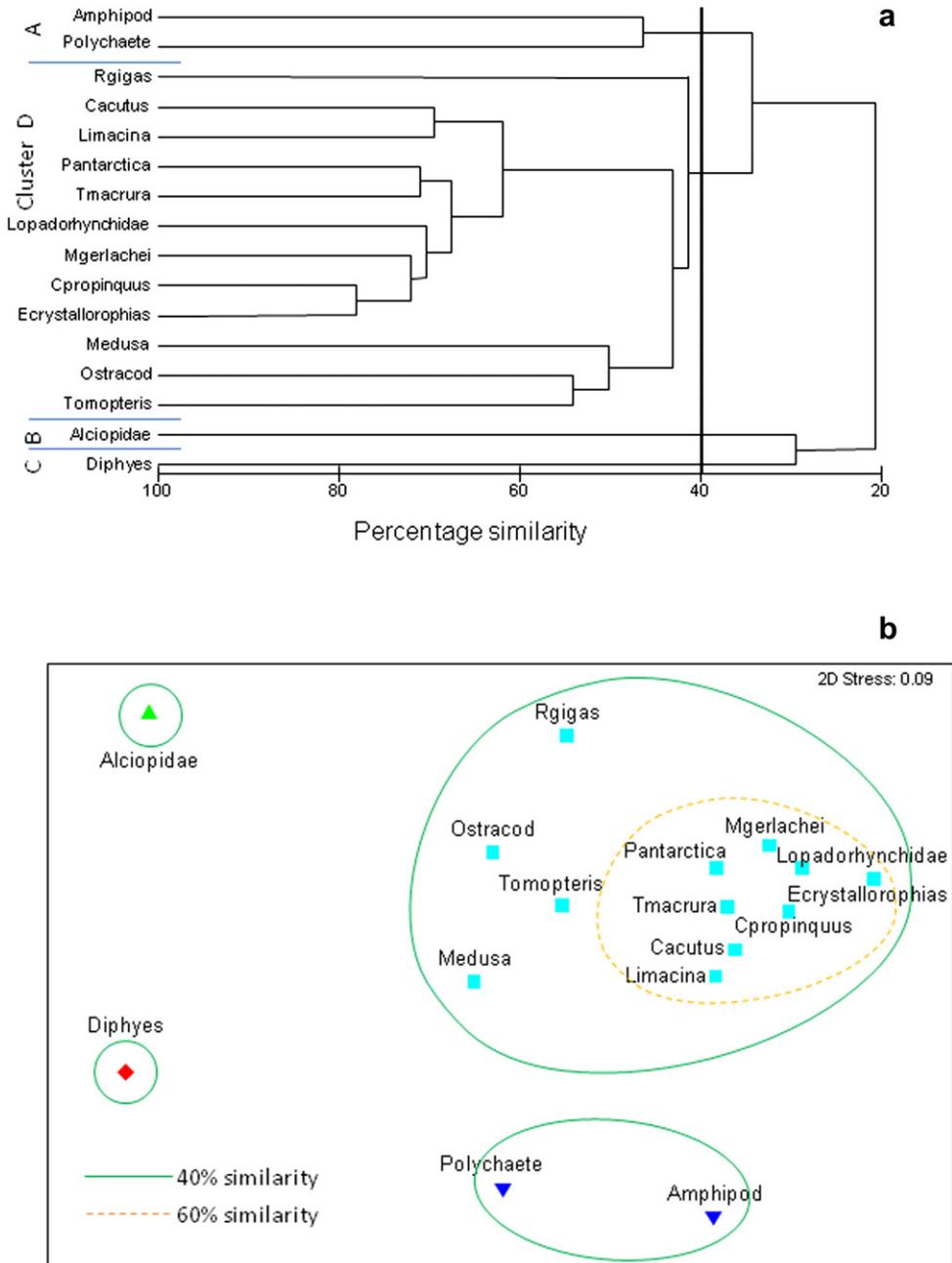


Fig. 7. Species associations. (a) Dendrogram of the inverse cluster analysis showing associations between species at a similarity of 40%. Bray–Curtis similarity index with UPGMA linkage. (b) NMDS inverse ordination plot. Groups identified at 40% similarity are indicated by solid lines and at 60% by the dashed line.

Fig. 3 shows the average sea ice concentrations for the study region during each November from 2003 to 2007, based on AMSR-E data. November 2003 (i.e. prior to the January 2004 survey) had the highest mean value for sea ice concentration (~60%), while 2004, 2005 and 2006 averaged around 40–45%. Sea ice concentration increased again in 2007 (~52%), before the last sampling survey in January 2008. The Mertz Glacier Polynya can be clearly identified in all maps in Fig. 3 by the low average SIC area west of the Mertz Glacier Tongue. Another region of low SIC values was also visible north-west of the Astrolabe Glacier in 2003, 2006 and 2007. This region corresponds with deep bathymetry in the Adélie Basin where there is a lack of anchor points for icebergs resulting in breakouts of unstable seasonable fast ice (Massom et al., 2009). 2003 and 2007 maps show high average SIC in the coastal region west of Commonwealth Bay. The southeast to northwest spatial trajectory of the breakout is implied in all maps by the increasing average SIC following the same direction.

3.2. Zooplankton species assemblages

A total of 27 taxa was identified from 117 sites sampled during the five summers from 2004 to 2008 (Table 2). The groups that accounted for most of the abundance included euphausiids (16–72%), copepods (17–34%) and polychaetes (10–44%). The remaining taxa present in the samples (1–6%) included chaetognaths, pteropods, siphonophores, amphipods and ostracods. Table 2 shows the mean abundance of each taxon collected in each year and highlights those that scored an IndVal of greater than 25%. The table also shows the taxa that contributed to the top 50% of abundance in each year, as determined by SIMPER analysis. All years had high abundances of *E. crystallorophias*, *Calanus propinquus*, *Metridia gerlachei* and polychaetes (>100 ind. 1000 m⁻³), although, of these taxa, only *E. crystallorophias*, *M. gerlachei* and *C. propinquus* met the criteria to be designated as indicator species in 2005. Other taxa that contributed high abundances were polychaetes in the family Lopadorhynchidae in 2004, *Calanoides acutus*, *Paraeuchaeta antarctica* and *T. macrura* in 2005, *T. macrura* in 2006, *P. antarctica* and *T. macrura* in 2007, and *C. acutus* and *T. macrura* in 2008.

Total mean abundance was highly variable between years (Fig. 4), with a minimum of 961 ind. 1000 m⁻³ recorded in 2004 (range 65–3407 ind. 1000 m⁻³) and a maximum of 15,627 ind. 1000 m⁻³ in 2005 (range 5109–33,869 ind. 1000 m⁻³) (Table 2). The abundances

of individual species also varied between years (Fig. 5). Biomass-dominant copepods, including *C. acutus*, *C. propinquus*, *M. gerlachei* and *Rhincalanus gigas*, generally reached their highest mean abundance in 2005, with secondary peaks in 2007 (*C. propinquus*, *M. gerlachei*, *R. gigas*) or 2008 (*C. acutus*). The carnivorous copepod *P. antarctica* was numerous in 2005 but was most common in 2007 (mean of 367 ind. 1000 m⁻³). *E. crystallorophias* was present each year, but reached particularly high abundance (10,819 ind. 1000 m⁻³) in 2005. Other taxa that were common in 2005 included polychaetes, particularly the family Lopadorhynchidae (1092 ind. 1000 m⁻³) and the euphausiid *T. macrura* (437 ind. 1000 m⁻³). Taxa that did not follow the trend of highest numbers in 2005 included the pteropods *Limacina helicina* (102 ind. 1000 m⁻³ in 2006) and *Clione* sp. (12 ind. 1000 m⁻³ in 2007), ostracods (67 ind. 1000 m⁻³ in 2007), the polychaete *Tomopteris* sp. (95 ind. 1000 m⁻³ in 2007), and *S. thompsoni* (34 ind. 1000 m⁻³ in 2007).

Spatially, within each year, abundances were also variable, and there were no uniform patterns in abundance from year to year (Fig. 6a). Taxonomic composition tended to vary across the region, except in 2005 when the sampling sites were all dominated by *E. crystallorophias* (Fig. 6b). In 2004 polychaetes were dominant between 141°E and 143°E, while *C. propinquus* and the Lopadorhynchidae were most numerous in water over the Adélie Depression. During January 2006 *Thysanoessa macrura* was abundant in the west of the Adélie shelf, except for close to the coast where *E. crystallorophias* was common. Community composition in 2007 and 2008 was dominated by the Lopadorhynchidae, *E. crystallorophias* and *T. macrura* (Fig. 6b), though deep waters near the Mertz Glacier contained considerable numbers of large copepods, especially *M. gerlachei*, *P. antarctica* and *C. propinquus*.

Sixteen taxa were identified as occurring in the survey region during each summer, and their associations were analysed using cluster and NMDS (Fig. 7). Four clusters were separated at 40% similarity (Fig. 7a). There were three small clusters of one or two taxa: (A) amphipods and unidentified polychaetes; (C) polychaetes belonging to the family Alciopidae; and (D) the siphonophore genus *Diphyes* spp. The remaining 12 species clustered together in the largest group, B, though eight of these 12 taxa clustered more tightly (Fig. 7b).

3.3. Zooplankton-environment analysis

A plot of the stations within each year based on the first two canonical axes from the CAP, for all taxa, is

shown in Fig. 8. Results from the ANOSIM indicated that the five years were significantly different at $P < 0.01$; i.e. the distances (from the Bray–Curtis similarity matrix) between pairs of samples between years were greater than the distances between samples within years. It is clear that there was more overlap in stations between some years (e.g. 2005 and 2007) than those sampled in other years (e.g. 2004). BIOENV analysis indicated that the suite of environmental variables that best correlated with patterns in the species distribution across the years included T_{0-100} and $S_{100-200}$ (R-statistic 0.140; $P < 0.01$).

4. Discussion

Twenty-seven mesozooplankton taxa were identified from the Bongo net deployed during five summer surveys in the Dumont d'Urville Sea. The suite of taxa recorded during the surveys was typical of that found in other southern shelf communities for organisms $> 500 \mu\text{m}$ (e.g. Hubold et al., 1988), though some species that are more typically found in oceanic communities, e.g. *R. gigas*, were also observed. As the region's bathymetry includes depressions where deep water circulation is significant the presence of characteristically oceanic species is not surprising. Euphausiids, copepods and polychaetes comprised the dominant groups, though their relative contributions varied from year to year. Common copepod species included the biomass-dominant calanoids *C. propinquus*, *C. acutus*, *M. gerlachei*, and *P. antarctica*. The main euphausiids identified were *E. crystallorophias* and *T. macrura*, with *E. superba* only caught sporadically. Due to the fact that adult *E. superba* were not sampled quantitatively they have not been

included in the present analysis. It should also be noted that the Bongo net likely undersampled many juvenile stages of the larger copepods. Mesozooplankton in the Southern Ocean are usually sampled with $200 \mu\text{m}$ mesh nets, although a more suitable size is $100 \mu\text{m}$ mesh, and these will still undersample juveniles stages of some cyclopoid species. Therefore, abundances of many of the copepod species are probably underestimated. In spite of this limitation our multiannual sampling program offers a means of examining temporal and spatial variation in Antarctic zooplanktonic species.

There was considerable temporal variation in the mean abundance of the mesozooplankton assemblage between the years, ranging from 961 individuals per 1000 m^3 in 2004 to 15,627 individuals per 1000 m^3 in 2005. Chlorophyll *a* concentrations also varied between years, with the highest mean concentration recorded in 2005. The high biomass of plankton measured in 2005 likely relates to the condition of the sea ice cover during the previous spring. While ice breakout in November 2004 began at a similar time to other years (early to mid-November) and the breakout period was also similar (approximately two weeks), the sea ice coverage in November 2004 was relatively low, indicating substantial areas of thinner ice. This was particularly evident in the western part of the survey region (Fig. 3). An extended period of thinner ice cover would have increased the amount of irradiation reaching the surface waters and facilitated primary production, which, in turn, would promote good conditions for recruitment of *E. crystallorophias*. January 2007, which had the second highest concentrations of zooplankton and chlorophyll *a*, followed similar spring conditions (November 2006; Fig. 3) when the sea ice cover also tended to be thinner over large areas.

Spatially, abundances varied and there were no clear trends with longitude. Although total abundances tended to be higher near the Mertz Glacier, this observation was not robust from year to year, and there was no clear zonation apparent that could be readily linked to the zones described by Beans et al. (2008) for phytoplankton groups examined during January 2004. On a latitudinal gradient *E. crystallorophias* was the only taxon that showed a distinct pattern, where it was less abundant at the stations that were further from the coast. Data presented in Table 2 and Fig. 6b show that most taxonomic groups were present each year, with mainly differences in the ratios of taxa, and higher abundances in the case of 2005, rather than significant changes in taxonomic composition accounting for differences between the years. This is supported by our analysis of species associations (Fig. 7) that highlighted the majority of taxa forming one large cluster at 60% similarity.

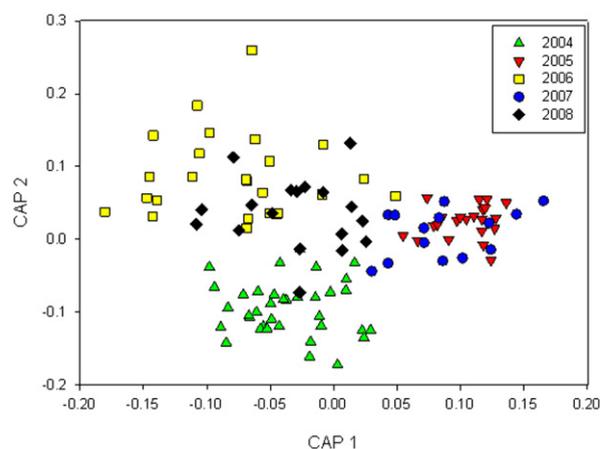


Fig. 8. Plot showing canonical analysis of principal coordinates for zooplankton-site relationships during the 5 summers between 2004 and 2008.

The sampling area covered ($\sim 33,000 \text{ km}^2$) is small compared to large-scale synoptic surveys such as BROKE ($873,000 \text{ km}^2$; Nicol et al., 2000) and BROKE-West ($>1.5 \text{ million km}^2$; Nicol et al., 2010), where differences in major water masses were largely responsible for major differences in zooplankton zonation. In the Dumont d'Urville Sea the sampling stations were under the influence of the Antarctic Coastal Current, and there is little evidence that warmer water from the north extruded onto the shelf (average temperatures $< -0.5 \text{ }^\circ\text{C}$). Therefore it was not surprising that only a small proportion of the distribution of zooplankton in this study was explained by water column characteristics (i.e. temperature and salinity). The tendency for some larger copepods to be more dominant near the Mertz Glacier, e.g. *R. gigas* and *M. gerlachei*, was possibly driven by differences in topography, water depth and proximity to the glacier. The distribution of *Pleuragramma antarcticum* larvae, examined during the same surveys, was clearly related to the presence of deep canyons over the shelf (Koubbi et al., 2011). In our study large numbers of unidentified polychaete larvae tended to have their main centres of distribution offshore from Dumont d'Urville Station where water depths were shallower. This is unsurprising if the larvae were predominantly offspring of benthic species, but this is not known. Overall, it is likely that variation in zooplankton distribution is largely related to a combination of localised features, such as the thickness and extent of sea ice cover, timing of sea ice break-out, the position and extent of the Mertz Polynya, local wind conditions and bathymetric features.

Undoubtedly there was a seasonal component to this survey that may also have influenced our observations of zooplankton distribution. The survey cruises were indeed not always conducted exactly over the same sampling period, although there was, at most, a 10-day lag between the start and end dates of surveys. This could be of particular concern for shorter-generation organisms such as appendicularians and some of the small cyclopid copepods, although these taxa were not included in our surveys. For larger calanoid copepods and euphausiids, which were the focus of this study, the difference in sampling times will influence growth more than abundance; i.e. development to later stages.

Previous assessments of latitudinal zonation patterns have indicated the presence of a neritic assemblage south of 67°S in Prydz Bay that was dominated by *E. crystallorophias* (Hosie, 1994), while Hunt et al. (2007) found a distinct division between the neritic and oceanic communities that appeared consistent between years. Intrusions of warmer waters moving south, or,

conversely, cool waters flowing northwards, can define the extent of the neritic and oceanic zones from year to year, but the presence of the communities associated with the water masses generally remains robust (e.g. Hosie et al., 2000). On the other hand longitudinal zonation is far less clear, particularly close to the coast where transport within the Antarctic Coastal Current results in species with widespread, often circum-Antarctic, distributions. In many regions it is probably meso-scale environmental features and conditions that determine relative abundances of species from year to year.

A significant event occurred in the Dumont d'Urville Sea in February 2010, when a large iceberg (designated B09B) collided with the Mertz Glacier Tongue (MGT), causing the calving of a very large (78 km long) iceberg and reducing the length of the tongue by 80% (Young et al., 2010). Initially, the recently-calved iceberg (designated C28) moved westwards across the Dumont d'Urville Sea and over the Adélie Depression, an area that is an important site of bottom water formation and is implicated in the world's deep ocean circulation. In the process of moving it disturbed the Mertz Polynya by dividing it into several smaller areas, thus diminishing the polynya's role as a sea ice 'factory'. Iceberg C28 has since split into several massive icebergs that have drifted across the edge of the shelf into deep water, and they are now well clear on the polynya. Iceberg B909 has remained grounded to the northeast of what remains of the MGT. It is likely that the future position of iceberg B909, and the altered geography of the MGT, will strongly influence ocean circulation in the Dumont d'Urville Sea, particularly bottom water formation. These physical changes are very likely to affect the stability of the water mass, circulation patterns and planktonic productivity in the region and we are fortunate to have the ICO²TA surveys to furnish a detailed picture of the 'before' scenario, prior to the calving of the massive iceberg. Changes to the planktonic communities will have flow-on effects up the food chain, thus making continuing biological surveys of the region both timely and important.

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