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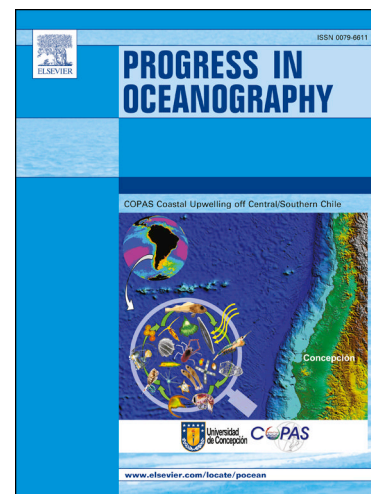
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Seasonal variation in the predatory impact of myctophids on zooplankton in the  
Scotia Sea (Southern Ocean)

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## Abstract

Myctophids are the biomass-dominant mesopelagic fishes in the Southern Ocean, but their trophic role within the pelagic food web south of the Antarctic Polar Front is poorly resolved from a seasonal perspective at the ocean-basin scale. In this study, the predatory impact of the predominant Southern Ocean myctophid community (*Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus braueri*, *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*, *Protomyctophum tenisoni*, *Protomyctophum choriodon*, *Krefflichthys anderssoni* and *Nannobranchium achirus*) on their zooplankton prey was examined during austral spring, summer and autumn in the Scotia Sea, one of the most productive regions of the Southern Ocean. Seasonal variations in diet and predation rates were apparent for all species. Based on the percentage index of relative importance, myctophids had high overlap in their diets, with all species mostly consuming copepods, small euphausiids and amphipods. Myctophid size was a key determinant of diet in the region, with larger species and intra-specific size classes consuming larger prey. Cluster analyses revealed myctophid feeding guilds that appeared to change seasonally, although there was little evidence of dietary specialisation. Myctophid predation on the daily productivity of most copepod species was relatively low across seasons (<7%), except for *Calanus simillimus* that was predated upon highly in summer (~26%). From the macrozooplankton component of the prey field, the myctophid community consumed substantial proportions of the euphausiid *Thysanoessa* spp. in each season (~7 to 76% daily productivity), particularly in summer. Relatively high proportions of the daily Antarctic krill (*Euphausia superba*) productivity (~8-58%) were also consumed by the larger myctophid species, particularly in summer by *Electrona antarctica*, suggesting increased competition for krill resources during the higher predator breeding season and possible reductions in food web stability during periods of reduced krill availability at this time. The amphipod *Themisto gaudichaudii* formed an important part of the larger myctophid species' diet in all seasons, with between 10 and 38% of its daily productivity being consumed. Myctophid predation on the daily productivity of salps was up to 4%, whilst their impact on ostracods and pteropods was negligible (<0.1% of daily productivity) in all seasons. This study demonstrates that Southern Ocean myctophids link secondary productivity to higher predators through both krill-independent and krill-dependent trophic pathways across seasons, with myctophids comprising a more krill-dependent pathway during austral summer.

## Key words

Myctophidae; predation rates; feeding ecology; food web; Southern Ocean

## 1.1 Introduction

Mesopelagic fish are probably the most abundant fishes on Earth (Irigoiien et al., 2014), yet they remain one of the least studied components of our world's oceans, with major gaps in our knowledge of their biology, ecology and behavioural adaptations. They have an important trophic role, both as zooplankton consumers and as prey of many higher marine predators, and may respire up to 10% of primary production in deep waters (Gjøsaeter & Kawaguchi, 1980; Irigoien et al., 2014; Pakhomov et al., 1996). Of the mesopelagic fish community, lanternfish, or myctophids (Family Myctophidae), are the most dominant in terms of diversity and abundance (Gjøsaeter & Kawaguchi, 1980), but all species around the globe are understudied and this has limited our understanding of how oceanic ecosystems and biogeochemical cycles operate.

Information on the ecology of myctophids is particularly scarce at high latitudes, such as the Southern Ocean, where they are difficult to sample at the appropriate spatial and temporal scales. What information we have indicates that there are 35 species of Southern Ocean myctophid fish, comprising an estimated biomass of between 70 and 200 million tonnes (Hulley, 1981; Lubimova et al., 1987), making the Southern Ocean one of the most diverse and biomass-rich myctophid fish communities worldwide. Myctophids are an integral component of the Southern Ocean ecosystem as they link primary consumers, such as copepods, amphipods and euphausiids (Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009), to a range of higher marine predators (Brown et al., 1999; Cherel et al., 2002; Cherel et al., 2010; Collins et al., 2007; Olsson & North, 1997; Rodhouse et al., 1992), providing a trophic pathway that is nominally independent of Antarctic krill (*Euphausia superba*), which otherwise dominate food webs south of the Antarctic Polar Front (APF) (Murphy et al., 2007b; Stowasser et al., 2012). In this region, myctophids are also an important conduit for the transfer of matter from the sea surface to mesopelagic depths through their extensive vertical migrations (Pakhomov et al., 1996).

The Southern Ocean is presently experiencing rapid broad-scale environmental change, particularly the Scotia Sea in the Atlantic sector, where evidence of increases in surface temperatures, reductions in winter sea ice extent and declines in krill stocks have been reported (Atkinson et al., 2004; Curran et al., 2003; de la Mare, 1997; Flores et al., 2012; Murphy et al., 2007a; Whitehouse et al., 2008). The Scotia Sea is one of the most productive regions of the Southern Ocean, containing around half of the circumpolar krill population, which in turn supports major populations of higher predators such as penguins, whales and seals in short efficient food chains (Atkinson et al., 2004; Holm-Hansen et al., 2004; Murphy et al., 2007b). The Scotia Sea is also the primary location of the Antarctic krill fishery, as well as fisheries for Patagonian toothfish (*Dissostichus eleginoides*) and mackerel icefish (*Champsocephalus gunnari*) (Constable et al., 2000; Everson, 2000). Environmental change may have already had a negative impact on krill biomass in this region (Atkinson et al., 2004) and may continue to do so under a scenario of sustained climate change in this region (Murphy et al., 2007a). The importance of myctophids as a krill-independent trophic pathway in the food web here may correspondingly increase. There is therefore a clear need for more comprehensive information on the ecology and trophodynamics of the myctophid community in the Scotia Sea, particularly from a seasonal perspective at the ocean-basin scale to facilitate robust ecosystem management (Constable et al., 2014).

Understanding temporal, spatial and ontogenetic patterns in diet is essential to understanding food web dynamics and resource partitioning, and recent studies have cast new light on the feeding ecology of several of the most common myctophids in the Scotia Sea (Lourenço et al., 2017; Saunders et al., 2014; Saunders et al., 2015b; Saunders et al., 2015c). These studies showed that myctophids consume mostly copepods, euphausiids and amphipods, with evidence of dietary segregation between species, probably related to inter-specific variations in body size, variations in vertical migratory behaviour and depth selection (Gaskett et al., 2001; Kozlov & Tarverdiyeva, 1989; Naumov et al., 1981; Pakhomov et al., 1996; Pusch et al., 2004; Rowedder, 1979; Shreeve et al., 2009). Spatial and temporal variation in prey consumption was also apparent for most myctophid species that broadly corresponded with spatial patterns in prey distribution and possibly seasonal changes in prey ontogeny (Lourenço et al., 2017; Saunders et al., 2014; Saunders et al., 2015c; Shreeve et al., 2009). Based on seasonally and spatially averaged data from across the Scotia Sea, a recent study showed that the overall predatory impact of the Scotia Sea myctophid community on the

productivity of most of their prey species, including Antarctic krill, was relatively low ( $<5\% \text{ C m}^{-2} \text{ d}^{-1}$ ) (Saunders et al., 2015a), which is consistent with other studies conducted in the region at more limited spatial and temporal scales (Shreeve et al., 2009). However, trophic relationships are likely to change both intra- and inter-annually, and it remains unclear how the predatory impact of myctophids on the zooplankton community varies temporally, and whether myctophids maintain a robust krill-independent trophic pathway at all times of the year.

This study examines and compares the diets of the Scotia Sea myctophid community at the ocean-basin scale during austral spring, summer and autumn using net-catch data collected as part of the most comprehensive myctophid fish survey in the Southern Ocean to date. The seasonal vertical distributions of myctophids were compared with those of their main prey species to investigate the extent of overlap between predators and prey at different times of year and to assess the extent of seasonal prey selectivity by myctophids. The predatory impact of myctophids on assemblages of their prey was also estimated in different seasons, together with sensitivity analyses to ascertain the level of variation around these estimates. To our knowledge, there have been no other studies that have focused upon seasonal variations in the predatory impact of an entire myctophid community on their zooplankton prey at the ocean-basin scale in the Southern Ocean, or elsewhere. Our data therefore provide important parameterizations for food web and ecosystem studies in the Southern Ocean and contribute to resolving the trophodynamics of the global mesopelagic fish community.

## 2.1. Materials and methods

### 2.1.1 Study region

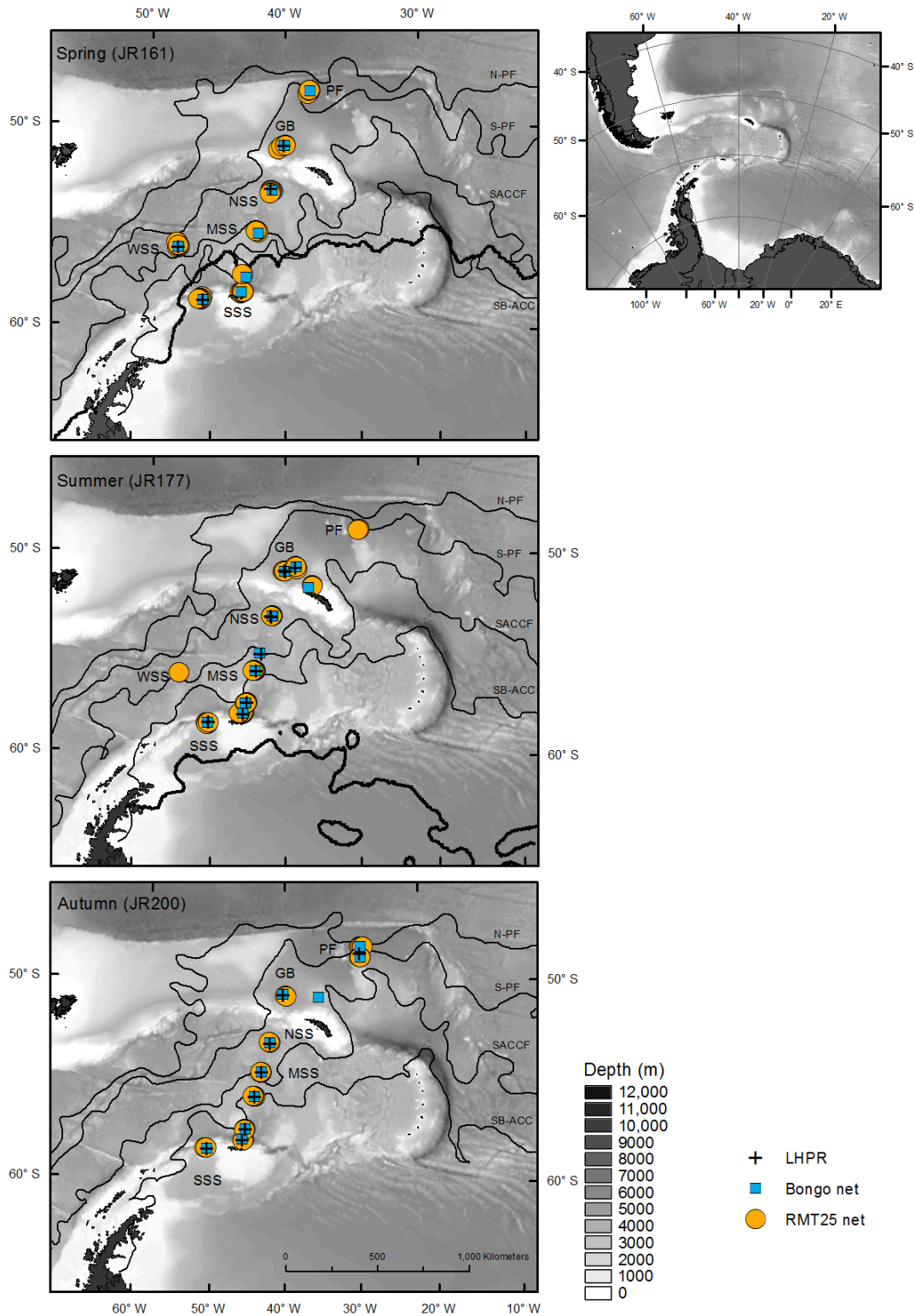
Three multidisciplinary research cruises were conducted in the Scotia Sea onboard RSS *James Clark Ross* during austral spring (October-December 2006; JR161), summer (January-February 2008; JR177) and autumn (March-April 2009; JR200). Six nominal stations were sampled repeatedly along a transect that spanned the latitudinal extent of the Scotia Sea ( $63^{\circ}\text{S}$  to  $50^{\circ}\text{S}$ ) between the sea ice zone (SIZ) and the Antarctic Polar Front (APF): Southern Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF; Fig. 1).

### 2.1.2 Net sampling

At each station, mesopelagic fish were collected by depth-stratified rectangular mid-water trawl nets (RMT25; Piatkowski et al. 1994) deployed between 0-200, 200-400 m, 400-700 and 700-1000 m. These zones were repeated by day and night in spring and summer, but only during periods of darkness in the autumn. Each net had 5 mm mesh size at the cod end and a flow meter to measure the filtered water volume. The zooplankton prey field was characterized by oblique Longhurst-Hardy Plankton Recorder (LHPR) tows to 1000 m during both day and night. The LHPR was fitted with a 380 mm diameter nose cone and 200  $\mu$ m mesh net and filtering gauzes. LHPR samples were collected at a depth resolution of around 20-25 m per sampling patch, but counts were averaged into the same depth horizons as the RMT25 hauls to facilitate direct comparisons of vertical distribution patterns. The prey field was also characterized using a paired Bongo net (180 mm diameter mouth) with 53  $\mu$ m mesh. All Bongo nets were deployed during times of daylight to a depth of 400 m. Further details of the net sampling are described in Collins et al. (2012) and Ward et al. (2012).

### 2.1.3 Sample processing

All RMT25 catches were sorted onboard to the lowest taxonomic level possible. Total catch weight per fish species was recorded and all fish were measured to the nearest mm (standard length, SL). Stomachs were dissected from a random subsample of 25 fish per species, or from each specimen where catches were small. These fish were weighed prior to dissections. All stomachs and LHPR samples were frozen at -20 °C for subsequent microscopic analysis at the laboratory. Bongo net samples were preserved in 4% formalin and seawater solution and analysed in the laboratory under a stereomicroscope.



**Fig.1** Map of the study area showing the locations of the 25 m<sup>2</sup> rectangular midwater trawl nets (RMT25), Longhurst-Hardy Plankton Recorder (LHPR) trawls and Bongo net hauls during the three surveys. Sampling stations were: 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) were: 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).

#### 2.1.4 Stomach contents and diet analysis

Fish stomach contents were thawed and sorted to the lowest taxonomic level possible. Individual prey items were enumerated and weighed. During instances in which prey was highly disaggregated, the weights of component species were estimated as a proportion of the total stomach contents weight.

Diet composition was expressed using percentage frequency of occurrence (%  $F$ ), percentage mass (%  $M$ ), percentage number (%  $N$ ) and percentage Index of Relative Importance (%  $IRI$ ) (Cortes, 1997). 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. The %  $IRI_{DC}$  was calculated for the following key diet (DC) categories to examine seasonal variations in diet following Shreeve et al. (2009): 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 gaudichaudi* and other taxa (mostly unidentified crustaceans, Mollusca, Ostracoda, Urochordata). The  $\pm 95\%$  confidence limits were calculated for the mean %  $IRI_{DC}$  using a bootstrapping technique, whereby each species dataset (individual stomachs) was re-sampled (with replacement) 1000 times (Main et al., 2009).

### 2.1.5 Diet comparison between myctophid species

Similarities in the diets of the myctophid species in each season 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 of 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 complete linking method and a SIMPER routine was used to determine which prey species contributed most to the resulting cluster groupings.

### 2.1.6 Predation impact on zooplankton productivity

We used the model detailed in Shreeve et al. (2009) to determine the proportion of prey productivity consumed by each myctophid species in each season:

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

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 prey species  $i$ ,  $P_j$  is the depth-integrated concentration of predator species  $j$  (ind. m<sup>-2</sup>),  $G$  is the gut passage time (hrs),  $Z_i$  is the depth-integrated concentration of prey species  $i$  (ind. m<sup>-2</sup>), and  $F_i$  is the growth rate of prey species  $i$  (μg C d<sup>-1</sup>).

The calculation was performed for each prey species  $i$  consumed by myctophid  $j$  three times to determine a best estimate of predation and the most plausible estimates of the upper and lower bounds as detailed in Shreeve et al. (2009). Parameter values in the equation above were calculated as detailed later.

#### 2.1.6.1 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*, *Krefflichthys anderssoni* and *Nannobranchium achirus*. The prey field was limited to 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 *Triconia* spp. (formerly *Oncaea* spp.), ostracods, salps and pteropods.

A non-parametric bootstrapping technique was used to generate values for  $N_{i,j}$ . 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. This process was repeated 100 times and the median of the series was used as the best estimate value, with the 25<sup>th</sup> and 75<sup>th</sup> percentiles comprising the lower and upper bounds, respectively.

#### 2.1.6.2 Depth-integrated myctophid concentrations ( $P_j$ )

Myctophid concentrations were derived from night-time RMT25 net catches in each season to avoid issues with daytime net avoidance. A total of 86 stratified hauls were deployed during this time, with 26 in spring, 24 in summer and 36 in autumn. Net catch concentrations were expressed as a depth-integrated concentration per net (ind. m<sup>-2</sup>) between 0 and 1000 m. The best estimate value for  $P_j$  was the median of the pooled net concentrations and the 25<sup>th</sup> and 75<sup>th</sup> percentile values comprised the upper and lower bounds.

#### 2.1.6.3 Depth-integrated prey species concentrations ( $Z_i$ )

A total of 24 LHPR deployments were undertaken, with 4 in spring, 11 in summer and 9 in autumn. LHPR concentrations of prey species were expressed as depth-integrated concentrations (ind. m<sup>-2</sup>) per haul between 0 and 1000 m. All LHPR hauls were pooled for each survey and the median of this series was used as our best estimate value. The 25<sup>th</sup> and

75<sup>th</sup> percentile values were used as the upper and lower bounds, respectively. Similarly, prey species concentrations (standardised to ind. m<sup>-2</sup>) were also derived from the 65 Bongo net hauls deployed between 0 and 400 m (12 in spring, 33 in summer and 20 in autumn). We selected the highest best estimate values from these two samplers for our calculations to provide the most conservative estimates of predation rates on the prey field.

#### 2.1.6.4 Growth rates of prey species ( $F_i$ )

Following Shreeve et al. (2009), species-specific growth rates ( $\mu\text{g C d}^{-1}$ ) were estimated from direct measurements of carbon weight (5 to 10 individuals per species), multiplied by the weight-specific growth rate of each species using the functions provided by Hirst et al. (2003). For the copepod species, a weight-specific growth rate function appropriate for adult broadcast spawning copepods at 5 °C was used. 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 due to the absence of functions for lower temperatures. Although these growth functions were derived at ambient water temperatures greater than those of our study region (Fig. 2), they are the most appropriate functions available at this time. Previous Southern Ocean estimates derived from these functions were considered to represent an upper limit to zooplankton production, such that calculations represent a minimum of the predatory impact of myctophids on zooplankton (Saunders et al., 2015a; Shreeve et al., 2009). However, to provide a more realistic perspective of the level of myctophid predation on their daily prey productivity in this study, we used a simple  $Q_{10}$  temperature value to scale down the zooplankton production estimates to values that are more representative of the ambient temperatures in the study region. A  $Q_{10}$  value of 2.3 was selected for this purpose, which is typical of metabolic processes in marine organisms (Clarke, 1991; Schmidt-Nielsen, 1997). The growth rate function provided by Bednarsek et al. (2012) was used for pteropods, assuming that the majority of this group was most likely comprised of *Limacina* species.

#### 2.1.6.5 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. In our calculations, temperature data collected at each station during the surveys (Venables et al., 2012) were averaged for each survey to provide an estimate of the overall ambient temperature between 0-1000 m. Seasonal mean temperatures in the region were 1.7, 1.6 and 0.8 °C, giving best estimates of gut passage times of 20 hrs in spring, 21 hrs in summer and 25 hrs in autumn, respectively. Minimum mean temperature values were 0.5, 0.1 and -0.3 °C, which gave slowest respective gut passage times of approximately 26, 28 and 31 hrs in spring, summer and autumn. Maximum mean temperatures were 2.1, 3.3 and 4.0 °C, so the fastest gut passage times were 19 hrs in spring, 15 hrs in summer and 13 hrs in autumn.

### 3.1 Results

#### 3.1.1 Oceanographic conditions

Temperature and salinity profiles showed the presence of three major water masses at each station across the Scotia Sea: Antarctic Surface Water (ASW) above ~50 m, Winter Water (WW) around 80 m and Circumpolar Deep Water (CDW) below ~200 m (Fig. 2). Latitudinal differences in these water mass properties were apparent, with waters becoming progressively cooler between the APF and the SIZ. Temperatures in the ASW varied the most along this latitudinal gradient (~+4 to -2 °C). Seasonal variations in water mass properties were also apparent at each station, as waters generally became progressively warmer between spring and autumn. In general, stations in the WSS and MSS lay close to the Southern Antarctic Circumpolar Current Front (SACCF) and had relatively similar water mass properties, whilst the NSS station showed characteristics of the southern edge of the APF, particularly during spring. The GB station, situated downstream of South Georgia, had water mass properties that were more similar to those in the middle of the Scotia Sea than the NSS, primarily due to a retroflexion of the SACCF. The northernmost PF stations were situated north of the southern edge of the APF, whilst the SSS stations were situated in regions where sea ice was

present in spring. A more detailed description of the oceanography is given in Venables et al. (2012).

### 3.1.2 Seasonal myctophid distribution patterns

*Electrona antarctica*, *Gymnoscopelus braueri*, *Krefftichthys anderssoni* and *Protomyctophum bolini* were the most abundant species caught during the three surveys (Fig. 3) (Collins et al., 2012; Lourenço et al., 2017; Saunders et al., 2014; Saunders et al., 2015b; Saunders et al., 2015c). In each season, *E. antarctica* was most abundant in the SIZ and least abundant at the northern stations situated in close proximity to the APF. *Gymnoscopelus braueri* occurred throughout the Scotia Sea in all seasons, whilst *K. anderssoni* was most abundant in the northern Scotia Sea and seldom occurred in regions south of the SACCF (56 °S).

*Protomyctophum bolini* was also most abundant in the northern Scotia Sea in all seasons, particularly in regions associated with APF waters. *Electrona carlsbergi* was mostly absent from the APF and GB stations, but it occurred in greatest abundance at the NSS station in spring and further south towards the SACCF in both summer and autumn. This front marked the southernmost boundary for the species. *Protomyctophum tenisoni*, *Gymnoscopelus fraseri*, *Protomyctophum choriodon* and *Nannobranchium achirus* were predominantly distributed in the northern Scotia Sea in all seasons in which they were caught, with *P. tenisoni* and *N. achirus* most abundant in waters associated with the APF, and *G. fraseri* and *P. choriodon* abundance greatest around the GB and NSS stations. However, *P. choriodon* was present in waters further south in autumn indicative of a possible seasonal migration. *Gymnoscopelus nicholsi* was distributed throughout the Scotia Sea during spring, summer, and autumn, but it occurred only in relatively small numbers at each station.

Due to possible issues with net avoidance by myctophids during day-light hours, only night time data were used to describe the seasonal vertical distribution patterns (Fig. 4). All species occupied ASW, WW and CDW at some stage during the three surveys. *Protomyctophum bolini*, *Protomyctophum tenisoni* and *Protomyctophum choriodon* were predominantly confined to the upper 400 m of the water column, with no evidence of seasonal variation in depth distribution. Both *Gymnoscopelus braueri* and *Gymnoscopelus nicholsi* were confined to waters above 400 m in spring, but occurred deeper in summer and autumn, indicative of

some seasonal variation in vertical distribution. *Electrona antarctica* was spread throughout the water column between 0 and 1000 m during all seasons, but the greatest concentrations occurred between 200 and 400 m in spring, whilst the majority of the population was distributed between 400 and 700 m in summer and between 0 and 200 m in autumn. *Electrona carlsbergi* and *Gymnoscopelus fraseri* were mostly distributed in the upper 400 m of the water column in all seasons, but there was evidence of a seasonal deepening in their depth distributions between spring (0 to 200 m) and autumn (200 to 400 m) for both of these species. *Krefflichthys anderssoni* and *Nannobrachium achirus* were mostly distributed below 400 m in CDW in all seasons, although there was still evidence of seasonal variation in their depth distributions in this thermally stable water mass. For instance, the majority of the *K. anderssoni* population was distributed between 200 and 400 m in spring, but peak concentrations occurred deeper between 400 and 700 m in summer and between 400 and 1000 m in autumn. Conversely, the *N. achirus* population was spread between 200 and 1000 m in spring, but predominantly distributed between 400 and 700 m in summer and between 400 and 1000 m in autumn.

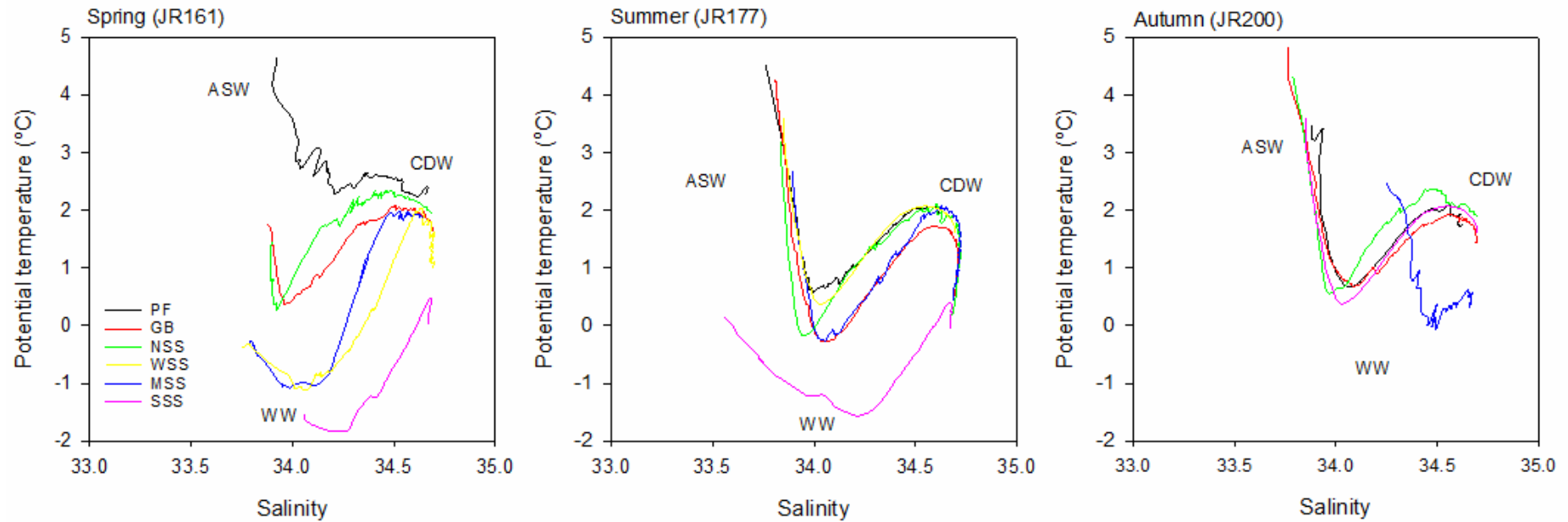
### 3.1.3 Abundance and vertical distribution patterns of prey species

Best estimates (median values) of depth-integrated macrozooplankton abundance varied substantially between seasons (Table 1). The amphipod *Themisto gaudichaudii* occurred mostly in the upper 200 m of the water column in each season and was most abundant in summer (589 ind. m<sup>-2</sup>; Table 1 and Fig 5). All euphausiid species were distributed predominantly above 200 m in each season. *Euphausia superba* and *Euphausia frigida* were most abundant in autumn, comprising depth-integrated abundances of 1,662 and 15 ind. m<sup>-2</sup>, respectively, whilst *Thysanoessa* spp. was most abundant in spring (707 ind. m<sup>-2</sup>). Pteropods, which were spread throughout the water column in spring and summer, but occurred only between 400 and 1000 m during autumn, were relatively abundant in all seasons, comprising a depth-integrated abundance of up to 8,801 ind. m<sup>-2</sup> in summer. Ostracods were also relatively abundant in the study area, particularly during spring where their depth-integrated abundance was 1,297 ind. m<sup>-2</sup>. Data on the vertical distribution of ostracods were only available for the spring-time, so it was not possible to examine seasonal variations in their depth distribution. During this time, these organisms were spread throughout the water column with peak concentrations occurring between 200 and 400 m. Salps were most

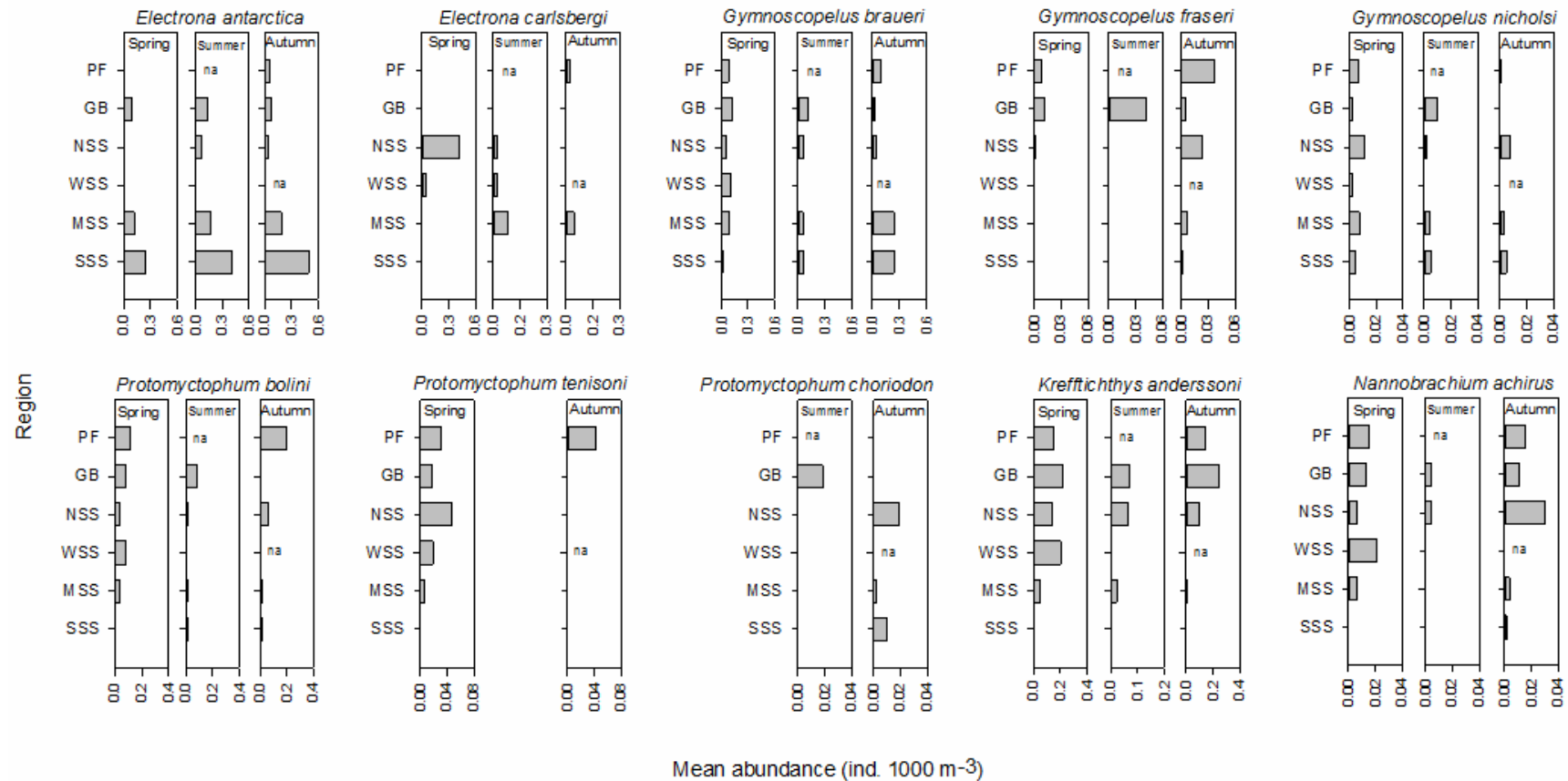
abundant in waters above 200 m in spring and summer, but the majority of the population was distributed between 200 and 400 m in autumn. However, the overall abundance of salps was relatively low during the study ( $<7$  ind.  $m^{-2}$ ).

High seasonal variation in depth-integrated abundance was also apparent for the copepod component of the prey field during the study. Overall, *Triconia* spp. was the most abundant copepod taxon encountered during the study, particularly during spring, but these copepods also had the greatest level of seasonal variation in abundance, with best estimates ranging between 196 and 113,498 ind.  $m^{-2}$  (Table 1). *Triconia* spp. were spread throughout the water column in spring and summer, but a clear seasonal deepening was evident in autumn, with the population mostly distributed below 400 m and the greatest concentrations occurring between 700 and 1000 m (Fig. 5). *Pleuromamma robusta* abundance varied between 89 and 46,207 ind.  $m^{-2}$ , with peak abundance occurring in summer and the majority of the population moving to depths below 200 m in this season. Copepods of the *Metridia* genus attained depth-integrated abundances between 7,465 and 21,491 ind.  $m^{-2}$ , with the greatest abundance occurring in autumn. *Metridia* spp. occurred throughout the water column in spring and autumn but was most abundant in the upper 400 m. However, peak concentrations occurred predominantly in the upper 200 m in summer. The abundance of *Calanus simillimus* ranged between 31 and 5,343 ind.  $m^{-2}$  and the species was most abundant in autumn. This species was distributed between 0 and 700 m in spring and autumn, but was confined to the upper 200 m in summer. A similar pattern in vertical distribution was apparent for *Rhincalanus gigas*, which attained depth-integrated abundances of between 96 and 2,967 ind.  $m^{-2}$  and was most abundant in spring. *Calanoides acutus* comprised depth-integrated abundances between 654 and 2,332 ind.  $m^{-2}$ . The species was most abundant in spring and the majority of the population was spread between 0 and 700 m at this time. The *C. acutus* population mostly occurred in the surface zone (0-200 m) in summer, but spread between 0 and 1000 m in autumn. There was no evidence of seasonal variation in the vertical distribution of *Paraeuchaeta* spp. which occurred between 0 and 1000 m in all seasons, with the greatest concentrations of the population occupying waters above 400 m. The abundance of these copepods varied between 123 and 688 ind.  $m^{-2}$ , with peaks in abundance occurring in spring.

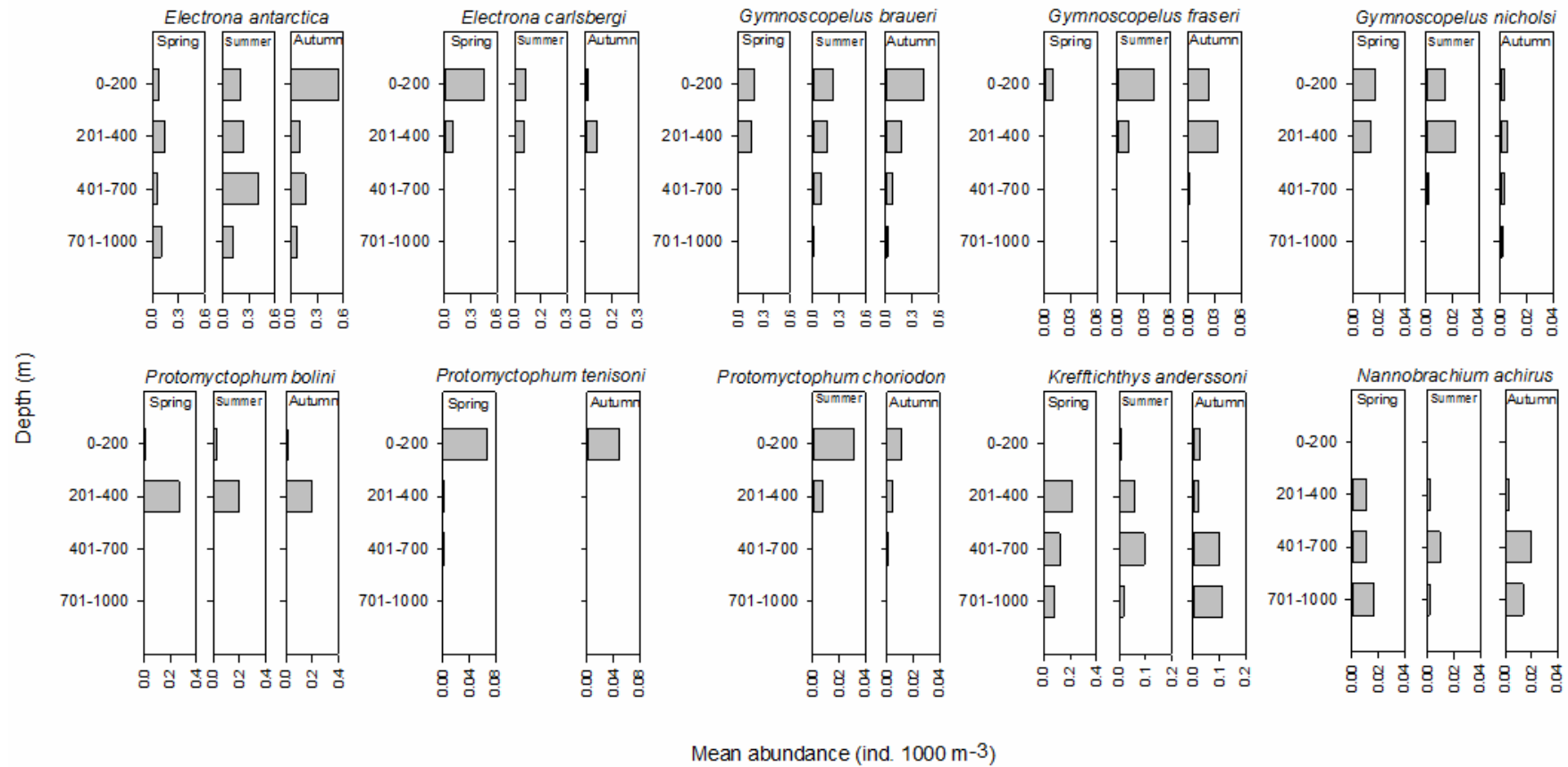




**Fig. 2** Typical water mass properties at each station across the Scotia Sea during spring (JR161), Summer (JR177) and autumn (JR200). Stations are: Polar Front (PF), Georgia Basin (GB), North Scotia Sea (NSS), Western Scotia Sea (WSS), Mid Scotia Sea (MSS) and Southern Scotia Sea (SSS). Water masses are: Antarctic Surface Water (ASW), Winter Water (WW) and Circumpolar Deep Water (CDW).



**Fig. 3** Mean abundance of myctophid fish across the study region during spring (JR161), summer (JR177) and autumn (JR200). Stations are PF: Polar Front, GB: Georgia Basin, NSS: North Scotia Sea, WSS: West Scotia Sea, MSS: Mid Scotia Sea and SSS: South Scotia Sea. Stations where no non-targeted net hauls were conducted are denoted as (na).



**Fig. 4** Night time vertical distribution of myctophid fish caught in the RMT25 net hauls during spring, summer and autumn.

Taxon	Sampler	Spring (JR161)			Summer (JR177)			Autumn (JR200)			
		Lower	Best	Upper	Lower	Best	Upper	Lower	Best	Upper	
<b>Myctophidae</b>	<i>Electrona carlsbergi</i>	RMT25	0.000	<b>0.004</b>	0.043	0.000	<b>0.021</b>	0.008	0.000	<b>0.001</b>	0.007
<b>Myctophidae</b>	<i>Electrona antarctica</i>	RMT25	0.006	<b>0.021</b>	0.077	0.120	<b>0.166</b>	0.283	0.017	<b>0.074</b>	0.271
<b>Myctophidae</b>	<i>Gymnoscopelus fraseri</i>	RMT25	0.000	<b>0.002</b>	0.003	0.000	<b>0.011</b>	0.022	0.001	<b>0.003</b>	0.010
<b>Myctophidae</b>	<i>Gymnoscopelus nicholsi</i>	RMT25	0.002	<b>0.002</b>	0.007	0.003	<b>0.008</b>	0.011	0.000	<b>0.001</b>	0.005
<b>Myctophidae</b>	<i>Gymnoscopelus braueri</i>	RMT25	0.029	<b>0.067</b>	0.093	0.066	<b>0.094</b>	0.133	0.015	<b>0.078</b>	0.186
<b>Myctophidae</b>	<i>Krefflichthys anderssoni</i>	RMT25	0.000	<b>0.045</b>	0.152	0.004	<b>0.010</b>	0.070	0.000	<b>0.012</b>	0.119
<b>Myctophidae</b>	<i>Nannobranchium achirus</i>	RMT25	0.000	<b>0.003</b>	0.012	0.000	<b>0.003</b>	0.007	0.001	<b>0.005</b>	0.008
<b>Myctophidae</b>	<i>Protomyctophum tenisoni</i>	RMT25	0.002	<b>0.006</b>	0.019	0.000	<b>0.000</b>	0.000	0.000	<b>0.011</b>	0.016
<b>Myctophidae</b>	<i>Protomyctophum bolini</i>	RMT25	0.001	<b>0.047</b>	0.074	0.020	<b>0.023</b>	0.055	0.002	<b>0.018</b>	0.039
<b>Myctophidae</b>	<i>Protomyctophum choriodon</i>	RMT25	0.000	<b>0.000</b>	0.000	0.000	<b>0.007</b>	0.011	0.000	<b>0.005</b>	0.006
<b>Amphipoda</b>	<i>Themisto gaudichaudii</i>	Bongo net	5.116	<b>20.686</b>	80.149	235.752	<b>589.380</b>	785.840	0.000	<b>23.574</b>	235.740
<b>Copepoda</b>	<i>Calanoides acutus</i>	Bongo net	1926.770	<b>2332.032</b>	2876.846	528.443	<b>1171.738</b>	1790.469	508.076	<b>654.469</b>	970.201
<b>Copepoda</b>	<i>Calanus simillimus</i>	Bongo net	87.553	<b>172.486</b>	415.881	2.523	<b>30.882</b>	219.106	0.000	<b>5343.440</b>	15244.520
<b>Copepoda</b>	<i>Metridia</i> spp.	Bongo net	3871.050	<b>8646.000</b>	10945.050	2082.476	<b>7465.480</b>	15323.880	12170.078	<b>21491.630</b>	46205.040
<b>Copepoda</b>	<i>Triconia</i> spp.	Bongo net	84062.700	<b>113498.400</b>	180465.600	117.876	<b>196.460</b>	628.672	47933.800	<b>62235.360</b>	87066.640
<b>Copepoda</b>	<i>Paraeuchaeta</i> spp.	Bongo net	491.250	<b>687.750</b>	1198.650	157.168	<b>275.044</b>	471.504	82.363	<b>122.847</b>	161.191
<b>Copepoda</b>	<i>Pleuromamma robusta</i>	Bongo net	0.000	<b>89.323</b>	357.293	33005.280	<b>46207.392</b>	103102.208	22.689	<b>196.450</b>	3143.200
<b>Copepoda</b>	<i>Rhincalanus gigas</i>	Bongo net	1355.850	<b>2967.150</b>	5511.825	314.336	<b>707.256</b>	27425.816	50.584	<b>95.921</b>	1131.632
<b>Euphausiacea</b>	<i>Euphausia frigida</i>	LHPR	0.000	<b>1.482</b>	122.860	0.609	<b>13.940</b>	28.350	4.517	<b>14.695</b>	48.745
<b>Euphausiacea</b>	<i>Euphausia superba</i>	LHPR	10.402	<b>62.635</b>	327.648	0.000	<b>28.650</b>	291.255	0.000	<b>1662.472</b>	13021.204
<b>Euphausiacea</b>	<i>Thysanoessa</i> spp.	LHPR	294.750	<b>707.400</b>	2534.850	6.089	<b>25.858</b>	46.553	0.000	<b>78.580</b>	412.545
<b>Ostracoda</b>	Ostracods	Bongo net	756.525	<b>1296.900</b>	1925.700	628.672	<b>1257.344</b>	3457.696	461.658	<b>785.800</b>	903.670
<b>Mollusca</b>	Pteropods	Bongo net	0.000	<b>275.100</b>	1257.600	1257.344	<b>8801.408</b>	106874.240	1257.280	<b>2671.720</b>	8486.640
<b>Urochordata</b>	Salps	LHPR	0.000	<b>0.000</b>	0.000	0.000	<b>7.144</b>	78.584	0.000	<b>1.436</b>	76.975

**Table 1.** Depth-integrated net catch concentrations (ind. m<sup>-2</sup>) of the most abundant myctophids and their zooplankton prey species north of the South Antarctic Circumpolar Current Front (SACCF) during the three surveys. The Lower, **Best** and Upper concentration estimates represent the 25<sup>th</sup> percentile, median and 75<sup>th</sup> percentile, respectively.

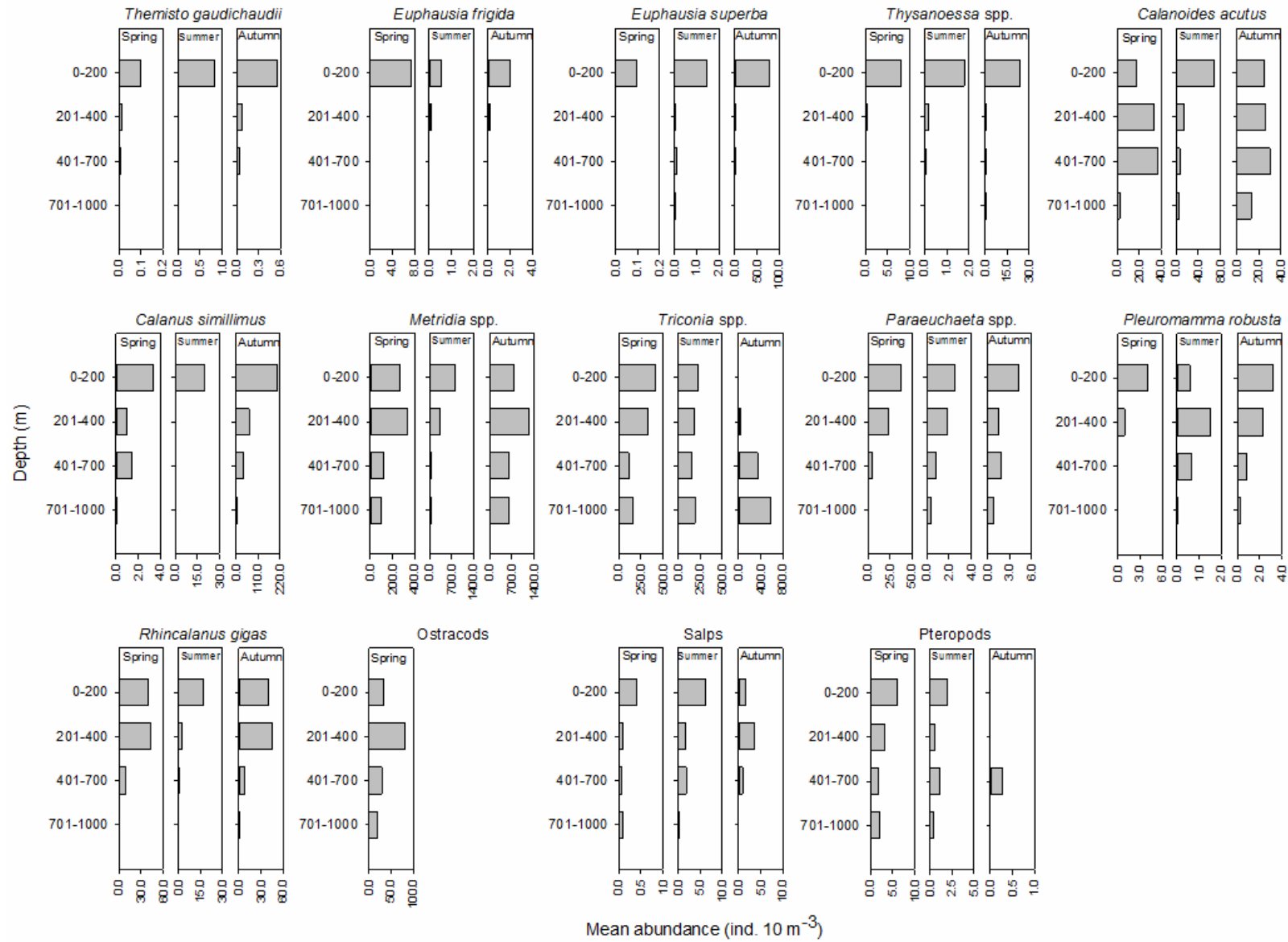


Fig. 5 Depth distributions of the main zooplankton in the diets of myctophids during spring (JR161), summer (JR177) and autumn (JR200).

### 3.1.4 Seasonal diet composition

A total of 1804 myctophid stomachs contained prey items and were used in the analysis (Table 2). For most species, these stomachs samples were obtained from a range of environments that covered their latitudinal range across the Scotia Sea in each season, and the overall size ranges and depth distributions of the sampled fish were representative of those found previously in the region (Collins et al., 2008; Donnelly & Torres, 2008; Hulley, 1981; Piatkowski et al., 1994; Pusch et al., 2004).

Based on percentage Index of Relative Importance, planktonic crustaceans mostly dominated the diets of all myctophids in each season (Supplementary 1; see Supplementary 2-4 for diet matrices by percentage frequency, percentage number and percentage mass). Seasonal variation in diet composition was apparent for all species that were sampled on multiple surveys. Only *Protomyctophum choriodon* and *Nannobranchium achirus* were sampled during single seasons, which prohibited a temporal examination of the diets of these species (Table 2).

#### 3.1.4.1 Southern Ocean *Electrona*

The diet of *Electrona antarctica* (24-115 mm SL) was dominated by the euphausiid *Euphausia superba* (41 %IRI), copepods *Metridia* spp. (34 %IRI) and unidentified pteropods (13 %IRI) in spring (Supplementary 1 and Fig. 6). Both *E. superba* and pteropods were predominantly distributed in the upper 200 m at this time, whilst *Metridia* spp. was most abundant above 400 m. These zones appeared to be only occupied by *E. antarctica* at night. During summer, the diet of *E. antarctica* switched to mostly the amphipod *Themisto gaudichaudii* (76 %IRI) and *E. superba* (11 %IRI) that were mostly confined to depths between 0 and 200 m. Although *E. antarctica* was present in this region at night during summer, the majority of the population was distributed between 400 and 700 m. The diet of *E. antarctica* in autumn was again dominated by *E. superba* (75 %IRI) and *Metridia* spp. (12% IRI) and there was strong overlap in the vertical distribution patterns of these prey species and *E. antarctica* (0 to 200 m) at this time.

Species	Season	SSS	MSS	WSS	NSS	GB	PF	Total	Mean SL (mm)	Range SL (mm)
<i>Electrona antarctica</i>	Spring (JR161)	104	22	0	0	34	2	162	72	31-113
	Summer (JR177)	59	39	2	5	88	10	203	71	25-115
	Autumn (JR200)	65	22	1	3	11	18	120	67	24-110
<i>Electrona carlsbergi</i>	Spring (JR161)	0	17	0	89	2	12	120	78	65-90
	Summer (JR177)	0	17	0	11	0	7	35	77	69-87
	Autumn (JR200)	0	17	0	2	0	11	30	76	69-84
<i>Gymnoscopelus braueri</i>	Spring (JR161)	58	12	9	18	31	28	156	84	34-139
	Summer (JR177)	28	17	0	9	33	10	97	80	37-162
	Autumn (JR200)	10	52	0	9	0	48	119	83	34-129
<i>Gymnoscopelus fraseri</i>	Spring (JR161)	0	0	0	2	3	6	11	80	60-115
	Summer (JR177)	0	0	0	0	55	10	65	64	39-90
	Autumn (JR200)	0	0	0	0	0	27	27	67	42-85
<i>Gymnoscopelus nicholsi</i>	Spring (JR161)	7	4	0	5	0	5	21	129	34-165
	Summer (JR177)	3	2	1	1	5	0	12	126	37-155
	Autumn (JR200)	0	4	0	2	0	1	7	117	34-151
<i>Krefftichthys anderssoni</i>	Spring (JR161)	1	18	18	39	50	47	173	50	25-74
	Summer (JR177)	1	0	0	24	40	0	65	44	30-71
	Autumn (JR200)	0	6	0	16	18	3	43	39	15-71
<i>Nannobrachium achirus</i>	Spring (JR161)	1	1	3	4	9	6	24	127	65-153
	Summer (JR177)	0	0	0	0	0	0	0	132	114-149
	Autumn (JR200)	0	0	0	0	0	0	0	128	88-167
<i>Protomyctophum bolini</i>	Spring (JR161)	10	9	28	19	18	39	123	47	23-66
	Summer (JR177)	2	0	0	9	58	9	78	45	27-60
	Autumn (JR200)	8	8	0	0	0	14	30	38	23-60
<i>Protomyctophum tenisoni</i>	Spring (JR161)	0	0	9	15	0	5	29	48	42-55
	Summer (JR177)	0	0	0	0	0	0	0	32	28-41
	Autumn (JR200)	0	0	0	0	0	17	17	39	32-44
<i>Protomyctophum choriodon</i>	Spring (JR161)	0	0	0	0	0	0	0	-	-
	Summer (JR177)	0	0	0	0	30	7	37	68	56-84
	Autumn (JR200)	0	0	0	0	0	0	0	73	55-85

**Table 2.** Numbers of myctophid stomachs containing prey items at each station in the Scotia Sea during the three surveys. Stations are: South Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), North Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF) The mean size and ranges (SL) of the fish from which stomach samples were extracted are also given for each survey.

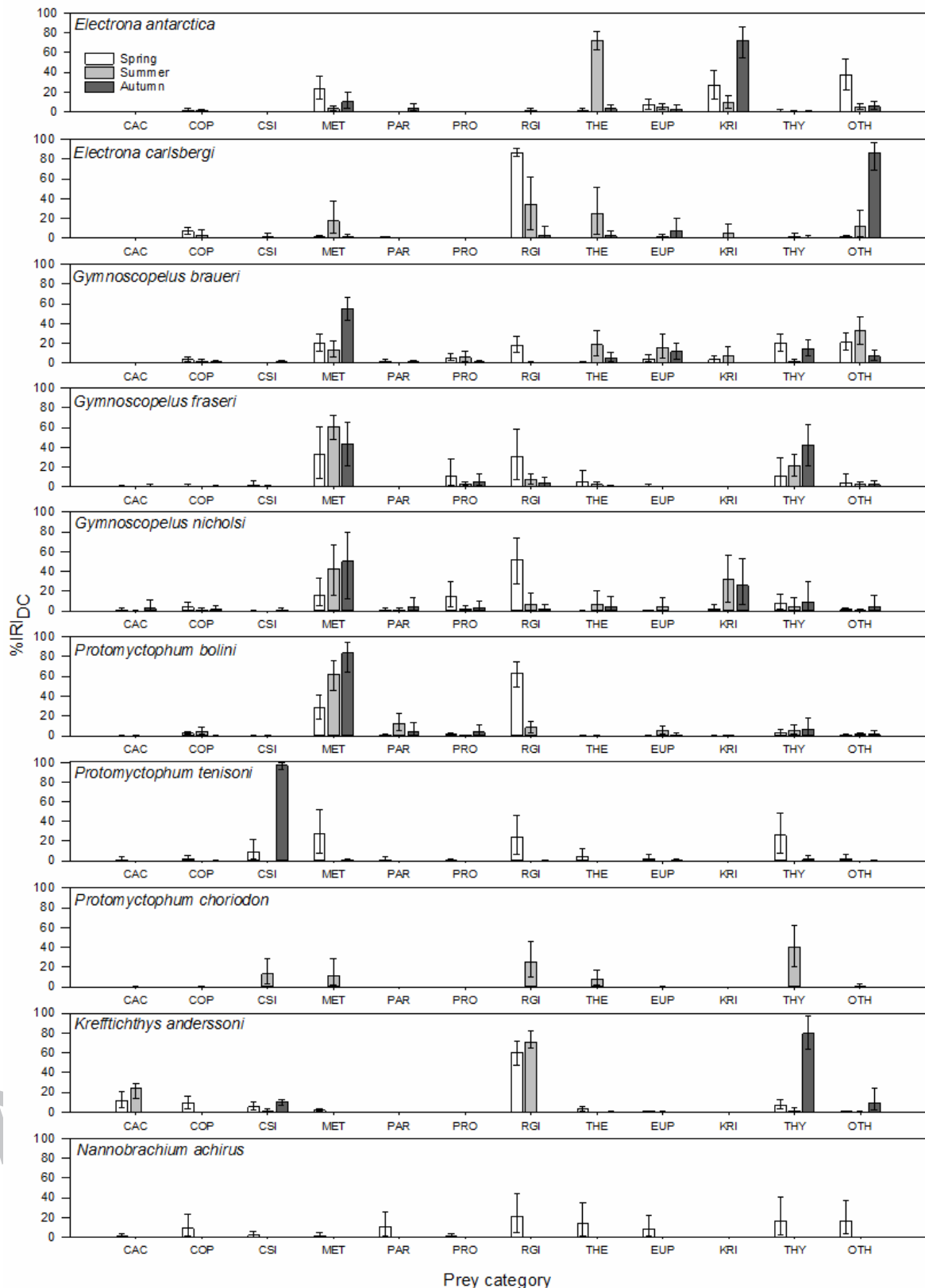
*Electrona carlsbergi* had a more restricted size range than *Electrona antarctica* in all seasons (65-90 mm SL). In spring, the species was predominantly distributed above 200 m and its diet was dominated by *Rhincalanus gigas* (85 %IRI) which was most abundant above 400 m. *Rhincalanus gigas* dominated the diet of *E. carlsbergi* in summer (43% IRI), although the species consumed relatively high proportions of *Themisto gaudichaudii* (27 %IRI) and *Metridia* spp. (20 %IRI). These prey species were most abundant between 0 and 200 m in summer, whilst *E. carlsbergi* was spread between 0 and 400 m. *Euphausia superba* was also consumed by the species during this season (4 %IRI). In autumn, *E. carlsbergi* was predominantly distributed between 200 and 400 m and it mostly consumed salps (81 %IRI) and unidentified euphausiids (9% IRI) that were also most abundant in this depth zone.

#### 3.1.4.2 Southern Ocean *Gymnoscopelus*

*Gymnoscopelus braueri* (34-162 mm SL) was spread mostly between 0 and 400 m in all seasons, similar to its main prey species. Its diet in spring comprised mostly *Metridia* spp. (26 %IRI), *Thysanoessa* spp. (26% IRI), *Rhincalanus gigas* (20 % IRI) and *Pleuromamma robusta* (7 %IRI), but *Euphausia superba* and ostracods were also important dietary components (4 %IRI). In summer, its vertical range extended to 700 m and the species took substantial proportions of *Themisto gaudichaudii* (26 %IRI), as well as *Metridia* spp. (20 %IRI), *E. superba* (10 %IRI), *P. robusta* (9 %IRI) and ostracods (8 %IRI). The diet of *G. braueri* switched back to mainly *Metridia* spp. (68 %IRI) and *Thysanoessa* spp. (16 %IRI), with *T. gaudichaudii* and *Euphausia triacantha* also being consumed (~4 %IRI).

Similar to *Gymnoscopelus braueri*, the diet of *Gymnoscopelus fraseri* (39-115 mm SL) was dominated by *Metridia* spp. (37 %IRI), *Rhincalanus gigas* (33 %IRI), *Thysanoessa* spp. (11% IRI) and *Pleuromamma robusta* (11 %IRI) in spring. This myctophid also took *Themisto gaudichaudii* at this time (4 %IRI), but *Euphausia superba* was absent from its diet in all seasons. The importance of *R. gigas* in its diet decreased in summer and autumn (7 and 3 %IRI, respectively), whilst there was a progressive increase in the consumption of *Thysanoessa* spp. between spring and autumn (20 and 43 %IRI, respectively). Overall, the vertical distribution of *G. fraseri* was similar to that of its main prey species in all seasons, with the greatest concentrations occurring above 200 or 400 m.





**Fig. 6** Diet composition of 10 myctophid species in the Scotia Sea in spring (JR161), summer (JR177) and autumn (JR200) expressed as the percentage index of relative importance (%IRI<sub>DC</sub>). Error bars are the bootstrapped 95% confidence intervals. THE: *Themisto gaudichaudii*, CAC: *Calanoides acutus*, CSI: *Calanus similimus*, 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 salps, unidentified crustaceans, ostracods, and pteropods).

*Gymnoscopelus nicholsi* (34-165 mm SL) resided mostly in the upper 400 m of the water column in each season and had a diet similar to that of the other *Gymnoscopelus* species. The diet of *G. nicholsi* was dominated by *Rhincalanus gigas* (46 %IRI), *Metridia* spp. (21 %IRI), and *Pleuromamma robusta* (18 %IRI) in spring, but *Metridia* spp. (44 to 64 %IRI) and *Euphausia superba* (25 to 38 %IRI) dominated its diet in summer and autumn. The species took *Thysanoessa* spp. in all seasons (3 to 10 %IRI) and *Themisto gaudichaudii* was an important dietary component in summer (5 %IRI).

#### 3.1.4.3 Southern Ocean *Protomyctophum*

*Protomyctophum bolini* (23-66 mm SL) was caught between 200 and 400 m at night in all seasons. This species mostly consumed copepods, with *Rhincalanus gigas* dominating its diet in spring (64 %IRI) and *Metridia* spp. dominating the diet in summer (66 %IRI) and autumn (87 %IRI). *Paraeuchaeta* spp., which were most abundant in waters above 400 m, formed a substantial part of the species' diet in summer (12 %IRI). *Thysanoessa* spp. were also consumed in each season (3 to 5 %IRI) and *Pleuromamma robusta* was predated in autumn (3 %IRI).

*Protomyctophum tenisoni* was absent during the summer survey, but it occurred between 0 and 200 m in spring and autumn. This species predated the copepods *Metridia* spp., *Rhincalanus gigas* and *Calanus simillimus* in spring, together with *Thysanoessa* spp. and *Themisto gaudichaudii*. However, its diet in autumn was comprised almost exclusively of *C. simillimus* (98 %IRI), which was most abundant in the upper 200 m of the water column.

Based on the available data from summer, the diet of *Protomyctophum choriodon* (55-85 mm SL) was dominated by *Thysanoessa* spp. (42 %IRI) which had an overlapping depth distribution with this myctophid species. *Protomyctophum choriodon* also consumed the copepods *Rhincalanus gigas* (26 %IRI), *Calanus simillimus* (13 %IRI) and *Metridia* spp. (12%IRI), as well as *Themisto gaudichaudii* (6 %IRI).

#### 3.1.4.4 Other Southern Ocean species

*Krefflichthys anderssoni* (15-74 mm SL) was predominantly a deeper-dwelling species during all seasons. In spring, the species occurred mainly between 200 and 400 m where its diet was mostly comprised of *Rhincalanus gigas* and *Calanoides acutus* that were also abundant at this depth interval. *Thysanoessa* spp. were also an important dietary component in spring. Both *R. gigas* and *C. acutus* dominated the diet of the *K. anderssoni* in summer, despite these copepods being predominantly situated above (0 to 200 m) the majority of the *K. anderssoni* population at night (400 to 700 m). Similarly, its diet in autumn was dominated by *Thysanoessa* spp. (78 %IRI) and *Calanus simillimus* (17 %IRI) that were distributed higher in the water column at night than the *K. anderssoni* population (0 to 200 m compared to 400 to 1000 m).

*Nannobrachium achirus* (65-167 mm SL) was the largest myctophid species studied and it occurred predominantly below 200 m in spring and below 400 m in summer and autumn. The sample size was relatively low for this species, but the available data from spring indicate that it consumed *Rhincalanus gigas* (25%IRI), *Thysanoessa* spp. (25 %IRI) and *Paraeuchaeta* spp. (15 %IRI) that were most abundant above 400 m. *Nannobrachium achirus* also took substantial proportions of mesopelagic fish (9 %IRI) and deep-water amphipods (6 %IRI).

#### 3.1.5 Size related diet patterns

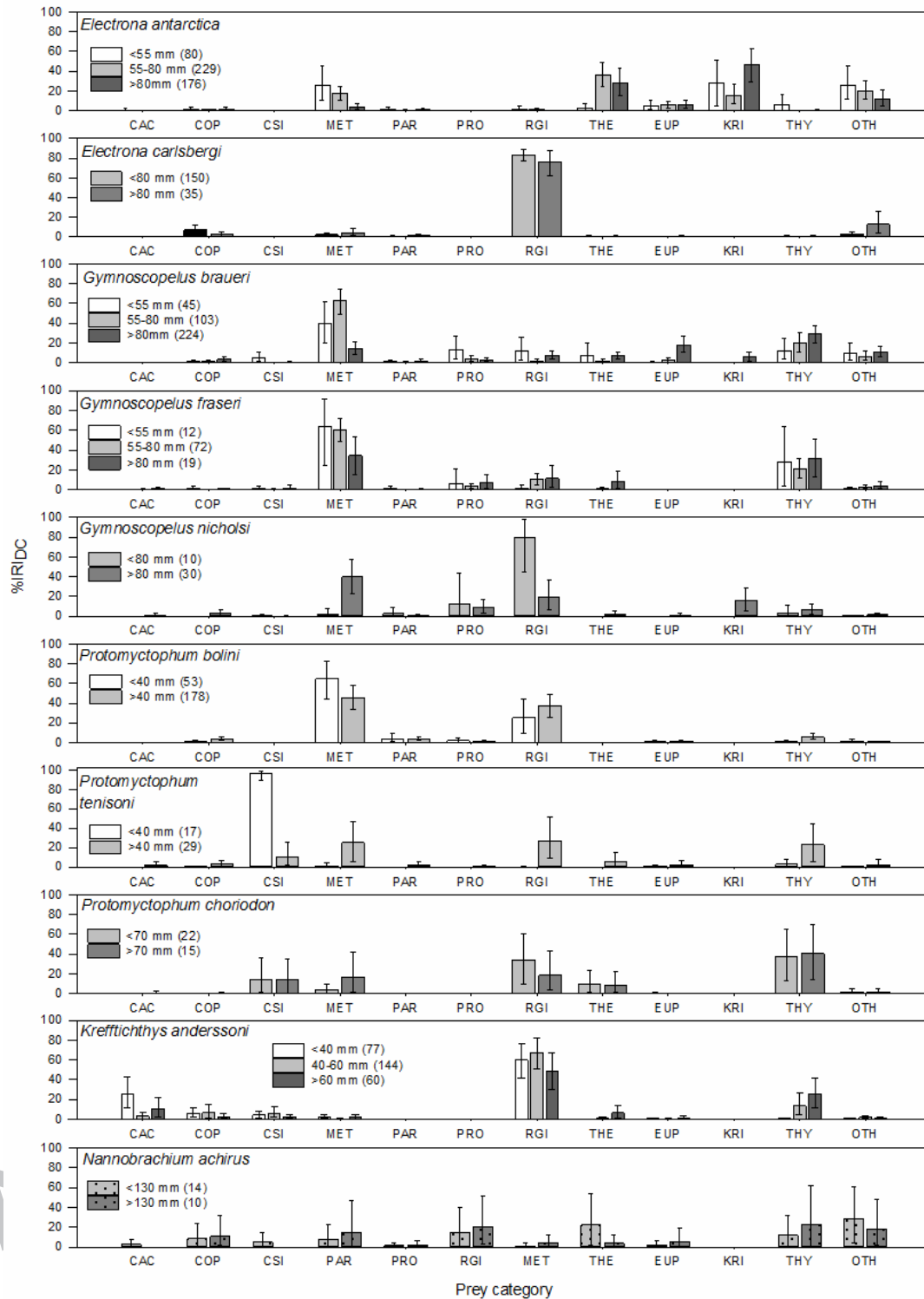
Although copepods were abundant in the diets of most myctophid size classes, there was a general change in diet with size for some species (Fig. 7). In *Electrona antarctica*, *Euphausia superba* was consumed by all size classes, but the largest sized specimens (>80 mm) consumed more *E. superba* and fewer copepods (*Metridia* spp.) than the smaller size classes. Only a few *E. antarctica* specimens <55 mm consumed *Themisto gaudichaudii*. There was also a decline in the prevalence of 'other prey taxa' in the diet with increasing size, which was dominated by unidentified pteropods. There was little evidence of size-related variations in the diet of *Electrona carlsbergi*, which had a limited size range and consumed mostly *Rhincalanus gigas* in the region, although salps were only consumed by specimens >80 mm.

Only *Gymnoscopelus braueri* specimens >80 mm consumed *Euphausia superba*, with this size class consuming the fewest copepods and the greatest proportions of ‘other euphausiids’. There was also a progressive increase in the consumption of *Thysanoessa* spp. with size in this species, although *Themisto gaudichaudii* was consumed by all size classes. Copepods of the *Metridia* genus and the euphausiid *Thysanoessa* spp. dominated the diets of all size classes in *Gymnoscopelus fraseri*, although *T. gaudichaudii* was only consumed by fish >80 mm and *Rhincalanus gigas* was predominantly taken by fish >55 mm. There was a clear switch in copepod selection with size in *Gymnoscopelus nicholsi*, with specimens >80 mm consuming fewer *Rhincalanus gigas* and more *Metridia* spp. than specimens <80 mm. Also, only specimens >80 mm consumed *E. superba*.

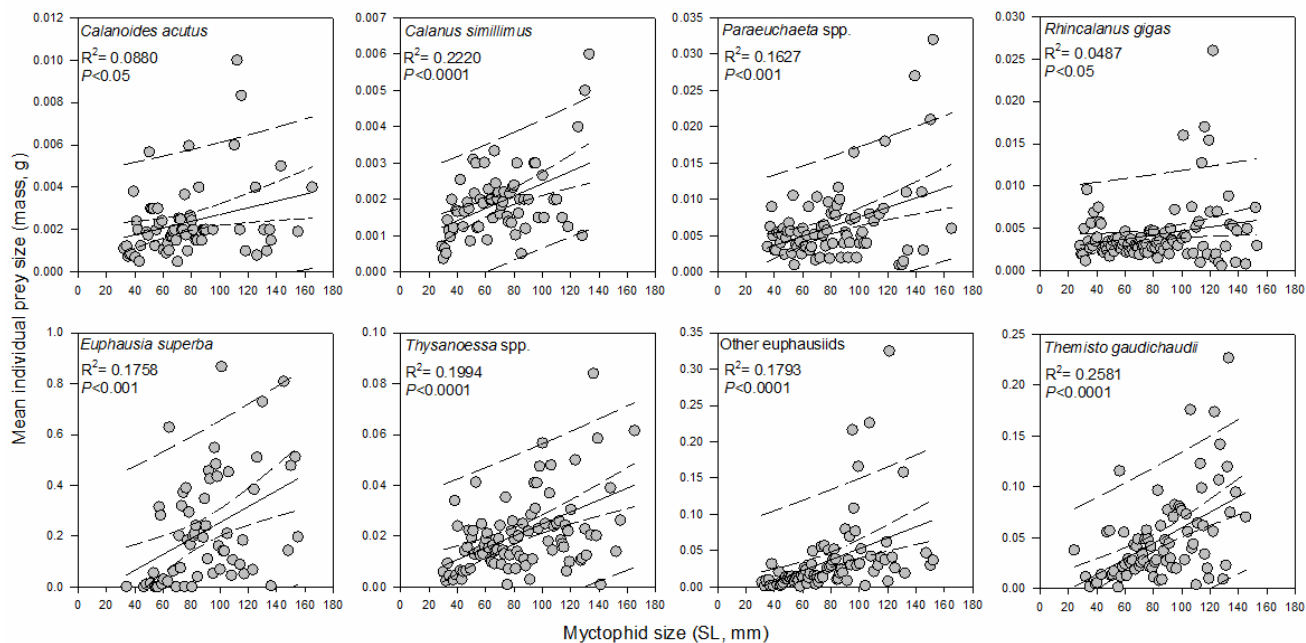
All species of the predominantly small *Protomyctophum* genus had relatively narrow size distributions in the region. Although *Protomyctophum bolini* specimens >40 mm took slightly greater proportions of *Thysanoessa* spp. and ‘other copepods’ than those <40 mm, there was little evidence of size-related variations in diet for this species. The diet of *Protomyctophum choriodon* was also similar across size classes. However, there was evidence of size-related variations in the diet of *Protomyctophum tenisoni*, with specimens >40 mm switching from mostly consumption of *Calanus simillimus* to consumption of *Metridia* spp., *Rhincalanus gigas* and *Thysanoessa* spp. This size class also took *Themisto gaudichaudii*.

The diet of *Krefflichys anderssoni* varied with size, with *Thysanoessa* spp. absent in the diet of fish <40 mm and consumption of this group greatest in specimens >60 mm. Also, *Themisto gaudichaudii* was only consumed by fish >60 mm and the consumption of *Calaniodes acutus* decreased with size in this species. There was little evidence of diet variations with size in *Nannobranchium achirus*, mostly because only large sized fish within a narrow size range were caught during the study.

In addition to these changes in species composition, the size of individuals within most prey species also increased with predator size (Fig. 8). The scatter plots suggest that both small and large fish take smaller prey, but that the size range (expressed as mass) of prey broadens with fish size. A significant ( $P < 0.05$ ) relationship between mean individual prey size consumed and myctophid size was apparent for *Calanoides acutus*, *Calanus simillimus*, *Paraeuchaeta* spp., *Rhincalanus gigas*, *Euphausia superba*, *Thysanoessa* spp., other euphausiids and *Themisto gaudichaudii*, with individual prey sizes in the diet increasing with increasing fish size. No significant relationship ( $P > 0.05$ ) was found for *Metridia* spp., *Pleuromamma robusta*, other copepods, or 'other taxa', suggesting that consumption of the different life cycle stages of these species was uniform across all myctophid size classes.



**Fig. 7** Diet composition of 10 myctophid species in the Scotia Sea by size class expressed as the percentage index of relative importance (%IRI<sub>DC</sub>). 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 salps, unidentified crustaceans, ostracods, and pteropods).



**Fig. 8** Relationship between mean individual prey size (expressed as mass, g) in myctophid stomachs and myctophid body size (SL, mm) for 8 key prey taxa consumed in the Scotia Sea. The solid black line is the regression fit to the observations, the short-dashed lines are the 95% confidence intervals of the regression, and the long-dashed lines are the 95% confidence intervals of the observations.

### 3.1.6 Diet comparisons between species

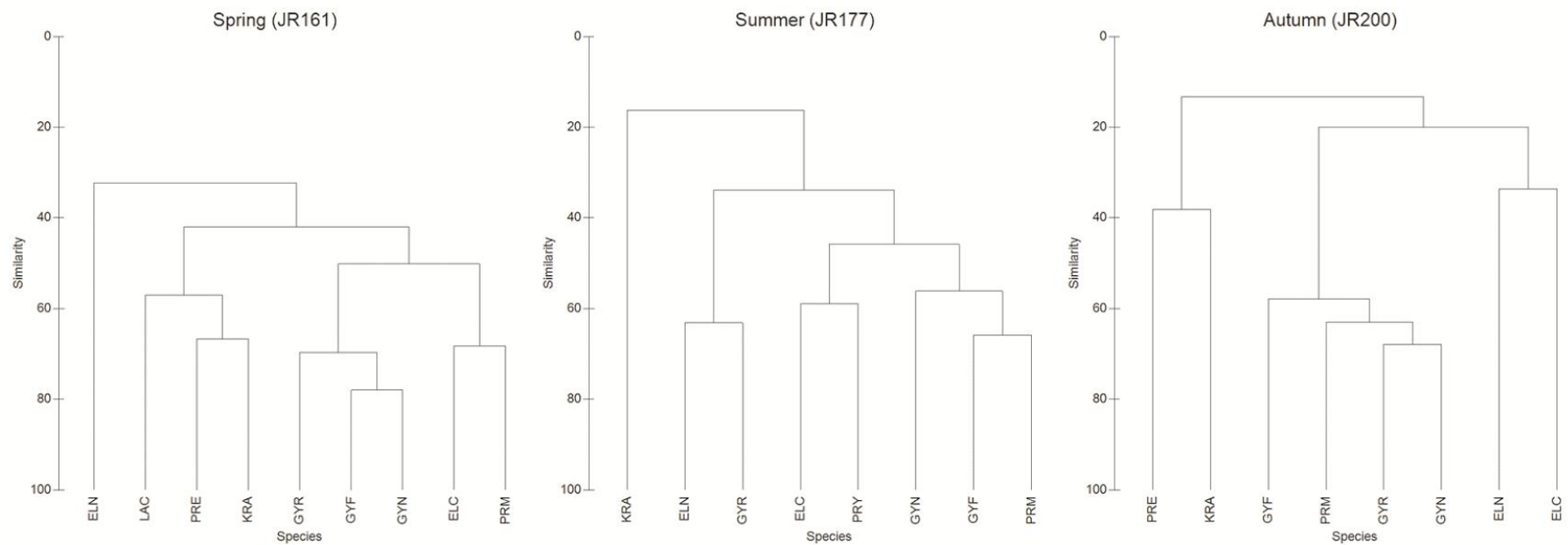
Overall, hierarchical cluster analysis indicated that myctophid feeding guilds varied seasonally in the Scotia Sea, but there was a high degree of dietary overlap between most species/guilds (Fig. 9). The analysis produced three clusters at the 58% similarity level for the spring data, with one outlier comprised of *Electrona antarctica* (Cluster 1). Unlike the other myctophid species, *E. antarctica* consumed mostly *Euphausia superba* and pteropods at this time. Cluster 2 grouped *Nannobranchium achirus*, *Protomyctophum tenisoni* and *Krefflichthys anderssoni* in a cluster that was dominated by the consumption of *Rhincalanus gigas* (28%), *Thysanoessa* spp. (22%) and *Calanus simillimus* (10%; Table 3). Cluster 3 contained the three *Gymnoscopelus* species in a cluster that was dominated by *R. gigas* (24%), *Metridia* spp. (23%), *Thysanoessa* spp. (15%) and *Pleuromamma robusta* (14%). *Electrona carlsbergi* and *Protomyctophum bolini* were grouped in Cluster 4 that was dominated by *R. gigas* (57%) and *Metridia* spp. (15%) consumption. Although these clusters were differentiated by the rankings of the composite prey species, the overall diet compositions of the cluster groups were broadly similar in terms of composition, with only one or two taxa unique to each

cluster and the same three species, *R. gigas*, *Metridia* spp. and *Thysanoessa* spp., dominating the groupings.

Three clusters and an outlier were also identified in summer at the 58% similarity level. The outlier (Cluster 1) comprised *Krefftichthys anderssoni*, which had a diet dominated by *Rhincalanus gigas* and *Calanoides acutus*. Cluster 2 grouped *Electrona antarctica* and *Gymnoscopelus braueri* in a cluster dominated by the consumption of *Themisto gaudichaudii* (29%), *Euphausia superba* (18 %) and unidentified euphausiids (11%). *Electrona carlsbergi* and *Protomyctophum choriodon* were grouped in Cluster 3 with these species consuming mostly *R. gigas* (35%), *Metridia* spp. (24%) and *T. gaudichaudii* (16%). Cluster 4 contained *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi* and *Protomyctophum bolini* in a group dominated by the consumption of *Metridia* spp. (49%), *R. gigas* (17%) and *Thysanoessa* spp. (14 %). Similar to spring, there was a relatively high degree of dietary overlap between Clusters 3 and 4, with *R. gigas*, *Metridia* spp., and *Thysanoessa* spp. ranked relatively highly in both feeding guilds. These species were also common to Cluster 2, with *Metridia* spp. being an important contributor.

Hierarchical cluster analysis identified three clusters in the autumn data at the 34% similarity level. Cluster 1 comprised *Protomyctophum tenisoni* and *Krefftichthys anderssoni* in a group that was dominated by just three species, *Calanus simillimus* (57%), *Thysanoessa* spp. (28 %) and *Metridia* spp. (15%). Cluster 3 grouped the three *Gymnoscopelus* species together with *Protomyctophum bolini*. This Cluster was dominated by consumption of *Metridia* spp. (31%), *Thysanoessa* spp. (18%) and *Pleuromamma robusta* (13%). *Paraeuchaeta* spp. were also important in this grouping. *Electrona antarctica* and *Electrona carlsbergi* were identified in Cluster 4, which was dominated by the consumption of *Themisto gaudichaudii* (15%), *Metridia* spp. (14%), unidentified euphausiids (13%), unidentified crustaceans (13%) and *Thysanoessa* spp. (10%).





**Fig. 9** 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 during spring (J161), summer (JR177) and autumn (JR200). Species codes are: ELN: *Electrona antarctica*, LAC: *Nannobrachium achirus*, GYR: *Gymnoscopelus braueri*, GYF: *Gymnoscopelus fraseri*, GYN: *Gymnoscopelus nicholsi*, PRM: *Protomyctophum bolini*, ELC: *Electrona carlsbergi*, KRA: *Krefflichthys anderssoni*, PRE: *Protomyctophum tenisoni*, PRC: *Protomyctophum choriodon*.

Spring JR161			Summer JR177			Autumn JR200											
Grp	Myctophid species	Prey species	Mean %IRI	Cont. %	Cum. %	Grp	Myctophid species	Prey species	Mean %IRI	Cont. %	Cum. %	Grp	Myctophid species	Prey species	Mean %IRI	Cont. %	Cum. %
2	<b>Average similarity: 62.45</b>					2	<b>Average similarity: 63.15</b>					1	<b>Average similarity: 46.53</b>				
	<i>P. tenisoni</i>	<i>R. gigas</i>	5.97	27.80	27.80		<i>E. antarctica</i>	<i>T. gaudichaudii</i>	6.90	29.35	29.35		<i>P. tenisoni</i>	<i>C. simillimus</i>	2.59	56.54	56.54
	<i>K. anderssoni</i>	<i>Thysanoessa</i> spp.	4.56	22.37	50.17		<i>G. braueri</i>	<i>E. superba</i>	3.23	18.45	47.80		<i>K. anderssoni</i>	<i>Thysanoessa</i> spp.	2.00	28.31	84.85
	<i>N. achirus</i>	<i>C. simillimus</i>	2.28	10.03	60.20			Unident. euphausiids	2.61	11.74	59.54			<i>Metridia</i> spp.	0.62	15.15	100.00
		<i>Metridia</i> spp.	2.81	7.89	68.09			<i>Metridia</i> spp. Unident.	3.20	11.17	70.71						
		<i>T. gaudichaudii</i> Unident.	1.59	7.47	75.56			crustaceans	2.30	6.74	77.45						
		euphausiids	1.18	5.54	81.10			<i>R. gigas</i>	1.22	6.04	83.48						
		<i>C. acutus</i>	1.86	5.40	86.50			<i>Thysanoessa</i> spp.	1.13	4.37	87.85						
		<i>C. propinquus</i>	0.89	3.17	89.67			Ostracods	1.60	2.59	90.45						
		<i>Paraeuchaeta</i> spp.	1.71	2.63	92.31												
3	<b>Average similarity: 73.28</b>					3	<b>Average similarity: 58.95</b>					2	<b>Average similarity: 58.86</b>				
	<i>G. braueri</i>	<i>R. gigas</i>	5.70	24.25	24.25		<i>E. carlsbergi</i>	<i>R. gigas</i>	5.80	34.57	34.57		<i>G. fraseri</i>	<i>Metridia</i> spp.	2.83	30.87	30.87
	<i>G. fraseri</i>	<i>Metridia</i> spp.	5.25	22.99	47.24		<i>P. choriodon</i>	<i>Metridia</i> spp.	3.97	23.63	58.20		<i>P. bolini</i>	<i>Thysanoessa</i> spp.	1.91	18.14	49.00
	<i>G. nicholsi</i>	<i>Thysanoessa</i> spp.	3.86	15.48	62.72			<i>T. gaudichaudii</i>	3.81	16.38	74.58		<i>G. braueri</i>	<i>P. robusta</i>	1.22	12.65	61.65
		<i>P. robusta</i> Unident.	3.41	14.05	76.76			<i>Thysanoessa</i> spp.	3.78	7.20	81.78		<i>G. nicholsi</i>	<i>Paraeuchaeta</i> spp.	1.03	9.40	71.05
		euphausiids	1.17	3.18	79.94			<i>C. simillimus</i> Unident.	2.33	6.94	88.72			<i>R. gigas</i>	0.80	4.52	75.56
		Ostracods	1.12	2.88	82.82			crustaceans	0.67	3.15	91.87			Ostracods	0.75	4.40	79.96
		<i>C. acutus</i>	0.68	2.51	85.33								<i>C. simillimus</i>	0.63	3.38	83.34	
		<i>T. gaudichaudii</i> <i>Paraeuchaeta</i> spp.	1.03	2.32	87.65								<i>C. acutus</i> Unident.	0.62	3.26	86.60	
			0.88	2.32	89.97								crustaceans	0.54	3.01	89.62	
		<i>Candacia</i> spp.	0.65	2.27	92.24								<i>Heterorhabdus</i> spp.	0.43	2.33	91.95	
4	<b>Average similarity: 68.24</b>					4	<b>Average similarity: 62.00</b>					3	<b>Average similarity: 54.66</b>				
	<i>E. carlsbergi</i>	<i>R. gigas</i>	8.62	56.61	56.61		<i>G. fraseri</i>	<i>Metridia</i> spp.	7.60	49.26	49.26		<i>E. antarctica</i>	<i>T. gaudichaudii</i>	1.31	15.19	15.19
	<i>P. bolini</i>	<i>Metridia</i> spp.	3.75	14.59	71.20		<i>G. nicholsi</i>	<i>R. gigas</i>	2.64	17.45	66.71		<i>E. carlsbergi</i>	<i>Metridia</i> spp. Unident.	1.49	13.82	29.01
		<i>Thysanoessa</i> spp. <i>Paraeuchaeta</i> spp.	1.40	7.27	78.47		<i>P. bolini</i>	<i>Thysanoessa</i> spp.	2.88	13.72	80.43			euphausiids	1.41	13.30	42.31
			1.09	5.84	84.32			<i>P. robusta</i>	1.09	4.87	85.30			Unident. crustaceans	1.17	12.55	54.86
		<i>Eucalanus</i> spp.	0.41	2.71	87.03			<i>Paraeuchaeta</i> spp.	1.54	3.57	88.87			<i>Thysanoessa</i> spp.	0.79	9.73	64.58
		<i>P. robusta</i>	0.76	2.62	89.65			<i>T. gaudichaudii</i>	1.28	3.45	92.32			Ostracods	0.82	7.81	72.40

Unident.  
euphausiids

0.35 1.99 91.64

<i>R. gigas</i>	0.84	7.08	79.48
<i>Paraeuchaeta</i> spp.	1.02	6.74	86.22
<i>C. simillimus</i>	0.55	6.38	92.6

**Table 3.** Results of SIMPER analyses showing percentage contributions of prey species to the myctophid groupings identified in each season by agglomerative hierarchical cluster analysis.

Table heading abbreviations are: Cluster group (Grp), Mean of transformed %IRI (Mean %IRI.), percentage contribution (Cont. %) and cumulative percentage (Cum. %).

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### 3.1.6 Consumption of prey productivity

The majority of stomachs examined in each season contained more than 1 species of prey, with some specimens containing more than 5 prey species. Copepod species were generally consumed in numbers of 10 or more for most myctophid species, whilst macrozooplankton taxa were often consumed in numbers of more than 5 individuals. 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 (Supplementary 5 and 6). The exceptions were some of the copepod species, notably *Metridia* spp. and *Rhincalanus gigas*, which were found in relatively high numbers in the stomachs of the predominant copepod feeders, such as *Gymnoscopelus fraseri*, *Gymnoscopelus nicholsi*, *Electrona carlsbergi* and *Protomyctophum bolini*. In these instances, the average prey numbers per stomach were  $>5$  in most seasons. *Thysanoessa* spp. was the most consumed macrozooplankton prey item, with the average prey numbers per stomach  $>1$  for the myctophids *G. fraseri*, *G. nicholsi*, *Krefftichthys anderssoni* and *Protomyctophum choriodon* in some seasons.

Best estimates of average depth-integrated concentrations across all 10 myctophid species in the upper 1000 m ranged between 0.001 and 0.155 ind.  $m^{-2}$  during the 3 surveys (Table 1). In the best estimate, myctophids consumed up to 7% of the daily productivity of key copepod taxa in the Scotia Sea in spring, with *Krefftichthys anderssoni* having the greatest overall impact, consuming ~4% of the *Calanus simillimus* production (Table 4). The impact of myctophid predation on macrozooplankton production in spring was relatively high, with a best estimate of consumption of around 38% of *Themisto gaudichaudii* daily production and 10% of *Euphausia superba* daily production (Table 4). Myctophids also consumed around 7% of *Thysanoessa* spp. daily production during this time. *Krefftichthys anderssoni* had the greatest impact on both *T. gaudichaudii* (29%) and *Thysanoessa* spp. (3%) daily production, whilst *Electrona antarctica* and *Gymnoscopelus braueri* were the main consumers of *E. superba* daily production (~4 to 6%). The impact of myctophids on salps, ostracods and pteropods was negligible in spring ( $<0.1\%$ ).

The predatory impact of myctophids on macrozooplankton production was highest in summer (Table 5). Myctophids consumed around 76% of the daily *Thysanoessa* spp. productivity and up to 53% of *Euphausia superba* productivity during this time. *Thysanoessa* spp. was impacted most by *Protomyctophum choriodon* (26%) and *Gymnoscopelus fraseri* (22%), whilst *Electrona antarctica* consumed the majority of *E. superba* daily production (30%). *Gymnoscopelus braueri* and *G. nicholsi* also consumed around 10% of the daily productivity of *E. superba* during this time. *Themisto gaudichaudii* daily production was impacted less in summer than in spring (9%), but myctophids consumed more *Euphausia frigida* (12%) production during summer. The impact of myctophids on the daily productivity of salps accounted for up to 4%, with only *Electrona carlsbergi* consuming this prey taxon. As in spring, myctophids had a negligible impact on ostracods and pteropods in summer. Of the copepod component of the prey field, myctophids consumed best estimates of <4% of daily productivity for all key species during summer, except *Calanus simillimus* that was impacted by up to 26%, with *P. choriodon* consuming the most of this species' daily production (16%).

In autumn, the predatory impact of myctophids on the copepod component of the prey field accounted for <3% of the daily production of most species, with *Paraeuchaeta* spp. being impacted the most during this time (Table 6). Myctophids consumed up to 27% of the daily productivity of key macrozooplankton taxa in autumn, with *G. braueri* and *K. anderssoni* having the greatest overall impact, each consuming ~11% of the daily *Thysanoessa* spp. production. *Themisto gaudichaudii* was impacted most by *E. antarctica* and *G. braueri* during this season, with up to 16% of this prey item consumed overall. *Electrona antarctica* had the greatest predatory impact on *E. superba*, consuming around 8% of this species' daily productivity in the region. Myctophids consumed around 3to 4% of the daily productivity of salps and *E. frigida*, but they had little overall impact on ostracods and pteropods.

## 4.1. Discussion

### 4.1.1. Sampling considerations

The present study provides the first detailed analysis of the trophodynamics and predatory impact of the Southern Ocean myctophid community on the zooplankton prey field in different seasons, and represents one of the most comprehensive studies undertaken to date

on the trophic ecology of myctophids in any oceanic region. However, the results of this study must be placed within the appropriate context of the associated sampling issues that arise with net sampling surveys of mesopelagic fish and zooplankton. For example, mesopelagic fish are capable of actively avoiding scientific nets, which together with the inherently patchy nature of their distribution patterns, may impact our net-based measurements of abundance, particularly when averaging over relatively broad spatial scales. Recent studies using underwater acoustics indicate that the abundance of mesopelagic fish may be at least an order of magnitude greater than that assumed from netting studies (Irigoien et al., 2014), suggesting that our study is likely to underestimate the overall predatory impact of myctophids in the Scotia Sea. Zooplankton aggregations are also inherently variable in space and time and, as a consequence, our net-based measurements of the prey field may be under-represented. Antarctic krill abundance, for example, varies substantially between years in the study region (Brierley et al., 1997), and repeated observations in each season are clearly required to examine the impact of inter-annual variations in prey abundance on the trophic ecology of Southern Ocean myctophids. However, the available data indicate that the study was not conducted during years of low krill abundance in the Scotia Sea (Fielding et al., 2014). A further consideration of our study is that our stomach samples were not collected in consecutive or repeated seasons, so possible inter-annual effects in myctophid diet cannot be accounted for. Also, our data might not adequately reflect the long-term diet of myctophids, although our results are consistent with observations from trophic studies using biochemical techniques that provide a more time-integrated synopsis of Southern Ocean myctophid diets (Cherel et al., 2010; Stowasser et al., 2012). Sampling myctophids and their prey at finer spatial and temporal scales is challenging in the remote Southern Ocean and our synoptic data provide the best window of observation into the feeding ecology of myctophids at an intra-annual time scale in the region to date.

Myctophid species	Estimate	<i>Themisto gaudichaudii</i>	<i>Euphausia frigida</i>	<i>Euphausia superba</i>	<i>Thysanoessa</i> spp.	<i>Calanoides acutus</i>	<i>Calanus simillimus</i>	<i>Metridia</i> spp.	<i>Triconia</i> spp.	<i>Pleuromamma robusta</i>	<i>Paraeuchaeta</i> spp.	<i>Rhincalanus gigas</i>	Ostracods	Pteropods	Salps
<i>Electrona carlsbergi</i>	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
	<b>Best</b>	<b>0.65</b>	<b>1.03</b>	<b>0.00</b>	<b>0.13</b>	<b>0.00</b>	<b>0.11</b>	<b>0.01</b>	<b>0.00</b>	<b>0.11</b>	<b>0.05</b>	<b>0.28</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	2.20	0.07	3.54	0.30	0.01	-	1.10	8.60	0.02	-	0.00
<i>Electrona antarctica</i>	Lower	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>0.95</b>	<b>0.00</b>	<b>5.75</b>	<b>0.14</b>	<b>0.01</b>	<b>0.04</b>	<b>0.02</b>	<b>0.00</b>	<b>0.08</b>	<b>0.01</b>	<b>0.00</b>	<b>0.01</b>	<b>0.02</b>	<b>0.00</b>
	Upper	-	-	-	1.08	0.06	0.30	0.28	0.00	-	0.12	0.21	0.05	-	0.00
<i>Gymnoscopelus fraseri</i>	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
	<b>Best</b>	<b>3.27</b>	<b>0.00</b>	<b>0.00</b>	<b>0.22</b>	<b>0.00</b>	<b>0.12</b>	<b>0.03</b>	<b>0.00</b>	<b>0.91</b>	<b>0.00</b>	<b>0.06</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	0.41	0.01	0.47	0.12	0.00	-	0.01	0.24	0.01	-	0.00
<i>Gymnoscopelus nicholsi</i>	Lower	0.06	0.00	0.02	0.01	0.00	0.01	0.01	0.00	0.07	0.00	0.05	0.00	0.00	0.00
	<b>Best</b>	<b>0.44</b>	<b>0.00</b>	<b>0.13</b>	<b>0.23</b>	<b>0.01</b>	<b>0.02</b>	<b>0.02</b>	<b>0.00</b>	<b>1.96</b>	<b>0.01</b>	<b>0.18</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	0.81	0.02	0.23	0.15	0.00	-	0.08	1.62	0.01	-	0.00
<i>Gymnoscopelus braueri</i>	Lower	0.00	0.00	0.13	0.04	0.00	0.00	0.01	0.00	0.03	0.01	0.02	0.01	0.00	0.00
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>3.70</b>	<b>1.45</b>	<b>0.01</b>	<b>0.25</b>	<b>0.05</b>	<b>0.00</b>	<b>2.06</b>	<b>0.11</b>	<b>0.14</b>	<b>0.04</b>	<b>0.01</b>	<b>0.00</b>
	Upper	-	-	-	2.36	0.03	1.18	0.21	0.00	-	0.37	0.69	0.17	-	0.00
<i>Krefflichthys anderssoni</i>	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
	<b>Best</b>	<b>28.95</b>	<b>0.00</b>	<b>0.00</b>	<b>3.48</b>	<b>1.19</b>	<b>3.89</b>	<b>0.04</b>	<b>0.00</b>	<b>0.17</b>	<b>0.02</b>	<b>1.55</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	16.69	6.95	40.26	0.45	0.00	-	0.48	15.47	0.03	-	0.00
<i>Nannobranchium achirus</i>	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
	<b>Best</b>	<b>0.16</b>	<b>0.00</b>	<b>0.00</b>	<b>0.09</b>	<b>0.00</b>	<b>0.03</b>	<b>0.00</b>	<b>0.00</b>	<b>0.03</b>	<b>0.02</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	0.44	0.01	0.24	0.00	0.00	-	0.11	0.08	0.01	-	0.00
<i>Protomyctophum tenisoni</i>	Lower	0.13	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>4.05</b>	<b>0.00</b>	<b>0.00</b>	<b>0.36</b>	<b>0.01</b>	<b>0.23</b>	<b>0.01</b>	<b>0.00</b>	<b>0.05</b>	<b>0.02</b>	<b>0.03</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	1.39	0.03	1.85	0.13	0.00	-	0.10	0.25	0.00	-	0.00
<i>Protomyctophum bolini</i>	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
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.76</b>	<b>0.00</b>	<b>0.09</b>	<b>0.23</b>	<b>0.00</b>	<b>1.63</b>	<b>0.12</b>	<b>1.02</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	1.66	0.02	0.29	1.11	0.00	-	0.35	4.46	0.03	-	0.00
Total	Lower	0.19	0.00	0.32	0.06	0.00	0.02	0.02	0.00	0.10	0.02	0.07	0.01	0.00	0.00
	<b>Best</b>	<b>38.47</b>	<b>1.03</b>	<b>9.58</b>	<b>6.86</b>	<b>1.23</b>	<b>4.76</b>	<b>0.40</b>	<b>0.00</b>	<b>7.00</b>	<b>0.36</b>	<b>3.27</b>	<b>0.06</b>	<b>0.03</b>	<b>0.00</b>
	Upper	-	-	-	27.04	7.21	48.35	2.76	0.01	-	2.72	31.62	0.33	-	0.00

**Table 4.** The impact of myctophid predation on the production of key zooplankton taxa expressed as a percentage of daily production consumed ( $\mu\text{g C m}^{-2} \text{d}^{-1}$ ) by each myctophid caught in the Scotia Sea during spring (JR161). Estimates represent the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentiles. Dashes denote instances where there was insufficient data to generate a confident estimate.

Myctophid species	Estimate	<i>Themisto gaudichaudii</i>	<i>Euphausia frigida</i>	<i>Euphausia superba</i>	<i>Thysanoessa</i> spp.	<i>Calanoides acutus</i>	<i>Calanus simillimus</i>	<i>Metridia</i> spp.	<i>Triconia</i> spp.	<i>Pleuromamma robusta</i>	<i>Paraeuchaeta</i> spp.	<i>Rhincalanus gigas</i>	Ostracods	Pteropods	Salps
<i>Electrona carlsbergi</i>	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
	<b>Best</b>	<b>1.42</b>	<b>0.00</b>	<b>2.54</b>	<b>1.92</b>	<b>0.01</b>	<b>4.33</b>	<b>0.04</b>	<b>0.09</b>	<b>0.00</b>	<b>0.00</b>	<b>1.27</b>	<b>0.01</b>	<b>0.00</b>	<b>4.34</b>
	Upper	3.17	-	-	-	0.01	-	0.08	0.12	0.00	0.00	1.69	0.01	0.00	-
<i>Electrona antarctica</i>	Lower	2.54	0.00	0.56	0.00	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>6.55</b>	<b>0.00</b>	<b>29.56</b>	<b>4.97</b>	<b>0.08</b>	<b>0.00</b>	<b>0.05</b>	<b>0.00</b>	<b>0.00</b>	<b>0.25</b>	<b>0.42</b>	<b>0.02</b>	<b>0.00</b>	<b>0.00</b>
	Upper	61.39	-	-	-	0.49	-	0.42	0.00	0.01	0.85	3.13	0.15	0.00	-
<i>Gymnoscopelus fraseri</i>	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
	<b>Best</b>	<b>0.04</b>	<b>0.00</b>	<b>0.00</b>	<b>21.56</b>	<b>0.02</b>	<b>1.94</b>	<b>0.14</b>	<b>0.00</b>	<b>0.00</b>	<b>0.07</b>	<b>0.23</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>
	Upper	0.66	-	-	-	0.11	-	1.32	0.00	0.01	0.17	1.38	0.10	0.00	-
<i>Gymnoscopelus nicholsi</i>	Lower	0.05	1.07	0.15	0.38	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>0.17</b>	<b>6.29</b>	<b>9.63</b>	<b>4.98</b>	<b>0.01</b>	<b>0.00</b>	<b>0.06</b>	<b>0.00</b>	<b>0.00</b>	<b>0.09</b>	<b>0.14</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	1.26	-	-	-	0.02	-	0.37	0.00	0.00	0.17	0.60	0.02	0.00	-
<i>Gymnoscopelus braueri</i>	Lower	0.29	0.00	0.15	0.42	0.00	0.00	0.01	0.00	0.07	0.00	0.00	0.01	0.00	0.00
	<b>Best</b>	<b>0.79</b>	<b>5.45</b>	<b>11.12</b>	<b>8.42</b>	<b>0.00</b>	<b>0.00</b>	<b>0.04</b>	<b>0.00</b>	<b>0.01</b>	<b>0.00</b>	<b>0.09</b>	<b>0.05</b>	<b>0.00</b>	<b>0.00</b>
	Upper	5.52	-	-	-	0.00	-	0.32	0.00	0.02	0.20	0.49	0.29	0.00	-
<i>Krefflichthys anderssoni</i>	Lower	0.00	0.00	0.00	0.02	0.03	0.05	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>2.13</b>	<b>0.40</b>	<b>3.19</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>1.29</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	0.00	-	-	-	6.80	-	0.06	0.00	0.00	0.00	26.71	0.00	0.00	-
<i>Protomyctophum bolini</i>	Lower	0.00	0.00	0.00	0.78	0.00	0.00	0.04	0.00	0.01	0.09	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>6.28</b>	<b>0.00</b>	<b>0.45</b>	<b>0.22</b>	<b>0.00</b>	<b>0.00</b>	<b>0.82</b>	<b>0.22</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>
	Upper	0.00	-	-	-	0.07	-	2.84	0.00	0.00	2.30	1.55	0.07	0.00	-
<i>Protomyctophum choriodon</i>	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
	<b>Best</b>	<b>0.31</b>	<b>0.00</b>	<b>0.00</b>	<b>25.72</b>	<b>0.02</b>	<b>15.83</b>	<b>0.05</b>	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	<b>0.65</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	2.46	-	-	-	0.08	-	0.36	0.00	0.00	0.03	3.11	0.02	0.00	-
Total	Lower	2.87	1.07	0.86	1.60	0.03	0.05	0.06	0.00	0.09	0.11	0.01	0.01	0.00	0.00
	<b>Best</b>	<b>9.28</b>	<b>11.74</b>	<b>52.85</b>	<b>75.99</b>	<b>0.53</b>	<b>25.73</b>	<b>0.60</b>	<b>0.09</b>	<b>0.01</b>	<b>1.25</b>	<b>4.33</b>	<b>0.11</b>	<b>0.00</b>	<b>4.34</b>
	Upper	74.46	-	-	-	7.57	-	5.79	0.12	0.04	3.71	38.66	0.67	0.00	-

**Table 5.** The impact of myctophid predation on the production of key zooplankton tax expressed as a percentage of daily production consumed ( $\mu\text{g C m}^{-2} \text{d}^{-1}$ ) by each myctophid caught in the Scotia Sea during summer (JR177). Estimates represent the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentiles. Dashes denote instances where there was insufficient data to generate a confident estimate.



Myctophid species	Estimate	<i>Themisto gaudichaudii</i>	<i>Euphausia frigida</i>	<i>Euphausia superba</i>	<i>Thysanoessa</i> spp.	<i>Calanoides acutus</i>	<i>Calanus simillimus</i>	<i>Metridia</i> spp.	<i>Triconia</i> spp.	<i>Pleuromamma robusta</i>	<i>Paraeuchaeta</i> spp.	<i>Rhincalanus gigas</i>	Ostracods	Pteropods	Salps
<i>Electrona carlsbergi</i>	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
	<b>Best</b>	<b>0.11</b>	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.01</b>	<b>0.12</b>	<b>0.00</b>	<b>0.00</b>	<b>2.80</b>
	Upper	-	0.00	-	-	0.02	-	0.00	0.00	0.00	0.21	5.29	0.01	0.00	-
<i>Electrona antarctica</i>	Lower	0.11	0.00	0.05	0.02	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>8.67</b>	<b>0.00</b>	<b>7.57</b>	<b>0.82</b>	<b>0.00</b>	<b>0.00</b>	<b>0.02</b>	<b>0.00</b>	<b>0.00</b>	<b>2.16</b>	<b>0.27</b>	<b>0.05</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	87.28	-	-	0.00	-	0.36	0.00	12.68	31.19	10.00	0.68	0.00	-
<i>Gymnoscopelus fraseri</i>	Lower	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>1.25</b>	<b>0.01</b>	<b>0.00</b>	<b>0.01</b>	<b>0.00</b>	<b>0.08</b>	<b>0.02</b>	<b>0.20</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	0.00	-	-	0.10	-	0.09	0.00	5.66	0.26	2.95	0.06	0.00	-
<i>Gymnoscopelus nicholsi</i>	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
	<b>Best</b>	<b>0.19</b>	<b>0.00</b>	<b>0.02</b>	<b>0.37</b>	<b>0.01</b>	<b>0.00</b>	<b>0.01</b>	<b>0.00</b>	<b>0.04</b>	<b>0.10</b>	<b>0.06</b>	<b>0.00</b>	<b>0.00</b>	<b>0.43</b>
	Upper	-	0.00	-	-	0.14	-	0.13	0.00	2.97	1.25	0.88	0.02	0.00	-
<i>Gymnoscopelus braueri</i>	Lower	0.05	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.03	0.05	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>6.07</b>	<b>4.07</b>	<b>0.08</b>	<b>11.25</b>	<b>0.03</b>	<b>0.02</b>	<b>0.07</b>	<b>0.00</b>	<b>0.45</b>	<b>0.68</b>	<b>0.56</b>	<b>0.04</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	-	-	-	0.17	-	0.67	0.00	26.08	6.11	6.86	0.47	0.00	-
<i>Krefftichthys anderssoni</i>	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
	<b>Best</b>	<b>0.48</b>	<b>0.00</b>	<b>0.00</b>	<b>10.95</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	0.00	-	-	0.22	-	0.01	0.00	0.00	0.00	0.00	0.00	0.00	-
<i>Protomyctophum tenisoni</i>	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
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.86</b>	<b>0.00</b>	<b>0.36</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.08</b>	<b>0.01</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	0.00	-	-	0.00	-	0.01	0.00	0.00	0.00	0.59	0.05	0.00	-
<i>Protomyctophum bolini</i>	Lower	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00
	<b>Best</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>1.22</b>	<b>0.00</b>	<b>0.00</b>	<b>0.06</b>	<b>0.00</b>	<b>0.44</b>	<b>0.37</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
	Upper	-	0.00	-	-	0.00	-	0.53	0.00	22.26	2.87	0.00	0.00	0.00	-
Total	Lower	0.16	0.00	0.05	0.36	0.00	0.00	0.01	0.00	0.05	0.29	0.01	0.01	0.00	0.00
	<b>Best</b>	<b>15.53</b>	<b>4.07</b>	<b>7.67</b>	<b>26.74</b>	<b>0.06</b>	<b>0.39</b>	<b>0.17</b>	<b>0.00</b>	<b>1.01</b>	<b>3.34</b>	<b>1.29</b>	<b>0.10</b>	<b>0.00</b>	<b>3.23</b>
	Upper	-	-	-	-	0.66	-	1.80	0.00	69.67	41.90	26.56	1.30	0.00	-

**Table 6.** The impact of myctophid predation on the production of key zooplankton tax expressed as a percentage of daily production consumed ( $\mu\text{g C m}^{-2} \text{d}^{-1}$ ) by each myctophid caught in the Scotia Sea during autumn (JR200). Estimates represent the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentiles. Dashes denote instances where there was insufficient data to generate a confident estimate.

#### 4.1.2 Seasonal variations in prey selection

The results of this study show that myctophids consume a range of meso- and macrozooplankton in different seasons, particularly copepods, euphausiids and amphipods. These results are consistent with other studies conducted in the Southern Ocean (Gaskett et al., 2001; Gerasimova, 1990; Kozlov & Tarverdiyeva, 1989; Naumov et al., 1981; Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009) and on high latitude myctophid communities elsewhere at a more limited temporal resolution (Hopkins & Gartner, 1992; Pepin, 2013; Suntsov & Brodeur, 2008; Tanaka et al., 2013; Williams et al., 2001). Overall, the data suggest distinct seasonal variations in prey selection for the biomass-dominant Southern Ocean myctophids. Most of the myctophid species that fed predominantly on copepods, particularly *Protomyctophum* and *Gymnoscopelus* species, switched between different copepod species across seasons, and species such as *Electrona carlsbergi* and *Krefflichthys anderssoni* clearly switched from copepods to macrozooplankton between seasons. Consistent with other studies in the northern Scotia Sea, *E. carlsbergi* also switched to non-crustacean food resources in autumn as its diet was dominated by salps during this time, indicating that this prey taxa could be seasonally important in the prey field (Shreeve et al., 2009). Seasonal variation was also apparent in the diets of the species that consumed substantial proportions of macrozooplankton, such as *Electrona antarctica*, which switched between amphipods, euphausiids and pteropods between seasons. However, these apparent seasonal variations in myctophid diet did not correspond well with the observed seasonal trends in the abundance of their main prey species in the region (Fielding et al., 2012; Ward et al., 2012), indicating that myctophid prey selection is not simply a function of seasonal variations in prey availability. It has been suggested that seasonal variations in myctophid diet may be related to changes in prey ontogeny, behaviour and condition, as well as variations in temporal abundance, as recent studies observed a tendency for Southern Ocean myctophids to consume older and larger copepodite stages (Saunders et al., 2015a; Shreeve et al., 2009). However, more data at an increased spatial and temporal resolution are required to examine this hypothesis.

#### 4.1.3 Vertical distribution patterns

In this study, there was little evidence that seasonal patterns in myctophid depth distributions were governed by seasonal changes in the depth distributions of their main prey species at the

vertical resolution of our data, suggesting that other behavioral mechanisms are responsible for temporal variations in myctophid depth selection. Most copepod prey species were distributed throughout the water column across seasons and were therefore available to most myctophid species, which were predominantly distributed above 400 m at night in all seasons. The noteworthy exceptions were the deeper-dwelling species that consumed substantial proportions of prey taxa that appeared to be distributed above their main depths of occupancy in all seasons. For example, *Krefftichthys anderssoni* consumed substantial proportions of *Thysanoessa* spp. and *Rhincalanus gigas*, particularly during summer and autumn, even though these prey species were distributed around 200 m above the myctophids. Although there was some evidence of diel vertical migration (DVM) for *K. anderssoni* (Lourenço et al., 2017), similar to that reported in other studies (Collins et al., 2008; Duhamel et al., 2000; Koubbi et al., 2001), only small fractions of the population appeared to inhabit regions above 200 m. Similarly, *Thysanoessa* spp., *R. gigas*, and *Themisto gaudichaudii*, were also substantial components of the diet of *Nannobrachium achirus* which mostly occurred below 400 m in all seasons and was markedly absent from the upper 200 m. This suggests limited DVM and foray-type foraging behavior in these deeper-dwelling myctophid species, whereby individuals distributed at depth undertake intermittent and unsynchronized vertical migrations into the surface layers to feed (Cottier et al., 2006).

Foray behavior is generally considered to reflect the requirement for individuals within populations to maintain their specific metabolic requirements within the environment in which they reside. Interestingly, a recent study showed both *Krefftichthys anderssoni* and *Nannobrachium achirus* to be sub-Antarctic species, with only non-reproducing migrants penetrating high latitude waters (Saunders et al., 2017). Both species occupied a narrow thermal range centered around 2 °C, suggesting that these fish need to maintain a vertical distribution that minimizes fluctuation in temperature throughout their latitudinal range. In the Scotia Sea, such thermally stable water masses are found predominantly within CDW in regions below 300 m (Venables et al., 2012), where the majority of the *K. anderssoni* and *N. achirus* populations were distributed. This implies that, unlike most other myctophid species in the region, the need to thermoregulate limits the capacity of these species to migrate vertically to feed in the zooplankton rich surface layers. Evidence that these two species have an alternative feeding strategy that focuses on deep living prey, such as mesopelagic copepods, amphipods and small decapods, was limited in this study, particularly for *K.*

*anderssoni*, indicating that forays to the upper layers are necessary once the requirement to feed on their preferred prey taxa overrides the requirement to thermoregulate. Also, such behavior may not necessarily be restricted to the night. We observed occasional aggregations of *K. anderssoni* above 200 m during the daytime in spring and summer (Lourenço et al., 2017), and acoustic studies in the Scotia Sea indicate that daytime surface aggregations of swimbladdered myctophid fish, such as *K. anderssoni*, are not uncommon (Saunders et al., 2013). Furthermore, higher predators, such as king penguins (*Aptenodytes patagonicus*) often catch their myctophid prey, particularly *K. anderssoni*, in the upper 300 m of the water column during daylight (Scheffer et al., 2010).

#### 4.1.4 Myctophid body size and diet

Our study further demonstrates that the size of the myctophid predator is a key determinant of diet in the Scotia Sea, with larger species and intra-specific size classes generally consuming larger prey (Shreeve et al., 2009). For example, the study showed that only the largest sized myctophid species, such as *Electrona antarctica*, *Gymnoscopelus nicholsi* and *Gymnoscopelus braueri*, consumed *Euphausia superba*, with size classes larger than 80 mm consuming the greatest proportions of the species. *Euphausia superba* was present in the diet of *E. antarctica* individuals <55 mm, although preliminary analysis indicates that only the calyptopes and furcillia stages were consumed by these fish. Our analyses also showed that larger sized myctophids include larger and older life stages of their main prey species in their diets (Fig. 8). However, more detailed determination of the predatory impact on the specific developmental stages of their prey species, particularly *E. superba*, is clearly a necessary further step towards understanding the structure and operation of the Scotia Sea food web. The amphipod *Themisto gaudichaudii* and the euphausiid *Thysanoessa* spp. were consumed by both large and small species in the region, although *T. gaudichaudii* was mostly taken by fish >55 mm, whilst only fish >40 mm took *Thysanoessa* spp. There was also a general decline in copepod consumption with size for most myctophid species, which corresponded with an increase in dietary breadth. Such size-related diet patterns most likely reflect an increase in myctophid predation capacity, such as gape and stomach size, as well changes in metabolic requirements and filtering capacity of the gill rakers (Karpouzi & Stergiou, 2003; Scharf et al., 2000).

#### 4.1.5 Niche partitioning

Resource partitioning is important in minimizing competition between coexisting species in pelagic ecosystems (Schoener, 1974), and such partitioning has been demonstrated in highly diverse low latitude myctophid communities (Clarke, 1980; Hopkins & Gartner, 1992), and at temperate and high latitudes (Cherel et al., 2010; Sassa & Kawaguchi, 2005; Shreeve et al., 2009; Watanabe et al., 2002). However, species tend also to exhibit a high degree of dietary overlap at high latitudes, such as the Southern Ocean, which could be a function of increased regional food availability that minimizes inter-specific food competition (Pakhomov et al., 1996). In the present study, there was some evidence of myctophid feeding guilds within the Southern Ocean myctophid community which appeared to change seasonally. Our cluster analysis, for example, showed that only *Gymnoscopelus fraseri* and *Gymnoscopelus nicholsi* occurred in the same group consistently across the three seasons, although *Krefflichthys anderssoni* and *Protomyctophum tenisoni*, the two smallest species, were also grouped together in seasons when both species were present. Overall, there was a relatively high degree of dietary overlap within this myctophid community across seasons, with several prey taxa common to all feeding guilds. Most feeding guilds were also centered around the consumption of copepods and small euphausiids in each season, with myctophid groupings defined predominantly by the differential contributions of a few key prey species in the diet, such as *Rhincalanus gigas*, *Metridia* spp., *Pleuromamma robusta* and *Thysanoessa* spp. Apart from *Thysanoessa* spp., our estimates of the level of myctophid predation impact on the daily productivity of these key copepod prey species was mostly relatively low, and the data indicate that myctophids maintain sufficient dietary breadths in each season that potentially minimises both the impact of seasonal changes in the prey field and the exhaustion of any one food source through inter-specific competition. Our results therefore support the hypothesis that inter-specific competition for these prey resources is minimal in the Scotia Sea because of their high availability in the water column and suggests that the myctophid community in this region is relatively stable in terms of resilience to short-term fluctuations within the zooplankton prey field.

Our study only found limited evidence of dietary segregation and specialization in myctophid species in the Scotia Sea, but instances where this was apparent were similar to those reported previously in the region (Shreeve et al., 2009). *Electrona antarctica*, for example, was

consistently identified as a predominant macrozooplankton feeder across seasons, consuming mostly *Euphausia superba* and *Themisto gaudichaudii*. However, *Gymnoscopelus braueri* and *Electrona carlsbergi*, two large and otherwise copepod and small euphausiid consuming species, were also clustered with *E. antarctica* in macroplankton feeding guilds in summer and autumn, respectively. This demonstrates that other large myctophids are opportunistic and highly selective feeders that may change feeding roles seasonally depending upon the prey resources available. Overall, our results correspond broadly with findings from other studies using time-integrated biochemical trophic markers in the Southern Ocean (Cherel et al., 2010; Stowasser et al., 2012), which show that myctophid species generally occupy a similar trophic level within the Southern Ocean food web, although some niche segregation occurs within the community based on inter-specific diet preference and habitat utilization.

#### 4.1.6 Food web implications

The significance of Antarctic krill in the diet of Southern Ocean myctophids in regions south of the Antarctic Polar Front has long been debated, primarily due to a lack of trophodynamics data at the appropriate spatial and temporal scales (Lancraft et al., 1989; Pakhomov et al., 1996; Pusch et al., 2004; Shreeve et al., 2009; Williams, 1985). However, a recent study in the Scotia Sea cast new light upon the role that krill plays in the feeding ecology of myctophids and the structure of the Scotia Sea food web (Saunders et al., 2015a). Based on data averaged across seasons and the entire Scotia Sea, this study showed that most myctophids in the region have a wide dietary breadth, consuming mostly copepods, small euphausiids and amphipods, but seldom consume Antarctic krill. However, krill were found to comprise a relatively high proportion of the diets of some large myctophid species, most notably *Electrona antarctica* (up to 43% by Index of Relative Importance). Although the overall predatory impact of these myctophids on the daily productivity of krill appeared relatively low (<3%, or ~6% when krill production estimates are adjusted to reflect ambient temperatures using a  $Q_{10}$  value of 2.3; see methods section), the annual removal of Antarctic krill by large myctophids at the Scotia Sea scale could amount to ~17 million tons, possibly making them the main consumers of krill in the region (Hill et al., 2007; Kock et al., 2012). Myctophids therefore appear to link secondary productivity to higher predators through both krill-independent and krill-dependent trophic pathways (Murphy et al., 2007b), although how

the dynamics of these pathways change in different seasons at the ocean-basin scale was unclear prior to our study.

In this study, we found that the respective roles of small versus large myctophids in this pathway varied. Small myctophids maintained a robust krill-independent trophic pathway at all times of year, consuming mostly copepods and small euphausiids, with all krill life stages absent in their diets. Antarctic krill comprised a substantial dietary component of the large myctophids *Electrona antarctica*, *Gymnoscopelus braueri* and *Gymnoscopelus nicholsi*, although consumption of this prey species varied intra-annually. Our calculations showed that their overall consumption of daily krill production was relatively high in all seasons (8-53%), particularly in summer, further suggesting that these large myctophids comprise a krill-dependent trophic pathway in all seasons, but with the level of dependence increasing substantially at certain times of year. The data further indicate that, although the proportions of krill consumed by large myctophids varies intra-annually, the overall level of predation impact that they exert on daily krill production at different times of year may be governed more by seasonal variations in myctophid abundance than seasonal increases in krill in the diet. This is consistent with the notion that, whilst krill consumption per unit myctophid biomass may be relatively low, they remain major consumers of krill due to their relatively high biomass and broad-scale distributions patterns (Hill et al., 2007). Factors that control seasonal variations in myctophid abundance in the region currently remain unclear, but seasonal migratory behavior may be important (Saunders et al., 2014).

Regardless of the mechanisms controlling seasonal variations in krill consumption by large myctophids, the summer is a critical time in the life cycles of many Southern Ocean higher predators, as it is a time when most species breed (Croxall et al., 1988). Consequently, there is an increased demand for krill at this time to ensure higher predator breeding and recruitment success (Croxall et al., 1999). Our results suggest that, because myctophids become more dependent on krill in the summer season, there could be increased resource competition for krill during this biologically sensitive time, which could have an impact on higher predator populations, particularly during periods of low krill availability (Murphy et al., 2007b). The results also imply that populations of some large myctophid species would be most susceptible to periods of low krill availability during the summer season, although there

appears to be some dietary flexibility within the main krill consuming species, particularly *Gymnoscopelus braueri* and *Gymnoscopelus nicholsi*, which may provide a buffer under such scenarios in the short-term. However, the extent to which both large and small myctophids are resilient to increased predation pressure and can sustain higher predator populations under scenarios of increased and prolonged reductions in krill stocks requires examination.

Myctophid predation had little impact on the productivity of most copepod species in the Scotia Sea during all seasons, except for *Calanus simillimus*, of which myctophids consumed up to 23% of its' daily productivity in summer. *Protomyctophum choriodon*, a predominantly northern species and likely seasonal migrant in the region (Reid et al., 2006), had the greatest impact on this copepod species during this time. Our results accord with other studies conducted in the region and show that the majority of myctophid species comprise a robust link between secondary production and higher predators, with myctophids unlikely to exhaust the copepod component of the prey field across seasons (Shreeve et al., 2009). Similarly, the predatory impact of myctophids on macrozooplankton such as pteropods, ostracods and salps was either relatively low or negligible in most seasons.

Our study showed that myctophid predation on the daily productivity of *Thysanoessa* species was high in each season (up to 76% in summer) and that these smaller euphausiids comprised a substantial proportion of the diets of most myctophid species, particularly *Krefflichthys anderssoni*, *Protomyctophum choriodon* and *Gymnoscopelus fraseri*. *Thysanoessa macrura* and *Thysanoessa vicini* are the most consistently found euphausiids in Antarctic waters and often exceed *Euphausia superba* in abundance in some regions (Daly & Macaulay, 1988). These small euphausiids are an important dietary component of penguins, sea birds and large predatory fish (Brown & Klages, 1987; Kock et al., 1994; Pichegru et al., 2011), but information on the ecology of Southern Ocean *Thysanoessa* species is limited and further studies are clearly warranted on this component of the food web. Given the high seasonal importance of these small euphausiids in the diets of most myctophid species in the Scotia Sea, they are likely to play a vital role in sustaining the relatively high levels of biomass in the region, which, in turn, is crucial in governing their capacity to maintain a robust krill-independent trophic pathway. Our study also showed that *Themisto gaudichaudii* was an important dietary component of most myctophids in the Southern Ocean and that their



predatory impact on this prey taxa may be high at certain times of year (38 % of daily productivity in spring). The species was particularly important in the diet of *Electrona antarctica*, which appears to be a predominant macro-plankton feeder. The ecological importance of this species in the northern Scotia Sea and at sub-Antarctic latitudes was highlighted by Shreeve et al. (2009) and Boucher et al. (2001), respectively.

#### 4.1.7 Possible expatriation perspective

Most of the biomass-dominant myctophid species found in the Scotia Sea appear to be non-reproducing migrants from waters north of the APF, the main exceptions being *Electrona antarctica* and possibly *Krefflichthys anderssoni*, the latter seemingly able to recruit successfully in waters around the South Georgian Shelf (Belchier & Lawson, 2013; Lourenço et al., 2017; Saunders et al., 2017). Furthermore, both inter-specific body size capacity and underlying temperature gradients are important controls of spatial patterns in myctophid distribution and population dynamics in the region, with only species capable of attaining a large body size able to penetrate colder waters at high latitudes (Saunders & Tarling, 2018). In this study, we found that only two of the largest-sized expatriate species, *Gymnoscopelus nicholsi* and *Gymnoscopelus braueri*, consumed Antarctic krill across seasons, although their overall individual consumption of krill was less than ~11% of its daily productivity. All of the expatriate species in the study were largely copepod and small euphausiid feeders in each season. Since Antarctic krill is predominantly absent in regions north of the APF, where most myctophid species populations appear to be centered (Hulley, 1981), it is possible that some of the appropriate sized expatriate myctophids are not accustomed to the behaviour of the species, which may explain its low seasonal occurrence in the diets of some large expatriate species in the Scotia Sea. Furthermore, Antarctic krill recruit predominantly under sea ice, with smaller larval stages occurring mostly in the SIZ and populations in the northern Scotia Sea being dominated by large adults (Tarling et al., 2007). Krill are therefore likely to be too large to consume for many of the smaller expatriate species that inhabit the northern Scotia Sea, such as *Protomyctophum* spp. and *K. anderssoni*. Since many of these species are unable to penetrate the colder waters of the SIZ, they are also unlikely to reach regions where krill stages within their prey size spectra occur.

Our data imply that the capacity of myctophids to maintain a robust krill-independent trophic pathway in the Southern Ocean food web is largely dependent upon inter-specific physiological characteristics, the underlying latitudinal temperature gradient, and oceanic transportation mechanisms that govern myctophid migration capacity and therefore enables the influx of major concentrations of expatriate myctophid biomass in the region. Given that most myctophid populations are centered in regions north of the AFP, perhaps as far north as the sub-tropical front (Hulley, 1981), studies are required further afield to understand key ecological processes that are likely to have a direct bearing on ecosystem processes at higher latitudes throughout the Southern Ocean. Our data also imply regional variation in food web structure in the Scotia Sea, whereby krill-dependent trophic pathways are likely to be more prevalent in the SIZ than in the northern sectors due to expatriation effects. For example, the diversity and abundance of the non-krill consuming myctophid community appears lower in the SIZ, whilst the abundance of *Electrona antarctica*, the main krill predating myctophid, is greatest in this region in all seasons. Such regional variability requires further examination to ascertain the resilience of Southern Ocean food web structure to sustained periods of low krill abundance, as well as possible climate related impacts on the ecology of myctophids, including shifts in distributional range.

#### 4.1.8 Conclusions

The myctophid community in the Scotia Sea appears to link secondary production to higher predators through both krill-dependent and krill-independent trophic pathways in each season. Large myctophid species, particularly *Electrona antarctica*, comprise the most krill-dependent trophic pathway of this community and may exert a relatively high predatory impact upon Antarctic krill, particularly during the higher predator breeding season in summer. Consequently, krill-consuming myctophids, and hence, the Southern Ocean mesopelagic food web, appear to be most sensitive to periods of low krill availability and sustained environmental change during this season. However, the overall myctophid community comprises a seasonally robust component of the Southern Ocean food web, as all species maintained a large dietary breadth in each season, did not exhaust their zooplankton prey field, and appeared not to be in direct competition for resources. Given the relatively high abundance of myctophids in the region, there is likely to be considerable flux of biomass passing through the Scotia Sea myctophid community in each season, which appears to be

mostly independent of Antarctic krill. However, the capacity of myctophids to maintain this krill-independent trophic pathway in this ecosystem appears to be largely dependent upon the influx of major concentrations of expatriate populations from regions outside of Antarctic waters. Studies into the sensitivities of Southern Ocean food ecosystems to environmental change therefore need to consider ocean transport mechanisms and ecological processes occurring in more remote regions to understand processes occurring at higher latitudes. Also, given that many expatriate species seem unable to penetrate the cold waters of the sea ice sector, and that high latitude communities are dominated by *E. antarctica*, krill-dependent trophic pathways are likely to be of greatest importance in the southernmost regions of the Scotia Sea. Further studies are warranted here to examine the trophodynamics and stability of the myctophid component of this regional food web.

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## Highlights

- The diet and predatory impact of Southern Ocean myctophids varies seasonally.
- Most myctophids have high overlap in diets across seasons.
- Myctophid predation on Antarctic krill is highest in summer.
- Food web stability may be lowest in summer during times of low krill availability.
- Myctophids provide both krill-dependent and krill-independent trophic pathways.