



Community structure and feeding ecology of mesopelagic fishes in the slope waters of King George Island (South Shetland Islands, Antarctica)

C. Pusch^{a,*}, P.A. Hulley^b, K.-H. Kock^c

^aAlfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, Columbusstrasse, 27568 Bremerhaven, Germany

^bIziko Museums of Cape Town, P.O. Box 61, 8000 Cape Town, Republic of South Africa

^cSea Fisheries Research Institute, Palmaille 9, 22767 Hamburg, Germany

Received 17 September 2003; received in revised form 18 June 2004; accepted 22 June 2004

Abstract

The role of mesopelagic fishes in the Southern Ocean ecosystem and more particular their trophic effect on the standing stock of mesozooplankton is at present poorly understood. To get a deeper insight in the Antarctic mid-water ecosystem the mesopelagic fish community of the King George Island slope (South Shetland Islands) was sampled with a pelagic trawl in 1996. The community structure was analysed and the feeding ecology was studied of the five most abundant species. A total of 18 mesopelagic fish species in 10 families was identified. Of these, the Myctophidae was the most important family by species number (9 species), individual number (98.5% of all individuals) and fish wet weight (87.3% of the total weight). The assemblage was numerically dominated by four myctophids (*Electrona antarctica*, *Gymnoscopelus braueri*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*) and one gempilyd (*Paradiplospinus gracilis*). Multivariate statistical analysis of the mesopelagic fish data reveals two major groups of stations according to the sampled depth: a shallow group of stations (295–450 m depth) and a deeper group of stations (440–825 m depth). The change in relative abundance of mesopelagic fish species at 440–450 m coincides with the presence of warmer and denser Circumpolar Deep Water at and below these depths. Deeper stations were characterized by a higher density and increased diversity of mesopelagic fish species. The community patterns identified correlated well with the vertical depth distribution of the most abundant species. Dietary analysis reveals that myctophids are mostly zooplanktivorous, while the gempilyd *P. gracilis* is classified as a piscivorous predator. The small *P. bolini* feed mainly on copepods of the species *Metridia gerlachei*, while the most important prey item of the larger myctophids *E. antarctica*, *G. braueri*, and *G. nicholsi* were various species of euphausiids. Investigation of feeding chronology showed that *G. nicholsi* and *P. bolini* were feeding day and night. Daily ration estimates for myctophid species ranged from 0.28% to 3.3% of dry body weight (0.5–5.94% of wet body weight). Krill (*Euphausia superba*) were the most important food of *E. antarctica* and *G. nicholsi*, accounting for 53.1% and 58.3% of the total food weight, respectively. The annual removal from the krill

*Corresponding author. Tel.: +49-471-4831-1652; fax: +49-471-4831-1425.

E-mail address: cpusch@awi-bremerhaven.de (C. Pusch).

stock by both species was estimated to amount to 11.1–26.7% in the South Shetland Islands region. This estimate emphasizes the important role of mesopelagic fish in the Antarctic ecosystem as a prevalent consumer of krill.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Marine fish; Myctophidae; Mesopelagic zone; Community structure; Stomach content; Predation; Daily ration

1. Introduction

One-quarter of all known fish species in the Southern Ocean live in the mesopelagic and bathypelagic zones (Kock, 1992). Myctophids are the dominant fish family in these zones, as far as diversity, biomass and abundance are concerned. Thirty-three myctophid species are known from the Southern Ocean, of which 11 have a circum-polar distribution. Although their geographical distribution and taxonomy have been described (Hulley, 1981; McGinnis, 1982), comparatively few studies have examined the vertical distribution of oceanic micronekton by intensive depth stratified sampling (Torres and Somero, 1988; Lancraft et al., 1989; Piatkowski et al., 1994; Duhamel, 1998). All these studies indicate that the common Antarctic myctophids are diel vertical migrators.

King George Island is located in the southern part of the Drake Passage and is strongly influenced by the Antarctic Circumpolar Current (ACC). The ACC is the major oceanographic feature of the Southern Ocean; it is an extensive eastward flowing circumpolar current (Hofmann et al., 1996). The upper waters of the ACC in the study area comprised Antarctic Surface Water (ASW) and the associated Circumpolar Deep Water (CDW), which flows from the Bellingshausen Sea into southern Drake Passage (Stein and Heywood, 1994). The study site on the slope of King George Island is characterized by a shelf-break front resulting in enhanced production and a higher krill abundance compared to oceanic waters. For this reason the area north of King George Island is one of the most important krill fishing regions of the Southern Ocean (Ichii et al., 1996).

Myctophids play a significant role as consumers of zooplankton in the food web of the Southern Ocean (Lancraft et al., 1989). As in the other

world oceans, they occupy the third level and are consumers of the second order. They are an important food source for the predators of higher trophic levels like benthopelagic fish (Bulman et al., 2002), seabirds (Guinet et al., 1996), fur seals (Cherel et al., 1997) and squid (Rodhouse et al., 1992; Phillips et al., 2001). Any estimation of energy transport within the pelagic system must include analyses of the individual diet composition of the mesopelagic fish and their rates of food consumption.

Although the diet composition of the most abundant myctophid species is documented (Rowedder, 1979a; Ascenio and Moreno, 1984; Williams, 1985; Kozlov and Tarverdiyeva, 1989; Lancraft et al., 1991; Hoddell et al., 2000) only a few studies have investigated feeding chronology (Rowedder, 1979a) and estimated daily rations (Gerasimova, 1990; Pakhomov et al., 1996).

Krill (*Euphausia superba*) plays an important role as the key prey item of a number of top predators, especially in the Atlantic Sector of the Southern Ocean (Barlow et al., 2002). Because of their high biomass (the total stock of the Southern Ocean was estimated by Lancraft et al. (1989) to account for 133–191 million tonnes), mesopelagic fish could be one of the most important predators of oceanic zooplankton (Lancraft et al., 1989; Pakhomov et al., 1996). Numerous studies have shown that myctophids play a significant role in the consumption of juvenile and adult krill (Rembiszewski et al., 1978; Rowedder, 1979a; Williams, 1985). This conclusion has more recently been challenged by a suggestion that a substantial consumption of krill occurs only during certain periods and within specific regions (Pakhomov et al., 1996).

Finally, it should be noted that a preliminary analysis of community structure of the mesopelagic fish assemblage from cruise ANT XIV/2 of RV

“Polarstern” has already been presented by [Hulley et al. \(1998\)](#), and the results used for a cladistic analysis of the myctophid tribe Electronini ([Hulley, 1998](#)). In the present study, however, community structure of the mesopelagic community over the slope of King George Island is analysed in greater detail. The community pattern and the vertical distribution are related to the feeding ecology of the most abundant mesopelagic fish species. Four myctophids and one gempylid are analysed with respect to diet, feeding chronology and daily rations. In conclusion, an estimation is made of the predation impact of the mesopelagic fish community on the krill stock in the region of King George Island.

2. Material and methods

2.1. Sampling

Data were collected during the cruise ANT XIV/2 of RV “Polarstern” in November/December 1996. The study area was located over the slope northwest of King George Island (South Shetland Islands), in southern Drake Passage ([Fig. 1](#)).

The sampling program consisted of 16 hauls, with the objective to sample three different depth horizons: 200–300 m, 400–500 m and near-bottom (2–28 m above seafloor) at soundings of 400, 600 and 800 m ([Table 1](#)) ([Kock et al., 1998](#)). Mesopelagic fish were sampled with a pelagic trawl PT-1088 with an estimated mouth opening of 200 m² (width 20 m and a height of 10–12 m). The mesh size was 12 mm in the cod end. It was expected that juvenile myctophids (SL < 30 mm) would not be sampled adequately with this net configuration ([Gartner et al., 1988](#)). An SCANMAR depth sensor controlled the sample depth and net opening during trawling. Towing time varied between 30 and 60 min; trawl speeds ranged from 3.5 to 4.0 knots. Ship speed was increased during net deployment and decreased during retrieval. This procedure minimizes the effects of net contamination by fish resident in water layers above the fishing depth. Station 73 was excluded from community analysis as the net snagged on the bottom during trawling ([Hulley et al., 1998](#)). All fishes were identified to species according to the most recent keys ([Gon and Heemstra, 1990](#)). Fish from the entire sample or a sub-sample of each species from each station were counted and weighed, and standard lengths (SL) were taken

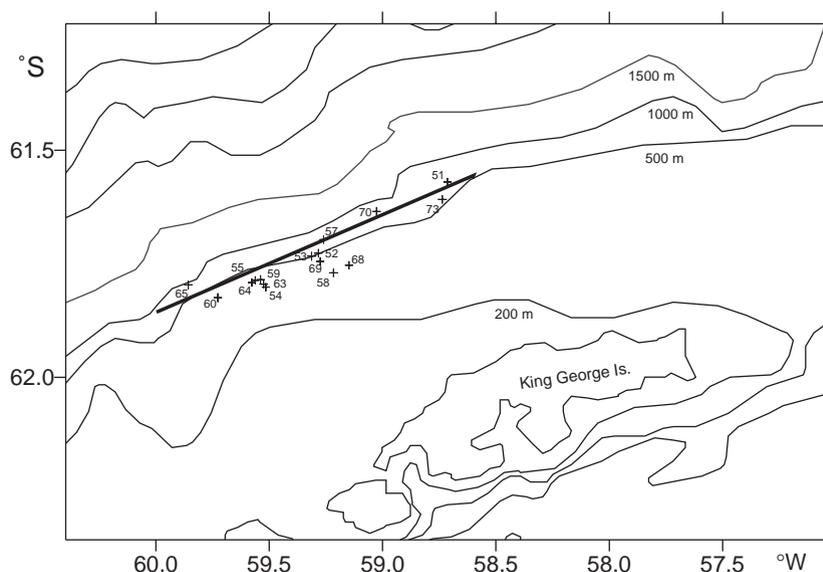


Fig. 1. Sampling localities in 1996. Line indicates hydrographic section through the study area.

Table 1
Station data for 16 PT-1088 trawl samples

ST	Sampling Longitude	Locality Latitude	Date 1996	Time (Local)	Day Time ^a	Global Radiation (wm2)	Sample Depth (m)	Bottom Depth (m)	Ship Speed (km)
51	58°43'W	61°36'S	30 November	16:49–17:49	Day	197.8	400–450	786–875	4.0
52	59°17'W	61°45'S	1 December	08:00–08:30	Day	75.0	415–515	660–730	4.0
53	59°19'W	61°45'S	1 December	10:57–11:27	Day	153.0	273–302	635–738	4.0
54	59°31'W	61°48'S	1 December	14:50–15:20	Day	230.3	283–295	475–652	4.0
55	59°34'W	61°47'S	1 December	17:35–18:05	Day	145.8	400–450	680–995	4.0
57	59°16'W	61°43'S	3 December	08:19–08:50	Day	179.7	397–465	730–790	4.0
58	59°13'W	61°47'S	3 December	20:26–21:26	Day	12.4	283–325	380–387	3.5
59	59°32'W	61°48'S	3 December	23:20–00:20	Night	0.0	431–495	850–1058	3.7
60	59°44'W	61°48'S	4 December	02:15–03:18	Night	0.0	380–440	681–690	3.5
63	59°32'W	61°48'S	4 December	20:30–21:11	Day	98.5	520–580	555–608	4.0
64	59°35'W	61°47'S	5 December	01:06–01:41	Night	0.0	610–640	731–792	4.0
65	59°51'W	61°49'S	5 December	04:26–04:56	Day	80.6	750–800	1287–1468	4.0
68	59°09'W	61°44'S	5 December	21:10–21:41	Day	46.0	340–360	360–367	3.5
69	59°17'W	61°46'S	6 December	01:01–01:32	Night	0.0	560–597	584–599	3.7
70	59°02'W	61°38'S	6 December	04:50–05:20	Day	23.0	790–825	810–833	3.7
73	58°44'W	61°36'S	6 December	21:07–21:10	Day	20.0	550–575	570–580	3.5

^aDefined by sunset 22:06 and sunrise 03:23.

to the nearest millimetre with sliding callipers. Hydrographic data were collected by conductivity, temperature and depth casts (CTD, 22 stations). The CTD was deployed at each station in advance of the trawl tows.

2.2. Diet analysis

Diet analysis was performed on the five most abundant mesopelagic fish species. A maximum of 20 individuals of these species was selected from each sample. In samples containing >20 specimens individuals were chosen haphazardly. Fish were weighed wet, measured (SL, mm below) and the whole stomach removed. The dry weight of fish specimens was determined by oven-drying specimens at 80 °C until constant weight was reached.

Prey organisms were identified to the lowest possible taxon and measured under a binocular microscope. Dry weight of the prey organisms was reconstructed by length–weight regressions taken from the literature (Mizdalski, 1988; Groeger et al., 2000).

Three indices, the frequency of occurrence (F_i) of each prey item in non-empty stomachs, the percentage of each food item by number (N_i) to the total number, and the percentage by dry weight

(DW_i) were calculated (George and Hadley, 1979). By the following equation, all three indices were combined to describe the prey utilization by the 'Relative Importance Index' (RI) for each prey category i (George and Hadley, 1979; Hyslop, 1980):

$$RI_i = \frac{(F_i + N_i + DW_i) \times 100}{\sum_{i=1}^s (F_i + N_i + DW_i)}, \quad (1)$$

where s is the number of prey categories.

Feeding chronology was analysed by the Stomach Content Index (SCI):

$$SCI(\%) = \frac{\text{dry weight of stomach content}}{\text{body dry weight}} \times 100. \quad (2)$$

In addition, the stage of digestion of each prey item was determined by the modified method of Percy et al. (1979): Stage 1 = undigested prey, Stage 2 = slightly digested with some appendages damaged, but body shape still preserved, Stage 3: body shape of prey deformed. The ratio of digestion stages was calculated for each time interval based on these criteria.

Daily ration (mean daily food consumption, C_w) of the four myctophids was investigated by the

method of Eggers (1977):

$$C_w = I \times 24/T, \quad (3)$$

where I is the daily average SCI (%) and T the gut passage time (h).

In this study, no gut passage time data were collected. Therefore, data from the literature were used. Two estimates of egestion times for Antarctic myctophids are available: the first estimate by Rowedder (1979a) for *Electrona antarctica* and the second by Gerasimova (1990) for *E. carlsbergi*. These studies estimated the egestion time to be 8 and 8.5 h, respectively. In our study, we used the 8.5 h suggested by Gerasimova. For the calculation of daily ration some authors (Pakhomov et al., 1996) have recommended the substitution of 24×10 in Eq. (3) for species that have an active feeding period of 10 h. Other authors argue that this substitution introduces a significant conservative bias (Williams et al., 2001). We calculated two alternative daily rations using both 10 and 24.

2.3. Data analysis

Density and biomass data for mesopelagic fish were calculated as individuals per filtered water volume. The filtered volume was calculated by multiplying the trawled distance of the vessel with the estimated mouth opening (200 m^2) of the PT-1088.

Community structure was investigated with the Primer-E5 Software package (Clarke and Warwick, 2001). To reduce the weighting of dominant species, the densities were square-root transformed prior to the computation of the triangular similarity matrices based on Bray-Curtis similarities (Field et al., 1982). The results of the latter were classified by hierarchical agglomerative cluster analysis using the group average linking method, and ordinated by a non-metric, multi-dimensional scaling technique (MDS).

The BIOENV sub-routine was used to relate the community patterns of the mesopelagic fish assemblage to six environmental variables: light intensity (W/m^2) (indicating time of day), minimum and maximum values of sample depth, bottom depth, temperature and salinity at the sampled depth horizon. Values of average light

intensity were log transformed to validate the use of normalized Euclidean distance for the calculation of the abiotic similarity matrix. We applied the Spearman Rank correlation to relate the biotic matrix based on mesopelagic fish abundances with the abiotic similarity matrix (Clarke and Ainsworth, 1993).

Two different water masses were discernible over the slope of King George Island, separated at a depth of 450 m (see Section 3). Mesopelagic fish samples above and below this depth were compared with different sub-routines of the Primer computer program.

One-way analysis of similarity, ANOSIM (Clarke and Warwick, 1994), was employed to test the hypothesis of no differences in mesopelagic fish assemblage above and below 450 m. This sub-routine compares the average rank similarities within the predefined groups of samples with the average similarity between groups. Values close to 1 indicate a strong separation between groups, while a value of 0 indicates no differences between groups.

The similarity percentage routine (SIMPER) (Clarke and Warwick, 1994), which was applied to square-root transformed mesopelagic fish abundances, identified the contribution from individual species to the dissimilarities between (the deep and the shallow) sample groups.

Various univariate indices were calculated in order to characterize the species assemblages of the deep and shallow group of samples: species number, Shannon's diversity index (H') (Shannon and Weaver, 1949) and Pielou's Evenness Index (J) (Pielou, 1975). As these indices are known to be influenced by sample size, we also calculated the taxonomic diversity Δ and taxonomic distinctness Δ^* , which consider the taxonomic relatedness of species (Warwick and Clarke, 1995). Taxonomic diversity Δ is empirically related to H' but contains, in addition, information on the taxonomic separation of the species in a sample, i.e. besides the distribution of individuals among species it also takes into account the distribution of species in the taxonomic system by weighting the co-occurrences of species according to the degree of separation in the hierarchical classification (1 = different species, 2 = different genera, 3 = different families, 4 = different orders). Δ^* is

derived from Δ but measures solely the taxonomic distinctness of species in a sample, without the contribution from species diversity.

Oceanographic data were obtained from the program Ocean Data View (Schlitzer, 2003). The results are presented as a section through the study area.

3. Results

3.1. Oceanographic conditions

The study area is situated in the Weddell-Scotia-Confluence, where water masses of the Weddell

Sea and Scotia Sea mingle. Analysis of vertical temperature and salinity sections through the study site revealed the existence of two different water masses in the slope region of King George Island (Fig. 2A–B). The water mass in the upper 200 m was composed of ASW, characterized by a temperature minimum in 50–150 m depth ($T < 0.5^\circ\text{C}$) and a low salinity (< 34.4). The origin of this water body is due to the cooling of the surface water during winter. The properties of this so-called winter water are stable year round (Hofmann et al., 1996). During our study the surface water temperature was slightly increased by enhanced solar radiation. The dominating water mass below 400 m depth,

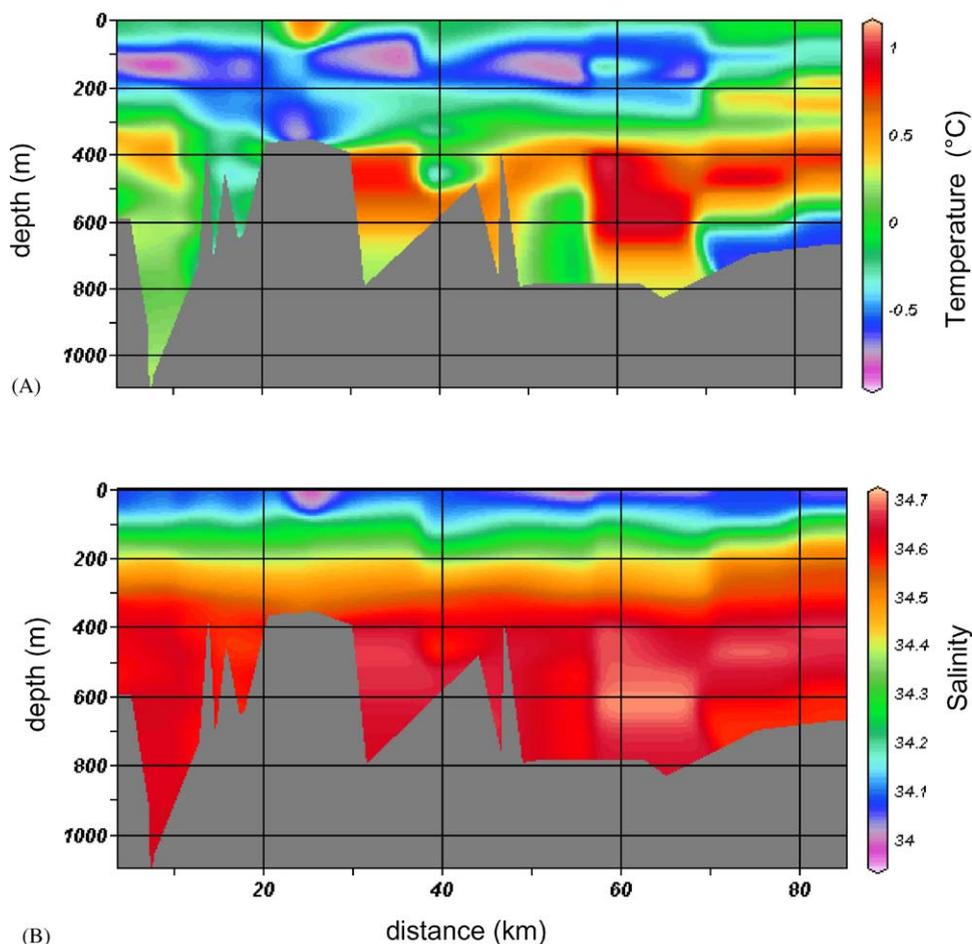


Fig. 2. (A–B) RV “Polarstern” cruise ANT XIV/2, east–west hydrographic section through the study area as indicated in Fig. 1, (A) temperature ($^\circ\text{C}$) and (B) salinity.

Circumpolar Deep Water, was characterized by higher temperature ($T > 0.5$ °C) and salinity ($S > 34.5$). A transition zone between these water masses occupies the depth range 200–400 m, in which the gradients of temperature and salinity were strongest.

3.2. Species composition

The total catch of mesopelagic fish taken on 15 pelagic trawl stations included 16 343 specimens with a wet weight of 122.5 kg (Table 2). Eighteen mesopelagic species belonging to 10 families and 13 genera were identified. The family Myctophidae was by far the most speciose (9 species), with all

other families represented by just one species. Three myctophids, *Gymnoscopelus fraseri*, *G. hintonoides* and *Protomyctophum choriodon*, were newly recorded for the South Shetland Island region.

Myctophids dominated the mesopelagic fish community by number and wet weight accounting for 98.5% of all sampled individuals and 87.3% of the total weight. *E. antarctica* was the most abundant species by number and weight. This myctophid accounted for 60.7% of all sampled individuals, followed by *P. bolini* (19.6%), *G. braueri* (13.8%) and *G. nicholsi* (4.0%). All other mesopelagic fish species were of numerically minor importance (<2% in total).

Table 2

Number of individual fish, density as number of individuals per 10^5 m³ filtered volume, wet weight in kg and biomass as g wet weight per filtered volume in 15 PT-1088 samples

Species	Abundance			Biomass		
	No. Inds.	(%)	Ind/ 10^5 m ³	kg	(%)	g ww/ 10^5 m ³
Astronestidae						
<i>Borostomias antarcticus</i>	1	(0.01)	0.00	0.01	(0.01)	0.05
Bathylagidae						
<i>Bathylagus antarcticus</i>	4	(0.02)	0.03	0.05	(0.04)	0.43
Chiasmodontidae						
<i>Chiasmodon niger</i>	1	(0.01)	0.00	0.02	(0.02)	0.09
Gempylidae						
<i>Paradiplospinus gracilis</i>	182	(1.11)	1.14	14.96	(12.21)	93.29
Gonostomatidae						
<i>Cyclothone</i> sp.	2	(0.01)	0.02	0.01	(0.01)	0.09
Melamphaidae						
<i>Poromitra crassiceps</i>	2	(0.01)	0.01	0.02	(0.02)	0.09
Microstomatidae						
<i>Nansenia antarctica</i>	3	(0.02)	0.02	0.09	(0.07)	0.66
Myctophidae						
<i>Electrona antarctica</i>	9931	(60.71)	59.48	67.93	(55.46)	407.98
<i>Gymnoscopelus braueri</i>	2253	(13.77)	20.23	13.71	(11.19)	122.72
<i>Gymnoscopelus fraseri</i>	2	(0.01)	0.01	0.02	(0.02)	0.14
<i>Gymnoscopelus hintonoides</i>	15	(0.09)	0.11	0.13	(0.11)	0.99
<i>Gymnoscopelus nicholsi</i>	647	(3.96)	4.2	21.15	(17.27)	136.81
<i>Gymnoscopelus opisthopterus</i>	27	(0.17)	0.13	0.96	(0.78)	4.52
<i>Krefflichthys anderssoni</i>	23	(0.14)	0.18	0.07	(0.06)	0.55
<i>Protomyctophum bolini</i>	3212	(19.63)	20.1	2.97	(2.42)	18.65
<i>Protomyctophum choriodon</i>	1	(0.01)	0.00	0.01	(0.01)	0.04
Notosudidae						
<i>Scopelosaurus hamiltoni</i>	3	(0.02)	0.02	0.27	(0.22)	1.48
Paralepididae						
<i>Notolepis coatsi</i>	34	(0.21)	0.22	0.11	(0.09)	0.71
Total	16 343			122.5		

In wet weight, *E. antarctica* accounted for 55.6% of total mesopelagic fish biomass, far exceeding *G. nicholsi* (17.3%), *G. braueri* (11.2) and the gempilyd, *Paradiplosinus gracilis* (12.2%).

3.3. Patterns of vertical distribution

Because of the sampling strategy (no samples above 273 m depth and only four night tows) no detailed conclusions about the vertical migration behaviour of the mesopelagic community can be

made. Nevertheless, some assumptions about the vertical distribution patterns of the more abundant species are possible. All four myctophids were more abundant, in the 273–825 m depth range, in daytime samples than in nighttime samples (Fig. 3A–D). This observation supports the results of earlier studies that the bulk of Antarctic myctophids migrate to epipelagic layers at night (Torres and Somero, 1988; Lancraft et al., 1989).

P. gracilis was concentrated in depths below 400 m during daytime (Fig. 3E). The distribution

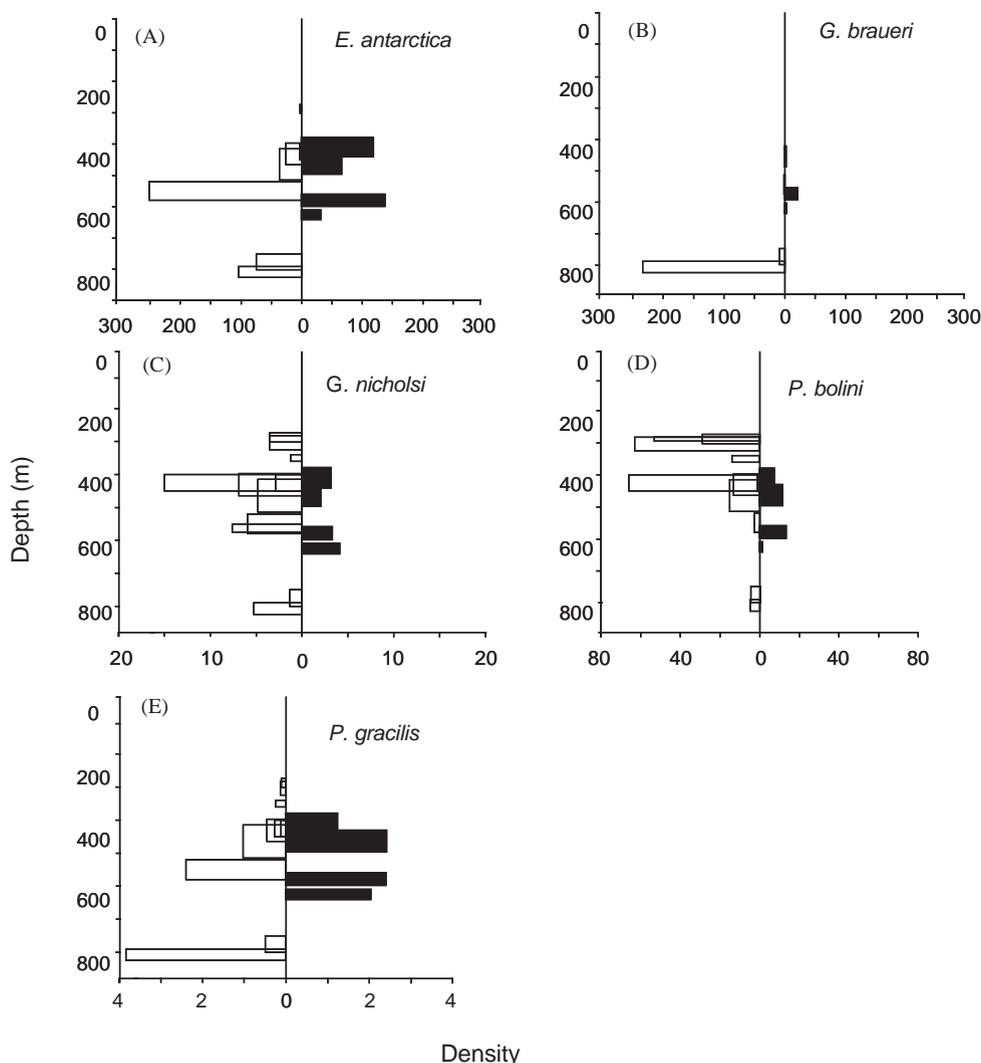


Fig. 3. (A–E) Vertical day/night distribution: (A) *E. antarctica*, (B) *G. braueri*, (C) *G. nicholsi*, (D) *P. bolini*, (E) *P. gracilis*, Density as individuals per 10^5 m^3 ; open bars = day tows; filled bars = night tows.

data show an increased density in this species between 400 and 500 m, suggesting vertical migration behaviour at least in mesopelagic depths. The four myctophids showed different daytime depth distributions: The bulk of *E. antarctica* individuals were found below 400 m depth (Fig. 3A) and the minimum depth of occurrence of *G. braueri* was 750 m (Fig. 3B). In contrast, *P. bolini* occurred over a depth range of 273–825 m, with the bulk of the population in the shallow 273–450 m interval (Fig. 3D). *G. nicholsi* occurred over the whole sampled depth range (273–825 m) with a centre of distribution between 400 and 597 m (Fig. 3C).

3.4. Community analysis

Cluster analysis based on densities of mesopelagic fish showed a clear separation of stations at an arbitrary level of 40% (Fig. 4). The first cluster comprises stations sampled at and above 450 m depth. The second cluster is exclusively composed of stations taken in depth > 450 m, with the exception of station 60, where sampling depth was 380–440 m.

The separation of stations at 450 m depth is confirmed by the ordination with MDS of the same assemblage data (Fig. 5). Again, station 60 was more closely associated with the deeper group of stations.

An exploratory analysis, BIOENV, was applied to examine which abiotic variables could best explain the observed patterns in the mesopelagic fish assemblage. The maximum matching coefficient was achieved by the abiotic variable maximum sample depth (51.7%) and supported therefore the result from the MDS and cluster analyses. Minimum sample depth (46.4%) and minimum and maximum salinity (34.9% and 28.6%, respectively) were further useful abiotic parameters to explain the observed pattern in the mesopelagic fish community. Other abiotic variables showed a low correlation with the biotic similarity matrix and yielded matching coefficients below 25%. Sample depth is thus the best environmental variable to explain the grouping of the samples in a manner consistent with the biotic pattern.

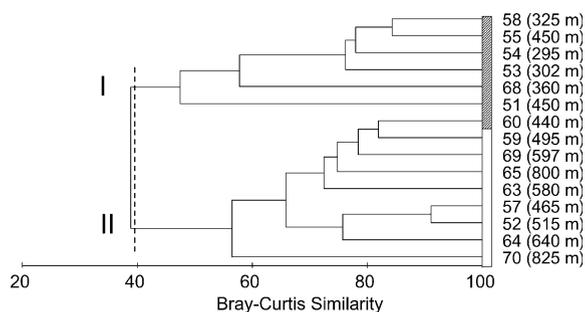


Fig. 4. Dendrogram representing the classification of 15 PT-1088 stations according to mesopelagic fish assemblage; Station number and maximum sampled depth are indicated. Hatching indicates shallow stations (depth 302–450 m).

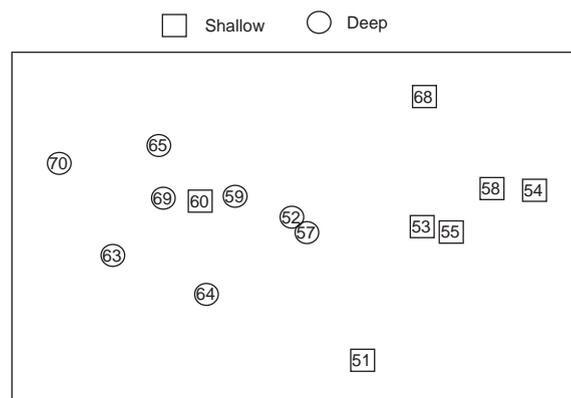


Fig. 5. MDS plot for 15 PT-1088 stations according to the mesopelagic fish assemblage; shallow and deep refer to the sampled depth; shallow = depth 302–450 m; deep = depth 465–825 m; stress (= goodness of fit) = 0.07.

An analysis of similarity (ANOSIM) was performed to test for statistical differences in species composition between shallow stations (295–450 m depth) and deep stations (465–825 m). A value of $R = 0.561$ supported the results of the classification and ordination of the data and indicated significant differences in species composition between shallow and deep stations ($P = 0.003$).

The similarity percentage procedure (SIMPER) was applied to identify those species that contribute most to the observed differences between shallow and deep samples (Table 3). Only three species were more abundant in the shallow group

Table 3
SIMPER analysis; discriminating species between “deeper” and “shallower” station groups as revealed by cluster analysis

Species	Avg. density (Ind./10 ⁵ m ³)		Contribution (%)	Cumulative Contribution (%)
	Shallow	Deep		
<i>Electrona antarctica</i>	19.01	94.89	43.33	43.33
<i>Protomyctophum bolini</i>	33.6	8.3	18.8	62.13
<i>Gymnoscopelus braueri</i>	0.01	37.93	16.35	78.48
<i>Gymnoscopelus nicholsi</i>	4.13	4.26	5.89	84.36
<i>Paradiplospinus gracilis</i>	0.3	1.88	5.22	89.59
<i>Notolepis coatsi</i>	0.05	0.37	2.29	91.88
<i>Krefflichthys anderssoni</i>	0	0.34	2.28	94.16
<i>Gymnoscopelus hintonoides</i>	0	0.2	1.67	95.82
<i>Gymnoscopelus opisthopterus</i>	0	0.24	1.19	97.02
<i>Bathylagus antarcticus</i>	0	0.06	0.5	97.52
<i>Nansenia antarctica</i>	0.01	0.03	0.47	97.99
<i>Scopelosaurus hamiltoni</i>	0	0.03	0.46	98.45
<i>Gymnoscopelus fraseri</i>	0	0.03	0.41	98.85
<i>Protomyctophum choriodon</i>	0	0.02	0.28	99.13
<i>Poromitra crassiceps</i>	0.01	0	0.25	99.38
<i>Cyclothone sp.</i>	0	0.04	0.25	99.62
<i>Chiasmodon niger</i>	0	0.01	0.2	99.82
<i>Borostomias antarcticus</i>	0.01	0	0.18	100

Species are ordered in decreasing contribution (%) to the total dissimilarity.

of samples, while 15 species were more abundant in the deeper group. The myctophid *P. bolini* was the best indicator species for samples taken above 450 m depth and accounted for 18.8% of the observed differences. Deeper stations were characterized by relatively higher abundances of *E. antarctica* and *G. braueri* and *P. gracilis*, which together accounted for 65% of the observed differences between the two groups of samples.

The calculation of several univariate indices for the species densities above and below 450 m depth reflected the observed differences between the mesopelagic fish assemblages (Table 4). The number of species (9) in depth between 273 and 450 m was lower, compared to 16 species in depths below 450 m (two individuals of *Cyclothone sp.* were not identified to species level). Also the average density of mesopelagic fish was 2.5 times higher in the deeper group samples. Shannon's diversity (H'), Pielou's evenness index (J) and the taxonomic diversity Δ were higher in samples taken below 450 m depth. However, the observed differences in diversity indices between the deeper and shallower group of samples were statistically

Table 4
Univariate indices of the deeper and shallower groups of stations over the slope of King–George Island

	Shallow	Deep
No. of species	9	16
Density (Ind./10 ⁵ m ³)	57.13	148.61
Pielou's evenness (J)	0.35	0.41
Shannon's diversity (H')	0.51	0.79
Taxonomic diversity (Δ)	10.03	14.64
Taxonomic distinctness (Δ^*)	35.87	37.02

not significant. The taxonomic distinctness Δ^* showed a high similarity between shallow and deep samples.

3.5. Feeding ecology

3.5.1. Food composition

The diet of *E. antarctica* was dominated by euphausiids in our samples. By number, euphausiids (47.8%) are followed by ostracods (15.6%) and then by copepods (26.7%) (Fig. 6A; Table 5). By dry weight (DW), euphausiids account for

Table 5

Diet composition of *E. antarctica*, *G. braueri*, *G. nicholsi*, *P. bolini* and *P. gracilis*, showing number and reconstructed dry weight of each food item; the respective percentage of the total number and the total dry weight is given in parenthesis; “-”: absent.

	<i>Electrona antarctica</i>			<i>Gymnoscopelus braueri</i>			<i>Gymnoscopelus nicholsi</i>			<i>Protomyctophum bolini</i>			<i>Paradiplospinus gracilis</i>		
SL range (mm)	57–113			69–121			123–172			33–53			284–469		
No. of fish examined	145			67			186			122			100		
No. of stomach empty (%)	84	(57.9)		46	(68.7)		51	(27.4)		21	(17.2)		72	(72)	
	No.	(%)	Weight (%)	No.	(%)	Weight (%)	No.	(%)	Weight (%)	No.	(%)	Weight (%)	No.	(%)	Weight (%)
Amphipoda	2	(2.2)	210.86 (13.9)	1	(3.2)	84.08 (23.5)	1	(0.1)	50.75 (0.8)	—	—	—	—	—	—
Cephalopoda	—	—	—	—	—	—	—	—	—	—	—	—	3	(8.3)	9900 (7.4)
<i>Psychroteuthis glacialis</i>	—	—	—	—	—	—	—	—	—	—	—	—	3	(8.3)	9900 (7.4)
Chaetognatha	5	(5.6)	3.9 (0.3)	2	(6.5)	1.56 (0.4)	21	(2.6)	241.78 (3.8)	4	(0.3)	3.12 (0.6)	—	—	—
Copepoda	24	(26.7)	5.42 (0.4)	7	(22.6)	1.97 (0.6)	517	(63.8)	235.67 (3.7)	1515	(96.6)	354.93 (84.2)	—	—	—
<i>Calanus propinquus</i>	1	(1.1)	0.8 (0.1)	—	—	—	23	(2.8)	21.84 (0.3)	8	(0.5)	6.21 (1.5)	—	—	—
<i>Gaidius</i> spp.	1	(1.1)	0.37 (0.0)	3	(9.7)	1.11 (0.3)	10	(1.2)	3.7 (0.1)	11	(0.7)	4.07 (1.0)	—	—	—
<i>Metridia gerlachei</i>	11	(12.2)	1.62 (0.1)	—	—	—	341	(42.1)	68.58 (1.1)	1438	(91.7)	319.83 (75.9)	—	—	—
<i>Pareuchaeta</i> spp.	1	(1.1)	1.35 (0.1)	—	—	—	67	(8.3)	95.82 (1.5)	13	(0.8)	15.87 (3.8)	—	—	—
<i>Rhincalanus gigas</i>	—	—	—	1	(3.2)	0.43 (0.1)	46	(5.7)	29.69 (0.5)	5	(0.3)	2.49 (0.6)	—	—	—
Unidentified calanoids	10	(11.1)	1.28 (0.1)	3	(9.7)	0.43 (0.1)	30	(3.7)	16.04 (0.3)	40	(2.6)	6.46 (1.5)	—	—	—
Euphausiacea	43	(47.8)	1292.07 (85.0)	13	(41.9)	268.66 (75.0)	226	(27.9)	4950.82 (77.9)	8	(0.5)	54.79 (13.0)	8	(22.2)	280.69 (0.2)
<i>Euphausia crystallorophias</i>	—	—	—	—	—	—	1	(0.1)	7.55 (0.1)	—	—	—	—	—	—
<i>E. frigida</i>	1	(1.1)	14.63 (1.0)	—	—	—	2	(0.2)	78.12 (1.2)	—	—	—	—	—	—
<i>E. superba</i>	14	(15.6)	807.23 (53.1)	—	—	—	67	(8.3)	3707.89 (58.3)	—	—	—	6	(16.7)	223.19 (0.2)
<i>E. triacantha</i>	1	(1.1)	19.96 (1.3)	1	(3.2)	36.82 (10.3)	4	(0.5)	163.74 (2.6)	—	—	—	1	(2.7)	45.4 (0.0)
<i>Euphausia</i> spp.	22	(24.4)	425.04 (28.0)	12	(38.7)	231.84 (64.8)	20	(2.5)	386.4 (6.1)	—	—	—	—	—	—
<i>Thysanoessa macrura</i>	5	(5.6)	25.21 (1.7)	—	—	—	132	(16.3)	607.12 (9.6)	8	(0.5)	54.79 (13.0)	1	(2.7)	12.1 (0.0)
Gastropoda	1	(1.1)	1.56 (0.1)	—	—	—	—	—	—	1	(0.1)	1.56 (0.4)	—	—	—
Ostracoda	14	(15.6)	4.78 (0.3)	8	(25.8)	1.74 (0.5)	39	(4.8)	8.76 (0.1)	41	(2.6)	7.13 (1.7)	—	—	—
Pisces	—	—	—	—	—	—	6	(0.7)	866.97 (13.6)	—	—	—	25	(69.4)	123868.28 (92.4)
<i>Electrona antarctica</i>	—	—	—	—	—	—	—	—	—	—	—	—	2	(5.6)	6435.36 (4.8)
<i>Gymnoscopelus nicholsi</i>	—	—	—	—	—	—	—	—	—	—	—	—	1	(2.7)	10162.92 (7.6)
<i>Gymnoscopelus braueri</i>	—	—	—	—	—	—	—	—	—	—	—	—	1	(2.7)	2270 (1.7)
<i>Neopageotopsis ionah</i>	—	—	—	—	—	—	2	(0.3)	408.25 (6.4)	—	—	—	—	—	—
<i>Protomyctophum bolini</i>	—	—	—	—	—	—	4	(0.5)	458.72 (7.2)	—	—	—	—	—	—
Polychaeta	1	(1.1)	1.84 (0.1)	—	—	—	—	—	—	—	—	—	—	—	—
Total	90		1520.43	31		358.01	810		1742.7	1569		7.13	36		134048.97

85.0% of the total stomach content, far exceeding amphipods (13.9%) and the other prey categories (< 2% in total). Euphausiids occurred in 65.6% of all filled stomachs, while ostracods and copepods occurred less frequently (21.1% and 23.0%, respectively). The RI values were 61.1% for euphausiids, 14.9% for copepods and 12.0% for ostracods, stressing the importance of euphausiids in the diet of *E. antarctica*.

The size distribution of the 145 individuals examined for food composition was unimodal and ranged from 57 to 113 mm (Fig. 7A). To investigate an ontogenetical shift in the prey size of *E. antarctica* we compared the ratio of euphausiids (largest prey item) to the total dry weight of stomach content in individuals smaller and larger than 80 mm SL. The ratio of euphausiids to the total dry weight of stomach contents was $60.7 \pm 49.0\%$ (avg. \pm SD) for 57–79 mm sized individuals, and $68.6 \pm 46.2\%$ for 80–113 mm SL fish. The difference was not significant (Mann–Whitney *U*-test, $p > 0.05$). Therefore, no significant shift in prey size was detectable over the size range examined.

In this study, feeding intensity of *E. antarctica* was low, with 57.9% of stomachs empty (Table 5). More than half of all euphausiids were not identifiable to species. Nevertheless, krill (*E. superba*) was the most important euphausiid in the diet of this myctophid, accounting for more than one-half (53.1%) of the overall food weight.

The prey composition of *G. braueri* was similarly dominated by euphausiids (Fig. 6B, Table 5). Euphausiids were most important by number ($N = 41.9\%$), DW (75.0% of total weight) and frequency of occurrence (61.9%). The RI reflected the high dietary value of euphausiids (52.9%), while ostracods, copepods and amphipods were of minor importance with RI values of 19.0%, 13.9% and 9.3%, respectively. Despite the high significance of euphausiids in the diet, the most abundant euphausiid, *E. superba*, was lacking (Table 5). The feeding intensity of *G. braueri* was noticeably low, with 68.7% of stomachs containing no identifiable food.

The diet of *G. nicholsi*, was numerically dominated by copepods and euphausiids (Fig. 6C, Table 5), accounting for 63.8% and 27.9% (N) of

the identifiable food items respectively, while other food items accounted for less than 5% each. In dry weight (DW) euphausiids made up 77.9% of the total prey, followed by fish (13.6%), chaetognaths (3.8%) and copepods (3.7%). The frequencies of occurrence for copepods, euphausiids, ostracods and chaetognaths were 77.7%, 62.9%, 22.9% and 15.5%, respectively, while the remaining prey categories accounted for less than 4.4% in total. The RI values were 44.0% for euphausiids and 37.9% for copepods, while the remaining prey categories accounted for <10%.

The size distribution of the 186 individuals of *G. nicholsi* examined for stomach content was unimodal and ranged from 123 to 172 mm (Fig. 7C). The ratio of euphausiids (largest prey item) to the total dry weight of the stomach content was $54.7 \pm 64.0\%$ (avg. \pm SD) for 123–144 mm SL individuals and $58.3 \pm 45.1\%$ for 145–172 mm SL fish. The difference was not statistically significant (Mann–Whitney *U* test, $p > 0.05$) and we therefore suggest that no substantial ontogenetic shift in prey size occurs over the size range examined.

Prey species composition showed that *G. nicholsi* fed on all five euphausiids species occurring in the Southern Ocean (Table 5). The most important euphausiid by food weight was *E. superba* (58.3% of total food weight), while *Metridia gerlachei* dominated numerically (42.1%). *G. nicholsi* was the only myctophid in our study that preyed on other mesopelagic fish (*Neopageotopsis ionah* and *Protomyctophum bolini*).

The food spectrum of *P. bolini*, a relatively small-sized myctophid (SL 33–53 mm, Fig. 7D), was dominated by copepods (Fig. 6D, Table 5). The *N*, *DW* and *F* values for copepods were 96.6%, 84.2% and 91.1%, respectively. The RI value of copepods was 82.0% followed by ostracods (10.0%) and euphausiids (6.2%).

The prey species composition showed that copepods of the genus *M. gerlachei* were by far the most important prey item, accounting for 91.7% of all identified food items (Table 5).

The diet of *P. gracilis*, the only non-myctophid in our analysis, consisted almost exclusively of fish (Fig. 6E, Table 5). The three trophic parameters *N*, *DW* and *F* for this prey category were 69.4%, 92.4% and 82.1%, resulting in an RI of 76.8%.

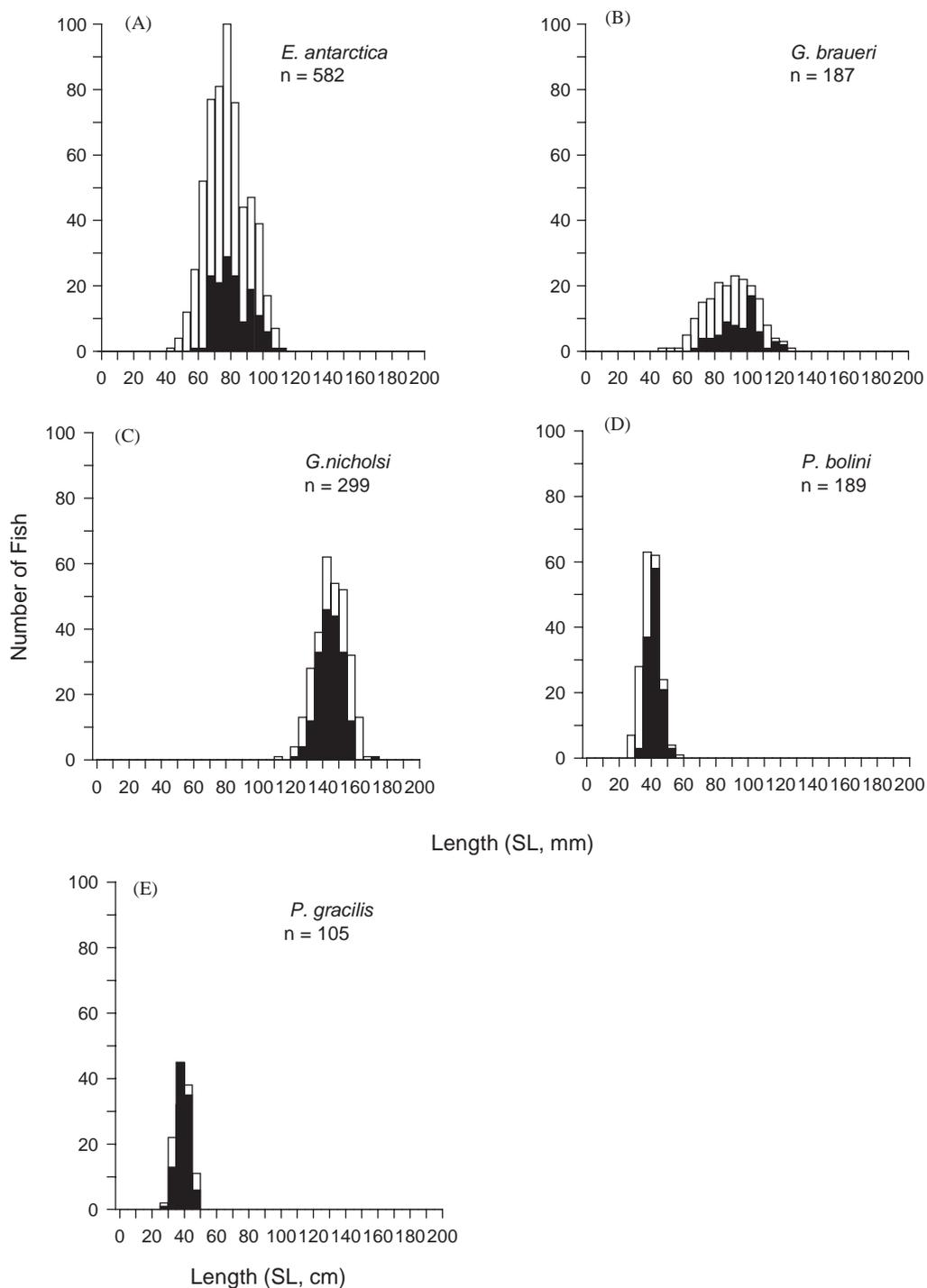


Fig. 7. (A–E) Length-frequency plots of (A) *E. antarctica* (B) *G. braueri* (C) *G. nicholsi* (D) *P. bolini* (E) *P. gracilis* showing size classes of fish measured (open bars) and sampled for diet analysis (filled bars); *n* total number of fish measured.

Most fishes found in the stomachs were not identifiable because of the advanced stage of digestion. Nevertheless, the common myctophids *E. antarctica*, *G. nicholsi* and *G. braueri* could be identified. Additional euphausiids and cephalopods (*Psychroteuthis glacialis*) were found in the stomachs of *P. gracilis*, accounting for RI values of 15.1% and 8.4%, respectively.

3.5.2. Feeding chronology

The influence of sample depth on feeding intensity was investigated by the calculation of the Stomach Content Index (SCI) for *E. antarctica*, *G. nicholsi* and *P. bolini*. We compared the SCIs of individuals taken in shallow (sample depth 295–440) and deep tows (465–825 m) and found no differences for *E. antarctica*, *G. nicholsi* and *P. bolini* (Mann–Whitney *U*-Test; $p > 0.05$). Therefore, it was concluded that sample depth had no major influence on the SCI of these species. *G. braueri* was taken in too low numbers in the upper depth horizon to be able to draw conclusions about the influence of sample depth on feeding behaviour.

The SCI of *E. antarctica* fluctuated between 0.0% and 0.9% (avg. 0.47) over a 24 h time period (Fig. 8A). Highest feeding activity was observed at night (0200–0300 h). Minimum values in feeding intensity were found for the intervals 0800–0900 h and 1100–1200 h. Nevertheless, no difference in feeding intensity was found between day and night samples (Mann–Whitney *U*-test, $p = 0.081$), because of the high variability of the SCI values during day. The proportion of undigested food items (Stage 1) was reduced during daytime except at one station during the time interval 1100–1200 h where results are based on a low number of fish (5) and food items (2) (Fig. 8C).

The average SCI of *G. braueri* was 0.22%, and values ranged from 0.04% to 0.4% (Fig. 8B). It is difficult to draw conclusions about the feeding chronology of this species because of the low overall feeding intensity. We found no statistical differences in SCI between day and night samples (Mann–Whitney *U*-test, $p = 0.867$). The proportion of fresh prey items was highest in the early evening (time interval 2000–2100 h) (Fig. 8D).

The average and range of SCI for *G. nicholsi* were calculated to be 0.29% and 0.12% to 0.55% (Fig. 9A). There was no statistical difference in feeding intensity between samples taken at day and night (Mann–Whitney *U*-test, $p = 0.178$). However, feeding intensity was increased during evening times at 2100–2200 h (average SCI 0.38%) and reached a maximum at 2300–2400 h (SCI 0.55%). The observation of intensified feeding at these time periods is supported by a higher proportion of undigested food items. We observed a decrease in feeding intensity after midnight and lasting until the early morning hours. The stomachs of *G. nicholsi* contained fresh food items during day and night (stage 1) (Fig. 9C). For this reason we suggest that feeding activity was taking place continuously.

In the small *P. bolini* average SCI (1.1%) was higher than in *G. nicholsi* (Fig. 9B). We excluded one station (58) with extraordinarily high stomach filling (SCI 10.6%), and which we interpret as an outlier. No difference in median SCI was found between daytime and nighttime samples (Mann–Whitney *U* test $p = 0.127$). Nevertheless, feeding activity was increased during hours of darkness when SCI values were above the average. A second peak in feeding intensity was observed in the morning hours from 0800 to 0900 h (SCI 1.7%). During the day, SCI reached a minimum value of 0.21 at 1400–1500 h. The highest proportions of undigested food items were recorded in the evening and before midnight (Fig. 9D).

3.5.3. Daily ration and the impact of predation on the krill stock

The daily ration estimate was highest for the small myctophid *P. bolini*, accounting for 2.48% of fish wet weight assuming a 10 h feeding period and 5.94% assuming that the species feeds 24 h a day (Table 6). The lowest daily ration was calculated for *G. braueri*, accounting for 0.5% wet body weight under the conservative assumption and 1.19% with a 24 h feeding period. The estimated daily rations of *G. nicholsi* are calculated to be only slightly higher than in *G. braueri* at 0.65% and 1.57%. *E. antarctica* took an intermediate position with daily rations of 1.06% and

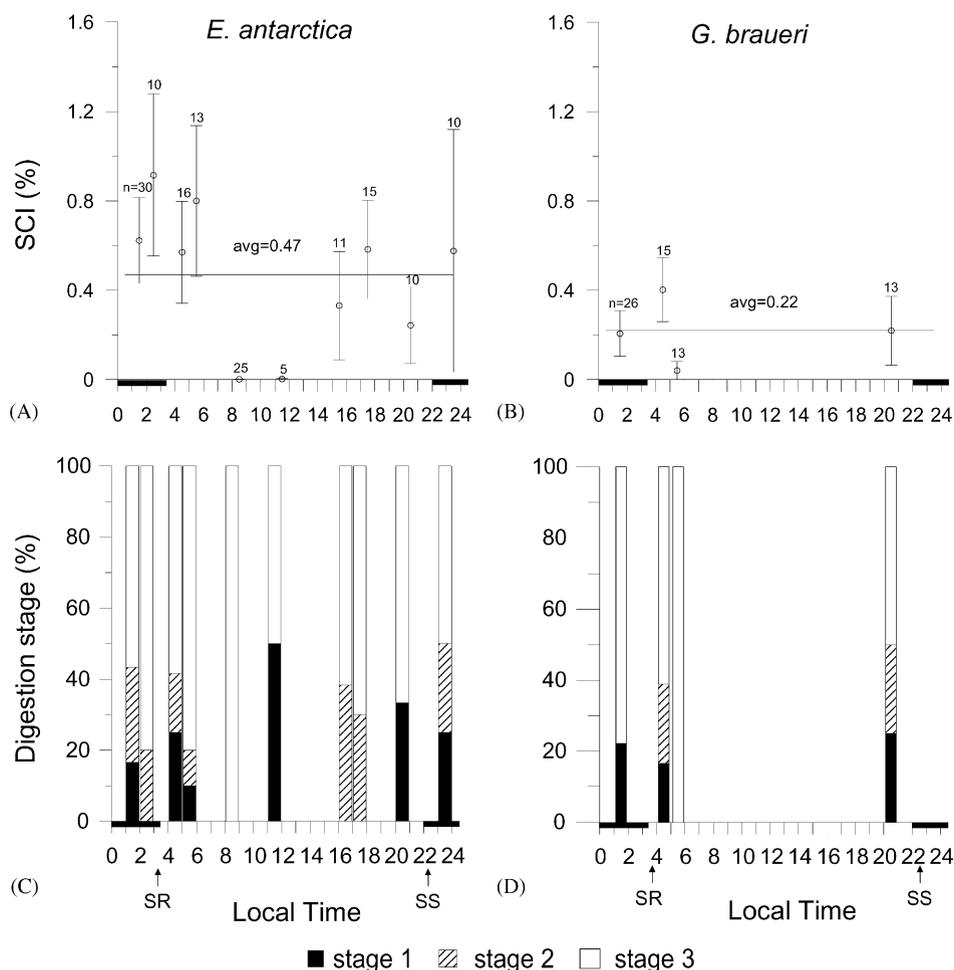


Fig. 8. (A–D) Diel changes in stomach content of *E. antarctica* and *G. braueri*: (A–B) Average Stomach Content Index (SCI); vertical bars = standard error; n = number of individuals examined. (C–D) Proportion of digestion stage (stage 1 = fresh food, stage 2 = slightly digested, stage 3 = only indigestible remains). Sunset (SS) and sunrise (SR) are indicated on the x -axis. Filled bars represent hours of darkness.

2.54% of wet body weight by the 10 and 24 h feeding period assumption.

Two myctophids in our study, *E. antarctica* and *G. nicholsi*, fed on krill (*E. superba*). Based on the food composition data and the daily rations, we assessed the predation impact of these myctophids on the krill stock in the study area.

E. superba was the most important prey item in the diet of *E. antarctica* and *G. nicholsi* and accounted for 53.1% and 58.3% of the total food weight in these species, respectively. The standing stock of krill biomass in the Elephant Island

region in the years 1996/1997 was estimated to be 92 g/1000 m³ (Siegel et al., 1998b). We estimated the biomass of *E. antarctica* and *G. nicholsi* to be 4.08 and 1.36 g/1000 m³, respectively, in slope waters off King George Island. The daily intake of krill by *E. antarctica* was assessed to be 1.06% of its body wet weight during a 10 h feeding period and 2.54% in 24 h.

The predation impact of *G. nicholsi* on krill was estimated to be 0.65% of body wet weight under the assumption of a 10 h feeding period and 1.57% assuming a 24 h feeding period.

Table 6
Daily ration and predation impact on the krill stock of four myctophid species

	<i>E. antarctica</i>	<i>G. braueri</i>	<i>G. nicholsi</i>	<i>P. bolini</i>
Avg. SCI (% body dry weight)	0.47	0.22	0.29	1.10
Feeding period (h)	10/24	10/24	10/24	10/24
Daily ration (% body dry weight)	0.59/1.41	0.28/0.66	0.36/0.87	1.38/3.3
Daily ration (% body wet weight) ^a	1.06/2.54	0.50/1.19	0.65/1.57	2.48/5.94
Proportion of <i>E. superba</i> in food weight (%)	53.1	0.00	58.30	0.00
Daily ration of <i>E. superba</i> (% body wet weight)	0.56/1.35	0.00	0.38/0.92	0.00
Predator density (g/1000 m ³)	4.08	1.20	1.36	0.19
Daily consumption of krill (mg/1000 m ³)	22.85/55.08	0.00	5.17/12.51	0.00
Annual consumption of krill (g/1000 m ³)	8.32/20.05	0.00	1.88/4.55	0.00
Percentage of krill stock removed (%) ^b	9.04/21.79	0	2.05/4.95	0

Daily rations were calculated for both 10 and 24 h periods of feeding.

^aConversion factor daily ration dw to ww 1.8.

^bTaking in account a krill biomass of 92 g/1000 m³ (Siegel et al., 1998b).

XIV/2 indicated an increased chlorophyll-*a* concentration in the vicinity of the Scotia-Weddell Confluence, which passed through the study site. A higher diversity of mesopelagic fish, resulting from an 'island effect', was described by Piatkowski et al. (1994) for an assemblage above the slope of South Georgia when compared to an oceanic station in the northern Scotia Sea. The snake mackerel *P. gracilis* is a characteristic species of slope habitats with benthopelagic life style (Nakamura, 1990) which was also recorded over the slope of South Georgia (Piatkowski et al., 1994).

However, our study supports the results of previous studies that characterize the Antarctic micronekton community as a low diversity oceanic faunal assemblage, compared to subtropical and tropical oceans, where species numbers are four to five times higher (Hopkins and Lancraft, 1984; Lancraft et al., 1989).

The dominant position of *E. antarctica*, *G. braueri*, *P. bolini* in the Antarctic micronekton assemblage have also been shown for the Scotia Sea and slope waters off South Georgia (Piatkowski et al., 1994). These species are assumed to be the most common myctophids of the Southern Ocean (Hulley, 1981). The high densities of *E. antarctica* over the slope of King George Island confirmed the importance of this species in the pelagic ecosystem south of the Antarctic Polar

Front (Rowedder, 1979b; Hulley, 1981; McGinnis, 1982; Lancraft et al., 1989; Hoddell et al., 2000). The size spectrum of *E. antarctica* suggested the presence of the age classes two and three during our study, according to the results of Greely et al. (1999).

The centre of distribution of *P. choriodon*, *G. fraseri* and *G. hintonoides* are known to be in the area of the South Polar Front and north of it (Hulley, 1981). The first records of these species in the South Shetland Islands region give support to the idea that frontal zones, such as the South Polar Front Zone, are not impervious barriers but may be penetrated by mesopelagic fish that are trapped in eddies (Kock, 1992).

4.2. Community structure

Our data showed a strong separation between samples taken above and below 450 m depth. These finding could be well correlated with the presence of warmer and denser CDW at and below this depth. Samples from the CDW showed a higher species diversity based on Shannon's diversity and Taxonomic diversity (Δ). In contrast the Taxonomic distinctness (Δ^*) showed a high degree of similarity between the deeper and lower mesopelagic fish community, due to the dominance of the family Myctophidae and the high

number of congeneric species in the lower mesopelagic assemblage.

The higher density of mesopelagic fish samples taken in the CDW compared to ASW are in accordance with the results of Piatkowski et al. (1994), who found a high similarity in species composition in lower mesopelagic depths (400–1000 m) sampled at two different stations in the Scotia Sea, while samples taken in the upper depth horizons were clearly separated geographically. They found the highest biomass and abundance in the upper layers of the CDW (400–800 m).

The analysis of the community structure of migratory species, like mesopelagic fish, has to consider the day/night distribution of the species. Because of our restricted sampling program (no samples above 273 m depth, only four night samples) conclusions about the vertical migration patterns of the mesopelagic fish can be drawn only from data in the literature (Lancraft et al., 1989; Piatkowski et al., 1994; Duhamel et al., 2000).

The results of the multivariate statistical analysis of the mesopelagic fish data can be best explained by diel migratory behaviour of the species. The most characteristic species, *E. antarctica* and *G. braueri*, in the group of deeper stations (as defined by SIMPER analysis) perform extensive vertical migrations (Torres and Somero, 1988; Lancraft et al., 1989; Piatkowski et al., 1994). During daylight, they stay in the core of the CDW (400–800 m) and migrate to the upper 200 m at night. A third species characteristic of deeper stations was *P. gracilis*, a species whose vertical distribution is probably confined to mesopelagic depths. The most characteristic species of shallow samples, *P. bolini*, also migrates vertically, but over a more restricted range as described by Piatkowski (1989) and Lancraft et al. (1989). Therefore, a substantial part of the population remains in the ASW (0–400 m depth) during daylight.

Duhamel et al. (2000) showed a clear change in the species composition of mesopelagic fish in the vicinity of the Polar Front at Kerguelen Island. A frontal system has also been described for the shelf-break zone north of King George Island that results in increased krill densities in this area (Ichii

et al., 1998). In our study, no influence of the shelf-break on the mesopelagic fish assemblage was discernable. This could be due to the relatively small horizontal extent of our study site. Therefore, further studies of community structure should cover a wider geographical area to fully encompass hydrographic features like frontal zones.

4.3. Feeding ecology

4.3.1. Food composition

Our data showed that Antarctic myctophids, like myctophids in other oceans, are primarily zooplanktivores. They feed mainly on copepods and euphausiids. The proportions of these main prey categories differed in the diets of the species examined. Large myctophids (>60 mm SL), *E. antarctica*, *G. braueri* and *G. nicholsi* fed mainly on euphausiids, while the smaller-sized *P. bolini* (53 mm maximum SL) preyed mainly on copepods. These results suggest niche separation by the utilization of different prey taxa.

More than 90% of the krill biomass is concentrated in the upper 100 m of the water column in the South Shetland Island region (Siegel, 1985). The diet analysis indicated that krill was the main prey item of *E. antarctica* and *G. nicholsi*. It can be assumed that *E. antarctica* and *G. nicholsi* were sampled below their main feeding depth, because the fishes examined in our study were taken in depths greater than 273 m. This assumption was supported by the low stomach filling in *E. antarctica* (57.9% empty stomachs) and the advanced digestion stage of krill found in the stomachs of *G. nicholsi* (46.3% digestion stage 3). In contrast, the proportion of heavily digested *Thysanoessa macrura*, a species characterized by a wider vertical distribution range (Lancraft et al., 1989), was much smaller (9.1% digestion stage 3). The high importance of *M. gerlachei* in the diet of *P. bolini* in our study re-confirmed the results of Ascenio and Moreno (1984). The vertical distribution maximum of *M. gerlachei* is in the upper and lower mesopelagic depths (Huntley and Escritor, 1992). It can be assumed that this copepod species was available over the whole vertical distribution range of *P. bolini*. In contrast to these findings,

Gaskett et al. (2001) described *P. bolini* as an euphausiid feeder, as this prey category made up more than the half of the food wet weight in their study that was undertaken close to the subantarctic Maquarie Island. Such differences support the findings of Pakhomov et al. (1996), namely that the food composition of myctophids varies by locality and probably by season. The same conclusion is true for the role of krill in the diets of *E. antarctica* and *G. nicholsi*. The importance of adult krill in the diet of both species has been described previously for several areas of the Southern Ocean (Rembiszewski et al., 1978; Rowedder, 1979a; Lubimova et al., 1983; Kozlov and Tarverdiyeva, 1989). However, Pakhomov et al. (1996) found no krill in the diet of *E. antarctica* and only small quantities in the diet of *G. nicholsi* sampled in the Prydz Bay, South Georgia and Lazarev Sea (Indian Sector) regions. Therefore, these authors suggest that krill only plays a significant role in the diet of myctophids only during certain time periods and within specific areas. An additional reason for the minor importance of krill in the diet of *E. antarctica* and *G. nicholsi* in their study could be result of size-dependent feeding. Numerous studies have shown that larger individuals of a population are able to consume larger prey items, which is often demonstrated by an ontogenetic switch from copepods to euphausiids as the main prey category (Young and Blaber, 1986; Williams et al., 2001). The size-ranges of *E. antarctica* (25–85 mm SL) and *G. nicholsi* (69–139 mm SL) examined by Pakhomov et al. (1996) were smaller than their size-ranges in our study, namely 57–113 mm SL and 123–172 mm, respectively. Nevertheless, the difference in diet composition cannot be explained entirely by predator length. In the present study the diet of the smaller-sized *E. antarctica* (57–79 mm) and *G. nicholsi* (123–144 mm), that is size ranges represented in Pakhomov's samples, have a similar food composition to larger individuals and is dominated by euphausiids. Therefore scarcity of *E. superba* in the diet of *E. antarctica* and *G. nicholsi* in Pakhomov's study may be due more to the effect of food availability than the effect of size-dependent feeding behaviour.

E. antarctica taken in samples from November to January (Rowedder, 1979a) and *P. bolini* sampled in February (Ascenio and Moreno, 1984) have been shown to prey heavily on development stages of krill. The breeding season of krill fluctuates in the Antarctic Peninsula region from the beginning of December until the end of March (Siegel et al., 1997). During our study, at the beginning of December, most female krill individuals were in a pre-spawning or early spawning condition (Siegel et al., 1998a). Therefore, it can be assumed that no krill development stages were available in the zooplankton community at the time of our study. In summary, our data indicate that krill was an important prey item for *E. antarctica* and *G. nicholsi* over the slope of King George Island. It can be expected that the dietary importance of krill for myctophids will be enhanced during the course of the austral summer, when krill abundance increases and their smaller development stages become available in the zooplankton (Siegel et al., 1997; Ichii et al., 1998). Our data also show that *P. gracilis* is an important predator of mesopelagic fish over the slope of King George Island, so confirming the results of Rembiszewski et al. (1978).

4.3.2. Feeding chronology

Except for *G. braueri*, all myctophids in the present study showed diurnal feeding patterns characterized by increased food intake during night. Nevertheless the day-night differences in feeding activity were not significant for any species. Pakhomov et al. (1996) suggested an active nocturnal feeding period of 8–10 h for Antarctic myctophids. Migratory myctophids, especially in nutrient poor tropical and subtropical waters, are reported to show a pronounced chronology of feeding activity, by feeding in the food rich epipelagic layer at night (Clarke, 1978; Kinzer and Schulz, 1985; Gartner et al., 1997). In contrast, in more productive areas, a number of migratory myctophids such as *Diaphus theta*, *Stenobrachius leucopsarus*, *Tarletonbeania crenularis* (Tyler and Percy, 1975), *Benthosema glaciale* (Kinzer, 1977), *Diaphus danae*, *Lampanyctus hectoris* (Young and Blaber, 1986) and *D. theta* (Moku et al., 2000) tend to feed continuously. It

should be noted that the Southern Ocean ecosystem is characterized by a seasonal high productivity near the pack ice and in the shelf regions like the slope region of King George Island (Hempel, 1985; Ichii et al., 1998).

In our study, *G. nicholsi* showed an increased feeding activity in the time period 2100–2400 h, while in *P. bolini* SCI was above the average from 2000 to 0300 h. However, neither species ceased feeding during the day, and both showed a second feeding activity peak in the time interval 0800–0900 h. A daily feeding period in *P. bolini* appears to be possible due to the relatively shallow daytime depth they occupy (273–500 m). This range overlaps with the vertical distribution range of its major prey item, *M. gerlachei* (Hernandez-Leon et al., 2001). The SCI of *E. antarctica* increased during the hours of darkness and in the early morning. In contrast during summer and autumn at South Georgia, South Sandwich and South Orkney Island Rowedder (1979a) observed the highest feeding activity of this species in the afternoon (1400 h) and second peak in the morning (0600 h). The different feeding patterns of *E. antarctica* observed by Rowedder suggest that the feeding chronology of mesopelagic fish can show a high regional and seasonal variability.

4.3.3. Daily ration and predation impact on the krill stock

Our estimates of daily rations (0.7–3.3% of dry body weight, assuming a 24 h feeding period) were in good agreement with the estimates of Pakhomov et al. (1996) for Antarctic myctophids. The latter ranged from 0.2% to 4.4% of dry body weight.

The estimates of daily ration given by Rowedder (1979a) for *E. antarctica* (5% of dry body weight) and by Gerasimova (1990) for *E. carlsbergi* (3.7–5.6 wet body weight) were higher than in our results. While feeding activity in migratory mesopelagic fish has been observed to reach maximum values in the food-rich epipelagic layers (Gartner et al., 1997), the calculations of daily rations in our study were based on individuals sampled from mesopelagic depths. *E. antarctica* and *G. braueri*, in particular, showed a low feeding activity (57.9% and 68.7% of all stomachs

examined were empty, Table 5). Because of this fact, our calculated daily rations could be underestimated. However, we suggest that our estimates are realistic, because we have re-calculated prey dry weights by length-weight regressions of undigested prey items. The use of re-calculated weight is expected to bias the SCI values in a positive direction (Hyslop, 1980). It is for this reason that we felt justified in applying the daily rations of myctophids in the calculation of their predation impact on the krill stock in the study area. Most estimates of the predation impact by mesopelagic fish on the zooplankton stock have been performed in tropical and subtropical waters. Despite differences in regions and methods of estimation used, all these studies indicate that mesopelagic fish are able to remove two to three times the standing stock of herbivorous zooplankton (Dalpadado and Gjoesaeter, 1988; Hopkins and Gartner, 1992; Gartner et al., 1997).

There has been only one previous estimate of zooplankton consumption by Antarctic mesopelagic fish. Naumov (1985) as cited in Pakhomov et al. (1996) on the basis of an assumed mesopelagic fish stock of 275 million tonnes in the Southern Ocean, estimated an annual consumption of 1085 million tonnes of meso- and macro zooplankton (excluding *E. superba*). This equates to an estimated predation impact equivalent to 40% of the annual secondary production.

We have calculated the annual removal of the krill stock in the Southern Ocean region by *E. antarctica* and *G. nicholsi*, which are thought to be two of the most abundant myctophids in the Southern Ocean, to be 11.1–26.7%. These results confirm the important position of mesopelagic fish in the Antarctic oceanic system, and give support to the suggestion of Lancraft et al. (1989) that they are the most prevalent predators on krill in the Antarctic ecosystem. However, the figures given in the present study should be treated with caution since they represent a “snapshot” of the mid-water fish community over the slope of King George Island. Because the feeding impact of mesopelagic fish on the krill stock is largely dependent on locality and season, future studies should be carried out at different seasons of the year to get

a more realistic picture of the Antarctic mesopelagic food web.

Acknowledgements

Special thanks to Dr. Volker Siegel (Sea Fisheries Research Institute) for his great assistance in the identification of zooplankton and his constructive comments on an earlier version of this manuscript. We also thank Captain Pahl and the crew of the RV 'Polarstern' for outstanding work at sea.

References

- Ascenio, G., Moreno, C.A., 1984. Dieta y selectividad alimentaria de *Protomyctophum bolini* Fraser-Brunner (Pisces; Myctophidae) en el paso Drake (Antarctica). Serie científica. Instituto Antartico chileno. 31, 85–91.
- Barlow, K.E., Boyd, I.L., Croxall, J.P., Reid, K., Staniland, I.J., Brierley, A.S., 2002. Are penguins and seals in competition for Antarctic krill at South Georgia? Marine Biology 140, 205–213.
- Bulman, C.M., He, X., Koslow, J.A., 2002. Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. Marine Freshwater Research 53, 59–72.
- Cherel, Y., Guinet, C., Tremblay, Y., 1997. Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croy, Kerguelen. Polar Biology 17, 87–90.
- Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology-Progress Series 92, 205–219.
- Clarke, K.R., Warwick, R.M., 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Natural Environmental Research Council, Plymouth (p. 144).
- Clarke, K.R., Warwick, R.M., 2001. Primer-E (5) Computer Program. Natural Environmental Research Council, Plymouth.
- Clarke, T.A., 1978. Diel feeding patterns of 16 species of mesopelagic fishes from Hawaiian waters. Fishery Bulletin 76, 495–513.
- Dalpadado, P., Gjoesaeter, J., 1988. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. Marine Biology 99, 555–567.
- 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-Verlag Italia, Milano (Italy), pp. 63–74.
- Duhamel, G., Koubbi, P., Ravier, C., 2000. Day and night mesopelagic fish assemblage off the Kerguelen Islands (Southern Ocean). Polar Biology 23, 106–112.
- Eggers, D.M., 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. Journal of the Fisheries Research Board of Canada 34, 290–294.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology-Progress Series 8, 37–52.
- Gartner Jr., J.V., Crabtree, R.E., Sulak, K.J., 1997. Feeding at depth. In: Randall, D.J., Farrel, A.P. (Eds.), Deep-Sea Fishes. Academic Press, San Diego, pp. 1–388.
- Gartner Jr., J.V., Conley, W.J., Hopkins, T.L., 1988. Escape-ment by fishes from midwater trawls: a case study using lanternfishes (Pisces: Myctophidae). Fishery Bulletin 87, 213–222.
- Gaskett, A.C., Bulman, C.M., He, X., Goldsworthy, S.D., 2001. Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. NewZealand Journal of Marine Freshwater Research 35, 469–476.
- George, E.L., Hadley, W.F., 1979. Food and habitat partitioning between Rock Bass (*Ambloplites rupestris*) and small-mouth Bass (*Micropterus dolomieu*) young of the year. Transactions of the American Fisheries Society 108, 253–261.
- Gerasimova, O.V., 1990. Feeding and food intake of *Electrona carlsbergi* (Taning, 1932) Myctophidae. Selenium Science Paper CCAMLR 7, 411–416.
- Gon, O., Heemstra, P.C., 1990. Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstone (462pp).
- 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. Marine Biology 133, 145–158.
- Groeger, J., Piatkowski, U., Heinemann, H., 2000. Beak length analysis of the Southern Ocean squid *Psychroteuthis glacialis* (Cephalopoda: Psychroteuthidae) and its use for size and biomass estimation. Polar Biology 23, 70–74.
- Guinet, C., Cherel, Y., Ridoux, V., Jouventin, P., 1996. Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–1985. Antarctic Science 8, 23–30.
- Hempel, G., 1985. Antarctic marine food webs. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), Antarctic Nutrient Cycles. Springer, Berlin, pp. 266–276.
- Hernandez-Leon, S., Portillo-Hahnefeld, A., Almeida, C., Becognee, P., Moreno, I., 2001. Diel feeding behaviour of krill in the Gerlache Strait, Antarctica. Marine Ecology-Progress Series 223, 235–242.
- 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 Research Part II 47, 2519–2541.
- Hofmann, E.E., Klinck, J.M., Lascara, C.M., Smith, D.A., 1996. Water mass distribution and circulation west of the Antarctic Peninsula and including Bransfield Strait. Antarctic Research Series 70, 61–80.

- Hopkins, T.L., Gartner Jr., J.V., 1992. Resource partitioning and predation impact of a low latitude myctophid community. *Marine Biology* 114, 185–197.
- Hopkins, T.L., Lancraft, T.M., 1984. The composition and standing stock of mesopelagic micronekton at 27°N 86°W in the eastern Gulf of Mexico. *Contributions to Marine Science* 27, 143–158.
- Hulley, P.A., 1981. Results of the research cruises of FRV “Walther Herwig” to South America LVIII. Family Myctophidae (Osteichthyes, Myctophiformes). *Archiv für Fischereiwissenschaft* 31, 1–300.
- Hulley, P.A., 1998. Preliminary investigations on the evolution of the tribe Electronini (Myctophiformes, Myctophidae). In: Di Prisco, G., Pisano, E., Clarke, A. (Eds.), *Fishes of Antarctica: a biological overview*. Springer-Verlag Italia, Milano, pp. 75–85.
- Hulley, P.A., Kock, K.H., Pusch, C., White, M.G., 1998. Mesopelagic fishes. *Berichte zur Polarforschung* 274, 17–22.
- Huntley, M.E., Escritor, F., 1992. Ecology of *Metridia gerlachei* Giesbrecht in the western Bransfield Strait, Antarctica. *Deep-Sea Research A* 39, 1027–1055.
- Hyslop, E.J., 1980. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* 17, 411–429.
- Ichii, T., Naganobu, M., Ogishima, T., 1996. Competition between the krill fishery and penguins in the South Shetland Islands. *Polar Biology* 16, 63–70.
- Ichii, T., Katayama, K., Obitsu, N., Ishii, H., Naganobu, M., 1998. Occurrence of Antarctic krill (*Euphausia superba*) concentrations in the vicinity of the South Shetland Islands: relationship to environmental parameters. *Deep-Sea Research I* 45, 1235–1262.
- Kinzer, J., 1977. Observations on feeding habits of the mesopelagic fish *Benthoosema glaciale* (Myctophidae) off NW Africa. In: Anderson, N.R., Zahuranec, B.J. (Eds.), *Oceanic Sound Scattering Prediction*. Plenum Press, New York, pp. 381–392.
- Kinzer, J., Schulz, K., 1985. Vertical distribution and feeding patterns of midwater fish in the central equatorial Atlantic. I. Myctophidae. *Marine Biology* 85, 313–322.
- Kock, K.-H., 1992. *Antarctic Fish and Fisheries*. Cambridge University Press, Cambridge (359pp).
- Kock, K.-H., Döllefeld, L., Hulley, P.A., Jählig, H.-P., Petzel, W., Pusch, C., Siegel, V., White, M.G., 1998. The composition of the fish fauna on the northern slope of King George Island. *Berichte zur Polarforschung* 274, 14–17.
- Kozlov, A.N., Tarverdiyeva, M.I., 1989. Feeding of different species of Myctophidae in different parts of the Southern Ocean. *Journal of Ichthyology* 29, 160–167.
- Lancraft, T.M., Torres, J.J., Hopkins, T.L., 1989. Micronekton and Macrozooplankton in the open waters near Antarctic Ice Edge Zones (AMERIEZ). *Polar Biology* 9, 225–233.
- Lancraft, T.M., Hopkins, T.L., Torres, J.J., Donnelly, J., 1991. Oceanic micronekton/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). *Polar Biology* 11, 157–167.
- Lubimova, T.G., Shust, K.V., Troyanovskij, F.M., Semenov, A.B., 1983. The ecology of mass species of myctophids from Atlantic Antarctica. *Antarktika* 22, 99–106.
- McGinnis, R.F., 1982. Biogeography of lanternfishes (Myctophidae) south of 30°. *Antarctic Research Series* 35, 1–110.
- Mizdalski, E., 1988. Weight and length data of zooplankton in the Weddell Sea in austral spring 1986 (ANTV/3). *Berichte zur Polarforschung* 55, 1–72.
- Moku, M., Kawaguchi, K., Watanabe, H., Ohno, A., 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. *Marine Ecology-Progress Series* 207, 129–140.
- Nakamura, I., 1990. Gempylidae. In: Gon, O., Heemstra, P.C. (Eds.), *Fishes of the Southern Ocean*. JLB Smith Institute of Ichthyology, Grahamstown, South Africa, pp. 402–403.
- Naumov, A.G., 1985. System analysis of the structure of the Antarctic waters community. In: Vinogradov, M.E., Flint, M.V. (Eds.), *Biological Basis of the Commercial Utilization of the Open Regions of the Ocean*. Nauka Press, Moscow, pp. 57–80 (in Russian).
- Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., 1996. Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology-Progress Series* 134, 1–14.
- Pearcy, W.G., Lorz, H.V., Peterson, W., 1979. Comparison of the feeding habits of migratory and non-migratory *Stenobrachius leucopsarus* (Myctophidae). *Marine Biology* 51, 1–8.
- Phillips, K.L., Jackson, G.D., Nichols, P.D., 2001. Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analysis. *Marine Ecology-Progress Series* 215, 179–189.
- Piatkowski, U., 1989. Macroplankton communities in Antarctic surface waters: spatial changes related to hydrography. *Marine Ecology-Progress Series* 55, 251–259.
- Piatkowski, U., Rodhouse, P.G., White, M.G., Bone, D.G., Symon, C., 1994. Nekton community of the Scotia Sea as sampled by the RMT 25 during austral summer. *Marine Ecology-Progress Series* 112, 13–28.
- Pielou, E.C., 1975. *Ecological Diversity*. Wiley, New York (165pp).
- Rembiszewski, J.M., Krzeptowski, M., Linkowski, T.P., 1978. Fishes (Pisces) as by-catch in fisheries of krill *Euphausia superba* Dana (Euphausiacea, Crustacea). *Polskie archiwum hydrobiologii* 25, 677–695.
- Rodhouse, P.G., White, M.G., Jones, M.R.R., 1992. Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front, Scotia Sea. *Marine Biology* 114, 415–421.
- Rowedder, U., 1979a. Feeding ecology of the myctophid *Electrona antarctica* (Guenther, 1878) (Teleostei). *Meeresforschung* 27, 252–263.
- Rowedder, U., 1979b. Some aspects of the biology of *Electrona antarctica* (Guenther, 1878) (Family Myctophidae). *Meeresforschung* 27, 244–251.
- Schlitzer, R., 2003. Ocean data view. <http://www.awi-bremerhaven.de/GEO/ODV>.

- Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University Illinois Press, Chicago (p. 111).
- Siegel, V., 1985. The distribution pattern of krill, *Euphausia superba*, west of the Antarctic Peninsula in February 1982. *Meeresforschung* 30, 292–305.
- Siegel, V., de la Mare, W.K., Loeb, V., 1997. Long-term monitoring of krill recruitment and abundance indices in the Elephant Island area (Antarctic Peninsula). *CCAMLR Science* 4, 19–35.
- Siegel, V., Kock, K.H., Petzel, W., Hulley, P.A., Pusch, C., Döllefeld, L., White, M.G., 1998a. Investigation on the krill stock and the epipelagic zooplankton community in the Elephant Island region. *Berichte zur Polarforschung* 274, 50–56.
- Siegel, V., Loeb, V., Groeger, J., 1998b. Krill (*Euphausia superba*) density, proportional and absolute recruitment and biomass in the Elephant Island region (Antarctic Peninsula) during the period 1977–1997. *Polar Biology* 19, 393–398.
- Stein, M., Heywood, R.B., 1994. Antarctic environment-physical oceanography: the Antarctic Peninsula and South-west Atlantic region of the Southern Ocean. In: El-Sayed, S.Z. (Ed.), *Southern Ocean Ecology—The Biomass Perspective*. Cambridge University Press, Cambridge, pp. 11–24.
- Torres, J.J., Somero, G.N., 1988. Vertical distribution and metabolism in Antarctic mesopelagic fishes. *Comparative Biochemistry and Physiology* 90B, 521–528.
- Tyler Jr., H.R., Percy, W.G., 1975. The feeding habits of three species of lanternfishes (Family Myctophidae) off Oregon, USA. *Marine Biology* 32, 9–11.
- Warwick, R.M., Clarke, K.R., 1995. New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology-Progress Series* 129, 301–305.
- Williams, A., Koslov, J.A., Terauds, A., Haskard, K., 2001. Feeding ecology of five fishes from the mid-slope micro-nekton community off southern Tasmania, Australia. *Marine Biology* 139, 1177–1192.
- Williams, R., 1985. Trophic relationships between pelagic fish and euphausiids in Antarctic waters. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), *Antarctic Nutrient Cycles and Food Webs*. Springer, Berlin, pp. 452–459.
- Young, J.W., Blaber, S.J.M., 1986. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. *Marine Biology* 93, 147–156.