Assemblages of micronektonic fishes and invertebrates in a gradient of regional warming along the Western Antarctic Peninsula

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ABSTRACT

Micronektonic fishes and invertebrates were sampled with 32 midwater trawls at nine sites along the Western Antarctic Peninsula (WAP) in the austral fall (March–April) of 2010. Study sites were located within four hypothesized hydrographic regions: near Joinville Island in Region I, at Croker Passage, near Anvers Island, and near Renaud Island in Region II, within Marguerite Bay and the Marguerite Trough in Region III, and near Charcot Island in Region IV. A total of 62 taxa representing 12 taxonomic groups of pelagic invertebrates and 9 families of fish were captured, but assemblages were dominated by only a few species. The most numerically abundant taxa were the euphausiids, *Thysanoessa macrura*, *Euphausia superba*, and *E. crystallorophias*, combining to contribute nearly 79% of the total catch. Biomass dominants included *E. superba*, which contributed more than 44% of the total catch, the notothenioid *Pleuragramma antarctica*, and the salp, *Salpa thompsoni*. A comparison of total catches among sites revealed that the largest volumetric abundances and biomasses were captured at the Marguerite Bay site.

Cluster analysis of abundance data identified distinct multispecies assemblages at Joinville Island in Region I, Croker Passage in Region II, Marguerite Bay in Region III, and Charcot Island in Region IV. A fifth distinct assemblage included samples from sites near Anvers and Renaud Island in Region II, and from the Marguerite Trough in Region III. Assemblages at Joinville Island and Croker Passage were both dominated by *E. superba* and *S. thompsoni*, but hydrographic conditions at Joinville Island favored a neritic assemblage, underscored by substantial numbers of *P. antarctica*. The assemblage at Croker Passage was more oceanic in nature with major inputs from the myctophid, *Electrona antarctica* and the hyperiid amphipod, *Themisto gaudichaudii*. Marguerite Bay and Charcot Island were well-mixed assemblages with strong representation by both neritic and oceanic fauna. The mid-peninsula assemblage was oceanic in character, being overwhelmingly dominated by *Thysanoessa macrura* and *T. gaudichaudii*.

Pleuragramma antarctica were captured at five sites: Joinville Island, Croker Passage, Marguerite Bay, and the two sites near Charcot Island. They were completely absent at the two sites near Anvers Island, at Renaud Island, and in the Marguerite Trough. One fish was captured in Croker Passage. The majority of fish captured in Marguerite Bay were larger than 150 mm standard length (SL), with very few fish of smaller size present. If resident populations of *Pleuragramma* reproduce and recruit locally rather than being sustained by larval advection, those populations will be highly susceptible to local disappearance. This may be the causative factor behind the absence of *Pleuragramma* from the mid-peninsula region. Continued warming and subsequent sea ice reductions may not only cause *Pleuragramma* population collapses in the Marguerite Bay and Charcot Island regions, but may also change the character of the faunal assemblages along the WAP to those of an oceanic system.

1. Introduction

Three regions of the globe are undergoing recent rapid regional warming: Northwestern North America, the central Siberian Plateau, and the Antarctic Peninsula and Bellingshausen Sea (Vaughan et al., 2003). All three have exhibited significantly higher increases in mean

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annual temperature during the twentieth century than the global mean of 0.6 ± 0.2 °C (X ± SD) (Vaughan et al., 2003). On the Antarctic Peninsula, mean annual air temperatures have warmed at a rate of 3.7 ± 1.6 °C century^{-1} (Turner et al., 2005; Vaughan et al., 2003) and sea surface temperatures have increased by more than 1 °C (Meredith and King, 2005) over the past 50 years, resulting in decreased winter sea ice and a change in the timing of its advance and retreat in the WAP, specifically in the vicinity of Anvers Island (Ducklow et al., 2007). Reductions in sea ice could directly impact population dynamics of fauna which, like the silverfish *Pleuragramma antarctica* (Vacchi et al., 2004) and the krill *Euphausia superba* (Marr, 1962; Quetin and Ross, 1991) have life history stages that rely on the presence of sea ice (Clarke et al., 2007). Freshwater inputs from increased glacial meltwater may impact phytoplankton assemblages by shifting dominance from diatoms to smaller cryptophytes (Moline et al., 2004). This in turn may impact grazing efficiencies of zooplankton causing further shifts in faunal composition and distribution, e.g. the encroachment of salps and other oceanic fauna into regions previously dominated by neritic species (Atkinson et al., 2004).

Several unique physical properties of the Western Antarctic Peninsula (WAP) shelf make it one of the most productive and diverse regions in the Southern Ocean. The bathymetry of the Antarctic shelf, which is much deeper than in other oceanic systems (200–500 m vs. <200 m; Dinniman and Klinck, 2004), enhances faunal mixing by effectively removing a natural barrier to deeper dwelling oceanic fauna (Eastman,

1993). Another attribute, which is unique to the WAP shelf, is the absence of a slope front zone and its associated steep temperature and salinity gradients. In other Antarctic coastal regions, water column temperatures are uniformly cold (−2 °C), and oceanic species are excluded from the shelf (DeWitt, 1970; Donnelly et al., 2004). The WAP is the only region of the Antarctic where oceanic fishes, primarily lanternfishes (Myctophidae), are prevalent on the shelf despite their lack of biological antifreezes (Cullins et al., 2011). Hydrographic conditions on the WAP shelf are also influenced by the proximity of the Antarctic Circumpolar Current (ACC) to the shelf break. As the ACC flows northeasterly along the shelf break, it encounters deep cross-shelf troughs and depressions that allow intrusions of warm, nutrient-rich Circumpolar Deep Water (CDW) onto the shelf (Dinniman and Klinck, 2004; Klinck et al., 2004; Smith et al., 1999b) providing yet another mechanism for enhanced faunal mixing in that region.

Faunal assemblages are influenced by local circulation patterns in the WAP region. Large-scale circulation on the shelf is clockwise, driven by the northeasterly flowing ACC at the shelf break and the southward flowing coastal current (Hofmann et al., 1996). Smaller sub-gyres also exist along the WAP shelf (Fig. 1) which may limit advection and locally retain fauna, especially in inner shelf regions (Murphy et al., 2012; Piñones et al., 2011, 2013a). A primary objective of this study was to test the hypothesis that four distinct hydrographic regimes exist from north to south along the WAP continental shelf (Fig. 1) and that the
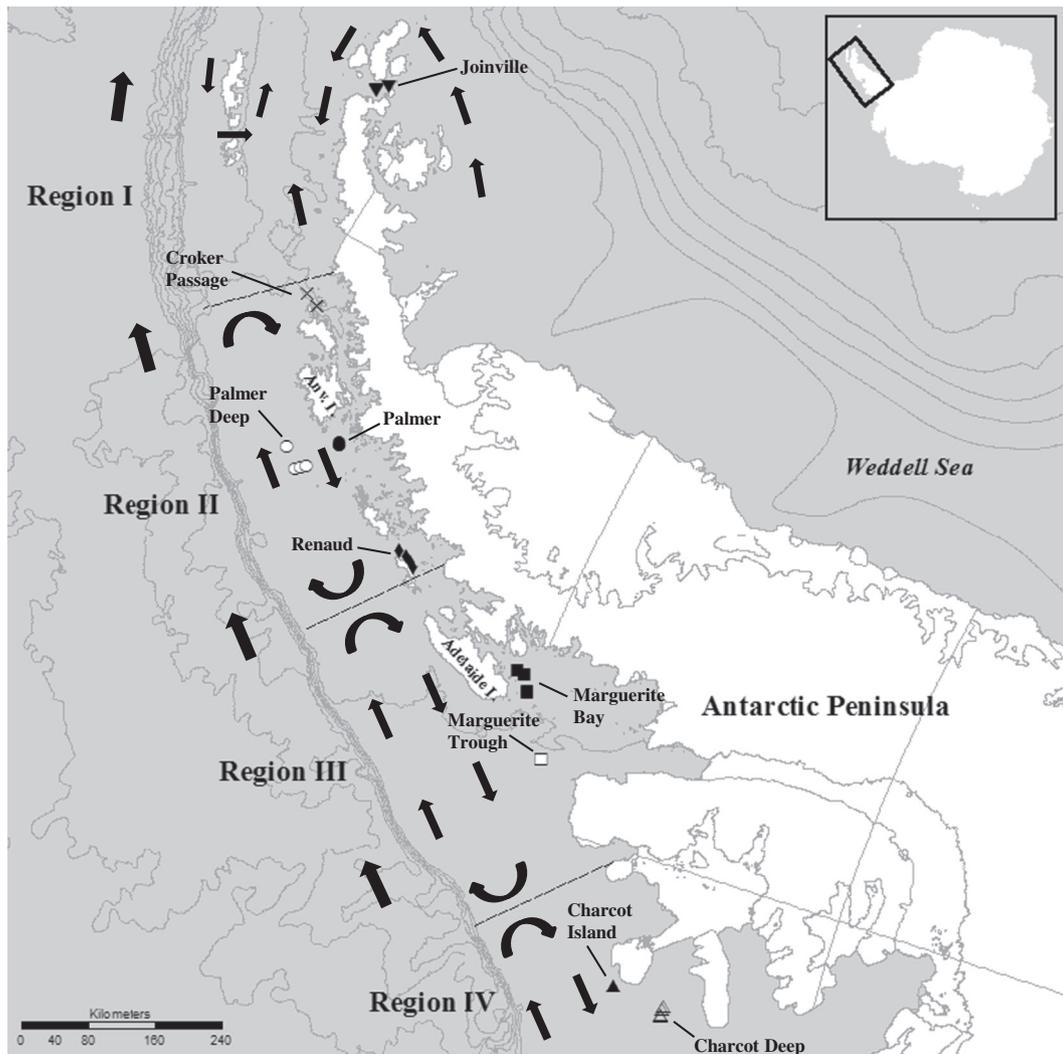

Fig. 1. Trawl, site, and region locations along the Western Antarctic Peninsula in 2010. Arrows indicate general water circulation patterns within the four regions (adapted from Hofmann et al., 1996; Piñones et al., 2011). Coastline and bathymetry data from the SCAR Antarctic Digital Database.

faunal assemblages within those regimes can be biologically discriminated. The regimes, designated as peninsular regions, were delineated as follows. Region I comprised the northern peninsula (Paulet-Joinville Island – Antarctic Sound), including the Bransfield Strait. It is strongly influenced by coldwater flow from the Weddell Sea and is roughly bounded on the south by Brabant Island; it contains no gyral circulation. Region II is the northern middle peninsula (Palmer-Renaud) community where regional warming has produced a marked decline in spring (November) sea ice (Ducklow et al., 2007; Stammerjohn et al., 2008a,b) and has exhibited change in its faunal composition over the last 25 years. Region III is the southern middle peninsula (Marguerite Bay) community including the Marguerite Bay system. It is defined by a gyral circulation bounded roughly on the north by Lavoisier Island and on the south by the southern lip of Lazarev Bay (on the southwestern flank of Alexander Island). Region IV is the southern peninsula (Charcot Island) community roughly defined by Lazarev Bay on the north and an as yet undefined boundary well south of Charcot Island. We believe that the gyral circulation in Region III reaches closure near Lazarev Bay, and a third gyral circulation is set up just north of Charcot Island, reaching closure further south (Piñones et al., 2011, 2013a,b). The four regions define the north-south extent of the project study area.

The four peninsular regions lie within a N-S gradient of recent rapid regional warming. Region I shows significant warming in mean annual temperature (3.4 ± 1.3 °C century^{-1}; Vaughan et al., 2003), but the cold waters originating in the Weddell Gyre (Stein, 1986; Thompson et al., 2009) keep water column temperatures in the Antarctic Sound at < 1 °C, more typical of those in the high Antarctic. Thus, Region I has the coldest water column despite being the furthest north. Warming is most pronounced in Region II (Vaughan et al., 2003), which shows the highest mean annual temperature rise (5.7 ± 2.0 °C century^{-1}) and shortest sea-ice season (Ducklow et al., 2007; Stammerjohn et al., 2008a; Vaughan et al., 2003). The meteorological station at Rothera Base, located at the mouth of Marguerite Bay in Region III shows a non-significant warming trend between 1979 and 1998 (Ducklow et al., 2007; Vaughan et al., 2003) accompanied by a decline in the number of ice days per year for the Marguerite Bay system (Ducklow et al., 2007; Stammerjohn et al., 2008a), though not as severe as the decline in the vicinity of Palmer Station in Region II. Data on annual temperature change in Region IV are lacking. However, the decline in sea ice days in the vicinity of Charcot Island is less than that exhibited by Marguerite Bay (Ducklow et al., 2007; Stammerjohn et al., 2008a), suggesting that regional warming effects are less pronounced as one moves south in the coastal region of the Antarctic Peninsula included in Regions III and IV.

In recent years, changes in diet composition have been observed in several predators from the vicinity of Anvers Island. Before the 1990s, *Pleuragramma antarctica* was a major component in south polar skua (*Catharacta lonnbergi*), kelp gull (*Larus dominicanus*), and Adélie penguin (*Pygoscelis adeliae*) diets (Neilson, 1983; Fraser, 1989, unpublished data; Fraser and Patterson, 1997). Recent studies show lower proportions of *P. antarctica* present in Adélie penguin diets (Fraser, unpublished data), suggesting that *Pleuragramma* numbers may have decreased in the Anvers Island region. Most nototheniods are benthic as adults, but *Pleuragramma* has a completely pelagic life history and is most commonly found below 100 m depth in the midwaters of the continental shelf and even deeper in coastal fjords (Cullins et al., 2011). Because the depth of the Antarctic continental shelf puts bottom fauna out of reach to many higher trophic level predators, *Pleuragramma* serve as a key prey source for several species of fishes (Eastman, 1985), flighted seabirds (Ainley et al., 1991; Fraser, 1989), penguins (Ainley, 2002; Bengtson et al., 1993; Cherel and Kooyman, 1998; Fraser and Patterson, 1997; Williams, 1995), and seals (Fuiman et al., 2002; La Mesa et al., 2004; Lowry et al., 1988; Oritsland, 1977), constituting an important component of the WAP ecosystem.

The present study examined the distribution of macrozooplanktonic/micronektonic faunal assemblages in the warming gradient along the WAP shelf, including taxonomic composition and distribution patterns in relation to local bathymetry and hydrography. Multivariate techniques were used to test for differences between the sites/regions sampled; identify unique multispecies assemblages; and quantify the contributions of both oceanic and neritic species to each assemblage. In this way, the abundance and biomass of *Pleuragramma* in the WAP shelf region were compared to the faunal assemblages with which they were associated, as well as densities recorded by previous studies.

2. Methods

2.1. Study sites and sample collection

Samples were collected at nine sites characterized by historic distributions of *P. antarctica* along the Western Antarctic Peninsula (Fig. 1) aboard the Research Vessel Ice Breaker (R.V.I.B.) *Nathaniel B. Palmer* during austral fall (March–April) 2010. Sites were located within four hypothesized hydrographic regions: Region I included the northernmost sampling site, which was located in Antarctic Sound near Joinville Island. Four sites were sampled in Region II. Those sites consisted of Croker Passage near the northern boundary of the region; Palmer located south of Anvers Island; Palmer Deep offshore of Anvers Island; and the pass to the east of Renaud Island. Sampling in Region III occurred at two sites in Marguerite Bay, one near the southern tip of Adelaide Island and one located mid-shelf within the Marguerite Trough. In Region IV, sampling occurred at two sites in the vicinity of Charcot Island, one nearshore (Charcot Island) and one offshore within a cross-shelf canyon (Charcot Deep).

Hydrographic data were collected at or near each site using a CTD. Characteristic water masses such as Antarctic Surface Water (AASW; temperature -1.8 to 1.0 °C, salinity 33.0 to 33.7), Winter Water (WW; temperature -1.5 °C, salinity 33.8 to 34.0), and modified Circumpolar Deep Water (mCDW; temperature 1.0 to 1.5 C, salinity 34.6 to 34.7) as defined by Smith et al. (1999b) were denoted on plots when present.

Macrozooplankton and micronekton were collected at each site with a 10-m^2 Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with six 3-mm mesh nets (Wiebe et al., 1976, 1985). A total of 32 trawls were successfully completed with seven conducted during the day and 25 at night (Table 1). For each trawl, the first net fished obliquely from surface to depth and each subsequent net fished a discrete depth layer up towards the surface. Most trawls fished to depths of 500 m and sampled depth strata of 0–50, 50–100, 100–200, 200–300, and 300–500 m. Three trawls fished to a depth of 1000 m and sampled depth strata of 0–100, 100–200, 200–300, 300–500, and 500–1000 m. One trawl fished to a depth of 331 m and sampled depth strata of 0–50, 50–100, 100–170, 170–225, and 225–331 m.

Specimens collected in the trawls were either preserved in a 10% buffered formalin solution or frozen and shipped to the laboratory for analysis. All micronektonic and macrozooplanktonic specimens were sorted, counted, identified to lowest possible taxon, and weighed (g wet mass). Standard length (mm SL) was measured for all fish specimens. After processing, samples were transferred to 50% isopropanol for long term storage.

2.2. Data analyses

Volumetric abundance and biomass values from each trawl were obtained by dividing the raw number or wet mass (WM) by the water volume filtered during each trawl (number or g WM $\times 10^4$ m^{-3}). Those standardized values were then used to compute the mean abundance and biomass of each individual taxon per site as well as the mean overall abundance and biomass for each site. Statistical comparisons between sites and regions were performed on the volumetric data (number or

Table 1
10-m^2 MOCNESS trawl data from nine sites sampled along the Western Antarctic Peninsula in 2010. Local time = GMT − 4 hours, TOD = Time of Day.

Region	Site	Trawl	Date (GMT)	Time (GMT)	TOD	Latitude (°S)	Longitude (°S)	Trawl Depth (m)	Bottom Depth (m)	Volume Filtered (m^3)
II	Palmer Deep	4	3/22/2010	18:58	Day	64 29.31	65 08.44	331	574	48,998
II	Palmer Deep	5	3/23/2010	5:54	Night	64 40.38	65 32.20	500	655	33,472
II	Palmer Deep	6	3/23/2010	8:12	Night	64 42.80	65 27.50	500	690	59,884
II	Palmer Deep	7	3/23/2010	11:00	Day	64 45.91	65 21.89	500	597	53,352
IV	Charcot Deep	11	3/29/2010	8:21	Night	70 25.13	76 16.36	500	813	65,327
IV	Charcot Deep	14	3/29/2010	18:57	Day	70 25.19	76 32.45	500	1259	65,327
IV	Charcot Deep	15	3/29/2010	22:05	Night	70 25.18	76 20.02	500	695	64,782
IV	Charcot Deep	16	3/30/2010	0:27	Night	70 25.19	76 34.43	500	1299	55,529
IV	Charcot Island	17	3/31/2010	2:07	Night	69 50.83	76 00.15	500	757	55,529
IV	Charcot Island	18	3/31/2010	4:28	Night	69 50.85	76 00.81	500	787	60,428
III	Marguerite Bay	19	4/3/2010	12:07	Day	67 46.73	68 06.06	500	860	121,390
III	Marguerite Bay	20	4/5/2010	22:43	Night	67 52.58	68 08.47	500	506	137,647
III	Marguerite Bay	21	4/6/2010	4:27	Night	67 52.42	68 08.13	500	685	124,111
III	Marguerite Trough	24	4/8/2010	0:33	Night	68 21.94	70 11.83	500	826	147,439
III	Marguerite Bay	25	4/8/2010	18:07	Day	67 52.54	68 08.26	500	680	130,643
III	Marguerite Bay	27	4/11/2010	4:32	Night	67 58.53	68 33.39	500	800	120,845
III	Marguerite Bay	28	4/11/2010	22:25	Night	67 58.50	68 33.33	500	564	153,503
II	Renaud	30	4/14/2010	3:22	Night	66 05.10	66 23.15	500	745	60,428
II	Renaud	31	4/14/2010	5:56	Night	66 05.10	66 22.86	500	>500	57,479
II	Renaud	34	4/15/2010	5:44	Night	66 17.93	66 38.93	500	500	135,056
II	Renaud	35	4/15/2010	10:41	Night	66 14.58	66 33.00	500	911	67,504
II	Renaud	36	4/16/2010	1:29	Night	66 10.80	66 27.24	500	657	98,527
II	Palmer	37	4/17/2010	21:39	Night	64 58.91	64 30.96	500	961	78,390
II	Palmer	38	4/18/2010	1:18	Night	64 59.97	64 33.94	1000	>1000	130,098
II	Palmer	39	4/18/2010	6:32	Night	65 00.03	64 33.83	500	899	107,238
II	Palmer	40	4/18/2010	11:15	Day	64 59.82	64 33.48	1000	>1000	127,377
II	Croker Passage	41	4/23/2010	13:30	Day	63 56.44	61 39.40	500	1174	125,200
II	Croker Passage	43	4/24/2010	2:33	Night	64 05.70	61 48.11	500	1040	63,694
II	Croker Passage	44	4/24/2010	6:21	Night	64 05.72	61 47.88	1000	1056	124,655
I	Joinville	45	4/25/2010	23:04	Night	63 25.11	56 42.48	500	781	120,301
I	Joinville	46	4/26/2010	3:36	Night	63 30.97	56 29.79	500	753	122,476
I	Joinville	47	4/26/2010	7:41	Night	63 25.59	56 43.70	500	935	62,059

g WM × 10^4 m^{-3}) using generalized linear mixed models in SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).

Vertical distributions for four common invertebrate species and two common fish species were compiled from nets that fished within the following depth strata: 0–50, 50–100, 100–200, 200–300, 300–500, and 500–1000 m. Mean volumetric abundance was calculated for each depth stratum and those values were used to determine the vertical range for each species. The peak range for each species was chosen as the stratum with the highest mean volumetric abundance for daytime and nighttime trawls. There were a total of seven daytime trawls and 25 nighttime trawls completed during the cruise. It should be noted that total numbers of individuals captured during daytime trawls were often substantially lower than total numbers captured during nighttime trawls, suggesting daytime net avoidance. A day–night disparity in total catch is a common shortcoming of net-based studies and may result in an underestimate of daytime abundance; however, day–night shifts in population maxima remain accurate. Because so little data are available on vertical distribution patterns for the species addressed in the present study, results from daytime trawls were included and contrasted with nighttime abundances.

Macrozooplankton/micronekton assemblage structure was analyzed by multivariate techniques using the PRIMER v6 software package (Clarke and Gorley, 2006) with PERMANOVA + v1.0.5 (Anderson et al., 2008). Volumetric abundance and biomass data were log (x+1) transformed to allow for a more even contribution from both common and rare taxa in each analysis (Clarke, 1993). Transformed data were then used to calculate Bray-Curtis similarity matrices, which were subsequently used in a one-way PERMANOVA (Anderson, 2001), with a maximum of 9999 permutations, to test for differences in assemblages present at the nine sites and in the four regions. Hierarchical cluster analysis dendrograms and MDS ordination plots were also generated from the similarity matrices. The SIMPER (analysis of similarity percentages) procedure was used to identify those taxa contributing most to the similarities within each resultant cluster group.

Mean integrated abundance (number m^{-2}) and biomass (g WM m^{-2}) for the 0–200 m stratum were determined by first selecting those nets from each trawl that sampled within 0–200 m. Integrated values were then calculated by dividing the total number or wet mass from each net by the water volume filtered by that net, multiplied by the vertical range, in meters, trawled by that net, and summed for each trawl. Mean integrated abundance and biomass were calculated for the 0–200 m stratum at each site. Because there were so few daytime trawls, those data were omitted from this analysis.

3. Results

3.1. Hydrography

Water column properties varied markedly among the sites (Fig. 2). At Joinville Island, Croker Passage, and Palmer, the water column was nearly isothermal and isohaline from the surface to 500 m depth; however, temperature and salinity ranges varied among the three sites. Joinville Island had the coldest water column with temperatures ranging from only −1.8 to −1.4 °C and salinities from 34.3 to 34.4. Salinity profiles were similar at Croker Passage and Palmer, ranging from approximately 33.8 at the surface to 34.6 at depth, but temperatures at Palmer were substantially warmer (0.6 to 1.0 °C) than those at Croker Passage (−0.5 to 0.1 °C). In addition, mCDW was present at depths below 375 m at Palmer.

The water column was stratified at the remaining six sites. At Palmer Deep and Marguerite Bay, a temperature minimum occurred between 90 and 200 m with coldest temperatures recorded at approximately 140 m. A similar temperature minimum occurred at Renaud Island and Marguerite Trough, but was slightly shallower and instead extended from 50 to either 150 or 200 m. At Charcot Island and Charcot Deep, the coldest temperatures occurred near the surface (<100 m) and were associated with AASW. WW was also present between 100 and 200 m at those two sites. Modified CDW was present at all six stratified sites and
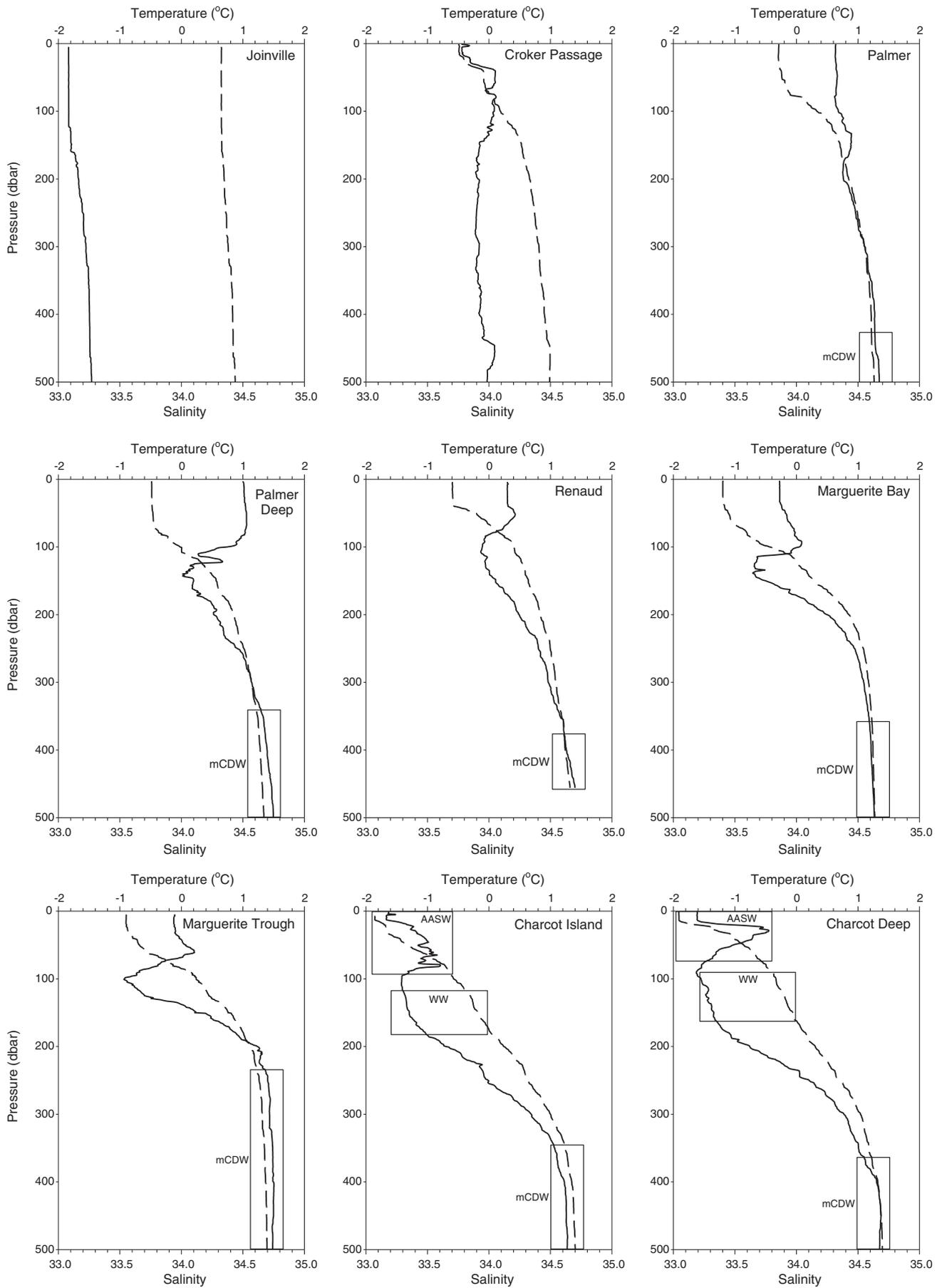
Fig. 2. Temperature (solid line) and salinity (dashed line) to 500 m depth at each site during the 2010 cruise. Boxes denote temperature and salinity ranges for AASW, WW, and mCDW.

first appeared between depths of 340 to 375 m at most sites. The only exception occurred in the Marguerite Trough where mCDW was detected at the much shallower depth of 230 m.

3.2. Taxonomic composition

A total of 62 taxa representing 12 taxonomic groups of pelagic invertebrates and 9 families of fish were collected during this study (Table 2). The gammarid amphipods were the most diverse taxonomic group overall with eight taxa, followed by the hyperiid amphipods and the nototheniid fish, each with six taxa. Diversity was greatest at the Croker Passage and Marguerite Bay sites, each with 39 taxa. Gammarids were also among the most diverse taxonomic groups at the majority of study sites, the exceptions being at the Palmer and Palmer Deep sites where numbers of euphausiid, hyperiid, and/or mysid taxa were greater. The myctophids were the most diverse fish family at all sites except Joinville Island, Charcot Island, and Charcot Deep. At Joinville Island, no myctophids were collected and the notothenioid family Channichthyidae was most diverse. At Charcot Island, myctophids and nototheniids were equally diverse whereas nototheniids were the most diverse fish family at Charcot Deep.

The most numerically abundant taxa included the euphausiids, *Thysanoessa macrura*, *Euphausia superba*, and *E. crystallorophias*, combining to contribute nearly 79% of the total catch. Those three species were also the most abundant taxa at all sites, except Croker Passage where the tunicate, *Salpa thompsoni*, was the numerical dominant. Among the fishes, the myctophid, *Electrona antarctica*, was the dominant fish species at the Croker Passage, Palmer, Renaud Island, Marguerite Trough, and Charcot Island sites. Another myctophid, *Protomyctophum bolini*, was dominant at Palmer Deep. Two nototheniids were numerical dominants at the remaining sites; *Pleuragramma antarctica* at Joinville Island and Marguerite Bay and *Trematomus* sp. at Charcot Deep.

With respect to biomass, *E. superba* was the dominant species, contributing more than 44% of the total catch. Other dominant biomass contributors included *P. antarctica* and *S. thompsoni*, which supplied 16% and 11% of the catch, respectively. Biomass dominants at each of the sites were similar to numerical dominants with the exception of Charcot Island, where *P. antarctica* contributed the most biomass overall. Among the fishes, *P. antarctica* was also the dominant biomass contributor at Joinville Island and Marguerite Bay. Other dominant fish taxa included the myctophids at five sites: *E. antarctica* at Palmer, Marguerite Trough, and Charcot Deep, *P. bolini* at Palmer Deep, and *Gymnoscopelus nicholsi* at Renaud Island. The paralepidid, *Notolepis coatsi*, contributed the most fish biomass at Croker Passage.

3.3. Vertical distributions

Discrete depth distributions for four common invertebrate and two common fish species are shown in Fig. 3. Four species, *E. superba*, *T. macrura*, *S. thompsoni*, and *E. antarctica*, were found throughout the sampled water column (surface to 1000 m). The remaining common species, *E. crystallorophias* and *P. antarctica*, were only present from the surface to 500 m. Peak daytime ranges were similar between the two fish species (300–500 m) but *E. antarctica* had nighttime peaks at 100–200 m as well as 300–500 m while *P. antarctica* was concentrated between 100–300 m. The euphausiids, *E. crystallorophias* and *E. superba* were most abundant at the surface (0–50 m) at night but both descended during the day with peak abundances of *E. crystallorophias* at 200–300 m and *E. superba* at 50–100 m. In contrast, the majority of *T. macrura* ascended from 200–300 m at night to 50–100 m in the day. The salp, *S. thompsoni*, behaved similarly, with the majority ascending from a peak nighttime distribution of 500–1000 m to the surface during the day.

3.4. Site comparisons

A comparison of total catches among sites showed that the largest volumetric abundances were captured at Marguerite Bay where the mean exceeded 1000 individuals $10^4 \, m^{-3}$ ($F_{8, 23} = 3.15$, $P = 0.01$; Fig. 4). At the Marguerite Trough site, mean abundances were an order of magnitude lower with only 146 individuals $10^4 \, m^{-3}$ captured. Although only one trawl was completed at Marguerite Trough, the total volume filtered was similar to that of Palmer Deep (147,439 vs. 195,705 m^3) where the mean abundance of 626 individuals $10^4 \, m^{-3}$ was significantly higher. Mean abundances among the remaining sites were similar, ranging from approximately 300 to 800 individuals $10^4 \, m^{-3}$. Mean volumetric biomass was also highest at the Marguerite Bay site (530 g WM $10^4 \, m^{-3}$), but the lowest biomasses were captured at the Marguerite Trough, Palmer, and Palmer Deep sites where mean values ranged from 17 to 41 g WM $10^4 \, m^{-3}$ ($F_{8, 23} = 7.82$, $P < 0.01$). Renaud Island had slightly higher mean biomass (73 g WM $10^4 \, m^{-3}$) and the remaining sites, Joinville Island, Croker Passage, Charcot Island and Charcot Deep, all had means near or slightly higher than 200 g WM $10^4 \, m^{-3}$.

Comparisons of total catches of dominant invertebrates and fish revealed that there were differences in abundance and biomass among sites for most of those taxa (Fig. 5). *E. superba* was present at all sites but was most prevalent at Joinville Island, Marguerite Bay, and Charcot Deep where mean volumetric abundances (ranging from 235 to 496 individuals $10^4 \, m^{-3}$; $F_{8, 23} = 11.61$, $P < 0.01$) and biomasses (ranging from 140 to 355 g WM $10^4 \, m^{-3}$; $F_{8, 23} = 9.59$, $P < 0.01$) were similar. Abundance and biomass of *E. superba* was one to two orders of magnitude lower at the remaining sites. The greatest quantities of *E. crystallorophias* were captured at the Marguerite Bay and Charcot Island sites where means of 507 individuals $10^4 \, m^{-3}$ and 172 individuals $10^4 \, m^{-3}$, respectively, were significantly higher than measures at the other sites ($F_{8, 23} = 21.17$, $P < 0.01$). The greatest biomasses of *E. crystallorophias* were also captured at those sites, but biomass was significantly higher at Marguerite Bay than at Charcot Island (102 vs. 29 g WM $10^4 \, m^{-3}$; $F_{8, 23} = 11.51$, $P < 0.01$). Very few *E. crystallorophias* were captured at Croker Passage, Palmer, and Renaud Island, while none were captured at Palmer Deep. Total catches of *T. macrura* were highest at the Palmer, Palmer Deep, and Renaud Island sites where mean abundances exceeded 386 individuals $10^4 \, m^{-3}$ ($F_{8, 23} = 12.02$, $P < 0.01$) and mean biomasses ranged from 14 to 23 g WM $10^4 \, m^{-3}$ ($F_{8, 23} = 7.45$, $P < 0.01$). The salp, *S. thompsoni*, was captured in greatest quantities at Croker Passage (203 individuals $10^4 \, m^{-3}$; $F_{8, 23} = 11.00$, $P < 0.01$; 145 g WM $10^4 \, m^{-3}$; $F_{8, 23} = 18.19$, $P < 0.01$), in moderate quantities at Joinville Island, and in relatively low quantities at the Palmer, Palmer Deep, Marguerite Trough, and Charcot Island sites. No *S. thompsoni* were captured at Renaud Island, Marguerite Bay, and Charcot Deep.

The lanternfish, *E. antarctica*, was present at all sites except Joinville Island but the largest catches were at the Charcot Island site where the means were 5 individuals $10^4 \, m^{-3}$ ($F_{8, 5.70} = 21.58$, $P < 0.01$) and 36 g WM $10^4 \, m^{-3}$ ($F_{8, 23} = 14.98$, $P < 0.01$). As mentioned earlier, *P. antarctica* was absent from the Palmer, Palmer Deep, Renaud Island, and Marguerite Trough sites. The largest *P. antarctica* abundances, with means between 3 and 4 individuals $10^4 \, m^{-3}$, were captured at Joinville Island and Charcot Island ($F_{8, 23} = 8.50$, $P < 0.01$); however, average biomass was significantly higher at the Charcot Island site (163 vs. 44 g WM $10^4 \, m^{-3}$; $F_{8, 23} = 3.79$, $P < 0.01$). No differences in abundance or biomass among sites were detected for other prevalent fishes such as *G. nicholsi*, *G. braueri*, *N. coatsi* or *P. bolini*.

3.5. Regional comparisons

Mean overall volumetric abundances were similar in the four regions and ranged from 334 to 1029 individuals $10^4 \, m^{-3}$ ($F_{3,28} = 2.90$, $P = 0.053$); however, mean overall volumetric biomass was significantly higher in Regions I, III and IV where catches exceeded 200 g WM

Table 2

Mean volumetric abundance (number individuals 10^4 m^{-3}) and biomass (g WM 10^4 m^{-3}) of each taxon at each site in 2010. n = number of trawls, VF = total volume filtered (m^3), SD = standard deviation.

Group	Taxa	Joinville (n=3), VF = 304,836				Croker Passage (n=3), VF = 313,549			
		# 10^4m^{-3}	SD	gWM 10^4m^{-3}	SD	# 10^4m^{-3}	SD	gWM 10^4m^{-3}	SD
Amphipoda	*Cyphocarus richardi*	0.03	0.05	0.006	0.010	8.02	6.98	4.250	3.786
Gammaridea	*Epimeria sp.*	0.06	0.10	0.002	0.003				
	Epimeriella macronyx	1.41	0.46	0.173	0.043	0.05	0.09	0.026	0.045
	Eusiroides stenopleura	0.03	0.05	0.011	0.019				
	Eusirus microps	0.57	0.29	0.367	0.185	0.03	0.05	0.029	0.051
	Eusirus properdentatus	0.14	0.05	0.325	0.194	1.17	1.30	1.267	1.688
	Orchomene plebs	13.93	3.78	6.945	2.219	1.71	0.37	0.215	0.090
	Parandania boecki					0.11	0.19	0.153	0.265
Amphipoda	*Cyllopus lucasii*	0.11	0.10	0.032	0.044	1.40	0.92	0.153	0.094
Hyperiidea	*Hyperia macrocephala*	0.08	0.08	0.049	0.048	0.08	0.08	0.003	0.003
	Hyperiella macronyx								
	Primno macropa	0.03	0.05	0.001	0.002	0.08	0.14	0.007	0.013
	Themisto gaudichaudi					18.62	11.40	1.627	1.087
	Vibilia stebbingi	0.03	0.05	0.002	0.003				
Decapoda	*Notocrangon antarcticus*								
	Pasiphea scotiae					0.05	0.09	0.024	0.041
Euphausiacea	*Euphausia crystallorophias*	14.76	6.59	2.461	0.987	0.48	0.56	0.060	0.058
	Euphausia superba	337.73	344.99	140.404	146.705	26.72	24.83	13.396	16.720
	Euphausia triacantha					0.29	0.25	0.042	0.038
	Thysanoessa macrura	34.57	22.98	1.153	0.201	36.96	32.86	1.357	1.149
Mysida	*Antarctomysis maxima*	19.96	5.06	8.452	2.176				
	Antarctomysis ohlinii	2.84	1.56	1.297	0.579	0.24	0.29	0.233	0.231
	Boreomysis sp.	0.03	0.05	0.002	0.003	0.03	0.05	0.002	0.004
	Dactylamblyops hodgsoni	0.54	0.38	0.039	0.032	0.13	0.23	0.021	0.036
	Mysidetes sp.	3.86	2.09	0.333	0.206	0.05	0.09	0.008	0.014
Cephalopoda	*Alluroteuthis antarcticus*					0.14	0.24	0.360	0.624
	Galliteuthis glacialis					0.05	0.09	0.268	0.465
Gastropoda	*Clione limacina*	0.05	0.09	0.001	0.002				
	Spongiobranchea australis					0.05	0.09	0.003	0.005
Polychaeta	*Tomopteris carpenteri*	0.11	0.13	0.106	0.150	0.05	0.09	0.030	0.053
Hydrozoa	*Calycopsis borchgrevinki*	0.19	0.05	0.393	0.190	0.21	0.12	0.319	0.218
	Crossota brunnea								
	Diphyes antarctica	0.60	0.16	0.150	0.036	0.13	0.05	0.064	0.023
	Leptomedusa	0.14	0.17	0.049	0.047	0.05	0.05	0.042	0.039
Scyphozoa	*Atolla wyvillei*								
	Periphylla periphylla					0.05	0.09	0.271	0.469
	Stygiomedusa gigantea[a]					0.03	0.05		
Chaetognatha	Chaetognath	1.12	0.30	0.088	0.056	0.35	0.61	0.015	0.026
	Pseudosagitta gazellae	2.32	0.67	0.704	0.200	0.46	0.39	0.165	0.027
Tunicata	*Salpa thompsoni*	40.02	0.75	23.940	3.073	203.25	96.35	145.350	55.022
Fish Family									
Bathydraconidae	*Gerlachea australis*								
Bathylagidae	*Bathylagus antarcticus*	0.03	0.05	0.010	0.017				
Channichthyidae	*Chionodraco rastrospinosus*	0.52	0.29	4.313	2.702	0.58	0.55	1.492	1.293
	Cryodraco antarcticus	0.27	0.33	1.216	1.200	0.11	0.09	0.475	0.438
	Dacodraco hunteri	0.03	0.05	0.155	0.269				
	Pagetopsis macropterus	0.27	0.32	1.175	0.582				
Gempylidae	*Paradiplospinus gracilis*								
Liparidae	*Edentoliparis terraenovae*								
	Paraliparis antarcticus	0.14	0.17	0.219	0.311				
Myctophidae	*Electrona antarctica*					1.10	0.41	8.457	4.153
	Electrona carlsbergi								
	Gymnoscopelus braueri					0.05	0.09	0.849	1.471
	Gymnoscopelus nicholsi					0.16	0.27	6.351	11.000
	Protomyctophum bolini								
Nototheniidae	*Aethotaxis mitopteryx*								
	Lepidonotothen larseni	0.05	0.09	9.131	15.815				
	Lepidonotothen squamifrons								
	Pagothenia borchgrevinki					0.03	0.05	0.092	0.160
	Pleuragramma antarctica	3.72	2.76	43.563	29.874	0.03	0.05	0.360	0.624
	Trematomus sp.								
Paralepididae	*Notolepis coatsi*					0.26	0.09	10.014	16.757
Zoarcidae	*Melanostigma gelatinosum*								
	Mean Total	480.27		247.265		303.37		197.855	
	Number of Taxa	35				39			

[a] No weights were recorded for these specimens.

Table 2 (continued)

Group	Taxa	Palmer (n=4), VF = 443,103				Palmer Deep (n=4), VF = 195,705			
		# $10^4 m^{-3}$	SD	gWM $10^4 m^{-3}$	SD	# $10^4 m^{-3}$	SD	gWM $10^4 m^{-3}$	SD
Amphipoda Gammaridea	*Cyphocarus richardi*	1.21	0.76	0.378	0.243				
	Epimeria sp.								
	Epimeriella macronyx								
	Eusiroides stenopleura								
	Eusirus microps								
	Eusirus properdentatus								
	Orchomene plebs	0.07	0.05	0.006	0.005	0.78	0.92	0.035	0.044
	Parandania boecki								
Amphipoda Hyperiidea	*Cyllopus lucasii*	0.10	0.13	0.009	0.012	0.12	0.14	0.014	0.017
	Hyperia macrocephala								
	Hyperiella macronyx								
	Primno macropa	0.86	0.73	0.062	0.054	0.26	0.07	0.011	0.010
	Themisto gaudichaudi	22.30	19.06	1.199	1.035	62.55	36.41	3.240	1.895
	Vibilia stebbingi								
Decapoda	*Notocrangon antarcticus*								
	Pasiphea scotiae	0.15	0.13	0.475	0.568				
Euphausiacea	*Euphausia crystallorophias*	0.08	0.16	0.006	0.011				
	Euphausia superba	13.00	10.21	10.927	9.306	1.93	1.63	1.821	1.606
	Euphausia triacantha	1.33	0.39	0.193	0.059	4.37	0.33	0.723	0.090
	Thysanoessa macrura	386.37	223.60	13.885	7.894	523.09	509.68	22.607	22.222
Mysida	*Antarctomysis maxima*								
	Antarctomysis ohlinii	0.02	0.04	0.000	0.000				
	Boreomysis sp.	21.55	13.78	1.227	0.787	1.50	1.63	0.078	0.084
	Dactylamblyops hodgsoni	0.65	1.00	0.035	0.047				
	Mysidetes sp.								
Cephalopoda	*Alluroteuthis antarcticus*								
	Galliteuthis glacialis								
Gastropoda	*Clione limacina*	0.09	0.11	0.007	0.009				
	Spongiobranchea australis	0.68	0.47	0.035	0.024	0.14	0.19	0.009	0.010
Polychaeta	*Tomopteris carpenteri*	0.18	0.12	0.058	0.025	0.13	0.16	0.085	0.106
Hydrozoa	*Calycopsis borchgrevinki*	0.16	0.13	0.221	0.224	0.58	0.41	0.277	0.270
	Crossota brunnea					0.07	0.15	0.002	0.004
	Diphyes antarctica	0.02	0.04	0.002	0.004				
	Leptomedusa								
Scyphozoa	*Atolla wyvillei*								
	Periphylla periphylla								
	Stygiomedusa gigantea[a]	0.06	0.08						
Chaetognatha	Chaetognath	4.34	4.11	0.091	0.072	17.05	12.85	0.705	0.627
	Pseudosagitta gazellae	4.15	3.71	0.758	0.588	8.87	3.36	2.013	1.366
Tunicata	*Salpa thompsoni*	0.26	0.51	0.012	0.023	3.82	6.82	0.478	0.557
Fish Family									
Bathydraconidae	*Gerlachea australis*								
Bathylagidae	*Bathylagus antarcticus*	0.16	0.18	0.036	0.056				
Channichthyidae	*Chionodraco rastrospinosus*								
	Cryodraco antarcticus								
	Dacodraco hunteri								
	Pagetopsis macropterus								
Gempylidae	*Paradiplospinus gracilis*	0.02	0.05	2.271	4.541				
Liparidae	*Edentoliparis terraenovae*								
	Paraliparis antarcticus								
Myctophidae	*Electrona antarctica*	1.63	0.75	7.776	4.219	0.24	0.32	0.336	0.426
	Electrona carlsbergi								
	Gymnoscopelus braueri	0.10	0.19	0.706	1.411				
	Gymnoscopelus nicholsi								
	Protomyctophum bolini					0.27	0.32	0.413	0.481
Nototheniidae	*Aethotaxis mitopteryx*								
	Lepidonotothen larseni								
	Lepidonotothen squamifrons								
	Pagothenia borchgrevinki								
	Pleuragramma antarctica								
	Trematomus sp.								
Paralepididae	*Notolepis coatsi*	0.43	0.31	0.469	0.573	0.13	0.16	0.082	0.132
Zoarcidae	*Melanostigma gelatinosum*								
	Mean Total	459.96		40.844		625.91		32.931	
	Number of Taxa	27				18			

[a] No weights were recorded for these specimens.

Table 2 (continued)

Group	Taxa	Renaud (n=5), VF = 418,995				Marguerite Bay (n=6), VF = 788,139			
		# $10^4 m^{-3}$	SD	gWM $10^4 m^{-3}$	SD	# $10^4 m^{-3}$	SD	gWM $10^4 m^{-3}$	SD
Amphipoda	*Cyphocarus richardi*	5.50	2.93	1.037	0.308	0.02	0.04	0.002	0.004
Gammaridea	*Epimeria sp.*								
	Epimeriella macronyx	0.03	0.07	0.003	0.006	5.62	1.34	1.238	0.260
	Eusiroides stenopleura	0.00	0.00	0.000	0.000				
	Eusirus microps	0.01	0.03	0.001	0.003	0.17	0.19	0.055	0.067
	Eusirus properdentatus	0.08	0.08	0.033	0.072	0.91	0.61	0.052	0.044
	Orchomene plebs	0.81	0.51	0.215	0.179	3.26	1.13	1.049	0.400
	Parandania boecki	0.02	0.05	0.001	0.001				
Amphipoda	*Cyllopus lucasii*	0.05	0.07	0.011	0.019	0.09	0.09	0.011	0.011
Hyperiidea	*Hyperia macrocephala*					0.01	0.03	0.001	0.002
	Hyperiella macronyx								
	Primno macropa	0.82	0.36	0.045	0.019	0.13	0.16	0.005	0.006
	Themisto gaudichaudi	211.00	92.47	11.905	5.298	34.60	23.44	2.209	1.478
	Vibilia stebbingi								
Decapoda	*Notocrangon antarcticus*	0.01	0.03	0.042	0.095	0.01	0.03	0.064	0.156
	Pasiphea scotiae								
Euphausiacea	*Euphausia crystallorophias*	3.26	1.66	0.368	0.215	507.46	305.54	102.438	65.746
	Euphausia superba	14.26	16.93	11.306	14.340	495.95	632.68	355.393	437.595
	Euphausia triacantha	23.70	31.01	4.826	6.367	0.28	0.27	0.047	0.047
	Thysanoessa macrura	548.24	287.18	20.912	12.158	71.11	58.06	4.861	4.194
Mysida	*Antarctomysis maxima*	0.31	0.42	0.005	0.006	0.90	0.66	0.030	0.019
	Antarctomysis ohlinii					37.04	28.45	6.840	3.685
	Boreomysis sp.	21.60	21.07	1.269	1.224	10.07	4.28	0.609	0.306
	Dactylamblyops hodgsoni	0.13	0.22	0.006	0.012	0.05	0.04	0.003	0.003
	Mysidetes sp.					0.01	0.03	0.001	0.001
Cephalopoda	*Alluroteuthis antarcticus*	0.02	0.05	0.584	1.306	0.01	0.03	0.004	0.010
	Galliteuthis glacialis								
Gastropoda	*Clione limacina*	0.13	0.14	0.013	0.016	2.19	1.65	0.177	0.137
	Spongiobranchea australis	0.85	1.01	0.044	0.050	0.31	0.18	0.015	0.009
Polychaeta	*Tomopteris carpenteri*	0.17	0.20	0.040	0.060	0.05	0.08	0.012	0.021
Hydrozoa	*Calycopsis borchgrevinki*	0.21	0.25	0.171	0.225	0.02	0.04	0.025	0.039
	Crossota brunnea								
	Diphyes antarctica								
	Leptomedusa					0.26	0.48	0.279	0.642
Scyphozoa	*Atolla wyvillei*					0.01	0.03	0.874	2.142
	Periphylla periphylla					0.04	0.07	0.029	0.056
	Stygiomedusa gigantea[a]					0.03	0.04		
Chaetognatha	Chaetognath	3.44	3.01	0.107	0.096	0.36	0.35	0.017	0.022
	Pseudosagitta gazellae	6.36	0.87	0.722	0.122	1.08	0.24	0.172	0.060
Tunicata	*Salpa thompsoni*								
Fish Family									
Bathydraconidae	*Gerlachea australis*								
Bathylagidae	*Bathylagus antarcticus*					0.12	0.19	0.167	0.406
Channichthyidae	*Chionodraco rastrospinosus*								
	Cryodraco antarcticus								
	Dacodraco hunteri								
	Pagetopsis macropterus					0.01	0.03	0.001	0.001
Gempylidae	*Paradiplospinus gracilis*								
Liparidae	*Edentoliparis terraenovae*	0.04	0.10	0.040	0.089	1.11	0.42	0.383	0.197
	Paraliparis antarcticus								
Myctophidae	*Electrona antarctica*	0.75	0.47	2.746	3.386	0.90	0.56	4.044	2.551
	Electrona carlsbergi	0.03	0.07	0.207	0.462				
	Gymnoscopelus braueri	0.03	0.08	1.249	2.794	0.05	0.09	0.512	0.982
	Gymnoscopelus nicholsi	0.26	0.37	9.970	13.146	0.04	0.04	1.661	2.270
	Protomyctophum bolini								
Nototheniidae	*Aethotaxis mitopteryx*								
	Lepidonotothen larseni								
	Lepidonotothen squamifrons	0.01	0.03	0.004	0.008				
	Pagothenia borchgrevinki								
	Pleuragramma antarctica					1.18	0.68	46.103	29.958
	Trematomus sp.					1.00	1.04	0.029	0.030
Paralepididae	*Notolepis coatsi*	0.18	0.13	0.026	0.024				
Zoarcidae	*Melanostigma gelatinosum*	0.72	0.78	5.244	6.569	0.01	0.03	0.244	0.599
	Mean Total	843.04		73.153		1176.48		529.657	
	Number of Taxa	33				39			

[a] No weights were recorded for these specimens.

Table 2 (continued)

Group	Taxa	Marguerite Trough ($n=1$), VF = 147,439				Charcot Island ($n=2$), VF = 115,957			
		# 10^4m^{-3}	SD	gWM 10^4m^{-3}	SD	# 10^4m^{-3}	SD	gWM 10^4m^{-3}	SD
Amphipoda	*Cyphocarus richardi*	1.02		0.202					
Gammaridea	*Epimeria sp.*								
	Epimeriella macronyx	0.14		0.030		0.26	0.14	0.025	0.014
	Eusiroides stenopleura								
	Eusirus microps	0.07		0.053		0.79	0.41	0.139	0.070
	Eusirus properdentatus	0.07		0.044		0.17	0.01	0.067	0.026
	Orchomene plebs	1.09		0.329		1.55	0.15	0.359	0.092
	Parandania boecki	0.20		0.011					
Amphipoda	*Cyllopus lucasii*	0.14		0.014		0.18	0.25	0.011	0.015
Hyperiidea	*Hyperia macrocephala*								
	Hyperiella macronyx								
	Primno macropa	0.41		0.014		0.08	0.12	0.003	0.004
	Themisto gaudichaudi	27.20		1.679		5.32	0.90	0.292	0.016
	Vibilia stebbingi								
Decapoda	*Notocrangon antarcticus*								
	Pasiphea scotiae					0.08	0.12	0.048	0.068
Euphausiacea	*Euphausia crystallorophias*	2.37		0.290		171.86	239.99	28.855	40.348
	Euphausia superba	1.56		1.316		15.70	14.31	4.397	0.045
	Euphausia triacantha	1.15		0.216		6.09	1.22	1.726	0.526
	Thysanoessa macrura	99.70		4.524		38.84	15.61	2.047	0.805
Mysida	*Antarctomysis maxima*					0.08	0.12	0.001	0.002
	Antarctomysis ohlinii	0.07		0.036					
	Boreomysis sp.	1.42		0.079		4.13	0.24	0.276	0.007
	Dactylamblyops hodgsoni								
	Mysidetes sp.					0.09	0.13	0.013	0.018
Cephalopoda	*Alluroteuthis antarcticus*								
	Galliteuthis glacialis								
Gastropoda	*Clione limacina*								
	Spongiobranchea australis	0.14		0.007		0.34	0.22	0.017	0.011
Polychaeta	*Tomopteris carpenteri*	0.34		0.190					
Hydrozoa	*Calycopsis borchgrevinki*	0.47		0.362		0.44	0.15	0.290	0.169
	Crossota brunnea								
	Diphyes antarctica					0.53	0.28	0.090	0.075
	Leptomedusa					0.09	0.13	0.017	0.024
Scyphozoa	*Atolla wyvillei*					0.25	0.35	0.330	0.466
	Periphylla periphylla								
	Stygiomedusa gigantea[a]								
Chaetognatha	Chaetognath	1.22		0.092		2.20	1.47	0.147	0.109
	Pseudosagitta gazellae	4.41		0.833		2.64	1.62	0.878	0.537
Tunicata	*Salpa thompsoni*	0.14		0.400		0.72	1.02	0.464	0.656
Fish Family									
Bathydraconidae	*Gerlachea australis*								
Bathylagidae	*Bathylagus antarcticus*	0.47		0.006					
Channichthyidae	*Chionodraco rastrospinosus*								
	Cryodraco antarcticus								
	Dacodraco hunteri								
	Pagetopsis macropterus					0.08	0.12	0.002	0.003
Gempylidae	*Paradiplospinus gracilis*								
Liparidae	*Edentoliparis terraenovae*	0.20		0.108					
	Paraliparis antarcticus								
Myctophidae	*Electrona antarctica*	1.02		4.196		4.89	0.81	35.981	3.550
	Electrona carlsbergi								
	Gymnoscopelus braueri	0.14		1.609		0.52	0.03	9.204	3.493
	Gymnoscopelus nicholsi								
	Protomyctophum bolini								
Nototheniidae	*Aethotaxis mitopteryx*								
	Lepidonotothen larseni								
	Lepidonotothen squamifrons								
	Pagothenia borchgrevinki								
	Pleuragramma antarctica					3.46	0.21	162.860	25.153
	Trematomus sp.	0.34		0.019		1.13	0.19	0.031	0.010
Paralepididae	*Notolepis coatsi*	0.34		0.031					
Zoarcidae	*Melanostigma gelatinosum*					0.35	0.02	4.498	1.292
	Mean Total	145.82		16.690		262.85		253.066	
	Number of Taxa	27				29			

[a] No weights were recorded for these specimens.

Table 2 (continued)

Group	Taxa	Charcot Deep ($n=4$), VF = 250,965			
		# 10^4m^{-3}	SD	gWM 10^4m^{-3}	SD
Amphipoda	*Cyphocarus richardi*	0.65	0.18	0.133	0.057
Gammaridea	*Epimeria sp.*				
	Epimeriella macronyx	0.17	0.19	0.029	0.034
	Eusiroides stenopleura				
	Eusirus microps	0.62	0.45	0.071	0.069
	Eusirus properdentatus	0.17	0.26	0.029	0.058
	Orchomene plebs	0.80	0.34	0.155	0.104
	Parandania boecki	0.04	0.08	0.016	0.032
Amphipoda	*Cyllopus lucasii*	0.23	0.15	0.037	0.025
Hyperiidea	*Hyperia macrocephala*	0.04	0.08	0.004	0.009
	Hyperiella macronyx	0.04	0.08	0.001	0.003
	Primno macropa	0.43	0.25	0.022	0.013
	Themisto gaudichaudi	1.92	0.80	0.136	0.050
	Vibilia stebbingi				
Decapoda	*Notocrangon antarcticus*				
	Pasiphea scotiae	0.09	0.18	0.013	0.026
Euphausiacea	*Euphausia crystallorophias*	39.95	23.99	6.076	3.868
	Euphausia superba	235.00	376.14	157.544	273.477
	Euphausia triacantha	0.54	0.40	0.128	0.072
	Thysanoessa macrura	65.07	17.28	3.694	1.164
Mysida	*Antarctomysis maxima*				
	Antarctomysis ohlinii				
	Boreomysis sp.	5.51	3.16	0.282	0.145
	Dactylamblyops hodgsoni	0.44	0.27	0.028	0.018
	Mysidetes sp.	0.78	1.19	0.042	0.069
Cephalopoda	*Alluroteuthis antarcticus*	0.04	0.08	0.077	0.153
	Galliteuthis glacialis				
Gastropoda	*Clione limacina*	0.15	0.12	0.012	0.010
	Spongiobranchea australis	0.21	0.16	0.010	0.008
Polychaeta	*Tomopteris carpenteri*	0.04	0.08	0.006	0.013
Hydrozoa	*Calycopsis borchgrevinki*	0.12	0.15	0.165	0.193
	Crossota brunnea	0.30	0.42	0.017	0.023
	Diphyes antarctica	0.27	0.26	0.045	0.060
	Leptomedusa				
Scyphozoa	*Atolla wyvillei*	0.20	0.15	0.244	0.169
	Periphylla periphylla	0.05	0.09	0.040	0.080
	Stygiomedusa gigantea[a]				
Chaetognatha	Chaetognath	10.39	4.80	0.467	0.181
	Pseudosagitta gazellae	2.75	0.57	1.248	0.126
Tunicata	*Salpa thompsoni*				
Fish Family					
Bathydraconidae	*Gerlachea australis*	0.04	0.08	0.002	0.003
Bathylagidae	*Bathylagus antarcticus*	0.20	0.19	0.039	0.054
Channichthyidae	*Chionodraco rastrospinosus*				
	Cryodraco antarcticus				
	Dacodraco hunteri				
	Pagetopsis macropterus	0.04	0.08	0.001	0.003
Gempylidae	*Paradiplospinus gracilis*				
Liparidae	*Edentoliparis terraenovae*				
	Paraliparis antarcticus				
Myctophidae	*Electrona antarctica*	0.43	0.26	1.709	1.071
	Electrona carlsbergi	0.15	0.22	1.221	1.899
	Gymnoscopelus braueri				
	Gymnoscopelus nicholsi				
	Protomyctophum bolini				
Nototheniidae	*Aethotaxis mitopteryx*	0.04	0.08	0.004	0.009
	Lepidonotothen larseni				
	Lepidonotothen squamifrons				
	Pagothenia borchgrevinki				
	Pleuragramma antarctica	0.19	0.29	0.006	0.010
	Trematomus sp.	2.21	1.02	0.044	0.019
Paralepididae	*Notolepis coatsi*				
Zoarcidae	*Melanostigma gelatinosum*				
	Mean Total	370.31		173.797	
	Number of Taxa	38			

[a] No weights were recorded for these specimens.

10^4 m^{-3} (F$_{3,28}$ = 6.58, P<0.01; Fig. 6). Most of the dominant taxa exhibited significant differences in abundance and biomass among the regions (Fig. 7). Catches of *E. superba* were greatest, and similar, in Regions I, III and IV where mean abundances ranged from 161 to 425 g WM 10^4 m^{-3} (F$_{3,28}$ = 14.71, P<0.01) and mean biomasses ranged from 106 to 304 g WM 10^4 m^{-3} (F$_{3,28}$ = 12.67, P<0.01). In contrast, *T. macrura* was most prevalent in Region II where mean abundance exceeded 400 individuals 10^4 m^{-3} (F$_{3,28}$ = 14.93, P<0.01) and mean
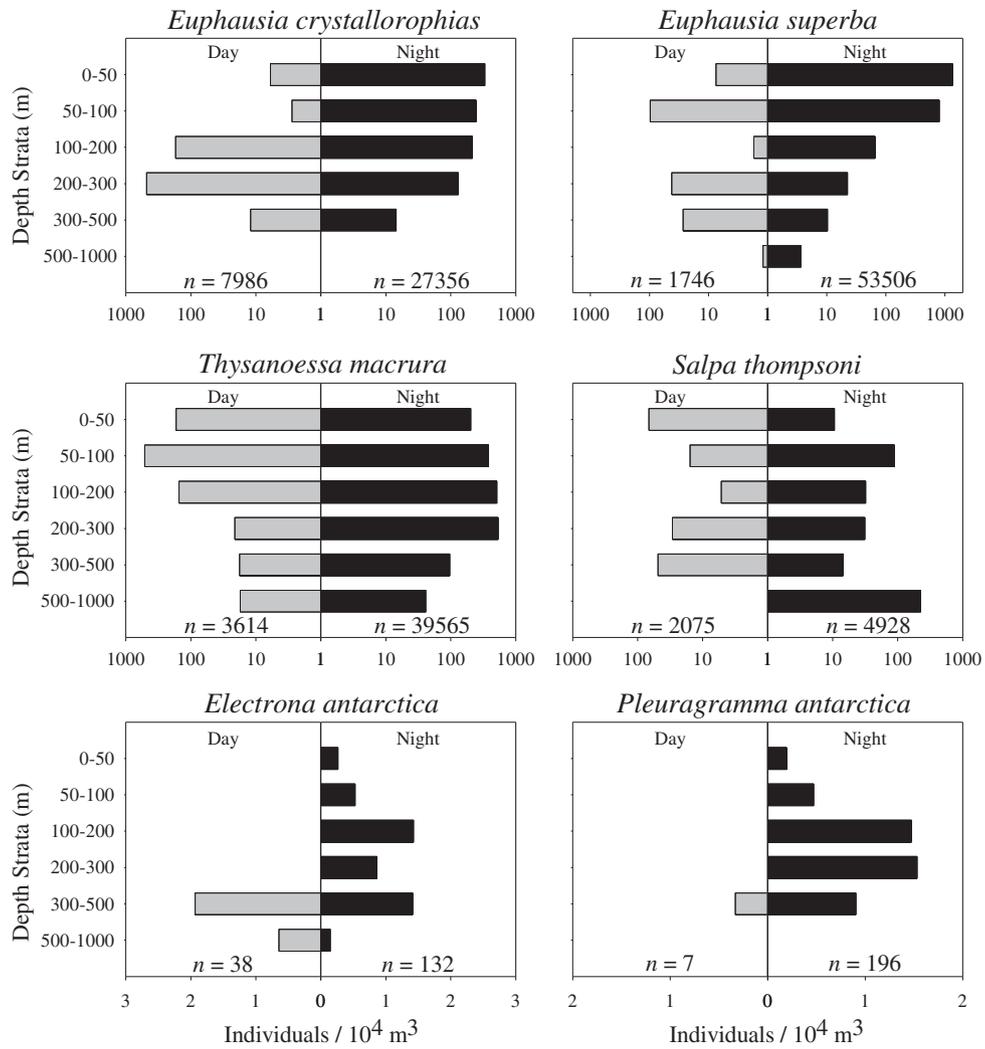
Fig. 3. Vertical distributions of common invertebrate and fish species collected during the 2010 cruise. n = number of individuals.

biomass was nearly 16 g WM 10^4 m^{-3} (F$_{3,28}$ = 9.18, P<0.01). The ice krill, *E. crystallorophias*, had significantly different catches in each region but the greatest abundance of 435 individuals 10^4 m^{-3} (F$_{3,28}$ = 41.05,

P<0.01) and biomass of 88 g WM 10^4 m^{-3} (F$_{3,28}$ = 22.54, P<0.01) were measured in Region III. Catches of *S. thompsoni* were greatest in Regions I and II where abundances ranged from 39 to 40 individuals
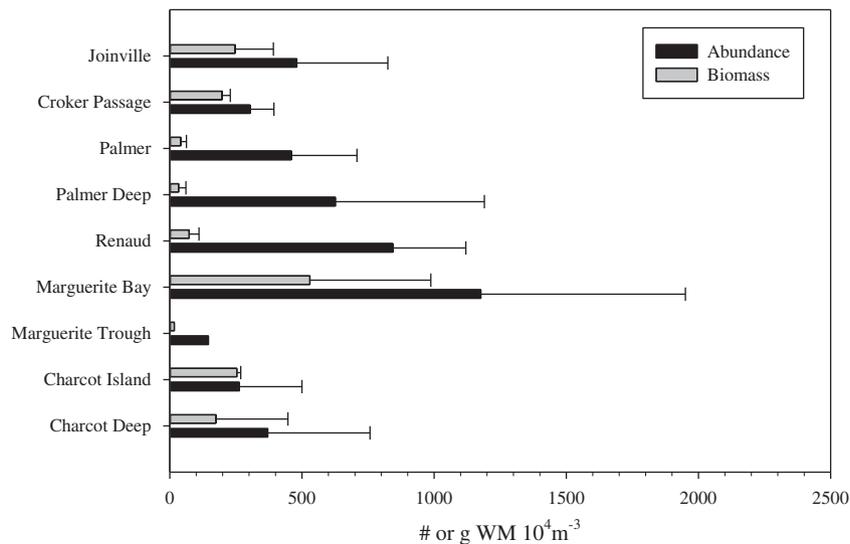
Fig. 4. Mean total volumetric abundance (±SD) (black bars) and biomass (±SD) (gray bars) at each site in 2010.
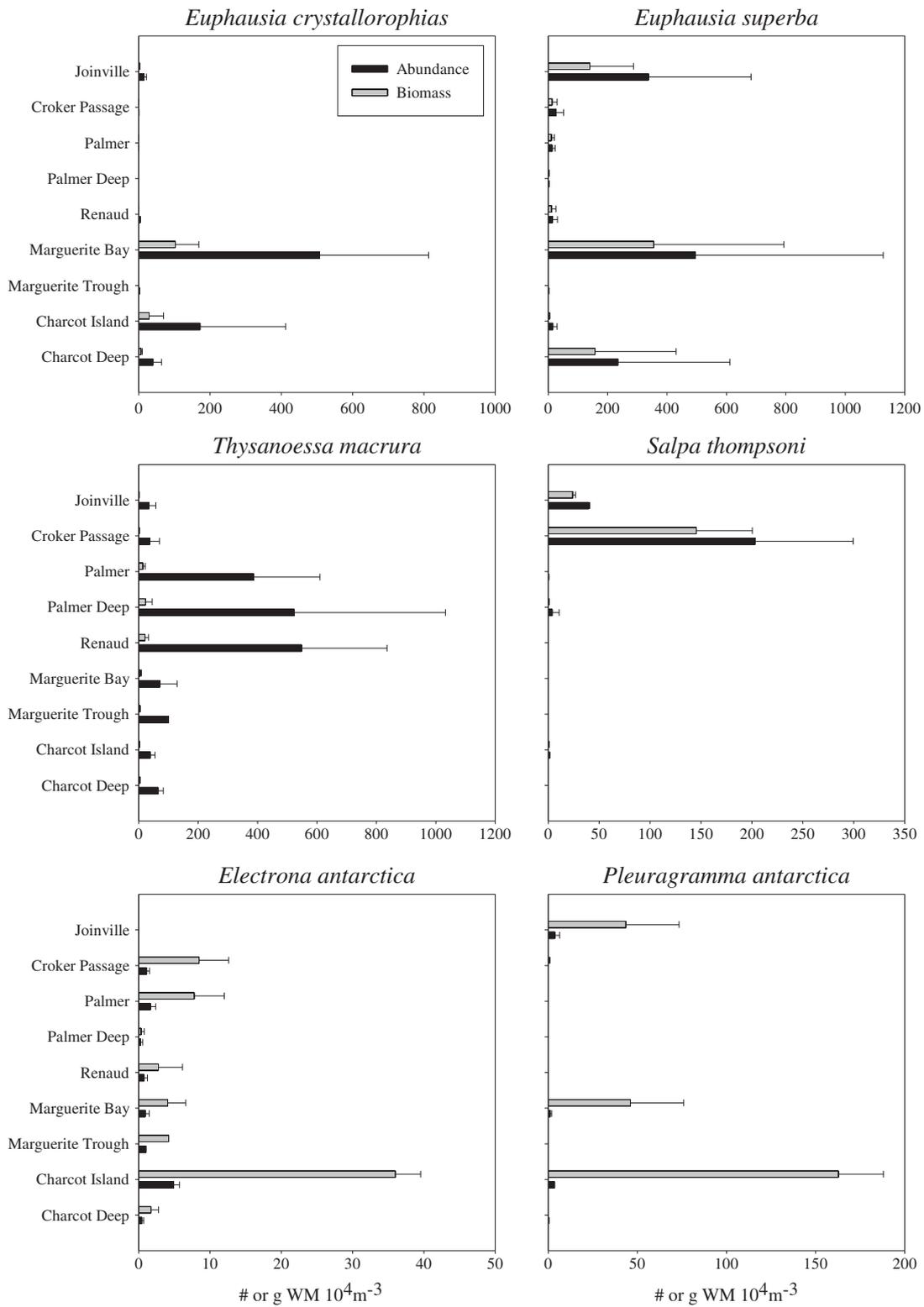
Fig. 5. Mean total volumetric abundance (±SD) (black bars) and biomass (±SD) (gray bars) of common invertebrate and fish species at each site in 2010.

10^4 m^{-3} (F$_{3,28}$= 5.68, P<0.01) and biomasses ranged from 24 to 27 g WM 10^4 m^{-3} (F$_{3,28}$= 5.60, P<0.01). The silverfish, *P. antarctica*, was present in greatest quantities in Region I where mean abundance was approximately 4 individuals 10^4 m^{-3} (F$_{3,28}$= 10.49, P<0.01). Biomasses of *P. antarctica* were greatest in Regions I, III and IV where catches ranged

from 40 to 54 g WM 10^4 m^{-3} (F$_{3,28}$= 10.51, P<0.01). The lanternfish, *E. antarctica*, had similar catches in Regions II, III and IV where abundances ranged from approximately 1 to 2 individuals 10^4 m^{-3} (F$_{3,28}$= 1.37, P<0.27) and biomasses ranged from 4 to 13 g WM 10^4 m^{-3} (F$_{3,28}$= 1.72, P= 0.79). No *E. antarctica* were captured in Region I.
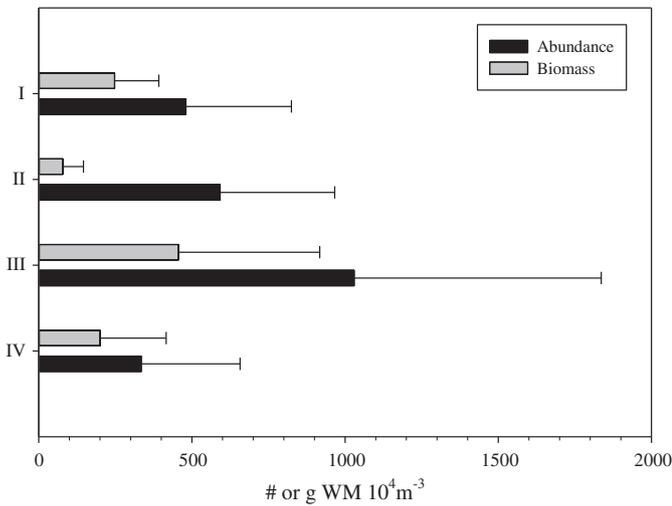
Fig. 6. Mean total volumetric abundance (±SD) (black bars) and biomass (±SD) (gray bars) in each region in 2010.

3.6. Multispecies assemblages

One-way PERMANOVA analyses of volumetric abundance and biomass revealed that there were significant differences in multispecies assemblages among sites (Abundance: $F_{8, 23} = 15.33$, $P < 0.01$; Biomass: $F_{8, 23} = 10.36$, $P < 0.01$) and among regions (Abundance: $F_{3, 28} = 9.91$, $P < 0.01$; Biomass: $F_{3, 28} = 6.55$, $P < 0.01$). Cluster analysis of abundance data separated trawls from the nine sites into five distinct clusters at the 60% similarity level (Fig. 8a). Groups A and B were more similar and comprised of trawls conducted at Joinville Island and Croker Passage, respectively. Group D included the trawls conducted in Marguerite Bay and Group E included the trawls from Charcot Island and Charcot Deep. Group C was composed of the remaining trawls which were from the Palmer, Palmer Deep, Renaud Island, and Marguerite Trough sites. At the 49% similarity level, biomass cluster groups were very similar to those on the abundance dendrogram, with the only differences occurring in Groups D and E (Fig. 9a). Instead of comprising one cluster group, the nearshore Charcot Island trawls clustered with Marguerite Bay in Group D, leaving only the Charcot Deep trawls in Group E. The MDS ordination plots show the 2-dimensional structure of the abundance and biomass data with resultant stress levels of 0.12 and 0.15, respectively (Figs. 8b and 9b).

SIMPER analysis of the abundance data identified the taxa that contributed the most to similarities within each resultant cluster group. Although most dominant taxa were present in all clusters, each contributed to the similarity within the clusters to varying degrees. In Group C, *T. macrura* and the oceanic hyperiid, *Themisto gaudichaudii*, were the two most abundant species combining to contribute more than 50% of the similarity within that group (Table 3a). The euphausiid *T. macrura* was also the dominant species in Group E but, in contrast, the secondary contributors were the euphausiids *E. crystallorophias* and *E. superba*. Species composition in Group D was similar to that of Group E, but instead *E. crystallorophias* was the ranking species contributing 19% to the similarity within the group. Groups A and B were similar in that the top two contributors were either *E. superba* or the oceanic *S. thompsoni*; however, in Group B, *S. thompsoni* contributed nearly twice that of *E. superba* (30% vs. 16%) whereas in Group A, percent contributions from each species were similar (14% vs. 18%). Bubble plot overlays of the MDS ordination plot show the abundance and distribution of the dominant invertebrate and fish species and how they relate to the abundance cluster groups (Fig. 10a).

Results from SIMPER analysis on biomass were similar to those of abundance with the major differences arising from the greater influence

of species that were less numerous but larger in size (Table 3b). In Group A, *P. antarctica* increased from contributing less than 4% to the similarity within the abundance cluster to nearly 15% of the similarity within the biomass cluster. The influence of *E. antarctica* also increased, especially in Group B where it was the second ranked contributor. The composition of Cluster Groups D and E was slightly different for biomass than for abundance (placement of Charcot Island trawls), and as a result *E. crystallorophias* rather than *T. macrura* was the ranking species in Group E. Fig. 10b shows the bubble plot overlays of biomass and distribution of the six common species.

3.7. Integrated abundance and biomass

A total of 31 invertebrate and 12 fish taxa were captured in the upper 200 m of the water column during the cruise. Of those taxa, 18 contributed 1% or more to either the total integrated abundance or biomass at a minimum of one site (Tables 4a and 4b). The euphausiids *T. macrura* and *E. superba* were dominant contributors of abundance and biomass in the 0–200 m layer at the majority of sites. The ice krill, *E. crystallorophias*, was the top contributor at Charcot Island and *S. thompsoni* was the top contributor at Croker Passage. Other taxa such as *T. gaudichaudii*, *E. antarctica*, *G. nicholsi*, and *P. antarctica* also supplied a substantial proportion of the catch among the sites. Mean total densities in the upper 200 m ranged from approximately 6 individuals m^{-2} at Marguerite Trough to 63 individuals m^{-2} at Marguerite Bay. Densities at the remaining sites fell between 15 and 30 individuals m^{-2}. Biomass estimates showed a similar pattern, with the lowest mean recorded at Marguerite Trough (0.4 g WM m^{-2}) and the highest at Marguerite Bay (33 g WM m^{-2}).

3.8. Pleuragramma antarctica size distributions

Size distributions of *P. antarctica* captured from each site are presented in Fig. 11. Standard lengths of all fishes ranged from 19 to 213 mm with three modal peaks occurring at the 45 mm (small), 115 mm (medium), and 155 mm (large) size class intervals. The small and medium modal groups were primarily composed of fish captured from Joinville Island, while those in the large modal group were dominated by fish captured at Marguerite Bay. The large modal group also included all of the fish captured at Charcot Island. Fewer fish were captured at Charcot Deep and those all fell into the small modal group. No fish from Charcot Island or Charcot Deep fell into the medium modal group. One fish, falling into the medium modal group, was captured from Croker Passage. No *P. antarctica* were captured from the Palmer, Palmer Deep, Renaud Island, or Marguerite Trough sites.

4. Discussion

4.1. Faunal composition in the warming gradient along the WAP

A total of 62 taxa were collected during the present study, but four species, *E. crystallorophias*, *E. superba*, *T. macrura*, and *S. thompsoni*, accounted for the majority of the catch, contributing more than 84% of the total abundance and 69% of the total biomass captured. Those species have previously been characterized as dominant taxa in various regions along the WAP including Bransfield Strait (Brinton and Townsend, 1991; Nordhausen, 1992; Piatkowski, 1985; Witek et al., 1985), Croker Passage (Lancraft et al., 2004), Gerlache Strait (Nordhausen, 1994a,b), the region extending from Anvers to Adelaide Island (Ross et al., 2008), and Marguerite Bay (Parker et al., 2011). Fishes constituted more than one-third of the taxa captured, but contributions to overall abundance were negligible, totaling less than 1% of the numbers captured. However, two important pelagic fish species, the Antarctic silverfish, *P. antarctica*, and the myctophid, *E. antarctica*, contributed substantial biomass, accounting for 16% and 4% of the total catch, respectively.
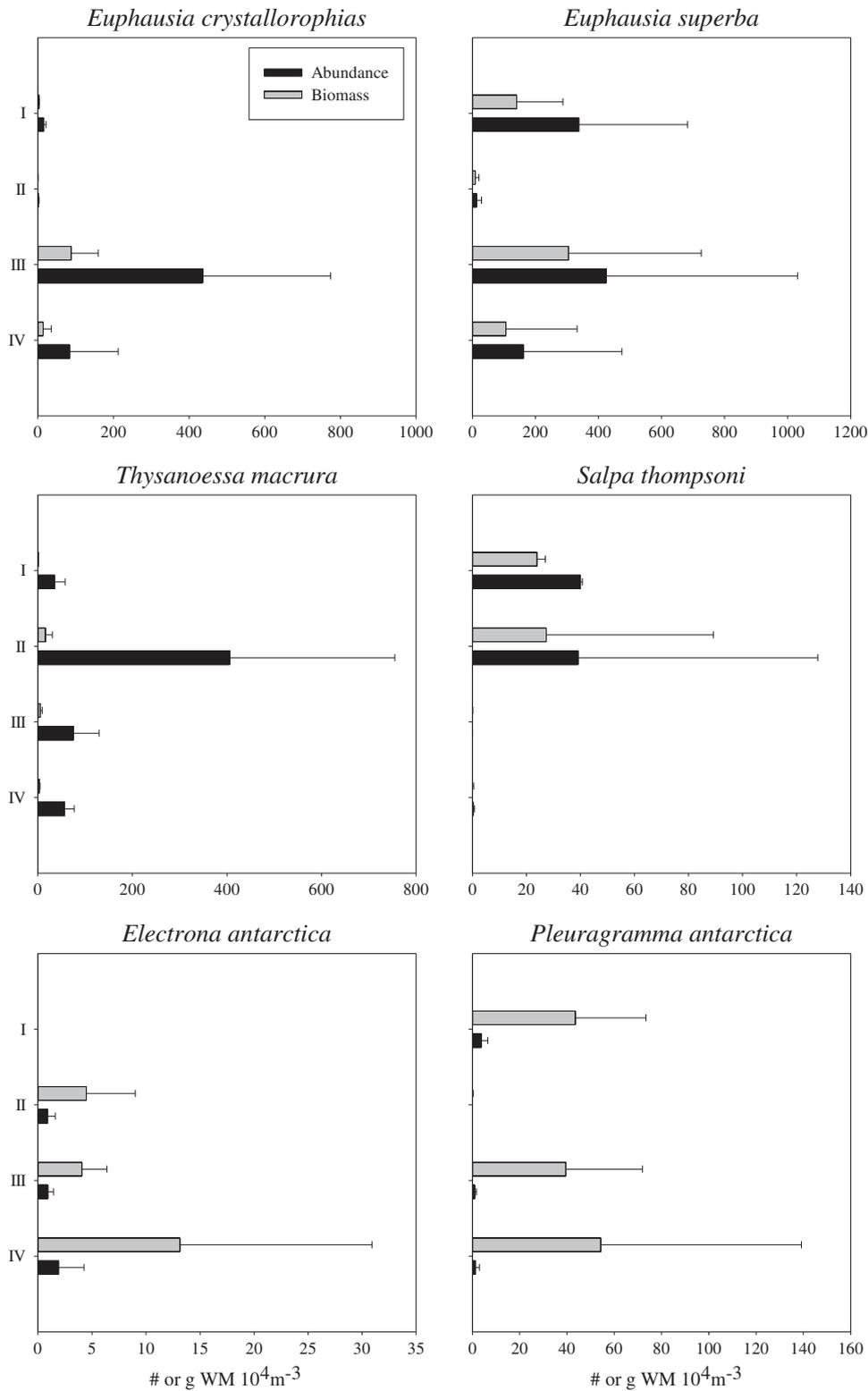
Fig. 7. Mean total volumetric abundance (±SD) (black bars) and biomass (±SD) (gray bars) of common invertebrate and fish species in each region in 2010.

Vertical depth ranges for most dominant species encompassed the entire sampled water column, but neither *E. crystallorophias* nor *P. antarctica* were captured at depths greater than 500 m. This may be an artifact of the trawling effort since the few deep trawls (surface to 1000 m) were conducted at sites (Croker Passage and Palmer) where both species were either absent or present at very low densities. However, a study in the Marguerite Bay region during 2001/2002 yielded

similar results (Donnelly and Torres, 2008; Parker et al., 2011), suggesting that the coastal distributions of both species may preclude their presence below 500 m at most of the present study sites. Deeper distributions of *P. antarctica* were recorded at Croker Passage in 1983 (Lancraft et al., 2004), but since only one fish was captured at that site in the present study (as well as being captured in a net that fished obliquely from the surface to depth) a valid comparison cannot be
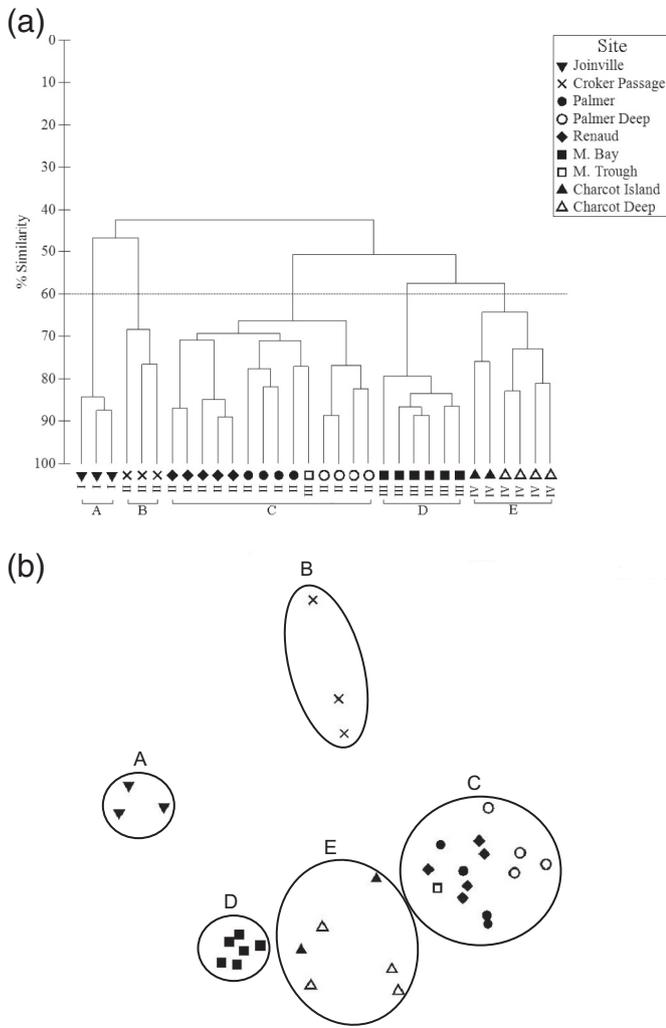
Fig. 8. (a) Percent similarity cluster dendrogram of micronekton/macrozooplankton volumetric abundance (number individuals 10^4 m^{-3}). Roman numerals along the abscissa represent hydrographic regions. Brackets represent cluster groups at the 60% similarity level. (b) Corresponding MDS ordination plot of abundance data.
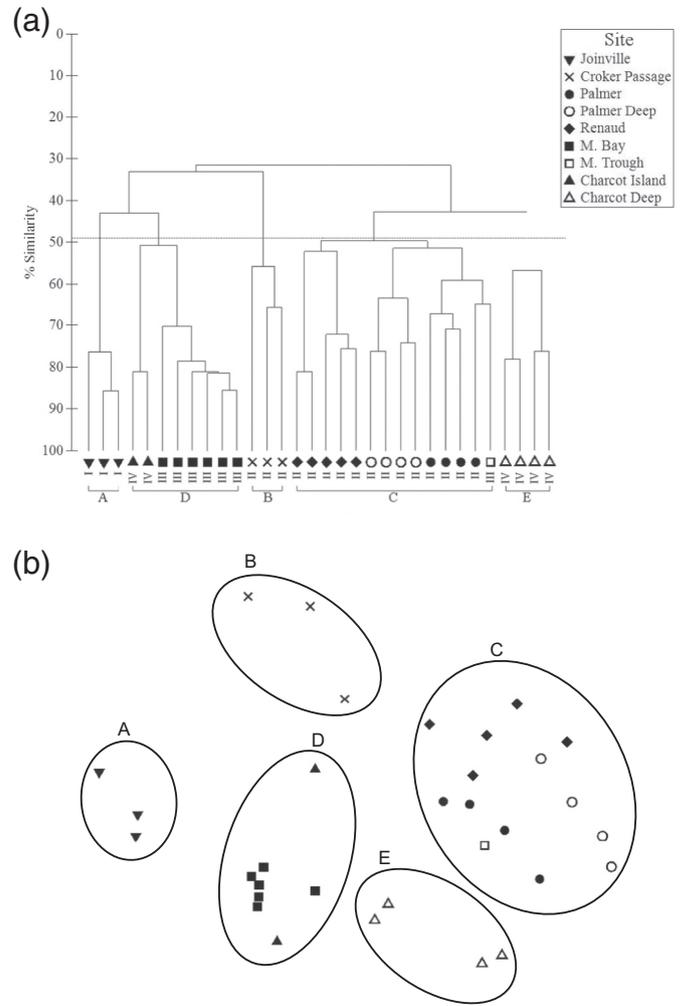
Fig. 9. (a) Percent similarity cluster dendrogram of micronekton/macrozooplankton volumetric biomass (g WM 10^4 m^{-3}). Roman numerals along the abscissa represent hydrographic regions. Brackets represent cluster groups at the 49% similarity level. (b) Corresponding MDS ordination plot of biomass data.

made. It should be noted that the WAP is the only region of the Antarctic whose temperature profile allows the intrusion of oceanic fishes into shelf waters. The lanternfishes, dominated by *E. antarctica*, are well established despite their lack of biological antifreezes (Cullins et al., 2011). In coastal regions where low temperature (−2.0 °C) ice-shelf water is present, e.g. the Ross Sea (Dinniman et al., 2003), oceanic species are excluded (DeWitt, 1970; Donnelly et al., 2004); their presence in the water column ends at the shelf break.

Micronektonic/macrozooplanktonic faunal assemblages along the WAP continental shelf were composed of a varying mix of neritic and oceanic species. The extent of mixing between the two assemblages as well as changes in the relative abundances of dominant species among sites were directly related to the unique bathymetry and hydrographic conditions present on the WAP shelf. Faunal mixing is maximized as CDW moves onto the shelf and mixes with cooler, fresher shelf waters (Donnelly and Torres, 2008; Parker et al., 2011). This was illustrated by the balance of oceanic and neritic fauna in assemblages at sites in the Marguerite Bay region and near Charcot Island. For example, taxonomic diversity was high at Charcot Deep, a site that was located nearshore but within a deep trench where fauna associated with cold, shelf waters mixed with oceanics transported onto the shelf within the warm, deep CDW layer. Although that assemblage was dominated by the euphausiid, *E. superba*, there was almost even representation by neritic and oceanic fauna. The assemblage in the Marguerite Trough was

also well mixed, but instead the ubiquitous euphausiid *T. macrura* was the predominant species. The character of the fauna suggests there was a weaker neritic influence at the Trough site, which was reflected in the warmer water column temperatures and the much shallower presence of mCDW at that site. Conversely, the assemblages at the most nearshore sites, Marguerite Bay and Charcot Island, were dominated by *E. crystallorophias* and *P. antarctica*, both of which are coastal species most commonly found in cold shelf waters (Hubold, 1984; Smith and Schnack-Schiel, 1990).

At the two northernmost sites, Joinville Island and Croker Passage, the absence of a mCDW layer strongly influenced the assemblages. Near Joinville Island, circulation is driven by cold surface waters moving westward from the Weddell Sea (Stein, 1986; Thompson et al., 2009) resulting in a water column more typical of higher latitude Antarctic shelf regions where temperatures are near freezing (−2 °C) from the surface to depth (Dinniman et al., 2003). The absence of oceanic species in the cold Weddell source water as well as the cold temperatures themselves excluded many oceanics from the Joinville Island assemblage, especially those fishes such as *E. antarctica* which lack antifreezes (Cullins et al., 2011). Instead, silverfish were not only abundant at Joinville Island, but captured at densities comparable to those recorded in Marguerite Bay and near Charcot Island. The water column at Croker Passage was also well mixed, but temperatures were slightly warmer with an average near 0 °C. The resulting assemblage at Croker Passage consisted

Table 3
Results of SIMPER analysis on (a) volumetric abundance data and (b) volumetric biomass data showing the taxa contributing the most to similarity within each cluster group. Values in parentheses represent overall similarity among samples within a cluster group. % Contribution = percentage contribution to overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

(a)

Group A (85.39% similarity)		Group B (71.14% similarity)		Group C (70.09% similarity)		Group D (83.11% similarity)		Group E (69.81% similarity)	
Joinville trawls		Croker Passage trawls		Palmer, Palmer Deep, Renaud, and Marguerite Trough trawls		Marguerite Bay trawls		Charcot Island and Charcot Deep trawls	
% Contribution		% Contribution		% Contribution		% Contribution		% Contribution	
Euphausia superba	17.94	*Salpa thompsoni*	30.38	*Thysanoessa macrura*	31.95	*Euphausia crystallorophias*	19.16	*Thysanoessa macrura*	21.24
Salpa thompsoni	13.85	*Euphausia superba*	15.83	*Themisto gaudichaudi*	20.48	*Euphausia superba*	14.86	*Euphausia crystallorophias*	14.73
Thysanoessa macrura	11.34	*Themisto gaudichaudi*	15.31	*Pseudosagitta gazellae*	9.77	*Thysanoessa macrura*	12.36	*Euphausia superba*	11.40
Antarctomysis maxima	10.67	*Thysanoessa macrura*	11.90	*Euphausia superba*	6.88	*Themisto gaudichaudi*	10.17	*Boreomysis sp.*	9.05
Orchomene plebs	9.38	*Orchomene plebs*	5.58	*Chaetognath*	6.69	*Antarctomysis ohlinii*	9.54	*Chaetognath*	8.35
Euphausia crystallorophias	9.07	*Cyphocarus richardi*	5.19	*Boreomysis sp.*	6.49	*Boreomysis sp.*	7.16	*Pseudosagitta gazellae*	6.49
Mysidetes sp.	4.42	*Cyllopus lucasii*	3.79	*Euphausia triacantha*	5.48	*Epimeriella macronyx*	6.01	*Themisto gaudichaudi*	5.77
Pseudosagitta gazellae	3.91	*Electrona antarctica*	3.70	*Cyphocarus richardi*	2.32	*Orchomene plebs*	4.31	*Trematomus sp.*	4.64
Antarctomysis ohlinii	3.71	*Eusirus properdentatus*	1.37	*Electrona antarctica*	2.01	*Clione limacina*	2.61	*Orchomene plebs*	3.08
Pleuragramma antarctica	3.70	*Pseudosagitta gazellae*	1.16	*Primno macropa*	1.65	*Pseudosagitta gazellae*	2.31	*Euphausia triacantha*	2.49
Epimeriella macronyx	2.82	*Notolepis coatsi*	1.16	*Spongiobranchea australis*	1.10	*Edentoliparis terraenovae*	2.01	*Electrona antarctica*	2.20
Chaetognath	2.44	*Chionodraco rastrospinosus*	1.02	*Euphausia crystallorophias*	1.09	*Pleuragramma antarctica*	1.71	*Eusirus microps*	2.00
Diphyes antarctica	1.49			*Orchomene plebs*	1.00	*Electrona antarctica*	1.62	*Pleuragramma antarctica*	1.05
Eusirus microps	1.18					*Eusirus properdentatus*	1.52		
Dactylamblyops hodgsoni	1.05					*Antarctomysis maxima*	1.38		
Chionodraco rastrospinosus	1.03					*Trematomus sp.*	1.07		

(b)

Group A (79.52% similarity)		Group B (59.01% similarity)		Group C (53.99% similarity)		Group D (66.01% similarity)		Group E (63.61% similarity)	
Joinville trawls		Croker Passage trawls		Palmer, Palmer Deep, Renaud, and Marguerite Trough trawls		Marguerite Bay and Charcot Island trawls		Charcot Deep trawls	
% Contribution		% Contribution		% Contribution		% Contribution		% Contribution	
Euphausia superba	19.62	*Salpa thompsoni*	41.88	*Thysanoessa macrura*	34.57	*Pleuragramma antarctica*	20.56	*Euphausia crystallorophias*	22.57
Salpa thompsoni	15.68	*Electrona antarctica*	16.94	*Themisto gaudichaudi*	16.13	*Euphausia crystallorophias*	19.86	*Thysanoessa macrura*	19.99
Pleuragramma antarctica	14.59	*Euphausia superba*	13.84	*Euphausia superba*	15.66	*Euphausia superba*	19.47	*Euphausia superba*	16.14
Antarctomysis maxima	10.34	*Themisto gaudichaudi*	5.87	*Electrona antarctica*	8.74	*Electrona antarctica*	9.96	*Pseudosagitta gazellae*	11.65
Orchomene plebs	9.28	*Cyphocarus richardi*	4.94	*Pseudosagitta gazellae*	8.11	*Thysanoessa macrura*	7.43	*Electrona antarctica*	10.55
Chionodraco rastrospinosus	6.01	*Thysanoessa macrura*	3.40	*Euphausia triacantha*	3.90	*Antarctomysis ohlinii*	5.25	*Chaetognath*	4.58
Euphausia crystallorophias	5.10	*Chionodraco rastrospinosus*	3.10	*Boreomysis sp.*	3.04	*Themisto gaudichaudi*	3.57	*Boreomysis sp.*	2.75
Thysanoessa macrura	3.52	*Notolepis coatsi*	1.42	*Cyphocarus richardi*	2.25	*Orchomene plebs*	2.94	*Atolla wyvillei*	2.00
Antarctomysis ohlinii	3.36	*Calycopsis borchgrevinki*	1.40	*Calycopsis borchgrevinki*	1.58	*Epimeriella macronyx*	2.60	*Themisto gaudichaudi*	1.54
Pagetopsis macropterus	2.82	*Orchomene plebs*	1.28	*Chaetognath*	1.24	*Boreomysis sp.*	1.97	*Electrona carlsbergi*	1.54
Pseudosagitta gazellae	2.25	*Eusirus properdentatus*	1.27			*Gymnoscopelus braueri*	1.52	*Cyphocarus richardi*	1.34
Cryodraco antarcticus	1.36	*Pseudosagitta gazellae*	1.25			*Pseudosagitta gazellae*	1.02	*Euphausia triacantha*	1.19
Calycopsis borchgrevinki	1.20	*Cryodraco antarcticus*	1.17					*Orchomene plebs*	1.16
Eusirus microps	1.10								

primarily of oceanic fauna and was overwhelmingly dominated by *S. thompsoni*, which is becoming increasingly more common in the northern WAP region (Atkinson et al., 2004).

At Renaud Island and the two Palmer sites, temperatures were even warmer than those at Croker Passage, generally exceeding 0 °C throughout the water column. Oceanic fauna were most prevalent in those assemblages but *T. macrura* dominated, as observed in the Marguerite Trough assemblage. In fact, *T. macrura* contributed more than 83% of the total number of individuals captured at the two Palmer sites and just over 65% at Renaud Island. Diversity at the Palmer Deep site was the lowest recorded in the study and contributions by the few neritic fauna present in the assemblage totaled less than 1%. Despite the fact that the Palmer and Renaud Island sites were located nearshore, *E. crystallorophias* was present only at very low densities and *P. antarctica* was completely absent from the assemblages.

4.2. Are multispecies assemblages related to hydrographic regimes along the WAP?

One of the goals of the present study was to investigate the existence of several distinct hydrographic regimes occurring along the WAP shelf. Physical factors such as the presence of persistent gyral circulation patterns, which act to retain fauna, and the extent and duration of seasonal

sea ice were used to define different regions. In addition, the expected composition of the faunal assemblages and the prevalence of ice-associated fauna like *E. crystallorophias* and *P. antarctica* were used to characterize those regions. Prior to this study, we hypothesized that there were four such regions occurring from north to south along the WAP (Fig. 1). The northernmost region (Region I), which extends from Joinville Island to just north of Brabant Island, was delineated by its lack of gyral circulation and the strong influence of coldwater flow from the Weddell Sea (Hofmann et al., 1996). Assemblages in this region were expected to contain high densities of *P. antarctica* and other neritic fauna. Region II was characterized by the existence of a clockwise gyral circulation pattern that encompassed the area from north of Brabant Island to just south of Renaud Island (Hofmann et al., 1996; Smith et al., 1999b). In addition, regional warming in this area has led to a substantial decrease in sea ice days, primarily due to later ice advance in the autumn/winter (Ducklow et al., 2007). Assemblages in Region II were predicted to be composed almost exclusively of oceanic fauna.

The Marguerite Bay system, which included Adelaide Island to the north and Alexander Island to the south, comprised Region III and was defined by a second cyclonic gyre that extended from Lavoisier Island to the southern extent of Lazarev Bay (Klinck et al., 2004). Lastly, Region IV was designated by an area extending from Lazarev Bay in the north to

an as yet undefined boundary south of Charcot Island. Observations in this region are limited, but simulated circulation distributions for the WAP continental shelf show a gyral circulation just north of Charcot Island (Piñones et al., 2011, Fig. 4) and simulated particle trajectories show that this area is a retention region (Piñones et al., 2013b). In Regions III and IV, the presence of cold shelf waters and warm CDW is expected to generate assemblages composed of both oceanic and neritic fauna.

Cluster analysis of the assemblages from each site identified five primary groups, which corresponded closely with the hypothesized regions and their expected faunal compositions. Distinct assemblages were identified at Joinville Island, Marguerite Bay, and Charcot Island, which coincided with Regions I, III and IV, respectively. Assemblages from the two Palmer sites, Renaud Island, and the Marguerite Trough clustered together and, with the exception of the Marguerite Trough site, fit within the geographical constraints of Region II. The Croker Passage assemblage grouped independently rather than within Regions I or II, most likely due to the overwhelming abundance of *S. thompsoni* in those samples. Because most taxa were captured throughout the study region, there were no apparent indicator species for any particular assemblage. Instead, changes in the relative abundance and biomass of major taxa were instrumental in determining differences among the multispecies assemblages (Siegel and Piatkowski, 1990). In addition, those species that have been typically classified as either oceanic or neritic fauna were useful in characterizing the multispecies assemblages.

The assemblages at Joinville Island and Croker Passage were more similar to each other than to the other three cluster groups. Although *E. superba*, *S. thompsoni*, and *T. macrura* were dominant contributors in both northern groups, hydrographic conditions at Joinville Island favored a neritic assemblage as evidenced by the substantial contributions from *P. antarctica* and the deep dwelling mysid, *Antarctomysis maxima*. In contrast, the assemblage at Croker Passage was more oceanic in nature with major inputs from *E. antarctica* and *T. gaudichaudii*. Assemblages at Marguerite Bay and Charcot Island grouped more closely due to strong neritic and oceanic influences, which functioned to maximize faunal mixing at those sites. This is demonstrated by the prevalence of the neritics, *E. crystallorophias* and *P. antarctica*, as well as the oceanics, *T. gaudichaudii* and *E. antarctica* in those assemblages. The final cluster assemblage included samples collected from several sites in the mid-peninsula region, roughly corresponding to Region II, and was overwhelmingly dominated by two species, *T. macrura* and *T. gaudichaudii*. Although *T. macrura* is not considered an oceanic species, but rather a ubiquitously distributed species (Kittel and Stepnik, 1983; Kittel et al., 1985; Nordhausen, 1994a,b; Piatkowski, 1985), abundances were an order of magnitude higher at most sites in Region II. Very few neritic fauna were present in the Region II assemblage. Most notable was the complete absence of *P. antarctica*.

Although samples for this study were collected over a two month period and thus only present a snapshot of the multispecies assemblages present at each of the study sites, results from cluster analyses provide support for the presence of distinct hydrographic regimes along the WAP. The unique hydrography of the WAP creates complex cross-shelf circulation processes that increase retention at inner shelf locations (Murphy et al., 2012; Piñones et al., 2011, 2013a), effectively
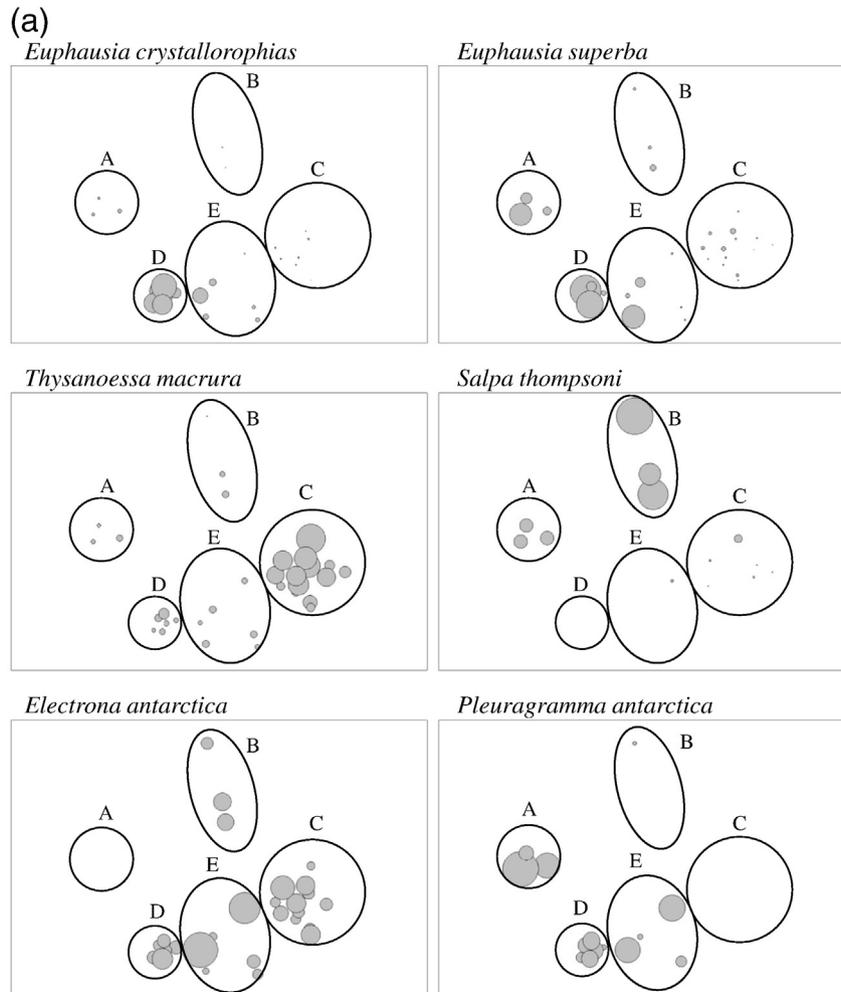

Fig. 10. Bubble plot overlays of the (a) abundance MDS ordination plot and the (b) biomass MDS ordination plot representing the relative abundance and biomass of several common species. The larger the bubble, the greater the number of individuals were captured at that site. Please note that bubble sizes are not consistent among species.
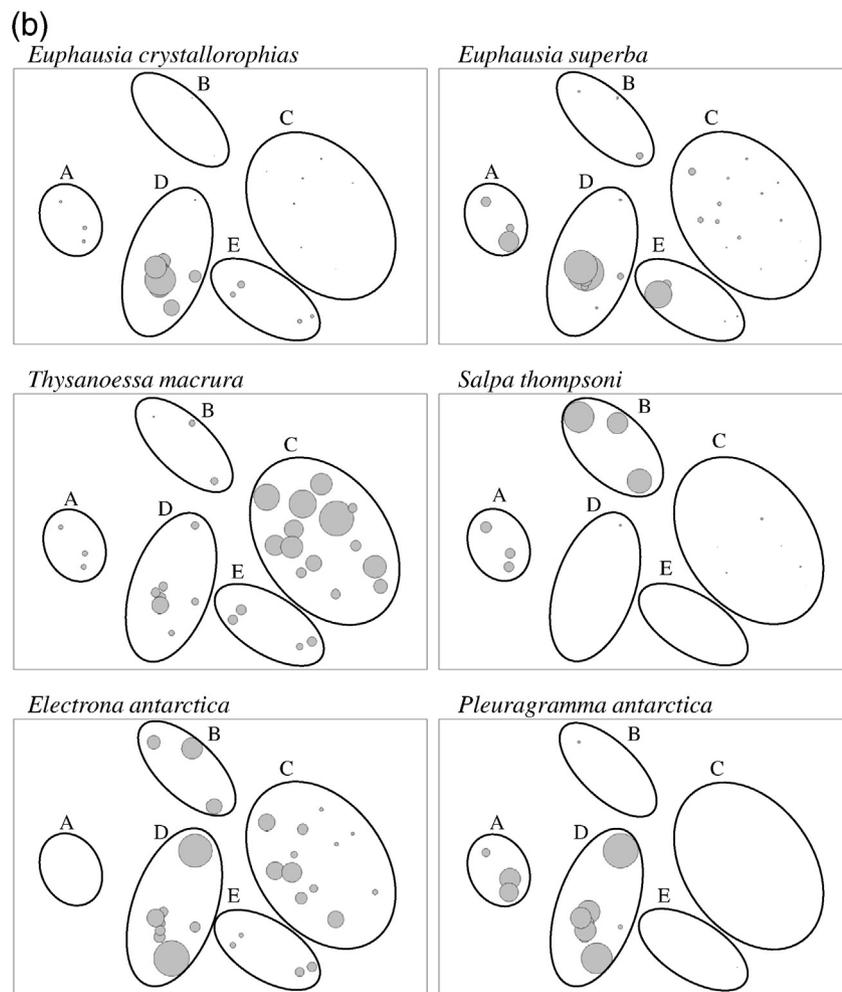
(b)

Euphausia crystallorophias

Euphausia superba

Thysanoessa macrura

Salpa thompsoni

Electrona antarctica

Pleuragramma antarctica

Fig. 10 (*continued*).

limiting connectivity between the regions. Simulated particle trajectories show essentially no exchange between the southern WAP continental shelf and the northern Peninsula-Bransfield Strait region (Piñones et al., 2013a, Fig. 7). In contrast, evidence from oceanographic observations (Moffat et al., 2008), and simulated particle trajectories (Piñones et al., 2011, 2013a,b), suggests that flow from the Antarctic coastal current connects the Marguerite Bay region to areas further south, such as Charcot Island.

4.3. Disappearance of Pleuragramma antarctica from the WAP shelf

Cluster analyses showed oceanic assemblages mixing inshore over the shelf during 2010, and a strong association of *Pleuragramma* with neritic assemblages constrained in coastal areas of the northern and south-western AP. Results suggest that faunal distributions on the WAP are responding to changes in local hydrography and sea-ice behavior, particularly when considered in light of information collected over the last forty years. Extensive sampling of larval and adult *P. antarctica* has occurred in the waters of the WAP shelf region. Consecutive sampling programs such as FIBEX and SIBEX (First and Second International Biomass EXperiments, respectively), RACER (Research on Antarctic Coastal Ecosystem Rates), and AMLR (Antarctic Marine Living Resources) have described *P. antarctica* distributions on the WAP since 1976 (Kellermann, 1986, 1987, 1989; Kellermann and Kock, 1988; Loeb, 1991; Rembiszewski et al., 1978; Skora and Sosinksi, 1983; Slosarczyk, 1986; Slosarczyk and Cielniaszek, 1985; Slosarczyk and Rembiszewski, 1982; White and North, 1987). There have also been several individual studies that, when taken collectively with the

sampling programs, provide a fairly good description of historical *P. antarctica* distributions on the WAP shelf (Daniels, 1982; Daniels and Lipps, 1982; Donnelly and Torres, 2008; Hubold and Tomo, 1989; Kellermann and Schadwinkel, 1991; Lancraft et al., 2004; Morales-Nin et al., 1998). Among those studies, juvenile and adult silverfish have been definitively captured in nets deployed in Croker Passage (Lancraft et al., 2004), northwest of Adelaide Island (Skora and Sosinksi, 1983) and in the Marguerite Bay region (Donnelly and Torres, 2008). In addition, Daniels (1982) reported schools of several thousand *Pleuragramma* observed under the ice near Palmer Station, Anvers Island.

Silverfish were captured at five sites during the present study: Joinville Island in Region I, Croker Passage in Region II, Marguerite Bay in Region III, and the two sites near Charcot Island in Region IV. They were completely absent at the two Palmer sites, at Renaud Island, and in the Marguerite Trough, all in Region II. They were nearly absent in Croker Passage (one fish was captured), where they were previously considered a dominant fish species (Reisenbichler, 1993) and where Lancraft et al. (2004) measured an integrated abundance of 88 individuals 10^3 m^{-2} in the upper 200 m of the water column in 1983. In Marguerite Bay, volumetric abundances of *P. antarctica* were also much lower than previously observed, with a mean of approximately 1 individual 10^4 m^{-3} compared to 45 individuals 10^4 m^{-3} in 2001 and 2002 (Donnelly and Torres, 2008). Biomass estimates in Marguerite Bay were more similar, at approximately 50 g WM 10^4 m^{-3} (Donnelly and Torres, 2008), suggesting that the fish caught in 2010 were substantially larger than those from the 2001/2002 study reported in Donnelly and Torres, 2008. In fact, the majority of fish captured from Marguerite

Table 4
Integrated (a) abundance (number individuals m⁻²) and (b) biomass (g WM m⁻²) of taxa collected from discrete night tows within the 0–200 meter depth stratum at each site in 2010.

Taxa	Joinville (n = 3) VF = 83,835 # m⁻²	SD	Croker Passage (n = 2) VF = 28,857 # m⁻²	SD	Palmer (n = 2) VF = 62,061 # m⁻²	SD	Palmer Deep (n = 2) VF = 21,187 # m⁻²	SD	Renaud (n = 5) VF = 136,255 # m⁻²	SD	Marguerite Bay (n = 4) VF = 170,964 # m⁻²	SD	Marguerite Trough (n = 1) VF = 54,985 # m⁻²	SD	Charcot Island (n = 2) VF = 26,137 # m⁻²	SD	Charcot Deep (n = 3) VF = 43,016 # m⁻²	SD
(a)																		
Alluroteuthis antarcticus									0.001	0.002								
Chaetognath	0.041	0.014			0.026	0.003	0.085	0.010	0.103	0.099	0.009	0.011	0.054		0.058	0.026	0.337	0.247
Euphausia crystallorophias	0.891	0.349							0.134	0.133	20.531	7.178	0.032		12.784	17.977	3.020	2.531
Euphausia superba	20.926	30.825	1.035	0.719	1.236	1.065	0.049	0.069	0.290	0.241	36.063	38.728	0.042		1.036	1.124	23.339	35.978
Euphausia triacantha			0.015	0.003	0.019	0.008	0.008	0.012	0.223	0.327	0.004	0.003	0.013		0.053	0.028		
Orchomene plebs	0.297	0.149	0.069	0.002	0.002	0.003			0.006	0.008	0.053	0.012	0.031		0.007	0.009	0.006	0.010
Primno macropa	0.001	0.002			0.007	0.010			0.012	0.009	0.001	0.003						
Pseudosagitta gazellae	0.021	0.018	0.014	0.019	0.049	0.028	0.031	0.043	0.047	0.023	0.012	0.014	0.095		0.022	0.013	0.028	0.019
Salpa thompsoni	0.421	0.288	13.197	14.552	0.027	0.038	0.658	0.931					0.005		0.061	0.087		
Themisto gaudichaudi			0.660	0.129	0.846	0.628	2.129	1.727	5.930	4.637	1.115	1.290	0.442		0.241	0.019	0.077	0.032
Thysanoessa macrura	0.194	0.057	0.734	0.881	16.904	4.490	14.626	7.437	19.611	8.107	4.730	2.705	5.569		0.604	0.186	2.302	1.141
Tomopteris carpenteri			0.007	0.010	0.002	0.002			0.007	0.014	0.002	0.005	0.011					
Edentoliparis terraenovae											0.004	0.005	0.009					
Electrona antarctica			0.035	0.050	0.032	0.005	0.015	0.022	0.021	0.028	0.007	0.014			0.076	0.000		
Gymnoscopelus braueri													0.003					
Gymnoscopelus nicholsi			0.014	0.020					0.009	0.021								
Melanostigma gelatinosum									0.004	0.007								
Pleuragramma antarctica	0.048	0.051									0.066	0.020					0.019	0.022
Mean Total	22.839		15.780		19.151		17.601		26.397		62.599		6.306		14.942		29.127	
Number of Taxa	9		10		11		8		14		13		12		10		8	
(b)																		
Alluroteuthis antarcticus									0.029	0.066								
Chaetognath	0.002	0.002			0.001	0.000	0.007	0.003	0.003	0.003	0.000	0.001	0.004		0.003	0.003	0.005	0.004
Euphausia crystallorophias	0.144	0.044							0.017	0.019	4.166	1.550	0.004		2.133	3.000	0.444	0.383
Euphausia superba	8.917	12.870	0.288	0.303	1.099	1.008	0.047	0.066	0.216	0.178	25.557	26.293	0.039		0.233	0.060	16.186	26.451
Euphausia triacantha			0.002	0.000	0.003	0.002	0.001	0.002	0.049	0.070	0.001	0.000	0.002		0.016	0.011		
Orchomene plebs	0.187	0.102	0.009	0.007	0.000	0.000			0.002	0.003	0.016	0.005	0.009		0.001	0.002	0.001	0.002
Primno macropa	0.000	0.000			0.001	0.001			0.001	0.000	0.000	0.000						
Pseudosagitta gazellae	0.005	0.006	0.006	0.008	0.009	0.005	0.006	0.009	0.007	0.005	0.002	0.002	0.023		0.002	0.002	0.013	0.006
Salpa thompsoni	0.186	0.126	12.133	12.140	0.001	0.002	0.057	0.081					0.015		0.039	0.056		
Themisto gaudichaudi			0.055	0.021	0.047	0.032	0.117	0.093	0.345	0.274	0.072	0.084	0.027		0.013	0.000	0.006	0.002
Thysanoessa macrura	0.009	0.003	0.026	0.031	0.590	0.194	0.563	0.170	0.691	0.302	0.323	0.197	0.250		0.027	0.007	0.110	0.050
Tomopteris carpenteri			0.004	0.006	0.001	0.002			0.002	0.003	0.001	0.001	0.007					
Edentoliparis terraenovae											0.002	0.005	0.005					
Electrona antarctica			0.373	0.527	0.145	0.036	0.023	0.033	0.153	0.238	0.009	0.018			0.502	0.239		
Gymnoscopelus braueri													0.019					
Gymnoscopelus nicholsi			0.585	0.827					0.368	0.824								
Melanostigma gelatinosum									0.039	0.071								
Pleuragramma antarctica	0.562	0.662									2.481	0.852					0.001	0.001
Mean Total	10.013		13.481		1.898		0.822		1.921		32.631		0.405		2.970		16.765	
Number of Taxa	9		10		11		8		14		13		12		10		8	

Bay in 2010 were larger than 150 mm SL (age class 10; Hubold and Tomo, 1989) compared to a majority of fishes sized 30–53 mm SL (age class 1) in 2001 and 55–72 mm SL (age class 2) in 2002 (Donnelly and Torres, 2008; Fig. 12). Comparison of the 2001, 2002, and 2010 *Pleuragramma* size distributions shows what appears to be the ageing of a single year class of fish, suggesting that very little larval recruitment had occurred in the vicinity of Marguerite Bay in the years preceding the present study. The question remains as to why a historically continuous distribution of juvenile and adult silverfish along the WAP shelf (Daniels and Lipps, 1982) was highly discontinuous at the time of the present study in early fall 2010, and what its implications are for silverfish on the WAP.

The prevailing consensus (e.g. Kellermann, 1996; La Mesa and Eastman, 2012; La Mesa et al., 2015) is that recruitment of *Pleuragramma* to the waters of the WAP shelf is by larval dispersal, a "larval pump", from spawning centers located in the western Weddell Sea (e.g. Larsen Bay) and the continental Bellingshausen Sea southwest of the Peninsula (Kellermann and Schadwinkel, 1991). The reason why
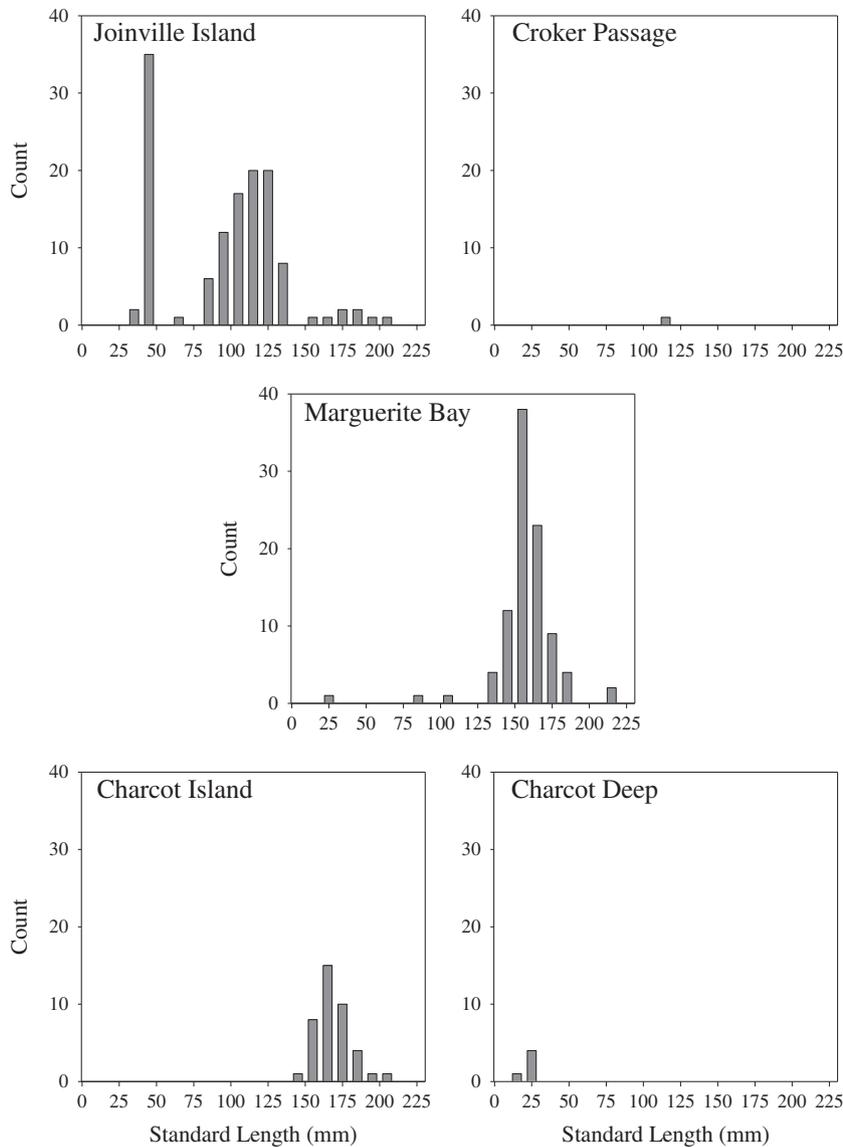
Fig. 11. Size distributions of *Pleuragramma antarctica* collected from each site during the 2010 cruise.

local reproduction on the WAP shelf has been ruled out is that very young post-larvae (<10 mm) have only been rarely captured on the peninsula in the many larval surveys conducted from the 1970's through the early 1990's (Kellermann, 1996), and that larvae were about an order of magnitude less abundant than at known spawning sites in the Weddell Sea itself (Kellermann, 1986). Larvae are assumed to be transported from the Weddell Sea via the Weddell Gyre/Antarctic Coastal Current as it flows through the Antarctic Sound and bends around Joinville Island (Fig. 1; Stein, 1983; Hofmann et al., 1996; La Mesa et al., 2015) and into the eastern Bransfield Strait. Larvae originating in the other hypothetical spawning site, the continental Bellingshausen Sea south of the peninsula, would be transported northeast in the upper 100 m of the Antarctic Circumpolar Current (ACC), merging with the general northeasterly flow at the shelf break along the peninsula, and making their way further inshore via the cross-shelf gyral flows in the vicinity of Alexander Island, Renaud Island, and the southern Bransfield Strait (Fig. 1; Hofmann et al., 1996; Piñones et al., 2011, 2013a). Once in shelf waters, post-larvae would presumably recruit to the WAP silverfish community.

The "larval pump" hypothesis is supported by a consistent presence of larval *Pleuragramma antarctica* in the Bransfield Strait from the 1970's

through the 1990's (Kellermann, 1986, 1996; Loeb, 1991; Morales-Nin et al., 1998) up through at least 2011 (La Mesa et al., 2015). Year-class strengths have been variable (Kellermann, 1996), but a steady larval supply has been present whenever sampling has taken place. Recent modeling of larval transport for *Pleuragramma* originating in the Weddell Sea strongly corroborates the dispersal path described above, both in terms of trajectory and timing relative to hatch-date (La Mesa et al., 2015). Once in the Bransfield Strait, larvae could be transported south via the Antarctic Peninsula Coastal Current (APCC), potentially to the Palmer Archipelago, the Biscoe Islands, and Marguerite Bay (Moffat et al., 2008; Niiler et al., 1991). Flow in the upper 200 m of the Gerlache Strait east of Anvers Island is generally north (Savidge and Amft, 2009), so dispersal of larvae further south via the Gerlache Strait would be severely constrained by the circulation (Fig. 1). Successful transport south would require that larvae be in the west central Bransfield Stait (Moffat et al., 2008; Niiler et al., 1991).

An alternative hypothesis to the "larval pump" of silverfish from the Weddell and Bellinghausen Seas is that successful reproduction has historically occurred on the WAP shelf beneath the winter sea ice. This would presume that larval sampling on the shelf missed young larvae produced locally in ice-covered embayments on the peninsula such as
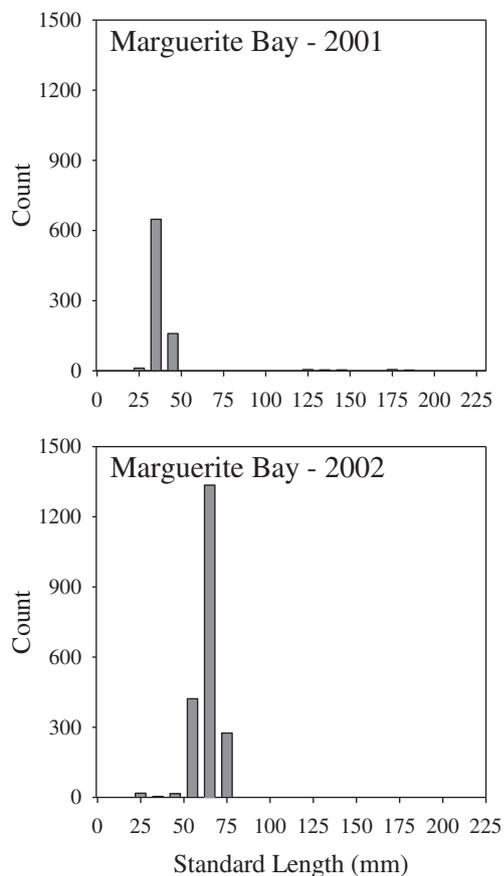
Fig. 12. Size distributions of *Pleuragramma antarctica* captured during the 2001 and 2002 SO GLOBEC cruises in the Marguerite Bay region of the Western Antarctic Peninsula (adapted from Donnelly and Torres, 2008).

Palmer Station's Arthur Harbor (cf. Daniels, 1982), Crystal Sound, and Marguerite Bay. Such local populations could have been founded by larvae transported from the Weddell and Bellingshausen Seas, but become established in their own right, recruiting from their own numbers and a steady larval supply from outside the WAP. A corollary to the presence of independent local populations is that they would be vulnerable to local population reductions, or even extinctions, in the face of unfavorable conditions brought about by a changing climate. The absence of silverfish from region II, which has been the most severely impacted by recent rapid regional warming, suggests such a population event, likely due to long-term absence of recruitment and either migration or mortality of adults.

Microchemical analyses of otolith nuclei conducted on fish captured during the present study revealed that there were no significant differences in isotopic ratios between fish captured in Marguerite Bay and near Charcot Island, and that ratios in those fish were significantly different than those from fish obtained from the Ross Sea (Ferguson, 2012). This suggests that *Pleuragramma* from Marguerite Bay and Charcot Island are part of one contiguous population. Genetic analyses performed on fish captured in the present study yielded similar results, with the Marguerite Bay and Charcot Island fish comprising a single, panmictic population that was differentiated from the Joinville Island fish (Agostini et al, 2015). Results of those studies coupled with the results presented here provide three lines of evidence, cluster analyses, otolith microchemical analyses, and genetic analyses, that there is little connectivity between silverfish populations in the northernmost region at Joinville Island and the two southernmost regions at Marguerite Bay and Charcot Island. Taken together, the observed results support a case for independent local populations of silverfish.

Region II, which shows the most pronounced effects of rapid regional warming in the study area, including mean annual temperatures that have increased by $5.7 \pm 2.0\,°\text{C century}^{-1}$ since 1951 (Vaughan et al., 2003) and a consistently earlier sea ice retreat at about the time-of-hatch for *Pleuragramma* eggs (November-December, Kellermann, 1996), also showed a virtual absence of silverfish. The fact that *Pleuragramma* spawns under coastal sea ice and that the eggs develop and hatch in a nursery of platelet ice when it is available (Vacchi et al., 2004, 2012) points to regional warming and its effects on seasonal sea ice dynamics as an important element in the species' absence in Region II. Phenology of reproduction in the local silverfish population may have been disrupted by early ice retreat, resulting in the absence of a sea ice refugium prior to hatching, with an accompanying change in predation pressure and altered prey spectrum for larvae, resulting in multiple years of poor local recruitment for larvae both originating in place and dispersing south.

Hydrographic information collected in the present study shows the increased landward influence of warm upper circumpolar deep water (UCDW) along the WAP over the last two decades described by Suprenand et al. (2013), Piñones et al. (2013b), Smith et al. (1999a), Martinson et al. (2008, Martinson, 2012) and Dinniman et al. (2012), effectively making the outer shelf a more oceanic system, particularly at depths below 200 m. In the present study, winter water was present only in the southernmost sites of region II, being absent at Anvers Island and Croker Passage. Previous studies concur with our results that *Pleuragramma antarctica* is a neritic species, not found in oceanic waters during its juvenile or adult stages (DeWitt, 1970; Donnelly and Torres, 2008; Donnelly et al., 2004; Lancraft et al., 1989, 1991) despite an entirely pelagic life history (La Mesa and Eastman, 2012). Increasing influence of upwelled warm oceanic waters (upper circumpolar deep water) on the shelf will likely constrict its distribution further to inner shelf locations, a trend observed in Marguerite Bay during the 2001, 2002 GLOBEC program (Donnelly and Torres, 2008). Further, any Weddell Sea larvae drifting south past Anvers Island and the Biscoe Islands will encounter a warmer water column and an altered prey spectrum.

Connectivity is key to understanding why silverfish were absent in Region II. The increasing eastward encroachment of oceanic water effectively pushes the neritic environment and its silverfish landward to refugia, such as Marguerite Bay and Charcot Island, that have retained some neritic character in their more predictable winter sea ice and presence of winter water. Limited access to the outer shelf also limits access to the northeasterly flow along the outer shelf and the "ascending limbs" of the gyre systems running along the WAP shelf (Fig. 1). Thus, south to north connectivity is restricted while north to south connectivity can persist along the APCC on the inner shelf. Re-population of Region II will have to be via larval dispersal mixing in from the north and whatever relict population has persisted in the face of the warming trend.

A recent study (La Mesa et al., 2014) examining the reproductive characteristics of *Pleuragramma* captured on the 2010 cruise described here, showed that the fish at Charcot Island and Marguerite Bay exhibited considerable reproductive potential, with high fecundities in the adult females. In the event of multiple strong ice years on the WAP shelf, successful reproduction, recruitment and rebound of *Pleuragramma* in the southern peninsula may be possible, perhaps restoring some continuity in its distribution along the peninsula. In contrast, continued warming and sea-ice retreat will likely cause their eventual disappearance.

5. Conclusions

Subtle changes in faunal composition and shifts in dominant taxa demonstrated the importance and influence of local hydrography on micronektonic fish and invertebrate distributions. On-shelf circulation patterns and identification of five different multispecies assemblages provide substantial support for the existence of distinct hydrographic regimes along the WAP shelf. Along with those findings, the disappearance

of *Pleuragramma* from Region II and the absence of younger year classes in Marguerite Bay suggest that populations within each region are sustained by local reproduction as well as larval advection. Region I is the exception since flow from the Weddell Sea provides a steady supply of larvae for recruitment. In the other regions, the unique hydrography of the WAP creates complex cross-shelf circulation processes that increase retention at inner shelf locations (Murphy et al., 2012; Piñones et al., 2011, 2013a), effectively limiting connectivity between the regions.

Mid-winter air temperatures in the vicinity of Region II have increased by nearly 6 °C over the past 50 years, resulting in an overall decrease in the extent and duration of the winter sea ice season (Fraser et al., 1992; Smith et al., 2003a,b). Sea ice has been forming later and retreating earlier over the last decade, leading to an almost two week decrease in the duration of the sea ice season (Ducklow et al., 2007; Stammerjohn et al., 2008a). If resident populations of ice-dependent species reproduce and recruit locally, the changes may render those populations highly susceptible to local extinction. This may be the causative factor behind the disappearance of *Pleuragramma* from Region II.

The disappearance of *Pleuragramma* from Region II underscores its life history's obligate tie to the sea-ice. Vacchi et al.'s (2004, 2012) identification of large numbers of *Pleuragramma* eggs in the platelet ice of Terra Nova Bay in the Ross Sea, confirmed that at a minimum, the early life history of silverfish is constrained to the sea ice. Sea ice is projected to decline and disappear from large areas of the WAP continental shelf, including the southern portion of the shelf, as a result of climate warming (Dinniman et al., 2012). Decreases in sea ice extent and duration have the potential to impact the population dynamics of several Antarctic species including upper trophic level predators such as penguins, seals and whales (Atkinson et al., 2004; Fraser and Hofmann, 2003; Lima and Estay, 2013). Continued warming and subsequent sea ice reductions may not only cause *Pleuragramma* population collapses in the Marguerite Bay and Charcot Island regions, but may also change the character of the faunal assemblages along the WAP to those of an oceanic system.

Acknowledgments

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