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

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15   This study investigated spatial and temporal patterns in distribution, population structure and

16   diet of Bolin's lanternfish *Protomyctophum bolini*, Tenison's lanternfish *Protomyctophum*

17   *tenisoni* and gaptooth lanternfish *Protomyctophum choriodon* in the Scotia Sea using data

18   collected by mid-water trawl nets during spring, summer and autumn. *Protomyctophum*

19   *bolini* was the most abundant species of the genus encountered throughout the Scotia Sea

20   with the greatest concentrations occurring around the Antarctic Polar Front (APF). This

21   species had a life cycle of 2+ years, but spatial differences in population structure were

22   apparent as the I-group was absent from all regions south of the APF, suggesting that the

23   species does not recruit in the Scotia Sea. *Protomyctophum tenisoni* occurred mostly in

24   waters characteristic of the APF and was absent from the southern Scotia Sea. It had a limited

25   and unimodal size range, but there was clear size-related sexual dimorphism with males

26   significantly larger than females. The species had a life cycle of ~2 years, but the I-group

27   occurred only in regions close to the APF suggesting that recruitment is restricted to these

28   waters. A seasonal southward migration for *P. choriodon* is likely as the species occurred

29   mostly to the southwest of South Georgia in summer, but extended to the sea-ice sectors in

30   autumn. *Protomyctophum choriodon* had a life cycle of 4+ years in the Scotia Sea and the

31   population was dominated by age-classes >3 years old. Larval stages were absent during the

32   surveys for all species. Diurnal variations in vertical distribution were apparent for all three

33   species. Inter-specific variations in diet were evident, but all species were primarily copepod

34   feeders, with *Metridia* spp. *Rhincalanus gigas* and *Calanus simillimus* generally dominating

35   their prey. Small euphausiids, principally *Thysanoessa* spp., were also an important

36   component of their diets, particularly for *P. choriodon* which had the largest body size. The

37 spatial and temporal variations in diet for both *P. bolini* and *P. tenisoni* were broadly

38 consistent with underlying abundance patterns within mesozooplankton community.

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40 Key words

41

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

43 **INTRODUCTION**

44

45 Mesopelagic fish are the most abundant fishes on earth comprising an estimated biomass in

46 excess of 11,000 million tons (Irigoien *et al.*, 2014). They are important conduits in the

47 transfer of energy through oceanic food webs, linking primary consumers to a range of top

48 marine predators, and contribute to the export of carbon from the surface layers to

49 mesopelagic depths through their extensive vertical migrations (Pakhomov *et al.*, 1996;

50 Smith, 2011; Irigoien *et al.*, 2014). These fish therefore play a major role in the function of

51 oceanic ecosystems and biogeochemical cycles around the globe. However, mesopelagic fish

52 remain one of the least studied components of the oceanic ecosystem, with major

53 uncertainties in the most basic aspects of their biology and ecology. Lanternfish, or

54 myctophids (family Myctophidae), are considered to be the dominant mesopelagic fishes in

55 most the world's oceans in terms of diversity and biomass (Gjøsaeter and Kawaguchi, 1980),

56 but little is known of their distribution of abundance, ecology or trophodynamics in all

57 regions in which they occur. Consequently, determining the ecology of myctophids is an

58 important step towards understanding the operation of oceanic ecosystems at a regional and,

59 ultimately, global level.

60

61 Myctophids are difficult to sample at an appropriate temporal and spatial resolution,

62 particularly in remote high latitude regions such as the Southern Ocean. This has not only

63 confounded our understanding of all myctophids in these regions, but has limited

64   investigations to the most abundant and frequently encountered species (Linkowski, 1985;

65   Greely *et al.*, 1999; Sassa and Kawaguchi, 2005; Dypvik *et al.*, 2012; Pepin, 2013; Saunders

66   *et al.*, 2014). There are many high latitude myctophid species for which virtually nothing is

67   known about their ecology. The genus *Protomyctophum* has 16 species that occur mostly at

68   high latitudes in all of the world's oceans and all species are examples of understudied

69   myctophids. The majority of information available on this genus refers to general patterns in

70   biogeography and morphology (Hulley, 1981; McGinnis, 1982), with only a few studies

71   reporting information on abundance and vertical distribution for species such as

72   *Protomyctophum arcticum* (Lütken 1892) (Kawaguchi and Mauchline, 1982; Fock and John,

73   2006) and bigeye lanternfish *Protomyctophum thompsoni* (Chapman 1942) (Pearcy *et al.*,

74   1977; Beamish *et al.*, 1999; Watanabe *et al.*, 1999) in the sub-Arctic, and Bolin's lanternfish

75   *Protomyctophum bolini* (Fraser-Brunner 1949) in the sub-Antarctic (Piatkowski *et al.*, 1994;

76   Pusch *et al.*, 2004; Collins *et al.*, 2008; Iwami *et al.*, 2011). Furthermore, few studies have

77   detailed information on *Protomyctophum* population dynamics (Kawaguchi and Mauchline,

78   1982), or trophodynamics (Oven *et al.*, 1990; Pakhomov *et al.*, 1996; Pusch *et al.*, 2004;

79   Sassa and Kawaguchi, 2005; Shreeve *et al.*, 2009) in any region, and those that exist are

80   spatially and temporally limited, often with small sample sizes. There is a clear need for new

81   data on all species within this genus, including the rarer ones, in order to resolve the

82   composition and dynamics of the high latitude mesopelagic fish community.

83

84   The majority of *Protomyctophum* species (10 out of 16 species) are found in the Southern

85   Ocean, where the most common species include *P. bolini*, gaptooth lanternfish

86　*Protomyctophum choriodon* (Hulley 1981) and Tenison's lanternfish *Protomyctophum*

87　*tenisoni* (Norman 1930) (Hulley, 1981). The Scotia Sea (Atlantic sector) is one the most

88　productive regions of Southern Ocean, sustaining high levels of secondary production, which

89　in turn supports major populations of whales, seals, penguins and commercially-targeted fish

90　(Atkinson *et al.*, 2001; Holm-Hansen *et al.*, 2004). In this region, myctophids, including the

91　*Protomyctophum* species, play an important role in the transfer of energy through the food

92　web as they consume herbivorous and omnivorous zooplankton, such as copepods and

93　euphausiids (including Antarctic krill, *Euphausia superba*) (Pakhomov *et al.*, 1996; Pusch *et*

94　*al.*, 2004; Shreeve *et al.*, 2009), and are preyed upon by several top marine predators,

95　including seals (e.g. *Arctocephalus gazella*, *Mirounga leonina*), penguins (*Aptenodytes*

96　*patagonicus*), squid (*Martialia hyadesi*) and large pelagic fish (*Dissostichus eleginoides*)

97　(Rodhouse *et al.*, 1992; Olsson and North, 1997; Brown *et al.*, 1999; Cherel *et al.*, 2002; Reid

98　*et al.*, 2006; Collins *et al.*, 2007). Myctophids comprise an estimated biomass of 4.5 million

99　tonnes in the Scotia Sea (Collins *et al.*, 2012), providing a major krill-independent trophic

100　pathway in the usually krill-dominated food web (Murphy *et al.*, 2007b). More

101　comprehensive data on the ecology of all myctophid species in this region is required in light

102　of recent evidence of ocean-warming (Whitehouse *et al.*, 2008), reductions in winter sea-ice

103　extent, (de la Mare, 1997; Curran *et al.*, 2003) and declining krill stocks in the Scotia Sea

104　(Atkinson *et al.*, 2004; Hill *et al.*, 2013), which could have an adverse impact on the Southern

105　Ocean ecosystem (Moline *et al.*, 2004; Murphy *et al.*, 2007a; Flores *et al.*, 2012). With

106　further long-term reductions in krill abundance, as predicted (Hill *et al.*, 2013), the

107　importance of myctophids as a krill-independent trophic pathway is likely to increase in the

108　region. Acquisition of new data on the distribution of abundance, population dynamics and

109   feeding ecology of all myctophids is therefore essential for understanding how pelagic food

110   webs are structured in the Scotia Sea, for determining their sensitivity to ongoing

111   environmental change, and for establishing effective ecosystem-based management strategies

112   throughout the Southern Ocean (Kock *et al.*, 2012).

113

114   In this paper we present new data on the distribution of abundance, population structure and

115   diet of, *P. bolini*, *P. choriodon* and *P. tenisoni*, in the Scotia Sea. An index of relative

116   importance (IRI), which combines prey occurrence, biomass and numbers, was used to

117   investigate spatial, temporal and ontogenetic variations in their respective diets. Our data

118   were derived from depth-discrete net samples collected between the ice-edge and Antarctic

119   Polar Front (APF) during austral spring, summer and autumn (2006-2009), and are the most

120   comprehensive for the *Protomyctophum* genus in any region of the world to date. Our study

121   provides important parameterizations for new food web and ecosystem studies in the Scotia

122   Sea that are required in order to cast new light on the potential impacts of ocean-climate

123   change on the operation of the Southern Ocean pelagic food webs and ecosystems. They also

124   contribute to resolving the composition and dynamics of the global mesopelagic fish

125   community.

126

127   **MATERIALS AND METHODS**

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129   STUDY LOCATION

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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).

140

NET SAMPLE COLLECTION AND PROCESSING

142

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

151 JR200. The RMT25 was deployed twice in succession to cover the four depth zones at each

152 station, with the upper nets (0-200 and 200-400 m) undertaken as close to local midday or

153 midnight as practical. The majority of nets were deployed in oceanic regions where bottom

154 depths exceeded 1500 m (see Collins *et al.* 2012). Additional targeted net hauls were

155 undertaken on acoustically detected fish aggreations during the surveys, mostly around the

156 Polar Front. These hauls were not used to generate estimates of abundance or biomass. Net

157 samples were sorted onboard to the lowest taxonomic level possible (Hulley, 1990) and total

158 catch weights per fish species were recorded using a motion-compensated balance. The

159 standard length (SL) of all fish were measured to the nearest mm. Where possible, sex and

160 maturity status was recorded for a subsample. Stomachs were dissected from a random

161 subsample of 25 fish per non-targeted haul, or from each fish where catches were small. All

162 stomachs were frozen for subsequent microscopic analysis.

163

164 STOMACH CONTENTS ANALYSIS

165

166 Fish stomachs contents were sorted to the lowest taxonomic level possible, subject to the

167 state of digestion, following Shreeve *et al.* (2009). Individual prey items were enumerated

168 and weighed. If the prey was highly disaggregated, the weights of the component species

169 were estimated as a proportion of the total weight of all components..

170

171

172   Diet was expressed as percentage frequency of occurrence (%F), percentage mass (%M),

173   percentage number (%N) and percentage Index of Relative Importance (%IRI) (Hynes, 1950;

174   Pinkas *et al.*, 1971; Hyslop, 1980; Cortes, 1997). The %IRI was calculated for prey species

175   and %IRI$_{DC}$ for prey categories (Main *et al.*, 2009). In the preliminary analysis, prey

176   categories were defined as: Amphipoda, Copepoda, Euphausiacea, Chordata, Ostracoda and

177   Unidentified crustacean, but a more detailed analysis was subsequently performed using the

178   following nine dominant prey categories: the copepods *Metridia* spp., *Rhincalanus gigas*,

179   *Pleuromamma robusta*, *Paraeuchaeta* spp., and *Calanus simillimus*, Other copepods, the

180   euphausiid *Thysanoessa* spp., the amphipod *Themisto gaudichaudii* and Other taxa (other

181   amphipods, *E. superba*, Ostracods, Chordates and unidentified crustaceans). Note that the

182   %IRI is not additive so the sum of the individual species' %IRI is not the same as the prey

183   category %IRI$_{DC}$ value (Hansson, 1998). The %IRI was calculated as:

184

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

185

187   where *i* is prey item.

188

189   The %IRI for each prey category was calculated in this way for all three myctophid species to

190   examine variations in diet between fish pooled by region, season (cruise), size and sex (Table

191   I). For spatial comparisons of diet, data were pooled for regions south of the South Antarctic

192   Circumpolar Current Front (SACCF; stations: SSS and MSS), between the SACCF and the

193   Southern Boundary of the Antarctic Polar Front (S-APF; stations WSS, NSS, GB) and north

194   of the S-APF (stations: PF) (Fig.1.) Data were also pooled for size-classes less than or greater

195   than the overall population mean for comparisons of each species' diet by size. The ±95%

196   confidence limits for the mean %IRI of each prey category were calculated using a

197   bootstrapping procedure that re-sampled (with replacement) each species' datasets

198   (individual stomachs) 1000 times (Main *et al.*, 2009).

199

200   LENGTH-FREQUENCY ANALYSIS

201

202   Due to the relatively low sample sizes per species at each station (<50 individuals), it was not

203   possible to investigate spatial variations in length-frequency distributions robustly during the

204   three surveys. Data were therefore pooled by survey for each species to give composite

205   length-frequency distributions for the study region as a whole. CMIX component fitting

206   software (de la Mare, 1994) was then used to fit normal distributions to the composite length-

207   frequency data and identify modes following the approach detailed in Saunders *et al.* (2007).

208   A series of runs were performed during the analysis based on the presence of one, two or

209   three cohorts in the data and we then determined the best component fit to the observed data

210   using a Chi-squared test. No constraints were placed on the mean length, variance or

211   proportions expected within each component when fitting the mixed distributions.

212   Differences between gender sizes and depth zones were investigated using Students t-tests

213   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

233   A total of 143 RMT25 non-targeted net hauls (i.e. hauls not directed at acoustical targets)

234   were undertaken during the three surveys. Weather and operational constraints meant that it

235   was not possible to sample all stations to the same degree on all surveys. Most notably,

236   sampling at the WSS station was mostly confined to the spring survey.

237

238   Several species of *Protomyctophum* were encountered during the surveys, including

239   Andriashev's lanternfish *Protomyctophum andriashevi* (Becker 1963), *P. tenisoni*, *P. bolini*,

240   *P. choriodon*, parallel lanternfish *Protomyctophum parallelum* (Lönnberg 1905) and jewelled

241   lanternfish *Protomyctophum gemmatum* (Hulley 1981) (Fig. 1). *Protomyctophum bolini* was

242   the most abundant species on each survey, comprising an overall mean abundance of 0.038-

243   0.070 ind. 1000 m^{-3} and a biomass of 0.052-0.080 g 1000 m^{-3} (Tables II and III). The species

244   was distributed throughout the Scotia Sea in regions north of the seasonal ice-edge and the

245   greatest concentrations occurred at the PF and GB stations (Fig. 1). *Protomyctophum tenisoni*

246   was absent from non-targeted net hauls during the summer survey, but comprised a relatively

247   high proportion of abundance during spring and autumn (0.012-0.021 ind. 1000 m^{-3}),

248   particularly around the PF (Fig. 1; Table II). This species was seldom encountered south of

249   the SACCF and comprised an overall mean biomass of <0.025 g 1000 m^{-3} on the two surveys

250   (Table III). *Protomyctophum choriodon* was absent in spring and was caught predominantly

251   around the GB in summer (Fig. 1). However, it occurred at all stations further south during

252   autumn, with the greatest concentrations generally in the SSS (Table II). The species had an

253   overall mean abundance and biomass of ~0.005 ind. 1000 m^{-3} and ~0.020 g 1000 m^{-3},

254   respectively (Tables II and III). *Protomyctophum parallelum*, *P. andriashevi* and *P.*

255   *gemmatum* were caught predominantly in APF waters during the spring survey. Overall, these

256   species comprised a relatively low abundance and biomass in the Scotia Sea (<0.050 ind.

257   1000 m^{-3} and <0.010 g 1000 m^{-3}).

258

259   VERTICAL DISTRIBUTION

260

261   The vertical distribution patterns of *P. bolini*, *P. tenisoni* and *P. choriodon* did not differ

262   between seasons or stations, so the data were aggregated to illustrate their overall depth

263   distributions in the region. Daytime catches of *P. bolini* were low and the species was mostly

264   spread between 201-700 m during this time (Fig. 2a). *Protomyctophum bolini* abundance and

265   biomass was substantially larger at night, where the species occurred higher in the water

266   column between 201-400 m. Only a few individuals were encountered above 200 m at night.

267   Daytime catches of *P. tenisoni* were also comparatively low and the species was distributed

268   mostly between 401-700 m (Fig. 2b). At night, both mean density and biomass increased

269   markedly and the species occurred solely in the upper 200 m of the water column, indicative

270   of some diurnal vertical migration (DVM). *Protomyctophum choriodon* was distributed

271   predominantly between 0-200 m during both day and night, although the species was also

272   present in deeper regions (201-400 m) during the night, but not during the daytime (Fig. 2c).

273   This suggests a night-time deepening of part of the population for this species. Of the other

274   *Protomyctophum* species encountered on the surveys, *P. parallelum* and *P. gemmatum* were

275 caught exclusively between 400 and 700 m, whilst *P. andriashevi* was predominantly

276 distributed between 200-400 m.

277

278 POPULATION SIZE STRUCTURE

279

280 The information available for *Protomyctophum* species indicate that spawning occurs in

281 spring (September/October) (Oven *et al.*, 1990). The following terminology was therefore

282 adopted to describe the population structure of these myctophids: 0-group covers the period

283 from hatching until 31 October the following year; I-group covers the period 1 November to

284 31 October the next year; II-group covers the subsequent period from 1 November until 31

285 October, and so on. Differentiation between the 0-goup and I-group in the population was

286 aided by comparisons of modal size, relative to the estimated spawning period, with

287 published growth rates of high latitude and temperate myctophids (Smoker and Pearcy, 1970;

288 Gjøsaeter, 1978; Linkowski, 1985; Greely *et al.*, 1999). Although the data were collected

289 without temporal repetition in non-consecutive seasons, and therefore interannual effects

290 cannot be accounted for, our analyses provide the most comprehensive synopsis of seasonal

291 variations in *Protomyctophum* population structure to date.

292

293 Length-frequency histograms for *P. bolini* showed one size-, and presumably age-, class in

294 the spring population that we assumed to be the newly recruited II-group containing ~2 year

295 old individuals based on realistic rates of growth (mode: 50 mm; Fig 3a). Both the newly

15

296 spawned 0-group and I-group were absent during this time. Approximately 5% of the II-

297 group was juvenile and all adults had developing gonads. There was little evidence of growth

298 of the II-group during the summer period (mode: 50 mm), indicating that it had attained its

299 terminal size prior to this season. The 0-group and I-group remained absent from the

300 population at this time, and the maturity structure of the II-group was very similar to that in

301 spring. By autumn, the I-group (~1 year olds) was evident in the population (mode: 38 mm),

302 together with the II-group that had reduced in magnitude from the previous season (mode: 51

303 mm). Juvenile stages dominated the I-group during the autumn and this cohort occurred

304 entirely at the PF and NSS stations, where water masses properties were characteristic of the

305 APF (Fig. 4a). This cohort would presumably overwinter and recruit into the new II-group

306 the following spring, indicating either increased growth rates during the overwinter period or

307 an influx of large fish into the population from other regions prior to spring. The remaining

308 II-group present in the autumn population either died out of the population, or became

309 indistinguishable in size from I-group individuals during the overwintering period, suggesting

310 that the species has a life span of at least two years.

311

312 *Protomyctophum tenisoni* had a limited size range of 30-55 mm during the surveys and

313 appeared to have a life cycle of approximately two years (Fig. 3b). Only one cohort was

314 present in the population during each survey and the 0-group was consistently absent. In

315 spring, only the newly recruited II-group (~2 yrs olds, mode: 53 mm) was evident in the

316 overwintered population and all individuals within this group were adults with developing

317 gonads. This age-group appeared to have died out by the summer period, as there was no

318   overlap of generations. The new I-group (~ 1 year olds) was first evident in the summer

319   population (mode: 36 mm) during target-hauls at the PF (Fig. 4b). Approximately 23% of this

320   group were juvenile, whilst ~76% of adults had immature gonads and the remainder had

321   developing gonads. The I-group had increased in size by autumn (mode: 44 mm) and would

322   presumably grow and recruit into the II-group the following October. All specimens were

323   adult at this time.

324

325   The overall size range of *P. choriodon* during the study was 55-85 mm and the species had a

326   life cycle of at least four years (Fig. 3c). The composite length-frequency histograms

327   indicated two size-classes in the population during the summer, the III-group (~3 year olds,

328   mode: 70 mm) and the IV-group (~4 year olds, mode: 82 mm). No juvenile stages were

329   present at this time and all adults had developing gonads. Too few samples were obtained in

330   autumn to analyse the population structure robustly, but the available data suggest that both

331   III- and IV- group specimens were present at this time. The 0-group, I-group and II-group

332   were consistently absent during the surveys.

333

334   Population analyses were not possible for *P. parallelum*, *P. andriashevi* and *P. gemmatum*

335   due to insufficient length-frequency data ($n < 30$). The size ranges for these three species was

336   29-53, 44-53 and 54-66 mm, respectively.

337

338   GENDER-BASED DIFFERENCES

339

340   There was no significant (*t*-test, *T*= -0.52, d.f. = 369, *P*> 0.05) difference in size between

341   adult *P. bolini* females and males and both sexes had a mean size of ~48 mm. The ratio of

342   females to males was close to 2:1 for this species at all stations across the Scotia Sea.

343   *Protomyctophum tenisoni* males were slightly, but significantly (*t*-test, *T*= -3.32, d.f. = 111,

344   *P*< 0.01) larger than females (means: 43.3 mm compared to 39.4 mm), and the ratio of

345   females to males was approximately 1:1 in all regions. The number of observations for *P.*

346   *choriodon* was relatively low, but no significant difference (*t*-test, *T*= -0.10, d.f. = 37, *P*>

347   0.05) in size between males and females was evident from the available data. Both sexes had

348   a mean size of ~69 mm and the ratio of females to males was consistently around 1:1.

349

350   DIET COMPOSITION

351

352   A total of 231, 46 and 37 stomachs were examined for *P. bolini*, *P. tenisoni* and *P.*

353   *choriodon*, respectively (Table IV). *Protomyctophum bolini* had a diet that was dominated by

354   copepods (94% IRI), with *Metridia* spp. (59% IRI), *R. gigas* (36 %IR) and *Paraeuchaeta* spp.

355   (4% IRI) the most predated species. Euphausiids, primarily *Thysanoessa* spp. (5% IRI), also

356   comprised an important component of the species' diet. The diet of *P. tenisoni* was similarly

357   dominated by copepods (90% IRI) and the euphausiid *Thysanoessa* spp. (10% IRI), although

358   *C. simillimus* (71% IRI) was a major dietary component, with smaller quantities of *Metridia*

359   spp. (7% IRI) and *R. gigas* (6% IRI). The diet of *P. choriodon* largely incorporated these

360 same prey species, although much greater proportions of *Thysanoessa* spp. (42% IRI) and

361 fewer copepods (63% IRI) were consumed. *Protomyctophum choriodon* also preyed upon the

362 amphipod *T. gaudichaudii*. None of the three *Protomyctophum* species consumed significant

363 quantities of *E. superba*.

364

365 DIET PATTERNS

366

367 The available data suggested spatial variation in diet for both *P. bolini* (Fig. 5a) and *P.*

368 *tenisoni* (Fig. 5b). The diet of *P. bolini* was dominated by *Metridia* spp. in regions south of

369 the SACCF, but there was a decrease in predation upon these copepods with decreasing

370 latitude towards the PF. Conversely, there was an increase in *R. gigas* predation along this

371 latitudinal gradient. *Protomyctophum bolini* also seldom preyed upon other copepods and

372 *Thysanoessa* spp. in the southernmost regions of the Scotia Sea, and predation on

373 *Paraeuchaeta* spp. occurred predominantly between the SACCF and the S-APF. The diet of

374 *P. tenisoni* was dominated by *C. simillimus* around the APF, but there was an increase in

375 occurrence of other prey items in the diet south of this front, principally *Metridia* spp.,

376 *Thysanoessa* spp. and *R. gigas*.

377

378 The data also suggested seasonal variation in the diet of these two myctophids. In spring, the

379 diet of *P. bolini* was dominated by *R. gigas*, but there was a clear reduction in the proportion

380 of this copepod in the diet in summer and autumn (Fig. 6a). *Metridia* spp. increased in the

381   species' diet between spring and autumn and predation on *Paraeuchaeta* spp. and

382   *Thysanoessa* spp. was highest in summer. No stomach samples were obtained for *P. tenisoni*

383   during summer, but there was a clear switch in prey from *Thysanoessa* spp., *R. gigas*,

384   *Metridia* spp. and other copepods, in spring to predominantly *C. simillimus* in autumn (Fig

385   6b).

386

387   Gender-based variations in diet were not apparent for *P. bolini*, *P. tenisoni*, or *P. choriodon*,

388   and there was no evidence of size-related variations in diet for any of the three species from

389   the available data.

390

391   **DISCUSSION**

392

393   This study, which surveyed the Scotia Sea from the ice-edge to the Antarctic Polar Front in

394   different seasons, provides important information on the distribution, population structure and

395   feeding ecology of *P. bolini*, *P. tenisoni* and *P. choriodon* in the Southern Ocean. Myctophid

396   fish are difficult to sample at high latitudes and their abundance, distribution and population

397   dynamics are inherently patchy and highly variable in space and time. Considering that the

398   data presented here were collected at a relatively low temporal and spatial resolution, and

399   without seasonal replication, such variability needs to be taken into account when interpreting

400   the results of this investigation. The relatively small sample sizes should also be taken into

401   consideration when interpreting the spatial and temporal patterns in diet, particularly for *P.*

402 *tenisoni*. Our data are, however, the best available to date and the results suggest that these

403 three understudied myctophids exhibit different life history, distribution, and diet patterns in

404 the Scotia Sea.

405

406 *PROTOMYCTOPHUM BOLINI*

407

408 *Protomyctophum bolini* was the most abundant of the three *Protomyctophum* species in this

409 study and the greatest concentrations of biomass and abundance were found north of the

410 SACCF in the northern Scotia Sea. *Protomyctophum bolini* is regarded as one of the most

411 common species in the ichthyofauna in the Southern Ocean (Hulley, 1981) and our estimates

412 of abundance/biomass accorded well with those of other studies from the Scotia Sea

413 (Piatkowski *et al.*, 1994; Pusch *et al.*, 2004; Collins *et al.*, 2008). The species has been

414 described as having a sub-Antarctic distribution pattern (Hulley, 1981), although relatively

415 high abundances have been previously reported at higher latitudes in the Scotia Sea,

416 including the South Shetland Islands and the Antarctic Peninsula (Pusch *et al.*, 2004;

417 Donnelly and Torres, 2008). In accordance with other studies, *P. bolini* was caught mostly

418 between 200-400 m and, although there were certain issues with daytime net avoidance, there

419 was some evidence of DVM similar to that observed previously (Hulley, 1981; Piatkowski *et*

420 *al.*, 1994; Duhamel *et al.*, 2000; Pusch *et al.*, 2004; Collins *et al.*, 2008; Donnelly and Torres,

421 2008). Seasonal and regional variation in depth distribution was not apparent for the species

422 from the available data, but the possibility of such variation has been indicated from previous

423   observations in the region (Piatkowski *et al.*, 1994; Collins *et al.*, 2008). Collins *et al.* (2012)

424   noted that the upper limit to species depth distribution at South Georgia was consistent with

425   the depth at which the base of the cold Winter Water layer occurred and hypothesised that

426   temperature is an important control on its vertical distribution. A similar trend seemed

427   apparent at the Antarctic Peninsula (Donnelly and Torres, 2008).

428

429   The data indicated that *P. bolini* had a life cycle of approximately two years in the Scotia Sea.

430   The species attained a maximum size of around 70 mm and there was no evidence of size-

431   related sexual dimorphism, which is consistent with other studies (Collins *et al.*, 2008).

432   During the study, there was a marked absence of newly spawned larvae and the 0-group

433   component of the population from all biological samplers (including Longhurst-Hardy

434   Plankton Recorder, RMT8 nets and Bongo nets) suggesting that recruitment for the species

435   was confined to waters north of the study region. Furthermore, the juvenile I-group was

436   entirely confined to waters characteristic of the APF in autumn and only the oldest stages (~2

437   year olds) were present in regions further south. This supports the notion that this

438   predominantly sub-Antarctic species only completes its life cycle in waters north of the APF

439   and that there is a distinct spatial separation in population structure between the Subtropical

440   Front (STF) and the Scotia Sea (Hulley, 1981; Pusch *et al.*, 2004; Collins *et al.*, 2008). It has

441   been suggested that the adults of this species migrate south of the APF to feed in the Scotia

442   Sea, leaving the juvenile component of the population in waters to the north of this front

443   (Hulley, 1981; Collins *et al.*, 2008). Similar patterns in behaviour have been suggested for

444   myctophids in the sub-Arctic (Sassa and Kawaguchi, 2005). However, it is also possible that

445   spawning, recruitment and sexual development are inhibited in the colder waters of the Scotia

446   Sea and the population structure in the Scotia Sea reflects an expatriate population.

447   *Protomyctophum* eggs, for example, have only been observed in regions north of the APF

448   (Efremenko, 1986), suggesting that the cold waters of the Scotia Sea may inhibit egg

449   survival.

450

451   *Protomyctophum bolini* fed mostly on copepods, particularly *Metridia* spp., and *R. gigas*,

452   which is in accordance with previous observations in the Scotia Sea (Pusch *et al.*, 2004).

453   Other studies have reported that the species feeds primarily on small euphausiids, but these

454   conclusions were based on relatively low sample sizes (Gaskett *et al.*, 2001; Shreeve *et al.*,

455   2009). Spatial variation in diet was indicated for *P. bolini*, which broadly reflected the

456   regional availability of the main prey species in the mesozooplankton community across the

457   Scotia Sea (Ward *et al.*, 2012). For example, predation on all copepods species other than

458   *Metridia* spp. was highest in regions north of the SACCF where their abundance was

459   markedly higher than that south of this front. The reduced availability of these copepods

460   south of the SACCF may therefore have resulted in the switch to predominantly *Metridia*

461   spp. predation in the region. The apparent seasonal variation in diet did not reflect the overall

462   seasonal pattern in copepod abundance, as the abundance of most prey-species north of the

463   SACCF was relatively similar across surveys (Ward *et al.*, 2012). However, there was a

464   tendency for older copepodite stages of *R. gigas* to be present in the region during spring,

465   which, may account for some of the observed seasonal changes in diet. Shreeve *et al.* (2009)

466   observed that myctophids tend to target the older copepodite stages, particularly adult

467   females. The switch from *R. gigas* predation in spring to predation on other copepods in

468   summer and autumn may therefore have been related to a reduction in the availability of

469   older *R. gigas* stages in the prey field. Differences in copepod behaviour, such as DVM,

470   reactivity to stimuli and seasonal diapause may also be important factors in temporal and

471   ontogenetic variations in myctophid predation (Shreeve *et al.*, 2009).

472

473   *PROTOMYCTOPHUM TENISONI*

474

475   *Protomyctophum tenisoni* is a particularly understudied species throughout the Southern

476   Ocean and, prior to this investigation, most aspects of the species' distribution, population

477   dynamics and trophic ecology were unknown, particularly in the Scotia Sea. In this study, *P.*

478   *tenisoni* was relatively abundant during the spring and autumn surveys and it was primarily

479   found near the APF. The species did not occur south of the SACCF, which agrees with other

480   observations that indicate that *P. tenisoni* is a predominantly sub-Antarctic species, with a

481   southern distributional limit around the Antarctic Convergence (~60 °S) (Hulley, 1981;

482   McGinnis, 1982). Our data showed that the species was distributed below 400 m during the

483   daytime, but moved up the water column to layers above 200 m at night, indicative of DVM

484   behaviour, and consistent with observations around the Kerguelen Islands (Indian sector)

485   (Duhamel *et al.*, 2000).

486

487   *Protomyctophum tenisoni* had a limited size range throughout the Scotia Sea, but there was

488   evidence of size-related sexual dimorphism that, to our knowledge, has not been previously

489   reported for a species within this genus (Collins *et al.*, 2008). Unlike many myctophid

490   species, such as Antarctic lanternfish *Electrona antarctica* (Günther 1878), Carlsberg's

491   lanterfish *Electrona carlsbergi* (Tåning 1932) and Brauer's lanternfish *Gymnoscopelus braueri*

492   (Lönnberg 1905) (Rowedder, 1979; Collins *et al.*, 2008), *P. tenisoni* males were larger in size

493   than females suggesting that selection mechanisms in growth and life history strategies could

494   differ between the sexes in this species (Parker, 1992)..

495

496   Our data also indicated that *P. tenisoni* had a life cycle of approximately two years and that

497   recruitment appeared to be confined to regions north of the APF, as evidenced by a marked

498   absence of larval stages and the 0-group during the surveys. Furthermore, I-group specimens

499   were absent in the Scotia Sea in all seasons. These trends are consistent with the notion that

500   *P. tenisoni* is a predominantly sub-Antarctic species, which spawns in regions towards the

501   STF, and that either ontogenetic migrations, or expatriate effects may be an important control

502   on spatial patterns in population structure. It has been reported that *P. tenisoni* reaches sexual

503   maturity at ~41 mm and attains a maximum size of around 54 mm (Hulley, 1981), which is

504   consistent with our findings. Our data suggested that cohort growth rates of *P. tenisoni* were

505   similar to that of *P. bolini*, although the species appears to spawn slightly earlier.

506

507 *Protomyctophum tenisoni* fed mostly upon copepods, with *C. simillimus* dominating this

508 component of the prey field. Small euphausiids of the *Thysanoessa* genus also comprised an

509 important part of the diet. To our knowledge, the only other data available on the

510 trophodynamics of *P. tenisoni* are from a study at Macquarie Island (Pacific sector of the

511 Southern Ocean), which reported that the species was predominantly a copepod feeder, but

512 also took high proportions of euphausiids and amphipods. However, information on prey

513 species composition was not detailed in that study and, similar to the present study, the

514 sample size was relatively low (Gaskett *et al.*, 2001). The diet of *P. tenisoni* appeared to vary

515 between the APF and regions further south from the available data collected during our study

516 and this corresponded broadly with spatial changes in the abundance of the main prey species

517 (Ward *et al.*, 2012). Data from the concurrent mesozooplankton survey showed that *C.*

518 *simillimus* abundance was markedly higher at the PF stations than at those between the

519 SACCF and S-PF, whilst the abundance of prey species such as *Metridia* spp., *R. gigas*, and

520 *Thysanoessa* spp. was comparatively lower. Thus *P. tenisoni* appeared to prey upon *C.*

521 *simillimus* in regions where its availability was highest, but then switched to other prey items

522 in regions where these species became increasingly abundant and the availability of *C.*

523 *simillimus* was reduced. However, it is also possible that seasonal effects could have

524 contributed to the apparent regional pattern in diet, as *P. tenisoni* stomachs were mostly

525 obtained at the PF front in autumn, during which time its diet was almost exclusively

526 comprised of *C. simillimus*. Further data are clearly warranted to substantiate spatial and

527 temporal trends inthe diet of this rarer myctophid species, and to examine the possibility of

528 ontogenetic variations in its diet robustly.

529

530   *PROTOMYCTOPHUM CHORIODON*

531

532   *Protomyctophum choriodon* was caught only on the summer and autumn surveys, but the

533   available data suggest the possibility of a seasonal southward migration for the species.

534   During the summer survey, *P. choriodon* occurred exclusively at the GB stations to the

535   northwest of South Georgia, but the species was distributed in regions further south in

536   autumn. Although *P. choriodon* is regarded as a sub-Antarctic species that is usually

537   associated with the APF and regions further north (Hulley, 1981), the species occurs

538   regularly in fur seal (*Arctocephalus gazella*) diets at South Georgia in late summer and

539   autumn (Reid *et al.*, 2006). The abundance of *P. choriodon* in fur seal diet samples is also

540   strongly correlated with sea-surface temperature (Reid *et al.*, 2006), supporting the idea that it

541   undertakes seasonal migrations to regions south of the APF during periods of elevated sea-

542   surface temperatures (Collins *et al.*, 2012). Alternatively, the seasonal increase in water

543   temperatures may simply enable the species to survive temporarily at higher latitudes and

544   expansion of its southern distributional range might not be a function of behaviour-specific

545   migrations *per se*.

546

547   During the study, *P. choriodon* was caught primarily above 400 m, with the species

548   distributed exclusively between 0-200 m during the day and peak concentrations also

549   occurring in this zone at night. These observations are consistent with those at South Georgia,

550   although the species was predominantly distributed between 200-400 m during the daytime in

551   this region, but occasional daytime catches have been made at depths of ~150 m (Collins *et*

552   *al.*, 2008). Acoustic studies have further reported that myctophid schools are not uncommon

553   above 200 m in the Scotia Sea during the daytime, particularly in off-shelf regions where they

554   can occur in the near-surface zone (Fielding *et al.*, 2012; Saunders *et al.*, 2013). Our data also

555   indicated a downward movement of part of the population at night, which could be a sinking

556   response following satiation after night-time feeding (Tarling and Johnson, 2006), or an

557   ontogenetic separation of the population that was not detected in the study due to the

558   relatively low sample sizes.

559

560   Population analyses were limited for *P. choriodon* due to its absence in spring and relatively

561   low sample sizes in summer and autumn. However, the available data suggested that the

562   species had a life cycle of at least four years. Other studies have reported that *P. choriodon*

563   reaches sexual maturity at ~77 mm, attains a maximum size of 95 mm and spawns once in

564   spring during its life cycle (Hulley, 1981; Oven *et al.*, 1990). An ontogenetic separation in the

565   population was suggested for the species, as specimens towards the STF tended to be

566   juveniles whereas mature adults were more prevalent in regions closer to the Scotia Sea

567   (Hulley, 1981). Collins *et al.* (2008) also observed a unimodal population structure of limited

568   size range (60-75 mm) at South Georgia during autumn and further hypothesised that the

569   species does not complete its life cycle south of the APF. These notions were supported by

570   our study as (i) there was no evidence of spawning in the study region, (ii) there was a

571   distinct absence of 0- and I-group specimens and (iii) the population was dominated by older

572   year-classes (>3 year old). Similar to *P. bolini* and *P. tenisoni*, this suggests that either the

573   species undertakes a stage-specific migration whereby older specimens actively move away

574   from the younger stages that reside north of the APF to the Scotia Sea, or that the species is

575   an expatriate in the Scotia Sea.

576

577   Although our sample size was relatively low, the diet of *P. choriodon* was broadly consistent

578   with that reported previously in the northern Scotia Sea and this species appears to be mostly

579   a copepod and euphausiid predator (Oven *et al.*, 1990; Shreeve *et al.*, 2009). Euphausiids

580   comprised a greater part of the diet than found in *P. bolini* and *P. tenisoni* and this could be a

581   function of its greater body size that enables it to predate larger prey items more effectively

582   (Karpouzi and Stergiou, 2003). There were too few data to investigate spatial and temporal

583   patterns in diet for this species in this study, although such variation has been suggested from

584   limited data in the region, as *P. choriodon* tended to predate small euphausiids more at higher

585   latitudes (Oven *et al.*, 1990). However, more quantitative data are warranted to substantiate

586   and quantify such trends in this species diet.

587

588   *PROTOMYCTOPHUM* NICHE SEPARATORS

589

590   In pelagic ecosystems, differences in diets, vertical distribution and life cycle strategies are

591   important niche separators that enable several species to co-exist within the same locality

592   (Barange, 1990). The *Protomyctophum* species studied in this investigation are similar in

593   appearance, have distribution patterns that overlap in the Scotia Sea region, and appear to be

594   adapted to the sub-Antarctic environment. However, data suggest that these species exhibit

595   different niche roles that may explain how they are able to avoid direct competition for

596   resources and co-exist in the region. For example, *P. choriodon* is a larger-sized species that

597   is able to predate larger prey items, such as euphausiids and amphipods, than either *P. bolini*

598   or *P. tenisoni*. Unlike *P. bolini* and *P. tenisoni*, *P. choriodon* appears to reside in the upper

599   200 m during the daytime, with part of the population moving to deeper depths of the water

600   column at night. The species may also undertake seasonal southward migrations and has a

601   greater juvenile growth rate than *P. bolini* and *P. tenisoni*, as well as a longer life cycle.

602   *Protomyctophum bolini* and *P. tenisoni* are similarly sized species that exhibit similar rates of

603   growth and have comparable life spans. They are also both predominantly copepod predators.

604   However, *P. tenisoni* appears to spawn slightly earlier than *P. bolini* and they seem to target

605   different copepod species, with *P. tenisoni* feeding mostly on *C. simillimus* and *P. bolini*

606   feeding on *Metridia* spp. and *R. gigas*. Both species appear to undertake DVM, but *P.*

607   *tenisoni* was distributed higher in the water column at night than *P. bolini*. *Protomyctophum*

608   *bolini* also appeared to have a distribution pattern that extended as far south as the sea-ice

609   sector in all seasons, whereas *P. tenisoni* had a distribution pattern that was more closely

610   associated with waters of the APF. These three myctophid species therefore seem to have

611   different niche roles in the Scotia Sea region and do not appear to be in direct competition for

612   resources in regions where they co-occur.

613

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615

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621

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