

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<sup>-3</sup>), 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<sup>-3</sup>.  
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 m<sup>2</sup>  
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<sub>DC</sub> 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<sub>DC</sub> 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<sup>-3</sup>. 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<sup>-3</sup> 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<sup>-3</sup>). 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<sup>-3</sup>. 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<sup>-3</sup> and a biomass of 0.62-1.28 g 1000 m<sup>-3</sup> (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<sup>-3</sup> and 1.84-2.60 g 1000  
264 m<sup>-3</sup>). 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<sup>-3</sup> and <0.39 g 1000 m<sup>-3</sup>) and PF (<0.05 ind. 1000 m<sup>-3</sup> and <0.42 g 1000 m<sup>-3</sup>)  
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<sup>-3</sup> and 0.62 g 1000 m<sup>-3</sup>) and biomass  
273 was greatest during the summer (survey mean: 1.28 g 1000 m<sup>-3</sup>), although summer and  
274 autumn densities were very similar (0.21 ind. 1000 m<sup>-3</sup>).

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<sup>-3</sup> and 3.33 g 1000 m<sup>-3</sup>, 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<sup>-3</sup> and <0.02 g m<sup>-3</sup>) and at the PF  
281 (<0.02 ind. 1000 m<sup>-3</sup> and <0.21 g 1000 m<sup>-3</sup>) 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<sup>-3</sup>  
284 and 0.80 g 1000 m<sup>-3</sup>), whilst both densities and biomass were very similar during the summer  
285 and autumn surveys (cruise means: ~0.03 ind. 1000 m<sup>-3</sup> and ~0.16 g 1000 m<sup>-3</sup>).

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<sub>DC</sub>  
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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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](http://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 ( $\pm 2$  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<sub>DC</sub>)  
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<sub>DC</sub>)  
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 <sub>DC</sub> 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<sub>DC</sub> 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
<b><i>E. antarctica</i></b>									
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
<b><i>E. carlsbergi</i></b>									
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<sup>-3</sup>) 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
<b><i>E. antarctica</i></b>									
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
<b><i>E. carlsbergi</i></b>									
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<sup>-3</sup>) of *Electrona antarctica* and *Electrona carlsbergi* in the  
946 Scotia Sea. *N* is the number of net hauls

947

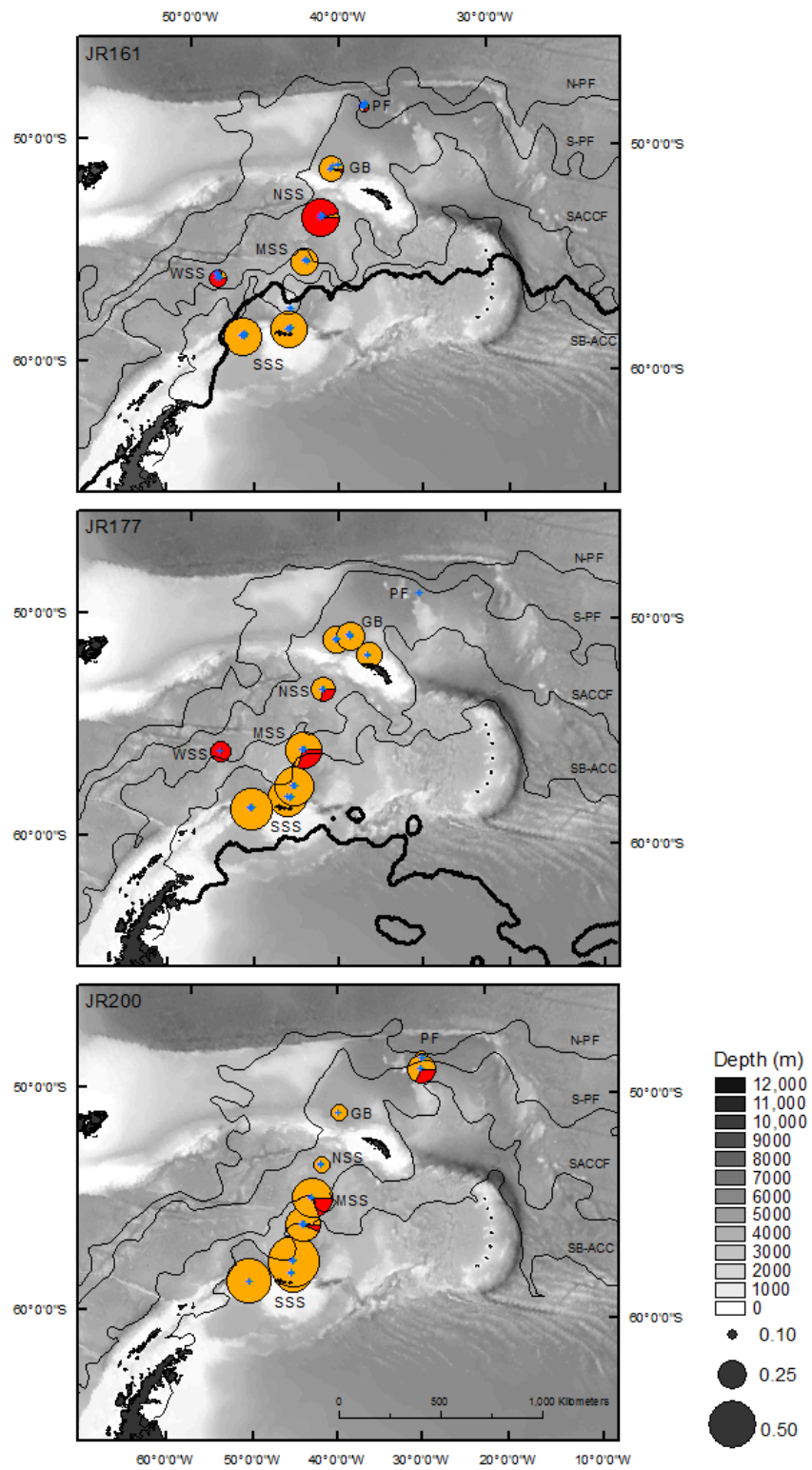
948

Prey	<i>E. antarctica</i>				<i>E. carlsbergi</i>			
	%F	%M	%N	%IRI	%F	%M	%N	%IRI
<b>Amphipoda</b>								
<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	<b>23.30</b>	<b>27.78</b>	<b>13.81</b>	<b>15.16</b>	<b>12.43</b>	<b>8.46</b>	<b>1.98</b>	<b>0.98</b>
<b>Copepoda</b>								
<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	<b>43.51</b>	<b>3.23</b>	<b>30.36</b>	<b>22.86</b>	<b>82.70</b>	<b>63.09</b>	<b>85.59</b>	<b>93.29</b>
<b>Decapoda</b>								
Unidentified decapods	0.21	1.12	0.05	0.01	0.00	0.00	0.00	0.00
Total	<b>0.21</b>	<b>1.12</b>	<b>0.05</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>
<b>Euphausiacea</b>								
<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	<b>36.49</b>	<b>61.14</b>	<b>42.97</b>	<b>59.44</b>	<b>28.65</b>	<b>15.88</b>	<b>2.70</b>	<b>4.04</b>
<b>Chordata</b>								
Unidentified fish	1.24	0.33	0.30	0.01	2.70	0.30	0.14	0.01
Total	<b>1.24</b>	<b>0.33</b>	<b>0.30</b>	<b>0.01</b>	<b>2.70</b>	<b>0.30</b>	<b>0.14</b>	<b>0.01</b>

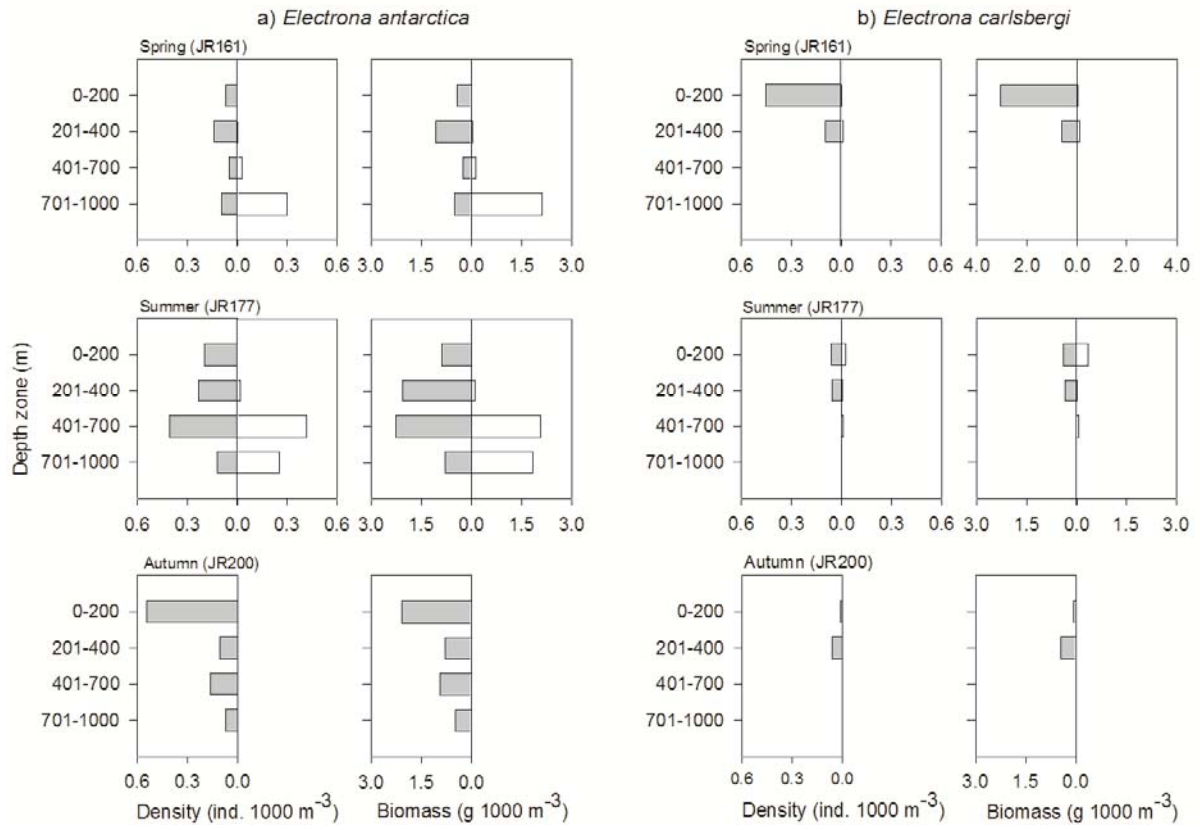
<b>Ostracoda</b>								
Unidentified ostracod	8.25	0.14	2.24	0.66	5.95	0.13	0.25	0.03
Total	<b>8.25</b>	<b>0.14</b>	<b>2.24</b>	<b>0.31</b>	<b>5.95</b>	<b>0.13</b>	<b>0.25</b>	<b>0.02</b>
<b>Mollusca</b>								
Unidentified pteropod	5.36	2.89	4.54	1.33	12.43	5.38	4.52	0.87
<i>Limacina</i> spp.	0.21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

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

# Figures

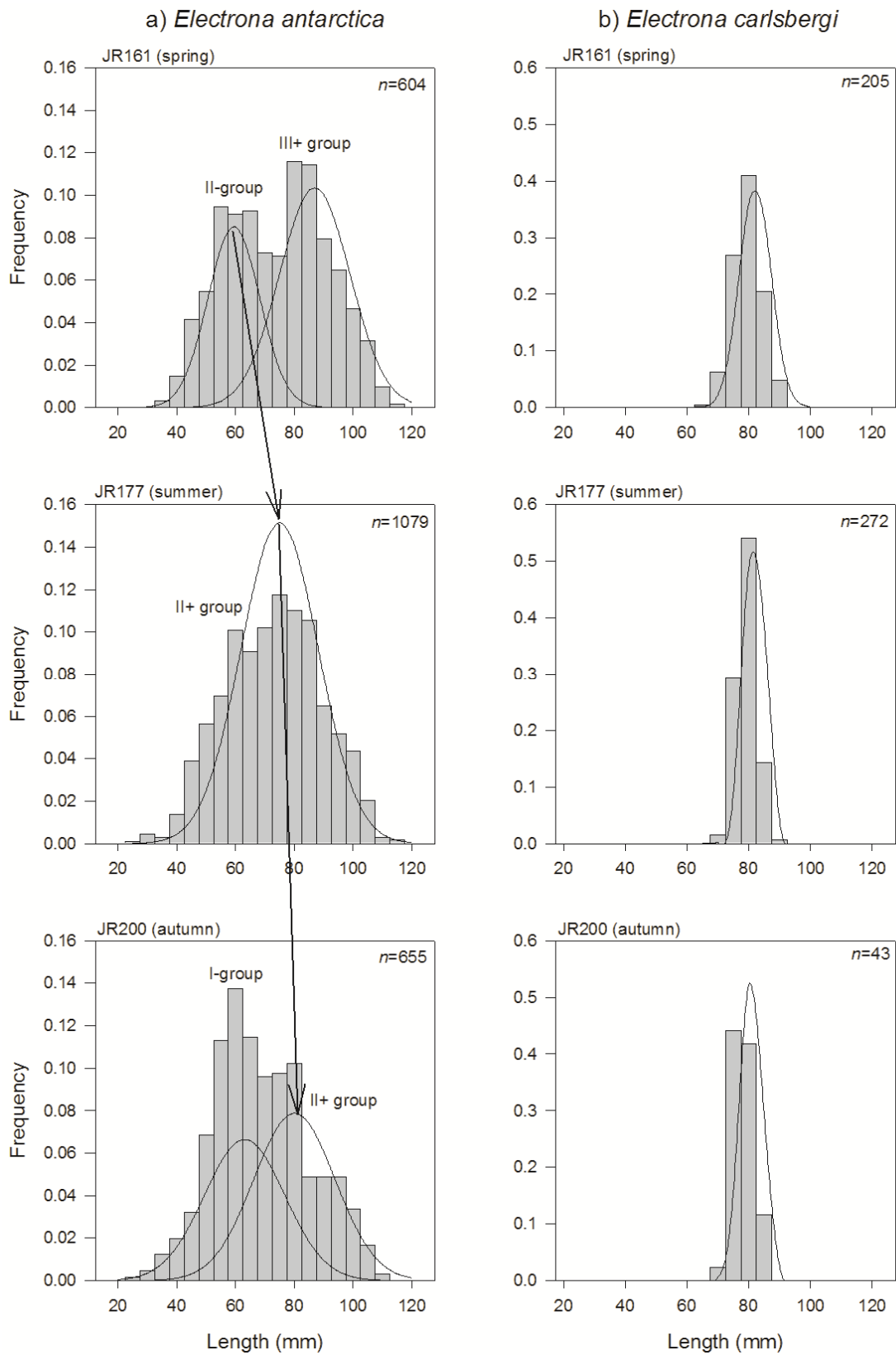


**Fig. 1**

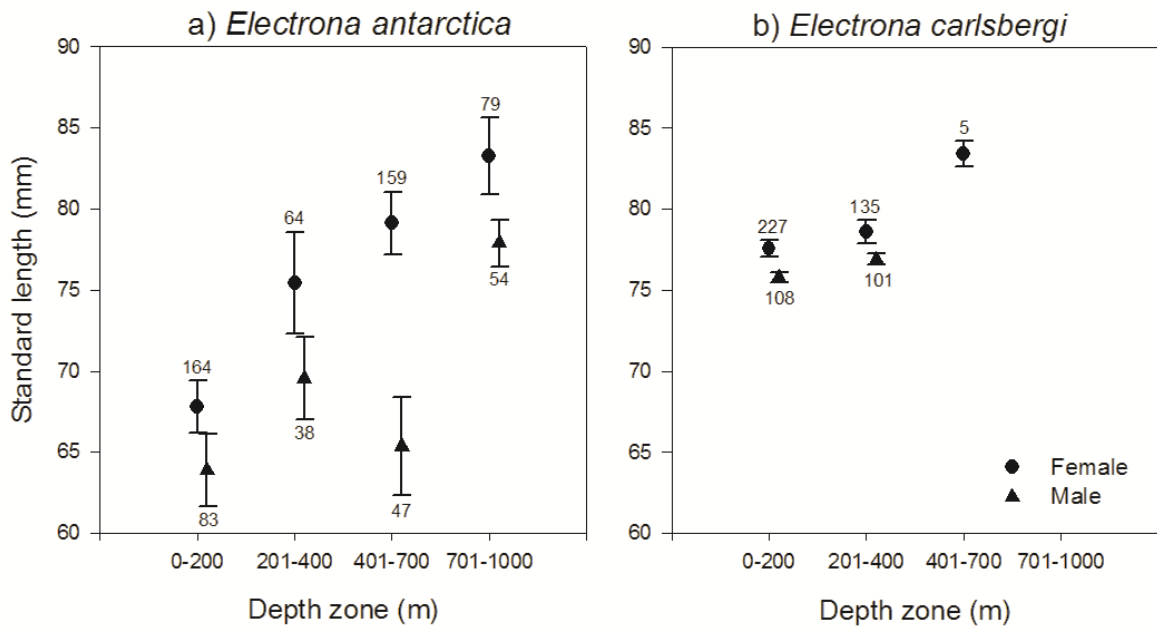


**Fig. 2**

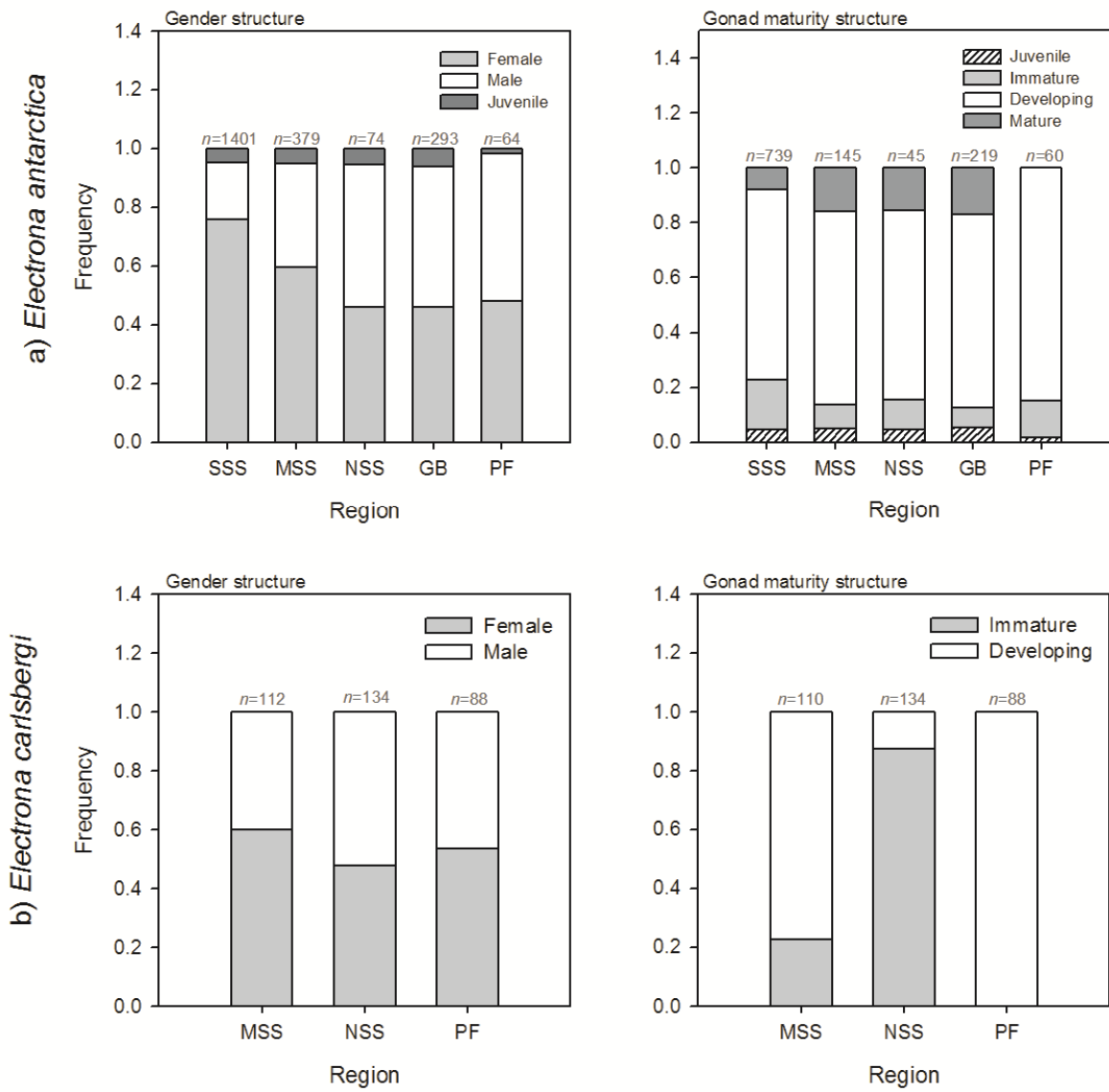




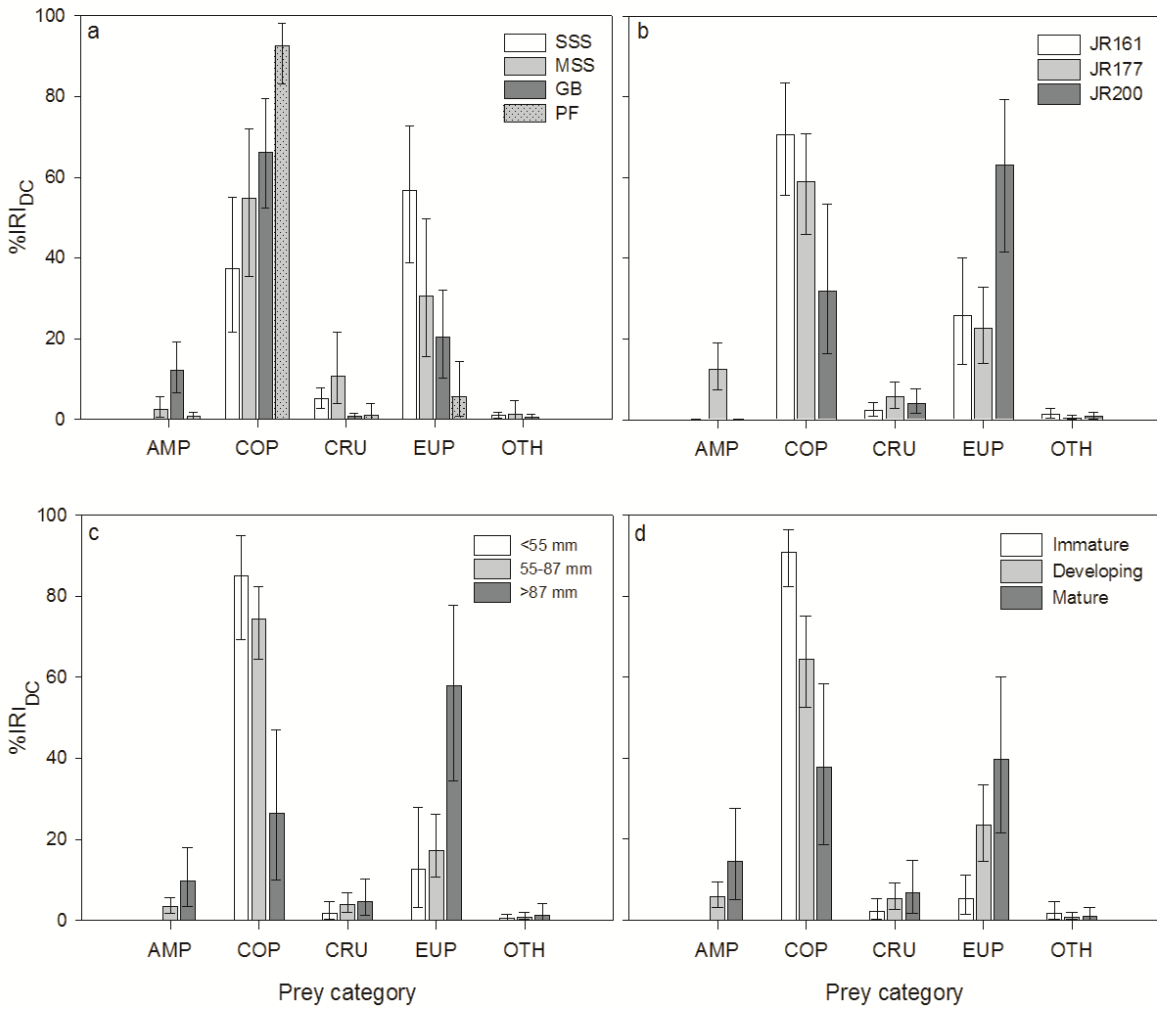
**Fig. 3**



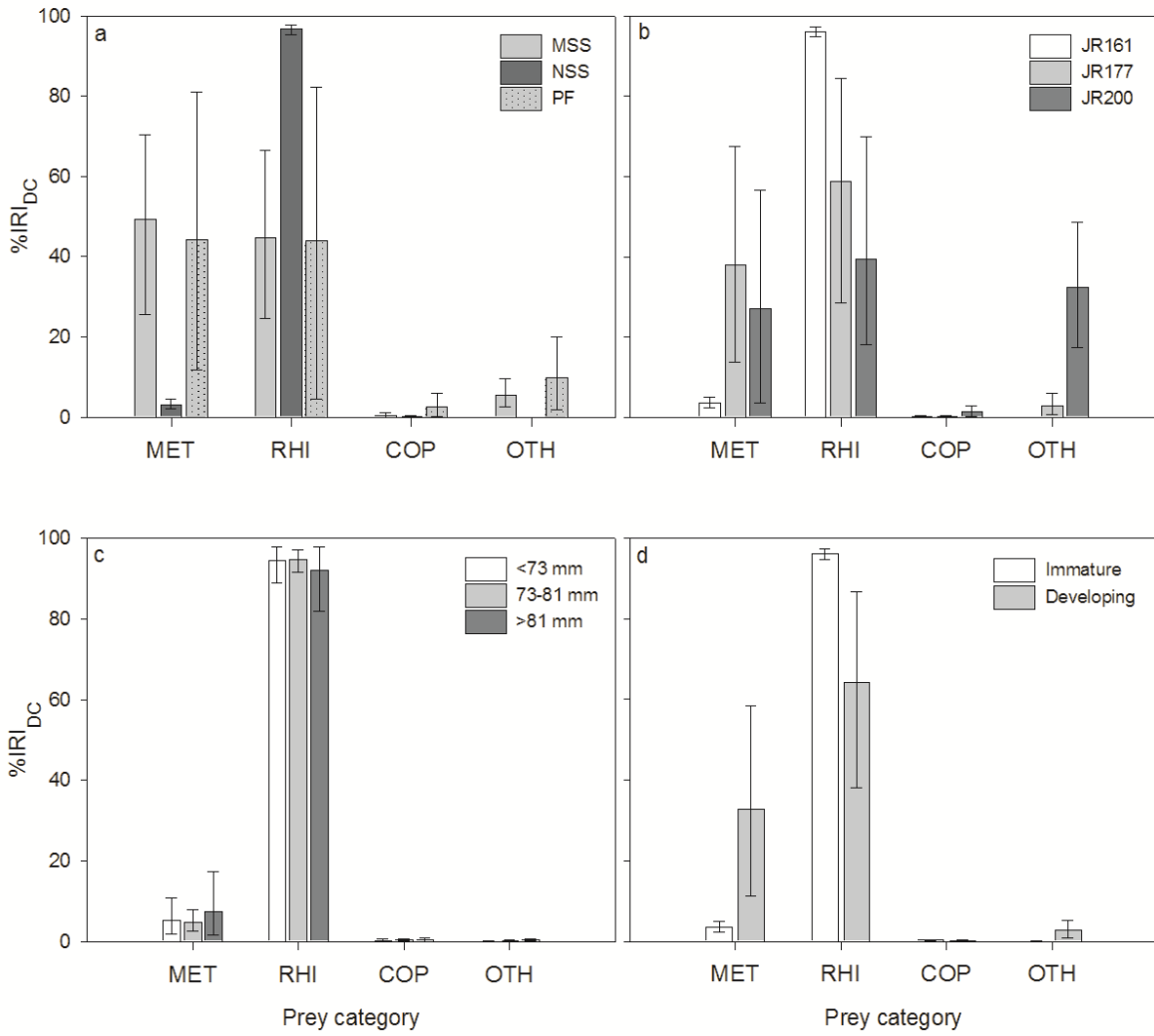
**Fig. 4**



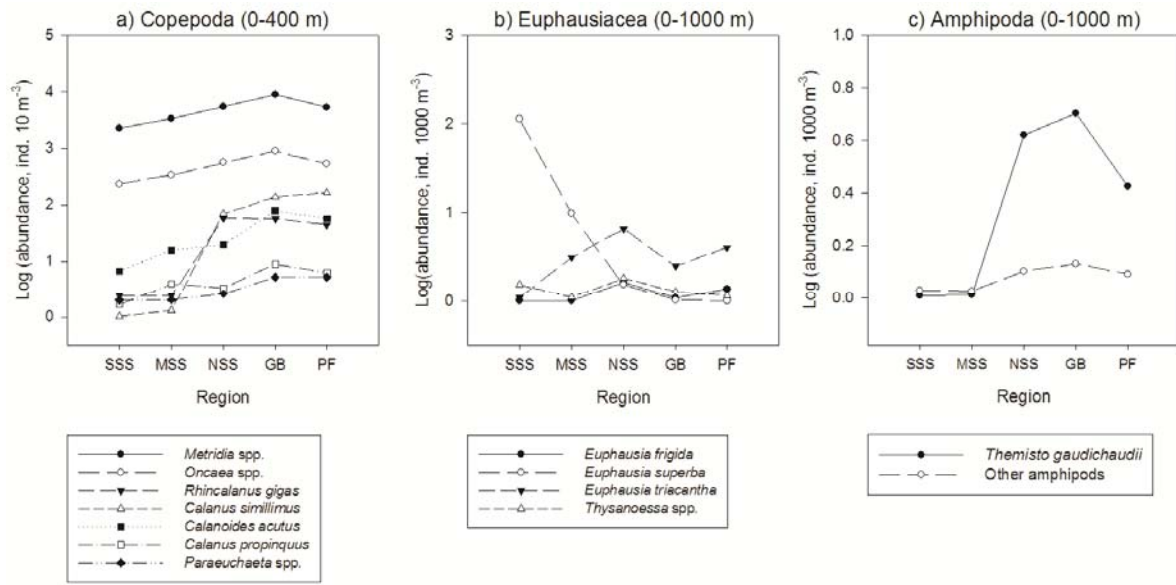
**Fig. 5**



**Fig. 6**



**Fig. 7**



**Fig. 8**