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E. A. Pakhomov · I. J. Ansorge · P. W. Froneman

Variability in the inter-island environment of the Prince Edward Islands (Southern Ocean)

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Abstract Variability in the oceanographic parameters and macrozooplankton and micronekton composition, densities and distributional patterns were investigated during a repeat survey conducted between the Prince Edward Islands in April 1998. Results of this study demonstrated the occurrence of pronounced water pulses along the inter-island trench. The location of the Subantarctic Front to the north of the island plateau, through its interactions with the island group, appeared to have a marked effect on the mesoscale dynamics of physical and biological parameters between and around the islands. Seawater temperature and salinity accounted for >40% of the variation in the zooplankton distribution during the trench studies. A total of 41 macroplankton and micronekton taxa, consisting of subantarctic, subtropical and Antarctic species, were identified. Numerical analyses revealed two major groupings of stations corresponding to an offshore and inshore region. Although there was no evidence for quantitative differences in macroplankton densities between the inshore surveys, offshore plankton biomass was at least three- to eightfold higher than during the trench surveys. The importance of water pulses in carrying stocks of large plankton between the islands appeared to be minimal, at least during the time when the investigation took place.

Introduction

The Prince Edward Islands, consisting of two small volcanic islands, Marion and Prince Edward, are located

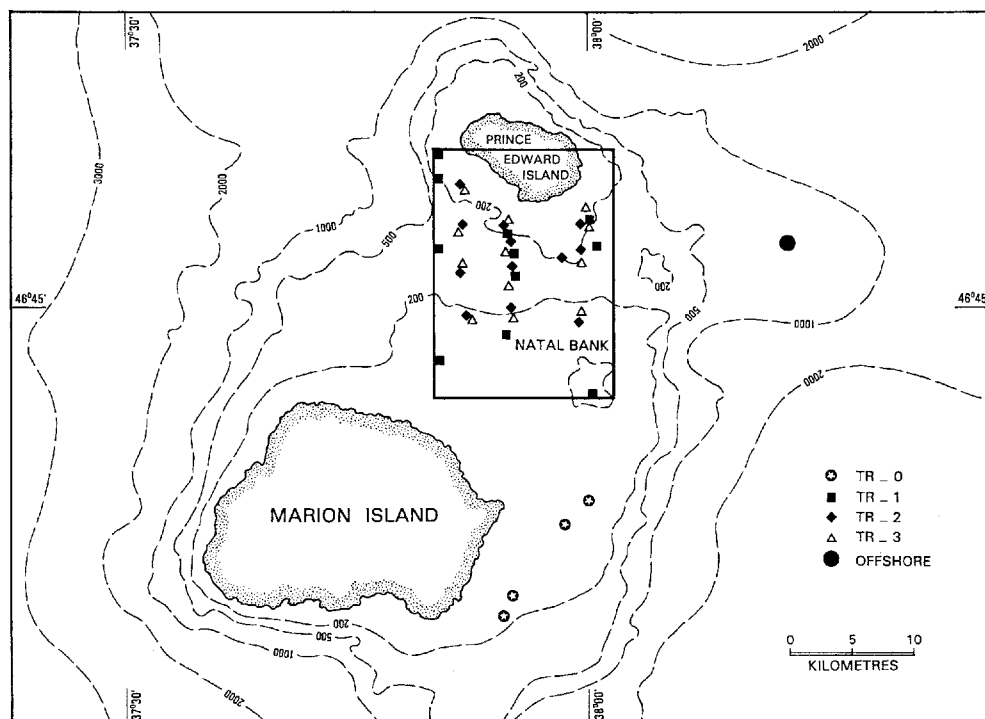
in the Indian sector of the Southern Ocean at 46°50'S and 37°50'E (Fig. 1). Rising from a depth of 3000 m, the islands are separated by a shallow plateau approximately 200 m deep. Previous investigations conducted around the Prince Edward Islands demonstrated that the island group lies directly in the path of the easterly-flowing Antarctic Circumpolar Current (ACC) within the Antarctic Polar Front Zone (APFZ). This zone is bounded to the north by the Subantarctic Front (SAF) and to the south by the Antarctic Polar Front (APF) (Lutjeharms and Valentine 1984; Duncombe Rae 1989a; Lutjeharms 1990). As a consequence of the shallow topography, the islands act as an obstacle to the ACC, resulting in substantial modifications within the oceanographic and biological environment, particularly in the downstream region (Ansorge et al. 1999; Froneman et al. 1999).

Typical of many subantarctic oceanic islands, the Prince Edward Islands accommodate large, seasonal populations of predatory birds and mammals, suggesting an adequate supply of food (Williams et al. 1979; Condy 1981; Perissinotto and McQuaid 1992). The mechanism that sustains the large numbers of predators on the islands has been termed a "life-support system" (Perissinotto and McQuaid 1992). It is now recognized that the "life-support system" of the islands includes two important components: an inshore and offshore component (Pakhomov and Froneman 1999a). The inshore component represents the trophic links between selected top predators and the rich benthic and demersal fish communities, while the offshore component establishes links between numerous penguins, flying birds, seals and the open-ocean allochthonous zooplankton and nekton (Perissinotto and McQuaid 1992; Pakhomov and Froneman 1999a, b). It has been suggested that the geographic location of the SAF in relation to the islands may substantially influence the oceanological conditions within and around the island group (Perissinotto and Duncombe Rae 1990; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov and Froneman 1999b; Perissinotto et al., in press). When the SAF lies far to the north

E. A. Pakhomov (✉) · P. W. Froneman
Southern Ocean Group,
Department of Zoology and Entomology, Rhodes University,
P.O. Box 94,
Grahamstown 6140, South Africa
e-mail: e.pakhomov@ru.ac.za

I. J. Ansorge
Department of Oceanography, University of Cape Town,
Rondebosch 7701,
Cape Town, South Africa

Fig. 1 Oceanographic/biological stations (CTD + RMT-8) occupied during the trench surveys in April 1998 (TR1 first trench survey; TR2 second trench survey; TR3 third trench survey; TR0 exploratory shelf survey; offshore downstream offshore station)



of the island plateau, the APFZ broadens and advective forces associated with these quiescent zones are weak. As a consequence, trapped eddies generally coupled with extensive phytoplankton blooms, resulting in little exchange of inshore/offshore waters, have been observed over the inter-island region of the Prince Edward Islands (Perissinotto and Duncombe Rae 1990). In contrast, when the SAF lies in close proximity to the islands, advective forces associated with the strong frontal flow prevail, and a flow-through system is established between the islands (see review, Pakhomov and Froneman 1999a). Consequently, eddies are absent between the islands (Perissinotto et al., in press).

Most recently the trophic importance of open-ocean macroplankton and micronekton stocks around the Prince Edward Islands has been studied in detail using large nets and acoustic surveys (Pakhomov and Froneman 1999b). In contrast, the importance of large plankton and nekton within the inter-island area is still poorly understood. The previously proposed "replenishing hypothesis" suggested that micronekton that were advected at night and consumed by the top predators during the day would be replenished during the following night (Perissinotto and McQuaid 1992). Recent investigations conducted between the islands have not supported this hypothesis, as the continuous advection of large plankton and nekton over the islands' saddle has not been confirmed (Pakhomov and Froneman 1999b).

In the center of the island plateau, a deep (> 200 m) and narrow (> 5 nautical miles) channel runs south-eastwards, dividing the plateau into northern and southern regions (Fig. 1). This channel may act as a

funnel to the flow associated with the Antarctic Circumpolar Current, possibly resulting in its acceleration through the islands. It has been hypothesized that, during a flow-through regime, pulses of water may occur between the islands (Miller 1982). The origin and frequency of such water pulses, as well as their importance in advection of large plankton between the islands, are unknown. The main aim of the present study is, therefore, to investigate the short-term variability of oceanographic and biological (macroplankton and micronekton) characteristics in the channel of the inter-island region of the Prince Edward Islands.

Materials and methods

All measurements and samples were collected during voyage 87 on board the mv *SA Agulhas* between 7 and 24 April 1998 in the inter-island region of the Prince Edward Islands (Fig. 1). The survey represented part of the third cruise of the Marion Island Oceanographic Study (MIOS III). An exploratory shelf survey (TR0; $n = 4$) was conducted during the evening (1700–2000 hours local time) on 7 April. The first trench survey (TR1; $n = 12$) was occupied between 13 and 14 April. The second trench survey (TR2; $n = 12$) was undertaken during 20 April, while the third survey (TR3; $n = 12$) was conducted between 23 and 24 April (Fig. 1). Surveys TR1 and TR3 were occupied from early afternoon to sunrise, while survey TR2 was conducted mainly during daylight hours. For a comparison, a single station was occupied at 12 midnight within the top 300 m in the downstream region of the islands, at approximately 46°42.07'S–38°13.35'E (Fig. 1).

Except for the TR0 survey, at each station a CTD (conductivity-depth-temperature) cast was undertaken using a Neil Brown Instrument System Mark IIIc underwater unit to within 10 m of the bottom. Station depths ranged from 80 m on the shelf to ~500 m in the western sector of the survey.

To locate and monitor the position of the SAF in relation to the Prince Edward Islands, three transects were carried out upstream of the islands along the 37°E meridian over a period of 4 weeks. These lines were occupied en route to the islands (4–5 April), during a northern transect (15–16 April) and during the return voyage to Cape Town (8–9 May). The front was identified by its subsurface expression ($T_{100} = 7^{\circ}\text{C}$), following the definition by Nagata et al. (1988). During these transects Sippican T7-XBTs (Expendable Bathythermograph) were deployed at 15' intervals to a maximum depth of 760 m. Prior to deployment, the XBTs were placed in a water bath for 5 min in order to minimize the difference between the probes' storage temperature ($\sim 22^{\circ}\text{C}$) and that of the sea-surface temperature (between 7 and 5 °C).

Macroplankton/micronekton samples were collected using a Rectangular Midwater Trawl (RMT-8) with a nominal mouth area of 8 m² and a mesh size of 5 mm. The trawl was towed obliquely from the bottom to the surface or between 300 and 0 m. Towing speed and duration varied between 1.5 and 3.3 knots and between 5 and 20 min, respectively. The trawl was equipped with a Universal Underwater Unit (U³, 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. This was calculated from the ship's average speed and the duration of trawling after the net was opened. In calculating the volume filtered, the effect of towing speed was also taken into consideration (Roe et al. 1980). Samples were preserved in 6% buffered formalin and examined in the laboratory within 3 months of collection. Tissue loss due to preservation may have been as high as 30% for crustaceans and 70% for gelatinous zooplankton (A. Slaughter, unpublished work). As there is no agreement yet on what correction factor to apply, no adjustments were made to correct for tissue loss due to formalin preservation. Therefore, the term "biomass" used throughout the paper is, in fact, equivalent to "formalin altered biomass". Entire catches were sorted and analyzed for taxonomic identification, numerical abundance and wet weight biomass. The dry weights of the main macrozooplanktonic and micronektonic groups were obtained by oven drying fixed specimens for 36 h at 60 °C.

To compare plankton communities, non-metric cluster analysis and multi-dimensional scaling were used in conjunction with the Bray-Curtis similarity index after log-transforming [$\log_{10}(x + 1)$]

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 Routine In Multivariate Ecological Research (PRIMER, Clarke and Warwick 1994) computer package, according to the procedure described by Field et al. (1982).

Results

Physical environment

During the course of the voyage, the Subantarctic Front (SAF) was crossed on three occasions. On each occasion the geographic position of the front, in relation to the islands, was shown to shift considerably. The SAF was first crossed during the voyage en route to the islands, where it was observed at 45°30'S (Fig. 2A). A week later, following the TR1 survey, the front was crossed again. On this occasion the SAF appeared to have shifted northwards to $\approx 45^{\circ}15'S$ (Fig. 2B). The final crossing occurred during the return voyage to Cape Town. Although this transect was occupied approximately 2 weeks after the final trench survey (TR3), the SAF was identified at $\approx 45^{\circ}40'S$ (Fig. 2C).

The oceanic environment in the inter-island region during the surveys clearly shows pronounced variability in the flow pattern of water between the islands. During the TR1 survey, an eddy-type feature, centering within the inter-island channel, was evident (Fig. 3A). Its position appears to be guided by the bathymetry, which narrows with distance from west to east. Subsurface (150 m) physical properties of this feature are colder (4.6 °C) and more saline (>34) than the surrounding

Fig. 2A–C Underway XBT temperature sections occupied along the 37°E to and from the Prince Edward Islands. The position of the SAF is determined by the intersection of the 7 °C isotherm and the 100 m depth line (marked as a *bold line*). **A** 4–5 April; **B** 15–16 April; **C** 8–9 May 1998

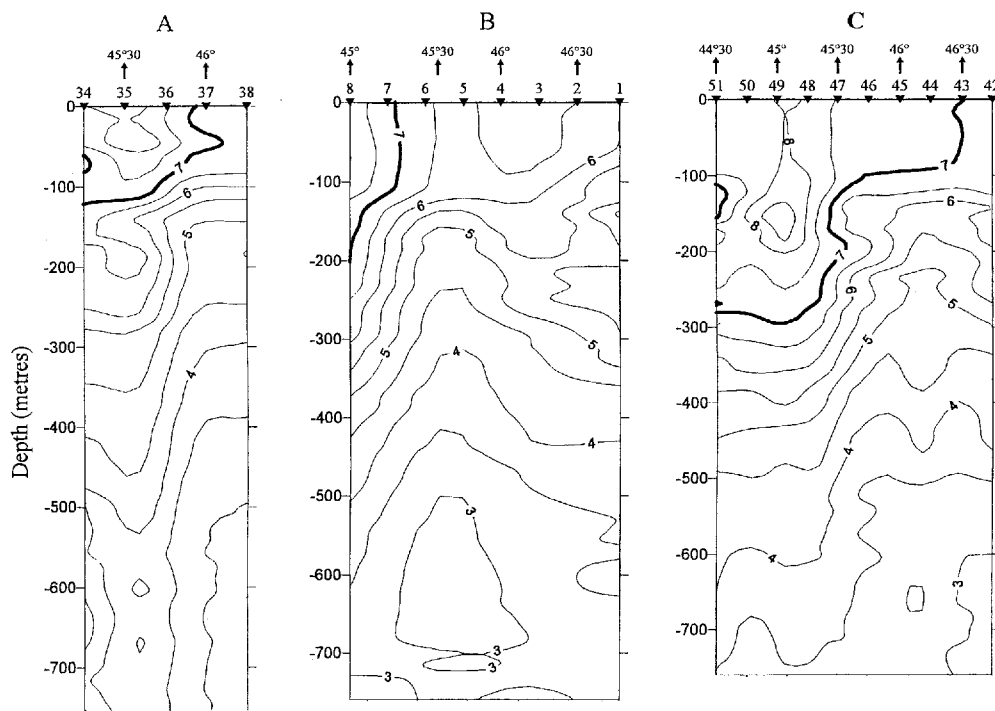
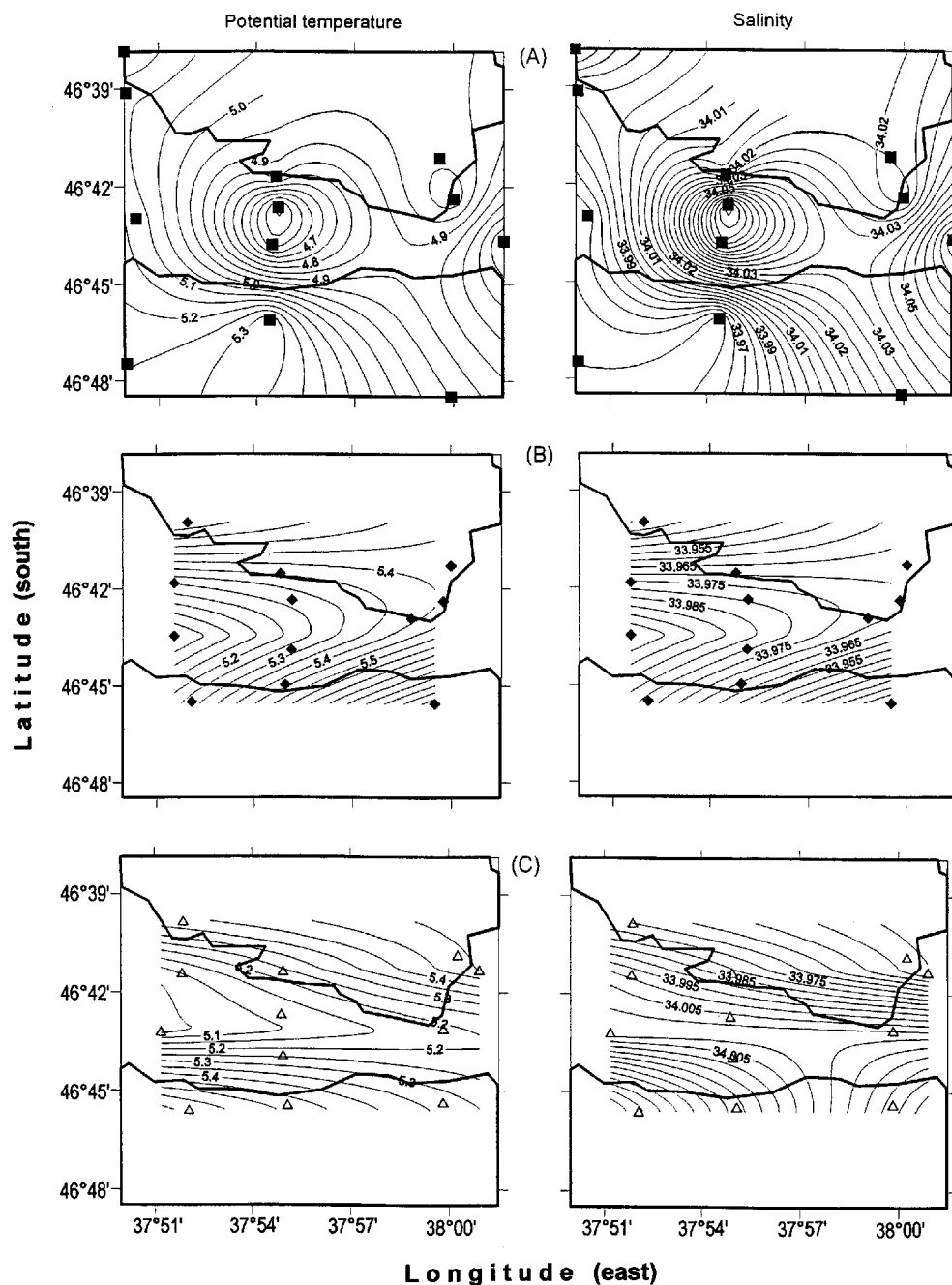


Fig. 3 Subsurface (150 m) potential temperature and salinity distributions for each trench survey (A–C TR1 to TR3), conducted over the shelf region between Prince Edward and Marion Island. The 200-m isobath is *outlined*, while *symbols* indicate the position of each hydrographic station



environment suggesting that this water body, indicative of modified Antarctic Surface Waters, may have originated from the southern part of the Antarctic Polar Frontal Zone. In the eastern corner of the trench, what may be the tail end of a similar feature can be observed. In contrast, water properties appear to become warmer ($> 5^{\circ}\text{C}$) and fresher (< 33.90) west of the central feature, suggesting that the flow through the shallow trench may occur in a series of pulses.

Physical properties identified during TR2 and TR3 showed very different distribution in the inter-island region (Fig. 3B, C). The eddy-type feature observed during TR1 was no longer present. Instead, the properties appeared to correspond to those associated with

northern APFZ waters. Seawater temperatures were higher ($> 5^{\circ}\text{C}$) and salinities lower (33.97–34.01), extending eastwards in the form of a tongue along the trench (Fig. 3B, C). However, along the northern and southern edges salinities appeared lower, < 33.96 . This is also clearly evident in the surface property distributions (not shown) and may possibly be due to the runoff of fresh water from the islands.

Plankton community structure and dynamics

A total of 41 macrozooplankton and micronekton taxa were identified in the RMT-8 samples (Table 1). The

Table 1 Abundance (ind. 1000 m⁻³, ± 1 SD) and biomass (mgDW 1000 m⁻³, ± 1 SD) estimates of macrozooplankton and micronekton during different surveys conducted in April 1998 around the Prince Edward Islands (*Offshore* downstream offshore station; *TR0* exploratory shelf survey; *TR1* to *TR3* first to third trench surveys)

Taxa	Abundance					Biomass				
	Offshore	TR0	TR1	TR2	TR3	Offshore	TR0	TR1	TR2	TR3
<i>Euphausia vallentini</i>	8.6	12.5 \pm 6.1	35.5 \pm 39.7	4.9 \pm 7.8	6.8 \pm 4.8	93.5	101 \pm 57.9	285 \pm 283	41.6 \pm 77.2	36.8 \pm 25.9
<i>E. longirostris</i>	56.6	—	<0.1	—	<0.1	1649.4	—	0.6 \pm 1.6	—	0.9 \pm 1.9
<i>E. similis</i>	0.2	—	<0.1	—	<0.1	4.9	—	0.7 \pm 1.5	—	0.3 \pm 1.1
<i>Nematoscelis megalops</i>	2.3	0.1 \pm 0.1	1.6 \pm 1.9	1.2 \pm 1.2	0.3 \pm 0.3	43.6	1.2 \pm 1.4	22.6 \pm 28.9	17.8 \pm 31.0	4.2 \pm 5.5
<i>Thysanoessa macrura</i>	—	—	<0.1	—	—	—	—	0.1 \pm 0.2	—	—
<i>T. vicina</i>	1.9	6.8 \pm 2.4	3.5 \pm 2.9	2.3 \pm 2.6	4.3 \pm 2.6	2.1	6.4 \pm 1.9	3.2 \pm 2.7	1.8 \pm 2.4	3.3 \pm 2.0
<i>T. gregaria</i>	—	0.5 \pm 0.6	0.5 \pm 0.5	0.3 \pm 0.3	0.8 \pm 0.6	—	3.4 \pm 3.9	3.4 \pm 4.1	1.8 \pm 2.2	5.4 \pm 4.5
<i>Stylocheiron longicorne</i>	0.2	—	<0.1	<0.1	0.2 \pm 0.2	0.2	—	<0.1	<0.1	0.4 \pm 0.8
<i>S. maximum</i>	—	—	<0.1	—	0.1 \pm 0.2	—	—	0.3 \pm 0.9	—	1.2 \pm 2.7
<i>Nauticaris marionis</i>	0.9	<0.1	2.3 \pm 2.1	0.8 \pm 1.2	0.9 \pm 1.0	5.6	1.9 \pm 3.2	18.2 \pm 17.6	8.7 \pm 17.8	6.9 \pm 8.1
<i>Themisto gaudichaudi</i>	0.2	3.4 \pm 2.6	1.0 \pm 1.5	0.7 \pm 1.5	0.2 \pm 0.3	3.2	54.7 \pm 43.8	14.2 \pm 24.3	10.4 \pm 24.3	3.6 \pm 4.7
<i>Primno macropa</i>	—	—	0.1 \pm 0.1	<0.1	<0.1	—	—	1.0 \pm 1.6	0.7 \pm 1.4	0.6 \pm 1.1
<i>Hyperoche medusarum</i>	—	—	<0.1	—	—	—	—	0.3 \pm 0.8	—	—
<i>Phronima atlantica</i>	—	—	<0.1	—	0.1 \pm 0.2	—	—	<0.1	—	0.7 \pm 1.3
<i>P. sedentaria</i>	—	—	—	—	<0.1	—	—	—	—	0.9 \pm 1.9
<i>Vibilia antarctica</i>	—	0.2 \pm 0.2	—	<0.1	—	—	0.5 \pm 0.7	—	0.2 \pm 0.6	—
<i>Cyllopus magellanicus</i>	—	0.1 \pm 0.1	<0.1	<0.1	—	—	1.5 \pm 1.9	0.1 \pm 0.5	<0.1	—
<i>Chuneola paradoxa</i>	—	—	—	<0.1	—	—	—	—	0.6 \pm 2.0	—
<i>Spongiobranchea australis</i>	0.7	0.8 \pm 0.4	0.6 \pm 0.6	<0.1	0.3 \pm 0.3	5.6	8.8 \pm 5.5	4.7 \pm 6.1	0.5 \pm 1.2	5.8 \pm 5.7
<i>Clio pyramidata</i>	—	1.2 \pm 0.9	0.1 \pm 0.2	0.1 \pm 0.3	0.5 \pm 0.5	—	1.8 \pm 1.8	<0.1	0.2 \pm 0.6	0.5 \pm 0.8
<i>Octopus</i> sp.	—	—	0.3 \pm 0.5	0.1 \pm 0.2	0.2 \pm 0.3	—	—	22.8 \pm 38.4	8.9 \pm 21.7	22.1 \pm 29.0
Cranchiidae	—	—	<0.1	<0.1	<0.1	—	—	1.4 \pm 3.6	0.2 \pm 0.8	1.9 \pm 4.5
Teuthida larvae	0.2	—	<0.1	—	<0.1	3.1	—	0.1 \pm 0.4	—	0.1 \pm 0.3
<i>Vanadis longissima</i>	—	<0.1	—	<0.1	<0.1	—	2.0 \pm 3.4	—	1.4 \pm 3.2	3.4 \pm 5.6
<i>Salpa thompsoni</i>	2.3	1.1 \pm 1.3	2.3 \pm 3.8	0.2 \pm 0.4	1.5 \pm 1.6	28.0	43.6 \pm 44.4	23.6 \pm 49.0	11.2 \pm 19.6	31.8 \pm 59.9
<i>Iasis zonaria</i>	—	<0.1	—	—	—	—	13.4 \pm 23.2	—	—	—
Tunica	0.2	—	—	<0.1	<0.1	2.0	—	—	0.6 \pm 2.0	2.1 \pm 3.3
<i>Sagitta gazellae</i>	7.6	34.0 \pm 11.1	21.9 \pm 6.9	11.8 \pm 7.5	27.6 \pm 10.6	30.3	329 \pm 107	149 \pm 83.1	85.3 \pm 59.1	193 \pm 77.8
<i>S. maxima</i>	—	5.6 \pm 2.6	4.3 \pm 5.5	0.8 \pm 0.9	3.5 \pm 1.8	—	3.6 \pm 0.7	4.1 \pm 4.6	0.3 \pm 0.4	1.9 \pm 0.9
<i>Eukrohnia hamata</i>	—	10.1 \pm 3.3	9.8 \pm 6.1	2.6 \pm 2.9	5.4 \pm 1.8	—	2.1 \pm 0.5	2.4 \pm 1.7	0.5 \pm 0.6	1.2 \pm 0.4
<i>Melophysa melo</i>	2.1	0.1 \pm 0.2	4.6 \pm 4.1	0.5 \pm 0.6	1.6 \pm 2.6	2.9	8.2 \pm 14.4	76 \pm 79	3.3 \pm 6.7	14.3 \pm 19.3
<i>Vogtia kuruae</i>	—	—	0.2 \pm 0.4	—	—	—	—	0.7 \pm 1.7	—	—
<i>Dimophyes arctica</i>	—	—	0.2 \pm 0.3	—	—	—	—	<0.1	—	—
<i>Zanclea costata</i>	—	—	0.1 \pm 0.3	—	—	—	—	<0.1	—	—
<i>Pegantha</i> sp.	1.2	<0.1	0.1 \pm 0.2	0.2 \pm 0.4	0.3 \pm 0.4	11.0	1.5 \pm 2.5	1.7 \pm 2.2	3.3 \pm 6.4	2.5 \pm 3.6
Hydromedusae	—	0.2 \pm 0.2	0.1 \pm 0.1	—	<0.1	—	11.3 \pm 11.6	8.3 \pm 13.5	—	7.5 \pm 13.5
<i>Beroe cucumis</i>	—	0.3 \pm 0.2	<0.1	<0.1	0.1 \pm 0.1	—	27.6 \pm 16.9	2.8 \pm 7.1	4.3 \pm 7.3	15.7 \pm 20.9
<i>Lepidonotothen larseni</i>	—	—	<0.1	—	<0.1	—	—	1.0 \pm 2.2	—	2.2 \pm 7.2
<i>Krefflichthys anderssoni</i>	0.4	—	<0.1	—	<0.1	12.3	—	0.7 \pm 2.3	—	0.4 \pm 1.3
<i>Electrona</i> sp. larvae	—	—	<0.1	—	—	—	—	0.2 \pm 0.8	—	—
Myctophid larvae	0.7	0.5 \pm 0.4	0.3 \pm 0.2	0.5 \pm 0.5	1.3 \pm 1.3	5.3	3.7 \pm 3.8	12. \pm 1.8	4.0 \pm 5.3	12.0 \pm 13.4
Total density	86.2	77.5 \pm 21.7	89.5 \pm 31.2	27.4 \pm 20.9	56.4 \pm 13.9	1903.1	628 \pm 129	651 \pm 239	208 \pm 172	383 \pm 142

taxa diversity was the highest (31–35 taxa) during the TR1 and TR3 surveys. The lowest number of taxa (17) was encountered at the offshore station, while during the TR0 and TR2 surveys intermediate diversities, e.g. 21–25 taxa, were found (Table 1). The majority of macroplankton and micronekton were represented by the subantarctic and Antarctic species widely distributed throughout the Southern Ocean (Table 1). There were, however, a number of species of subtropical origin, including the salp *Iasis zonaria*, the hyperiids *Chuneola paradoxa*, *Phronima sedentaria* and *P. atlantica*, the euphausiids *Thysanoessa gregaria* and *Stylocheiron longicorne*, the siphonophore *Vogtia kuruae* and the jellyfish *Zanclea costata* (Table 1). Only a single Antarctic species proper, the euphausiid *Thysanoessa macrura*, was encountered during TR1 at the core of the eddy-like feature (Table 1).

The hierarchical cluster and ordination analyses revealed the presence of the three groupings of stations (Fig. 4). The first group consisted of the station that was occupied in the offshore region. The second group comprised seven daytime stations conducted during the TR2 survey. Finally, the third group was composed of all other stations occupied during surveys TR0, TR1 and TR3, as well as nighttime stations of the TR2 survey (Fig. 4). A one-way ANOVA similarity test showed significant differences between the communities found at the offshore station and all trench surveys (TR0 to TR3, $P < 0.01$ in all cases). The euphausiid, *Euphausia longirostris*, which was virtually absent between the islands, accounted for more than 50% of the dissimilarity

between the groupings between the offshore and inshore regions. The zooplankton community identified during the TR2 survey was also significantly different from these found during the TR1 and TR3 surveys ($P < 0.05$). This, however, was largely associated with the differences in average densities of the most abundant species (Table 1). Indeed, the SIMPER analysis showed that the average dissimilarity was the highest (73–78%) between the offshore and inshore groupings of stations, while it ranged from 33 to 65% (mean $51 \pm 12\%$) between the inshore groupings of stations. During all inshore surveys, a similar community was observed. Here, *E. vallentini*, *Sagitta gazellae* and *Eukrohnia hamata* were responsible for >78% of the average similarity between stations.

Average plankton densities, calculated during different surveys, are presented in Fig. 5. The highest average abundance levels (76–90 ind. 1000 m^{-3}) were found at the offshore station and during the TR0 and TR1 surveys. The lowest average abundance [27 ind. 1000 m^{-3} , significantly different ($P < 0.05$) from TR0 and TR1 surveys only] was calculated for the TR2 survey (Table 1, Fig. 5A). Similarly, the average macroplankton biomass was found to be the lowest (208 mgDW 1000 m^{-3}) during the TR2 survey. Except for TR2, mean biomass levels during TR0, TR1 and TR3 were not significantly different from one another ($P > 0.05$, Fig. 5B, Table 1), ranging from 383 to 650 mgDW 1000 m^{-3} . The offshore station had a significantly higher total biomass (1903 mgDW 1000 m^{-3}) compared with inshore surveys (Table 1, Fig. 5B).

Throughout the investigation, euphausiids and chaetognaths dominated macroplankton samples, accounting for almost 90% of total abundance and 65–95% of total zooplankton stock. At the offshore station, euphausiids (mainly *Euphausia longirostris*) were the predominant group, contributing up to 80% to total abundance and 95% of the total biomass (Fig. 5). Chaetognaths' contribution did not exceed 10% by abundance and 2% by biomass. In contrast, in the samples collected during all the inshore surveys, with the exception of the TR1 survey, chaetognaths dominated zooplankton stock, composing 55–73% and 41–60% of total zooplankton abundance and standing stock, respectively (Table 1, Fig. 5). Euphausiids, mostly *Euphausia vallentini* and *Nematoscelis megalops*, were the second most important group of zooplankton, accounting for 13–30% of total zooplankton densities. During TR1, the euphausiids' contribution to both total abundance and biomass was slightly higher than chaetognaths' contribution (Table 1, Fig. 5). Throughout the surveys, gelatinous zooplankton (range 1–12% of both abundance and biomass), hyperiids (<1–10%) and salps (<1–9%) were identified as the third, fourth and fifth most important groups (Table 1, Fig. 5).

Average biomass of the most important taxonomic groups of macroplankton and micronekton demonstrated extreme short-term variations throughout the course of the investigation (Fig. 6). However, the

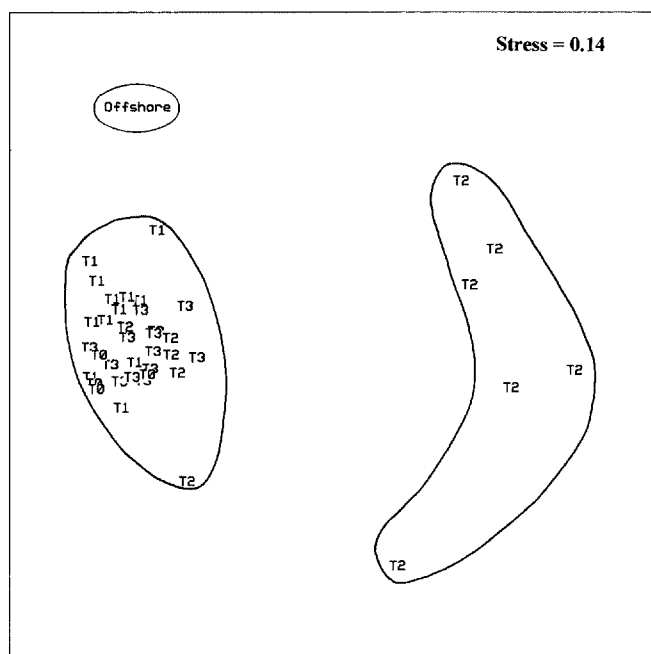


Fig. 4 Results of ordination analysis of the zooplankton community structure during the inshore and offshore surveys conducted in April/May 1998 between the Prince Edward Islands (T0 TR0 stations; T1 TR1 stations; T2 TR2 stations; T3 TR3 stations)

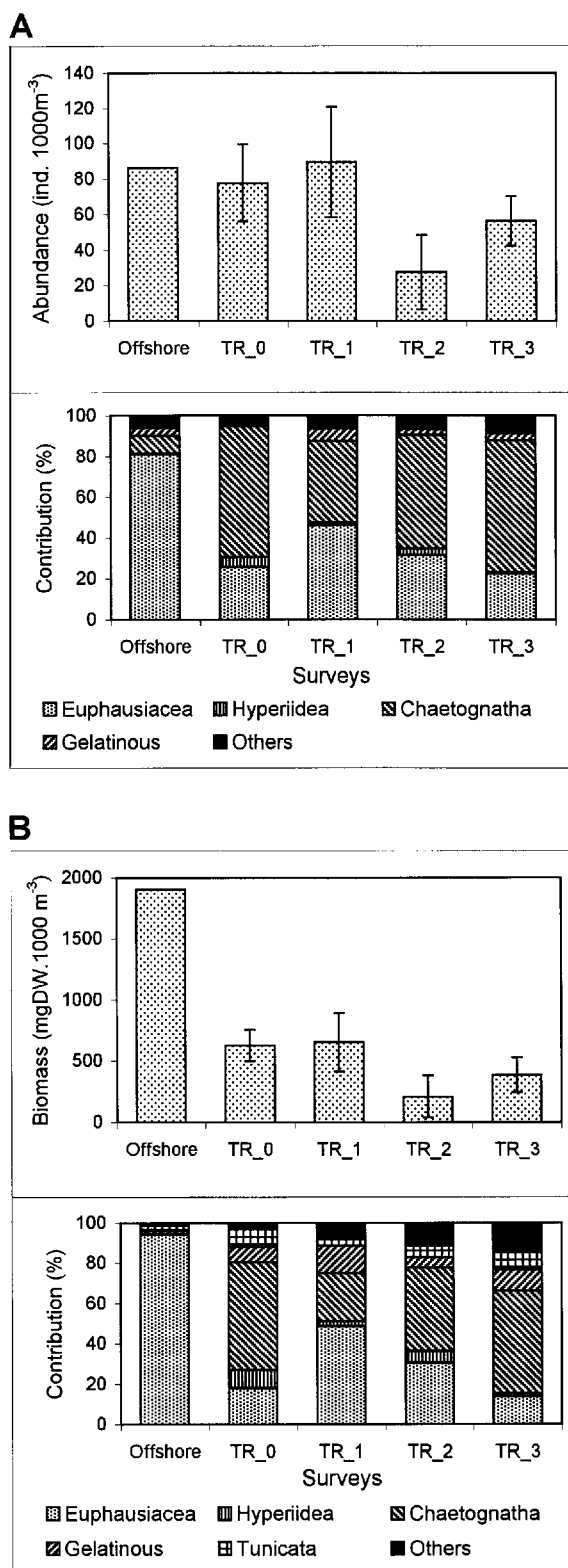


Fig. 5 Average total and percentage distribution of macroplankton/micronekton abundance (A) and biomass (B) during different surveys conducted in April/May 1998 between the Prince Edward Islands. Bars show one standard deviation

differences between both average abundance and biomass among all surveys were not significant ($P > 0.5$).

Plankton distribution

The spatial distribution of macroplankton/micronekton densities showed different patterns during TR1 to TR3 surveys (Fig. 7). During TR1, the highest plankton densities (both abundance and biomass) corresponded to the station occupied at the northern periphery of the cold eddy-like feature and at the southwestern corner of the survey (Fig. 7A). The lowest plankton densities were encountered over the southern central and eastern parts of the survey in association with the warmer ($> 5^{\circ}\text{C}$) waters (Figs. 3A, 7A). During TR2, the lowest zooplankton densities coincided with the cold water intrusion observed between the islands (Figs. 3B, 7B). During the TR3 survey, a gradual north-south increase in plankton densities was observed (Fig. 7C). The intrusion of colder waters separated low and high densities of zooplankton found north and south of the trench, respectively (Figs. 3C, 7C). Overall, the spatial distribution of zooplankton densities showed reasonable consistency with the small-scale oceanographic features recorded between the islands (Figs. 3, 7).

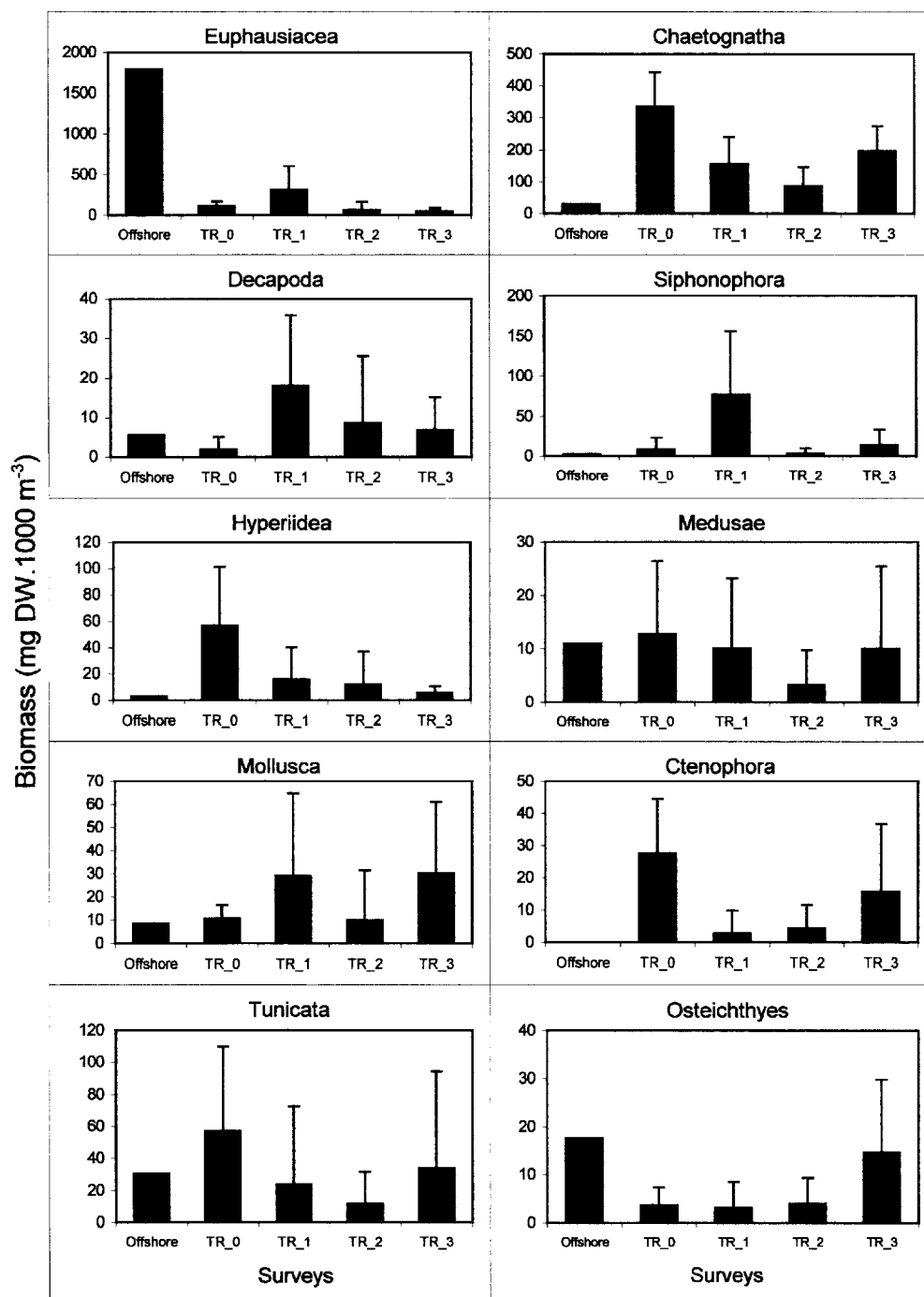
No significant correlations were found between temperature/salinity and abundance/biomass values for each trench survey. ($P > 0.05$ in all cases). However, pooled data produced several significant ($P < 0.05$) negative correlations between zooplankton densities and water temperature at 150 m depth and salinity at the surface (Table 2).

Discussion

Temperature sections obtained during this study using XBT probes clearly demonstrated the short-term variability in the position of the SAF (Fig. 2). During the period of 5 weeks the front, initially recorded at $\sim 45^{\circ}15'\text{S}$, shifted ~ 30 min of latitude to the south. Such fluctuations are consistent with previous observations in the vicinity of the islands (Nagata et al. 1988; Duncombe Rae 1989a; Lutjeharms 1990). It is documented that the position of the SAF relative to the island plateau influences oceanological conditions around and between the islands (Perissinotto and Duncombe Rae 1990; Ansorge et al. 1999; Froneman et al. 1999; Pakhomov and Froneman 1999b). Therefore, during the TR1 survey, when the SAF was located in its northernmost position relative to the island plateau, the trapping of water in the inter-island region may have occurred due to the reduced flow intensity in the vicinity of the islands (Perissinotto and Duncombe Rae 1990). Duncombe Rae (1989b) suggested that an eddy-like feature may be "constrained to the inter-island channel".

It is documented that the prolonged water trapping between the islands is generally associated with elevated phytoplankton concentrations and primary production rates (Perissinotto and Duncombe Rae 1990). As no enhancements in primary production or chlorophyll

Fig. 6 Total biomass of major taxonomic groups of macroplankton/micronekton during different surveys conducted in April/May 1998 between the Prince Edward Islands. Bars show one standard deviation



concentration were observed during the study (M. Balarin, unpublished data), it is likely that a parcel of colder, more saline water was moving through the inter-island region during the TR1 survey rather than water being trapped. During the TR2 and TR3 surveys, the SAF had shifted considerably southwards. According to the hypothesis of Perissinotto and Duncombe Rae (1990), under these conditions advective forces would dominate between the islands preventing the retention of water in the inter-island region. Distributional patterns of physical parameters during the TR2 and TR3 surveys

demonstrated consistency with the above hypothesis. It is apparent that, during the present study, the SAF was located too close to the island plateau to induce the proper water trapping between the islands.

While the exact origin of water parcels sampled during different trench surveys is unclear, their physical properties are characteristic of APFZ waters. Duncombe Rae (1989a) showed that the formation of the Antarctic Intermediate Water originating from the APF develops northwards across the APFZ. Waters in the southern part of the APFZ are, therefore, more

Fig. 7 Abundance and biomass distributions during each trench survey (A–C TR1 to TR3) conducted in April 1998 between the Prince Edward Islands

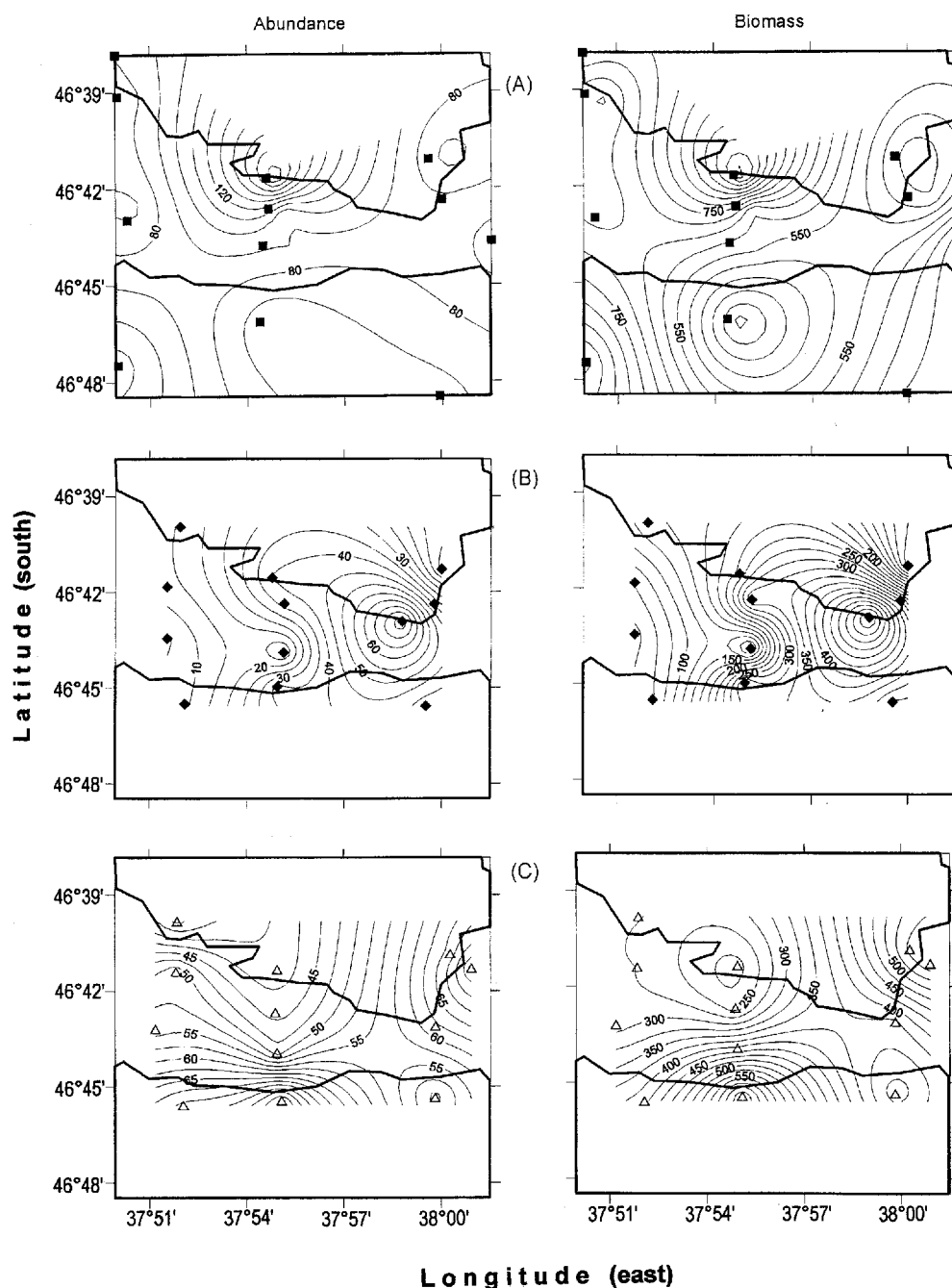


Table 2 Significant ($P < 0.05$) pairwise correlations between log-transformed zooplankton densities (abundance as ind. 1000 m^{-3} and biomass as mgDW 1000 m^{-3}) and environmental parameters

Pair of variables	Valid number	R^2
Abundance and temperature at 150 m	33	-0.48
Biomass and temperature at 150 m	33	-0.41
Abundance and surface salinity	35	-0.48
Biomass and surface salinity	35	-0.51

characteristic of Antarctic waters (Ansorge et al. 1999). As the southern boundary of the APFZ, the APF, is spatially stable (Sievers and Emery 1978; Nagata et al.

1988; Belkin and Gordon 1996), it is not unreasonable to suggest that the position of the SAF could also have a direct influence on the modification of the waters in the trench. On occasions when the SAF is situated far to the north, the APFZ broadens considerably. As a consequence, during the TR1 survey, waters encountered between the islands could be advected from the southern part of the APFZ. Indeed during the survey, the Antarctic euphausiid, *T. macrura*, was identified in samples collected in the trench. In contrast, during the TR2 and TR3 surveys, the waters encountered across the trench were more influenced by the Subantarctic Surface Waters, which may be linked to the presence of the SAF

close to the island plateau. No Antarctic species were found during these surveys, while subantarctic and some subtropical species were well represented.

It is evident that during the present study short-term episodic events occurred between the islands. Similar short-term dynamics in water pulsing has also been demonstrated at the Antarctic Ob and Lena seamounts (Lanin 1985; Pakhomov and Semelkina 1995). Here, Taylor Columns ("hydrodynamic traps" after Lanin 1985) were established and removed from the seamount summit on the synoptic scale, which was closely correlated to the wind stress and current speeds in the vicinity of the seamounts (Lanin 1985). A good consistency between proposed pulses of water and the position of the SAF in the northern proximity of the Prince Edward Islands should also be noted (Pakhomov and Froneman 1999a; this study). Although it is obvious that water parcels with different physical characteristics were observed during the TR1 to TR3 surveys, numerical analyses of zooplankton data did not identify different plankton assemblages during the surveys. This is most likely the result of limited number of samples collected and an enormous inter-sample variability in zooplankton densities. Alternatively, the lack of distinct groupings may indicate the extreme dynamic processes that occur in the region of the islands, resulting in a well-mixed plankton community (Ansorge et al. 1999; Froneman et al. 1999).

Colder waters appeared to be more productive in terms of macroplankton/micronekton standing stock. Seawater temperature and salinity accounted for >40% of the variation in the zooplankton distribution between the islands, providing indirect evidence for close association of zooplankton assemblages with water masses/parcels of different origin. This is in accordance with the most recent studies on mesozooplankton conducted in the vicinity of the Prince Edward Islands (Hunt 2000). During years when the SAF is found in close proximity to the islands, water temperature and salinity accounted for as much as 70% of zooplankton variability, suggesting close coincidence of physical and biological heterogeneity through the increased mesoscale variability. Alternatively, during years when the SAF only slightly interacted with the island plateau, physics explained only <30% of the variation in zooplankton distribution, reflecting homogeneity in environmental and biological parameters (Hunt 2000).

Due to the similarity in the processes operating around oceanic islands and seamounts, it is important to understand the biological consequences of short-term events for the Prince Edward Archipelago inter-island ecosystem (Genin and Boehlert 1985; Boehlert and Genin 1987; Genin et al. 1988, 1994; Darnitski 1991; Dower and Mackas 1996; Mullineaux and Mills 1997). Recent studies conducted around the islands (Pakhomov and Froneman 1999b) have demonstrated that, in contrast with the seamount scenario (Isaacs and Schwartzlose 1965; Kashkin 1984; Tseitlin 1985; Genin et al. 1988; Pakhomov 1993), macrozooplankton and

micronekton stocks are not transported over the inter-island region as suggested by Perissinotto and McQuaid (1992). Indeed, during the present study the macrozooplankton community identified within the inter-island region was significantly different from the offshore community. Also, while there was little evidence for quantitative differences in macroplankton densities between the inshore surveys, offshore zooplankton biomass was at least three- to eightfold higher than during the trench surveys. The biological consequences of water pulses, with regard to the amount of large plankton transported over the inter-island saddle, appeared therefore to be negligible. This cannot be attributed to predation or/and net avoidance as samples were taken largely during the nighttime.

A few other findings of the present study that are of importance should be mentioned. Firstly, numerous juveniles of the bottom-dwelling shrimp *Nauticaris marionis* were sampled for the first time at the offshore region. Although this is hardly surprising, it provides conclusive evidence that waters from the inter-island region were swept downstream. Secondly, although zooplankton distribution was extremely patchy, elevated densities of plankton were often associated with the shallow shelf regions rather than with the trench. This could be possible through the differences in the water retention over the shelf and trench regions, similar to that observed around South Georgia and the Kerguelen Archipelago (Atkinson and Peck 1990; Pakhomov 1995) or through the combination of high allochthonous mesozooplankton stock input with low predation by selected birds, and local benthic and fish communities (Pakhomov and Froneman 1999a).

In conclusion, results of the present study demonstrated the occurrence of pronounced water pulses through the inter-island region of the Prince Edward Islands. The location of the SAF to the north of the island plateau appears to determine water dynamics (trapping or retention) on different time scales in the trench between the islands. However, even during the flow-through scenario, some degree of water retention over the shallow part of the island's shelf may occur. The biological consequences of water pulses observed within the inter-island trench with regard to the food supply to top predators appear to be minimal at least during the time when the present investigation took place. The frequency of water pulses and their importance as potential carriers of macroplankton and nekton stocks over the inter-island saddle, as well as the effect of the SAF on the inter-island environment, should be further investigated, particularly including a temporal aspect of these events.

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