

Feeding ecology of myctophid fishes in the northern Scotia Sea

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ABSTRACT: The diets of 9 species of myctophid fishes, *Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus fraseri*, *G. nicholsi*, *G. braueri*, *Protomyctophum bolini*, *P. choriodon*, *Krefflichthys anderssoni* and *Nannobranchium achirus*, were investigated during austral autumn in the northern Scotia Sea. Based on the percent index of relative importance (%IRI), the data suggest dietary specialisation in some species, which may permit resource partitioning. Hierarchical agglomerative cluster analysis of Bray-Curtis similarity (60% threshold) separated the myctophid community into distinct feeding guilds. One group (*G. braueri* and *E. antarctica*) fed principally on *Themisto gaudichaudii*, another (*P. choriodon* and *G. fraseri*) primarily on copepods (*Metridia* spp. and *Rhincalanus gigas*), and a third group (*G. nicholsi* and *P. bolini*) consumed copepods and euphausiids (mostly *Metridia* spp. and *Euphausia frigida*). The diets of *E. carlsbergi* and *K. anderssoni* differed from the other species, with *E. carlsbergi* being the only species that consumed salps. There was a general switch in diet from copepods to euphausiids and amphipods as the myctophid predator size increased. Dietary specialisation is likely the result of a combination of predator size, gape size, filtering capacity of the gill rakers and the vertical distribution of predators and prey. Antarctic krill were only consumed by the larger myctophids, which represented a numerically minor part of the myctophid community, supporting the concept that myctophids can provide a krill-independent link between secondary production and higher trophic levels. However, the northern Scotia Sea is dominated by adult krill, which are only suitable as prey for larger fish. In the northern Scotia Sea, myctophid predation had a very small impact on copepod production but a higher impact on macrozooplankton, with a best-estimate of 4% of the daily production of *Themisto gaudichaudii* and 6% of that of *Euphausia superba* being consumed.

KEY WORDS: Southern Ocean · Diet · Predation mortality · Copepods · Euphausiid · Predator · Prey

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INTRODUCTION

Lantern fish or myctophids (Family Myctophidae) are the dominant mesopelagic fish in most of the world's oceans, playing a key role in oceanic foodwebs (Gjøsaeter & Kawaguchi 1980, Mann 1984, Hopkins & Gartner 1992, Tsarin 1997) and, through their extensive vertical migrations, contributing to the export of carbon from the surface to mesopelagic depths. Myctophids consume herbivorous and omnivorous zooplankton (e.g. copepods & amphipods) (Pakhomov et al. 1996, Williams et al. 2001, Pusch et al. 2004) and are in

turn consumed by a range of oceanic top predators (Tsarin 1997, Olsson & North 1997, Cherel et al. 2002), thus providing a key link in the open ocean food web. Consequently, determining the trophic ecology of abundant myctophid species is essential in understanding the operation of ocean ecosystems.

Whilst the food web of the Southern Ocean is often perceived to be dominated by Antarctic krill *Euphausia superba*, it is clear that other trophic pathways are both regionally and seasonally important, with myctophids providing a key alternative (Hempel 1985, Murphy et al. 2007). Furthermore, with evidence of a

long-term decline in krill (Atkinson et al. 2004), the importance of these krill-independent pathways is likely to increase. The Southern Ocean myctophid fauna includes approximately 35 species in 12 genera (Hulley 1990), with an estimated biomass of between 70 and 200 million tonnes (Mt) (Lubimova et al. 1987). In the Southern Ocean, myctophids are the primary prey of several important species such as king penguins (Olsson & North 1997), elephant seals (Cherel et al. 2008) and the squid *Martialia hyadesi* (Rodhouse et al. 1992), and are regionally and seasonally important to many other predators, such as fur seals (Guinet et al. 2001, Reid et al. 2006). Despite their abundance and ecological significance, data on the ecology of myctophids are remarkably sparse, globally and particularly in the Southern Ocean.

Determining diet is essential to understanding food web dynamics and resource partitioning (Ross 1986), but studies of Southern Ocean myctophid diets have, so far, been restricted to the most abundant species on limited spatial and temporal scales, in some cases with very small sample sizes (Rowedder 1979, Naumov et al. 1981, Kozlov & Tarverdiyeva 1989, Gerasimova 1990, Pakhomov et al. 1996, Gaskett et al. 2001, Pusch et al. 2004). Important parameters, such as daily rations, have only been estimated in a small number of studies (Gerasimova 1990, Pakhomov et al. 1996, Pusch et al. 2004). The predation impact of myctophids on prey species has received very little attention, with the only Southern Ocean estimates being derived for myctophid predation mortality on Antarctic krill (Williams 1985, Pakhomov et al. 1996, Pusch et al. 2004).

The northern Scotia Sea area is one of the most productive regions in the Southern Ocean (Atkinson et al. 2001) and, although generally krill-dominated, has a substantial, depth-stratified myctophid fauna that includes 15 species in 5 genera (Collins et al. 2008a). Here, we investigate the diet of the most abundant myctophid species in the mesopelagic community of the northern Scotia Sea, NW of South Georgia, during the austral autumn. An index of relative importance (IRI), which combines prey occurrence, biomass and numbers, is used to describe the diet, with comparisons undertaken by generating bootstrap confidence intervals. Vertical distributions of prey species are compared with vertical distributions of myctophids to examine the degree of overlap between predators and prey and to determine whether

there is a degree of prey selectivity. The impact of myctophids on assemblages of prey species was estimated and sensitivity analyses were run to provide confidence intervals around these estimates and to highlight parameters that require further attention.

MATERIALS AND METHODS

Oceanographic, acoustic and biological data were collected in the northern Scotia Sea NW of South Georgia during RRS 'James Clark Ross' Cruise 100 between 12 March and 2 April 2004. The study area is between the mean locations of the Antarctic Polar Front (APF) and the Southern Antarctic Circumpolar Current Front (SACCF).

Five acoustic transects, running from east to west, were undertaken with net hauls targeting acoustically detected putative aggregations of fish. In addition, 3 stations (A, B and C) were studied intensively during the cruise (Fig. 1). Stns A and B were within the known foraging area of Antarctic fur seals, with Stn A over the shelf break at approximately 53° 30' S, 37° 30' W (water depth ~1000 m) and Stn B north of the shelf break at approximately 53° 20' S, 38° W (depth ~2500 m). Stn C was located at an oceanic site (depth 3750 m) that has been sampled repeatedly over the past decade by a Longhurst-Hardy Plankton Recorder (LHPR) (Ward et al. 2006).

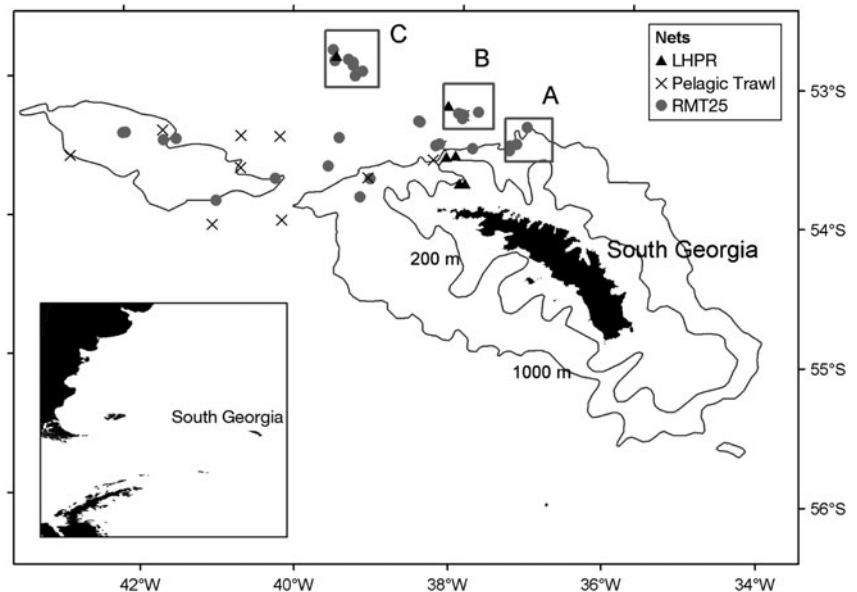


Fig. 1. Locations of 25 m² rectangular midwater trawls (RMT25), pelagic trawls and Longhurst-Hardy Plankton Recorder (LHPR) deployments. Stns A, B and C (boxed areas) show the 3 main oceanographic regions targeted. Stn A was over the shelf break (water depth <1000 m), B was north of the shelf break, (depth around 2500 m) and C was in oceanic water (depth around 3750 m). Insert shows larger geographical area

Net sampling. Targeted net hauls were undertaken along the acoustic transects using an opening and closing 25 m² rectangular midwater trawl (RMT25) and an International Young Gadoid Pelagic Trawl (YGP) (see Collins et al. 2008a). To determine the vertical distribution of the nekton community, Stns A, B & C (Fig. 1) were fished intensively with depth stratified RMT25 hauls (surface to 200 m, 200–400 m, 400–600 m, 600–800 m and 800–1000 m) repeated day and night. The abundance and depth distribution of the zooplankton prey were characterised by oblique LHPR tows to 1000 m made during nighttime and early dawn. The details of hauls and analyses are covered in Ward et al. (2006). Briefly, the LHPR was equipped with a 380 mm diameter nose cone and a 200 µm mesh net and filtering gauzes. The sampler's gauze advance mechanism was set to 90 s, which resulted in a depth resolution of around 20 m per patch. Samples were frozen at –20°C and transported back to the UK where they were thawed and the species identified and enumerated under a stereomicroscope at 10× magnification. Counts were averaged into the same depth horizons as used for the above RMT hauls to enable appropriate comparisons between the sample sets.

Sample processing. Net haul catches were sorted to the lowest taxonomic level using published guides (Hulley 1981, Hulley 1990, Boltovskoy 1999). Fish were separated from invertebrates and measured (standard length, SL, to the nearest mm). Stomachs were dissected from a sub-sample of the 9 most abundant myctophid species (*Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus fraseri*, *G. nicholsi*, *G. braueri*, *Protomyctophum bolini*, *P. choriodon*, *Krefflichthys anderssoni* and *Nannobranchium achirus* (see Collins et al. 2008a), and the stomach with contents frozen for subsequent microscopic analyses. Note that Collins et al. (2008a) incorrectly used the name *Lampamyctus achirus* rather than *Nannobranchium achirus*.

Stomach content analyses. In the laboratory, stomach contents were thawed prior to being sorted into species or taxonomic groups. Contents were identified to the lowest taxonomic level the state of digestion would allow. Individual prey items were weighed. If the prey was highly disaggregated, the weights of the component species were estimated as a proportion of the total contents weight. Items that were completely undigested were considered to represent trawl feeding and were excluded from subsequent analyses.

Diet was expressed using percent mass (%M), percent frequency of occurrence (%F), percent number (%N) and percent Index of Relative Importance (%IRI; see Cortes 1997). Percent mass was based on the weight of prey found in the stomach and not on reconstituted mass. The %IRI was calculated for prey species and %IRI_{DC} for prey categories (amphipods, cope-

pods, decapods, euphausiids, mysids, unidentified crustacea, salps and molluscs). Note that %IRI is not additive, so the sum of the individual species' %IRI values is not the same as the prey category %IRI_{DC} value (see Hansson 1998). The %IRI was calculated as:

$$\%IRI_i = \frac{(\%N_i + \%M_i) \times \%F_i}{\sum_{i=1}^n (\%N_i + \%M_i) \times \%F_i} \times 100 \quad (1)$$

Confidence limits for the %IRI of each prey category were obtained using a bootstrap technique, whereby each species dataset (individual stomachs) was re-sampled (with replacement) 1000 times (see Main et al. 2009).

Analysis of feeding guilds in the myctophid community. Similarities in the diets of the myctophid species were investigated using the Plymouth Routines in Multivariate Ecological Research (PRIMER v.6) software package (Clarke & Warwick 2001, Clarke & Gorley 2006). Values of %IRI for each of the dietary components (excluding unidentified crustaceans) for each fish species were square-root transformed. *Nannobranchium achirus* was excluded because sample numbers were insufficient (see Table 2). Bray-Curtis similarities were then calculated for each pair of fish species to produce a similarity matrix, which was classified by hierarchical agglomerative cluster analysis using the group average linking method. A SIMPER routine was applied to the resulting clusters to determine which prey species contributed to which grouping.

Determination of impact of myctophids on prey species assemblages. We used the following function to evaluate the proportion of the productivity of different prey species consumed by each myctophid species:

$$I_{i,j} = \frac{N_{i,j} \cdot C_i \cdot P_j \cdot 24}{Z_i \cdot F_i} / G \quad (2)$$

where $I_{i,j}$ is the proportion of the production of prey species i consumed by myctophid species j per day, $N_{i,j}$ is the number of individuals of prey species i in the stomach of myctophid species j , C_i is the carbon mass of species i , P_j is the depth-integrated concentration (ind. m⁻²) of predator species j , G is the gut passage time (in h), Z_i is the depth-integrated concentration (ind. m⁻²) of prey species i and F_i is the growth rate of species i (µg C d⁻¹).

There are a number of ways of calculating values for these parameters. Our approach was to run the calculation of each prey species i consumed by each myctophid species j 3 times: the first time to derive our best estimate, the second time to derive an upper bound value and the third time to derive a lower bound value. The upper bound is based on (1) our upper estimate of the number of prey items i eaten by myctophid spe-

cies j , (2) our upper estimated concentration of j , (3) our lower estimated concentration of i and (4) the fastest gut passage time. Conversely, the lower bound value combines (1) our lower estimate of the number of species i in the stomachs of myctophid species j , (2) our lower estimated concentration of j , (3) our upper estimated concentration of i and (4) the slowest gut passage time. We detail below how these values were derived for each parameter:

Numbers of individuals of prey species i in myctophid j ($N_{i,j}$): The dataset was restricted to the 9 most common taxa found in myctophid stomachs: the amphipod *Themisto gaudichaudii*, the euphausiids *Euphausia frigida*, *E. superba* and *Thysanoessa* spp., the copepods *Metridia* spp., *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus*, and salps. Seven myctophid species were considered in our analysis: *Electrona carlsbergi*, *E. antarctica*, *Gymnoscopelus fraseri*, *G. nicholsi*, *G. braueri*, *Protomyctophium bolini*, and *P. choriodon*. *Krefflichthys anderssoni* and *Nannobranchium achireus* were excluded due to small sample size.

The data were non-normally distributed, so a non-parametric bootstrapping technique was used to generate upper and lower bounds. For each myctophid species, 30 individuals were randomly extracted and the average number of items of each prey species in this random data set was determined. This process was repeated 100 times. The median of this series was used as our best estimate value, the 25th percentile value as the lower bound and the 75th percentile value as the upper bound.

Depth-integrated concentration of myctophid species (P_j): Myctophid concentrations were evaluated from RMT25 catches. Over the course of the cruise, 4 major RMT25 sampling series were carried out, 2 during the day and 2 at night. During each series, the entire water column between 0 and 1000 m was sampled in 200 m depth intervals. Net catch concentrations (ind. m^{-3}) were multiplied by the respective depth interval (m) and combined to give a depth integrated concentration per net (ind. m^{-2}) between 0 and 1000 m for the 4 net sampling series. Our best estimate value was the median of the 4 values, with the 75th percentile the upper bound and the 25th percentile the lower bound.

Depth-integrated concentration of prey species (Z_j): Two LHPR deployments between 0 and 1000 m were carried out during the cruise. The LHPR provides a depth resolution of between 10 and 20 m, with each interval being sampled for an equal amount of time, filtering similar volumes of water. Accordingly, data were averaged over all depth-discrete samples to obtain a mean concentration (ind. m^{-3}), and then multiplied by 1000 to give a depth-integrated concentration (ind. m^{-2}). Our best estimate was determined from averaging concentrations of each respective zooplank-

ton species over the 2 deployments. The lower of the 2 values was used as the lower bound value, the higher value as the upper bound value.

Growth rate of prey species (F_j): Species-specific growth rates ($\mu g C d^{-1}$) were estimated from direct measurements of the carbon weight, multiplied by the weight-specific growth rate of each species according to Hirst et al. (2003). Carbon weight measurements were made on 5 to 10 individuals of each species. Hirst et al. (2003) provided functions to estimate the weight-specific growth rate of zooplankton based on individual carbon weight and temperature ($\pm 5^\circ C$). For the copepod species (*Calanoides acutus*, *Calanus simillimus* and *Rhincalanus gigas*), we used a function appropriate for adult broadcast spawning copepods at $5^\circ C$; for the euphausiids (*Euphausia superba*, *E. frigida* and *Thysanoessa* spp.) and the amphipod *Themisto gaudichaudii*, a function covering all crustaceans (excluding copepods) at $5^\circ C$ was used, while a function for Thaliaceans at $15^\circ C$ was used for the salps (a function for $5^\circ C$ was not available given the lack of suitable data at lower temperatures).

Gut passage time (G): Pakhomov et al. (1996) provided data on the gut passage time of a number of different planktivorous fish species mainly feeding on mesozooplankton species from a variety of locations with different ambient temperatures. Our examination of these data showed that there was distinct temperature dependence in the gut passage time of planktivorous fish that was best explained by a negative exponential curve, with an intercept (c) lower than zero. An exponential model that includes a term for the lower temperature limit (c) is:

$$y = c + a^{(-bx)} \quad (3)$$

The model is fitted using least squares, i.e. estimates of a , b and c are found that minimise the sums of squares of the deviations from the fitted model. A conspicuous feature of the relationship between gut passage time and temperature is the increased variation at lower temperature. This was allowed for by using weighted least squares in which the more variable points are given less weight. Here, we assumed that the standard deviation of passage time increases in proportion to the mean passage time. The model was fitted using the statistical package Genstat, giving values and standard errors (SE) of: $a = 24.92$ (SE = 5.72), $b = 0.265$ (SE = 0.065), $c = 4.50$ (SE = 0.630). Fitted values and 95% confidence limits were calculated for temperatures in the range of -1 to $22^\circ C$ in steps of $0.1^\circ C$ (Fig. 2).

Excluding the surface mixed layer (between 3 and $4^\circ C$), temperature profiles at the time of the study (Collins et al. 2008a) varied from around 1.3 to $1.9^\circ C$. Taking a characteristic temperature of $1.75^\circ C$ would

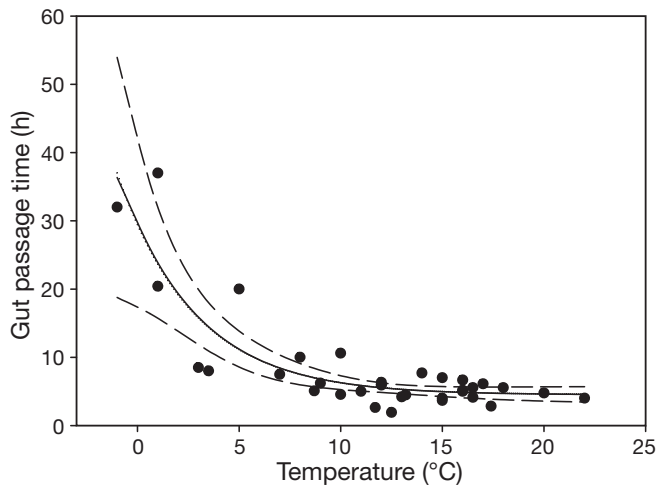


Fig. 2. Exponential curve (solid line) fitted to the relationship between gut passage time and temperature in planktivorous fishes (with lower asymptote), with upper and lower 95% confidence interval (dashed lines). Data from Pakhomov et al. (1996)

equate to a gut passage time of 20.2 h, which we applied as our best estimate value. 95% confidence intervals fitted to Eq. (3) give a fastest gut passage time of 14.3 h and a slowest gut passage time of 26.0 h. This level of variance in passage time simulates to a degree the variance in gut passage time between prey species, as described by Andersen (1999) and Andersen & Beyer (2008). More intensive investigations of species-specific gut passage times for Southern Ocean zooplankton would be needed to constrain these estimates further.

RESULTS

Myctophid distribution

A detailed analysis of the distribution of the myctophid species is given in Collins et al. (2008a) and only nighttime vertical distribution is illustrated here (Fig. 3). Three species had a restricted vertical distribution, with *Electrona carlsbergi* and *Protomyctophum bolini* caught primarily between 200 and 400 m and *Protomyctophum choriodon* caught in the upper 200 m. *Nannobranchium achirus* was primarily caught below 600 m, whilst all other species were caught throughout the sampled depth range. Note that sampling depths were arbitrary and thus may not have resolved vertical distributions of the species.

Abundance and vertical distribution of zooplankton

Best-estimates of macrozooplankton depth-integrated abundance varied between 21 ind. m⁻² for *Euphausia superba* to 31500 ind. m⁻² for *Thysanoessa* spp. (Table 1). The euphausiids were mainly found in the upper water column above 600 m (Fig. 4). *Thysanoessa* spp. were found mainly concentrated above 200 m. *Euphausia frigida* and *E. superba* were found a little deeper in the water column, at a modal depth between 200 and 400 m. The amphipod *Themisto gaudichaudii*, which had a depth-integrated abundance of 364 ind. m⁻², was principally found in the upper 200 m. Salps were found mainly above 400 m and had a depth-integrated abundance of 2688 ind. m⁻².

Copepods occurred at higher concentrations than macrozooplankton, with best estimates of depth-integrated concentrations typically ranging between 10⁵ and 10⁶ ind. m⁻² (Table 1). The numerically dominant species were *Oithona* spp., *Ctenocalanus* spp.,

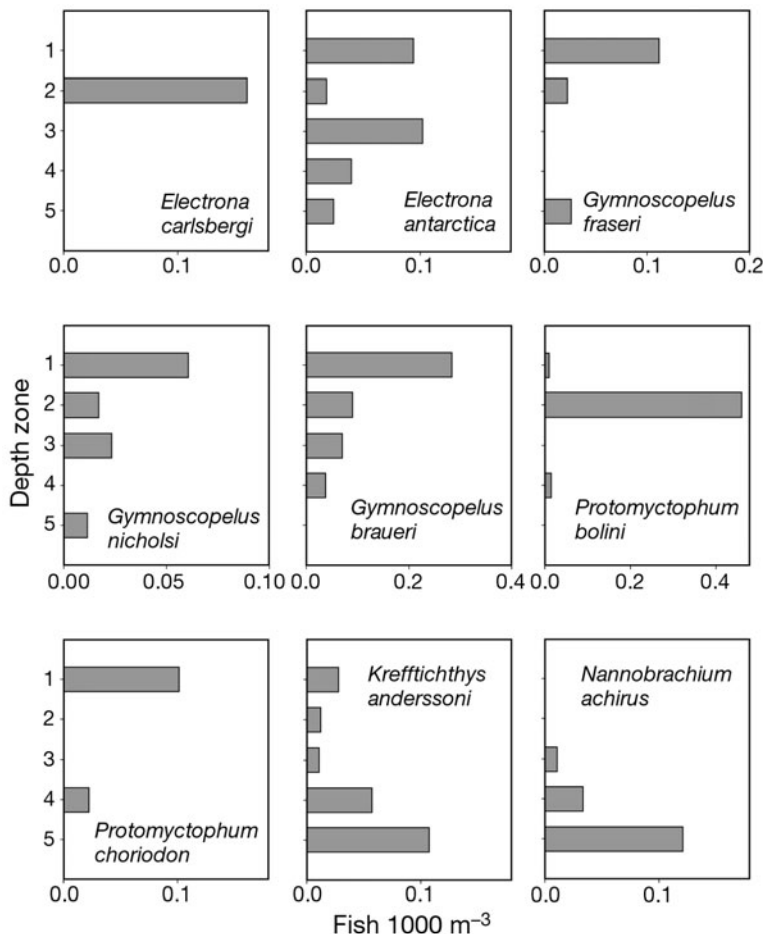


Fig. 3. Nighttime vertical distribution of myctophid fish caught in non-target RMT25 net hauls. Depth zones are 1: 0–200 m; 2: 200–400 m; 3: 400–600 m; 4: 600–800 m; 5: 800–1000 m. Modified from Collins et al. (2008a)

Table 1. Depth-integrated (0–1000 m) net-catch concentration of the most abundant fish and zooplankton taxa NW of South Georgia in March–April 2004. There are 3 estimates for each prey species, representing a best estimate (median, **bold**) and the lower and upper bounds (25th and 75th percentile respectively).

Taxon	Sampling device	Concentration (ind. m ⁻²)		
		Lower	Best	Upper
<i>Electrona carlsbergi</i>	RMT25	0.02	0.04	0.06
<i>E. antarctica</i>	RMT25	0.04	0.05	0.06
<i>Gymnoscopelus fraseri</i>	RMT25	0.03	0.05	0.07
<i>G. nicholsi</i>	RMT25	0.02	0.02	0.02
<i>G. braueri</i>	RMT25	0.04	0.05	0.09
<i>Protomyctophum bolini</i>	RMT25	0.06	0.10	0.13
<i>P. choriodon</i>	RMT25	0.02	0.02	0.03
<i>Themisto gaudichaudii</i>	LHPR	51.8	364.4	677.0
<i>Euphausia frigida</i>	LHPR	303.4	1124.1	1944.7
<i>E. superba</i>	LHPR	0.00	21.3	42.6
<i>Thysanoessa</i> spp.	LHPR	29603.5	31476.7	33350.0
<i>Metridia</i> spp.	LHPR	6104.4	1126311.1	2246517.8
<i>Calanoides acutus</i>	LHPR	44320.9	45910.9	47501.0
<i>Rhincalanus gigas</i>	LHPR	125101.3	172712.3	220323.2
<i>Calanus simillimus</i>	LHPR	41091.1	46925.1	52759.1
Salps	LHPR	1392.6	2688.6	3984.7

Oncaea spp. and *Microcalanus* spp. (Fig. 4). *Oithona* spp. was most numerous between 200 and 400 m whilst *Oncaea* spp. was concentrated in deeper water (600 to 1000 m). *Ctenocalanus* spp. was found throughout the water column whilst *Calanus propinquus* had a bimodal peak, one at 0 to 200 m and another between 800 and 1000 m. The large predatory copepod *Paraeuchaeta antarctica* was found in low numbers mainly between 200 and 400 m (Fig. 4). The larger, biomass-dominant copepods *Rhincalanus gigas* and *Calanoides acutus* were found at all depths but were concentrated at around 400 to 600 m and 800 to 1000 m, respectively. *Calanus simillimus* was concentrated at the surface. *Metridia* spp. were evenly distributed throughout the water column with slightly higher abundances in the upper 400 m.

Dietary composition

Stomach contents of 718 fish were examined microscopically (Table 2). Size ranges and depth of sampled fish reflected the size and vertical distribution of captured fish (see Table 1 in Collins et al. 2008a). Planktonic crustaceans dominated the diets of all myctophid species (Tables 3 to 6; Fig. 5) but, in some cases, stomach contents were too far digested to identify the specific composition. Note the large error bars around the % IRI_{DC} values for the prey categories of *Krefflichthys anderssoni* and *Nannobranchium achirus* (Fig. 5), which reflect uncertainty about the results as a consequence of the small sample sizes (Table 2).

The diet of *Electrona antarctica* (47 to 112 mm SL) was dominated by amphipods, notably the hyperiid amphipod *Themisto gaudichaudii* (Table 3; Fig. 5). Although *E. antarctica* was spread throughout the water column, *T. gaudichaudii* was found predominantly in the upper 200 m, which *E. antarctica* appeared to occupy during the hours of darkness only. *Electrona carlsbergi*, by contrast, was found only in the 200 to 400 m depth horizon and had a more limited size range (71 to 93 mm SL). The main prey of *E. carlsbergi* were copepods (*Metridia* spp. and *Rhincalanus gigas*), euphausiids, the amphipod *T. gaudichaudii* and salps, with *T. gaudichaudii* (19% IRI) the single most important species (Table 3). *E. carlsbergi* was the only species found to eat significant quantities of salps.

The 3 species of *Gymnoscopelus* had distinctly different diets (Table 4; Fig. 5). *Gymnoscopelus fraseri* (46 to 112 mm SL; mean 77 mm) was mostly caught in the upper 400 m and had a diet dominated by copepods, with *Metridia* spp. (mostly *M. gerlachei*) making up 79% IRI and *Rhincalanus gigas* 7% IRI. The slightly larger conspecific *Gymnoscopelus braueri* (46 to 133 mm

Table 2. Myctophid fish sampled for stomach analysis. Numbers of individuals sampled in each depth layer, with mean size and size range; SL given as mean (range)

Fish species	Depth layer (m)						Total	SL (mm)
	0–200	200–400	400–600	600–800	800–1000	0–1000		
<i>Electrona carlsbergi</i>	0	158	0	0	0	0	158	80 (71–93)
<i>Electrona antarctica</i>	21	23	30	14	2	36	126	84 (47–112)
<i>Gymnoscopelus fraseri</i>	25	26	5	0	0	0	56	77 (46–112)
<i>Gymnoscopelus nicholsi</i>	25	59	5	0	0	0	89	111 (52–149)
<i>Gymnoscopelus braueri</i>	16	48	20	6	0	8	98	103 (46–133)
<i>Protomyctophum bolini</i>	2	58	1	0	0	0	61	49 (38–78)
<i>Protomyctophum choriodon</i>	53	31	0	0	0	0	84	73 (51–85)
<i>Krefflichthys anderssoni</i>	4	2	12	5	0	7	30	39 (17–73)
<i>Nannobranchium achirus</i>	0	0	1	3	4	8	16	133 (117–140)

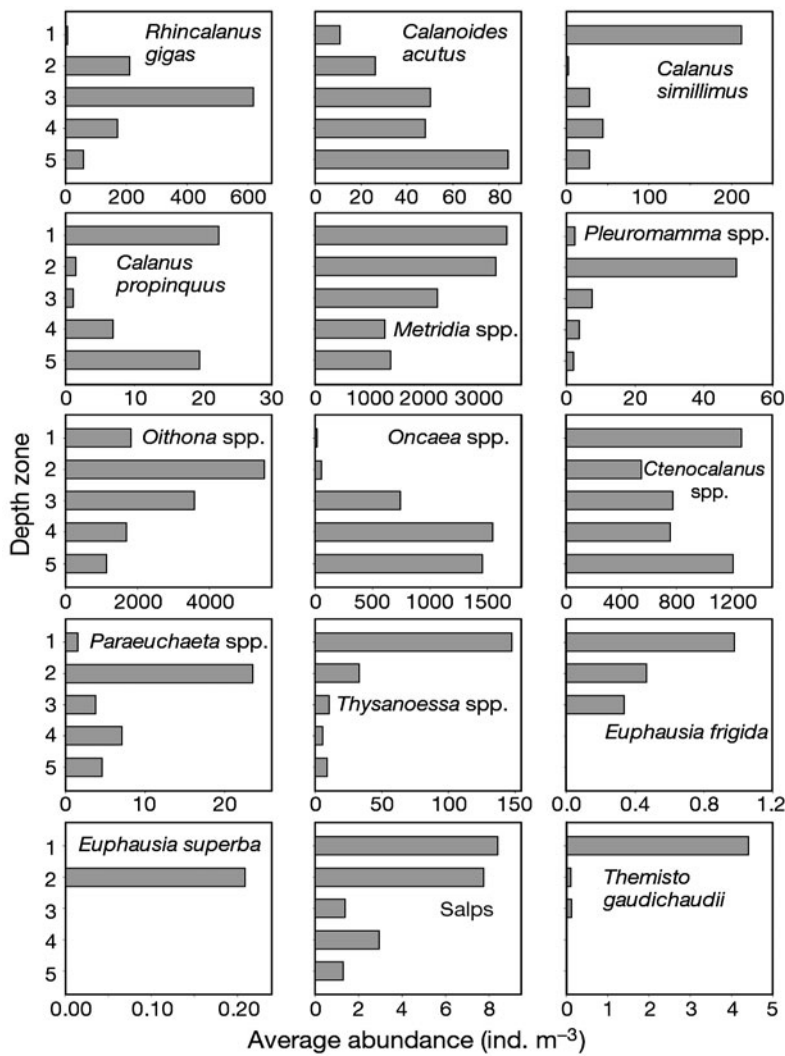


Fig. 4. Depth distribution of the key zooplankton species in the diets of myctophids in this study, and of the biomass-dominant zooplankton. Depth zones as in Fig. 3

SL; mean 103 mm) reached its maximum abundance in the upper 200 m at night and principally consumed the amphipod *Themisto gaudichaudii* (56% IRI) and Antarctic krill *Euphausia superba* (10% IRI), both of which were mainly caught in the surface waters. *Antarctomysis* spp. (7.8% IRI) and the copepods *Metridia* spp. and *R. gigas* (1% IRI combined) also made small contributions to the diet. *Gymnoscopelus nicholsi* was one of the larger myctophid species sampled (52 to 144 mm SL; mean 111 mm) and, although caught throughout the water column, reached its maximum abundance in the upper 200 m at night. The diet was varied and included euphausiids, copepods and amphipods with *Metridia* spp., *T. gaudichaudii*, and *Euphausia frigida* the most common prey species. *E. superba* was also consumed.

Protomyctophum bolini (38 to 78 mm SL; mean 49 mm) was mainly caught between 200 and 400 m and fed mostly on copepods and euphausiids (Table 5; Fig. 5). The principal prey species were the copepod *Metridia* spp. and *Euphausia frigida*, which were both abundant in the same depth zone as the fish. *Protomyctophum choriodon* (51 to 85 mm SL; mean 73 mm) was found mainly in the top 200 m and was primarily a copepod consumer (Table 5), particularly of *Metridia* spp. and *Calanoides acutus* (38 and 27% IRI, respectively), but also consumed *Rhincalanus gigas* and *Calanus simillimus* (10 and 6% IRI, respectively).

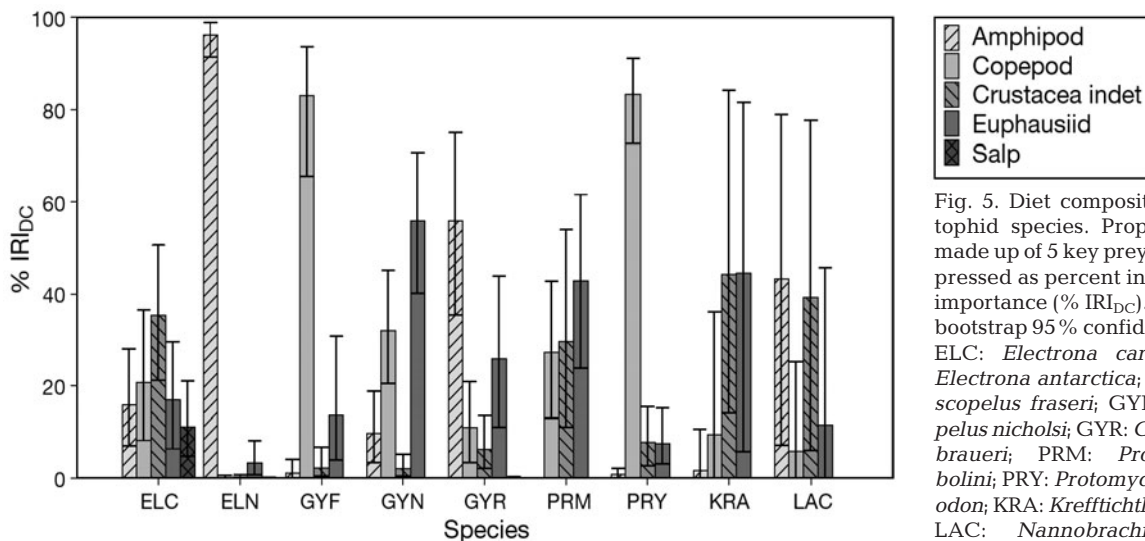


Fig. 5. Diet composition of 9 myctophid species. Proportion of diet made up of 5 key prey categories expressed as percent index of relative importance (% IRI_{DC}). Error bars are bootstrap 95% confidence intervals. ELC: *Electrona carlsbergi*; ELN: *Electrona antarctica*; GYF: *Gymnoscopelus fraseri*; GYN: *Gymnoscopelus nicholsi*; GYR: *Gymnoscopelus braueri*; PRM: *Protomyctophum bolini*; PRY: *Protomyctophum choriodon*; KRA: *Krefflichthys anderssoni*; LAC: *Nannobranchium achirus*. Crustacea indet. represents a group with visibly crustacean characters but too digested to identify further

Table 3. *Electrona carlsbergi* and *Electrona antarctica*. Diet composition. Percent number (N), mass (M), frequency of occurrence (F) and index of relative importance (IRI) of items of each prey species are given with sums for prey categories. See 'Materials and methods' for calculation of % IRI. Note that % occurrence and % IRI are not additive and that grouping the prey into categories influences the resulting %IRI_{DC} values

Prey	<i>Electrona carlsbergi</i>				<i>Electrona antarctica</i>			
	% N	% M	% F	% IRI	% N	% M	% F	% IRI
Amphipoda								
<i>Themisto gaudichaudii</i>	9.61	26.96	20.89	19.48	70.97	80.65	84.25	98.78
Total	9.61	26.96	20.89	15.47	70.97	80.65	84.25	96.51
Copepoda								
<i>Calanoides acutus</i>	13.92	1.72	6.33	2.53	0.00	0.00	0.00	0.00
<i>Calanus propinquus</i>	0.20	0.02	0.63	0.00	0.00	0.00	0.00	0.00
<i>Calanus simillimus</i>	10.98	1.36	3.80	1.20	1.21	0.04	0.79	0.01
<i>Heterorhabdus</i> spp.	0.20	0.02	0.63	0.00	0.00	0.00	0.00	0.00
<i>Metridia</i> spp.	10.00	0.40	14.56	3.86	0.00	0.00	0.00	0.00
<i>Oithona</i> spp.	0.20	0.01	0.63	0.00	0.00	0.00	0.00	0.00
<i>Paraeuchaeta</i> spp.	0.78	0.16	2.53	0.06	3.22	0.60	3.15	0.06
<i>Pleuromamma</i> spp.	0.59	0.07	1.90	0.03	0.00	0.00	0.00	0.00
<i>Rhincalanus gigas</i>	10.00	2.06	8.23	2.53	0.00	0.00	0.00	0.00
Unidentified copepods	0.20	0.01	0.63	0.00	0.00	0.00	0.00	0.00
Total	47.06	5.85	20.25	21.71	4.44	0.64	3.94	0.15
Euphausiacea								
<i>Euphausia frigida</i>	0.20	0.40	0.63	0.01	1.61	3.64	2.36	0.10
<i>Euphausia superba</i>	0.59	7.15	1.90	0.37	1.61	4.46	1.57	0.07
<i>Euphausia triacantha</i>	0.00	0.00	0.00	0.00	1.61	4.01	2.36	0.10
<i>Thysanoessa</i> spp.	0.78	0.54	2.53	0.09	0.40	0.09	0.79	0.00
Unidentified euphausiids	8.24	25.05	15.19	12.90	13.31	3.95	4.72	0.63
Total	9.80	33.16	20.25	17.62	18.55	16.16	11.81	3.10
Unidentified crustaceans								
Total	14.51	26.82	41.14	34.44	2.82	2.47	5.51	0.22
Salps								
Total	19.02	7.21	20.25	10.76	3.23	0.09	0.79	0.02

The sample size of both *Kreftlichthys anderssoni* and *Nannobranchium achirus* was small, and a large proportion of the stomach contents could not be identified beyond the classification of Crustacea (Table 6). *K. anderssoni*, which was most abundant in the 600 to 1000 m depth layer, was one of the smaller species studied (17 to 73 mm SL; mean 39 mm) and fed principally on the euphausiid *Thysanoessa* spp. (24% IRI), which was found predominately in the top 400 m. *N. achirus* (mean SL 133 mm) was mainly caught deeper than 600 m and principally ate *Themisto gaudichaudii* (48% IRI), along with some Antarctic krill (3% IRI).

Grouping all myctophids species together, there was a clear change in diet with size (Fig. 6). Smaller fish (< 75 mm SL) consumed significantly more copepods (62% IRI_{DC}) than the larger size classes, with the older copepodite stages predominating. Specifically, most of the consumed *Calanoides acutus* were Copepodite stage CV, *Metridia* spp. were Stage CVI females, *Rhincalanus gigas* were Stage CIII to CVI females and *Calanus simillimus* were Stage CV and CVI males and females. There was a greater range of *Paraeuchaeta antarctica* developmental stages, with stages from CII upwards being found, although Stage CV and CVI

females and males were the most abundant. Amphipods, such as *Themisto gaudichaudii*, were the most abundant dietary item (43% IRI_{DC}) in medium-sized (76 to 100 mm SL) myctophids, while copepods (43% IRI_{DC}) were also taken. Euphausiids, including Antarctic krill, were only a major component (45% IRI_{DC}) of the diet of fish larger than 100 mm SL.

Feeding guild analysis

Hierarchical cluster analysis (excluding the prey category 'unidentified crustacea') produced 5 clusters at the 60% similarity level; however, 2 of them (Clusters 2 and 5) consisted of single species (Fig. 7). Cluster 2 grouped *Gymnoscopelus braueri* and *Electrona antarctica* together in a cluster dominated by the consumption of *Themisto gaudichaudii* (83% contribution). Clusters 3 and 4 were both dominated by copepod feeders, with *Gymnoscopelus fraseri* and *Protomyctophum choriodon* in a cluster dominated by *Metridia* spp. (40%) and *Rhincalanus gigas* (16%) and *Gymnoscopelus nicholsi* and *Protomyctophum bolini* in a cluster that mainly consumed *Metridia* spp. (32%) and *Euphausia frigida* (21%).

Table 4. *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi* and *Gymnoscopelus braueri*. Diet composition. Percent number (N), mass (M) frequency of occurrence (F) and index of relative importance (IRI) of items of each prey species are given with sums for prey categories. See 'Materials and methods' for calculation of % IRI. Note that % occurrence and % IRI are not additive and that grouping the prey into categories influences the resulting IRI_{DC} values

Prey	<i>Gymnoscopelus fraseri</i>				<i>Gymnoscopelus nicholsi</i>				<i>Gymnoscopelus braueri</i>			
	% N	% M	% F	% IRI	% N	% M	% F	% IRI	% N	% M	% F	% IRI
Amphipoda												
<i>Themisto gaudichaudii</i>	0.63	8.23	8.93	1.32	3.98	29.47	24.72	19.48	28.51	43.55	47.96	73.49
Total	0.63	8.23	8.93	0.88	3.98	29.47	24.72	9.36	28.51	43.55	47.96	56.03
Copepoda												
<i>Aetideus</i> spp.	0.00	0.00	0.00	0.00	0.12	0.03	1.12	0.00	0.00	0.00	0.00	0.00
<i>Calanoides acutus</i>	2.20	2.98	16.07	1.39	2.65	0.46	13.48	0.99	0.80	0.04	1.02	0.02
<i>Calanus propinquus</i>	0.08	0.11	1.79	0.01	0.24	0.04	2.25	0.01	0.00	0.00	0.00	0.00
<i>Calanus simillimus</i>	1.18	1.60	12.50	0.58	6.39	1.00	17.98	3.13	3.61	0.20	5.10	0.41
<i>Candacia</i> sp.	0.08	0.21	1.79	0.01	0.36	0.09	2.25	0.02	0.40	0.04	1.02	0.01
<i>Drepanopus forcipatus</i>	0.08	0.04	1.79	0.00	0.00	0.00	0.00	0.00	0.80	0.01	1.02	0.02
<i>Gaidius tenuispinus</i>	0.08	0.11	1.79	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Haloptolis</i> sp.	0.08	0.11	1.79	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Heterorhabdus</i> spp.	0.31	0.43	3.57	0.04	0.96	0.15	3.37	0.09	0.00	0.00	0.00	0.00
<i>Metridia</i> spp.	82.20	33.58	41.07	79.59	38.55	2.00	35.96	34.36	20.48	0.37	9.18	4.07
<i>Oithona</i> spp.	0.00	0.00	0.00	0.00	0.12	0.01	1.12	0.00	0.00	0.00	0.00	0.00
<i>Paraeuchaeta</i> spp.	0.86	4.18	8.93	0.75	0.60	0.28	5.61	0.08	2.81	0.26	2.04	0.13
<i>Pleuromamma</i> spp.	0.55	0.64	7.14	0.14	1.45	0.17	7.87	0.30	2.01	0.09	5.10	0.23
<i>Rhincalanus gigas</i>	4.00	12.30	25.00	6.82	6.87	1.71	21.35	4.31	7.63	0.58	8.16	1.43
Unidentified calanoid copepods	1.10	1.49	1.79	0.08	0.48	0.05	3.37	0.04	0.00	0.00	0.00	0.00
Unidentified copepods	0.00	0.00	0.00	0.00	0.24	0.05	1.12	0.01	1.20	1.00	3.06	0.14
Total	92.78	57.77	50.00	84.11	59.04	6.03	43.82	32.28	39.76	2.59	16.33	11.21
Decapoda												
Unidentified decapods	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.93	1.02	0.03
<i>Gennadus</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.20	3.90	2.04	0.22
Total	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.61	4.84	3.06	0.32
Euphausiacea												
<i>Euphausia frigida</i>	1.49	3.79	10.71	0.95	14.34	15.04	20.22	14.00	2.81	0.56	4.08	0.29
<i>Euphausia superba</i>	0.00	0.00	0.00	0.00	1.08	22.66	6.74	3.77	5.62	36.58	11.22	10.07
<i>Euphausia triacantha</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.40	0.19	1.02	0.01
<i>Thysanoessa</i> spp.	1.65	13.48	7.14	1.81	9.28	6.83	15.73	5.97	5.22	0.98	6.12	0.81
Unidentified euphausiids	2.20	8.51	19.64	3.52	7.83	11.55	20.22	9.23	3.61	3.22	5.10	0.74
Total	5.33	25.78	37.50	13.04	32.53	56.08	56.18	56.35	17.67	41.53	27.55	26.44
Mysidacea												
<i>Antarctomysis</i> spp.	0.86	7.98	19.64	2.91	3.73	7.32	15.73	4.10	9.24	7.11	22.45	7.80
Total	0.86	7.98	19.64	1.94	3.73	7.32	15.73	1.97	9.24	7.11	22.45	5.95
Ostracoda												
Total	0.39	0.25	0.00	0.03	0.00	0.00	0.00	0.00	0.40	0.07	0.00	0.01
Unidentified crustaceans												
Total	0.00	0.00	0.00	0.00	0.48	1.06	2.25	0.04	0.00	0.00	1.02	0.00
Mollusca												
Thecate pteropod	0.00	0.00	0.00	0.00	0.24	0.04	2.25	0.02	1.20	0.04	1.02	0.03
Total	0.00	0.00	3.57	0.00	0.24	0.04	2.25	0.01	1.20	0.04	1.02	0.02
Salps												
Total	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.61	0.28	1.02	0.03

Consumption of prey productivity

The majority of myctophid stomachs examined contained more than one species of prey, with some fish containing 5 or more prey species. Where a prey species was present in the stomach of a myctophid, it was commonly found in numbers >10 or more. However, when averaged for a particular myctophid species, the

number of prey items frequently became <1 because of the large numbers of stomachs from which a prey species was absent (Table 7). The exception were some of the copepod species, most notably *Metridia* spp., which were found in relatively high numbers in the stomachs of *Gymnoscopelus fraseri*, *Krefftichthys anderssoni* and *Protomyctophum choriodon*, such that average prey numbers per stomach were >1. The same

Table 5. *Protomyctophum bolini* and *Protomyctophum choriodon*. Diet composition. Percent number (N), mass (M) frequency of occurrence (F) and index of relative importance (IRI) of items of each prey species are given with sums for prey categories. See 'Materials and methods' for calculation of % IRI. Note that % occurrence and % IRI are not additive and that grouping the prey into categories influences the resulting IRI_{DC} values

Prey	<i>Protomyctophum bolini</i>				<i>Protomyctophum choriodon</i>			
	% N	% M	% F	% IRI	% N	% M	% F	% IRI
Ampipoda								
<i>Themisto gaudichaudii</i>	0.00	0.00	0.00	0.00	0.65	5.10	14.29	1.34
Total	0.00	0.00	0.00	0.00	0.65	5.10	14.29	0.85
Copepoda								
<i>Calanoides acutus</i>	1.02	0.41	1.64	0.05	27.89	22.11	33.33	27.18
<i>Calanus propinquus</i>	0.51	0.20	1.64	0.02	0.19	0.15	3.57	0.02
<i>Calanus simillimus</i>	3.57	1.42	4.92	0.52	8.89	6.00	23.81	5.78
<i>Candacia</i> sp.	0.00	0.00	0.00	0.00	0.14	0.19	3.57	0.02
<i>Drepanopus forcipatus</i>	0.00	0.00	0.00	0.00	0.19	0.05	2.38	0.01
<i>Gaidius tenuispinus</i>	0.00	0.00	0.00	0.00	0.05	0.04	1.19	0.00
<i>Heterorhabdus</i> spp.	1.02	1.29	1.64	0.08	0.19	0.15	3.57	0.02
<i>Metridia</i> spp.	44.90	4.40	18.03	18.97	40.27	11.95	44.05	37.52
<i>Paraeuchaeta</i> spp.	1.53	2.78	4.92	0.23	1.21	1.67	10.71	0.50
<i>Pleuromamma</i> spp.	1.02	0.41	3.28	0.10	0.51	0.42	11.90	0.18
<i>Rhincalanus gigas</i>	1.02	0.68	3.28	0.12	7.50	12.58	29.76	9.74
<i>Scaphocalanus</i> spp.	0.00	0.00	0.00	0.00	0.19	0.15	1.19	0.01
<i>Scolecithricella</i> spp.	0.00	0.00	0.00	0.00	0.65	0.52	1.19	0.02
Copepoda unid.	0.51	0.20	1.64	0.02	3.82	3.01	8.33	0.93
Calanoid copepods unid.	2.04	1.69	3.28	0.26	0.84	1.36	1.19	0.04
Total	57.14	13.46	31.15	27.96	92.50	60.35	53.57	84.64
Euphausiacea								
<i>Euphausia frigida</i>	12.76	34.10	22.95	22.94	0.98	3.76	5.95	0.46
<i>Thysanoessa</i> spp.	6.12	5.55	9.84	2.45	2.65	8.01	23.81	4.14
Euphausiid unid.	6.12	11.98	14.75	5.70	0.84	2.79	10.71	0.63
Total	25.00	51.62	44.26	43.12	4.47	14.56	36.90	7.26
Mysidacea								
<i>Antarctomysis</i> spp.	0.00	0.00	0.00	0.00	0.23	1.67	3.57	0.11
Total	0.00	0.00	4.92	0.00	0.23	1.67	3.57	0.07
Ostracoda								
<i>Gigantocypris</i> spp.	0.00	0.00	0.00	0.00	0.05	0.01	1.19	0.00
Unidentified ostracods	3.06	0.54	4.76	0.38	0.00	0.00	0.00	0.00
Total	3.06	0.54	4.76	0.23	0.05	0.01	1.19	0.00
Unidentified crustaceans								
Total	14.80	34.37	45.90	48.15	2.05	18.06	34.52	11.32
Total	14.80	34.37	45.90	28.69	2.05	18.06	34.52	7.18
Mollusca								
<i>Limacina</i> spp.	0.00	0.00	0.00	0.00	0.05	0.24	1.19	0.01
Total	0.00	0.00	0.00	0.00	0.05	0.24	1.19	0.00

was true of *Calanoides acutus*, *Rhincalanus gigas* and *Calanus simillimus* in the stomachs of *P. choriodon*. Average numbers >1 were also found for the euphausiid *Thysanoessa* spp. in the stomachs of *K. anderssoni* and *Gymnoscopelus nicholsi*.

The best estimates of the average depth-integrated concentration of the 9 myctophid species in the upper 1000 m of the water column around South Georgia ranged between 0.02 and 0.1 ind. m⁻² (Table 1; see also Collins et al. 2008a). As a best estimate, myctophids consumed up to 0.02% of the daily productivity (in terms of C m⁻² d⁻¹) of key copepod species in the NW South Georgia region (Table 8). *Protomyctophum choriodon* had the largest overall

impact, taking 0.01% d⁻¹ of the *Calanoides acutus* production.

The impact of myctophid predation on macrozooplankton production was greater than that of copepods (Table 8). The myctophid community consumed a best estimate of 3.85% of *Themisto gaudichaudii* daily production and 6.26% of *Euphausia superba* daily production. The former was impacted most by *Electrona antarctica* and *Gymnoscopelus braueri*, while *G. braueri* and *Gymnoscopelus nicholsi* had the largest impact on the latter. Myctophids consumed a lower proportion of *Euphausia frigida* and *Thysanoessa* spp. productivity, accounting for 0.06% d⁻¹ and 0.02% d⁻¹, respectively. The impact of myctophids on salps was negligible.

Table 6. *Kreftlichthys anderssonii* and *Nannobranchium achirus*. Diet composition. Percent number (N), mass (M) frequency of occurrence (F) and index of relative importance (IRI) of items of each prey species are given with sums for prey categories. See 'Materials and methods' for calculation of % IRI. Note that % occurrence and % IRI are not additive and that grouping the prey into categories influences the resulting IRI_{DC} values

Prey	<i>Kreftlichthys anderssonii</i>				<i>Nannobranchium achirus</i>			
	% N	% M	% F	% IRI	% N	% M	% F	% IRI
Ampipoda								
<i>Themisto gaudichaudii</i>	1.38	10.70	3.45	1.19	20.83	42.38	25.00	34.35
<i>Vibilia antarctica</i>	0.00	0.00	0.00	0.00	4.17	2.65	6.25	0.93
Amphipoda	0.00	0.00	0.00	0.00	8.33	6.51	6.25	2.02
Total	1.38	10.70	3.45	0.82	33.33	51.54	37.50	48.04
Copepoda								
<i>Calanoides acutus</i>	1.38	1.55	3.45	0.29	0.00	0.00	0.00	0.00
<i>Calanus simillimus</i>	10.09	3.66	3.45	1.35	0.00	0.00	0.00	0.00
<i>Candacia</i> sp.	0.00	0.00	0.00	0.00	4.17	0.43	6.25	0.62
<i>Metridia</i> spp.	21.56	2.61	6.90	4.75	12.50	0.26	6.25	1.73
Unidentified copepods	0.46	0.50	3.45	0.09	4.17	3.94	6.25	1.10
Total	33.49	8.31	10.34	8.51	20.83	4.62	12.50	4.80
Euphausiacea								
<i>Euphausia frigida</i>	9.17	6.87	3.45	1.58	4.17	0.43	6.25	0.62
<i>Euphausia superba</i>	0.00	0.00	0.00	0.00	4.17	17.55	6.25	2.95
<i>Thysanoessa</i> spp.	38.99	42.24	10.34	23.97	4.17	1.46	6.25	0.76
Unidentified euphausiids	7.34	10.92	6.90	3.59	0.00	0.00	0.00	0.00
Total	55.50	60.03	20.69	47.06	12.50	19.43	18.75	9.04
Unidentified crustaceans	9.63	20.95	72.41	63.18	33.33	24.40	43.75	54.91
Total	9.63	20.95	72.41	43.61	33.33	24.40	43.75	38.12

DISCUSSION

The present study provides the first detailed analysis of myctophid diets from the northern Scotia Sea and represents one of the most detailed studies undertaken in the Southern Ocean. However, it is important to recognise the spatial and temporal limitations of this study, which focused on a relatively small area NW of

South Georgia during the austral autumn. Understanding the trophic role of myctophids in the Southern Ocean requires key data on spatial, temporal and ontogenetic variability in both diets and consumption rates.

In general, myctophids consume a range of larger mesozooplankton and smaller macrozooplankton species, particularly euphausiids, amphipods and calanoid copepods, which is consistent with studies carried out

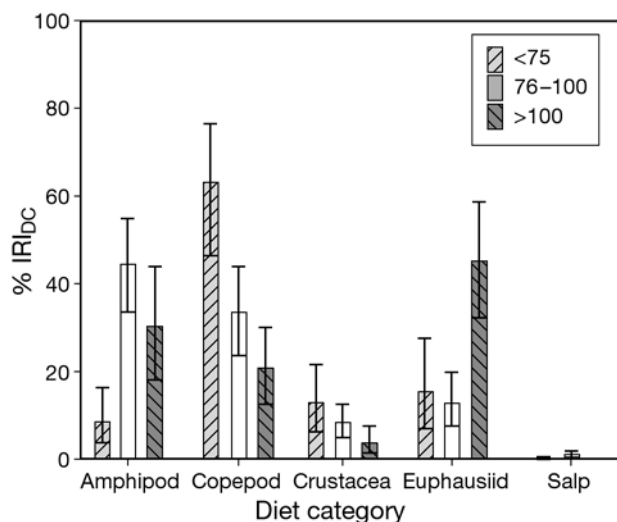


Fig. 6. Diet composition, expressed as percent index of relative importance by prey categories (% IRI_{DC}) of all myctophid species grouped by size category (mm SL)

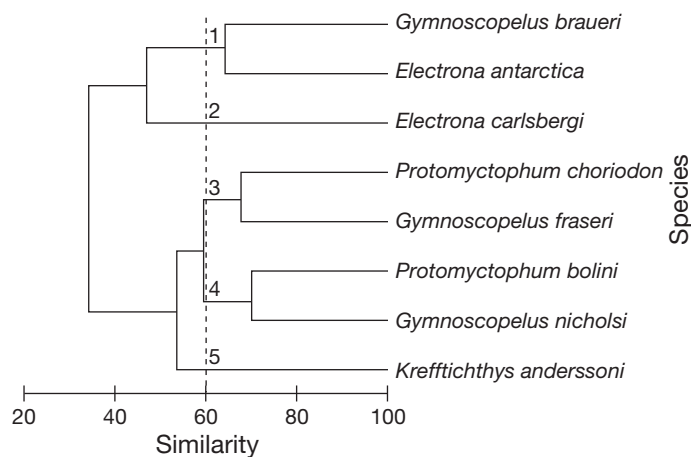


Fig. 7. Cluster diagram (group average) of Bray-Curtis similarity of the dietary composition (% IRI data, excluding the category 'unidentified crustacea') of the 8 myctophid species with n > 20 stomach content samples

Table 7. Estimates of the number of individuals of key prey taxa within the stomachs of different myctophid species around South Georgia in March–April 2004. There are 3 estimates for each prey species, representing a best estimate (**bold**) and the upper and lower bounds to this estimate. Only 7 of the 9 species of myctophids were included because of low sample numbers in the remaining 2 species

Myctophid species	Estimate	Prey species							Salps	
		<i>Themisto gaudichaudii</i>	<i>Euphausia frigida</i>	<i>Euphausia superba</i>	Thysanoessa spp.	Metridia spp.	<i>Calanoides acutus</i>	<i>Rhincalanus gigas</i>		<i>Calanus similimus</i>
<i>Electrona carlsbergi</i>	Upper	0.38	0.03	0.03	0.03	0.43	0.17	0.50	0.26	0.70
	Best	0.27	0.00	0.00	0.03	0.27	0.10	0.23	0.03	0.55
	Lower	0.20	0.00	0.00	0.00	0.17	0.07	0.13	0.00	0.43
<i>Electrona antarctica</i>	Upper	1.54	0.03	0.07	0.03	0.00	0.00	0.00	0.00	0.00
	Best	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gymnoscopelus fraseri</i>	Upper	0.14	0.40	0.00	0.40	16.23	0.40	1.10	0.27	0.00
	Best	0.07	0.17	0.00	0.17	11.67	0.27	0.35	0.13	0.00
	Lower	0.03	0.07	0.00	0.03	7.98	0.13	0.23	0.03	0.00
<i>Gymnoscopelus nicholsi</i>	Upper	0.43	1.68	0.13	1.13	4.30	0.33	0.80	0.77	0.00
	Best	0.32	0.97	0.07	0.87	3.10	0.23	0.63	0.45	0.00
	Lower	0.23	0.70	0.03	0.47	2.25	0.13	0.43	0.30	0.00
<i>Gymnoscopelus braueri</i>	Upper	0.90	0.13	0.17	0.13	0.72	0.07	0.20	0.13	0.00
	Best	0.70	0.03	0.10	0.07	0.30	0.00	0.13	0.03	0.00
	Lower	0.57	0.03	0.07	0.00	0.10	0.00	0.03	0.00	0.00
<i>Protomyctophum bolini</i>	Upper	0.00	0.50	0.00	0.27	2.06	0.07	0.03	0.18	0.00
	Best	0.00	0.50	0.00	0.27	02.06	0.07	0.03	0.18	0.00
	Lower	0.00	0.33	0.00	0.07	0.96	0.00	0.00	0.00	0.00
<i>Protomyctophum choriodon</i>	Upper	0.21	0.23	0.00	0.88	16.92	9.86	2.56	3.08	0.00
	Best	0.17	0.10	0.00	0.47	8.63	7.80	1.90	2.15	0.00
	Lower	0.13	0.03	0.00	0.30	5.70	5.18	1.27	1.38	0.00

in other parts of the Southern Ocean (Rowedder 1979, Naumov et al. 1981, Kozlov & Tarverdiyeva 1989, Gerasimova 1990, Pakhomov et al. 1996, Gaskett et al. 2001, Pusch et al. 2004) and on myctophid communities elsewhere (e.g. Young & Blaber 1986, Hopkins & Gartner 1992, Williams et al. 2001). It is, however, important to note that soft-bodied and easily digested prey, such as salps, may be underestimated in studies such as this.

Partitioning of resources is key to the coexistence of species that would otherwise be potential competitors (Schoener 1974), and such partitioning has been demonstrated in highly diverse low latitude myctophid assemblages (Hopkins & Gartner 1992). In the present study, there was evidence of dietary segregation and specialisation (e.g. *Electrona antarctica*) that is linked, in part, to the vertical distribution and size of the fish predators (Collins et al. 2008a). It is difficult to disentangle active prey selection from simply feeding on the appropriate sized prey at a predator species' feeding depth. Nevertheless, there is clear niche separation between species, whatever the cause. Similarity analysis clearly demonstrated 2 clusters that were dominated by copepod consumers (*Protomyctophum bolini*, *Protomyctophum choriodon*, *Gymnoscopelus fraseri* and *Gymnoscopelus nicholsi*), and another dominated by consumers of the amphipod *Themisto gaudichaudii* (*Electrona antarctica* and *Gymnoscopelus braueri*). The size of the fish (predator) is a key determinant of diet, with larger prey, such as Antarctic krill, only being consumed by the largest myctophids. In addition, prey size (Fig. 8, also see Jennings et al. 2001), gape size of the fish (Karpouzi & Stergiou 2003) and the filtering capability of the gill rakers probably influence diet selectivity. Similar dietary specialisation has been reported in other mesopelagic fish communities in the Southern Ocean (Gaskett et al. 2001), although the results differed somewhat to those of the present study, probably reflecting seasonal and regional differences in predator size and prey fields. Interestingly, the most abundant copepods in the area, which were the small

Table 8. Effect of myctophid predation on the production of 9 key zooplankton taxa expressed as a % of daily production (in units of $\mu\text{g carbon m}^{-2} \text{d}^{-1}$) consumed by each myctophid species NW of South Georgia in March–April 2004. There are 3 estimates for each prey species, representing a best estimate (median; **bold**) and the lower and upper bounds (25th and 75th percentiles, respectively). N/A: insufficient data available to make a confident estimate. Only 7 of the 9 species of myctophids were included because of low sample numbers in the remaining 2 species

% of daily production	Estimate	<i>Themisto gaudichaudii</i>	<i>Euphausia frigida</i>	<i>Euphausia superba</i>	Thysanoessa spp.	Metridia spp.	<i>Calanoides acutus</i>	<i>Rhincalanus gigas</i>	<i>Calanus similimus</i>	Salps
<i>Electrona carlsbergi</i>	Upper	6.80	0.10	N/A	0.00	0.02	0.00	0.00	0.00	0.03
	Best	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Electrona antarctica</i>	Upper	30.09	0.11	N/A	0.00	0.00	0.00	0.00	0.00	0.00
	Best	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gymnoscopelus fraseri</i>	Upper	2.92	1.33	N/A	0.01	0.92	0.00	0.00	0.00	0.00
	Best	0.11	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gymnoscopelus nicholsi</i>	Upper	2.58	1.61	N/A	0.01	0.07	0.00	0.00	0.00	0.00
	Best	0.17	0.16	1.20	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.05	0.05	0.21	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gymnoscopelus braueri</i>	Upper	23.25	0.56	N/A	0.00	0.05	0.00	0.00	0.00	0.00
	Best	1.07	0.02	5.05	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.25	0.00	0.90	0.00	0.00	0.00	0.00	0.00	0.00
<i>Protomyctophum bolini</i>	Upper	0.00	3.12	N/A	0.01	0.22	0.00	0.00	0.00	0.00
	Best	0.00	0.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Lower	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Protomyctophum choriodon</i>	Upper	1.62	0.29	N/A	0.01	0.36	0.03	0.00	0.01	0.00
	Best	0.10	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	Lower	0.03	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Total	Upper	67.25	7.11	N/A	0.05	1.64	0.04	0.01	0.03	0.03
	Best	3.85	0.63	6.26	0.02	0.00	0.02	0.00	0.01	0.00
	Lower	0.95	0.14	1.11	0.00	0.00	0.01	0.00	0.00	0.00

cyclopoid *Oithona* spp. and *Oncaea* spp. and the calanoid *Ctenocalanus* spp., were absent from myctophid stomachs. These species may either be too small for retention by gill-rakers or too unprofitable to exploit.

The amphipod *Themisto gaudichaudii* was a key dietary item of 2 myctophid species, *Gymnoscopelus braueri* and *Electrona antarctica*, with *E. antarctica* feeding almost exclusively on *T. gaudichaudii*. Such dietary specialisation is somewhat surprising given the range of capture depth and size of *E. antarctica* examined here. In other parts of the Southern Ocean, the diet of *E. antarctica* is reported to be more diverse, being dominated by copepods in both the Lazarev Sea (Pakhomov et al. 1996) and near Macquarie Island (Gaskett et al. 2001) and dominated by euphausiids in the South Shetland Islands (Pusch et al. 2004). *T. gaudichaudii* clearly plays a key role in the northern Scotia Sea, where it is also an important prey of notothenid fish (Collins et al. 2008b, Main et al. 2009) and seabirds (Croxall et al. 1997), particularly in krill-poor years. It is also a key species on the Patagonian shelf and in other sub-Antarctic areas (Bocher et al. 2001).

There was some evidence of prey selection within the copepod portion of the diet. Copepod prey was dominated by older copepodite stages of *Rhincalanus gigas* and *Metridia* spp., particularly females. Older female polar copepods are generally more lipid rich than other stages (Hagen & Schnack-Schiel 1996) and may be actively targeted by myctophids. Alternatively, the behaviour of these species may make them particularly susceptible to myctophid predation. *Metridia* spp. is a very active copepod that undergoes a diel vertical migration of around 200 m (Ward et al. 2006). *R. gigas* is relatively inactive and only reacts slowly to stimuli (Shreeve et al. 2002). Both behaviours, in different ways, may increase vulnerability to predation from an active fish predator. Hopkins & Gart-

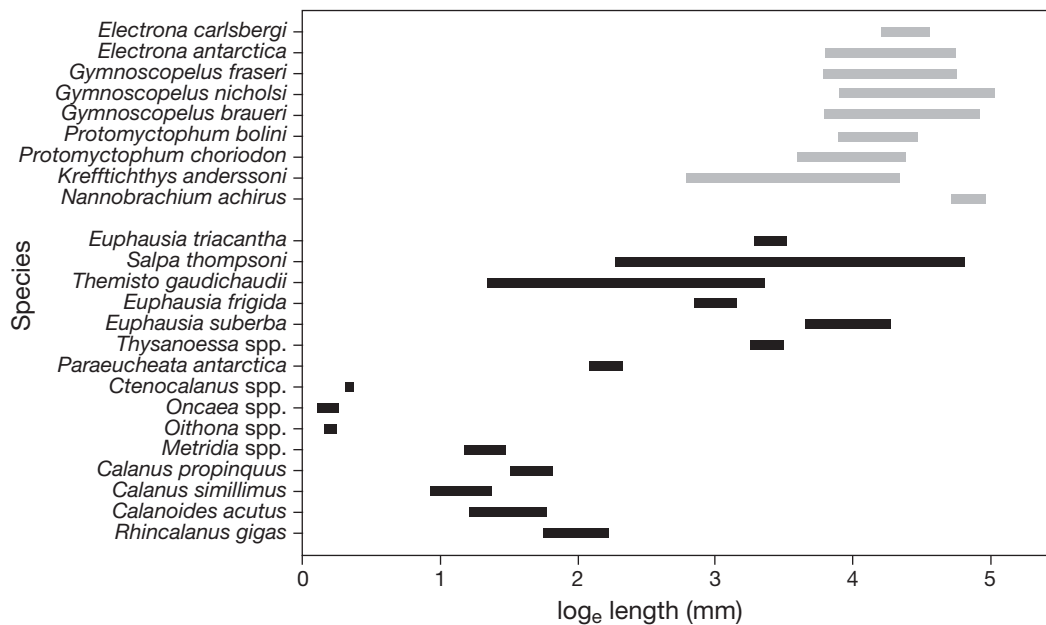


Fig. 8. Size range (natural log length, mm) of myctophid predators (SL) and prey species (TL). Grey bars: predator sizes from the present study; black bars: prey species with sizes taken from Boltovskoy (1999) and Kirkwood (1984)

ner (1992) similarly found that myctophids preferentially consumed the intermediate to late growth stages of copepods in the Gulf of Mexico.

Adult Antarctic krill *Euphausia superba* are probably one of the largest prey species that can be handled by myctophids and, consequently, were only consumed by the larger myctophids (notably larger *Gymnoscopelus braueri*, *G. nicholsi* and *Nannobranchium achirus*). The significance of krill in the diet of Southern Ocean myctophids has been the source of debate in the literature (Williams 1985, Pakhomov et al. 1996, Pusch et al. 2004). The data presented here largely support the concept that myctophids provide an important krill-independent link between secondary production and higher predators (Murphy et al. 2007). However, it should be recognised that, while our study area (NW of South Georgia) is home to large populations of Antarctic krill, most of the krill in this area are large adults (Tarling et al. 2007), which are probably too large for most myctophids. It is possible that myctophids consume significant amounts of krill further south in the Scotia Sea, where krill are generally younger and smaller.

The presence of both Antarctic krill and *Themisto gaudichaudii* in the diet of *Nannobranchium achirus* was interesting, as this species was generally caught deeper than 600 m (Collins et al. 2008a) and krill and *T. gaudichaudii* are generally concentrated in the upper 400 m. There is no evidence that *N. achirus* migrates to the surface to feed; however, during this study, krill were caught in RMT25 samples taken between 800

and 1000 m, which supports the recent observations of krill actively feeding at abyssal depths in Marguerite Bay (Clarke & Tyler 2008).

Two myctophid species, *Protomyctophum bolini* and *Electrona carlsbergi*, did not show any evidence of vertical migration (at least to the resolution of the sampling), and both consumed prey that was abundant in the 200 to 400 m depth zone which they occupied. In other species (e.g. *Gymnoscopelus braueri* and *E. antarctica*), there was some evidence of diel vertical migration (see Collins et al. 2008a), but likely net avoidance in the upper 400 m during daylight makes interpretation of day and night patterns difficult. Diel migrations are probably related to feeding and daylight avoidance of visual predators (Robison 2003). The dominance of the largely surface-dwelling *Themisto gaudichaudii* in the diet of *P. bolini* and *E. carlsbergi* suggests that they either feed near the surface at night or during the day, but are missed by daylight nets. Evidence from other studies supports the concept that diurnally vertically migrating myctophids predominantly feed at night, whilst those with weak or no migration show less distinct changes in stomach fullness (Williams et al. 2001).

One implication of the above behavioural pattern is that at least some species of myctophids are carrying prey below the pycnocline before carrying out the processes of digestion and egestion. This behaviour would contribute to the active flux of carbon from the mixed layers to the ocean interior (Longhurst et al. 1990). A number of studies have indicated that such active flux

may be greater than first considered (Michaels et al. 1994, Tarling & Johnson 2006) and that this process may explain some of the imbalances presently found in carbon export models (Smith 1992, Michaels et al. 1994). Tarling & Johnson (2006) estimated that Antarctic krill could export 2.3×10^{13} g C yr⁻¹ into the interior of the Southern Ocean through hunger/satiation vertical migrations. Given that krill biomass estimates (100 Mt; Atkinson et al. 2008) are roughly equivalent to those of myctophids in the Southern Ocean (70 to 200 Mt; Lubimova et al. 1987), it is possible that myctophids are contributing a similar order of active carbon flux in this ocean region.

Even though copepods were a major prey item of myctophids, myctophid predation had little impact on copepod productivity in this region. Macrozooplankton species were affected to a greater extent, particularly *Themisto gaudichaudii* and *Euphausia superba*. In the former instance, our best estimate was that 3.9% of daily production (in terms of carbon) was consumed by myctophids, principally by *Electrona antarctica* and *Gymnoscopelus braueri*. For the latter, a best estimate of 6.3% of daily productivity was consumed by a combination of *G. braueri* and *Gymnoscopelus nicholsi*. However, some caution is warranted as to the overall impact of myctophid predation across wider ocean regions, given the patchy nature of macrozooplankton aggregations. Furthermore, these results must be placed in the wider context of seasonal and latitudinal changes in trophic relationships. Prey and predator sizes will change and there will sometimes be mismatches between prey availability and predator demand.

We found that the myctophid community in this region maintains a large dietary breadth, which is one way of minimising the impact of seasonal mismatches. In addition, there is good evidence of dietary segregation between species, related to inter-specific differences in body size and variations in migratory behaviour and depth selection. These differences potentially minimise competition and the exhaustion of any one particular food resource. There is likely to be a considerable flux of biomass through the myctophid community, which is largely independent of Antarctic krill. Together, these findings reveal the myctophid community to be a robust component of the mesopelagic system, capable of exploiting a wide range of food sources and of acting as a major link between lower and higher trophic levels in this region.

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