

E. A. Pakhomov · P. W. Froneman

## Macroplankton/micronekton dynamics in the vicinity of the Prince Edward Islands (Southern Ocean)

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**Abstract** Combined trawling (rectangular midwater trawl, RMT-8 net) and acoustic (120 kHz) surveys in the upstream and downstream region of the Prince Edward Islands were undertaken during April and May 1996 and 1997. A total of 49 species of macroplankton and micronekton were encountered within the region investigated. Mesopelagic fishes, euphausiids, chaetognaths and tunicates dominated numerically and by biomass. Average abundance and biomass of macroplankton/micronekton in the top 300 m layer were low, 18 individuals  $1000\text{ m}^{-3}$  and 288 mg dry wt  $1000\text{ m}^{-3}$ , respectively. Numerical analysis revealed the presence of two major groups of stations broadly corresponding to the offshore (upstream and downstream) and inshore (inter-island) realms. Planktonic samples and acoustic measurements revealed that elevated densities of macroplankton/micronekton were associated with the subantarctic front region and in close proximity to the island plateau. Based on trawling and acoustic survey results, it is suggested that large plankton and micronekton are mostly washed around rather than across the inter-island shelf region. This is in contrast with the “replenishing hypothesis” previously proposed for this region by other investigators.

### Introduction

Isolated oceanic islands in the subantarctic zone of the Southern Ocean have been shown to affect strongly the physico-chemical structure of the adjacent oceanic environment (Duncombe Rae 1989) and are regions of

enhanced biological productivity (Perissinotto et al. 1990; Perissinotto and Duncombe Rae 1990; Pakhomov 1995). The Prince Edward Island group, comprising two small volcanic islands, is situated directly in the path of the easterly-flowing Antarctic circumpolar current (ACC), between the subantarctic (SAF) and antarctic (APF) polar fronts (Lutjeharms 1985, 1990). Like many subantarctic oceanic islands, the Prince Edward Island group supports huge (> 5 million) seasonal populations of seabirds and mammals (Williams et al. 1979; Condy 1981; Perissinotto and McQuaid 1992).

Previous multi-year oceanographic studies conducted in the vicinity of the Prince Edward Islands provided much of the information on the species composition and spatio-temporal distribution of different components of plankton assemblages (see review by Pakhomov and Froneman 1999). It has been shown that the mesoscale oceanographical and biological processes around the islands appear to be affected by interactions of the free-stream ACC with the local topography (Allanson et al. 1985). Furthermore, it has been postulated that the meridional shifts in the position of the SAF may affect the background productivity around the Prince Edward Islands (Pakhomov and Froneman 1999; Perissinotto et al. 1999).

The uniqueness of the island-group ecosystem is thought to be the result of a close marine–terrestrial interaction known as the “life-support system” which ultimately provides food for the entire community of seabirds and mammals on the islands. The life-support mechanism includes two important components, an inshore and offshore component. The inshore food component, comprising demersal fishes, the caridean shrimp *Nauticaris marionis* and other benthic organisms, is of crucial importance to only a few land-based inshore predators (Espitalier-Noel et al. 1988; Adams and Klages 1989; Perissinotto and McQuaid 1990). In contrast, because of the higher number of offshore feeding predators on the islands (Adams and Brown 1989), the offshore component appears to substantially outweigh the inshore component, suggesting that the adjacent

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E.A. Pakhomov (✉) · P.W. Froneman  
Southern Ocean Group, Department of Zoology and Entomology,  
Rhodes University, P.O. Box 94, Grahamstown 6140,  
South Africa

Fax: 0027(0)46 622 4377; e-mail: zoep@warthog.ru.ac.za

environment largely supports the vast numbers of land-based predators on the Prince Edward Islands.

According to Perissinotto and McQuaid (1992), the advection of zooplankton from the upstream region associated with the ACC is able to supply much of the food necessary for the survival of the land-based predators. It had been hypothesized that plankton and micronekton are depleted over the islands' shelf during the day, and are replenished by advection of allochthonous zooplankton and micronekton from the upstream offshore waters by a wind-induced surface Ekman drift during the night (Perissinotto 1989; Perissinotto et al. 1990; Perissinotto and McQuaid 1992). This hypothesis was first proposed and tested for the small, shallow, abrupt topographic features such as seamounts and banks (Isaaks and Schwartzlose 1965; Pakhomov 1993; Genin et al. 1994, 1988). The observed fish densities in these regions suggested the necessity of allochthonous energy input for population maintenance (Tseitlin 1985). In contrast, the Prince Edward Islands are located on a shallow distinct plateau that rises steeply from a depth of  $> 3000$  m. As the entire plateau rises above the surface and forms an obstacle to the current, it was suggested that the water would largely flow around rather than over the shallow plateau (Roden 1987). As a consequence, the replenishing hypothesis (Perissinotto and McQuaid 1992) would fail to explain how allochthonous plankton and micronekton can be delivered into the inter-island region.

The main objective of this study was, therefore, to test the replenishing hypothesis using data collected during combined trawling and acoustic oceanographic surveys

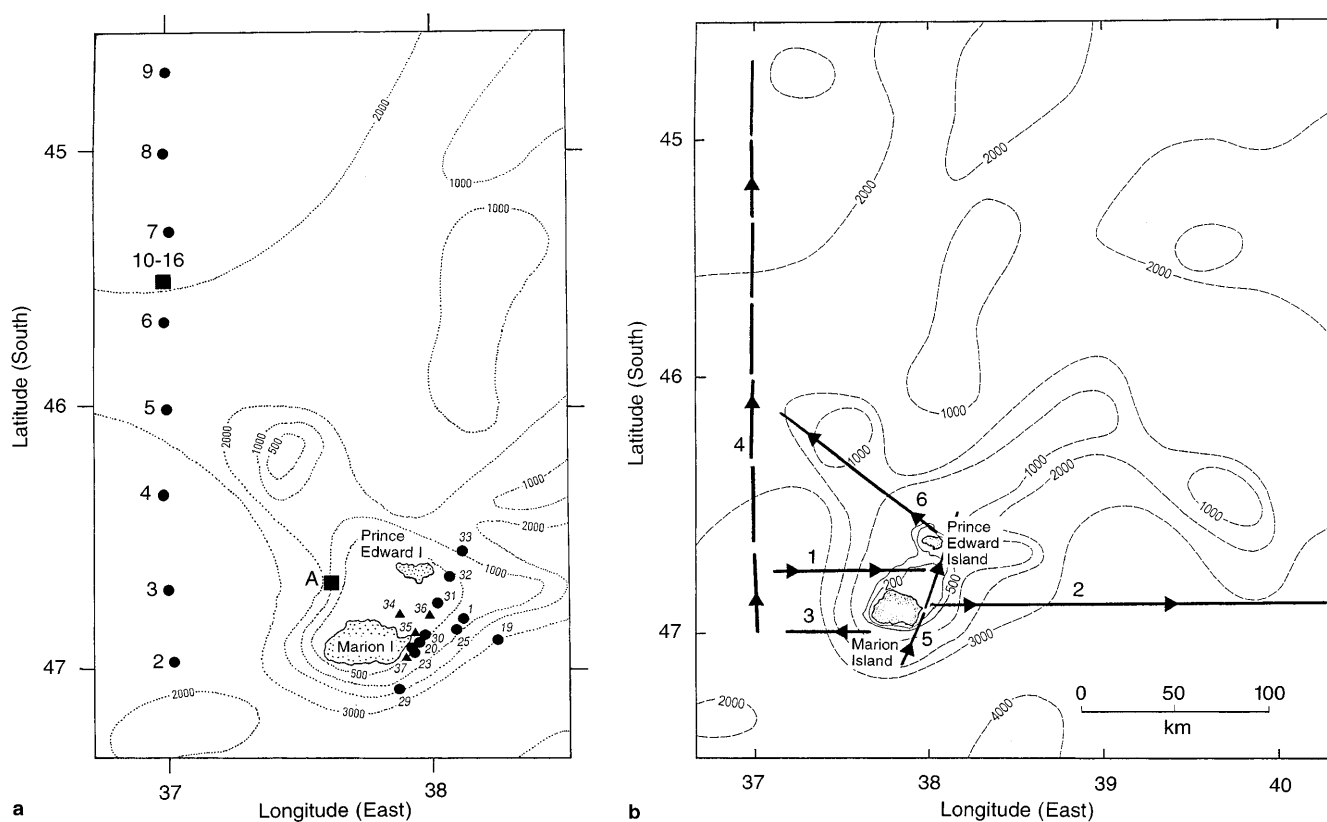
conducted in the upstream, downstream and inter-island regions during April and May 1996 and 1997.

## Materials and methods

An oceanographic survey was conducted in the vicinity of the Prince Edward Islands during the 81st voyage of the MV "SA Agulhas" in April and May 1996. The survey covered the upstream, inter-island and downstream regions of the islands (Fig. 1a). In the upstream region, samples were collected throughout a 24 h cycle along the 37°E meridian between 47° and 44°30'S. The position of the SAF along the transect was identified after setting up CTD (conductivity-temperature-depth) stations to a depth of 300 m. A single 24 h station was then occupied at the SAF (Station 10-16; Fig. 1a). At this station, samples were collected at  $\approx 4$  h intervals in the top 300 m. This was followed by an intensive inter-island trawling survey during the two subsequent nights to eliminate the net avoidance and bias associated with vertical migrations of plankton. In addition, during the 84th voyage of the MV "SA Agulhas" in May 1997, a further 24 h station in the immediate upstream vicinity of the islands (Station A, depth  $\approx 1000$  m; Fig. 1a) was occupied. A series of tows in the depth strata 400 to 200, 200 to 150, 150 to 100, 100 to 50 and 50 to 0 m were conducted at midday and midnight in order to examine the vertical migration patterns of the macrozooplankton and micronekton.

Samples were collected using a rectangular midwater trawl (RMT-8) with a nominal mouth area of  $8 \text{ m}^2$  and mesh size of 4.5 mm. The volume filtered by the trawl was determined by multiplying the effective mouth area of the trawl by the distance travelled. This was calculated from the ship's speed and the duration of

**Fig. 1** Position of RMT-8 net tows (a) and acoustic transects (b) in vicinity of Prince Edward Islands during April and May 1996 [● oblique tows; ▲ near-bottom tows; ■ 24 h stations (10-16 = 1996; A = 1997)] Depth contours are in metres



trawling after the net had opened in the water. In calculating the volume filtered, the effect of towing speed was also taken into consideration (Roe et al. 1980). During April and May 1996, the trawl was towed obliquely between 0 and 300 m in the oceanic stations, or from the bottom to the surface within the inter-island region. In addition, in the shelf area of the islands, several tows were conducted in the close proximity to the bottom. Towing speed and duration varied between 1.5 and 3.5 knots and 5 and 20 min, respectively. The trawl was fitted with a universal underwater unit (U<sup>3</sup>; Robertson et al. 1981) that monitored continuously depth and temperature as well as the opening and closing times of the trawl. Samples were preserved in 4 to 6% buffered formalin and examined in the laboratory within 1 mo of collection. Catches were sorted and analyzed for taxonomic identification, numerical abundance and dry weight biomass. The dry weight of the main macrozooplanktonic and micronektonic groups were obtained by oven-drying fixed specimens for 36 h at 60 °C. No adjustments were made to correct for tissue loss due resulting from formalin preservation.

Surface size-fractionated chlorophyll *a* (chl *a*) concentrations were determined at each CTD station along the 37°E meridian between 47° and 44°30'S. In addition, in the inter-island region chl *a* concentrations were measured at a single station (46°55'S; 37°56'E, bottom depth ≈140 m). At this station, samples were collected daily at midday between 29 April and 17 May 1996. Chl *a* was measured from 250 ml aliquots obtained from the shipboard pump. The pump outlet was positioned ≈5 m below the sea surface, and the seawater was supplied to the laboratory via PVC piping. Water samples were gently filtered through a serial filtration unit and fractionated into the pico- (<2.0 µm), nano- (2.0 to 20.0 µm) and micro- (>20.0 µm) size fractions. Chl *a* concentrations were then determined fluorometrically after extraction in 90% acetone for 24 h (Holm-Hansen and Riemann 1978).

To compare plankton communities, non-metric cluster analysis and multidimensional scaling were used in conjunction with the Bray–Curtis similarity index after log transformation [ $\log_{10}(x+1)$ ] of the species' abundance data. Significance levels and sources of difference between plankton assemblages were tested using the analysis of similarity (ANOSIM) and similarity percentages (SIMPER) programmes of the "Plymouth routines in multivariate

ecological research" (PRIMER; Clarke and Warwick 1994) computer package, according to the procedure described by Field et al. (1982).

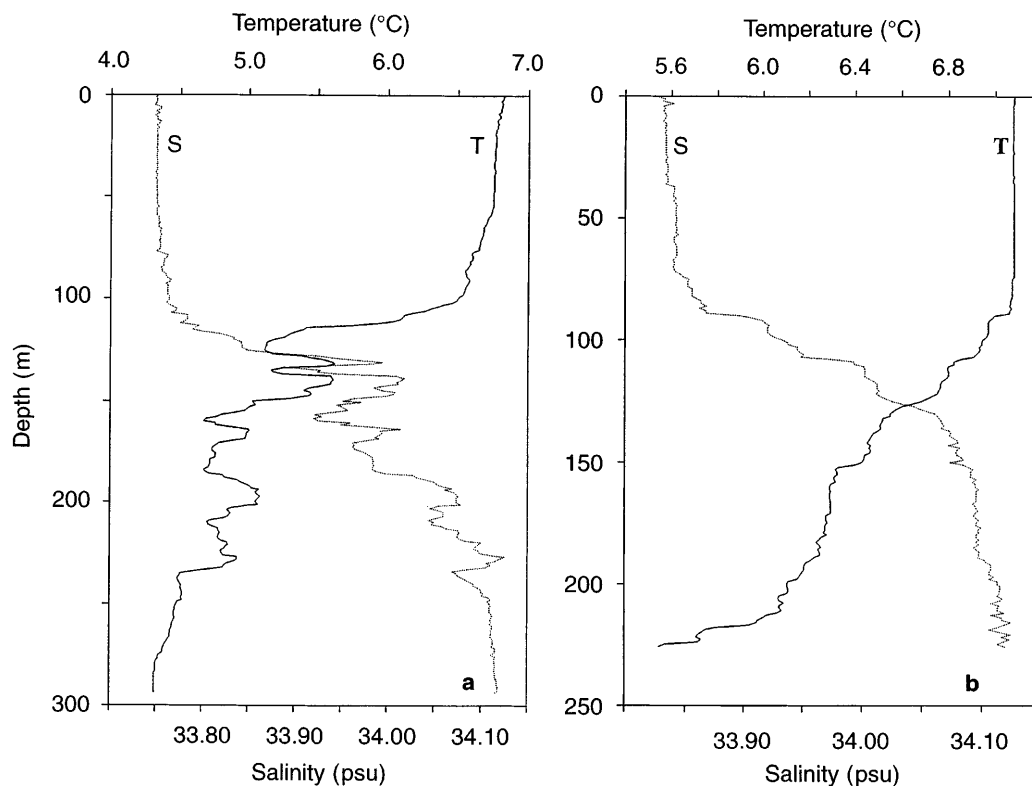
Throughout the April and May 1996 survey while en route to and from the islands as well as towards the downstream region, macrozooplankton/micronekton densities within the top 250 m were estimated acoustically using a Simrad EK500 echo sounder operated at frequency of 120 kHz (Fig. 1b). The output parameter of the sounder echo-integrator was  $S_a$  (m<sup>2</sup> nm<sup>-2</sup>; Simrad 1991), the mean backscatter area per unit of horizontal area. A depth-stratified (every 5 m depth) and integrated quantitative estimates of  $S_a$  were stored on a personal computer along the survey path every 1 min (≈2 nm). In order to detect only large plankton and micronekton, the volume backscatter strengths ( $S_v$ ) threshold value for echo integration was set for -80 dB (Simrad 1991). The underlying background noise level was then subtracted from the entire data set following the procedure described by Watkins and Brierley (1996).

## Results

### Physical environment, position of SAF, chlorophyll dynamics

Analysis of the CTD data showed that during April and May 1996 the waters in the upstream and inter-island regions displayed seasonal stratification (Fig. 2). The surface mixed-layer extended to a depth of ≈100 to 110 m in both regions. Active mixing processes were evident in the upstream region of the islands below

**Fig. 2** Water-column profiles of temperature and salinity (practical salinity units, *psu*) in upstream (**a**, Station 3) and inter-island (**b**, 46°44.7S; 37°52.9E) regions of Prince Edward Islands during April and May 1996



120 m (Fig. 2), probably because this station was in close proximity to the SAF.

The SAF is predominantly a subsurface front, and can be identified by the most vertically orientated isotherms and halynotherms (Lutjeharms and Valentine 1984). As a result, latitudinal positions of the surface and subsurface expressions may differ. Indeed, seawater temperature and salinity data collected along 37°S during April and May 1996 indicated that the subsurface position of the SAF lay between 46°20' and 46°S with its surface expression located further north between 46° and 44°50'S (Fig. 3).

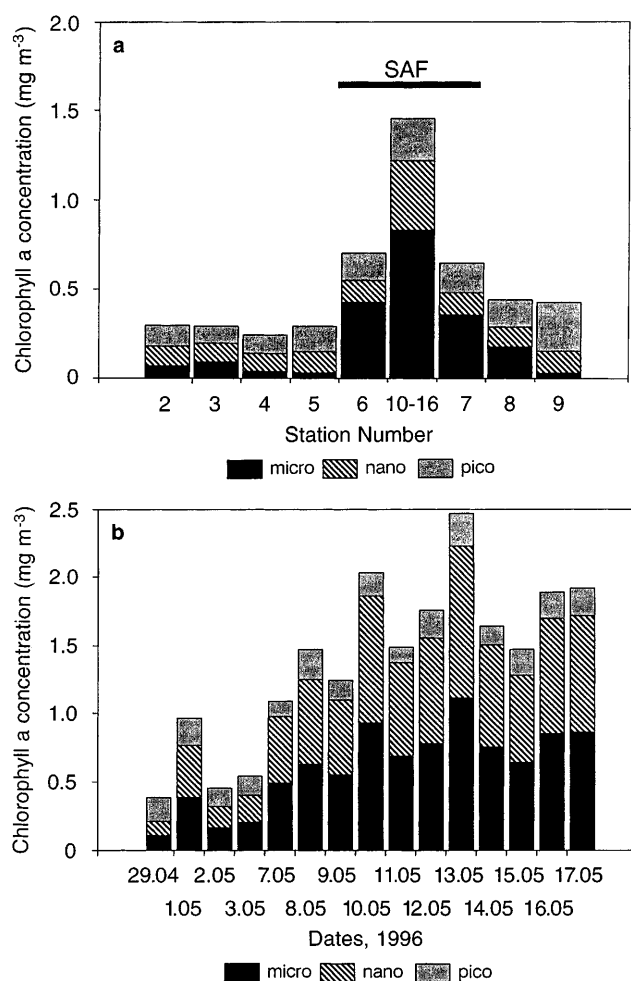
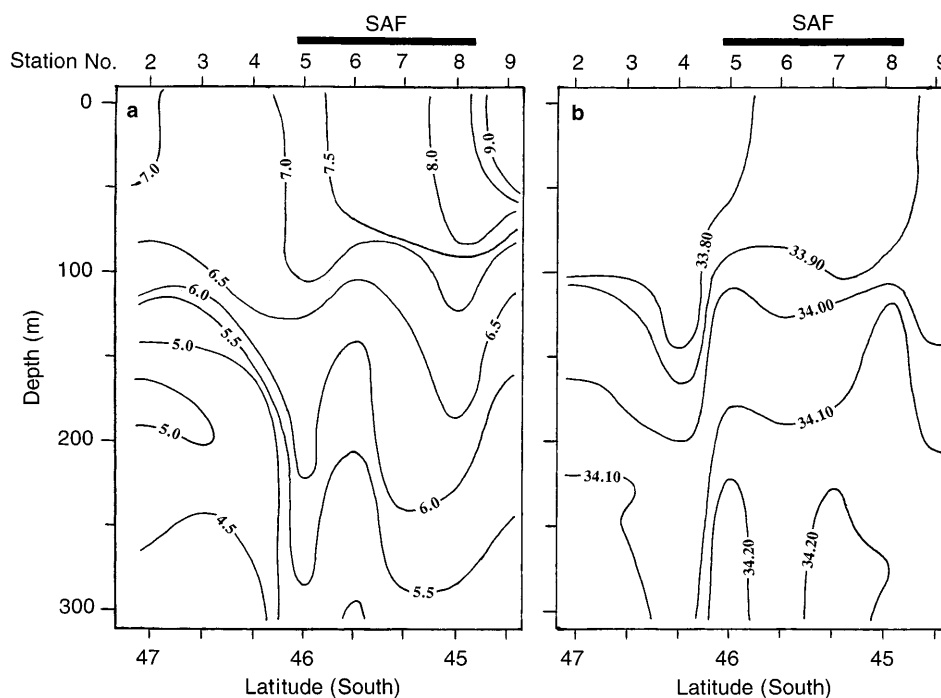
Surface chl *a* concentrations along the 37°E transect ranged from 0.3 to 1.4  $\mu\text{g l}^{-1}$ . Generally chl *a* levels did not exceed 0.5  $\mu\text{g l}^{-1}$  (Fig. 4a). At these stations, nano- and picophytoplankton constitute the fractions contributing most (80%) to the total chl *a* concentrations. The highest chl *a* levels (0.7 to 1.4  $\mu\text{g l}^{-1}$ ) were recorded at the SAF, where microphytoplankton cells accounted for the bulk ( $\approx 60$  to 70%) of the total phytoplankton stock (Fig. 4a).

The surface chl *a* concentrations in the inter-island region between 29 April and 17 May 1996, showed a gradual increase in chl *a* biomass over the shelf region during the period of observation (Fig. 4b). A four-fold increase in total chl *a* concentrations (from  $\sim 0.5$  to  $\sim 2.0$   $\mu\text{g l}^{-1}$ ) was observed over the period of 2 wk; this was largely attributable to an increase in nano- and microphytoplankton concentrations (Fig. 4b).

#### Macroplankton/micronekton communities: composition, distribution, biomass

A total of 49 macrozooplankton and micronekton species were identified in the RMT-8 samples (Table 1).

**Fig. 3** Temperature (a, °C) and salinity (b, psu) profiles along 37°E transect during May 1996 (SAF subantarctic front)



**Fig. 4** Surface chlorophyll *a* distribution along 37°E transect (a) and between Prince Edward Islands (b) during April and May 1996

Among these, 21 species were recorded for the first time in the vicinity of the Prince Edward Islands (Miller 1982; Allanson et al. 1985; Boden and Parker 1986; Gon and Klages 1988). The highest number of species (12) was identified in the fish group. In the offshore samples, mesopelagic fishes of the family Myctophidae formed the bulk of the fishes identified, while in the inter-island region, fishes of the family Nototheniidae, particularly *Lepidonotothen larseni*, dominated. This was followed by euphausiids and amphipods, which comprised 8 and 6 species, respectively. Among the euphausiids *Euphausia longirostris*, *E. vallentini*, *E. similis* and *Nematoscelis megalops* dominated, while among the amphipods *Themisto gaudichaudi* and *Primno macropa* were most frequently encountered. Other groups were less numerous and generally comprised 2 to 4 species (Table 1).

With the exception of Stations 3 and 8, all samples were collected during the night. In the vicinity of the Prince Edward Islands within the top 300 m, total macroplankton abundance ranged from 7.3 to 50.7 individuals  $1000\text{ m}^{-3}$  (av =  $17.5 \pm 9.6$  individuals  $1000\text{ m}^{-3}$ ). Total biomass varied between 40 and 1140 mg dry wt  $1000\text{ m}^{-3}$  (mean  $288 \pm 272$  mg dry wt  $1000\text{ m}^{-3}$ ) (Fig. 5). The spatial distribution of macroplankton was not uniform, with maximum densities (both abundance and biomass) being recorded for the 24 h station occupied at the SAF (Stations 10 to 16; Fig. 1a). Generally, increased macroplankton abundance and biomass were found in the upstream (average 34.8 individuals  $1000\text{ m}^{-3}$  and 815 mg dry wt  $1000\text{ m}^{-3}$ , respectively) and downstream (23.0 individuals  $1000\text{ m}^{-3}$  and 420 mg dry wt  $1000\text{ m}^{-3}$ ) regions. Between the islands, the average abundance and dry biomass were 13.1 individuals  $1000\text{ m}^{-3}$  and 63 mg dry wt  $1000\text{ m}^{-3}$ , respectively (Table 2). Average abundance and biomass levels in the near-bottom samples conducted between the islands were characterized by comparable densities of macroplankton/micronekton (15.1 individuals  $1000\text{ m}^{-3}$  and 333 mg dry wt  $1000\text{ m}^{-3}$ ) at offshore stations. Unfortunately, the number of observations was too small to identify any significant differences in average density between the regions ( $P > 0.05$ ).

The composition of macroplankton/micronekton also differed between the different regions. In the upstream and downstream regions of the islands, nighttime tows were dominated by euphausiids, tunicates and mesopelagic myctophid fishes which collectively accounted for  $> 75\%$  of the catch by dry mass (Fig. 5). In the daytime tows and in the inter-island area, chaetognaths were the most important contributors to total biomass (Fig. 5). The taxonomic composition of near-bottom inter-island samples revealed the clear predominance of either the bottom-dwelling decapod *Nauticaris marionis* (Station 20/1) or demersal fishes of the family Nototheniidae (Stations 35 and 36; Fig. 5, Tables 1 and 2). On two occasions, the near-bottom samples were dominated by chaetognaths and octopus larvae (Stations 34 and 37).

#### Macroplankton/micronekton communities: cluster and ordination analyses

Results of the hierarchical cluster-analysis revealed the presence of two major groups of stations (Fig. 6a). These broadly corresponded to the offshore group, which included stations occupied in the upstream and downstream regions, and the inshore group comprising stations within the inter-island region. Exceptions were Stations 3 and 8, which were incorporated into the inshore group by the cluster analysis but were sampled during the daytime in the offshore region (Fig. 6a). The ordination analysis revealed a similar pattern, although the separation between the offshore and inshore groups was more distinct (Fig. 6b). Indeed, the one-way ANOVA similarity test clearly showed that the differences between the two groups identified with the hierarchical cluster analysis were significant ( $P < 0.05$ ).

The results of the SIMPER analysis revealed an average similarity of 42% between stations within the offshore group. Four species (in order of importance: *Sagitta gazellae*, *Euphausia longirostris*, *Salpa thompsoni* and *E. vallentini*), which accounted for  $\approx 75\%$  of the group numerical abundance, were responsible for  $\approx 84\%$  of the group-average similarity index. Within the inshore group of stations the average similarity index was higher, 52%. Here, two species of chaetognaths, *Sagitta gazellae* and *Eukrohnia hamata*, which contributed  $\approx 77\%$  to the group abundance, accounted for 95% of the similarity index between stations.

Comparison of the two groups identified with the numerical analyses revealed that species' richness was substantially higher in the offshore group than in the inshore group (42 vs 25; Table 1). The average dissimilarity between the groups was  $\approx 70\%$ . Five macroplankton species (in order of importance: *Eukrohnia hamata*, *Euphausia longirostris*, *Sagitta gazellae*, *Euphausia vallentini* and *Salpa thompsoni*) accounted for 55% of the dissimilarity. Among these the chaetognaths *Eukrohnia hamata*, *Sagitta gazellae* and the euphausiid *Euphausia vallentini* were generally common to both groups of stations, although their abundance was 1.4 to 4.3 times higher in the inshore group. The salp *Salpa thompsoni* was also found in both realms (Table 1), but its abundance was 22 times higher in the offshore group. In contrast, the euphausiid *E. longirostris* was not found in the inshore samples (Table 1).

#### Macroplankton/micronekton: vertical migrations

A 24 h station occupied in the immediate vicinity of the SAF during April and May 1996 revealed a clear diel pattern in macroplankton/micronekton biomass within the top 300 m (Fig. 7). Generally, euphausiids (e.g. *Euphausia longirostris*, *E. vallentini* and *Nematoscelis megalops*, tunicates and mesopelagic fishes migrated into the top 300 m layer during the night.

During May 1997, at a 24 h station immediately upstream of the islands, the overall biomass of mac-

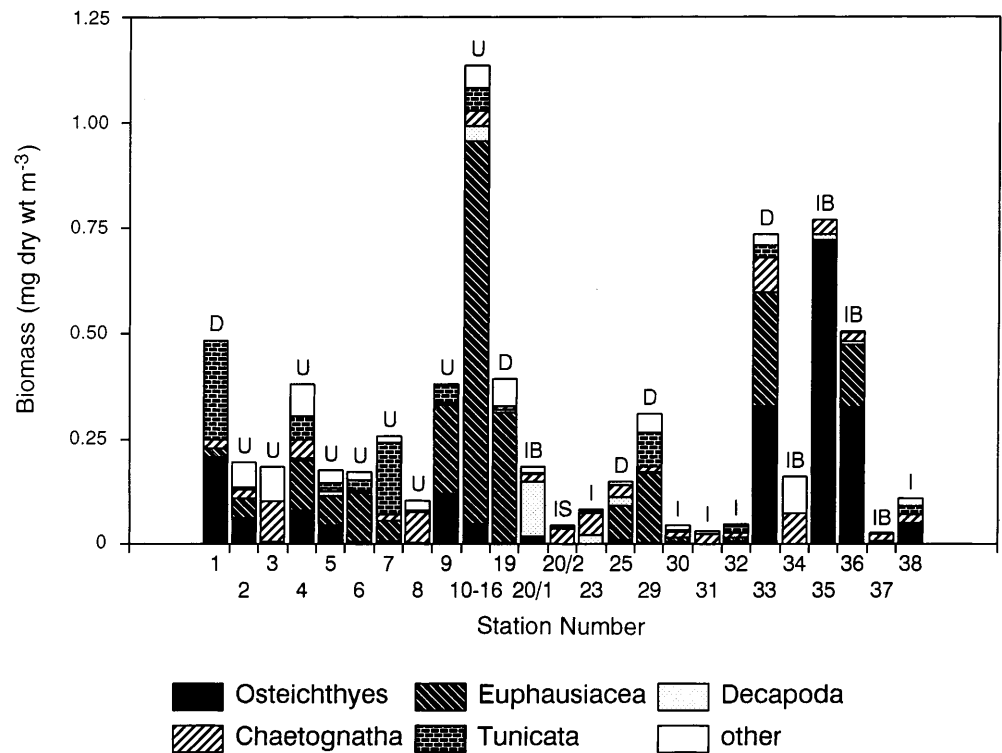
**Table 1** Species list and frequency of occurrence (for 1996 only) in RMT-8 samples in vicinity of Prince Edward Islands during April and May 1996 and 1997 (*na* species recorded only during May 1997; \* species with new records for the region; – species not recorded)

Taxa	Upstream	Downstream	Inter-island, oblique tows	Inter-island, near-bottom tows
Hydromedusae				
<i>Pegantha</i> sp.*	33.3	20.0	–	20.0
Hydromedusae gen. sp.	33.3	40.0	33.3	20.0
Siphonophora				
<i>Melophysa melo</i> *	55.5	60.0	33.3	40.0
<i>Diphyes</i> sp.*	22.2	40.0	16.7	20.0
Ctenophora				
<i>Beroe</i> sp.*	55.5	40.0	–	–
Polychaeta				
<i>Travislopsis levinseni</i> *	na	na	na	na
<i>Vanadis (longissima)</i> *	33.3	20.0	16.7	–
Euphausiacea				
<i>Euphausia similis</i>	77.8	80.0	–	–
<i>E. similis</i> var. <i>armata</i>	44.4	20.0	–	–
<i>E. longirostris</i>	88.9	100.0	–	–
<i>E. vallentini</i>	55.5	80.0	33.3	40.0
<i>Bentheuphausia amblyops</i> *	na	na	na	na
<i>Nematoscelis megalops</i>	88.9	80.0	33.3	60.0
<i>Stylocheiron maximum</i> *	100.0	20.0	–	–
<i>Thysanoessa gregaria</i> *	11.1	20.0	–	–
Amphipoda				
<i>Themisto gaudichaudi</i>	44.4	–	16.7	20.0
<i>Phronima sedentaria</i>	44.4	40.0	50.0	20.0
<i>Primno macropa</i>	44.4	–	16.7	40.0
<i>Hyperietta dilatata</i> *	33.3	–	–	–
<i>Cylopus magellanicus</i> *	11.1	–	–	–
<i>Vibilia</i> sp.	11.1	20.0	–	–
Decapoda				
<i>Acanthephira pelagica</i> *	11.1	–	–	–
<i>Sergestes (arcticus)</i> *	44.4	60.0	–	–
<i>Petalidium foliaceum</i> *	na	na	na	na
<i>Nauticaris marionis</i>	–	–	33.3	80.0
Mollusca				
<i>Clio pyramidata</i>	55.5	40.0	100.0	80.0
<i>Spongiobranchia australis</i>	55.5	40.0	66.7	20.0
<i>Cymbulia peroni</i> *	22.2	–	–	–
<i>Galiteuthis glacialis</i> *	11.1	–	–	–
<i>Gonatus</i> sp.*	22.2	–	–	–
<i>Octopus</i> sp. (larvae)	–	–	33.3	40.0
Chaetognatha				
<i>Sagitta gazellae</i>	100.0	100.0	100.0	100.0
<i>S. maxima</i>	55.5	60.0	33.3	20.0
<i>Eukrohnia hamata</i>	88.9	80.0	100.0	100.0
Tunicata				
<i>Salpa thompsoni</i>	77.8	60.0	83.3	–
<i>Iasis zonaria</i> *	33.3	20.0	–	–
Tunica	33.3	60.0	33.3	20.0
Osteichthyes				
Myctophidae				
<i>Protomyctophum bolini</i>	22.2	–	–	–
<i>P. normani</i>	22.2	–	–	–
<i>Protomyctophum</i> sp. (larvae)	44.4	40.0	16.7	–
<i>Gymnoscopelus braueri</i>	11.1	–	–	–
<i>G. bolini</i>	22.2	20.0	–	–
<i>Gymnoscopelus</i> sp. (larvae)	11.1	–	16.7	–
Gonostomatidae				
<i>Vincigueria attenuata</i>	22.2	40.0	16.7	–

**Table 1** (continued)

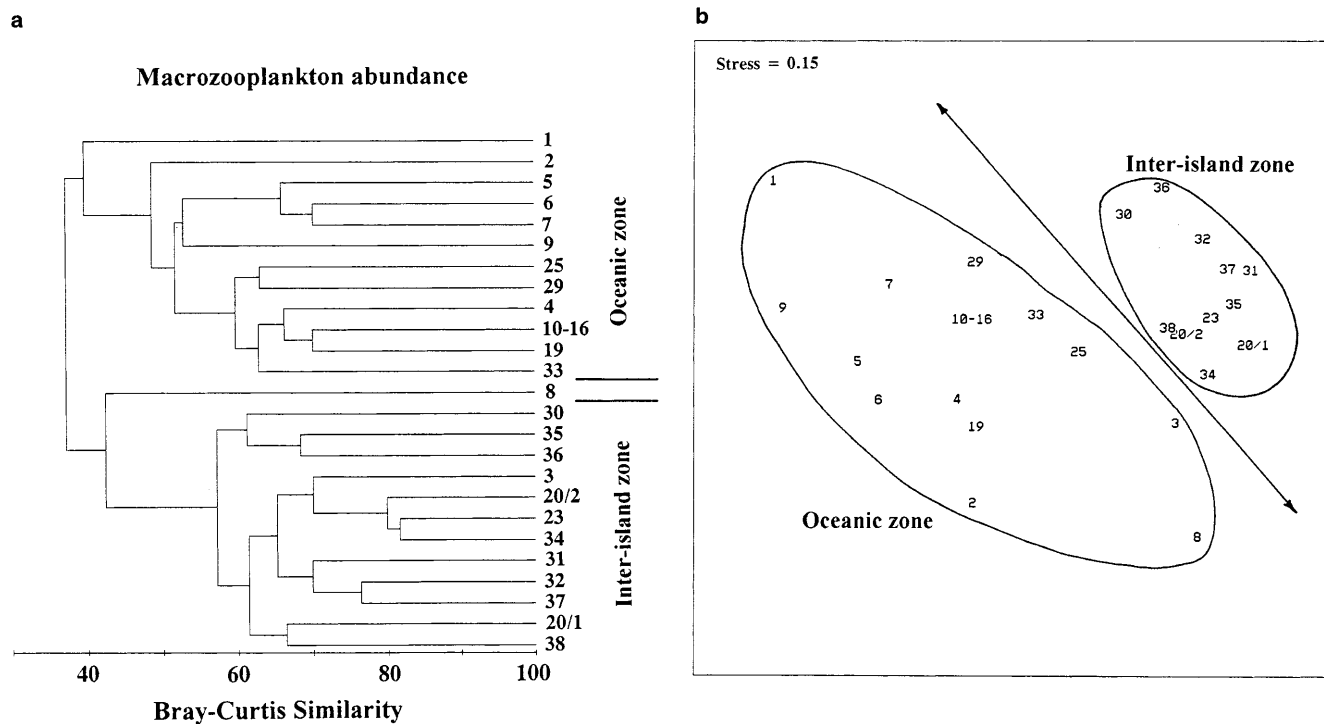
Taxa	Upstream	Downstream	Inter-island, oblique tows	Inter-island, near-bottom tows
Stomiidae				
<i>Stomias boa boa</i> *	—	20.0	—	—
Paralepididae				
<i>Stemonosudis</i> sp.*	—	—	16.7	—
Carapidae				
<i>Echiodon cryomargarites</i> *	33.3	—	—	—
Nototheniidae				
<i>Lepidonotothen larseni</i>	—	20.0	16.7	60.0
<i>L. squamifrons</i> (larvae)	—	—	—	40.0
No. of stations	9	5	6	5

**Fig. 5** Spatial distribution of macroplankton/micronekton in vicinity of Prince Edward Islands during April and May 1996. (*U* upstream tows; *D* downstream tows; *I*, *IB*, *IS* inter-island oblique, near-bottom, and surface tows, respectively)



**Table 2** Abundance (*A*) and biomass (*B*) of major groups of macroplankton/micronekton in vicinity of Prince Edward Islands during April and May 1996 (nighttime tows only). (Gelatinous zooplankton include Hydromedusae, Siphonophora and Ctenophora)

Group	Upstream		Downstream		Inter-island oblique tows		Inter-island, near-bottom tows	
	A (%)	B (%)	A (%)	B (%)	A (%)	B (%)	A (%)	B (%)
Gelatinous zooplankton	8.3	10.6	5.7	6.6	2.2	8.4	2.0	5.7
Polychaeta	0.1	0.1	0.1	0.1	0.2	1.3	—	—
Euphausiacea	37.7	52.6	43.0	40.9	6.4	7.7	20.2	9.3
Amphipoda	1.3	0.8	0.4	0.3	0.6	1.5	0.8	0.1
Decapoda	0.5	2.0	0.5	1.6	0.2	5.2	5.2	9.6
Mollusca	1.3	0.7	0.5	0.1	3.9	4.0	1.4	1.0
Chaetognatha	38.7	9.4	31.4	8.0	83.2	42.1	65.7	10.4
Tunicata	10.6	12.6	17.2	16.5	2.3	14.3	0.5	0.3
Osteichthyes	1.3	11.2	1.2	25.9	1.0	15.5	4.2	63.6
Total A (individuals 1000 m <sup>-3</sup> )	34.8 ± 44.4		23.0 ± 4.9		13.1 ± 4.8		15.1 ± 5.2	
Total B (mg dry wt 1000 m <sup>-3</sup> )	815 ± 1414		420 ± 197		63 ± 27		333 ± 270	

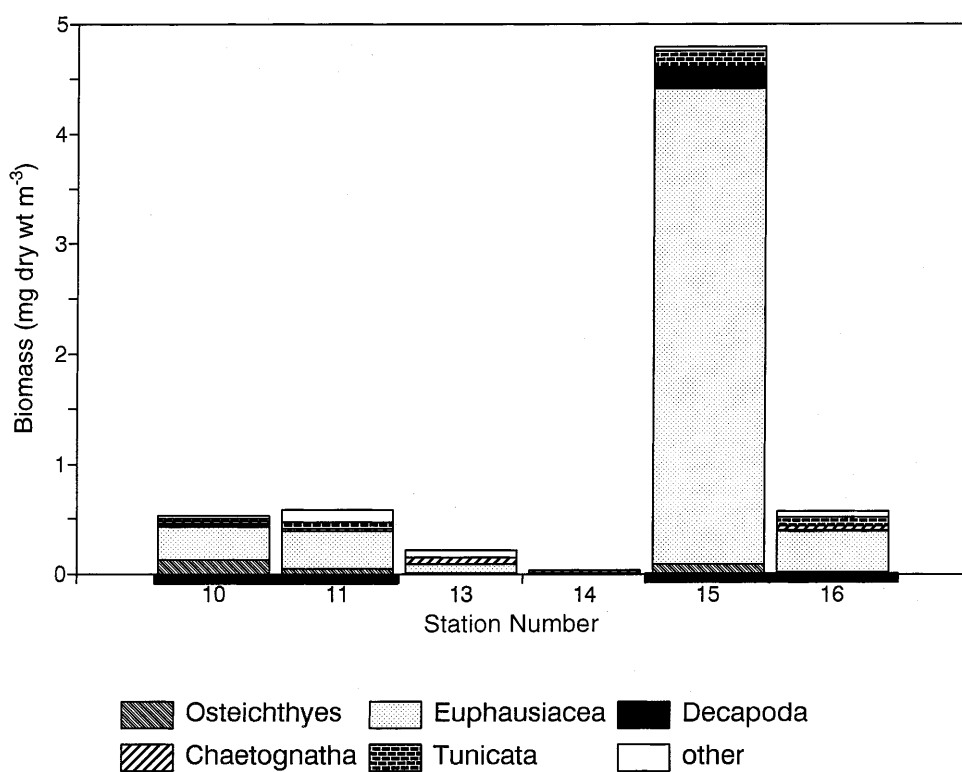


**Fig. 6** Cluster (a) and ordination (b) analyses of macroplankton/micronekton community structure in vicinity of Prince Edward Islands during April and May 1996

roplankton and micronekton was similar in the top 400 m during day ( $153 \text{ mg dry wt m}^{-2}$ ) and night ( $125 \text{ mg dry wt m}^{-2}$ ) tows (Fig. 8a). The results showed that gelatinous zooplankters (e.g. jellyfish, siphono-

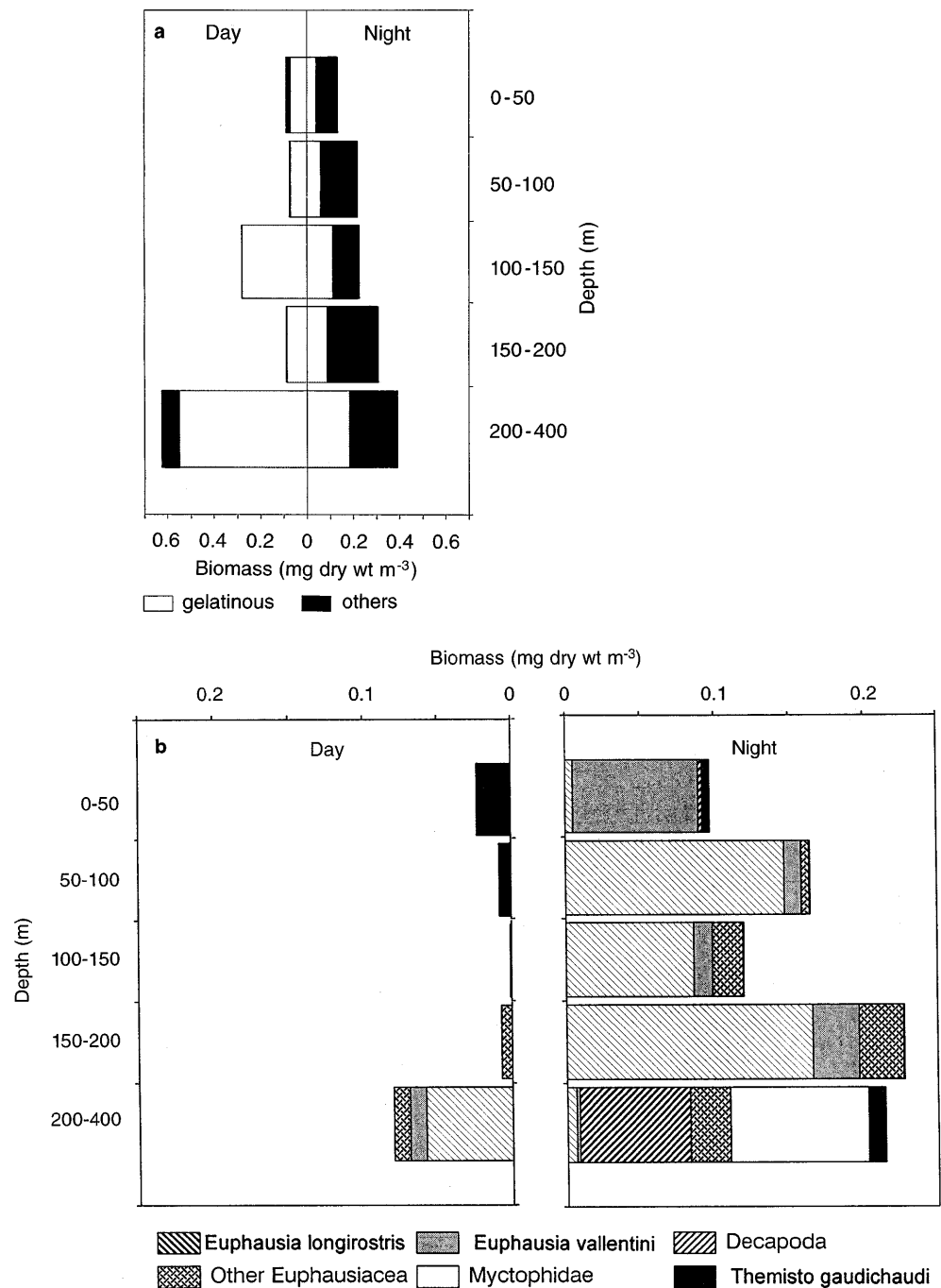
phores and chaetognaths) had similar vertical distribution patterns during the day and night. Meso- and macroplanktonic euphausiids (e.g. *Euphausia longirostris*, *E. vallentini* and *Nematoscelis megalops*) appeared to undertake marked vertical migrations. *E. vallentini* and *N. megalops* were recorded in the top 50 m, while the remaining species were found at depths  $< 200 \text{ m}$ . During the daytime, these species were all

**Fig. 7** Biomass of macroplankton/micronekton during 24 h sampling cycle at Subantarctic Front (Station 10–16, 6 and 7 May 1996) (Black bars on abscissa period of darkness)





**Fig. 8** Vertical distribution of total (a) and migrating (b) macroplankton during 24 h sampling cycle in upstream region of Prince Edward Islands (Station A, 20 and 21 May 1997)



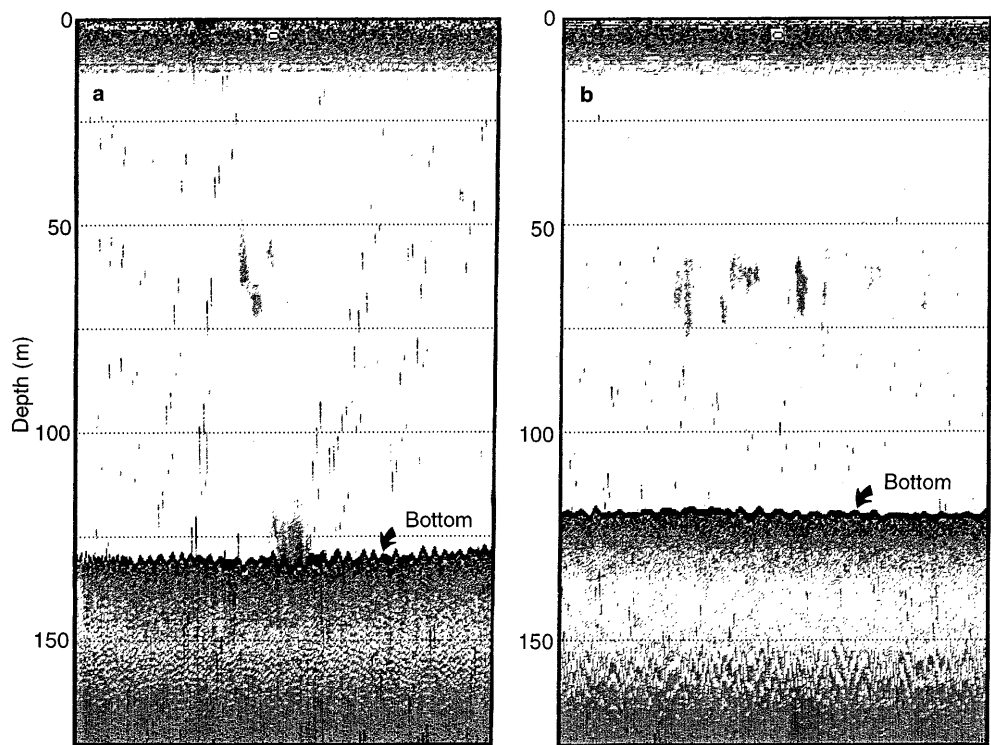
recorded at depths >200 m. Micronektonic decapods and fishes of the family Myctophidae were found only in the nighttime tows conducted deeper than 200 m (Fig. 8b). The vertical distribution of the hyperiid *Themisto gaudichaudi* displayed no clear diel pattern, and was observed in the upper 100 m during both day and night (Fig. 8b).

#### Acoustic studies

Short acoustic transects conducted between the islands during darkness showed that during April and

May 1996 no acoustic targets were observed over the island shelf. In contrast during April and May 1997 surveys conducted during the nighttime and at dawn, small schools of zooplankton were regularly observed over the island shelf at depths between 50 and 100 m (Fig. 9). These schools tended to descend, sometimes to the shelf floor, after sunrise. The identification tows, conducted using a Bongo net (Froneman and Pakhomov 1998a), revealed that copepods, euphausiids, particularly *Euphausia vallentini*, *Nematoscelis megalops* and *Thysanoessa* spp., and the hyperiid *T. gaudichaudi* numerically dominated these samples.

**Fig. 9** Echo charts (EK500 Simrad, 120 kHz) showing swarms of mesozooplanktonic euphausiids and hyperiids at dawn (local time 05:40 to 05:55 hrs) of 4 May 1997 (a) and at sunrise (06:35 to 06:50 hrs) of 23 May 1997 (b) between Prince Edward Islands



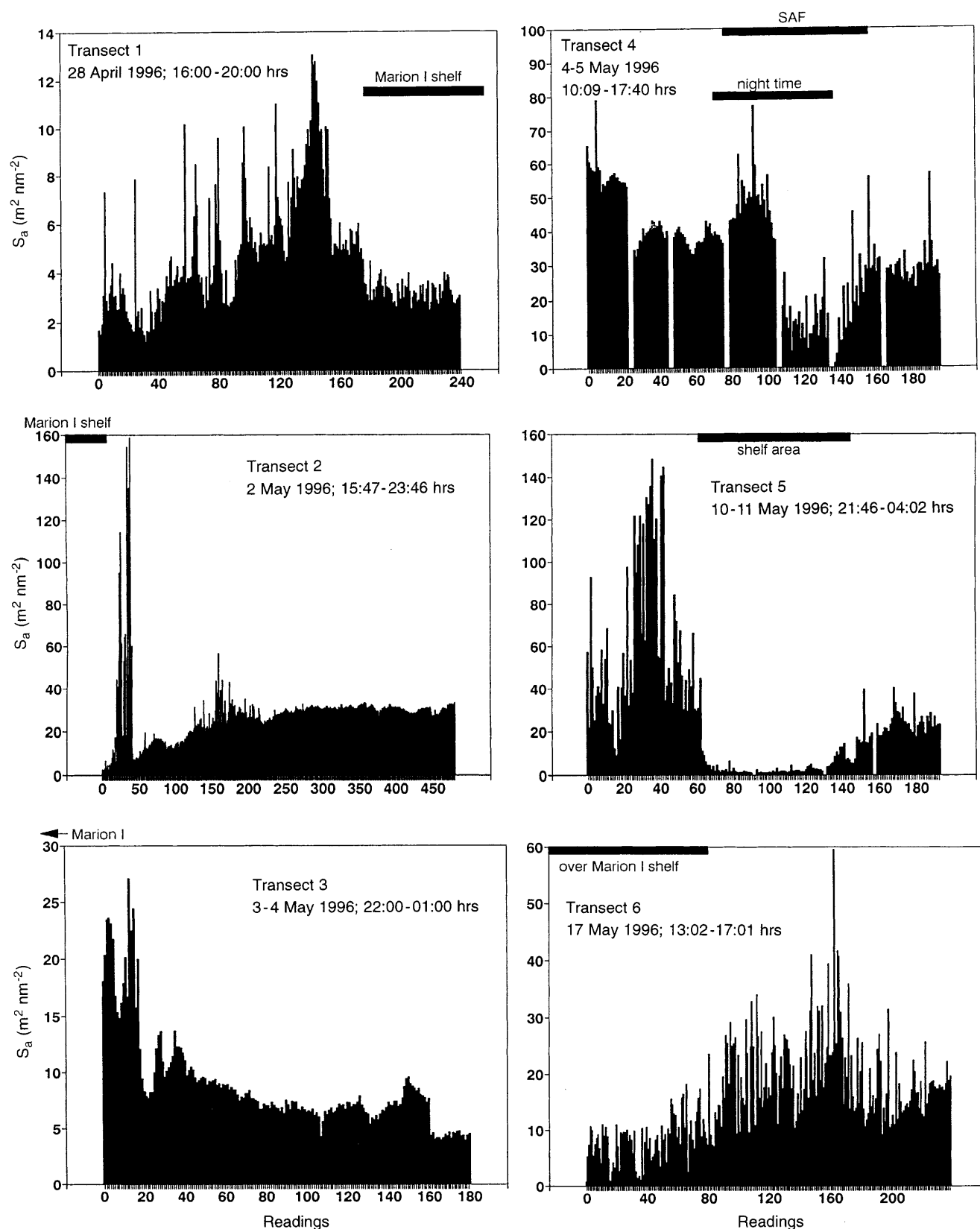
The continuous record of acoustic backscatter ( $S_a$ ) along 37°S (Transect 4), reflecting the macroplankton/micronekton distribution, showed that backscatter was most intense in the region south of the SAF (Fig. 10). It dropped substantially after the frontal zone had been crossed. Transects in the upstream region and across the island shelf from the south to north (Transects 1, 3, 5 and 6), generally showed increased backscatter in close proximity to the island shelf (Fig. 10). A single downstream transect (Transect 2) indicated that backscatter was highest on the offshore leeward side of the islands. Smaller increases in backscatter were also observed further downstream at a distance of  $\approx 70$  to 80 km from the islands (Fig. 10). Generally, the backscatter levels gradually increased towards the downstream region and, by the end of the transect, were almost double those observed in the immediate proximity of the Prince Edward Islands (Fig. 10).

## Discussion

Previous investigations in the vicinity of the Prince Edward Islands have shown that the zooplankton community structure demonstrated tremendous interannual variability particularly with respect to the contribution of the major taxonomic groups (Allanson et al. 1985; Boden and Parker 1986). The numerous planktonic studies undertaken around the Prince Edward Island group were, however, largely concentrated on the species composition, origin and distributional pattern of meso-

zooplankton (see review by Pakhomov and Froneman 1999). Macroplankton/micronekton within the top 50 m were investigated only once, during May and June 1980 (Miller 1982). Miller's study was combined with detailed acoustic measurements, but was unfortunately largely restricted to the island shelf. A macroscale oceanographic, acoustic and Bongo-net survey in April and May 1989, did not sample macroplankton (Perissinotto and McQuaid 1992). Thus, the present study is the first extensive examination of the macroplankton/micronekton community in the top 300 m of the water column in the vicinity of the Prince Edward Islands including the upstream region.

The total number of species identified in this study is similar to those previously reported for the same area (Miller 1982; Allanson et al. 1985; Boden and Parker 1986). However, at least 21 new species of macroplankton/micronekton for the region were recorded (Table 1). This can partially be attributed to the sampling design used in the present study, as 15 of the 21 species found were recorded in the offshore stations occupied in either the upstream or downstream regions (Table 1). Previous studies, although conducted during the same season, generally lacked offshore observations. It is also noteworthy that the macroplanktonic euphausiid *Euphausia longirostris* was very common in our offshore samples, but was virtually absent during previous investigations. Only during a single survey, in May and June 1980, in the offshore region were small numbers of *E. longirostris* recorded in samples collected at night (Miller 1982). It is also notable that a few subtropical species were encountered in the vicinity of the



**Fig. 10** Two-dimensional plots of acoustic backscattering ( $S_a$ ) at 120 kHz along transects in vicinity of Prince Edward Islands (Fig. 1b) during April and May 1996

islands during April and May 1996. These included the siphonophore *Melophysa melo*, the euphausiid *Stylocheiron maximum*, the salp *Iasis zonaria*, the pteropod

*Cymbulia peroni* and the fish *Echiodon cryomargarites*. However, the macroplankton and micronekton fauna found during this study were generally of subantarctic origin. This agrees well with early studies, which showed that although the plankton community is mainly subantarctic, a mixture of subtropical and antarctic species is a common feature of waters in the vicinity of the Prince Edward Islands (Miller 1982; Allanson et al. 1985; Boden and Parker 1986).

The abundance and biomass estimates of this study were among the lowest in the literature (Pakhomov et al. 1994). However, previous estimates (abundance range 130 to 4850 individuals  $\text{m}^{-3}$  and biomass 9 to 57 mg dry wt  $\text{m}^{-3}$ , Pakhomov and Froneman 1999) were largely obtained using nets with a finer mesh, and thus they reflected mesozooplankton densities which are not directly comparable with our own estimates. The densities recorded in our study comprised mainly macroplankton and micronekton, and are similar to these obtained by Miller (1982) for the Prince Edward Island region and by Pakhomov et al. (1994) for the subtropical convergence and the APF. The similarity is probably due to the fact that the same sampling gear (RMT-8) was used in all studies. It is noteworthy that our macroplankton densities (range 0.06 to 0.8 mg dry wt  $\text{m}^{-3}$ ) are similar to these obtained using a Bongo net (range 0.04 to 1.45 mg dry wt  $\text{m}^{-3}$ ) during the same study (Froneman and Pakhomov 1998a). Our biomass estimates were, however, substantially lower than that of the nekton standing stock (2.8 to 8 mg dry wt  $\text{m}^{-3}$ ) in the top 200 m of the APF region and near South Georgia (Piatkowski et al. 1994).

Previous studies have shown that no holoplanktonic endemism, either algal or faunal, is associated with the Prince Edward Island pelagic subsystem (Allanson et al. 1985; Miller 1985; Boden and Parker 1986; Boden 1988). When the bottom-dwelling shelf species are omitted, the analysis of the macroplankton/micronekton community structure conducted in this study confirms these earlier findings. A few pelagic species display substantial differences in distribution and concentration between the offshore and inshore realms. Three hypotheses could explain these discrepancies. Firstly, the predation impact on some species may be higher between the islands than in the offshore regions (Perissinotto and McQuaid 1992). Secondly, the physical environment may limit transportation into the inter-island region. Finally, behavioral features of pelagic animals may prevent them from being washed over the island shelf.

This study revealed that in the inter-island region the average macroplankton/micronekton biomass was nearly an order of magnitude lower than in the upstream and downstream regions (Table 2). A similar pattern was observed during April and May 1989 using a Bongo net (Perissinotto and McQuaid 1992). The lower biomass in the inter-island region was attributed to the high predation pressure of predators feeding on the plankton trapped within the shallow waters between the islands

during the day. As Bongo net samples are composed mainly of mesozooplankton (e.g. copepods, pteropods, small euphausiids), the general decrease in zooplankton biomass could be due to three major factors: predation impact by demersal fish (Blankley 1982; Perissinotto and McQuaid 1992), predation impact by the bottom caridean shrimp *Nauticaris marionis* (Perissinotto and McQuaid 1990), or/and predation impact by chaetognaths (Froneman and Pakhomov 1998b; Froneman et al. 1998). Little information is available regarding the first two factors. There is some evidence that mesozooplankton accounts for a significant proportion of fish and shrimp diets. Recently, however, it was shown that chaetognaths are able to consume daily up to 5% of copepod standing stock, or up to 103% of copepod production (Froneman and Pakhomov 1998b). A combination of vertical migrations and net avoidance may further account for the substantial underestimation in zooplankton biomass over the shelf region. Shallow depths would prevent zooplankton migrating into their usual depth range, and thus would enhance prey encounter-rates with chaetognaths and bottom-dwelling fishes and shrimps. It is possible that zooplankton biomass was elevated in close proximity to the island shelf. Unfortunately, the near-bottom layers could not be sampled efficiently by our nets.

The decrease in macroplankton/micronekton densities over the shelf region cannot be attributed to net avoidance, as samples were largely collected during the night. It is also unlikely that small nototheniid fishes, shrimps and chaetognaths may prey efficiently upon animals  $\geq 20$  mm in length. Predation impact by flying birds and penguins may, therefore, primarily be responsible for the biomass depletion in this region. Indeed, it is generally recognised that most myctophids, pelagic shrimps and squid are the staple food of many top predators on the islands (Adams and Brown 1989; Cooper and Brown 1990). There are, however, a few exceptions, e.g. the macroplanktonic euphausiid *Euphausia longirostris* and two species of salps. These organisms were virtually absent from the inter-island samples in the present study, and have never been found in the stomachs of any top predators (Cooper and Brown 1990). All major consumers of food on the islands, e.g. king, macaroni and rockhopper penguins as well as albatrosses, are known to forage mainly in offshore waters (Adams and Brown 1989; Cooper and Brown 1990; Bost et al. 1997). Therefore, factors other than predation must be responsible for the poor macroplankton/micronekton densities in the Prince Edward Island inter-island region.

The physical environment, particularly current flow, may account for the low macroplankton/micronekton densities between the islands. The Prince Edward Islands Plateau acts as an obstacle to current flow. Flow acceleration would unavoidably occur around the islands, with relatively calm areas in the immediate upstream and downstream proximity of the islands (Boehlert and Genin 1987; Roden 1987; Heywood et al. 1990). Because the inter-island saddle is shallow, most of the water

would be expected to go around the islands rather than over the shelf. Previously, it has been suggested that water containing allochthonous plankton would be transported to the shelf region between the islands during the night (Perissinotto and McQuaid 1992), thus replenishing the planktonic stock depleted during the previous day. However, preliminary calculations indicated that the daily food requirements of the island-based predators could not be covered by the replenished planktonic stock (Perissinotto and McQuaid 1992). Also, the replenishment hypothesis is in direct contradiction to the results of our RMT-8 net trawls, which revealed very poor macroplankton/micronekton densities within the inter-island region.

Perissinotto and McQuaid (1992) suggested that interactions between vertical migrations, surface Ekman drift and bottom topography may be responsible for conveying food to the islands' top predators. In our opinion, besides physical parameters, behavioral patterns of allochthonous zooplankters may also contribute to this process. Our observations at the 24 h stations clearly indicated that the migrational patterns of the various zooplankton/micronekton groups are different. For example, mesozooplanktonic species (e.g. many copepods, small euphausiids and hyperiids) migrate to surface layers at night, while macroplanktonic/micronektonic animals tend to stay deeper (usually at > 100 m depth). Since Ekman drift only applies only to the upper 20 m of the water column, and since only a limited volume of water may drift over the shallow inter-island saddle, larger animals will generally not be advected across the islands' shelf. As a result, macroplankton/micronekton would largely drift around the islands, forming a belt of high concentrations in close proximity to the island shelf. Indeed, the acoustic data obtained in this study confirm this suggestion (Fig. 10). The behavioral patterns of plankton and micronekton, particularly vertical migrations, would therefore largely be responsible for the absence of large plankters between the islands. This hypothesis may also partially explain why cluster analysis grouped the daytime upstream samples with the inter-island samples during this study.

Results of previous studies in the region of the Prince Edward Islands have suggested that the position of the SAF in the vicinity of the island group may be important determinants of the macro- and mesoscale oceanographic conditions (see review by Pakhomov and Froneman 1999): (1) Where the SAF lies far to the north of the islands, the interaction between the ACC and the archipelago results in the formation of eddies in the inter-island region with which phytoplankton blooms are associated (Perissinotto and Duncombe Rae 1990); (2) in contrast, where the SAF is in close proximity to the islands, advection forces prevail and a flow-through system is established between the islands, with a pronounced Rossby wave in the downstream region (Perissinotto et al. 1999). These scenarios have important implications for the inter-island realm dynamics.

Oceanographic surveys during April and May 1996 and 1997 revealed that the position of the SAF in the vicinity of the Prince Edward Islands was substantially different between years. During the 1996 survey, it lay far to the north of the islands, and as a result a phytoplankton bloom was observed between the islands. During the 1997 season, neither water trapping nor phytoplankton bloom occurred between the islands (Pakhomov and Froneman unpublished data). Our results thus provide further evidence for the two scenarios mentioned above. The RMT-8 samples and acoustic data revealed that no macroplankton/micronekton were represented over the island shelf, while mesozooplankton appeared to drift over the inter-island region only during April and May 1997. This indicates that even the advection of allochthonous mesozooplankton across the island shelf differs substantially between the two flow-pattern scenarios. Apparently the advection of mesozooplankton across the island shelf is lower during periods when the SAF lies far to the north of the island group because the water exchange between the upstream and the inter-island regions is limited. At this stage, we can only speculate about the consequences of this limitation for the bottom-dwelling communities, but it is not unreasonable to suggest that the feeding conditions would be substantially better during the second scenario.

Our acoustic data always showed strong backscatter in regions immediately downstream from the islands. Indeed, the upstream macroplankton concentrations during the April and May 1996 cruise (excluding the SAF stations) were on average about half those of the downstream region (240 vs 420 mg dry wt 1000 m<sup>-3</sup>), providing some evidence for the accumulation of larger animals in the latter region. The acoustic survey of the downstream region revealed increased macroplankton/micronekton concentrations not only in the immediate vicinity of the islands, but also further downstream. This could indicate that the elevated concentrations of large plankton and micronekton observed in the lee of the islands are carried downstream.

In conclusion, the replenishment hypothesis proposed by Perissinotto and McQuaid (1992) failed to explain the macroplankton/micronekton distribution patterns around and between the Prince Edward Islands. The findings of this study indicate that the larger pelagic organisms, which constitute an important food source for many land-based predators, are mostly washed around islands rather than drifting between them. There is evidence that macroplankton/micronekton concentrate in close proximity around the islands, particularly in the downstream region. This region probably represents an important foraging ground for some of the land-based predators. This is partly supported by the distributional pattern of all the major penguin colonies (e.g. king, rockhopper and macaroni penguins) which are concentrated on the westward side of the islands (Williams 1978; Adams and Wilson 1987; Watkins 1987).

Miller (1982) reported high backscatter in the deepest channel between Marion and the Prince Edward Islands. To date, however, there are no data available on the potential flow-through capacity of the inter-island saddle. Also, we do not know whether a limited amount of large plankton and nekton may be carried over the shelf region. Little is known about the pulses of water which theoretically may occur between the islands, and these will be the subject of future investigations. The mesozooplankton and macroplankton/micronekton food supplies over the island shelf and in the vicinity of the islands appeared to indicate two different oceanographic scenarios: availability of small allochthonous zooplankton may be substantially limited when the SAF is far from the islands, but is probably sufficient when the SAF is in close proximity to them. Large zooplankton and micronekton may be more accessible to the top predators on the islands in both scenarios as the result of either accumulation on the leeward side of the islands, or the close interaction of the SAF with the Prince Edward Islands plateau.

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