

1 The trophodynamics of Southern Ocean *Electrona* (Myctophidae) in the Scotia
2 Sea

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22 **Abstract**

23 The Scotia Sea is one of the most productive regions of the Southern Ocean, but its surface
24 waters are experiencing a rapid increase in temperature, which may be changing the
25 behaviour and distribution of many myctophids and their prey-species. *Electrona antarctica*
26 and *Electrona carlsbergi* are two of the most abundant myctophids in the region, but their
27 ecology is poorly understood and their response to ongoing environmental change is difficult
28 to determine. This study investigated spatial and temporal patterns in their abundance,
29 population structure and diets using mid-water trawl nets deployed across the Scotia Sea
30 during spring, summer and autumn. *E. antarctica* was the most numerically abundant species
31 (0.09-0.21 ind. 1000 m⁻³), with greatest concentrations occurring in the sea-ice sectors. *E.*
32 *carlsbergi* occurred in more northern regions, comprising densities of 0.02-0.11 ind. 1000 m⁻³.
33 There was evidence of seasonal variation in depth distribution, size-related sexual
34 dimorphism, and size-specific vertical stratification for both species. Latitudinal trends in sex
35 ratio and female body-size were apparent for *E. antarctica*. Its diet varied between regions,
36 seasons and size-classes, but overall, *Euphausia superba*, *Metridia* spp. and *Themisto*
37 *gaudichaudii* were the dominant prey items. *E. carlsbergi* appeared not to recruit in the
38 Scotia Sea. Its diet was dominated by copepods, particularly *Rhincalanus gigas* and *Metridia*
39 spp., but regional, seasonal and ontogenetic variations were evident. This study contributes to
40 our understanding of how mid-water food webs are structured in the Southern Ocean and
41 their sensitivity to ongoing environmental change.

42

43 **Keywords**

44 Myctophidae, *Electrona*, Feeding ecology, Antarctic krill, Copepod, Scotia Sea

45

46 **Introduction**

47 Myctophid fish (Myctophidae) are one of the most diverse and abundant mesopelagic fish
48 groups in the world's oceans (Gjøsaeter and Kawaguchi 1980). They consume herbivorous
49 and omnivorous zooplankton (e.g. copepods and euphausiids), and are in turn consumed by a
50 range of higher predators including birds, marine mammals and large pelagic fish. This taxa

51 also contributes to the active export of carbon from the sea surface to the mesopelagic layers
52 through their extensive vertical migrations (Pakhomov et al. 1996). They therefore have an
53 important role in the transfer of energy through the pelagic ecosystem.

54

55 In the Southern Ocean there are 33 species of myctophid fish (McGinnis 1982; Hulley 1990),
56 comprising an estimated biomass of 70-130 million tonnes (Lubimova et al. 1987; Collins et
57 al. 2012). The Scotia Sea area (Atlantic sector) is one of the most productive regions in the
58 Southern Ocean (Atkinson et al. 2001; Atkinson et al. 2004), where myctophids form an
59 important dietary component of many higher predators, including penguins (*Aptenodytes*
60 *patagonicus* and *Eudyptes chrysolophus*) seals (*Arctocephalus gazella* and *Mirounga*
61 *leonina*), squid (*Martialia hyadesi*) and toothfish (*Dissostichus eleginoides*) (Olsson and
62 North 1997; Cherel et al. 2002; Dickson et al. 2004; Reid et al. 2006; Collins et al. 2007). In
63 turn, they are the predators of copepods, amphipods and euphausiids, including Antarctic krill
64 (*Euphausia superba*), with some evidence of dietary specialisation occurring in certain
65 myctophids (Pakhomov et al. 1996; Pusch et al. 2004; Shreeve et al. 2009; Cherel et al. 2010;
66 Stowasser et al. 2012). Despite their ecological importance, there are few data on the ecology
67 of myctophids, globally and particularly in the Scotia Sea.

68

69 The Scotia Sea ecosystem is often perceived to be dominated by Antarctic krill, which has a
70 pivotal role in transferring energy from primary producers to abundant higher predators in
71 short, but efficient food chains (Murphy et al. 2007b). Whilst this concept of a simple krill-
72 dominated food web is valid over certain spatial and temporal scales, it is now clear that other
73 trophic pathways, such as myctophid fish, are both regionally and seasonally important
74 (Murphy et al. 2007b). Ocean temperatures in the Scotia Sea have increased markedly in
75 recent decades (Whitehouse et al. 2008), which together with evidence of reductions in
76 winter sea-ice extent (de la Mare 1997; Curran et al. 2003) and evidence of long-term
77 reductions in krill abundance (Atkinson et al. 2004), have raised concerns for the health of
78 the Scotia Sea ecosystem (Moline et al. 2004; Murphy et al. 2007a). With the possibility of
79 further reductions in krill abundance under currently predicted ocean-climate change
80 scenarios (Hill et al. 2013), the importance of krill-independent food web pathways, such as
81 myctophid fish, is likely to increase in the Scotia Sea. Therefore, more comprehensive data

82 on the ecology of myctophid fish and their role within the Scotia Sea food web are required
83 to understand, and ultimately predict, the possible impacts of long-term, broad-scale
84 environmental change on the Scotia Sea ecosystem (Kock et al. 2012).

85

86 Several species of myctophid fish are found commonly in the Scotia Sea and two of the most
87 abundant species in the region are *Electrona antarctica* and *Electrona carlsbergi* (Hulley
88 1981; McGinnis 1982; Collins et al. 2008; Collins et al. 2012). Both species reach an adult
89 size of between 80 and 100 mm SL (standard length). The gill rakers, used for filtering and
90 capturing prey, are slightly more numerous in *E. carlsbergi*, which possess 8-10 primary and
91 19-25 secondary rakers compared to respectively 3-5 and 12-16 primary and secondary rakers
92 in *E. antarctica* (Hulley 1990). Both species feed primarily on hyperiid amphipods,
93 euphausiids and copepods, with the former species known to consume a comparatively higher
94 proportion of copepods, in line with the greater frequency of their gill-rakers. Nevertheless,
95 their respective diets overlap in regions where they co-occur (Shreeve et al. 2009).

96

97 Although some aspects of the distribution and abundance of these two species have been
98 reported, most of the available data are limited to small sample sizes collected over relatively
99 small spatial and temporal scales (Rowedder 1979b; Hulley 1981; Naumov et al. 1981;
100 McGinnis 1982; Zasel'sliy et al. 1985; Lancraft et al. 1989; Piatkowski et al. 1994; Pusch et
101 al. 2004; Collins et al. 2008). There is currently a paucity of basic information on the regional
102 and seasonal distribution of abundance, vertical distribution and population dynamics of *E.*
103 *antarctica* and *E. carlsbergi* in the Scotia Sea, and there is a clear need for contemporary net
104 haul data to resolve these issues. Furthermore, there are few quantitative data on the diet and
105 feeding ecology of these two species. Determining patterns in diet is essential to
106 understanding food web dynamics and resource partitioning (Ross 1986), but trophodynamic
107 studies on *E. antarctica* and *E. carlsbergi* in the Scotia Sea have been similarly limited in
108 their sample coverage (Rowedder 1979a; Naumov et al. 1981; Gorelova and Efremenko
109 1989; Kozlov and Tarverdiyeva 1989; Gerasimova 1990; Pakhomov et al. 1996; Pusch et al.
110 2004; Shreeve et al. 2009). Furthermore, the predation impact of myctophids on the prey field
111 is unresolved at appropriate temporal and spatial scales and further data are required to permit
112 robust quantitative investigations (Pakhomov et al. 1996; Pusch et al. 2004; Shreeve et al.

113 2009). The trophodynamic role of myctophids in the Southern Ocean is therefore poorly
114 understood (Kock et al. 2012).

115

116 In this paper, we present new data on the distribution of abundance, population structure and
117 feeding ecology of *E. antarctica* and *E. carlsbergi* in the Scotia Sea using net samples
118 collected during three multi-disciplinary research cruises (November 2006, January 2008 and
119 March 2009) that surveyed across the Scotia Sea from the ice-edge to the Antarctic Polar
120 Front (Collins et al. 2012). Regional, seasonal and ontogenetic patterns in *E. antarctica* and
121 *E. carlsbergi* diet were investigated using an index of relative importance (IRI) of prey
122 occurrence, biomass and numbers, together with bootstrapped confidence intervals. These
123 data comprise the most comprehensive for *E. antarctica* and *E. carlsbergi* in any Southern
124 Ocean region. In the first instance, this allows us to address how these superficially similar
125 and abundant species, are able to co-occur over large areas of the Scotia Sea. Secondly,
126 through focussing on these biomass-dominant myctophid species, it provides an important
127 contribution to our understanding of the sensitivities of, and controls on Southern Ocean mid-
128 water food webs.

129

130 **Methods and materials**

131 Study location

132 Three multi-disciplinary research cruises were conducted in the Scotia Sea onboard RRS
133 *James Clark Ross* during the austral spring (cruise JR161; October-December 2006), austral
134 summer (JR177; January-February 2008) and austral autumn (JR200; March-April 2009).
135 The surveys covered the region from the seasonal ice-edge to the Antarctic Polar Front (Fig.
136 1). During each survey, oceanographic (Venables et al. 2012), acoustic (Fielding et al. 2012)
137 and biological data (Collins et al. 2012; Korb et al. 2012; Ward et al. 2012; Whitehouse et al.
138 2012) were collected at a series of stations along a transect from the edge of the sea-ice to the
139 Polar Front (PF). Stations were spread across different water masses and frontal zones to
140 sample the diversity of environments in the Scotia Sea.

141

142 Net sampling

143 Mesopelagic fish and invertebrates were collected using an opening and closing rectangular
144 mid-water trawl net (RMT25) (Piatkowski et al. 1994). The RMT25 incorporates two 25 m²
145 nets that can be opened and closed sequentially via an electronic downwire control unit to
146 sample two depth-discrete layers. Each net had a cod-end mesh of 5 mm and was fitted with a
147 protective cod-end to minimise damage to the samples. The RMT25 was towed obliquely at
148 ~2.5 knots for 30-60 min in each depth zone, and each deployment was monitored in real-
149 time using a custom-built net monitoring system that logged depth and temperature. Both nets
150 were closed during deployment and veering, but opened sequentially during hauling.

151

152 Net hauls were undertaken at six nominal stations across the study site: Southern Scotia Sea
153 (SSS), Mid Scotia Sea (MSS), Western Scotia Sea (WSS), Northern Scotia Sea (NSS),
154 Georgia Basin (GB), and the Polar Front (PF) (Fig. 1 and Appendix table 1). At each station,
155 depth-stratified hauls were undertaken at 0-200 m, 200-400 m, 400-700 m, and 700-1000 m.
156 These depth zones were repeated by day and by night during the spring and summer cruises,
157 but all hauls were conducted during hours of darkness during the autumn survey. The
158 uppermost depth-zones (0-200 m and 200-400 m) were sampled as close to local midday or
159 midnight as practical. On occasion, additional net hauls were deployed to target acoustically-
160 detected fish aggregations. These hauls, deployed mostly at the PF during summer, were
161 omitted from the calculations of fish density and biomass.

162

163 Sample processing

164 RMT25 net hauls were sorted onboard to the lowest taxonomic level using published guides
165 (Gon and Heemstra 1990; Hulley 1990). Total catch weights for each fish species were
166 obtained using a motion-compensated balance. All fish were measured to the nearest mm
167 (standard length, SL). Where possible, the sex and maturity status of the fish were recorded
168 from a sub-sample following dissection. We recorded gonad maturity status for according to
169 the following nominal categories: (1) Juvenile (gonad absent), (2) Immature (gonad visible,
170 but immature and reduced), (3) Developing (gonad visible and maturing), (4) Mature (gonad
171 fully developed), (5) Gravid female (gonad full of oocytes and ready to spawn), and (6)

172 Spawned female (gonad large, but no/few oocytes visible). Stomachs were dissected from a
173 sub-sample of 25 fish per haul, or from each fish where net catches were small. All stomachs
174 were frozen for subsequent microscopic analysis back in the laboratory.

175

176 Stomach content analysis

177 Fish stomachs were thawed prior to contents being sorted into species or taxonomic groups
178 following Shreeve et al. (2009). Contents were identified to the lowest taxonomic level the
179 state of digestion would allow and individual prey items were enumerated and weighed. If the
180 prey was highly disaggregated, the weights of the component species were estimated as a
181 proportion of total stomach weight. Items that were completely undigested were considered
182 to represent trawl feeding and were therefore excluded from the analysis.

183

184 Myctophid diet was expressed using percent mass (%M), percent frequency of occurrence
185 (%F), percent number (%N) and percent Index of Relative Importance (%IRI) (Cortes 1997).
186 The %IRI was calculated for prey species and %IRI_{DC} for prey categories (see Main et al.
187 2009 and Shreeve et al. 2009). Prey categories for *E. antarctica* were amphipods, copepods,
188 decapods, euphausiids, unidentified crustaceans, salps and molluscs (Shreeve et al. 2009).
189 The diet of *E. carlsbergi* was predominantly comprised of copepods and the following
190 dominant prey categories were used for this species: *Metridia* spp., *Rhincalanus gigas*,
191 *Paraeuchaeta* spp. *Calanus* spp. *Oncea* spp., and ‘Other taxa’ (euphausiids, amphipods,
192 salps, unidentified crustaceans and molluscs). Note that the %IRI is not additive, so the sum
193 of the individual species’ %IRI values is not the same as the prey category %IRI_{DC} value
194 (Hansson 1998). The %IRI was calculated as:

195

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

196

197 where *i* is prey item.

198

199 The %IRI for each prey category was calculated for data (where $n > 30$) collated by region,
200 cruise (a proxy for season), size class, and sex and gonad maturity status (Table 1). Fish size
201 classes for each species were derived from the composite length-frequency distributions for
202 the lower percentiles (sizes below $\mu - \sigma$), mid-percentile (sizes within $\mu \pm \sigma$) and upper
203 percentile (sizes above $\mu + \sigma$). The $\pm 95\%$ confidence limits for the mean %IRI of each prey
204 category were calculated using a bootstrapping technique, whereby each species dataset
205 (individual stomachs) was re-sampled (with replacement) 1000 times (Main et al. 2009).

206

207 Length-frequency analyses

208 A series of Kolmogorov-Smirnov tests were conducted on the length-frequency data to
209 investigate possible differences in population structure between surveys and regions across
210 the Scotia Sea. The tests were performed for each species where there were > 60 individuals
211 for the comparisons. Component-fitting software (CMIX) was used to fit normal distributions
212 to the composite length-frequency data and identify modes (de la Mare 1994). This method
213 fits a mixed distribution using a maximum likelihood estimator that assumes the data have an
214 Aitchison delta distribution (Aitchison 1955). The number of expected cohorts in the data
215 must be specified by the user before initiating the fitting procedure. We therefore conducted a
216 series of runs based on the presence of one or two cohorts and then determined the best fit to
217 the data using a Chi-squared test.

218

219 Regional and vertical differences between gender sizes were investigated using a series of
220 Students t-tests. The tests were first performed for each survey, where possible, to investigate
221 the possibility of temporal bias. Although the numbers of observations were often low on
222 each survey, the general underlying trends in gender size variation were consistent across all
223 surveys. Therefore, data were collated from all surveys for further analysis. A similar
224 approach was adopted for the analysis of regional variations in sex ratios and gonad maturity
225 status.

226

227 **Results**

228 Oceanographic conditions

229 The physical oceanography of the Scotia Sea during each survey is detailed in Venables et al.
230 (2012) and Whitehouse et al. (2012), so only the main features of the study sites are detailed
231 here. Net sampling stations covered the main oceanographic regimes of the Scotia Sea during
232 the three surveys (Fig. 1). Stations in the SSS were situated south of the Southern Boundary
233 of the Antarctic Circumpolar Current (SB-ACC) where mean temperatures in the Antarctic
234 Surface Waters (AASW; above ~90 m) ranged from -1.6 to 1.5 °C and mean Chlorophyll *a*
235 (hereafter Chl *a*) concentrations were around 0.2-0.4 mg m⁻³. These stations lay within the
236 receding ice-edge during the spring survey. Further north, stations in the WSS and MSS lay
237 between the SB-ACC and South Antarctic Circumpolar Current Front (SACCF). Mean
238 temperatures and Chl *a* concentrations in the AASW ranged from -0.2 to 2.1 °C and 0.2-2.6
239 mg m⁻³ in these regions. Stations in the NSS and GB were situated between the SACCF and
240 the Antarctic Polar Front (APF). Mean temperature and Chl *a* concentrations were similar in
241 the AASW in these two regions during each survey (~1.5-4.0 °C and ~0.2-1.0 mg m⁻³). All
242 PF stations were situated in waters north of the southern Polar Front (S-PF). Surface waters in
243 this region had a mean temperature >4.0 °C during all surveys with mean Chl *a*
244 concentrations ranging between 0.2-0.6 mg m⁻³. Winter Water (WW; ~100 to 200 m) and
245 Circumpolar Deep Water (CDW; >200 m) were evident at all stations located between the
246 SB-ACC and APF. Mean temperatures in the WW ranged between 0.2-1.0 °C. Mean water
247 temperature in the CDW (~0.8 °C) varied by <0.5 °C between surveys and by ~1.0 °C
248 between regions.

249

250 Distribution and abundance

251 A total of 143 non-targeted net hauls were conducted in the Scotia Sea during the three
252 surveys (JR161: *n*= 50, JR177: *n*=57, JR200: *n*=36; Table 2). Most stations were sampled
253 repeatedly to a varying degree during the surveys, although sampling in the WSS was
254 predominantly confined to the spring survey (JR161) (Fig. 1, Table 2). *E. antarctica* and *E.*
255 *carlsbergi* were the two principle species encountered during the surveys. Only five
256 specimens of *Electrona subaspera* (107-119 mm SL) were caught between 0-400 m at the PF
257 station during the three surveys.

258

259 *E. antarctica*: The species occurred at most stations throughout the Scotia Sea (Fig. 1) and
260 was the most abundant of the two species encountered during the surveys, comprising
261 densities between 0.09-0.21 ind. 1000 m⁻³ and a biomass of 0.62-1.28 g 1000 m⁻³ (survey
262 means; Tables 2 and 3). Densities and biomass for this species were highest south of the SB-
263 ACC in the SSS sector during all three surveys (0.25-0.49 ind. 1000 m⁻³ and 1.84-2.60 g 1000
264 m⁻³). The species also had a relatively high density around the MSS stations, near the
265 SACCF, and around the GB. However, the species was not found commonly in proximity to
266 the SACCF at the WSS stations. *E. antarctica* densities and biomass were low in the NSS
267 (<0.07 ind. 1000 m⁻³ and <0.39 g 1000 m⁻³) and PF (<0.05 ind. 1000 m⁻³ and <0.42 g 1000 m⁻³)
268 regions, and the species seldom occurred north of the S-PF. As net sampling was
269 undertaken in different years and there was a relatively high degree of patchiness in numbers
270 of fish sampled between hauls/stations, seasonal trends in density/biomass of *E. antarctica*
271 were difficult to substantiate. However, the lowest densities and biomass were generally
272 observed during spring (survey mean: 0.09 ind. 1000 m⁻³ and 0.62 g 1000 m⁻³) and biomass
273 was greatest during the summer (survey mean: 1.28 g 1000 m⁻³), although summer and
274 autumn densities were very similar (0.21 ind. 1000 m⁻³).

275

276 *E. carlsbergi*: This species was caught predominantly in the NSS during spring, where the
277 mean density and biomass was 0.42 ind. 1000 m⁻³ and 3.33 g 1000 m⁻³, respectively (Tables 2
278 and 3). The species occurred mostly around the MSS and WSS during summer and autumn
279 and was always absent south of the SB-ACC in the SSS. Densities and biomass were also
280 markedly low in both the GB region (<0.01 ind. 1000 m⁻³ and <0.02 g m⁻³) and at the PF
281 (<0.02 ind. 1000 m⁻³ and <0.21 g 1000 m⁻³) during all surveys. Again, seasonal trends were
282 difficult to substantiate, but the available data suggested that the greatest densities and
283 biomass were generally observed during the spring survey (survey mean: 0.11 ind. 1000 m⁻³
284 and 0.80 g 1000 m⁻³), whilst both densities and biomass were very similar during the summer
285 and autumn surveys (cruise means: ~0.03 ind. 1000 m⁻³ and ~0.16 g 1000 m⁻³).

286

287 Vertical distribution

288 *E. antarctica*: Clear differences between day and night hauls were apparent with consistently
289 greater densities and biomasses of fish caught during the night (Fig. 2a). Daytime abundance
290 and biomass was greatest between 701-1000 m in spring and between 401-700 m in summer.
291 Very few specimens were caught above 400 m during the daytime. At night, the species was
292 distributed throughout the water column (0-1000 m), but there were some differences in
293 depth distribution between surveys. The greatest night-time concentrations occurred between
294 201-400 m in spring, while the majority of the population was distributed between 401-700 m
295 in summer, and between 0-200 m in autumn.

296

297 *E. carlsbergi*: Few specimens were caught during the day and the species was largely
298 confined to the upper 400 m of the water column during the night (Fig. 2b). The species was
299 predominantly distributed between 0-200 m in spring and was spread between 0-400 m in the
300 summer. Its vertical distribution was deepest in autumn when most of the population occurred
301 between 201-400 m.

302

303 Population size structure

304 *E. antarctica*: The overall size ranged between 25-115 mm SL on each survey and larval
305 stages (<20 mm) were not observed during the study. A series of K-S tests conducted on
306 length-frequency data aggregated by region on each survey (where $n > 60$) showed that there
307 were no significant ($P > 0.05$) regional differences in composite length-frequency distributions
308 across the Scotia Sea. Published data indicate that peak spawning for *E. antarctica* occurs
309 throughout the Scotia Sea in autumn/early-winter (April-June) (Lubimova et al. 1987) and
310 hatching occurs between June and August (Kellermann 1989b; Kellermann 1989a). We
311 therefore consider individuals as belonging to a 0-group from the time of hatching until June
312 the following year, to a I-group from 1 July to 30 June the next year, and so on.

313 Differentiation between the 0-group and I-group cohorts in the initial population was aided
314 by published growth rates for the species (Greely et al. 1999). Although the data were not
315 collected in consecutive seasons, the overall seasonal pattern in population structure appeared
316 to be as follows. The general life span of *E. antarctica* was at least three years. Two size-,
317 and presumably age-, classes were present in the spring population: the newly recruited II-

318 group (~2 year old; mode: 54 mm) and III+ group (>3 year old; 87 mm). The summer length-
319 frequency distribution was unimodal (II+ group: 75 mm) as the II-group evident in spring had
320 increased in size and was now indistinguishable in size from III+ group individuals. The
321 newly spawned 0-group was absent from the population during all surveys. By autumn, the I-
322 group was first evident in the population (~1 year old; mode: 63 mm), together with the II+
323 group which had again increased in size from the previous season (mode: 80 mm). These two
324 cohorts would presumably over-winter and recruit into the II-group and III+ group the
325 following June.

326

327 *E. carlsbergi*: The species had a narrower size range (65-90 mm SL) than that of *E.*
328 *antarctica* and the composite length-frequency distributions were always unimodal (81-82
329 mm; Fig. 3b). No juvenile specimens (<50 mm SL) were caught during the surveys. K-S tests
330 showed that there were no significant differences ($P>0.05$) in *E. carlsbergi* length-frequency
331 distribution between surveys or between regions.

332

333 Gender-based differences

334 *E. antarctica*: On each survey, adult females were always significantly larger (Students t-
335 tests, $P<0.001$) than adult males, the difference in mean size being ~5 mm. The mean size of
336 adult males was not significantly different between regions (~69 mm, $P>0.05$), but regional
337 differences in the size of females were evident, as females at the PF (86 mm) and in the GB
338 (78 mm) had a significantly larger ($P<0.01$) mean size than those in NSS (75 mm), MSS (73
339 mm) and SSS (72 mm). Analyses of mean fish size by depth zone revealed evidence of
340 vertical stratification, with larger fish positioned predominantly deeper in the water column
341 than smaller fish (Fig. 4a). For example, there was a difference in mean fish size of ~15 mm
342 between the 0-200 and 701-1000 m depth zones, regardless of gender.

343

344 *E. carlsbergi*: Adult females had a significantly larger (Students t-tests, $P<0.05$) mean size
345 than adult males during each survey, the difference consistently being ~2 mm. However,
346 there were no significant ($P>0.05$) regional or temporal differences in the mean size of either

347 sex. There was some evidence of vertical stratification in size classes in this species, as the
348 mean size of specimens distributed between 401-700 m was approximately 6 mm larger than
349 that observed in the 0-200m depth zone (Fig. 4b). However, only a few fish ($n= 5$) were
350 observed below 400 m, and there were no significant differences ($P>0.05$) in fish size
351 between 0-200 m and 201-400 m for this species.

352

353 Patterns in sex and gonad maturity status

354 *E. antarctica*: Juvenile specimens comprised ~5% of the population in each region, except
355 the PF where they were seldom observed (~1%). There was a latitudinal decrease in the ratio
356 of adult females to males between the SSS and regions further north (Fig. 5a). The ratio of
357 females to males was ~4:1 in the SSS, which decreased to ~2:1 in the MSS and then to ~1:1
358 in the NSS, GB and PF regions. Also, the proportion of specimens with immature gonads in
359 the SSS (18%) was double that in more northern regions, whilst the proportion of specimens
360 with mature gonads was lower by half (~8%). No fish with mature gonads were caught at the
361 PF and gravid and spawned females were absent during all three surveys.

362

363 *E. carlsbergi*: All specimens caught on the three surveys were adults. Regional comparisons
364 were only possible for the PF, NSS and MSS for this species. There was little evidence of
365 regional variation in the sex ratios of adult *E. carlsbergi* and the ratio of females to males was
366 approximately 1:1 at all stations (Fig. 5b). Mature, Gravid and Spawned females were absent
367 on all surveys. However, there was some evidence of regional variations in gonad maturity
368 status between the Immature and Developing components of the populations. All fish
369 observed at the PF had gonads in the developing stages, whereas the majority of the
370 population (~88%) in the NSS had immature gonads. Around 77% of the population had
371 gonads in the developing phase in the MSS.

372

373 General diet composition

374 *E. antarctica*: A total of 485 stomachs were examined for this species. The species had a
375 relatively broad diet in the Scotia Sea region, predated several species of amphipods,

376 copepods, euphausiids, as well as other groups such as ostracods and molluscs (Table 4).
377 Unidentifiable (digested) crustaceans were a further major component. Its diet was dominated
378 by *E. superba* (43% IRI), the amphipod *Themisto gaudichaudii* (30% IRI) and copepods
379 within the *Metridia* genus (16% IRI)

380

381 *E. carlsbergi*: A total of 185 stomachs were examined. The diet of *E. carlsbergi* was largely
382 dominated by copepods (93% IRI), with other prey groups comprising only minor parts of the
383 diet (Table 4). The diet was mostly dominated by *Rhincalanus gigas* (82% IRI). Other
384 important components included *Metridia* spp. and *Oncaea* spp. (~5% IRI).

385

386 Spatial patterns in diet

387 *E. antarctica*: There was a latitudinal trend in the relative importance of copepods and
388 euphausiids in the diet, with copepod predation highest at the northernmost PF stations, but
389 decreasing progressively southwards along the transect to the SSS stations (Fig. 6a).
390 Conversely, euphausiids were of greatest importance in the diet at the SSS stations but this
391 decreased northward to the PF stations. Predation on amphipods occurred predominantly at
392 the GB stations and less so in the SSS or at the PF.

393

394 *E. carlsbergi*: Spatial variations in diet were also apparent for this species (Fig. 7a). Its diet
395 was comprised exclusively of two copepods species in the NSS region, with *R. gigas* being
396 the dominant prey species (~97% IRI) and *Metridia* spp. occurring in minor proportions. By
397 contrast, almost equal proportions of these two species were consumed (~42% IRI) around
398 the MSS and PF, and other prey items, most notably pteropods and *T. gaudichaudii*, also
399 occurred in the diet in these regions (~7% IRI). However, it should be noted that the % IRI_{DC}
400 values at the PF were associated with high error bars due to the relatively low sample sizes
401 obtained there (Table 2).

402

403 Temporal patterns in diet

404 *E. antarctica*: Although net sampling was conducted in different years, there was evidence of
405 seasonal variations in diet for both myctophid species (Fig. 6b). Copepods comprised the
406 most important prey group for *E. antarctica* during spring (71% IRI), followed by
407 euphausiids (26% IRI). However, the proportion of copepods in the diet was reduced during
408 summer (59% IRI) as amphipods became part of the diet. During the autumn, the proportion
409 of copepods in the diet was further reduced (32% IRI) as euphausiids increased substantially
410 and dominated the diet (63% IRI).

411

412 *E. carlsbergi*: The diet in spring was predominantly comprised of *R. gigas* (96% IRI), but
413 there was a clear reduction in the proportion of this species in the diet during summer (59%
414 IRI) and autumn (39% IRI), as *Metridia* spp. increased as a dietary component (Fig. 7b).
415 There was also an increase in the proportion of other, non-copepod prey groups during
416 autumn (<3% compared to 32% IRI). Pteropods and *T. gaudichaudii* were the principle prey
417 species in this category.

418

419 Ontogenetic patterns in diet

420 *E. antarctica*: Specimens in the largest size category (>87 mm) predated the greatest
421 proportions of euphausiids (58% IRI) and fewest proportions of copepods (26% IRI; Fig. 6c).
422 This size group also predated the greatest proportions of amphipods (10% IRI). The smallest
423 size class (<55 mm) took the greatest quantities of copepods (85% IRI), but the lowest
424 proportions of euphausiids (13% IRI) and no amphipods. The diet of the mid-percentile
425 category (55-87 mm) was similar to that of the smallest size category, although the
426 proportion of euphausiids was slightly higher (17% IRI) and the proportions of copepods
427 slightly lower (74% IRI). Trends in diet by gonad maturity class were similar to those by size
428 class (Fig. 6d) and there were no differences in diet between males and females.

429

430 *E. carlsbergi*: The proportion of each prey group consumed by this species was similar across
431 all adult size classes (Fig. 7c). However, there were differences in diet between gonad
432 maturity stages (Fig. 7d). Although no mature specimens were encountered on the surveys,

433 fish with immature gonads took considerably more *R. gigas* than those with developing
434 gonads (96% compared to 64% IRI), and much less *Metridia* spp. (4% compared to 34%
435 IRI). There was no difference in diet between male and females for this species.

436

437 **Discussion**

438 Distribution

439 *E. antarctica* was the most abundant of the two principal *Electrona* species encountered in
440 the Scotia Sea. The species was distributed throughout the region south of the APF, with the
441 greatest concentrations occurring south of the SB-ACC where water temperatures were
442 frequently below zero. This pattern is in accordance with other studies in the Southern Ocean
443 that reported that this Antarctic species is most frequently encountered in the sea-ice sectors
444 and has a northern distributional limit of around 5° north of the APF (Rowedder 1979b;
445 Hulley 1981; McGinnis 1982). In contrast, *E. carlsbergi* was primarily distributed in the
446 more northern sectors of the Scotia Sea, and did not occur in waters south of the SB-ACC. *E.*
447 *carlsbergi* has been described as a sub-Antarctic species that has a distribution that is highly
448 associated with the AFP (Hulley 1981; McGinnis 1982; Zasel'sliy et al. 1985; Efremenko
449 1986). The distributional range of the species in the Southern Ocean is generally considered
450 to be between the Subtropical Front (hereafter STF; ~40 °S) and ~60 °S, with the greatest
451 concentrations occurring predominantly around ~50 °S within the Antarctic Intermediate
452 waters of the APF. The species has also been observed in high abundance at South Georgia
453 (Collins et al. 2008). In our study, *E. carlsbergi* did not occur in high abundance at the PF nor
454 around the GB (including South Georgia), but was predominantly found in the NSS and MSS
455 (~56-58 °S), indicating a relatively high degree of spatial variability in its distribution in the
456 Scotia Sea.

457

458 It is possible that *E. carlsbergi* is a highly migratory species in the Southern Ocean and
459 variations in distribution could be related to underlying oceanographic conditions, such as
460 changes in frontal positions, eddy formations and temperature (Collins et al. 2012).
461 Variations in its distribution could also be related to ontogenetic changes in the lifecycle and
462 intra-specific migrations. Studies have reported that *E. carlsbergi* forms dense, mono-specific

463 schools, particularly in regions around the APF, and that there is a high degree of spatial
464 heterogeneity in population structure throughout its distributional range (Hulley 1981;
465 McGinnis 1982; Zasel'sliy et al. 1985; Efremenko 1986; Collins et al. 2008). The available
466 data from these studies indicate that discrete schools at the APF consist exclusively of adults
467 and that juveniles tend to dominate populations in regions further north towards the STF.
468 However, juveniles are markedly absent south of the APF. Many mesopelagic fish species
469 undertake specific spawning migrations, traversing relatively long distances and a range of
470 different environments (Krause and Ruxton 2002). It has therefore been suggested that the
471 species undertakes distinct spawning migrations, with adults spawning in the northern regions
472 of the APF and then migrating away from the newly spawned cohort back to regions further
473 south (Hulley 1981; McGinnis 1982; Zasel'sliy et al. 1985; Efremenko 1986; Collins et al.
474 2008). A further possibility is that *E. carlsbergi* occurs only as an expatriate in regions south
475 of the APF, perhaps via oceanographic transportation (fronts or eddies), and that populations
476 occurring in the Scotia Sea are not self-sustaining. As a more northerly sub-Antarctic species,
477 *E. carlsbergi* may have a lifecycle that is adapted to predominantly warmer temperatures than
478 those that occur in the Scotia Sea, such that recruitment is inhibited in the region. The early
479 larval stages may be sensitive to colder temperatures (Ross et al. 1988), which might explain
480 why no larvae or juveniles have thus far been caught south of the APF, even though post-
481 spawning females have been reported in these waters (Oven et al. 1990).

482

483

484 Vertical distribution

485 *E. antarctica* had a broad night-time depth distribution (0-1000 m), spanning all three
486 overlying water masses (AASW, WW and CDW) (Venables et al. 2012). During the daytime,
487 the species was confined to depths below 400 m, suggesting some diel vertical migration
488 (DVM) at night, although daytime net avoidance may also have been inherent (Collins et al.
489 2012; Kaartvedt et al. 2012). These patterns are in accordance with Collins et al. (2008) and
490 Pusch et al. (2004), although others studies have reported that the species has a much more
491 restricted vertical range of around 0-250 m in the region (Andriashev 1965; Hulley 1981).
492 Concurrent with Collins et al. (2008), *E. carlsbergi* was limited to the upper 400 m of the
493 water column, but also occupied AASW, WW and CDW. DVM was not apparent for *E.*

494 *carlsbergi* at the vertical resolution of our net sampling, but such behaviour has been
495 observed during acoustic studies (Zasel'sliy et al. 1985; Kozlov et al. 1991). The vertical
496 distribution of *E. carlsbergi* was previously reported to be mainly around 0-100 m in the
497 Scotia Sea region, but populations, including both juveniles and adults, were restricted to
498 depths below ~500 m in waters near the STF (Hulley 1981; McGinnis 1982). Such regional
499 differences suggest that latitudinal variations in temperature are an important control on the
500 vertical distribution of *E. carlsbergi* (Hulley 1981; McGinnis 1982).

501

502 Different temporal patterns in night-time vertical distribution were evident for both species
503 by the net catches across cruises, indicative of seasonal variation. *E. antarctica* appeared to
504 be distributed deeper in summer than in autumn and spring, whilst the depth distribution of *E.*
505 *carlsbergi* appeared to increase from spring to autumn. Studies at high latitudes in the North
506 Atlantic have reported a distinct seasonal deepening of mesopelagic fish that corresponds
507 with a winter deepening of prey organisms, particularly copepods, that comprise the deep
508 scattering layers (DSL) (Anderson et al. 2005; Dypvik et al. 2012; Pepin 2013). Many high
509 latitude copepods over-winter at depth and it has been hypothesised that mesopelagic fish and
510 other zooplankton move down the water column to predate these organisms (Atkinson 1998;
511 Astthorsson and Gislason 2003; Dypvik et al. 2012). The seasonal increase in depth
512 distribution of *E. carlsbergi* was consistent with this hypothesis, as overwintering copepod
513 stages were seen to be undergoing their seasonal descent during autumn (Ward et al. 2012)
514 and the species is considered to comprise the principle component of the DSL in other
515 regions, such as the Pacific sector (Linkowski 1983). However, the pattern in *E. antarctica*
516 depth distribution was not consistent with this notion. It is possible that large portions of the
517 *E. antarctica* population remain at depth in summer to avoid predation when light intensities
518 are greatest, but then move up to the surface layers in autumn when periods of darkness are
519 increased.

520

521 Vertical size structure

522 Ontogenetic patterns in vertical distribution were apparent for both *Electrona* species, with
523 larger fish caught predominantly deeper in the water column. Similar patterns were reported

524 for *E. antarctica* adults at South Georgia (Collins et al. 2008), and *E. antarctica* larvae were
525 found higher (above ~200 m) in the water column than juveniles (~200-1000 m) off Lutzow-
526 Holm Bay (Indian sector) (Moteki et al. 2009). However, the reasons for this behaviour are
527 unclear. Collins et al. (2008) suggested that ontogenetic patterns in *Electrona* depth
528 distribution could be a function of downward spawning migrations of gravid females.
529 However, no gravid females were observed in our study and the trend was apparent for
530 males, as well as females, indicating that ontogenetic migrations within this genus are not just
531 simply related to the spawning behaviour of females.

532

533

534 Population structure

535 Regional variation in composite length-frequency distributions was not apparent for *E.*
536 *antarctica*, but there was clear evidence of seasonal growth and recruitment in the Scotia Sea
537 that was highly consistent with other population studies (Rowedder 1979b; Greely et al.
538 1999). *E. antarctica* larval stages typically occur throughout the Scotia Sea in summer
539 (January to April) (McGinnis 1982; Efremenko 1986), but these stages were not caught with
540 any zooplankton/micro-nekton sampling device during our study. It is probable that the
541 species has a narrow and variable spawning window, such that the early larval stages were
542 missed within the timeframe of our summer survey. However, the data are still consistent
543 with a lifespan of around three to four years (Rowedder 1979b; Greely et al. 1999). Although
544 the overall population size structure of *E. antarctica* did not vary between regions, size-
545 related sexual dimorphism was apparent and there was a consistent decline in the mean size
546 of females from the PF to the SSS, a trend that was not apparent for males. Similar findings
547 were reported by Rowedder (1979b). We also observed a corresponding latitudinal cline in
548 sex ratio, with the ratio of females to males increasing towards the southernmost sectors of
549 the Scotia Sea. This retention of females in the sea-ice sectors suggests that the region is the
550 main spawning grounds for the species, and that females may undertake distinct spawning
551 migrations. Retention of newly recruited females in the region, or a greater influx of
552 spawning females of a predominantly younger age/size-class (first-time spawners), may have
553 caused a reduction in the mean size of females in the sea-ice sectors.

554 There was no evidence of regional or temporal variation in the length-frequency distributions
555 for *E. carlsbergi*, and the presence of single, adult cohorts of a limited size range (65-90 mm
556 SL) is highly consistent with other, albeit limited, studies in the Scotia Sea (Hulley 1981;
557 McGinnis 1982; Zasel'sliy et al. 1985; Efremenko 1986; Oven et al. 1990; Collins et al.
558 2008). The diet of king penguins (*A. patagonicus*) at the sub-Antarctic Crozet Archipelago
559 also consisted exclusively of *E. carlsbergi* specimens of the same size range (Cherel and
560 Ridoux 1992). *E. carlsbergi* juveniles (<70 mm SL) and larvae (~7-15 mm SL) have only
561 been recorded in regions north of the APF in summer (January) (Hulley 1981; McGinnis
562 1982) and specimens that occur in the Scotia Sea are exclusively adults, mostly around two
563 years of age (Zasel'sliy et al. 1985; Oven et al. 1990). It has been estimated from otoliths that
564 the species has a life span of two to three years and that spawning occurs either late-
565 winter/early-spring (August-September) (Lubimova et al. 1987) or late-spring/early-summer
566 (November-December) (Zasel'sliy et al. 1985). The overall patterns in population structure
567 and distribution are therefore consistent with the concept that *E. carlsbergi* is either an
568 expatriate in the Scotia Sea from regions north of the APF, or a highly migratory species that
569 has ontogenetically segregated populations between the Scotia Sea and northern APF.

570

571 General diet patterns

572 Several studies have focussed on the diet of *E. antarctica* and *E. carlsbergi* in various regions
573 throughout the Southern Ocean, including the Scotia Sea (Rowedder 1979a; Naumov et al.
574 1981; Gorelova and Efremenko 1989; Pusch et al. 2004; Shreeve et al. 2009), Lazarev Sea
575 (Gerasimova 1990; Pakhomov et al. 1996; Flores et al. 2008), near Macquarie Island (Gaskett
576 et al. 2001) and the Kosmonavtov Sea (Kozlov and Tarverdiyeva 1989). However, the
577 majority of these studies were either based on small sample sizes collected at relatively small
578 spatial scales, or were only semi-quantitative, making it difficult to substantiate and compare
579 trends in diet in the Southern Ocean. The diet of *E. antarctica* in our study was broadly
580 consistent with that previously reported from the Scotia Sea in that the species is considered
581 to be an opportunistic feeder with a diverse diet, but feeding predominantly on copepods and
582 euphausiids, principally *E. superba*. Also, *T. gaudichaudii* appears to comprise an important
583 part of *E. antarctica* diet in waters around South Georgia in all studies. The diet of *E.*

584 *carlsbergi* was similarly consistent with these previous studies, which report that the species
585 feeds opportunistically, but is predominantly a copepod predator.

586

587 *E. antarctica* diet patterns

588 The largest specimens and those present in the southernmost regions of the Scotia Sea
589 predated the greatest amounts of euphausiids, predominantly *E. superba*. However, krill
590 predation decreased with decreasing latitude northwards to the PF, whilst the proportion of
591 copepods in the diet increased along this cline. This trend corresponded with the regional
592 distributional patterns of the main prey species that were present in the water column during
593 the surveys (Fig. 8). Data from the concurrent zooplankton survey (Ward et al. 2012) and our
594 RMT25 nets showed a marked latitudinal decrease in the abundance of *E. superba*, along
595 with an increase in abundance of all predated copepod species from the SSS to the PF. Data
596 from the acoustic survey also showed that *E. superba* schools were smaller, contained fewer
597 individuals, and were positioned further apart in the north compared to the south (Fielding et
598 al. 2012). These results therefore indicate that *E. superba* was less available to *E. antarctica*
599 in the northern regions of the Scotia Sea, which resulted in a shift towards copepods in the
600 diet. Size-dependant feeding behaviour on krill could be an additional factor (Pakhomov et al.
601 1996; Pusch et al. 2004; Shreeve et al. 2009). *E. superba* tend to be larger in the northern
602 sectors of the Scotia Sea compared to the sea-ice sectors that are important sites for krill
603 recruitment (Nicol 2006; Tarling et al. 2007), a trend that was also apparent in our study
604 (Fielding et al. 2012). Krill in the northern regions may therefore be too large for *E.*
605 *antarctica* to predate as well as being too patchy to exploit as a primary food source.

606

607 *E. antarctica* did not appear to predate great quantities of other smaller euphausiids, such as
608 *Euphausia triacantha*, *Thysanoessa* spp. and *Euphausia frigida* in the study region. These
609 euphausiids were found commonly in the northern regions of the Scotia Sea, particularly *E.*
610 *triacantha* which had a relatively high abundance in the northern regions, similar to that of *T.*
611 *gaudichaudii* (Fig. 8). These smaller euphausiids have comparable energy content to
612 similarly sized *E. superba* (Reinhardt and Vanvleet 1986), yet *E. antarctica* still favoured

613 copepods and *T. gaudichaudii* over smaller euphausiids, suggesting a degree of resource
614 selectivity within the species.

615

616 There appeared to be seasonal variation in the diet of *E. antarctica* that did not reflect
617 seasonal changes in prey abundance (Fielding et al. 2012; Ward et al. 2012). The temporal
618 pattern in *E. antarctica* diet broadly reflected the seasonal change in copepod ontogeny in the
619 region, as adult females and older copepodite stages dominated in the overwintered spring
620 population whilst younger stages (particularly stage CIII) dominated the post-spawned
621 population in autumn (Ward et al. 2012). Shreeve et al. (2009) reported a tendency for
622 myctophids, including *E. antarctica* and *E. carlsbergi*, to target older copepodite stages. The
623 switch from copepods to krill in the diet in autumn may therefore have been a function of a
624 reduction in older copepod stages in the prey field. However, more data at an increased
625 temporal resolution are clearly warranted to substantiate links between copepod ontogeny and
626 myctophid predation.

627

628 *E. carlsbergi* diet patterns

629 Spatial variation in *E. carlsbergi* diet was apparent which broadly reflected the spatial
630 patterns in copepod abundance, and there was a relatively high overlap in the broad-scale
631 distribution of abundance of *E. carlsbergi* and its main prey species, *R. gigas* (Fig. 8). The
632 abundance of all the main copepod species was considerably greater in regions north of the
633 SB-ACC than in those situated south of this front during all surveys, particularly *R. gigas*,
634 where there was a marked decrease in abundance between the NSS and MSS. There was also
635 a tendency for more advanced copepodite stages to occur north of the SB-ACC (Ward et al.
636 2012). These differences in feeding environment, as well as marked differences in water
637 temperature, may explain the observed broad-scale distribution of *E. carlsbergi* that appeared
638 to be restricted by the SB-ACC. Thus this predominantly sub-Antarctic species may not only
639 be intolerant of the colder waters south of the SB-ACC (Collins et al. 2012), but there may
640 also be insufficient food of the right quality (i.e. older *R. gigas* stages) in the region for its
641 survival at these higher latitudes. There was also evidence of seasonal variation in diet but,
642 similar to *E. antarctica*, the drivers of this trend were unclear from our data.

643

644 A relatively high degree of copepod species selection by *E. carlsbergi* was apparent, as the
645 species clearly predated *R. gigas* and *Metridia* spp. in favour of other abundant species, such
646 as *Calanoides acutus* and *Calanus simillimus* (Fig. 8). These copepods had a comparatively
647 high abundance in each region north of the SB-ACC, were similar in size to *R. gigas* and
648 *Metridia* spp. and occurred within the vertical range of *E. carlsbergi*, but they did not occur
649 often in the diet. *E. carlsbergi* also tended not to predate the smaller copepod species, such as
650 *Oithona* spp. and *Ctenocalanus* spp., despite the numerical dominance of these zooplankton
651 throughout the region (Ward et al. 2012). However, an exception to this was the relatively
652 high proportion of the deeper-dwelling *Oncaea* spp. in the diet. It has been suggested that
653 small copepods may either be too small for retention by gill-rakers or too unprofitable to
654 exploit for several myctophid species (Shreeve et al. 2009). Our results indicated that *E.*
655 *carlsbergi* is a species capable of retaining small copepods such as *Oncaea* spp., so it is
656 apparent that selectivity in copepod predation occurred for reasons other than size alone.
657 Shreeve et al. (2009) also suggested that the behaviour of certain copepods species may make
658 them more susceptible to predation by myctophids than others. For example, *Metridia*
659 copepods undergo extreme DVM in excess of 200 m, whilst *R. gigas* is relatively inactive
660 and reacts slowly to stimuli (Shreeve et al. 2002; Ward et al. 2006). Also, *R. gigas* is a
661 species that undertakes prolonged periods of winter dormancy at depth whereas *Metridia* spp.
662 does not and remains active throughout the year (Hagen and Schnack-Schiel 1996). These
663 different behaviour patterns may increase their vulnerability not only to different myctophid
664 species, but also to different ontogenetic stages within the same species. Ontogenetic copepod
665 selectivity for *E. carlsbergi* was evident in this study.

666

667 Potential *Electrona* niche separators

668 Differences in lifecycle strategies, vertical distribution, population dynamics and diets are
669 important niche separators in marine ecosystems (Barange 1990), and may explain, to a
670 certain extent, the co-existence of the two *Electrona* species in the Scotia Sea region. From
671 data presented here and elsewhere, it appears that, although *E. antarctica* and *E. carlsbergi*
672 are superficially very similar-looking species and their distributions overlap in the Scotia Sea,
673 they have different niche roles. *E. antarctica* appears to be a deep-dwelling species with a life

674 cycle that is predominantly adapted to the cold Antarctic waters. The species is distributed
675 throughout the Scotia Sea south of the APF, with the greatest concentrations occurring in the
676 sea-ice sectors. *E. antarctica* also appears to spawn and recruit successfully throughout the
677 Scotia Sea in autumn/winter to produce viable self-sustaining populations in the region. The
678 species has a diet that is dominated by Antarctic krill in the southern regions of the Scotia
679 Sea, but the species switches to *Metridia* spp. and *T. gaudichaudii* in other regions. By
680 contrast, *E. carlsbergi* is a sub-Antarctic species that is predominantly distributed in the
681 warmer waters north of the APF and has a southern distributional limit around the SB-ACC
682 in the sea-ice sector. It appears unable to reproduce successfully in the colder waters of the
683 Scotia Sea, so the species is either an expatriate here, possibly due to oceanographic
684 processes, or it produces ontogenetically segregated populations and undertakes intra-specific
685 spawning migrations to regions elsewhere. *E. carlsbergi* also has narrower depth distribution
686 than *E. antarctica*, possibly spawns at different times (spring), and exhibits a pattern of
687 seasonal vertical migration that differs from that of *E. antarctica*. Furthermore, the species
688 predated predominantly copepods, particularly *R. gigas*, and not euphausiids. These two
689 myctophid species therefore seem to have very different niche roles in the Scotia Sea region,
690 and do not appear to be in direct competition for resources in regions where they are both
691 abundant. This is supported by biochemical studies that also indicate strong niche segregation
692 in terms of diet and habitat type within the *Electrona* genus in the Southern Ocean (Cherel et
693 al. 2010; Stowasser et al. 2012).

694

695 Conclusions

696 This study provides new insight into the ecology and trophodynamics of two biomass
697 dominant myctophid species, *E. antarctica* and *E. carlsbergi*, within the Scotia Sea
698 ecosystem. Temperature is an important control on the spatial and vertical distribution
699 patterns of both species. Surface waters in the northern parts of the study regions are
700 experiencing a rapid increase in temperature, which is likely to be changing the behaviour
701 and distribution of both myctophid prey-species and myctophids. The study contributes to our
702 understanding of how mid-water food webs are structured in the Southern Ocean and their
703 sensitivity to ongoing environmental change.

704

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709 **References**

- 710 Aitchison J (1955) On the distribution of a positive random variable having a discrete probability
711 mass at the origin. *J AM Stat Assoc* 50:901-908
- 712 Anderson CIH, Brierley AS, Armstrong F (2005) Spatio-temporal variability in the distribution of epi-
713 and meso-pelagic acoustic backscatter in the Irminger Sea, North Atlantic, with implications
714 for predation on *Calanus finmarchicus*. *Mar Biol* 146:1177-1188
- 715 Andriashev AP (1965) A general review of the Antarctic fish fauna. *Monogr Biol* 15:491-550
- 716 Astthorsson OS, Gislason A (2003) Seasonal variations in abundance, development and vertical
717 distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic
718 Current. *J Plankton Res* 25:843-854
- 719 Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. *J Mar Syst*
720 15:289-311
- 721 Atkinson A, Siegel V, Rothery P (2004) Long-term decline in krill stock and increase in salps within the
722 Southern Ocean. *Nature* 432:100-103
- 723 Atkinson A, Whitehouse MJ, Priddle J, Cripps GC, Ward P, Brandon M (2001) South Georgia,
724 Antarctica: a productive, cold water, pelagic ecosystem. *Mar Ecol Prog Ser* 216:279-308
- 725 Barange M (1990) Vertical migration and habitat partitioning of 6 euphausiid species in the North
726 Benguela upwelling system. *J Plankton Res* 12:1223-1237
- 727 Cherel Y, Fontaine C, Richard P, Labat J-P (2010) Isotopic niches and trophic levels of myctophid
728 fishes and their predators in the Southern Ocean. *Limnol Oceanogr* 55:324-332
- 729 Cherel Y, Putz K, Hobson KA (2002) Summer diet of king penguins (*Aptenodytes patagonicus*) at the
730 Falkland Islands, southern Atlantic Ocean. *Polar Biol* 25:898-906
- 731 Cherel Y, Ridoux V (1992) Prey species and nutritive value of food fed during summer to king
732 penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis*
733 134:118-127
- 734 Collins MA, Ross KA, Belchier M, Reid K (2007) Distribution and diet of juvenile Patagonian toothfish
735 on the South Georgia and Shag Rocks Shelves (Southern Ocean). *Mar Biol* 152:135-147
- 736 Collins MA, Stowasser G, Fielding S, Shreeve R, Xavier JC, Venables HJ, Enderlein P, Cherel Y, Van de
737 Putte A (2012) Latitudinal and bathymetric patterns in the distribution and abundance of
738 mesopelagic fish in the Scotia Sea. *Deep-Sea Res Part II* 59:189-198

- 739 Collins MA, Xavier JC, Johnston NM, North AW, Enderlein P, Tarling GA, Waluda CM, Hawker EJ,
740 Cunningham NJ (2008) Patterns in the distribution of myctophid fish in the northern Scotia
741 Sea ecosystem. *Polar Biol* 31:837-851
- 742 Cortes E (1997) A critical review of methods of studying fish feeding based on analysis of stomach
743 contents: application to elasmobranch fishes. *Can J Fish Aquat Sci* 54:726-738
- 744 Curran MAJ, van Ommen TD, Morgan VI, Phillips KL, Palmer AS (2003) Ice core evidence for sea ice
745 decline since the 1950s. *Science* 302:1203-1206
- 746 de la Mare W (1994) Estimating krill recruitment and its variability. *CCAMLR Sci* 1:55-69
- 747 de la Mare WK (1997) Abrupt mid-twentieth-century decline in Antarctic sea extent from whaling
748 records. *Nature* 389:387-400
- 749 Dickson J, Morley SA, Mulvey T (2004) New data on *Martialia hyadesi* feeding in the Scotia Sea
750 during winter; with emphasis on seasonal and annual variability. *J Mar Biol Assoc UK* 84:785-
751 788
- 752 Dypvik E, Rostad A, Kaartvedt S (2012) Seasonal variations in vertical migration of glacier lanternfish,
753 *Benthoosema glaciale*. *Mar Biol* 159:1673-1683
- 754 Efremenko VN (1986) Distribution of eggs and larvae of Myctophidae in the southern Atlantic. *J*
755 *Ichthyol* 26:141-147
- 756 Fielding S, Watkins JL, Collins MA, Enderlein P, Venables HJ (2012) Acoustic determination of the
757 distribution of fish and krill across the Scotia Sea in spring 2006, summer 2008 and autumn
758 2009. *Deep-Sea Res Part II* 59:173-188
- 759 Flores H, de Putte APV, Siegel V, Pakhomov EA, Van Franeker JA, Meesters HWG, Volckaert FAM
760 (2008) Distribution, abundance and ecological relevance of pelagic fishes in the Lazarev Sea,
761 Southern Ocean. *Mar Ecol Prog Ser* 367:271-282
- 762 Gaskett AC, Bulman C, He X, Goldsworthy SD (2001) Diet composition and guild structure of
763 mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *New Zeal J Mar Fresh*
764 35:469-476
- 765 Gerasimova OV (1990) Feeding and food intake of *Electrona carlsbergi* (Taning, 1932) Myctophidae.
766 *CCAMLR Sel Sci Pap* 7:411-416
- 767 Gjøsaeter J, Kawaguchi K (1980) A review of the world resources of mesopelagic fish. FAO (Food and
768 Agriculture Organization of the United Nations) Fisheries Technical Paper:1-151
- 769 Gon O, Heemstra PC (1990) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology,
770 Grahamstown

- 771 Gorelova TA, Efremenko VN (1989) On the food composition of the larvae of two species of lantern
772 anchovies (Myctophidae) from the Scotia Sea. J Ichthyol 29:106-109
- 773 Greely TM, Gartner JV, Torres JJ (1999) Age and growth of *Electrona antarctica* (Pisces :
774 Myctophidae), the dominant mesopelagic fish of the Southern Ocean. Mar Biol 133:145-158
- 775 Hagen W, Schnack-Schiel SB (1996) Seasonal lipid dynamics in dominant Antarctic copepods: Energy
776 for overwintering or reproduction? Deep-Sea Res Part I 43:139-158
- 777 Hansson S (1998) Methods of studying fish feeding: a comment. Can J Fish Aquat Sci 55:2706-2707
- 778 Hill SL, Phillips T, Atkinson A (2013) Potential climate change effects on the habitat of Antarctic krill
779 in the Weddell quadrant of the Southern Ocean. Plos One 8:1-12
- 780 Hulley PA (1981) Results of the research cruises of FRV "Walther Herwig" to South America. 58.
781 Family Myctophidae (Osteichthyes, Myctophiformes). Arch Fischereiwiss 31:1-300
- 782 Hulley PA (1990) Myctophidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B.
783 Smith Institute of Ichthyology, Grahamstown, pp 146-178
- 784 Kaartvedt S, Staby A, Aksnes DL (2012) Efficient trawl avoidance by mesopelagic fishes causes large
785 underestimation of their biomass. Mar Ecol Prog Ser 456:1-6
- 786 Kellermann A (1989a) Fish eggs and larvae. Ber Polarforsch 62:157-158
- 787 Kellermann A (1989b) The larval fish community in the zone of seasonal ice cover and its seasonal
788 and interannual variability. Arch Fischereiwiss 39:89-109
- 789 Kock KH, Barrera-Oro E, Belchier M, Collins MA, Duhamel G, Hanchet S, Pshenichnov L, Welsford D,
790 Williams R (2012) The role of fish as predators of krill (*Euphausia superba*) and other pelagic
791 resources in the Southern Ocean. CCAMLR Sci 19:115-169
- 792 Korb RE, Whitehouse MJ, Ward P, Gordon M, Venables HJ, Poulton AJ (2012) Regional and seasonal
793 differences in microplankton biomass, productivity, and structure across the Scotia Sea:
794 Implications for the export of biogenic carbon. Deep-Sea Res Part II 59:67-77
- 795 Kozlov AN, Shust K, Zemsky AV (1991) Seasonal and inter-annual variability in the distribution of
796 *Electrona carlsbergi* in the Southern Polar Front area (the area to the north of South Georgia
797 is used as an example). CCAMLR Sel Sci Pap 7:337-368
- 798 Kozlov AN, Tarverdiyeva MI (1989) Feeding of different species of Myctophidae in different parts of
799 the Southern Ocean. J Ichthyol 29:160-167
- 800 Krause J, Ruxton GD (2002) Living in Groups. Oxford University Press, Oxford

- 801 Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters
802 near Antarctic Ice Edge Zones (AMERIEZ). *Polar Biol* 9:225-233
- 803 Linkowski TB (1983) *Electrona carlsbergi* (Taning, 1932), the principle component of a deep
804 scattering layer in the Pacific sector of the Antarctic Ocean. *Pol Polar Res* 4:71-78
- 805 Lubimova T, Shust K, Popkov V (1987) Specific features in the ecology of Southern Ocean
806 mesopelagic fish of the family Myctophidae. Nauka Press, Moscow
- 807 Main CE, Collins MA, Mitchell R, Belchier M (2009) Identifying patterns in the diet of mackerel icefish
808 (*Champscephalus gunnari*) at South Georgia using bootstrapped confidence intervals of a
809 dietary index. *Polar Biol* 32:569-581
- 810 McGinnis RF (1982) Biogeography of lanternfishes (Myctophidae) south of 30 °S. American
811 Geophysical Union, Washington DC
- 812 Moline MA, Claustre H, Frazer TK, Schofields O, Vernet M (2004) Alteration of the food web along
813 the Antarctic Peninsula in response to a regional warming trend. *Glob Change Biol* 10:1973-
814 1980
- 815 Moteki M, Horimoto N, Nagaiwa R, Amakasu K, Ishimaru T, Yamaguchi Y (2009) Pelagic fish
816 distribution and ontogenetic vertical migration in common mesopelagic species off Lutzow-
817 Holm Bay (Indian Ocean sector, Southern Ocean) during austral summer. *Polar Biol* 32:1461-
818 1472
- 819 Murphy EJ, Trathan PN, Watkins JL, Reid K, Meredith MP, Forcada J, Thorpe SE, Johnston NM,
820 Rothery P (2007a) Climatically driven fluctuations in Southern Ocean ecosystems. *Proc R Soc*
821 *B* 274:3057-3067
- 822 Murphy EJ, Watkins JL, Trathan PN, Reid K, Meredith MP, Thorpe SE, Johnston NM, Clarke A, Tarling
823 GA, Collins MA, Forcada J, Shreeve RS, Atkinson A, Korb R, Whitehouse MJ, Ward P,
824 Rodhouse PG, Enderlein P, Hirst AG, Martin AR, Hill SL, Staniland IJ, Pond DW, Briggs DR,
825 Cunningham NJ, Fleming AH (2007b) Spatial and temporal operation of the Scotia Sea
826 ecosystem: a review of large-scale links in a krill centred food web. *Phil Trans R Soc Lond B*
827 362:113-148
- 828 Naumov AG, Svetlov MF, Kozlov AN, Pinskaya IA (1981) Some features of the distribution and
829 feeding of *Electrona carlsbergi* (Taning) (Myctophidae) in the Scotia Sea. *J Ichthyol* 21:467-
830 472
- 831 Nicol S (2006) Krill, currents, and sea-ice: *Euphausia superba* and its changing environment.
832 *Bioscience* 56:111-120
- 833 Olsson O, North AW (1997) Diet of the King Penguin *Aptenodytes patagonicus* during three summers
834 at South Georgia. *Ibis* 139:504-512

- 835 Oven LS, Konstantinova MP, Shevchenko NF (1990) Aspects of of reproduction and feeding of
836 myctophids (Myctophidae) in the southwest Atlantic. J Ichthyol 30:115-127
- 837 Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid
838 fishes in the Southern Ocean. Mar Ecol Prog Ser 134:1-14
- 839 Pepin P (2013) Distribution and feeding of *Benthosema glaciale* in the western Labrador Sea: Fish-
840 zooplankton interaction and the consequence to calanoid copepod populations. Deep-Sea
841 Res Part I 75:119-134
- 842 Piatkowski U, Rodhouse PG, White MG, Bone DG, Symon C (1994) Nekton community of the Scotia
843 Sea as sampled by the RMT 25 during austral summer. Mar Ecol Prog Ser 112:13-28
- 844 Pusch C, Hulley PA, Kock KH (2004) Community structure and feeding ecology of mesopelagic fishes
845 in the slope waters of King George Island (South Shetland Islands, Antarctica). Deep-Sea Res
846 Part I 51:1685-1708
- 847 Reid K, Davis D, Staniland IJ (2006) Spatial and temporal variability in the fish diet of Antarctic fur
848 seal (*Arctocephalus gazella*) in the Atlantic sector of the Southern Ocean. Can J Zool
849 84:1025-1037
- 850 Reinhardt SB, Vanvleet ES (1986) Lipid composition of 22 species of Antarctic midwater zooplankton
851 and fish. Mar Biol 91:149-159
- 852 Ross RM, Quetin LB, Kirsch E (1988) Effect of temperature on development times and survival of
853 early larval stages of *Euphausia superba* Dana. J Exp Mar Biol Ecol 121:55-71
- 854 Ross ST (1986) Resource partitioning in fish assemblages- A review of field studies. Copeia:352-388
- 855 Rowedder U (1979a) Feeding ecology of the myctophid *Electrona antarctica* (Gunther, 1878)
856 (Teleostei). Meeresforschung 27:252-263
- 857 Rowedder U (1979b) Some aspects of the biology of *Electrona antarctica* (Gunther, 1878) (Family
858 Myctophidae). Meeresforschung 27:244-251
- 859 Shreeve RS, Collins MA, Tarling GA, Main CE, Ward P, Johnston NM (2009) Feeding ecology of
860 myctophid fishes in the northern Scotia Sea. Mar Ecol Prog Ser 386:221-236
- 861 Shreeve RS, Ward P, Whitehouse MJ (2002) Copepod growth and development around South
862 Georgia: relationships with temperature, food and krill. Mar Ecol Prog Ser 233:169-183
- 863 Stowasser G, Atkinson A, McGill RAR, Phillips RA, Collins MA, Pond DW (2012) Food web dynamics in
864 the Scotia Sea in summer: A stable isotope study. Deep-Sea Res Part II 59:208-221

- 865 Tarling GA, Cuzin-Roudy J, Thorpe SE, Shreeve RS, Ward P, Murphy EJ (2007) Recruitment of
866 Antarctic krill *Euphausia superba* in the South Georgia region: adult fecundity and the fate of
867 larvae. Mar Ecol Prog Ser 331:161-179
- 868 Venables H, Meredith MP, Atkinson A, Ward P (2012) Fronts and habitat zones in the Scotia Sea.
869 Deep-Sea Res Part II 59:14-24
- 870 Ward P, Atkinson A, Tarling G (2012) Mesozooplankton community structure and variability in the
871 Scotia Sea: A seasonal comparison. Deep-Sea Res Part II 59:78-92
- 872 Ward P, Shreeve R, Tarling GA (2006) The autumn mesozooplankton community at South Georgia:
873 biomass, population structure and vertical distribution. Polar Biol 29:950-962
- 874 Whitehouse MJ, Atkinson A, Korb RE, Venables HJ, Pond DW, Gordon M (2012) Substantial primary
875 production in the land-remote region of the central and northern Scotia Sea. Deep-Sea Res
876 Part II 59:47-56
- 877 Whitehouse MJ, Meredith MP, Rothery P, Atkinson A, Ward P, Korb RE (2008) Rapid warming of the
878 ocean around South Georgia, Southern Ocean, during the 20th century: Forcings,
879 characteristics and implications for lower trophic levels. Deep-Sea Res Part I 55:1218-1228
- 880 Zasel'sliy VS, Kudrin BD, Poletayev VA, Chechenin SC (1985) Some features of the biology of
881 *Electrona carlsbergi* (Taning) (Myctophidae) in the Atlantic sector of the Antarctic. J Ichthyol
882 25:163-166
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885

886 **Figure legends**

887

888 **Fig. 1** Map of the Scotia Sea and the distribution of *Electrona antarctica* (yellow) and
889 *Electrona carlsbergi* (red) density during the surveys. The size of the pies is proportional to
890 the log total of fish densities per net. Blue crosses denote non-targeted net haul positions.
891 Sampling stations are: Southern Scotia Sea (SSS), Western Scotia Sea (WSS), Mid-Scotia
892 Sea (MSS), North Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF). Mean frontal
893 positions determined during the cruises from dynamic height data (Venables et al. 2012) are:
894 northern Polar Front (N-PF), southern Polar Front (S-PF), Southern Antarctic Circumpolar
895 Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB-
896 ACC). The heavy black line shows the position of the 15% ice-edge cover for 24/10/2006 and
897 for 15/01/2008. The ice-edge occurred well south of the transect during autumn 2009
898 (JR200). Bathymetry data are taken from the GEBCO_08 grid (version 20091120,
899 www.gebco.net)

900

901 **Fig. 2** Mean vertical distribution of (a) *Electrona antarctica* and (b) *Electrona carlsbergi* in
902 the Scotia Sea by day (open bars) and by night (filled bars) during the three surveys. No net
903 hauls were collected during daytime on the autumn survey (JR200)

904 **Fig. 3.** Length-frequency (mm, SL) distributions of (a) *Electrona antarctica* and (b)
905 *Electrona carlsbergi* in the Scotia Sea during the three surveys. Mixture distributions (solid
906 lines) were determined using CMIX (see methods). The progression of identified cohorts
907 through time is aided by solid arrows

908 **Fig. 4** Mean standard length (± 2 standard error) of (a) *Electrona antarctica* and (b) *Electrona*
909 *carlsbergi* in each depth zone sampled by the RMT25 in the Scotia Sea. Filled circles and
910 triangles denote adult males and females, respectively. The number of samples measured in
911 each zone is also given

912 **Fig. 5** Regional comparisons of the gender structure and gonad maturity status of (a)
913 *Electrona antarctica* and (b) *Electrona carlsbergi* in the Scotia Sea. The number of samples
914 analysed in each zone is also shown. Both males and females are included in the population
915 maturity structure

916 **Fig. 6** Variation in *Electrona antarctica* diet in the Scotia Sea by (a) region, (b) survey, (c)
917 size class and (d) gonad maturity status illustrated by mean %IRI of prey categories (%IRI_{DC})
918 with 95% confidence intervals (error bars). AMP: amphipods, COP: copepods, CRU:
919 unidentified crustaceans, EUP: euphausiids, OTH: other taxa (Decapoda, Chordata,
920 Ostracoda, Urochordata, Mollusca, Unidentified crustaceans and Other taxa)

921 **Fig. 7** Variations in *Electrona. carlsbergi* diet in the Scotia Sea by (a) region, (b) survey, (c)
922 size class and (d) gonad maturity status illustrated by mean %IRI of prey categories (%IRI_{DC})
923 with 95% confidence intervals (error bars). MET: *Metridia* spp., RHI: *Rhincalanus gigas*,
924 COP: copepods (e.g. *Calanus* spp., *Paraeuchaeta* spp., *Oncaea* sp., unidentified copepods),
925 OTH: other taxa (Amphipoda, Euphausiacea, Urochordata, Mollusca, Unidentified
926 crustaceans and Other taxa)

927 **Fig. 8** Mean abundance of the dominant prey taxa sampled during the surveys. (a) Copepoda,
928 (b) Euphausiacea and (c) Amphipoda. Copepods were collected with a Longhurst-Hardy
929 Plankton Recorder (LHPR) for all species, except *Metridia* spp. and *Oncaea* spp. that were
930 collect with a 200 µm Bongo net. These data are summarised from Ward et al. (2012).
931 Euphausiids and amphipods were obtained from the RMT25 net deployed for mesopelagic
932 fish

% IRI _{DC} comparison	Pooled samples	Category	<i>E. antarctica</i> (n)	<i>E. carlsbergi</i> (n)
Regional	All surveys	SSS	228	0
		MSS	83	51
		WSS	3	0
		NSS	8	102
		GB	133	2
		PF	30	30
Cruises (seasons)	All regions	JR161 (spring)	162	120
		JR177 (summer)	203	35
		JR200 (autumn)	120	30
Sex (adults)	All data	Male	140	80
		Female	316	79
Stage	All data	Juvenile	14	0
		Gonad immature	52	115
		Gonad developing	194	45
		Gonad mature	76	0
Size	All data	Low percentile	85	41
		Mid percentile	301	113
		Upper percentile	99	31

934

935 **Table 1** The number of *Electrona antarctica* and *Electrona carlsbergi* stomach samples that
936 were pooled for comparisons of %IRI_{DC} between regions, cruises (seasons), depth zone and
937 ontogenetic status. Comparisons were not performed for categories with <30 stomachs. The
938 percentile size categories refer to the portions of the composite length-frequency distributions
939 (Fig. 3), where Low percentile = size classes below $\mu - \sigma$, Mid percentile = size classes within
940 $\mu \pm \sigma$, and Upper percentile = size classes above $\mu + \sigma$

Region	JR161			JR177			JR200		
	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range
<i>E. antarctica</i>									
SSS	17	0.25	0.00-1.26	19	0.41	0.00-1.29	10	0.49	0.05-1.85
WSS	8	0.01	0.00-0.06	1	0.00	0.00	0	-	-
MSS	4	0.12	0.12-0.23	9	0.17	0.00-0.50	12	0.19	0.04-0.56
NSS	8	0.01	0.00-0.04	8	0.07	0.00-0.09	4	0.03	0.02-0.11
GB	5	0.09	0.00-0.18	10	0.14	0.00-0.39	2	0.07	0.02-0.11
PF	8	0.004	0.00-0.03	10	0.00	0.00	8	0.05	0.00-0.21
All	50	0.09	0.00-1.26	57	0.21	0.00-1.29	36	0.21	0.00-1.85
<i>E. carlsbergi</i>									
SSS	17	0.00	0.00	19	0.00	0.00	10	0.00	0.00
WSS	8	0.05	0.00-0.21	1	0.02	0.02	0	-	-
MSS	4	0.00	0.00	9	0.08	0.00-0.39	12	0.04	0.00-0.22
NSS	8	0.42	0.00-2.13	8	0.02	0.00-0.08	4	0.00	0.00
GB	5	0.003	0.00-0.02	10	0.001	0.00-0.01	2	0.00	0.00
PF	8	0.003	0.00-0.02	10	0.00	0.00	8	0.03	0.00-0.28
All	50	0.11	0.00-2.13	57	0.03	0.00-0.39	36	0.02	0.00-0.28

941

942 **Table 2** Mean abundance (ind. 1000 m⁻³) of *Electrona antarctica* and *Electrona carlsbergi* in
943 the Scotia Sea. *N* is the number of net hauls

Region	JR161			JR177			JR200		
	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range	<i>n</i>	Mean	Range
<i>E. antarctica</i>									
SSS	17	1.84	0.00-8.51	19	2.60	0.00-9.00	10	2.35	0.56-6.24
WSS	8	0.08	0.00-0.53	1	0.00	0.00	0	-	-
MSS	4	0.68	0.23-1.19	9	0.87	0.00-3.08	12	0.93	0.04-2.30
NSS	8	0.04	0.00-0.16	8	0.39	0.00-0.88	4	0.07	0.02-0.15
GB	5	0.47	0.00-0.87	10	0.79	0.00-2.22	2	0.30	0.26-0.33
PF	8	0.01	0.00-0.08	10	0.00	0.00	8	0.42	0.00-1.92
All	50	0.62	0.00-8.51	57	1.28	0.00-9.00	36	1.04	0.00-6.24
<i>E. carlsbergi</i>									
SSS	17	0.00	0.00	19	0.00	0.00	10	0.00	0.00
WSS	8	0.32	0.00-1.21	1	1.39	1.39	0	-	-
MSS	4	0.00	0.00	9	0.52	0.00-2.38	12	0.29	0.00-1.44
NSS	8	3.33	0.00-15.53	8	0.16	0.00-0.62	4	0.00	0.00
GB	5	0.02	0.00-0.11	10	0.01	0.00-0.11	2	0.00	0.00
PF	8	0.01	0.00-0.10	10	0.00	0.00	8	0.21	0.00-2.34
All	50	0.80	0.00-15.53	57	0.16	0.00-2.38	36	0.15	0.00-2.34

944

945 **Table 3** Mean biomass (g 1000 m⁻³) of *Electrona antarctica* and *Electrona carlsbergi* in the
946 Scotia Sea. *N* is the number of net hauls

947

948

Prey	<i>E. antarctica</i>				<i>E. carlsbergi</i>			
	%F	%M	%N	%IRI	%F	%M	%N	%IRI
Amphipoda								
<i>Themisto gaudichaudii</i>	22.27	27.09	13.36	30.05	10.81	7.67	1.86	1.15
<i>Primno macropa</i>	0.21	0.07	0.05	0.00	0.00	0.00	0.00	0.00
<i>Cyphocaris richardi</i>	0.21	0.00	0.05	0.00	0.00	0.00	0.00	0.00
<i>Hyperia</i> spp.	0.21	0.27	0.05	0.00	0.00	0.00	0.00	0.00
<i>Vibilia</i> spp.	0.62	0.22	0.15	0.01	0.00	0.00	0.00	0.00
Unidentified amphipod	0.62	0.13	0.15	0.01	1.62	0.80	0.11	0.02
Total	23.30	27.78	13.81	15.16	12.43	8.46	1.98	0.98
Copepoda								
<i>Aetideus</i> spp.	1.24	0.03	0.30	0.01	2.16	0.06	0.14	0.00
<i>Calanoides acutus</i>	3.09	0.16	1.55	0.18	7.03	0.59	0.64	0.10
<i>Calanus propinquus</i>	2.68	0.18	1.40	0.14	3.78	0.26	0.20	0.02
<i>Calanus simillimus</i>	2.27	0.07	0.60	0.05	17.84	1.03	2.09	0.62
<i>Candacia</i> sp.	0.82	0.03	0.25	0.01	2.70	0.11	0.11	0.01
<i>Clausocalanus</i> spp.	0.00	0.00	0.00	0.00	4.86	0.09	0.34	0.02
<i>Ctenocalanus</i> spp.	0.00	0.00	0.00	0.00	0.54	0.01	0.02	0.00
<i>Drepanopus forcipatus</i>	0.00	0.00	0.00	0.00	0.54	0.01	0.02	0.00
<i>Eucalanus</i> spp.	0.41	0.01	0.10	0.00	7.57	0.97	0.89	0.16
<i>Gaidius</i> spp.	2.27	0.05	0.55	0.04	0.54	0.01	0.02	0.00
<i>Haloptilus</i> spp.	0.00	0.00	0.00	0.00	0.54	0.01	0.02	0.00
<i>Heterorhabdus</i> spp.	0.82	0.02	0.20	0.01	3.78	0.11	0.25	0.02
<i>Metridia</i> spp.	26.80	0.79	16.65	15.59	48.11	2.24	8.38	5.70
<i>Oithona</i> spp.	0.00	0.00	0.00	0.00	1.62	0.09	0.30	0.01
<i>Oncaea</i> spp.	0.00	0.00	0.00	0.00	28.11	2.17	13.77	5.00
<i>Paraeuchaeta</i> spp.	8.45	0.91	3.14	1.10	22.16	4.22	2.32	1.53
<i>Pleuromamma robusta</i>	3.30	0.09	0.95	0.11	9.73	0.55	0.73	0.11
<i>Rhincalanus gigas</i>	5.15	0.59	4.09	0.80	69.73	50.37	54.78	81.78
<i>Scolecithricella</i> spp.	0.00	0.00	0.00	0.00	1.62	0.06	0.09	0.00
Unidentified copepods	2.47	0.30	0.60	0.04	3.24	0.15	0.48	0.01
Total	43.51	3.23	30.36	22.86	82.70	63.09	85.59	93.29
Decapoda								
Unidentified decapods	0.21	1.12	0.05	0.01	0.00	0.00	0.00	0.00
Total	0.21	1.12	0.05	0.00	0.00	0.00	0.00	0.00
Euphausiacea								
<i>Euphausia frigida</i>	1.44	1.20	0.60	0.09	1.62	0.82	0.09	0.02
<i>Euphausia superba</i>	14.85	51.11	35.74	43.01	1.62	5.32	0.07	0.10
<i>Euphausia triacantha</i>	0.21	0.05	0.05	0.00	0.00	0.00	0.00	0.00
<i>Thysanoessa</i> spp.	4.95	2.47	2.39	0.80	15.68	5.50	1.32	1.19
Unidentified euphausiids	15.67	6.32	4.19	4.50	11.35	4.24	1.23	0.69
Total	36.49	61.14	42.97	59.44	28.65	15.88	2.70	4.04
Chordata								
Unidentified fish	1.24	0.33	0.30	0.01	2.70	0.30	0.14	0.01
Total	1.24	0.33	0.30	0.01	2.70	0.30	0.14	0.01

Ostracoda								
Unidentified ostracod	8.25	0.14	2.24	0.66	5.95	0.13	0.25	0.03
Total	8.25	0.14	2.24	0.31	5.95	0.13	0.25	0.02
Mollusca								
Unidentified pteropod	5.36	2.89	4.54	1.33	12.43	5.38	4.52	0.87
<i>Limacina</i> spp.	0.21	0.82	1.89	0.02	0.00	0.00	0.00	0.00
Unidentified Cephalopoda	0.00	0.00	0.00	0.00	1.08	0.10	0.05	0.00
Total	5.57	3.71	6.43	0.88	13.51	5.49	4.57	1.03
Urochordata								
Salps	0.62	0.02	0.25	0.01	8.65	4.29	2.93	0.70
Total	0.62	0.02	0.25	0.00	8.65	4.29	2.93	0.47
Unidentified crustacean								
Total	14.23	2.50	3.44	1.32	7.03	2.11	0.30	0.12
Other taxa								
Polychaeta	0.21	0.02	0.05	0.00	0.00	0.00	0.00	0.00
Chaetognatha	0.21	0.00	0.05	0.00	0.54	0.02	0.02	0.00
Siphonophora	0.00	0.00	0.00	0.00	1.08	0.22	1.52	0.02
Gelatinous mass	0.21	0.00	0.05	0.00	0.00	0.00	0.00	0.00
Total	0.62	0.02	0.15	0.00	1.62	0.25	1.55	0.02
Number of full stomachs	485				185			
Number of empty stomachs	205				11			

Table 4 All prey items identified from *Electrona antarctica* and *Electrona carlsbergi* stomachs collected in the Scotia Sea.

Figures

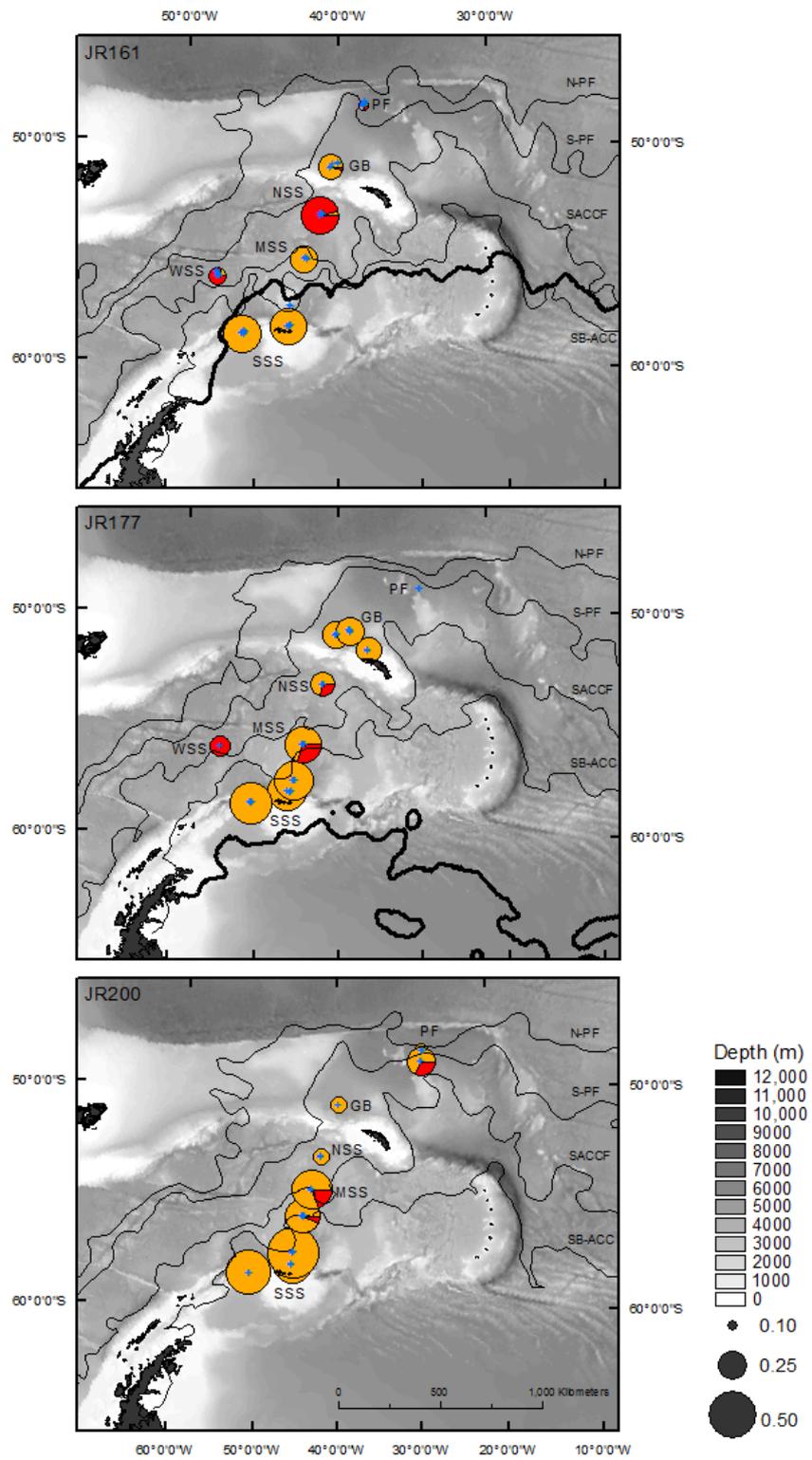


Fig. 1

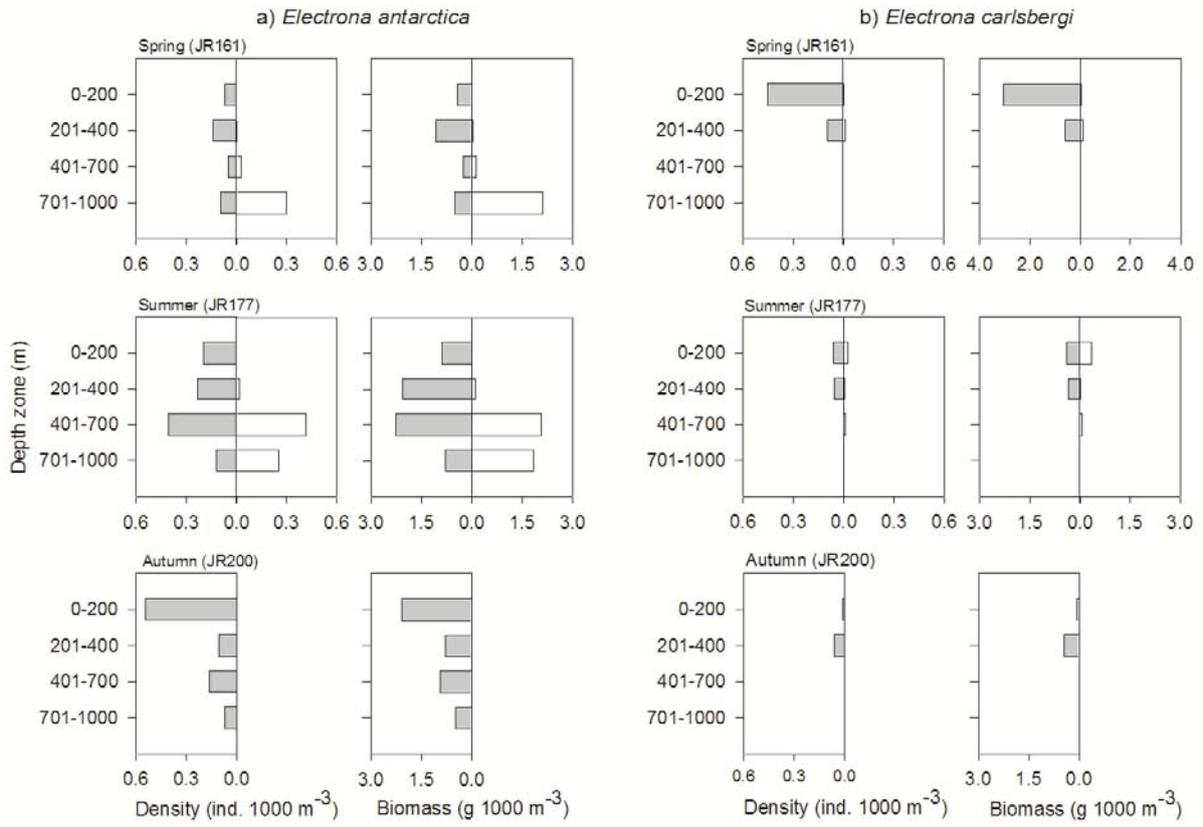


Fig. 2

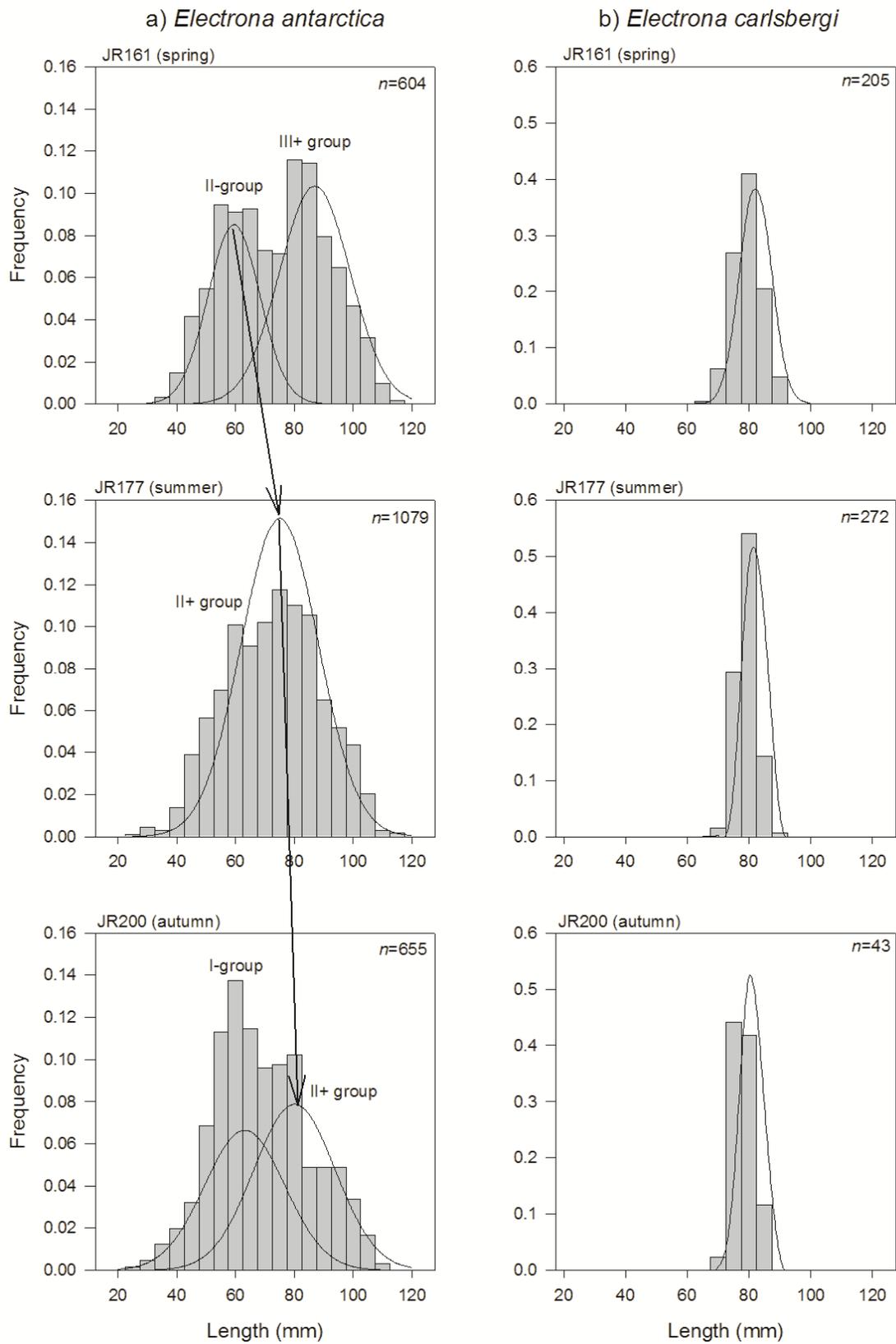


Fig. 3

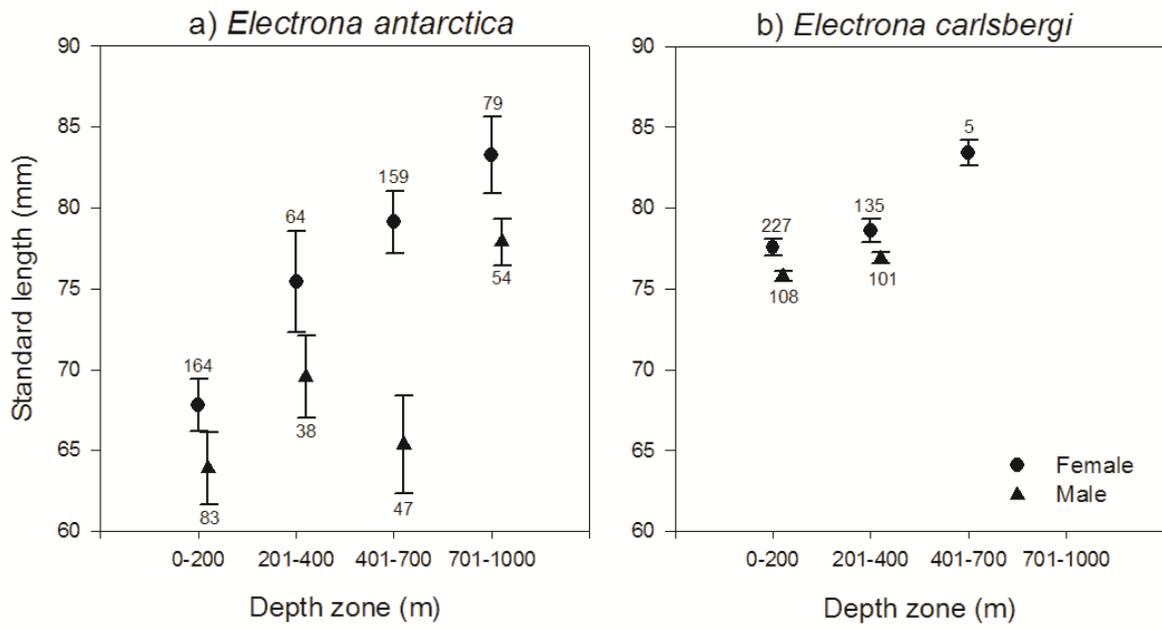


Fig. 4

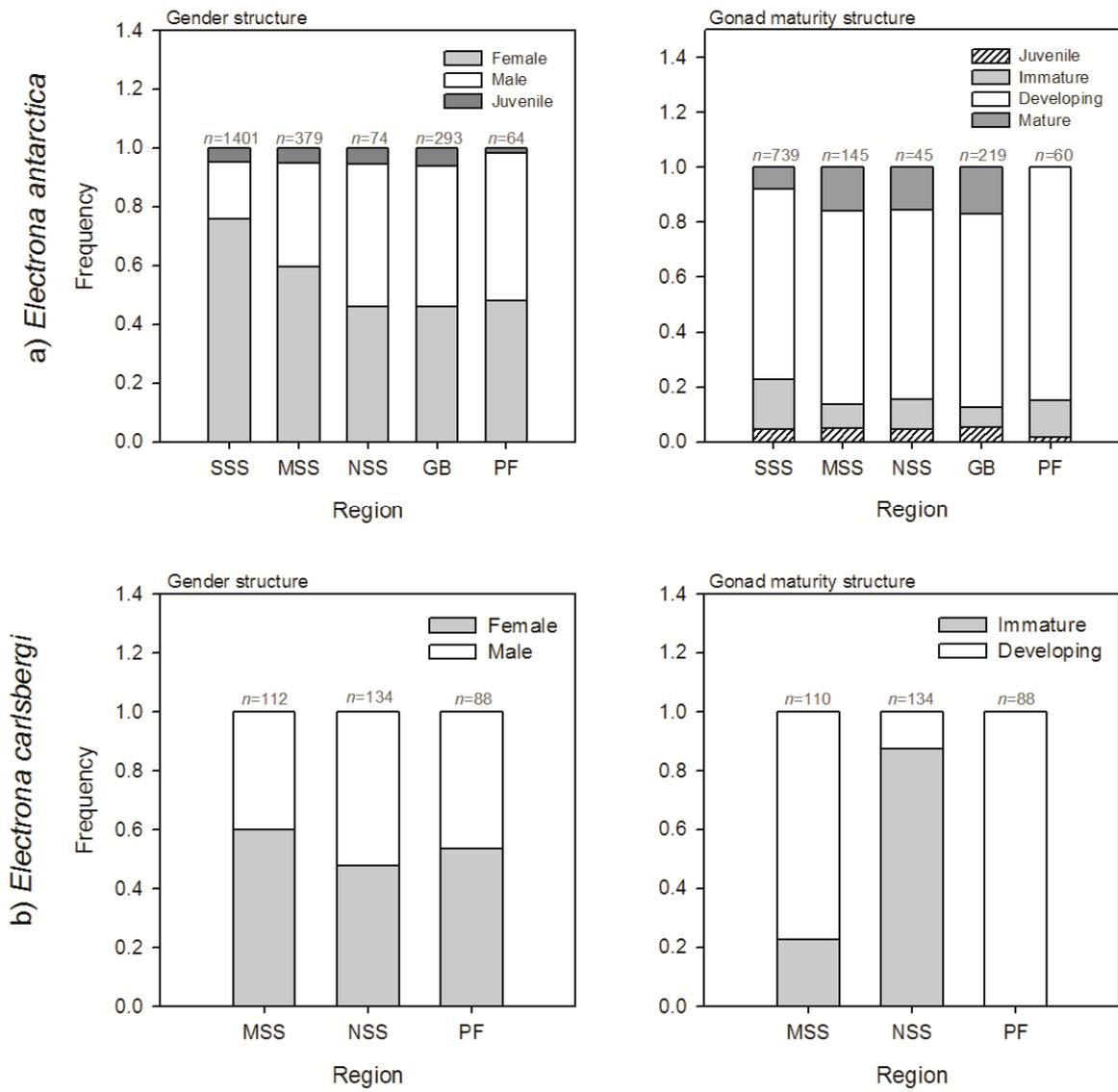


Fig. 5

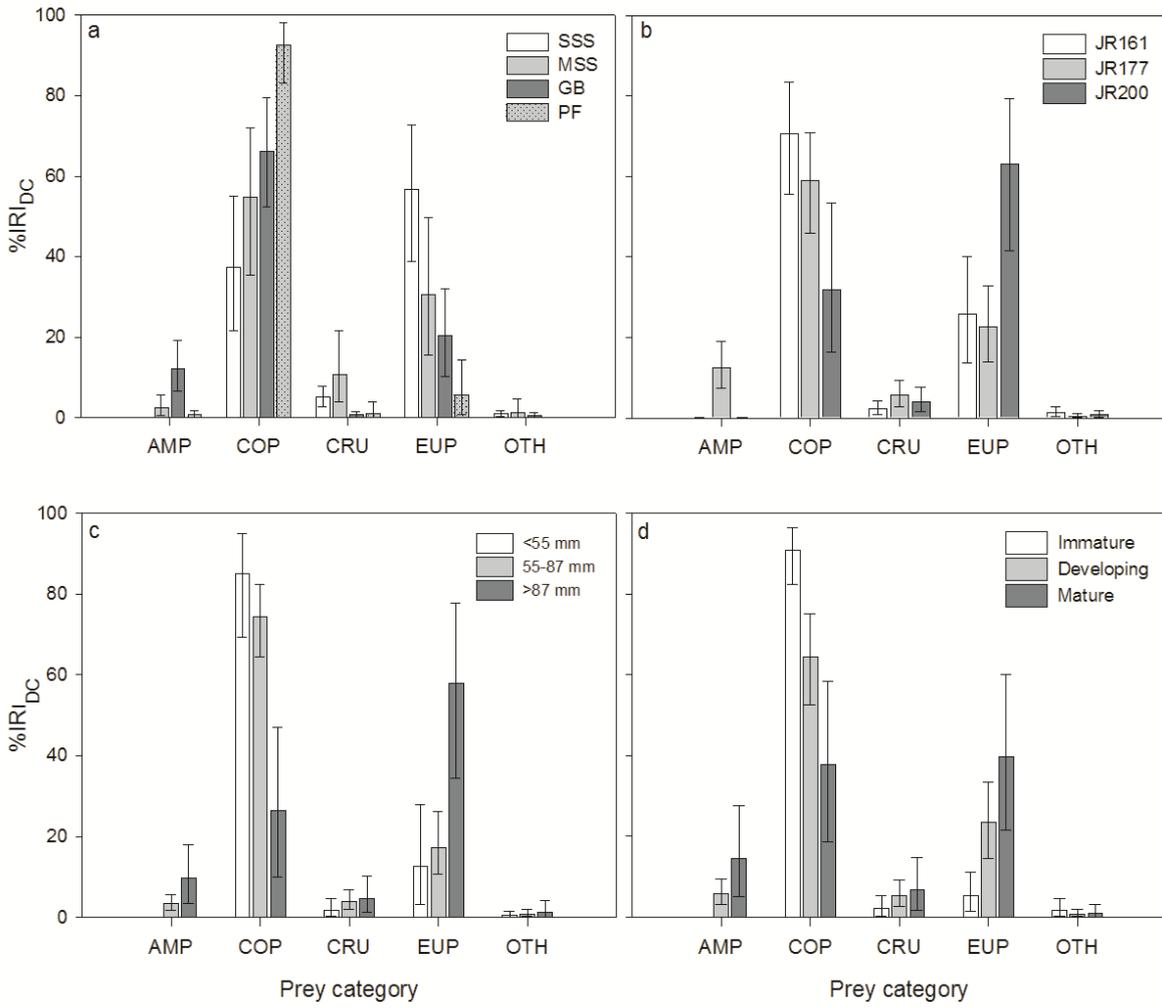


Fig. 6

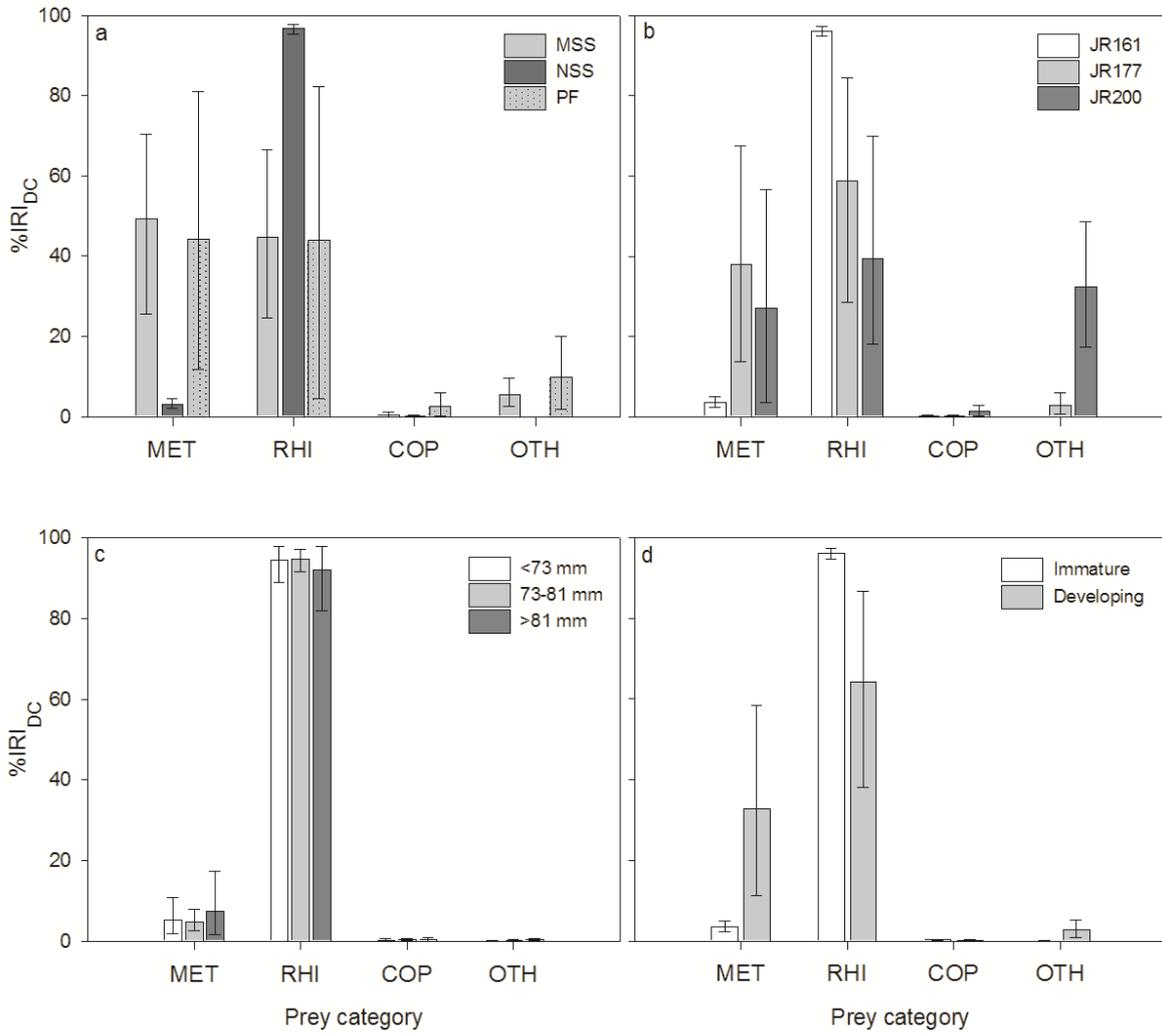


Fig. 7

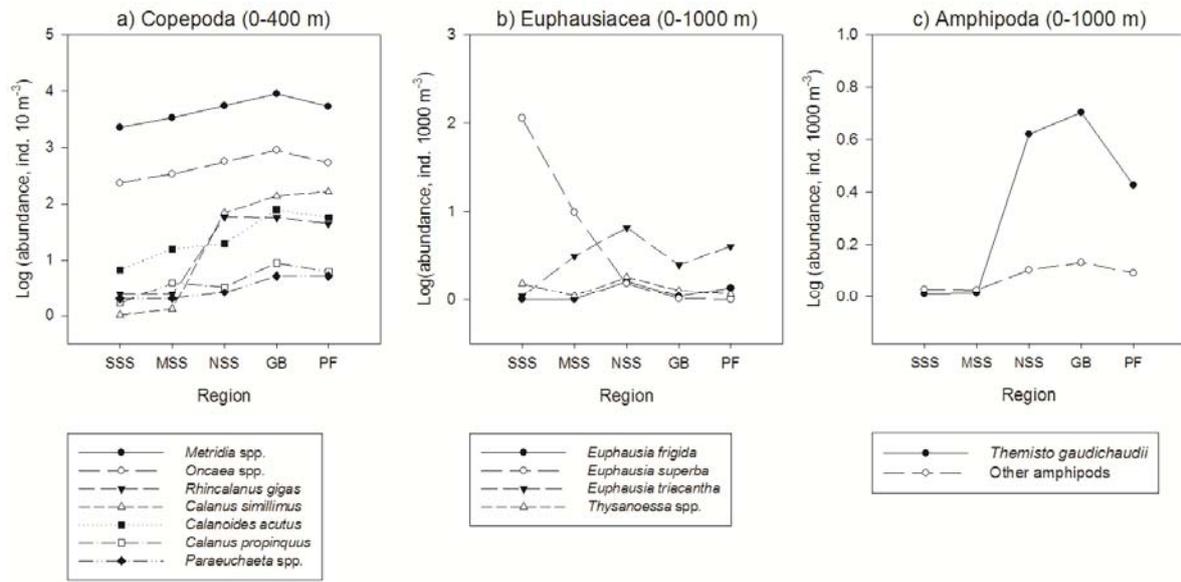


Fig. 8