Trophodynamics of *Protomyctophum* (Myctophidae) in the Scotia Sea (Southern Ocean)

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This study investigated spatial and temporal patterns in distribution, population structure and diet of Bolin's lanternfish *Protomyctophum bolini*, Tenison's lanternfish *Protomyctophum tenisoni* and gaptooth lanternfish *Protomyctophum choriodon* in the Scotia Sea using data collected by mid-water trawl nets during spring, summer and autumn. *Protomyctophum bolini* was the most abundant species of the genus encountered throughout the Scotia Sea with the greatest concentrations occurring around the Antarctic Polar Front (APF). This species had a life cycle of 2+ years, but spatial differences in population structure were apparent as the I-group was absent from all regions south of the APF, suggesting that the species does not recruit in the Scotia Sea. *Protomyctophum tenisoni* occurred mostly in waters characteristic of the APF and was absent from the southern Scotia Sea. It had a limited and unimodal size range, but there was clear size-related sexual dimorphism with males significantly larger than females. The species had a life cycle of ~2 years, but the I-group occurred only in regions close to the APF suggesting that recruitment is restricted to these waters. A seasonal southward migration for *P. choriodon* is likely as the species occurred mostly to the southwest of South Georgia in summer, but extended to the sea-ice sectors in autumn. *Protomyctophum choriodon* had a life cycle of 4+ years in the Scotia Sea and the population was dominated by age-classes >3 years old. Larval stages were absent during the surveys for all species. Diurnal variations in vertical distribution were apparent for all three species. Inter-specific variations in diet were evident, but all species were primarily copepod feeders, with *Metridia* spp. *Rhincalanus gigas* and *Calanus simillimus* generally dominating their prey. Small euphausiids, principally *Thysanoessa* spp., were also an important component of their diets, particularly for *P. choriodon* which had the largest body size. The spatial and temporal variations in diet for both *P. bolini* and *P. tenisoni* were broadly consistent with underlying abundance patterns within mesozooplankton community.

Key words

Myctophid fish, *Protomyctophum*, Feeding ecology, Antarctic krill, Copepod, Scotia Sea

INTRODUCTION

Mesopelagic fish are the most abundant fishes on earth comprising an estimated biomass in excess of 11,000 million tons (Irigoien *et al.*, 2014). They are important conduits in the transfer of energy through oceanic food webs, linking primary consumers to a range of top marine predators, and contribute to the export of carbon from the surface layers to mesopelagic depths through their extensive vertical migrations (Pakhomov *et al.*, 1996; Smith, 2011; Irigoien *et al.*, 2014). These fish therefore play a major role in the function of oceanic ecosystems and biogeochemical cycles around the globe. However, mesopelagic fish remain one of the least studied components of the oceanic ecosystem, with major uncertainties in the most basic aspects of their biology and ecology. Lanternfish, or myctophids (family Myctophidae), are considered to be the dominant mesopelagic fishes in most the world's oceans in terms of diversity and biomass (Gjøsaeter and Kawaguchi, 1980), but little is known of their distribution of abundance, ecology or trophodynamics in all regions in which they occur. Consequently, determining the ecology of myctophids is an important step towards understanding the operation of oceanic ecosystems at a regional and, ultimately, global level.

Myctophids are difficult to sample at an appropriate temporal and spatial resolution, particularly in remote high latitude regions such as the Southern Ocean. This has not only confounded our understanding of all myctophids in these regions, but has limited investigations to the most abundant and frequently encountered species (Linkowski, 1985; Greely *et al.*, 1999; Sassa and Kawaguchi, 2005; Dypvik *et al.*, 2012; Pepin, 2013; Saunders *et al.*, 2014). There are many high latitude myctophid species for which virtually nothing is known about their ecology. The genus *Protomyctophum* has 16 species that occur mostly at high latitudes in all of the world's oceans and all species are examples of understudied myctophids. The majority of information available on this genus refers to general patterns in biogeography and morphology (Hulley, 1981; McGinnis, 1982), with only a few studies reporting information on abundance and vertical distribution for species such as *Protomyctophum arcticum* (Lütken 1892) (Kawaguchi and Mauchline, 1982; Fock and John, 2006) and bigeye lanternfish *Protomyctophum thompsoni* (Chapman 1942) (Pearcy *et al.*, 1977; Beamish *et al.*, 1999; Watanabe *et al.*, 1999) in the sub-Arctic, and Bolin's lanternfish *Protomyctophum bolini* (Fraser-Brunner 1949) in the sub-Antarctic (Piatkowski *et al.*, 1994; Pusch *et al.*, 2004; Collins *et al.*, 2008; Iwami *et al.*, 2011). Furthermore, few studies have detailed information on *Protomyctophum* population dynamics (Kawaguchi and Mauchline, 1982), or trophodynamics (Oven *et al.*, 1990; Pakhomov *et al.*, 1996; Pusch *et al.*, 2004; Sassa and Kawaguchi, 2005; Shreeve *et al.*, 2009) in any region, and those that exist are spatially and temporally limited, often with small sample sizes. There is a clear need for new data on all species within this genus, including the rarer ones, in order to resolve the composition and dynamics of the high latitude mesopelagic fish community.

The majority of *Protomyctophum* species (10 out of 16 species) are found in the Southern Ocean, where the most common species include *P. bolini*, gaptooth lanternfish

Protomyctophum choriodon (Hulley 1981) and Tenison's lanternfish *Protomyctophum tenisoni* (Norman 1930) (Hulley, 1981). The Scotia Sea (Atlantic sector) is one the most productive regions of Southern Ocean, sustaining high levels of secondary production, which in turn supports major populations of whales, seals, penguins and commercially-targeted fish (Atkinson *et al.*, 2001; Holm-Hansen *et al.*, 2004). In this region, myctophids, including the *Protomyctophum* species, play an important role in the transfer of energy through the food web as they consume herbivorous and omnivorous zooplankton, such as copepods and euphausiids (including Antarctic krill, *Euphausia superba*) (Pakhomov *et al.*, 1996; Pusch *et al.*, 2004; Shreeve *et al.*, 2009), and are preyed upon by several top marine predators, including seals (e.g. *Arctocephalus gazella*, *Mirounga leonina*), penguins (*Aptenodytes patagonicus*), squid (*Martialia hyadesi*) and large pelagic fish (*Dissostichus eleginoides*) (Rodhouse *et al.*, 1992; Olsson and North, 1997; Brown *et al.*, 1999; Cherel *et al.*, 2002; Reid *et al.*, 2006; Collins *et al.*, 2007). Myctophids comprise an estimated biomass of 4.5 million tonnes in the Scotia Sea (Collins *et al.*, 2012), providing a major krill-independent trophic pathway in the usually krill-dominated food web (Murphy *et al.*, 2007b). More comprehensive data on the ecology of all myctophid species in this region is required in light of recent evidence of ocean-warming (Whitehouse *et al.*, 2008), reductions in winter sea-ice extent, (de la Mare, 1997; Curran *et al.*, 2003) and declining krill stocks in the Scotia Sea (Atkinson *et al.*, 2004; Hill *et al.*, 2013), which could have an adverse impact on the Southern Ocean ecosystem (Moline *et al.*, 2004; Murphy *et al.*, 2007a; Flores *et al.*, 2012). With further long-term reductions in krill abundance, as predicted (Hill *et al.*, 2013), the importance of myctophids as a krill-independent trophic pathway is likely to increase in the region. Acquisition of new data on the distribution of abundance, population dynamics and feeding ecology of all myctophids is therefore essential for understanding how pelagic food webs are structured in the Scotia Sea, for determining their sensitivity to ongoing environmental change, and for establishing effective ecosystem-based management strategies throughout the Southern Ocean (Kock *et al.*, 2012).

In this paper we present new data on the distribution of abundance, population structure and diet of, *P. bolini*, *P. choriodon* and *P. tenisoni*, in the Scotia Sea. An index of relative importance (IRI), which combines prey occurrence, biomass and numbers, was used to investigate spatial, temporal and ontogenetic variations in their respective diets. Our data were derived from depth-discrete net samples collected between the ice-edge and Antarctic Polar Front (APF) during austral spring, summer and autumn (2006-2009), and are the most comprehensive for the *Protomyctophum* genus in any region of the world to date. Our study provides important parameterizations for new food web and ecosystem studies in the Scotia Sea that are required in order to cast new light on the potential impacts of ocean-climate change on the operation of the Southern Ocean pelagic food webs and ecosystems. They also contribute to resolving the composition and dynamics of the global mesopelagic fish community.

MATERIALS AND METHODS

STUDY LOCATION

Oceanographic, acoustic and biological data were collected at stations across the Scotia Sea during three cruises on the RRS *James Clark Ross* (Fielding *et al.*, 2012; Korb *et al.*, 2012; Venables *et al.*, 2012; Ward *et al.*, 2012; Whitehouse *et al.*, 2012). JR161 was undertaken in November 2006 (spring), JR177 in January 2008 (summer) and JR200 in March 2009 (autumn). Dependent on ice and weather conditions, six regional locations were sampled during the surveys: Southern Scotia Sea (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS), Georgia Basin (GB) and the Polar Front (PF) (Fig. 1). Stations were spread across the predominant water masses and frontal zones that occur in the region (Rintoul *et al.*, 2001).

NET SAMPLE COLLECTION AND PROCESSING

Mesopelagic fish were collected using a Rectangular Midwater Trawl net (RMT25; Piatkowski *et al.*, 1994) that comprised two opening and closing nets with a 5 mm mesh at the cod-end. Each net had a flow meter to estimate the filtered water volume and was operated by an electronic downwire net monitoring system that also provided real-time information on depth, temperature and salinity. At each station, depth-stratified hauls were undertaken at 0-200 m, 201-400 m, 401-700 m and 701-1000 m, with the net towed at ~2.5 knots for 30-60 mins in each depth zone. These zones were repeated by day and by night during JR161 and JR177, but sampling was only conducted during hours of darkness on

JR200. The RMT25 was deployed twice in succession to cover the four depth zones at each station, with the upper nets (0-200 and 200-400 m) undertaken as close to local midday or midnight as practical. The majority of nets were deployed in oceanic regions where bottom depths exceeded 1500 m (see Collins *et al.* 2012). Additional targeted net hauls were undertaken on acoustically detected fish aggreations during the surveys, mostly around the Polar Front. These hauls were not used to generate estimates of abundance or biomass. Net samples were sorted onboard to the lowest taxonomic level possible (Hulley, 1990) and total catch weights per fish species were recorded using a motion-compensated balance. The standard length (SL) of all fish were measured to the nearest mm. Where possible, sex and maturity status was recorded for a subsample. Stomachs were dissected from a random subsample of 25 fish per non-targeted haul, or from each fish where catches were small. All stomachs were frozen for subsequent microscopic analysis.

STOMACH CONTENTS ANALYSIS

Fish stomachs contents were sorted to the lowest taxonomic level possible, subject to the state of digestion, following Shreeve *et al.* (2009). Individual prey items were enumerated and weighed. If the prey was highly disaggregated, the weights of the component species were estimated as a proportion of the total weight of all components..

Diet was expressed as percentage frequency of occurrence (%F), percentage mass (%M), percentage number (%N) and percentage Index of Relative Importance (%IRI) (Hynes, 1950; Pinkas *et al.*, 1971; Hyslop, 1980; Cortes, 1997). The %IRI was calculated for prey species and $\%IRI_{DC}$ for prey categories (Main *et al.*, 2009). In the preliminary analysis, prey categories were defined as: Amphipoda, Copepoda, Euphausiacea, Chordata, Ostracoda and Unidentified crustacean, but a more detailed analysis was subsequently performed using the following nine dominant prey categories: the copepods *Metridia* spp., *Rhincalanus gigas*, *Pleuromamma robusta*, *Paraeuchaeta* spp., and *Calanus simillimus*, Other copepods, the euphausiid *Thysanoessa* spp., the amphipod *Themisto gaudichaudii* and Other taxa (other amphipods, *E. superba*, Ostracods, Chordates and unidentified crustaceans). Note that the %IRI is not additive so the sum of the individual species' %IRI is not the same as the prey category $\%IRI_{DC}$ value (Hansson, 1998). The %IRI was calculated as:

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

where *i* is prey item.

The %IRI for each prey category was calculated in this way for all three myctophid species to examine variations in diet between fish pooled by region, season (cruise), size and sex (Table I). For spatial comparisons of diet, data were pooled for regions south of the South Antarctic Circumpolar Current Front (SACCF; stations: SSS and MSS), between the SACCF and the

Southern Boundary of the Antarctic Polar Front (S-APF; stations WSS, NSS, GB) and north of the S-APF (stations: PF) (Fig.1.) Data were also pooled for size-classes less than or greater than the overall population mean for comparisons of each species' diet by size. The ±95% confidence limits for the mean %IRI of each prey category were calculated using a bootstrapping procedure that re-sampled (with replacement) each species' datasets (individual stomachs) 1000 times (Main *et al.*, 2009).

LENGTH-FREQUENCY ANALYSIS

Due to the relatively low sample sizes per species at each station (<50 individuals), it was not possible to investigate spatial variations in length-frequency distributions robustly during the three surveys. Data were therefore pooled by survey for each species to give composite length-frequency distributions for the study region as a whole. CMIX component fitting software (de la Mare, 1994) was then used to fit normal distributions to the composite length-frequency data and identify modes following the approach detailed in Saunders *et al.* (2007). A series of runs were performed during the analysis based on the presence of one, two or three cohorts in the data and we then determined the best component fit to the observed data using a Chi-squared test. No constraints were placed on the mean length, variance or proportions expected within each component when fitting the mixed distributions. Differences between gender sizes and depth zones were investigated using Students t-tests performed on data aggregated across all surveys.

RESULTS

OCEANOGRAPHIC CONTEXT

Detailed descriptions of the oceanographic regime are given in Venables *et al.* (2012) and Whitehouse *et al.* (2012), so only a brief overview is given here. During each cruise, stations in the SSS were situated south of the Southern Boundary in the colder waters of the Seasonal Ice Zone. Stations in the WSS and MSS lay close to the South Antarctic Circumpolar Front (SACCF) and had relatively similar water mass properties. The NSS station showed characteristics of the southern edge of the Antarctic Polar Front (APF), particularly during JR161. 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 retroflection of the flow of the SACCF. The northernmost PF stations were situated north of the southern edge of the APF where surface water temperatures were warmer than those in regions further south.

DISTRIBUTION

A total of 143 RMT25 non-targeted net hauls (i.e. hauls not directed at acoustical targets) were undertaken during the three surveys. Weather and operational constraints meant that it was not possible to sample all stations to the same degree on all surveys. Most notably, sampling at the WSS station was mostly confined to the spring survey.

Several species of *Protomyctophum* were encountered during the surveys, including Andriashev's lanternfish *Protomyctophum andriashevi* (Becker 1963), *P. tenisoni*, *P. bolini*, *P. choriodon*, parallel lanternfish *Protomyctophum parallelum* (Lönnberg 1905) and jewelled lanternfish *Protomyctophum gemmatum* (Hulley 1981) (Fig. 1). *Protomyctophum bolini* was the most abundant species on each survey, comprising an overall mean abundance of 0.038-0.070 ind. 1000 m^{-3} and a biomass of 0.052-0.080 g 1000 m^{-3} (Tables II and III). The species was distributed throughout the Scotia Sea in regions north of the seasonal ice-edge and the greatest concentrations occurred at the PF and GB stations (Fig. 1). *Protomyctophum tenisoni* was absent from non-targeted net hauls during the summer survey, but comprised a relatively high proportion of abundance during spring and autumn (0.012-0.021 ind. 1000 m^{-3}), particularly around the PF (Fig. 1; Table II). This species was seldom encountered south of the SACCF and comprised an overall mean biomass of <0.025 g 1000 m^{-3} on the two surveys (Table III). *Protomyctophum choriodon* was absent in spring and was caught predominantly around the GB in summer (Fig. 1). However, it occurred at all stations further south during autumn, with the greatest concentrations generally in the SSS (Table II). The species had an overall mean abundance and biomass of ~0.005 ind. 1000 m^{-3} and ~0.020 g 1000 m^{-3}, respectively (Tables II and III). *Protomyctophum parallelum*, *P. andriashevi* and *P.*

gemmatum were caught predominantly in APF waters during the spring survey. Overall, these species comprised a relatively low abundance and biomass in the Scotia Sea (<0.050 ind. 1000 m^{-3} and <0.010 g 1000 m^{-3}).

VERTICAL DISTRIBUTION

The vertical distribution patterns of *P. bolini*, *P. tenisoni* and *P. choriodon* did not differ between seasons or stations, so the data were aggregated to illustrate their overall depth distributions in the region. Daytime catches of *P. bolini* were low and the species was mostly spread between 201-700 m during this time (Fig. 2a). *Protomyctophum bolini* abundance and biomass was substantially larger at night, where the species occurred higher in the water column between 201-400 m. Only a few individuals were encountered above 200 m at night. Daytime catches of *P. tenisoni* were also comparatively low and the species was distributed mostly between 401-700 m (Fig. 2b). At night, both mean density and biomass increased markedly and the species occurred solely in the upper 200 m of the water column, indicative of some diurnal vertical migration (DVM). *Protomyctophum choriodon* was distributed predominantly between 0-200 m during both day and night, although the species was also present in deeper regions (201-400 m) during the night, but not during the daytime (Fig. 2c). This suggests a night-time deepening of part of the population for this species. Of the other *Protomyctophum* species encountered on the surveys, *P. parallelum* and *P. gemmatum* were caught exclusively between 400 and 700 m, whilst *P. andriashevi* was predominantly distributed between 200-400 m.

POPULATION SIZE STRUCTURE

The information available for *Protomyctophum* species indicate that spawning occurs in spring (September/October) (Oven *et al.*, 1990). The following terminology was therefore adopted to describe the population structure of these myctophids: 0-group covers the period from hatching until 31 October the following year; I-group covers the period 1 November to 31 October the next year; II-group covers the subsequent period from 1 November until 31 October, and so on. Differentiation between the 0-goup and I-group in the population was aided by comparisons of modal size, relative to the estimated spawning period, with published growth rates of high latitude and temperate myctophids (Smoker and Pearcy, 1970; Gjøsaeter, 1978; Linkowski, 1985; Greely *et al.*, 1999). Although the data were collected without temporal repetition in non-consecutive seasons, and therefore interannual effects cannot be accounted for, our analyses provide the most comprehensive synopsis of seasonal variations in *Protomyctophum* population structure to date.

Length-frequency histograms for *P. bolini* showed one size-, and presumably age-, class in the spring population that we assumed to be the newly recruited II-group containing ~2 year old individuals based on realistic rates of growth (mode: 50 mm; Fig 3a). Both the newly spawned 0-group and I-group were absent during this time. Approximately 5% of the II-group was juvenile and all adults had developing gonads. There was little evidence of growth of the II-group during the summer period (mode: 50 mm), indicating that it had attained its terminal size prior to this season. The 0-group and I-group remained absent from the population at this time, and the maturity structure of the II-group was very similar to that in spring. By autumn, the I-group (~1 year olds) was evident in the population (mode: 38 mm), together with the II-group that had reduced in magnitude from the previous season (mode: 51 mm). Juvenile stages dominated the I-group during the autumn and this cohort occurred entirely at the PF and NSS stations, where water masses properties were characteristic of the APF (Fig. 4a). This cohort would presumably overwinter and recruit into the new II-group the following spring, indicating either increased growth rates during the overwinter period or an influx of large fish into the population from other regions prior to spring. The remaining II-group present in the autumn population either died out of the population, or became indistinguishable in size from I-group individuals during the overwintering period, suggesting that the species has a life span of at least two years.

Protomyctophum tenisoni had a limited size range of 30-55 mm during the surveys and appeared to have a life cycle of approximately two years (Fig. 3b). Only one cohort was present in the population during each survey and the 0-group was consistently absent. In spring, only the newly recruited II-group (~2 yrs olds, mode: 53 mm) was evident in the overwintered population and all individuals within this group were adults with developing gonads. This age-group appeared to have died out by the summer period, as there was no overlap of generations. The new I-group (~ 1 year olds) was first evident in the summer population (mode: 36 mm) during target-hauls at the PF (Fig. 4b). Approximately 23% of this group were juvenile, whilst ~76% of adults had immature gonads and the remainder had developing gonads. The I-group had increased in size by autumn (mode: 44 mm) and would presumably grow and recruit into the II-group the following October. All specimens were adult at this time.

The overall size range of *P. choriodon* during the study was 55-85 mm and the species had a life cycle of at least four years (Fig. 3c). The composite length-frequency histograms indicated two size-classes in the population during the summer, the III-group (~3 year olds, mode: 70 mm) and the IV-group (~4 year olds, mode: 82 mm). No juvenile stages were present at this time and all adults had developing gonads. Too few samples were obtained in autumn to analyse the population structure robustly, but the available data suggest that both III- and IV- group specimens were present at this time. The 0-group, I-group and II-group were consistently absent during the surveys.

Population analyses were not possible for *P. parallelum*, *P. andriashevi* and *P. gemmatum* due to insufficient length-frequency data ($n < 30$). The size ranges for these three species was 29-53, 44-53 and 54-66 mm, respectively.

GENDER-BASED DIFFERENCES

There was no significant (*t*-test, *T*= -0.52, d.f. = 369, *P*> 0.05) difference in size between adult *P. bolini* females and males and both sexes had a mean size of ~48 mm. The ratio of females to males was close to 2:1 for this species at all stations across the Scotia Sea. *Protomyctophum tenisoni* males were slightly, but significantly (*t*-test, *T*= -3.32, d.f. = 111, *P*< 0.01) larger than females (means: 43.3 mm compared to 39.4 mm), and the ratio of females to males was approximately 1:1 in all regions. The number of observations for *P. choriodon* was relatively low, but no significant difference (*t*-test, *T*= -0.10, d.f. = 37, *P*> 0.05) in size between males and females was evident from the available data. Both sexes had a mean size of ~69 mm and the ratio of females to males was consistently around 1:1.

DIET COMPOSITION

A total of 231, 46 and 37 stomachs were examined for *P. bolini*, *P. tenisoni* and *P. choriodon*, respectively (Table IV). *Protomyctophum bolini* had a diet that was dominated by copepods (94% IRI), with *Metridia* spp. (59% IRI), *R. gigas* (36 %IR) and *Paraeuchaeta* spp. (4% IRI) the most predated species. Euphausiids, primarily *Thysanoessa* spp. (5% IRI), also comprised an important component of the species' diet. The diet of *P. tenisoni* was similarly dominated by copepods (90% IRI) and the euphausiid *Thysanoessa* spp. (10% IRI), although *C. simillimus* (71% IRI) was a major dietary component, with smaller quantities of *Metridia* spp. (7% IRI) and *R. gigas* (6% IRI). The diet of *P. choriodon* largely incorporated these same prey species, although much greater proportions of *Thysanoessa* spp. (42% IRI) and fewer copepods (63% IRI) were consumed. *Protomyctophum choriodon* also preyed upon the amphipod *T. gaudichaudii*. None of the three *Protomyctophum* species consumed significant quantities of *E. superba*.

DIET PATTERNS

The available data suggested spatial variation in diet for both *P. bolini* (Fig. 5a) and *P. tenisoni* (Fig. 5b). The diet of *P. bolini* was dominated by *Metridia* spp. in regions south of the SACCF, but there was a decrease in predation upon these copepods with decreasing latitude towards the PF. Conversely, there was an increase in *R. gigas* predation along this latitudinal gradient. *Protomyctophum bolini* also seldom preyed upon other copepods and *Thysanoessa* spp. in the southernmost regions of the Scotia Sea, and predation on *Paraeuchaeta* spp. occurred predominantly between the SACCF and the S-APF. The diet of *P. tenisoni* was dominated by *C. simillimus* around the APF, but there was an increase in occurrence of other prey items in the diet south of this front, principally *Metridia* spp., *Thysanoessa* spp. and *R. gigas*.

The data also suggested seasonal variation in the diet of these two myctophids. In spring, the diet of *P. bolini* was dominated by *R. gigas*, but there was a clear reduction in the proportion of this copepod in the diet in summer and autumn (Fig. 6a). *Metridia* spp. increased in the species' diet between spring and autumn and predation on *Paraeuchaeta* spp. and *Thysanoessa* spp. was highest in summer. No stomach samples were obtained for *P. tenisoni* during summer, but there was a clear switch in prey from *Thysanoessa* spp., *R. gigas*, *Metridia* spp. and other copepods, in spring to predominantly *C. simillimus* in autumn (Fig 6b).

Gender-based variations in diet were not apparent for *P. bolini*, *P. tenisoni*, or *P. choriodon*, and there was no evidence of size-related variations in diet for any of the three species from the available data.

DISCUSSION

This study, which surveyed the Scotia Sea from the ice-edge to the Antarctic Polar Front in different seasons, provides important information on the distribution, population structure and feeding ecology of *P. bolini*, *P. tenisoni* and *P. choriodon* in the Southern Ocean. Myctophid fish are difficult to sample at high latitudes and their abundance, distribution and population dynamics are inherently patchy and highly variable in space and time. Considering that the data presented here were collected at a relatively low temporal and spatial resolution, and without seasonal replication, such variability needs to be taken into account when interpreting the results of this investigation. The relatively small sample sizes should also be taken into consideration when interpreting the spatial and temporal patterns in diet, particularly for *P.*

tenisoni. Our data are, however, the best available to date and the results suggest that these three understudied myctophids exhibit different life history, distribution, and diet patterns in the Scotia Sea.

PROTOMYCTOPHUM BOLINI

Protomyctophum bolini was the most abundant of the three *Protomyctophum* species in this study and the greatest concentrations of biomass and abundance were found north of the SACCF in the northern Scotia Sea. *Protomyctophum bolini* is regarded as one of the most common species in the ichthyofauna in the Southern Ocean (Hulley, 1981) and our estimates of abundance/biomass accorded well with those of other studies from the Scotia Sea (Piatkowski *et al.*, 1994; Pusch *et al.*, 2004; Collins *et al.*, 2008). The species has been described as having a sub-Antarctic distribution pattern (Hulley, 1981), although relatively high abundances have been previously reported at higher latitudes in the Scotia Sea, including the South Shetland Islands and the Antarctic Peninsula (Pusch *et al.*, 2004; Donnelly and Torres, 2008). In accordance with other studies, *P. bolini* was caught mostly between 200-400 m and, although there were certain issues with daytime net avoidance, there was some evidence of DVM similar to that observed previously (Hulley, 1981; Piatkowski *et al.*, 1994; Duhamel *et al.*, 2000; Pusch *et al.*, 2004; Collins *et al.*, 2008; Donnelly and Torres, 2008). Seasonal and regional variation in depth distribution was not apparent for the species from the available data, but the possibility of such variation has been indicated from previous observations in the region (Piatkowski *et al.*, 1994; Collins *et al.*, 2008). Collins *et al.* (2012) noted that the upper limit to species depth distribution at South Georgia was consistent with the depth at which the base of the cold Winter Water layer occurred and hypothesised that temperature is an important control on its vertical distribution. A similar trend seemed apparent at the Antarctic Peninsula (Donnelly and Torres, 2008).

The data indicated that *P. bolini* had a life cycle of approximately two years in the Scotia Sea. The species attained a maximum size of around 70 mm and there was no evidence of size-related sexual dimorphism, which is consistent with other studies (Collins *et al.*, 2008). During the study, there was a marked absence of newly spawned larvae and the 0-group component of the population from all biological samplers (including Longhurst-Hardy Plankton Recorder, RMT8 nets and Bongo nets) suggesting that recruitment for the species was confined to waters north of the study region. Furthermore, the juvenile I-group was entirely confined to waters characteristic of the APF in autumn and only the oldest stages (~2 year olds) were present in regions further south. This supports the notion that this predominantly sub-Antarctic species only completes its life cycle in waters north of the APF and that there is a distinct spatial separation in population structure between the Subtropical Front (STF) and the Scotia Sea (Hulley, 1981; Pusch *et al.*, 2004; Collins *et al.*, 2008). It has been suggested that the adults of this species migrate south of the APF to feed in the Scotia Sea, leaving the juvenile component of the population in waters to the north of this front (Hulley, 1981; Collins *et al.*, 2008). Similar patterns in behaviour have been suggested for myctophids in the sub-Arctic (Sassa and Kawaguchi, 2005). However, it is also possible that spawning, recruitment and sexual development are inhibited in the colder waters of the Scotia Sea and the population structure in the Scotia Sea reflects an expatriate population. *Protomyctophum* eggs, for example, have only been observed in regions north of the APF (Efremenko, 1986), suggesting that the cold waters of the Scotia Sea may inhibit egg survival.

Protomyctophum bolini fed mostly on copepods, particularly *Metridia* spp., and *R. gigas*, which is in accordance with previous observations in the Scotia Sea (Pusch *et al.*, 2004). Other studies have reported that the species feeds primarily on small euphausiids, but these conclusions were based on relatively low sample sizes (Gaskett *et al.*, 2001; Shreeve *et al.*, 2009). Spatial variation in diet was indicated for *P. bolini*, which broadly reflected the regional availability of the main prey species in the mesozooplankton community across the Scotia Sea (Ward *et al.*, 2012). For example, predation on all copepods species other than *Metridia* spp. was highest in regions north of the SACCF where their abundance was markedly higher than that south of this front. The reduced availability of these copepods south of the SACCF may therefore have resulted in the switch to predominantly *Metridia* spp. predation in the region. The apparent seasonal variation in diet did not reflect the overall seasonal pattern in copepod abundance, as the abundance of most prey-species north of the SACCF was relatively similar across surveys (Ward *et al.*, 2012). However, there was a tendency for older copepodite stages of *R. gigas* to be present in the region during spring, which, may account for some of the observed seasonal changes in diet. Shreeve *et al*. (2009) observed that myctophids tend to target the older copepodite stages, particularly adult females. The switch from *R. gigas* predation in spring to predation on other copepods in summer and autumn may therefore have been related to a reduction in the availability of older *R. gigas* stages in the prey field. Differences in copepod behaviour, such as DVM, reactivity to stimuli and seasonal diapause may also be important factors in temporal and ontogenetic variations in myctophid predation (Shreeve *et al.*, 2009).

PROTOMYCTOPHUM TENISONI

Protomyctophum tenisoni is a particularly understudied species throughout the Southern Ocean and, prior to this investigation, most aspects of the species' distribution, population dynamics and trophic ecology were unknown, particularly in the Scotia Sea. In this study, *P. tenisoni* was relatively abundant during the spring and autumn surveys and it was primarily found near the APF. The species did not occur south of the SACCF, which agrees with other observations that indicate that *P. tenisoni* is a predominantly sub-Antarctic species, with a southern distributional limit around the Antarctic Convergence (~60 °S) (Hulley, 1981; McGinnis, 1982). Our data showed that the species was distributed below 400 m during the daytime, but moved up the water column to layers above 200 m at night, indicative of DVM behaviour, and consistent with observations around the Kerguelen Islands (Indian sector) (Duhamel *et al.*, 2000).

Protomyctophum tenisoni had a limited size range throughout the Scotia Sea, but there was evidence of size-related sexual dimorphism that, to our knowledge, has not been previously reported for a species within this genus (Collins *et al.*, 2008). Unlike many myctophid species, such as Antarctic lanternfish *Electrona antarctica* (Günther 1878), Carlsberg's lanterfish *Electrona carlsbergi* (Tåning 1932) and Brauer's lanterfish *Gymnoscopelus braueri* (Lönnberg 1905) (Rowedder, 1979; Collins *et al.*, 2008), *P. tenisoni* males were larger in size than females suggesting that selection mechanisms in growth and life history strategies could differ between the sexes in this species (Parker, 1992)..

Our data also indicated that *P. tenisoni* had a life cycle of approximately two years and that recruitment appeared to be confined to regions north of the APF, as evidenced by a marked absence of larval stages and the 0-group during the surveys. Furthermore, I-group specimens were absent in the Scotia Sea in all seasons. These trends are consistent with the notion that *P. tenisoni* is a predominantly sub-Antarctic species, which spawns in regions towards the STF, and that either ontogenetic migrations, or expatriate effects may be an important control on spatial patterns in population structure. It has been reported that *P. tenisoni* reaches sexual maturity at ~41 mm and attains a maximum size of around 54 mm (Hulley, 1981), which is consistent with our findings. Our data suggested that cohort growth rates of *P. tenisoni* were similar to that of *P. bolini*, although the species appears to spawn slightly earlier.

Protomyctophum tenisoni fed mostly upon copepods, with *C. simillimus* dominating this component of the prey field. Small euphausiids of the *Thysanoessa* genus also comprised an important part of the diet. To our knowledge, the only other data available on the trophodynamics of *P. tenisoni* are from a study at Macquarie Island (Pacific sector of the Southern Ocean), which reported that the species was predominantly a copepod feeder, but also took high proportions of euphausiids and amphipods. However, information on prey species composition was not detailed in that study and, similar to the present study, the sample size was relatively low (Gaskett *et al.*, 2001). The diet of *P. tenisoni* appeared to vary between the APF and regions further south from the available data collected during our study and this corresponded broadly with spatial changes in the abundance of the main prey species (Ward *et al.*, 2012). Data from the concurrent mesozooplankton survey showed that *C. simillimus* abundance was markedly higher at the PF stations than at those between the SACCF and S-PF, whilst the abundance of prey species such as *Metridia* spp., *R. gigas*, and *Thysanoessa* spp. was comparatively lower. Thus *P. tenisoni* appeared to prey upon *C. simillimus* in regions where its availability was highest, but then switched to other prey items in regions where these species became increasingly abundant and the availability of *C. simillimus* was reduced. However, it is also possible that seasonal effects could have contributed to the apparent regional pattern in diet, as *P. tenisoni* stomachs were mostly obtained at the PF front in autumn, during which time its diet was almost exclusively comprised of *C. simillimus*. Further data are clearly warranted to substantiate spatial and temporal trends inthe diet of this rarer myctophid species, and to examine the possibility of ontogenetic variations in its diet robustly.

PROTOMYCTOPHUM CHORIODON

Protomyctophum choriodon was caught only on the summer and autumn surveys, but the available data suggest the possibility of a seasonal southward migration for the species. During the summer survey, *P. choriodon* occurred exclusively at the GB stations to the northwest of South Georgia, but the species was distributed in regions further south in autumn. Although *P. choriodon* is regarded as a sub-Antarctic species that is usually associated with the APF and regions further north (Hulley, 1981), the species occurs regularly in fur seal (*Arctocephalus gazella*) diets at South Georgia in late summer and autumn (Reid *et al.*, 2006). The abundance of *P. choriodon* in fur seal diet samples is also strongly correlated with sea-surface temperature (Reid *et al.*, 2006), supporting the idea that it undertakes seasonal migrations to regions south of the APF during periods of elevated sea-surface temperatures (Collins *et al.*, 2012). Alternatively, the seasonal increase in water temperatures may simply enable the species to survive temporarily at higher latitudes and expansion of its southern distributional range might not be a function of behaviour-specific migrations *per se*.

During the study, *P. choriodon* was caught primarily above 400 m, with the species distributed exclusively between 0-200 m during the day and peak concentrations also occurring in this zone at night. These observations are consistent with those at South Georgia, although the species was predominantly distributed between 200-400 m during the daytime in this region, but occasional daytime catches have been made at depths of ~150 m (Collins *et al.*, 2008). Acoustic studies have further reported that myctophid schools are not uncommon above 200 m in the Scotia Sea during the daytime, particularly in off-shelf regions where they can occur in the near-surface zone (Fielding *et al.*, 2012; Saunders *et al.*, 2013). Our data also indicated a downward movement of part of the population at night, which could be a sinking response following satiation after night-time feeding (Tarling and Johnson, 2006), or an ontogenetic separation of the population that was not detected in the study due to the relatively low sample sizes.

Population analyses were limited for *P. choriodon* due to its absence in spring and relatively low sample sizes in summer and autumn. However, the available data suggested that the species had a life cycle of at least four years. Other studies have reported that *P. choriodon* reaches sexual maturity at ~77 mm, attains a maximum size of 95 mm and spawns once in spring during its life cycle (Hulley, 1981; Oven *et al.*, 1990). An ontogenetic separation in the population was suggested for the species, as specimens towards the STF tended to be juveniles whereas mature adults were more prevalent in regions closer to the Scotia Sea (Hulley, 1981). Collins *et al.* (2008) also observed a unimodal population structure of limited size range (60-75 mm) at South Georgia during autumn and further hypothesised that the species does not complete its life cycle south of the APF. These notions were supported by our study as (i) there was no evidence of spawning in the study region, (ii) there was a distinct absence of 0- and I-group specimens and (iii) the population was dominated by older year-classes (>3 year old). Similar to *P. bolini* and *P. tenisoni*, this suggests that either the species undertakes a stage-specific migration whereby older specimens actively move away from the younger stages that reside north of the APF to the Scotia Sea, or that the species is an expatriate in the Scotia Sea.

Although our sample size was relatively low, the diet of *P. choriodon* was broadly consistent with that reported previously in the northern Scotia Sea and this species appears to be mostly a copepod and euphausiid predator (Oven *et al.*, 1990; Shreeve *et al.*, 2009). Euphausiids comprised a greater part of the diet than found in *P. bolini* and *P. tenisoni* and this could be a function of its greater body size that enables it to predate larger prey items more effectively (Karpouzi and Stergiou, 2003). There were too few data to investigate spatial and temporal patterns in diet for this species in this study, although such variation has been suggested from limited data in the region, as *P. choriodon* tended to predate small euphausiids more at higher latitudes (Oven *et al.*, 1990). However, more quantitative data are warranted to substantiate and quantify such trends in this species diet.

PROTOMYCTOPHUM NICHE SEPARATORS

In pelagic ecosystems, differences in diets, vertical distribution and life cycle strategies are important niche separators that enable several species to co-exist within the same locality (Barange, 1990). The *Protomyctophum* species studied in this investigation are similar in appearance, have distribution patterns that overlap in the Scotia Sea region, and appear to be adapted to the sub-Antarctic environment. However, data suggest that these species exhibit different niche roles that may explain how they are able to avoid direct competition for resources and co-exist in the region. For example, *P. choriodon* is a larger-sized species that is able to predate larger prey items, such as euphausiids and amphipods, than either *P. bolini* or *P. tenisoni*. Unlike *P. bolini* and *P. tenisoni*, *P. choriodon* appears to reside in the upper 200 m during the daytime, with part of the population moving to deeper depths of the water column at night. The species may also undertake seasonal southward migrations and has a greater juvenile growth rate than *P. bolini* and *P. tenisoni*, as well as a longer life cycle. *Protomyctophum bolini* and *P. tenisoni* are similarly sized species that exhibit similar rates of growth and have comparable life spans. They are also both predominantly copepod predators. However, *P. tenisoni* appears to spawn slightly earlier than *P. bolini* and they seem to target different copepod species, with *P. tenisoni* feeding mostly on *C. simillimus* and *P. bolini* feeding on *Metridia* spp. and *R. gigas*. Both species appear to undertake DVM, but *P. tenisoni* was distributed higher in the water column at night than *P. bolini*. *Protomyctophum bolini* also appeared to have a distribution pattern that extended as far south as the sea-ice sector in all seasons, whereas *P. tenisoni* had a distribution pattern that was more closely associated with waters of the APF. These three myctophid species therefore seem to have different niche roles in the Scotia Sea region and do not appear to be in direct competition for resources in regions where they co-occur.

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