

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

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## Abstract

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

## Keywords

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

## Introduction

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

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

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

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

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

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

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

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

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

## Methods and materials

### Study location

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

## Net sampling

Mesopelagic fish and invertebrates were collected using an opening and closing rectangular mid-water trawl net (RMT25) (Piatkowski et al. 1994). The RMT25 incorporates two 25 m<sup>2</sup> nets that can be opened and closed sequentially via an electronic downwire control unit to sample two depth-discrete layers. Each net had a cod-end mesh of 5 mm and was fitted with a protective cod-end to minimise damage to the samples. The RMT25 was towed obliquely at ~2.5 knots for 30-60 min in each depth zone, and each deployment was monitored in real-time using a custom-built net monitoring system that logged depth and temperature. Both nets were closed during deployment and veering, but opened sequentially during hauling.

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

## Sample processing

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

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

#### Stomach content analysis

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

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

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

where *i* is prey item.

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

#### Length-frequency analyses

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

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

## Results



## Oceanographic conditions

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

## Distribution and abundance

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

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>).

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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>).

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287 Vertical distribution

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

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

#### Population size structure

*E. antarctica*: The overall size ranged between 25-115 mm SL on each survey and larval stages (<20 mm) were not observed during the study. A series of K-S tests conducted on length-frequency data aggregated by region on each survey (where  $n > 60$ ) showed that there were no significant ( $P > 0.05$ ) regional differences in composite length-frequency distributions across the Scotia Sea. Published data indicate that peak spawning for *E. antarctica* occurs throughout the Scotia Sea in autumn/early-winter (April-June) (Lubimova et al. 1987) and hatching occurs between June and August (Kellermann 1989b; Kellermann 1989a). We therefore consider individuals as belonging to a 0-group from the time of hatching until June the following year, to a I-group from 1 July to 30 June the next year, and so on. Differentiation between the 0-group and I-group cohorts in the initial population was aided by published growth rates for the species (Greely et al. 1999). Although the data were not collected in consecutive seasons, the overall seasonal pattern in population structure appeared to be as follows. The general life span of *E. antarctica* was at least three years. Two size-, and presumably age-, classes were present in the spring population: the newly recruited II-

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

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

#### Gender-based differences

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

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

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

#### Patterns in sex and gonad maturity status

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

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

#### General diet composition

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

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

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

#### Spatial patterns in diet

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

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

#### Temporal patterns in diet

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

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

#### Ontogenetic patterns in diet

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

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

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

## Discussion

### Distribution

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

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



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

#### Vertical distribution

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

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

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

#### Vertical size structure

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

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

#### Population structure

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

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

#### General diet patterns

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

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

#### *E. antarctica* diet patterns

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

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

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

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

#### *E. carlsbergi* diet patterns

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

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

## Conclusions

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



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## Figure legends

**Fig. 1** Map of the Scotia Sea and the distribution of *Electrona antarctica* (yellow) and *Electrona carlsbergi* (red) density during the surveys. The size of the pies is proportional to the log total of fish densities per net. Blue crosses denote non-targeted net haul positions. Sampling stations are: Southern Scotia Sea (SSS), Western Scotia Sea (WSS), Mid-Scotia Sea (MSS), North Scotia Sea (NSS), Georgia Basin (GB) and Polar Front (PF). Mean frontal positions determined during the cruises from dynamic height data (Venables et al. 2012) are: northern Polar Front (N-PF), southern Polar Front (S-PF), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB-ACC). The heavy black line shows the position of the 15% ice-edge cover for 24/10/2006 and for 15/01/2008. The ice-edge occurred well south of the transect during autumn 2009 (JR200). Bathymetry data are taken from the GEBCO\_08 grid (version 20091120, [www.gebco.net](http://www.gebco.net))

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

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

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

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



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

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

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

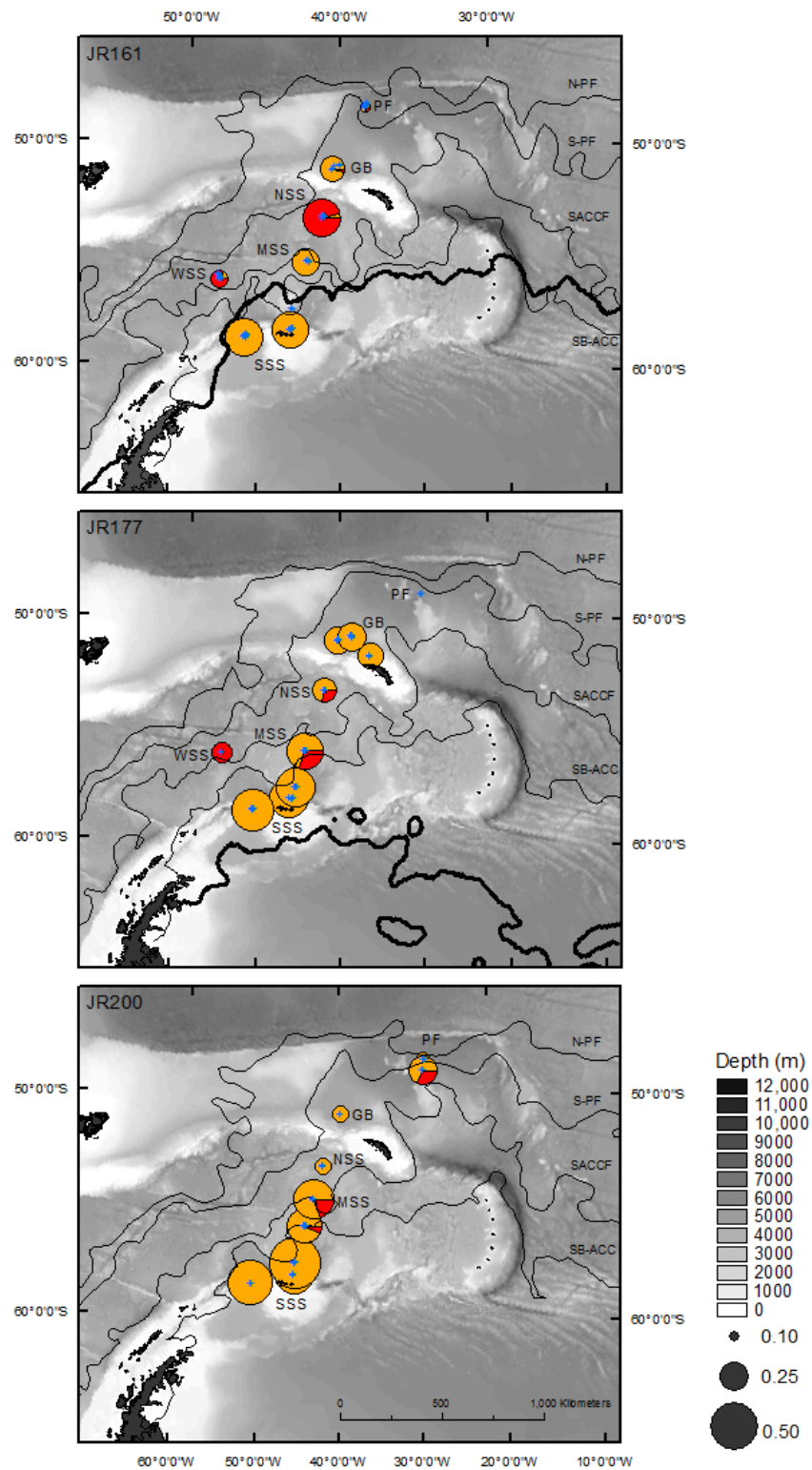
**Table 3** Mean biomass (g 1000 m<sup>-3</sup>) of *Electrona antarctica* and *Electrona carlsbergi* in the Scotia Sea. *N* is the number of net hauls

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>

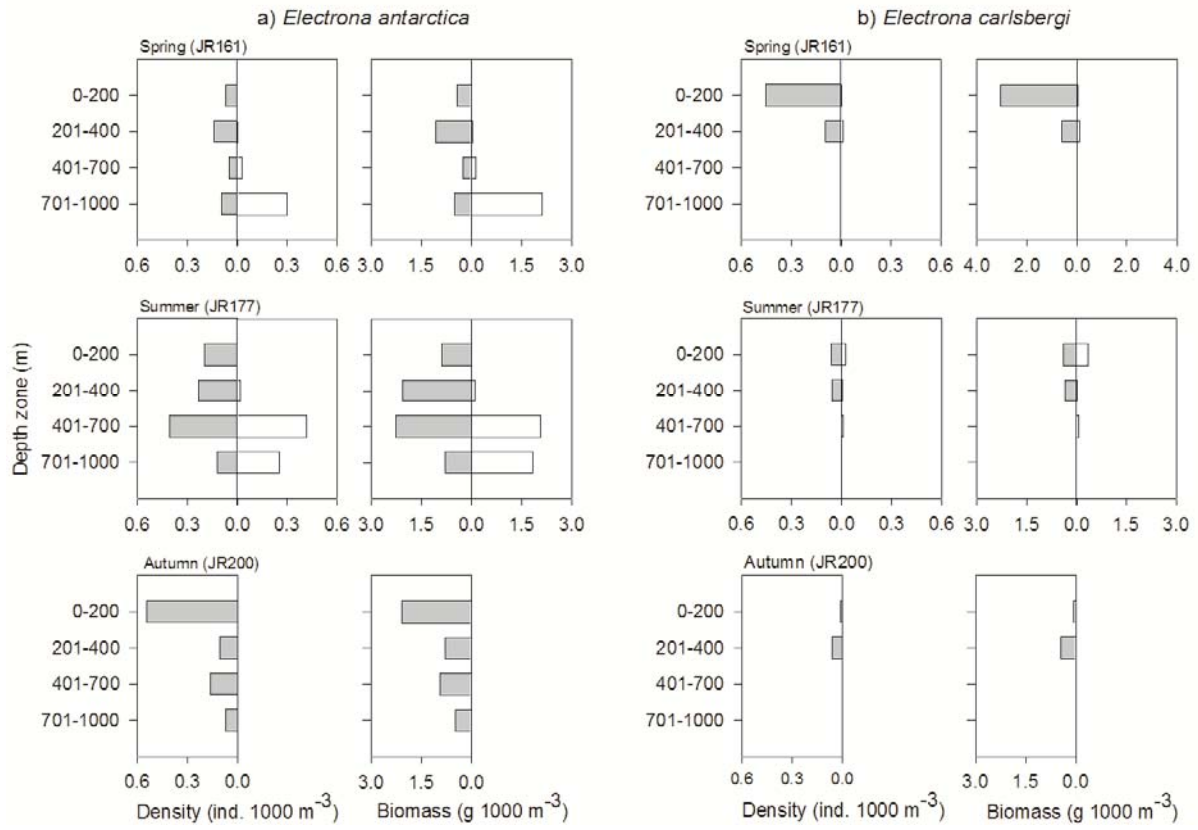
<b>Ostracoda</b>								
Unidentified ostracod	8.25	0.14	2.24	0.66	5.95	0.13	0.25	0.03
Total	<b>8.25</b>	<b>0.14</b>	<b>2.24</b>	<b>0.31</b>	<b>5.95</b>	<b>0.13</b>	<b>0.25</b>	<b>0.02</b>
<b>Mollusca</b>								
Unidentified pteropod	5.36	2.89	4.54	1.33	12.43	5.38	4.52	0.87
<i>Limacina</i> spp.	0.21	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>	14.23	2.50	3.44	1.42	7.03	2.11	0.30	0.12
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>0.13</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

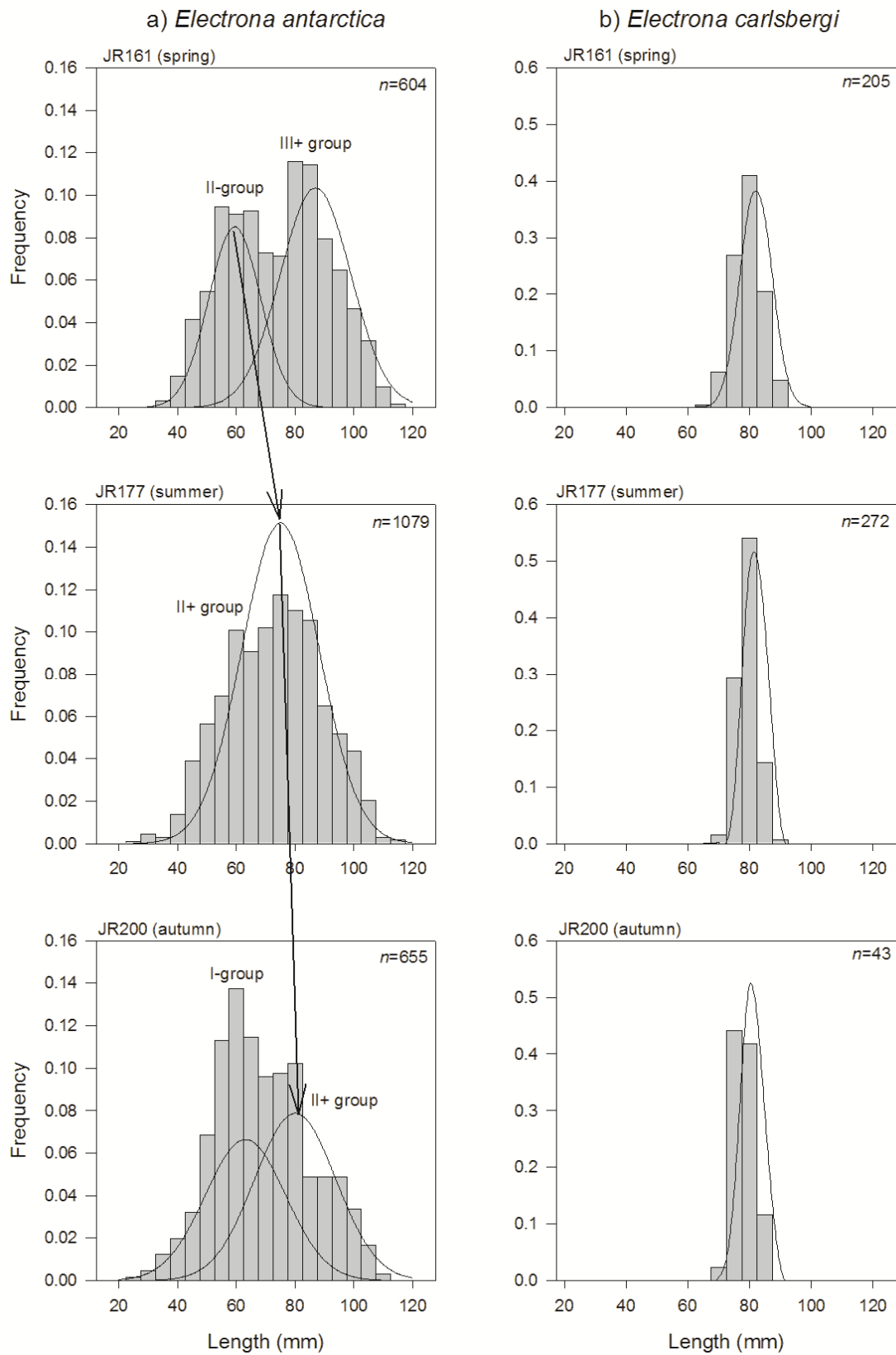


**Fig. 1**

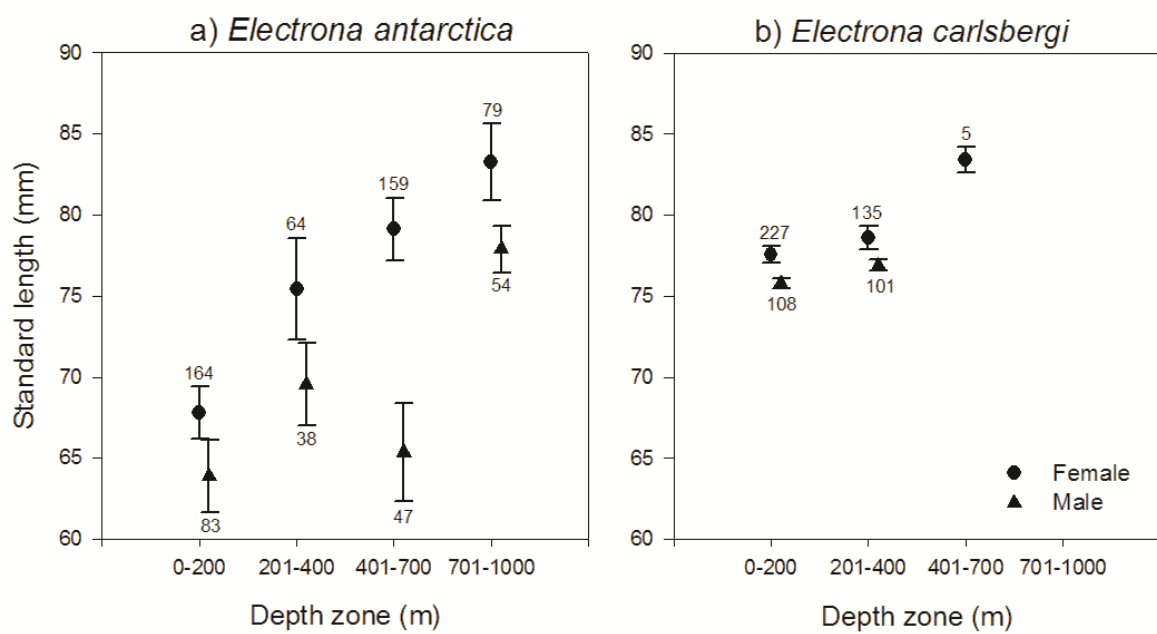


**Fig. 2**

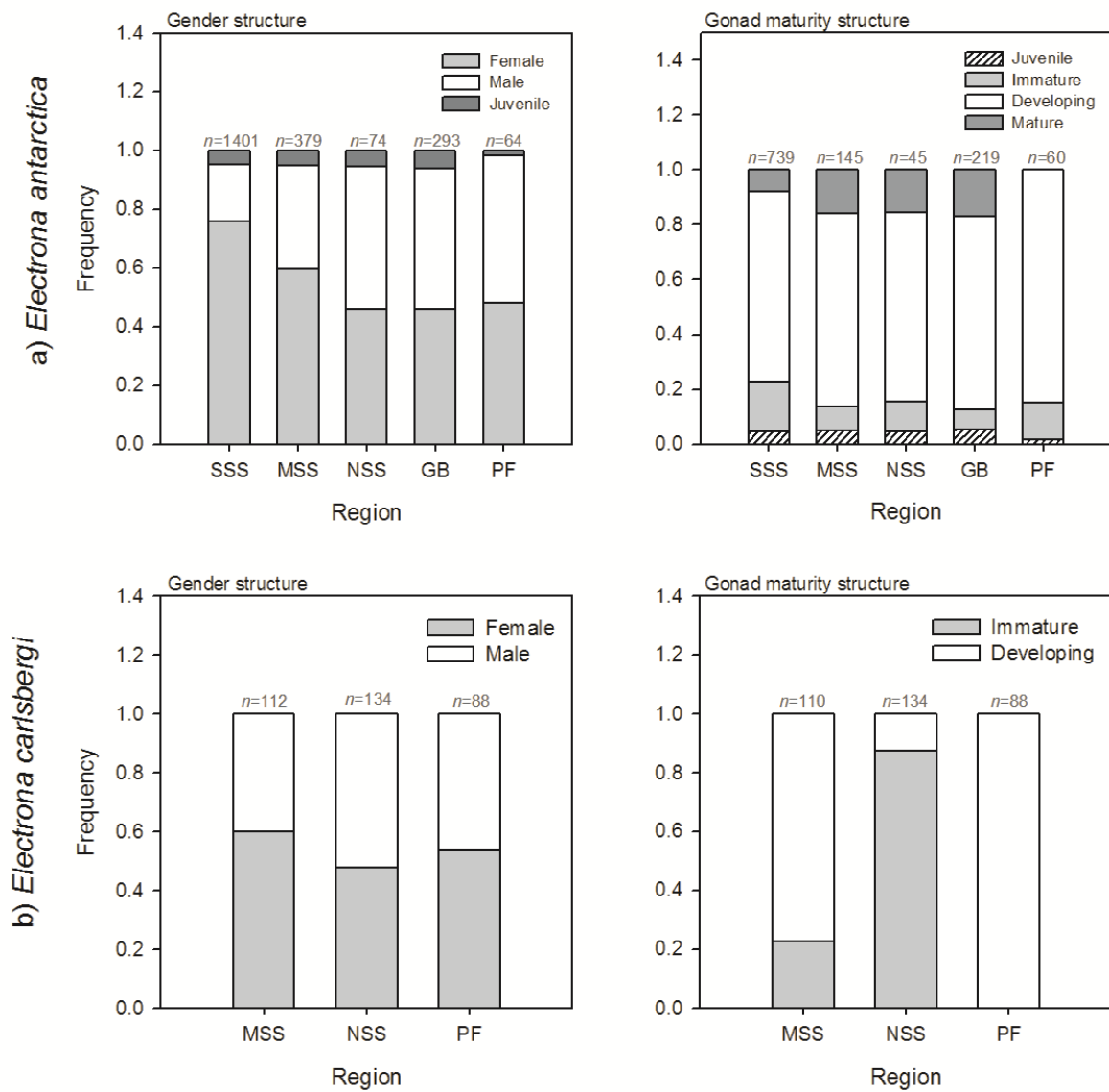




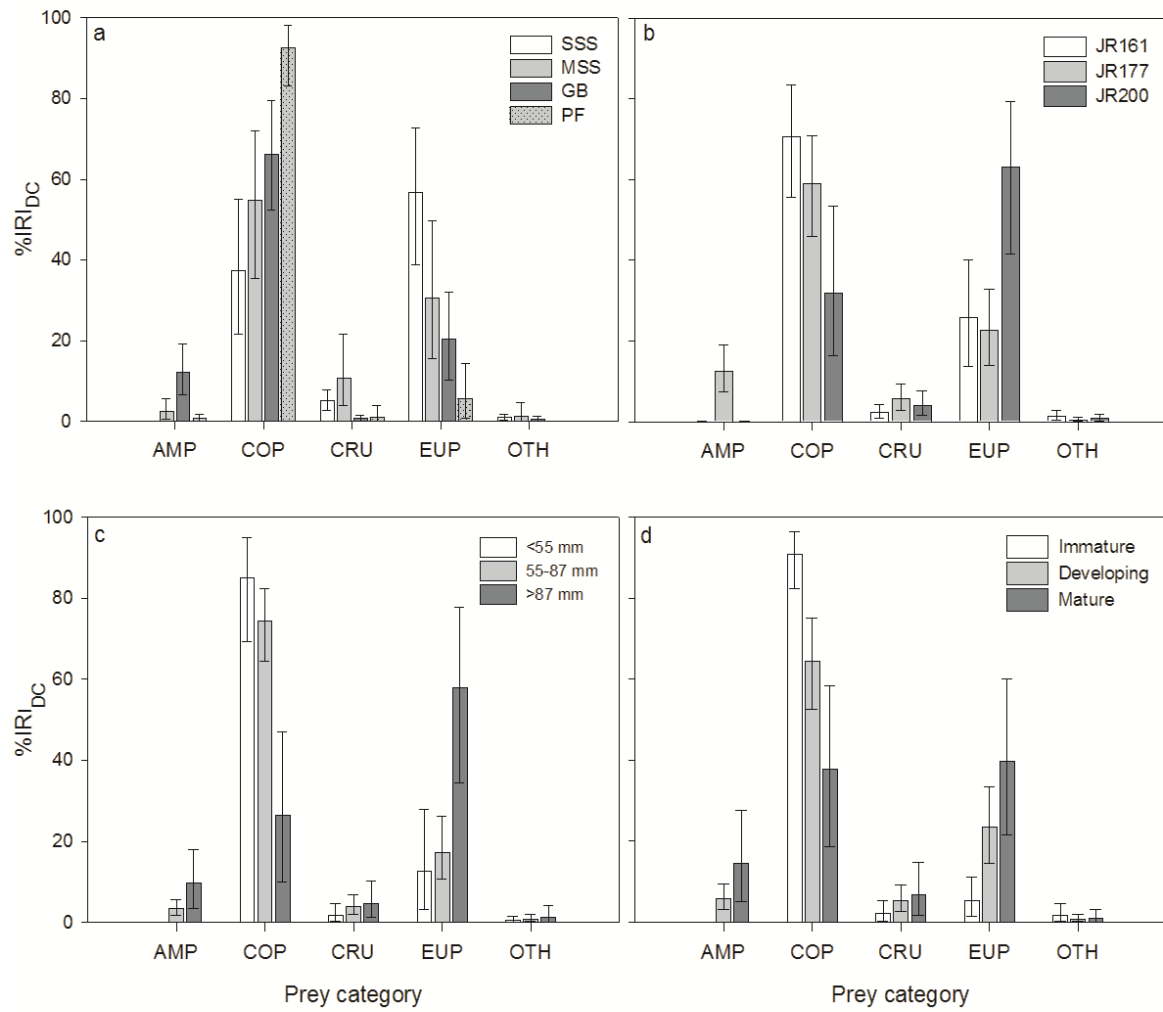
**Fig. 3**



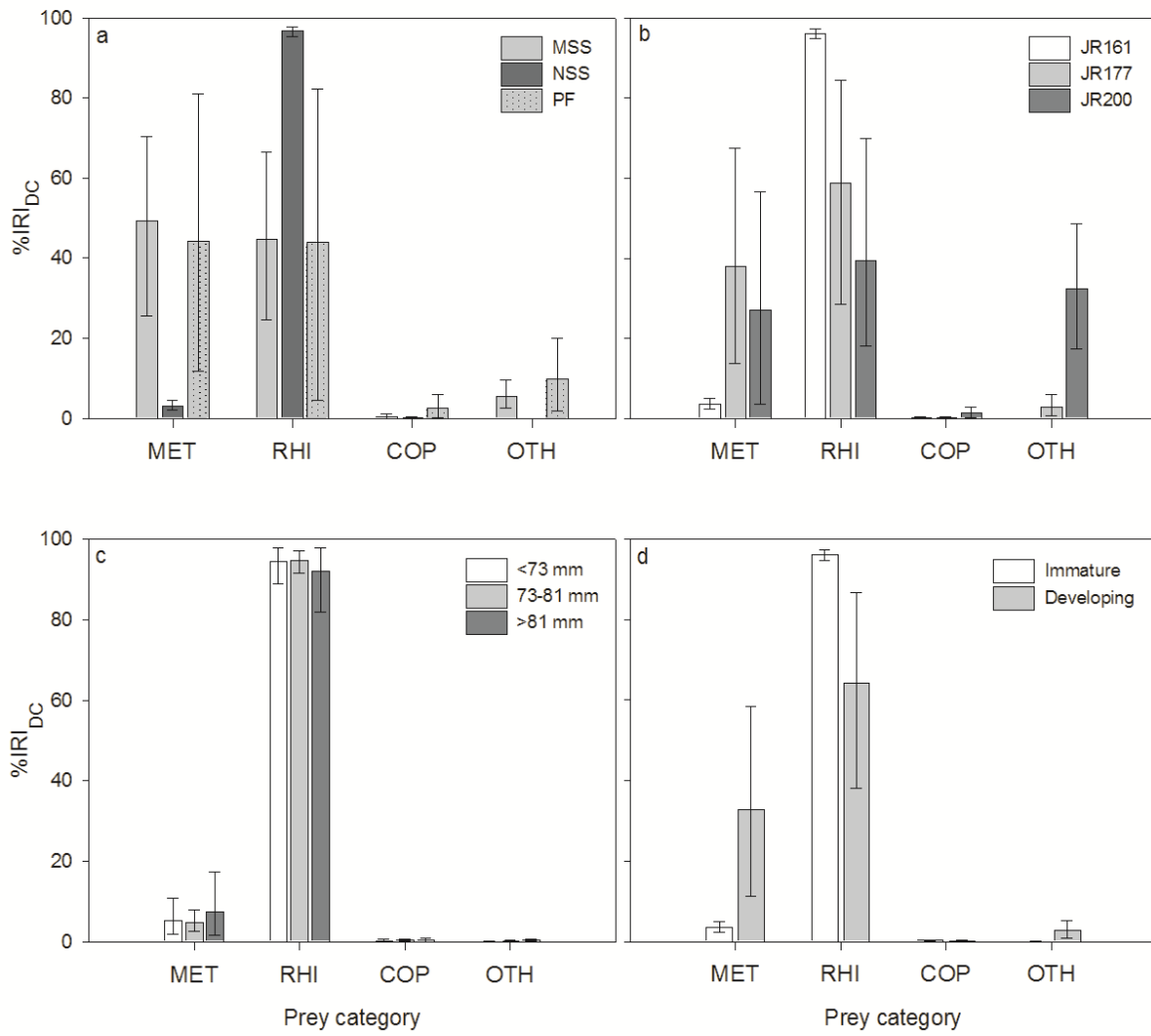
**Fig. 4**



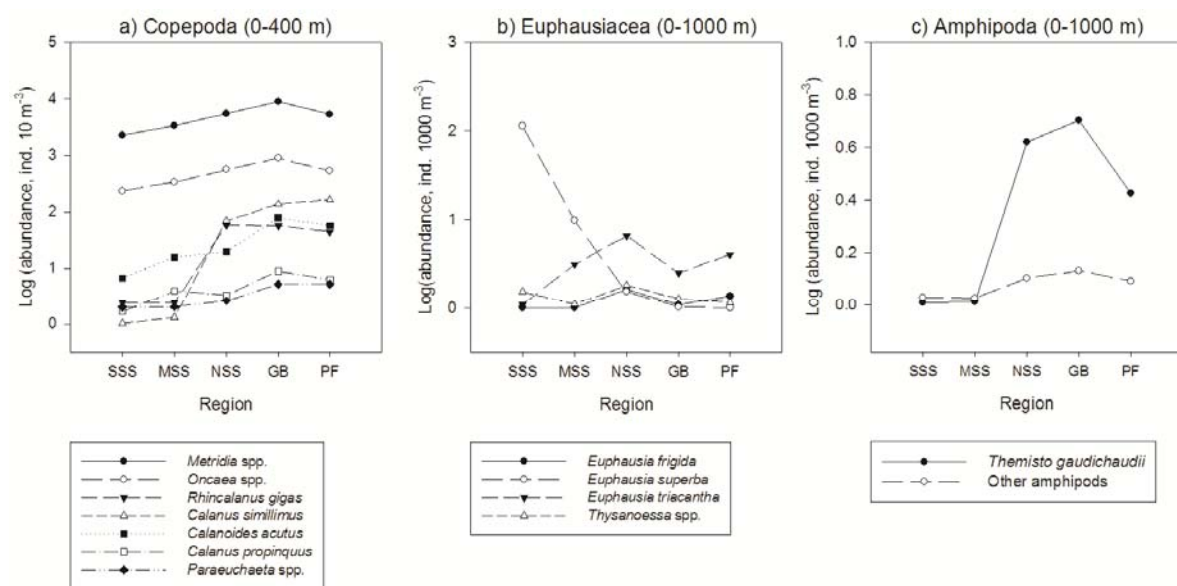
**Fig. 5**



**Fig. 6**



**Fig. 7**



**Fig. 8**