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Composition and spatial variability of macroplankton and micronekton within the Antarctic Polar Frontal Zone of the Indian Ocean during austral autumn 1997

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Abstract Net sampling and continuous acoustic measurements within the Antarctic Polar Frontal Zone (APFZ) and in the vicinity of the Prince Edward Islands were conducted during austral autumn (April/May) 1997 to describe the composition and distribution of macrozooplankton and micronekton, and to investigate their relations to the prevailing oceanographic regime in the area. Two major circulation patterns associated with the Subantarctic (SAF) and Antarctic Polar (APF) Fronts existed in the oceanic environment surrounding the Prince Edward Islands, promoting high cross-frontal mixing both upstream and downstream of the islands. Average abundance and biomass of macroplankton/micronekton in the top 300-m layer were 21 ind. 1000 m^{-3} and 467 mg DW 1000 m^{-3}, respectively. Pelagic crustaceans (euphausiids and amphipods), fish, chaetognaths and gelatinous zooplankton dominated numerically and by biomass. Continuous acoustic measurements displayed elevated pelagic biomass at the SAF and APF. Although four groupings of stations were identified using cluster analysis, a single macroplankton/micronekton community was recognized in the top 300-m layer throughout the offshore area of the APFZ. A modification of the APFZ community was observed within the inter-island region. Subantarctic species dominated zooplankton samples throughout the APFZ, although subtropical species were also well represented at stations occupied in the northern region of the APFZ. A biological response reflected in macroplankton community composition, resulting from an extensive cross-frontal mixing, was observed within the APFZ around the Prince Edward Islands.

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Introduction

The Antarctic Polar Frontal Zone (APFZ) represents a circumpolar belt of water bounded by the Subantarctic (SAF) and Antarctic Polar (APF) Fronts and forms the northern part of the eastward-flowing Antarctic Circumpolar Current (ACC) (Deacon 1983; Hofmann and Whitworth 1985). The Prince Edward Islands (46°45′S, 37°50′E) lie directly in the path of the ACC (Pakhomov and Froneman 1999a). The islands promote "an island-mass effect" and accommodate large populations of top predators (Williams et al. 1979; Condy 1981; Boden 1988; Perissinotto and Duncombe Rae 1990; Perissinotto and McQuaid 1992; Pakhomov and Froneman 1999a).

Recent investigations have shown that both the SAF and the APF are characterized by an enhanced macroplankton/micronekton standing stock (Pakhomov and McQuaid 1996; Ansorge et al. 1999; Pakhomov et al. 1999). Extensive oceanographic surveys undertaken in the vicinity of the Prince Edward Islands have shown that the position of these fronts demonstrate a high degree of latitudinal variability (Nagata et al. 1988; Duncombe Rae 1989; Lutjeharms 1990). Although many of the land-based top predators are able to travel long distances to forage within the nearby frontal systems (Bost et al. 1997; Guinet et al. 1997; Weimerskirch et al. 1997), it is hypothesized that elevated macroplankton and micronekton biomass associated with the SAF and APF may be transported to the island ecosystem via physical mechanisms (Pakhomov and Froneman 1999a). Previous investigations have largely been restricted to the immediate proximity or inter-island region of the Prince Edward Islands (Pakhomov and Froneman 1999a, b). As a consequence, little is known on the interaction between the offshore macroplankton stock and the predators on the islands.

Oceanographic studies conducted within the APFZ are scarce throughout the entire Southern Ocean. In April/May 1989 and 1997, two mesoscale surveys covering >100,000 km^2 were carried out around the Prince Edward Islands, with the main objective of understanding the influence of the islands on the downstream physical environment (van Ballegooyen et al. 1989; Pakhomov et al. 1998). During the 1989 expedition, some zooplankton samples were collected using a Bongo net, which is considered an appropriate gear for catching mesozooplankton only. During the 1997 survey, both a Bongo and Rectangular Midwater Trawl (RMT-8) nets were employed, and continuous acoustic measurements were also undertaken (Pakhomov et al. 1998). Surface phytoplankton and mesozooplankton distributions during April/May 1997 were found to be consistent with the prevailing oceanographic regime around the islands (Froneman et al. 1999). As previous studies concentrated on mesozooplankton and little or no information on macrozooplankton and micronekton are available for the remote offshore upstream and downstream regions of the Prince Edward Islands, the main aims of this study are to describe the community structure and distribution patterns of large plankton and to relate them to the physical environment within the APFZ around the islands using material from the 1997 expedition.

Materials and methods

Macrozooplankton/micronekton samples were collected during the 84th voyage of the mv *SA Agulhas* in the upstream and downstream areas of the Prince Edward Islands between 8 and 18 May 1997 (Fig. 1). The survey consisted of a grid of eight north-south transects. Each transect generally consisted of nine alternate CTD (conductivity-depth-temperature) stations to a depth of 1500 m using a Neil Brown Instrument system and XBT (expendable bathythermograph) stations to a depth of 760 m. CTD and XBT stations were occupied at ≈15-nautical mile intervals. At selected CTD stations, a zooplankton sample was collected throughout the 24-h cycle using an RMT-8 with a nominal mouth area of 8 m^2 and a mesh size of 5 mm (Fig. 1). Generally, at the oceanic stations the trawl was towed obliquely between 300 and 0 m. At stations 131 and 133, only deep-water layers between 500 and 300 m were sampled. In addition, in the shelf area between the islands three near-bottom tows were conducted. Towing speed and duration varied between 1.5 and 3.3 knots and between 10 and 40 min. The trawl was equipped with a Universal Underwater Unit (U^3: Robertson et al. 1981) which continuously monitored depth and temperature, as well as the opening and closing times of the trawl. The volume filtered by the trawl was determined by multiplying the effective mouth area of the trawl by the distance travelled (Roe et al. 1980). This was calculated from the ship's speed and the duration of trawling after the net was opened. Samples were preserved in 6% buffered formalin and examined in the laboratory within 2 months after collection. No adjustments were made to correct for tissue loss due to formalin preservation. Entire catches were sorted and analysed for species composition, numerical abundance and wet weight biomass. The dry weights of the main macrozooplanktonic and micronektonic taxa were then estimated by using conversion factors obtained by oven-drying fixed specimens for 36 h at 60 °C.

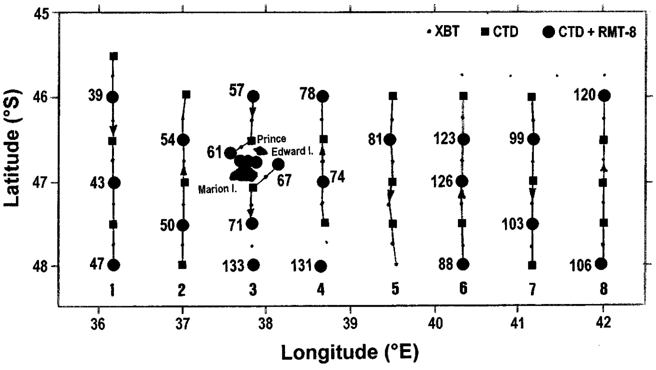

Fig. 1 Positions of hydrographic stations, RMT-8 net tows and acoustic transects around the Prince Edward Islands during May 1997

To compare plankton communities, hierarchical cluster analysis and multidimensional scaling were used in conjunction with the Bray-Curtis similarity index, after log transforming [$\log_{10}(x + 1)$] the species abundance data. Significance levels and sources of difference between zooplankton assemblages associated with the different group of stations were tested using the similarity analysis programs ANOSIM and SIMPER of the Plymouth Routines In Multivariate Ecological Research computer package (PRIMER) (Clarke and Warwick 1994).

Between the CTD stations, macrozooplankton/micronekton densities within the top 250 m were determined acoustically using a SIMRAD EK500 echosounder operated at frequency of 120 kHz (Fig. 1). In order to detect large plankton and micronekton, the volume backscattering strengths (S_v) threshold value for echo integration was set for −80 db. The output parameter of the sounder echo integrator was S_a (m^2 nm^{-2}; Simrad 1991), the mean backscattering area per unit of horizontal area. This gave depth-stratified (every 5 m depth), integrated, quantitative estimates along the survey path every 3 min (≈5 nm). The underlying background noise level was then subtracted from the entire data set (for each transect separately), following the procedure described by Watkins and Brierley (1996).

Results

Physical environment

The detailed description of the oceanographic conditions in the vicinity of the Prince Edward Islands during May 1997 are published elsewhere (Froneman et al. 1999). Here, we concentrate on the description of two most important features relevant to the plankton distribution, i.e. the position of the SAF and APF to the north and south of the island group, and the mesoscale eddies found in the downstream region.

Upstream of the Prince Edward Islands between 36 and 37°E, the SAF was registered at 47°20′S (Fig. 2A). In this area, the SAF merged with the APF forming an intensive frontal feature with subsurface temperatures ranging from 7.8 to 5.2 °C (Fig. 2A). A high temperature gradient, ca. 0.05 °C/km, was observed in this area. Towards the islands, the SAF and APF appeared to branch, resulting in the SAF being topographically deflected north of the island group. Here, the SAF lay close to the islands' northern edge as an intense near-zonal jet (Fig. 2B). Further downstream, the SAF was found slightly meandering along 46°S (Fig. 2). In contrast, the APF continued to meander eastwards south of 48°S. The APF was again encountered in the south-eastern part of the survey grid (Fig. 2A).

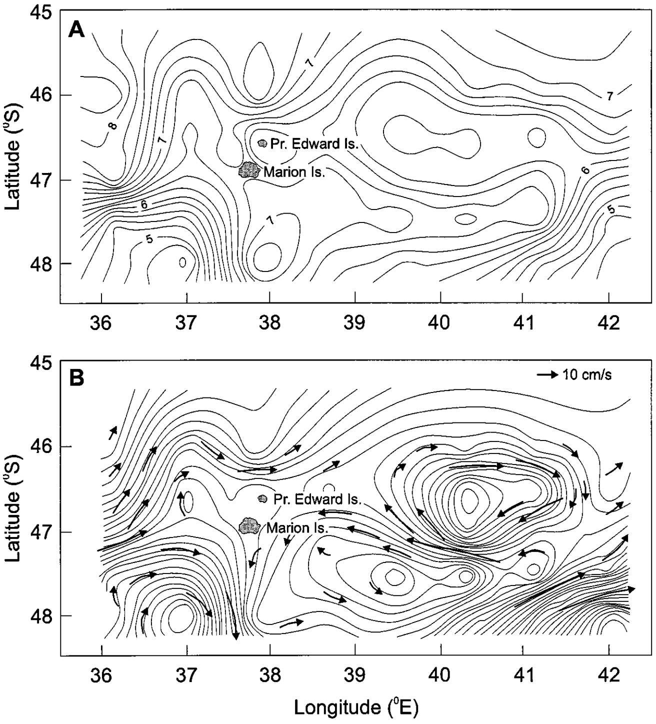

Fig. 2 Temperature at 100 m depth (**A**; °C) and geopotential anomalies (**B**; 0 m/ref. 1500 m) around the Prince Edward Islands during May 1997

Two mesoscale physical features were observed downstream of the Prince Edward Islands. Firstly, at ≈40°E and 46°30′S, a cyclonic cold-core (< 6 °C) eddy extending down to 1500 m depth was evident from both the dynamic height and subsurface temperature distribution pattern (Fig. 2). Secondly, south of the Prince Edward Islands extending eastwards, a warm anticyclonic feature (>6.6 °C) was observed (Fig. 2).

Plankton community structure

A total of 54 macrozooplankton and micronekton taxa were identified in the RMT-8 samples (Table 1). The highest species numbers, ten and nine, were encountered in the fish and euphausiid groups, respectively. Mesopelagic fish formed the bulk of the fish collected in the offshore stations, while within the inter-island region only one species, belonging to the family Nototheniidae, *Lepidonotothen larseni*, was found. Among euphausiids, *Euphausia longirostris*, *E. vallentini*, *E. similis*, *Nematoscelis megalops* and *Thysanoessa* spp. dominated. These groups were followed by squid and decapods, which comprised six and five species, respectively. Other groups were less numerous and generally comprised 2–4 species (Table 1).

Numerically, euphausiids were the most prominent group, accounting for 43% of total average abundance. They were followed by chaetognaths (26%), hyperiid amphipods (12%) and gelatinous (cnidarians and ctenophores) zooplankton (11%). In terms of biomass, euphausiids again dominated RMT-8 samples contributing, on average, 30% of total dry mass. The second and third most important groups consisted of gelatinous zooplankton and hyperiid amphipods, which accounted for 24 and 12% of the total biomass, respectively. These were followed by fish (11%) and chaetognaths (8%). Other groups contributed <4% to total abundance and < 6% to total biomass.

Macroplankton and micronekton were mostly represented by subantarctic and common Southern Ocean species (Table 1). There were, however, several species of subtropical origin, including the salp *Iasis zonaria*, the pteropod *Cymbulia* sp., the euphausiid *Thysanoessa gregaria* and the fishes *Echiodon cryomargarites* and *Diplophos rebainsi*. Generally, subtropical species were found in the northwestern part of the survey (Fig. 3). Results of the hierarchical cluster analysis revealed the presence of four major groupings of stations (Fig. 4A). The first grouping combined four stations occupied within the inter-island region. The second grouping comprised two mesopelagic stations, where samples were collected between 300 and 500 m depth. Groupings 3 and 4 comprised stations occupied in both the upstream and downstream areas of the island group (Fig. 4A). Only a single outliner, stn. 88, was found. This station was characterized by the lowest species number ($n = 3$) and densities (0.6 ind. 1000 m^{-3}, 27 mg DW 1000 m^{-3}) of macroplankton and micronekton during the entire study.

The highest number of species ($n = 44$) was recorded in grouping 4, followed by grouping 3 ($n = 27$). Groups 1 and 2 had the lowest number of species ($n = 16$) (Table 1). One-way ANOSIM test showed significant differences between the inshore (grouping 1) and offshore groups of stations (3 and 4, $P < 0.05$). Group 2 was significantly different from grouping 4 ($P < 0.05$) but not from grouping 3 ($P > 0.05$). Finally, no differences were found between groupings 1 and 2 ($P > 0.05$), while groupings 3 and 4 were significantly different from each other ($P < 0.05$). The overall dissimilarity was the highest (71%) between groupings 1 and 3. In order of importance, *Euphausia vallentini*, *Thysanoessa* spp., *Sagitta gazellae, Themisto gaudichaudi*, *Euphausia longirostris*, *Nauticaris marionis* and *Lepidonotothen larseni*, were responsible for > 50% of the between grouping-average dissimilarity index. The same species also accounted for > 40% of the average dissimilarity (65%) index between groupings 1 and 4. The lowest average dissimilarities were found between groupings 1 and 2 (61%), with *Euphausia longirostris*, *Euphausia vallentini*, *Thysanoessa* spp., *Nematoscelis megalops*, *Salpa thompsoni* and *Themisto gaudichaudi* major contributors to the dissimilarity index, and between groupings 3 and 4 (63%), with *Melophysa melo*, *Sagitta gazellae*, *Themisto gaudichaudi*, *Stylocheiron maximum* and *Euphausia vallentini* as major contributors.

Average macrozooplankton densities of different groupings are presented in Table 1. The highest abundance and biomass values were calculated within the groupings 2 and 4. Grouping 3 was characterized by the lowest abundance and biomass densities. No significant differences in average biomass values were found between all groupings ($P > 0.05$), while the average abundance of grouping 3 was significantly lower than average abundances of groupings 2 and 4 ($P < 0.05$).

Taxonomic composition was also different between groups of stations identified with hierarchical analysis (Table 1). The zooplankton community of grouping 1 was dominated by gelatinous zooplankton, euphausiids, chaetognaths, squid and notothenioid fish, both numerically (>97%) and by biomass (>95%). Within

Table 1 Composition, average abundance (*A*, ind. 1000 m^{-3}) and biomass (*B*, mg DW 1000 m^{-3}) of macrozooplankton and micronekton around the Prince Edward Islands during autumn 1997. Groups were identified with cluster analysis (species origin: *subtropical, **Antarctic/Subantarctic, ***Subantarctic)

Taxa	Grouping 1 ($n = 4$)		Grouping 2 ($n = 2$)		Grouping 3 ($n = 9$)		Grouping 4 ($n = 10$)	
	A	B	A	B	A	B	A	B
Cnidaria								
Pegantha sp.	–	–	–	–	–	–	0.1	1.9
Hydromedusae	0.3	60.1	0.5	51.9	0.2	16.0	0.1	11.9
*Melophysa melo**	1.0	11.8	16.7	197.6	0.3	7.0	0.6	8.1
*Vogtia spinosa****	–	–	–	–	–	–	<0.1	0.4
Vogtia sp.	–	–	0.6	2.9	–	–	–	–
Diphyes sp.	–	–	–	–	<0.1	0.1	<0.1	0.1
Siphonophora unidentified	<0.1	0.1	–	–	–	–	0.1	1.3
Ctenophora								
Beroe sp.	0.2	4.4	–	–	–	–	<0.1	97.6
Euphausiacea								
*Euphausia vallentini****	7.1	43.6	0.6	4.4	0.5	3.6	10.9	91.1
*E. longirostris****	–	–	0.3	6.9	0.6	11.5	7.7	201.4
*E. similis****	–	–	0.5	6.0	0.3	7.0	1.0	22.5
E. similis var *armata****	–	–	0.1	3.1	–	–	0.7	15.2
*Stylocheiron maximum****	–	–	1.0	17.8	<0.1	0.3	0.2	3.9
*Nematoscelis megalops****	0.2	1.1	1.1	14.3	0.3	3.1	2.4	35.1
*Thysanoessa gregaria**	–	–	–	–	<0.1	0.1	<0.1	0.2
Thysanoessa spp.	3.8	2.5	<0.1	<0.1	<0.1	<0.1	2.1	1.6
*Bentheuphausia ambylops***	–	–	–	–	–	–	<0.1	0.2
Decapoda								
*Nauticaris marionis****	0.6	9.2	–	–	–	–	–	–
Nematocarcinus sp.	–	–	–	–	–	–	<0.1	0.1
Sergestes sp.	–	–	–	–	0.2	6.8	0.3	9.6
*Acanthephyra pelagica****	–	–	–	–	–	–	<0.1	1.9
*Petalidium foliaceum***	–	–	–	–	–	–	<0.1	0.2
Amphipoda								
*Themisto gaudichaudi***	0.2	2.2	–	–	2.2	37.1	0.7	12.6
*Phronima sedentaria**	–	–	–	–	<0.1	1.5	0.1	2.2
*Primno macropa***	<0.1	<0.1	0.1	1.3	–	–	<0.1	0.2
Vibilia sp.	–	–	–	–	–	–	<0.1	<0.1
Mollusca								
*Spongiobranchaea australis***	–	–	–	–	<0.1	0.3	0.1	2.4
*Clio pyramidata****	–	–	–	–	–	–	<0.1	0.1
Cymbulia sp.*	–	–	–	–	–	–	<0.1	0.6
Travisiopsis sp.	–	–	–	–	–	–	<0.1	<0.1
*Galiteuthis glacialis***	–	–	–	–	<0.1	1.5	–	–
*Alluroteuthis antarctica***	0.2	15.6	–	–	–	–	–	–
Chiroteuthis sp.**	–	–	–	–	–	–	<0.1	116.1
Histioteuthis sp.**	–	–	–	–	–	–	<0.1	6.4
Moroteuthis sp.**	0.1	9.0	–	–	<0.1	1.1	–	–
Brachioteuthis sp.**	–	–	–	–	–	–	<0.1	4.2
Teuthoidea unidentified	–	–	–	–	–	–	<0.1	0.5
Octopoda unidentified***	<0.1	1.4	–	–	<0.1	0.3	–	–
Tunicata								
*Salpa thompsoni****	–	–	0.2	0.9	0.2	5.3	1.9	23.9
*Iasis zonaria**	–	–	–	–	<0.1	1.8	0.1	6.3
Tunicata unidentified	–	–	–	–	<0.1	1.5	0.1	2.1
Chaetognatha								
*Sagitta gazellae***	6.0	49.0	12.5	60.6	1.8	7.9	2.6	12.8
*Eukrohnia hamata***	0.9	0.1	1.4	0.1	0.3	<0.1	0.9	0.1

Table 1 (*Continued*)

Taxa	Grouping 1 (*n* = 4)		Grouping 2 (*n* = 2)		Grouping 3 (*n* = 9)		Grouping 4 (*n* = 10)	
	A	B	A	B	A	B	A	B
Osteichthyes								
*Lepidonotothen larseni****	0.5	22.4	–	–	–	–	–	–
Gymnoscopelus spp.	–	–	–	–	<0.1	0.4	<0.1	5.3
*G. braueri***	–	–	–	–	<0.1	1.6	0.1	34.0
*Protomyctophum normani****	–	–	–	–	<0.1	6.1	0.2	56.1
*Krefftichthys anderssoni***	–	–	–	–	<0.1	0.4	–	–
*Vinciguerria attenuata****	–	–	–	–	–	–	<0.1	0.17
*Stomias boa boa****	–	–	<0.1	15.2	–	–	–	–
*Echiodon cryomargarites**	–	–	–	–	<0.1	0.4	<0.1	1.0
Stemonosudis sp.*	–	–	–	–	–	–	<0.1	0.2
*Diplophos rebainsi**	–	–	–	–	–	–	<0.1	139.6
Fish larvae	–	–	<0.1	<0.1	–	–	–	–
Total	20.9	232.5	35.6	382.8	7.2	122.9	33.7	931.2
Standard deviation	11.2	161.4	4.2	72.8	2.2	57.9	29.8	812.6
Number of species		16		16		27		44

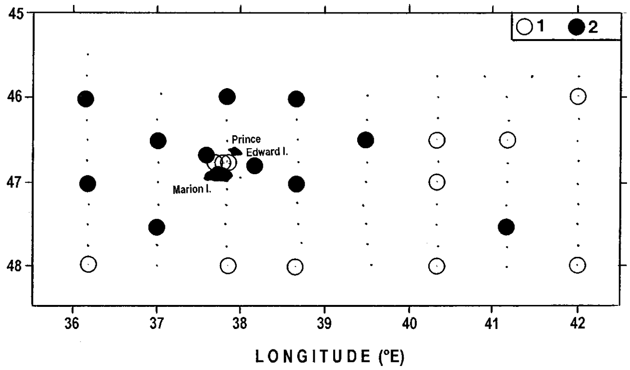

Fig. 3 Distribution of subtropical species of macroplankton around the Prince Edward Islands during May 1997 (*1* no finding; *2* subtropical species found)

grouping 2, only gelatinous zooplankton and chaetognaths were prominent taxonomic groups (89% of total abundance and 82% of dry mass). The zooplankton taxonomic composition of groupings 3 and 4 was generally similar, with higher emphasis on hyperiid amphipods, particularly *Themisto gaudichaudi* in grouping 3 and squid in grouping 4 (Table 1). The SIMPER analysis showed that the average similarity between stations was the highest (73%) within grouping 2. The least homogenous community (average similarity 44%) was found in grouping 3. The average similarity between stations in groupings 1 and 4 was similar, 57% and 56%, respectively.

Ordination analysis showed a slightly different grouping composition than the one obtained with the dendrogram (Fig. 4B). In contrast with cluster analysis, groupings 3 and 4 were closely grouped by the ordination analysis. Stn. 106 was an outlier, spatially coinciding with the northern proximity of the APF. Stns. 43, 74 and 88 formed a separate grouping with low species richness (≤8) and densities (≤6 ind. 1000 m^{-3}) of macroplankton/micronekton (Fig. 4B). This grouping coincidentally comprised stations conducted within the colder/warmer water interfaces upstream and downstream of the Prince Edward Islands (Fig. 1).

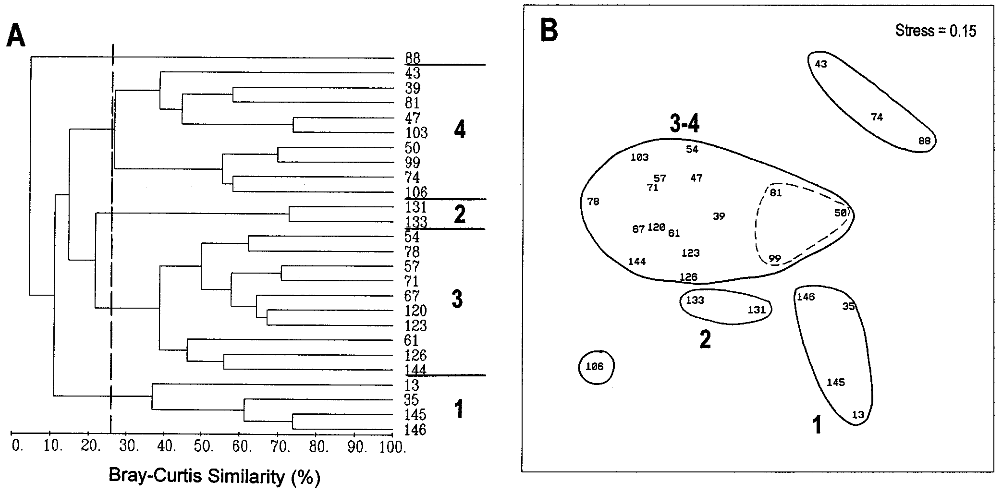

Fig. 4 Results of cluster (**A**) and ordination (**B**) analyses of the macroplankton/micronekton community structure around the Prince Edward Islands during May 1997

Plankton distribution

Within the top 300 m, total macroplankton abundance ranged from 0.6 to 120.4 ind. 1000 m^{-3} (average 21.4 ± 23.3 ind. 1000 m^{-3}). The total biomass varied between 27 and 2880 mg DW 1000 m^{-3} (mean 467 ± 645 mg DW 1000 m^{-3}). There were no significant differences in both average abundance and biomass levels between samples collected during daytime and night-time ($P > 0.05$).

The spatial distribution of macroplankton was not uniform, with high densities (both abundance and biomass) recorded between 37 and 39°E and in close proximity to the islands (Fig. 5). The elevated abundances (> 40 ind. 1000 m^{-3}) of macroplankton south of the islands were associated with siphonophores and chaetognaths (stns. 131, 133), while at northern stations, euphausiids (*Euphausia vallentini*, *Euphausia longirostris*, *Nematoscelis megalops*, *Thysanoessa* spp.) and salps (*Salpa thompsoni*) dominated (Fig. 5A). At stations with enhanced biomass euphausiids, salps and mesopelagic fish dominated samples (Fig. 5B).

Continuous acoustic records along eight transects showed that backscattering strengths were consistently elevated in the northern and southern parts of the survey (Figs. 5B, 6). The northern belt of high pelagic biomass coincided with the southern boundary of the SAF. Pronounced backscattering strength enhancement was also observed upstream of the islands, along transect 1 in the region where the SAF and APF merged (Fig. 6). The southern belt of enhanced pelagic biomass coincided with the northern proximity of the APF (Figs. 2, 6). The elevated macroplankton/micronekton densities and backscattering strengths generally matched in the northern part of the survey, while no such coincidence was found in the southern part of the area investigated (Figs. 5, 6). As a consequence, relationships between zooplankton densities, both abundance and biomass, and acoustic backscatterers were not significant ($P > 0.05$).

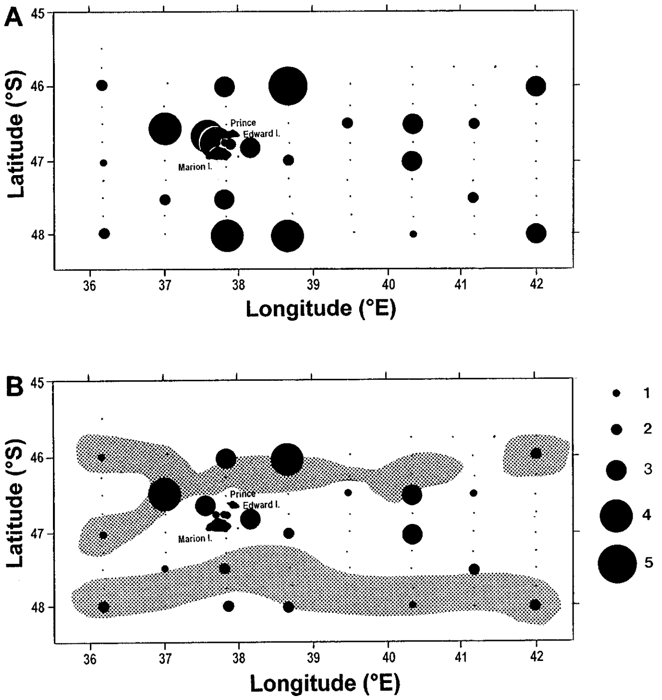

Fig. 5 Spatial distribution of macroplankton/micronekton abundance (**A**) and biomass (**B**) around the Prince Edward Islands during May 1997. *Shaded areas* indicate elevated pelagic biomass by using acoustic data. For **A**: *1* < 5; *2* 5–9; *3* 10–29; *4* 30–100; *5* >100 ind. 1000 m^{-3}. For **B**: *1* <100; *2* 100–499; *3* 500–1000; *4* >1000 mg DW 1000 m^{-3}

Discussion

Results of the April/May 1997 survey showed two separate flow patterns around the Prince Edward Islands. To the north of the islands, the flow associated with the SAF was substantially affected by the Southwest Indian Ridge and Del Cano Rise (Froneman et al. 1999). In contrast, the APF appeared to exist as a meandering flow almost unaffected by bathymetry. While a distinct downstream wake was observed during April/May 1989 (Ansorge et al. 1999), during the 1997 survey the SAF downstream of the islands remained predominantly zonal (Froneman et al. 1999). In the upstream region, a confluence of the SAF and the APF was recorded for the first time, indicating the extreme mesoscale variability in frontal positions in the vicinity of the Prince Edward Islands. A similar process was observed further upstream between 30 and 34°E where two fronts merged as a result of bottom topography (Read and Pollard 1993; Holliday and Read 1998). The biological consequences of such features are as yet unknown. However, enhanced biological productivity generally associated with both frontal features may be sufficient to provide the pulse of elevated zooplankton and micronekton biomass recorded during this study.

Two counter-rotating eddies, probably generated from instabilities of the SAF and APF, were observed in the downstream region of the Prince Edward Islands. Observations south of Australia have shown that eddies may enhance the associated zonal flow (Emery and Savchenko 1977). During April/May 1997, eddies created a front-like structure in the downstream region, which subsequently increased the spatial heterogeneity in the zooplankton distribution pattern. These eddies also acted as a distinct barrier to the downstream geostrophic flow, resulting in the build-up of the APFZ (Froneman et al. 1999). The origin of the cold-core eddy (CCE) was not determined. However, the presence of the cold-water gymnosomate pteropod, *Spongiobranchaea australis*, in zooplankton within the CCE suggests that the eddy may have resulted from a meander of the APF that was cut off (Joyce and Patterson 1977; Sievers and Emery 1978; Koshlyakov et al. 1985). This was subsequently supported by the copepod composition from mesozooplankton samples (Froneman et al. 1999).

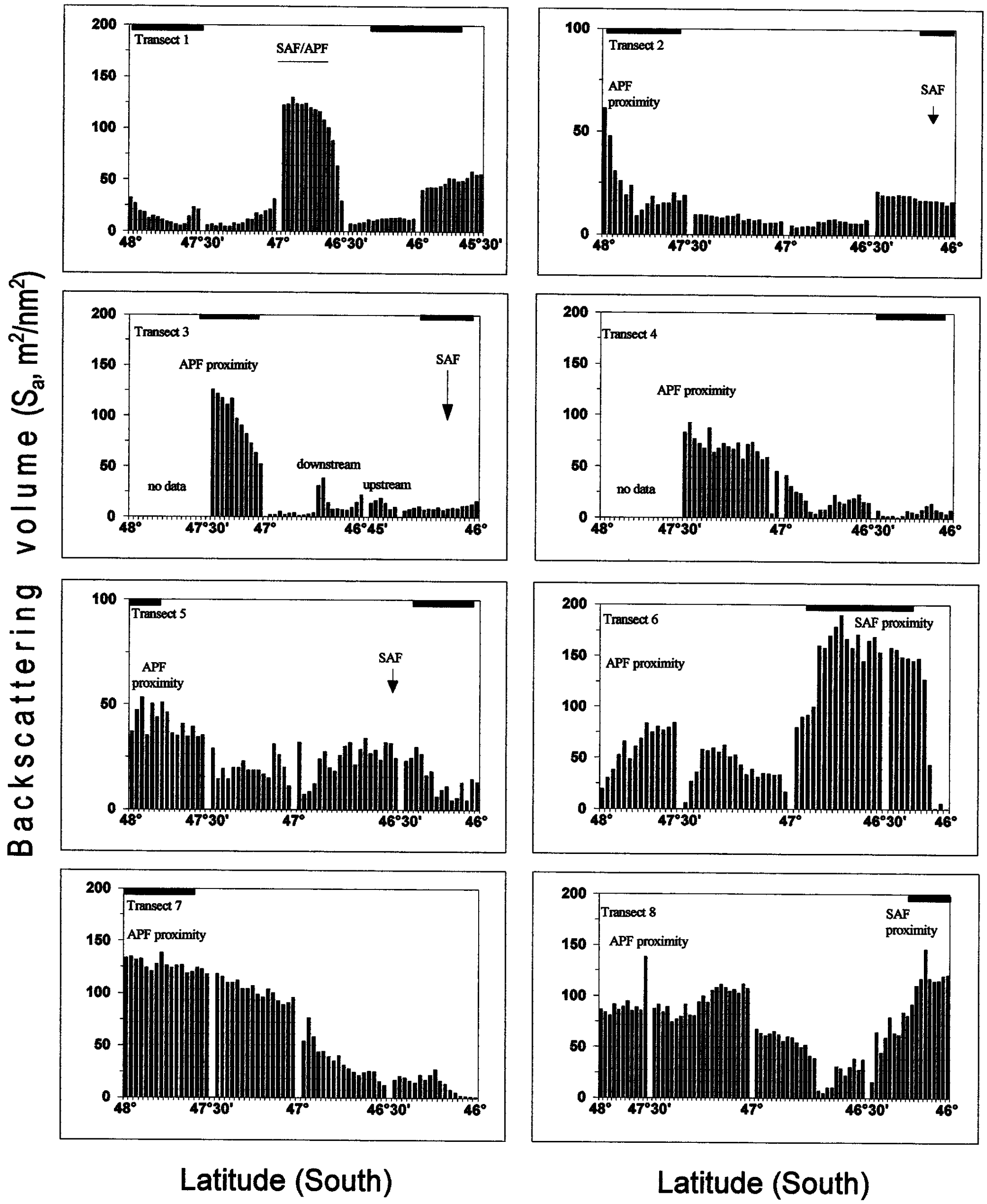

Fig. 6 Two-dimensional plots of acoustic backscattering (S_a) at 120 kHz along the transects conducted within the Polar Frontal Zone around the Prince Edward Islands during May 1997. All transects plotted from south to north (*SAF* Subantarctic Front; *APF* Antarctic Polar Front). Period of darkness is indicated by thickening of the upper horizontal axis

Similarly, the warm-core eddy (WCE) observed downstream of the islands may also be a result of a breakdown of a southward-penetrating SAF meander, with the subsequent advection of warm Subantarctic Surface Waters across the SAF (Sievers and Emery 1978), as the spatial distribution of subtropical species in the area investigated corresponded well with the position of the WCE (Figs. 2, 3).

Previous studies indicated that the zooplankton community in the vicinity of the Prince Edward Islands is generally subantarctic in origin with a minimal addition of Antarctic and subtropical species (Miller 1982a, 1985; Allanson et al. 1985). In the late 1970s, the contribution of Antarctic species was substantial while almost no subtropical species were encountered (Grindley and Lane 1979). In contrast, during April/May 1997, subtropical species sampled as far south as 47°30′S were more frequently found within the APFZ than Antarctic species. Mesoscale eddies, having their origins from nearby frontal systems, were hypothesized to advect aliens into the region (Boden and Parker 1986). During the April/May 1997 survey, a substantial cross-frontal transport of the Subantarctic Surface Waters into the APFZ was evident upstream and downstream of the Prince Edward Islands (Froneman et al. 1999). A similar situation, only in the downstream region, was encountered during a previous study conducted in 1989 (Ansorge et al. 1999). This may indicate long-term large-scale changes in the environment surrounding the Prince Edward Islands (Smith 1991).

The mixing of communities within the APFZ has previously been postulated to be due to the positional variability of the SAF and APF (Boden and Parker 1986). Also, the upstream community would seem to determine the structure of the inter-island community (Miller 1985; Froneman and Pakhomov 1998). This was confirmed by several studies where well-mixed microphytoplankton and mesoplankton communities were observed within the APFZ and between the Prince Edward Islands (Froneman and Pakhomov 1998; Ansorge et al. 1999; Froneman et al. 1999). Most recently, however, a study conducted in close proximity to the islands showed that behavioural patterns, particularly mesoscale spatial distribution and diel vertical migrations, differ between meso- and macrozooplankton, which may affect the interaction between plankton and the prevailing oceanographic regime (Pakhomov and Froneman 1999b).

Although a reasonable consistency was found between different water masses and mesozooplankton assemblages (Ansorge et al. 1999; Froneman et al. 1999), no macroplankton communities associated with water masses within the surveyed area were identified. This is probably due to low sampling resolution coupled with extensive cross-frontal mixing. Our results are, however, consistent with findings of a similar study conducted around the Kerguelen Archipelago, which employed a substantially higher sampling resolution (Pakhomov 1995). Except for the mesopelagic stations (grouping 2), only two major macroplankton assemblages were identified during April/May 1997. The first community, although consisting of two significantly different groupings of stations, represented a typical APFZ community (Pakhomov 1995; Pakhomov and Froneman 1999b), with a substantial presence of subtropical species. It is noteworthy that differences between groupings were related to zooplankton numerical abundance, which is likely a result of natural patchiness, diel migrations and net avoidance, rather than to the presence/absence of species. The second community (grouping 1), identified within the inter-island region, was a modification of the first assemblage. It was characterized by low species diversity, presence of shelf species, and absence of some large euphausiid species, e.g. *Euphausia longirostris*, *Euphausia similis* and *Stylocheiron maximum*, between the islands, which could be attributed to the "island-mass effect" (Coutis and Middleton 1999; Pakhomov and Froneman 1999b).

The macroplankton/micronekton biomass values obtained in this study fall well within the range (40–8000 mg DW 1000 m^{-3}) previously reported for the Subantarctic and Antarctic Polar Frontal Zones of the Southern Ocean (Table 2). The low Antarctic biomass values are, however, generally lower than those found in high Antarctic regions (Table 2). Despite weak correlation between zooplankton densities and acoustic backscattering values, the spatial distribution of large zooplankton based on net samples demonstrated some consistency with acoustic measurements, as elevated backscattering strengths were closely associated with the SAF and APF. The APFZ proper was characterized, however, by a relatively low pelagic biomass. Interestingly, the SAF was found to have higher pelagic biomass than the APF, which was supported by net samples. During studies conducted in April/May 1989 and 1996, the highest densities of large zooplankton (>20 mm) concentration were also confined to the SAF (Froneman and Pakhomov 1998; Ansorge et al. 1999; Pakhomov and Froneman 1999b). This is in contradiction to previous studies, which regarded the APF as the region of the highest biomass of mesopelagic fish and crustaceans (Linkowski 1983; Zemsky 1987; Pakhomov et al. 1994; Pakhomov and McQuaid 1996; Pakhomov et al. 1999). Whether this is a regional feature or an artifact due to net avoidance is as yet unknown.

Although little is known about seasonal variability in the SAF productivity, there is evidence that during early and late austral summer, the SAF has strong chlorophyll and acoustic backscattering strength signals

Table 2 Macroplankton biomass in different regions of the Southern Ocean (*IK* Isaacs-Kidd trawl, *BMS* Melnikov's trawl, *TT* Tucker trawl, *PEI* Prince Edward Islands, *STC* Subtropical Convergence, *APF* Antarctic Polar Front)

Region, season, layer	Gear	Mean (range) biomass (mg DW 1000 m^{-3})	Source
Pacific Subantarctic, summer, 0–200 m	IK	655	Barchatov (1988)
Gough Island, early summer, 0–50 m	RMT-8	260	Miller (1982b)
STC, winter, 0–300 m	RMT-8	337–780	Pakhomov et al. (1994)
APF, summer, 0–300 m	RMT-8	613	Pakhomov et al. (1994)
APF, summer, 0–200 m	RMT-25	8000	Piatkowski et al. (1994)
APF, summer, 0–200 m	BMS	525	Voronina et al. (1994)
South Georgia, summer, 0–200 m	RMT-25	2800	Piatkowski et al. (1994)
Kerguelen Archipelago, summer, 0–200 m	BMS	2490	Pakhomov (1995)
PEI, winter, 0–50 m	RMT-8	140	Miller (1982a)
PEI, autumn 1989, 0–300 m	Bongo	509 (40–2970)	Ansorge et al. (1999)
PEI, autumn 1996, 0–300 m	Bongo	392 (40–1450)	Froneman and Pakhomov (1998)
PEI, autumn 1996, 0–300 m	RMT-8	288 (40–1140)	Pakhomov and Froneman (1999b)
PEI, autumn 1997, 0–300 m	Bongo	745 (390–2560)	Froneman et al. (1999)
PEI, autumn 1997, 0–300 m	RMT-8	467 (20–9100)	This study
Weddell Sea, summer, 0–300 m	RMT-8	4000–11333	Boysen-Ennen et al. (1991)
Bellingshausen Sea, summer, 0–200 m	RMT-8	6500–10000	Siegel and Harm (1996)
Ross Sea, summer, 0–800 m	TT	210–800	Hopkins (1987)
Scotia Sea, summer, 0–1000 m	TT	2377–3132	Lancraft et al. (1989)
Scotia Sea, summer, 0–200 m	TT	1027–1447	

(R. Perissinotto, E.A. Pakhomov, P.W. Froneman, unpublished work). The spatio-temporal persistence of elevated macroplankton/micronekton stocks with the SAF may have important implications for the Prince Edward Island ecosystem. It is well documented that apex predators, such as king penguins, albatrosses and seals, forage within the major frontal systems of the Southern Ocean, including the SAF or APF, while others, e.g. gentoo, macaroni and rockhopper penguins, rely mainly on inshore and near-offshore food resources (Pakhomov and Froneman 1999a). It has been hypothesized that plankton stocks associated with the frontal systems to the north and, perhaps, to the south of the islands may be transferred to the island ecosystem by physical forces (Boden and Parker 1986; Froneman and Pakhomov 1998; Pakhomov and Froneman 1999a). Although there is little evidence to support this hypothesis, the elevated macroplankton and micronekton stocks associated with the SAF, due to its close proximity to the islands, may enhance pelagic biomass at the north and leeward sides of the islands' plateau (Pakhomov and Froneman 1999b). Under these conditions, elevated prey biomass would become more accessible to both the far and near-shore foraging top predators on the Prince Edward Islands.

In conclusion, although the southern boundary of the APFZ, the APF, was clearly encountered during the survey, a well-mixed macrozooplankton community with little influence by Antarctic species persisted within the APFZ around the Prince Edward Islands during April/May 1997. The presence of a single offshore community suggests large mesoscale mixing upstream and downstream of the islands, driven by physical forces rather than by behavioural responses of zooplankton (Pakhomov and Froneman 1999b). The SAF position in relation to the island plateau appeared to be a major factor enhancing the cross-latitudinal water and macroplankton/micronekton exchange within the APFZ and around the Prince Edward Islands. Indeed, a notable presence of subtropical species was a confirmation of an extensive cross-frontal penetration of Subantarctic Surface Waters into the APFZ (see also Froneman et al. 1999).

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