Mesozooplankton interactions with the shelf around the sub-Antarctic Prince Edward Islands archipelago

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Mesozooplankton surveys were conducted in April/May for four consecutive years (1996–1999) in the vicinity of the Prince Edward Islands (PEIs), Southern Ocean. The PEIs are located in the Polar Frontal Zone, directly in the path of the east-flowing Antarctic Circumpolar Current. Zooplankton were collected by oblique tows using a Bongo net fitted with 300 μm mesh. The abundance, biomass and average size of the mesozooplankton in the upstream (USR), inter-island (IIR) and downstream (DSR) regions indicated that some groups and species were significantly affected by their interaction with the shallow shelf waters of the PEIs. Total mesozooplankton abundance and biomass were typically highest in the DSR, but no consistent pattern was evident in the USR and IIR. Copepods, euphausiids and fish were generally of a low average size in the IIR. This small size was largely attributed to the reduced abundance, or complete absence, of mesopelagic species from the shelf region. Of total biomass, the mesopelagic species Euphausia longirostris, Euphausia similis, Pleuromamma abdominalis, Paraeuchaeta biloba and Oncaea antarctica together contributed an average of 16% to the USR, 2% to the IIR and 15% to the DSR. Conversely, epipelagic species showed no consistent pattern of abundance and biomass distribution between regions. The low incidence of mesopelagic species over the island shelf was attributed mainly to reduced advection of deep water into the shelf region (average depth = 200 m), rather than predation, particularly during the through-flow mode between the islands. This resulted in substantial regional differences in euphausiid community structure. The epipelagic species Euphausia vallentini and Thysanoessa vicina completely dominated the IIR, comprising on average 89% of total euphausiid biomass in this region. However, predation may be important during the water-trapping mode between the islands. Advection of zooplankton into the IIR appeared to be affected by the proximity of the Subantarctic Front (SAF). In 1996, when the SAF was far north of the PEIs, reduced current velocities resulted in some degree of water retention over the shelf and an increased predation impact. Conversely, when the SAF was close to the PEIs in 1999, more large plankton were transported over the island shelf. High current velocities and productivity associated with the SAF appear to increase the biomass and size of allochthonous zooplankton/nekton advected into the IIR, and consequently may have increased the availability of prey to land-based predators. The long-term southward movement of the SAF recently observed in the vicinity of the PEIs may therefore have important implications for the ecosystem of these islands.

INTRODUCTION

Within the oceanic environment, islands and seamounts are topographic features that impact significantly on plankton populations and communities. Depletion of zooplankton stocks over seamounts can result in daily gap formation in downstream regions (Genin *et al.*, 1988, 1994; Haury *et al.*, 1995; Dower and Mackas, 1996). Biomass reduction has been attributed to a combination of trapping of migratory zooplankton, predation and daytime advection of low-biomass surface waters over the shallow topography. Indeed, biomass reduction has been

observed over shallow island shelf waters and their downstream regions (Grindley and Lane, 1979; Perissinotto, 1989; Atkinson and Peck, 1990; Perissinotto and McQuaid, 1992). On the contrary, both seamounts and islands are recognized to be regions of locally enhanced production through the 'island mass effect' (Genin and Boelhert, 1985; Heywood *et al.*, 1990; Coutis and Middleton, 1999).

The Prince Edward Island (PEI) archipelago is located in the Indian sector of the Southern Ocean, within the Polar Frontal Zone (PFZ) of the easterly flowing Antarctic Circumpolar Current (ACC) (Figure 1). The archipelago comprises two islands, Marion and Prince Edward, separated by a shallow shelf region ~200 m deep (Pakhomov and Froneman, 1999). The PEIs are bounded to the north by the Subantarctic Front (SAF) and to the south by the Antarctic Polar Front (APF). Oceanographic studies have shown that hydrodynamic conditions in the vicinity of the PEIs may be strongly influenced by the proximity of the SAF (Ansorge and Lutjeharms, 2000; Pakhomov *et al.*, 2000; Perissinotto *et al.*, 2000).

The shelf waters of the PEIs are relatively rich in benthic fish fauna, although no studies have yet quantified their biomass (Gon and Klages, 1988). The islands themselves support large breeding populations of seabirds and seals, estimated at 4–6 million individuals (Williams *et al.*, 1979; Perissinotto and McQuaid, 1992). The predation impact of vertebrate predators on zooplankton populations in the vicinity of the PEIs is, therefore, expected to be seasonally high (Grindley and Lane, 1979; Perissinotto, 1989). The PEIs do not have an endemic holoplankton and predators are, therefore, supported mainly by oceanic species (Allanson *et al.*, 1985; Boden and Parker, 1986). Large copepods, euphausiids, decapods, hyperiid amphipods, pelagic fish and the neritic decapod *Nauticaris marionis* have all been recorded in the diets of vertebrate predators (ave birds and fish) at the PEIs, with the lantern fish, euphausiids *Euphausia vallentini* and *Thysanoessa vicina*, and *N. marionis* being the principal prey species (Steele and Klages, 1986; Gartshore *et al.*, 1988; Brown *et al.*, 1990; Perossinotto and McQuaid, 1992).

Together, the interplay of hydrodynamics and predation is expected to influence plankton population structure. A mesozooplankton study conducted in April/May 1989 observed reduced biomass levels over the shelf and in the downstream region of the PEIs, a feature attributed to predation (Perissinotto and McQuaid, 1992). A macroplankton/micronekton study at the PEIs also observed reduced biomass over the island shelf (Pakhomov and Froneman, 1999) and these authors proposed that three factors could explain these discrepancies: (i) predation impact; (ii) hydrodynamics; and (iii) zooplankton behaviour.

Between 1996 and 1999, annual mesozooplankton surveys were carried out at the PEIs during the austral autumn (April/May) to investigate the structural patterns of the plankton community. The data collected during these surveys provided an excellent opportunity to investigate the above three hypotheses. In the light of possible predation effects, zooplankton size structure, and particularly euphausiid population structure, was given special attention.

METHOD

Each of the four surveys used in this analysis was of similar design and included a transect in the upstream region (USR) along 37°E, and two transects crossing both the shelf waters of the inter-island region (IIR) and the downstream region (DSR) (Figure 2). For the purpose of this study, shelf waters were defined as all areas of <300 m depth.

Mesozooplankton samples were collected using a Bongo net with a mouth area of 0.25 m^2 and a mesh size of 300 µm. 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. All of the 1996, 1997 and 1999 samples used in the analysis were collected at night (between 19:00 and 07:00 h). A large number of both day and night samples were collected in 1998, and these were used to investigate diel variation. In the case of the 1998 samples, night-time net tows were conducted to a maximum depth of 200 m, while daytime net tows were conducted to 300 m. The volume of water filtered during each tow was determined using an electronic flow meter. Samples were fixed in 4–6% buffered formalin. Zooplankton were identified to species, and abundance was determined from subsamples, obtained using a Folsom plankton splitter, ranging between 1/2 and 1/32 aliquots of the total, depending on sample size. All subsamples contained 200–500 animals. The entire sample was analysed for low-abundance species not encountered in subsamples. Abundance was expressed as number of individuals per cubic metre. The dry weight of all species was measured to the nearest 0.001 mg, 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 (Mizdalski, 1988). Biomass data were expressed as milligrams dry weight per cubic metre. No corrections were applied for loss of weight due to preservation. Average zooplankton size was calculated at each station in terms of milligrams dry weight per individual. Owing to the large number of copepods sampled, the size of individual copepods was determined from stage-specific
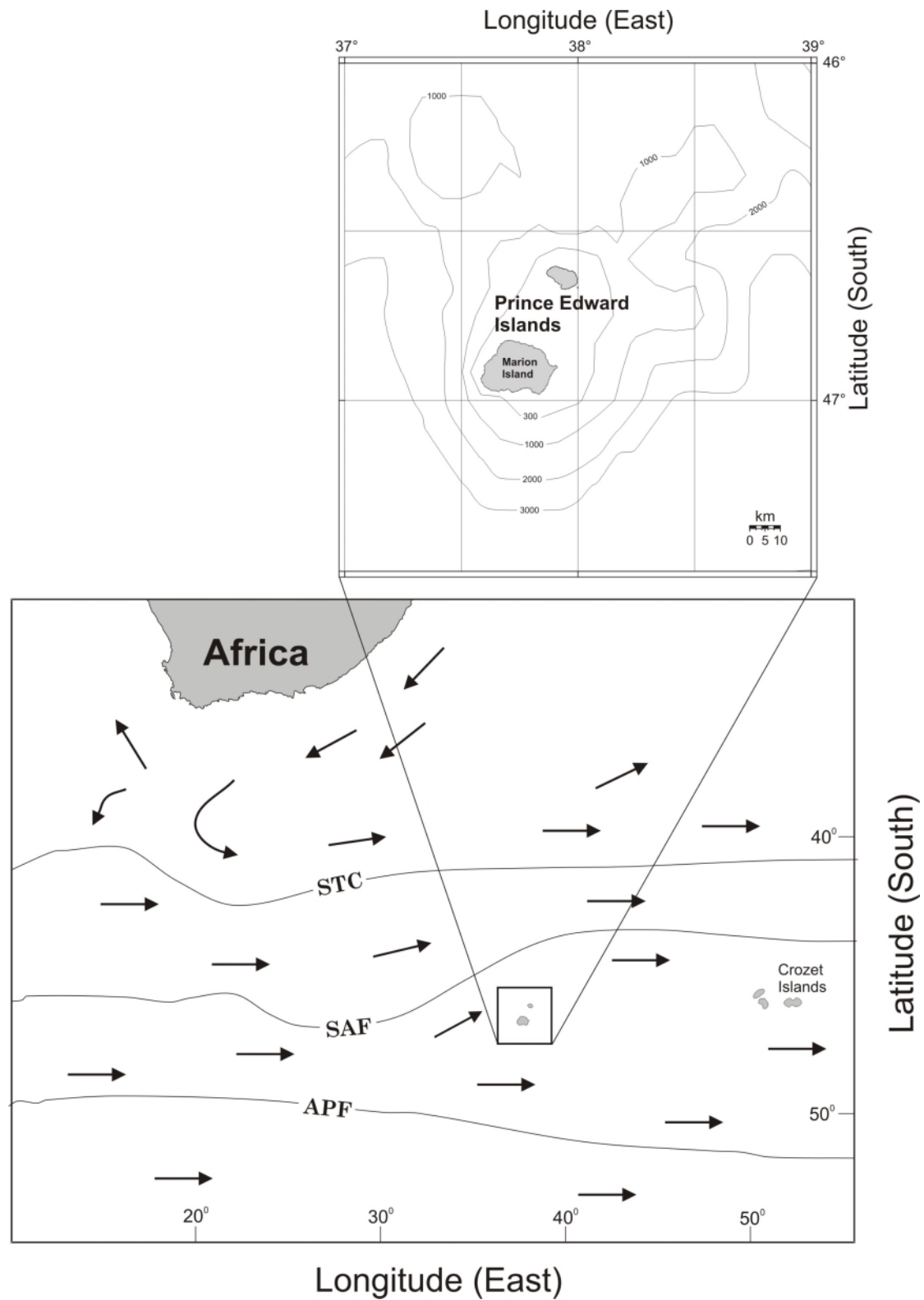
Fig. 1. Map illustrating the location of the PEIs in relation to South Africa and the average position of major frontal systems of the Southern Ocean. STC, Subtropical Convergence; SAF, Subantarctic Front; APF, Antarctic Polar Front. The insert shows local bottom topography in the vicinity of the PEIs.
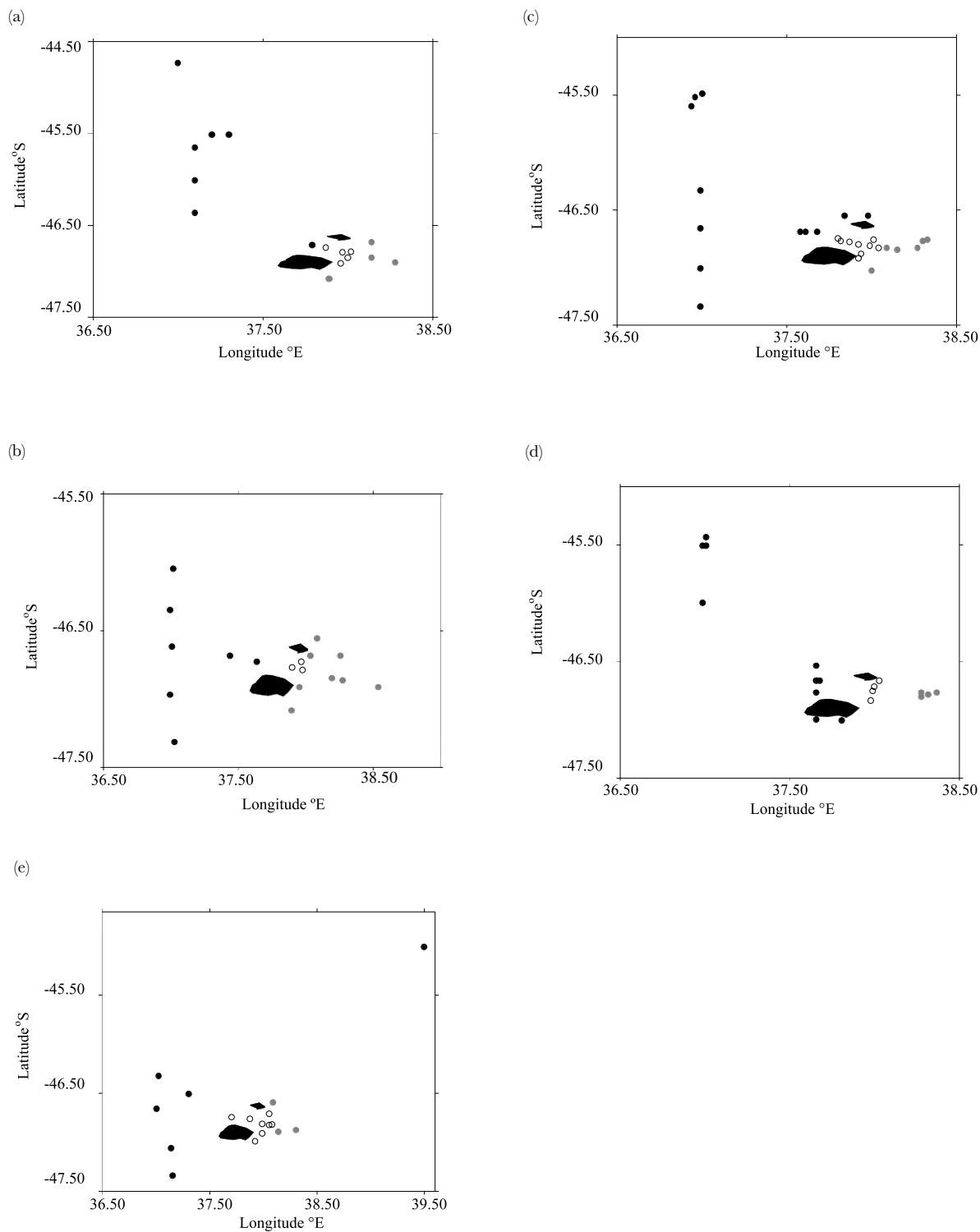
Fig. 2. The location of Bongo net hauls conducted in (**a**) 1996, (**b**) 1997, (**c**) 1998 night-time samples, (**d**) 1998 daytime samples and (**e**) 1999. Black circles indicate upstream samples, open circles indicate shelf samples and grey circles indicate downstream samples.

averages for a minimum of 20 individuals from each stage/species.

Over 120 species were identified during this study. The analysis focused on major zooplankton groupings and the most common species. A subset of common species was selected based on their occurrence in >50% of the stations in all surveys (Table I). All euphausiids were included due to their role as prey species. Prior to analysis, data were normalized by $\log_{10}(x + 1)$ transformation. The distribution of abundance, biomass and size of zooplankton groups between regions, and between day and night samples, was investigated using one-way ANOVA. Subsequently, differences between regions were investigated using Newman–Keuls multiple range tests (Zar, 1984).

An oceanographic survey was conducted in conjunction with each zooplankton survey in order to determine the positions of the SAF and APF in relation to the PEIs. This required a minimum of an upstream transect along 37°E. CTD casts were carried out using a Neil Brown Instrument Mark IIIc underwater unit. The position of the SAF was determined by the position of the 7°C isotherm at 100 m, and that of the APF by the position of the 2°C isotherm at 200 m.

RESULTS

In 1996, there was no significant difference in total abundance and total biomass between regions. Euphausiid biomass was significantly lower in the IIR than the DSR and all species except *T. vicina* occurred at lowest abundance and biomass in the IIR (Table IIA and B). The hyperiid *Primno macropa* had significantly higher abundance and biomass in the IIR, while the converse was true for the mesopelagic copepod *Oncaea antarctica*. Average copepod, euphausiid and total zooplankton sizes were significantly lower in the IIR, while pteropods,

Table I: Species occurring at 50% of stations in all surveys and their vertical distribution patterns

	Depth	References
Protomyctophum sp.	>200 m	Pakhomov and Froneman, 1999
Eukrohnia hamata	E	O'Sullivan, 1982a
Sagitta gazellae	E	O'Sullivan, 1982a
Primno macropa	0–500 m; E	Guglielmo and Ianora, 1997; Boltovskoy, 1999
Themisto gaudichaudii	0–500 m; E	Guglielmo and Ianora, 1997; Boltovskoy, 1999
Euphausia vallentini	N 50–100 m; D <50 m	Mauchline and Fisher, 1969; Pakhomov and Froneman, 1999
Euphausia longirostris	N 100–200 m	Pakhomov and Froneman, 1999
Euphausia similis	<300 m	Boltovskoy, 1999
Nematoscelis megalops	M; D 300–500 m; N >100 m	Mauchline and Fisher, 1969; Boltovskoy, 1999
Stylocheiron maximum	M	Mauchline and Fisher, 1969
Thysanoessa vicina	N <50 m	Mauchline and Fisher, 1969
Thysanoessa gregaria	N 400 m; D <200 m	Mauchline and Fisher, 1969
Aetideus armatus	E/M	Boltovskoy, 1999
Calanus simillimus	E <250 m, seasonally M	Atkinson and Sinclair, 2000; Boltovskoy, 1999
Clausocalanus laticeps	E <250 m	Atkinson and Sinclair, 2000; Boltovskoy, 1999
Clausocalanus brevipes	E <250 m	Guglielmo and Ianora, 1995; Boltovskoy, 1999
Ctenocalanus vanus	E <250 m	Atkinson and Sinclair, 2000; Boltovskoy, 1999
Heterorhabdus austrinus	M	Boltovskoy, 1999
Metridia lucens	0–700 m[a]; M[b]	Guglielmo and Ianora, 1995[a]; Atkinson and Sinclair, 2000[b]
Oithona frigida	E	Boltovskoy, 1999
Oncaea antarctica	M >250 m	Atkinson and Sinclair, 2000; Boltovskoy, 1999
Paraeuchaeta biloba	M	Guglielmo and Ianora, 1995; Boltovskoy, 1999
Pleuromamma abdominalis	E/M	Boltovskoy, 1999
Rhyncalanus gigas	E	Atkinson and Sinclair, 2000
Scolecithricella minor	E <250 m	Atkinson and Sinclair, 2000; Boltovskoy, 1999
Limacina retroversa	E	Boltovskoy, 1999
Tomopteris sp.	E	O'Sullivan, 1982b

All euphausiids were included in this list because of their contribution as prey species. E, epipelagic; M, mesopelagic; N, night; D, day.

Table IIA: Average abundance (individuals m⁻³) of zooplankton groups recorded from the USR, IIR and DSR regions of the PEIs in 1996, 1997 and 1999

	1996				1997				1999			
	USR	IIR	DSR	P	USR	IIR	DSR	P	USR	IIR	DSR	P
Gelatinous	0.456	0.164	0.273		0.127	0.109	0.204		0.057	0.021	0.361	
Polychaeta	0.169	0.177	0.056		0.051	0.011	0.064		0.048	0.039	0.084	
Pteropoda	10.045	2.841	1.072		X0.226	Y1.147	XY0.484	*	4.483	11.292	6.932	
Ostracoda	7.404	5.453	5.174		4.123	3.691	7.077		X5.304	X2.269	Y11.645	**
Copepoda	78.911	107.32	58.724		X31.956	Y116.09	Y73.506	**	Y56.228	X25.674	Y57.275	*
Euphausiacea	3.761	3.358	2.900		X2.385	Y5.801	XY3.281	*	4.024	4.043	2.557	
Decapoda	0.001	–	–		0.002	–	<0.001		0.001	0.039	0.014	
Hyperiidea	0.529	1.305	0.722		X0.254	Y0.879	XY0.535	*	0.950	0.868	1.037	
Chaetognatha	12.474	14.011	11.096		2.269	2.645	4.677		X6.694	X4.209	Y15.781	**
Osteichthyes	0.068	0.165	0.086		0.153	0.149	0.431		0.098	0.112	0.051	
Total	106.41	129.35	74.929		X37.423	Y125.96	Y83.203	**	XY72.58	X46.304	Y84.092	*
Protomyctophum sp.	0.035	0.109	0.071		0.147	0.119	0.421		0.070	0.021	0.025	
E. hamata	7.743	11.665	7.855		2.005	1.138	3.804		5.009	3.346	12.416	
S. gazellae	3.609	4.973	3.241		X0.264	XY0.630	Y0.874	*	1.685	0.863	3.365	
P. macropa	X0.472	Y1.185	X0.563	*	X0.222	Z0.799	ZY0.474	*	X0.605	Y0.716	XY0.679	*
T. gaudichaudii	0.105	0.192	0.160		0.031	0.080	0.061		0.312	0.153	0.326	
E. vallentini	0.186	0.043	0.351		0.220	0.856	0.789		0.254	0.569	0.424	
E. longirostris	0.050	–	0.132		0.021	–	0.015		0.040	0.020	0.027	
E. similis	0.010	–	–		0.011	–	0.001		0.060	–	0.036	
N. megalops	0.008	–	0.010		0.095	–	0.038		0.048	0.034	0.039	
S. maximum	0.067	0.108	0.031		0.079	0.159	0.037		0.031	0.028	0.018	
T. vicina	3.061	3.372	2.302		1.944	4.766	2.398		3.501	3.354	1.995	
T. gregaria	0.013	0.017	0.000		0.016	0.019	0.003		0.071	0.023	0.008	
A. armatus	0.341	0.859	0.806		0.047	0.097	0.187		0.251	0.088	0.143	
C. simillimus	1.300	3.230	1.620		0.229	0.683	0.706		2.447	7.012	7.261	
C. laticeps	0.670	2.162	0.979		X0.276	X0.744	Y1.120	*	0.738	0.592	1.257	
C. brevipes	38.531	45.795	19.945		X3.903	Z69.992	YZ18.683	***	12.683	8.510	7.154	
C. vanus	0.179	0.000	0.000		5.544	14.391	14.492		0.026	0.000	0.000	
H. austrinus	0.604	0.081	0.588		0.476	0.227	0.587		0.454	0.425	0.758	
M. lucens	12.144	20.085	18.637		6.360	14.671	14.107		22.630	3.941	8.820	
O. frigida	3.903	11.342	2.967		1.860	6.375	7.233		1.443	0.513	0.711	
O. antarctica	Y1.448	X0.104	Y0.541	*	0.356	–	0.219		Y0.995	X0.018	Y1.167	*
P. biloba	0.121	0.000	0.000		Y0.797	–	X0.149	*	0.488	0.059	1.319	
P. abdominalis	5.235	1.798	1.994		Y1.662	–	Y1.371	*	1.231	0.019	3.052	
R. gigas	0.916	0.793	1.169		0.000	0.000	0.115		1.676	0.489	3.340	
S. minor	1.506	2.386	2.137		0.582	1.457	1.692		0.835	0.428	1.587	
L. retroversa	6.284	2.908	0.763		0.186	0.896	0.353		4.259	10.882	6.851	
Tomopteris sp.	0.117	0.088	0.045		0.032	0.000	0.048		0.048	0.127	0.077	

Significant differences between regions, determined by Newman–Keuls multiple range tests, are indicated by different letters. *$P < 0.05$; **$P < 0.01$; ***$P < 0.005$.

Table IIB: Average biomass (mg dry wt m^{-3}) of zooplankton groups recorded from the USR, IIR and DSR regions of the PEIs in 1996, 1997 and 1999

	1996				1997				1999			
	USR	IIR	DSR	*P*	USR	IIR	DSR	*P*	USR	IIR	DSR	*P*
Gelatinous	0.329	0.222	0.107		0.035	0.092	0.163		0.269	0.051	0.147	
Polychaeta	0.021	0.092	0.021		0.004	<0.001	0.002		0.006	0.001	0.007	
Pteropoda	1.649	0.288	0.111		X0.035	Y0.190	X0.043	*	0.659	1.375	0.709	
Ostracoda	0.255	0.271	0.178		0.142	0.127	0.244		X0.203	X0.078	Y0.401	**
Copepoda	3.901	2.865	2.462		1.728	2.557	2.292		X2.234	X1.071	Y3.823	**
Euphausiaceae	XY1.976	X0.723	Y3.197	*	2.844	5.896	4.688		3.72	3.781	5.693	
Decapoda	0.033	–	–		0.002	–	1.172		0.007	0.148	0.148	
Hyperiidea	0.069	0.181	0.123		0.102	0.044	0.108		0.832	0.120	0.659	
Chaetognatha	1.228	1.299	1.096		0.232	0.200	0.320		1.046	0.461	1.079	
Osteichthyes	0.608	0.063	0.165		0.409	0.019	0.055		0.254	0.052	0.206	
Total	9.809	5.732	7.282		5.391	8.970	8.843		9.056	7.061	12.496	
Protomyctophum sp.	0.005	0.018	0.010		0.031	0.017	0.018		0.026	0.005	0.004	
E. hamata	0.503	1.336	0.756		0.115	0.096	0.245		0.720	0.187	0.652	
S. gazellae	0.586	0.258	0.340		0.116	0.077	0.076		0.326	0.274	0.427	
P. macropa	X0.040	Y0.100	X0.059	*	0.024	0.034	0.028		0.057	0.018	0.045	
T. gaudichaudii	0.035	0.049	0.065		0.078	0.011	0.078		0.725	0.102	0.606	
E. vallentini	0.545	0.097	0.946		0.517	4.162	3.047		1.143	2.681	3.228	
E. longirostris	XY0.533	–	Y1.660	*	0.359	–	0.205		XY0.214	X0.010	Y0.517	*
E. similis	0.072	–	–		0.099	–	0.021		0.215	–	0.349	
N. megalops	0.016	–	0.071		Y1.058	–	X0.386	*	0.453	0.309	0.593	
S. maximum	0.032	0.021	0.026		0.026	0.009	0.016		0.005	0.005	0.036	
T. vicina	0.535	0.643	0.427		0.742	1.607	0.997		1.355	0.692	0.894	
T. gregaria	0.033	0.061	0.063		0.042	0.118	0.015		0.289	0.083	0.075	
A. armatus	0.014	0.035	0.033		0.002	0.004	0.008		0.010	0.004	0.006	
C. simillimus	0.143	0.345	0.194		0.011	0.067	0.039		0.183	0.517	0.608	
C. laticeps	0.013	0.042	0.019		0.005	0.014	0.022		0.014	0.012	0.024	
C. brevipes	0.768	0.913	0.398		X0.078	Z1.395	Y0.372	*	0.253	0.170	0.143	
C. vanus	0.003	0.000	0.000		0.107	0.278	0.280		0.001	0.000	0.000	
H. austrinus	0.116	0.057	0.140		0.113	0.054	0.139		0.055	0.003	0.091	
M. lucens	0.278	0.434	0.556		0.164	0.273	0.266		0.343	0.122	0.251	
O. similis	0.001	0.000	0.000		0.000	0.000	0.001		0.000	0.000	0.000	
O. frigida	0.012	0.034	0.009		X0.006	XY0.019	Y0.022	*	0.004	0.002	0.002	
O. antarctica	Y0.013	X0.001	X0.005	*	0.003	0.000	0.002		0.009	0.000	0.011	
P. biloba	0.038	0.000	0.000		Y0.254	X0.000	X0.047	*	Y0.126	X0.005	Y0.244	**
P. abdominalis	1.297	0.446	0.494		0.412	0.000	0.340		Y0.305	X0.005	Z0.757	***
R. gigas	0.186	0.161	0.237		0.000	0.000	0.010		0.311	0.073	0.562	
S. minor	0.029	0.046	0.041		0.011	0.028	0.032		0.016	0.008	0.030	
L. retroversa	0.158	0.083	0.014		X0.032	Y0.172	X0.041	*	0.570	1.335	0.696	
Tomopteris sp.	0.013	0.006	0.007		0.002	0.000	0.002		0.002	0.001	0.006	

Significant differences between regions, determined by Newman–Keuls multiple range tests, are indicated by different letters. *$P < 0.05$; **$P < 0.01$; ***$P < 0.005$.
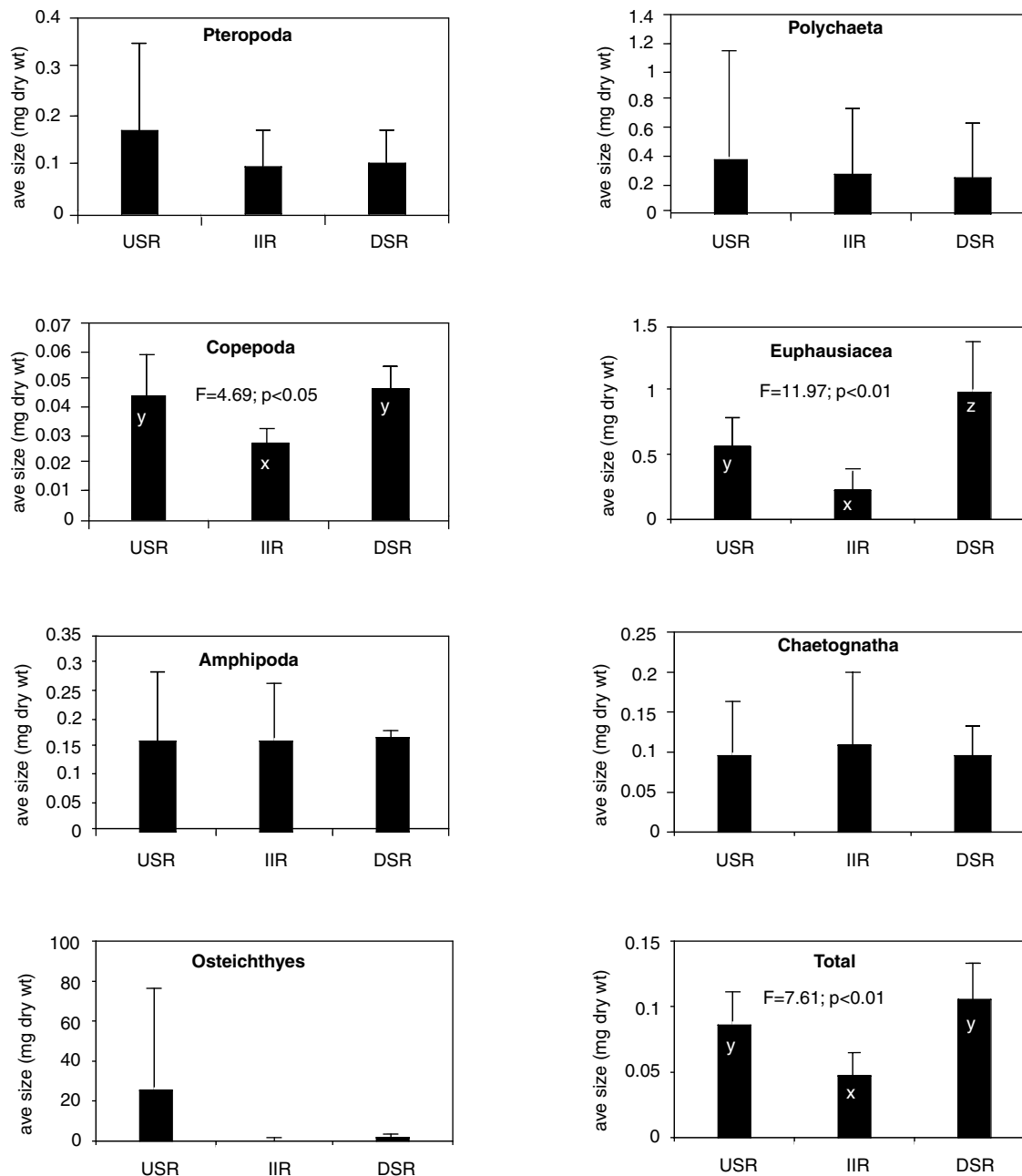
Fig. 3. Average size (mg dry wt ind.$^{-1}$) of major mesozooplankton groups recorded from the USR, IIR and DSR regions of the PEIs. Significance levels, determined by one-way ANOVA, are indicated by F and P. Significant differences between regions, determined by Newman–Keuls multiple range tests, are indicated by different letters. DN in (c) denotes significant differences in average size between day and night samples, independent of regional variation. (**a**) 1996; (**b**) 1997; (**c**) 1998; (**d**) 1999.

polychaetes and chaetognaths were of a similar average size in the USR, IIR and DSR (Figure 3a). Fish biomass and average size were relatively high in the USR in comparison to the IIR and DSR.

In 1997, total abundance was significantly lower in the USR and highest in the IIR, and this was reflected by the abundance levels of pteropods, copepods, euphausiids and amphipods (Table IIA). *Sagitta gazellae* and *Clausocalanus laticeps* were significantly more abundant in the DSR, while *P. macropa* and *Clausocalanus brevipes* were most abundant in the IIR. The mesopelagic copepods *O. antarctica*, *Paraeuchaeta biloba* and *Pleuromamma abdominalis*, and
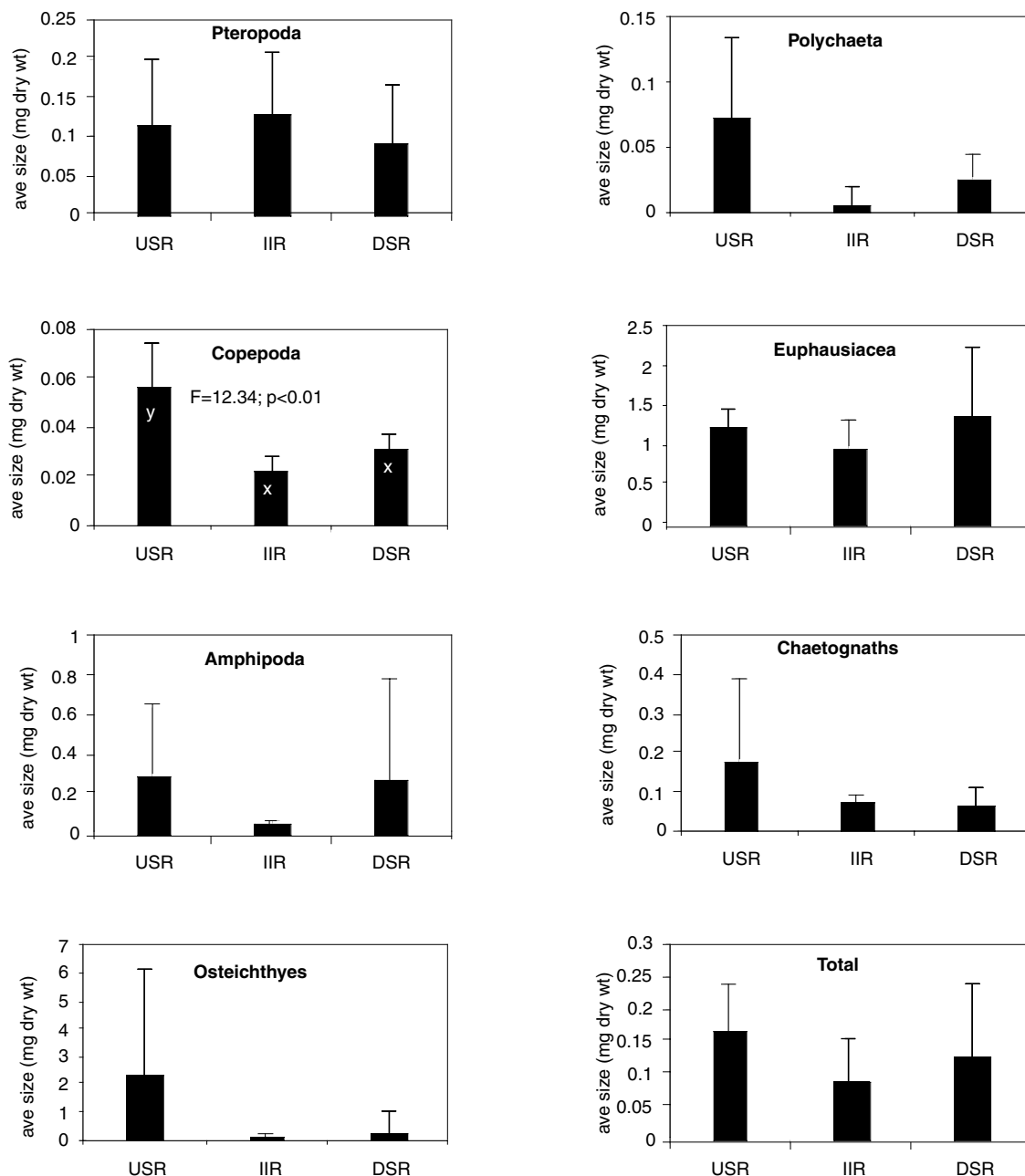
Fig. 3b.

the euphausiids *Euphausia longirostris*, *Euphausia similis* and *Nematoscelis megalops*, were all absent from the IIR. There was no significant difference in total biomass between regions, although lowest levels were observed in the USR. Pteropods, dominated by *Limacina retroversa*, and *C. brevipes* occurred at significantly higher biomass in the IIR. *Paraeuchaeta biloba* and *N. megalops* occurred at highest

biomass in the USR. The average size of polychaetes, copepods, chaetognaths and fish was highest in the USR, while polychaetes, amphipods and total zooplankton were smallest in the IIR (Figure 3b).

The 1998 day/night comparison revealed significant diel variation in total zooplankton abundance and biomass, both being significantly higher at night than
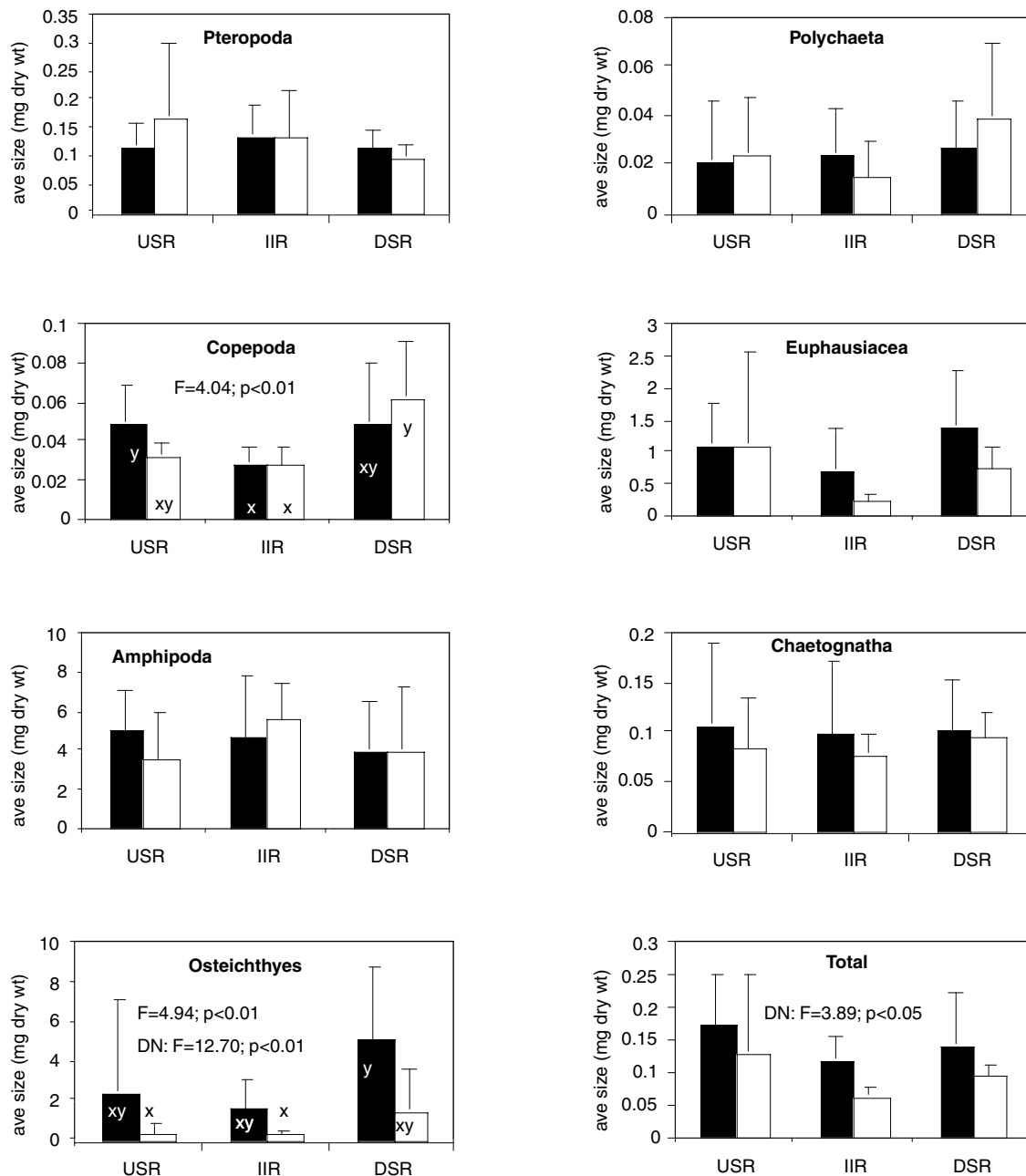
Fig. 3c.

during the day. The night-time abundance of pteropods and euphausiids, and biomass of euphausiids, amphipods and fish, were significantly higher than daytime levels and this was reflected by the diel variation of species within these groups (Table IIIA and B). Significant diel variation was also observed for the copepods *C. laticeps, C. brevipes* and *P. abdominalis*.

Total abundance and biomass were highest in the

DSR, and gelatinous plankton, chaetognaths and fish all occurred at significantly higher levels in the DSR and lowest levels in the USR and IIR, respectively. The euphausiids *E. longirostris* and *E. similis*, and the copepod *O. antarctica*, were all absent from the IIR. *Calanus simillimus* was characterized by high densities in the DSR, and *Oithona frigida* by high daytime density in the IIR.

Pteropods, polychaetes, amphipods and chaetognaths
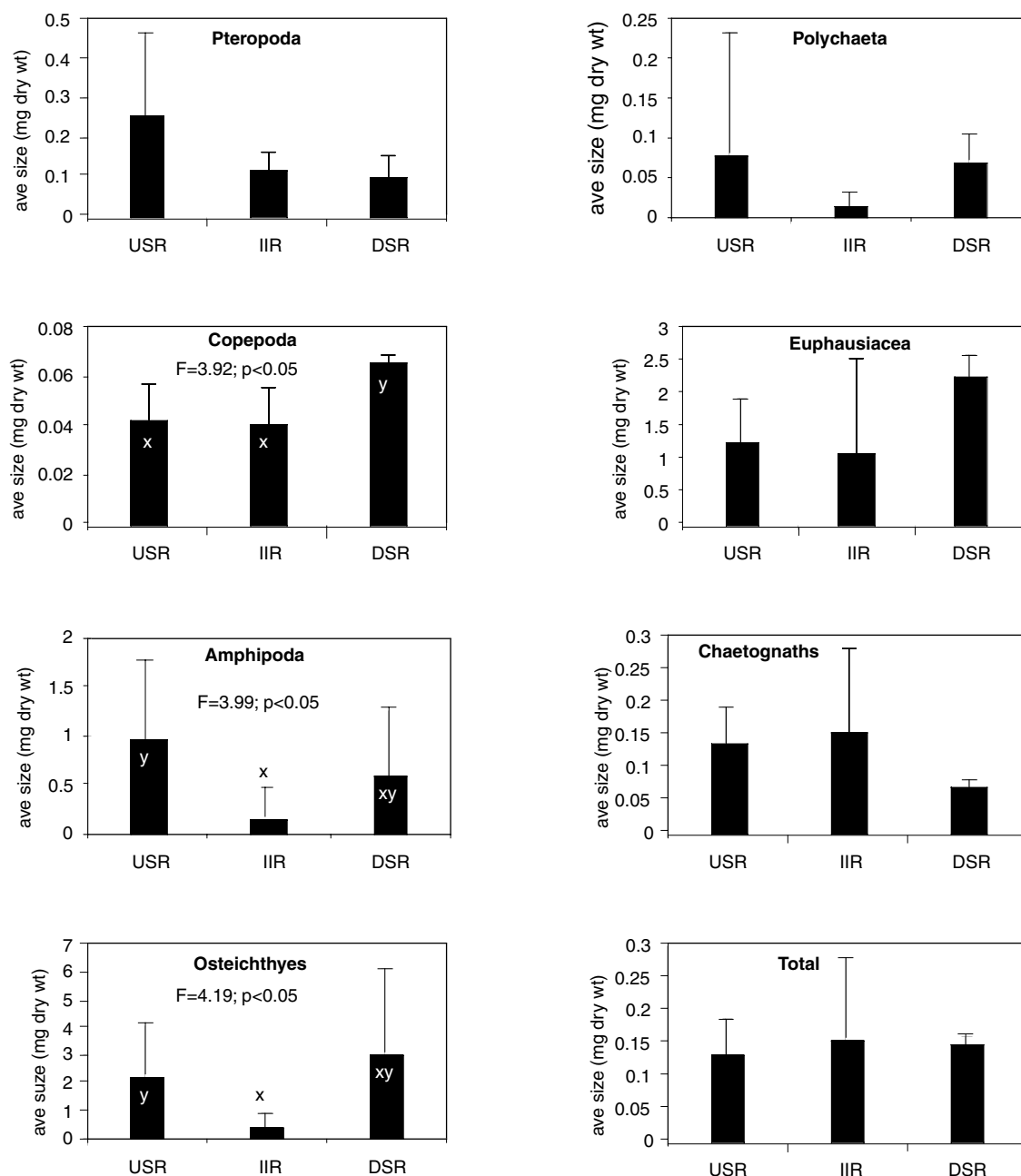
Fig. 3d.

demonstrated little diel and/or regional variation in size, but the average sizes of fish and total zooplankton were significantly higher at night than during the day (Figure 3c). Copepods, euphausiids, fish and total zooplankton were all of a smaller average size in the IIR, during both night and day, copepods and fish significantly so.

In 1999, both abundance and biomass were relatively low in the IIR and highest in the DSR (Table IIA and B).

Ostracods and chaetognaths occurred at significantly higher abundance and biomass in the DSR, and had relatively low levels in the IIR. Copepods occurred at significantly lower abundance in the IIR. Both ostracods and copepods had significantly higher biomass levels in the DSR. As in previous years, the copepods *P. biloba*, *P. abdominalis* and *O. antarctica* occurred at lowest levels in the IIR. Pteropods were of a larger average size in the USR

(Figure 3d). The euphausiids *E. similis* and *E. longirostris* were absent from the IIR, with the exception of a single *E. longirostris* furcilia larva. *Primno macropa* was recorded at highest levels in the IIR.

The average size of polychaetes, amphipods and fish was smallest in the IIR. Euphausiids and copepods were of a larger average size in the DSR, but showed little difference in average size between the USR and IIR. Chaetognaths and total zooplankton were slightly larger in the IIR.

The percentage contribution of the principal euphausiid species differed substantially between regions and years (Figure 4). *Euphausia vallentini* and *T. vicina* were consistently important components of the euphausiid community, particularly in the IIR, where their combined biomass contributed, on average, 89% to total euphausiid biomass. The 1996 and day 1998 surveys were characterized by >50% contributions of *T. vicina* to total euphausiid biomass. The other euphausiid species generally occurred at reduced biomass in the IIR, with *E. longirostris* and *E. similis* typically being completely absent. The upstream and downstream regions had increased contributions of species other than *E. vallentini* and *T. vicina* to total euphausiid biomass.

In general, the average size of *E. vallentini* and *T. vicina* was similar between regions, although both were slightly smaller in the IIR in 1999, and *E. vallentini* was slightly smaller in the IIR in 1996 (Figure 5). *Euphausia longirostris* and *E. similis* demonstrated similar size between USR and DSR in all years, with the exception of 1999, when *E. longirostris* in the DSR were substantially larger than those in the USR. Both *N. megalops* and *Stylocheiron maximum* were generally of a smaller average size in the IIR, while *Thysanoessa gregaria* showed no consistent pattern.

The positions of oceanic fronts along 37°E, in the region directly upstream of the islands, are illustrated in Figure 6. The SAF showed a high degree of variation between surveys. In both 1996 and 1998, the SAF was located to the north of its average position, while in 1997 and 1999 it was located to the south of its average position. In 1999, both the SAF and the APF were in close proximity to the PEIs.

DISCUSSION

The regional patterns of mesozooplankton abundance, biomass and size observed during this study indicated that some groups and species were significantly affected by their interaction with the shallow topography of the PEIs. Consistently low levels of abundance and biomass of certain species, and low average size of copepods, euphausiids, fish and total plankton, were observed in the IIR.

Reduced biomass, together with a reduction in average size, may implicate predator selection of the larger fraction of the mesozooplankton community. The dominant land-based predators of mesozooplankton are macaroni and rockhopper penguins, white-chinned petrels, blue petrels and Salvin's prions (Brown, 1989; Cooper and Brown, 1990). During the breeding season, macaroni and rockhopper penguins are very abundant and comprise an estimated 20% of total avian biomass. However, both species moult (at which time no feeding occurs) in April and then leave the islands to spend the winter at sea (Brown, 1989). Their impact on mesozooplankton populations at the time of our surveys (April–May) would therefore have been negligible. Similarly, white-chinned petrels and Salvin's prions both finish their reproductive cycles by April and the majority would have departed the islands by the time our surveys were conducted (Cooper and Brown, 1990). This leaves blue petrels as the major avian mesozooplankton predators. Together, white-chinned petrels, blue petrels and Salvin's prions have ~20% of the food consumption of macaroni and rockhopper penguins (Brown, 1989). As blue petrels comprise only 4% of the combined abundance of this trio, they would not be expected to impact significantly on mesozooplankton stocks during the survey periods. To date, no comprehensive survey of demersal fish populations has been conducted in the PEI ecosystem and although species composition is relatively well known, the biomass of fish stocks has yet to be quantified (Gon and Klages, 1988). The impact of demersal fish predation on mesozooplankton can therefore not be established, but must be assumed to play a role in the reduced on-shelf biomass. However, the timing of the surveys does seem to coincide with a period of relatively low predation pressure in the seasonal cycle of the PEIs.

Analysis of species-specific distribution patterns gives increased insight into the possible impact of predation. The dominant species of euphausiid, *E. vallentini* and *T. vicina*, showed no significant variation in abundance, biomass or average size between regions, despite their being the principal prey items of land-based vertebrate predators (Gartshore *et al.*, 1988; Brown *et al.*, 1990). Any predation occurring at the time of the surveys, therefore, did not have a significant effect on the population structure of these two species. By contrast, the two large mesopelagic euphausiids, *E. longirostris* and *E. similis*, were almost entirely absent from the IIR, an occurrence that cannot be explained by predation alone, particularly as neither of these species has previously been recorded from the gut contents of either inshore- or offshore-feeding birds (Steele and Klages, 1986; Brown and Klages, 1987; Gartshore *et al.*, 1988; Cooper and Brown, 1990). Amongst the common mesozooplankton species
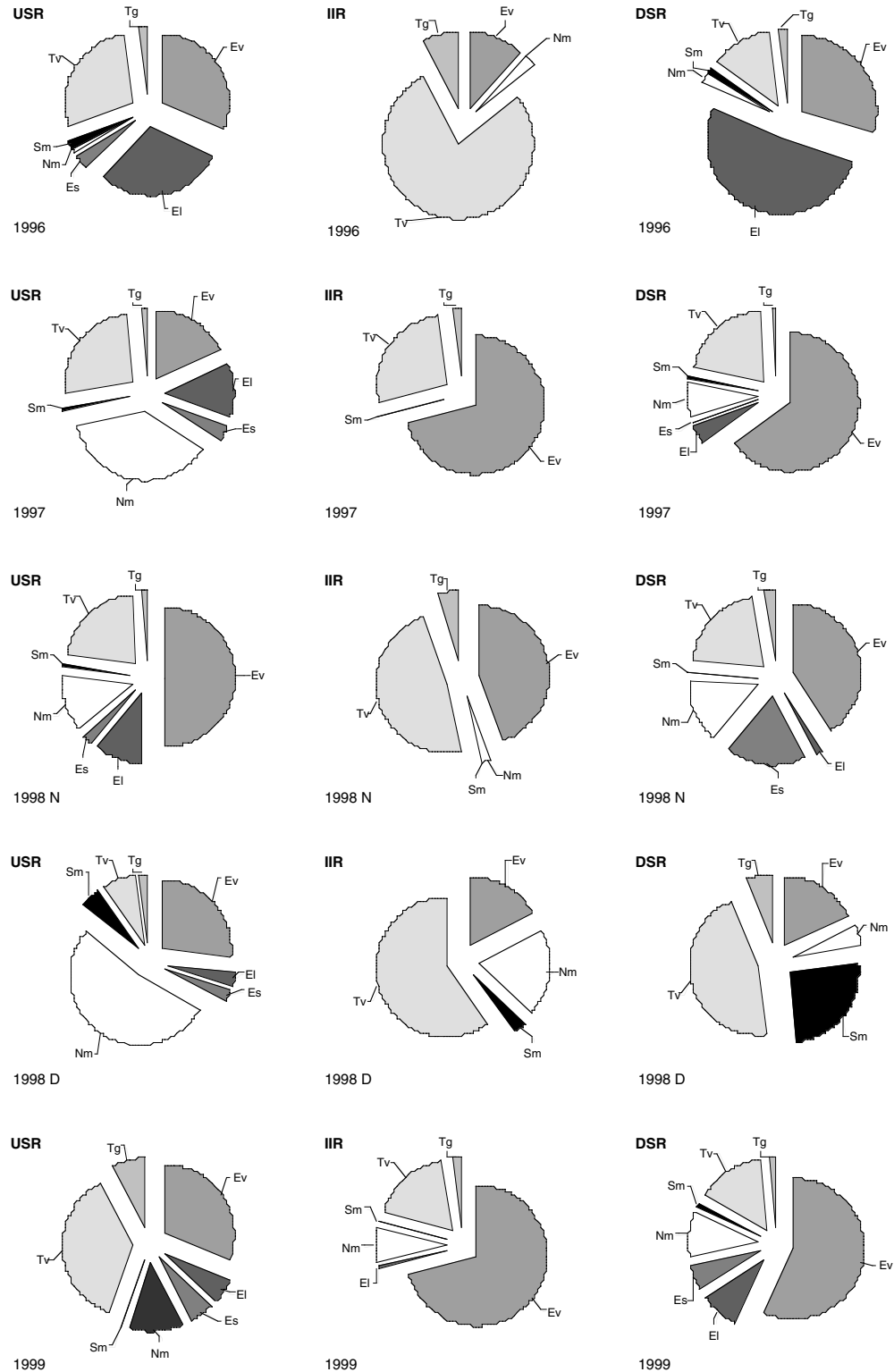
Fig. 4. The percentage contribution of the principal euphausiid species, collected at the PEIs, to total euphausiid biomass in the USR, IIR and DSR regions of all surveys. Ev, *Euphausia vallentini*; El, *Euphausia longirostris*; Es, *Euphausia similis*; Tv, *Thysanoessa vicina*; Nm, *Nematoscelis megalops*; Sm, *Stylocheiron maximum*; Tg, *Themisto gaudichaudii*.
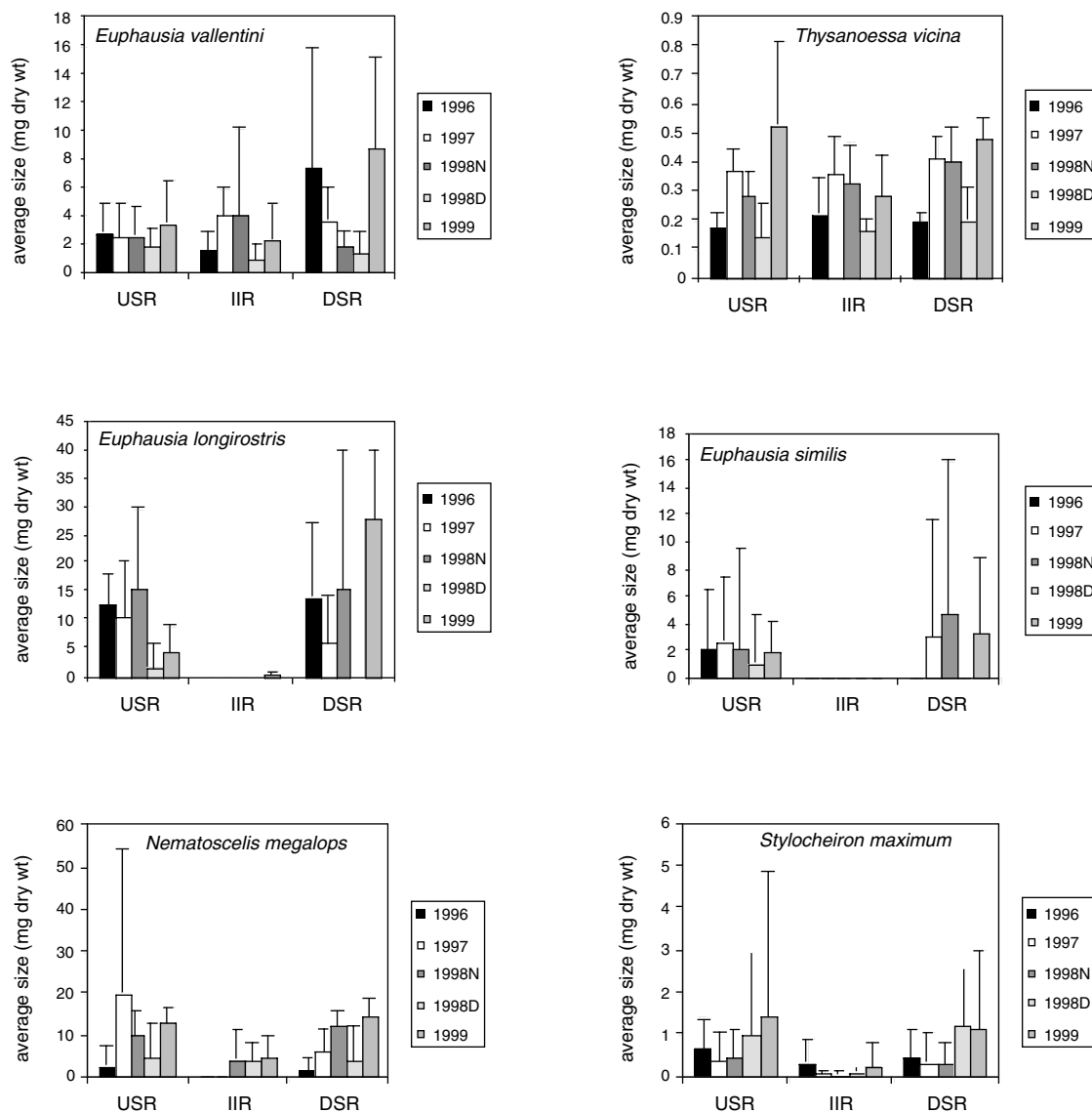
Fig. 5. The average size (mg dry wt individual^{-1}) of the principal euphausiid species recorded from the USR, IIR and DSR regions of the PEIs for each of the four surveys conducted between 1996 and 1999 (1998N, night samples; 1998D, day samples).

collected, the mesopelagic copepods *P. biloba*, *P. abdominalis* and *O. antarctica* all occurred at lowest abundance and biomass in the IIR. Conversely, the typically epipelagic species found within the gelatinous plankton, pteropods, ostracods, many of the copepod species, amphipods, the highly abundant euphausiids *E. vallentini* and *T. vicina*, and chaetognaths, showed no consistent pattern of abundance and biomass distribution between regions. The single exception being the hyperiid amphipod *P. macropa*, which occurred at highest abundance and biomass in the IIR in 1996, 1997 and 1999.

The depth zones occupied by mesozooplankton species

were, therefore, an important factor in determining their occurrence and densities on the PEI shelf, and point to a possible role of diel migration patterns in this regard. A seamount study by Genin *et al.* recorded reduced abundance levels of strongly migrating zooplankton, including *Euphausia pacifica* and *Pleuromamma* spp., in patches downstream of a seamount, formed by daytime advection of these species around the shallow topography (Genin *et al.*, 1994).

The significant night-time increase in abundance and biomass observed in 1998 was associated with a significant increase in average zooplankton size. This was
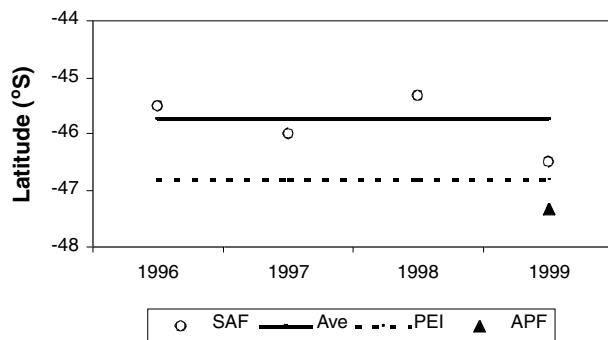
Fig. 6. Positions of oceanographic fronts recorded along 37°E at the time of the April/May surveys (1996–1999). The position of the SAF is indicated by ○ and the position of the APF by ▲. The average position (Ave) of the SAF (indicated by the solid line) in the vicinity of the PEIs was determined from 11 crossings between 1987 and 1999. The latitude of the PEIs is indicated by the dotted line. Figure modified from Hunt *et al.* (Hunt *et al.*, 2001b).

indicative of both an increased contribution of larger planktonic groups (e.g. euphausiids) and an increase in the average size of some groups (particularly copepods and fish). Daytime net avoidance may have contributed to these patterns, but diel vertical migration is expected to have been the dominant factor. There was a clear night-time increase in the biomass of mesopelagic species above 200 m (the maximum sampling depth). There was also a significant increase in the contribution of epipelagic migrators including *E. vallentini*, *T. vicina*, *Ctenocalanus* sp. and *Clausocalanus* sp. Fish had a size-related vertical distri-bution, with larger individuals migrating into the sampling zone at night. Although fish biomass generally did not vary significantly between regions, average size was always lowest in the IIR, indicating either a predation effect or size-differentiated advection due to deeper depths occupied by larger specimens. A similar pattern was evident for the euphausiids *N. megalops* and *S. maximum*.

The obvious absence of some mesopelagic species from the PEI shelf in this study, and the low average size of some species, indicated that differential advection, rather than predation, was an important factor in determining the abundance, biomass and size distributions of meso-zooplankton. It is worth noting that a community struc-ture analysis using abundance data from the same data set did not identify a unique shelf community (Hunt *et al.*, 2001a). Rather, station groupings generally comprised a mix of on- and off-shelf stations. The use of abundance data focused the analysis on species occurring at high densities, including copepods, chaetognaths and pteropods, many of which are epipelagic. However, the importance of mesopelagic species is evident when their

relative contribution to biomass is examined. Of total biomass, *E. longirostris*, *E. similis*, *P. abdominalis*, *P. biloba* and *O. antarctica* together contributed an average of 16% to the USR, 2% to the IIR and 15% to the DSR (Figure 7). The absence of mesopelagic species from the shelf also resulted in large regional differences in euphausiid community structure. An aspect to consider in future studies is the seasonal migration of many Antarctic copepods. Some species occupy surface waters in summer but overwinter at depth, including *C. simillimus*, which is an important component of the PEI copepod community (Atkinson, 1998). These species may be absent, or occur at low abundance, over the PEI shelf waters during the winter months.

The PEIs are an obstacle to current flow and, as a result, flow acceleration will occur around them (Roden, 1987). Given an average horizontal flow of $U \sim 0.20$ m s^{-1} and with $N = 0.0046$ s^{-1} (Brunt–Väisälä frequency), vertical excursions (U/N) onto the shelf would not exceed 45 m [U from Ansorge and Lutjeharms (Ansorge and Lutjeharms, 2002); N from Perissinotto and Duncombe Rae (Perissinotto and Duncombe Rae, 1990)]. There would therefore be a limited amount of advection of waters below the depth of the island shelf (average depth = 200 m). However, even with some vertical transport, strong-swimming plankton such as euphausiids would not necessarily be transported out of their depth preference (Mackas *et al.*, 1997). The bulk of water below 200 m would be expected to pass around the PEI shelf, rather than over it, taking with it most mesopelagic species and deep migrators. The high average biomass of mesozoo-plankton recorded in the DSR during this study indicates that there may be a mechanism that concentrates plankton in this region.

Mesozooplankton size and biomass distribution at the PEIs need to be considered in concert with the prevailing
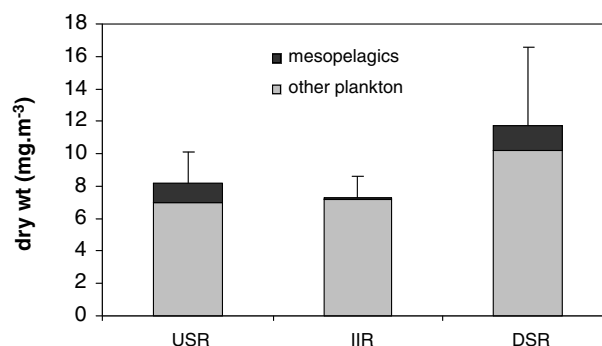
Fig. 7. Average biomass (mg m^{-3}) of mesozooplankton recorded in the USR, IIR and DSR of the PEIs for the four surveys conducted between 1996 and 1999. The dark shading indicates the contribution of mesopelagic species to total biomass.

Table IIIA: Average abundance (individuals m^{-3}) of zooplankton groups recorded from the USR, IIR and DSR regions of the PEIs, during both day and night in 1998

	Night			Day			P REG	P D/N
	USR	IIR	DSR	USR	IIR	DSR		
Gelatinous	X0.236	X 0.150	XY0.519	X0.200	X0.327	Y0.783	*	
Polychaeta	0.088	0.057	0.167	0.073	0.042	0.123		
Pteropoda	7.365	10.721	16.991	5.437	2.183	8.064		*
Ostracoda	4.274	5.354	7.610	3.834	6.932	5.896		
Copepoda	31.182	39.456	87.192	17.068	38.622	31.264		
Euphausiacea	Y4.067	Y4.374	Y3.599	X0.488	X1.417	X0.772	**	***
Decapoda	0.016	0.019	–	0.001	0.019	0.000		
Amphipoda	0.150	0.176	0.293	0.201	0.147	0.091		
Chaetognatha	X5.092	X4.933	Y11.853	X6.332	X6.711	Y11.698	*	
Osteichthyes	0.140	0.197	0.166	0.085	0.106	0.137		
Total	XY52.616	XY65.444	Y128.408	X33.725	XY56.528	XY58.862	*	*
Protomyctophum sp.	0.127	0.179	0.138	0.083	0.102	0.136		
E. hamata	3.853	3.322	10.315	5.098	4.938	9.240	*	
S. gazellae	1.239	1.611	1.538	1.234	1.772	2.459		
P. macropa	0.017	0.029	0.031	0.014	0.019	0.009		
T. gaudichaudii	0.119	0.141	0.262	0.178	0.128	0.082		
E. vallentini	0.712	0.377	0.654	0.071	0.050	0.046		***
E. longirostris	Y0.028	–	X0.002	X0.005	–	–	*	
E. similis	0.004	–	0.030	0.002	–	–		
N. megalops	0.054	0.003	0.057	0.034	0.011	0.001		
S. maximum	0.064	0.033	0.078	0.049	0.038	0.111		
T. vicina	3.198	3.921	2.750	0.321	1.279	0.608		***
T. gregaria	0.007	0.012	0.018	0.004	–	0.006		
A. armatus	0.222	0.265	0.035	0.180	0.358	0.547		
C. simillimus	XY2.850	XY2.994	Y45.547	X1.200	XY1.484	Y9.590	**	
C. laticeps	0.784	2.754	1.064	0.395	0.439	0.904		*
C. brevipes	8.521	14.151	11.422	5.437	8.791	4.934		*
C. vanus	5.569	8.879	8.537	2.936	6.549	2.216		*
H. austrinus	0.216	0.046	0.459	0.134	0.018	0.136		
M. lucens	4.141	2.930	5.019	1.771	6.524	2.997		
O. frigida	X1.659	XY2.591	XY2.899	X1.595	Y7.804	XY2.567	*	
O. antarctica	XY0.156	–	XY0.488	XY0.152	XY0.049	Y0.731	**	
P. biloba	0.408	0.029	0.390	0.205	0.119	0.283		
P. abdominalis	1.392	0.160	0.827	0.014	0.477	0.024		**
R. gigas	0.102	0.101	0.133	0.011	0.257	0.621		
S. minor	1.716	1.371	2.904	0.971	3.176	0.520		
L. retroversa	6.074	9.141	14.423	4.808	1.296	6.542		*
Tomopteris sp.	0.080	0.054	0.125	0.065	0.024	0.096		

One-way ANOVAs were used to investigate differences between day and night samples independent of regional variation. Newman–Keuls multiple range tests were used to investigate regional differences and diel variation between regions, and significant differences between regions are indicated by different letters. REG, differences between regions; D/N, differences between day and night samples. *$P < 0.05$; **$P < 0.01$; ***$P < 0.005$.

Table IIIB: Average biomass (mg dry wt m^{-3}) of zooplankton groups recorded from the USR, IIR and DSR regions of the PEIs, during both day and night in 1998

	Night			Day			P REG	P D/N
	USR	IIR	DSR	USR	IIR	DSR		
Gelatinous	0.090	0.122	0.109	0.115	0.023	0.404		
Polychaeta	0.003	0.002	0.006	0.003	0.001	0.006		
Pteropoda	0.869	1.700	2.185	0.707	0.204	0.838		
Ostracoda	0.147	0.185	0.262	0.132	0.239	0.203		
Copepoda	1.566	1.129	7.588	0.545	1.070	2.174		
Euphausiaceae	Y4.132	Y2.747	Y4.508	X0.648	X0.369	X0.405	**	***
Decapoda	0.216	0.049	0.000	0.005	0.008	0.006		
Amphipoda	0.727	0.817	1.428	0.402	0.693	0.296		*
Chaetognatha	0.472	0.443	1.302	0.546	0.462	1.087		
Osteichthyes	X0.201	X0.213	Y0.884	X0.029	X0.032	X0.046	**	**
Total	XY8.423	XY7.407	Y18.272	X3.131	XY3.103	XY5.465	*	*
Protomyctophum sp.	0.092	0.179	0.237	0.024	0.030	0.040		***
E. hamata	X0.277	X0.237	Y1.070	XY0.332	XY0.325	XY0.750	**	
S. gazellae	0.196	0.206	0.232	0.215	0.137	0.337		
P. macropa	0.668	0.760	1.405	0.359	0.682	0.278		*
T. gaudichaudii	0.044	0.023	0.023	0.040	0.011	0.018		
E. vallentini	2.081	1.221	1.833	0.172	0.063	0.072		***
E. longirostris	Y0.438	–	X0.084	X0.024	–	–	*	*
E. similis	0.103	–	0.837	0.018	–	–		
N. megalops	0.562	0.052	0.679	0.344	0.072	0.021		
S. maximum	0.017	0.004	0.011	0.028	0.010	0.103		*
T. vicina	0.884	1.334	0.968	0.049	0.218	0.185		***
T. gregaria	0.047	0.136	0.098	0.013	–	0.025		*
A. armatus	0.009	0.011	0.001	0.007	0.014	0.022		
C. simillimus	X0.296	XY0.324	Y6.259	X0.112	X0.155	XY1.323	**	
C. laticeps	0.015	0.054	0.021	0.008	0.009	0.018		
C. brevipes	0.170	0.282	0.228	0.108	0.175	0.098		*
C. vanus	0.108	0.172	0.165	0.057	0.127	0.043		*
H. austrinus	0.051	0.011	0.109	0.032	0.004	0.032		
M. lucens	0.098	0.081	0.100	0.033	0.094	0.089		
O. frigida	X0.005	X0.008	X0.009	X0.005	Y0.023	X0.008	*	
O. antarctica	0.001	–	0.004	0.001	<0.001	0.007	*	
P. biloba	0.130	0.009	0.124	0.065	0.038	0.090		
P. abdominalis	0.345	0.040	0.205	0.003	0.118	0.006		*
R. gigas	0.016	0.009	0.024	0.002	0.024	0.126		
S. minor	0.033	0.026	0.056	0.019	0.061	0.010		
L. retroversa	0.817	1.426	1.854	0.645	0.142	0.824		
Tomopteris sp.	0.003	0.002	0.005	0.003	0.001	0.004		

One-way ANOVAs were used to investigate differences between day and night samples independent of regional variation. Newman–Keuls multiple range tests were used to investigate regional differences and diel variation between regions, and significant differences between regions are indicated by different letters. REG, differences between regions; D/N, differences between day and night samples. $*P < 0.05$; $**P < 0.01$; $***P < 0.005$.

hydrodynamic conditions. The proximity of the SAF to the PEIs appeared to be a major determinant of hydrodynamics in the vicinity of the islands and the flow regime over the island shelf (Perissinotto and Duncombe Rae, 1990; Ansorge and Lutjeharms, 2000; Pakhomov *et al.*, 2000). Approximately 75% of the ACC baroclinic transport is associated with the SAF and APF, while the PFZ between them is a region of weak flow (Nowlin and Klinck, 1990). However, both of these fronts show a high degree of positional variability in the vicinity of the PEIs (Lutjeharms and Valentine, 1984; Nagata *et al.*, 1988). It has been suggested that when the SAF lies far to the north of the islands, lower ACC current velocities result in water retention over the PEIs shelf and the formation of eddies in the downstream region (Perissinotto *et al.*, 2000). The trapping of water over the island shelf and the associated build-up of fresh water and nutrient run-off can result in extensive phytoplankton blooms with chlorophyll *a* biomass an order of magnitude greater than values typical of the PFZ (Perissinotto and Duncombe Rae, 1990). Conversely, when high ACC current velocities are recorded in the vicinity of the PEIs, advective forces prevail and a flow-through system is established between the islands. The occurrence of high current velocities correlates well with the SAF being in close proximity to the archipelago (Ansorge and Lutjeharms, 2000; Pakhomov *et al.*, 2000). Prevailing current velocity would also be expected to affect the amount of vertical transport over the shelf. At the same N values, it could vary from 21.7 m at 10 cm s^{-1} to <55 m at 25 cm s^{-1}.

In both 1996 and 1998, the SAF was to the north of its average position. In theory, conditions should have favoured water retention over the island shelf (Perissinotto and Duncombe Rae, 1990). In 1996, increasing chlorophyll *a* values recorded through the survey indicated the development of a phytoplankton bloom, providing biological evidence for water retention in the IIR (Pakhomov and Froneman, 1999). The increased residence time of water in the IIR would be expected to enhance the impact of predation on zooplankton stocks, while advective replenishment would be greatly reduced. This was supported by the low total zooplankton biomass and significantly lower average zooplankton size in the IIR in 1996. Indeed, 1996 was the only year in which euphausiid biomass and size were significantly lower in the IIR. *Euphausia vallentini* occurred at low biomass levels in the IIR and fish biomass was also extremely low in the IIR relative to the off-shelf waters. It is worth noting that the substantial decreases in zooplankton biomass in the PEIs shelf region recorded in March 1976 and April/May 1983 both coincided with periods of increased water retention between the islands (Grindley and Lane, 1979; Perissinotto and Duncombe Rae, 1990).

There was little evidence for water retention in 1998, although elevated microphytoplankton biomass in the IIR, a feature characteristic of phytoplankton blooms associated with water retention, indicated that the advection of water over the shallower shelf waters was reduced (Hunt, 2000). A CTD survey conducted after the completion of this study's mesozooplankton survey observed limited water movement over the shelf (Pakhomov *et al.*, 2000). This is consistent with the slow current velocities predicted when the SAF is far to the north of the islands. In 1997, although no water retention was observed, current velocities in the vicinity of the islands remained relatively low (Ansorge and Lutjeharms, 2002). Both the 1997 and 1998 surveys demonstrated a similar pattern of reduced zooplankton size in the IIR.

The 1999 survey was conducted while both the SAF and APF were in close proximity to the PEIs. This was the only survey during which average zooplankton size in the IIR was comparable with that in the USR and DSR. In particular, average copepod and euphausiid size in the IIR was similar to that in the USR. Stronger advective forcing during periods of high current flow may transport a higher proportion of large, deep-water plankton onto the island shelf. However, the absence of mesopelagic species from the IIR, and small average size of fish in this region, indicated that even in the above scenario deep-water advection into the IIR was limited. Possibly a more important contributor to the large average size of plankton in the IIR may have been constant replenishment of zooplankton stocks from the upstream region due to high-velocity flows, coupled with the biological enhancement associated with the SAF and APF (Lutjeharms *et al.*, 1985; Pakhomov and McQuaid, 1996).

In conclusion, the PEIs shelf region was generally characterized by low average zooplankton size and biomass. The study seemed to be conducted during a period of relatively low predation pressure, although the importance of fish could not be assessed. The vertical distribution of mesozooplankton appeared to be the major factor determining their absence or occurrence on the island shelf. Mesopelagic species were typically absent, while strongly migrating night-time epipelagic species occurred at reduced densities. Conversely, epipelagic species showed no consistent distribution differences between regions. It is possible that the size distribution of species over the island shelf may be affected by changes in vertical migration behaviour with age. Predation may be of greater importance in determining zooplankton distribution patterns and population size structure during the summer season (December–March), and particularly during periods of on-shelf water retention. The biomass of mesozooplankton was consistently high in the region downstream of the island shelf, suggesting a concentrating

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