Predatory impact of the myctophid fish community on zooplankton in the Scotia Sea (Southern Ocean)

[1*]Ryan A. Saunders, [2]Martin A. Collins, [1]Peter Ward, [1]Gabriele Stowasser, [1]Simeon L. Hill, [1]Rachael Shreeve and [1]Geraint A. Tarling

[1]British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK

[2]Government of South Georgia and South Sandwich Islands, Government House, Stanley, Falkland Islands

[*]Corresponding author: Email: ryaund@bas.ac.uk, Tel: +44(0)1223 221275, Fax: +44 (0)1223 362616

Running header: Predation rates of Southern Ocean myctophids

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ABSTRACT

Myctophids are the most abundant mesopelagic fishes in the Southern Ocean, but their trophic role within the predominantly krill-based food web in regions south of the Antarctic Polar Front (APF) is poorly resolved. This study therefore examined the diets of 10 species of myctophid fishes, *Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus braueri*, *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi*, *Krefftichthys anderssoni*, *Protomyctophum bolini*, *Protomyctophum tenisoni*, *Protomyctophum choriodon* and *Nannobrachium achirus*, in the Scotia Sea, together with their predatory impact on the underlying zooplankton community. Myctophids and their prey were sampled in different seasons by scientific nets deployed across the Scotia Sea from the sea ice zone to the APF. Based on the percentage index of relative importance, myctophids had high overlap in their diets, although the data suggest dietary specialisation in some species. There was also a distinct switch in diet from copepods to euphausiids and amphipods with increasing myctophid size. Myctophid predation impacted daily copepod production by between 0.01 and 5%, with *Calanus simillimus* being most impacted. Total annual consumption of copepods was around 1.5 million tonnes (Mt) per year. All myctophids predated the euphausiid *Thysanoessa* spp., consuming ~12 % of its daily productivity and around 4 Mt per year. However, only larger myctophid species preyed upon *Euphausia superba*, consuming 2% of its daily productivity, which could amount to as much as 17 Mt per year. *Themisto gaudichaudii* was also an important dietary component, with 4% of its daily productivity being consumed, amounting to around 2 Mt per year. This study demonstrates that myctophids link secondary productivity to higher predators both through krill-dependent and krill-independent trophic pathways.

KEY WORDS

Myctophidae; Predation rates; Feeding ecology; Scotia Sea; Southern Ocean

INTRODUCTION

The estimated global biomass of mesopelagic fish is in excess of 11,000 million tons, making them a major contributor to the function of oceanic ecosystems and global biogeochemical cycles (Irigoien et al. 2014). Mesopelagic fish transfer energy through pelagic food webs, linking primary consumers and omnivorous macro-zooplankton to higher marine predators. They also contribute to the export of carbon from the sea surface to mesopelagic depths through their extensive vertical migrations (Pakhomov et al. 1996, Smith 2011, Irigoien et al. 2014). Nevertheless, despite their ecological importance, this group of fishes remain one of the least investigated components of the oceanic ecosystem, with major uncertainties in their abundance, biology and ecology. Of the mesopelagic fishes, myctophids (family Myctophidae) are considered one of the most diverse and numerically abundant families (Gjøsaeter & Kawaguchi 1980). Determining the ecology of myctophids therefore constitutes an important step towards understanding the operation of oceanic ecosystems at both regional and global scales.

Our understanding of myctophids is confounded primarily due to difficulties in sampling them appropriately at the necessary spatial and temporal scales. This is particularly so in remote, high latitude regions such as the Southern Ocean. One example of a high latitude region where myctophids are considerably understudied is the Scotia Sea in the Atlantic sector of the Southern Ocean; one of the most productive regions of the Southern Ocean (Holm-Hansen et al. 2004). This region is also subject to broad-scale, long-term environmental change, with marked increases in sea-surface temperatures and substantial reductions in both winter sea ice extent and Antarctic krill stocks (de la Mare 1997, Curran et al. 2003, Atkinson et al. 2004, Murphy et al. 2007a, Whitehouse et al. 2008). There is therefore an imminent need for more information on all components of the Scotia Sea pelagic ecosystem, particularly myctophids, in order to understand and predict the manifestations of this change, both in the Scotia Sea and throughout the Southern Ocean.

There are 33 species of myctophid fish in the Scotia Sea comprising an estimated biomass of 4.5 million tonnes (Mt; Collins et al. 2012) . Although the food web of the Scotia Sea is predominantly centred on Antarctic krill (Murphy et al. 2007b), it is clear that other trophic pathways are both regionally and seasonally important, with myctophids providing a key alternative (Murphy et al. 2007b, Stowasser et al. 2012). Myctophids in the Scotia Sea are the primary prey of king penguins (*Aptenodytes patagonicus*), elephant seals (*Mirounga leonina*) and squid (*Martialia hyadesi*) and are important dietary components for many other predators, including fur seals (*Arctocephalus gazella*), Cape petrels (*Daption capense*) and toothfish (*Dissostichus eleginoides*) (Olsson & North 1997, Casaux et al. 1998, Brown et al. 1999, Dickson et al. 2004, Reid et al. 2006, Collins et al. 2007). In turn, they are predators of copepods, amphipods and euphausiids, including Antarctic krill (Pusch et al. 2004, Shreeve et al. 2009, Saunders et al. 2014, Saunders et al. 2015a). Under a scenario of regional ocean-warming and declines in krill stocks, the role of myctophids in food webs may become increasingly important. However, the extent to which myctophids can potentially support the ecosystem against such change is unknown, primarily due to uncertainties in their distribution of abundance and trophodynamics.

Determining diet is essential to understanding food web dynamics and resource partitioning (Ross 1986), but studies of Southern Ocean myctophid diets have been predominantly restricted to the most abundant species on limited spatial and temporal scales, often 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, Shreeve et al. 2009). Recent studies have cast new light on the diet and feeding ecology of myctophids in the Scotia Sea at more appropriate spatial and temporal scales (Saunders et al. 2014, Saunders et al. 2015a, b), but parameters important to the determination of their trophic role, such as daily rations, have rarely been estimated (Gerasimova 1990, Pakhomov et al. 1996, Pusch et al. 2004, Shreeve et al. 2009). Also, only a few studies considered predation impact of Southern Ocean myctophids on their prey species, focussing on a small range of prey species at limited spatial and temporal scales (Williams 1985, Pakhomov et al. 1996, Pusch et al. 2004, Shreeve et al. 2009).

In this study, we examine and compare the diets of the most abundant myctophid species across the entire latitudinal extent of the Scotia Sea (63°S to 50°S), spanning the sea-ice zone (SIZ) to the Antarctic Polar Front (APF). Furthermore, we integrate over the austral spring, summer and autumn to gain a seasonally averaged perspective. Vertical distributions of myctophids are compared with those of their prey species to investigate the spatial overlap between predators and prey and to assess the extent of prey selectivity. The predation impact of myctophids on prey assemblages was also estimated and sensitivity analyses used to determine confidence intervals around these estimates. These data are the most comprehensive for any region of the Southern Ocean to date, and provide important parameterisations for new food web and ecosystem studies in the region. They also contribute to resolving the composition and dynamics of the global mesopelagic fish community that is a prerequisite for understanding global ecosystem and biogeochemical processes.

MATERIALS AND METHODS

Oceanographic, acoustic and biological data were collected in the Scotia Sea during three research cruises on board RSS *James Clark Ross* in October-December 2006 (JR161, austral spring), January-February 2008 (JR177, austral summer) and March-April 2009 (JR200, austral autumn). The study area covered regions from the SIZ to the APF, with sampling stations distributed across several prevailing water masses and frontal zones (Fig. 1). Six nominal stations were sampled repeatedly across the study site during the surveys: Southern Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS), Georgia Basin (GB) and the Polar Front (PF).

Net sampling

Mesopelagic fish were collected with a rectangular midwater trawl net (RMT25; Piatkowski et al. 1994) . Depth stratified hauls were undertaken at each station covering depth intervals between 0-200, 200-400, 400-700 and 700-1000 m. These zones were repeated day and night in spring and summer, but only during hours of darkness in the autumn. The abundance and vertical distribution of the zooplankton prey were characterised by oblique Longhurst-Hardy Plankton Recorder (LHPR) tows to 1000 m during both day and night. The LHPR was equipped with a 0.38 m diameter nose cone and a 200 µm mesh net and filtering gauzes. The gauze advance mechanism was set to 90 s during the spring and 120 s during summer and autumn, which resulted in a depth resolution of around 20-25 m per patch. The prey field was further characterised using a paired Bongo net (180 mm diameter mouth) fitted with 53 µm mesh. Bongo nets were deployed to 400 m and hauled vertically to the surface during hours of daylight. Further details of the net samplers, haul deployments and analyses are described in Collins et al. (2012) and Ward et al. (2012).

Sample processing

RMT25 net haul catches were sorted onboard to the lowest possible taxonomic level (Hulley 1990). Total catch weights per fish species were recorded using a motion compensated balance and all fish were measured to the nearest mm using standard length (SL). Stomachs were dissected from a random sub-sample of 25 fish per non-targeted net haul, or from each specimen where catches were small. All stomachs were frozen for subsequent microscopic analysis. LHPR samples were frozen at -20 °C and transported back to the laboratory where species were identified and enumerated under a stereomicroscope. Counts were averaged into the same depth horizons as used for the RMT25 net hauls to enable direct comparisons of vertical distributions. Bongo net samples were preserved in 4% formalin and seawater solution and subsequently aliquots were analysed under a stereomicroscope back at the laboratory.

Stomach contents analysis

Following Shreeve et al. (2009), fish stomach contents were thawed and sorted to the lowest taxonomic level that the state of digestion would allow. Individual prey items were enumerated and weighed. If the prey was highly disaggregated, the weights of component species were estimated as a proportion of the weight of the total contents.

Diet was expressed using four measures: 1) percentage frequency of occurrence (%*F*), 2) percentage mass (%*M*), 3) percentage number (%*N*) and 4) percentage Index of Relative Importance (%IRI) (Cortes 1997). The %IRI was calculated for prey species and $\%IRI_{DC}$ was calculated for prey categories (Main et al. 2009, Shreeve et al. 2009). The initial prey categories used in the analysis were defined according to order (Amphipods, Copepods, Euphausiids, Ostracods, Molluscs, Urochordata and Other taxa), but a more detailed analysis was performed subsequently for the most numerically dominant prey categories: the copepods *Metridia* spp., *Pleuromamma robusta*, *Rhincalanus gigas*, *Calanoides acutus*, *Calanus simillimus*, *Paraeuchaeta* spp., "Other copepods", the euphausiids *Euphausia superba*, *Thysanoessa* spp., "Other euphausiids", the amphipod *Themisto gaudichaudii* and "Other taxa" (mostly Unidentified crustaceans, Mollusca, Ostracoda, Urochordata). The %IRI was calculated as:

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

where *i* is prey item.

95% confidence limits for the mean %IRI of each prey category were calculated using a bootstrapping technique, whereby each species dataset (individual stomachs) was re-sampled (with replacement) 1000 times (Main et al. 2009).

Diet comparison between myctophid species

Similarities in the diets of the myctophid species were examined using the Plymouth Routines in Multivariate Ecological Research (PRIMER version 6) software package (Clarke & Warwick 2001). The %IRI values for each diet component for each myctophid species were first square root transformed and a Bray-Curtis similarity index was then calculated for each pair of species. Hierarchical agglomerative cluster analysis was performed on this data set using the group average linking method and a SIMPER routine was used to determine which prey species contributed most to the resulting cluster groupings.

Predation impact of myctophids

Following Shreeve et al. (2009), we used the following function to determine the proportion of prey productivity consumed by each myctophid species:

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

Where $I_{i,j}$ is the proportion of 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 stomachs of myctophid species j, C_i is the carbon mass of species i, P_i is the depth-integrated concentration of predator species j (ind. m^{-2}), G is the gut passage time (hrs), Z_i is the depth-integrated concentration of prey species i (ind. m^{-2}), and F_i is the growth rate of prey species i (µg C d^{-1}). We extended this calculation to estimate total consumption of each prey taxon by myctophids using the equation:

$$Q_i = A\, D\, 365\, R\, \left(\frac{\sum_j N_{i,j}\, C_i\, P_i}{\sum_{i,j} N_{i,j}\, C_i\, P_i}\right)$$

Where Q_i is the total annual consumption of prey taxon i, A is the approximate area of the Scotia Sea (2 million km^2), D is the mean density of myctophids (2.23 tonnes km^2 ±0.79 SD, and R is the daily food intake of myctophids as a percentage of body mass (1.5%) All values were taken from Collins et al. (2012). R is a mean daily ration (% dry body weight) calculated from data presented in Pakomov et al. (1996) for Antarctic and high sub-Antarctic myctophids. 95% confidence intervals were calculated around our annual consumption estimates to represent the variation in mean myctophid density observed in the Scotia Sea.

We used the approach of Shreeve et al. (2009) to derive the most plausible estimates and their upper and lower bounds. The upper bound is based on the upper estimate of the number of prey items i eaten by myctophid j, the upper estimated concentration of myctophid j, the lower estimated concentration of prey i, and the fastest gut passage time. Conversely, the lower bound is derived from the lower estimate of the number of prey species i in the stomachs of myctophid species j, the lower estimated concentration of myctophid j, the upper estimated concentration of prey species i, and the slowest gut passage time. The most plausible estimate uses the median values for each of the above parameters. Each of these parameter values were calculated as detailed below.

Numbers of individuals of prey species *i* in the stomachs of myctophid *j* ($N_{i,j}$)

Ten myctophid species were considered in our analysis: *Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus braueri*, *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*, *Protomyctophum tenisoni*, *Protomyctophum choriodon*, *Krefftichthys anderssoni* and *Nannobrachium achirus*. The dataset was restricted to the most common prey taxa found in the myctophid stomachs: the amphipod *Themisto gaudichaudii*, the euphausiids *Euphausia superba*, *Euphausia frigida* and *Thysanoessa* spp., the copepods *Metridia* spp., *Rhincalanus gigas*, *Calanoides acutus*, *Calanus simillimus*, *Pleuromamma robusta*, *Paraeuchaeta* spp., and *Oncaea* spp., ostracods, salps and pteropods.

The following non-parametric bootstrapping technique was used to generate the upper and lower bounds: for each myctophid species, 30 individuals were extracted at random and the mean number of items of each prey species in this subset was calculated and the process repeated 100 times. The median of the series was used as the best estimate value, with the 25th and 75th percentiles comprising the lower and upper bounds, respectively.

Depth-integrated myctophid concentrations (P_i)

Myctophid concentrations were determined from the RMT25 net catches that were aggregated for all surveys and regions across the Scotia Sea. Only night-time hauls were used in the analysis to avoid potential bias due to daylight net avoidance in the upper regions of the water column (Collins et al. 2012). A total of 117 stratified net hauls were deployed during this time. At each station, the entire water column between 0-1000 m was sampled in depth-discrete intervals. Net catch concentrations (ind. m^{-3}) were therefore 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. Our best estimate value for P_i was the median of the pooled net concentrations, with the 25th percentile representing the lower bound and the 75th percentile comprising the upper bound.

Depth-integrated prey species concentrations (Z_i)

A total of 24 LHPR deployments were undertaken during the study, each sampling the whole water column between 0-1000 m at a depth resolution of approximately 20-25 m. Net catch concentrations of prey species (ind. m^{-3}) were multiplied by the respective depth interval and summed to give depth-integrated concentrations (ind. m^{-2}) per haul between 0-1000 m. All LHPR hauls were pooled for all surveys and the median of this series was used as the best estimate value, the 25th percentile value as the lower bound and the 75th percentile value as the upper bound.

Prey species abundance estimates (standardised to ind. m^{-2}) were also calculated from 65 Bongo net hauls deployed between 0-400 m. These data were pooled for all surveys and the median, 25th, and 75th percentile values were selected to represent the best estimate values and their associated upper/lower bounds. We assumed that all zooplankton sampling devices would most likely underestimate the actual concentrations of prey species present in the water column. Therefore, the median LHPR and Bongo net values were scrutinised and the highest estimates for each species were selected for use in our calculations. This approach, which applied mostly to copepods, was adopted to provide the most conservative estimates of myctophid predation rates on the prey field. Some prey species exhibited a high degree of patchiness during the surveys and were absent in several of the net hauls. On occasion, this resulted in 25th percentile values of zero for these species (Table 1) and in such instances, it was not possible to calculate an upper bound for $I_{i,j}$.

Growth rate of prey species (F_i)

Following Shreeve et al. (2009), species-specific growth rates (µg C d^{-1}) were estimated from direct measurements of carbon weight, multiplied by the weight-specific growth rate of each species using the functions provided by Hirst et al. (2003). Mean carbon weight measurements were calculated from around 10 to 60 individuals of each species during the surveys. For the copepod species, we used a weight-specific growth rate function appropriate for adult broadcast spawning copepods at 5 °C. A function covering all crustaceans (excluding copepods) at 5 °C was selected for the euphausiids, amphipods and ostracods, whilst a function suitable for Thaliaceans at 15 °C was used for salps. Although these functions were derived at temperatures greater than those of our study region, particularly for Thaliaceans, they are the most appropriate functions available in the scientific literature to date. We consider estimates derived from these functions to represent an upper limit to zooplankton production, which means that our calculations represent a minimum of the predatory impact of myctophids on zooplankton. We assumed that the majority of pteropods collected during the surveys were most probably *Limacina* species, so the growth rate function provided by Bednaršek et al. (2012) was used for this prey group.

Gut passage time (*G*)

The temperature-specific gut passage time function detailed in Shreeve et al. (2009) was used in our analysis:

$$y = 4.50 + 24.92^{(-0.265x)}$$

where *y* is gut passage time (hrs) and *x* is temperature.

This model was derived from data on the gut passage time of a number of different planktivorous fish from various locations with different ambient water temperatures (Pakhomov et al. 1996). In our calculations, temperature data collected at each station during the surveys (Venables et al. 2012) were collated and averaged to provide an estimate of the overall ambient temperature between 0-1000 m across the Scotia Sea. The mean temperature in the region was 0.67 °C, giving an estimated gut passage time of 25.4 hrs that was used as our best estimate value. Mean temperature values varied between -0.30 and 2.0 °C, which gave a slowest gut passage time of 31.2 hrs and a fastest gut passage time of 19.1 hrs. This level of variance simulates to a degree the variance in gut passage time between prey species in other studies (Andersen 1999, Andersen & Beyer 2008), although further investigations are required to provide more robust species-specific gut passage times for Southern Ocean zooplankton.

RESULTS

Myctophid distribution

Detailed descriptions of the horizontal and vertical distributions of the myctophids are given in Collins et al. (2012) and Saunders et al. (2014, 2015a, b), so only an overview is given here. These studies also provide information on their seasonal and regional biomass. *Electrona antarctica* and *Gymnoscopelus braueri* were the most abundant species encountered on the surveys (Fig. 2). These two species occurred throughout the Scotia Sea, including the sea ice sectors, where *E. antarctica* was most abundant. *Gymnoscopelus nicholsi* had a similar distribution pattern, but occurred only in small numbers. *Krefftichthys anderssoni* and *Protomyctophum bolini*, and *Electrona carlsbergi* were the most abundant species in the northern Scotia Sea, but they seldom occurred at the southernmost stations. *Protomyctophum tenisoni*, *Nannobrachium achirus*, *Gymnoscopelus fraseri* and *Protomyctophum choriodon* were also distributed predominantly in the northern regions, with the abundance of *P. tenisoni* and *N. achirus* being highest in regions associated with the APF and *G. fraseri* and *P. choriodon* highest around the Georgia Basin.

Only night time data were used here to illustrate the vertical distribution of the myctophid species because of possible daytime net avoidance in the upper water column (Fig. 3). Six species were distributed predominantly in the upper 400 m of the water column, with *Electrona carlsbergi*, *Protomyctophum bolini*, and *Protomyctophum tenisoni* restricted exclusively to this zone and *Protomyctophum choriodon*, *Gymnoscopelus fraseri* and *Gymnoscopelus nicholsi* occurring only in low abundance in regions deeper than 400 m. *Electrona antarctica*, *Gymnoscopelus braueri* and *Krefftichthys anderssoni* were caught throughout the sampled depth range, whilst *Nannobrachium achirus* was distributed predominantly below 400 m.

Abundance and vertical distribution of zooplankton prey species

Best estimates (median values) of depth-integrated macrozooplankton abundance varied between 37 ind. m^{-2} for *Euphausia frigida* to 636 ind. m^{-2} for *Euphausia superba* (Table 1). All euphausiid species occurred predominantly in the upper 200 m of the water column along with the amphipod *Themisto gaudichaudii* (Fig. 4), which had a depth-integrated abundance of 236 ind. m^{-2}. Salps were found mainly above 400 m and had a depth-integrated abundance of 47 ind. m^{-2}. Pteropod counts were only available from the Bongo net hauls, so it was not possible to examine their vertical distribution. These organisms had a depth-integrated concentration of 2829 ind. m^{-2}. Ostracods comprised a depth-integrated abundance of 943 ind. m^{-2} and were spread throughout the water column, with the greatest concentrations above 400 m.

Copepods generally occurred in greater concentrations than macrozooplankton, with best estimates of depth-integrated abundance ranging between 118 and 12181 ind. m^{-2}. The most abundant copepod species were *Pleuromamma robusta*, *Metridia* spp. and *Oncaea* spp. (Table 1). These three species were found throughout the water column, but the highest concentrations occurred mostly above 400 m (Fig 4). *Calanoides acutus*, *Calanus simillimus* and *Paraeuchaeta* spp. were found at all depths, but maximal concentrations were in the upper 200 m. *Rhincalanus gigas* occurred predominantly above 700 m, with the greatest concentrations spread between the surface and 400 m.

Diet compositions

A total of 1804 myctophid stomachs contained prey items and were used in the analysis (Table 2). Empty stomachs were excluded from the analysis. For each myctophid species, the size ranges, depths and locations of the sampled fish were representative of those found previously in the Scotia Sea region (Hulley 1981, McGinnis 1982, Pusch et al. 2004, Collins et al. 2008).

Planktonic crustaceans dominated the diets of all myctophid species (Supplementary 1 to 4; Fig. 5). The diet of *Electrona antarctica* (24-115 mm SL) was dominated by *Euphausia superba* and *Themisto gaudichaudii* (Supplementary 1; Fig. 5). These species were distributed predominantly in the upper 200 m, a region that *E. antarctica* appeared to occupy only at night. By contrast, *Electrona carlsbergi* was found in greatest abundance above 200 m at night and had a smaller size range (68-88 mm SL). *Electrona carlsbergi* was predominantly a copepod feeder (93 %IRI) with *Rhincalanus gigas*, *Metridia* spp. and *Oncaea* spp. the most predated species (Supplementary 1; Fig. 5).

The three *Gymnoscopelus* species had diets that were dominated by copepods and euphausiids, although there were some differences in their respective diets (Supplementary 2; Fig 5). *Gymnoscopelus braueri* (mean: 82 mm SL) reached its maximum abundance in the upper 200 m at night and had a diet dominated by the copepod *Metridia* spp. and the euphausiid *Thysanoessa* spp. (Supplementary table 2). *Themisto gaudichaudii* and *Euphausia superba* also formed an important part of this species' diet (~5 %IRI). Similarly, the abundance of *Gymnoscopelus fraseri* (mean: 67 mm SL) was highest between 0 and 200 m at night and the species predated mostly *Metridia* spp., although *Rhincalanus gigas* formed a substantial part of the diet (10 %IRI) and *E. superba* was absent. By contrast, *Gymnoscopelus nicholsi* (mean: 126 mm SL), which was spread between the surface and 400 m at night, had a diet dominated by *Metridia* spp., *R. gigas* and *E. superba* (Supplementary 2). This species also took substantial proportions of *Pleuromamma robusta* (10 %IRI).

Protomyctophum bolini (mean: 49 mm SL) was mainly caught between 200-400 m at night and fed mostly on copepods (Supplementary 3; Fig. 5). The principle prey species were *Metridia* spp., *Rhincalanus gigas* and *Thysanoessa* spp.. *Protomyctophum tenisoni* (mean: 42 mm SL) occurred in the top 200 m at night and also predated copepods, particularly *Calanus simillimus* (75 %IRI), together with substantial proportions of the euphausiid *Thysanoessa* spp. (10 %IRI). By contrast, the main copepod prey species of *Protomyctophum choriodon* (mean: 70 mm SL) was *R. gigas* and this myctophid species predated much greater proportions of *Thysanoessa* spp. (42 %IRI) than *P. bolini* and *P. tenisoni* (Supplementary 3). *Protomyctophum choriodon* abundance was greatest above 200 m at night and *Themisto gaudichaudii* also comprised an important component of the species' diet (5 %IRI).

Krefftichthys anderssoni (mean: 51 mm SL), which was most abundant between 200 and 700 m, fed mostly on copepods, particularly *Rhincalanus gigas* (59 %IRI). This myctophid also took relatively high proportions of *Calanoides acutus* (16 %IRI) and the euphausiid *Thysanoessa* spp. (14 %IRI; Supplementary 4 and Fig. 5). *Nannobrachium achirus* (mean: 132 mm SL) was the largest myctophid species studied and it occurred in highest abundance below 400 m. The sample size was relatively small for this species, but the available data indicate that it was a copepod, euphausiid and amphipod feeder, with *R. gigas* (25 %IRI), *Thysanoessa* spp. (25 %IRI) and unidentified non-hyperiid amphipods (6 %IRI) the main dietary components within these groups (Supplementary 4; Fig. 5). *Nannobrachium achirus* also took relatively high proportions of the copepod *Paraeuchaeta* spp. (15 %IRI) and was the only species to predate fish (9 %IRI).

Copepods were the dominant prey items in all myctophid size classes, although there was a distinct change in diet with size (Fig. 6). The smallest sized fish (<55 mm SL) consumed significantly more copepods than the larger size classes, with the older copepodite stages usually predominant (CV and CVI stages of *Metridia* spp., *Calanoides acutus*, and *Calanus simillimus*). A greater range in developmental stages was only apparent for *Paraeuchaeta* spp., with stages from CII upwards being present and the CIII stage being the most abundant in myctophid diets. Euphausiids and amphipods increased proportionally in the diet with increasing fish size. Euphausiids (~30 $\%IRI_{DC}$) and amphipods (~5 $\%IRI_{DC}$), including the species *Euphausia superba* and *Themisto gaudichaudii*, were most abundant in the largest sized fish (>82 mm SL; Fig. 6). There was a further increase in diet breadth with increasing size, as other taxa became more prevalent in larger sized fish. The "Other taxa" category was dominated by unidentified crustaceans, ostracods, pteropods and salps.

Consumption of prey productivity

The majority of stomachs examined contained more than one species of prey, with some myctophids containing more than 5 prey species. For most myctophid species, each copepod prey species was consumed in numbers of 10 or more, whilst the main macrozooplankton taxa predated were commonly found in numbers of 5 or more. However, when averaged out for a particular myctophid species, the number of prey items was mostly <1 because of the large numbers of stomachs from which a prey species was absent (Table 3). The exception were some of the copepod species, particularly *Metridia* spp. and *Rhincalanus gigas*, which were found in relatively high numbers in the stomachs of the predominant copepod feeders, such as *Electrona carlsbergi*, *Gymnoscopelus nicholsi* and *Gymnoscopelus fraseri*. In these instances, the average prey numbers per stomach were >1. *Thysanoessa* spp. was the only macrozooplankton prey item to be taken in sufficient quantities such that the average prey numbers per stomach was greater than 1 (Table 3). This prey item was most abundant in the stomachs of *Protomyctophum bolini* and *G. fraseri*.

Best estimates of average depth-integrated concentration across all 10 myctophid species in the upper 1000 m ranged between 0.003 and 0.155 ind. m^{-2} (Table 1). As a best estimate, myctophids consumed up to ~5 % of the daily productivity (C m^{-2} d^{-1}) of key copepod taxa in the Scotia Sea, with *Krefftichthys anderssoni* having the greatest overall impact, taking ~2 % of the *Calanus simillimus* production (Table 4). The impact of myctophid predation on macrozooplankton production was also relatively high (Table 4), with a best estimate of ~4 % of *Themisto gaudichaudii* daily production and ~12 % of *Thysanoessa* spp. daily production. *Themisto gaudichaudii* and *Thysanoessa* spp. were impacted most by *Electrona antarctica* and *K. anderssoni*, respectively. Myctophids also consumed around 2 % of *Euphausia superba* daily production, with *E. antarctica* impacting this prey species the most. The impact of myctophids on salps and ostracods accounted for up to 0.1 % d^{-1}, but their impact on pteropods was negligible.

Annual consumption of zooplankton

Estimates of the total annual consumption of zooplankton across the whole Scotia Sea were dominated by the diet of *Electrona antarctica*, the most common myctophid species. Our data suggest that the main taxa consumed by myctophids were *Euphausia superba*, *Thysanoessa* spp. and *Themisto gaudichaudii*, with 16,808,493, 3,754,095 and 2,245,883 t yr^{-1} of these species being eaten, respectively (Table 5). The estimated annual consumption of all key copepods was around 1.5 Mt yr^{-1}, with *Rhincalanus gigas* being predated the most 1,135,180 t yr^{-1}). The estimated consumption of the other main macrozooplankton taxa, such as salps and ostracods, was <0.5 Mt yr^{-1} (Table 5).

Diet comparisons between species

Hierarchical cluster analysis produced 5 clusters at the 60 % similarity level, although two of these clusters were comprised of single species (Cluster 1: *Electrona antarctica* and Cluster 2: *Nannobrachium achirus*; Fig.7). Cluster 3 grouped *Gymnoscopelus braueri*, *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi* and *Protomyctophum bolini* together in a cluster dominated by the consumption of the copepod *Metridia* spp. (36%; Table 6). Cluster 4 contained *Electrona carlsbergi* and *Krefftichthys anderssoni* in a cluster dominated by the consumption of *Rhincalanus gigas* (54%), and *Protomyctophum tenisoni* and *Protomyctophum choriodon* were grouped in Cluster 5 that was dominated by the consumption of *Calanus simillimus* (25%) and *Thysanoessa* spp. (22%). There was substantial overlap between the composite length-frequency distributions of fish within each cluster dominated by copepod consumption, indicating that this clustering reflected differences in feeding selectivity rather than size-related differences in feeding patterns (e.g. the median fish size for clusters 3, 4 and 5 was 72, 73 and 64 mm SL, respectively). However, there was also a high degree of overlap in the overall diets of Clusters 3, 4 and 5, as *R. gigas*, *Metridia* spp. and *Thysanoessa* spp. all occurred within the top 3 to 4 most consumed prey species in each cluster, contributing a total of ~57-69 % to the groupings (Table 6). *Themisto gaudichaudii* and *C. simillimus* were also common to the 3 clusters, suggesting that other, less dominant species were important contributors to these clusters. Most notably, *Pleuromamma robusta*, ostracods and *Euphausia superba* were unique in the grouping of Cluster 3 (contributing 13 %, collectively), as were unidentified euphausiids and unidentified crustaceans in the grouping of Cluster 4 (contributing ~8 %, collectively).

DISCUSSION

The present study provides a comprehensive analysis of myctophid diets and their predatory impact on zooplankton communities in the Southern Ocean and represents one of the most detailed studies undertaken on the trophic role of myctophids in any oceanic region. These results must be placed within a context of the associated sampling issues inherent with net-based surveys of mesopelagic fish and zooplankton. Such issues include active net avoidance by myctophids and the patchy nature of both myctophid and zooplankton aggregations which may, for example, impact estimates of abundance averaged over relatively broad spatial and temporal scales. Indeed, recent acoustic studies have reported that the abundance of mesopelagic fishes may be at least an order of magnitude greater than previously assumed from net survey data, suggesting that the role of mesopelagic fish in oceanic ecosystems may be underestimated in net-based trophodynamics studies (Irigoien et al. 2014). A further consideration is that seasonal variations were not resolved in the study since the data were integrated over the three seasons. Although this approach does not provide a seasonal synopsis, it does provide a more accurate view of the average situation during the productive months because the data are more representative of myctophid diets over the longer-term.

Niche partitioning

The results of our study show that myctophids consume a range of mesozooplankton and macrozooplankton, particularly copepods, euphausiids and amphipods, which is consistent with studies carried out in other parts of the Southern Ocean (Naumov et al. 1981, Kozlov & Tarverdiyeva 1989, Gerasimova 1990, Pakhomov et al. 1996, Gaskett et al. 2001, Pusch et al. 2004, Shreeve et al. 2009) and on the myctophid community elsewhere (Hopkins & Gartner 1992, Williams et al. 2001, Suntsov & Brodeur 2008, Pepin 2013, Tanaka et al. 2013).

Resource partitioning is key to minimising inter-specific competition and enabling the coexistence of species in a region (Schoener 1974), and such partitioning has been demonstrated in highly diverse low latitude myctophid communities (Clarke 1980, Hopkins

& Gartner 1992) and at high and temperate latitudes (Watanabe et al. 2002, Sassa & Kawaguchi 2005, Shreeve et al. 2009, Cherel et al. 2010). However, species tend to exhibit a high degree of overlap in their diets in high latitude regions and it has been suggested that inter-species food competition is avoided because of high regional food availability (Pakhomov et al. 1996). In the present study, there was evidence of dietary segregation and specialisation for some myctophid species that is linked, in part, to horizontal and vertical distribution and individual size (see Shreeve et al. 2009 for an overview of the size ranges of myctophids and their prey species). *Electrona antarctica*, for example, occurred mostly in the sea-ice sectors and, unlike the other myctophids, had a diet dominated by *Euphausia superba* and *Themisto gaudichaudii*. Also, *Nannobrachium achirus* was the largest species encountered and was caught predominantly below 400 m, and had a diet that included substantial amounts of deep water amphipods and small fish. Thus these species appear to have different niches from the other myctophids. Furthermore, similarity analysis identified 3 clusters that were dominated by copepod consumers, but preferential selection of certain copepod species appeared to separate their niches. Of the predominantly smaller myctophid species, *Electrona carlsbergi* and *Krefftichthys anderssoni*, which had different depth distributions, targeted mostly *Rhincalanus gigas*, whilst *Protomyctophum tenisoni* and *Protomyctophum choriodon* favoured *Calanus simillimus*. In contrast, the group comprising the three larger-sized *Gymnoscopelus* species and *Protomyctophum bolini* took mostly *Metridia* spp. These results are broadly consistent with concurrent studies using trophic biomarkers, such as stable isotopes and fatty acids, which provide complimentary time-integrated synopses of predator diets and habitats (Stowasser et al. 2012, Tarling et al. 2012). Similar niche partitioning was also observed for most of the studied myctophid species at lower latitudes (Kerguelen Islands, southern Indian Ocean) using these techniques, where strong segregation between the genera *Electrona*, *Gymnoscopelus* and *Protomyctophum* was observed (Cherel et al. 2010). However, there was also a high degree of overlap in the overall diets of all myctophids in our study, with *R. gigas*, *Metridia* spp., and *Thysanoessa* spp. predated substantially by all species. This suggests that inter-specific competition for these prey items may be reduced in the Scotia Sea because of their high availability in the water column (Pakhomov et al. 1996).

Prey selection

The overall distribution patterns of *Krefftichthys anderssoni* and *Electrona carlsbergi* broadly matched that of its main prey, *Rhincalanus gigas*, as did the distribution patterns of *Protomyctophum tenisoni* and *Protomyctophum choriodon* and their preferred prey species, *Calanus simillimus*. These myctophids and prey items occurred mostly in the northern regions of the Scotia Sea and were less abundant in regions south of the SACCF (Ward et al. 2012, Saunders et al. 2014). Similarly, *Electrona antarctica* occurred in highest abundance in the SIZ where its main prey species, *Euphausia superba*, was also most abundant. The trend was less obvious for the *Gymnoscopelus* species and *Protomyctophum bolini*, but the abundance of these species was generally higher in the northern regions, which broadly matched the distribution pattern of *Metridia* spp. in the region.

The most abundant copepod species in the region, which were the small copepods *Oithona* spp. and *Ctenocalanus* spp., were not predated much by any of the myctophids. These prey species may either be too small to retain by the gill rakers or too unprofitable to exploit (Shreeve et al. 2009). The exception to this was the consumption of *Oncaea* spp. by *Electrona carlsbergi*, which suggests that myctophids are capable of retaining small copepods, but there is a high degree of prey selectivity. Further evidence of prey selectivity within the copepod community was apparent, as all myctophids tended to predate the older copepodite stages, particularly CVI females that are generally considered to be more lipid rich than other stages (Hagen & Schnack-Schiel 1996, Shreeve et al. 2009). A relatively high degree of selectivity was also apparent in the macrozooplankton component of the prey field. Myctophids appeared to select the euphausiid *Thysanoessa* spp. in preference to *Euphausia frigida,* which is a similar sized euphausiid and had a similar depth distribution and abundance in the Scotia Sea. Likewise, *Euphausia triacantha,* a euphausiid similar in size to *Euphausia superba*, was seldom predated by any of the larger myctophid species even though its abundance was relatively high in the region (Saunders et al. 2014). These euphausiids have comparable energy content in terms of total lipids, although there are some differences in component lipid composition, which may be important in resource selectivity by myctophids (Reinhardt & Vanvleet 1986, Ruck et al. 2014). Differences in euphausiid aggregation and escape behaviour may also be an important factor in myctophid predation on these organisms (Daly & Macaulay 1988, Brierley et al. 1998).

Body size effects on diet

The results showed that myctophid size was an important determinant of diet, as larger sized fish clearly predated a broader range of prey taxa and took bigger prey items, such as *Euphausia superba* and *Themisto gaudichaudii*. Adult Antarctic krill are probably one of the largest prey species that can be predated by myctophids, and as a consequence, were only consumed by the largest myctophids. An increase in trophic level with increasing myctophid size was also detected during stable isotope analyses (Tarling et al. 2012). The ability to predate larger-sized organisms is most likely controlled by gape size and body size such that only the larger-sized myctophids are able to capture and consume these animals (Karpouzi & Stergiou 2003).

Food-web implications

The significance of krill in the diet of Southern Ocean myctophids has been the source of debate in the scientific literature (Williams 1985, Lancraft et al. 1989, Pakhomov et al. 1996, Pusch et al. 2004). Our results support the concept that the myctophids, particularly the small species, provide an important krill-independent link between secondary production and higher predators (Murphy et al. 2007b). Myctophid predation accounted for approximately 2% of the daily krill productivity in the Scotia Sea, with *Electrona antarctica* consuming the majority of this productivity. Whilst this level of predation impact is relatively low, it is still indicative of major quantities of krill biomass being consumed by myctophids in the Scotia Sea on an annual basis. Collins et al. (2012) estimated that zooplankton consumption by myctophids in the Scotia Sea was approximately 25 Mt y^{-1}. We used our diet data to partition this consumption estimate amongst prey taxa to estimate the cumulative impact of myctophid predation on their prey biomass throughout the year. The data suggests that myctophids in the Scotia Sea consume around 17 Mt of *Euphausia superba* per year (± 6 Mt SD), supporting the notion that large myctophids are possibly the main consumers of this species in the region (Lancraft et al. 1989, Pusch et al. 2004, Hill et al. 2007).

Myctophids consume both larval and adult stages of krill. However, there are currently no independent estimates of krill biomass or production that encompass all the developmental stages of krill that myctophids consume. Our estimate of krill density (637 ind. m^{-2}), which encompassed larval and post-larval stages, is higher than that reported for post-larval krill in the Scotia Sea (16-256 ind. m^{-2}), suggesting that krill biomass and production are also higher than that estimated in the region (Hewitt et al. 2004, Atkinson et al. 2009). Determination of biomass of the whole life-cycle of krill, together with the predatory impact of myctophids on the specific developmental stages, is a necessary further step towards understanding high latitude Southern Ocean food webs and ecosystem function.

Our result showed that myctophid predation on the daily productivity of *Thysanoessa* species was high. These smaller euphausiids comprised a substantial proportion of the diets of all myctophids, particularly *Krefftichthys anderssoni*, indicating that they have a key role in the Southern Ocean ecosystem. *Thysanoessa* species, such as *T. macrura* and *T. vicini*, are the most consistently found euphausiid in Antarctic waters (Nordhausen 1994, Boltovskoy 1999, Haraldsson & Siegel 2014) and often exceed *Euphausia superba* in abundance in some regions (Daly & Macaulay 1988). These smaller euphausiids are an important dietary component of penguins, sea birds and mackerel ice fish (Brown & Klages 1987, Kock et al. 1994, Main et al. 2009, Pichegru et al. 2011), but information on the trophic role of Southern Ocean *Thysanoessa* within Antarctic ecosystems is limited. Given their importance in the diet of Southern Ocean myctophids, resolving the trophodynamics of *Thysanoessa* species in this region is an important part of predicting how myctophids will respond in this rapidly changing environment (Flores et al. 2012). Myctophids also predated a substantial proportion of the daily productivity of *Themisto gaudichaudii* and the ecological importance of this species in the northern Scotia Sea and at sub-Antarctic latitudes was highlighted by Shreeve et al. (2009) and Bocher et al. (2001), respectively.

Even though copepods were the main prey item of myctophids, myctophid predation had relatively little impact on the productivity of most copepod species in the Scotia Sea region. The exceptions were the larger copepods *Rhincalanus gigas* and *Calanus simillimus* of which myctophids consumed between 3-5% of their daily productivity. The myctophid species that had the greatest impact on these copepods was *Krefftichthys anderssoni* due to its relatively high abundance in the northern Scotia Sea. This predominant APF species was one of the smallest myctophid encountered on the surveys, but it also predated the greatest proportions of *Thysanoessa* spp. productivity and was the second highest consumer of *Themisto gaudichaudii* productivity. *Krefftichthys anderssoni* is the primary prey of king penguins (Olsson & North 1997, Bost et al. 2002, Cherel et al. 2002) and an important dietary component of other predators (Rodhouse et al. 1992, Casaux et al. 1998, Deagle et al. 2008, Cherel et al. 2010), indicating that it has an important role in the operation of the Scotia Sea ecosystem, despite it being a species that typically resides in waters of the APF. Given that *K. anderssoni* and the other sub-Antarctic species (e.g. *Electrona carlsbergi*, *Gymnoscopelus fraseri* and *Protomyctophum tenisoni*) are possibly expatriates, or seasonal migrants, in the Scotia Sea (Hulley 1981), it is clear that further studies are warranted in regions north of the APF in order to gain better insight into the trophodynamics and ecology of these myctophids which are likely to have a direct bearing on ecosystem dynamics in regions at higher latitudes, such as the Scotia Sea.

In conclusion, the myctophid community in the Scotia Sea maintained a large dietary breadth, but there was some evidence of dietary segregation between species, related to their horizontal distribution, inter-specific variations in body size, variations in vertical migratory behaviour and depth selection. These differences potentially minimise the impact of seasonal changes in the prey field and minimise competition and the exhaustion of any one particular food resource. There is likely to be a considerable flux of biomass through the Scotia Sea myctophid community, which appears largely independent of Antarctic krill. This indicates that the myctophid community is a robust component of the Southern Ocean mesopelagic system that is able to exploit a wide range of food resources and provide a major link between lower and upper trophic levels in the Southern Ocean.

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TABLES

Taxon	Sampling device	Sampling depth (m)	Concentration (ind. m^{-2}) Lower	**Best**	Upper
Myctophidae					
Electrona carlsbergi	RMT25	0-1000	0.002	**0.015**	0.207
Electrona anarctica	RMT25	0-1000	0.003	**0.155**	0.586
Gymnoscopelus fraseri	RMT25	0-1000	0.002	**0.007**	0.048
Gymnoscopelus nicholsi	RMT25	0-1000	0.002	**0.004**	0.015
Gymnoscopelus braueri	RMT25	0-1000	0.002	**0.078**	0.431
Krefftichthys anderssoni	RMT25	0-1000	0.002	**0.067**	0.346
Nannobrachium achirus	RMT25	0-1000	0.003	**0.006**	0.033
Protomyctophum tenisoni	RMT25	0-1000	0.002	**0.006**	0.084
Protomyctophum bolini	RMT25	0-1000	0.002	**0.032**	0.143
Protomyctophum choriodon	RMT25	0-1000	0.002	**0.003**	0.030
Amphipoda					
Themisto gaudichaudii	Bongo	0-400	0.000	**235.740**	628.672
Copepoda					
Calanoides acutus	LHPR	0-1000	569.040	**1018.730**	2187.315
Calanus simillimus	Bongo	0-400	0.000	**117.900**	7858.400
Metridia spp.	Bongo	0-400	3143.360	**11237.512**	21570.210
Oncaea	Bongo	0-400	196.460	**6522.472**	71664.960
Pleuromamma robusta	Bongo	0-400	78.580	**12180.520**	46207.392
Paraeuchaeta spp.	Bongo	0-400	117.876	**275.044**	471.504
Rhincalanus gigas	Bongo	0-400	157.168	**1178.760**	5343.440
Euphausiacea					
Euphausia frigida	LHPR	0-1000	1.218	**37.340**	482.553
Euphausia superba	LHPR	0-1000	0.000	**636.693**	13021.204
Thysanoessa spp.	LHPR	0-1000	0.000	**134.571**	1150.767
Ostracoda					
Ostracods	Bongo	0-400	628.640	**943.008**	1729.200
Mollusca					
Pteropods	Bongo	0-400	628.800	**2829.024**	14459.456
Urochordata					
Salps	LHPR	0-1000	0.000	**46.957**	766.109

Table 1. Depth-integrated net catch concentrations of the most abundant myctophid fish and zooplankton taxa in the Scotia Sea during the three surveys. The concentration estimates are the 25th percentile (lower), **median**, 75th percentile (upper)

Species	SSS	MSS	WSS	NSS	GB	PF	Total	Mean SL (mm)	Range SL (mm)
Electrona antarctica	228	83	3	8	133	30	485	71	24-115
Electrona carlsbergi	0	51	0	102	2	30	185	77	68-90
Gymnoscopelus braueri	96	81	9	36	64	86	372	82	34-162
Gymnoscopelus fraseri	0	0	0	2	58	43	103	67	39-115
Gymnoscopelus nicholsi	10	10	1	8	5	6	40	126	34-165
Protomyctophum bolini	20	17	28	28	76	62	231	49	23-66
Protomyctophum tenisoni	0	0	9	15	0	22	46	42	32-55
Protomyctophum choriodon	0	0	0	0	30	7	37	70	55-85
Krefftichthys anderssoni	2	24	18	79	108	50	281	51	15-74
Nannobrachium achirus	1	1	3	4	9	6	24	132	65-167

Table 2. Numbers of myctophid stomachs containing prey items from each station during the three surveys. The mean size (SL) and size ranges of the fish specimens from which the stomachs were extracted are also given. Regions are South Scotia Sea (SSS), Mid Scotia Sea (MSS) West Scotia Sea (WSS), North Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF)

Myctophid species	Estimate	*Themisto gaudichaudii*	*Euphausia frigida*	*Euphausia superba*	*Thysanoessa* spp.	*Calanoides acutus*	*Calanus simillimus*	*Metridia* spp.	Oncaea spp.	*Pleuromamma robusta*	*Paraeuchaeta* spp.	*Rhincalanus gigas*	Ostracods	Pteropods	Salps
Electrona	Lower	0.10	0.00	0.00	0.17	0.03	0.30	1.47	1.06	0.10	0.33	11.99	0.03	0.00	0.13
carlsbergi	**Best**	**0.23**	**0.00**	**0.00**	**0.27**	**0.10**	**0.43**	**1.87**	**2.42**	**0.13**	**0.50**	**13.78**	**0.03**	**0.10**	**0.60**
	Upper	0.51	0.03	0.03	0.50	0.23	0.67	2.50	4.02	0.23	0.67	15.04	0.07	0.27	0.97
Electrona	Lower	0.27	0.00	0.20	0.03	0.00	0.00	0.46	0.00	0.00	0.03	0.03	0.03	0.03	0.00
antarctica	**Best**	**0.38**	**0.00**	**0.43**	**0.07**	**0.03**	**0.02**	**0.63**	**0.00**	**0.03**	**0.10**	**0.10**	**0.10**	**0.10**	**0.00**
	Upper	0.54	0.03	1.84	0.14	0.10	0.03	0.87	0.00	0.07	0.20	0.20	0.13	0.30	0.00
Gymnoscopelus	Lower	0.06	0.00	0.00	1.35	0.14	0.23	8.24	0.00	0.77	0.06	1.29	0.33	0.00	0.00
fraseri	**Best**	**0.11**	**0.00**	**0.00**	**1.73**	**0.24**	**0.53**	**10.08**	**0.00**	**1.04**	**0.10**	**1.75**	**0.46**	**0.00**	**0.00**
	Upper	0.21	0.00	0.00	2.27	0.37	0.70	11.93	0.00	1.34	0.16	2.48	0.57	0.00	0.00
Gymnoscopelus	Lower	0.17	0.00	0.27	0.83	0.30	0.10	6.91	0.03	2.96	0.36	5.58	0.17	0.03	0.00
nicholsi	**Best**	**0.27**	**0.23**	**0.35**	**1.00**	**0.43**	**0.17**	**9.00**	**0.03**	**4.07**	**0.43**	**10.13**	**0.23**	**0.03**	**0.10**
	Upper	0.30	0.23	0.44	1.17	0.60	0.20	11.75	0.07	5.01	0.54	13.05	0.31	0.07	0.10
Gymnoscopelus	Lower	0.03	0.00	0.03	0.23	0.00	0.03	0.79	0.00	0.17	0.03	0.13	0.13	0.00	0.00
braueri	**Best**	**0.07**	**0.00**	**0.07**	**0.30**	**0.03**	**0.07**	**1.13**	**0.00**	**0.23**	**0.07**	**0.23**	**0.17**	**0.03**	**0.00**
	Upper	0.10	0.03	0.07	0.40	0.03	0.13	1.47	0.00	0.33	0.10	0.38	0.23	0.07	0.03
Krefftichthys	Lower	0.07	0.00	0.00	0.77	2.82	0.63	0.37	0.00	0.00	0.00	4.85	0.00	0.00	0.00
anderssoni	**Best**	**0.17**	**0.00**	**0.00**	**1.13**	**4.62**	**1.12**	**0.58**	**0.00**	**0.00**	**0.02**	**6.02**	**0.00**	**0.00**	**0.00**
	Upper	0.83	0.00	0.00	1.67	6.97	1.74	0.80	0.00	0.04	0.07	7.57	0.00	0.00	0.00
Nannobrachium	Lower	0.00	0.00	0.00	0.30	0.03	0.10	0.07	0.00	0.03	0.20	0.37	0.10	0.00	0.00
achirus	**Best**	**0.03**	**0.00**	**0.00**	**0.37**	**0.10**	**0.12**	**0.10**	**0.00**	**0.07**	**0.30**	**0.50**	**0.13**	**0.03**	**0.00**
	Upper	0.07	0.00	0.00	0.47	0.10	0.17	0.13	0.00	0.10	0.33	0.63	0.17	0.07	0.00
Protomyctophum	Lower	0.13	0.00	0.00	0.40	0.07	7.48	1.00	0.00	0.00	0.03	0.53	0.00	0.00	0.00
tenisoni	**Best**	**0.25**	**0.00**	**0.00**	**0.57**	**0.13**	**9.03**	**1.53**	**0.13**	**0.00**	**0.10**	**0.70**	**0.03**	**0.00**	**0.00**
	Upper	0.40	0.00	0.00	0.70	0.21	10.50	1.90	0.13	0.07	0.17	0.83	0.10	0.00	0.00
Protomyctophum	Lower	0.00	0.00	0.00	0.17	0.00	0.00	5.23	0.00	0.17	0.27	2.15	0.00	0.00	0.00
bolini	**Best**	**0.00**	**0.00**	**0.00**	**0.23**	**0.00**	**0.03**	**6.67**	**0.00**	**0.30**	**0.37**	**2.97**	**0.07**	**0.00**	**0.00**
	Upper	0.03	0.00	0.00	0.30	0.03	0.10	8.59	0.00	0.50	0.53	3.43	0.13	0.00	0.00
Protomyctophum	Lower	0.73	0.00	0.00	3.47	0.17	5.76	2.06	0.00	0.00	0.03	4.38	0.13	0.00	0.00
choriodon	**Best**	**0.93**	**0.00**	**0.00**	**4.28**	**0.30**	**7.53**	**6.12**	**0.00**	**0.07**	**0.07**	**6.07**	**0.23**	**0.00**	**0.00**
	Upper	1.28	0.00	0.00	5.11	0.54	10.56	7.35	0.00	0.11	0.08	8.01	0.33	0.00	0.00

Table 3. Estimates of the number of individuals of key prey taxa within the stomachs of different myctophids in the Scotia Sea. The Lower, **Best** and Upper estimates are the 25th percentile, median and 75th percentile values of the data set, respectively

Myctophid species	Estimate	*Themisto gaudichaudii*	*Euphausia frigida*	*Euphausia superba*	*Thysanoessa* spp.	*Calanoides acutus*	*Calanus simillimus*	*Metridia* spp.	Oncaea spp.	*Pleuromamma robusta*	*Paraeuchaeta* spp.	*Rhincalanus gigas*	Ostracods	Pteropods	Salps
Electrona	Lower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00
carlsbergi	**Best**	**0.16**	**0.00**	**0.00**	**0.32**	**0.00**	**0.18**	**0.01**	**0.01**	**0.00**	**0.13**	**0.80**	**0.00**	**0.00**	**0.10**
	Upper	-	-	-	-	0.38	-	0.71	6.93	2.93	7.61	-	0.04	0.03	-
Electrona	Lower	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
antarctica	**Best**	**2.75**	**0.00**	**2.26**	**0.82**	**0.02**	**0.07**	**0.03**	**0.00**	**0.00**	**0.27**	**0.06**	**0.02**	**0.00**	**0.00**
	Upper	-	-	-	-	0.45	-	0.69	0.00	2.36	6.46	-	0.22	0.09	-
Gymnoscopelus	Lower	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
fraseri	**Best**	**0.03**	**0.00**	**0.00**	**0.90**	**0.01**	**0.09**	**0.02**	**0.00**	**0.00**	**0.01**	**0.04**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.14	-	0.78	0.00	3.86	0.42	-	0.08	0.00	-
Gymnoscopelus	Lower	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00
nicholsi	**Best**	**0.05**	**0.23**	**0.05**	**0.31**	**0.01**	**0.02**	**0.01**	**0.00**	**0.00**	**0.03**	**0.15**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.07	-	0.24	0.01	4.60	0.45	-	0.01	0.00	-
Gymnoscopelus	Lower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
braueri	**Best**	**0.24**	**0.00**	**0.18**	**1.86**	**0.01**	**0.14**	**0.03**	**0.00**	**0.01**	**0.09**	**0.07**	**0.02**	**0.00**	**0.00**
	Upper	-	-	-	-	0.11	-	0.86	0.00	8.70	2.38	-	0.28	0.02	-
Krefftichthys	Lower	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
anderssoni	**Best**	**0.52**	**0.00**	**0.00**	**6.06**	**1.01**	**2.02**	**0.01**	**0.00**	**0.00**	**0.02**	**1.54**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	18.71	-	0.38	0.00	0.87	1.27	-	0.00	0.00	-
Nannobrachium	Lower	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
achirus	**Best**	**0.01**	**0.00**	**0.00**	**0.18**	**0.00**	**0.02**	**0.00**	**0.00**	**0.00**	**0.03**	**0.01**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.03	-	0.01	0.00	0.20	0.61	-	0.02	0.00	-
Protomyctophum	Lower	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
tenisoni	**Best**	**0.08**	**0.00**	**0.00**	**0.29**	**0.00**	**1.57**	**0.00**	**0.00**	**0.00**	**0.01**	**0.02**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.14	-	0.22	0.09	0.34	0.77	-	0.02	0.00	-
Protomyctophum	Lower	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
bolini	**Best**	**0.00**	**0.00**	**0.00**	**0.59**	**0.00**	**0.03**	**0.06**	**0.00**	**0.00**	**0.21**	**0.36**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.04	-	1.67	0.00	4.32	4.20	-	0.05	0.00	-
Protomyctophum	Lower	0.02	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
choriodon	**Best**	**0.12**	**0.00**	**0.00**	**0.96**	**0.00**	**0.57**	**0.00**	**0.00**	**0.00**	**0.00**	**0.07**	**0.00**	**0.00**	**0.00**
	Upper	-	-	-	-	0.13	-	0.30	0.00	0.20	0.12	-	0.03	0.00	-
Total	Lower	0.05	0.00	0.00	0.12	0.01	0.01	0.01	0.00	0.02	0.02	0.04	0.00	0.00	0.00
	Best	**3.97**	**0.23**	**2.49**	**12.29**	**1.06**	**4.70**	**0.17**	**0.01**	**0.02**	**0.82**	**3.12**	**0.05**	**0.00**	**0.11**
	Upper	-	-	-	-	20.19	-	5.86	7.04	28.38	24.29	-	0.74	0.14	-

Table 4. The impact of myctophid predation on the production of the key zooplankton taxa expressed as a percentage of daily production consumed (µg C m^{-1} d^{-1}) by each myctophid species caught in the Scotia Sea during the study. The Lower, **Best** and Upper estimates represent the 25^{th} percentile, median and 75^{th} percentile values of the data set, respectively. Instances where there was insufficient data (i.e. where 25^{th} percentile estimates were zero) to make a confident estimate are denote by a dash (-)

Estimate	*Themisto gaudichaudii*	*Euphausia frigida*	*Euphausia superba*	*Thysanoessa* spp.	*Calanoides acutus*	*Calanus simillimus*	*Metridia* spp.	*Oncea*	*Pleuromamma robusta*	*Paraeuchaeta* spp.	*Rhincalanus gigas*	Ostracods	Pteropods	Salps
Lower 95%	686,455	4,316	5,137,520	1,147,440	33,843	14,459	53,818	37	8,600	29,318	346,968	331	43	67,311
Mean	**2,245,883**	**14,120**	**16,808,493**	**3,754,095**	**110,723**	**47,305**	**176,078**	**121**	**28,136**	**95,922**	**1,135,180**	**1,083**	**140**	**220,222**
Upper 95%	3,805,311	23,924	28,479,466	6,360,750	187,604	80,152	298,338	206	47,672	162,525	1,923,393	1,835	237	373,133

Table 5. Estimated total annual consumption of zooplankton biomass (tonnes yr^{-1}) for the whole Scotia. The 95% confidence intervals around these estimates reflect the level of variation in myctophid density observed during the study

Cluster group	Myctophid species	Prey species	Average abundance	Percentage contribution	Cumulative percentage
3	*Gymnoscopelus braueri*	**Average similarity: 68.82**			
	Gymnoscopelus fraseri	*Metridia* spp.	6.89	35.59	35.59
	Gymnoscopelus nicholsi	*Rhincalanus gigas*	4.28	18.10	53.68
	Protomyctophum bolini	*Thysanoessa* spp.	3.46	14.44	68.12
		Pleuromamma robusta	2.15	8.84	76.96
		Paraeuchaeta spp.	1.11	3.79	80.75
		Themisto gaudichaudii	1.24	3.70	84.45
		Ostracods	0.92	2.49	86.94
		Calanus simillimus	0.57	1.92	88.85
		Euphausia superba	1.52	1.91	90.77
4	*Electrona carlsbergi*	**Average similarity: 64.01**			
	Krefftichthys anderssoni	*Rhincalanus gigas*	8.59	54.02	54.02
		Metridia spp.	1.79	7.95	61.97
		Thysanoessa spp.	2.31	7.24	69.21
		Themisto gaudichaudii	1.05	6.84	76.05
		Unidentified euphausiids	0.84	5.52	81.57
		Calanus simillimus	1.36	5.22	86.80
		Paraeuchaeta spp.	0.39	2.61	89.41
		Unidentified crustaceans	0.46	2.27	91.68
5	*Protomyctophum tenisoni*	**Average similarity: 63.77**			
	Protomyctophum choriodon	*Calanus simillimus*	6.16	25.43	25.43
		Thysanoessa spp.	4.82	21.83	47.26
		Metridia spp.	3.02	17.91	65.16
		Rhincalanus gigas	3.76	17.02	82.18
		Themisto gaudichaudii	1.66	6.34	88.52
		Calanoides acutus	0.41	2.85	91.37

Table 6. Results of a SIMPER analysis showing percentage contributions of prey species to the myctophid groupings identified by agglomerative hierarchical cluster analysis (see Figure 7)

FIGURES

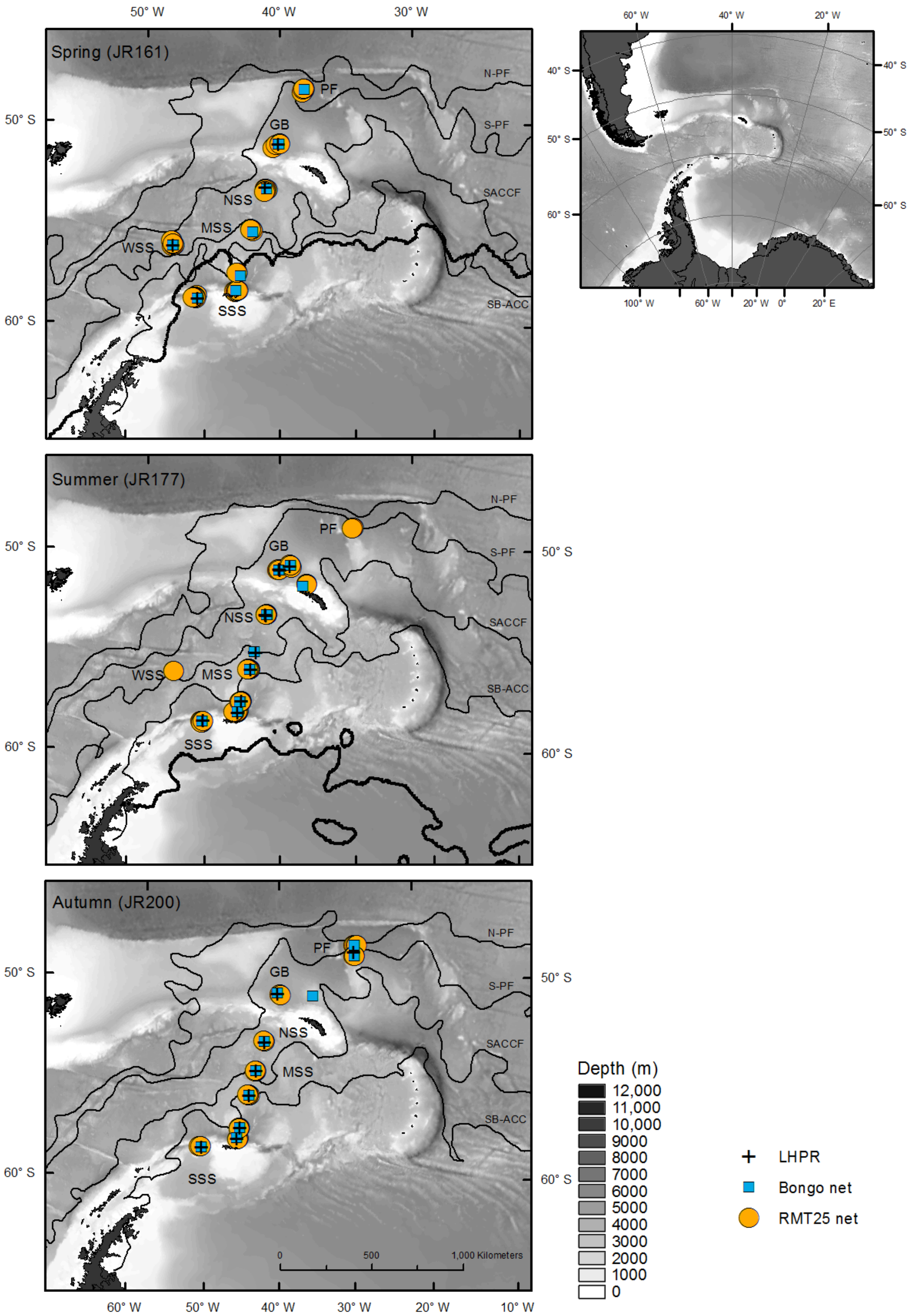

Fig. 1. Locations of 25 m^2 rectangular midwater trawls (RMT25), Longhurst-Hardy Plankton Recorder (LHPR) trawls and Bongo net hauls during the three surveys. Sampling stations are: Southern Scotia Sea (SSS), Western Scotia Sea (WSS), Mid-Scotia Sea (MSS), North Scotia

Sea (NSS), Georgia Basin (GB) and Polar Front (PF). Mean frontal positions determined during the cruises from dynamic height data (Venables et al. 2012) are: northern Antarctic Polar Front (N-PF), southern Antarctic Polar Front (S-PF), South Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB-ACC). The heavy black line shows the position of the 15% ice-edge cover for 24/10/2006 and for 15/01/2008. The ice-edge occurred well south of the transect during autumn 2009 (JR200). Bathymetry data are from the GEBCO_08 grid (version 20091120, www.gebco.net)

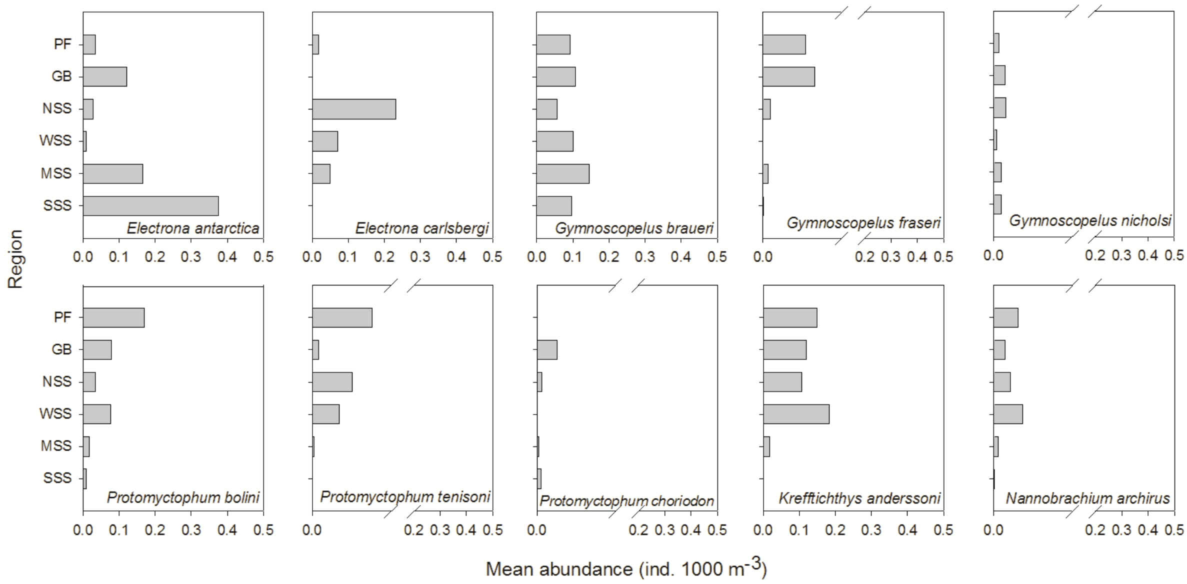

Fig. 2. Mean abundance of myctophid fish at each station during the three surveys. Regions are PF: Polar Front, GB: Georgia Basin, NSS: North Scotia Sea, WSS: West Scotia Sea, MSS: Mid Scotia Sea and SSS: South Scotia Sea. The breaks in the abundance axis start at 0.05 ind. 1000 m^{-3}. Comprehensive descriptions of these species distribution patterns are given in Collins et al. (2012) and Saunders et al. (2014, 2015a, b)

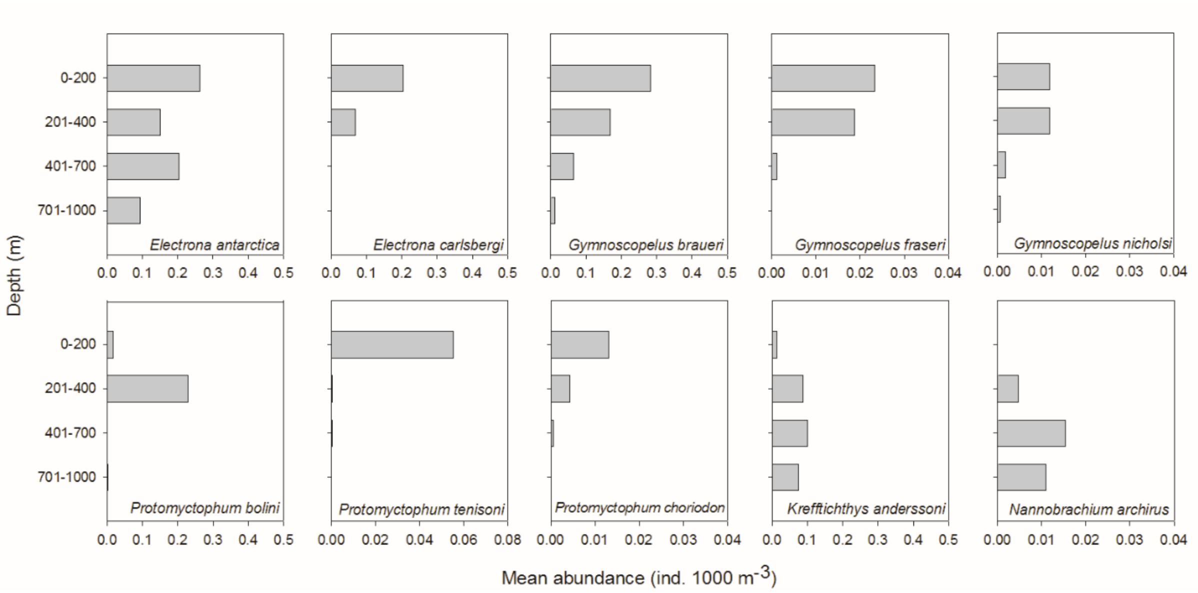

Fig. 3. Night time vertical distribution of myctophid fish caught in the RMT25 net hauls during the three surveys. These data are modified from Saunders et al. (2014, 2015a, b)

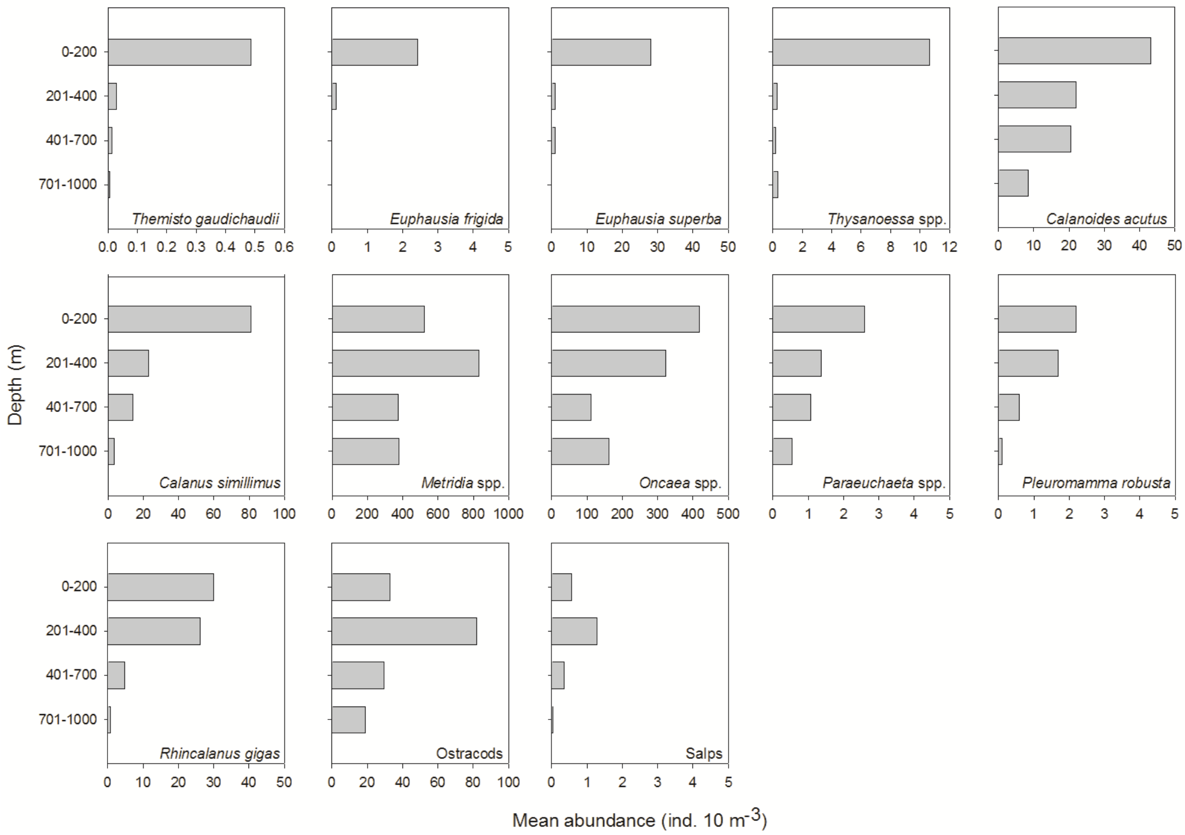

Fig. 4. Depth distribution of the main zooplankton species in the diets of myctophid fish in the Scotia Sea during this study. All depth distributions were derived from LHPR samples.

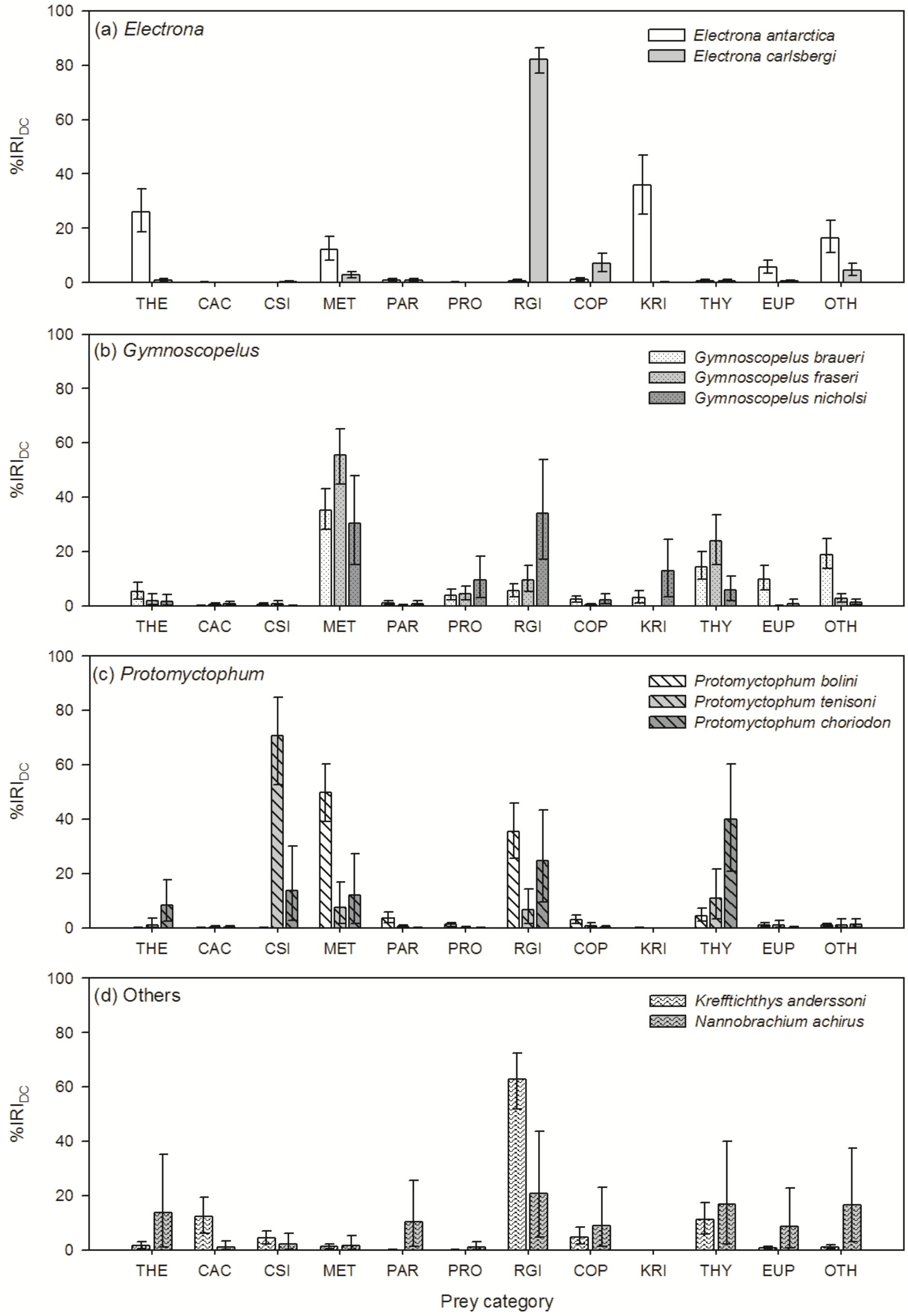

Fig. 5. Diet composition of 10 myctophid species in the Scotia Sea expressed as the percentage index of relative importance (%IRI_{DC}). Error bars are the bootstrapped 95% confidence intervals. THE: *Themisto gaudichaudii*, CAC: *Calanoides acutus*, CSI: *Calanus simillimus*, MET: *Metridia* spp., PAR: *Paraeuchaeta* spp., PRO: *Pleuromamma robusta*, RGI: *Rhincalanus gigas*, COP: other copepods, KRI: *Euphausia superba*, THY: *Thysanoessa* spp., EUP: other euphausiids, OTH: other taxa (predominantly unidentified crustaceans, ostracods and pteropods)

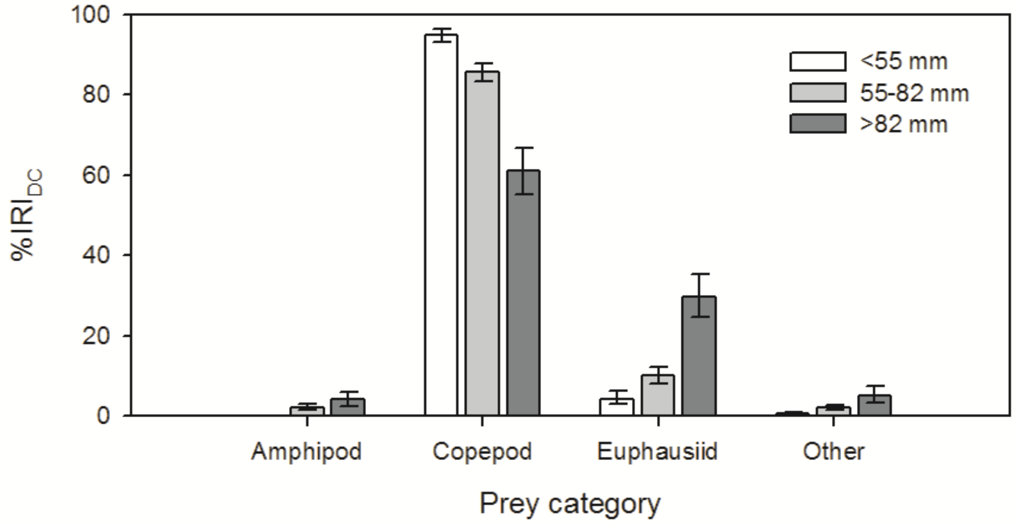

Fig. 6. Diet composition, expressed as percentage index of relative importance by prey category (% IRI_{DC}) of all myctophid species grouped by size category (mm SL). The Other category was dominated by unidentified crustaceans, ostracods, pteropds and salps. The size classes were derived from the 25th and 75th percentiles of the pooled length-frequency data

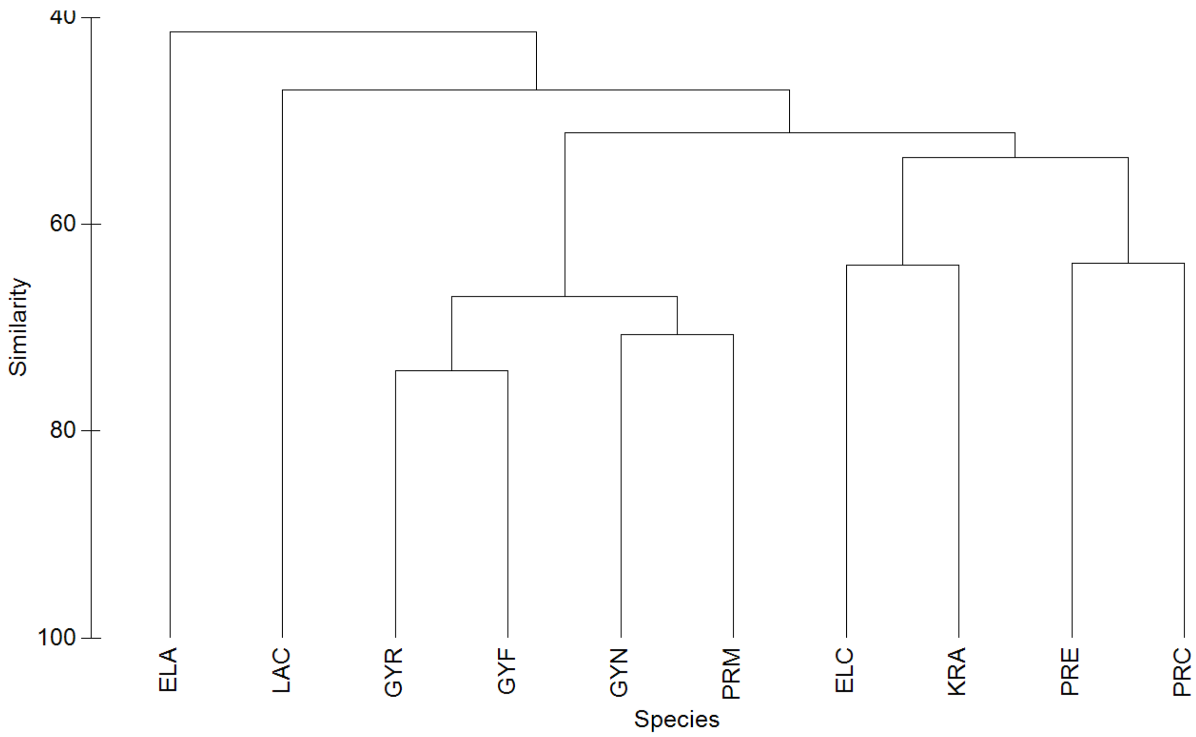

Fig. 7. Cluster diagram of a Bray-Curtis similarity matrix of the dietary composition (%IRI data for all prey items) of the ten myctophid species caught in the Scotia Sea. Cluster 1: *Electrona antarctica* (ELA), Cluster 2: *Nannobrachium achirus* (LAC), Cluster 3: *Gymnoscopelus braueri* (GYR), *Gymnoscopelus fraseri* (GYF), *Gymnoscopelus nicholsi* GYN), *Protomyctophum bolini* (PRM), Cluster 4: *Electrona carlsbergi* (ELC), *Krefftichthys anderssoni* (KRA), Cluster 5: *Protomyctophum tenisoni* (PRE), *Protomyctophum choriodon* (PRC)

SUPPLIMENTARY INFORMATION

	Electrona antarctica				*Electrona carlsbergi*			
Prey	**%F**	**%M**	**%N**	**%IRI**	**%F**	**%M**	**%N**	**%IRI**
Amphipoda								
Themisto gaudichaudii	22.27	27.09	13.36	30.05	10.81	7.67	1.86	1.15
Other amphipods	1.86	0.69	0.45	0.02	1.62	0.80	0.11	0.02
Total	**23.30**	**27.78**	**13.81**	**15.16**	**12.43**	**8.46**	**1.98**	**0.98**
Copepoda								
Calanoides acutus	3.09	0.16	1.55	0.18	7.03	0.59	0.64	0.10
Calanus propinquus	2.68	0.18	1.40	0.14	3.78	0.26	0.20	0.02
Calanus simillimus	2.27	0.07	0.60	0.05	17.84	1.03	2.09	0.62
Eucalanus spp.	0.41	0.01	0.10	0.00	7.57	0.97	0.89	0.16
Metridia spp.	26.80	0.79	16.65	15.59	48.11	2.24	8.38	5.70
Oncaea spp.	0.00	0.00	0.00	0.00	28.11	2.17	13.77	5.00
Paraeuchaeta spp.	8.45	0.91	3.14	1.10	22.16	4.22	2.32	1.53
Pleuromamma robusta	3.30	0.09	0.95	0.11	9.73	0.55	0.73	0.11
Rhincalanus gigas	5.15	0.59	4.09	0.80	69.73	50.37	54.78	81.78
Other copepods	7.63	0.43	1.89	0.11	22.16	0.71	1.80	0.07
Total	**43.51**	**3.23**	**30.36**	**22.86**	**82.70**	**63.09**	**85.59**	**93.29**
Euphausiacea								
Euphausia frigida	1.44	1.20	0.60	0.09	1.62	0.82	0.09	0.02
Euphausia superba	14.85	51.11	35.74	43.01	1.62	5.32	0.07	0.10
Euphausia triacantha	0.21	0.05	0.05	0.00	0.00	0.00	0.00	0.00
Thysanoessa spp.	4.95	2.47	2.39	0.80	15.68	5.50	1.32	1.19
Unidentified euphausiids	15.67	6.32	4.19	4.50	11.35	4.24	1.23	0.69
Total	**36.49**	**61.14**	**42.97**	**59.44**	**28.65**	**15.88**	**2.70**	**4.04**
Ostracoda								
Unidentified ostracods	8.25	0.14	2.24	0.66	5.95	0.13	0.25	0.03
Total	**8.25**	**0.14**	**2.24**	**0.31**	**5.95**	**0.13**	**0.25**	**0.02**
Mollusca								
Unidentified pteropods	5.57	3.71	6.43	1.35	12.43	5.38	4.52	0.87
Unidentified Cephalopoda	0.00	0.00	0.00	0.00	1.08	0.10	0.05	0.00
Total	**5.57**	**3.71**	**6.43**	**0.88**	**13.51**	**5.49**	**4.57**	**1.03**
Urochordata								
Salps	0.62	0.02	0.25	0.01	8.65	4.29	2.93	0.70
Total	**0.62**	**0.02**	**0.25**	**0.00**	**8.65**	**4.29**	**2.93**	**0.47**
Unidentified crustacean	14.23	2.50	3.44	1.42	7.03	2.11	0.30	0.12
Total	**14.23**	**2.50**	**3.44**	**1.32**	**7.03**	**2.11**	**0.30**	**0.13**
Other taxa								
Polychaeta	0.21	0.02	0.05	0.00	0.00	0.00	0.00	0.00
Chaetognatha	0.21	0.00	0.05	0.00	0.54	0.02	0.02	0.00
Siphonophora	0.21	0.00	0.05	0.00	1.08	0.22	1.52	0.02
Unidentified decapods	0.21	1.12	0.05	0.01	0.00	0.00	0.00	0.00
Unidentified fish	1.24	0.33	0.30	0.01	2.70	0.30	0.14	0.01
Total	**2.06**	**1.47**	**0.50**	**0.02**	**4.32**	**0.55**	**1.68**	**0.03**

Supplementary 1. Diet composition of *Electrona antarctica* and *Electrona carlsbergi* by percentage frequency of occurrence (%F), percentage number (%N), percentage mass (%M) and percentage index of relative importance (%IRI). These data are summarised from Saunders et al. (2014). Note that %F and %IRI are not additive and that grouping prey into categories influences the resulting $\%IRI_{DC}$ values

	Gymnoscopelus braueri				*Gymnoscopelus fraseri*				*Gymnoscopelus nicholsi*			
Prey	**%*F***	**%*M***	**%*N***	**%IRI**	**%*F***	**%*M***	**%*N***	**%IRI**	**%*F***	**%*M***	**%*N***	**%IRI**
Amphipoda												
Themisto gaudichaudii	8.06	15.84	2.98	4.97	10.68	16.44	1.14	1.70	22.50	5.53	0.95	1.77
Other amphipods	1.61	2.14	0.53	0.03	0.97	0.62	0.06	0.01	0.00	0.00	0.00	0.00
Total	**9.41**	**17.98**	**3.50**	**2.32**	**11.65**	**17.06**	**1.20**	**1.45**	**22.50**	**5.53**	**0.95**	**0.94**
Copepoda												
Calanoides acutus	2.15	0.23	0.79	0.07	15.53	1.36	1.65	0.42	22.50	0.52	1.71	0.61
Calanus propinquus	1.08	0.18	0.44	0.02	4.85	0.44	0.29	0.03	12.50	0.37	0.57	0.14
Calanus simillimus	6.18	0.57	3.24	0.77	18.45	1.97	3.02	0.83	10.00	0.07	0.57	0.08
Candacia sp.	3.49	0.43	1.23	0.19	6.80	0.30	0.40	0.04	17.50	0.42	1.04	0.31
Heterorhabdus spp.	2.15	0.15	0.70	0.06	3.88	0.22	0.23	0.02	7.50	0.10	0.47	0.05
Metridia spp.	34.95	3.94	37.22	47.06	80.58	18.57	60.55	57.68	80.00	2.59	32.73	34.38
Paraeuchaeta spp.	7.80	2.79	2.80	1.43	10.68	0.99	0.63	0.16	25.00	1.07	1.61	0.82
Pleuromamma robusta	15.86	1.87	7.97	5.11	43.69	5.08	6.39	4.53	42.50	3.01	16.13	9.90
Rhincalanus gigas	15.32	4.55	8.76	6.67	48.54	11.48	10.60	9.70	52.50	10.62	35.77	29.63
Other copepods	7.80	0.78	2.63	0.22	2.91	0.10	0.17	0.00	15.00	0.23	0.57	0.04
Total	**64.25**	**15.50**	**65.76**	**59.97**	**93.20**	**40.52**	**83.92**	**78.98**	**90.00**	**19.01**	**91.18**	**63.84**
Euphausiacea												
Euphausia frigida	2.42	3.78	1.40	0.41	0.00	0.00	0.00	0.00	2.50	2.69	0.66	0.10
Euphausia superba	5.38	20.11	2.01	3.89	0.00	0.00	0.00	0.00	20.00	61.81	1.33	15.36
Euphausia triacantha	1.88	9.54	0.70	0.63	0.00	0.00	0.00	0.00	2.50	1.48	0.09	0.05
Thysanoessa spp.	23.39	14.70	9.72	18.69	52.43	38.73	10.95	23.56	45.00	7.90	3.70	6.35
Unidentified euphausiids	9.68	9.98	3.24	4.19	3.88	0.20	0.34	0.02	5.00	0.79	0.19	0.06
Total	**40.86**	**58.12**	**17.08**	**35.30**	**54.37**	**38.92**	**11.29**	**18.59**	**67.50**	**74.66**	**5.98**	**35.04**
Ostracoda												
Unidentified ostracods	14.52	1.18	6.57	3.68	29.13	1.14	2.74	1.02	20.00	0.11	0.95	0.26
Total	**14.52**	**1.18**	**6.57**	**1.29**	**29.13**	**1.14**	**2.74**	**0.77**	**20.00**	**0.11**	**0.95**	**0.14**
Mollusca												
Unidentified pteropods	3.49	2.57	1.31	0.40	0.97	0.10	0.06	0.00	5.00	0.13	0.19	0.02
Total	**3.49**	**2.57**	**1.31**	**0.16**	**0.97**	**0.10**	**0.06**	**0.00**	**5.00**	**0.13**	**0.19**	**0.01**
Urochordata												
Salps	1.34	1.41	0.61	0.09	0.00	0.00	0.00	0.00	2.50	0.33	0.28	0.02
Total	**1.34**	**1.41**	**0.61**	**0.03**	**0.00**	**0.00**	**0.00**	**0.00**	**2.50**	**0.33**	**0.28**	**0.01**
Unidentified crustacean	11.83	2.79	3.85	1.40	0.97	0.10	0.06	0.00	5.00	0.20	0.19	0.02
Total	**11.83**	**2.79**	**3.85**	**0.90**	**0.97**	**0.10**	**0.06**	**0.00**	**5.00**	**0.20**	**0.19**	**0.01**
Other taxa												
Appendicularian	0.27	0.04	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chaetognatha	0.81	0.06	0.26	0.01	10.68	2.15	0.68	0.27	7.50	0.03	0.28	0.03
Siphonophora	0.54	0.05	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified fish	1.08	0.31	0.35	0.01	0.97	0.02	0.06	0.00	0.00	0.00	0.00	0.00
Total	**2.69**	**0.46**	**1.31**	**0.03**	**11.65**	**2.17**	**0.74**	**0.21**	**7.50**	**0.03**	**0.28**	**0.02**

Supplementary 2. Diet composition of *Gymnoscopelus braueri*, *Gymnoscopelus fraseri* and *Gymnoscopelus nicholsi* by percentage frequency of occurrence (%F), percentage number (%N), percentage mass (%M) and percentage index of relative importance (%IRI). These data are summarised from Saunders et al. (2015a) . Note that %F and %IRI are not additive and that grouping prey into categories influences the resulting $\%IRI_{DC}$ values

	Protomyctophum bolini				*Protomyctophum tenisoni*				*Protomyctophum choriodon*			
Prey	**%F**	**%M**	**%N**	**%IRI**	**%F**	**%M**	**%N**	**%IRI**	**%F**	**%M**	**%N**	**%IRI**
Amphipoda												
Themisto gaudichaudii	0.87	0.59	0.07	0.01	8.70	5.62	2.14	0.82	32.43	13.24	3.92	5.77
Other amphipods	0.43	1.13	0.04	0.01	0.00	0.00	0.00	0.00	5.41	2.67	0.31	0.08
Total	**1.30**	**1.72**	**0.11**	**0.02**	**8.70**	**5.62**	**2.14**	**0.48**	**35.14**	**15.91**	**4.23**	**5.16**
Copepoda												
Calanoides acutus	1.73	0.24	0.26	0.01	6.52	1.01	1.15	0.17	8.11	0.54	1.44	0.17
Calanus propinquus	8.23	2.26	1.46	0.43	4.35	0.58	0.33	0.05	10.81	0.44	0.52	0.11
Calanus simillimus	3.03	0.54	0.71	0.05	56.52	37.61	71.33	75.26	32.43	9.14	30.34	13.29
Eucalanus spp.	3.90	0.52	0.45	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Candacea sp.	6.06	1.25	0.90	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Metridia spp.	46.32	21.22	59.38	52.50	30.43	6.34	11.37	6.59	43.24	4.60	22.19	12.02
Paraeuchaeta spp.	22.94	8.64	3.21	3.82	6.52	1.73	0.82	0.20	5.41	0.37	0.21	0.03
Pleuromamma robusta	14.72	2.44	3.25	1.18	2.17	1.15	0.33	0.04	5.41	0.14	0.31	0.02
Rhincalanus gigas	45.02	31.42	24.85	35.62	28.26	11.96	5.27	5.95	62.16	16.66	23.22	25.72
Other copepods	5.63	1.37	0.78	0.03	10.87	1.01	1.32	0.08	5.41	0.10	0.21	0.01
Total	**84.42**	**69.88**	**95.25**	**94.20**	**82.61**	**61.38**	**91.93**	**89.70**	**78.38**	**31.99**	**78.43**	**63.14**
Euphausiacea												
Euphausia superba	0.87	2.42	0.11	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thysanoessa spp.	17.32	17.06	2.09	4.66	30.43	22.19	4.12	9.79	64.86	47.16	15.79	42.37
Unidentified euphausiids	10.82	6.06	0.97	1.07	13.04	4.18	0.99	0.82	5.41	0.54	0.31	0.05
Total	**29.00**	**25.54**	**3.18**	**5.63**	**43.48**	**26.37**	**5.11**	**9.69**	**67.57**	**47.70**	**16.10**	**31.45**
Ostracoda												
Unidentified ostracods	4.33	0.38	0.64	0.06	4.35	0.43	0.49	0.05	10.81	0.24	0.93	0.13
Total	**4.33**	**0.38**	**0.64**	**0.03**	**4.35**	**0.43**	**0.49**	**0.03**	**10.81**	**0.24**	**0.93**	**0.09**
Unidentified crustacean	10.82	2.48	0.82	0.27	2.17	1.01	0.16	0.03	8.11	4.16	0.31	0.21
Total	**10.82**	**2.48**	**0.82**	**0.13**	**2.17**	**1.01**	**0.16**	**0.02**	**8.11**	**4.16**	**0.31**	**0.15**
Other taxa												
Unidentified fish	0.00	0.00	0.00	0.00	2.17	5.19	0.16	0.14	0.00	0.00	0.00	0.00
Total	**0.00**	**0.00**	**0.00**	**0.00**	**2.17**	**5.19**	**0.16**	**0.08**	**0.00**	**0.00**	**0.00**	**0.00**

Supplementary 3. Diet composition of *Protomyctophum bolini*, *Protomyctophum tenisoni* and *Protomyctophum choriodon* by percentage frequency of occurrence (%F), percentage number (%N), percentage mass (%M) and percentage index of relative importance (%IRI). These data are summarised from Saunders et al. (2015b). Note that %F and %IRI are not additive and that grouping prey into categories influences the resulting $\%IRI_{DC}$ values

Prey	*Krefftichthys anderssoni* %F	%M	%N	%IRI	*Nannobrachium achirus* %F	%M	%N	%IRI
Amphipoda								
Themisto gaudichaudii	10.28	4.12	3.15	1.33	4.17	9.36	1.59	1.46
Primno macropa	2.13	0.57	0.12	0.03	4.17	1.09	1.59	0.36
Vibilia spp.	1.06	0.23	0.05	0.01	0.00	0.00	0.00	0.00
Unidentfied amphipod	0.35	0.03	0.02	0.00	8.33	19.19	4.76	6.41
Total	**12.77**	**4.95**	**3.34**	**0.91**	**16.67**	**29.64**	**7.94**	**8.81**
Copepoda								
Calanoides acutus	19.86	14.08	32.33	16.40	8.33	0.39	3.17	0.95
Calanus propinquus	5.32	1.46	1.11	0.24	8.33	1.09	6.35	1.99
Calanus simillimus	19.15	6.10	12.89	6.47	12.50	1.17	4.76	2.38
Clausocalanus spp.	3.90	0.07	0.39	0.03	0.00	0.00	0.00	0.00
Ctenocalanus spp.	1.06	0.15	0.86	0.02	0.00	0.00	0.00	0.00
Cornucalanus spp.	0.00	0.00	0.00	0.00	4.17	1.56	1.59	0.42
Drepanopus forcipatus	0.35	0.05	2.53	0.02	0.00	0.00	0.00	0.00
Eucalanus spp.	3.55	1.40	1.74	0.20	0.00	0.00	0.00	0.00
Heterorhabdus spp.	0.00	0.00	0.00	0.00	4.17	0.70	1.59	0.31
Metridia spp.	17.38	1.01	2.70	1.15	12.50	0.23	4.76	2.00
Microcalanus spp.	0.71	0.01	0.03	0.00	0.00	0.00	0.00	0.00
Paraeuchaeta spp.	2.48	0.42	0.25	0.03	25.00	7.64	11.11	15.05
Pleuromamma robusta	1.77	0.16	0.17	0.01	8.33	0.47	3.17	0.97
Rhincalanus gigas	51.42	33.70	30.55	58.77	29.17	7.96	19.05	25.28
Scolecithricella spp.	0.00	0.00	0.00	0.00	4.17	0.23	1.59	0.24
Unidentified copepods	4.61	0.84	2.27	0.11	4.17	0.39	1.59	0.26
Total	**69.15**	**59.46**	**87.82**	**87.90**	**58.33**	**21.84**	**58.73**	**66.08**
Euphausiacea								
Thysanoessa spp.	22.34	29.46	6.11	14.14	25.00	17.08	14.29	25.17
Unidentified euphausiids	10.28	2.79	0.60	0.62	8.33	3.82	3.17	1.87
Total	**32.62**	**32.25**	**6.71**	**10.97**	**33.33**	**20.90**	**17.46**	**17.98**
Chordata								
Unidentified fish	0.35	0.01	0.02	0.00	12.50	17.00	4.76	8.73
Total	**0.35**	**0.01**	**0.02**	**0.00**	**12.50**	**17.00**	**4.76**	**3.83**
Ostracoda								
Unidentified ostracods	1.77	0.62	1.39	0.06	12.50	0.31	4.76	2.04
Total	**1.77**	**0.62**	**1.39**	**0.03**	**12.50**	**0.31**	**4.76**	**0.89**
Mollusca								
Unidentified pteropods	0.00	0.00	0.00	0.00	4.17	6.86	1.59	1.13
Total	0.00	0.00	0.00	0.00	4.17	6.86	1.59	0.50
Urochordata								
Salps	0.71	0.69	0.03	0.01	0.00	0.00	0.00	0.00
Total	**0.71**	**0.69**	**0.03**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Unidentified crustacean	14.54	2.03	0.69	0.36	16.67	3.43	4.76	2.95
Total	**14.54**	**2.03**	**0.69**	**0.18**	**16.67**	**3.43**	**4.76**	**1.92**

Supplementary 4. Diet composition of *Krefftichthys anderssoni* and *Nannobrachium achirus* by percentage frequency of occurrence (%F), percentage number (%N), percentage mass (%M) and percentage index of relative importance (%IRI). Note that %F and %IRI are not additive and that grouping prey into categories influences the resulting $\%IRI_{DC}$ value