Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea, Southern Ocean

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ABSTRACT: The distribution and abundance of larval and postlarval fishes was investigated in the Lazarev Sea, Southern Ocean, in March and April 2004. The upper 200 m of the water column were sampled with an 8 m^2 rectangular midwater trawl at 93 stations. The larval species community clustered in a diverse coastal community with high densities of Antarctic silverfish *Pleuragramma antarcticum* larvae and a less diverse offshore community dominated by Antarctic jonasfish *Notolepis coatsi* and the lanternfish *Electrona antarctica*. No postlarval fish were caught in coastal areas. The offshore community of postlarval fishes consisted of the deep-sea smelt *Bathylagus antarcticus*, and the lanternfishes *Gymnoscopelus braueri*, *G. nicholsi* and *E. antarctica.* The latter species clearly dominated, occurring at mean individual and wet mass densities of 0.17 individuals m^{-2} and 0.26 g m^{-2}, respectively. A generalized additive model significantly related the density of postlarval *E. antarctica* to the abundance of Antarctic krill *Euphausia superba*, ocean depth and sea surface temperature. The diet of *E. antarctica* was dominated by copepods and euphausiid larvae. Mean energy density of *E. antarctica* in the upper 200 m was 2.8 kJ m^{-2}, which is equivalent to 36 % of the energy stored in Antarctic krill stocks and probably would be considerably higher if a greater depth range were considered. This suggests that *E. antarctica* is a major energy transmitter in the food web of the Lazarev Sea, challenging the classical krill-dominated food web paradigm of the Southern Ocean.

KEY WORDS: Antarctic · Southern Ocean · Fish abundance · Fish ecology · Fish larvae · Energy · Food web

INTRODUCTION

Pelagic offshore waters form the largest marine realm in the Antarctic, accounting for 89 % of the marine primary production (Arrigo et al. 1998). In the early years of pelagic ecosystem research, studies focused on the role of Antarctic krill *Euphausia superba*, which forms a major food source of many species of fish, squid, birds and mammals (González & Rodhouse 1998, Wienecke et al. 2000, Casaux et al. 2004, Flores et al. 2004). With time it has become increasingly clear that the Antarctic food web is more complex than the simplistic diatom–krill–top predator concept initially assumed. Especially the importance of pelagic fishes as energy transmitters may have been underestimated (Ainley & DeMaster 1990, Barrera-Oro 2002).

The mesopelagic ichthyofauna of the Southern Ocean comprises 73 species belonging to 24 families

(Kock 1992). It is dominated, in species number as well as biomass, by the family Myctophidae or lanternfishes (Barrera-Oro 2002). Thirty-five species of myctophids are known from the Southern Ocean (Hulley 1990). Lanternfishes are major consumers of mesozooplankton (Pakhomov et al. 1996, Pusch et al. 2005) and an important, often dominating part of the diet of a number of bird and mammal species (Barrera-Oro 2002, Casaux et al. 2004). South of the Antarctic Polar Front (APF), the myctophid *Electrona antarctica* is the most abundant lanternfish (Sabourenkov 1990). With the exception of the Ross Sea, it exhibits an almost ubiquitous distribution between the APF and the continental shelf (Hulley 1990).

Other abundant non-myctophid, mesopelagic and epipelagic fishes in the Southern Ocean belong to the families Bathylagidae (deep-sea smelts) and Paralepididae (barracudinas). The deeper-dwelling bathylagid *Bathylagus antarcticus*, for example, is widely distributed in the Southern Ocean. It is found at depths down to 4000 m, but vertical migration extends up to the surface layer (Lancraft et al. 1989, Gon 1990). The paralepidid *Notolepis coatsi* (Antarctic jonasfish) is known to occur between the surface and 2000 m depth (Post 1990).

The early stages of most Antarctic fish species are usually epipelagic. Larvae of Bathylagidae, Myctophidae and Paralepididae are common in oceanic near-surface waters (Hoddell et al. 2000, Fisher et al. 2004). In high Antarctic shelf waters, the nototheniid *Pleuragramma antarcticum* (Antarctic silverfish) is the dominating pelagic species (White & Piatkowski 1993, Hoddell et al. 2000). Spatial separation has been hypothesized between the different life stages of *P. antarcticum*; larvae feed on zooplankton in the surface layer of the shelf waters and move into deeper layers farther offshore when they become juveniles. Mature adults return to the shelf for spawning (Hubold 1992, Maes et al. 2006).

The Lazarev Sea belongs to the less intensively investigated sectors of the Southern Ocean. Between the Antarctic Circumpolar Current in the north and the Coastal Current in the south, large areas are influenced by the eastern extension of the Weddell Gyre with an eastward flow in the north and branches turning south and west in the central Lazarev Sea (Klatt et al. 2005). The major part of the Lazarev Sea covers deep sea and a narrow shelf borders the Antarctic continent.

A scientific survey in austral autumn 2004 provided an opportunity to sample the pelagic ichthyofauna of the Lazarev Sea and to evaluate the results in the light of various abiotic and biological datasets collected in parallel. The objectives of this study are to (1) investigate the distribution of larval and postlarval fishes in the top 200 m layer of the Lazarev Sea, (2) assess the role of different biotic and abiotic factors in controlling the distribution of the most abundant species, *Electrona antarctica*, and (3) evaluate the ecological relevance of myctophid fishes to the pelagic ecosystem.

MATERIALS AND METHODS

Sampling scheme. Larval and postlarval fish were collected between 7 and 26 April 2004 during an expedition with RV 'Polarstern' (ANT XXI-4). The cruise was mainly dedicated to surveying the distribution and abundance of Antarctic krill *Euphausia superba* on behalf of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). The station grid in the Lazarev Sea (CCAMLR statistical Subarea 48.6) included 4 longitudinal transects along the 0°, 2°, 4° and 6° W meridian and extended from 61° S to the continental coast at approximately 71° S (Fig. 1b). Latitudinal spacing between stations was 20 nautical miles (n miles) (37.0 km).

A rectangular midwater trawl (RMT 8+1) net was used as the routine sampling device. It consisted of an RMT 1 (mesh size = 0.33 mm) mounted above an RMT 8 with net opening areas of 1 and 8 m^2, respectively. The RMT 8 had a mesh size of 4.5 mm at the opening and a mesh size of 0.85 mm at the cod end. A calibrated mechanical impeller flow meter mounted outside the net opening allowed the volume of water passing through the net to be estimated. At each station, standard double oblique hauls were conducted, reaching to a depth of 200 m at a trawling speed of 2.5 knots (4.5 km h^{-1}).

Environmental data. Ocean depth, sea surface temperature and surface salinity were continuously recorded by the ship's sensors. Based on RMT 8 and RMT 1 samples, euphausiid larval and postlarval abundance data (individuals [ind.] 1000 m^{-3}) were collected following the procedures described in Siegel et al. (2004). Surface water total chlorophyll concentration (mg m^{-3}) at each sampling station was obtained from a public database based on the NASA Ocean Biogeochemical model (NOBM: NASA 2007, Gregg & Casey 2007).

The proportion of the sea surface covered by sea ice was monitored by an observer on board while the ship travelled between stations according to the method described in Van Franeker et al. (1997). Total ice coverage was estimated for each station as a function of latitude using a linear model with a logit link function (explained deviance = 67.4 %, p < 0.001). The same method was applied to estimate the proportion of the sea surface covered by pack-ice floes excluding young ice (explained deviance = 34.2 %, p < 0.05).
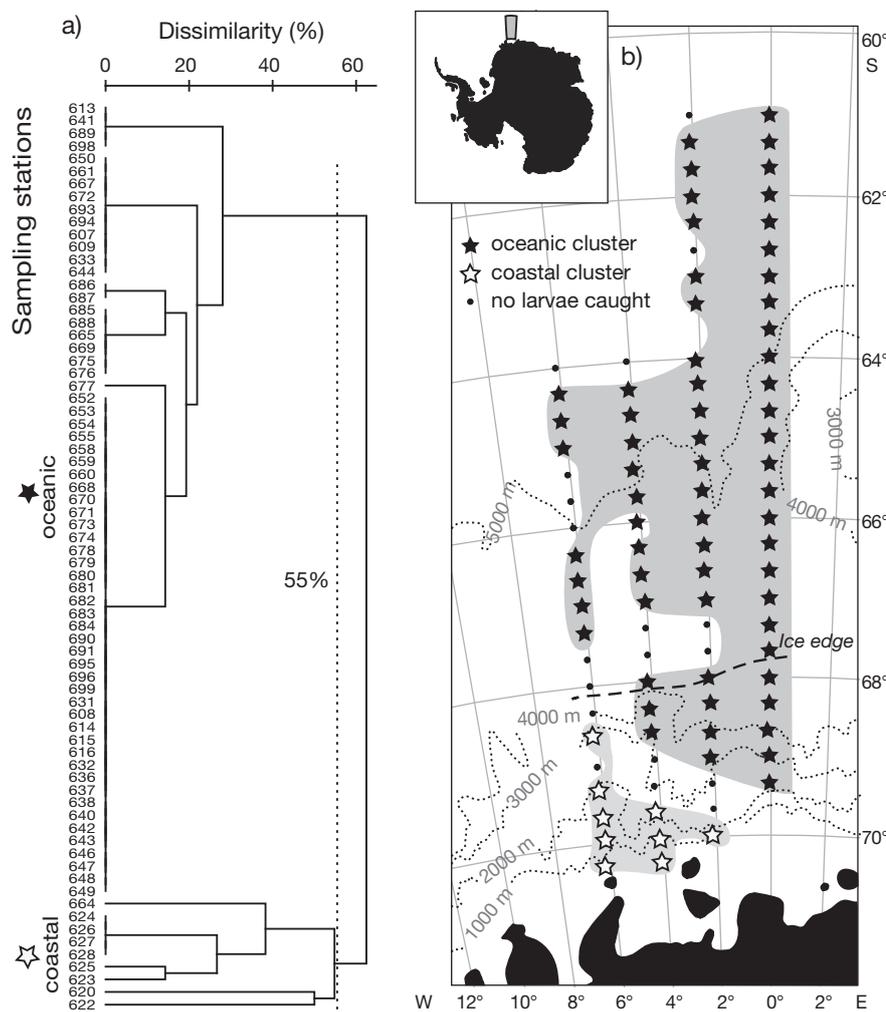
Fig. 1. (a) Cluster dendrogram of stations according to the species composition of larval fishes and (b) geographic distribution of species clusters in polar stereographic projection. Stations where fish larvae were caught were grouped in a coastal and an oceanic cluster. Geographic overview of the Antarctic continent in inset shows the survey area shaded in grey

From the 14 stations where a sufficient number of fish were caught, the diet was analysed in 139 *Electrona antarctica*. Stomachs were collected from the fish immediately after thawing and fixed in 4% hexamine-buffered formaldehyde solution in seawater. After fixation, stomachs were dissected under a stereoscopic microscope. Food items were identified to species level and ontogenetic stage if possible. In the case of strongly digested crustaceans, the number of ingested individuals was assumed to be half the number of facet eyes. Calanoid copepods were grouped in the size classes of small (<3 mm) and large (≥3 mm). Reconstructed dry weight was calculated for major taxonomic groups of prey species using published data on mean individual dry mass (Donnelly et al. 1994, Torres et al. 1994, Hagen 2001).

Data analysis — fish larvae. A hierarchical cluster analysis of sampling sites was performed to investigate the spatial structure of larval species communities. Unidentified larvae and stations where no larvae were caught were excluded from the analysis. A dissimilarity matrix based on the Bray-Curtis index was constructed using presence–absence data of species at each station. Clusters were fused by group-average linking. The density of fish larvae was estimated at each station based on the number of individuals per volume of water filtered and expressed as the number of individuals per surface area (ind. $m^{-3} \times 200$ m = ind. m^{-2}). Overall density per species was calculated as the average over all stations.

Fish data. All larval and postlarval fish were collected from the RMT 8 and identified to species level. Larvae were either frozen or preserved in 70% ethanol. We measured the standard length (SL) of each postlarval fish to the lower full millimeter immediately after capture. One-third of the postlarval fish were preserved on 4% hexamine-buffered formaldehyde solution in seawater; the rest were frozen at –20°C. In the home laboratory, the frozen fish were thawed and blotted dry with paper tissue. Wet weight (WW) was estimated to an accuracy of 0.01 g. The length–weight relationship obtained from these specimens was used to calculate the WW of the remaining fish (Table 1).

Table 1. *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri*. Parameters of the length–weight regressions. The wet weight (WW) in g was expressed as a function of the standard length (SL) in mm according to the equation: $\log_{10}(WW) = a + b\log_{10}(SL)$. N = sample size

Species	N	a	b	R^2	p
Bathylagus antarcticus	24	−5.5296	3.0949	0.90	<0.001
Electrona antarctica	649	−5.2708	3.21570	0.97	<0.001
Gymnoscopelus braueri	35	−5.2182	3.0709	0.91	<0.001

Data analysis: postlarval fish. Daylight hauls (solar radiation > 10 W m^{-2}) were excluded from analysis of postlarval fish to avoid an underestimation of density and biomass due to vertical migration into deeper layers at daytime (Piatkowski et al. 1994, Pusch et al. 2005, Loots et al. 2007). Similar to density estimates of larvae, number of individuals, wet biomass and energy densities of postlarval fishes were calculated and expressed in ind. m^{-2}, g m^{-2} and kJ m^{-2}, respectively. Energy density was estimated based on the sum of the individual energy contents of adult *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri*. Individual energy contents were calculated using the mean wet mass energy content in *B. antarcticus* and *G. braueri* and the relationship between SL and energy content estimated from a subsample of fish from the same survey in *E. antarctica* (Van de Putte et al. 2006).

Generalized additive models (GAMs, Hastie & Tibshirani 1990) were used to investigate the relationship of environmental variables with the individual density of *Electrona antarctica* using a suite of publicly available physical and biological datasets and euphausiid abundance data obtained simultaneously by RMT sampling. Data included: ocean depth, surface temperature, surface salinity, surface water total chlorophyll concentration, total ice coverage, abundance of postlarval *Euphausia superba*, abundance of larval *E. superba*, abundance of postlarval euphausiid *Thysanoessa macrura*, and abundance of larval *T. macrura*.

GAMs can be considered as an extension of generalized linear models (GLMs, McCullagh & Nelder 1989). They extend the implicit linear relationship between response and explanatory variables of GLMs by fitting higher order smoothing functions to explanatory variables. The flexibility of the smoothing function is determined by the degrees of freedom associated with the smoothing term. One degree of freedom is equivalent to a GLM; the flexibility of the smoother increases at higher degrees of freedom.

Fish density is comparable with count data, which are typically modeled using a Poisson error distribution (McCullagh & Nelder 1989). We used a Poisson error distribution with a correction for overdispersion (in R termed quasipoisson) combined with a log link function. The number of fish caught per station was used as the discrete response variable. To relate the number of fish to actual densities, the amount of filtered water was used as an offset variable.

The 2 shelf stations with depths less than 500 m were excluded. *Electrona antarctica* is an offshore species and was not caught at these localities. To obtain an equal spread over the entire range of the data, depth values were log-transformed, and a 4th-root transformation was applied to the euphausiid abundance data.

Collinearity of variables was assessed by calculating correlation coefficients and variance inflation factors (VIF). The VIF values of all variables were <10, a value below which colinearity is usually not regarded as serious (Quinn & Keough 2002).

Models were fitted with smoothing splines using cross-validation to obtain the optimal degrees of freedom for each variable. The best model was estimated by stepwise forward selection based on the lowest deviance. Significance of decreasing deviance was confirmed with the *F*-test (Quinn & Keough 2002). Regression assumptions were assessed visually by plotting the response variable against fitted values and residuals against variables. The procedure was repeated using ice floe coverage instead of total ice coverage as a descriptor of sea ice conditions. Statistical calculations were performed with the R (R Development Core Team 2006) and Brodgar (Highland Statistics 2006) software packages.

RESULTS

Larval fish

Ninety-three stations were sampled for fish larvae. At 74 of these stations, 903 fish larvae were collected. They comprised at least 10 species belonging to 7 families. *Electrona antarctica*, *Notolepis coatsi* and *Pleuragramma antarcticum* dominated the species community, altogether accounting for 97% of the larvae caught (Table 2).

A hierarchical cluster analysis separated the stations into 2 groups at a dissimilarity level of 55% (Fig. 1a). Most stations of one cluster were located in the southern shelf and slope region of the survey area, which is, therefore, referred to as the coastal cluster (Fig. 1b). Sea ice was common in this region. At only one station was a single specimen of *Notothenia kempi* caught, at a bottom depth of 4100 m. The species composition of the coastal cluster consisted exclusively of notothenioid larvae. It was dominated by *Pleuragramma antarcticum*, which was encountered at 7 of the 9 stations in this cluster. Due to the high numbers of *P. antarcticum* larvae, overall density of larvae in the coastal cluster was considerably higher than in the oceanic cluster (Table 3).

Stations deeper than 3000 m formed an oceanic cluster (Fig. 1b). Larvae of *Electrona antarctica* and *Notolepis coatsi* were found throughout this region. *N. coatsi* were more abundant than *E. antarctica* larvae (Table 3). On the easternmost transect, larvae of *Bathylagus antarcticus* were encountered at 8 stations, and a single *Muraenolepis* sp. larvae was obtained.

Table 2. Species composition of larval fishes in the Lazarev Sea, March and April 2004. F_O = frequency of occurrence (percentage of stations where fish larvae were caught), F_R = relative frequency (percentage of the total number of fish sampled), N = number of fish larvae caught

Taxonomic group and species	N	No. of stations	F_O (%)	F_R (%)
Bathylagidae				
Bathylagus antarcticus	16	8	8.6	1.8
Myctophidae				
Electrona antarctica	262	55	59.1	29.0
Muraenolepidae				
Muraenolepis sp.	1	1	1.1	0.1
Paralepididae				
Notolepis coatsi	362	60	64.5	40.1
Bathydraconidae				
Akarotaxis nudiceps	1	1	1.1	0.1
Racovitza glacialis	1	1	1.1	0.1
Channichthyidae				
Channichthyidae spp.	4	3	3.2	0.4
Nototheniidae				
Notothenia kempi	2	2	2.2	0.2
Pleuragramma antarcticum	248	7	7.5	27.5
Nototheniidae sp.	1	1	1.1	0.1
Unidentified	5	3	3.2	0.5
No fish	–	20	21.5	–
Total	**903**	**93**	**–**	**100.0**

Table 3. Densities (ind. m^{-2}) of dominant species of fish larvae in the spatial clusters shown in Fig. 1

Cluster	— Coastal — Mean	SD	— Oceanic — Mean	SD	— Total — Mean	SD
Bathylagus antarcticus	0.000	–	0.014	0.046	0.010	0.038
Electrona antarctica	0.000	–	0.221	0.258	0.152	0.237
Notolepis coatsi	0.000	–	0.307	0.241	0.211	0.246
Pleuragramma antarcticum	1.454	2.194	0.000	–	0.141	0.778
All species	1.526	2.215	0.546	0.372	0.523	0.825

Table 4. Species composition of postlarval fishes in the Lazarev Sea, March and April 2004. F_O = frequency of occurrence (percentage of stations where fish were caught), F_R = relative frequency (percentage of total number of fish sampled), N = number of fish caught

Taxonomic group and species	N	No. of stations	F_O (%)	F_R (%)	Length range (mm)
Bathylagidae					
Bathylagus antarcticus	40	7	11.5	3.7	29–130
Myctophidae					
Electrona antarctica	987	42	68.9	90.2	21–102
Gymnoscopelus braueri	65	20	32.8	5.9	64–132
Gymnoscopelus nicholsi	2	2	3.3	0.2	158–180
No fish	–	19	31.1	–	–
Total	1094	61	–	100.0	–

Postlarval fish

Species composition and distribution patterns

The analysis was limited to the 61 stations sampled in darkness because large parts of the populations of the species caught are known to dwell at depths below 200 m during daylight. In total, 1094 individuals of 4 species were caught. *Electrona antarctica* clearly dominated the species community. It was caught at most stations throughout the oceanic part of the area of investigation (Table 4, Fig. 2a). The distribution of *Gymnoscopelus braueri* was similar to that of *E. antarctica*, but it occurred in much lower numbers. *Bathylagus antarcticus* was collected at 7 localities (Fig. 2b). Twenty-nine of the 40 individuals sampled were caught at a single locality at 69°S, 6°W. Two *G. nicholsi* were caught at 2 stations in the northern part of the survey area (Table 4).

The overall average number of individuals, biomass and energy densities of postlarval *Bathylagus antarcticus*, *Electrona antarctica* and *Gymnoscopelus braueri* are shown in Table 5. Highest densities of *E. antarctica* were found between 66° and 68°S (Fig. 2a). The length-frequency distribution of the postlarval *E. antarctica* covered almost the entire known size range (Hulley 1990) and was dominated by fish between 25 and 39 mm SL, averaging at 43.6 mm (Fig. 3). The low numbers caught of *B. antarcticus* and *G. braueri* preclude a meaningful analysis of their distribution patterns and size distributions.

Density of postlarval *Electrona antarctica* in relation to environmental variables

The relationship of the density of postlarval *Electrona antarctica* with a number of environmental variables was explored using GAMs. The GAM with the lowest deviance included abundance of postlarval *Euphausia superba*, ocean depth, sea surface temperature and abundance of *Thysanoessa macrura* larvae. This model explained 78.3% of the deviance (Table 6). The smooth term of the latter variable, however, was insignificant (Table 7). Excluding the abundance of *T. macrura* larvae led to an increase in unexplained deviance of only 4%, suggesting that a combination of postlarval krill abundance, depth and
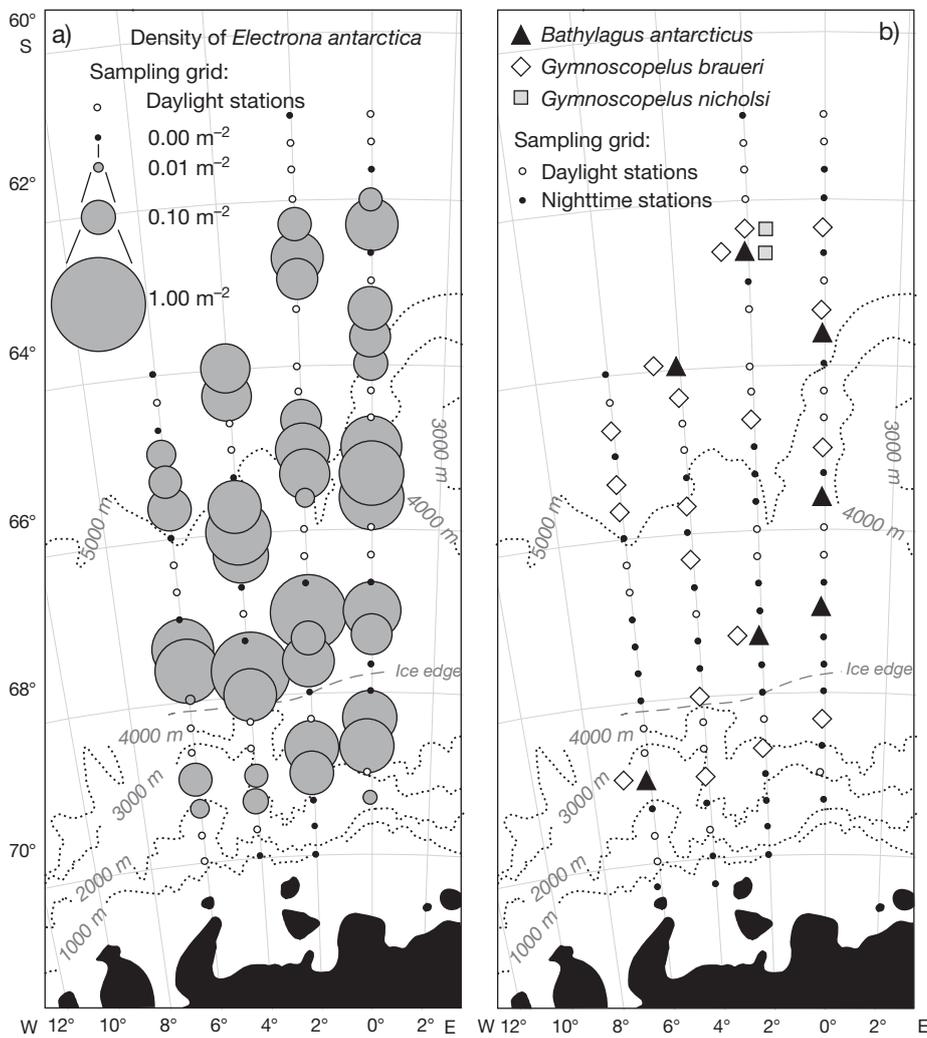
abundance of postlarval krill had a negative effect on the fitted density of the lanternfish (Fig. 4a,b). The effect of sea surface temperature on modeled fish density was largely neutral, although it significantly improved the overall model fit in combination with the other variables (Fig. 4c). Large confidence intervals indicate that model reliability was low at depths shallower than ca. 3200 m, postlarval krill abundances above 80 ind. m^{-2} and sea surface temperatures below –1.7°C (Fig. 4).

Diet of *Electrona antarctica*

Stomachs of 139 postlarval fish were investigated for their content. The fish had a mean SL of 43.9 mm, ranging between 20 and 79 mm. Stomachs were not collected from the few larger fish obtained, which were sacrificed entirely for energy investigations (Van de Putte et al. 2006). Of the total examined, 120 stomachs contained food items. Most of the stomach contents, however, were at an advanced stage of digestion. At least 12 prey species were found. The majority of prey items were copepods (Table 8). Calanoid copepods ≥ 3 mm were the most numerous, accounting for 28% of the number of prey items. Among them, *Metridia gerlachei* was the most frequently identified species. The second most frequent large copepod species identified was *Pareuchaeta antarctica*. Among the copepods < 3 mm in size (16% of food items), *Aetidiopsis minor* and *Scolecithricella minor* were the only identifiable prey species. Euphausiids accounted for 28% of the food items. A small number of furcilia larvae and adult euphausiids could be identified as *Thysanoessa macrura*. Ostracods (6.6%) and amphipods (5.7%; e.g. *Hyperiella dilatata*) were less frequent (Table 8). *Limacina* spp. (1.9%) were found occasionally.

Fig. 2. Spatial distribution of postlarval fishes (polar stereographic projection). (a) Individual density of *Electrona antarctica* (daylight stations excluded from analysis) and (b) stations where *Bathylagus antarcticus*, *Gymnoscopelus braueri* and *Gymnoscopelus nicholsi* were caught (all stations included)

Table 5. Individual, biomass and energy densities of the 3 most abundant species of postlarval fish

Species	Density (ind. m^{-2})		Biomass (g m^{-2})		Energy (kJ m^{-2})	
	Mean	SD	Mean	SD	Mean	SD
Bathylagus antarcticus	0.005	0.027	0.012	0.082	0.036	0.246
Electrona antarctica	0.170	0.172	0.261	0.255	2.827	2.723
Gymnoscopelus braueri	0.011	0.026	0.074	0.175	0.614	1.534

sea surface temperature was the best predictor of the density of postlarval *E. antarctica* (Table 6).

Postlarval krill abundances between 2 and 11 ind. m^{-3} and depths between 3800 and 4500 m positively affected the fitted density of *Electrona antarctica*. Low
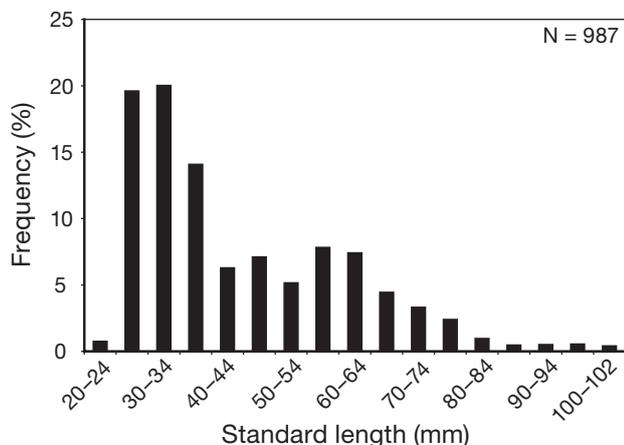
Fig. 3. *Electrona antarctica.* Length–frequency distribution of postlarvae. The percentage of the total number of fish is shown for each 5 mm length class

DISCUSSION

Only a few fish surveys have been conducted in the less intensively investigated sectors of the Southern Ocean (Hoddell et al. 2000, Granata 2002, Donnelly et al. 2004). Our study forms the first published record on the distribution of postlarval fishes in the pelagic waters of the Lazarev Sea and contributes new data on the distribution of fish larvae, 23 yr after the data collection of the most recent published record (Efremenko 1991). The restricted fishing depth (0–200 m) of the survey limited the chances of sampling the full range of deep-dwelling species. Because the natural depth distributions of the postlarval fishes caught exceed 200 m at night (Collins et al. 2008), and due to possible net avoidance by larger fish, their individual and biomass densities were probably underestimated. With few exceptions (Piatkowski et al. 1994, Duhamel et al. 2000, Collins et al. 2008), however, data collected with relatively small macrozooplankton nets present the best information on mesopelagic fish in the Southern Ocean available to date (Lancraft et al. 2004, Donnelly

Table 6. *Electrona antarctica*. Comparison of generalized additive models relating the density of fish to combinations of stepwise added environmental variables. p = *F*-test significance of change in deviance compared with the model in the preceding row. The model discussed in the text is highlighted in **bold** and shaded

Model no.	Variables	Deviance	Explained deviance	p
1	Postlarval krill abundance	624.1	42.1%	0.003
2	Model 1 + ocean depth	498.0	53.8%	0.008
3	**Model 2 + sea surface temperature**	**247.6**	**74.5%**	**0.032**
4	Model 3 + larval *Thysanoessa macrura* abundance	233.6	78.3%	0.041

Table 7. Model parameters of smoothing terms of the 2 most parsimonious models (from Table 6). df = degrees of freedom, p = significance of smoother. The model analyzed in the discussion is highlighted in **bold** and shaded

Smoother for variable	Model 3		Model 4	
	df	**p**	df	p
Postlarval krill abundance	**6.6**	**<0.001**	4.7	<0.001
Ocean depth	**6.6**	**0.005**	4.1	0.001
Sea surface temperature	**9.0**	**0.041**	2.7	0.019
Larval *Thysanoessa macrura* abundance	**–**	**–**	1.6	0.168

et al. 2006). In this sense, the standardized, spatially dense sampling scheme of the present study provided a dependable dataset for minimum abundance estimates of Antarctic mesopelagic fishes.

Larval fish

Ten species of larval fish belonging to 7 families were collected. The taxonomic richness was small compared with reports from nearby areas, such as Efremenko (1991) who found 25 species from 8 families in the Lazarev Sea in autumn, and White & Piatkowski (1993) who reported 18 species from 8 families from the adjacent Weddell Sea in summer. Comparability among studies is often complicated by the difference in depth ranges sampled and sampling gears used. More importantly, extensive sampling of the diverse shelf-associated species assemblage in these studies probably contributed to an elevated species richness compared with our more oceanic sampling scheme. In high Antarctic offshore waters, species numbers comparable with our findings are representative for a sampling depth between 100 and 300 m (Kaufmann et al. 1995, Morales-Nin et al. 1995, Fisher et al. 2004).

A distinct separation into coastal and oceanic species communities was apparent from the cluster analysis. This pattern reflects the contrast between the shelf-associated species community dominated by notothenioids and the offshore community of mesopelagic fishes in the Southern Ocean (DeWitt 1970, Hoddell et al. 2000, Granata 2002). The 6 notothenioid species encountered on the few shelf stations can be considered as a subsample of the coastal ichthyoplankton community of the Lazarev Sea (Efremenko 1991, White & Piatkowski 1993). Many species of this taxonomic group are endemic to high Antarctic waters (Loeb et al. 1993). Three of these, *Akarotaxis nudiceps*,
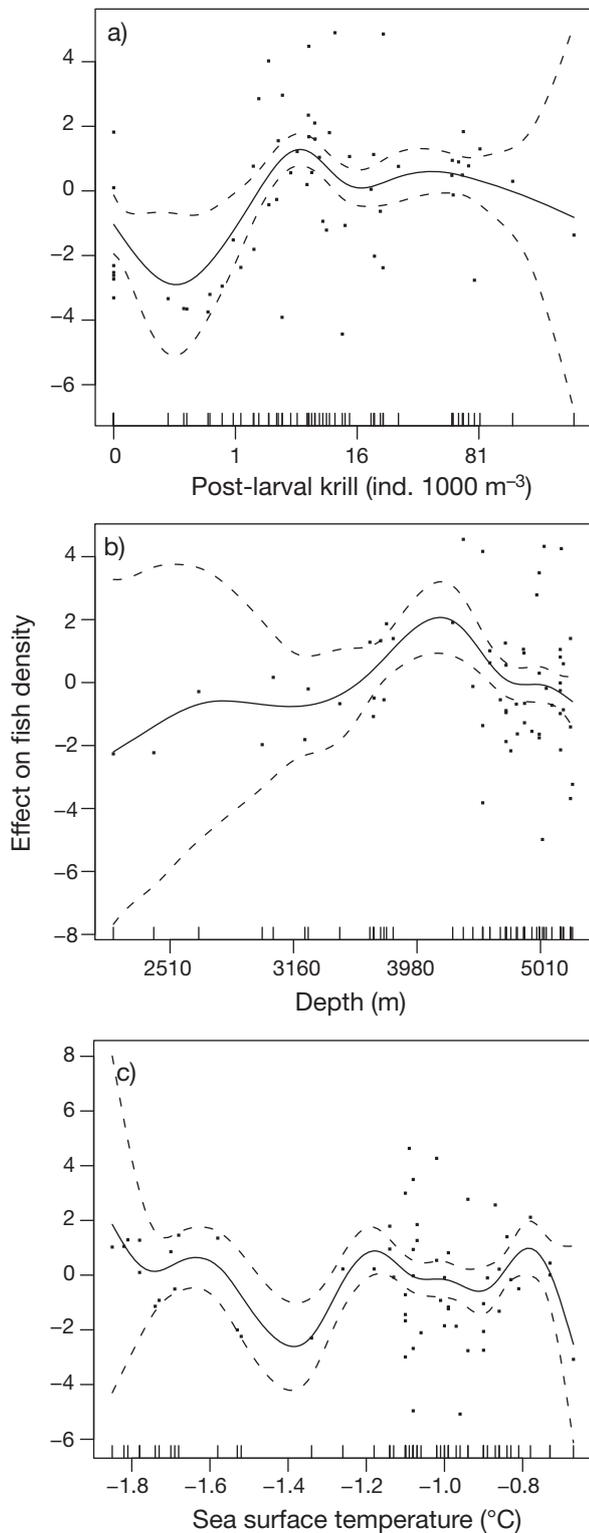
Fig. 4. *Electrona antarctica.* Generalized additive model of the numerical density of postlarvae. Effect of additive smoothing functions of (a) postlarval *Euphausia superba* abundance, (b) ocean depth and (c) surface sea temperature on the fitted density of fish. Dashed lines show 95% confidence intervals of smoothers

Rakovitza glacialis and *Pleuragramma antarcticum*, were collected during the present survey. The dominance of *P. antarcticum* larvae often observed in Antarctic shelf and slope waters could be confirmed for the Lazarev Sea (Kaufmann et al. 1995, Hoddell et al. 2000, Granata 2002).

The ichthyoplankton composition was less diverse in offshore waters. *Electrona antarctica* and *Notolepis coatsi* larvae occurred widely in the offshore parts of the survey area. They are typically the dominant species of fish larvae in the oceanic part of the Southern Ocean south of the APF (Morales-Nin et al. 1995, Hoddell et al. 2000, Fisher et al. 2004). *Muraenolepis* sp. and *Bathylagus antarcticus* have been reported to be scarce in high Antarctic surface waters (Kaufmann et al. 1995, Morales-Nin et al. 1995). The elevated frequency of *B. antarcticus* larvae in the east of the survey area might be related to upwelling of deeper water layers close to the Maud Rise seamount (Holland 2001).

As a consequence of their planktonic mode of life, a pronounced role of bottom topography and prevailing currents in structuring the distribution of larval fish communities is typical (Koubbi et al. 1991, White & Piatkowski 1993, Hoddell et al. 2000). In the ocean around the Antarctic continent, separation of coastal and offshore waters is enhanced by a latitudinal succession of circumpolar current systems with longitudinal flow, such as the westward flowing Coastal Current. In the Lazarev Sea, the northern boundary of this current system largely coincides with the shelf break, forming an effective physical barrier between oceanic and coastal ichthyoplankton communities (Klatt et al. 2005).

Postlarval fish

Species composition and distribution patterns

Four species of postlarval fish were collected in offshore waters: *Bathylagus antarcticus* (Bathylagidae) and *Electrona antarctica*, *Gymnoscopelus braueri* and *G. nicholsi* (Myctophidae). The absence of these mesopelagic fishes from the coastal areas reflected the spatial separation observed in the larval community. Shelf-associated postlarval fish were probably not sampled representatively at the few shelf and slope stations of the survey, leaving no evidence of postlarval *Pleuragramma antarcticum*, the dominating pelagic species on the Antarctic shelf. A range of species similar to our findings with *E. antarctica* as the most common postlarval fish was reported from the upper 200 m of the water column in various areas of the Southern Ocean (Hoddell et al. 2000, Lancraft et al. 2004, Donnelly et al. 2006).

Table 8. *Electrona antarctica.* Diet composition from 139 fish sampled (20 to 79 mm SL); 19 stomachs were empty. Proportional dry weights were reconstructed based on published mean individual weights. DW = dry weight, N = number of diet items

Prey item	N	Proportional N (%)	Mean ind. DW (mg)	Proportional DW (%)
Ostracods	21	6.6	0.54[a]	4.55
Copepods	166	52.6	0.68[a]	44.80
Postlarval euphausiid	8	2.5	3.94[b]	12.57
Euphausiid furcilia	13	4.1	0.85[c]	4.41
Euphausiid calyptotis	67	21.2	0.22[c]	5.87
Euphausiids total	88	27.8		22.85
Amphipods	18	5.7	3.87[b]	27.81
Others	23	7.3	–	–
Total	316	100.0	–	100.0

[a]From Donnelly et al. (1994); [b]from Torres et al. (1994); [c]from Hagen (2001)

The density of *Electrona antarctica* individuals (0.170 ind. m^{-2}) was substantially higher compared with values reported for the upper 200 m, which range between 0.011 (Lancraft et al. 2004) and 0.099 ind. m^{-2} (Kaufmann et al. 1995). The majority of *E. antarctica* sampled in the Lazarev Sea were juveniles. The 2 major modes in the length-frequency distribution (30 to 34 mm and 55 to 59 mm) correspond to the length classes of 1 and 2 year old fish (Fig. 3; Greely et al. 1999). Due to the dominance of juveniles, high individual densities were not reflected in biomass density (0.261 g WW m^{-2}), which was at the lower end of the range reported from the western Weddell Sea and adjacent waters (Lancraft et al. 1989, Donnelly et al. 2006), but considerably higher than values reported from the Ross Sea, the Scotia Sea and the APF (Piatkowski et al. 1994, Donnelly et al. 2004, Collins et al. 2008). The low numerical and biomass densities of *Bathylagus antarcticus* and *Gymnoscopelus braueri* in the Lazarev Sea were in the range reported from the near-surface layer (Kaufmann et al. 1995, Donnelly et al. 2006).

Density of postlarval *Electrona antarctica* in relation to environmental variables

Postlarval *Electrona antarctica* density could best be modeled by a GAM including abundance of postlarval *Euphausia superba*, ocean depth and sea surface temperature. Ocean depths between about 3800 and 4500 m had a positive effect on the modeled density of *E. antarctica*, whereas low abundances of postlarval krill negatively affected the fitted fish density (Fig. 4a,b).

A growing number of studies has exemplified the benefit of GAMs in ecological datasets, including marine and fisheries ecology (Maravelias et al. 2007, Zarauz et al. 2007). Loots et al. (2007) modeled the habitat use of *Electrona antarctica* as a function of bathymetry, sea surface temperature and chlorophyll *a* (chl *a*) concentration in the Kerguelen Archipelago. They argued that chl *a* concentration inversely reflected food availability. Unlike the findings of Loots et al. (2007), surface chlorophyll concentration did not significantly contribute to the predicted density of *E. antarctica* in our model. Chlorophyll concentration cannot always be correlated to food availability because it indicates algal standing stock rather than the primary production rate. Instead, abundance of postlarval krill was the most significant component. In less productive waters, postlarval krill can be expected to be scarce. The same holds true for copepods and euphausiid larvae, the primary prey of *E. antarctica* (Table 8). The negative effect of declining postlarval krill abundance on the modeled density of *E. antarctica* indicates that both species responded to similar environmental constraints. Despite differences in approach, hydrographical setting, zoogeographic zone and environmental variables, the investigations of Loots et al. (2007) and ours agree in relating the distribution of *E. antarctica* to hydrography and food availability. It can be assumed that the inclusion of a parameter more directly reflecting food availability, such as overall mesozooplankton biomass, would increase model performance, when available.

Ecological significance of fish: the case of *Electrona antarctica*

The environmental variables positively affecting the modeled density of *Electrona antarctica* in the Lazarev Sea occur widely in the Southern Ocean, indicating a huge potential of this species in the pelagic ecosystem. The diet of *E. antarctica* was dominated by copepods with respect to numerical and dry mass proportions (Table 8). The food composition of *E. antarctica* is known to vary with area and season and has been reported to shift towards a higher proportion of euphausiids in larger fish (Rowedder 1979, Williams 1985). The proportion of euphausiids in the diet might have been somewhat underestimated because the largest fish (SL ≥ 80 mm) were very scarce and not

available for stomach analysis. This study confirms the dominance of copepods in the diet of postlarval *E. antarctica* <90 mm SL in the Lazarev Sea reported by Pakhomov et al. (1996).

The taxonomical range of the diet composition reflected a typical catholic diet, indicating that *Electrona antarctica* can rely on a diversity of resources (Sabourenkov 1990). A diverse prey spectrum in combination with diel vertical migration enables *E. antarctica* to exploit both mesopelagic and epipelagic resources. Through diel vertical migration, the fish acts as an effective energy store and carrier between the mesopelagic and epipelagic realms. Such a 'biological pump' (Radchenko 2007) could work both downwards and upwards. The myctophid's high energy storage capacity effectively binds resources in periods of elevated epipelagic secondary production, enhancing a fast transfer into deeper layers (Donnelly et al. 1990, Van de Putte et al. 2006). During times of poor epipelagic food availability, the myctophid can rely on these reserves as well as deeper living zooplankton, providing energy to the top predators at the surface by nocturnal upward migration.

The relative importance of myctophids for the Southern Oceanic ecosystem is often distorted by the omnipresence of Antarctic krill and the under-representation of pelagic fishes in many sampling schemes. The perceived limited ecological significance of myctophids contrasts with their common presence in the diets of a range of Antarctic marine bird and seal species (Ainley et al. 2003, Connan et al. 2007, Luque et al. 2007). Ichii et al. (2007) recently demonstrated that non-breeding chinstrap penguins *Pygoscelis antarctica* and lactating Antarctic fur seals *Arctocephalus gazella* perform foraging trips to obtain energy-rich myctophids, even when krill is abundant close to their breeding colonies. While biomass density of *Electrona antarctica* (0.3 g m^{-2}) was low compared with the concurrently sampled Antarctic krill, which were in the order of 1.9 g m^{-2} (V. Siegel unpubl. data), energy density of the fish averaged 2.8 kJ m^{-2} (Table 5). For comparison, a tentative estimate of the energy density of Antarctic krill in the area of investigation, based on an average wet weight energy content of 4.1 kJ g^{-1} (Torres et al. 1994), calculates to 7.8 kJ m^{-2}. Thus, *E. antarctica* in the upper 200 m alone represented 36% of the energy density of Antarctic krill. This figure is probably an underestimate of the total population's energy content due to the shallow sampling depth. In high Antarctic oceanic waters, about 24 to 70% of the biomass of *E. antarctica* between the surface and 1000 m depth has been reported to occur in the upper 200 m at night (Lancraft et al. 1989, Donnelly et al. 2006). In contrast, krill biomass estimates are unlikely to change when a wider depth range is considered

(Siegel 2005). Thus, *E. antarctica* may have formed an energy resource similar in magnitude to the more abundant krill.

Assuming 2 major trophic pathways in the high Antarctic (Hopkins et al. 1993), the energy flow starting with phytoplankton and protozoans will mainly flow either (1) via krill, or (2) via copepods and myctophids to the top predators, partly comprising intermediate trophic steps via cephalopods and large fishes. The latter food web contains an additional trophic level, which would be associated with about 90% energy loss. Interestingly, estimates of bulk biomass in the Southern Ocean were very similar for krill (67 to 297 × 10^6 t; Atkinson et al. 2004, Siegel 2005) and myctophids (70 to 275 × 10^6 t; Gjosaeter & Kawaguchi 1980, Naumov 1985, Lubimova et al. 1987). Currently, there is an accepted paradigm that total biomass of Antarctic krill and copepods in the Antarctic are equal (Voronina 1998). Yet, the annual krill production to biomass (P/B) ratio coefficient is about 1 (Pakhomov 2000, Siegel 2000), while for copepods it is at least 6 to 7 for large calanoid copepods and perhaps higher for small copepods (Voronina 1984). This leads to the conclusion that energy flow through the copepod community could be several (up to 10) times higher than through krill, largely accounting for an extra trophic level and explaining why the total biomass of myctophids and Antarctic krill in the Southern Ocean can be expected to be in the same order of magnitude.

By comparing krill and myctophid energy stocks sampled simultaneously, this study provided new evidence that the copepod–fish–top predator link is probably as important as the traditionally emphasized krill trajectory in the Southern Ocean food web. However, better knowledge of trophic interactions at all trophic levels is necessary to obtain an accurate picture of the role of fish in the pelagic food web, and more precise estimates of mesopelagic fish stocks and their distribution are needed that are based on sampling schemes specifically tailored for that purpose.

Concluding remarks

This study provided a novel baseline assessment of the pelagic ichthyofauna of the Lazarev Sea. A wide and abundant distribution of larval and postlarval fishes and a pronounced role of *Electrona antarctica* in the pelagic energy budget in autumn provided evidence that pelagic fishes play an important role in the ecosystem of the Southern Ocean, challenging the traditional krill-centered concept of the Southern Ocean food web. It was demonstrated that the distribution of an ecologically important species such as *E. antarctica* can be related to a limited set of environmental vari-

ables. On a larger scale, similar models may help to explain the distribution of *E. antarctica* and its response to a changing environment. In the context of ecosystem management, a closer look at mesopelagic fishes could add a new perspective relating to the ecological consequences of human activities in the Antarctic marine environment. This aspect might become more important in the future with respect to bycatch in the expanding krill fisheries and potentially developing fisheries directed at mesopelagic fish.

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