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Spatial distribution of pelagic fish off Adélie and George V Land, East Antarctica in the austral summer 2008

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Abstract

Pelagic fish assemblages and community structure were examined along longitudinal and meridian transects off Adélie and George V Land, East Antarctica, in the austral summer 2008. Fish were sampled with an RMT 8 net principally from six discrete depth layers (0–50–100–200–500–1000–2000 m) in the oceanic zone and from three depth layers (0–50–100–200 m) over the continental shelf zone. A total of 20,281 individuals from 27 species were collected. *Pleuragramma antarcticum* was the most dominant species by number (18,710 inds), followed by *Chionodraco hamatus* (768), *Trematomus newnesi* (375), *Cyclothone microdon* (101), *Electrona antarctica* (92), *Bathylagus antarcticus* (51) and *Notolepis coatsi* (54). Cluster analysis revealed that the fish community was clearly divided at the Antarctic Slope Front into separate oceanic and shelf assemblages, being dominated by mesopelagic fish and notothenioids, respectively. The Southern Boundary of Antarctic Circumpolar Current likely restricted a more northern distribution of notothenioids in the upper 200 m. Mesopelagic fish dominated the large biomass below 500 m and notothenioids dominated that in the upper 100 m. It is considered that mesopelagic fish in the oceanic zone would unlikely be eaten by seabirds because no distinctive diel vertical migration to the surface layer was observed. In the neritic zone, notothenioids (*C. hamatus*, *T. newnesi* and *P. antarcticum*) possibly play an important role as prey items for flying seabirds, penguins and other notothenioids fish especially in the shallow depth stratum (0–100 m).

Keywords: Pelagic fish; Community structure; East Antarctica; Mesopelagic fish; Notothenioids

1. Introduction

While krill have been identified as a key trophic component, pelagic fish are also important elements of the food web in the Southern Ocean. Among the pelagic fish, Antarctic myctophids or lantern fish have

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Table 1
Abundance (number 100 m⁻²) of fish collected off Adélie and George V Land, Indian sector, East Antarctica, by an RMT 8 in the austral summer.

	Stn.	14	15	16	17	18	19	20	21
Bathylagidae	Bathylagus antarcticus	19.4 (2)	3.2 (1)	50.4 (6)	18.5 (4)	35.8 (7)		118.9 (24)	31.4 (7)
Gonostomatidae	Cyclothone microdon	139.3 (21)	48.5 (11)	127.2 (18)	64.7 (15)	35.8 (7)	30 (10)	68.2 (13)	25.3 (6)
Paralepididae	Notolepis coatsi	15.3 (11)	27.4 (7)	24.7 (7)	3.2 (2)	18.2 (5)	28.9 (13)	14 (3)	18.8 (4)
Myctophidae	Electrona antarctica Gymnoscoplelus braueri Krefftichthys anderssoni Protomyctophum bolini	70.7 (15) 15.3 (3)	29.7 (7) 4.4 (1) 4.4 (1)	73.7 (29) 1.2 (1) 4.3 (3)	27.7 (6)	23.3 (5) 5.1 (1)	1.8 (1) 4.9 (1)		51.3 (12) 4.2 (2) 4.9 (1)
Macrouridae	Cynomacrurus piriei		4.4 (1)						
Melamphaidae	Melamphaes microps					5.1 (1)			
Nototheniidae	Pleuragramma antarcticum Trematomus lepidorhinus Trematomus newnesi								
Artedidraconidae	Artedidraco loennbergi Artedidraco shackletoni Artedidraco skottsbergi Artedidraco Type A Artedidraco Type B Pogonophryne sp.							1.4 (2)	
Bathydraconidae	Bathydraco antarcticus Cygnodraco mawsoni Prionodraco evansii Racovitzia glacialis								3.2 (1) 0.8 (1)
Channichthydae	Chaenodraco wilsoni Chionodraco hamatus Cryodraco antarcticus Dacodraco hunteri Pagetopsis sp.								(1)
	Total	260.0 (52)	122.0 (29)	281.5 (64)	117.3 (28)	123.3 (26)	108.2 (41)	227.5 (48)	139.9 (34)

Abundance values represent number of fish in the 100 m^2 water column from surface to the maximum depth samples at each station. Number in parenthesis indicates individual number collected.

been considered as one of the key families in the oceanic realm from the subantarctic zone to the Antarctic continental shelf with their biogeographic patterns following major water masses and fronts (Piatkowski, 1989; Hulley, 1992; Koubbi et al., 2011). Some studies revealed that myctophids and notothenioids dominated oceanic and shelf zones, respectively, near the Antarctic continental shelf (Hoddell et al., 2000; Barrera-Oro, 2002; Flores et al., 2008; Van de Putte et al., 2010) but also in the subantarctic zone (Koubbi et al., 1991; Duhamel, 1998; Duhamel et al., 2000).

Several papers have studied fish assemblages in East Antarctica (Hulley et al., 1989; Hoddell et al., 2000; Donnelly et al., 2004; Moteki et al., 2009; Van de Putte et al., 2010; Koubbi et al., 2010). In the most southern part of this ocean, one species of lantern fish

Electrona antarctica dominates the mesopelagic fish fauna in terms of biomass and abundance (Greely et al., 1999). On the continental shelf, notothenioids are the dominant fish but this group has more benthic species than pelagic ones (Eastman, 2005) which was confirmed in our study area by Koubbi et al. (2010) and Causse et al. (2011). Few notothenioids have pelagic larvae (Loeb et al., 1993; North and Kellermann, 1989; Koubbi et al., 2009), whereas for others the larvae have not been described yet because of probable non-pelagic early life with parental care (Gon and Heemstra, 1990). Some icefish have larvae or juveniles linked with krill swarms (Kock, 2005), while other species are adapted to extreme conditions and are cryopelagic like Pagothenia borchgrevinki. Other species of notothenioids are benthopelagic or even pelagic feeding on plankton.

22	23	42	24	25	26	27	11	Total	Depth (m)
								277.6 (51)	500-2000
								539 (101)	500-2000
		0.7(1)	1.5 (1)					152.7 (54)	100-2000
								333 (92)	50-1000
								16.5 (6)	100-1000
								14.5 (4)	500-1000
								33.7 (10)	0-2000
								4.4 (1)	500-1000
								5.1 (1)	1000-2000
19.0 (30)	18.7 (27)	64.2 (37)	468.2 (552)	22.0 (61)	3539.7 (6047)	7510.9 (11949)	56.3 (29)	11699 (18732)	0-500
		0.7(2)	370 (20)			10.3 (17)		381 (39)	0-200
		8.2 (11)	19.5 (276)	16.7 (31)	5.7 (10)	11.9 (19)	11.6 (6)	73.6 (353)	0-200
0.6(1)								0.6 (1)	0-50
	0.7(1)				1.7 (3)			2.4 (4)	0-50
			0.7 (1)		1.1 (2)			1.8 (3)	0-50
			3.7 (3)				1.9(1)	5.6 (4)	0-200
								1.4(2)	0-50
						0.6(1)		0.6(1)	0-50
0.6(1)								0.6 (1)	50-100
								3.2 (1)	0-200
		2.2 (3)	1.5 (1)			8.3 (14)		12.0 (18)	0-200
								0.8 (1)	50-100
		0.7(1)						0.7 (1)	0-50
0.6(1)		5.9 (8)	389.8 (292)	21.7 (41)	25.2 (44)	84 (180)	390.2 (201)	917.4 (768)	0-200
		1.4(2)						1.4(2)	0 - 100
		4.2 (2)	1.5 (1)		0.6(1)	10.9 (20)	3.9 (2)	21.1 (26)	0-200
		1.1(1)			0.6(1)	1.2 (2)		2.9 (4)	0-200
20.8 (33)	19.4 (28)	89.3 (68)	1256.4 (1147)	60.4 (133)	3574.6 (6108)	7638.1 (12202)	463.9 (239)	14502.6 (20281)	

Pleuragramma antarcticum is the only species which has all pelagic life stages and has a huge biomass over the continental shelf. Its larval stages dominate (90–99%) the neritic ichthyoplankton, including in East Antarctica (Koubbi et al., 1997, 2007, 2011; Hoddell et al., 2000). During its life, this species forages on different planktonic organisms and switches its feeding mode from omnivorous on copepods, euphausiids nauplii and phytoplankton in early stages (Koubbi et al., 2007; Vallet et al., 2011) to foraging mainly on krill, either ice krill Euphausia crystallorophias or Antarctic krill Euphausia superba (Hubold, 1985; Hubold and Ekau, 1990; Kellermann, 1987; Takahashi and Nemoto, 1984). This change in diet has been identified by studies of the diet contents (Koubbi et al., 2007; Vallet et al., 2011), stable isotopes (Giraldo et al., 2011) and lipid trophic markers (Mayzaud et al., 2011). P. antarcticum is also a micronektonic species that is intermediate between mesozooplankton and larger predators such as large fish like Antarctic toothfish (Dissostichus eleginoides) and also seabirds and seals (Kozlov, 1995; Gaskett et al., 2001; Murphy et al., 2007; Flores et al., 2008; Van de Putte et al., 2010).

The mid-trophic level occupied by P. antarcticum and krill species could be indicative of a wasp-waist ecosystem, as hypothesized by Koubbi et al. (2011). Therefore studies on the spatial distribution and community structure of pelagic fish provide fundamental information for the understanding of the pelagic ecosystem. Although many studies were carried out in the epipelagic layer and mainly on two dimensions (latitude and longitudes), few studied have been made on the vertical distribution of pelagic fish both in the neritic and the oceanic zone. Of these studies, only Moteki et al. (2009) conducted discrete depth sampling down to 2000 m, while the others sampled an upper depth stratum of several hundred meters. Moteki et al. (2009) found that in Lützow Holm Bay (33-45°E), E. antarctica, Notolepis coatsi, Bathylagus antarcticus, and Cyclothone microdon were the four most dominant species (94% by number). Furthermore, this study revealed that B. antarcticus and C. microdon had large abundances in the 500-2000 m depth layers.

A multidisciplinary survey was conducted off Adélie and George V Land in January and February 2008 by the Training and Research Vessel (TRV)

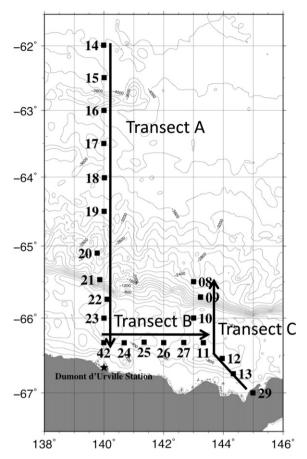


Fig. 1. Sampling stations off Adélie and George V Land in the Indian Ocean sector in austral summer, 2008. RMT sampling in the present study was conducted along transects A and B.

Umitaka Maru of Tokyo University of Marine Science and Technology (TUMSAT) as a part of the Collaborative East Antarctic Marine Census (CEAMARC). In this survey, intensive pelagic trawl sampling principally down to 2000 m using a Rectangular Midwater Trawl (RMT), was undertaken to gather information on marine biota of East Antarctica. Based on these net samples, Ono et al. (2011) studied the community structure of the euphausiid species in the meso- and bathypelagic layers, and showed that some euphausiid species occur in large abundances in the mesopelagic layer as well as in the upper 200 m. The present study aims to describe fish assemblages and community structure off Adélie and George V Land in the austral summer of 2008 and using an RMT 8, in order to provide more information on the pelagic ecosystem of East Antarctica. For this purpose, we made discrete depth sampling from the surface to 2000 m in the oceanic zone and through to the shelf waters.

During the present survey, fish were also sampled by a large International Young Gadoid Pelagic Trawl (IYGPT) trawl along transects A-C. The results of the IYGPT sampling are described in Koubbi et al. (2010, 2011).

2. Materials and methods

2.1. Net sampling and sample analysis

Research cruises were conducted from 28 January to 8 February 2008 on the TRV Umitaka Maru off Adélie and George V Land in the Indian Ocean sector (Table 1; Fig. 1). The 22 sampling stations were arranged in three transects. However, we only used samples from transects A and B, because the opening/ closing system on the RMT net was mechanically nonoperational after station 11. Transect A was run along 140°E and transect B along 66°20'S. Stations 14 to 19 were situated in the Oceanic Zone with bottom depths >3000 m; stations 20 and 21 were over the continental slope with bottom depths between 1000 and 3000 m; and the remaining stations were in the shelf zone (George V Shelf), mostly in depths of 200-400 m. However, bottom depths at stations 42 and 11 were slightly deeper, namely 480 m and 720 m respectively. The topography, simplified bottom circulation and benthic communities observed by underwater video on George V Shelf are documented in Post et al. (2011). Fish were sampled using a rectangular midwater trawl (RMT 1 + 8) equipped with three sets of nets linked to an opening/closing mechanism (Baker, 1973). Oblique tows were conducted from deeper layer to shallower layer, and one or two hauls were made at each station. The sampling depth layers were 0-50-100-200 m for the epipelagic layer (shallow hauls) at all stations. In addition, deep hauls sampled the 200-500-1000-2000 m depth strata, and were undertaken at stations 14, 16, 18 and 20, while the 200-500-1000 m depth strata were sampled at stations 15, 17, 19 and 21. At stations 42 and 27, only a 200-500 m depth stratum was sampled as a deep haul. Samples from surface to 200 m were collected as a part of the deep cast at stations 19 and 11 due to mechanical trouble with the opening/closing equipment. To estimate the effects of luminescence levels on vertical distributions, stations were divided into day and night periods. Night periods were defined as when average values of photosynthetically active radiation (PAR) during sampling were less than 20% of maximum values. The PAR values were recorded using a PAR sensor (LI-190SB, LI-COR Inc.) equipped on

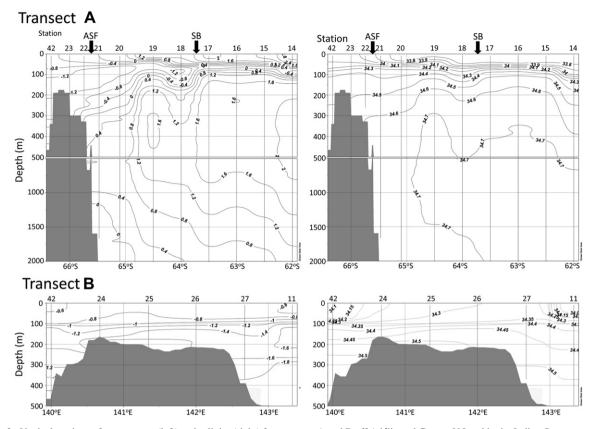


Fig. 2. Vertical sections of temperature (left) and salinity (right) for transects A and B off Adélie and George V Land in the Indian Ocean sector in austral summer, 2008. Arrows indicate approximate position of the Antarctic Slope Front (ASF) and the Southern Boundary of Antarctic Circumpolar Current (SB).

the top deck of the vessel. The night stations were identified as 16, 19, 20, 22, 42, 26 and 11. We used only samples from the 8 m² net for this study. The station data are presented in Ono et al. (2011).

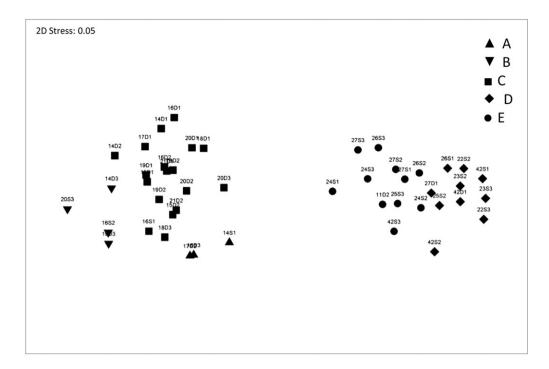
Large specimens were sorted on board, and were fixed in 5% buffered formalin. A part of the fish samples were frozen for barcoding (Dettai et al., 2011) and stable isotope analysis (Cherel et al., 2011; Giraldo et al., 2011). The remaining fish were fixed in 5% buffered formalin with other plankton and sorted at the TUMSAT laboratories. The number of individuals and wet weights to the nearest 0.01 g were determined for seven dominant species (E. antarctica, N. coatsi, B. antarcticus, C. microdon, Chionodraco hamatus, Trematomus newnesi, P. antarcticum). Before the wet weight was determined with an electric balance, each specimen was blotted dry on filter paper, and repeated several times until the filter paper was no longer moist. Identification of species was based on morphology using Gon and Heemstra (1990) and North and Kellermann (1989), but some specimens were identified by barcoding (Dettai et al., 2011).

2.2. Hydrographic observations

At each station and before undertaking the RMT tow, salinity and temperature data were collected at each sampling station using a conductivity-temperature-depth (CTD) profiler (Sea-Bird Electronics, SBE911) to depths of 2000 m, or just above the bottom in shallower depths. The accuracy of temperature and conductivity were 10^{-3} degrees and 3.10-4 S m⁻¹ (2.10^{-3} in terms of salinity), respectively. The location of Southern Boundary of the Antarctic Circumpolar Current (SB) was defined by the southern limit of maximum potential temperature warmer than $1.5\,^{\circ}\text{C}$ (Sokolov and Rintoul, 2002). The terminology of the water masses is in accordance with Bindoff et al. (2000) and Tomczak and Liefrink (2005).

2.3. Data analysis

The Bray—Curtis similarity index was used to compare fish species composition with respect to station and depth (Field et al., 1982). Abundances were



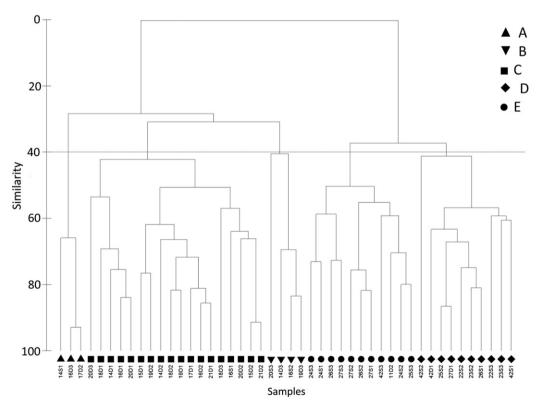


Fig. 3. Dendrogram representing the classification of samples collected by an RMT 8 based on Bray—Curtis similarities for fish species assemblages and nMDS plots of the samples with groupings at 40% similarity. Labels of samples indicate station number and depth strata; in stations 14, 16, 18 and 20, D1: 1000–2000 m; D2: 500–1000 m; D3:, 200–500 m; in stations 15, 17, 19 and 21, D1: 500–1000 m; D2: 200–500 m; D3: 0–200 m; in 42, D1: 200–500 m; in all stations, S1: 100–200 m; S2: 50–100 m; 0–50 m.

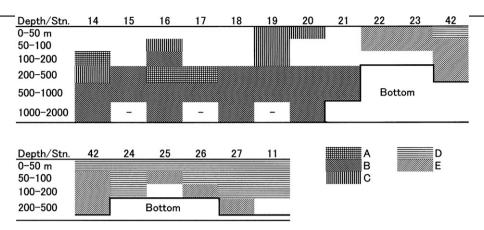


Fig. 4. Schematic of the fish community structures off Adélie and George V Land in the Indian Ocean sector based on the cluster analysis shown in Fig. 3.

fourth-root transformed to decrease the undue influence of high abundance species according to Field et al. (1982). Samples for which fewer than three specimens were caught were excluded from the analysis. Unweighted-pairs group linkage and non-metric multidimensional scaling (nMDS) were performed based on the similarity matrix. The SIMPER (similarity percentage) routine identified those species contributing to the similarity within the observed clusters. These statistical analyses were conducted using the PRIMER v6 software package (PRIMER-E; Clarke and Gorley, 2006).

3. Results

3.1. Oceanographic conditions

On transect A, the Antarctic Slope Front (ASF) was located between stations 21 and 22, while the SB was located between stations 17 and 18 (Fig. 2). North of the ASF, the water column was well stratified. Summer Surface Water (SSW) characterized by low salinity and high temperature, covered the surface to ca. 50 m depth. The core of Modified Circumpolar Deep Water (MCDW), represented by warm, highly saline water,

Table 2 Characteristics of each group identified by the hierarchical clustering.

Group	Av. Abund. (<i>n</i> 105 m ⁻³)	Av. species no.	Species richness	No. samples
A	10.5	1.7	2	3
В	76.5	3.6	9	18
C	31.3	2.3	4	4
D	1146.5	5.2	14	11
Е	49.8	1.9	8	10

was observed deeper than 100 m depth. Between 50 and 100 m, cold Winter Water (WW) was present, especially south of SB. A lens-like eddy structure, with anomalous feature of cooler and fresher waters at the surface down to ca. 300 m depth was observed at around 64°S. This was similar to that reported by Hirawake et al. (2003).

By contrast, the water column was less stratified south of ASF but vertical stratification was observed in the George V Basin when compared to the Adélie Bank and the Adélie Basin to the west (Koubbi et al., 2010). Water temperatures were less than $-0.6~^{\circ}\text{C}$ from surface to bottom. Salinity ranged from 34.0 to 34.6.

3.2. Community structure of fish collected by RMT 8

A total of 20,281 individuals from 27 species in 10 families were collected (Table 1). *P. antarcticum* was the most dominant species by number (18,710 inds), followed by *C. hamatus* (768), *T. newnesi* (375), *C. microdon* (101), *E. antarctica* (92), *B. antarcticus* (51), *N. coatsi* (54).

The fish community was clearly divided between stations 21 and 22 (Table 1). From station 14 to 21, typical mesopelagic fish (Myctophidae, Bathylagidae, Gonostomatidae, Paralepididae) dominated the ichthyofauna, while from station 22 to 11 and with the exception of two paralepidid specimens, only notothenioid families occurred.

Hierarchical clustering and nMDS plots revealed five clusters (A–E) at 40% similarity, although the cluster groups A–C and D–E were totally dissimilar (Fig. 3). Cluster group (A–C) was composed of oceanic samples, while cluster group (D–E) comprised

Table 3 Average similarity, abundance, and related values within a cluster (SIMPER analysis).

Species	Av. Si (%)	Si/SD(Si)	Contrib. (%)	Cum. %	Av. abund. (n 104 m ⁻³)
Group A (Av. simlarity: 74.94)					
Notolepis coatsi	60.01	5.79	80.08	80.08	1.68
Protomyctophum bolini	14.93	0.58	19.92	100	0.63
Group B (52.15)					
N. coatsi	13.02	1.13	24.97	24.97	1.73
Electrona antarctica	12.86	0.98	24.65	49.62	4.48
Cyclothone microdon	12.40	0.82	23.77	73.4	4.59
Bathylagus antarcticus	11.81	0.84	22.64	96.04	2.57
Gymnoscoplelus braueri	1.10	0.26	2.12	98.15	0.25
P. bolini	0.85	0.20	1.63	99.79	0.27
Krefftichthys andersoni	0.11	0.08	0.21	100	0.16
Group C (57.28)					
E. antarctica	38.46	7.35	67.15	67.15	2.16
P. bolini	18.82	0.91	32.85	100	1.00
Group D (56.08)					
Pleuragramma antarcticum	27.14	2.40	48.39	48.39	1981.76
Chionodraco hamatus	16.37	3.25	29.19	77.58	79.10
Trematomus newnesi	7.79	1.20	13.89	91.47	43.78
Dacodraco hunteri	2.09	0.58	3.72	95.19	2.54
Prionodraco evansii	1.56	0.45	2.79	97.98	1.69
Trematomus lepidorhinus	0.54	0.24	0.96	98.93	4.46
Artedidraco sp. (Type A)	0.39	0.24	0.7	99.63	0.49
Artedidraco skottsbergi	0.12	0.13	0.21	99.84	0.33
Pagetopsis sp.	0.09	0.13	0.16	100	0.32
Group E (57.98)					
P. antarcticum	55.87	4.18	96.36	96.36	33.55
C. hamatus	2.11	0.26	3.64	100	0.67

Av. Si: average contribution of species i to the similarity within the cluster. SD(Si): standard deviation of Si, high Si/SD(Si) ration indicates that a given species is typical to all staions in the cluster.

shelf samples. The two clusters were clearly separated by the ASF. Group B comprised samples taken below 200 m (Fig. 4), and had the second largest value of average abundance (76.5) (Table 2). The species contributing most to the similarity within this group were N. coatsi, E. antarctica, C. microdon and B. antarcticus (Table 3). These four species contributed almost the same percentages within the group (22.6-25.0%). Group A represented part of the 100-500 m community north of the SB (stations 14, 16, and 17). This group recorded the lowest values for average abundance, average species number and species richness (Table 2). N. coatsi contributed 80.1% to the similarity within this group (Table 3). Group C represented partly a surface community at stations 16, 19 and 20, and the 200-500 m community at station 14 (Fig. 4). This group had the second smallest values in average abundance and species richness (Table 2). Two myctophid species, E. antarctica and Protomyctophum bolini, contributed 100% to the similarity of Group C (Table 3).

Groups D and E were composed of shelf samples (Fig. 4). Group D was mainly observed in the surface

to 200 m depth strata from at stations 42 to 11. Group D had the highest values in average abundance, average species number and species richness (Table 2). The species contributing most to the similarity within this group were *P. antarcticum*, *C. hamatus* and *T. newnesi* and these species contributed to more than 90% of the similarity (Table 3). Group E comprised near-bottom samples from station 42 to 27, although samples in the 0–100 m stratum at stations 22 and 23 belonged to group E (Fig. 4). This group had comparatively high species richness (8), although the average species number was 1.9 (Table 2). The main species in this group was *P. antarcticum*, which contributed 96.4% to the similarity within group E (Table 3).

3.3. Vertical distribution in dominant species

The vertical distribution patterns of the biomass of the seven dominant species are shown in Fig. 5. In oceanic waters, a large biomass was found mainly in the meso- and bathypelagic layers and was more-orless uniformly distributed among sampling stations.

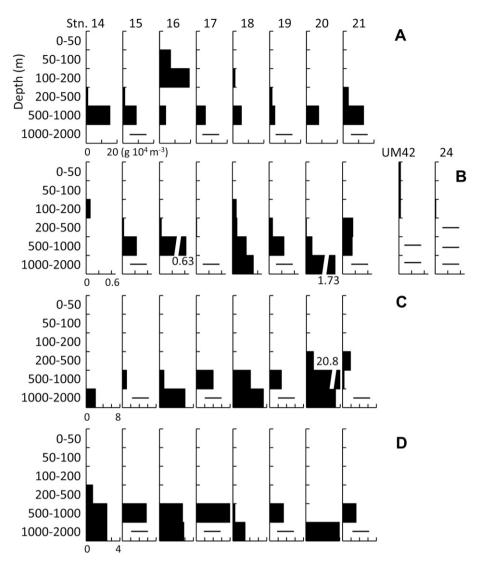


Fig. 5. Vertical distribution of biomass for the seven dominant species off Adélie Land in the Indian Ocean sector. A, *Electrona antarctica*; B, *Notolepis coatsi*; C, *Bathylagus antarcticus*; D, *Cyclothone microdon*; E, *Chionodraco hamatus*., F, *Trematomus newnesi*; G, *Pleuragrammma antarcticum*.

E. antarctica was distributed mainly in the 500–1000 m depth stratum except at station 16, where most of the fish were observed in the 50–200 m depth stratum. N. coatsi exhibited a wide distribution from the surface to 2000 m, although the biomass was larger in the deeper layer from 500 to 2000 m. In shelf waters (stations 42 and 24), a very small biomass was recorded in the surface waters (0–200 m). For B. antarcticus and C. microdon, the largest biomass was recorded from the 500–2000 m layers, and none of these fish were caught in the surface layers (0–200 m).

The vertical distribution patterns of shelf species varied horizontally. However, *C. hamatus* and *T. newnesi* had similar patterns, being found in the surface

(0–50 m) layer throughout the shelf stations but with a larger biomass in the 100–200 m layer at station 24. *P. antarcticum* was also distributed throughout the shelf sampling stations, although a smaller biomass was observed at stations 42 through 25. The largest biomass in this species was observed from the surface to 100 m at stations 22, 23, 26 and 27.

4. Discussion

4.1. Community structure and vertical distribution

The fish community is clearly divided by Antarctic Slope Front (ASF) into separate oceanic and shelf

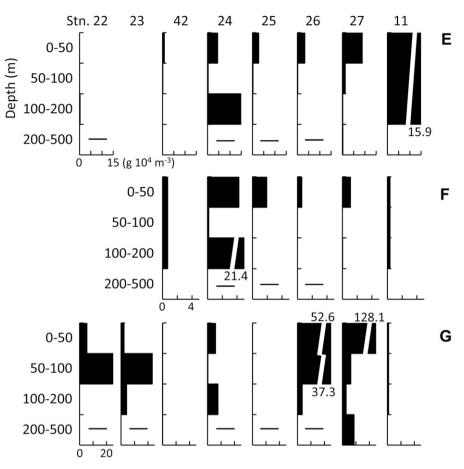


Fig. 5. (continued).

communities, with mesopelagic fish and notothenioids dominating respectively. This fact partly agrees with previous results (Flores et al., 2008; Van de Putte et al., 2010), although most of these surveys were conducted in the upper 200 m. In the Weddell Sea and West Antarctic Peninsula (White and Piatkowski, 1993; Donnelly and Torres, 2008), fish communities are not so clearly divided above the continental slope, with mesopelagic fish and notothenioids distributions overlapping. By contrast, the oceanic and neritic communities are clearly divided in the Ross Sea and eastern Indian sector (Hoddell et al., 2000; Donnelly et al., 2004). A few notothenioids (Cygnodraco mawsoni and Racovitzia glacialis) were distributed north of the shelf break (station 21, just north of ASF) in the present study. No mesopelagic fish were present south of ASF, except for the two specimens of N. coatsi. Only two larvae of Artedidraco type B (notothenioid species) were distributed from the ASF to the SB where cold shelf water was dominant in a subsurface layer (50-200 m depth). A neritic-oceanic mixed distribution on the West Antarctic Peninsula shelf was explained by the presence of CDW on the shelf (Donnelly and Torres, 2008). However, input of MCDW was not detected in this study. The resulting fish assemblages were clearly divided into neritic and oceanic groups similar to those in Ross Sea (Donnelly et al., 2004). The euphausiid community structure is affected by the SB (Ono et al., 2011), although the SB is less likely to affect mesopelagic fish distribution than the ASF. Contrarily, shallower assemblages (0–200 m) taken by a large trawl (IYGPT) was clearly divided at the SB, although the number of fish collected in the area north of the SB was very few (18 individuals in total, only *Krefftichthys anderssoni*).

The abundance of fish in the upper 200 m of the oceanic zone was very low during mid-summer off Adélie Land. This fact is also confirmed by the IYGPT sampling during the CEAMARC survey (Koubbi et al., 2011). The oceanic fish community, represented by *E. antarctica*, is known to undertake diel vertical migration (DVM). *E. antarctica* was collected mainly

between 500 and 1000 m in the present study, which agrees with the daytime distribution in previous studies (Lancraft et al., 1989, 2004). At station 16, where sampling was conducted at night, E. antarctica was abundant in the 50-200 m layers, suggesting some DVM. However, such DVM was not apparent at station 19 and 20 (night-time sampling). During the present cruise, where the night period was very short, DVM if present may be undertaken over a very short time period making it difficult to follow by net sampling. In fact, the IYGPT sampling suggested possible DVM by E. antarctica (Koubbi et al., 2011). However, no distinctive pattern (identifiable as fish) was observed in the 38 and 70 kHz echograms in the upper 200 m, which were taken by the quantitative echo-sounder in all regions of the study area (K. Amakasu, personal communication). If DVM was not present in summer season in high Antarctic zone, seabirds would hardly feed on mesopelagic fish as observed by Ainley et al. (1991). Further detailed study on DVM by fish at high latitudes and during austral summer conditions is necessary to understand the oceanic ecosystem in the high Antarctic Zone. Some information about DVM under midnight sun conditions by zooplankton is available (Nishikawa and Tsuda, 2001; Tanimura et al., 2008).

B. antarcticus and C. microdon may play key roles as predators on zooplankton, and as prey items for squid or large pelagic fish in meso- and bathypelagic ecosystems. However, most of studies conducted in the oceanic area in the high Antarctic Zone have targeted layers from the surface to 1000 m. B. antarctica has a lower energy content level than C. microdon (Donnelly et al., 1990). However, since the dominance of both species in the lower meso- and bathypelagic layers of the high Antarctic Zone has been established in Lützow-Holm Bay, Indian Ocean sector (Moteki et al., 2009) and in our study area from the IYGPT with adult fish (Koubbi et al., 2010, 2011), these species are likely to have a large biomass throughout the oceanic zone. This could also apply to E. antarctica and N. coatsi off Adélie Land. Therefore, these mesoand bathypelagic species are likely to have an impact as predators on copepods, euphausiids and gelatinous zooplankton (Hopkins and Torres, 1989; Hopkins et al., 1993; Lancraft et al., 1991).

In the neritic zone, notothenioid fish (C. hamatus, T. newnesi and P. antarcticum) possibly have an important role as prey items for flying seabirds, penguins and other notothenioids fish in the shallow depth stratum (0–100 m) even during daytime. P. antarcticum larvae mainly feed on diatoms and

copepods (Koubbi et al., 2007; Vallet et al., 2011) whereas juveniles and adults shift toward copepods and euphausiids (Giraldo et al., 2011; Mayzaud et al., 2011) off Adélie and George V Land, and *C. hamatus* feeds on *P. antarcticum* larvae in the Ross Sea (La Mesa et al., 2004). However, the existence of any depth segregation between both these species was not clear.

4.2. Diversity

Van de Putte et al. (2010) conducted RMT sampling in the upper 200 m layer of the Cosmonaut Sea and Prydz Bay regions and collected very few fish in 2005/2006; in fact no fish were collected in 65 of the 125 hauls. The numbers of *P. antarcticum, C. hamatus*, and *T. newnesi* were 113, 9, and 3, respectively, although these are the most dominant species of the neritic zone (Van de Putte et al., 2010). In 2005/06, low chlorophyll *a* concentrations and low zooplankton abundance were observed in this area. These are likely to have resulted in the low fish abundance (Toda et al., 2010).

The number of notothenioid species collected in this study was fairly large, 18 species being recorded in surface layer of the shelf alone. By contrast, Hoddell et al. (2000) and Van de Putte et al. (2010), who sampled in the Cosmonaut Sea and Prydz Bay regions, collected only 13 and 11 species of notothenioids respectively. In several studies of pelagic fish communities in West Antarctica, 11-17 species were collected by Piatkowski (1989), Loeb (1991) and Donnelly and Torres (2008), although 29 species of notothenioids have been reported from pelagic waters of the Weddell Sea by White and Piatkowski (1993). The latter was a compilation of several papers. The number of notothenioid species in the present study is considered large for a single survey in comparison with that in the Weddell Sea. This indicates that the neritic zone off Adelie and George V Land is an important nursery area for notothenioids in the Indian Ocean sector (Koubbi et al., 1997, 2009, 2011), as it is in the Weddell Sea. The gyre-like oceanic circulation could support the retention of larval fish, with a resulting high diversity in the shelf zone.

Twenty-six species of mesopelagic fish are recorded by a large trawl, IYGPT (Koubbi et al., 2011), although only eight species by an RMT 8 in this study. High species diversity and abundance in the meso- and bathypelagic zones, which was revealed in the CEA-MARC, would suggest that further studies on more precise distribution patterns of nektonic animals and their DVM are required to understand oceanic ecosystem in the high Antarctic Zone.

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References

- Ainley, D.G., Fraser, W.R., Smith Jr., W.O., Hopkins, T.L., Torres, J.J., 1991. The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. J. Mar. Syst. 2, 111–122.
- Baker, A., de, C., Clarke, M.R., Harris, M.J., 1973. The N.I.O. combination net (RMT 1+8) and further development of Rectangular Midwater Trawls. J. Mar. Biol. Assoc. UK 53, 167–184.
- Barrera-Oro, E., 2002. The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. Ant. Sci. 14 (4), 293–309.
- Bindoff, N.L., Rosenberg, M.A., Warner, M.J., 2000. On the circulation and water masses over the Antarctic continental slope and rise between 80 and 150°E. Deep Sea Res. II 47, 2299–2326.
- Causse, R., Ozouf-Costaz, C., Koubbi, P., Lamy, D., Eléaume, M., Dettai, A., Duhamel, G., Busson, F., Pruvost, P., Post, A., Beaman, R.J., Riddle, M.J., 2011. Demersal ichthyofaunal shelf communities from the Dumont d'Urville Sea (East Antarctica). Polar Sci. 5 (2), 272–285.
- Cherel, Y., Koubbi, P., Giraldo, C., Penot, F., Tavernier, E., Moteki, M., Ozouf-Costaz, C., Causse, R., Chartier, A., Hosie, G., 2011. Isotopic niches of fishes in coastal, neritic and oceanic waters off Adélie Land, Antarctica. Polar Sci. 5 (2), 286–297.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Dettai, A., Lautredou, A.-C., Bonillo, C., Goimbault, E., Busson, F., Causse, R., Couloux, A., Cruaud, C., Duhamel, G., Denys, G., Hautecoeur, M., Iglesias, S., Koubbi, P., Lecointre, G., Moteki, M., Pruvost, P., Tercerie, S., Ozouf, C., 2011. The actinopterygian diversity of the CEAMARC cruises: barcoding and molecular taxonomy as a multi level tool for new findings. Deep Sea Res. II 58, 250–263.

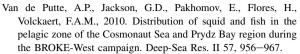
- Donnelly, J., Torres, J.J., Hopkins, T.L., Lancraft, T.M., 1990. Proximate composition of Antarctic mesopelagic fishes. Mar. Biol. 106, 13–23.
- Donnelly, J., Torrres, J.J., Sutton, T.T., Simoniello, C., 2004. Fishes of the eastern Ross Sea, Antarctica. Polar Biol. 27, 637–650.
- Donnelly, J., Torres, J.J., 2008. Pelagic fishes in the Marguerite Bay region of the West Antarctic Peninsula continental shelf. Deep-Sea Res. II 55, 523-539.
- Duhamel, G., 1998. The pelagic fish community of the Polar Frontal zone of the Kerguelen islands. In: Di Prisco, G., Pisano, E., Clarke, A. (Eds.), Fishes of Antarctica: A Biological Overview. Springer, Berlin Heidelberg New York, pp. 63-74.
- Duhamel, G., Koubbi, P., Ravier, C., 2000. Day and night mesopelagic fish assemblages off the Kerguelen islands (Southern Ocean). Polar Biol. 23, 106–112.
- Eastman, J.T., 2005. The nature of the diversity of Antarctic fishes. Polar Biol. 28, 93–107.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.
- Flores, H., Van de Putte, A.P., Siegel, V., Pakhomov, E.A., van Franeker, J.A., Meesters, E.H.W.G., Volckaert, F.A.M., 2008. Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea, Southern Ocean. Mar. Ecol. Prog. Ser. 367, 271–282.
- Gaskett, A.C., Bulman, C., He, X., Goldsworthy, S.D., 2001. Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. N.Z. J. Mar. Freshwat. Res. 35, 469–476.
- Giraldo, C., Cherel, Y., Vallet, C., Mayzaud, P., Tavernier, E., Moteki, M., Hosie, G.W., Koubbi, P., 2011. Ontogenic changes in the feeding ecology of the early life stages of the Antarctic silverfish (*Pleuragramma antarcticum*) documented by stable isotopes and diet analysis in the Dumont d'Urville sea (East Antarctica). Polar Sci. 5 (2), 252–263.
- Gon, O., Heemstra, P.C., 1990. Fishes of the Southern Ocean. JLB Smith Institute of Ichthyology, Grahamstown.
- Greely, T.M., Gartner Jr., J.V., Torres, J.J., 1999. Age and growth of Electrona antarctica (Pisces: Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Mar. Biol. 133, 145-158.
- Hirawake, T., Kudou, S., Aoki, S., Rintoul, S.R., 2003. Eddies revealed by SeaWiFS ocean colour images in the Antarctic Divergence zone near 140°E. Geophys. Res. Lett. 30, 1458.
- Hoddell, R.J., Crossley, A.C., Williams, R., Hosie, G.W., 2000. The distribution of Antarctic pelagic fish and larvae (CCAMLR division 58.4.1). Deep Sea Res II 47, 2519–2541.
- Hopkins, T.L., Torres, J.J., 1989. Midwater food web in the vicinity of the marginal ice zone in the western Weddell Sea. Deep Sea Res. 36A, 543–560.
- Hopkins, T.L., Ainley, D.G., Torres, J.J., Lancraft, T.M., 1993. Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biol. 13, 389–397.
- Hubold, G., 1985. Stomach contents of the Antarctic Silverfish Pleuragramma antarcticum from the southern and eastern Weddell Sea (Antarctica). Polar Biol. 5 (12), 43–48.
- Hubold, G., Ekau, W., 1990. Feeding patterns of post-larval and juvenile notothenioids in the southern Weddell Sea (Antarctica). Polar Biol. 10 (4), 255–260.
- Hulley, P.A., Camus, P., Duhamel, G., 1989. Ichthyological results of cruise MD-42/SIBEX-II. Part 1. Fishes from RMT-8 stations,

- with additional records of lantern fishes (Myctophidae: Osteichthys) from the Indian and Atlantic sectors of the southern ocean. Cybium 13 (1), 83–99.
- Hulley, P.A., 1992. Upper-slope distributions of oceanic lanternfishes (family: Myctophidae). Mar. Biol. 114, 365–383.
- Kellermann, A., 1987. Food and feeding ecology of postlarval and juvenile *Pleuragramma antarcticum* (Pisces; Notothenioidei) in the seasonal pack ice zone off the Antarctic Peninsula. Polar Biol. 7, 307–315.
- Kellermann, A., 1989. Catalogue of early life stages of Antarctic notothenioid fishes. In: Kellermann (Ed.), Identification Key and Catalogue of Larval Antarctic Fishes. BIOMASS Sci Ser, Vol. 10. Alfred-Wegener-Institut, Bremerhaven, pp. 45–136.
- Kock, K.-H., 2005. Antarctic icefishes (Channichthyidae): a unique family of fishes. A review, Part 1. Polar Biol. 28, 862–895.
- Koubbi, P., Ibanez, F., Duhamel, G., 1991. Environmental influences on spatio-temporal oceanic distribution of ichthyoplankton around the Kerguelen islands (Southern Ocean). Mar. Ecol. Progr. Ser. 72, 225–238.
- Koubbi, P., Hureau, J.-C., Vacchi, M., White, M., 1997. Results of the preliminary survey on the coastal distribution of fish larvae in Adelie land (Southern Ocean) during January—February 1996. Cybium 21 (4), 381–392.
- Koubbi, P., Vallet, C., Razouls, S., Grioche, A., Hilde, D., Courcot, L., Janquin, M.A., Vacchi, M., Hureau, J.C., 2007. Condition and diet of larval *Pleuragramma antarcticum* (Nototheniidae) from Terre Adélie (Antarctica) during summer. Cybium 31, 67–76.
- Koubbi, P., Duhamel, G., Hecq, J.-H., Beans, C., Loots, C., Pruvost, P., Tavenier, E., Vacchi, M., Vallet, C., 2009. Ichthyoplankton in the neritic and coastal zone of Antarctica and Subantarctic islands: a review. J. Mar. Syst. 78, 547–556.
- Koubbi, P., Ozouf-Costaz, C., Goarant, A., Moteki, M., Hulley, P.-A.,
 Causse, R., Dettai, A., Duhamel, G., Pruvost, P., Tavernier, E.,
 Post, A., Beaman, R.J., Rintoul, S., Hirawake, T., Hirano, D.,
 Ishimaru, T., Riddle, M., Hosie, G., 2010. Estimating the biodiversity of the East Antarctic shelf and oceanic zone for ecoregionalisation: example of the ichthyofauna of the CEAMARC (Collaborative East Antarctic marine Census) CAML surveys.
 Polar Sci. 4, 115–133.
- Koubbi, P., Moteki, M., Duhamel, G., Goarant, A., Hulley, P.-A., Ishimaru, T., Pruvost, P., Tavernier, E., Vacchi, M., Hosie, G., 2011. Ecoregionalization of myctophid fish in the Indian sector of the Southern Ocean: results from generalized dissimilarity models. Deep Sea Research II 58, 170–180.
- Koubbi, P., Hulley, P.-A., Pruvost, P., Henri, P., Labat, J.-P., Wadley, V., Hirano, D., Moteki, M., 2011. Size distribution of meso- and bathypelagic fish in the Dumont d'Urville Sea (East Antarctica) during the CEAMARC surveys. Polar Sci. 5 (2), 195–210.
- Kozlov, A., 1995. A review of the trophic role of mesopelagic fish of the family Myctophidae in the Southern Ocean ecosystem. CCAMLR Sci. 2, 71–77.
- La Mesa, M., Eastman, J.T., Vacchi, M., 2004. The role of notothenioids fish in the food web of the Ross Sea shelf waters: a review. Polar Biol. 27, 321–338.
- Lancraft, T.M., Torres, J.J., Hopkins, T.L., 1989. Micronecton and zooplankton in the open waters near Anarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biol. 9, 225–233.
- Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., 1991.

 Oceanic micronektonic/macrozooplanktonic community

- structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biol. 11, 157–167.
- Lancraft, T.M., Reisenbichler, K.M., Robinson, B.H., Hopkins, T.L., Torres, J.J., 2004. A krill dominated micronecton community in Croker Passage, Antarctica with an estimate of fish predation. Deep-Sea Res. II 51, 2247–2260.
- Loeb, V.J., 1991. Distribution and abundance of larval fishes collected in the western Bransford Strait region, 1986–87. Deep-Sea Res. 38, 1251–1260.
- Loeb, V.J., Kellermann, A., Koubbi, P., North, A.W., White, M., 1993. Antarctic larval fish assemblages: a review. Bull. Mar. Sci. 53 (2), 416–449.
- Mayzaud, P., Chevallier, J., Tavernier, E., Moteki, M., Koubbi, P., 2011. Lipid composition of the high Antarctic fish *Pleuragramma* antarcticum. Influence of age class. Polar Sci. 5 (2), 264–271.
- Moteki, M., Horimoto, N., Nagaiwa, R., Amakasu, K., Ishimaru, T., Yamaguchi, Y., 2009. Pelagic fish distribution and ontogenetic vertical migration in common mesopelagic species off Lützow-Holm Bay (Indian Ocean sector, Southern Ocean) during austral summer. Polar Biol. 32, 1461–1472.
- Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meradith, M.P.,
 Thorp, S.E., Johnston, N.M., Clarke, A., Tarling, G.A.,
 Collins, M.A., Forcada, S.E., Shreeve, R.S., Atkinson, A.,
 Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G.,
 Enderlein, P., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.J.,
 Pond, D.W., Briggs, D.R., Cunningham, N.J., Fleming, A.H.,
 2007. Spatial and temporal operation of the Scotia Sea
 ecosystem: a review of large-scale links in a krill centred food
 web. Phil. Trans. R. Soc. B. 362, 113–148.
- Nishikawa, J., Tsuda, R., 2001. Diel vertical migration of the tunicate Salpa thompsoni in the Southern Ocean during summer. Polar Biol. 24, 299–302.
- North, A.W., Kellermann, A., 1989. Key to the early stages of Antarctic fish. In: Kellermann (Ed.), Identification Key and Catalogue of Larval Antarctic Fishes. BIOMASS Sci Ser, Vol. 10. Alfred-Wegener-Institut, Bremerhaven, pp. 1–44.
- Ono, A., Moteki, M., Amakasu, K., Toda, R., Horimoto, N., Hirano, D., Ishimaru, T., Hosie, G.W., 2011. Euphausiid community structure and population of Euphausia superba off Adélie Land in the Southern Ocean during austral summers 2003, 2005 and 2008. Polar Sci. 5 (2), 146–165.
- Piatkowski, U., 1989. Macronekton communities in Antarctic surface waters: spatial changes related to hydrography. Mar. Ecol. Prog. Ser. 55, 251–259.
- Post, A.L., Beaman, R.J., O'Brien, P.E., Eléaume, M., Riddle, M.J., 2011. Community structure and benthic habitats across the George V Shelf, East Antarctica: trends through space and time. Deep Sea Res. II. 58, 105–118.
- Sokolov, S., Rintoul, S.R., 2002. Structure of the Southern Ocean fronts at 140°E. J. Mar. Syst. 37, 151–184.
- Takahashi, M., Nemoto, T., 1984. The food of some Antarctic fish in the western Ross Sea in summer 1979. Polar Biol. 3, 237–239.
- Tanimura, A., Hattori, H., Miyamoto, Y., Hoshiai, T., Fukuchi, M., 2008. Diel changes in vertical distribution of *Oithona similis* (Cyclopoida) and *Oncea curvata* (Poecilostomatoida) under sea ice in mid-summer near Syowa Station, Antarctica. Polar Biol. 31, 561–567.
- Toda, R., Moteki, M., Ono, A., Horimoto, N., Tanaka, Y., Ishimaru, T., 2010. Structure of the planktonic cnidarian community in Lützow-Holm Bay in the Indian sector of the Southern Ocean. Polar Sci., 387–404.

Tomczak, M., Liefrink, S., 2005. Interannual variations of water mass volumes in the Southern Ocean. J. Atmos. Ocean Sci. 10, 31–42.
Vallet, C., Beans, C., Koubbi, P., Courcot, L., Hecq, J.-H., Gaffart, A., 2011. Food preference of larvae of Antarctic silverfish Pleuragramma antarcticum Boulenger, 1902 from Terre Adelie coastal waters during summer 2004. Polar Sci. 5 (2), 239–251.



White, M.G., Piatkowski, U., 1993. Abundance, horizontal and vertical distribution of fish in eastern Weddell Sea micronekton. Polar Biol. 13, 41–53.



