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Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during the BROKE-West campaign

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ABSTRACT

The composition and distribution of squid and fish collected by Rectangular Midwater Trawls in the upper 200 m were investigated during the BROKE-West (Baseline Research on Oceanography, Krill and the Environment-West) survey (January–March 2006) in CCAMLR Subdivision 58.4.2 of the Southern Ocean. A total of 332 individuals were collected, with the most abundant fish species being *Pleuragramma antarcticum* (34%), *Notolepis coatsi* (27%) and *Electrona antarctica* (26%); and the most abundant squid being *Galiteuthis glacialis* (64%). Abundances of all species were among the lowest recorded using this type of gear. Cluster analysis revealed two distinct communities: a notothenioid-dominated coastal community and an oceanic community dominated by mesopelagic fish and squid. Environmental factors related to this segregation were explored using Redundancy Analysis (RDA). The notothenioid *P. antarcticum* was associated with shallow areas with high chlorophyll *a* concentrations. Larval stages of *E. antarctica*, *N. coatsi* and *G. glacialis* were found over deeper water and were positively correlated with higher temperatures and a deeper-reaching mixed layer. Postmetamorphic stages of *E. antarctica* were caught mostly after sunset and were negatively correlated with solar elevation. The observation of higher densities in the eastern part of the sampling area reflects a temporal rather than a geographical effect. Samples of the three most abundant fishes, *E. antarctica*, *P. antarcticum* and *N. coatsi*, were analysed for gut content. All species fed on a variety of mesozooplankton including copepods, amphipods and euphausiids, which is consistent with previous reports on similar life stages. Mean body energy density was highest for *E. antarctica* (27 kJ g⁻¹), while it was similar for *P. antarcticum* and *N. coatsi* (22 kJ g⁻¹). The high energy content emphasizing the importance as a food resource for top predators in the Southern Ocean.

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1. Introduction

Species composition of fish and squid in the pelagic realm is not random, as they migrate between locations with favourable conditions, resulting in distinct distributions and assemblages (Kock, 1992; Jackson et al., 2002). These differences in distribution are often related to hydrographical properties such as water depth, density, temperature, the presence of seamounts or islands, or the position of fronts (Reid et al., 1991; Loots et al., 2007). Vertical distributional differences may be related to ontogenetic shifts within species, often larval stages are found in the pelagic

zone enhancing survival by niche segregation and dispersal by surface currents.

Two distinct fish assemblages characterize the pelagic Southern Ocean (Efremenko and Pankratov, 1988). The oceanic assemblage is dominated by meso- and bathypelagic fish while the coastal assemblage is characterized by the dominance of notothenioid juveniles (Koubbi et al., 1991; Kock, 1992; Pakhomov et al., 1995). The pelagic Antarctic shelf zone is dominated by the nototheniid *Pleuragramma antarcticum* and pelagic larvae and juveniles of four notothenioid families: Artedidraconidae, Bathydraconidae, Nototheniidae and Channichthyidae (Williams and Duhamel, 1994; Hoddell et al., 2000). Larvae and fingerlings of *P. antarcticum* live close to the surface, often in association with krill swarms, while adults stay closer to the bottom (Hubold et al., 1985). In the oceanic zone south of the Antarctic Polar Front (APF) lanternfish (family Myctophidae) of

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the genus *Electrona* and Paralepididae of the genus *Notolepis* are among the most abundant in terms of biomass and numbers (Efremenko and Pankratov, 1988; Kock, 1992). Larvae of *Electrona antarctica* and *Notolepis coatsi* are abundant in the surface layers (Efremenko and Pankratov, 1988; Hoddell et al., 2000). Older individuals are mainly distributed between 200 and 600 m depth during daytime and shift upward above 200 m at night (Torres and Somero, 1988). *E. antarctica* migrates to the upper 100 m and has been reported close to the surface.

Southern Ocean squid are generally absent from the shelf zone and their distribution is often linked to broad-scale hydrography (Jackson et al., 2002; Collins and Rodhouse, 2006). The circumantarctic pelagic squid *Galiteuthis glacialis* is restricted to cold Antarctic waters, displays ontogenetic descent and is one of the most abundant and widely distributed of the Antarctic squids (Rodhouse and Clarke, 1986; Jackson et al., 2002; Collins and Rodhouse, 2006).

Historically, Antarctic macrozooplankton dynamics have been mainly studied in either the Atlantic or Indian sectors of the Southern Ocean, with efforts concentrating in the vicinity of the Antarctic Peninsula (Piatkowski, 1985; Hopkins, 1987; Hopkins and Torres, 1989; Siegel and Piatkowski, 1990), Prydz Bay regions (Pakhomov, 1989, 1993; Hosie, 1994), and recently the Cosmonaut Sea (Hunt et al., 2007). Larval and juvenile squid and fish, a component of macroplankton, have at times been documented (Lubimova et al., 1988; Filippova and Pakhomov, 1994). Nevertheless data on distribution patterns in many areas remain disjointed and the underlying mechanisms responsible for their distribution are poorly understood.

The study area during BROKE-West was the CCAMLR statistical zone 58.4.2, which includes the Cosmonaut Sea to the west and Prydz Bay area to the east. To date only a few studies have investigated the distribution of fish in the Prydz Bay region (Pankratov and Pakhomov, 1988; Gerasimchuk et al., 1990; Williams and Duhamel, 1994), and only a single study documented fish larval distribution in the Cosmonaut Sea (Efremenko and Pankratov, 1988). This large-scale survey, comparable to the BROKE-West campaign in design but using different gear over a greater depth range, was only carried out once during the summer of 1984 (Lubimova et al., 1988). Another dataset comparable to the BROKE-West campaign was available from the BROKE-east sampling campaign in 1996, which took place in the area immediately to the east of the present study and used a similar methodology (Hoddell et al., 2000; Nicol et al., 2000).

Geographically there are two major water bodies in the area. To the west there is the Cosmonaut Sea with an intrusion of the eastern boundary of the Weddell Gyre. To the east there is the Cooperation Sea characterized by the Prydz Bay Gyre. To the south both gyral systems are bordered by the fast and narrow westward-flowing Antarctic Slope Current. The eastward flowing Antarctic Circumpolar Current (ACC) forms the northern boundary of the two gyral systems but has a more southern extension in the Cooperation Sea. The ACC is characterized by the southern ACC front and its southern limit is formed by the Southern Boundary (SB). Detailed descriptions of the oceanographic patterns observed during BROKE-West are available from Williams et al. (2010) and Meijers et al. (2010).

This paper represents a baseline assessment of the nektonic squid and fish fauna in the pelagic zone of the Cosmonaut and Cooperation Seas. The aim is to investigate the abiotic factors responsible for the spatial and temporal structuring of the oceanic and coastal communities. The role of key species is further explored by investigating their role as consumers and as potential food sources for top predators.

2. Material & methods

2.1. Sampling procedure

Samples were collected during the BROKE-West cruise of RV “Aurora Australis” (05/06 V3) in the CCAMLR statistical subarea 58.4.2, between January 2 and March 17, 2006 (Fig. 1).

The sampling grid consisted of 11 longitudinal transects between 30° and 80°E and 52°S south to the Antarctic coastline. Fish were caught using Rectangular Midwater Trawl nets (RMT 8 + 1), consisting of a RMT 1 mounted above a RMT 8 with a mouth area of 1 and 8 m² and a cod end mesh size of 0.33 and 0.85 mm, respectively. Two types of methods were used: target trawls and routine trawls. Target trawls were not pre-planned and were aimed at acoustically detected aggregations. The net was lowered to the depth of the aggregation, and opened and closed remotely. Routine hauls consisted of a standard double oblique tow from the surface down to 200 m and back again to the surface. Towing speed was approximately 2.5 knots (4.5 km h⁻¹). Further details on the sampling procedure are outlined in Kawaguchi et al. (2010).

Fish and squid were sorted from the total catch of the RMT 8 and identified to species level wherever possible. Fish standard length was measured onboard to the lowest mm below and fish were preserved on absolute ethanol, formalin or initially frozen at -80 °C and stored at -20 °C. Squid were preserved in absolute ethanol onboard; measuring of the mantle length to the lowest mm below and identification was done in the laboratory.

2.2. Stomach content

Formalin preserved samples and a small subsample of stomachs taken from a few larger frozen fish designated for energy measurements were analysed in the lab. Stomach content was analysed according to the method described in Pakhomov et al. (1996). Results from stomach content analyses were expressed as a percentage of each food item of the total number of food items counted (N, %).

2.3. Water and energy content

Dry mass and energy content was determined from frozen specimens. To prevent errors due to the loss of body fluids during dissection, water and energy contents were determined for whole individuals only. Only for the few larger specimens caught, stomach content was analyzed before desiccation. Frozen fish were thawed, blotted dry and total wet weight (WW) was determined to the nearest mg. Fish were freeze-dried until complete desiccation (constant mass). After drying, they were re-weighed to determine the total dry weight (DW). Water content was calculated as the difference between WW and DW, expressed as %WW. Individual DW and WW energy content, expressed as kJ g⁻¹, was determined by an isoperibol bomb calorimeter calibrated with benzoic acid. After homogenizing, either the whole fish or a subsample (0.1–0.6 g) was used for calorimetry, depending on the size of the fish.

2.4. Additional data

The RMT net used for sampling was equipped with a CTD, providing detailed data on conductivity, temperature (C°), salinity (PSU), pressure (dBar) and fluorescence (Gorton, 2006). Additional oceanographic information such as mixed-layer depth (MLD) and position of fronts was provided by Williams et al. (2010). Solar azimuth, elevation and day length were calculated as a measurement of light conditions, according to a procedure used by NOAA (Cornwall, 2007).

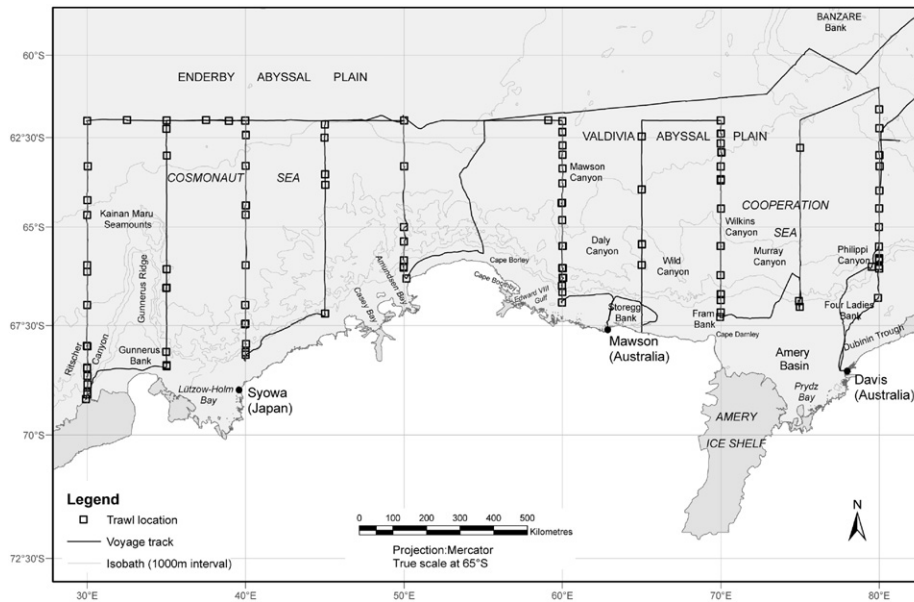


Fig. 1. Station grid sampled during BROKE-West. The trawl locations as well as the main oceanic and bathymetric features in the area are indicated. Map produced by the Australian Antarctic Data Centre © Commonwealth of Australia.

Table 1
Overview of fish caught by routine, target and combined RMT-8 nets.

	No. of individuals						No. of stations						Mean Number per 10^5 m^3		
	All trawls		Routine trawls		Target trawls		All trawls		Routine trawls		Target trawls		All trawls	Routine trawls	Target trawls
	n	%	n	%	n	%	n	%	n	%	n	%			
Total fish	332	100	183	55.12	149	44.88									
Total stations							125	50			75				
Empty							65	52	13	26	52	69.33			
Myctophidae															
<i>Electrona antarctica</i> all	87	26	73	39.89	14	9.4	27	21.6	21	42	6	8	2.392	3.211	1.95
<i>E. antarctica</i> larvae	56	17	48	26.23	8	5.37	21	16.8	16	32	5	6.67	1.438	2.142	1.022
<i>E. antarctica</i> Postmetamorphic	31	9.3	25	13.66	6	4.03	11	8.8	8	16	3	4	0.955	1.069	0.928
<i>Gymnoscopelus braueri</i>	1	0.3	0	-	1	0.67	1	0.8	0	-	1	1.33	0.101	-	0.177
<i>Protomyctophum bollini</i>	1	0.3	1	0.55	0	-	1	0.8	1	2	0	-	0.023	0.058	-
Paralepididae															
<i>Notolepis coatsi</i>	88	27	77	42.08	11	7.38	33	26.4	24	48	9	12	2.016	3.358	1.184
Macrouridae															
Macrouridae sp.	1	0.3	1	0.55	0	-	1	0.8	1	2	0	-	0.015	0.038	-
Arteidraconidae															
<i>Arteidraco scottsbergi</i>	1	0.3	1	0.55	0	-	1	0.8	1	2	0	-	0.013	0.033	-
<i>Pogonophryne marmorata</i>	3	0.9	1	0.55	2	1.34	3	2.4	1	2	2	2.67	0.095	0.046	0.135
Bathydraconidae															
<i>Bathyraco</i> sp.	5	1.5	2	1.09	3	2.01	4	3.2	2	4	2	2.67	0.231	0.103	0.334
<i>Cygnodraco mawsoni</i>	4	1.2	1	0.55	3	2.01	3	2.4	1	2	2	2.67	0.246	0.059	0.391
<i>Gerlachea australis</i>	1	0.3	1	0.55	0	-	1	0.8	1	2	0	0	0.022	0.056	-
<i>Gymnodraco acuticeps</i>	3	0.9	3	1.64	0	-	3	2.4	3	6	0	0	0.055	0.136	-
Channichthyidae															
<i>Chionodraco</i> sp.	9	2.7	2	1.09	7	4.7	5	4	2	4	3	4	0.295	0.073	0.468
<i>Cryodraco antarcticus</i>	2	0.6	0	-	2	1.34	2	1.6	0	0	2	2.67	0.086	-	0.152
<i>Pagetopsis maculatus</i>	5	1.5	1	0.55	4	2.68	4	3.2	1	2	3	4	0.206	0.046	0.33
Nototheniidae															
<i>Pleuragramma antarcticum</i>	113	34	13	7.1	100	67.11	11	8.8	6	12	5	6.67	3.417	0.552	5.627
<i>Trematomus</i> sp.	3	0.9	1	0.55	2	1.34	3	2.4	1	2	2	2.67	0.119	0.046	0.176
Unidentified spp.	5	1.5	5	2.73	0	-	3	2.4	3	6	0	-	0.083	0.206	-

2.5. Data analysis

For each species the total number of individuals, frequency of occurrence and individual densities were calculated for the routine and target trawls separately and combined. Individual densities of all species were calculated (ind. per 10^5 m^3). Fish

community structure was investigated by hierarchical cluster analysis for routine and target trawls separately. Clustering was done based on a Bray-Curtis dissimilarity matrix of presence-absence data of each species per station excluding zero catch stations, using the Unweighted Pair Group Method with Arithmetic mean (UPGMA).

For the most abundant and frequent species, association with environmental variables was analysed using a direct gradient analysis. Redundancy Analysis (RDA) was the optimal method based on the methodology of Leps and Smilauer (2003). RDA is an extension of Principal Component Analysis that explicitly models response variables as a function of explanatory variables. In order to meet the requirements for redundancy analysis, only routine stations were included and species abundance data for each station was $\log(X+1)$ transformed.

For the energy content analysis, fish of *E. antarctica* and *P. antarcticum* were divided in size classes. In order to obtain biologically more relevant categories we calculated age based on reliable age-size regressions available in the literature (Hubold and Tomo, 1989; Greely et al., 1999). Since these categories do not correspond to real age classes, we refer to them as age groups (Table 4).

3. Results

3.1. Diversity and abundance of all species

One hundred twenty five trawls resulted in a total of 332 fish and larvae collected at 60 stations (Table 1). A total of 16 fish taxa were identified. Three species belonging to three different taxa comprised 87% of the total catch: i.e. various stages of the nototheniid *Pleuragramma antarcticum* (34%), larval stages of the paralepidid *Notolepis coatsi* (27%), and larval and postmetamorphic stages of the myctophid *Electrona antarctica* (26%). The remaining catch was dominated by a variety of notothenioids (12%).

The frequency of occurrence of species showed a slightly different pattern: *P. antarcticum* was not so dominant (9%), while *N. coatsi* (26%) and *E. antarctica* (22%) showed similar proportions. Catch success and composition were remarkably different between routine and target trawls. Target trawls caught fish less frequently than routine trawls, as shown by the number of trawls lacking fish (69 vs. 26%, respectively). While *E. antarctica* and *N. coatsi* were more abundant in routine trawls, target trawls were numerically dominated by *P. antarcticum* (Table 1).

Table 2A total of 58 squid paralarvae and small juveniles were collected at 37 of the 125 stations (Table 2). Not all squid could be identified to species level, resulting in 21% unidentified individuals, 16% unidentified cranchiid squid, and only one positively identified species, *Galiteuthis glacialis*. Both in routine and target trawls (63 and 67%, respectively) the most abundant species was *G. glacialis*, totalling 64% of all squid caught. The occurrences of squid in the trawls were lower than those of fish. Especially the target trawls were often void of squid (85%); about half of the routine trawls (52%) didn't catch squid either. All squid

were small juveniles or paralarvae with an average size of 11.8 mm and ranging in size between 4.3 mm and 35.6 mm (Table 2).

3.2. Abundance and distribution of common species

Although numerically the most abundant, *P. antarcticum* (n=113) did not occur in many trawls (8%). This was due to one target trawl with a large catch (n=94) of fingerlings (size range 56–93 mm SL) in the western section of the sampling area (Figs. 2 and 3). Size-wise, the large catch probably corresponds to age group 2+ as calculated based on the size-age regression in Hubold and Tomo (1989). The remainder of the size range of *P. antarcticum* was poorly sampled with some larvae and postlarvae, and several adult specimens (age group >5+) caught in the vicinity of Prydz Bay. *P. antarcticum* was mostly confined to the shelf area (depth <1000 m), only occurring at two oceanic stations close to the shelf (Fig. 3).

N. coatsi was the second most abundant species (n=88) and the most frequently occurring (26% of all trawls). It was frequently caught in routine trawls (48%) but hardly present in target trawls (12%). The bulk constituted of postlarvae and small juveniles (size range 20–55 mm SL) (Fig. 2). The two largest adult specimens were caught in a single target trawl near Prydz Bay. *N. coatsi* occurred evenly throughout the oceanic zone and was occasionally caught in the margin of the Antarctic Slope (Fig. 3).

E. antarctica was the third most abundant species (n=87) and occurred the second most frequently (22%). Total numbers were similar to *N. coatsi*. The bulk of *E. antarctica* were larval stages smaller than 20 mm SL. Size classes larger than 30 mm SL were relatively evenly represented, not allowing the distinction of separate cohorts (Fig. 2). Because of differences in ecology and behaviour, the distribution of larval and post-metamorphic stages of *E. antarctica* is shown separately (Fig. 3). Except for the westernmost transect, larval stages were abundant and widespread in the oceanic regions. Postmetamorphic specimens were more frequent in the eastern part of the sampling area.

3.3. Other fish species

Two postmetamorphic myctophids, *Protomyctophum bolini* and *Gymnoscopelus braueri*, were sampled in the central northern part of the sampling area (Appendix 1). A single macrourid was caught on the first transect to the west of Gunnerus Ridge. A range of nototheniid species were caught mainly over the continental shelf but also in the north-eastern part of the Cooperation Sea towards BANZARE Bank. Two species of larval atredidraconids were caught close to the continental slope (depth ~1000 m).

Table 2
Overview of squid caught by routine, target and combined RMT-8 nets.

	No. of individuals						No. of stations						Mean Number per 10 ⁵ m ³			
	All trawls		Routine trawls		Target trawls		All trawls		Routine trawls		Target trawls		All trawls	Routine trawls	Target trawls	
	n	%	n	%	n	%	n	%	n	%	n	%				
Total Squid	58		43	0.74	15	0.3										
Total Stations																
Empty							88	70	24	48	64	85.33				
Unidentified squid	12	20.7	8	18.6	4	27	11	8.8	7	14	4	5.33	0.206	0.155	0.257	
<i>Galiteuthis glacialis</i>	37	63.8	27	62.8	10	67	24	19	16	32	8	10.67	0.508	0.498	0.519	
Unidentified cranchiid	9	15.5	8	18.6	1	6.7	6	4.8	5	10	1	1.33	0.078	0.136	0.021	

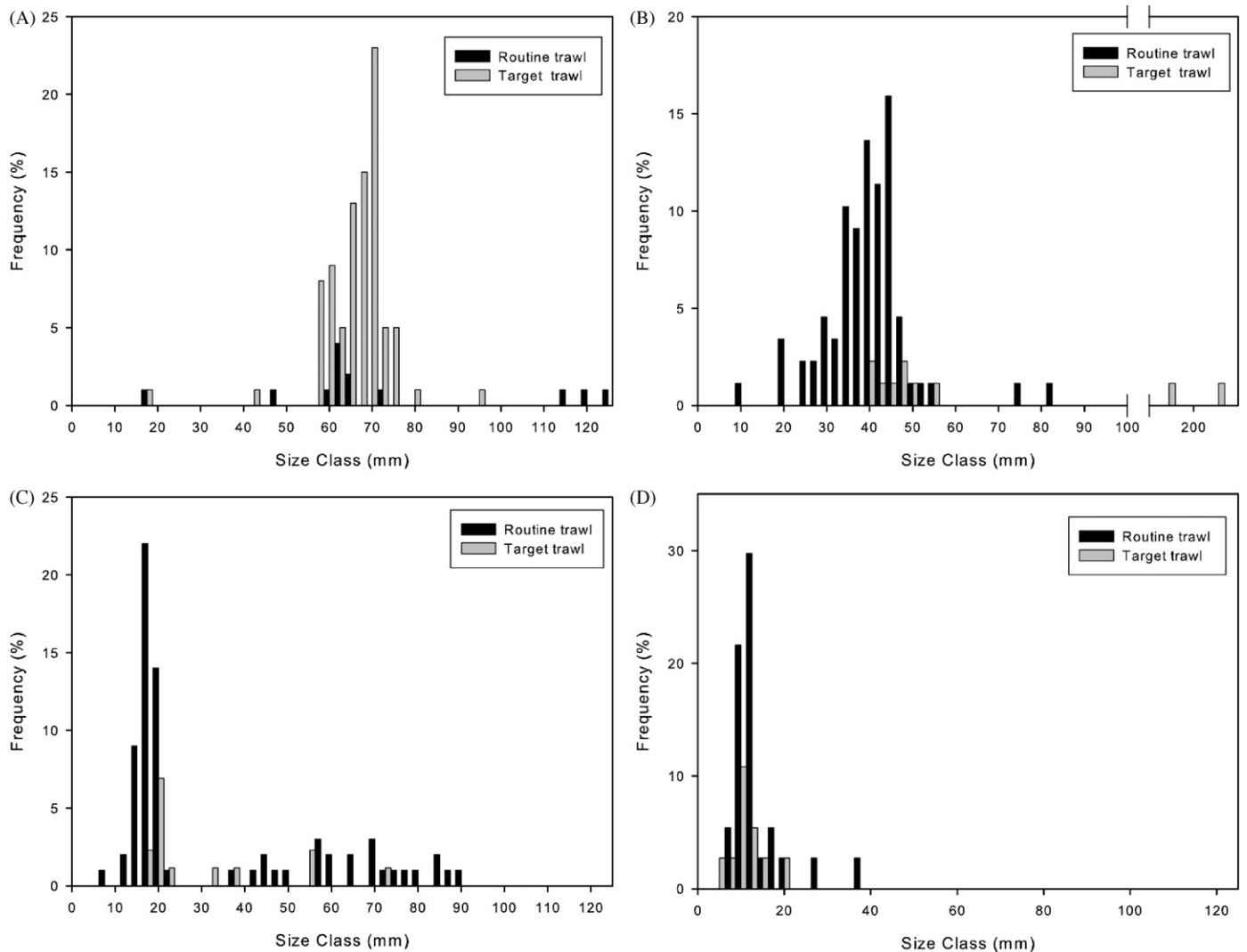


Fig. 2. Size-frequency histogram for target and routine trawls of (A) *Pleuragramma antarcticum*, (B) *Notolepis coatsi*, (C) *Electrona antarctica* and (D) *Galiteuthis glacialis*.

Artedidraco scottsbergi was caught once in the vicinity of Amundsen Bay. *Pogonophryne marmorata* occurred three times at the shelf break to the north of Amery Basin. Similarly, the larvae of the bathydracoids *Gymnodraco acuticeps* and *Gerlachea australis* were caught at the continental slope. A number of unidentified *Bathydraco* species and *Cygnodraco mawsoni* larvae were caught over deeper areas (1000–2000 m) in the southern Cooperation Sea. Larval channichthyids were mostly restricted to the Cooperation Sea, with only one specimen of *Pagetopsis maculatus* found west of Gunnerus Bank. The remainder of *P. maculatus* and some *Chionodraco* sp. larvae were found at the continental shelf and slope (500–1000 m) of the Cooperation Sea. In the north, *Cryodraco antarcticus* larvae occurred over deeper waters (1000–2000 m) in the vicinity of BANZARE Bank.

3.4. Squid

The majority of *Galiteuthis glacialis* were small paralarvae (4–20 mm ML) and several small juveniles (20–36 mm) (Fig. 2). They were distributed over the whole sampling area, but more dominant in the Cooperation Sea and almost lacking in the South-western part of the Cosmonaut Sea (Fig. 3). There were a few (n=12) small oegopsid non-cranchiid species, which were not

identified to the species level. Unidentified squid were found throughout the sampling area. Unidentified cranchiids were found around the Southern Boundary (SB) of the Antarctic Circumpolar Current (Appendix 2).

3.5. Community structure

Only the fish data were integrated in the cluster analysis. After exclusion of stations lacking fish, analysis was performed on routine and target stations separately, reflecting the differences in methodology and resulting catch composition.

The cluster analysis of the routine trawls (Appendix 3) showed a cluster of outliers above the 98% dissimilarity level. These outliers included uniquely occurring species. Below this level the stations were further subdivided into a cluster corresponding to coastal stations and a larger cluster representing oceanic stations at 85% dissimilarity composed of two smaller subclusters (Oceanic 1 and 2) at the 67% dissimilarity level.

Pleuragramma antarcticum had a significantly higher abundance at the coastal stations (Fig. 4). A range of notothenioids was found in the coastal stations. The oceanic community was determined by *Notolepis coatsi* and *Electrona antarctica*. Cluster Oceanic 1 corresponds to two smaller clusters of *N. coatsi*,

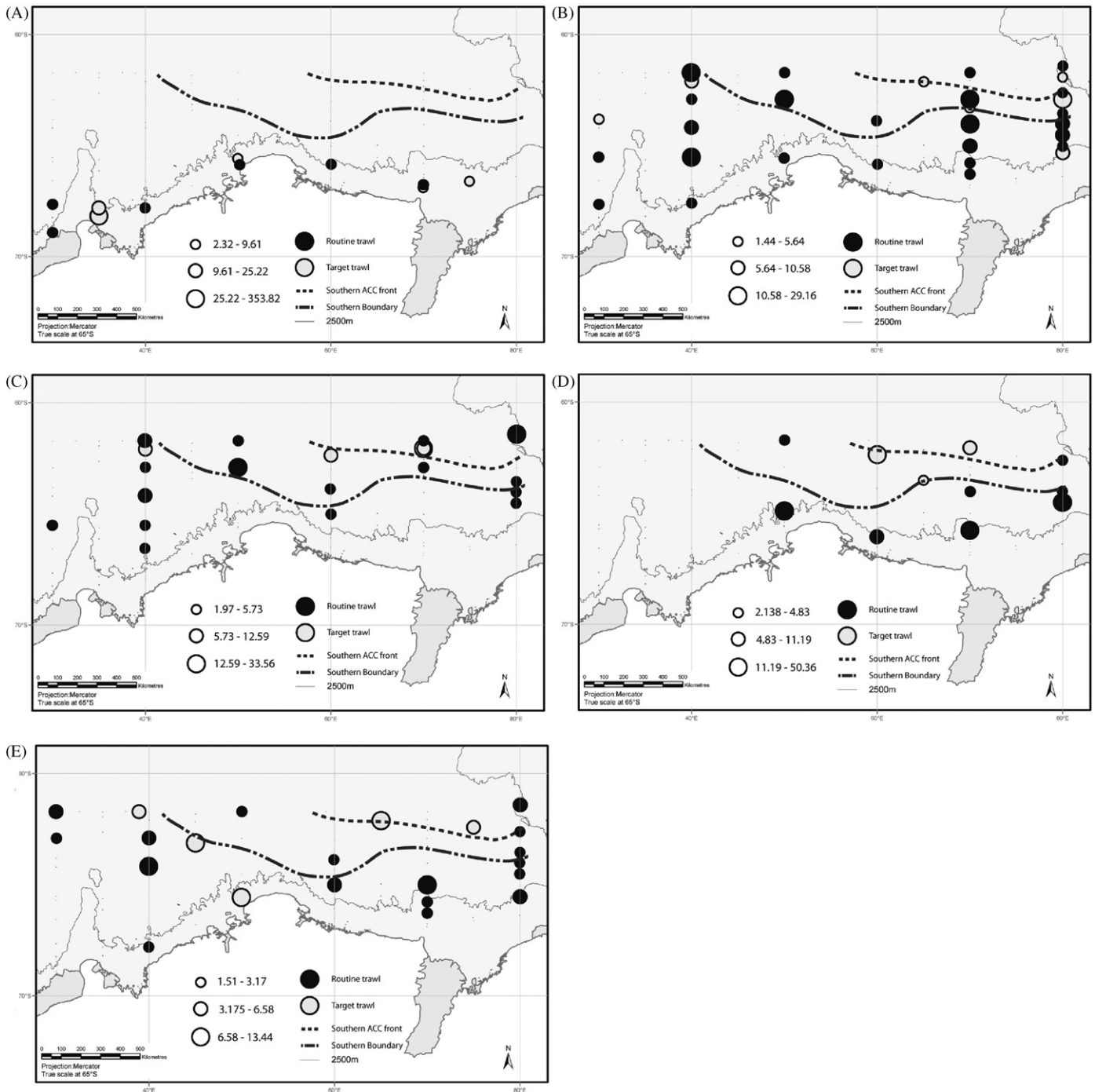


Fig. 3. Distribution in the sampling area, size of circles indicates densities ($\text{ind.} \cdot 10^5 \text{ m}^{-3}$) of (A) *Pleuragramma antarcticum*, (B) *Notolepis coatsi*, (C) larval *E. antarctica*, (D) postmetamorphic *E. antarctica* and (E) *Galiteuthis glacialis*.

and *N. coatsi* and *E. antarctica* larvae. The other oceanic group corresponds to the stations where postmetamorphic *E. antarctica* also occurred.

For the target trawls (Appendix 4), two clusters were distinguished at the 99% level. These clusters also correspond to a coastal and an oceanic community. Similar to the pattern observed in the routine stations the coastal community was dominated by *P. antarcticum*. In the coastal cluster all except one station, station 109 northeast of the sampling area around BANZARE Bank, were located on the shelf and slope (Appendix 4). The station yielded two channichthyid larvae, causing the clustering with the other channichthyids in the coastal zone.

The oceanic community was also composed of several subclusters. All the oceanic subclusters contained *N. coatsi* and, similar to the routine stations, the stations with *E. antarctica* postmetamorphic individuals were only differentiated from other oceanic stations at a level below 50%.

3.6. Redundancy analysis

An RDA analysis was used to explore the association between the main species and environmental variables (Fig. 5). Significance of the first axis and all other axes was confirmed

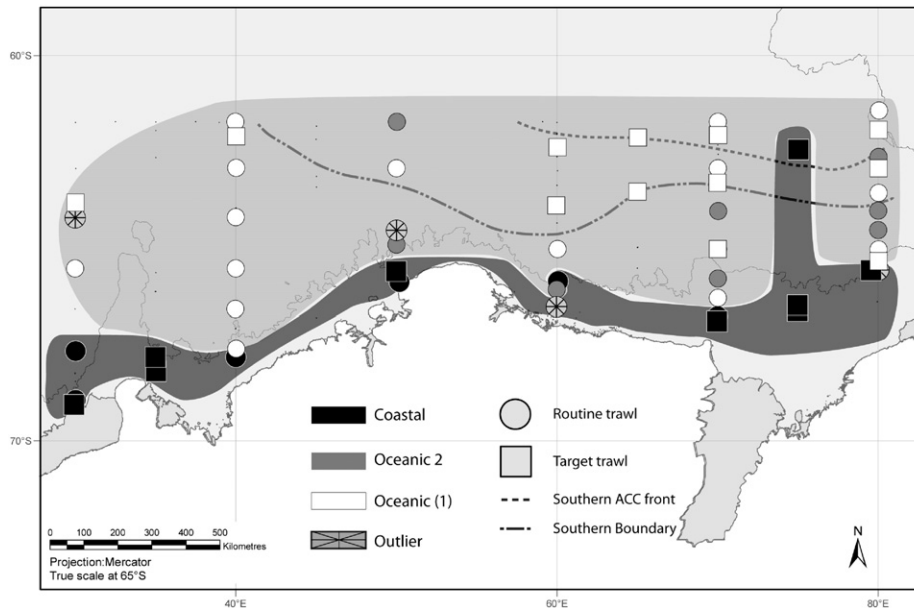


Fig. 4. Geographic distribution of species clusters for routine (\square) and target (\circ) trawls. Legend for cluster assignment on figure. Results of both assignments were grouped to represent the coastal (dark grey) and oceanic (light grey) communities (not considering outliers)

using a Monte Carlo test ($p=0.002$ in both cases). The first axis corresponds to the division into a coastal and oceanic community, explaining 31.2% of the total variability in the species data. *P. antarcticum* was strongly correlated with shallow waters and high chlorophyll *a* values. The oceanic larvae of the fishes *N. coatsi* and *E. antarctica* grouped together as well, as did the paralarvae of the squid *G. glacialis*. All were strongly positively correlated with temperature and salinity and, to a lower extent, mixed-layer depth.

The distribution of *E. antarctica* juveniles and adults was unrelated to the other species. On the second axis, explaining 5% of total variability, *E. antarctica* showed a strong negative correlation with solar elevation, corresponding to a pronounced night time occurrence in the catches. Similar to the other oceanic species, the thickness of the Mixed Layer was positively correlated with postmetamorphic *E. antarctica*.

3.7. Stomach content

Stomach content was analysed for subsamples of *Electrona antarctica* ($n = 7$; SL = 57–79 mm), *Pleuragramma antarcticum* ($n = 10$; SL = 57–73 mm) and *Notolepis coatsi* ($n = 2$; SL = 193–203 mm). Five of the seven analysed stomachs of *E. antarctica* contained food items. Copepods, mainly *Rhincalanus gigas* and *Paraeuchaeta* sp., were found most frequently (57%) and accounted for the majority of prey items in the stomachs (50%). They were followed by hyperiids and euphausiids. However, hyperiids, mainly *Hyperiella* sp. and *Cylopus* sp., appeared to dominate by mass among the prey items accounting for 65% of the food bolus. Euphausiids were the second most important prey items by mass, but only *Thysanoessa macrura* was identified to species level.

Main prey items of *P. antarcticum* fingerlings were copepods followed by larval stages of euphausiids, mainly *E. superba*, and juvenile hyperiids, *Primno macropa*. Among copepods, small cyclopoids (*Oithona similis*) and calanoids (mostly *Scaphocalanus* sp. and *Ctenocalanus* sp.) were most numerous. Copepods were present in all stomachs while hyperiids (40%) and euphausiids (30%) were observed less frequently. The average number of prey

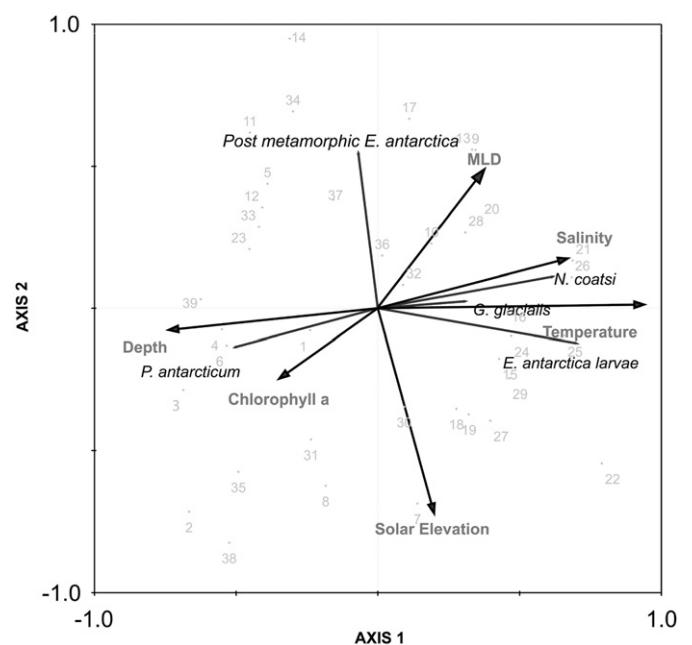


Fig. 5. Species-environment biplot diagram summarizing the effect of environmental variables on the abundance of *Electrona antarctica* larvae and juvenile and adult stages, *Notolepis coatsi*, *Pleuragramma antarcticum* and *Galiteuthis glacialis*. The first explanatory variable is displayed on the X-axis, the second on the Y-axis, (MLD = Mixed-Layer Depth).

per stomach was 13.4 ± 7.8 ranging from 6 to 30. Only Antarctic krill, *Euphausia superba*, has been found in stomachs of two *N. coatsi* subadults. Seven to eight euphausiids per gut were counted.

3.8. Energy content

Three species were analysed for energy content: *Electrona antarctica*, *Notolepis coatsi* and *Pleuragramma antarcticum*

(Table 3). Although the number of samples was relatively low for *E. antarctica*, the size range was well covered. Only a small size range, corresponding to age group 2+ and 3+ fingerlings, and several specimens of at least age group 5+ (Hubold and Tomo, 1989) were available from *P. antarcticum*. Stomachs were extracted before energy measurements in age group 5+ *P. antarcticum*. The same treatment was applied for the three *N. coatsi* specimens. WW energy content differed between *E. antarctica* and *P. antarcticum* (Table 3).

The DW energy content was significantly different between *E. antarctica* and both other species, but not between *N. coatsi* and *P. antarcticum*. Water content differed significantly between all species (Table 3). Analysis by size-based age groups of *E. antarctica* showed increasing mean DW energy content from age group 0 to age group 3 of 23.38 kJ g⁻¹ to 29.14 kJ g⁻¹. DW energy content of age group 0 and 1 were significantly different in comparison to all age groups.

The opposite trend was apparent for water content (Table 4) with age group 2 and 3 being significantly different. Mean DW energy of the combined age 2+ and 3+ age groups of *P. antarcticum* (21.83 kJ g⁻¹) was significantly different from the > 5+ age group (25.52 kJ g⁻¹) ($p=0.01$) (Table 4). The average energy content of *N. coatsi* was the lowest among all three species.

4. Discussion

4.1. Species distribution and abundance

With at least 17 different taxa comprising a mixture of notothenioid species and mesopelagic fish such as myctophids and paralepidids, species diversity observed during BROKE-West was slightly lower in comparison to other studies in the Southern Ocean (Hubold, 1990; Morales-Nin et al., 1995). Species composition is in accordance with Efremenko and Pankratov (1988) in the same area, although these authors reported a wider variety of oceanic species but used different gear over a wider depth range. The combination of *Galiteuthis glacialis* occurring throughout the sampling area accompanied by a suite of non-cranchiid squid is

characteristic for the Southern Ocean (Piatkowski and Hagen, 1994; Jackson et al., 2002).

The BROKE-east dataset (1996) was best suited for a quantitative comparison because of the similarities in used gear and sampling strategy. During both campaigns large differences were observed in the catch ratio between target and routine samples. Because of the methodology, target trawls will be biased towards species associated with the targeted zooplankton aggregations or towards misidentified large aggregations that attract the attention of the scientist on watch. In comparison to the BROKE-east campaign algorithms to identify krill aggregation from acoustic profiles had improved and the amount of bycatch fish in target trawls was reduced. Because of this bias in target trawls analysis within and comparison with other surveys will be limited to the samples collected by routine trawls.

Overall densities of fish were among the lowest observed in the Southern Ocean (Hubold, 1990; Morales-Nin et al., 1995). Total fish density for routine trawls was more than 10 times lower than during the BROKE-east campaign (Hoddell et al., 2000). A similar overall pattern was observed for squid, with *Galiteuthis glacialis* numerically dominant in the oceanic Southern Ocean (Collins and Rodhouse, 2006). Yet compared to BROKE-east, overall densities were again significantly lower. Two possible causes of these differences are differences in sampling season and productivity, these will be addressed in more detail below.

4.2. Spatial patterns

Both for the target and routine trawls, cluster analysis identified a coastal and an oceanic community as observed during BROKE-east for fish and zooplankton (Hoddell et al., 2000; Hosie et al., 2000). The coastal pelagic community had the highest diversity, consisting of a range of notothenioid species dominated by *P. antarcticum*. The notothenioids of the coastal community were found in the highly productive areas of the continental slope. Productivity in the Cooperation Sea zone is higher than in the Cosmonaut Sea (Lubimova et al., 1988). The Cosmonaut coastal community was species poor and dominated by

Table 3

Samples size, mean values for size, water content, wet (WW) and dry weight (DW) energy density of all investigated species.

	Known range (mm)	n	Size range (mm)	Mean size (mm)	Water content (%)	WW energy density (kJ g ⁻¹)	DW energy density (kJ g ⁻¹)
<i>Electrona antarctica</i>	0-102	24	15-90	57.38 (21.15)	73.67 (3.98)	7.26 (1.68)*	27.21 (2.76)*
<i>Notolepis coatsi</i>	0-380	3	108 -203	168 (52.20)*	79.82 (1.25)	4.42 (0.33)	21.90 (0.73)
<i>Pleuragramma antarcticum</i>	0-250	16	57 -124	72.75 (19.12)	85.72 (7.13)*	3.27 (1.91)	22.29 (2.05)

Standard deviation in parentheses Variation between species significant for all three variables (ANOVA: $P < 0.01$) * Values significantly different from all other values in the same column (Tukey's HSD: $P < 0.05$).

Table 4

Mean energy and water content of age groups based on reported size range for *Electrona antarctica* and *Pleuragramma antarcticum*.

Class/group	Size range (mm)	N	Water content (%)	WW energy content (Kj g ⁻¹)	DW energy content (Kj g ⁻¹)
<i>Electrona antarctica</i>			NS	S	S
Age group 0	0-31	2	78.97 (0.82)	4.92 (0.59)	23.38 (1.9)
Age group 1	32-53	8	76.43 (4.07)	5.95 (1.54)	24.91 (2.54)
Age group 2	54-77	9	71.49 (2.11)	8.29 (0.73)	29.04 (0.75)
Age group 3	78-102	5	71.07 (2.13)	8.44 (0.8)	29.14 (0.61)
<i>Pleuragramma antarcticum</i>			S	S	S
Age group 2	52-95	14	87.93 (1.05)*	2.64 (0.25)*	21.83 (0.44)*
Age group > 5	> 105	2	70.24 (2.77)*	7.59 (0.65)*	25.52 (1.18)*

Standard deviation in parentheses.

S indicates an overall significant difference between age groups.

* Values significantly different from all other values in the same column (Tukey's HSD: $P < 0.05$).

N = sample size.

P. antarcticum, a species associated with higher chlorophyll a concentrations (Fig. 5). In the shelf-break zone of the Prydz Bay area there was a higher diversity of all notothenioid families dominated by bathydraconids and channichthyids. This pattern was also observed, using different sampling gear over a wider depth range, by Efremenko and Pankratov (1988). Channichthyid larvae such as *Chionodraco* sp. occurred in the vicinity of the slope break as well as over deeper waters in the Prydz Bay area; they have been reported in the western region of the BROKE-east sampling area (Hoddell et al., 2000). Similar distribution patterns for bathydraconid larvae have been reported (Williams and Duhamel, 1994; Hoddell et al., 2000). The north-westerly flow in the Prydz Bay gyre may transport larvae to the deeper water near BANZARE bank as shown in one target trawl (St-109), which was grouped in the coastal cluster because it was exclusively composed of channichthyids. Consequently, larvae can be lost or they can return to the shelf in the eastern part of the bay, indicating such larval retention within the Prydz Bay area. This pattern indicates a close hydrological and biological association between the Cooperation Sea and the western part of the BROKE-West sampling area.

The oceanic community was relatively species poor. A number of abundant circumantarctic mesopelagic species were not caught: *Bathylagus antarcticus*, *Gymnoscopelus nicholsi*, *Electrona carlsbergi* and *Krefflichthys anderssoni*. These species have been reported in the Cooperation Sea and the Cosmonaut Sea but in samples covering a wider depth range (Efremenko and Pankratov, 1988; Williams and Duhamel, 1994). No geographical or temporal patterns were apparent for the larval stages of *E. antarctica* and *N. coatsi*. These species appear to be general throughout the oceanic zone of the sampling area and the rest of the Southern Ocean (Hubold, 1990; Morales-Nin et al., 1995; Hoddell et al., 2000). Densities of larval *E. antarctica* and *N. coatsi* were positively correlated with temperature, salinity and to a lower extent mixed-layer depth. These environmental variables were more elevated in the eastern part of the sampling area due to the earlier onset of melting (and later sampling) in the east and the stronger influence of the Southern Antarctic Circumpolar Current bringing warmer and more saline water into the eastern area (Meijers et al., 2010; Williams et al., 2010).

Within the oceanic community there was a further subdivision to the east caused by the presence of juvenile and adult *E. antarctica*. A similar pattern was observed during BROKE-east, where this pattern was related to higher densities of all stages of *E. antarctica*. However, closer inspection of the BROKE-east data shows that these stations also have relatively more juvenile and adult *E. antarctica* (Hoddell et al., 2000). RDA analysis showed that the abundance of postmetamorphic stages of *E. antarctica* was strongly correlated with the solar elevation and mostly independent of any other variable evaluated. This may have two reasons. First of all *E. antarctica*, similar to other myctophids and squid, is known to display diurnal vertical migration, with an average daytime depth distribution below the fishing depth of this campaign (Torres and Somero, 1988). Additionally, net detection and avoidance are likely to increase with improving light conditions (Collins et al., 2008). Our clustering and RDA analyses suggest that the eastward distribution pattern in both campaigns is most likely an artefact of campaign planning. Because stations in the west were sampled earlier in the season, when hours of darkness were diminished, the probability to catch postmetamorphic *E. antarctica* was reduced to virtually zero even if they would have been present. The distribution of different ontogenetic stages of *E. antarctica* is determined by various environmental factors. These different life stages of *E. antarctica* and other fishes should thus be analysed separately in order not to distort any stage specific effects.

Catching squid using an RMT-8 net in the pelagic layer (< 200 m depth) is difficult for reasons similar to those discussed for *E. antarctica*. Furthermore the distributional patterns and environmental associations of *G. glacialis* paralarvae show strong similarities with *E. antarctica* and *N. coatsi* larvae, but they are likely to occur at a greater depth (Rodhouse and Clarke, 1986; Collins and Rodhouse, 2006).

4.3. Feeding ecology

Albeit limited, the data on the stomach contents of the three most abundant fish species caught during BROKE-West indicate that they were all planctivorous predators consuming mainly either copepods or euphausiids and hyperiids. *E. antarctica* has previously been described as a small zooplankton consumer (Gorelova and Efremenko, 1989; Kozlov and Tarverdieva, 1989; Gerasimchuk et al., 1990; Sabourenkov, 1991; Pakhomov et al., 1995, 1996).

The diet of *N. coatsi* has not been studied systematically; information is mainly based on an occasional stomach analysis of fish caught as bycatch during the krill fishery. On those occasions, usually only Antarctic krill 30–40 mm long were found in the stomachs of subadult and adult *N. coatsi* (Gerasimchuk et al., 1990; Pakhomov, 1997).

The feeding ecology of *P. antarcticum* is perhaps best studied among the three species investigated here. Findings are in line with the literature (see below). *P. antarcticum* yearlings consume mainly cyclopid and small calanoid copepods as well as copepod nauplii (Gorelova and Gerasimchuk, 1981; Kellermann, 1986; Pakhomov et al., 1995). The fingerlings' main prey items are calanoid copepods and Antarctic krill larvae, with some regional preferences (Gorelova and Gerasimchuk, 1981; Hubold, 1985; Gerasimchuk et al., 1990; Pakhomov and Pankratov, 1992; Williams and Duhamel, 1994; Pakhomov et al., 1996). Finally, adults of *P. antarcticum*, although supplementing their diet with copepods, consume mainly Antarctic neritic krill *Euphausia crystallophias* and at times juvenile Antarctic krill *E. superba* (Gorelova and Gerasimchuk, 1981; Gerasimchuk et al., 1990; Williams and Duhamel, 1994).

All three species appear to have a stage during their life cycle, when mesozooplankton is the dominant prey, putting them in the food web between small zooplankton and large-sized top predators. Further in-depth studies on the role of both myctophids and juvenile notothenioids are required to assess their significance in the ecosystem of the Southern Ocean.

4.4. Energy content

The mean energy content of *E. antarctica* samples was in the low range of the published data (for an overview see, Van de Putte et al., 2006). WW energy content was of the same order of magnitude as the spring data collected by Donnelly et al. (1990). These results are consistent with a reduction in energy content after reduced food availability during the winter months or spawning at the end of winter (Donnelly et al., 1990). Another factor contributing to the observed differences may be the lower productivity in the area compared to the productive Scotia Sea. DW energy measurements for age group 0 individuals were relatively high, which can be attributed to the high energy reserves at spawning or feeding on phytoplankton at the onset of the spring primary production peak.

The energy content of *P. antarcticum* was low in comparison with all age groups of *E. antarctica* and showed a large variation among the fingerlings, indicating that there is a lot of variation in energy content within cohorts. This variation may be attributed to the variable success in foraging in winter. Both *P. antarcticum* and *E. antarctica* are important prey items of Antarctic birds and

mammals. While the energy content of *P. antarcticum* fingerlings was comparable to Antarctic krill (Torres et al., 1994), that of subadults was comparable to the energy content of *E. antarctica* and could be higher for full grown adults, emphasising its role as an important food source for top predators in the coastal zone. The high energy content of *E. antarctica* suggests a pronounced importance in the offshore pelagic food web of the Southern Ocean (Flores et al., 2008).

4.5. Conclusions

The communities of fish and squid observed during BROKE-West are congruent with previous observations in the Southern Ocean, not only in regards to distribution patterns but also in terms of feeding regime of the species investigated. The strongest

differentiation was observed between the coastal notothenioid community and the mesopelagic oceanic community. Notothenioids such as *P. antarcticum* are correlated to the colder shelf zone and high chlorophyll *a* concentrations. The apparent subdivision of the oceanic community is most likely an artefact of seasonal changes in light conditions and behavioural responses of mesopelagic fish such as *E. antarctica*. The paralarvae of *G. glacialis* were related to similar environmental signals as the pelagic larvae of *E. antarctica* and *N. coatsi*. The lower energy content and low abundances of fish and squid in the area could suggest a low productivity in the BROKE-West area. This would be in contrast to the high observed primary production observed during the BROKE-West survey period in comparison to the BROKE-east campaign. However, zooplankton stock will only increase after a period in increased productivity. As such, the observed difference is due to a temporal effect. Lack of data within

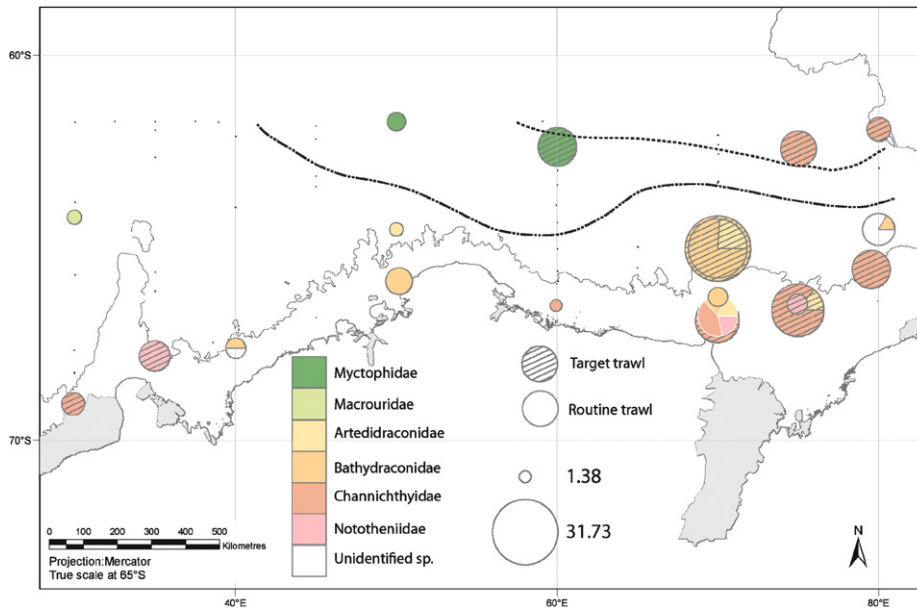


Fig. A1.

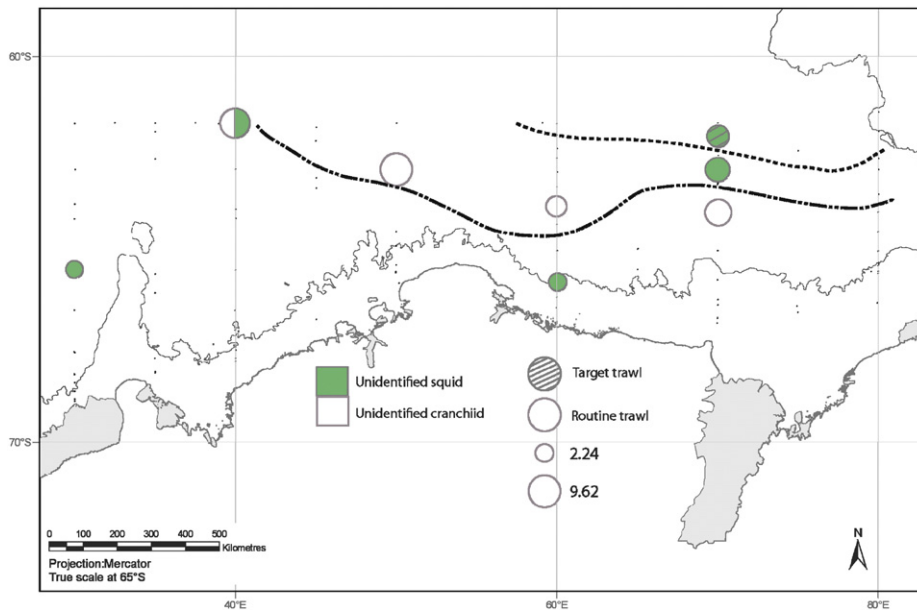


Fig. A2.

the area of investigation preclude us to determine whether the observed low densities of fish and squid are a temporal anomaly or typical for the area. In order to improve the understanding of the distribution of fish and squid as well as their role within the system, more sampling is needed through time, be it from a seasonal or an interannual perspective, with access to more sophisticated sampling gear deployed over a greater depth range.

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Appendix 1

Distribution in the sampling area, the size of the circles indicates densities ($\text{ind.}10^5 \text{m}^{-3}$) of fish according to family excluding *P. antarcticum*, *N. coatsi* and *E. antarctica* (Fig. A1).

Appendix 2

Distribution in the sampling area, the size of the circles indicates densities ($\text{ind.}10^5 \text{m}^{-3}$) of squid excluding *G. glacialis* (Fig. A2).

Appendix 3

UPGMA clustering dendrogram based on dissimilarity of species composition of routine trawls. Stations were grouped in one coastal and two oceanic (oceanic 1 and 2) clusters (Fig. A3).

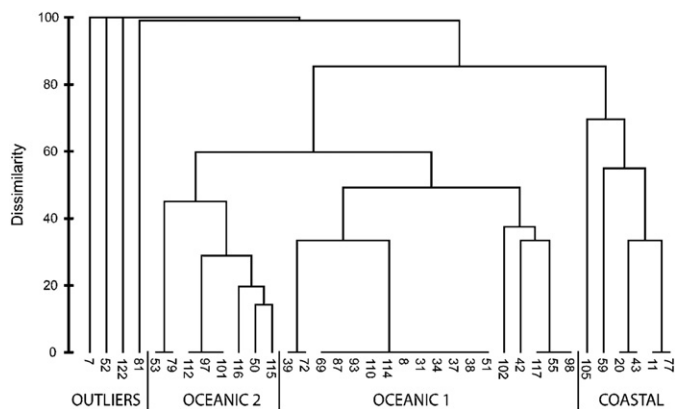


Fig. A3.

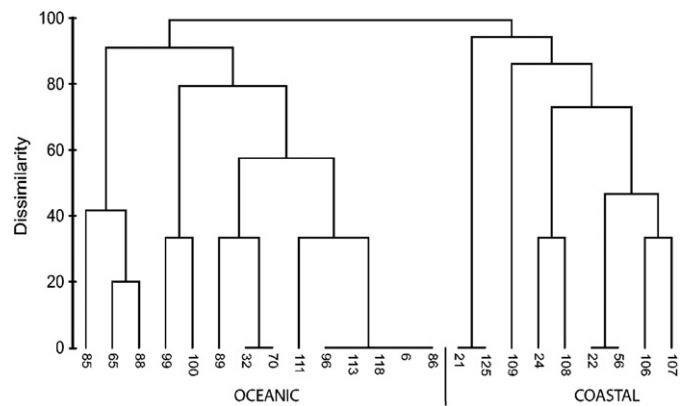


Fig. A4.

Appendix 4

UPGMA clustering dendrogram based on Bray-Curtis dissimilarity of species composition and density of target trawls. Stations were grouped in one coastal and one cluster (Fig. A4).

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