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Pelagic fishes in the Marguerite Bay region of the West Antarctic Peninsula continental shelf

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Abstract

Pelagic fishes in the Marguerite Bay region of the western Antarctic Peninsula (WAP) continental margin were sampled using a 10-m² MOCNESS as part of the Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program. Sixty-two tows were completed during the course of four cruises conducted during the austral fall and winter, 22 each during the austral fall, and 9 each during the austral winter. Six thousand and sixty individuals of 34 species representing 13 families were collected in the fall, while 672 individuals of 22 species from 10 families were collected in the winter. Nearly all of the notothenioid specimens collected (families Artedraconidae, Bathydraconidae, Channichthyidae, and Nototheniidae) were either larvae or young juveniles (0–2 years). Conversely, except for the paralepidid *Notolepis coatsi* and the occasional juveniles of the bathylagid *Bathylagus antarcticus*, the gonostomatid *Cyclothone kobayashii*, or the myctophid *Electrona antarctica*, the non-notothenioid specimens collected were predominantly adults. In the fall, the nototheniids *Pleuragramma antarcticum* and *Trematomus scotti*, and the myctophid *E. antarctica* numerically dominated the overall assemblage, collectively accounting for 89.7% of the total catch. In the winter, *E. antarctica*, *Cyclothone microdon*, and *B. antarcticus* were the numerical dominants, each contributing 14–20% of the total.

The pelagic fish community within the Marguerite Bay region of the WAP continental shelf is a variable mixture of mesopelagic and neritic fauna. At one extreme is an oceanic assemblage exhibiting high-diversity indices and characterized by the genera *Electrona*, *Gymnoscopelus*, *Protomyctophum*, *Bathylagus*, *Cyclothone*, and *Notolepis*. Minor components of this group include numerous less common mesopelagic genera (e.g., *Paradiplospinus*, *Lampanyctus*, *Benthalbella*, *Borostomias*) and the occasional larval/juvenile notothenioid. At the other extreme is a coastal assemblage with low-diversity indices dominated by larval and juvenile notothenioids, particularly *Pleuragramma antarcticum*. This assemblage is also characterized by a numerically low but consistent liparid and zoarcid component, with the latter group often contributing disproportionately to the total biomass. The degree of overlap between the two assemblages and the relative dominance of representative species is directly related to local hydrographic conditions, in particular the presence of Circumpolar Deep Water (CDW). The unique hydrographic conditions of the WAP shelf and the accompanying spatial heterogeneity in pelagic ichthyofauna provide a striking contrast to the continental margin areas of the Ross, Weddell, Davis, and Dumont d'Urville Seas where sharp temperature gradients near the shelf break result in a clear separation of oceanic and coastal assemblages.

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Keywords: Pelagic fishes; Continental Shelf; Distribution; Assemblage; Western Antarctic Peninsula; Marguerite Bay

1. Introduction

Pelagic fishes are an important component of Antarctic ecosystems. They are major contributors to the total water-column biomass in both oceanic (Lancraft et al., 1989,

1991) and coastal areas (DeWitt, 1970; Hubold and Ekau, 1987; Williams, 1985a), and are important zooplankton consumers, particularly on krill (Kock, 1992; Lancraft et al., 1991, 2004; Pusch et al., 2004; Rowedder, 1979; Williams, 1985b). In turn, pelagic fishes are fed upon by numerous upper-level predators including squid (Lubimova, 1985; Nemoto et al., 1985), birds (Ainley et al., 1991; Croxall et al., 1985; Volkman et al., 1980), and seals

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(Øritsland, 1977; Plötz, 1986). Clearly, pelagic fishes play a central role in energy transfer within the Antarctic food web.

In most Antarctic regions, such as the Ross Sea, the pelagic fish assemblage changes as you move shoreward from oceanic to neritic waters, likely due to the very cold ($\sim -2^\circ\text{C}$) waters prevailing over most Antarctic continental shelves (DeWitt, 1970; Donnelly et al., 2004; Hoddell et al., 2000; Hubold and Ekau, 1987; White and Piatkowski, 1993). Oceanic species vanish at the shelf break and are replaced by notothenioids, largely *Pleura-gramma antarcticum*. In contrast, along the western Antarctic Peninsula (WAP), deep troughs and depressions allow intrusions of Circumpolar Deep Water (CDW) onto the shelf (Hoffmann et al., 1996; Smith et al., 1999), producing a warm deep layer and potentially mixing offshore and coastal fauna.

In a review, Kellermann (1996) used the limited data available to describe a midwater fish assemblage within the WAP margin composed of both oceanic (i.e. myctophids, bathylagids, paralepidids, gonostomatids) and shelf (i.e. notothenioids) representatives. However, data on species distribution and abundance were largely limited to larval or juvenile notothenioids (Kellermann, 1986a; Kellermann and Kock, 1988; Kellermann and Schadwinkel, 1991). Lancraft et al. (2004) found that except for *Electrona antarctica*, common oceanic species were absent or rare in the deep basins of Croker Passage vic Anvers Island, probably due to a restricted influx of offshore CDW. Their

data underscore the importance of both bathymetry and local hydrography on coastal pelagic assemblages.

As part of the Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) program, the present study sampled pelagic fishes in the Marguerite Bay region of the WAP continental margin. Bathymetric features within this area include the Marguerite Trough, a deep channel that transects the shelf, as well as several other potentially interconnected channels and depressions. Faunal assemblages together with distribution and abundance patterns are examined in relation to physical and environmental conditions.

2. Methods

2.1. Study area

Field work was done on four cruises conducted during the austral fall and winter. Cruises 1 (2001) and 3 (2002) were aboard the Antarctic Research Support Vessel (A.R.S.V.) *Laurence M. Gould* from April to June; cruises 2 (2001) and 4 (2002) were aboard the Research Vessel Ice Breaker (R.V.I.B.) *Nathaniel B. Palmer* from July to September.

Station designations are based on nomenclature established for the multi-day sampling sites occupied during the *L. M. Gould* process cruises and are shown in Fig. 1A (fall) and B (winter). Process Site 1 was at, or seaward of, the shelf break at the mouth of Marguerite Trough, a deep

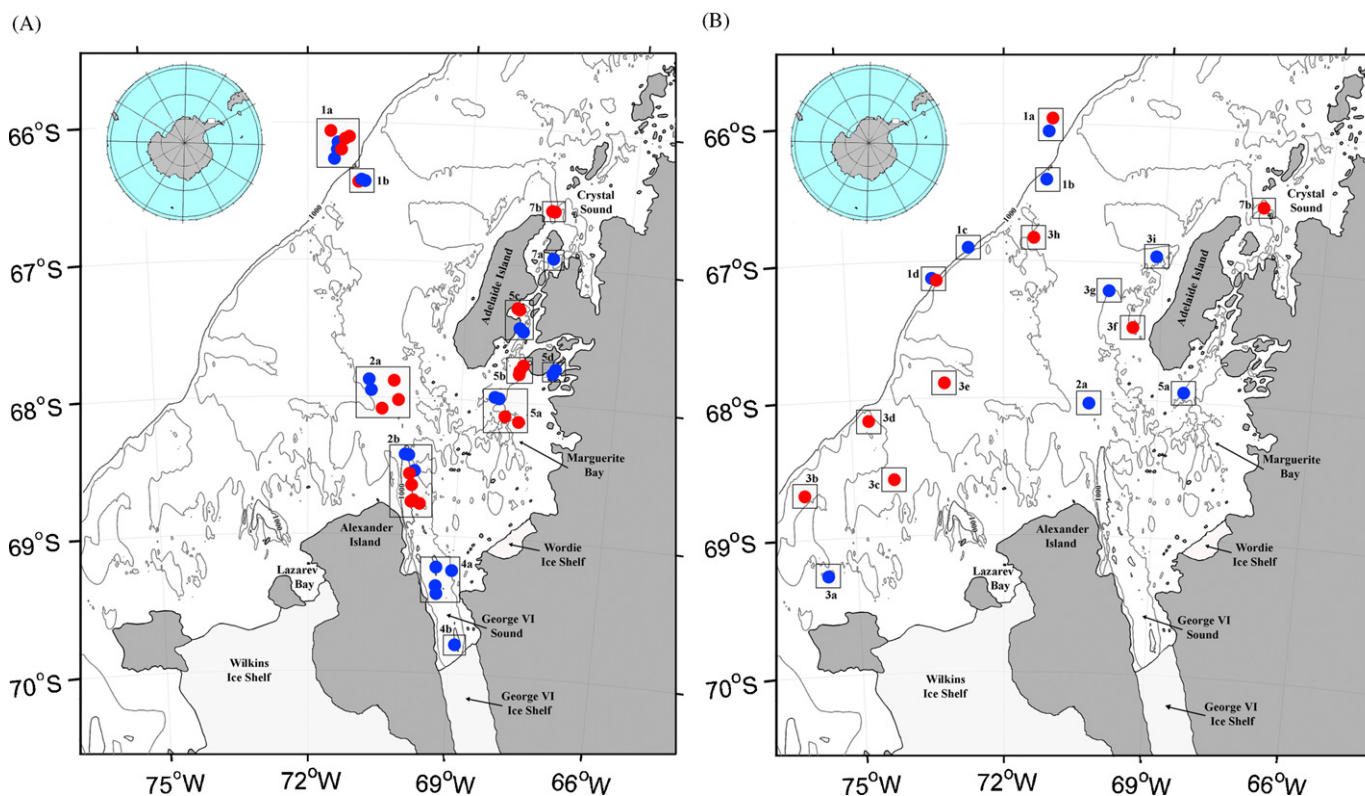


Fig. 1. Trawling sites for (A) fall and (B) winter SO GLOBEC cruises; blue circles: 2001 and red circles: 2002. Station designations as in Table 1.

canyon transecting the shelf in a south–southeast direction: station 1a was off-shelf, station 1b was in the vicinity of the shelf margin, stations 1c and 1d were at the shelf break south of the trough. Process Site 2 was mid-shelf, within the axis of Marguerite Trough: station 2a was seaward of Marguerite Bay, station 2b was at the southwest mouth of the bay. Process Site 3 was officially in Lazarev Bay on the western side of Alexander Island; however, no trawl samples were collected from that location due to uncertain bottom topography and high sea-ice concentrations. Instead, trawling station 3 comprised numerous locations across the continental shelf outside of Marguerite Bay: stations 3a–h were shallow tows (≤ 350 m); stations 3c, 3f, and 3i were deep tows (≥ 470 m). Process Site 4 was in south Marguerite Bay within the axis of Marguerite Trough: station 4a was at the mouth of George VI Sound, station 4b was at the southern end of George VI Sound near the permanent ice shelf. Process Site 5 was in north Marguerite Bay: station 5a was in the open bay, station 5b was between Adelaide and Pourquoi Pas Islands at the mouth of Laubeuf Fjord, station 5c was in the interior of Laubeuf Fjord, station 5d was on the southern side of Pourquoi Pas Island in Bourgeois Fjord. Process Site 7 was in the Crystal Sound area northeast of Adelaide Island: station 7a was in the southwest corner of the sound in Hanusse Bay, station 7b was at the entrance to the sound in Matha Strait.

Hydrographic data for each trawl station were provided by CTD casts conducted either directly before or after trawling and supported by data collected by conductivity, temperature, and pressure sensors mounted on the trawl frame.

2.2. Specimen collection and analysis

Samples were collected with a 10 m² MOCNESS (MOC-10) outfitted with six 3 mm mesh nets. The initial net fished obliquely to depth with each subsequent net fishing a discrete depth layer upward to the surface. At stations with depths > 1000 m, layers sampled were 0–1000, 1000–500, 500–200, 200–100, 100–50, and 50–0 m. At stations with depths > 500 m, layers sampled were 0–500, 500–300, 300–200, 200–100, 100–50, and 50–0 m. At stations with depths < 500 m, sample layers were modified to provide optimal coverage of the water column with the five discrete-depth nets.

A total of 62 MOC-10 trawls were done, 22 each in the fall of 2001 and 2002, and 9 each in the winter of 2001 and 2002 (Table 1). Trawls were conducted at various times throughout the day. In the fall, 37 trawls occurred at night (18:00–06:00 h), 1 in daylight, and 6 at dusk. In the winter, seven trawls occurred at night, seven in daylight, and four at twilight. Towing speed for all tows was 1.5–2.2 knots. Tows in pack ice were conducted in leads created by the ship's wake with the A-frame in to minimize the chance of hooking the wire on ice floes. When ice conditions dictated, the ship first traversed a trawling transect prior to

deployment and then backtracked over the same course through the created lead to insure that adequate speed could be maintained for the duration of the tow.

All samples were preserved in a 5–10% buffered formaldehyde solution, shipped to the laboratory for analysis, and then stored in 50% isopropanol. Fish were sorted from each sample, identified to lowest possible taxon, enumerated, measured (mm; standard length (SL)), and weighed (mg; wet mass (WM)). WM of formalin-preserved specimens has been found to not differ significantly from fresh specimen WM (Lancraft, Donnelly and Torres, unpublished data). For many catches, selected specimens were removed from the sample prior to preservation and stored frozen. These specimens were identified to species and measured prior to freezing and their WM determined from regressions generated from numerous previous datasets (Donnelly and Torres, unpublished data).

2.3. Data

Species' abundance and biomass are expressed as normalized values (#, gWM 10⁴ m⁻³ water volume filtered). Discrete-depth values were calculated for each species by dividing their number or WM in the catch by the water volume filtered for a particular depth stratum. Total integrated values within the 0–200, 0–500, and 0–1000 m layers were calculated by summing all the individual nets within each depth range, including both discrete-depth and oblique net tows. Tows in which a species was not caught were still included in the total volume filtered for a depth layer.

Shannon's diversity index (H' ; Shannon and Weaver, 1949), Pielou's evenness (J' ; Pielou, 1966), and hierarchical cluster analyses were done using PRIMER (Plymouth Routines In Multivariate Ecological Research) software (Clarke and Warwick, 2001). Cluster dendrograms were generated from Bray–Curtis similarity matrices of $\log(y+1)$ -transformed abundance and biomass data. Similarity matrices were generated using group-average distance measures. Potential temperature vs. salinity (θ – S) plots were generated using Ocean Data View software (Schlitzer, 2005).

3. Results

3.1. Interannual comparisons

Six fall and two winter sites were sampled in both 2001 and 2002. In most cases, potential temperature vs. salinity (θ – S) profiles at stations sampled in both years showed only slight inter-annual differences. For the fall cruises, at the off-shelf and shelf-edge sites (stations 1a and 1b), water temperatures at all depths were slightly cooler (0.1–0.5 °C) in 2001. Sub-surface hydrography in 2001 (–1.72 °C, 34.1‰) indicated remnant winter water (WW), although no such signature was evident in 2002. At the fall sites

Table 1
10-m² MOCNESS trawl data for four SO GLOBEC cruises (2001 and 2002)

Cruise	Season	Trawl number	Station	Date (GMT)	Time (GMT)	Latitude (°S)	Longitude (°W)	Trawl depth (m)	Bottom depth (m)	Volume filtered (m ³)
1	Fall	1	1a	5/1/01	1:22	66 12.23	71 24.77	1000	2954	140,758
1	Fall	3	1a	5/2/01	23:25	66 15.44	71 25.08	1000	2812	138,304
1	Fall	4	1a	5/3/01	23:50	66 9.08	71 24.00	1000	2986	180,947
1	Fall	5	1b	5/4/01	19:55	66 24.49	70 59.36	500	542	76,950
1	Fall	6	1b	5/5/01	0:40	66 25.18	70 58.81	500	542	56,815
1	Fall	7	5a	5/6/01	23:20	67 56.98	68 20.81	500	790	108,518
1	Fall	8	5a	5/7/01	0:13	67 56.68	68 21.12	500	803	94,311
1	Fall	9	5c	5/8/01	0:50	67 25.24	67 51.50	400	445	41,429
1	Fall	10	5d	5/9/01	1:30	67 46.30	67 18.50	300	380	42,646
1	Fall	11	5d	5/10/01	18:20	67 45.9	67 17.9	400	453	44,391
1	Fall	12	5c	5/11/01	23:13	67 27.40	67 50.4	400	495	62,191
1	Fall	13	4a	5/13/01	19:45	69 14.7	69 13.8	500	958	66,815
1	Fall	14	4a	5/14/01	0:30	69 14.95	69 2.2	500	634	59,168
1	Fall	15	4a	5/14/01	22:50	69 24.2	69 13.7	500	983	60,860
1	Fall	16	4a	5/15/01	2:12	69 20.16	69 13.79	700	892	98,121
1	Fall	17	4b	5/17/01	2:16	69 47.96	68 52.04	800	1050	83,995
1	Fall	18	2b	5/18/01	17:35	68 24.84	70 0.22	500	1016	37,755
1	Fall	19	2b	5/18/01	21:38	68 31.9	69 53.6	500	790	98,076
1	Fall	20	2b	5/19/01	2:12	68 24.57	69 59.95	500	944	75,101
1	Fall	21	2a	5/19/01	23:10	67 56.65	70 32.47	500	760	54,560
1	Fall	22	2a	5/20/01	2:07	67 50.46	70 35.02	500	805	79,078
1	Fall	23	7a	5/30/01	1:30	66 54.14	67 16.9	400	525	49,312
2	Winter	1	1a	7/30/01	14:28	66 2.38	71 13.38	1000	3100	93,156
2	Winter	2	3g	8/1/01	20:46	67 12.86	70 0.12	300	433	35,831
2	Winter	3	1c	8/3/01	19:51	66 53.62	72 36.9	1000	1190	101,758
2	Winter	4	2a	8/5/01	15:25	68 2.16	70 19.8	500	820	62,292
2	Winter	5	5a	8/8/01	14:01	67 55.2	68 30.8	500	650	39,673
2	Winter	6	1d	8/10/01	16:03	67 7.86	73 19.51	1000	1826	112,383
2	Winter	7	3a	8/21/01	18:54	69 16.33	75 38.84	300	338	32,116
2	Winter	8	1b	8/24/01	13:45	66 23.01	71 19.72	800	839	38,862
2	Winter	9	3i	8/25/01	12:18	66 58.16	69 24.61	466	546	33,838
3	Fall	2	7b	4/17/02	5:05	66 38.1	67 26.0	300	380	34,350
3	Fall	3	7b	4/17/02	9:30	66 38.3	67 25.9	300	387	44,324
3	Fall	4	5c	4/20/02	0:05	67 18.1	67 50.3	500	628	41,798
3	Fall	5	5c	4/20/02	2:42	67 18.2	67 50.2	450	650	43,382
3	Fall	6	5b	4/22/02	2:37	67 45.8	68 06.8	500	715	52,208
3	Fall	7	5b	4/22/02	19:07	67 46.9	68 07.2	500	827	66,420
3	Fall	8	5b	4/23/02	2:45	67 42.5	68 04.8	500	614	49,943
3	Fall	9	1a	4/24/02	21:45	66 05.1	71 13.8	1000	3041	75,142
3	Fall	10	1a	4/25/02	3:00	66 07.4	71 16.3	500	2974	45,826
3	Fall	11	1a	4/25/02	22:33	66 12.8	71 21.3	1000	2994	79,089
3	Fall	12	1a	4/27/02	14:45	66 03.2	71 27.8	1000	3186	95,905
3	Fall	13	1b	4/28/02	2:28	66 25.4	71 06.1	400	545	50,476
3	Fall	14	2b	5/2/02	1:20	68 45.2	69 52.8	800	1055	79,972
3	Fall	15	2b	5/3/02	0:36	68 45.1	69 53.1	800	1016	69,839
3	Fall	16	2b	5/4/02	0:38	68 46.5	69 49.4	716	676	76,439
3	Fall	17	2b	5/4/02	17:05	68 38.4	69 52.6	750	861	85,524
3	Fall	18	2b	5/4/02	23:33	68 32.6	69 54.3	750	820	87,855
3	Fall	19	2a	5/7/02	0:08	68 05.1	70 21.8	750	864	92,175
3	Fall	20	2a	5/7/02	17:44	68 00.2	70 02.9	750	832	114,263
3	Fall	21	2a	5/7/02	23:33	67 52.4	70 08.9	500	676	74,030
3	Fall	22	5a	5/10/02	1:27	68 05.8	68 14.9	400	302	39,433
3	Fall	23	5a	5/11/02	2:13	68 07.9	68 01.2	400	493	38,062
4	Winter	1	7b	8/7/02	23:07	66 32.5	67 5.8	500	1200	50,052
4	Winter	2	3b	8/12/02	1:00	68 40.0	76 8.6	350	430	40,933
4	Winter	3	3c	8/15/02	23:00	68 34.4	74 9.0	500	677	35,017
4	Winter	4	3d	8/17/02	19:12	68 8.8	74 35.5	350	417	18,971
4	Winter	6	1d	8/21/02	1:58	67 9.2	73 14.7	1000	> 1000	89,936
4	Winter	7	3e	8/24/02	1:32	67 53.2	73 5.9	250	376	21,548
4	Winter	9	1a	9/2/02	19:07	65 57.2	71 2.8	1000	3562	136,246
4	Winter	10	3h	9/6/02	17:48	66 49.2	71 25.3	400	479	54,798
4	Winter	11	3f	9/8/02	1:37	67 28.0	69 32.1	500	> 500	63,692

Station designations described in text; local time = GMT-4h.

within Marguerite Bay (stations 5a and 5c), surface water temperatures were 1.0 °C cooler in 2002, a consequence of a higher pack ice presence in that year (Perovich et al., 2004). Surface water temperatures were also cooler at the two sites within Marguerite Trough (stations 2a and 2b) but less so (0.4 °C) than that at the two inner-bay sites. Below a depth of 100–130 m at all four shelf stations, the θ – S profiles for both years mirrored each other. No inter-annual differences were observed at either of the two coincident winter sites (stations 1a and 1d).

Catch assemblages at coincident stations were similar between years (e.g., 57–83% overlap in occurrence of common species). No inter-annual differences in total abundance or biomass occurred at the off-shelf or shelf edge stations (1a–d) in either season. At the inner-shelf stations (2a, 2b, 5a, 5c), differences in total abundance and/or biomass resulted primarily from variability in the catches of three species: *E. antarctica*, *P. antarcticum*, and/or *Trematomus scotti*, but the only consistent inter-annual changes involved the nototheniid species. In the surface layer at stations 2b, 5a, and 5c, *T. scotti* had much higher abundance (43–49 ×) and biomass (102–144 ×) in 2001. Sampling at the inner bay sites, however, occurred 2–3 weeks earlier in 2002, which resulted in the majority of *T. scotti* individuals being slightly smaller than those from 2001 (17–20 mmSL vs. 20–26 mmSL). The difference in abundances between years likely reflects the inefficiency of 3 mm mesh nets in sampling specimens <20 mmSL. *P. antarcticum* had similar abundances in both years but biomass increased (0–34 ×) at these same stations in 2002 due to an increase in mean specimen size. In 2001, 7% of the *P. antarcticum* caught were 24–28 mmSL (age class 0, Hubold, 1985a), 90% were 30–53 mmSL (age class 1), and 3% were >125 mmSL (age 6+). In 2002, 1% were age class 0, 6% were age class 1, 93% were age class 2 (55–72 mmSL), and 0.3% were adults. These data suggest that the same population year-class accounted for the majority of specimens collected in successive years.

For both years, the total volume filtered (2,286,696 m³ vs. 1,947,645 m³), the number of specimens caught (16.2 individuals 10⁴ m⁻³ vs. 15.5 individuals 10⁴ m⁻³), and the overall sample biomass (19.2 gWM 10⁴ m⁻³ vs. 35.7 gWM 10⁴ m⁻³) were similar. Because of a generally consistent hydrography, an absence of significant differences in community assemblage, and a level of variability in species' abundance and biomass within that normally encountered in pelagic samples, catch data for stations sampled in both 2001 and 2002 were combined for the tabular presentation of seasonal values. Station catch data were not combined for the calculation of diversity indices or for cluster analyses.

3.2. Hydrographic setting

Representative plots of potential temperature vs. salinity (θ – S) for the 12 fall trawling stations and 16 winter trawling stations are shown in Fig. 2A and B. In the fall,

dispersed temperature and salinity values for Antarctic Surface Water (AASW) reflect temporal and spatial changes in heat flux within the near-surface layer. Warmest surface temperatures occurred at station 7a in Crystal Sound; coldest surface temperatures occurred at station 4b in George VI Sound. The temperature minimum of –1.7 °C at a salinity of 34.1‰ occurred at station 5d (Bourgeois Fjord) and indicates remnant WW. During the winter, surface conditions indicated that considerable seasonal cooling had occurred, with θ – S values representative of WW at most stations. Only stations 3a and 5a did not yet show a definite WW surface signature.

Water with temperatures of 1.0–2.0 °C and salinities of 34.6–34.74‰ represent CDW, which may be sub-divided into Upper CDW (UCDW) and Lower CDW (LCDW) (Sievers and Nowlin, 1984; Smith et al., 1999). In both seasons, UCDW was present off-shelf and at the shelf edge (stations 1a–d). LCDW was present only off-shelf in the fall but also along the shelf edge in the winter. Water with characteristics intermediate between AASW and UCDW (1.0–1.5 °C, 34.3–34.6‰), referred to as modified CDW (MCDW; Hoffmann and Klinck, 1998a), occurred throughout the study area in both seasons, and was the predominant sub-surface water mass both within and outside of Marguerite Bay.

3.3. Species abundance and biomass

Thirty-four species representing 13 families were collected in the fall (Table 2), while 22 species from 10 families were collected in the winter (Table 3). Nearly all of the nototheniid specimens collected (families Artedraconidae, Bathydraconidae, Channichthyidae, and Nototheniidae) were either larva or young juveniles (0–2 years). Conversely, except for the paraplepidid *Notolepis coatsi* and the occasional juveniles of the bathylagid *Bathylagus antarcticus*, the gonostomatid *Cyclothone kobayashii*, or the myctophid *E. antarctica*, the non-nototheniid specimens collected were predominantly adults.

In the fall, the nototheniids *P. antarcticum* and *T. scotti*, and the myctophid *E. antarctica* numerically dominated the overall assemblage, collectively accounting for 89.7% of the total catch. Four other species contributed greater than 1% of the collection: the myctophids *Protomyctophum bolini* and *Gymnoscopelus braueri*, the gonostomatid *Cyclothone microdon* and *B. antarcticus*. In terms of biomass, *Pleuragramma antarcticum* and *E. antarctica* remained the dominant species while the contribution from *T. scotti* and *C. microdon* decreased considerably. Species that were not abundant but contributed disproportionately to the total biomass included the myctophid *G. nicholsi*, the zoarcid *Melanostigma gelatinosum*, and the gempylid *Paradiplospinus gracilis*.

In the winter, *E. antarctica*, *C. microdon*, and *B. antarcticus* were the numerical dominants, each contributing 14–20% of the total. Seven additional species contributed 4–10%: *T. scotti*, *Lepidonotothen squamifrons*, *Pleuragramma*

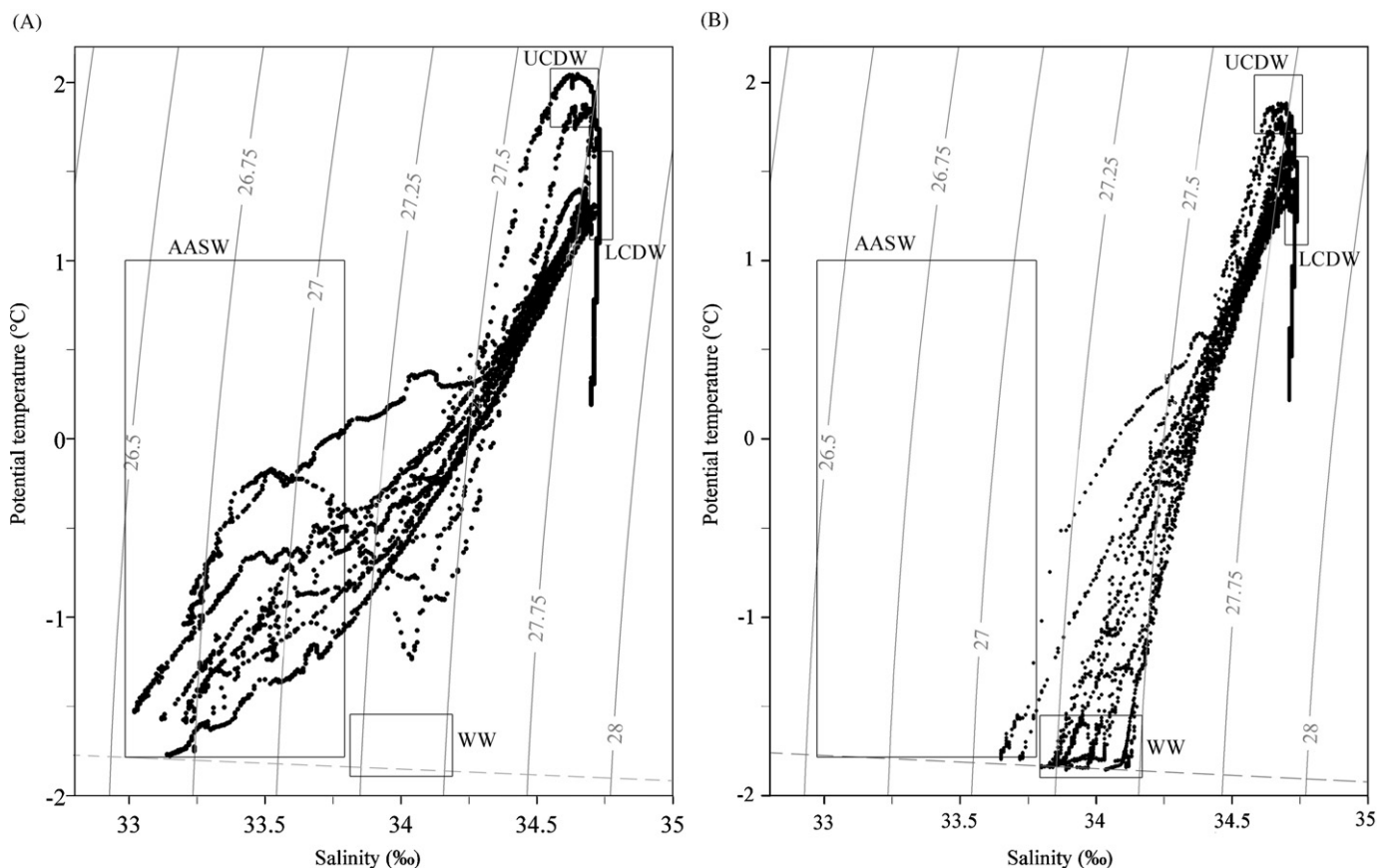


Fig. 2. Plot of potential temperature vs. salinity for each station during the (A) fall and (B) winter. Boxes show temperature and salinity ranges for UCDW, LCDW, AASW, and WW water masses. Light vertical lines are contours of equal potential density at the surface (σ_0). Freezing point of seawater shown by dashed line.

antarcticum, *G. braueri*, *Protomyctophum bolini*, *N. coatsi*, and the channichthyid *Chaenodraco wilsoni*. In terms of biomass, *E. antarctica* and *B. antarcticus* remained dominant while the contributions from *C. microdon* and the four notothenioid species decreased. Biomass sub-dominants (4–8% of the total) also included *M. gelatinosum* and the myctophids, *G. braueri* and *G. opisthopterus*.

Three times as many fishes were caught in the fall than in the winter (19.06 individuals 10^4 m^{-3} vs. 6.37 individuals 10^4 m^{-3}). This was due to primarily 38- and 7-fold lower catches, respectively, of *Pleuragramma antarcticum* and *T. scotti* during the winter. Total biomass over the study area, however, was similar between the two seasons (28.05 gWM 10^4 m^{-3} vs. 22.97 gWM 10^4 m^{-3}).

3.4. Station assemblages

Cluster analyses of fall abundance (Fig. 3A) and biomass (Fig. 3B) indicated two primary groupings: one including the mid-shelf and shelf-edge site (stations 1 and 2a), and one including the inner-bay sites (stations 4 and 5). Station 2b was transitional between both groups, clustering differently for abundance than for biomass, as well as showing different group affinities between sample years. Station 7b was

isolated in the fall abundance dendrogram because two *E. antarctica* were the only fish caught at that site.

Fall stations 1, 2a, and 7 were dominated by oceanic genera (e.g., *Electrona*, *Protomyctophum*, *Gymnoscopelus*, *Cyclothone*, *Bathylagus*) with little occurrence of notothenioid specimens. Abundance and biomass values for these stations ranged from 0.3 to 5.3 individuals 10^4 m^{-3} and 4.7 to 27.0 gWM 10^4 m^{-3} . Although station 2b exhibited similar values (3.7 individuals 10^4 m^{-3} and 14.8 gWM 10^4 m^{-3}), there was a greater contribution from notothenioid species, particularly *Pleuragramma antarcticum* and *T. scotti* at this site. Abundance and biomass values were higher for stations 4 and 5, ranging from 17.4 to 102.3 individuals 10^4 m^{-3} and 9.3 to 141.3 gWM 10^4 m^{-3} . These sites were dominated numerically by *T. scotti* and *P. antarcticum*; however, there were notable biomass contributions from non-notothenioid specimens, particularly *E. antarctica*, *B. antarcticus*, *Seleniolychus laevifasciatus*, and *M. gelatinosum*.

Diversity measures for the fall stations also highlighted the assemblage differences between inner- and outer-shelf sites (Table 4). In terms of abundance, both diversity (H') and evenness (J') were higher for stations 1, 2 and 7a (0.4–0.9) than for stations 4 and 5 (0.1–0.4). In terms of

Table 2
Total pelagic fish abundance (individual 10^4 m^{-3}) and biomass (gWM 10^4 m^{-3}) for each station during the fall (2001 and 2002 combined)

Family	Genus species (mmSL)	Station											
		1a (755,971)		1b (184,241)		2a (414,106)		2b (610,563)		4a (284,964)		4b (83,995)	
		Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM
Artedidraconidae	<i>Pogonophryne marmorata</i> (24)												
Bathydraconidae	<i>Prionodracon evansii</i> (40–54)												
	<i>Psilodracon breviceps</i> (141)												
	<i>Racovitzia glacialis</i> (38–44)									0.11	0.030		
	<i>Vomeridens infuscipinis</i> (47–157)												
Bathylagidae	<i>Bathylagus antarcticus</i> (25–166)	0.37	1.501			0.34	0.265	0.26	1.195	0.14	1.373	0.24	2.845
Channichthyidae	<i>Chaenodracon wilsoni</i> (102–105)							0.02	0.154	0.04	0.270		
	<i>Chionodracon hamatus</i> (62–80)							0.02	0.051				
	<i>Cryodraco antarctica</i> (111–121)											0.12	1.191
Gonostomatidae	<i>Cyclothone kobayashii</i> (24–55)	0.19	0.046			0.07	0.015	0.05	0.013				
	<i>Cyclothone microdon</i> (34–65)	0.94	0.651	0.05	0.048								
	<i>Cyclothone</i> spp. (30–60)	0.34	0.123										
Gempylidae	<i>Paradiplospinus gracilis</i> (377–388)	0.01	0.860	0.05	3.632								
Liparidae	<i>Edentoliparis terraenovae</i> (13–63)							0.11	0.024				
Macrouridae	<i>Cyanomacrurus piriei</i> (82–285)	0.05	0.910										
Myctophidae	<i>Electrona antarctica</i> (23–117)	1.63	4.864	3.37	17.631	2.78	16.606	0.61	3.615	0.04	0.415		
	<i>Electrona carlsbergi</i> (71–85)	0.13	0.967	0.16	1.133								
	<i>Gymnoscopelus braueri</i> (74–160)	0.45	1.435	0.05	0.211	0.58	5.943	0.13	1.508	0.14	2.197		
	<i>Gymnoscopelus nicholsi</i> (140–169)	0.04	1.480	0.05	1.465	0.07	2.217	0.07	2.457				
	<i>Gymnoscopelus opisthopterus</i> (66–135)	0.03	0.084							0.04	0.344		
	<i>Lampanyctus achirus</i> (100)	0.01	0.092										
	<i>Krefflichthys anderssoni</i> (36)	0.01	0.006										
	<i>Protomyctophum bolini</i> (35–66)	0.70	0.982	1.03	1.540	0.43	0.892	0.13	0.243				
Nototheniidae	<i>Lepidonotothen squamifrons</i> (22–29)	0.04	0.001	0.22	0.007	0.34	0.015	0.10	0.004	0.07	0.003		
	<i>Nototheniops larseni</i> (22–26)												
	<i>Nototheniops nudifrons</i> (31–36)							0.05	0.019				
	<i>Pleuragramma antarcticum</i> (24–208)	0.04	0.047			0.02	0.483	0.51	4.427	3.44	2.559	45.00	6.437
	<i>Trematomus eulepidotus</i> (36)												
	<i>Trematomus lepidorhinus</i> (28–37)							0.08	0.025	0.25	0.093		
	<i>Trematomus newnesi</i> (33)								0.04	0.009			
	<i>Trematomus scottii</i> (17–26)					0.12	0.008	1.31	0.091	12.91	0.960	3.57	0.264
Paralepididae	<i>Notolepis coatsi</i> (45–176)	0.30	0.268	0.33	0.101	0.10	0.068	0.18	0.203	0.11	0.015		
Stomiidae	<i>Borostomias antarcticus</i> (152–185)	0.03	1.006										
Zoarcidae	<i>Melanostigma gelatinosum</i> (57–185)							0.03	0.795	0.11	0.997		
	<i>Selenolychnus laevifasciatus</i> (139–172)					0.02	0.458					0.12	4.236
	Total	5.32	15.324	5.32	25.769	4.88	26.971	3.65	14.823	17.41	9.265	49.05	14.974

Table 2 (continued)

Family	Genus species (mmSL)	5a (280,324)		5b (168,574)		5c (188,800)		5d (87,037)		7a (42,271)		7b (78,674)		ALL (3,179,514)	
		Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM
Arteidraconidae	<i>Pogonophryne marmorata</i> (24)					0.05	0.025							0.003	0.001
Bathdraconidae	<i>Prionodracon evansii</i> (40–54)					0.26	0.142	0.57	0.412					0.03	0.020
	<i>Psilodracon breviceps</i> (141)							0.11	4.205					0.003	0.115
	<i>Racovitzia glacialis</i> (38–44)													0.01	0.003
	<i>Vomeridens infuscipinis</i> (47–157)	0.14	0.066	0.06	1.168									0.02	0.068
Bathylagidae	<i>Bathylagus antarcticus</i> (25–166)													0.20	0.819
Channichthyidae	<i>Chaenodracon wilsoni</i> (102–105)													0.01	0.054
	<i>Chionodracon hamatus</i> (62–80)	0.11	0.196	0.06	0.064									0.02	0.030
	<i>Cryodracon antarctica</i> (111–121)					0.05	0.177							0.01	0.042
Gonostomatidae	<i>Cyclothone kobayashii</i> (24–55)													0.06	0.015
	<i>Cyclothone microdon</i> (34–65)													0.23	0.158
	<i>Cyclothone</i> spp. (30–60)													0.08	0.029
Gempylidae	<i>Paradiplospinus gracilis</i> (377–388)													0.01	0.415
Liparidae	<i>Edentoliparis terraenovae</i> (13–63)	0.46	0.202	0.47	0.175	0.90	0.380	0.34	0.436	0.95	0.774			0.16	0.077
Macrouridae	<i>Cyanomacurus piriei</i> (82–285)													0.01	0.216
Myctophidae	<i>Electrona antarctica</i> (23–117)	0.57	6.596	0.95	8.574	0.21	2.687			0.47	5.559	0.25	4.688	1.19	6.458
	<i>Electrona carlsbergi</i> (71–85)													0.04	0.296
	<i>Gymnoscopelus braueri</i> (74–160)	0.04	0.341	0.06	0.753	0.11	2.855			0.24	0.994			0.24	1.867
	<i>Gymnoscopelus nicholsi</i> (140–169)													0.03	1.197
	<i>Gymnoscopelus opisthapterus</i> (66–135)					0.05	1.123							0.01	0.117
	<i>Lampanyctus achirus</i> (100)													0.003	0.022
	<i>Krefflichthys anderssoni</i> (36)													0.003	0.002
	<i>Protomyctophum bolini</i> (35–66)													0.31	0.486
Nototheniidae	<i>Lepidonotothen squamifrons</i> (22–29)													0.09	0.004
	<i>Nototheniops larseni</i> (22–26)	0.07	0.003			0.16	0.014	0.11	0.007	0.24	0.023			0.02	0.002
	<i>Nototheniops nudifrons</i> (31–36)	0.11	0.033			0.05	0.023	0.23	0.098					0.03	0.011
	<i>Pleuragramma antarcticum</i> (24–208)	15.95	33.822	99.78	130.153	34.80	31.306	29.53	20.230					11.18	13.619
	<i>Trematomus eulepidotus</i> (36)			0.06	0.019									0.003	0.001
	<i>Trematomus lepidorhinus</i> (28–37)	0.50	0.117			0.16	0.034	0.11	0.035					0.09	0.026
	<i>Trematomus newnesi</i> (33)													0.003	0.001
	<i>Trematomus scotti</i> (17–26)	16.34	1.196	0.71	0.024	5.77	0.381	50.44	3.129	0.47	0.025			4.73	0.327
Paralepididae	<i>Notolepis coatsi</i> (45–176)	0.04	0.004	0.06	0.061	0.05	0.003							0.16	0.123
														0.01	0.172
Stomiidae	<i>Borostomias antarcticus</i> (152–185)														
Zoarcidae	<i>Melanostigma gelatinosum</i> (57–185)	0.04	1.159	0.12	0.261	0.16	1.190	1.15	21.908					0.07	1.028
	<i>Selenolychus laevifasciatus</i> (139–172)													0.01	0.172
	Total	34.35	43.736	102.33	141.252	42.80	40.339	82.61	50.461	2.37	7.375	0.25	4.688	19.06	27.990

Values in parentheses in each station column heading are total volume filtered (m³).

Table 3
Total pelagic fish abundance (individual 10^4 m^{-3}) and biomass (gWM 10^4 m^{-3}) for each station during the winter (2001 and 2002 combined)

Family	Genus species (mmSL)	Station																
		1a (225,997)		1b (38,862)		1c (101,758)		1d (202,318)		2a (62,293)		3a (32,116)		3b (40,933)		3c (35,018)		
		Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	
Bathylagidae	<i>Bathylagus antarcticus</i> (21–164)	1.68	16.431	1.03	2.704	0.98	7.278	1.73	13.278	0.16	0.037	0.31	0.016			0.29	1.623	
Channichthyidae	<i>Chaenodraco wilsoni</i> (24–32)							0.05	0.0068	0.64	0.0607					0.86	0.0778	
	<i>Chionodraco hamatus</i> (23–106)	0.04	0.002					0.05	0.002									
Gonostomatidae	<i>Pagetopsis macropterus</i> (19–21)																	
	<i>Cyclothone kobayashii</i> (28–45)	0.22	0.135		0.20	0.051	0.20	0.051										
Liparidae	<i>Cyclothone microdon</i> (32–66)	0.93	0.758		2.56	1.907	4.15	3.466										
	<i>Edentoliparis terraenovae</i> (19–43)																	
Myctophidae	<i>Paraliparis meganchus</i> (130)																	
	<i>Electrona antarctica</i> (36–96)	2.04	13.137	2.06	10.539	2.26	12.312	0.99	6.277	0.64	4.815	0.31	3.113			1.14	7.132	
Myctophidae	<i>Gymnoscopelus braueri</i> (62–120)	0.22	1.872	2.57	15.696	0.10	0.285	0.40	2.544									
	<i>Gymnoscopelus nicholsi</i> (151)							0.05	2.392									
Myctophidae	<i>Gymnoscopelus opisthopterus</i> (51–158)	0.04	2.488					0.10	2.905									
	<i>Lampanyctus achirus</i> (121–141)							0.15	2.429									
Nototheniidae	<i>Protomyctophum bolini</i> (39–56)	0.40	0.658		0.59	1.122		0.05	0.053	0.32	0.626		0.49	1.022	0.57	1.337		
	<i>Lepidonotothen squamifrons</i> (24–33)	0.66	0.048	1.03	0.081			0.35	0.027	0.64	0.056		0.24	0.011	0.57	0.034		
Nototheniidae	<i>Pleuragramma antarcticum</i> (24–132)							0.30	0.025			5.92	0.774					
	<i>T. lepidorhinus</i> (42–45)																	
Paralepididae	<i>T. scotti</i> (19–26)			0.26	0.026	0.88	0.085	0.10	0.010					0.49	0.027	0.57	0.028	
	<i>Notolepis coatsi</i> (41–94)	0.18	0.048		0.49	0.089		0.64	0.220	0.64	0.132	0.31	0.086	0.49	0.057			
Scopelarchidae	<i>Benthalbella macropinna</i> (205)							0.05	2.094									
Stomiidae	<i>Borostomias antarcticus</i> (170)							0.05	1.5923									
Zoarcidae	<i>Melanostigma gelatinosum</i> (80–162)																	
	Total	6.42	35.577	6.95	29.047	8.06	23.129	9.39	37.375	3.05	5.726	6.85	3.990	1.71	1.117	4.00	10.233	
		3d (18,971)		3e (21,548)		3f (63,692)		3g (35,831)		3h (54,798)		3i (30,969)		5a (39,673)		7b (50,052)		All (1,054,827)
		Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	Number	gWM	
Bathylagidae	<i>Bathylagus antarcticus</i> (21–164)									0.18	0.006					0.86	6.926	
Channichthyidae	<i>Chaenodraco wilsoni</i> (24–32)	0.53	0.0714					6.14	0.4831			0.97	0.1189			0.20	0.0175	
	<i>Chionodraco hamatus</i> (23–106)									0.18	0.026					0.20	1.437	
Gonostomatidae	<i>Pagetopsis macropterus</i> (19–21)															0.60	0.0350	
	<i>Cyclothone kobayashii</i> (28–45)															0.10	0.044	
Liparidae	<i>Cyclothone microdon</i> (32–66)							0.28	0.112							1.25	1.015	
	<i>Edentoliparis terraenovae</i> (19–43)												0.50	0.0912	1.00	0.4543	0.07	
Myctophidae	<i>Paraliparis meganchus</i> (130)				0.16	5.0462										0.01	0.3047	
	<i>Electrona antarctica</i> (36–96)				2.51	12.731						0.97	7.685			2.00	13.650	
Myctophidae	<i>Gymnoscopelus braueri</i> (62–120)															0.80	6.909	
	<i>Gymnoscopelus nicholsi</i> (151)															0.20	2.516	
Myctophidae	<i>Gymnoscopelus opisthopterus</i> (51–158)															0.03	1.090	
	<i>Lampanyctus achirus</i> (121–141)															0.03	0.466	
Nototheniidae	<i>Protomyctophum bolini</i> (39–56)				0.94	2.068	0.28	0.607	0.18	0.416						0.28	0.548	
	<i>Lepidonotothen squamifrons</i> (24–33)	1.05	0.054	1.39	0.064			0.56	0.040			0.65	0.063			0.40	0.029	
Nototheniidae	<i>Pleuragramma antarcticum</i> (24–132)											0.32	0.070	1.26	10.051	0.29	0.409	
	<i>T. lepidorhinus</i> (42–45)													0.50	0.323	0.02	0.012	
Paralepididae	<i>T. scotti</i> (19–26)	2.11	0.150	5.57	0.451			5.86	0.558					4.03	0.354	0.65	0.057	
	<i>Notolepis coatsi</i> (41–94)			0.93	0.150					0.18	0.026					0.20	0.133	
Scopelarchidae	<i>Benthalbella macropinna</i> (205)															0.01	0.402	
Stomiidae	<i>Borostomias antarcticus</i> (170)															0.01	0.3054	
Zoarcidae	<i>Melanostigma gelatinosum</i> (80–162)				0.79	5.9579										0.60	11.309	
	Total	3.69	0.275	7.89	0.666	4.40	25.803	13.12	1.799	0.73	0.474	2.91	7.937	6.30	10.820	5.79	36.460	
																6.37	22.552	

Values in parentheses in each station column heading are total volume filtered (m^3).

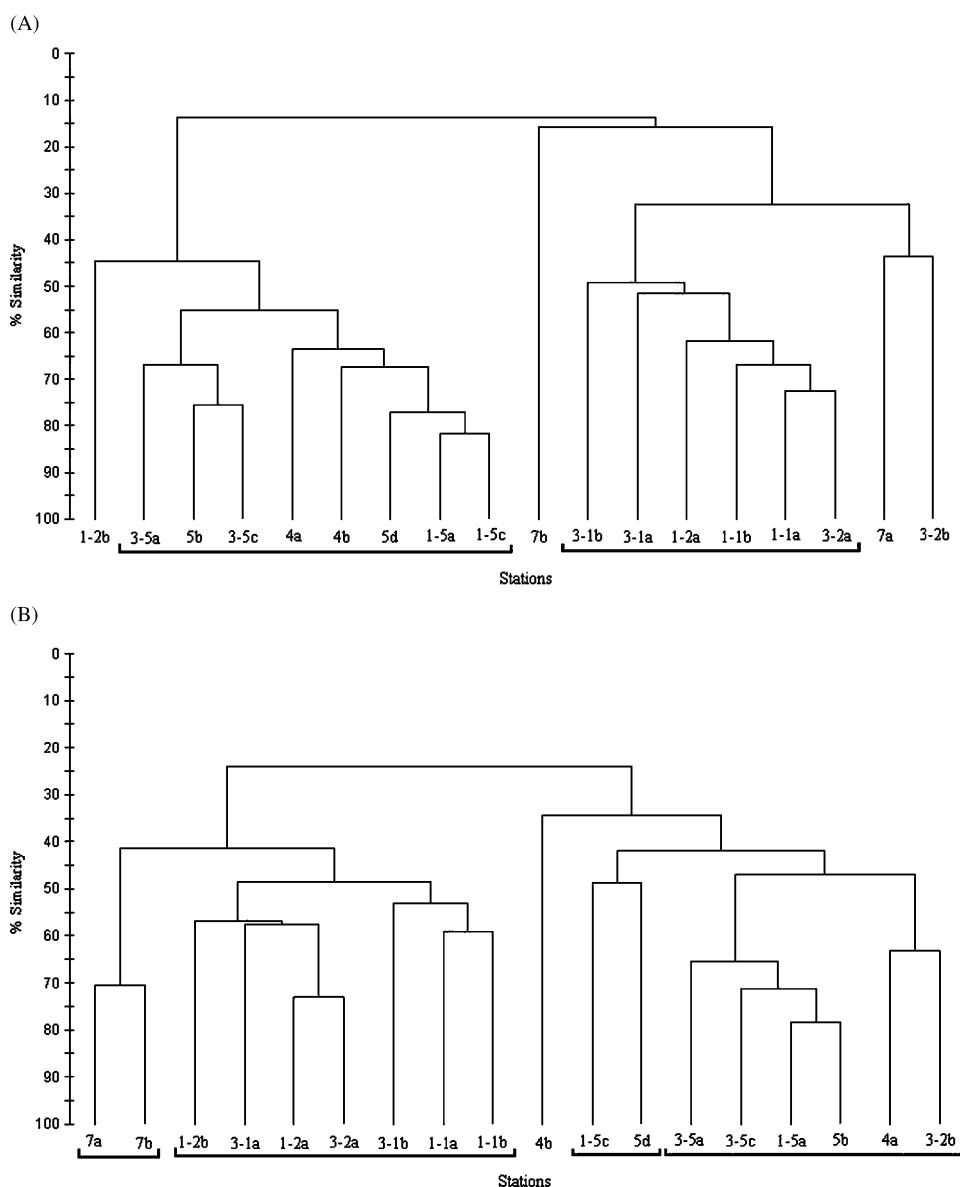


Fig. 3. Percent similarity cluster dendrograms of (A) fish abundance (number of individual 10^4 m^{-3}) and (B) biomass ($\text{gWM } 10^4 \text{ m}^{-3}$) by station during fall. Stations sampled in both years are distinguished by a 1- (2001) or 3- (2002) prefix.

biomass, diversity indices remained high for stations 1 and 2, while greater contributions from non-notothenioid species at station 4 and 5 are reflected in increased values for both *H'* and *J'*.

Cluster analyses of winter abundance (Fig. 4A) and biomass (Fig. 4B) were influenced by the greater spread in mid-shelf sample sites (i.e. station 3) compared to the fall. Two station groupings were maintained in both the abundance and biomass dendrograms: a shelf-edge cluster incorporating the station 1 sample sites; and a deep (540–820 m water depth), mid-shelf cluster including stations 2a, 3c, and 3i. As in the fall, station 1 exhibited a typical oceanic faunal assemblage with only the occasional occurrence of a larval nototheniid or juvenile channichthyid. Specimen abundance ranged from 6.4 to 9.4 individuals 10^4 m^{-3} and catch biomass was high

(23.1–35.6 $\text{gWM } 10^4 \text{ m}^{-3}$). The mid-shelf cluster stations contained a mixture of oceanic genera (e.g., *Electrona*, *Bathylagus*, *Notolepis*) and notothenioid genera (e.g., *Chaenodraco*, *Pleuragramma*, *Trematomus*). Specimen abundance was evenly distributed between both faunal groups, ranging from 2.9 to 4.0 individuals 10^4 m^{-3} . Biomass ranged from 5.7 to 10.2 $\text{gWM } 10^4 \text{ m}^{-3}$, and was accounted for predominantly by oceanic specimens, particularly *E. antarctica*.

A third, less-consistent winter cluster included several mid-shelf sites (stations 3d, 3e, 3g) and the inner-bay site (station 5a). These stations contained mainly notothenioid genera (*Trematomus*, *Lepidonotothen*, *Chaenodraco*) with minor occurrences of oceanic specimens or the lipid *Edentoliparis terraenovae*. Specimen abundance ranged from 3.7 to 13.1 individuals 10^4 m^{-3} . Biomass was low at

Table 4
Diversity and evenness indices for total fish abundance (individual 10^4 m^{-3}) and biomass (gWM 10^4 m^{-3}) for each station

Station	Cruise	Abundance (individual 10^4 m^{-3})		Biomass (gWM 10^4 m^{-3})	
		Diversity (H')	Evenness (J')	Diversity (H')	Evenness (J')
Fall					
1a	1	0.8358	0.7503	0.8401	0.7542
	3	0.8219	0.7171	0.8889	0.7755
1b	1	0.5977	0.6264	0.5807	0.6086
	3	0.3809	0.6327	0.1804	0.2997
2a	1	0.7364	0.8155	0.6123	0.6781
	3	0.6048	0.6048	0.4382	0.4382
2b	1	0.6693	0.6427	0.7438	0.7142
	3	0.9434	0.8022	0.7457	0.6340
4a	1	0.3669	0.3293	0.8267	0.7422
4b	1	0.1411	0.2019	0.5682	0.8129
5a	1	0.4242	0.4074	0.3145	0.3020
	3	0.1843	0.2369	0.3541	0.4551
5b	3	0.0682	0.0682	0.1487	0.1487
5c	1	0.3692	0.3869	0.3590	0.3763
	3	0.1451	0.1520	0.3510	0.3678
5d	1	0.3603	0.3776	0.5242	0.5493
7a	1	0.6388	0.9139	0.3287	0.4702
7b	3	0	na	0	na
Winter					
1a	2	0.6648	0.7867	0.5094	0.6028
	4	0.6837	0.6837	0.5064	0.5064
1b	2	0.6150	0.8799	0.4101	0.5867
1c	2	0.7496	0.8301	0.5045	0.5586
1d	2	0.7220	0.6690	0.5653	0.5239
	4	0.8343	0.7489	0.9235	0.8290
2a	2	0.7401	0.9511	0.2606	0.3349
3a	2	0.2380	0.3954	0.2679	0.4450
3b	4	0.5871	0.9751	0.1598	0.2653
3c	4	0.7429	0.9546	0.3831	0.4923
3d	4	0.4151	0.8699	0.4341	0.9098
3e	4	0.3491	0.7316	0.3586	0.7516
3f	4	0.4675	0.7765	0.5248	0.8717
3g	2	0.4401	0.6297	0.5819	0.8325
3h	4	0.6021	1.0000	0.2134	0.3545
3i	2	0.5693	0.9455	0.0757	0.1258
5a	2	0.4393	0.7297	0.1414	0.2348
7b	4	0.8153	0.8544	0.6269	0.6570

Station and cruise number designations as in Table 1.

stations 3d, 3e, and 3g ($0.3\text{--}1.8 \text{ gWM } 10^4 \text{ m}^{-3}$), but higher at station 5a ($10.8 \text{ gWM } 10^4 \text{ m}^{-3}$) due to the presence of three larger juvenile (118–132 mmSL) *Pleuragramma* specimens.

The remaining winter mid-shelf sample sites showed varying affinities. Stations 3b and 3h had a mixed assemblage with low specimen abundance ($0.7\text{--}1.7$ individuals 10^4 m^{-3}) and low biomass ($0.5\text{--}1.1 \text{ gWM } 10^4 \text{ m}^{-3}$) accounted for predominantly by *Protomyctophum bolini*.

Stations 3f and 7b, both deep mid-shelf sites, had assemblages dominated by myctophids, liparids, and zoarcids ($4.4\text{--}5.4$ individuals 10^4 m^{-3}) with high biomass ($25.8\text{--}28.0 \text{ gWM } 10^4 \text{ m}^{-3}$). Station 3a had intermediate abundance and biomass with an assemblage dominated by *Pleuragramma* numerically but by *Electrona* gravimetrically.

Diversity measures for the winter stations (Table 4) were less consistent than in the fall, but in general were higher for the shelf-edge (station 1) and deep mid-shelf (stations 2a, 3i, 3c, 3f) sites.

3.5. Depth distributions

Discrete-depth distributions were compiled for eight common species (Table 5). *B. antarcticus* and *C. microdon* were concentrated below 500 m in both seasons. A few *C. microdon* individuals were collected in shallow waters during the winter; however, *B. antarcticus* was never found above 100 m. Juvenile *N. coatsi* were also only caught below 100 m. *E. antarctica* and *G. braueri* were dispersed throughout the water column in the fall with peak levels found between 100 and 500 m. In the winter, both species only occurred regularly below 200 m. *Protomyctophum bolini* exhibited the narrowest depth range of the six oceanic genera, occurring almost exclusively within 200–500 m during both fall and winter. Trawling schedule constraints in both sampling years precluded an adequate examination of diel changes in vertical distribution. Previous studies (Hulley, 1981; Lancraft et al., 1989; 1991, 2004) have reported that *B. antarcticus*, *E. antarctica*, *G. braueri*, *G. nicholsi*, *P. bolini*, and *N. coatsi* all undertake diel vertical migrations.

The nototheniids *Pleuragramma antarcticum* and *T. scotti* occurred predominantly in epipelagic waters. All of the *T. scotti* specimens were larvae (17–26 mmSL) whereas 39% of the *P. antarcticum* specimens were age class 0–1 (<55 mmSL) and 59% were juveniles (age class 2–3, 55–90 mmSL). Larval *T. scotti* occurred predominantly (90%) in the 0–50 m layer while both larval and juvenile *P. antarcticum* had peak occurrences (71–80%) in the 100–200-m layer. Larger *P. antarcticum* (age class 5+, 113–208 mmSL), which were caught only sporadically, occurred mainly in the 200–500 m layer.

The depth distributions of total fish abundance and biomass in the fall reflected the observed changes in faunal assemblage, changing from the shelf edge through the mid-shelf trough and into the inner bay. At the off-shelf site (station 1a), abundance and biomass were highest below 100 m. *E. antarctica*, *Gymnoscopelus* spp., and *Protomyctophum bolini* dominated from 100 to 500 m, with *B. antarcticus*, *C. microdon*, and *E. antarctica* common below 500 m. At the shelf edge (station 1b) and upper, mid-shelf trough site (station 2a), abundance and biomass increased in epipelagic waters although both measures remained highest at sub-pycnocline depths. At the lower, mid-shelf site (station 2b) and the inner bay sites (stations 4

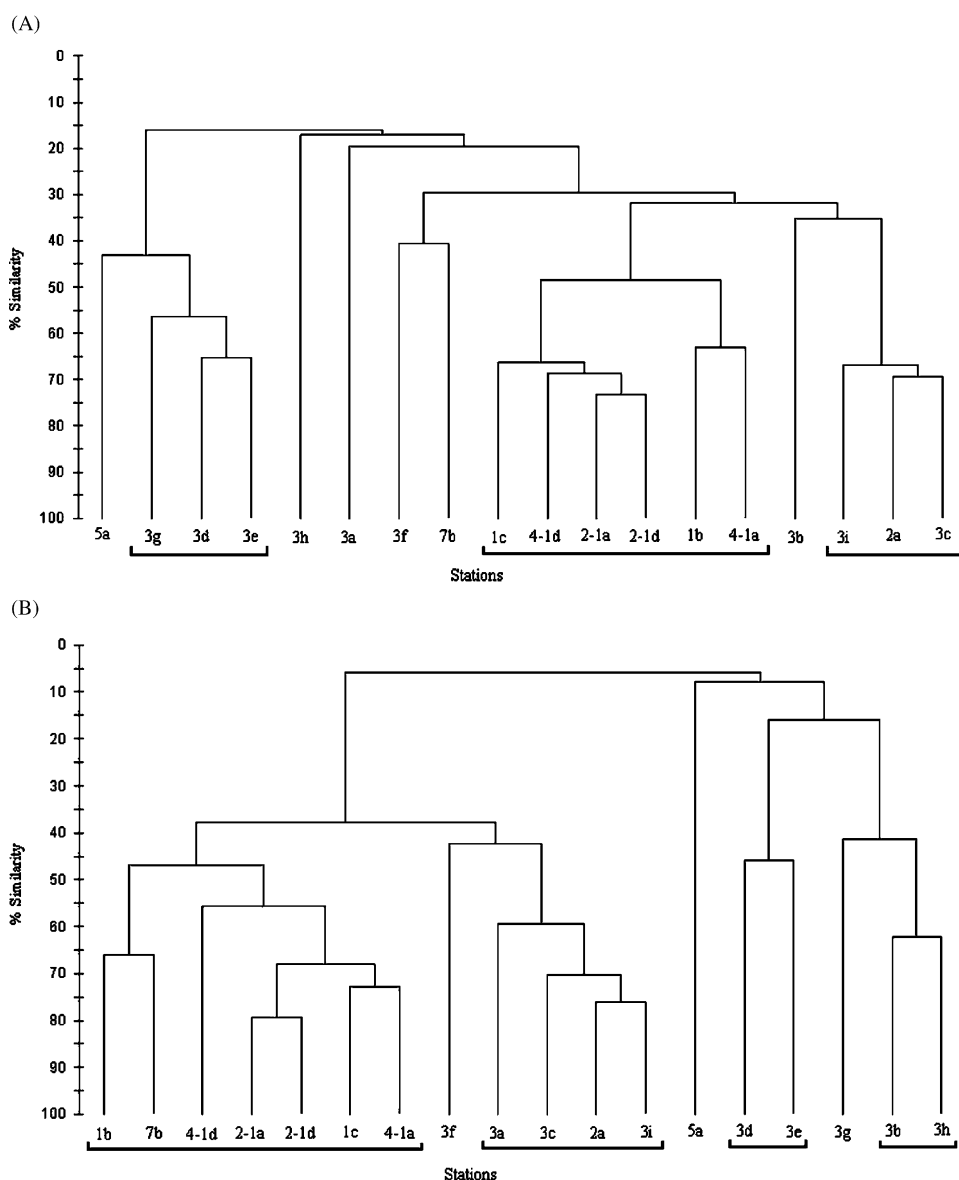


Fig. 4. Percent similarity cluster dendrograms of (A) fish abundance (number of individual 10^4 m^{-3}) and (B) biomass ($\text{gWM } 10^4 \text{ m}^{-3}$) by station during winter. Stations sampled in both years are distinguished by a 1- (2001) or 3- (2002) prefix.

and 5), abundance was highest at shallower depths with peak values at individual sites corresponding to the predominance of particular species. At station 4, abundance maxima in the 0–50 m (4a) and 50–200 m (4b) depth layers were due to the numerical dominance of *T. scotti* (4a) and *P. antarcticum* (4b). Biomass was more evenly distributed, particularly at station 4b, due to the presence of deeper-living, non-nototheniid specimens (e.g., *Gymnoscopelus*, *Bathylagus*, *Melanostigma*, and *Seleniolychus*). At stations 5a and 5d, peak abundance values in the 0–50-m and the 100–200-m layers again reflected high numbers of *T. scotti* and *P. antarcticum* specimens, while the deeper biomass peaks reflected the contributions from *Electrona* (5a) and *Melanostigma* (5d). At stations 5b and 5c, juvenile *Pleuragramma* in the 100–200-m layer dominated the catch in both numbers and biomass.

In the winter, there were few specimens and very little biomass in the upper 200 m at any station. Peak abundance values in the 0–50-m layer were attributable primarily to larval *L. squamifrons*, *T. scotti*, and *C. wilsoni* with the only notable surface water biomass peak coming from a single 110 mmSL specimen of *Gymnoscopelus nicholsi* caught at station 7b. At the shelf edge (station 1), abundance and biomass peaks occurred in both the 200–500 and 500–1000-m layers. In the upper mesopelagic layer, *E. antarctica* and *Protomyctophum bolini* dominated the catch numerically with *G. nicholsi*, *B. antarcticus*, and *Benthabella macropinna* also contributing to the total biomass. Below 500 m, *B. antarcticus*, *E. antarctica*, and *C. microdon* predominated with additional biomass contributions coming from *G. opisthopterus* and *Borostomias antarcticus*. Below 200 m on the shelf in the winter, catches

Table 5
Depth distributions for commonly caught pelagic fish. Abundance (individual 10^4 m^{-3}) and biomass (gWM 10^4 m^{-3}) data compiled from discrete-depth nets for all trawls that a species was caught

Species	Season	Trawl time	No. of tows	n	0–50 m			50–100 m			100–200 m			200–500 m			500–1000 m		
					Individual 10^4 m^{-3}	gWM 10^4 m^{-3}	mmSL range	Individual 10^4 m^{-3}	gWM 10^4 m^{-3}	mmSL range	Individual 10^4 m^{-3}	gWM 10^4 m^{-3}	mmSL range	Individual 10^4 m^{-3}	gWM 10^4 m^{-3}	mmSL range	Individual 10^4 m^{-3}	gWM 10^4 m^{-3}	mmSL range
<i>Bathylagus antarcticus</i>	Fall	N	17	43						0.10	0.505	32–99	0.36	2.073	36–129	0.84	4.474	25–166	
	Winter	D	5	38									0.65	7.332	24–163	3.63	27.471	44–64	
		N	3	33												2.68	21.274	34–150	
<i>Cyclothone microdon</i>	Fall	D/N	4	49												4.63	3.393	34–65	
	Winter	D	2	59	2.59	2.283	53	1.71	1.774	56	0.70	0.795	59			7.51	6.369	32–60	
		N	3	39												5.56	4.138	40–58	
<i>Electrona antarctica</i>	Fall	N	31	283	0.25	1.869	68–83	1.29	5.962	31–78	3.05	16.259	28–105	1.68	10.083	28–117	0.40	2.243	23–79
	Winter	D	6	21				0.60	2.566	68				1.08	7.221	36–95	0.82	4.997	65–89
		N	7	69						0.19	1.474	81	3.80	22.275	50–105	0.89	5.186	54–89	
<i>Gymnoscopehus braueri</i>	Fall	N	19	59	0.16	1.032	88–98				0.75	5.283	74–116	0.61	5.564	80–160	0.26	4.016	100–142
	Winter	D	3	9										0.13	0.375	77	0.94	6.589	81–120
		N	3	9										0.94	8.112	85–120	0.11	1.091	108
<i>Protomyctophum bolini</i>	Fall	N	18	87						0.05	0.222	66	1.56	2.392	35–59				
	Winter	D	3	3										0.37	0.682	39–55			
		N	4	19										1.75	3.482	48–55			
<i>Notolepis coatsi</i>	Fall	N	20	41						0.09	0.008	45–50	0.53	0.145	45–95	0.52	0.243	57–111	
	Winter	D	3	12						1.46	0.268	41–58	0.57	0.182	50–86	0.40	0.125	55–58	
		N	6	12						0.19	0.019	45	0.90	0.164	43–69				
<i>Pleuragramma antarcticum</i>	Fall	N	23	2769	9.48	2.860	24–71	26.67	22.972	25–130	101.97	90.647	23–188	2.47	19.808	35–208	0.11	0.022	39
	Winter	D	4	28	6.62	0.779	28–35	11.96	1.616	24–37	1.17	0.374	26–51	0.16	1.852	118			
<i>Trematomus scotti</i>	Fall	N	24	1465	97.24	6.789	17–26	8.65	0.544	17–24	0.25	0.013	20–24	0.15	0.008	19–22			
	Winter	D	3	12	10.52	0.879	20–26												
		N	5	38	6.93	0.635	20–26	2.79	0.224	22–24	3.11	0.287	22–26						

were generally greater at the deep (> 500 m water depth) sites (e.g., stations 2a, 3f, 3i, 7b) than at the shallower sites (e.g., stations 3b, 3d, 3e, 3g, 3h) with *E. antarctica* being the principal abundance and biomass component.

4. Discussion

4.1. Fish assemblages and hydrographic influences

The pelagic fish community within the Marguerite Bay region of the WAP continental shelf is a variable mixture of mesopelagic and neritic fauna. At one extreme is an oceanic assemblage exhibiting high-diversity indices and characterized by the genera *Electrona*, *Gymnoscopelus*, *Protomyctophum*, *Bathylagus*, *Cyclothone*, and *Notolepis*. Minor components of this group include numerous less common mesopelagic genera (e.g., *Paradiplospinus*, *Lampanyctus*, *Benthalbella*, *Borostomias*) and the occasional larval/juvenile notothenioid. At the other extreme is a coastal assemblage with low-diversity indices dominated by larval and juvenile notothenioids, particularly *Pleuragramma antarcticum*. This assemblage is also characterized by a numerically low but consistent liparid and zoarcid component, with the latter group often contributing disproportionately to the total biomass.

The degree of overlap between the two assemblages and the relative dominance of representative species is directly related to local hydrographic conditions. A purely oceanic assemblage just off-shelf as well as along the shelf break reflects unaltered CDW and indicates the proximity of the Antarctic Circumpolar Current to the continental margin in this area. Slight modifications in CDW (~1.4 °C temperature maximum, 34.72‰ salinity maximum) have negligible effect on the faunal makeup and further cooling and freshening is necessary before an evenly mixed oceanic–neritic assemblage develops (~1.3–1.4 °C temperature max, ~34.7–34.72‰ salinity max). Within the axis of Marguerite Trough, this degree of CDW modification was found near the southwest entrance to Marguerite Bay (station 2b), roughly 200 km in from the mouth of the trough. A similar hydrography and faunal mixture also occurred in Matha Strait (station 7b), which has a continuous bathymetric connection to the main trough via deep canyons north of Adelaide Island. Persistence of an oceanic ichthyofauna in Marguerite Trough and its extensions well shoreward of the shelf break underscores the findings of hydrographic studies identifying this deep bathymetric feature as an important conduit for CDW influx onto the shelf (Dinniman and Klinck, 2004; Hoffmann and Klinck, 1998b; Klinck et al., 2004; Prézelin et al., 2000).

As the incoming CDW flows across the shelf, bottom depth also influences the particular species that predominate in the mixed assemblage. Oceanic species with vertical distributions that include epipelagic depths such as *E. antarctica* and *G. braueri* have more widespread distributions across the shelf and are not as restricted to

the basins and canyons as are the deeper-living *Bathylagus antarcticus* and *C. microdon*. Similarly, with the neritic component, bottom depth does not influence the horizontal distribution of larval and juvenile notothenioids in epipelagic waters whereas zoarcids and to a lesser extent, liparids, only occur at deep-water sites. Vertical migration patterns also factor into the extent of a species' horizontal distribution. Diel ranges of *E. antarctica*, *G. braueri*, *G. nicholsi*, and *N. coatsi* regularly extend to epipelagic waters affording these species unrestricted access to both shallow and deep shelf sites. *B. antarcticus*, *G. opisthopterus*, and *P. bolini* also undergo daily migrations, but their depth ranges are deeper, extending only to upper mesopelagic depths.

When sub-surface temperature/salinity maxima are below 1.3 °C and 34.7‰, the pelagic fish assemblage is more neritic in nature, at least in terms of the numerically dominant species. Regular inputs of oceanic water (four to six intrusions per year; Klinck et al., 2004), however, result in sustained widespread coverage of MCDW across the area which places distributional constraints on a nototheniid-dominated shelf assemblage. One consequence of this is that high abundances of *T. scotti* and *P. antarcticum* larvae and juveniles were found only within Marguerite Bay in and around the northern bay coastal fjords and also deep inside George VI Sound. In addition to the general clockwise circulation inside Marguerite Bay, results from drifter and acoustic-Doppler current profile (ADCP) measurements (Beardsley et al., 2004; Klinck et al., 2004; Zhou et al., 2004) indicate the presence of a small gyre within the northern half of the bay and mesoscale eddies within the fjords, features that would favor the retention and accumulation of larval/juvenile nototheniids at the northern bay sites. Although adult *P. antarcticum* were caught infrequently (43 individuals), most (86%) of these specimens occurred at the northern bay sites as well.

Elevated abundance of *Pleuragramma* at the northern bay sites is likely influenced by trophic conditions as well as hydrography. *P. antarcticum* feed on copepods and krill (Hubold, 1985b; Kellermann, 1986b), groups that were both found to have elevated biomass in the northern bay, particularly in the austral fall (Ashjian et al., 2004; Lawson et al., 2004; Zhou and Dorland, 2004). Outside of Marguerite Bay, cold, less-saline waters can be found close to shore along the western side of Adelaide Island and in an expanded area west of Alexander Island south of the bay (Dinniman and Klinck, 2004; Klinck et al., 2004). The shelf west of Alexander Island was also found to be an area of elevated zooplankton biomass (Ashjian et al., 2004; Lawson et al., 2004). Although not sampled for ichthyofauna in the present study, those areas could potentially exhibit a *Pleuragramma*-dominated fish assemblage as well.

The unique hydrographic conditions of the WAP shelf and the accompanying spatial heterogeneity in pelagic ichthyofauna provides a striking contrast to the continental margin areas of the Ross, Weddell, Davis, and Dumont d'Urville Seas where sharp temperature gradients near the

shelf break result in a clear separation of oceanic and coastal assemblages (DeWitt, 1970; Donnelly et al., 2004; Hoddell et al., 2000; Hubold and Ekau, 1987; White and Piatkowski, 1993). The neritic midwater habitat developed recently in the geochronology of the Antarctic and as noted by White and North (1987), the influence of temperature on the geographical distribution of pelagic fishes likely stems from the evolutionary histories of the different groups. The oceanic species represent families with cosmopolitan distributions that have adapted secondarily to the Southern Ocean whereas the notothenioids have evolved within the Antarctic coastal environment since the waters began cooling 50 million years ago (Eastman, 1993; Kock, 1992).

4.2. Seasonal changes

The similarity in total biomass between fall and winter results from the tradeoff of high biomass inner-shelf sites in the fall (station 5) with high biomass shelf edge (stations 1c and 1d) and deep-water shelf (stations 3c, 3i, 3f, 7b) sites in the winter. At the off-shelf site, total biomass in the 0–1000-m layer increased two-fold in the winter due to the combined effect of greater catches of *Bathylagus* and *Cyclothone* in deep waters and an increase in the mean sizes of *Bathylagus*, *Cyclothone*, *Electrona*, and *Gymnoscopelus*. At the two Marguerite Trough sites (stations 1b and 2a), if we take into account the effect of daytime tows, biomass was comparable between seasons. By far the greatest seasonal change was observed at the northern Marguerite Bay site (station 5a). Here the large decrease in abundance and biomass from fall to winter resulted primarily from a seven-fold lower catch of *P. antarcticum* and *T. scotti*. Although myctophids comprised a minor numerical component at this station in the fall, their winter-time absence accounted for 16% of the biomass decline. Hydrographic conditions and sampling depths were the same at this site in both seasons; however, trawling effort was much reduced in the winter compared to the fall (39,673 m³ vs. 202,829 m³ volume filtered) and the single winter-time tow occurred during the day. Net avoidance during the daytime tow could contribute to the myctophid absence but is less likely to be a factor with the larval and juvenile nototheniids. There is no *a priori* reason to expect nototheniids to have low abundance at this location in the winter and in fact, adult *Pleuragramma* occurred in similar concentrations in both seasons (1.1 individuals 10⁴ m⁻³ vs. 0.8 individuals 10⁴ m⁻³). Juvenile *Pleuragramma* and larval *T. scotti* tend to aggregate and while a seasonal change in distribution cannot be discounted, it is more likely that the single winter tow did not represent an accurate sampling of the resident population.

A seasonal pattern that was consistently evident in both years was the winter-time deepening of abundance and biomass peaks. This was due primarily to the movement of myctophids out of epipelagic waters, at both on-shelf and off-shelf stations. At stations 1a, 1b, and 2a in 2001, the winter deepening appears to even extend below 500 m, but

this additional depression results from the fact that the winter-time tows at these sites were conducted during the day. Winter-time deepening of the depth of maximum occurrence for *Bathylagus*, *Cyclothone*, and *Electrona* is consistent with the findings of Lancraft et al. (1991) for oceanic waters. *G. braueri* was also more common at deeper depths during the winter in the present study, but no seasonal change in vertical distribution was observed for this species in the 1991 study. Of the common oceanic species collected in the present study, only *N. coatsi* and *Protomyctophum bolini* showed no seasonal change in abundance with depth.

A deeper winter depth distribution for the dominant oceanic species means that for areas of the shelf moderately influenced by CDW intrusions, ichthyofaunal biomass will be lower at shallow sites and elevated at deep-water sites. This consequence is evident when comparing winter-time catches from various shelf locations. All five shallow-water sites (stations 3b, 3d, 3e, 3g, 3h) had low biomass (0.3–1.8 gWM 10⁴ m⁻³) and an assemblage consisting primarily of small notothenioids and/or an occasional oceanic species. Conversely, the deep-water sites (stations 2a, 3c, 3i, 3f, 7b) had high biomass (5.7–36.5 gWM 10⁴ m⁻³) accounted for mainly by *Electrona* with additional input from other myctophids, *Bathylagus*, and the zoarcid *Melanostigma*. Biomass at deep mid-shelf sites was at times as high as that seen at the shelf-edge and off-shelf sites. From a trophodynamic perspective, deep-water shelf locations would offer improved foraging for piscivores such as seals and deep-diving penguins whose feeding ranges extend to mesopelagic depths.

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