1 Title: Life cycle, distribution and trophodynamics of the lanternfish

2 *Krefftichthys anderssoni* (Lönnberg, 1905) in the Scotia Sea

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19

20 **Abstract:**

21 Myctophid fish play an important role in the Southern Ocean pelagic food web. The

22 rhombic lanternfish *Krefftichthys anderssoni* is one of the most common myctophids in

23 the region, but its ecology is poorly known. This study examines spatial and temporal

24 patterns in the species distribution of abundance, life cycle, population structure and

25 diet using samples collected by mid-water trawl nets deployed in different seasons

26 across the Scotia Sea. Virtually absent from the sea-ice zone, the species was most

27 abundant in the northern Scotia Sea around the Georgia Basin at depths below 400 m

28 associated with the Circumpolar Deep Water. The species migrates during night to the

29 upper 400 m following their main preys: the copepods *Rhincalanus gigas* and

30 *Calanoides acutus*, and euphausiids of genus *Thysanoessa*. Larvae length distribution

31 and post-larvae length frequency analysis suggested a life cycle of $\approx$ 3 years with

32 spawning and recruitment strongly connected with the APF and the South Georgia

33 shelf. Spatial distribution, population structure and diet changed both seasonally and

34 ontogenetically. To date, the present study is the most comprehensive for *K. anderssoni*

35 in the Scotia Sea and contributes to resolving how pelagic food webs and ecosystems

36 operate in the Southern Ocean.

37

38 **Introduction:**

39 Mesopelagic fishes are among the most abundant vertebrate group on earth, and yet they

40 remain one of the least studied components of the open-ocean ecosystem (Gjøsaeter &

41 Kawaguchi 1980, Irigoien et al. 2014). They occupy an important trophic status, as

42 zooplankton consumers and as prey to many higher marine predators, and may respire

43 up to 10% of primary production in deep waters (Pakhomov et al. 1996, Smith 2011,

44 Irigoien et al. 2014). Lanternfish (family Myctophidae) are considered to be the

45 dominant fishes within the global mesopelagic fish community, including the Southern

46 Ocean (Gjøsaeter and Kawaguchi 1980).

47 In the Southern Ocean, the family Myctophidae is represented by 12 genera and

48 24 resident species plus 44 species occasionally recorded south of the sub-Tropical front

49 (Duhamel et al. 2014), comprising an estimated biomass of 70-130 million tonnes (Mt)

50 (Lubimova et al. 1987). Myctophids play an important ecological role in the offshore

51 pelagic food-web in this region (Barrera-Oro 2002; Saunders et al. in press). They are a

52 key dietary component of sea birds, seals, cetaceans, squid and large predatory fish

53 (Rodhouse et al. 1992, Olsson and North 1997, Cherel et al. 2002, Reid et al. 2006,

54 Collins et al. 2007, Cherel et al. 2008), and are themselves predators of

55 macrozooplankton, such as a copepods, amphipods and euphausiids, including Antarctic

56 krill (*Euphausia superba*) (Pakhomov et al. 1996, Williams et al. 2001, Shreeve et al.

57 2009; Saunders et al., 2015c). Myctophids are particularly important to the ecosystem in

58 this region as they provide a major krill-independent trophic pathway in an otherwise

59 krill-dominated food web (Murphy et al. 2007b). However, despite their ecological

60 importance, very little is known about the ecology of key myctophid species in the

61 region. Acquisition of new data on the ecology of myctophid fish, particularly their

62 trophic ecology, is therefore an essential prerequisite for understanding the operation of

63 the Southern Ocean ecosystem and carbon cycles, and for establishing sustainable

64 ecosystem management policies.

The rhombic lanternfish *Krefftichthys anderssoni* (Lönnberg, 1905) is one of the most common myctophid fish in the Scotia Sea (Hulley 1981, McGinnis 1982, Piatkowski et al. 1994, Collins et al. 2008), benefiting from the high levels of productivity conditions that sustain an abundant zooplankton community upon which they feed (Holm-Hansen et al. 2004)It has a distribution in the Southern Ocean and adjacent seas and is found from the Weddell-Scotia confluence to 32ºS-33ºS in the Peruvian Current, and to 34ºS in the Falkland Current (Hulley 1981). *Krefftichthys anderssoni* has a patchy distribution pattern and population structure throughout this range (Hulley 1981, Koubbi et al. 2001, Collins et al. 2008, Duhamel et al. 2014). It has been reported that the life cycle of this broadly Antarctic species is strongly associated with the Antarctic Polar Front (APF), with the most suitable habitats for the larvae found both off- and on-shelf in waters influenced by the APF (Hulley 1981, Koubbi et al. 2001, Koubbi et al. 2011, Duhamel et al. 2014). In the Scotia Sea, *K. anderssoni* has been caught from the surface up to 1000 m but only deeper than 400 m during daylight, which is indicative of diel vertical migration (DVM) (Piatkowski et al. 1994, Collins et al. 2008). Possible seasonal variations in depth distribution have yet to be investigated for this species.

Of the Southern Ocean myctophid fish community, *K. anderssoni* appears to be one of the most important species in the pelagic food web. It comprises a crucial part of the diet of many predators in the region, particularly the squid *Martialia hyadesi* (Rodhouse et al. 1992), Patagonian toothfish *Dissostichus eleginoides* (Collins et al. 2007), king penguins *Aptenodytes patagonicus* (Bost et al. 1997; Bost et al. 2002; Cherel et al. 1996), macaroni penguins *Eudyptes chrysolophus* (Klages et al. 1989; Waluda et al. 2010), grey-headed albatrosses *Thalassarche chrysostoma* (Xavier et al. 2003) and Antarctic fur seals *Arctocephalus gazella* (Green et al. 1989 Cherel et al. 1997; Daneri et al. 2005). Based on biochemical analyses, this relatively small myctophid species (up to ≈ 80 mm standard length; Hulley, 1981) is also considered a high level predator (trophic level = 3.8) in this food web, feeding on crustacean suspension feeders and other zooplankton (Stowasser et al. 2012), mainly copepods and small euphausiids (Gaskett et al. 2001, Shreeve et al. 2009). However, the exact diet composition of this species remains unresolved since previous trophic studies are limited to relatively small sample sizes collected over restricted spatial and temporal

97   scales (Pakhomov et al. 1996, Gaskett et al. 2001, Shreeve et al. 2009, Cherel et al.

98   2010). Recent trophic studies of other Southern Ocean species have shown that diets of

99   other myctophid species vary spatially, temporally and ontogenetically, with the

100   possibility of resource partitioning between co-existing species, such as *Electrona*

101   *carlsbergi*, *Gymnoscopelus braueri*, and *Protomyctophum bolini* (Shreeve et al. 2009,

102   Saunders et al. 2014, Saunders et al. 2015a). However, such variation has yet to be

103   examined for *K. anderssoni* and there remain major uncertainties in the species' diet

104   composition. New studies are required to assess the extent of resource overlap between

105   this species and other potential competitors in the same region.

106   Myctophids comprise an estimated biomass of around 4.5 Mt in the Scotia Sea

107   (Collins et al. 2012) and new knowledge about their ecology and trophodynamics in the

108   Atlantic sector of Scotia Sea constitutes a major step towards understanding ecosystem

109   dynamics at the broader scale of the Southern Ocean. In this paper, new data is

110   presented concerning the distribution, abundance, length structure and feeding ecology

111   of *K. anderssoni*, in the Scotia Sea, using net samples collected during three

112   multidisciplinary research cruises (November 2006, January 2008 and March 2009) that

113   surveyed the Scotia Sea from the sea-ice zone (SIZ) to the APF (ref Tarling et al DSR

114   summary paper). This information is important for resolving the structure and

115   evaluating the stability of the Southern Ocean food web that is presently subject to

116   sustained ocean-climate change (Moline et al. 2004, Murphy et al. 2007a, Flores et al.

117   2012). The Scotia Sea is one of the most productive regions of the Southern Ocean

118   (Holm-Hansen et al. 2004), sustaining abundant secondary consumers, major

119   populations of higher predators and important commercial fisheries (Everson 1992,

120   Constable et al. 2000, Murphy et al. 2007b, Atkinson et al. 2009).

121

Materials and Methods

123   This study takes advantage of the information collected on *K. anderssoni* during the

124   three multidisciplinary cruises conducted onboard RRS *James Clark* during austral

125   spring, summer and autumn of consecutive years. The cruises were designed to cover all

126   the major water masses and oceanographic regimes across Scotia Sea. Without being

127   species targeted, extended depth and latitudinal sampling in the three surveys allowed

128 the study of the composition and distribution of the mesopelagic fish at the community

129 level (Collins et al. 2012; Van de Putte et al. 2012) and at species level (Saunders et al

130 2014; Saunders et al. 2015a; Saunders et al. 2015b). Data on *K. anderssoni* captured

131 seasonally in the same stations and through an extended depth range was used to follow

132 the species distribution, abundance and trophodynamics in relation to major

133 oceanographic regimes, latitude and depth. Post-larvae length frequency analysis

134 combined with larvae abundance and length data collected during the British Antarctic

135 Survey's long-term ichthyoplankton monitoring programme (Belchier and Lawson

136 2013) were used to help determine the species life cycle.

137 **Study location and oceanographic background**

138 Three cruises were conducted during the austral spring (cruise JR161, October –

139 December 2006), austral summer (JR177, January – February 2008) and autumn (JR

140 200, March – April 2009). The cruises covered one transect from the sea ice zone (SIZ)

141 to the APF (Figure 1). During each survey, oceanographic (Venables et al. 2012),

142 acoustic (Fielding et al. 2012) and biological data (Collins et al. 2012; Korb et al. 2012;

143 Ward et al. 2012a; Whitehouse et al. 2012) were collected at a six fixed stations that

144 were spread across the different water masses and frontal zones in the region, following

145 a transect line from east of the South Orkneys to west of South Georgia, following an

146 ERS satellite altimeter track. These stations were named as follows: southern Scotia Sea

147 (SSS), mid- Scotia Sea (MSS), western Scotia Sea (WSS), northern Scotia Sea (NSS),

148 Georgia Basin (GB) and the polar front (PF, Figure 1).

149

150 **Fish sampling and processing**

151 Mesopelagic fish and invertebrates were collected using an opening and closing

152 rectangular mid-water trawl net (RMT 25) (Piatkowski et al. 1994). The RMT 25 is a

153 set of two 25 m^2 nets that can be opened and closed sequentially via an electronic down-

154 wire control unit to sample two depth-discrete layers. Each net had a cod-end mesh of 5

155 mm and was fitted with a protective cod-end to minimise damage to the samples. The

156 RMT 25 was towed obliquely at ≈ 2.5 knots for 30 – 60 min in each depth stratum, and

157 each deployment was monitored in real time using a custom-built net monitoring system

158 that logged depth and environment temperature. Both nets were closed during

159 deployment and veering, but opened sequentially during hauling. At each station, depth-
160 stratified hauls were undertaken at 0-200 m, 200-400 m, 400-700 m and 700 – 1000 m.
161 These depth strata were repeated day and night during the spring and summer cruises,
162 but all hauls were conducted at night during autumn due to reduced daylight hours. The
163 upper-most depth strata (0-200 m and 200 – 400 m) were sampled as close to local
164 midday or midnight as practical. The sampling depth range and stratification were
165 defined *a priori* to be coincident with predator vertical foraging ranges and also to
166 facilitate comparisons between BAS surveys. The targeted mesopelagic community
167 perform dial migratory movements between the deeper waters near 1000 m and the
168 shallow layer with abundance peaks around 400 m during the day and upper to 200 m
169 during the night (Piatkowski et al. 1994; Collins et al. 2008). Additionally, the predators
170 (e.g. king penguin and Antarctic fur seal) dive to forage predominantly above the 200 m
171 (Bost et al. 2002; Guinet et al. 2001) setting the limit for the most superficial depth
172 strata.

173   RMT 25 net haul catches were sorted on board to the lowest taxonomic level
174 possible using published guides (Hulley 1981, 1990). Total catch weights for each fish
175 species were obtained using a motion- compensated balance. All fish were measured to
176 the nearest 1 mm (standard length, hereafter SL). Stomachs were dissected from a
177 random sub-sample of 25 fish per haul, or from each fish when net catches were poor
178 (see Table 1 for sample size for length frequency and stomach content analyses). All
179 stomachs were frozen for subsequent microscopic analysis.

Length frequency analysis, LFA

181 Length-frequency data aggregated by season, region and depth strata were plotted as
182 histograms of 5 mm SL classes. The resulting distributions were tested for normality
183 with the Shapiro-Wilks test and based on the results obtained, a series of Kolmorov-
184 Smirnov tests were conducted on the length frequency distributions to investigate
185 possible differences in population structure between seasons, regions and depth strata
186 across the Scotia Sea. For each factor, the tests were performed pairwise, comparing
187 levels with n >60 individuals. The package R Mixdist (Macdonald, 2014) was used to
188 fit normal distributions to the composite length-frequency distributions. Mixdist fits a
189 mixture of distributions model using an algorithm defined by Macdonald and Green

190   (1988). The algorithm identifies a set of overlapping normal (or log-normal) component

191   distributions that gives the best fit for a specific mixture distribution. The number of

192   expected cohorts and approximate mean SL per cohort is specified by the user *a priori*

193   by visual inspection of the length histograms as initial fitting parameters. The analysis

194   was constrained to fixed variance between mixture components and all components

195   were assumed to be normal. The analysis was only conducted in data sets with $n > 60$

196   (Table 1). A series of runs were conducted based on the presence of two or three cohorts

197   and the best fit was determined by the analysis of the goodness-of-fit in larger χ^2 value

198   obtained with significance level *p < 0.05*.

Larvae sampling and data analysis

200   Larval length data were collected from Cumberland Bay larval study, South Georgia

201   (54º17'S, 36º20'W), as part of the British Antarctic Survey's long-term ichthyoplankton

202   monitoring program (Belchier and Lawson 2013). These inshore surveys were

203   conducted on a weekly basis between January 2002 and October 2008, with 1 to 5 hauls

204   conducted each month and 20 to 39 hauls per year. Larval fish samples were collected

205   from a total of 219 oblique plankton tows conducted with a RMT with a 1 m^2 opening

206   (RMT1) and net mesh size of 610 µm that was towed for 30 minutes from the surface to

207   a maximum depth of 25 m. The tows were conducted in an approximately north to south

208   direction over water depths of ≈ 25 m and the volume of water filtered was calculated

209   from swept area of the net calculated from GPS derived vessel speed and trawl duration

210   data. The *K. anderssoni* collected represented approximately 37% of the larvae

211   collected occurring in 35 % of the hauls (Belchier and Lawson, 2013). For each sampled

212   month a maximum of 200 *K. anderssoni* larvae were measured, with standard length

213   (SL) ranging between 2 mm and 19 mm. Further details about the larval fish sampling

214   procedures are described in Belchier and Lawson (2013). Variability among sampling

215   years and sampling months was analysed with type III ANOVA for unbalanced

216   samples. The mean larval month was then determined by calculating the average length

217   of the mean length obtained in each month sampled.

Diet analysis

219   Following Shreeve et al (2009), prey species were identified to the highest level that the

220   state of digestion would allow using standard zooplankton identification guides

221 (Boltovskoy 1999). Individual prey items were then counted and weighed. If the prey

222 was highly disaggregated, the weights of component species were estimated as a

223 proportion of the weight of total contents.

224   *Krefftichthys anderssoni* diet was expressed using percentage mass (%M),

225 percentage frequency of occurrence (%F), percentage number (%N), and an Index of

226 Relative Importance (%IRI, Cortés 1997). Percentage mass was based on the weight of

227 prey found in the stomach and not on estimated original mass. The %IRI was calculated

228 for prey specimens and the % IRI_{DC} for key diet categories (hereafter DC) (Main et al.

229 2009; Shreeve et al. 2009). The %IRI was calculated as:

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

231   Diet categories were selected for the prey taxa > 1% IRI of the diet: *Themisto*

232 *gaudichaudii* (thm), *Thysanoessa* spp. (thy), *Calanoides acutus* (cac), *Calanus*

233 *simillimus* (cas), *Metridia* spp. (met) and *Rhincalanus gigas* (rcg). The % IRI_{DC} was

234 calculated with data aggregated by region, season and size class (Table 1). The fish size

235 classes small (< 32 mm SL), medium (32-60 mm SL) and large (> 60 mm SL) were

236 derived from the length-frequency analyses. The 95% confidence limits for the mean %

237 IRI of each DC were calculated using bootstrapping technique, whereby each species

238 dataset (individual stomachs) was re-sampled with replacement 1000 times following

239 Main et al. (2009).

240

241 **Results**

242 **Oceanographic conditions**

243 *Krefftichthys anderssoni* was mainly captured in the regions north of the Southern

244 Boundary of the Antarctic Circumpolar Current (SB-ACC), so only oceanographic

245 conditions in the northern Scotia Sea are described here. Stations in the WSS and MSS

246 lay close to the South Antarctic Circumpolar Current Front (SACCF), where mean

247 temperatures and Chl *a* concentration in the Antarctic surface waters (AASW) ranged

248 from -0.2ºC to 2.1 ºC and 0.2 – 2.6 mg m^{-3}, respectively. Stations in the NSS and GB

249 were situated between SACCF and the APF. Mean temperature and Chl *a* concentrations

250 were similar in the AASW in these two regions during each survey (≈1.5- 4.0 ºC and ≈

251 0.2-1.0 mg m^{-3}). The APF stations were situated in waters close to the southern Antarctic

252 Polar Front (S-PF). The APF stations of spring 2006 (JR161) lay north to that S-PF, where

253 surface waters in this region had a mean temperature > 4ºC during all surveys with mean

254 Chl *a* concentrations ranging between 0.2 mg m^{-3} and 0.6 mg m^{-3}. Winter water (WW;

255 100-200 m) and Circumpolar Deep Water (CDW; > 200 m) were evident at all stations

256 located between SB-ACC and APF. Mean temperatures in the WW ranged between 0.2ºC

257 and 1.0ºC. Mean water temperature in the CDW (≈ 0.8 ºC) varied by < 0.5 ºC between

258 surveys and by ≈ 1.0ºC between regions. More detailed descriptions of the oceanographic

259 conditions can be found in Venables et al. (2012) and Whitehouse et al. (2012).

260

Distribution and abundance

262 A total of 143 non-targeted net hauls were conducted during the three surveys (Table 2).

263 All stations were sampled repeatedly to a varying degree during the study period except

264 the WSS, where sampling was confined to the spring survey. *Krefftichthys anderssoni*

265 abundance and biomass was variable, however the distribution pattern was consistent

266 between sampling years with species being predominantly distributed in the northern

267 Scotia Sea (NSS, GB and PF) and seldom occurred in the sea-ice sector (SSS) (n=2).

268 Higher densities and biomass were found in spring 2006 (0.12 ind.1000 m^{-3}; 0.20 g

269 1000 m^{-3}), and the lower densities and abundance in summer 2008 (0.04 ind.1000 m^{-3};

270 0.05 g 1000 m^{-3}) (Table 2).   The species was most abundant in spring around the GB

271 (0.22 ind. 1000 m^{-3} and 0.25 g 1000 m^{-3}) and least abundant in the MSS regions in

272 autumn (< 0.02 ind. 1000 m^{-3} and < 0.04 g 1000 m^{-3}; Table 2).

273 *Krefftichthys anderssoni* was most abundant at depths greater than 400 m during

274 daytime, although the species was caught at the surface layers (0-200 m) during this

275 time, suggesting daylight surface schooling of part of the population (Figure 2). During

276 the night-time, the species was distributed higher in the water column, with peaks in

277 abundance situated around 201-400 m, indicative of some DVM (Figure 2). There was

278 also evidence of seasonal variation in the species' depth distribution. Peaks in both

279 night-time abundance and biomass occurred at depths 201-400 m during the spring, but

280 occurred progressively deeper in summer (401-700 m) and autumn (700-1000 m; Figure

281 2). The data show an increasingly dominance of larger specimens in the deepest regions

282   of the water column during summer and autumn, as the mean size of specimens between

283   700-1000 m was at least 15 mm larger than that observed at depths higher up the water

284   column (e.g. 34 mm at 401-700 m compared to 49 mm at 700-1000 m in autumn). Such

285   size stratification was not apparent in spring.

286

287   **Life history and length frequency structure**

288   The larval mean length varied both with sampling year ($F = 196.50$, $p < 0.0001$) and

289   sampling month ($F = 150.74$, $p < 0.0001$), and the interaction between the two factors

290   ($F = 151.00$, $p < 0.0001$). The smallest larvae (mean SL = 5.71 mm ± 0.73, SD) were

291   captured in June, whilst the largest larvae were captured in March (mean SL = 14.25

292   mm ±1.46, SD; Figure 3). These results indicate that the species is most likely a winter

293   spawner, and therefore individuals are considered as belonging to a 0-group from the

294   time of hatching until the 31st July of the following year, to a group I from the 1st

295   August to the 31st July of the next year, and so on.

296   The overall size range of *K. anderssoni* post-larval stages was 15-75 mm, SL and

297   the series of Kolmorov-Smirnov tests between seasons, regions and depth strata did not

298   show significant differences between frequency distributions (for all pairwise

299   comparisons $p > 0.05$). Overall, length-frequency analyses suggested that the species

300   had a post-larval life cycle of ≈ 2 years (Figure 4). Although the data were not collected

301   in consecutive seasons, the overall seasonal pattern in population structure appeared to

302   be as follows. The spring population contained two size/age- classes, the group 1^{+}

303   (mode: 35 mm), composed by fishes hatched in the previous year winter, and group 2^{+}

304   (mode: 60 mm). There was only little growth for these two cohorts by summer and a

305   spreading of the group 2^{+} (mode: 60 mm) distribution as a result of the decreasing of the

306   population growth rate. Larvae hatched the previous winter were first evident as the

307   group 0^{+} (mode: 20 mm) in the population in autumn. Both the group 1^{+} (mode: 43 mm)

308   and remnants of the group 2^{+} (mode: 59 mm) were also evident at this time, suggesting

309   a relatively high rate of summer growth for the group 1^{+}. The autumn groups 0 and 1

310   would presumably overwinter and recruit into the new 1^{+}- and 2^{+}, respectively, the

311   following July/August. Kolmorov-Smirnov tests revealed significant ($p < 0.01$) spatial

312   variation in the population structure of *K. anderssoni* across the Scotia Sea (Figure 5,

313   bar diagrams on the left column). Three cohorts were present in the population at the

314   PF, the 0-group (mode: 20 mm), group 1 (mode: 39 mm) and group 2 (mode: 57 mm),

315   indicating that recruitment and growth had occurred in this region. By contrast, the

316   group 0 was notably absent in regions south of the APF in the Scotia Sea, with only

317   group 1 and group 2 specimens present in the population in the northern sector (GB and

318   NSS), and mainly 2 group specimens present at the southernmost range of the species

319   core distribution (MSS). This suggests that the species does not recruit in the oceanic

320   regions of the Scotia Sea and that populations become dominated by older and larger

321   specimens with increasing latitude into colder waters. The analyses also showed that the

322   species' population structure varied with depth, as the 0 group was predominantly

323   confined to the surface waters (0-200 m) and only 1 and 2 group specimens were

324   present in the deeper layers (> 200 m; Figure 5 bar diagrams on the right column).

325

326   **Diet analysis**

327   A total of 374 stomachs were examined during the analysis, of which 97 (24 %) were

328   found to be empty. The diet of *K. anderssoni* was mainly composed of copepods (80 %

329     $IRI_{Copepoda}$, 70 % F), notably the species *Rhincalanus gigas* (59 % IRI), *Calanoides*

330   *acutus* (14% IRI) and *Calanus simillimus* (7 %IRI). Euphausiacea (10% $IRI_{Euphausiacea}$,

331   32 % F), represented mostly by *Thysanoessa* spp. (14 % IRI), were the second most

332   important prey group consumed. The species also consumed the amphipod *Themisto*

333   *gaudichaudii* but it only comprised a relatively minor part of the diet (10 % F, 1% IRI)

334   (Table 4).

335   Based on the index of relative importance of the dominant prey taxa (%IRI_{DC}),

336   seasonal, spatial and ontogenetic differences in the diet of *K. anderssoni* were apparent.

337   Whilst the copepods *R. gigas* (spring: 61%IRI; summer: 72%IRI) and *C. acutus* (spring:

338   10 %IRI; summer: 24 %IRI) dominated the diet in spring and summer, there was a clear

339   switch to *Thysanoessa* spp. in the autumn (78% IRI) (Figure 6A). *Krefftichthys*

340   *anderssoni* consumed mostly the copepods *Calanoides acutus* (30-40 %IRI), *Metridia*

341   *sp* (18 % IRI) and *Calanus simillimus* (14% IRI) in the MSS and NSS, but further north

342   its diet was dominated by *R. gigas* (59% IRI) and *Thysanoessa* spp. (27% IRI) in the

343   GB and by *R. gigas* at the PF (73 % IRI) (Figure 6B). Although, the diet of all *K.*

344 *anderssoni* size classes were dominated by the copepod *R. gigas*, size-related variations

345 in diet were still apparent as there was a progressive increase in *Thysanoessa* spp.

346 consumption with increasing fish size (26 %IRI in larger fish), whilst smaller/younger

347 individuals preyed more on *C. acutus* (29 % IRI)) (Figure 6C).

348

Discussion

349

350 *Krefftichthys anderssoni* is one of the most important myctophid species in the Scotia

351 Sea, as a key prey species for a wide range of Southern Ocean marine predators (Guinet

352 et al. 1996; Waluda et al. 2010). However, to our knowledge, this study is the first to

353 detail information about the species distribution, life cycle, population structure and

354 feeding ecology in different seasons at the ocean-basin scale in any region of the Southern

355 Ocean. Myctophid fish are difficult to sample in this region and exhibit a relatively high

356 degree of patchiness in their distribution patterns and population dynamics. Since data

357 were collected in different years, and therefore possible inter-annual effects cannot be

358 accounted for, such variation should be taken into consideration when interpreting the

359 results.

360

Distribution patterns

361

362 During this study, *K. anderssoni* was caught between the APF and SACCF, which is

363 consistent with other studies of this broadly Antarctic species in the region (Hulley

364 1981, McGinnis 1982, Duhamel et al. 2014). The species was most abundant in the

365 northern regions of the Scotia Sea, particularly around the NSS and GB often attaining a

366 greater abundance and biomass than some of the other larger myctophid species, such as

367 *E. antarctica* and *G. braueri* (Saunders et al. 2014, Saunders et al. 2015a). Although

368 previous studies have hypothesized a close association between *K. anderssoni* and the

369 APF (e.g. Koubbi et al. 2001), the present data supports the concept that it also occurs

370 in high abundance south of this front in the northern Scotia Sea (Piatkowski et al. 1994,

371 Collins et al. 2008).

372

Vertical distribution

373

Krefftichthys anderssoni occurred predominantly below 200 m in circumpolar deep

water (CDW) (Venables et al. 2012). There was evidence of DVM within this water

mass, with individuals moving from below 400 m during the day to depths between

201-400 m at night. These results are consistent with other studies in the region

(Piatkowski et al. 1994, Collins et al. 2008). Daytime net avoidance in the upper regions

of the water column has been reported widely for many Southern Ocean myctophids

(Collins et al. 2008), but part of the *K. anderssoni* population was caught in the surface

layers (0-200 m) during daylight hours in our study. Daytime surface aggregations have

been reported previously for this species off the Kerguelen Islands (Indian sector of the

Southern Ocean), which is consistent with both acoustic studies of myctophid schools at

South Georgia (Saunders et al. 2013) and foraging studies of higher predators, such as

king penguins, in the northern Scotia Sea (Scheffer et al. 2010). Similar behaviour has

also been reported for myctophids of the *Protomyctophum* genus in this region

(Saunders et al. 2015b). Our data suggested that the daytime surface aggregations were

attributable to age 0+ and age 1 reflecting the extended surface feeding by juveniles in

the warmer and more food-rich layers of the water column following DVM (Venables et

al. 2012, Ward et al. 2012a).

There was clear seasonal variation in the depth distribution of *K. anderssoni*, with

relatively high concentrations of specimens moving progressively to deeper layers of

the water column between spring and autumn. Such behaviour is similar to that of other

myctophids in the region, such as *Electrona carlsbergi*, *Gymnoscopelus fraseri* and *G.

nicholsi*, although these species tend to be distributed higher in the water column (above

400 m) than *K. anderssoni* during all seasons (Saunders et al. 2014; 2015a). A seasonal

deepening of mesopelagic fish populations is generally assumed to be a response to the

winter deepening of food resources within the deep scattering layers (DSL), such as

overwintering copepods (Atkinson 1998, Dypvik et al. 2012, Pepin 2013). To a certain

extent, our observations are in accordance with this hypothesis, as there was a seasonal

deepening of the overwinter stages of the copepods *R. gigas* and *C. acutus* in the region

(Ward et al. 2012a). However, these copepods, particularly *R. gigas*, occurred

predominantly in regions above 400 m, as did the euphausiids *Thysanoessa* spp., which

were the other main prey group consumed by *K. anderssoni*. The data further indicated

that the seasonal migration was age-specific, suggesting that factors other than predation

406 on the DSL might also be important in driving this behaviour. For example, the
407 aggregation of large, mature adults at depth in autumn may reflect mating behavior prior
408 to spawning in winter.

409

Population dynamics

411 *Krefftichthys anderssoni* had a life cycle of around 3 years, with seasonal growth
412 apparent for all cohorts and clear spatial variation in population structure across the
413 Scotia Sea (Hulley 1981, McGinnis 1982, Collins et al. 2008). Length-frequency
414 analyses indicated that spawning and recruitment were predominantly confined to
415 regions around the APF in oceanic waters and that the population became increasingly
416 dominated by larger and older specimens with increasing latitude. This trend, which is
417 also apparent for several other myctophids in the region (Saunders et al. 2014; Saunders
418 et al. 2015a), is indicative of an oceanic expatriate proportion of the population in the
419 Scotia Sea that could be related to temperature following oceanic transportation of
420 individuals from regions further north. For example, recruitment of this typically sub-
421 Antarctic species may be inhibited in the cold oceanic waters of the Scotia Sea with
422 only the larger specimens, being able to tolerate the colder temperatures at increased
423 latitudes. Ontogenetic feeding/spawning migrations have also been suggested for
424 myctophids in this region (Hulley 1981, McGinnis 1982, Zasel'sliy et al. 1985, Collins
425 et al. 2008), although the adaptive advantage of such behavior between regions of
426 comparable food availability is unclear (Atkinson 1998, Ward et al. 2002; Ward et al.
427 2012a).

428   Small *K. anderssoni* appeared in June and July, suggesting that the species as a
429 winter spawner. Our data support the notion that the shelf waters around South Georgia
430 are an important region for spawning and recruitment of *K. anderssoni* south of the APF
431 (Collins et al. 2008, Belchier and Lawson 2013). Other studies have reported that the
432 species has a life cycle and distribution pattern that is closely coupled with waters of the
433 APF (Piatkowski et al. 1994; Koubbi et al. 2001; Koubbi et al. 2011), possibly due to
434 the warmer water temperatures and food availability associated with this region.
435 Similarly, environmental conditions around the South Georgia shelf may be suitable for
436 spawning, growth and recruitment of the species (Atkinson et al. 2001), enabling it to

437   form a self-sustaining population in the northern Scotia Sea, a region south of its core

438   distributional range. Interestingly, *K. anderssoni* could be the only myctophid species

439   that recruits successfully in the Scotia Sea south of the APF, as 0-group specimens and

440   larvae are notably absent in population studies of all other common species in the

441   region, including *E. carlsbergi*, *G. braueri*, *G. nicholsi* and *Protomyctophum bolini*

442   (Rowedder 1979, Linkowski 1985, Piatkowski et al. 1994, Greely et al. 1999, Pusch et

443   al. 2004, Collins et al. 2008, Donnelly and Torres 2008, Belchier and Lawson 2013,

444   Saunders et al. 2014; Saunders et al. 2015a). Eggs of these species have been reported

445   in the Scotia Sea, although most appear to be associated with regions of the APF,

446   (Efremenko 1986), suggesting that recruitment may be confined to warmer waters

447   further north.

448

449   **Diet patterns**

450   *Krefftichthys anderssoni* preyed on the most abundant species of the Southern Ocean

451   zooplankton community (Boltovskoy, 1999; Ward et al. 2012a), particularly copepods

452   and small euphausiids. The most important species consumed were the copepods *R.*

453   *gigas, C. acutus*, and *C. simillimus* and the euphausiids *Thysanoessa* spp., which

454   became of greater importance in the diet during autumn. The results are broadly

455   consistent with the spatially and temporally limited observations in the Scotia Sea and

456   elsewhere (Pakhomov et al. 1996, Gaskett et al. 2001, Shreeve et al. 2009) and suggest

457   that the diet of *K. anderssoni* depends on the seasonality and depth of zooplankton

458   abundance (Atkinson et al. 2001). *Calanoides acutus, C. simillimus* and *R. gigas* are

459   amongst the most abundant copepods of the Southern Ocean in the upper 400 m of the

460   water column, with a depth distribution that changes throughout the year (Ward et al.

461   2012a). Our data showed a relatively high overlap between the vertical distribution

462   patterns of *K. anderssoni* and these prey species in each season, suggesting that the

463   species feeds on both diel and seasonally migrating copepods following DVM to

464   regions higher in the water column at night (Ward et al. 2006; Ward et al. 2012a). There

465   was also high overlap in the horizontal distribution patterns of *K. anderssoni* and these

466   prey species across the Scotia Sea that may explain the southernmost extent of its

467   broad-scale distribution pattern. For instance, there was a marked decrease in the

abundance of the main copepods, particularly *R. gigas*, *C. acutus* and *C. simillimus*, in regions south of the SACCF, which constituted the approximate boundary to the species' southern range in the Scotia Sea (Ward et al. 2012a). This suggests that the species survival at these increased latitudes may be inhibited by both low water temperatures and insufficient availability of its main food source. While in spring and summer, the diet was dominated by the copepods, mostly *R. gigas* followed by *C. acutus*, the species' diet shifted to euphausiids in the autumn with *Thysanoessa* spp. being present in 77% of the 77 stomachs analysed. This change in prey is related to the prey abundance and biomass. During spring and summer, the copepods *R. gigas* and *C. acutus* aggregate between 400 m and 600 m (Ward et al. 2012a) overlapping the depth distribution of *K. anderssoni*, and in autumn, the *Thysanoessa* spp becomes more abundant (Piatkowski et al. 1994; Ward et al. 2012a). It is noteworthy that even in autumn *Thysanoessa* spp is a shallower water species (aggregating in the upper 400 m) and is far less abundant than copepods in the same region (Ward et al. 2012a). Shreeve et al. (2009) already had identified the importance of these euphausiids in the diet of *K. anderssoni* during autumn. In the Artic, species of the genus *Thysanoessa* are known to form swarms and to conduct DVM (Cottier et al. 2006). It is most likely that the Antarctic species have the same behavior and could be consumed when moving to deeper waters where large *K. anderssoni* aggregate during autumn. The diet preferences also changed in relation to the species ontogeny. While the smaller (age-group 0) and medium (age-group I) groups fed preferentially on copepods, the large and older animals (age-group II) fed preferentially on *Thysanoessa* spp. Such changes of prey with predator size may be related to increased gape and swimming speed with predator size.

Considering our results, *K. anderssoni* seems to be a selective predator. Previous studies comparing the fatty acids signature of myctophids with their potential preys off the Kerguelen Plateau indicate that copepods of the genus *Oncaea* can contribute as much as 19% of the diet of *K. anderssoni* (Connan et al. 2010). However, our results show that, in the Scotia Sea *K. anderssoni* do not feed directly on these small but highly abundant copepods, such as *Oncaea* and *Oithona* spp. (Ward et al. 2012a). Also, only in the Mid Scotia region does the genus *Metridia* (mean sized and abundant copepods) feature substantially in *K. anderssoni* diet (18 %IRI). In contrast, *Protomyctophum*

500 *bolini*, an equally small myctophid, feeds mostly on *Metridia* spp. (Saunders et al.

501 2015b). Other aspect that confirms the selectivity in the *K. anderssoni* feeding behavior

502 is, as explained above, their preference of feeding on *Thysanoessa spp.* an apparently

503 less abundant euphausiid (Piatkowski et al. 1994; Shreeve et al. 2009). The selective

504 predation seems to be common to several myctophid species in the Scotia Sea. In their

505 study, Saunders et al (2015c) showed that several myctophid feed preferentially on the

506 most nutritive prey as the copepodite older stages and on the euphausiid *Thysanoessa*

507 spp, rather than the most abundant copepods as *Oithona* spp and *Oncaea* spp.

508

Niche separation between co-existing myctophids

510 *Krefftichthys anderssoni* co-exists, in the Scotia Sea, with several other myctophid

511 species (Collins et al. 2008; Collins et al. 2012; Saunders et al. 2014; Saunders et al.

512 2015a; Saunders et al. 2015b). From these, *P. bolini*, *E. carlsbergi* and *G. fraseri* have

513 similar distribution, life span or feeding habits to *K. anderssoni*. These species are

514 indeed warmer water and cosmopolitan species that help to define the bioregion north of

515 the SACCF (Ward et al. 2012b). However, a detailed analysis of the four species life

516 cycle strategies, diet, population dynamics and vertical distribution allows niches

517 separation to be considered (Barange 1990). *Krefftichthys anderssoni* and *P. bolini* are

518 the smallest myctophid species found in the Scotia Sea with similar life span of 2 years

519 (Saunders et al. 2015a). However, *P. bolini* seems to be less abundant than *K.*

520 *anderssoni* and its vertical distribution is limited to 400 m, performing DVM to

521 shallower waters (0-200 m) in spring and summer (Push et al. 2004; Saunders et al.

522 2015b). *Krefftichthys anderssoni* had a wider vertical distribution with abundance

523 maxima between the 400 and 700 m. Its vertical distribution is also ontogenetically

524 driven, with the bigger and older individuals being more abundant in the deeper waters,

525 particularly below the 700 m. This is particularly relevant when both species seem to

526 share at least one important prey, the copepod *R. gigas* (Saunders et al. 2015a). The

527 larger DVM performed by *K. anderssoni* and the limited depth range of *P. bolini*

528 suggests that while *K. anderssoni* feeds mainly during the night when it ascends to the

529 shallower layers, *P. bolini* feeds constantly on the most common copepods around 400

m. *Krefftichthys anderssoni* also shows greater dietary diversity, with *Calanus acutus* and *C. simillimus* being common prey to the species.

Electrona carlsbergi adults are particularly abundant in NSS during spring, apparently competing with the *K. anderssoni* for prey (mainly *R. gigas* and *Metridia* spp.) (Shreeve et al. 2009; Saunders et al. 2014). However, *E. carlsbergi* attains significantly large sizes and has a larger life span (75 - 85 mm SL within 5 years, Linkowsky 1985) exhibiting a different life cycle strategy. Moreover, *E. carlsbergi* has a patchy distribution limited by depth, season and area to the upper strata of the water column (0-200 m) in NSS during spring. During spring, *K. anderssoni* is more abundant in GB area along the entire water column performing large DVM. This means that, although feeding on the same main prey (*R. gigas)* during spring, both these myctophid species do not seem to compete directly for space and prey.

Gymnoscopelus fraseri is the least abundant of the three species sharing the same area with *K. anderssoni* (Saunders et al. 2015a). Although having a similar life span, *G. fraseri* attains a larger size (40 - 115 mm SL), which means that it has a higher growth rate and a different life cycle strategy. Both species are particularly abundant in the northern areas of the sampling area, namely NSS, GB and PF, but the vertical distribution of *G. fraseri* is limited to the upper 200 m of the water column, and only in autumn does the species appear to descend to depths of around 400 m. During this season, the *K. anderssoni* population is dominated by older animals that aggregate deeper (401-1000 m) and in southern areas of NSS and MSS. Nevertheless, there could be some spatial overlap between the two species during spring, when *K. anderssoni* juveniles aggregate near the surface, although these specimens are very small (15- 25 mm SL) in comparison with *G. fraseri* adults and feed mainly on *C. acutus* which is seldom consumed by *G. fraseri* (Saunders et al. 2015a).

The differences found between the four species growth rates, diet, spatial and vertical distribution appear sufficient to avoid direct competition for food and space in the northern Scotia Sea region. Indeed, previous studies on isotopic niches of myctophids of Kerguelen region (Cherel et al. 2010) and in the oceanic waters off Adélie land (Cherel et al. 2011) showed that the differences found in the Nitrogen stable isotope ratio (^{15}N:^{14}N, δ^{15}N) and in the Carbon stable isotope ratio (^{13}C:^{12}C, δ^{13}C) signatures revealed a strong niche segregation between the myctophid genera *Gymnoscopelus*, *Electona* and *Protomyctphum*. When comparing the stable isotope

563 signatures of these species groups with *K. anderssoni*, in both studies the results show

564 that the later present a significantly low $\delta^{15}N$ signature in the muscle, most probably due

565 to the species small size and due to its diet dominated by herbivorous and omnivorous

566 copepods (Atkinson 1998; Ward et al. 1996) that have a lower $\delta^{15}N$ signature

567 (Stowasser et al. 2012). The apparent *K. anderssoni* specialization to feed on

568 *Thysanoessa* spp. during autumn also contributes to the niche separation between these

569 and the other myctophid species (Shreeve et al. 2009).

570

Conclusion

572 This study provides new insight into the ecology and trophodynamics of one of the most

573 abundant myctophid species in the Scotia Sea, which is important for understanding the

574 structure and dynamics of the Southern Ocean food web and ecosystem. These data also

575 contribute to resolving the biology, adaptations and dynamics of the global mesopelagic

576 fish community, which is an essential prerequisite for understanding the functioning of

577 the global open-ocean ecosystem and its biogeochemical cycles.

578

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Figures

Fig. 1 Map of the Scotia Sea and of the non-targeted net hauls position conducted in the spring cruise (● JR161), the summer cruise (● JR177), and autumn cruise (● JR200). Mean frontal positions determined during the cruises from dynamic height data (Venables et al. 2012) are as follow: northern Antarctic Polar Front (N-PF), southern Antarctic Polar Front (S-PF), south Antarctic Circumpolar Current Front (SACCF) and southern boundary of the Antarctic Circumpolar Current (SB-ACC). The heavy *black line* shows the position of the 15% ice-edge cover for 24/10/2006 (JR161) and the *grey line* shows the position of the 15% ice-edge cover for 15/01/2008 (JR177). The ice-edged occurred well south of the transects during autumn 2009 (JR200).

Fig. 2 Mean vertical distribution of the rhombic lanternfish *Krefftichthys anderssoni* density (individuals 1000 m^{-3}) and biomass (g 1000 m^{-3}) across the Scotia Sea during the day and night. No net hauls were collected during the daytime in autumn 2009 (JR200).

Fig. 3 Rhombic lanternfish *Krefftichthys anderssoni* larval mean standard length by month. The red dot indicates the mean SL while the box limits indicate the 25%, 50% and 75 % quartiles

Fig. 4 Rhombic lanternfish *Krefftichthys anderssoni* standard length-frequency (mm, SL) distribution in the Scotia Sea by season. Mixture distributions (solid lines) were determined using Mixdist package in R.

Fig. 5 Rhombic lanternfish *Krefftichthys anderssoni* length-frequency (mm, SL) distribution in the Scotia Sea by sampling region (bar diagrams in the left column) and by depth strata (bar diagrams in the right column). PF- polar front; GB – Georgia Basin; NSS – northern Scotia Sea; MSS - mid- Scotia Sea. The curves indicate the normal distribution of the three age groups identified based on the mixture of distributions analysis. The green line represents the age-group 0; the blue line represents the age-group 1 and the orange line indicates the age-group 2.

Fig. 6 Variations in rhombic lanternfish *Krefftichthys anderssoni* diet in the Scotia Sea by (a) season, (b) region and (c) size. Diet is expressed as mean % IRI of the dominant prey categories (% IRI$_{DC}$) with 95% confidence intervals. cac - *Calanoides acutus*; cas -

847   *Calanus simillimus*; rcg - *Rhincalanus gigas*; met - *Metridia* spp.; thm - *Themisto*
848   *gaudichaudii*; thy - *Thysanoessa* spp.