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## Short-term variation and long-term changes in the oceanographic environment and zooplankton community in the vicinity of a sub-Antarctic archipelago

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**Abstract** Mesozooplankton community structure in the vicinity of the Prince Edward Islands (PEIs) was investigated during six surveys conducted in late austral summer (April/May) from 1996 to 1999. Zooplankton samples were collected by oblique tows using a Bongo net fitted with 300- $\mu\text{m}$  mesh. Surface temperature, average temperature and chlorophyll *a* were measured in conjunction with each net tow. The positions of the Sub-Antarctic Front (SAF) and the Antarctic Polar Front (APF), in relation to the islands, were determined by CTD and/or XBT transects to the west of the islands (upstream). Both fronts were characterized by a high degree of latitudinal variation. Changes in position of the fronts occurred rapidly, the SAF moving up to  $\sim 120$  km in a 2-week period. Consequently, the oceanographic environment in the vicinity of the PEIs was subject to a high degree of intra- and inter-survey variation. The positions of the SAF and APF appeared to have a significant impact on phytoplankton biomass in the vicinity of the PEIs, possibly through the alteration of local oceanographic flow dynamics. Water retention over the island shelf in 1996, associated with location of the SAF far to the north of the PEIs, corresponded to enhanced chlorophyll-*a* concentrations ( $\sim 1.54$  mg  $\text{m}^{-3}$ ). Conversely, when the fronts were close to the islands, as in 1997 and 1999, higher current velocity limited water retention and chlorophyll-*a* concentrations in the inter-island region were relatively low ( $\sim 0.4$  mg  $\text{m}^{-3}$ ). Cluster analyses showed that, in many instances, there was greater similarity among zooplankton communities from different surveys than among communities within surveys, indicating that short-term variability exceeded in-

ter-annual variability. The population structure of the copepod *Calanus simillimus* indicated that there was inter-annual variation in the timing of the biological season. Differences in the population structure of species, and consequently their contribution to abundance and biomass, may therefore have been an important contributor to inter-annual variation in community structure. Evidence is provided of a long-term southward shift in the position of the SAF. It is postulated that this may affect the PEIs by increasing the proportion of allochthonous energy input, because the PEIs now lie in the path of the front, altering the trophodynamics of the island ecosystem. Lower mesozooplankton biomass associated with warmer sub-Antarctic water may have important negative consequences for higher trophic levels that depend on mesozooplankton for food.

### Introduction

The sub-Antarctic Prince Edward Island archipelago, comprising Marion Island and Prince Edward Island, is located in the Indian Ocean sector of the Southern Ocean at approximately 46°50'S and 37°50'E (Fig. 1). The islands lie directly in the path of the easterly flowing Antarctic Circumpolar Current (ACC). More specifically, they are located in the Antarctic Polar Frontal Zone (APFZ). The APFZ, bounded to the south by the Antarctic Polar Front (APF) and to the north by the Sub-Antarctic Front (SAF) (Lutjeharms and Vallentine 1984), is the region of transition between Antarctic and sub-Antarctic waters (Deacon 1983; Lutjeharms 1985). The SAF and APF have steep physical gradients (Emery 1977; Lutjeharms 1985; Nowlin and Klinck 1986) which represent important biogeographic boundaries (Backus 1985; Boden et al. 1988; Pakhomov et al. 1994; Tarling et al. 1995) and are often regions of enhanced biological productivity (Lutjeharms et al. 1985; Laubscher et al. 1993). Consequently, meridional fluctuations in the positions of the SAF and APF have important implications

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for the island systems with which they come into contact; e.g. Kerguelen, South Georgia and the Prince Edward Islands (Lutjeharms and Vallentine 1984; Nagata et al. 1988). Changes in the positions of the fronts alter the physical conditions and the zooplankton dynamics (Priddle et al. 1988; Pakhomov 1995; Ansorge et al. 1999; Froneman et al. 1999).

The interaction of currents with oceanic islands is dependent upon the velocity of the approaching current (Coutis and Middleton 1999; Perissinotto et al. 2000). For example, it has been suggested that during periods of low current velocity, frictional forces result in water retention over the Prince Edward Island (PEI) shelf (Perissinotto and Duncombe Rae 1990). Conversely, during periods of high current velocity, advective forces prevail, resulting in the flow of water over the shelf and eddy shedding into the downstream region (Allanson et al. 1985; Perissinotto et al. 2000; Ansorge and Lutjeharms, submitted). Since the SAF and APF are regions of enhanced current flow (Hofmann 1985; Nowlin and Klinck 1986), variability in the position of these fronts is expected to contribute to short-term hydrodynamic variability in the vicinity of sub-Antarctic islands. Hydrodynamics affect ecosystem functioning and are of particular importance to changes in the contribution of allochthonous and autochthonous production (Perissinotto et al. 1990; Perissinotto and McQuaid 1992).

Since 1951, average air temperature at Marion Island has increased by almost 1 °C. This corresponded to a similar increase in average sea-surface temperature (Smith and Steenkamp 1990), suggesting that the SAF may have moved southwards. This is supported by biotic changes observed at the PEIs since 1976 (Pakhomov et al. 2000b). Long-term studies in the Benguela upwelling region and the northern hemisphere have

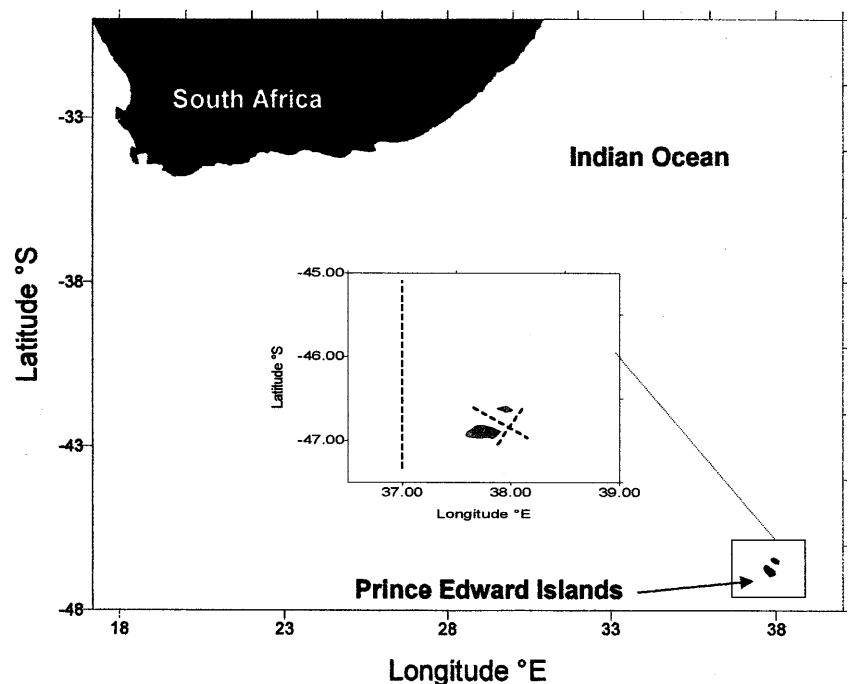
revealed decadal changes in zooplankton dynamics associated with long-term climatic changes (Roemmich and McGowan 1995; Verheye and Richardson 1998; Verheye et al. 1998; Mackas and Tsuda 1999). However, only a few long-term studies have been conducted in the sub-Antarctic region of the Southern Ocean (e.g. Razouls et al. 1998).

Data collected during the Marion Island Oceanographic Survey (MIOS), conducted in the vicinity of the PEI archipelago between 1996 and 1999, provided us with the opportunity to investigate short-term and inter-annual variation in zooplankton community structure and the physical environment. A detailed description of the individual MIOS cruises and the spatial distribution patterns of zooplankton in relation to the physical environment are presented elsewhere (Hunt et al., submitted). In this paper we investigate temporal variation (short-term and inter-annual) in zooplankton community structure. Furthermore, the MIOS data, in combination with data collected since 1976, were used to investigate long-term environmental changes and their possible ecological impacts.

## Materials and methods

Data were collected in late austral summer (April/May) during four cruises conducted between 1996 and 1999 in the vicinity of the PEIs. All cruises formed part of the MIOS programme, undertaken aboard the M.V. "SA Agulhas". Since the ACC flows west to east we refer to regions as being upstream (west) and downstream (east) of the islands. A repeat survey comprising a line of stations in the region upstream of the islands, as well as two transects over the island shelf (< 300 m deep) and downstream, were conducted each year (Fig. 1). In addition, secondary surveys of slightly different design were conducted in 1997 and 1999, also sampling the

**Fig. 1** Map illustrating the position of the Prince Edward Islands (PEI) in relation to South Africa. The *inset* illustrates transects along which nets were deployed during the annual repeat survey



upstream, inter-island and downstream regions. The number of stations conducted during each survey is given in Tables 1 and 2. The positions of the sampling stations conducted during each survey are presented in Hunt et al. (submitted).

An oceanographic survey was conducted corresponding to each zooplankton survey in order to locate the positions of the SAF and the APF. The APF was defined by the position of the 2 °C isotherm at 200-m depth (Lutjeharms and Emery 1984), and the SAF by the position of the 7 °C isotherm at 100-m depth (Nagata et al. 1988). Vertical temperature profiles were obtained using either a CTD (conductivity-temperature-depth) probe fitted with a Neil Brown Instrument system Mark 3B underwater unit, or Sippican T7 XBT (expendable bathythermograph) probes. The CTD was laboratory-calibrated before and after each cruise. Pressure was calibrated against a Budenberg Dead Weight Tester, and temperature was calibrated against a Hewlett Packard 1804A quartz thermometer. Prior to deployment, XBT's were calibrated against sea-surface temperature with a Crawford bucket (Crawford 1972). Oceanographic stations generally corresponded to net tows.

All net tows used in the analysis presented in this paper were conducted at night (between 7 p.m. and 7 a.m.). Mesozooplankton samples were collected using a Bongo net with a mouth area of 0.25 m<sup>2</sup> and a mesh size of 300 µm. This mesh size may under-sample smaller zooplankton species; however, this bias would have been consistent through all the surveys. The net was fitted with a Universal Underwater Unit (U<sup>3</sup>) which monitored temperature and depth continuously during each tow (Robertson et al. 1981). Towing speed varied between 1.5 and 2.5 knots and the net was towed obliquely between 300 m and the surface, or between the bottom and the surface over the island shelf. During 1998 all night tows were made to a maximum depth of 200 m. The volume of water filtered during each tow was calculated from data collected by an electronic flowmeter. Surface temperature and chlorophyll-*a* concentration were measured in conjunction with each net tow and the continuous temperature measurements recorded by the U<sup>3</sup> were used to obtain an integrated water temperature averaged over the water column for the duration of each tow. Samples were fixed in 4–6% buffered formalin. The abundance of all mesozooplankton species was determined from sub-samples, obtained using a Folsom plankton splitter, ranging between 1/2 and 1/32 aliquots of the total, depending on sample size. All sub-samples contained 200–500 animals. The entire sample was analysed for low-abundance species not encountered in sub-samples, including some large (>20 mm) species and some rare species. Abundance was expressed as number of individuals per cubic metre (ind m<sup>-3</sup>). The dry weight of all species was measured to the nearest microgram, after being oven-dried at 60 °C for 36 h, using a Sartorius Micro MC1 electronic microbalance. Large individuals from the whole sample were wet weighed and subsequently converted to dry weights using regressions derived from Mizdalski (1988). Biomass data were expressed as mg dry weight m<sup>-3</sup>. No corrections were applied for loss of weight during preservation. For the copepod *Calanus simillimus*, different maturity stages, determined by length measurements and morphology, were enumerated and weighed separately. The different maturity stages were pooled for the statistical analysis.

#### Numerical analysis

One-way ANOVA was run on surface and average temperature, and chlorophyll-*a* values to investigate differences between surveys. Values were normalized by log<sub>10</sub>(*x*+1) transformation prior to analysis. Newman–Keuls multiple-range tests were used to identify differences between the six surveys (Zar 1984).

Zooplankton community structure was investigated using Plymouth Routines in Multivariate Ecological Research (PRIMER) (Clarke and Warwick 1994). Prior to analysis, all data were transformed using the function log<sub>10</sub>(*x*+1) to reduce the weighting of highly abundant species (Legendre and Legendre 1983). After transformation, cluster analysis (*q*-type) was used to group stations based on the Bray–Curtis similarity measure and complete linkage classification of abundance data (Field et al. 1982). The similarity of zooplankton communities within and among surveys was de-

termined using the similarity programme SIMPER (Clarke and Warwick 1994).

Inverse (*r*-type) cluster analysis was used to identify species associations. Species were grouped based on the Bray–Curtis similarity measure and complete linkage classification of their abundance levels. A sub-set of common dominant species was used in the analysis to avoid the random association of rare, low-abundance species (Field et al. 1982). For the purpose of this study the sub-set was defined as those species identified by the SIMPER analysis as responsible for 80% of the similarity within groups and 80% of the dissimilarity between groups. This placed most species within the selection criteria set by Field et al. (1982), and all species within the selection criteria used by Tarling et al. (1995). In an inverse analysis, perfectly correlated species, which always occur together but in different abundances, might be separated from one another because their abundance levels are not the same. To overcome this, the data used in the inverse analysis were not log-transformed but standardized (Field et al. 1982). This establishes the relative abundance of a species in any one net tow, enabling the similarity between species with different abundance levels to be determined. One-way ANOVA was run on abundance values, normalized by log<sub>10</sub>(*x*+1) transformation, to investigate differences in species abundance levels. Subsequently, Newman–Keuls multiple-range tests were used to identify differences in species abundance levels between the six surveys.

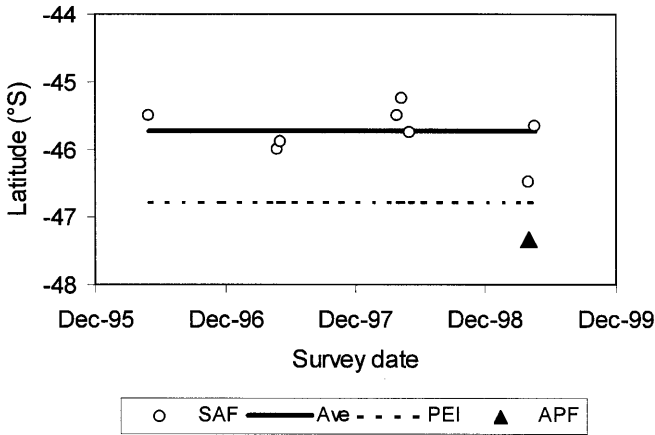
The similarity matrices produced by *q*-type cluster analysis were ordinated using non-metric multidimensional scaling (NMDS). The ordination scores, which summarized the zooplankton community in terms of the abundance data, were regressed against surface and average temperature to determine the effect of these physical variables on community structure (Hosie 1994).

Abundance data focus the analysis on small, high-abundance species, whereas biomass data put greater emphasis on large, low-abundance species which can make a large contribution to total biomass (Hopkins 1985; Rodhouse et al. 1994). Consequently biomass data focus the community-structure analysis on a different species set from that highlighted by abundance data. The methodology described above for the analysis of community structure based on abundance data was therefore also applied to biomass data.

## Results

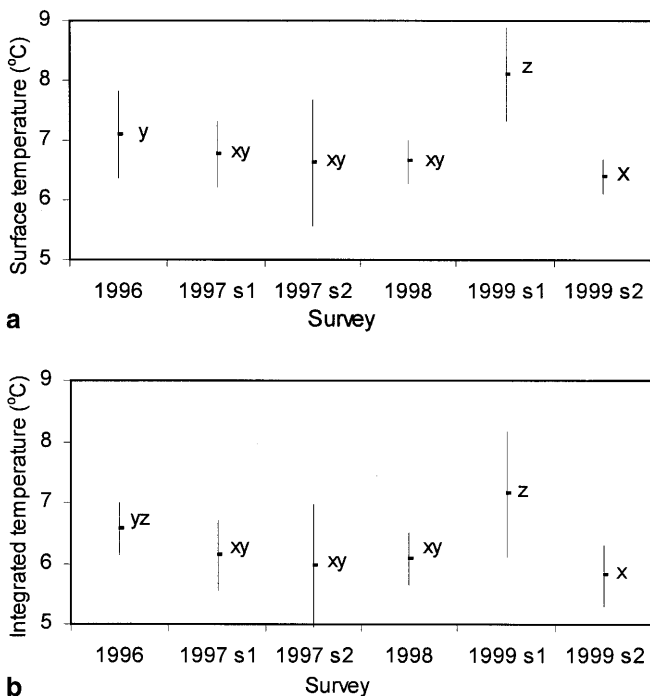
### Physical environment

The position of the SAF showed a high degree of variability between surveys both within and among years (Fig. 2). The positions given for 1998 is represent three crossings along the 37°E meridian. The SAF shifted 50 km north between 5 April and 17 April, and 20 km south between 17 April and 8 May (Pakhomov et al. 2000a). During survey 1 of 1999 the SAF was particularly close to the islands, but, upon completion of survey 2, it was located near its average position, having moved ~120 km northwards in just 2 weeks. During survey 2 of 1997, the steep thermal gradient along 37°E indicated that the APF was near to 48°S, although it was not crossed by the ship (Froneman et al. 1999). The APF was, however, encountered in the downstream region at 47°30'S and 42°E (Froneman et al. 1999). During survey 1 of 1999, the APF was located at 47°20'S along 37°E (Fig. 2). However, during survey 2 it was not crossed, despite sampling up to 48°S, indicating that the APF had moved >80 km since survey 1.



**Fig. 2** The position of the Sub-Antarctic Front (SAF) (indicated by O) along 37°E recorded during six surveys conducted between 1996 and 1999. The average position (*Ave*) of the SAF in the vicinity of the PEIs was determined from 11 crossings between 1987 and 1999. The latitude of the PEIs is indicated by the *dotted line*. The location of the Antarctic Polar Front during survey 1 of 1999 (along 37°E) is indicated by ▲

A one-way ANOVA showed that surface and average temperature differed significantly between surveys ( $P < 0.005$ ). Surface and integrated temperature were highest during survey 1 of 1999 and lowest during survey 2 of 1999 (Fig. 3a, b). The large drop in integrated temperature between surveys 1 and 2 of 1999 reflected



**Fig. 3** Average and standard deviation of surface (a) and integrated temperature (b) recorded for the six surveys conducted between 1996 and 1999. Significant differences ( $P < 0.05$ ) between surveys, determined by Newman-Keuls multiple-range *U*-tests of survey pairs, are indicated by different letters. Sharing of a letter indicates no significant difference

the northward movement of the SAF. There was no significant difference in surface or integrated temperature between surveys 1 and 2 of 1997, 1998 and survey 2 of 1999.

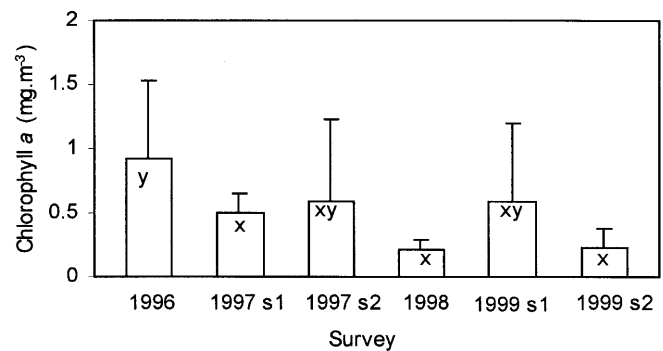
### Chlorophyll *a*

A one-way ANOVA showed that surface chlorophyll-*a* concentrations differed significantly between surveys ( $P < 0.001$ ), with the highest values being observed in 1996 (Fig. 4). During the 1996 survey, survey 2 of 1997 and survey 1 of 1999, chlorophyll-*a* concentrations at bloom levels were recorded at some stations. This was reflected in the high standard deviations recorded for chlorophyll-*a* concentrations during these surveys.

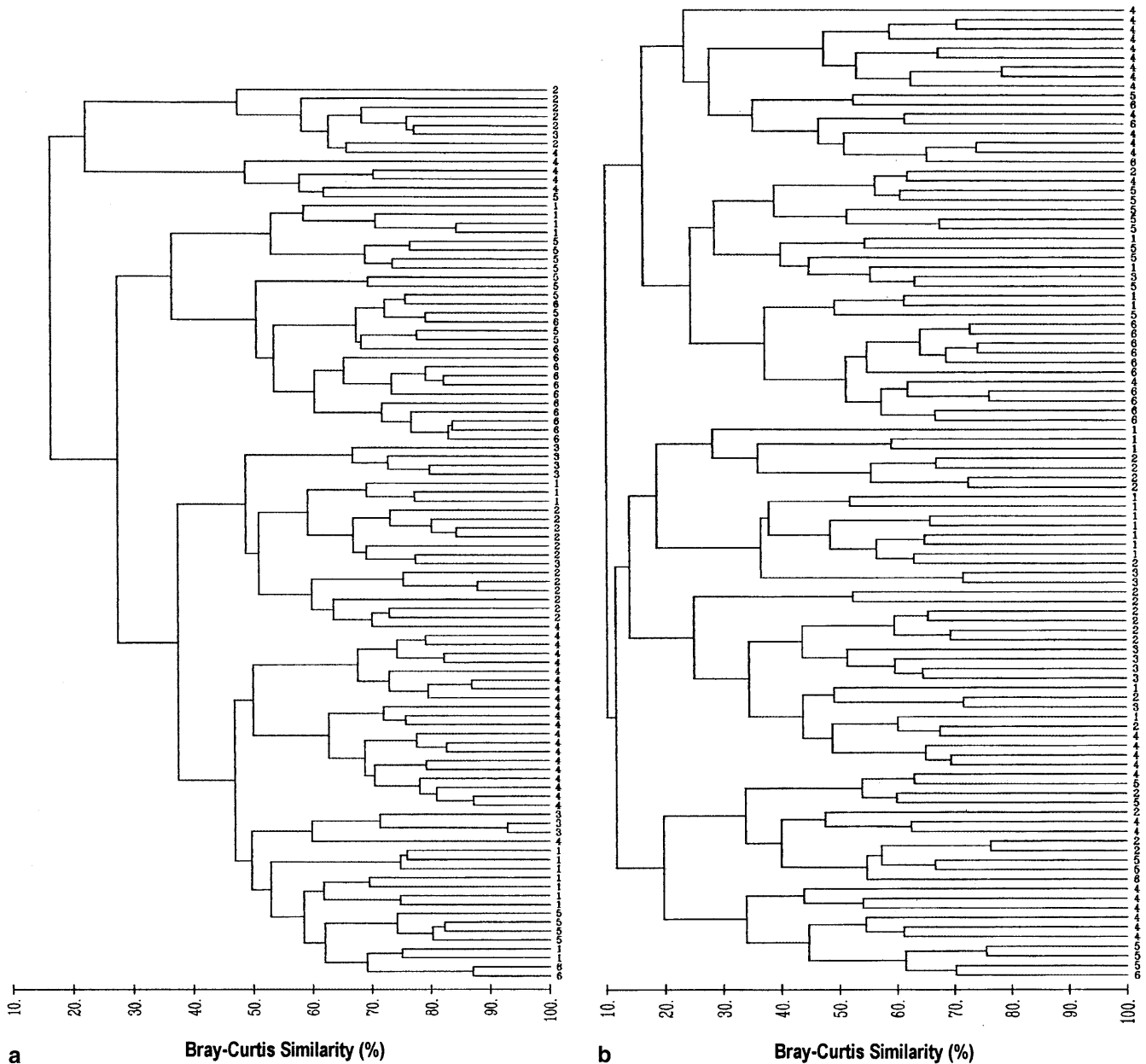
### Zooplankton

In the cluster analyses of abundance and of biomass data (Fig. 5a, b), stations from the six surveys did not form completely separate, survey-specific clusters. Some stations from the same survey did cluster together, but in most cases there was greater similarity between stations from different surveys. The biomass dendrogram was characterized by greater mixing of stations from different surveys than the abundance dendrogram, indicating a higher degree of within-survey heterogeneity in the biomass data.

SIMPER analysis identified a high degree of similarity in zooplankton community structure between stations within all surveys, exceeding 60% in all cases. The similarity between surveys was greater than 50% in all cases, and exceeded 60% between surveys 1 and 2 of 1997, and surveys 1 and 2 of 1999. Twenty-five and 28 species were responsible for 80% of the similarity within, and dissimilarity between, surveys in the abundance and biomass analyses, respectively (Tables 1, 2). The species clusters identified by inverse (*r*-type) analysis generally showed no specific survey associations (data are not



**Fig. 4** Average chlorophyll-*a* concentrations ( $\text{mg m}^{-3}$ ) and standard deviations recorded for the six surveys conducted between 1996 and 1999. Significant differences ( $P < 0.05$ ) between surveys, determined by Newman-Keuls multiple-range *U*-tests of survey pairs, are indicated by different letters. Sharing of a letter indicates no significant difference



**Fig. 5** **a** Dendrogram of the cluster analysis comparing zooplankton abundance data between surveys. The Bray-Curtis similarity index was used after  $\log_{10}(x+1)$  transformation of species abundance data. [1 1996, 2 survey 1 1997, 3 survey 2 1997, 4 1998, 5 survey 1 1999, 6 survey 2 1999] **b** Dendrogram of the cluster analysis comparing zooplankton biomass data between surveys. The Bray-Curtis similarity index was used after  $\log_{10}(x+1)$  transformation of species abundance data. [1 1996, 2 survey 1 1997, 3 survey 2 1997, 4 1998, 5 survey 1 1999, 6 survey 2 1999]

shown). However, cluster 1 of the abundance analysis (Fig. 5a) was dominated by species occurring at highest abundance during 1998. Cluster 5 of the abundance analysis and cluster 1 of the biomass analysis (Fig. 5b) contained species that occurred at significantly higher densities during 1996.

Total zooplankton abundance during all surveys was dominated by copepods (Fig. 6a; Table 3), this group

comprising 52–88% of the total. Copepods were particularly numerous in 1997, with abundance levels during survey 2 being significantly higher ( $P < 0.01$ ) than in any other survey. Pteropods, ostracods, euphausiids and chaetognaths also made relatively large contributions (2–20%) to total abundance (Table 3). Total zooplankton biomass was dominated by euphausiids and copepods during all surveys (Fig. 6b; Table 4), these two groups contributing up to 87% of total biomass. Euphausiid biomass was relatively low during 1996 and survey 2 of 1997, and was exceeded by copepod biomass. Pteropods, ostracods, hyperiids, chaetognaths and fish made relatively large contributions (1–18%) to total biomass (Table 4). There was no significant difference in total biomass between surveys, although values recorded in 1998 and 1999 were higher than those recorded in 1996 and 1997.

**Table 1** Average abundance (ind m<sup>-3</sup>) of species used in the inverse (*r*-type) analysis. Species clusters are indicated by shared numbers (\* indicates a species not part of a cluster). Significance levels, determined by one-way ANOVA, are indicated by *P*

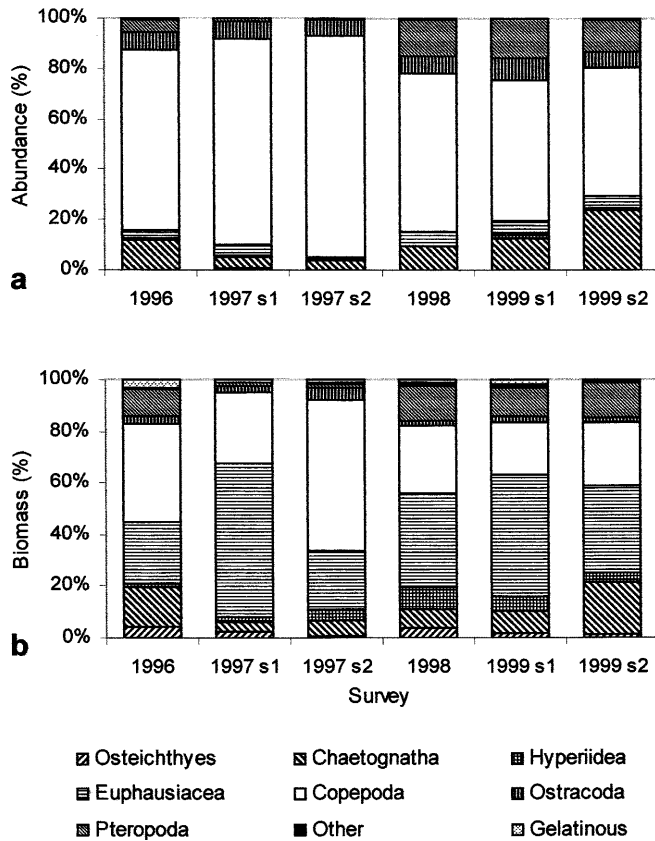
Cluster	Species	1996 (16)	1997-s1 (18)	1997-s2 (9)	1998 (27)	1999-s1 (15)	1999-s2 (15)	<i>F</i>	<i>P</i>
1	<i>Limacina helicina</i>	1.197	0.110	0.080	1.539	0.230	0.021	11.54	< 0.01
1	<i>Oithona similis</i>	0.321	0.116	0.000	<u>1.506</u>	0.012	0.120	10.98	< 0.01
1	<i>Ctenocalanus vanus</i>	0.089	<u>10.996</u>	<u>12.565</u>	<u>7.269</u>	0.009	0.000	48.97	< 0.001
2	<i>Rhincalanus gigas</i>	<u>0.949</u>	<u>0.051</u>	<u>1.742</u>	<u>0.108</u>	<u>1.411</u>	<u>0.964</u>	5.60	< 0.01
2	<i>Aetideus armatus</i>	<u>0.586</u>	0.117	<u>0.379</u>	0.196	<u>0.156</u>	<u>0.284</u>	3.26	< 0.01
3	<i>Oncaea antarctica</i>	<u>0.885</u>	0.236	0.259	0.177	<u>0.566</u>	<u>0.208</u>	3.31	< 0.01
3	<i>Heterorhabdus austrinus</i>	<u>0.437</u>	0.484	0.315	0.213	<u>0.306</u>	0.325	–	–
3	<i>Pleuromamma abdominalis</i>	3.565	1.256	3.370	0.875	0.982	0.427	3.09	< 0.01
*	<i>Paraeuchaeta biloba</i>	<u>0.060</u>	0.376	<u>2.561</u>	0.282	0.433	0.730	15.19	< 0.005
4	<i>Euphausia vallentini</i>	<u>0.191</u>	<u>0.579</u>	<u>0.125</u>	<u>0.592</u>	<u>0.432</u>	<u>0.676</u>	3.12	< 0.01
4	<i>Limacina retroversa</i>	<u>4.060</u>	<u>0.379</u>	0.906	<u>8.849</u>	<u>7.833</u>	<u>12.195</u>	14.05	< 0.01
4	<i>Calanus simillimus</i>	1.862	0.516	13.888	<u>12.06</u>	5.445	<u>19.359</u>	13.47	< 0.01
4	<i>Primno macropa</i>	<u>0.673</u>	0.430	0.419	0.024	<u>0.670</u>	<u>0.832</u>	22.13	< 0.005
4	<i>Clausocalanus laticeps</i>	1.120	0.729	2.746	1.477	<u>0.761</u>	1.118	–	–
4	<i>Scolecithricella minor</i>	1.883	1.221	2.871	1.860	0.776	1.334	–	–
4	<i>Sagitta gazellae</i>	3.858	0.596	0.763	1.423	1.595	1.836	19.80	< 0.005
4	<i>Eukrohnia hamata</i>	<u>8.752</u>	2.660	5.130	5.067	5.533	<u>21.016</u>	12.93	< 0.01
4	<i>Thysanoessa vicina</i>	2.949	<u>2.616</u>	0.842	<u>3.335</u>	<u>3.166</u>	<u>3.636</u>	3.96	< 0.01
4	<i>Oithona frigida</i>	5.529	5.001	<u>16.213</u>	2.224	0.876	3.056	9.93	< 0.01
4	<i>Metridia lucens</i>	15.753	11.188	<u>47.463</u>	3.940	11.398	5.057	11.35	< 0.01
4	<i>Clausocalanus brevipes</i>	<u>35.701</u>	<u>21.487</u>	<u>17.552</u>	10.952	9.743	7.554	5.76	< 0.01
4	Ostracods	<u>6.989</u>	<u>5.364</u>	<u>9.734</u>	5.336	4.995	6.133	–	–
5	<i>Metridia gerlachei</i>	<u>0.824</u>	0.000	0.000	0.002	0.000	0.000	7.16	< 0.01
5	<i>Euchaeta longiceps</i>	<u>0.556</u>	0.057	0.000	0.005	0.154	0.148	8.09	< 0.01
5	<i>Ctenocalanus citer</i>	<u>1.243</u>	0.000	0.000	0.000	0.000	0.000	26.43	< 0.001

(– indicates no significant difference). Significantly higher levels of abundance, identified by Newman–Keuls multiple-range tests, are underlined. Values in brackets represent number of stations for each survey

**Table 2** Average biomass (mg m<sup>-3</sup>) of species used in the inverse (*r*-type) analysis. Species clusters are indicated by shared numbers (\* indicates a species not part of a cluster). Significance levels, determined by one-way ANOVA, are indicated by

Cluster	Species	1996 (16)	1997-s1 (18)	1997-s2 (9)	1998 (27)	1999-s1 (15)	1999-s2 (15)	<i>F</i>	<i>P</i>
*	<i>Gymnoscopelus braueri</i>	0.002	0.140	0.035	0.024	0.000	0.008	–	–
*	<i>Limacina helicina</i>	0.539	0.005	0.001	0.018	0.007	0.002	–	–
1	<i>Clio pyramidata</i>	<u>0.138</u>	0.000	0.000	0.027	0.020	0.001	12.99	< 0.005
1	<i>Melophysa melo</i>	<u>0.145</u>	0.030	0.061	0.001	0.012	0.000	3.72	< 0.01
*	<i>Nauticaris marionis</i>	<u>0.000</u>	0.000	0.000	0.101	0.095	0.103	–	–
*	<i>Thysanoessa gregaria</i>	0.048	0.043	0.060	0.086	0.154	0.190	–	–
2	<i>Themisto gaudichaudii</i>	0.046	0.067	<u>0.317</u>	0.033	<u>0.411</u>	<u>0.291</u>	4.72	< 0.01
2	<i>Rhincalanus gigas</i>	<u>0.193</u>	0.004	<u>0.222</u>	0.015	<u>0.243</u>	<u>0.166</u>	4.57	< 0.01
3	<i>Euphausia similis</i>	<u>0.036</u>	0.048	0.000	0.227	<u>0.137</u>	<u>0.035</u>	–	–
3	<i>Calanus simillimus</i>	0.207	0.033	0.585	<u>1.583</u>	0.415	<u>1.462</u>	5.56	< 0.01
*	<i>Gymnoscopelus</i> spp	0.247	0.000	0.006	<u>0.029</u>	0.047	<u>0.031</u>	–	–
4	<i>Limacina retroversa</i>	0.103	0.059	0.084	<u>1.235</u>	<u>0.952</u>	<u>1.609</u>	11.61	< 0.005
4	<i>Primno macropa</i>	0.060	0.028	0.024	<u>0.856</u>	<u>0.036</u>	<u>0.110</u>	20.42	< 0.001
4	<i>Protomyctophum</i> spp	0.010	0.023	0.008	<u>0.151</u>	0.012	0.067	8.63	< 0.01
4	<i>Ctenocalanus vanus</i>	0.002	0.213	<u>0.251</u>	<u>0.141</u>	0.000	0.000	16.01	< 0.005
5	<i>Euphausia longirostris</i>	0.681	<u>0.231</u>	<u>0.674</u>	0.221	0.171	0.281	–	–
5	<i>Nematoscelis megalops</i>	0.026	<u>0.583</u>	<u>0.447</u>	<u>0.423</u>	<u>0.410</u>	0.445	2.53	< 0.05
5	<i>Paraeuchaeta biloba</i>	0.019	<u>0.120</u>	<u>0.763</u>	0.090	0.090	0.094	18.75	< 0.001
6	<i>Metridia lucens</i>	0.387	0.227	<u>0.668</u>	0.093	0.223	0.163	11.62	< 0.005
6	<i>Oithona frigida</i>	0.017	0.015	<u>0.057</u>	0.007	0.003	0.010	11.00	< 0.005
6	<i>Clausocalanus brevipes</i>	<u>0.712</u>	0.428	<u>0.331</u>	0.218	0.194	0.158	6.18	< 0.01
6	<i>Heterorhabdus austrinus</i>	<u>0.104</u>	0.115	0.065	0.051	0.037	0.041	–	–
6	<i>Pleuromamma abdominalis</i>	0.884	0.311	0.879	0.217	0.243	0.113	2.80	< 0.05
6	<i>Euphausia vallentini</i>	0.533	2.249	0.389	1.752	2.235	1.415	–	–
6	<i>Sagitta gazellae</i>	0.443	0.092	0.118	0.207	0.319	0.692	7.95	< 0.01
6	<i>Eukrohnia hamata</i>	0.775	0.170	0.371	0.553	0.457	<u>1.762</u>	14.20	< 0.005
6	<i>Thysanoessa vicina</i>	0.535	1.000	0.295	<u>1.046</u>	<u>0.961</u>	<u>1.583</u>	6.32	< 0.01
6	Ostracods	0.241	<u>0.185</u>	0.427	<u>0.184</u>	<u>0.172</u>	<u>0.217</u>	–	–

*P* (– indicates no significant difference). Significantly higher levels of biomass, identified by Newman–Keuls multiple-range tests, are underlined. Values in brackets represent number of stations for each survey



**Fig. 6** Percentage contribution of zooplankton groups to **a** total abundance and **b** total biomass recorded for the six surveys conducted between 1996 and 1999

### Sources of variation in community structure

Surface temperature accounted for a significant amount of variation in zooplankton community structure during all years of study (Table 5). Integrated temperature accounted for a significant amount of variation in com-

munity structure in terms of both abundance and biomass in 1999, and in terms of biomass in 1997. However, neither surface nor integrated temperature accounted for a significant amount of variation in zooplankton community structure in the combined analysis.

### Population structure of *Calanus simillimus*

*C. simillimus* was sampled at different stages in its seasonal cycle between 1996 and 1999. Atkinson (1991) proposed that the life cycle of *C. simillimus* could contain two generations per year, including a main spawning in spring and a second in April/May by the adults of the spring generation. Despite the 1996 and 1997 surveys being conducted 1–3 weeks later in the year they were characterized by the almost complete absence of stage 5 copepodites (C5) and adults (Fig. 7). This indicates that, in 1996 and 1997, sampling occurred relatively early in the phenological season, with 1997, dominated by C2, being the earliest. The 1999 surveys were conducted later in the season than in 1996, containing some adults and being dominated by C4, whereas the dominance of adults in 1998 indicated that this survey was conducted latest in the phenological season.

## Discussion

### Physical environment and phytoplankton response

The high degree of positional variability exhibited by the SAF and APF during this study agrees with previous investigations in the region of the PEIs (Lutjeharms and Vallentine 1984; Nagata et al. 1988). A significant feature of this variation was the high speed at which it occurred. Rapid variation in the width of the APFZ has

**Table 3** Abundance (ind  $m^{-3}$ ), with standard deviations (SD), of zooplankton groups for the six surveys between 1996 and 1999. One-way ANOVA was run on all data, normalized by  $\log_{10}(x+1)$  transformation, to determine whether species abundance levels

differed significantly between surveys. Significant differences are indicated by *P*. Significantly higher ( $P < 0.05$ ) levels of abundance identified by Newman-Keuls multiple-range tests, are underlined

Group	1996	SD	1997 s1	SD	1997 s2	SD	1998	SD	1999 s1	SD	1999 s2	SD	<i>F</i>	<i>P</i>
Hydromedusae	0.105	0.135	0.046	0.056	0.023	0.030	0.007	0.126	0.002	0.006	0.047	0.087	–	–
Siphonophora	0.192	0.169	0.109	0.085	0.164	0.142	0.185	0.257	0.085	0.150	0.271	0.257	–	–
Pteropoda	5.550	7.690	0.494	0.520	0.986	1.827	<u>10.506</u>	10.995	8.119	14.993	<u>12.793</u>	10.171	15.01	<0.005
Other	0.148	0.032	0.059	0.014	0.097	0.023	<u>0.105</u>	0.028	0.057	0.015	<u>0.102</u>	0.023	–	–
Ostracoda	6.989	3.742	5.364	2.883	9.734	7.833	5.336	4.834	4.995	4.453	6.310	4.475	–	–
Copepoda	75.752	51.104	59.082	41.588	<u>134.791</u>	69.381	45.844	60.919	37.039	21.129	47.726	17.990	6.1	<0.01
Decapoda	0.001	0.002	0.001	0.004	0.000	0.001	0.013	0.026	0.021	0.040	0.023	0.046	–	–
Euphausiacea	3.420	1.796	3.352	1.899	1.102	0.596	4.065	2.560	3.774	2.559	4.733	4.702	4.43	<0.01
Hyperideia	<u>0.820</u>	0.623	<u>0.483</u>	0.327	0.456	0.316	<u>0.189</u>	0.165	<u>0.927</u>	0.614	<u>1.091</u>	0.614	16.39	<0.01
Chaetognatha	<u>12.610</u>	7.771	3.256	2.377	5.893	3.683	6.490	5.408	7.128	5.380	<u>23.360</u>	10.870	15.81	<0.05
Tunicata	0.022	0.044	0.004	0.015	0.000	0.000	0.007	0.035	0.006	0.012	0.001	0.002	–	–
Osteichthyes	0.103	0.071	0.276	0.402	0.138	0.080	0.164	0.107	0.096	0.069	0.151	0.102	–	–
Total	105.713	51.284	72.526	43.313	<u>153.384</u>	72.127	72.950	72.587	65.250	25.399	96.609	30.929	4.27	<0.01

**Table 4** Biomass ( $\text{mg m}^{-3}$ ), with standard deviations (SD), of zooplankton groups for the six surveys between 1996 and 1999. One-way ANOVA was run on all data, normalized by  $\log_{10}(x+1)$  transformation, to determine whether species abundance and

biomass levels differed significantly between surveys. Significant differences are indicated by *P*. Significantly higher ( $P < 0.05$ ) levels of biomass, identified by Newman-Keuls multiple-range tests, are underlined

Group	1996	SD	1997 S1	SD	1997 S2	SD	1998	SD	1999 S1	SD	1999 S2	SD	<i>F</i>	<i>P</i>
Hydromedusae	0.036	0.085	0.016	0.063	0.002	0.003	0.034	0.114	0.000	0.000	0.001	0.002	–	–
Siphonophora	0.163	0.296	0.063	0.107	0.090	0.105	0.039	0.104	0.044	0.078	0.013	0.012	–	–
Pteropoda	0.839	2.226	0.065	0.093	0.085	0.168	1.418	1.710	1.005	1.845	0.623	1.214	7.68	<0.005
Other	0.044	0.023	0.003	0.001	0.004	0.001	0.025	0.012	0.006	0.003	0.007	0.003	–	–
Ostracoda	0.241	0.129	0.185	0.099	0.336	0.270	0.184	0.167	0.172	0.153	0.217	0.154	–	–
Copepoda	2.977	2.656	1.932	0.894	4.694	1.642	2.716	6.846	1.795	1.149	2.921	1.205	4.85	<0.01
Decapoda	0.015	0.058	0.037	0.107	0.067	0.202	0.116	0.319	0.098	0.165	0.103	0.269	–	–
Euphausiacea	1.890	1.546	4.172	3.140	1.880	1.205	3.768	2.946	4.097	4.108	4.094	4.010	3.26	<0.01
Hyperiidia	0.118	0.083	0.095	0.159	0.352	0.454	0.906	1.050	0.466	0.863	0.421	0.480	8.14	<0.005
Chaetognatha	1.217	0.818	0.261	0.161	0.437	0.305	0.760	0.928	0.776	0.740	2.455	1.035	18.77	<0.001
Tunicata	0.041	0.122	0.023	0.095	0.000	0.000	0.010	0.030	0.100	0.166	0.041	0.149	–	–
Osteichthyes	0.327	0.940	0.187	0.589	0.051	0.088	0.351	0.460	0.151	0.204	0.152	0.130	–	–
Total	7.907	4.254	7.522	4.288	7.998	2.357	10.326	11.745	8.712	5.531	12.049	4.550	0.92	0.47

**Table 5** Significant  $R^2$  values ( $P < 0.05$ ) for the multiple regression of environmental variables against NMDS ordination scores, for the abundance (A) and biomass (B) analyses from 1996 to 1999,

and for all years combined (– indicates no significant difference). The two surveys conducted in 1997 and in 1999 were merged for the purpose of this analysis

	1996		1997		1998		1999		Combined	
	A	B	A	B	A	B	A	B	A	B
Surface temperature	0.49	–	0.37	0.42	0.28	0.69	0.59	0.72	–	–
Integrated temperature	–	–	–	0.45	–	–	0.66	0.77	–	–

previously been recorded by Sievers and Emery (1978). Nowlin and Klinck (1986) recorded frontal shifts of as much as 100 km in 10 days within the ACC. The oceanographic environment in the vicinity of the PEIs is therefore highly dynamic and subject to rapid change, features which have important ecological implications.

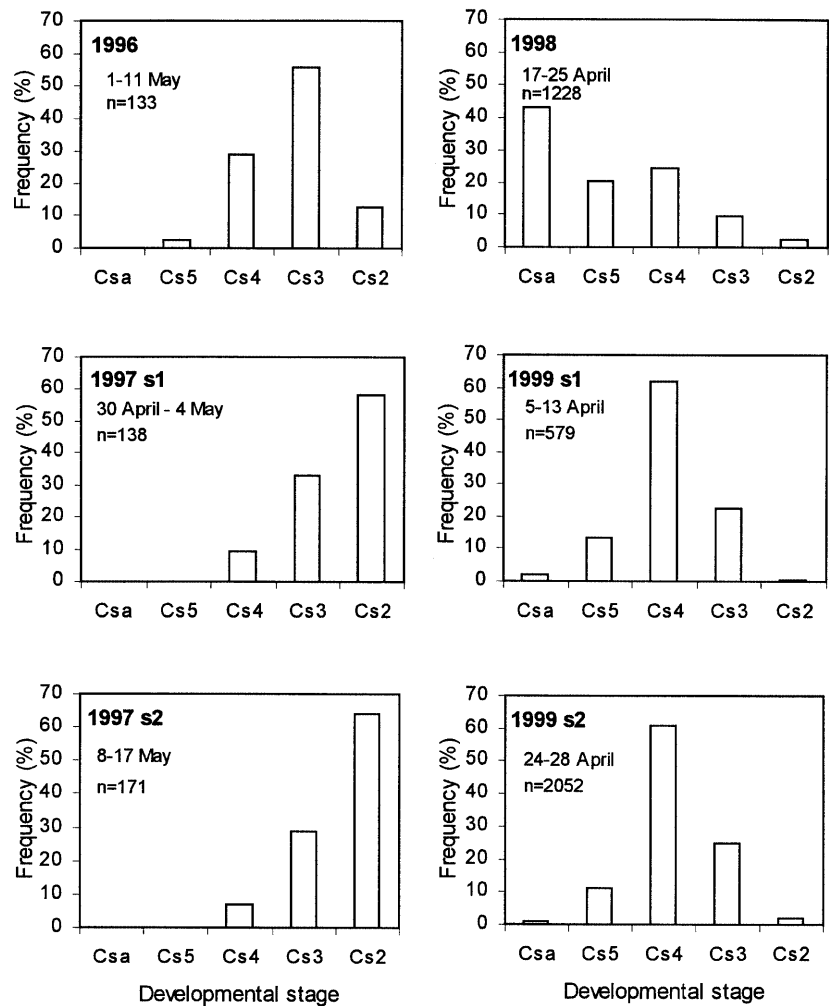
Periods of water retention over the island shelf, when the fronts are far from the islands, are conducive to phytoplankton blooms due to increased water-column stability and the island-mass effect (Perissinotto and Duncombe Rae 1990). The oceanographic environment during 1996, 1998 and survey 2 of 1999 favoured water retention and consequently enhanced phytoplankton biomass and primary production levels over the island shelf. High shelf-phytoplankton biomass was observed in 1996, indicating the occurrence of a bloom (Fig. 3; Pakhomov and Froneman 1999a). By contrast, in 1998, shelf-phytoplankton biomass and production levels were low (Balarin 1999). Despite the SAF being far to the north of the islands, oceanographic surveys revealed that sporadic pulses of off-shelf water passed over the shelf (Pakhomov et al. 2000a). However, elevated microphytoplankton concentrations at some shelf stations (Hunt 2000), a feature typical of phytoplankton blooms at the PEIs (Allanson et al. 1985; Boden 1988; Pakhomov and Froneman 1999a, b), indicated that some production enhancement did occur during 1998. The residence time of water during 1998 may have been too short to result in a full-

scale phytoplankton bloom, since bloom development requires a minimum of ~15 days (Perissinotto and Duncombe Rae 1990). This time lag may also have been responsible for the low chlorophyll-*a* concentrations recorded over the shelf during survey 2 of 1999, since, 2 weeks prior to this survey, the SAF had been observed close to the islands.

It has been hypothesized that, when the SAF is close to the islands, the elevated phytoplankton biomass sometimes recorded at these fronts may be transported into the island system (Froneman and Pakhomov 1998). This was not supported by the present study. Although average chlorophyll-*a* concentrations were relatively high in 1997 and survey 1 of 1999, no enhancement of phytoplankton biomass was observed at the SAF or APF and levels were within the typical range of the APFZ (Laubscher et al. 1993; Fiala et al. 1998; Pakhomov et al. 1999). Averaged phytoplankton biomass for survey 2 of 1997 was greatly enhanced by a single upstream station situated to the north of the SAF (chlorophyll *a* =  $2.3 \text{ mg m}^{-3}$ ), as evidenced by the high standard deviation recorded for this survey. The relatively high average chlorophyll-*a* concentration recorded during survey 1 of 1999 was largely due to three off-shelf downstream stations with high chlorophyll-*a* concentrations ( $1.3\text{--}2.4 \text{ mg m}^{-3}$ ; Hunt 2000). The low phytoplankton biomass recorded at the SAF and APF during this survey (Pakhomov et al. 1999) suggests that these three stations represented the remnants of a



**Fig. 7** Percentage frequency of occurrence of developmental stages of *C. simillimus* for the six surveys (s1 survey 1, s2 survey 2) conducted between 1996 and 1999. Cs2 to Cs5 = *C. simillimus* copepodite stages 2–5; Csa = *C. simillimus* adult



phytoplankton bloom in the island-shelf region being swept downstream, owing to the close proximity of the SAF.

It is possible that low chlorophyll-*a* levels observed at the SAF and APF during survey 2 of 1997 and survey 1 of 1999 may have been due to increased grazing pressure (Perissinotto 1992). The high zooplankton densities during survey 2 of 1997 support this; however, it was clearly not the case during survey 1 of 1999, when densities were the lowest of any survey. In the vicinity of the PEIs, zooplankton grazing has been shown to have a significant impact only on pico- and nanophytoplankton (Perissinotto and Boden 1989). As phytoplankton blooms at the SAF and PEIs are dominated by microphytoplankton (Froneman et al. 1995; Pakhomov and Froneman 1999 a, b), grazing would not be expected to reduce total phytoplankton biomass significantly (Perissinotto 1992). This was particularly relevant in 1997 when the average zooplankton size was relatively small, since the smaller zooplankton size fractions feed preferentially on pico- and nanophytoplankton (Perissinotto 1992; Froneman and Perissinotto 1996). Consequently, it would appear that the low chlorophyll-*a* biomass observed at the

SAF and APF in 1997 and 1999 was due to low levels of production.

It is evident that there is a strong relationship between the position of the SAF and APF, and phytoplankton production and biomass. This relationship is based on the physical interaction between the ACC and the islands, and the response of phytoplankton to the oceanographic environment, resulting in a dynamic ecosystem characterized by rapid short-term variability.

#### Zooplankton community structure

Each of the six surveys conducted between 1996 and 1999 was characterized by the presence of a number of separate zooplankton communities (Hunt et al., submitted). However, the cluster analysis of combined survey data showed that, in many instances, there was greater similarity among communities from different surveys than among communities from the same survey. This points to a high degree of inter-annual similarity in the zooplankton community structure within the APFZ. Different communities were identified by variation in species densities rather than variation in taxonomic

make-up. The dominance of copepods and euphausiids is consistent with previous studies in the vicinity of the PEIs and within the APFZ (Foxton 1966; Hopkins 1971; Grindley and Lane 1979; Boden and Parker 1986; Perissinotto 1989; Pakhomov et al. 2000b), with the exception of a survey conducted in May 1982 at the PEIs when chaetognaths dominated both abundance and biomass (Boden and Parker 1986).

The contribution of sea temperature to variation in community structure varied widely between surveys, ranging from very high values of up to 70%, to more usual levels of ~30%, which is similar to those observed by Hosie (1994) in the Prydz Bay region. Within surveys, temperature differences were an indicator of separate water masses and, correspondingly, separate zooplankton communities (Hunt et al., submitted). However, in the combined analysis of all surveys, temperature was not an important factor. Across surveys, structurally different communities occurred at similar temperatures and, conversely, similar communities occurred at different temperatures. In general, all the observed communities were typical of the APFZ (Ansoerge et al. 1999; Froneman et al. 1999; Pakhomov et al. 2000b). Although physical conditions may place the limits on zooplankton community structure, biological interactions within the available species set may play an important role in determining the composition of the prevailing community within any particular region (Margalef 1967; Levin 1977; Colebrook 1986).

Inter-annual differences in the population structure of *C. simillimus* indicated that the timing of this species' seasonal cycle varied between years. This needs to be considered in the interpretation of community structure. The total abundance and biomass of copepods exhibit strong seasonal variation in quantity and in vertical distribution in the water column (Atkinson 1989; 1991; 1998; Ward et al. 1995; Schnack-Schiel et al. 1998). After spring reproduction, total copepod biomass increases to a maximum in autumn by growth and development of copepodites from the copepodite 1 stage to the copepodite 5 stage (Vidal and Smith 1986; Schnack-Schiel et al. 1998; Goldblatt et al. 1999). Other mesozooplankton groups also show strong seasonal cycles (Knox 1994). The higher average zooplankton size and total zooplankton biomass recorded during 1998 and 1999 (Fig. 8) may therefore be the result of sampling later in the biological season.

Different zooplankton communities occurred within and between surveys because of the hydrodynamic variability of the region, biological interactions and inter-annual variation in the timing of the biological season. However, this variation in community structure was relatively small-scale, and all communities were characteristic of the APFZ. Therefore, despite the dynamic nature of the PEI ecosystem, the observed biological variability occurs within relatively narrow limits. Large-scale changes in zooplankton community structure may therefore have a significant effect on this ecosystem.

## Long-term changes

A combination of data from MIOS and previous oceanographic studies in the vicinity of the PEIs shows a trend of increasing sea-surface temperature with time (Fig. 9a), corresponding to the long-term trend of warming in air and sea-surface temperature observed by Smith and Steenkamp (1990). This increased temperature may reflect a southward shift in the mean position of the SAF, as suggested by the data of 30 crossings of the SAF upstream of the PEIs between 1959 and 1999 (Pakhomov et al. 2000b). Such a shift would not only increase sea temperature in the vicinity of the islands but also favour a flow-through environment, preventing water retention over the island shelf and the development of associated phytoplankton blooms. The decrease in average chlorophyll-*a* concentrations observed in the vicinity of the islands (Fig. 9b), since the first oceanic survey in 1976, therefore supports the suggestion of a southward movement of the SAF.

Such a movement would also alter the composition of zooplankton communities interacting with the island system, resulting in an increased dominance of sub-Antarctic and sub-tropical species (Pakhomov et al. 2000b). Although the SAF has been observed to be a region of high productivity (Laubscher et al. 1993; Froneman and Pakhomov 1998), in many studies both phytoplankton and zooplankton biomass show little difference from levels recorded in the inter-frontal regions (Lutjeharms et al. 1985; Pakhomov and McQuaid 1996; Froneman et al. 1999; Pakhomov et al. 1999a, b; Hunt 2000). Data from this study indicate that mesozooplankton abundance and biomass levels tend to decrease with increasing temperature (Fig. 10). Consequently, southward movement of the SAF may result in a reduction in mesozooplankton biomass in the waters surrounding the PEIs, producing a bottom-up effect on top-predator populations.

The PEI benthic shelf environment is characterized by a high biomass of the caridean shrimp *Nauticaris*

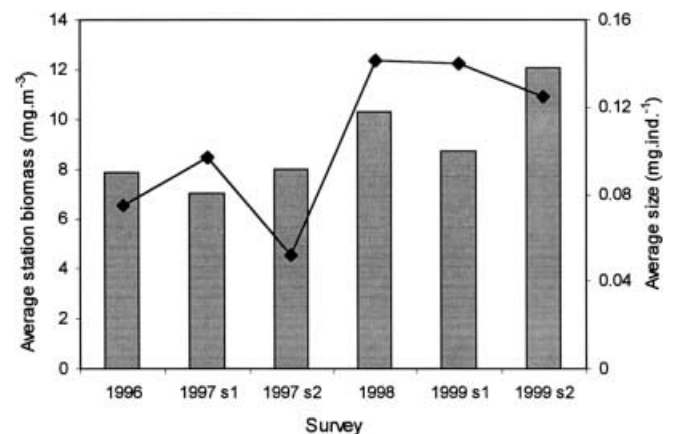
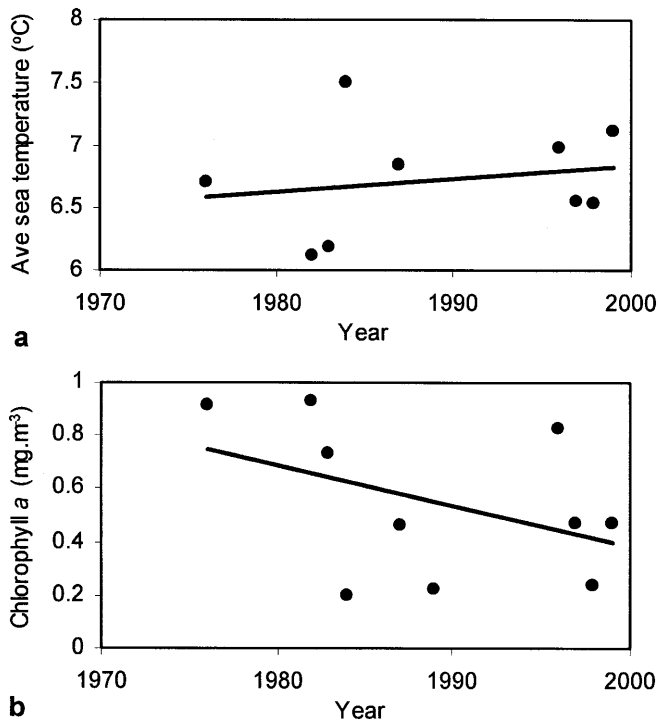


Fig. 8 Average zooplankton biomass (columns) and average individual zooplankton size (line) recorded per net station for each of the six surveys conducted between 1996 and 1999 (s1 survey 1, s2 survey 2)



**Fig. 9** Average sea-surface temperature (a) and chlorophyll-*a* concentration ( $\text{mg m}^{-3}$ ) (b) recorded during PEI surveys between 1976 and 1999. Data for these graphs were taken from several sources (El-Sayed et al. 1979; Allanson et al. 1985; Boden and Parker 1986; Boden 1988; Duncombe Rae 1989a, b; Ansorge et al. 1999; Pakhomov and Froneman 1999b)

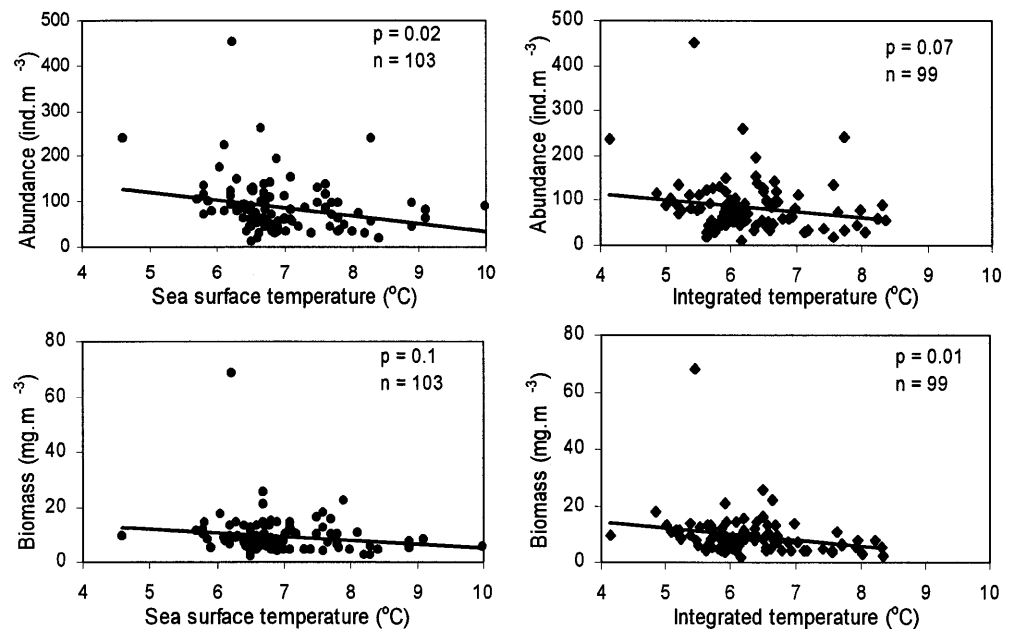
*marionis*. *N. marionis* is an important component in the diet of many inshore-feeding land-based predators (Brown and Klages 1987) and is considered a key element in the PEI ecosystem (Perissinotto et al. 1990). Short-term fluctuations in the position of the SAF and

APF may result in inter-annual variation in *N. marionis* biomass through the effect of the degree of shelf-water retention on the recruitment success of this species (Kuu 1998). Inter-annual variation in *N. marionis* biomass is evident from stomach-content analyses of inshore-feeding predators, with *N. marionis* being almost completely replaced by allochthonous zooplankton in some years (Brown and Klages 1987; Brown et al. 1990). Switching between allochthonous zooplankton and *N. marionis*-dominated diets may be due either to increased availability of allochthonous zooplankton in a flow-through scenario or short-term fluctuations in *N. marionis* biomass attributable to high predation pressure, or to both these factors. These fluctuations may be further affected by the Antarctic Circumpolar Wave (ACW) (White and Peterson, 1996), although at this stage it is difficult, without a complete, year-round, data set, to separate the inter-annual cycle of the ACW from short-term fluctuations in the position of the SAF and APF.

Furthermore, the role of *N. marionis* in the PEI ecosystem may be significantly affected by the long-term southward movement of the SAF. Sedimentation of bloom material, after inter-island blooms, forms an important energy source for benthic suspension feeders (Perissinotto et al. 1990), which in turn are consumed by *N. marionis* (Kuu 1998). Although phytoplankton may also be transported to the benthos during a flow-through scenario, oceanic phytoplankton biomass is generally low (Perissinotto et al. 1990; Pakhomov and Froneman 1999b). A southward shift in the position of the SAF may therefore result in a long-term reduction of *N. marionis* biomass through the restructuring of the inter-island food web.

Sub-Antarctic climate change is considered to be responsible for changes in the dynamics of the terrestrial

**Fig. 10** Regressions of zooplankton abundance ( $\text{ind m}^{-3}$ ) and biomass ( $\text{mg m}^{-3}$ ) against sea temperature (surface and integrated). Significance levels are indicated by *P. t*-tests showed that all slopes were significantly different from zero ( $P < 0.01$ )



ecosystem observed at the PEIs during recent decades (Smith and Steenkamp 1990; Chown and Smith 1993). It has yet to be proven conclusively that this climate change has been accompanied by the southward movement of the SAF. However, if this is the case, the close relationship between the position of the fronts and the biota demonstrated by this study suggests that the PEI ecosystem may have experienced dramatic changes in the past half century and will experience further dramatic change in the future.

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