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Prey composition and daily rations of myctophid fishes in the Southern Ocean

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ABSTRACT: The feeding ecology of myctophids was studied using data collected during 5 South African scientific cruises to the Southern Ocean from 1985 to 1995. A total of 362 specimens, comprising 36 species, were analyzed for gut contents. Myctophid biomass levels, estimated from Bongo net tows, are among the lowest yet recorded for the Southern Ocean. Peak biomass levels were associated with the main frontal zones and with a permanent polynya region in the Lazarev Sea. Results show that all myctophid species are opportunistic mesozooplankton feeders exhibiting a high degree of overlap in their food spectrum and consuming primarily the most abundant species of copepods, euphausiids, hyperiids and pteropods. Daily rations were estimated using 3 different approaches and ranged from 0.2 to 4.4% of dry body weights. Generally, the daily food intake was equivalent to 0.5 (lower mean) to 2.9 (upper mean) of dry body weight for Antarctic and subantarctic species, and between 1.2 and 3.8% for temperate and subtropical species. Antarctic krill, *Euphausia superba*, was usually poorly represented in the stomachs of all but 1 myctophid species. The results of this study therefore do not support the hypothesis that krill plays a major role in the feeding ecology and budget of myctophids.

KEY WORDS: Myctophid fishes · Antarctica · Feeding · Daily ration

INTRODUCTION

The Southern Ocean exhibits a distinct myctophid or lanternfish (family Myctophidae) fauna of ~40 endemic species (Bekker 1983, 1985). There are almost no truly epipelagic myctophids south of the Subtropical Convergence (STC) and most species are meso- and bathypelagic migrators (Gon & Heemstra 1990). The total biomass of mesopelagic fish in the Southern Ocean (south of the STC) has been estimated from survey data and model calculations to range between 212 and 396 million t (Lubimova et al. 1987). South of 40°S the biomass of myctophids alone ranges from 70 to 200 million t (Tseitlin 1982, Lubimova et al. 1987, Lancraft et al. 1989). This large myctophid stock has attracted some research attention in the past and recently the economic and general ecological importance of myctophids, as a link between meso- and macrozooplankton and top predators (e.g. fish, squid, birds and mammals), has stimulated great interest (Lubimova et al. 1987, Kozlov & Tarverdieva 1989, Perissinotto & McQuaid 1992, Sabourenkov 1992). Dense concentrations of myctophids are generally recorded in the Antarctic Polar Front Zone (APFZ), in the region between the Subantarctic Front and the Antarctic Polar Front (APF) (Chindonova 1987, Lubimova et al. 1987). However, the highest densities are consistently found within the major frontal systems, including the Marginal Ice Zone (Chindonova 1987, Lancraft et al. 1989, 1991, Filin et al. 1991, Kozlov et al. 1991, Pakhomov et al. 1994).

A recent model of the Antarctic pelagic subsystem suggests that approximately 23% of the total primary production may be indirectly ingested by pelagic fish and squid (Huntley et al. 1991). Myctophids may, thus, represent a pathway accounting for a substantial export of organic carbon from the euphotic zone to the deep ocean through their diurnal vertical migrations and production of large, fast-sinking faeces. Therefore, any effort towards a correct estimation of energy transfer within the pelagic subsystem of the Southern Ocean must include analyses of the individual diet

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composition of these fishes and their rates of food consumption. Although, the diet of the most common and abundant myctophid species is well documented (Rowedder 1979, Naumov et al. 1981, Williams 1985, Hopkins & Torres 1989, Kozlov & Tarverdieva 1989, Oven et al. 1990, Lancraft et al. 1991, Sabourenkov 1991, Hopkins et al. 1993), to date there are only 2 estimates of daily rations available in the literature (Rowedder 1979, Gerasimova 1991).

The main aims of this study are to estimate daily rations of myctophid fishes in the Southern Ocean (including the STC region) and to provide further information on the feeding ecology of these important components of the mesopelagic subsystem.

MATERIALS AND METHODS

Myctophids were collected during 5 South African cruises to the Southern Ocean (Fig. 1, Table 1). Two cruises were undertaken aboard RV 'Africana', to the Prydz Bay region in March 1985 and to South Georgia in February 1994 (Fig. 1). During both cruises, samples were collected using the Polish Krill Trawl 1641 with a nominal mouth area of ~30 m^2 and a mesh size of 7 mm. In the Prydz Bay region, trawls were towed obliquely between the surface and ~80 m depth, while in the South Georgia shelf region tows were undertaken as close as possible to the bottom. During the northbound leg of the South Georgia cruise (March 1994), an additional tow was made in the mid-Atlantic region of the STC (Fig. 1).

The other 3 cruises were undertaken aboard the SA 'Agulhas', and formed part of the South African Antarctic Marine Ecosystem Study (SAAMES). The first, SAAMES II, took place during the period January to February 1993 along a transect between SANAE and Cape Town (Fig. 1). During the second cruise, SAAMES III (June to July 1993), the area of investigation was limited to the region south of Africa situated in the vicinity of the Subtropical Convergence (Fig. 1). The third survey, SAAMES IV (December 1994 to January 1995), was carried out in the Marginal Ice Zone (MIZ) of the Lazarev Sea (Fig. 1). During these surveys, fish were collected using a Bongo net with a mouth area of 0.5 m^2 and a mesh size of 0.3 to 0.5 mm as well as with a Rectangular Midwater Trawl (RMT-8) with a nominal mouth area of 8 m^2 and a mesh size of 4.5 mm (Baker et al. 1973). Both nets were fitted with an Universal Underwater Unit (U^3; Robertson et al. 1981). The volume filtered by the Bongo net was calculated using electronic flowmeter data while for the RMT-8 this was determined by multiplying the effective mouth area of the trawl by the distance travelled (Roe et al. 1980). This was calculated from the ship's speed and the tow duration after the trawl was opened in the water. Towing speed varied between 1.5 and 4 knots and usually nets were towed obliquely between 0 and 300 m. During the SAAMES IV survey only, some deep tows were made with the RMT-8 trawl to a depth of 1000 m.

Samples were preserved in 4 to 6% buffered formalin and examined in the laboratory. All myctophids isolated from the samples were identified to the species level and their standard body length (accuracy:

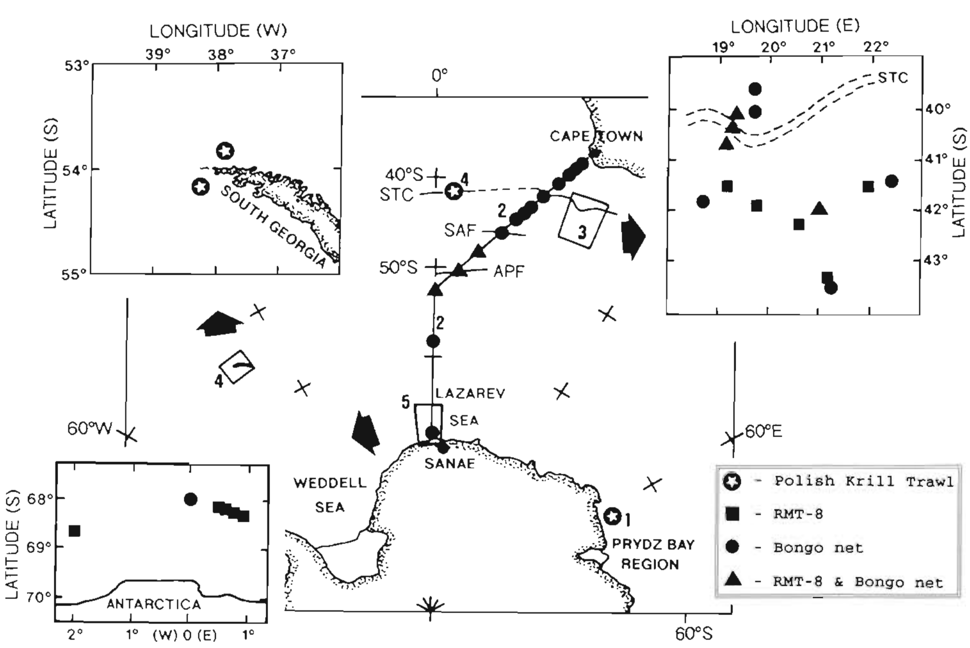

Fig. 1. Position of the stations where myctophids were collected in the Atlantic and Indian sectors of the Southern Ocean during 1: March 1985; 2: January to February 1993, SAAMES II; 3: June to July 1993, SAAMES III; 4: February to March 1994; 5: December 1994 to January 1995, SAAMES IV. STC: Subtropical Convergence; SAF: Subantarctic Front; APF: Antarctic Polar Front

Table 1. List of myctophid species examined for gut contents. APF: Antarctic Polar Front; STC: Subtropical Convergence; AD: Antarctic Divergence; AZ: Antarctic Zone; STZ: Subtropical Zone; SAZ: Subantarctic Zone

Species	Distribution	Sampling period: Mar 1985	Jan–Feb 1993	Jun–Jul 1993	Feb–Mar 1994	Dec 1994–Jan 1995	Total
Electrona antarctica	AZ	14	2	–	–	36	52
E. paucirastra	STC	–	–	–	8	–	8
E. subaspera	SAZ	–	–	1	1	–	2
E. carlsbergi	SAZ	–	2	–	–	–	2
Metelectrona herwigi	STC	–	–	–	12	–	12
Protomyctophum normani	STC	–	1	22	15	–	38
P. bolini	STC–AD	–	5	–	–	–	5
P. horiodon	36–51°S	–	3	–	1	–	4
P. luciferum	34–48°S	–	1	1	–	–	2
P. andriashevi	STC–APF	–	4	–	–	–	4
Diaphus taaningi	STZ	–	1	16	–	–	17
D. hudsoni	SAZ	–	–	3	15	–	18
D. efflugens	19°S–STC	–	–	1	–	–	1
D. luetkeni	STZ	–	–	2	–	–	2
D. meadi	STC	–	–	2	–	–	2
Bentosema suborbitale	50°N–50°S	–	2	4	–	–	6
Gymnoscopelus nicholsi	STC–APF	6	–	–	27	–	33
G. opisthopterus	AZ	25	–	–	–	7	32
G. bolini	SAZ	–	3	7	–	–	10
G. microlampas	STC–APF	–	1	–	–	–	1
Ceratoscopelus warmingi	42°N–45°S	–	3	11	31	–	45
Symbolophorus boops	SAZ–STC	–	–	2	24	–	26
S. evermanni	STZ	–	–	1	–	–	1
S. barnardi	30°S–STC	–	2	–	–	–	2
Hygophum hanseni	STZ, STC	–	2	2	–	–	4
H. higomii	STZ, STC	–	–	5	–	–	5
Lampanyctus alatus	STZ–STC	–	–	3	–	–	3
L. australis	SAZ, STC	–	2	2	–	–	4
L. pusillus	STZ	–	1	1	–	–	2
Krefftichthys andersoni	STC–AD	–	3	–	–	–	3
Lobianchia dolfeni	50°N–40°S	–	–	3	–	–	3
Lampadema ponifex	STZ	–	–	2	–	–	2
Diogenichthys atlanticus	50°N–48°S	–	–	3	–	–	3
Scopelopsis multipunctatus	25°S–STC	–	–	2	–	–	2
Notoscopelus resplendens	47°S–STC	–	5	–	–	–	5
Bolinichthys supralateralis	STZ–STC	–	1	–	–	–	1
Total		45	40	100	134	43	362

~0.5 mm) and wet weight (accuracy: ~1 mg) measured. Dry weight was obtained by oven-drying specimens at 60°C for 48 h. Prey items were isolated from myctophid gut contents, counted and where possible identified. In total 362 specimens, comprising 36 species of myctophids, were examined for gut contents (Table 1). Stomach contents were then dried at 60°C for 36 h. Results from stomach content analyses were expressed as a percentage of each food item to the total number of food items counted. The degree of stomach fullness was estimated according to the procedure suggested by Sameoto (1989). The index of stomach fullness (ISF), expressed as a percentage of body weight, was calculated by dividing the dry weight of the stomach contents by the dry weight of the fish body.

To estimate daily rations of myctophids, 3 independent approaches were followed.

Approach 1. The mean specific daily ration (C_w) was calculated using Baikov's relation (Baikov 1935, Eggers 1977), $C_w = I \times 24/T$, where I is the daily average ISF in % and T is the gut passage time in hours. Samples collected at our 24 h stations indicated that myctophid stomachs contain fresh food throughout the night. This suggests that fish could feed for at least 8 to 10 h d^{-1}. Taking this into account, Baikov's equation can be amended as follows: $C_w = I \times 10/T$. Since the gut passage time for the species studied is unknown, data on gut passage time versus temperature from the literature were used. Given that both fish size and food type may significantly affect the gut evacuation rate

(Fänge & Grove 1979), only published data on gut passage time of fish with similar characteristics in terms of size range (3 to 10 cm) and diet composition (zooplankton) were selected (Table 2). In some cases, both published and field data, collected at 24 h stations within the STC region (SAAMES III), were used to calculate gut evacuation rates (k) and gut passage time ($1/k$), assuming an exponential model of food evacuation. A regression model between $1/k$ and temperature was calculated from the values presented in Table 2. This equation was very similar to the model derived from data obtained by Tyler (1970) from young cod maintained at temperatures of 2 to 19°C. The 1/k values were also comparable to those published by Fänge & Grove (1979).

Approach 2. Given the well documented diurnal vertical migrations and the predominantly nighttime feeding activity in myctophids (e.g Hopkins & Baird 1977, Clarke 1978, Kinzer & Schulz 1985, Gon & Heemstra 1990), the assumption was made that 'the daily ration per fish is equal to the amount of fresh food found in a full stomach' (Sameoto 1988, 1989). For this purpose, values of ISF of full stomachs (100% of stomach fullness, according to Sameoto 1989) for all myctophid species investigated were transformed using the arcsin operator and combined to calculate a regression equation between the standard fish body length (in mm) and ISF (in % of body weight). Maximum daily ration derived in this way may be underestimated because fish may maintain a full stomach even while digesting or when food is transferred from the stomach to the hind gut during nighttime (Sameoto 1988). Therefore, 2 regressions were calculated (Fig. 2): in the first all data points were considered while in the sec-

Table 2. Available estimates of gut evacuation rate (k) and gut passage time ($1/k$) versus temperature in a selected range of fish species. The relationship between $1/k$ and water temperature (T) from data presented in the table is a power function of the form: $1/k = 24.3 \times T^{-0.6}$ ($R^2 = 57.1\%$, $p < 0.001$)

Fish species	T (°C)	k (h^{-1})	$1/k$ (h)	Source
Clupea harengus (larvae)	7.0	0.133	7.5	Blaxter (1963)
Clupea harengus (larvae)	9.0	0.161	6.2	Blaxter (1963)
Clupea harengus (larvae)	11.0	0.200	5.0	Blaxter (1963)
Clupea harengus (larvae)	15.0	0.250	4.0	Blaxter (1963)
Lampanyctus mexicanus[a]	12.0	0.166	6.02	Holton (1969)
Pungitius pungitius	5.0	0.050	20.0	Cameron et al. (1973)
Pungitius pungitius	15.0	0.143	7.0	Cameron et al. (1973)
Perca flavescens	22.0	0.250	4.0	Nobel (1973)
Diaphus taaningi	13.0	0.238	4.20	Baird et al. (1975)
Brevoortia tyrranus	16.0	0.200	5.0	Kjeldson et al. (1975)
Lagodon rhomboides	16.5	0.180	5.55	Kjeldson et al. (1975)
Lagodon rhomboides	16.0	0.194	5.15	Kjeldson et al. (1975)
Leiostomus anthurus	17.0	0.164	6.1	Kjeldson et al. (1975)
Hygophum proximum	12.5	0.520	1.92	Clarke (1978)
Valenciennellus tripunctatus	10.0	0.220	4.55	Clarke (1978)
Danaphos oculatus	8.0	0.100	10.0	Clarke (1978)
Vincigueria nimbaria	11.7	0.380	2.63	Clarke (1978)
Electrona antarctica[a]	3.0	0.118	8.5	Rowedder (1979)
Notothenia angustifrons	1.0	0.027	37.0	Targett (1981)
Notothenia larseni	1.0	0.049	20.4	Targett (1981)
Pleuronectes platessa[a]	10.0	0.094	10.6	Jobling (1986)
Brama brama (juveniles)	14.0	0.130	7.69	Krasnopeyor (1990)
Brama brama (juveniles)	16.0	0.150	6.67	Krasnopeyor (1990)
Brama brama (juveniles)	18.0	0.180	5.55	Krasnopeyor (1990)
Brama brama (juveniles)	20.0	0.210	4.76	Krasnopeyor (1990)
Electrona carlsbergi[a]	3.5	0.125	8.0	Gerasimova (1991)
Clupea harengus (juveniles)	17.4	0.352	2.84	Arrhenius & Hansson (1994)
Clupea harengus (juveniles)	16.5	0.242	4.13	Arrhenius & Hansson (1994)
Clupea harengus (juveniles)	15.0	0.272	3.67	Arrhenius & Hansson (1994)
Clupea harengus (juveniles)	13.2	0.223	4.48	Arrhenius & Hansson (1994)
Clupea harengus (juveniles)	8.7	0.197	5.08	Arrhenius & Hansson (1994)
Diaphus taaningi[a]	12.0	0.169	5.92	This study
Protomyctophum normani[a]	12.0	0.158	6.33	This study
Pagothenia borchgrevinki[b]	−1.0	0.031	32.0	Montgomery et al. (1989)

[a] k and $1/k$ were calculated from an exponential model of the decline of food weight in stomachs versus time
[b] Value presented for comparison only and not included in the calculation of the regression equation

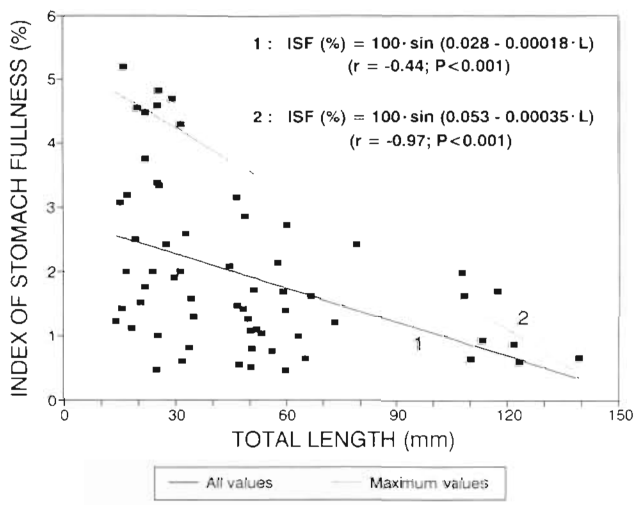

Fig. 2. Relationships between the index of stomach fullness (ISF, only stomachs with 100% fullness were considered; Sameoto 1989) and fish standard length for myctophids species collected in the Southern Ocean. 1. relationship obtained for all values of ISF; 2: relationship calculated for the maximum ISF values for each 5 mm fish length size class

ond only the maximum values for each 5 mm fish size class were selected. Maximum values provide a more accurate estimate of the daily rations.

Approach 3. The last approach was based on estimates of fish metabolic energy requirements and net conversion efficiency, $K_2 = P/P + R$ (where P is production and R is metabolic energy needs). Average values for K_2 in adult cold-water fish are ~0.2 (Vinberg 1956, Brett & Groves 1979). Thus, $P/R = 0.25$. Since the consumption $C = P + R/U$ (where U is the coefficient of assimilation), and assuming $U \sim 0.8$ (Hopkins & Baird 1977), a value for C of ~$1.56 \times R$ is obtained. Under natural conditions, R is equal to ~$2 \times R_{st}$ (Vinberg 1956), where R_{st} is the basic metabolic needs. R_{st} values for Antarctic species were derived from Torres & Somero (1988). For subantarctic and temperate species, average R_{st} values obtained by Torres et al. (1979) using species held at 5°C and 10°C, respectively, were used. Values of caloric content (kcal g^{-1} wet wt) were available in the literature for the following species: *Electrona carlsbergi*: 1.7 (Gerasimova 1991); *E. antarctica* and *Gymnoscopelus* spp.: 1.6; *G. nicholsi*: 2.8; *G. opisthopterus* and other species: 1.1 (Donnelly et al. 1990).

For example, according to Vinberg's equation the total daily energy requirements of *Electrona antarctica* estimated by doubling the basic metabolic requirements are:

$$C_w = 1.56 \times 2 \times R_{st} \times 24 \times 4.86 \times 100/W \times 1000$$

where $R_{st} = 0.044 \times W^{0.946}$ ml O_2 h^{-1} (Torres & Somero 1988), 4.86 cal ml^{-1} O_2 is the oxycaloric coefficient and W is the average wet weight of the fish in grams. Since the caloric content of copepods and euphausiids (the staple food items of myctophids) is ~0.7 kcal g^{-1} wet wt (Vinogradov & Shushkina 1987), then the above equation can be reduced to:

$$C_w = 3.656 \times W^{-0.054}.$$

To take into account the energy spent for reproduction, C_w must be further increased by ~19% (Tseitlin 1989)

RESULTS

Myctophid biomass distribution

Biomass levels, derived from Bongo net samples collected only during the nighttime tows and from the upper 300 m layer along the SANAE to Cape Town transect, ranged from <0.01 to 1.1 g dry wt m^{-2} (Fig. 3). Average biomass throughout the transect was 0.138 g dry wt m^{-2} (Table 3). Mesoscale enhancements in myctophid biomass generally co-occurred with high mesozooplankton densities (Fig. 3). The highest levels were recorded at a station situated at 60° S, immediately north of the MIZ (Fig 3). The second major peak in biomass was observed in the northern vicinity of the APF, extending across the APFZ. Minor peaks were found in the polynya region off SANAE and in the southern vicinity of the APF. In addition, 2 small but consistent biomass enhancements were associated with the STC and the continental slope/shelf of South Africa (Fig. 3). Biomass levels available in the literature are also presented in Table 3 for comparison with the data obtained during this study.

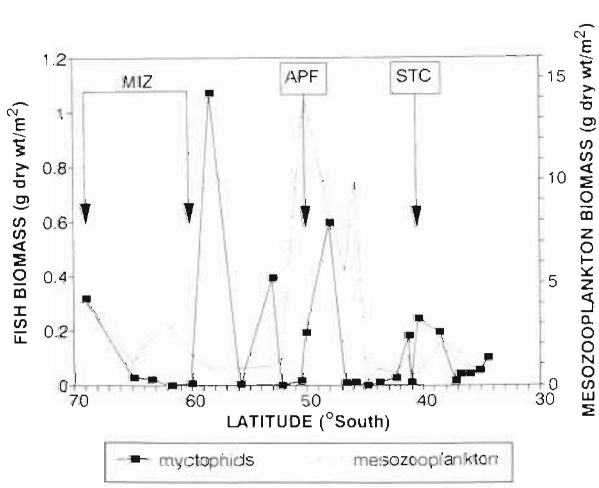

Fig. 3. Myctophid fish and mesozooplankton biomass along the transect from SANAE to Cape Town obtained from samples collected with 0 to 300 m oblique nighttime Bongo net tows during January to February 1993, SAAMES II

Table 3. Estimates of myctophid biomass in the Southern Ocean. APFZ: Antarctic Polar Front Zone (48 to 54°S); APF: Antarctic Polar Front; STC: Subtropical Convergence; MIZ: Marginal Ice Zone

Region	Method	Mean biomass (g wet wt m^{-2})	(g dry wt m^{-2})	Dominant species	Source
Atlantic sector	Combined	3.0	0.9	Various species	Gjøsaeter &
Indian sector	Combined	3.1–4.7	0.93–1.41	Various species	Kawaguchi (1980)
Pacific sector	Combined	4.5	1.35	Various species	
Atlantic sector, 40–54°S	Net (max.) (0–1000 m)	5–15	1.5–4.5	Various species	Chindonova (1987)
Atlantic sector, APFZ	Acoustic & net	5.3–9.9 (40–45)[a]	1.6–3.0 (12–13.5)[a]	Various species	Zemsky (1987)
Atlantic sector, APFZ	Acoustic	3.82–6.48 Max. 70–100	1.15–6.48 Max. 21–30	*Electrona carlsbergi*	Filin et al. (1991)
Atlantic sector, APFZ	Acoustic	1.6–11.72	0.48–3.52	*Electrona carlsbergi*	Kozlov et al. (1991)
Atlantic sector, MIZ	Net (0–1000 m)	–	0.36–0.73	Various species	Lancraft et al. (1991)
Atlantic sector, APF	Net (0–300 m)	–	Max. 0.117	Various species	Pakhomov et al. (1994)
STC	Net (0–300 m)	–	Max. 0.302	Various species	
Atlantic sector	Bongo net	–	0.138	Various species	This study
	(0–300 m)	–	Max. 1.07	*Electrona antarctica*	This study
Lazarev Sea, MIZ	Net (0–1000 m)	–	0.087	*Electrona antarctica*	Pakhomov et al.
	Net (0–1000 m)	–	Max. 0.806	*Electrona antarctica*	(unpubl.)

[a]In swarms

Water content and gravimetric analysis

Water content, expressed as a percentage of wet weight, ranged from 60% in *Gymnoscopelus nicholsi* to 80.9% in *G. microlampas* (Table 4). Generally, water content showed an inverse correlation with fish size. The values of water content obtained in this study are within the range reported for temperate myctophids (e.g. Neighbors & Nafpaktitis 1982, Baily & Robison 1986) and also almost identical to the levels obtained by Donnelly et al. (1990) for several Antarctic species.

Values for the coefficients a and b of the power function, obtained from the regression of standard length versus dry body weight, were generally similar in all species investigated and ranged from 0.0001 to 0.006 and from 2.7 to 3.7, respectively (Table 4).

Stomach content composition

The number of items per stomach examined generally ranged from 1 to 20 (Table 5a, b). Stomachs with more than 30 food items were very rare and contained a monospecific food type. The maximum number of food items in 1 stomach (185) was recorded for *Krefftichthys andersoni* (Table 5b). Average values of ISF ranged from 0.16 to 1.97% of dry body weight. Three species, i.e. *Bentosema suborbitale*, *Lampadema ponifex* and *K. andersoni*, had average ISFs as high as 2.4 to 4.5% of dry body weight (Table 5a, b).

Copepods were the most important component in the diet of almost all myctophid species examined. In general, they accounted for >50% by number of all prey items identified (Table 5a, b). Medium-sized (≤5 mm) bioluminescent species of the genera *Metridia* and *Pleuromamma* (exhibiting a large pigment spot on the cephalothorax) as well as large (5 to 8 mm) species of the genera *Calanus*, *Rhincalanus* and *Euchaeta* were the dominant copepods consumed. Small (≤12 mm) euphausiids, mainly *Euphausia* spp. and *Thysanoessa* spp., hyperiids, mostly *Themisto gaudichaudi* and *Primno macropa*, and the pteropod, *Limacina* spp., formed the next most abundant components of the myctophids diet (Table 5a, b). Antarctic krill *Euphausia superba*, with a total length of 33 to 43 mm, was an important food item only in the adults of *Gymnoscopelus opisthopterus*. Most krill individuals found in fish stomachs were, however, undigested. Euphausiids were in general more important in the diet of fish with a standard length >40 mm, e.g *Electrona paucirastra*, *Metelectrona hervigi*, *Gymnoscopelus nicholsi* and *G. opisthopterus* (Tables 4 & 5a).

Daily rations

Although estimates of daily rations for the most abundant myctophid species vary considerably (0.23 to 4.4% of dry body wt), the values derived from the 3 different approaches used in this study are in reasonable agreement with each other and with those reported in the literature (Table 6). Consistently lower daily rations were obtained only when using the first approach, probably due to the limited number of fish examined.

Table 4. Relationships between standard length, body dry weight and water content of the myctophid species analysed. Parameter values were fitted to the power function: $y = a \times x^b$, where y is the body dry weight (mg) and x is the standard length (mm)

Species	n	Size range (mm)	DW as % of WW Range	Mean	SD	*a*	*b*	*r*
Electrona antarctica	52	25–85	12.7–32.6	25.3	5.47	0.0002	3.706	0.995
E. paucirastra	8	48.5–65.8	24.8–27.7	26.0	0.95	0.0008	3.312	0.988
E. subaspera	2	21.6–47	19.1–22.3	20.2	2.95	–	–	–
E. carlsbergi	2	13.2–17.6	18.8–19.7	19.2	0.67	–	–	–
Metelectrona herwigi	12	46.3–57	31–38.7	34.6	2.35	0.0011	3.363	0.916
Protomyctophum normani	58	17.5–55.5	16.9–34.7	25.9	4.33	0.0032	2.990	0.963
P. bolini	5	53–57	29.5–34.4	31.0	1.78	–	–	–
P. horiodon	4	25.4–75.5	20.7–28.5	25.3	3.02	0.0006	3.332	0.998
P. luciferum	2	24–35	21.8–26.3	24.1	2.27	–	–	–
P. andriashevi	4	23.7–51.6	25.6–32.0	27.8	2.61	0.0009	3.300	0.997
Diaphus taaningi	17	12.4–59.5	20–25.7	22.8	1.56	0.0006	3.337	0.995
D. hudsoni	18	15–47.3	22.8–34.7	29.3	3.52	0.0012	3.236	0.903
D. efflugens	1	72.8	–	20.7	–	–	–	–
D. luetkeni	2	31.6–32.9	23.5–24.4	24.0	0.65	–	–	–
D. meadi	2	17–36	22.4–23.5	22.9	0.79	–	–	–
Bentosema suborbitale	6	11–29	20.4–27.6	23.4	2.60	0.0030	2.920	0.994
Gymnoscopelus nicholsi	33	69.1–139	31.4–46.2	40.0	3.45	0.0009	3.296	0.952
G. opisthopterus	32	64–153.5	14.7–31.6	20.2	5.59	0.00003	3.873	0.980
G. bolini	10	24.3–98.1	20.6–30.4	24.4	3.42	0.0004	3.377	0.996
G. microlampas	1	32.6	–	19.1	–	–	–	–
Ceratoscopelus warmingi	60	16.5–74.6	16.5–27.8	21.7	2.58	0.0004	3.361	0.995
Symbolophorus boops	26	25–96.1	21.4–27.5	24.6	1.67	0.0002	3.517	0.997
S. evermanni	1	22.1	–	22.2	–	–	–	–
S. barnardi	2	23–24.7	20–23	21.5	1.51	–	–	–
Hygophum hanseni	4	20.5–39.4	22.2–25.0	23.5	1.20	0.0022	2.993	0.966
H. higomii	5	14.5–16.3	17.9–20.9	20.0	1.08	–	–	–
Lampanyctus alatus	3	19.6–30.5	21–24.6	22.9	1.46	0.0009	3.070	0.999
L. australis	4	25–37	23.5–25.9	24.4	0.98	0.0001	3.871	0.952
L. pusillus	2	21.4–31.4	20.5–26.7	23.6	4.38	–	–	–
Krefftichthys andersoni	3	14–52.1	25.6–38.1	33.9	5.85	0.0002	3.854	0.999
Lobianchia dolleni	3	34–38	23.5–25.7	24.7	0.92	–	–	–
Lampadema ponifex	2	19.5–20	20.7–20.9	20.8	0.14	–	–	–
Diogenichthys atlanticus	3	14–18.1	19.9–21.0	20.6	0.59	–	–	–
Scopelopsis multipunctatus	2	16.7–17.2	21.3–22.3	21.8	0.55	–	–	–
Notoscopelus resplendens	5	42.4–56.4	22.4–24.9	23.3	0.87	0.0057	2.728	0.958
Bolinichthys supralateralis	1	17.1	–	19.5	–	–	–	–

Generally, the daily consumption of Antarctic and high-subantarctic species ranged from 0.5 (lower mean) to 2.92% (upper mean) of dry body weight (Table 6). Daily rations for the temperate and subtropical species ranged between 1.34 and 3.85%.

DISCUSSION

Feeding ecology

The results of this study indicate that Southern Ocean myctophids occupy an important trophic status as zooplankton consumers. Mesozooplanktonic organisms, such as copepods, euphausiids, hyperiids and pteropods, constitute the bulk of myctophid diets. As in most other regions of the world ocean, these fish constitute the tertiary level of the pelagic trophic system and are consumers of the second order (e.g. Hopkins & Baird 1977, Clarke 1978, 1980, Gordon et al. 1985, Duka 1986, Kawamura & Fujii 1988).

While studying the feeding ecology of a synoptic collection of 14 tropical myctophid species, Clarke (1980) found a high degree of feeding specialisation between species. In contrast, myctophids from temperate and high latitude regions appear to exhibit a high degree of overlap in their food spectrum (e.g. Tyler & Pearcy 1975, Scotto di Carlo et al. 1982, Young & Blaber 1986). In this study, we found no substantial differences in the prey items of myctophid species collected within the same region (Table 5a, b). This may reflect low inter-species food competition because of high regional food availability. This hypothesis is supported by the observation that at all stations myctophids fed on the most abundant species of mesozooplankton (e.g. Voronina 1984, Barange et al. in press, Pakhomov & McQuaid in

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Table 5a. Diet composition of 20 myctophid species collected in the Southern Ocean during the period 1985–1995. EA: *Electrona antarctica*; EP: *E. paucirastra*; ES: *E. subaspera*; EC: *E. carlsbergi*; MH: *Metelectrona herwigi*; PN: *Protomyctophum normani*; PB: *P. bolini*; PH: *P. horiodon*; PL: *P. luciferum*; PA: *P. andriashevi*; DT: *Diaphus taaningi*; DH: *D. hudsoni*; DE: *D. efflugens*; DL: *D. luetkeni*; DM: *D. meadi*; BS: *Bentosema suborbitale*; GN: *Gymnoscopelus nicholsi*; GO: *G. opisthopterus*; GB: *G. bolini*; GM: *G. microlampas*

Stomach contents	EA	EP	ES	EC	MH	PN	PB	PH	PL	PA	DT	DH	DE	DL	DM	BS	GN	GO	GB	GM
Copepoda																				
Rhincalanus gigas	1.0	–	–	–	–	–	–	–	–	12.5	–	–	–	–	–	–	10.9	2.8	2.3	–
Rhincalanus spp.	–	–	–	–	–	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calanus propinquus	20.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Calanus simillimus	–	–	–	–	–	–	6.7	–	–	–	–	–	–	–	–	–	18.1	–	6.8	–
Calanus spp.	–	–	4.2	–	–	–	–	–	11.1	–	0.9	–	–	–	–	4.5	3.6	–	2.3	–
Calanoides acutus	5.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.0	–	–	–
Clausocalanus spp.	3.6	–	–	–	–	–	–	–	–	6.3	–	–	–	–	–	–	1.2	–	–	–
Ctenocalanus spp.	3.6	–	–	–	–	–		–	22.2	25.0	–	–	–	–	–	–	–	–	–	–
Scaphocalanus spp.	–	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	–	–	–
Metridia gerlachei	25.2	–	–	–	–	–	20.0	–	–	–		–	–	–	–	–	–	–	–	–
Metridia lucens	–	45.0	16.7	–	–	–	–	–	–	–	1.7	–	–	–	–	–	–	–	6.8	–
Metridia spp.	1.8	–	–	–	8.8	2.3	–	–	–	–	9.4	1.6	–	–	11.1	–	10.2	–	–	20.0
Pleuromamma abdominalis	–	–	–	–	–	0.9	–	–	–	–	1.7	–	–	–	–	–	–	–	31.8	–
Pleuromamma spp.	–	2.5	29.2	–	11.7	70.6	–	11.1	33.3	12.5	56.4	40.9	50.0	16.7	33.3	36.4	0.2	–	4.6	20.0
Paraeuchaeta antarctica	1.8	–	–	–	–	–	26.7	–	–	–	–	–	–	–	–	–	0.4	13.9	–	–
Euchaeta spp.	4.7	–	–	–	1.5	–	33.3	11.1	–	6.3	0.9	–	–	–	–	–	5.4	–	2.3	–
Scolecitricella spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–
Candacia spp.	–	–	–	–	–	–	–	11.1	–	–	–	–		–	–	–	0.6	–	4.5	–
Calanoida	8.2	–	–	33.3	5.9	14.2	–	33.3	–	25.0	9.4	6.6	–	66.7	33.3	13.6	10.8	–	11.4	–
Oithona spp.	–	–	–	33.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Oncaea spp.	–	–	4.2	–	–	0.5	–	–	–	–	5.1	6.2	–	–	22.2	22.7	–	–	–	40.0
Ostracoda																				
Conchoecinae	0.9	–	–	–	–	–	–	–	22.2	6.2	6 0	9.6	–	–	–	4.6	1.2	–	11.4	–
Euphausiacea																				
Euphausia superba	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.5	16.7	–	–
Euphausia frigida	–	–	–	–	–	–	6.7	–	–	–	–	–	–	–	–	–	4.8	–	–	–
Euphausia triacantha	–	–	–	–	–	–	–	11.1	–	–	–	–	–	–	–	–	0.6	–	–	–
Euphausia spinifera	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euphausia similis	–	2.5	–	–	26.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euphausia (furcilia)	1.4	–	–	–	–	0.9	–	–	–	–	0.8	–	–	–	–	18.2	1.4	–	2.3	–
Thysanoessa macrura	3.6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.8	16.7	–	–
Thysanoessa vicina	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	16.1	–	–	–
Thysanoessa gregaria	–	5.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thysanoessa spp.	0.5	10.0	4.2	–	5.9	3.2	–	–	–	–	–	1.6	–	–	–	–	0.2	–	–	–
Nematoscelis megalops	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Euphausiacea	0.9	10.0	–	–	7.3	2.3	–	–	–	–	0.8	3.3	–	–	–	–	0.8	11.1	9.1	–
Mysidacea																				
Antarctomysis maxima	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–
Amphipoda																				
Themisto gaudichaudi	–	–	–	–	1.5	–	–	22.2	–	–	–	–	–	–	–	–	1.8	–	–	–
Primno macropa	0.9	–	–	–	–	–	13.3	–	–	6.2	–	–	–	–	–	–	–	–	–	–
Vibilia antarctica	1.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–
Hyperiella dilatata	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phronima sedentaria	–	–	–	–	1.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scina spp.	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyperiidea	0.9	–	–	–	–	–	–	–	–	–	–	3.3	–	–	–	–	–	2.8	–	–
Polychaeta																				
Rhinchonerella bongraini	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polychaeta	0.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	4.5	–

Table 5a (continued; Table 5b overleaf)

Stomach contents	EA	EP	ES	EC	MH	PN	PB	PH	PL	PA	DT	DH	DE	DL	DM	BS	GN	GO	GB	GM
Mollusca																				
Limacina spp.	1.4	20.0	41.7	–	25.0	0.5	–	–	–	–	2.6	1.6	–	–	–	–	0.2	–	–	–
Allurotheutis antarcticus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.5	–	–
Chaetognatha																				
Eukrohnia hamata	3.6	–	–	–	–	–	–	–	–	–	–	1.6	–	–	–	–	1.6	2.8	–	–
Sagitta spp.	1.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.0	–	–	–
Chaetogntha	2.7	–	–	33.3	–	–	–	–	–	–	1.7	1.6	–	16.6	–	–	–	2.8	–	20.0
Tunicata																				
Oikopleura spp.	–	5.0	–	–	–	–	–	–	–	–	–	6.2	–	–	–	–	–	–	–	–
Salpa spp.	–	–	–	–	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	–	–
Salpa thompsoni	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.1	–	–
Salpidae	–	–	–	–	–	–	–	–	–	–	0.9	6.2	–	–	–	–	–	–	–	–
Osteichthyes																				
Myctophidae	–	–	–	–	–	–	–	–	–	–	–	–	50.0	–	–	–	–	–	–	–
Fish scales	0.9	–	–	–	1.5	3.7	–	–	–	–	0.9	3.3	–	–	–	–	–	13.8	–	–
Total food items	219	40	24	3	68	218	15	9	9	16	117	61	2	6	18	22	498	36	44	5
No. of items per stomach	1–21	1–21	12	1–2	1–21	1–39	2–7	2–4	3–6	3–7	1–47	1–7	2	2–4	9	2–5	1–38	1–6	1–10	5
Average ISF values (%)	0.73	0.49	1.24	0.67	0.96	1.27	0.53	1.46	0.35	1.25	0.57	0.52	0.28	0.26	1.94	2.78	0.49	0.38	0.16	1.02

press). This is further confirmed by the spatial covariance between high myctophid densities and mesozooplankton biomass enhancement (Fig. 3). Antarctic, subantarctic and temperate/subtropical species of myctophids can, therefore, be classified as opportunistic mesozooplankton predators, with dietary preferences being solely a function of prey availability (Hopkins & Baird 1977).

Our data do not allow serious consideration of dietary changes during the life span of myctophids. The results do, however, show that euphausiids and hyperiids are more important in the diet of adult fish compared to the earlier stages. The available literature indicates that small euphausiids (such as *Thysanoessa* spp.) and hyperiids (mainly *Themisto gaudichaudi*) are the most consistent components in the food of adult Antarctic myctophids (Naumov et al. 1981, Kozlov & Tarverdieva 1989, Oven et al. 1990). This agrees with the conceptual model of a relationship between fish size and prey size, biomass and diversity as suggested for tropical myctophid species by Scotto di Carlo et al. (1982). Some studies have shown that adults of the most abundant Antarctic myctophids feed on krill, rather than copepods (Rowedder 1979, Naumov et al. 1981, Zasel'sljy et al. 1985, Kozlov & Tarverdieva 1989, Oven et al. 1990). This has important implications since it has been suggested that mesopelagic fish, and not seabirds and mammals, may be the dominant predators of krill in the Antarctic oceanic system (Lancraft et al. 1989).

Surprisingly, in this study Antarctic krill *Euphausia superba* was usually poorly represented in the stomachs of myctophids, with a few krill juveniles recorded in some stomachs of *Gymnoscopelus nicholsi* collected within the shelf region of South Georgia and in the Prydz Bay region (Table 5a). Only *Gymnoscopelus opisthopterus* exhibited an important krill component in its gut contents. In the Lazarev Sea and in the Prydz Bay region, krill was absent from all stomachs of *Electrona antarctica*, even when specimens of this myctophid were collected as a by-catch in krill trawls in the Prydz Bay region (O. Gon pers. comm.). These results suggest that the role of Antarctic krill in the feeding ecology of myctophids may have been greatly overestimated in the past. Previous studies have shown that Antarctic krill comprises 50 to 90% of the total mass of the food bolus only in the stomachs of a few Antarctic species, e.g. *G. nicholsi*, *G. opisthopterus* and *E. antarctica* (Rowedder 1979, Kozlov & Tarverdieva 1989, Sabourenkov 1991). We suggest that a substantial consumption of krill by myctophids occurs only during certain periods and within specific regions. This is quite obvious in the case of the most abundant myctophid, *Electrona carlsbergi*, for which *E. superba* is an important food source only during the summer season (Naumov 1985, Zasel'sljy et al. 1985, Kozlov & Tarverdieva 1989, Oven et al. 1990). This question has important implications for Southern Ocean carbon flux and more attention is certainly required to determine the role that Antarctic krill has in the feeding budget of myctophids.

Table 5b. Diet composition of a further 14 myctophid species collected in the Southern Ocean during the period 1985-1995. CW: *Ceratoscopelus warmingi*; SB: *Symbolophorus boops*; SBR: *S. barnardi*; HH: *Hygophum hanseni*; HHI: *H. higomii*; LAL: *Lampanyctus alatus*; LAU: *L. australis*; LP: *L. pusillus*; KA: *Krefftichthys andersoni*; LD: *Lobianchia dolfeni*; LP: *Lampadema ponifex*; DA: *Dio-genichthys atlanticus*; SM: *Scopelopsis multipunctatus*; NR: *Notoscopelus resplendens*

Stomach contents	CW	SB	SBR	HH	HHI	LAL	LAU	LP	KA	LD	LP	DA	SM	NR
Copepoda														
Rhincalanus gigas	–	–	–	–	–	–	–	–	1.7	–	–	–	–	–
Calanus simillimus	–	–	–	–	–	–	–	–	61.8	–	–	–	–	17.5
Calanus australis	–	–	–	–	9.5	–	–	–	–	–	–	–	–	–
Calanus spp.	1.2	–	33.3	–	–	–	–	–	–	16.7	–	–	–	–
Calanoides acutus	–	–	–	–	–	–	–	–	3.6	–	–	–	–	–
Clausocalanus spp.	1.5	–	–	–	–	–	–	–	11.2	–	–	–	–	–
Microcalanus spp.	–	–	–	–	4.8	–	–	–	–	–	–	–	–	–
Ctenocalanus spp.	2.4	–	–	–	–	–	–	–	5.7	–	–	–	–	–
Metridia gerlachei	–	–	–	–	–	–	–	–	7.8	–	–	–	–	–
Metridia lucens	30.1	82.0	–	3.4	–	–	–	–	–	8.3	–	–	–	–
Metridia spp.	1.8	–	–	–	–	–	–	–	4.2	–	–	–	–	–
Pleuromamma abdominalis	–	–	–	48.3	–	–	–	33.3	–	16.7	–	–	–	–
Pleuromamma spp.	40.4	1.6	33.3	44.8	28.6	46.2	72.7	–	–	50.0	–	10.5	–	25.0
Lucicutia spp.	–	–	–	–	–	–	–	–	–	–	20.0	–	–	–
Candacia spp.	0.6	–	–	–	42.9	–	–	–	–	–	–	–	–	–
Calanoida	3.3	–	–	–	–	7.7	18.2	33.3	–	8.3	–	5.3	100.0	–
Oithona spp.	–	–	–	–	–	–	–	–	–	–	–	26.3	–	–
Oncaea spp.	2.7	–	–	–	9.5	23.1	–	–	–	–	60.0	47.4	–	–
Corycaeus spp.	–	–	–	–	4.8	–	–	–	–	–	–	–	–	–
Ostracoda														
Conchoecinae	0.6	0.7	–	–	–	–	–	16.7	–	–	–	–	–	–
Euphausiacea														
Euphausia similis	2.4	1.3	–	–	–	–	–	–	–	–	–	–	–	–
Euphausia (furcilia)	5.1	2.0	–	3.4	–	15.2	–	–	–	–	20.0	–	–	–
Thysanoessa gregaria	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Thysanoessa spp.	1.8	0.6	–	–	–	–	–	–	3.6	–	–	–	–	12.5
Nematoscelis megalops	0.3	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Euphausiacea	1.5	–	–	–	–	–	–	–	0.3	–	–	–	–	37.5
Decapoda														
Zoea decapoda	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Amphipoda														
Themisto gaudichaudi	–	0.7	–	–	–	7.7	–	–	–	–	–	–	–	–
Phronima sedentaria	–	1.3	–	–	–	–	–	–	–	–	–	–	–	–
Hyperiidea	0.3	2.3	33.3	–	–	–	9.1	–	–	–	–	–	–	–
Polychaeta														
Polychaeta	–	–	–	–	–	–	–	–	–	–	–	–	–	12.5
Mollusca														
Limacina spp.	3.3	1.3	–	–	–	–	–	–	–	–	–	–	–	–
Chaetognatha														
Eukrohnia hamata	0.3	1.3	–	–	–	–	–	–	–	–	–	–	–	–
Sagitta spp.	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–
Tunicata														
Oikopleura spp.	0.3	0.6	–	–	–	–	–	–	–	–	–	10.5	–	–
Salpa spp.	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Osteichthyes														
Protomyctophum normani	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Myctophidae	–	0.3	–	–	–	–	–	–	–	–	–	–	–	–
Fish scales	–	–	–	–	–	–	–	16.7	–	–	–	–	–	–
Total food items	332	305	3	29	21	13	11	6	358	12	5	19	2	8
No. of items per stomach	2–63	1–54	1–2	2–15	1–9	2–9	2–4	3	1–185	3–6	2–3	2–17	2	1–4
Average ISF values (%)	1.33	0.87	0.71	0.85	1.71	1.97	1.94	2.42	4.46	0.48	1.94	0.76	0 25	0.37

Generally, the number of food items found in the stomachs of the myctophid species analysed in this study is comparable with those recorded for tropical and temperate mesopelagic fish (e.g. Kinzer & Schulz 1985, Gorelova & Prutko 1985) and often similar to the values found for the tropical species *Diaphus taaningi* (Baird et al. 1975). The number of food items in a stomach is, however, a function of fish size and food composition. Therefore, the ISF is a more objective parameter for comparisons. In this study, the values of ISF were also in good agreement with those (<4% of dry body wt) obtained for many species of myctophids throughout the World Ocean (Baird et al. 1975, Clarke 1978, Young & Blaber 1986, Duka 1986, Kawamura & Fujii 1988, Sameoto 1988, 1989, Kozlov & Tarverdieva 1989, Oven et al. 1990). Maximum values (up to ~5% of dry body weight; Fig. 3) were, however, lower than those recorded in tropical-temperate (up to 10 to 17%) and even in Antarctic (up to 26%) species (Holton 1969, Clarke 1978, Kawamura & Fujii 1988, Sameoto 1988, Kozlov & Tarverdieva 1989). The highest values of ISF recorded in the literature were derived from Antarctic myctophids that had been feeding on krill (Kozlov & Tarverdieva 1989). However, the presence in these stomachs of a limited number (2 to 4) of consistently undigested individuals of *Euphausia superba* leads us to the conclusion that krill might have been eaten just before the catch or, more likely, in the net after capture. Our own findings seem to support this conclusion. Thus, these maximum ISFs can be regarded as the maximum daily food intake and are most probably found only occasionally in nature.

Table 6. Daily rations of the most abundant myctophids of the Southern Ocean estimated using different approaches (1, 2, 3)

Species	Mean length (mm)	Daily ration (% dry body wt) 1	2 Mean	2 Max.	3
Antarctic and high-subantarctic species					
Electrona antarctica	52.8	0.46	1.86	3.45	3.34
Electorna carlsbergi	70.0[a]	0.75	1.56	2.85	2.55
Gymnoscopelus nicholsi	115.3	0.53	0.76	1.26	3.92
Gymnoscopelus opisthopterus	113.1	0.24	0.80	1.34	1.47
Temperate and subtropical species					
Electrona paucirastra	58.1	0.9	1.77	3.26	3.4
Metelectrona herwigi	49.7	2.07	1.92	3.56	3.2
Gymnoscopelus bolini	56.6	0.23	1.80	3.32	2.9
Protomyctophum normani	29.3	2.32	2.28	4.27	3.4
Diaphus taaningi	40.5	1.04	2.08	3.88	4.4
Diaphus hudsoni	40.4	0.95	2.08	3.88	3.0
Ceratoscopelus warmingi	51.3	2.43	1.89	3.50	4.4
Symbolophorus boops	74.7	1.59	1.48	2.68	3.6

[a]Mean length taken from Filin et al. (1991)

Daily rations

Unfortunately, only 2 previous estimates of daily rations for Antarctic myctophids are available in the literature. The daily ration of ~5% of dry body weight, calculated by Rowedder (1979) for *Electrona antarctica*, is likely to represent an overestimate. This is because of the bias associated with the extrapolation to the entire year of levels of food intake obtained during the summer and within a region of high krill biomass. Despite this, Rowedder's estimate may still be considered as the upper limits of the daily consumption during summer. The estimation of the daily ration for *E. carlsbergi* obtained using an energy budget approach (Gerasimova 1991) appears more realistic. According to this estimate, *E. carlsbergi* would require 3.7 to 5.6% of its wet body weight daily, or 2.5 to 3.7% of dry body weight.

Daily rations of *Diaphus taaningi* in continental waters off Venezuela were 0.8% of dry body weight, assuming ~3.5 h of feeding (Baird et al. 1975). However, extending the feeding period to ~6 h, the daily intake could be as high as 1.35% of dry body weight (Table 6). Sameoto (1988, 1989) showed that for the subarctic species *Bentosema glaciale* (which occupies a similar habitat to the Antarctic species) the daily ration ranges from 1.7% of dry body weight in adults to 8% in juveniles. Daily consumption rates of tropical and subtropical species of myctophids from other oceanic regions are higher, ranging generally between 5 and 13% of body weight (Holton 1969, Clarke 1978, Tseitlin & Gorelova 1978, Childress et al. 1980).

The values of daily rations obtained in this study, using 3 different approaches, seem realistic as they are in good agreement with those obtained for other Antarctic, although non-myctophid, fishes (e.g. Targett 1981, Pakhomov & Tseitlin 1992). A theoretical maximum daily ration for Antarctic myctophids can be estimated from the highest ISF recorded in the literature, ~26% of wet body weight (Kozlov & Tarverdieva 1989). Assuming that the digestion time of Antarctic krill is as long as 2 d (Targett 1981, Pakhomov & Tseitlin 1992, Table 2), maximum daily rations may reach ~13% of wet body weight, or ~8% of dry body weight.

Due to the well-known problem of net avoidance and of the shallow towing technique employed in this study, our myctophid biomass estimates are likely to be grossly underestimated. We cannot therefore address the question of their feeding impact on zooplankton adequately. Few estimates of myctophid predation impact are available. In the upper layer of the equatorial Pacific, Gorelova (1984) concluded that myctophids may consume from 2 to 31% (average ~10%) of zooplankton standing stock daily. This suggests that myctophids may be among the most important consumers of oceanic zooplankton, not only in the epi- and mesopelagic layers but also in near surface waters (Gorelova 1984). In contrast, the predation impact of the most important subarctic myctophid species, *Bentosema glaciale*, never exceeded 0.2% of zooplankton standing stock (Sameoto 1988, 1989).

The only estimate of zooplankton consumption by Antarctic mesopelagic fish was made by Naumov (1985). The total stock of mesopelagic fish in the Southern Ocean was estimated to be close to 275 million t and the year ration was assumed as 600% of fish body weight, equivalent to an across-the-year daily ration of ~1.64% of body weight (Naumov 1985). Thus, mesopelagic fish would consume 1085 million t of meso- and macrozooplankton (excluding *Euphausia superba*). As the entire Southern Ocean occupies an area of ~38.1 million km^2 (El-Sayed 1978), the average annual consumption could be equal to ~28.5 g wet wt m^{-2} or ~6.3 g dry wt m^{-2} The mean mesozooplankton biomass measured along our transect from SANAE to Cape Town was 3 g dry wt m^{-2} (Fig. 3). Using a P/B coefficient of ~5 yr^{-1}, as estimated for Antarctic copepods (Voronina 1984), the secondary production will be around 15 g dry wt m^{-2} yr^{-1}. Thus, Antarctic mesopelagic fish predation impact could be equivalent to ~40% of the annual secondary production.

On the basis of their high biomass levels, Lancraft et al. (1989) suggested that mesopelagic fish are probably the dominant predators in the Antarctic oceanic system. The results of this study show that myctophids may be among the most important consumers of secondary standing stock and production in the Southern Ocean. A more accurate assessment of the trophic importance of myctophids in the Southern Ocean requires further detailed information on their distribution, migrations, predation impact, seasonality of feeding rates and, also, estimates of their consumption by other predators.

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