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Invertebrate micronekton and macrozooplankton in the Marguerite Bay region of the Western Antarctic Peninsula

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ABSTRACT

Invertebrate micronekton and macrozooplankton in the Marguerite Bay region of the Western Antarctic Peninsula (WAP) were sampled using a 10-m^2 MOCNESS as part of the Southern Ocean Global Ecosystem Dynamics (SO GLOBEC) program. A total of 62 trawls were completed during four separate cruises in the austral fall (April–June) and winter (July–September) of 2001 and 2002. Crustaceans dominated the system in both seasons, accounting for 32 of the 55 species captured in the fall and 30 of the 48 species captured in winter. In both seasons, a very few species made up the majority of the catch. In the fall, the euphausiids *Euphausia crystallorophias*, *Euphausia superba*, and *Thysanoessa macrura*, and the mysid *Antarctomysis ohlinii* numerically dominated the assemblage, contributing over 85% of the total. In the winter, the same three euphausiids and the chaetognath *Pseudosagitta gazellae* were the numerical dominants, comprising over 90% of the catch. A significant increase in total abundance and biomass was observed from 2001 to 2002.

The invertebrate micronekton/macrozooplankton communities found in the Marguerite Bay region of the WAP were a mixture of oceanic and neritic fauna: a direct result of local hydrographic conditions. Near the shelf break and in the outer reaches of the Marguerite Trough, a deep canyon transecting the shelf in a south-southeast direction, the communities were more diverse, dominated by oceanic species such as *Euphausia triacantha*, *Salpa thompsoni*, and *Themisto gaudichaudi*. The assemblages present in the nearshore fjords exhibited lower diversity and were dominated by neritic species such as *E. crystallorophias* and *A. ohlinii*. At the mid-shelf and mid-trough locations, the assemblages were composed of a variable mixture of oceanic and neritic fauna. The faunal mixing and overall species composition in those areas is the result of episodic Circumpolar Deep Water (CDW) intrusions onto the shelf via deep bathymetric features such as the Marguerite Trough.

Species diversity and integrated abundance for the upper 200 m of the water column were similar between seasons in the WAP study region, but integrated biomass was nearly three times greater in fall than in winter. Integrated estimates from the WAP study region were similar to those from other studies conducted in the Scotia and Weddell Seas, but were orders of magnitude lower than estimates from a study in Croker Passage, primarily due to a large catch of *E. superba*. In contrast, species diversity in the WAP was higher than recorded in any of the previously mentioned studies, which is due to the mixing of typical oceanic fauna with endemic nearshore fauna.

1. Introduction

The continental shelf in the Marguerite Bay region of the Western Antarctic Peninsula (WAP) comprises a varying mixture of oceanic and neritic fauna. The mix is a result of at least three physical properties of the WAP shelf that remove barriers to shelfward movement of open ocean species. First, its depth, though typical of the Antarctic continental shelf (200–500 m; Eastman, 1993), is far greater than that found in more temperate systems (200 m maximum; Sverdrup et al., 1942), resulting in an environment with little to no depth limitation on distributions of open ocean fauna (Eastman, 1993). Second, and unique to the WAP shelf, is the absence of a steep temperature and salinity gradient, or slope front, at the shelf break, further increasing the potential for faunal mixing (Klinck et al., 2004). Many species, especially fish, are sensitive to the sharp temperature gradients encountered at the shelf break in most Antarctic coastal systems (cf. Cullins et al., 2011) and as a result there is a clear demarcation between oceanic and coastal assemblages in other Antarctic regions. A third prominent physical feature of the WAP shelf region is the proximity of the Antarctic Circumpolar Current (ACC), which flows in a northeasterly direction near the shelf break. Many cross-shelf troughs and depressions are found on the WAP shelf, providing a route for intrusions of warm, oceanic Circumpolar Deep Water (CDW) and yet another

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mechanism for mixing open ocean and coastal assemblages (Hofmann et al., 1996; Smith et al., 1999; Klinck et al., 2004).

CDW is nutrient-rich water mass associated with the ACC, characterized by temperatures ranging from 1.0 to 2.0 °C and salinities from 34.6 to 34.74. CDW intrusions onto the shelf occur when the ACC is deflected by changes in topography (Dinniman and Klinck, 2004). CDW typically resides at depths below 200 m, resulting in a water mass structure at depth that is nearly oceanic in character. In our study area, the Marguerite Trough, a deep canyon transecting the shelf in a south-southeast direction near Adelaide Island, enhances the extent of CDW intrusions by providing a deep connection between the outer shelf and inner reaches of Marguerite Bay. In 2001, Klinck et al. (2004) identified two to three CDW intrusions onto the shelf near Marguerite Bay, leading them to estimate a possible 4–6 intrusions/year in this region.

The importance of those CDW intrusions is three-fold. First, they may serve as an integral part of the life history of many species. For example, the presence or absence of CDW can greatly influence the success or failure of larval hatching in Antarctic krill (*Euphausia superba*). *E. superba* embryos sink after release in the water column, hatch at depth and then ascend to the surface during larval development (Marr, 1962). The fairly shallow depth and warm temperature of the CDW allow the larvae in turn to hatch at shallower depths and develop faster thus increasing their chances of survival (Hofmann et al., 1992; Hofmann and Husrevoglu, 2003). Second, the influx of nutrients into surface waters via upwelling of CDW onto the shelf can create areas of enhanced biological production (Prezelin et al., 2004). Finally as CDW moves shelfward the diffusion of heat and nutrients into cooler surface waters will influence annual sea ice formation (Dinniman and Klinck, 2004).

Due to its unique physical properties, the WAP shelf region is one of the most productive areas in the Southern Ocean and also serves as an important nursery ground for the Antarctic krill, *E. superba* (Marr, 1962; Siegel, 1988; Atkinson et al., 2001). Most descriptions of the Antarctic pelagic ecosystem have focused on *E. superba* due to its overwhelming abundance and widespread distribution, and its ecological importance as a primary food source for fishes, seabirds, penguins, seals, and whales (Marr, 1962; Laws, 1985, Knox, 1994). However, there are not only three other abundant species of euphausiid, but also an entire suite of micronektonic and macrozooplanktonic species that play a role in the ecology of the WAP ecosystem (Piatkowski, 1985; Lancraft et al., 1989, 1991, 2004). By describing the contributions of all species present in the study area and relating their distributions to the local hydrography, we will approach a more complete understanding of the WAP shelf ecosystem.

As part of the Southern Ocean Global Ecosystem Dynamics (SO GLOBEC) program, the present study examined the invertebrate micronekton/macrozooplankton communities found in the Marguerite Bay region of the WAP including the taxonomic composition, interannual variability, and distribution patterns of those communities during the fall and winter in 2001 and 2002. Multivariate techniques were used to identify unique multispecies assemblages and to quantify the contributions of both oceanic and neritic species to those assemblages. Finally we compared the integrated abundance and biomass of the WAP pelagic community to several other oceanic ecosystems both within and outside of the Southern Ocean.

2. Methods

2.1. Study area

The present study took place during four cruises to the Marguerite Bay region of the Western Antarctic Peninsula. Cruises 1 and 3 sampled during the austral fall aboard the Antarctic Support Research Vessel (A.S.R.V.) *Laurence M. Gould* (April–June 2001 and 2002 inclusive) and cruises 2 and 4 were aboard the Research Vessel Ice Breaker (R.V.I.B.) *Nathaniel B. Palmer* during the winter season (July–September 2001 and 2002 inclusive). Fall cruises had a process sampling strategy, occupying six sites for 5–6 days at each of six locations within the study region. Winter cruises aboard the *RVIB Palmer* sampled along a predetermined survey grid comprised of stations at 20 km intervals along 12–14 across-shelf transects (Hofmann et al., 2004).

Each general process site was sampled at multiple locations (Fig. 1). For purposes of discussion, each general process site will be termed "site" and the sampling stations within the site will be termed "stations". Process site 1 was located near the shelf break at the mouth of the Marguerite Trough. Samples were collected from four stations (1a–1d) within site 1. Process site 2 was located approximately mid-shelf within the Marguerite Trough and included stations 2a and 2b. Process site 3 was a generic mid-shelf designation that included several different stations located on the continental shelf outside of Marguerite Bay. Stations 3a, 3b, 3d, 3e, 3g, and 3h were shallow, with bottom depths less than 350 m while stations 3c, 3f, and 3i had bottom depths of greater than 470 m. Process site 4 was located at the southern end of the Marguerite Trough in George VI Sound. Stations within site 4 (4a and 4b) were only sampled in fall 2001. Process site 5 was in northern Marguerite Bay and included four stations (5a–5d) located southeast of Adelaide Island. Process site 7 was northeast of Adelaide Island in Crystal Sound and included stations 7a and 7b. The missing process site 6, originally located south of Marguerite Bay, was not sampled during any of the four cruises due to heavy ice conditions.

2.2. Specimen collection

Macrozooplankton and micronekton were collected with a 10-m^2 Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with six 3-mm mesh nets (Wiebe

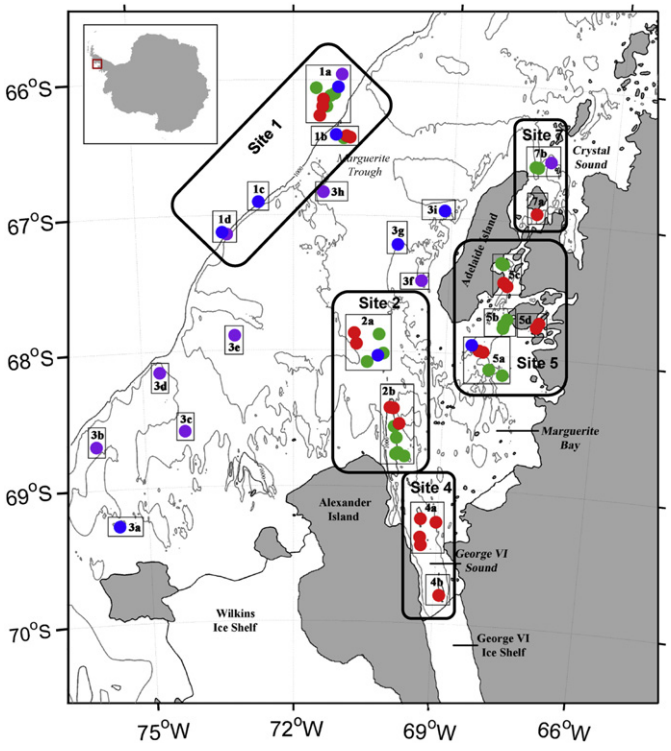

Fig. 1. Trawl locations for fall and winter SO GLOBEC cruises. Large rectangles represent sampled sites while smaller rectangles represent sampled stations within each site. Red circles = Fall 2001, blue circles = Winter 2001, green circles = Fall 2002, purple circles = Winter 2002.

et al., 1976, 1985). Towing speed for all trawls was 1.5–2.2 knots. During those trawls, the first net fished obliquely from surface to depth with each subsequent net fishing a discrete depth layer upward to the surface. Trawls reaching depths of 400 m or less sampled depth strata of 0–50, 50–100, 100–150, 150–200, and 200–400 m. Trawls reaching depths between 400 and 500 m sampled depth strata of 0–50, 50–100, 100–200, 200–300, and 300–400 or 500 m. Trawls reaching depths between 700 and 1000 m sampled depth strata of 0–50, 50–100, 100–200, 200–500, and 500–700 or 1000 m. A total of 62 trawls were completed during the four cruises with 22 occurring during each fall cruise and 9 per winter cruise (Table 1). Most trawls (49 of 62) were conducted at night, or dusk, with only a few occurring during the day.

Table 1
10-m^2 MOCNESS trawl data from four SO GLOBEC cruises conducted in 2001 and 2002 near the Marguerite Bay region of the Western Antarctic Peninsula. Trawls are organized by season and station. Local time=GMT—4 h, TOD=time of day.

Season	Site	Station	Cruise	Trawl	Date (GMT)	Time (GMT)	TOD	Latitude (°S)	Longitude (°S)	Trawl depth(m)	Bottom depth (m)	Volume filtered (m^3)
Fall	1	1a	1	1	4/30/2001	2:22	Night	66 12.23	71 24.77	1000	2954	140,758
Fall	1	1a	1	3	5/2/2001	23:25	Night	66 15.44	71 25.08	1000	2812	138,304
Fall	1	1a	1	4	5/3/2001	23:50	Night	66 09.08	71 24.00	1000	2986	180,947
Fall	1	1a	3	12	4/27/2002	14:45	Day	66 03.20	71 27.80	1000	3186	95,905
Fall	1	1a	3	9	4/24/2002	21:45	Night	66 05.10	71 13.80	1000	3041	75,142
Fall	1	1a	3	10	4/25/2002	3:00	Night	66 07.40	71 16.30	500	2974	45,826
Fall	1	1a	3	11	4/25/2002	22:33	Night	66 12.80	71 21.30	1000	2994	79,089
Fall	1	1b	1	5	5/4/2001	19:55	Night	66 24.49	70 59.36	500	542	76,950
Fall	1	1b	1	6	5/5/2001	0:40	Night	66 25.18	70 58.81	500	542	56,815
Fall	1	1b	3	13	4/28/2002	2:28	Night	66 25.40	71 06.10	400	545	50,476
Fall	2	2a	1	21	5/19/2001	23:10	Night	67 56.65	70 32.47	500	760	54,560
Fall	2	2a	1	22	5/20/2001	2:07	Night	67 50.46	70 35.02	500	805	79,078
Fall	2	2a	3	20	5/7/2002	17:44	Day	68 00.20	70 02.90	750	832	114,263
Fall	2	2a	3	19	5/7/2002	0:08	Night	68 05.10	70 21.80	750	864	92,175
Fall	2	2a	3	21	5/7/2002	23:33	Night	67 52.40	70 08.90	500	676	74,030
Fall	2	2b	1	18	5/18/2001	17:35	Day	68 24.84	70 00.22	500	1016	37,755
Fall	2	2b	1	19	5/18/2001	21:38	Night	68 31.90	69 53.60	500	790	98,076
Fall	2	2b	1	20	5/19/2001	2:12	Night	68 24.57	69 59.95	500	944	75,101
Fall	2	2b	3	17	5/4/2002	17:05	Day	68 38.40	69 52.60	750	861	85,524
Fall	2	2b	3	14	5/2/2002	1:20	Night	68 45.20	69 52.80	800	1055	79,972
Fall	2	2b	3	15	5/3/2002	0:36	Night	68 45.10	69 53.10	800	1016	69,839
Fall	2	2b	3	16	5/4/2002	0:38	Night	68 46.50	69 49.40	716	676	76,439
Fall	2	2b	3	18	5/4/2002	23:33	Night	68 32.60	69 54.30	750	820	87,855
Fall	4	4a	1	13	5/13/2001	19:45	Dusk	69 14.70	69 13.80	500	958	66,815
Fall	4	4a	1	14	5/14/2001	0:30	Night	69 14.95	69 02.20	500	634	59,168
Fall	4	4a	1	15	5/14/2001	22:50	Night	69 24.20	69 13.70	500	983	60,860
Fall	4	4a	1	16	5/15/2001	2:12	Night	69 20.16	69 13.79	700	892	92,823
Fall	4	4b	1	17	5/17/2001	2:16	Night	69 47.96	68 52.04	800	1050	83,995
Fall	5	5a	1	7	5/6/2001	23:20	Night	67 56.98	68 20.81	500	790	108,518
Fall	5	5a	1	8	5/7/2001	0:13	Night	67 56.68	68 21.12	500	803	94,311
Fall	5	5a	3	22	5/10/2002	1:27	Night	68 05.80	68 14.90	400	302	39,433
Fall	5	5a	3	23	5/11/2002	2:13	Night	68 07.90	68 01.20	400	493	38,062
Fall	5	5b	3	7	4/22/2002	19:07	Day	67 46.90	68 07.20	500	827	66,420
Fall	5	5b	3	6	4/22/2002	2:36	Night	67 45.80	68 06.80	500	715	46,974
Fall	5	5b	3	8	4/23/2002	2:45	Night	67 42.50	68 04.80	500	613	49,943
Fall	5	5c	1	9	5/8/2001	0:50	Night	67 25.24	67 51.50	400	445	41,429
Fall	5	5c	1	12	5/11/2001	23:13	Night	67 27.40	67 50.40	400	495	62,191
Fall	5	5c	3	4	4/20/2002	0:05	Night	67 18.10	67 50.30	500	628	41,798
Fall	5	5c	3	5	4/20/2002	2:42	Night	67 18.20	67 50.20	444	650	43,382
Fall	5	5d	1	11	5/10/2001	18:20	Day	67 45.90	67 17.90	400	453	44,391
Fall	5	5d	1	10	5/9/2001	1:30	Night	67 46.30	67 18.50	300	380	42,646
Fall	7	7a	1	23	5/30/2001	1:30	Night	66 51.14	67 16.90	400	525	42,271
Fall	7	7b	3	2	4/17/2002	5:05	Night	66 38.10	67 26.00	300	380	24,752
Fall	7	7b	3	3	4/17/2002	9:30	Night	66 38.30	67 25.90	300	387	29,662
Winter	1	1a	2	1	7/30/2001	14:28	Day	66 02.38	71 13.38	1000	3100	89,751
Winter	1	1a	4	9	9/2/2002	19:07	Dusk	65 57.20	71 02.80	1000	3562	136,246
Winter	1	1b	2	8	8/24/2001	13:45	Day	66 23.01	71 19.72	800	839	38,862
Winter	1	1c	2	3	8/3/2001	19:51	Dusk	66 53.62	72 36.90	1000	1190	101,758
Winter	1	1d	2	6	8/10/2001	16:03	Day	67 07.86	73 19.51	1000	1826	112,383
Winter	1	1d	4	6	8/21/2002	1:58	Night	67 09.20	73 14.70	1000	>1000	89,936
Winter	2	2a	2	4	8/5/2001	15:25	Day	68 02.16	70 19.80	500	820	62,292
Winter	3	3a	2	7	8/21/2001	18:54	Dusk	69 16.33	75 38.84	300	338	32,116
Winter	3	3b	4	2	8/12/2002	1:00	Night	68 40.00	76 08.60	350	430	40,933
Winter	3	3c	4	3	8/15/2002	23:00	Night	68 34.40	74 09.00	500	677	35,017
Winter	3	3d	4	4	8/17/2002	19:12	Dusk	68 08.80	74 35.50	350	417	18,971
Winter	3	3e	4	7	8/24/2002	1:32	Night	67 53.20	73 05.90	250	376	21,548
Winter	3	3f	4	11	9/8/2002	1:37	Night	67 28.00	69 32.10	500	>500	63,692
Winter	3	3g	2	2	8/1/2001	20:46	Night	67 12.86	70 00.12	300	433	35,831
Winter	3	3h	4	10	9/6/2002	17:48	Day	66 49.20	71 25.30	400	479	54,798
Winter	3	3i	2	9	8/25/2001	12:18	Day	66 58.16	69 24.61	466	546	30,969
Winter	5	5a	2	5	8/8/2001	14:01	Day	67 55.20	68 30.80	500	650	39,673
Winter	7	7b	4	1	8/7/2002	23:07	Night	66 32.50	67 05.80	500	1200	50,052

Specimens collected during each cruise were preserved in a 5–10% buffered formaldehyde solution and shipped to the laboratory for analysis. All invertebrate micronektonic and macrozooplanktonic specimens were sorted, counted, identified to lowest possible taxon, and weighed (g wet mass). Numerically abundant species, 3 euphausiids and 1 mysid, were first sorted into 20 mm size classes (0–20, 21–40, and 41–60 mm) and then enumerated and weighed. Large collections of euphausiids at times required subsampling. Those were initially sorted to remove any non-euphausiid taxa, which were then enumerated and weighed. The remaining euphausiids were then subsampled using a Motoda splitter (Motoda, 1959). Counts and weights of the subsampled euphausiids were used to estimate the total number and wet mass of euphausiids in the sample. The larval furcilia stage of *E. superba* was considered independently from adult *E. superba* in all analyses except for the size class distributions. After processing, samples were transferred to 50% isopropanol for long term storage. All fish collected in the samples were processed and analyzed by Donnelly and Torres (2008).

2.3. Data analysis

Volumetric abundance and biomass values from each trawl were obtained by dividing the raw number or wet mass by the water volume filtered during each trawl (# 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 cruise as well as the mean overall abundance and biomass for each cruise. Statistical comparisons between cruises were performed on the volumetric data (# or g WM $\times 10^4$ m^{-3}) using generalized linear mixed models in SAS version 9.2 (SAS Institute Inc., Cary, NC, USA).

Seasonal vertical distributions for 11 common species were compiled from nets that fished within the following depth strata: 0–50, 50–100, 100–200, 200–500, and 500–1000 m. For vertical distributions, standardized volumetric values were calculated from total abundances and total volumes filtered per depth stratum. Those values were used to determine vertical ranges for each species. The peak range was chosen as the stratum with the highest recorded abundance.

Invertebrate macrozooplankton/micronekton assemblage structure was analyzed by multivariate techniques using the PRIMER v6 software package (Clarke and Gorley, 2006). 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). For each cruise, mean volumetric abundance and biomass at each sampled station were used to calculate Bray–Curtis similarity matrices that were subsequently used to generate hierarchical cluster analysis dendrograms and MDS ordination plots. Because many stations were only sampled with one trawl during the cruises, significant differences in multispecies assemblages were determined by the SIMPROF procedure. The SIMPROF (similarity profile permutation test) procedure assumes no *a priori* structure to the data and tests the null hypothesis that there is no meaningful structure. When SIMPROF is conducted in conjunction with cluster analysis, it creates a dendrogram that displays statistically significant structure in the data. Those groups denoted by a solid dark line are found to have significant structure ($P<0.05$), while those denoted by lighter dashed lines are found to have to no further significant structure ($P>0.05$) and may simply represent a clustering of random variability (Clarke et al., 2008). The SIMPER (analysis of similarity percentages) procedure was used to identify those taxa contributing most to the similarities within each resultant cluster group. Shannon's diversity index (H') and Pielou's evenness (J') were also calculated for the fall and winter abundance cluster groups (Shannon and Weaver, 1949; Pielou, 1966).

For regional comparisons, each taxon's integrated abundance (# m^{-2}) and biomass (g WM m^{-2}) for the 0–200 m stratum in both fall and winter was calculated by dividing the total number or wet mass by the water volume filtered for the depth stratum sampled by each net. Those values were then multiplied by the vertical range, in meters, for each depth stratum and summed. Because there were so few daytime trawls, those data were omitted from this analysis.

3. Results

3.1. Taxonomic composition

A total of 58 taxa (55 in the fall, 48 in the winter) belonging to sixteen different taxonomic groups were collected during this study (Tables 2 and 3). Although the catch was fairly diverse, only a few species accounted for the majority of the total abundance and biomass. Three euphausiids, *Euphausia crystallorophias*, *E. superba*, and *Thysanoessa macrura*, and one mysid, *Antarctomysis ohlinii*, ranked as the most abundant taxa in each individual cruise, with the only exceptions occurring during the 2002 winter cruise when both *E. crystallorophias* and *A. ohlinii* were outnumbered by the chaetognath, *Pseudosagitta gazellae* and the amphipod *Epimeriella macronyx*. Interannual differences were observed in taxon contributions to total abundance. In fall 2001, the numerically dominant species was *A. ohlinii,* but that shifted to *E. cystallorophias* in fall 2002. Abundance rankings also differed between winter cruises with *E. superba* displacing *T. macrura* as the ranking species in 2002.

With respect to biomass, *E. superba* was the dominant species in three of the four cruises (not in winter 2001) contributing from 41% to 73% of the catch. The other numerically dominant species' (*E. crystallorophias*, *T. macrura*, and *A. ohlinii*) also contributed substantially to total biomass, but were occasionally out-ranked by the large scyphozoans *Atolla wyvillei* and *Periphylla periphylla*. Removal of the scyphozoans from the analyses revealed that the four numerically dominant species accounted for no less than 78% of the captured biomass during any individual cruise. Biomass rankings were nearly identical during both fall cruises, but there was a shift from winter 2001 to 2002. In winter 2001, *E. crystallorophias*, *T. macrura*, and *E. superba* all supplied similar contributions to biomass, ranging from 10% to 13% of the catch. However, in winter 2002, *E. superba* dominated and accounted for more than 70% of the captured biomass.

Size distributions of the dominants during each of the four cruises are shown in Fig. 2. *A. ohlinii* and *T. macrura* had fairly consistent size class breakdowns throughout the four cruises with the majority of individuals captured falling into the small (0–20 mm) size class. However, both *E. crystallorophias* and *E. superba* exhibited a different pattern. In fall and winter 2001 (cruises 1 and 2), the majority ($>88\%$) of captured *E. crystallorophias* were in the 21–40 mm size class. In 2002, the number of individuals in the small size class increased and this shifted the size class distributions to a nearly equal spread between 0–20 and 21–40 mm individuals. *E. superba* exhibited a similar pattern, shifting from a large size class dominated distribution in 2001 to a small to intermediate size class dominated distribution in 2002.

3.2. Interannual comparisons

The total volume filtered during each fall cruise (1,737,762 vs. 1,406,961 m^3) was similar, but both the mean number of specimens (300.209 vs. 1289.075 individuals 10^4 m^{-3}; $P=0.0004$) and

Table 2
Mean abundance (no. of individuals $\times 10^4$ m^{-3}) and biomass (g WM $\times 10^4$ m^{-3}) of each species during fall 2001 and 2002. n=number of trawls, VF=total volume filtered (m^3), SD=standard deviation.

Taxonomic group	Taxa	Fall 2001 (n=22) VF=1,737,762 m^3				Fall 2002 (n=22) VF=1,406,961 m^3			
		10^4 m^{-3}	SD	g WM $\times 10^4$ m^{-3}	SD	10^4 m^{-3}	SD	g WM $\times 10^4$ m^{-3}	SD
Amphipoda-Gammaridea	*Cyphocaris richardi*	0.398	0.84	0.0737	0.14	0.653	1.06	0.1597	0.25
	Epimeria sp.	0.010	0.05	0.0002	0.00	0.032	0.11	0.0016	0.01
	Epimeriella macronyx	7.617	13.70	2.4137	4.88	35.246	40.01	7.9833	8.12
	Eusiroides stenopleura	0.003	0.01	0.0007	0.00	0.021	0.06	0.0027	0.01
	Eusirus microps	0.364	0.37	0.1786	0.25	1.209	1.39	0.6195	0.79
	Eusirus properdentatus	11.280	9.87	0.8288	0.92	7.207	8.50	3.8042	3.94
	Orchomene plebs	1.900	1.81	0.4435	0.51	4.918	4.09	1.3096	1.34
	Parandania boecki	0.024	0.07	0.0025	0.01	0.083	0.19	0.0225	0.06
Amphipoda-Hyperiidaea	*Cyllopus lucasii*	0.425	0.46	0.0472	0.06	1.113	1.00	0.1420	0.12
	Hyperia macrocephala	0.146	0.20	0.0403	0.06	0.177	0.19	0.0599	0.09
	Hyperiella macronyx	0.003	0.02	0.0002	0.00				
	Hyperoche medusarum								
	Lanceola sayana					0.017	0.06	0.0032	0.01
	Pegohyperia princeps					0.006	0.03	0.0033	0.02
	Primno macropa	1.472	1.30	0.0753	0.07	2.179	2.47	0.1428	0.15
	Scina sp.								
	Themisto gaudichaudi	9.375	11.17	0.8659	1.08	24.602	36.76	2.1247	3.35
	Vibilia stebbingi								
Decapoda	*Gennadas kempi*	0.013	0.04	0.0111	0.04	0.106	0.26	0.1169	0.32
	Notocrangon antarcticus					0.019	0.09	0.1005	0.47
	Pasiphaea scotiae	0.033	0.06	0.0774	0.19	0.106	0.16	0.2059	0.48
	Petalidium foliaceum	0.018	0.05	0.0086	0.02	0.084	0.18	0.0526	0.10
Euphausiacea	*Euphausia crystallorophias*	32.056	105.58	5.0500	17.53	579.111	1067.65	77.4045	164.23
	Euphausia frigida	0.503	0.96	0.0177	0.03	0.998	2.92	0.0457	0.13
	Euphausia superba	69.820	115.16	52.3377	95.80	422.249	528.13	109.3476	124.24
	Euphausia superba furcilia	8.757	12.25	0.1108	0.17				
	Euphausia triacantha	3.472	6.13	0.6921	1.24	11.242	21.72	2.1429	4.02
	Thysanoessa macrura	29.197	29.84	2.2378	1.86	44.273	59.45	3.6892	3.79
Lophogastrida	*Eucopia australis*	0.003	0.02	0.0025	0.01	0.006	0.03	0.0053	0.02
	Neognathophausia gigas	0.003	0.02	0.0010	0.00	0.025	0.06	0.0241	0.08
Mysida	*Antarctomysis maxima*	3.686	7.08	0.2961	0.59	4.966	6.63	1.1633	2.13
	Antarctomysis ohlinii	85.195	158.40	18.2028	41.03	89.696	130.72	34.1691	54.26
	Boreomysis sp.	4.819	6.86	0.2604	0.37	17.286	32.52	1.4189	2.82
	Dactylamblyops hodgsoni	0.410	1.05	0.0228	0.06	0.212	0.37	0.0195	0.03
	Mysidetes sp.	0.018	0.06	0.0010	0.00	0.038	0.15	0.0034	0.01
Ostracoda	*Gigantocypris muelleri*	0.039	0.08	0.0308	0.06	0.114	0.20	0.1070	0.17
Cephalopoda	*Alluroteuthis antarcticus*	0.009	0.03	0.0016	0.01	0.084	0.14	0.0686	0.12
	Bathyteuthis abyssicola	0.003	0.02	0.0125	0.06	0.015	0.05	0.0756	0.27
	Galiteuthis glacialis					0.010	0.03	0.0025	0.01
	Mesonychoteuthis hamiltoni					0.006	0.03	0.0018	0.01
Gastropoda	*Clio pyramidata*	0.037	0.09	0.0043	0.01	0.020	0.07	0.0187	0.06
	Clione antarctica	0.049	0.09	0.0065	0.01	0.016	0.06	0.0038	0.01
	Gymnosome	0.190	0.18	0.0158	0.02	0.346	0.52	0.0258	0.05
	Spongiobranchaea australis					0.016	0.04	0.0008	0.00
Nemertea	*Obnemertes* sp.					0.028	0.08	0.0290	0.08
Polychaeta	*Tomopteris carpenteri*	0.307	0.25	0.1347	0.14	0.251	0.27	0.2878	0.38
	Vanadis antarctica					0.006	0.03	0.0040	0.02
Hydrozoa	*Calycopsis borchgrevinki*	0.195	0.27	0.2440	0.36	0.332	0.67	0.4409	0.61
	Crossota brunnea	15.591	65.53	1.2500	5.36	0.876	2.45	0.0863	0.25
	Diphyes antarctica	0.091	0.13	0.0198	0.03	0.088	0.16	0.0297	0.06
	Leptomedusa	0.287	0.51	0.1139	0.23	0.693	0.77	1.0911	1.31
Scyphozoa	*Atolla wyvillei*	0.220	0.45	4.8986	10.10	0.652	1.00	9.5986	14.93
	Periphylla periphylla	0.094	0.17	8.6019	30.17	0.227	0.38	1.8173	3.89
	Stygiomedusa gigantea[a]	0.006	0.03			0.017	0.05		
Ctenophora	*Beroe* sp.	0.003	0.02	0.0041	0.02	0.009	0.04	0.0313	0.15
Chaetognatha	*Eukrohnia hamata*	0.029	0.14	0.0018	0.01	0.880	3.44	0.0192	0.08
	Pseudosagitta gazellae	3.584	4.61	0.3812	0.52	5.443	3.95	1.7302	1.31
	Sagitta marri					0.450	1.79	0.0103	0.04
Tunicata	*Salpa thompsoni*	8.456	14.07	2.7538	4.91	30.614	92.54	6.3599	16.34
	Mean total	300.209		102.775		1289.075		268.128	

[a] No weights were recorded for these specimens.

Table 3
Mean abundance (no. of individuals $\times 10^4$ m^{-3}) and biomass (g WM $\times 10^4$ m^{-3}) of each species during winter 2001 and 2002. n=number of trawls, VF=total volume filtered (m^3), SD=standard deviation.

Taxonomic group	Taxa	Winter 2001 (n=9) VF=543,635 m^3				Winter 2002 (n=9) VF=511,192 m^3			
		10^4 m^{-3}	SD	g WM 10^4 m^{-3}	SD	10^4 m^{-3}	SD	g WM 10^4 m^{-3}	SD
Amphipoda-Gammaridea	*Cyphocaris richardi*	0.247	0.21	0.0451	0.06	0.387	0.56	0.1442	0.23
	Epimeria sp.								
	Epimeriella macronyx	4.968	13.10	1.1939	3.37	11.752	18.23	2.8760	4.51
	Eusiroides stenopleura								
	Eusirus microps	0.224	0.67	0.1058	0.32	0.564	0.78	0.1452	0.21
	Eusirus properdentatus	2.844	7.27	0.4134	1.08	2.355	4.26	2.9765	5.91
	Orchomene plebs	0.688	1.09	0.1336	0.33	3.789	5.15	0.8080	1.11
	Parandania boecki	0.023	0.05	0.0009	0.00	0.008	0.02	0.0013	0.00
Amphipoda-Hyperiidaea	*Cyllopus lucasii*	0.480	0.63	0.0576	0.09	1.553	2.84	0.3208	0.61
	Hyperia macrocephala	2.374	5.55	0.4104	1.12	0.410	0.33	0.0628	0.09
	Hyperiella macronyx	0.450	1.35	0.0218	0.07	0.258	0.77	0.0115	0.03
	Hyperoche medusarum	0.036	0.11	0.0013	0.00				
	Lanceola sayana								
	Pegohyperia princeps	0.021	0.04	0.0141	0.03	0.021	0.04	0.0089	0.02
	Primno macropa	1.624	0.70	0.1002	0.07	2.517	1.96	0.1375	0.08
	Scina sp.	0.011	0.03	0.0005	0.00				
	Themisto gaudichaudi	5.811	14.14	0.6412	1.59	1.572	3.40	0.1685	0.36
	Vibilia stebbingi					0.012	0.04	0.0006	0.00
Decapoda	*Gennadas kempi*	0.091	0.16	0.0741	0.14	0.049	0.15	0.0471	0.14
	Notocrangon antarcticus	0.028	0.08	0.0507	0.15				
	Pasiphaea scotiae	0.215	0.22	0.1473	0.26	0.037	0.08	0.0394	0.08
	Petalidium foliaceum	0.241	0.43	0.1563	0.28	0.070	0.18	0.0578	0.14
Euphausiacea	*Euphausia crystallorophias*	76.989	204.56	8.5115	22.60	3.337	9.76	0.2600	0.76
	Euphausia frigida								
	Euphausia superba	11.383	23.26	6.4765	13.49	585.688	944.20	121.7746	241.76
	Euphausia superba furcilia	0.977	2.13	0.0072	0.01				
	Euphausia triacantha	1.133	1.24	0.1286	0.14	7.504	5.54	1.5886	1.18
	Thysanoessa macrura	135.843	87.33	6.8471	3.86	195.532	133.17	11.7656	8.52
Lophogastrida	*Eucopia australis*	0.041	0.09	0.0171	0.04	0.025	0.07	0.0153	0.05
	Neognathophausia gigas	0.069	0.12	0.0874	0.14	0.016	0.05	0.0292	0.09
Mysida	*Antarctomysis maxima*	0.924	2.77	0.1077	0.32	0.336	0.51	0.0527	0.11
	Antarctomysis ohlinii	16.878	50.57	2.6205	7.85	0.488	1.47	0.0831	0.25
	Boreomysis sp.	1.094	2.44	0.0671	0.16	9.924	27.99	0.7625	2.16
	Dactylamblyops hodgsoni					0.116	0.22	0.0097	0.02
	Mysidetes sp.								
Ostracoda	*Gigantocypris muelleri*	0.103	0.18	0.0862	0.16	0.145	0.24	0.1879	0.31
Cephalopoda	*Alluroteuthis antarcticus*	0.032	0.07	0.0106	0.03	0.029	0.06	0.0572	0.15
	Bathyteuthis abyssicola	0.010	0.03	0.0356	0.11				
	Galiteuthis glacialis								
	Mesonychoteuthis hamiltoni								
Gastropoda	*Clio pyramidata*	0.332	0.38	0.0294	0.05	0.185	0.33	0.0189	0.04
	Clione antarctica	0.307	0.53	0.0571	0.08	0.112	0.14	0.0109	0.01
	Gymnosome	0.190	0.17	0.0246	0.02	0.557	0.55	0.0327	0.04
	Spongiobranchaea australis					0.110	0.30	0.0021	0.01
Nemertea	*Obnemertes* sp.	0.011	0.03	0.0159	0.05	0.012	0.04	0.0416	0.12
Polychaeta	*Tomopteris carpenteri*	0.428	0.30	0.3792	0.37	0.566	0.78	0.4518	0.51
	Vanadis antarctica	0.036	0.11	0.0377	0.11				
Hydrozoa	*Calycopsis borchgrevinki*	0.476	0.38	0.7604	0.81	0.441	0.64	0.7877	1.07
	Crossota brunnea								
	Diphyes antarctica	0.290	0.15	0.0685	0.06	4.521	11.96	0.3630	0.47
	Leptomedusa	0.370	0.53	0.7537	1.02	0.157	0.35	0.4595	1.12
Scyphozoa	*Atolla wyvillei*	1.070	1.33	24.5645	29.66	0.433	0.73	10.3710	17.19
	Periphylla periphylla	0.226	0.35	8.9417	14.01	0.215	0.29	1.9844	3.08
	Stygiomedusa gigantea[a]					0.026	0.05		
Ctenophora	*Beroe* sp.	0.012	0.04	0.0138	0.04	0.012	0.04	0.0337	0.10
Chaetognatha	*Eukrohnia hamata*								
	Pseudosagitta gazellae	9.157	5.93	1.6314	1.42	12.736	8.51	5.9743	4.73
	Sagitta marri								
Tunicata	*Salpa thompsoni*	1.322	2.17	0.2238	0.44	8.104	8.11	1.5002	1.73
	Mean Total	280.078		66.073		856.683		166.424	

[a] No weights were recorded for these specimens.

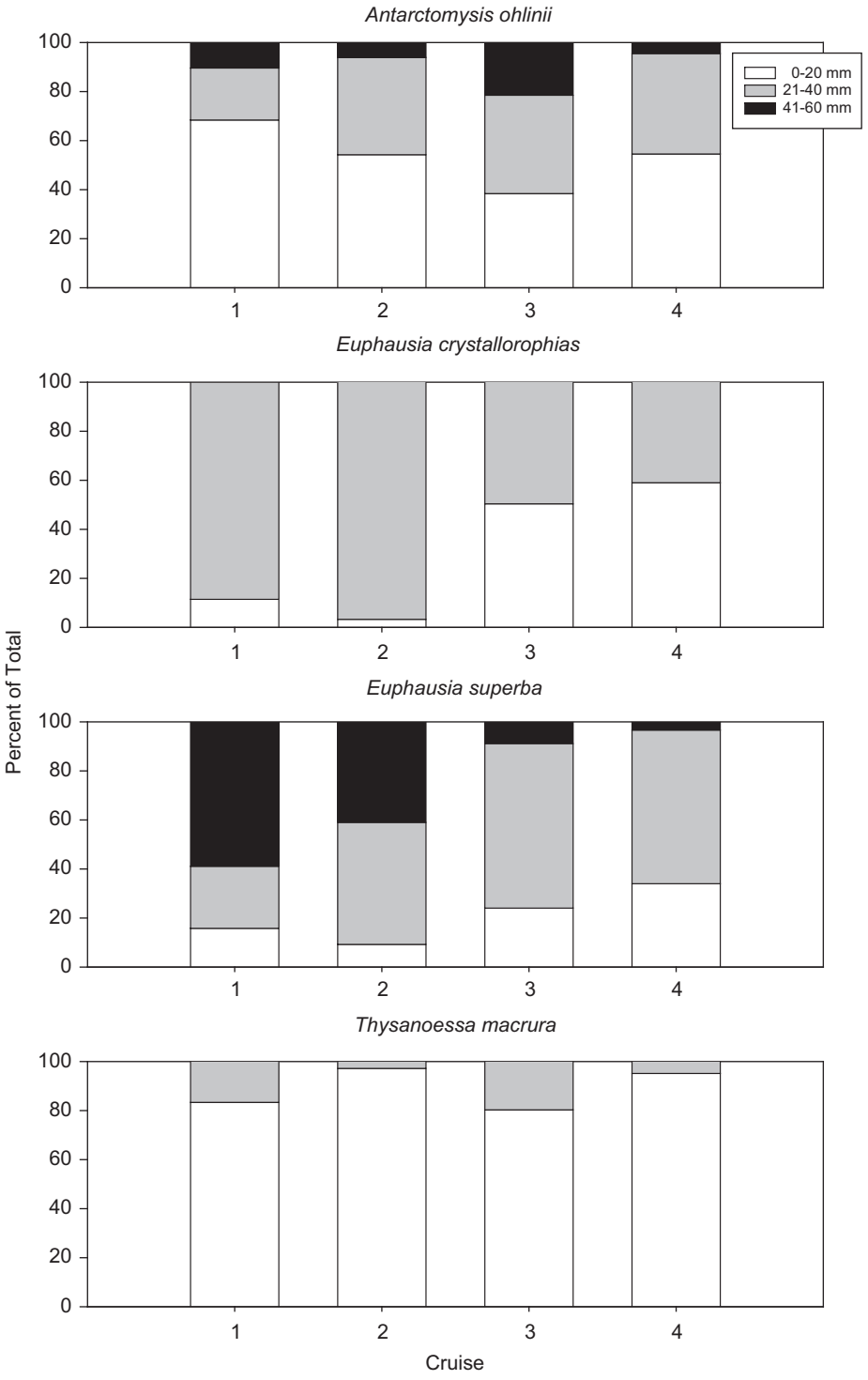

Fig. 2. Size distributions of dominant species collected during the four SO GLOBEC cruises.

the mean biomass (102.775 vs. 268.128 g WM $\times 10^4$ m^{-3}; $P=0.0009$) were significantly higher in 2002 (Table 2). Although mean abundances of most individual taxa were also higher in 2002, there were significant differences in only a few of those taxa due to a high variability in numbers per catch. The amphipods *E. macronyx*, *Eusirus microps*, and *Orchomene plebs* and the leptomedusae all exhibited significant increases in both abundance and biomass ($P<0.05$). Three species, *Alluroteuthis antarcticus*, and the crustaceans *Cyphocarus richardi* and *Gigantocypris muelleri*, significantly increased in number only ($P<0.05$). Several other species significantly increased in biomass only and included *E. superba*, the amphipods *Cyllopus lucasii* and *Eusirus properdentatus*, the mysid *Antarctomysis maxima*, and *P. gazellae* ($P<0.05$). In contrast, the furcilia stage of *E. superba* showed a significant decrease in abundance and biomass from fall 2001 to 2002 ($P<0.04$), which is due to the fact that none were captured in the fall 2002 trawls.

Clearly the trend within the fall data was that first, similar volumes were sampled in each year. Second, if the entire suite of samples were compared between years, the totals in numbers and

biomass were far higher in 2002. Yet, for the majority of individual species, no significant differences were observed between years in either mean numbers or mean biomass. In order to address this conundrum, all trawls that were conducted at a station that was only sampled in either 2001 or 2002 were removed from the data set for further comparisons. Six stations (1a, 1b, 2a, 2b, 5a, and 5c) were sampled in both 2001 and 2002 during the fall cruises (Table 4) for a total of 31 trawls (14 in 2001 and 17 in 2002). As with the total data set, the marked increase in total numbers and biomass from 2001 to 2002 remained significant. When catches from duplicate stations were compared between years, there were also significant increases in both total numbers and biomass at stations 2b and 5a ($P<0.01$), and in numbers at stations 1a and 5c ($P<0.04$). It was concluded that the high variability in numbers per catch was the reason for the large, statistically significant interannual difference when total numbers and biomass were compared without being mirrored by a similar significant change in individual species numbers, even though large interannual differences were observed in individual species' means.

During the winter cruises, total volumes filtered in 2001 and 2002 were similar (543,635 vs. 511,192 m^3). Although the mean total abundance (280.078 vs. 856.683 individuals $10^4\,m^{-3}$; $P=0.0110$) was significantly higher in winter 2002, there was no significant effect of year in mean total biomass (66.073 vs. 166.424 g WM $\times 10^4\,m^{-3}$; $P=0.258$, Table 3). Looking at individual species, the euphausiids *E. crystallorophias*, *E. superba*, and *Euphausia triacantha*, the tunicate *Salpa thompsoni*, the amphipods *Hyperia macrocephala* and *O. plebs*, and the hydrozoan *Diphyes antarctica* all exhibited significant increases in abundance from winter 2001–2002 ($P<0.05$). Both *E. properdentatus* and *P. gazellae* also had significantly higher biomass in winter 2002 ($P<0.02$). Two stations (1a and 1d) were each sampled once in winter 2001 and winter 2002 (Table 4). Because there was only one sample per station, no statistical comparisons between years were conducted.

Table 4
Total number of trawls sampled at each station during each of the four cruises.

Station	Fall		Winter		Total
	Cruise 1	Cruise 3	Cruise 2	Cruise 4	
1a	3	4	1	1	9
1b	2	1	1		4
1c			1		1
1d			1	1	2
2a	2	3	1		6
2b	3	5			8
3a			1		1
3b				1	1
3c				1	1
3d				1	1
3e				1	1
3f				1	1
3g			1		1
3h				1	1
3i			1		1
4a	4				4
4b	1				1
5a	2	2	1		5
5b		3			3
5c	2	2			4
5d	2				2
7a	1				1
7b		2		1	3
Total	22	22	9	9	62

Although fewer trawls were completed during the winter cruises, statistical comparisons between cruises that occurred during the same year, i.e., fall 2001 vs. winter 2001 and fall 2002 vs. winter 2002, revealed no significant differences in either total abundance or biomass ($P>0.05$). Four stations were sampled in both seasons (1a, 1b, 2a, and 5a) in 2001, and two stations were sampled in both seasons (1a and 7b) in 2002 (Table 4). As with the total data set, there were no statistical differences between stations that were sampled in both seasons within each year.

3.3. Vertical distributions

Seasonal discrete depth distributions were compiled for 10 common species by pooling data from each of the fall cruises and each of the winter cruises (Fig. 3). The euphausiids *E. crystallorophias*, *E. superba*, *E. triacantha*, and *T. macrura* were found throughout the sampled water column but peak abundances differed among the species. During the fall cruises, *E. crystallorophias* and *E. superba* were most abundant between 100 and 200 m during the day, but both species ascended at night with peak *E. superba* abundances at the surface (0–50 m) and *E. crystallorophias* peaking between 50 and 100 m. *E. triacantha* also ascended at night, moving from a peak range of 200–500 m during the day to 100–200 m at night. In contrast, *T. macrura* descended from a peak range of 50–100 m during the day to 100–200 m at night. In the winter, all four euphausiids were again found throughout the water column with the exception of *E. crystallorophias*, which was only found from the surface to 200 m at night. Winter daytime peak distributions of both *E. crystallorophias* and *E. superba* were deeper than in the fall, with the majority of *E. crystallorophias* found between 200 and 500 m and *E. superba* between 500 and 1000 m. *E. superba* was still concentrated at the surface at night, but *E. crystallorophias* peaked at 100–200 m in the winter. Peak distributions of *E. triacantha* and *T. macrura* were nearly the same in winter as in fall, with *E. triacantha* concentrated at 200–500 m and *T. macrura* concentrated at 50–100 m in both day and night trawls.

Other common species exhibited similar peak distributions during both day and night, and fall and winter. *A. ohlinii*, *E. macronyx*, and *E. properdentatus* were concentrated between 200 and 500 m, with the only major exception being slightly higher abundances of *E. macronyx* between 100 and 200 m at night in the fall. No winter nighttime values for *A. ohlinii* are shown in Fig. 3 since it was not captured in any of those corresponding trawls. Both *S. thompsoni* and *Themisto gaudichaudi* were concentrated at the surface with the only exception occurring during the daytime in winter when peak distributions of both were found deeper in the water column.

3.4. Multispecies assemblages

Cluster and SIMPROF analyses of fall abundance (Fig. 4A) and biomass (Fig. 5A) divided the 12 sampled stations from 2001 and 2002 into two primary groups: an offshore group that included trawls occurring at the off-shelf, shelf-edge, and outer trough sites (stations 1a, 1b, and 2a) and an inshore group that included the trawls from the bay and fjord sites (stations 4a, 5a–d, and 7a,b). Trawls from station 2b were split, with trawls from fall 2001 clustering with the offshore group and those from fall 2002 clustering with the inshore group. On the abundance dendrogram (Fig. 4A), the offshore group further divided into two significant clusters that were defined as an oceanic and a transitional cluster. The oceanic cluster included trawls that were conducted seaward of the shelf break (station 1a) while the transitional cluster included trawls conducted on the shelf within the Marguerite

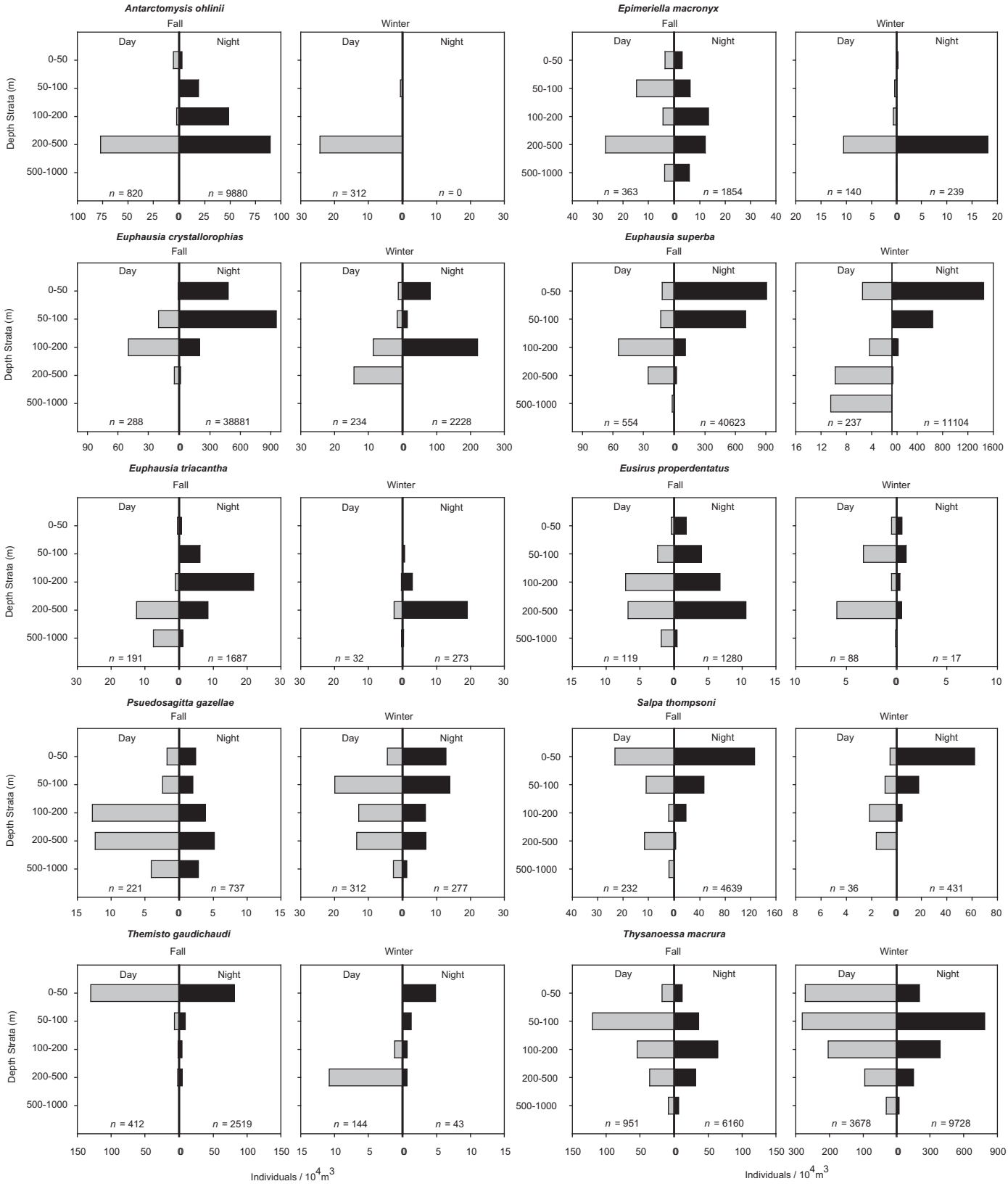

Fig. 3. Vertical distributions of 10 common species collected during the four SO GLOBEC cruises.

Trough (stations 2a and 2b). Trawls from station 1b were split between the two offshore clusters with those from 2001 falling into the transitional cluster and those from 2002 falling into the oceanic cluster.

Unlike the abundance data, with biomass there were no significant sub-groups within the offshore cluster (Fig. 5a). MDS ordination plots calculated from the similarity matrices show the same group structure for both abundance and biomass with

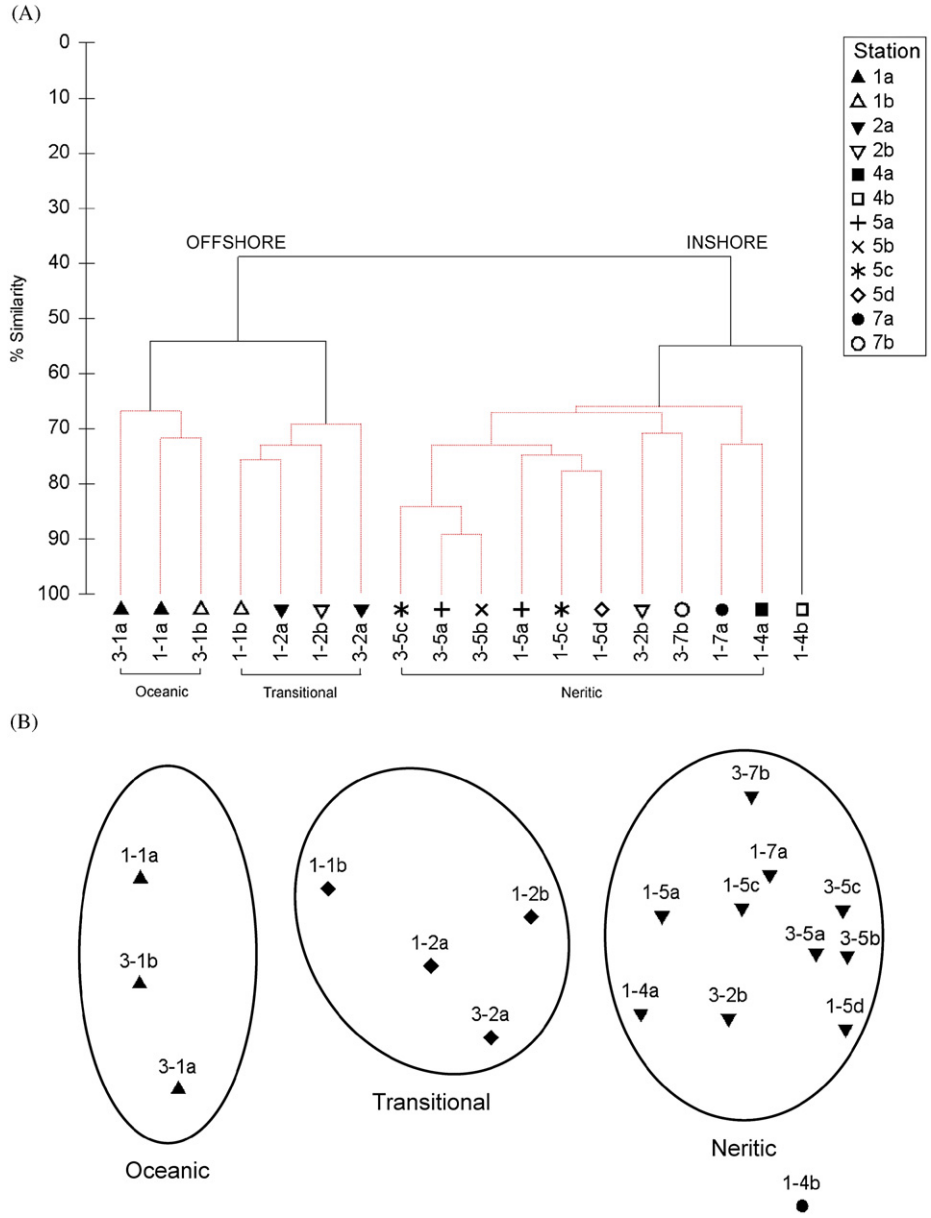

Fig. 4. (A) Percent similarity cluster dendrogram of fall invertebrate micronekton/macrozooplankton abundance (no. of individuals $\times 10^4\,m^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 3, station 1a is designated as 3-1a). (B) Corresponding MDS ordination plot of fall abundance data.

resultant stress levels of <0.1 (Figs. 4B and 5B). In fall 2001, one trawl was conducted at station 4b deep within George VI Sound near the permanent ice-shelf. Both abundance and biomass data from that trawl clustered as an outlier, which is likely due to the unusual nature of the catch. It was dominated by the neritic euphausiid *E. crystallorophias* (82%), yet also had several oceanic species underscoring the connection between ocean and shelf provided by the Marguerite Trough.

A SIMPER analysis conducted on the fall abundance data identified the taxa that contributed the most to similarities within each cluster group. The species *E. triacantha* and *S. thompsoni* were most abundant in the oceanic cluster and contributed over 20% each to the similarity within that group. In the neritic cluster, *E. superba*, *T. macrura*, *E. crystallorophias*, and *A. ohlinii* were the most numerous species and contributed nearly 50% to the similarity within that cluster. Dominant taxa in the transitional cluster included several species (*E. superba*, *T. macrura*, *T. gaudichaudi*, and *P. gazellae)* that were present to varying degrees in each of the three cluster groups (Table 5). The remainder of the taxa in the transitional cluster included species that were also present in either the oceanic or the neritic cluster, with the only exceptions being *Euphausia frigida* and *E. superba furcilia*. Abundance and distribution of several dominant species and how they relate to the three major clusters are shown in Fig. 6 as bubble plot overlays of the fall abundance MDS ordination.

During the winter cruises, 16 stations were sampled, each with one trawl per cruise. Site 3, which was only sampled during the winter cruises, included several stations (3a–3i) that were found at various locations on the continental shelf. Due to the presence of sea ice, only two trawls were completed at the more inshore sites during the winter cruises: one at station 5a in 2001 and one at station 7b in 2002. The rest of the samples were collected from site 1 at the shelf break and include the samples from stations 1a and 1d that occurred in both years. Cluster and SIMPROF analyses of winter abundance and biomass divided the samples into four and five significant groups, respectively. Like fall abundance,

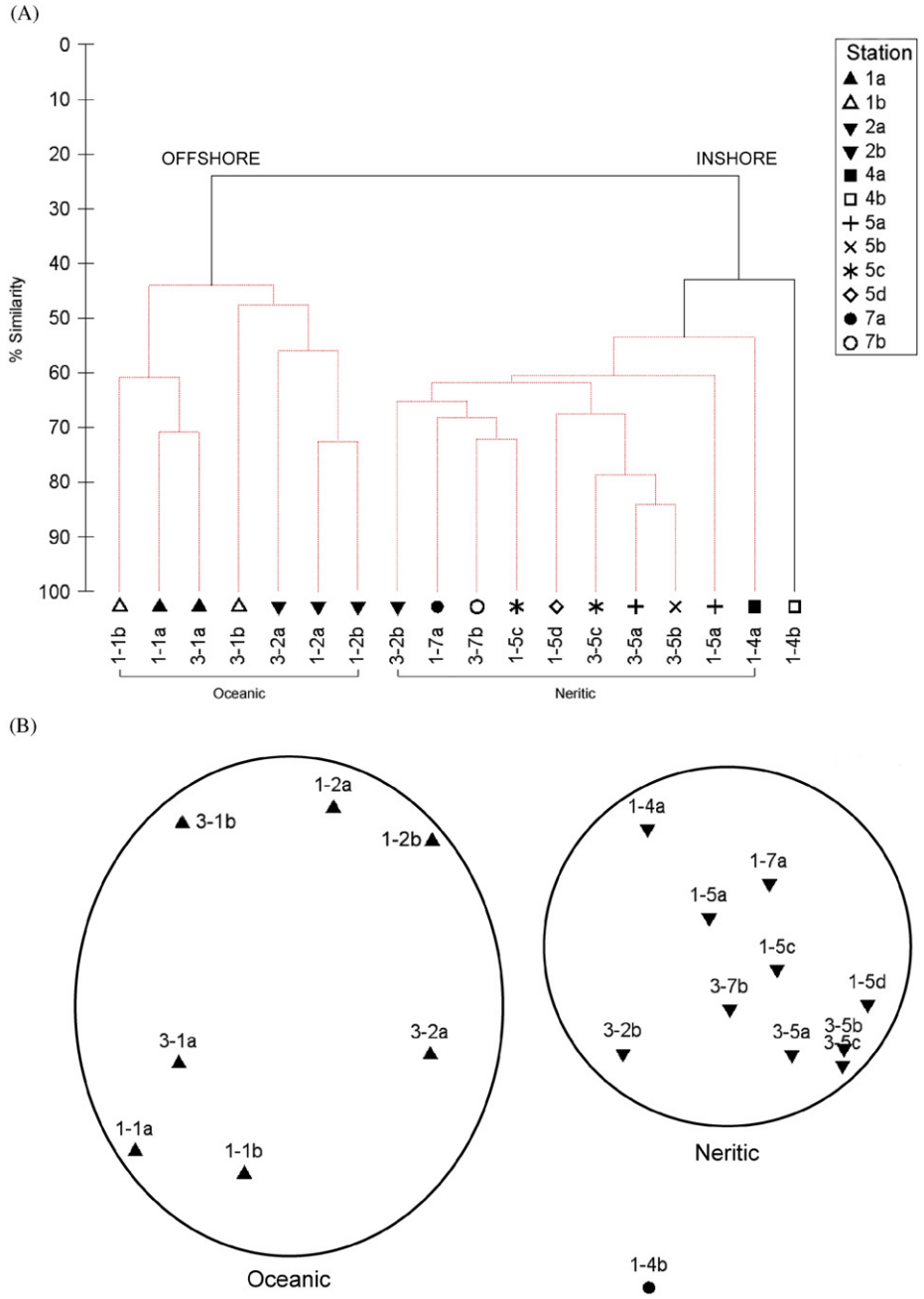

Fig. 5. (A) Percent similarity cluster dendrogram of fall invertebrate micronekton/macrozooplankton biomass (g WM $\times 10^4$ m^{-3}). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 3, station 1a is designated as 3-1a). (B) Corresponding MDS ordination plot of fall biomass data.

winter abundance clustered into an offshore and inshore group, with the offshore group further dividing into oceanic and transitional clusters. However, the addition of site 3 created another significant cluster group within the offshore branch that was defined as a mid-shelf cluster (Fig. 7A). The oceanic cluster included all samples from site 1, the transitional cluster included the trawls completed at station 2a as well as two of the mid-shelf trawls completed in 2001 (stations 3g and 3i), and the mid-shelf cluster contained the rest of the site 3 trawls. Not surprisingly those samples collected from stations 5a and 7b formed the inshore group (neritic cluster).

Results from winter biomass were less clear than those from winter abundance. Overall the samples still divided into an offshore and inshore group, however in this case the transitional group divided into its own significant cluster rather than nesting within the offshore group, and the mid-shelf cluster fell into the inshore group (Fig. 8A). Removal of several jellyfish species (*A. wyvillei*, *Calycopsis borchgrevinki*, and *P. periphylla*) from the cluster analysis yielded a slightly less complex clustering pattern with those stations that clustered originally as oceanic and transitional combining into one offshore group and the mid-shelf and neritic group clustering within the inshore group (Fig. 8B). The MDS ordination plots of winter abundance and biomass (without jellyfish) are shown in Figs. 7B and 8C.

Results of the SIMPER analysis of winter abundance revealed that *T. macrura* dominated in three of the four clusters, contributing from 25% to nearly 40% of the similarity within each cluster group (Table 6). Several other taxa (*E. macronyx*, *E. superba*, *E. crystallorophias*, *P. macropa*, *P. gazellae*, and *S. thompsoni*) were also present in either 3 or 4 of the cluster groups suggesting that

Table 5
Results of SIMPER analysis on fall abundance data showing the species contributing the most to similarity within each significant cluster. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution = percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

Oceanic (68.47% similarity)		**Transitional (71.53% similarity)**		**Neritic (69.90% similarity)**	
% Contribution		**% Contribution**		**% Contribution**	
Euphausia triacantha	22.60	*Thysanoessa macrura*	20.31	*Euphausia superba*	17.88
Salpa thompsoni	21.82	*Themisto gaudichaudi*	14.62	*Thysanoessa macrura*	10.10
Themisto gaudichaudi	17.56	*Salpa thompsoni*	12.08	*Euphausia crystallorophias*	10.06
Thysanoessa macrura	9.27	*Pseudosagitta gazellae*	10.30	*Antarctomysis ohlinii*	10.06
Euphausia superba	6.43	*Euphausia superba*	7.45	*Eusirus properdentatus*	9.03
Calycopsis borchgrevinki	4.10	*Euphausia superba furcilia*	6.00	*Epimeriella macronyx*	8.92
Primno macropa	3.70	*Boreomysis* sp.	5.62	*Antarctomysis maxima*	5.38
Pseudosagitta gazellae	2.49	*Primno macropa*	4.87	*Themisto gaudichaudi*	5.15
Cyllopus lucasii	2.48	*Eusirus properdentatus*	4.11	*Boreomysis* sp.	5.09
Atolla wyvillei	1.86	*Orchomene plebs*	2.21	*Orchomene plebs*	4.75
Euphausia frigida	1.73	*Euphausia frigida*	2.15	*Pseudosagitta gazellae*	4.32
Diphyes antarctica	1.38	*Euphausia triacantha*	1.73	*Eusirus microps*	1.97
		Cyllopus lucasii	1.61	*Euphausia superba furcilia*	1.46
		Antarctomysis ohlinii	1.14	Leptothecatae	1.15
				Primno macropa	1.10

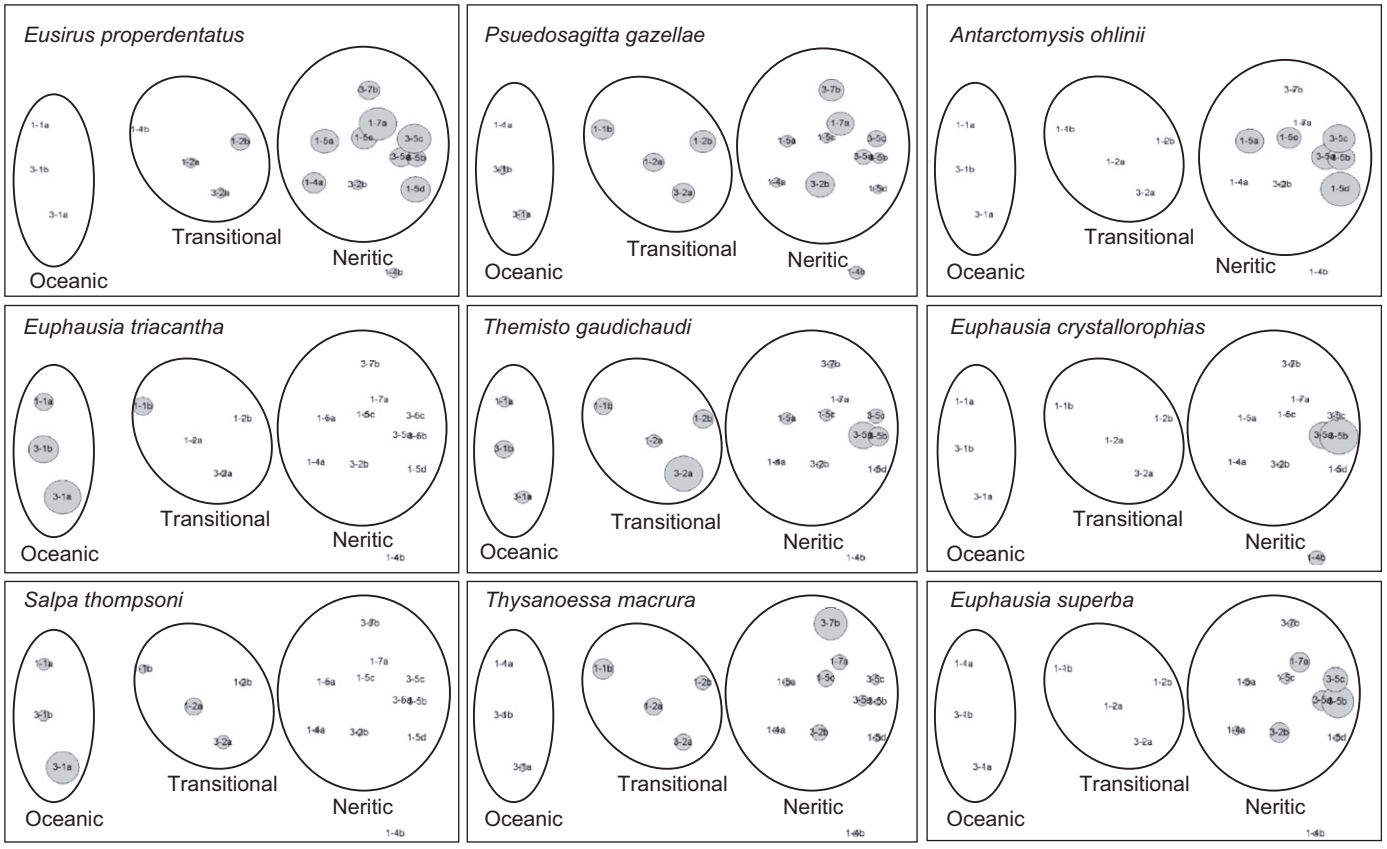

Fig. 6. Bubble plot overlays of the fall abundance MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that site. Please note that bubble sizes are not consistent among species.

there was more species overlap in the winter samples as compared to the fall samples. Fig. 9 shows the bubble plots of the abundance and distribution of four euphausiid species captured in the winter trawls.

Diversity indices for fall and winter were calculated with abundance data from each sampled station. Mean values for each significant cluster are presented in Table 7. In both fall and winter, more species were collected from the oceanic clusters, but the highest diversity and evenness indices occurred in the fall transitional cluster and in the winter neritic cluster.

3.5. Integrated abundance and biomass in the upper 200 m

A total of 37 taxa were present in the upper 200 m of the water column during the cruises. In the fall, *E. crystallorophias* and *E. superba* contributed both the highest numbers and the most biomass to the upper 200 m of the water column (Table 8). Other species such as *S. thompsoni*, *A. ohlinii*, *T. macrura*, *E. triacantha*, and *T. gaudichaudi* also supplied a substantial proportion of the total catch in the 0–200 m layer while *P. periphylla* and *A. wyvillei* contributed to total biomass. During the winter, *E. superba* and

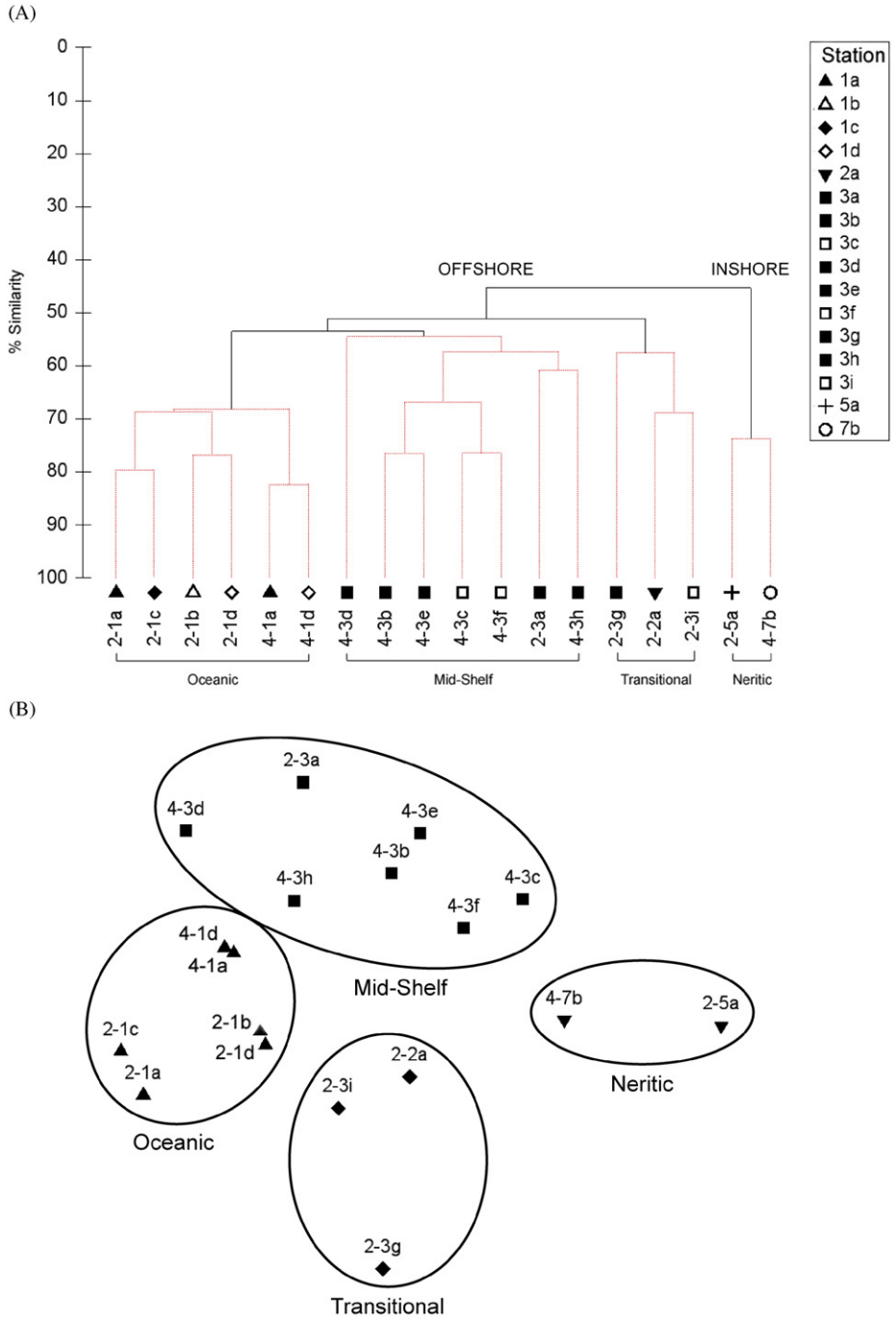

Fig. 7. (A) Percent similarity cluster dendrogram of winter invertebrate micronekton/macrozooplankton abundance (no. of individuals $\times 10^4\ m^{-3}$). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 2, station 1a is designated as 2-1a). (B) Corresponding MDS ordination plot of winter abundance data.

T. macrura were the dominant taxa, contributing over 94% in number and 85% in biomass. Total densities in each season were similar, but total biomass was approximately three times greater in fall than in winter.

4. Discussion

4.1. Dominant species and interannual differences

A total of 58 invertebrate taxa were collected during the four cruises to the Marguerite Bay region of the WAP in 2001 and 2002. Of those, four species, *E. crystallorophias*, *E. superba*, *T. macrura*, and *A. ohlinii*, accounted for the vast majority of the total abundance and biomass, contributing from 74% to 92% of the total number during each individual cruise. Many previous studies have also reported *E. superba* and *T. macrura* as dominant species throughout the WAP region (Kittel and Stepnik, 1983; Kittel et al., 1985; Lancraft et al., 1989, 1991, 2004; Nordhausen, 1992, 1994a, b) with others listing *E. crystallorophias* and *A. ohlinii* as dominants in nearshore environments (Lancraft et al., 2004; Ross et al., 1996). Interestingly each of the dominants ranked as the top numerical contributor in only one cruise. In the fall, *A. ohlinii* dominated in 2001 and *E. crystallorophias* dominated in 2002, while in the winter, *T. macrura* dominated in 2001 and *E. superba* dominated in 2002. Biomass contributions from the four dominants were also

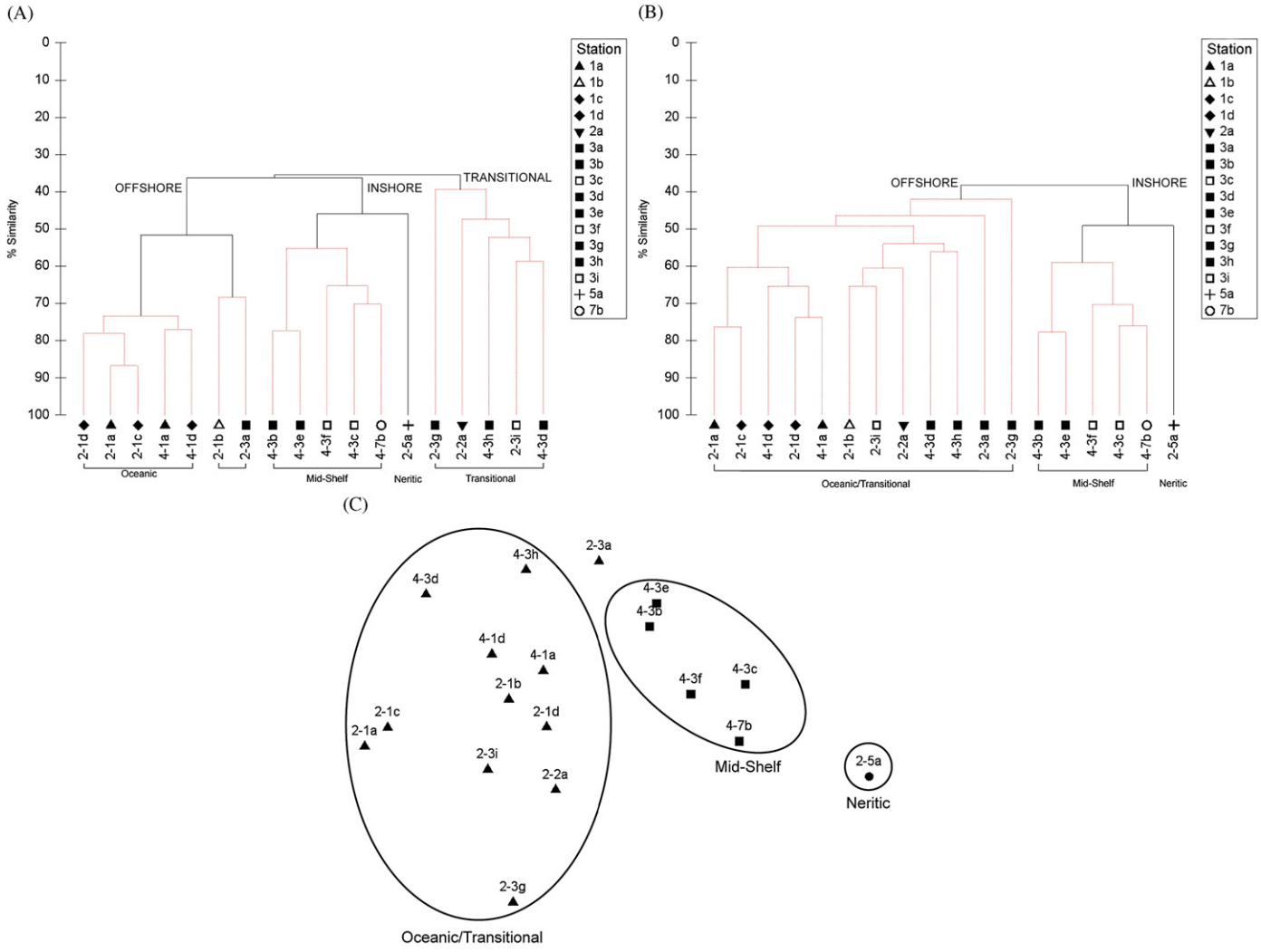

Fig. 8. (A) Percent similarity cluster dendrogram of winter invertebrate micronekton/macrozooplankton biomass (g WM $\times 10^4$ m^{-3}). Numbers along the abscissa represent the cruise and station number (Ex. Cruise 2, station 1a is designated as 2-1a). (B) Winter biomass cluster dendrogram minus the jellyfish taxa. (C) Corresponding MDS ordination plot of winter biomass data minus the jellyfish taxa.

Table 6
Results of SIMPER analysis on winter abundance data showing the species contributing the most to similarity within each significant cluster. Values in parentheses represent the overall similarity among samples within a cluster group. % Contribution=percentage contribution to the overall similarity among samples within a cluster group. Only those taxa that contributed 1% or more to overall group similarity are listed.

Oceanic (70.66% similarity)		**Transitional (61.45% similarity)**		**Neritic (73.78% similarity)**		**Mid-Shelf (60.44% similarity)**	
% Contribution		**% Contribution**		**% Contribution**		**% Contribution**	
Thysanoessa macrura	39.70	*Thysanoessa macrura*	32.91	*Euphausia superba*	15.16	*Thysanoessa macrura*	25.71
Pseudosagitta gazellae	13.18	*Euphausia crystallorophias*	20.40	*Euphausia crystallorophias*	12.07	*Euphausia superba*	20.19
Euphausia triacantha	7.00	*Pseudosagitta gazellae*	14.86	*Epimeriella macronyx*	10.62	*Pseudosagitta gazellae*	15.03
Euphausia superba	6.96	*Primno macropa*	4.84	*Eusirus properdentatus*	8.95	*Salpa thompsoni*	7.89
Atolla wyvillei	6.85	*Eusirus properdentatus*	3.79	*Thysanoessa macrura*	8.74	*Primno macropa*	6.66
Primno macropa	4.20	*Tomopteris carpenteri*	3.53	*Themisto gaudichaudi*	8.60	*Euphausia triacantha*	4.92
Cyphocaris richardi	2.39	*Cyllopus lucasii*	3.27	*Antarctomysis ohlinii*	5.96	*Epimeriella macronyx*	2.58
Periphylla periphylla	2.27	*Themisto gaudichaudi*	3.27	*Orchomene plebs*	5.14	*Orchomene plebs*	2.42
Calycopsis borchgrevinki	2.19	*Epimeriella macronyx*	2.75	*Pseudosagitta gazellae*	5.14	*Hyperia macrocephala*	2.03
Salpa thompsoni	1.92	*Salpa thompsoni*	1.97	*Boreomysis* sp.	4.45	*Diphyes antarctica*	2.02
Euphausia crystallorophias	1.79	*Orchomene plebs*	1.41	*Eusirus microps*	3.91	*Cyllopus lucasii*	1.86
Diphyes antarctica	1.39	*Euphausia superba*	1.18	*Primno macropa*	3.64	Gymnosome	1.60
Pasiphaea scotiae	1.34	*Hyperia macrocephala*	1.06	*Antarctomysis maxima*	2.45	*Eusirus properdentatus*	1.37
Petalidium foliaceum	1.27			*Tomopteris carpenteri*	1.66	*Themisto gaudichaudi*	1.15
				Euphausia triacantha	1.43	*Tomopteris carpenteri*	1.06

high, ranging from 37% to 84% of the total during each of the cruises. In winter 2002, their biomass contributions were diminished (37%) due to the capture of several large scyphozoans, *A. wyvillei* and *P. periphylla*. When the scyphozoans were removed from consideration, biomass contributions from the four dominants increased and ranged from 75% to 87%.

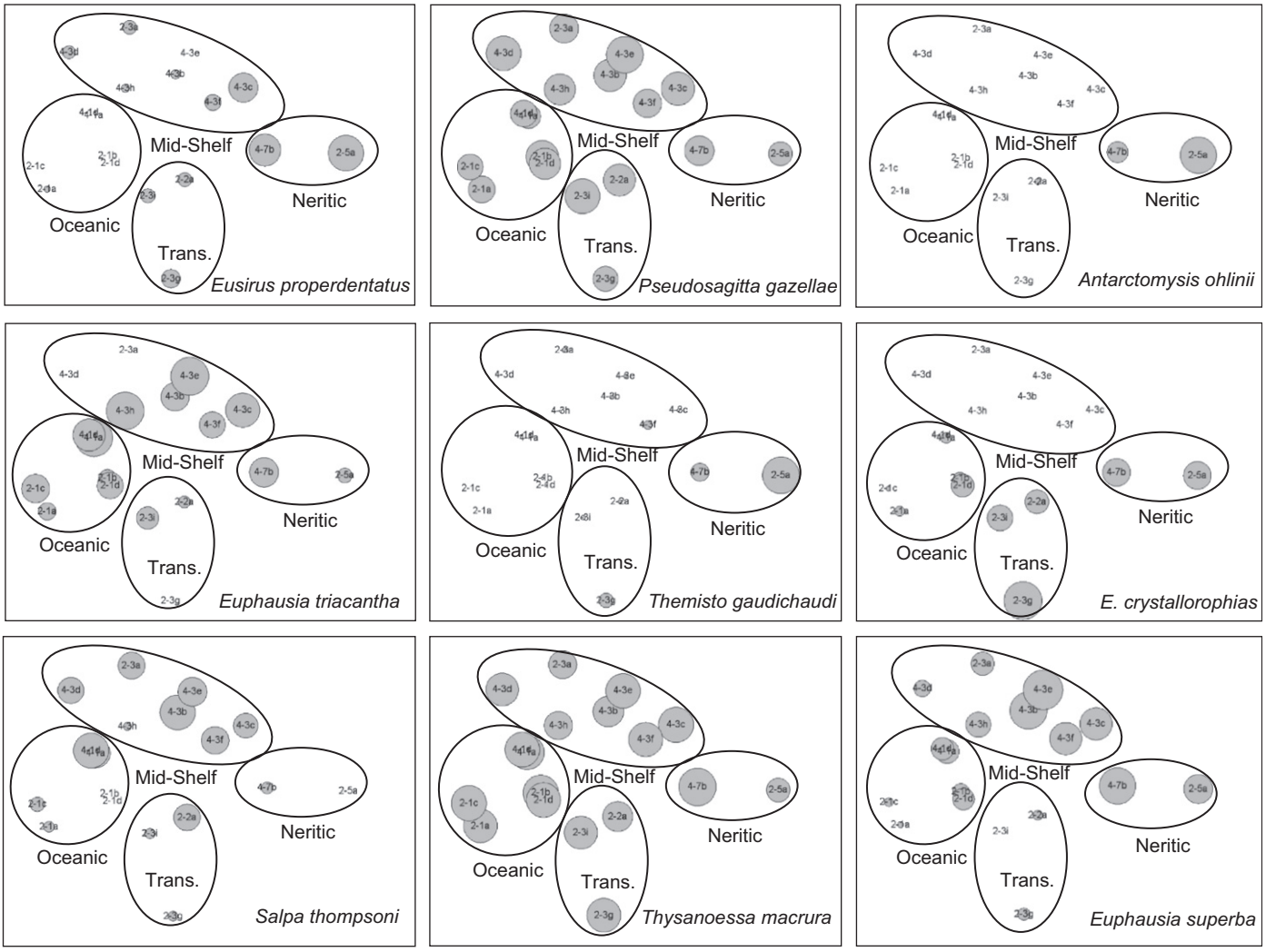

Fig. 9. Bubble plot overlays of the winter abundance MDS ordination plot representing the relative abundance of several common species. The larger the bubble, the greater the number of individuals were captured at that site. Please note that bubble sizes are not consistent among the species.

Table 7
Mean diversity (H') and evenness (J') for fall and winter abundance cluster groups depicted in Figs. 4 and 7.

Cluster	Diversity (H')		Evenness (J')	
	Mean	S.D.	Mean	S.D.
Fall				
Oceanic	1.63	0.25	0.51	0.10
Transitional	1.87	0.22	0.57	0.06
Neritic	1.40	0.34	0.44	0.11
Outlier	0.82		0.26	
Winter				
Oceanic	0.71	0.20	0.21	0.06
Mid-Shelf	1.26	0.60	0.43	0.20
Transitional	1.16	0.51	0.39	0.15
Neritic	1.48	0.63	0.48	0.21

Contributions by fish taxa to total abundance and biomass in the SO GLOBEC study were described by Donnelly and Torres (2008) and were relatively low in the fall and winter seasons. Although fishes comprised approximately two-thirds of the species found in the study, their contribution to total abundance in fall and winter ranged from only 1.5% to 3% (Donnelly and Torres, 2008). However, fish constituted a larger proportion of the biomass, contributing between 16% and 19% in both seasons (Donnelly and Torres, 2008).

Despite the fact that there were few significant differences in abundance or biomass of the dominant euphausiids, there was nearly an order of magnitude increase in both measures in 2002. Interannual comparisons of mean abundance and biomass of each dominant revealed that while all four species increased in number and wet mass between fall cruises, that was not the case between winter cruises. In winter 2002, both *E. crystallorophias* and *A. ohlinii* decreased in abundance and were outnumbered by *P. gazellae* and *E. macronyx*. In fact, the numerical catches of those two species decreased by more than 20-fold from winter 2001 to 2002. Winter distributions of those two species (Fig. 9) show that catches of *A. ohlinii* were limited to stations 5a and 7b where the deep, nearshore fjords are located. *E. crystallorophias* was also present at the fjord stations, but there were also substantial catches in the transitional cluster as well as at some of the stations in the oceanic cluster. This suggests that *E. crystallorophias* distributions tend to spread out onto the shelf during the winter when ice extent has increased. It is likely then that *P. gazellae* and *E. macronyx* outnumbered *A. ohlinii* and *E. crystallorophias* in winter 2002 for two reasons: (1) the more ubiquitous distributions of *P. gazellae* and *E. macronyx* allowed for greater numbers to be captured and (2) the decreased number of trawls

Table 8
Integrated abundance (no. of individuals m^{-2}) and biomass (g WM m^{-2}) of species collected from discrete night tows within the 0–200 m depth stratum during the fall and winter cruises.

Taxa	0–200 m stratum			
	Fall ($n=31$)		Winter ($n=6$)	
	m^{-2}	g WM m^{-2}	m^{-2}	g WM m^{-2}
Antarctomysis maxima	0.27	0.0493		
Antarctomysis ohlini	1.56	0.6144	0.06	0.0102
Atolla wyvillei	0.01	0.2427		
Boreomysis sp.	0.03	0.0018	0.03	0.0039
Calycopsis borchgrevinki	0.03	0.0447	0.05	0.1299
Clio pyramidata	0.01	0.0004		
Clione antarctica	0.01	0.0015	0.03	0.0024
Cyllopus lucasii	0.05	0.0062	0.03	0.0049
Cyphocaris richardi	0.02	0.0019		
Diphyes antarctica	0.01	0.0044	0.02	0.0055
Epimeria sp.	0.01	0.0006		
Epimeriella macronyx	0.31	0.0810	0.03	0.0080
Eukrohnia hamata	0.04	0.0007		
Euphausia crystallorophias	19.04	2.6078	0.04	0.0047
Euphausia frigida	0.30	0.0134		
Euphausia superba	11.93	3.7781	14.68	1.9428
Euphausia triacantha	0.72	0.1084	0.04	0.0077
Eusirus microps	0.03	0.0190	0.04	0.0072
Eusirus properdentatus	0.14	0.0652	0.02	0.0187
Gennadas kempi			0.01	0.0151
Gymnosome	0.01	0.0011	0.02	0.0013
Hyperia macrocephala	0.01	0.0041	0.03	0.0051
Hyperiella macronyx	0.01	0.0004		
Lanceola sayana	0.02	0.0020		
Leptomedusa	0.05	0.0572		
Orchomene plebs	0.09	0.0194	0.05	0.0085
Periphylla periphylla	0.01	0.8018		
Primno macropa	0.02	0.0014	0.04	0.0017
Pseudosagitta gazellae	0.08	0.0135	0.17	0.0473
Sagitta marri	0.03	0.0004		
Salpa thompsoni	1.79	0.4404	0.69	0.1140
Spongiobranchaea australis	0.01	0.0009	0.01	0.0003
Themisto gaudichaudi	0.47	0.0412	0.09	0.0089
Thysanoessa macrura	0.81	0.0763	13.50	0.6386
Tomopteris carpenteri	0.01	0.0063	0.01	0.0308
Vanadis antarctica	0.01	0.0071		
Vibilia stebbingi			0.01	0.0005
Total	37.96	9.11	29.72	3.02

that were completed in sites 5 and 7 reduced the chances of catching *A. ohlinii* and to some degree *E. crystallorophias*.

Sea ice coverage and formation differed in both timing and extent during the cruises in 2001 and 2002. In fall 2001, much of the study region, including portions of Marguerite Bay, remained open and free of ice until late June. In contrast, the ice edge extended well past the islands west of the Antarctic Peninsula in 2002 and this is echoed in the more offshore distribution of sample stations during those cruises (Perovich et al., 2004). The delayed sea ice formation in 2001 may have reduced spawning and recruitment success leading to the dearth of larval krill in the 2002 trawls. However, the abundance of larval krill in 2001 is reflected in the size increment data for both years. In fall 2001, the majority of captured *E. superba* were large (41–60 mm) but that decreased steadily over the following cruises such that large krill represented less than 10% of the total catches in 2002. The decrease in large *E. superba* was accompanied by an increase in small (0–20 mm) and intermediate (21–40 mm) sized individuals in 2002, which implies that a substantial number of larvae from 2001 survived and overwintered in the local region (Daly, 2004). *E. crystallorophias* exhibited similar size distribution patterns, with the occurrence of small-sized individuals increasing to over 50% in 2002. This suggests that the dramatic increase in both *E. superba* and *E. crystallorophias* abundance/biomass in 2002 is the result of a successful spawning and recruitment season in 2001.

Although mean abundance and biomass were higher in fall than in winter within each year, there were no significant differences detected between seasons. However, several other studies conducted in this region (Lascara et al., 1999; Ashjian et al., 2004; Lawson et al., 2004), noted a substantial decrease in both density and biomass captured in the winter when compared to the fall. Because of the nature of the present study and the differences in sampling sites/stations between seasons, a rigorous assessment of seasonal variations in taxon abundance and biomass is not possible.

4.2. Distributions and hydrographic influences

The invertebrate micronekton/macrozooplankton assemblages found in the Marguerite Bay region of the WAP were composed of a varying mixture of oceanic and neritic species: a product of the local hydrography. In most oceanic regions, the continental shelf is less than 200 m deep and the subsequent change in depth at the shelf break acts as a natural barrier between oceanic and shelf fauna. However, the Antarctic, specifically the WAP continental shelf, is much deeper, ranging in depth from 200 to 500 m (Dinniman and Klinck, 2004). As a result there is less filtering out of oceanic species from the shelf community (Eastman, 1993).

The proximity of the ACC to the shelf break is another unique attribute of the WAP region that enhances species mixing (Dinniman and Klinck, 2004). Oceanic fauna located near the shelf break are associated with the warmer waters of the ACC and when ACC-associated CDW intrudes onto the shelf, it potentially carries those oceanic fauna along with it. Those sub-surface CDW intrusions typically occur near anomalous bathymetric features such as the Marguerite Trough and are estimated to happen from 4 to 6 times per year (Klinck et al., 2004). As the CDW moves farther onto the shelf, it becomes slightly cooler and fresher, referred to as modified CDW (Hofmann and Klinck, 1998), as it mixes with shelf waters containing resident neritic fauna. Donnelly and Torres (2008), who described the fish assemblages from these same trawls, reported that modified CDW was present throughout the study region in both seasons.

Cluster analysis of the fall and winter samples identified three primary groups, defined as oceanic, transitional, and neritic assemblages, primarily due to their geographic location. In the Antarctic, the oceanic region is typically found in the deeper waters (>2000 m) offshore of the continental shelf; the neritic region is located on the continental shelf in coastal regions (Ross et al., 1996). The transitional zone is defined as the area between and represents a region of mixing between oceanic and neritic waters rather than a distinctly different physical or biological environment. Siegel and Piatkowski (1990) identified and described three similar assemblages in a more northerly region of the WAP during fall, winter, and spring seasons in the 1980s and concluded that differences between the assemblages were not due to differences in species composition, but rather due to changes in abundances of those species. This was borne out by the ubiquitous distributions of many of the taxa encountered in the present study. As a result, there were very few species that served as ideal indicators for any particular assemblage. Instead, those species that contributed most to similarities within an assemblage as well as those that have been typically characterized as either oceanic or neritic fauna were most useful in describing the assemblages and the degree of mixing within each assemblage. Species such as the ice krill, *E. crystallorophias*, along with the deep, fjord-favoring mysids, *A. ohlinii* and *A. maxima*, and the

gammarid amphipods, *E. properdentatus* and *E. macronyx*, were most abundant at nearshore stations while the oceanics, *E. triacantha* and *S. thompsoni*, were most common at the shelf break/off-shelf stations.

Fish taxa collected during the SO GLOBEC study exhibited distribution patterns similar to those of the invertebrate micronekton/microzooplankton component. Oceanic genera such as *Electrona*, *Gymnoscopelus*, *Protomyctophum*, *Bathylagus*, *Cyclothone*, and *Notolepsis* dominated at the offshore stations, while the notothenioids such as the Antarctic silverfish *Pleuragramma antarcicum* were most abundant nearshore (Donnelly and Torres, 2008).

For simplicity, only those species listed in Tables 5 and 6 will be discussed with respect to their distributions and contributions to each assemblage. In the fall, faunal mixing was maximal in the transitional assemblage and included samples collected primarily from site 2, located approximately 150–200 km shoreward of the shelf break within the trough near the mouth of Marguerite Bay. Within that assemblage, there was a nearly even mix of neritic and oceanic taxa contributing to the structure of that group. The oceanic assemblage, collected near the shelf break at site 1, contained the largest number of taxa but was dominated by oceanic species such *E. triacantha*, *S. thompsoni*, and *T. gaudichaudi*. In contrast, the assemblage present at the nearshore sites (sites 4, 5, and 7) had the lowest species number and diversity and evenness indices. *E. superba* dominated in that assemblage along with the neritics, *A. ohlinii* and *E. crystallorophias*, with *T. gaudichaudi* being the only oceanic species present.

During the winter, faunal mixing was prevalent in both the mid-shelf and transitional clusters, but species distributions, especially those of the four abundant euphausiids, were much broader than in the fall. While *E. crystallorophias* was confined to nearshore sites in the fall, its distribution extended across the shelf reaching the shelf break in the winter (Figs. 6 and 9). In fact, average *E. crystallorophias* abundances in the transitional and neritic zones were nearly identical in the winter. Siegel and Piatkowski (1990) reported a similar pattern for *E. crystallorophias* in the spring, when distributions extended into the transitional zone. In the opposite extreme, the CDW-associated euphausiid, *E. triacantha*, was also more widespread in winter and present in all assemblages suggesting that CDW, or modified CDW, was indeed present on the inner shelf during the winter, corroborating the findings of Donnelly and Torres (2008). In the fall, *E. superba* occurred predominantly at nearshore sites, a pattern reported by Lancraft et al. (2004) in the Croker Passage, but during the winter abundances were more evenly distributed among all assemblages. *T. macrura* exhibited wide-ranging distributions not only in winter, but throughout the study. This species is commonly described as having a uniform and ubiquitous distribution (Kittel et al., 1985; Nordhausen, 1994a; Piatkowski, 1985) and was abundant in each of the described assemblages serving as a top contributor in both the fall and winter transitional groups.

Water column depth also influences distributions, especially the prevalence and persistence of oceanic fauna as CDW moves across the shelf. Several deeper dwelling oceanics, such as the decapods *Gennadus kempi* and *Pasiphea scotiae*, were captured, although in low densities, at the offshore station, but were completely absent at any of the shelf stations. Those species are most likely limited in horizontal extent by the depths encountered as they move shelfward. In contrast, oceanic fauna with shallower distributions, such as *S. thompsoni* and *Themisto gaudichaudi* were more widespread across the shelf and were present in nearly all assemblages.

Vertical depth ranges for most species in this study were fairly broad and encompassed the entire sampled water column (surface to 1000 m). Of the common species, only the euphausiids demonstrated marked diel vertical migrations. Both *E. crystallorophias* and *E. superba* migrated during both seasons while *E. triacantha* migrations were only evident during the fall. Studies by Lancraft et al. (1989, 2004) in the Scotia Sea and Croker Passage during the fall, and by Nordhausen (1994a) in Gerlache Strait and Crystal Sound during the winter, found no evidence of DVM by any of those species. However, Lancraft et al. (1991) found that *E. superba* did vertically migrate during the winter in the Scotia Sea. Several species also exhibited seasonal differences in vertical distribution patterns. Maximum densities of *E. crystallorophias* were deeper during both the day and night in the winter. Peak daytime abundances of *E. superba* were also deeper in the winter, but nighttime peaks were still at the surface. In fact, *E. superba* comprised nearly 80% of the catch in surface waters with *T. macrura* being the only other major contributor. *T. macrura* exhibited no diel vertical migration patterns or seasonal differences in depth distributions.

4.3. Regional comparisons

Invertebrate species diversity in the WAP study region was relatively high (55 taxa in the fall; 48 taxa in the winter) due to the mixing of typical Antarctic oceanic fauna with endemic nearshore fauna. In comparison, species lists for invertebrate micronekton/macrozooplankton collected from oceanic regions in the Scotia and Weddell Seas ranged from only 27 to 29 species (Lancraft et al., 1989). However, a winter study in the Scotia Sea in the vicinity of the Weddell-Scotia Confluence, an area of faunal mixing, reported a total of 40 species, a number more similar to the WAP study (Lancraft et al., 1991). Hydrographic conditions in the Confluence are comparable to those of the WAP shelf in that there is mixing of the colder and warmer water masses of the Weddell Gyre and the ACC, and their associated fauna, which enhances local diversity (Lancraft et al., 1991). Diversity in Croker Passage (32 species), which like the WAP study region included a mixture of both oceanic and nearshore fauna, was also lower than that seen in the present study (Lancraft et al., 2004) and may arise from the lack of a well developed CDW layer, thus excluding deeper dwelling oceanic fauna such as *Euphausia triacantha* (Lancraft et al., 2004). A summer study in the permanent ice zone of the Ross Sea reported a total of 31 species, which is also lower than the present study, but similar to species counts in the Scotia Sea, Weddell Sea, and Croker Passage (Hopkins, 1987).

Fish diversity in the SO GLOBCEC study region was also high when compared to other studies. Donnelly and Torres (2008) reported a total of 34 and 22 species for the fall and winter, while numbers in the Weddell Sea and Croker Passage reached only about a third to half of that total (Lancraft et al., 1989, 2004). Fish diversity in the Scotia Sea, which is heavily influenced by the ACC, was again more similar to the WAP study region with 15 and 17 species reported in the fall and winter (Lancraft et al., 1989, 1991).

Mean total integrated abundance and biomass for the upper 200 m of the water column were calculated for purposes of comparison to other regional studies. Because direct comparisons between studies can be misleading due to differences in sampling design and gear, we have chosen to compare data only from studies that reported nighttime integrated values for the 0–200 m stratum. For that reason, comparisons will be limited to results presented by Lancraft et al. (1989, 1991, 2004).

Integrated biomass of invertebrate micronekton and macrozooplankton from the WAP study region (Table 8) was nearly three times greater in the fall than in the winter (9.11 vs. 3.02 g WM m^{-2}), which was likely due to a reduced catch of

E. crystallorophias in the winter (2.62 vs. 0.005 g WM m^{-2}). Total fall integrated biomass from the WAP was also greater than the value reported from the Scotia Sea in the fall (9.11 vs. 4.58 g WM m^{-2}; Lancraft et al., 1989). However, the WAP winter biomass was only half that reported in the Scotia Sea in winter (3.02 vs. 7.65 g WM m^{-2}; Lancraft et al., 1991) and can be attributed to a smaller *E. superba* catch. Integrated biomass in Croker Passage during the fall (187.64 g WM m^{-2}; Lancraft et al., 2004) was two orders of magnitude higher than that seen in the WAP study region during the fall. This was due to an inordinately large catch of *E. superba*, which was almost 50 times greater (3.78 vs. 174.81 g WM m^{-2}; Lancraft et al., 2004) than the catch in the WAP study region.

Invertebrate micronekton and macrozooplankton integrated abundances were more similar than biomass estimates for the WAP study region in fall and winter (37.96 vs. 29.72 individuals m^{-2}). Abundances reported in the Weddell Sea (11.56 individuals m^{-2}) and in both the winter and fall Scotia Sea studies (12.95 and 21.63 individuals m^{-2}) were also similar, but, like the biomass estimate, abundance in the Croker Passage (801.28 individuals m^{-2}) was substantially higher than in the WAP study region (Lancraft et al., 1989, 1991, 2004). *E. superba* alone supplied 98% of the catch in Croker Passage, which is indicative of a strong neritic influence. During fall in the WAP study region, *E. crystallorophias* dominated, though not to the same extent as *E. superba* in Croker Passage, which underscores the strong neritic influence on the WAP community.

When compared to other oceanic ecosystems, there were notable differences in species assemblages. In most oceanic regions, decapod species are both diverse and abundant (Hopkins and Lancraft, 1984), but in the WAP region there were only four species present; three oceanic and one neritic species found in the fjords (*Notocrangon antarcticus*). The reduced presence of decapods in Antarctic pelagic communities has been noted in several other studies (Piatkowski, 1985; Lancraft et al., 1989, 1991, 2004). Amphipods are another group that differs in relative abundance and diversity in Antarctic communities. In fact, in some Antarctic regions amphipods may occasionally contribute a substantial portion of the overall abundance and biomass. In the WAP study, there were a total of 8 gammarid and 10 hyperiid amphipods represented throughout the cruises. *T. gaudichaudi* was present in sufficient densities to serve as a major contributor in nearly all identified assemblages while *E. macronyx* served that purpose in the nearshore assemblages. In contrast, amphipods are much less common in subtropical regions, like the eastern Gulf of Mexico, where only 25 individuals were collected during a summer study (Hopkins and Lancraft, 1984).

Total species diversity in the WAP region was low in comparison to diversities found in mid-latitude oceanic regions. For example, in the eastern Gulf of Mexico, the number of identified invertebrate micronekton and macrozooplankton species, as well as the number of fish species, was nearly double that found in the WAP study region (Hopkins and Lancraft, 1984; Donnelly and Torres, 2008). In contrast, total integrated abundance and biomass in the WAP region was high compared to the Gulf of Mexico and Hawaii (Hopkins and Lancraft, 1984; Maynard et al., 1975). In the pelagic community as in most others, species diversity, abundance, and biomass all tend to scale with temperature in that diversity increases when moving from polar to equatorial regions while abundance and biomass decline.

5. Conclusion

In both seasons, crustaceans dominated the system accounting for 35 of the 58 taxa encountered during the four cruises. However, a very few species made up a majority of the catch in either season. In the fall, the euphausiids *E. crystallorophias*, *E. superba*, and *T. macrura*, and the mysid *A. ohlinii* numerically dominated the assemblage while in the winter, the same three euphausiids and the chaetognath *P. gazellae* were the numerical dominants. A significant increase in total abundance and biomass was also observed from 2001 to 2002.

Three broad groupings of invertebrate micronektonic/macrozooplanktonic taxa were identified in the waters of the WAP shelf, an oceanic, neritic, and mixed or transitional assemblage. The change in faunal composition was a cross-shelf gradient rather than a sharp boundary at the shelf break and was largely due to changes in relative species abundance with some changes in species composition.

Species diversity and integrated abundance for the upper 200 m of the water column were similar between seasons in the WAP study region, but integrated biomass was nearly three times greater in fall than in winter. Integrated estimates from the WAP study region were similar to those from other studies conducted in the Scotia and Weddell Seas, but were orders of magnitude lower than estimates from a study in Croker Passage, primarily due to a large catch of *E. superba*. In contrast, species diversity in the WAP was higher than recorded in any of the previously mentioned studies, which is due to the mixing of typical oceanic fauna with endemic nearshore fauna.

Results of the present study show that abundance and distribution of invertebrate micronekton and macrozooplankton in the WAP shelf region are highly variable in both space and time. Siegel (2000) described three categories of factors that potentially influence distributions of euphausiids, which can likely be applied to all taxa in the WAP shelf ecosystem. These categories include behavioral factors such as vertical or ontogenetic migrations, life history-related factors such mortality and recruitment success or failure, and physical factors such as temperature and circulation patterns. Only through a better understanding of all of these factors can we hope to gain a complete understanding of the WAP shelf ecosystem.

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