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Life cycle, distribution and trophodynamics of the lanternfish *Krefftichthys anderssoni* (Lönnberg, 1905) in the Scotia Sea

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Abstract Myctophid fish play an important role in the Southern Ocean pelagic food web. The lanternfish *Krefftichthys anderssoni* is one of the most common myctophids in the region, but its ecology is poorly known. This study examines spatial and temporal patterns in the species distribution of density, life cycle, population structure and diet using samples collected by mid-water trawl nets deployed in different seasons across the Scotia Sea. Virtually absent from the sea-ice zone, the species was most abundant in the northern Scotia Sea around the Georgia Basin at depths below 400 m that are associated with the Circumpolar Deep Water. The species migrated during night from waters deeper than 700 m to waters above the 400 m following their main prey species: the copepods *Rhincalanus gigas* and *Calanoides acutus* and euphausiids of the *Thysanoessa* genus. Larvae length distribution and post-larvae length-frequency analyses suggested a life cycle of ∼3 years with spawning and recruitment strongly connected with APF and the South Georgia shelf. Our results show that species spatial distribution, population structure and diet changed both seasonally and ontogenetically. This study is the most comprehensive examination of the ecology of *K. anderssoni* in the Southern Ocean to date and contributes to resolving how pelagic food webs and ecosystems operate in the region.

Keywords Southern Ocean · Myctophids · Distribution · Trophic ecology

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Introduction

Mesopelagic fishes are amongst the most abundant vertebrate group on earth, yet they remain one of the least studied components of the open-ocean ecosystem (Gjøsaeter and Kawaguchi 1980; Irigoien et al. 2014). They occupy an important trophic status, as both zooplankton consumers and prey to many higher marine predators, and may respire up to 10 % of primary production in deep waters (Pakhomov et al. 1996; Smith 2011; Irigoien et al. 2014). Lanternfish (family Myctophidae) are considered to be the dominant fishes within the global mesopelagic fish community in terms of biomass and diversity, including the Southern Ocean (Gjøsaeter and Kawaguchi 1980).

In the Southern Ocean, the family Myctophidae is represented by 12 genera and, with 24 resident species, plus 44

species occasionally recorded south of the sub-Tropical front (Duhamel et al. 2014), comprising an estimated biomass of 70–130 million tonnes (Mt) (Lubimova et al. 1987). Myctophids play an important ecological role in the open-ocean food web in this region (Barrera-Oro 2002; Saunders et al. 2015c). They are a key dietary component of sea birds, seals, cetaceans, squid and large predatory fish (Rodhouse et al. 1992; Olsson and North 1997; Cherel et al. 2002; Reid et al. 2006; Collins et al. 2007; Cherel et al. 2008) and are themselves predators of macrozooplankton, such as copepods, amphipods and euphausiids, including Antarctic krill (Euphausia superba) (Pakhomov et al. 1996; Williams et al. 2001; Shreeve et al. 2009). Myctophids are particularly important to the ecosystem in this region as they provide a major krill-independent trophic pathway in an otherwise krill-dominated food web (Murphy et al. 2007b). However, despite their ecological importance, very little is known about the ecology of key myctophid species in the region. Acquisition of new data on the ecology of myctophid fish, particularly their trophic ecology, is therefore an essential prerequisite for understanding the operation of the Southern Ocean ecosystem and carbon cycles and for establishing sustainable ecosystem management policies.

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

Of the Southern Ocean myctophid fish community, *K. anderssoni* appears to be one of the most important species in the pelagic food web. It comprises a crucial part of the diet of many predators in the region, particularly the squid *Martialia hyadesi* (Rodhouse et al. 1992), Patagonian toothfish *Dissostichus eleginoides* (Collins et al. 2007), King Penguins *Aptenodytes patagonicus* (Cherel et al. 1996; Bost et al. 1997, 2002), Macaroni Penguins *Eudyptes chrysolophus* (Klages et al. 1989; Waluda et al. 2010), Grey-headed Albatrosses *Thalassarche chrysostoma* (Xavier et al. 2003) and Antarctic fur seals *Arctocephalus gazella* (Green et al. 1989; Cherel et al. 1997; Daneri et al. 2005). Based on biochemical analyses, this relatively small myctophid species (up to ∼80 mm standard length; Hulley, 1981) is also considered a high-level predator (trophic level = 3.8) in this food web, feeding on crustacean suspension feeders and other zooplankton (Stowasser et al. 2012), with copepods and small euphausiids often dominating its diet (Gaskett et al. 2001; Shreeve et al. 2009). However, the exact diet composition of this species remains unresolved since previous trophic studies are limited to relatively small sample sizes collected over restricted spatial and temporal scales (Pakhomov et al. 1996; Gaskett et al. 2001; Shreeve et al. 2009; Cherel et al. 2010). Recent trophic studies of other Southern Ocean species have shown that the diets of other myctophid species vary spatially, temporally and ontogenetically, with the possibility of resource partitioning between coexisting species, such as *Electrona carlsbergi*, *Gymnoscopelus braueri* and *Protomyctophum bolini* (Shreeve et al. 2009; Saunders et al. 2014, 2015a). However, such variation has yet to be examined for *K. anderssoni*, and there remain major uncertainties in the species' diet composition at different times of year and stages of ontogeny. New studies are therefore required to assess the extent of resource overlap between this species and other potential competitors in the same region.

In this study, we focus on the ecology of *K. anderssoni* in the Scotia Sea (Atlantic sector). The Scotia Sea is one of the most productive regions of the Southern Ocean (Holm-Hansen et al. 2004), sustaining abundant secondary consumers, major populations of higher predators and important commercial fisheries (Everson 1992; Constable et al. 2000; Murphy et al. 2007b; Atkinson et al. 2009). Myctophids comprise an estimated biomass of around 4.5 Mt in this region (Collins et al. 2012), so new information about their ecology and trophodynamics in this important sector would constitute a major step towards understanding ecosystem dynamics at the broader scale throughout the Southern Ocean. In this paper, we present new data on the distribution, density, population structure and feeding ecology of *K. anderssoni*, in the Scotia Sea, using net samples collected during three multidisciplinary research surveys (November 2006, January 2008 and March 2009) that surveyed the Scotia Sea from the sea-ice zone to the APF (Tarling 2012). This information is important for

resolving the structure the Southern Ocean food web and for evaluating its stability in a region that is presently subject to sustained ocean climate change (Moline et al. 2004; Murphy et al. 2007a; Flores et al. 2012). The information is also important for resolving the dynamics of the mesopelagic fish community at both a regional and global scale.

Materials and methods

This study makes use of biological and oceanographic data collected during three multidisciplinary research surveys conducted onboard RRS *James Clark* during austral spring, summer and autumn. The surveys were designed to cover all of the major water masses and oceanographic regimes across a transect spanning the entire Scotia Sea sampling the mesopelagic fish community between 0 and 1000 m in each region (Fig. 1). Although surveys were not conducted in consecutive seasons, this approach enables a first synoptic examination of the seasonal and broad-scale variation in the composition and distribution of the mesopelagic fish at the community level (Collins et al. 2012; van de Putte et al. 2012) and at species level (Saunders et al. 2014; 2015a, b) in relation to the prevailing environmental conditions. We also utilize time-series data on larval size distribution collected during the British Antarctic Survey's long-term ichthyoplankton monitoring programme (Belchier and Lawson 2013) to underpin the species life cycle characteristics.

Study location and oceanographic background

Three surveys were conducted during the austral spring (survey JR161, October–December 2006), austral summer (JR177, January–February 2008) and autumn (JR 200, March–April 2009). The cruises surveyed a transect spanning from the sea-ice zone (SIZ) to the APF. 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. 2012a; Whitehouse et al. 2012) were collected at a six fixed stations that were spread across the different water masses and frontal zones in the region, following a transect line from east of the South Orkneys to west of South Georgia. These stations were named as follows: 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).

Fish sampling and processing

Mesopelagic fish and invertebrates were collected using an opening and closing rectangular mid-water trawl net (RMT 25) (Piatkowski et al. 1994). The RMT 25 is a set of two 25-m^2 nets that can be opened and closed sequentially via an electronic down-wire 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 minimize damage to the samples. The RMT 25 was towed obliquely at ~ 2.5 knots for 30–60 min in each depth stratum, and each deployment was monitored in real time using a custom-built net monitoring system that logged depth and environment temperature. Both nets were closed during deployment and veering, but opened sequentially during hauling. At each station, depth-stratified hauls were undertaken at 0–200, 201–400, 401–700 and 701–1000 m. These depth strata were repeated day and night during the spring and summer surveys, but all hauls were conducted at night during autumn due to the reduced daylight hours in this season. The upper-most depth strata (0–200 and 200–400 m) were sampled as close to local midday or midnight as practical. Our sampling depth range and strata were defined a priori to cover the predominant vertical range of the myctophid fish community and capture possible their diel vertical migrations, whilst being coincident with the known vertical foraging ranges of higher predators. They were also selected to facilitate comparisons between previous surveys in the region. The targeted mesopelagic community perform diel migratory movements between the deeper waters near 1000 m and the shallow layer with density peaks around 400 m during the day and upper to 200 m during the night (Piatkowski et al. 1994; Collins et al. 2008). Additionally, the predators (e.g. King Penguin and Antarctic fur seal) dive to forage predominantly above the 200 m (Guinet et al. 2001; Bost et al. 2002) setting the limit for the most superficial depth strata.

RMT 25 net haul catches were sorted on board to the lowest taxonomic level possible using published guides (Hulley 1981; 1990). Total catch weights for each fish species were obtained using a motion-compensated balance. All fish were measured to the nearest 1 mm (standard length, hereafter SL). When possible, the sex and maturity stage of the fish were recorded. Stomachs were dissected from a random sub-sample of 25 fish per haul, or from each fish when net catches were low (Table 1). All stomachs were frozen for subsequent microscopic analysis back at the laboratory.

Length-frequency analysis, LFA

Length-frequency data aggregated by season, region and depth strata were plotted as histograms of 5-mm SL classes. The resulting distributions were tested for normality with the Shapiro–Wilks test, and based on the results obtained, a series of Kolmorov–Smirnov tests were conducted on the length-frequency distributions to investigate
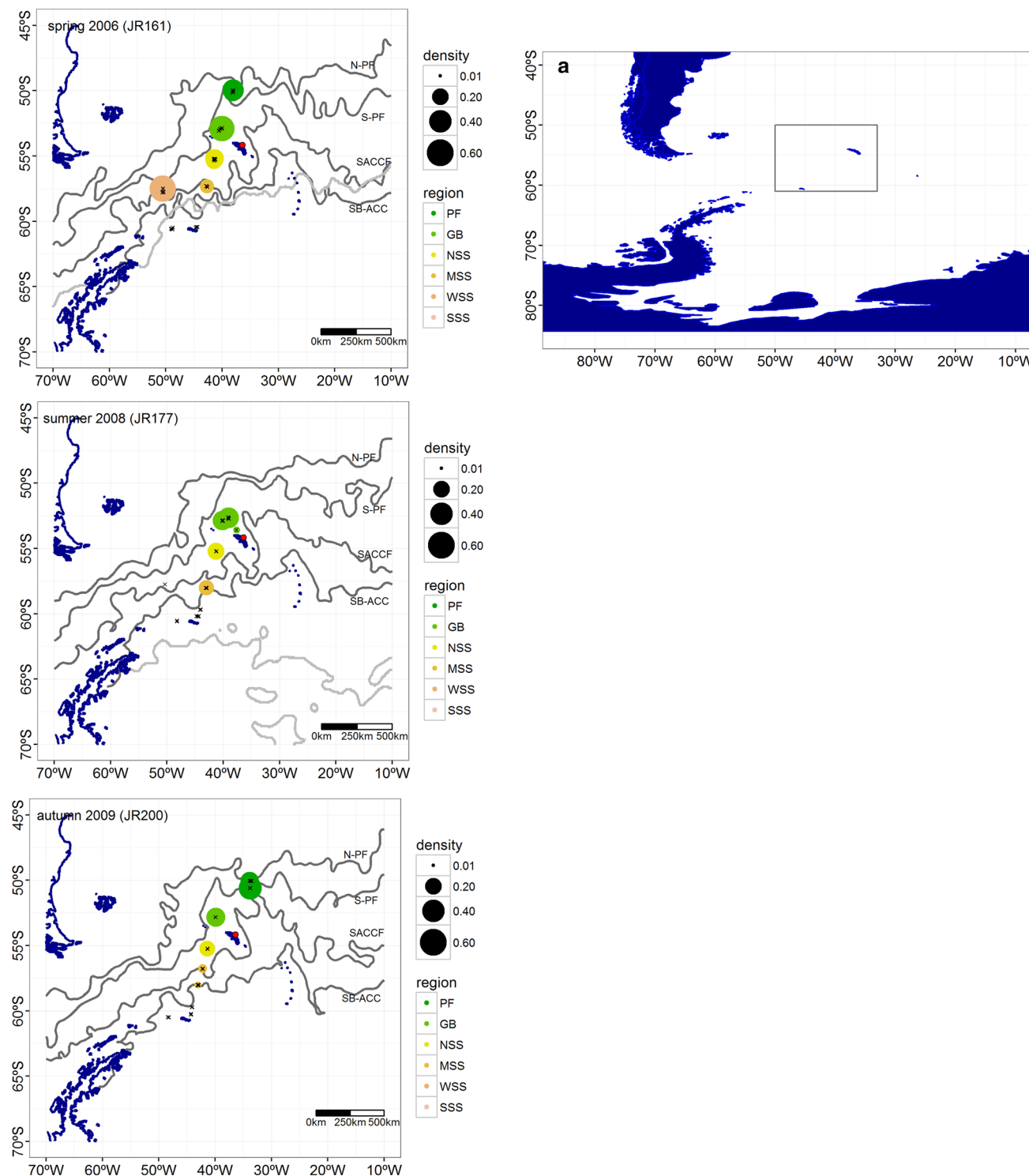
Fig. 1 Maps of the Scotia Sea showing the RMT 25 approximate sampling area of the three surveys (**a**) and of the non-targeted net hauls position with *Krefftichthys anderssoni* density by net haul (individuals per 1000 m³) conducted in the spring 2006 (JR161), the summer 2008 (JR177) and autumn 2009 (JR200). *Red circle* indicates the location of the Cumberland Bay ichthyoplankton surveys. Mean frontal positions determined during the surveys from dynamic height data (Venables et al. 2012) are as follows: northern Antarctic Polar

Front (N-PF), southern Antarctic Polar Front (S-PF), south Antarctic Circumpolar Current Front (SACCF) and southern boundary of the Antarctic Circumpolar Current (SB-ACC). The heavy *black line* shows the position of the 15 % ice-edge cover for 24 October 2006 (spring 2006, JR161), and the *grey line* shows the position of the 15 % ice-edge cover for 15 January 2008 (summer 2008, JR177). The ice edge occurred well south of the transects during autumn 2009 (autumn 2009, JR200). (Color figure online)

Table 1 Numbers of rhombic lanternfish *Krefftichthys anderssoni* samples by pooled dataset used for the population structure analysis and for comparison of %IRI$_{DC}$ between seasons, regions and sizes (only for diet comparisons)

Factor for comparison	Pooled samples	Category	N_{LF}	N_{DA}
Season	All regions	Spring 2006 (JR161)	690	218
		Summer 2008 (JR177)	186	79
		Autumn 2009 (JR200)	226	77
Region	All seasons	SSS	2	
		WSS	157	49
		MSS	40	12
		NSS	241	78
		GB	406	154
		PF	258	79
Size	All regions and seasons	Small (<32 mm SL)		20
		Medium (32–60 mm SL)		251
		Large (>60 mm SL)		103

N_{LF} number of individuals used for length-frequency analysis, N_{DA} number of individuals used for diet analysis, *SSS* southern Scotia Sea, *WSS* western Scotia sea *MSS* mid-Scotia Sea, *NSS* northern Scotia Sea, *GB* George Basin, *PF* Polar Front

possible differences in population structure between seasons, regions and depth strata across the Scotia Sea. For each factor, the tests were performed pairwise, comparing levels with $n > 60$ individuals. The package R Mixdist was used to fit normal distributions to the composite length-frequency distributions. Mixdist fits a mixture of distributions model using an algorithm defined by Macdonald and Green (1988). The algorithm identifies a set of overlapping normal component distributions that gives the best fit for a specific mixture distribution. The number of expected cohorts and approximate mean SL per cohort is specified by the user a priori by visual inspection of the length histograms as initial fitting parameters. The analysis was constrained to fixed variance between mixture components, and all components were assumed to be normal. The analysis was only conducted in datasets with $n > 60$ (Table 1). A series of runs were conducted based on the presence of two or three cohorts, and the best fit was determined by the analysis of the goodness-of-fit based on the larger χ^2 value obtained with a significance level of $p < 0.05$.

Larvae sampling and data analysis

Larval length data were collected from Cumberland Bay larval study, South Georgia (54°17′S, 36°0′W), as part of the British Antarctic Survey's long-term ichthyoplankton monitoring programme (Belchier and Lawson 2013). These inshore surveys were conducted on a weekly basis between January 2002 and October 2008, with 1–5 hauls conducted each month and 20–39 hauls per year. Larval fish samples were collected from a total of 219 oblique plankton tows conducted with a RMT with a 1-m^2 opening (RMT1) and net mesh size of 610 µm that was towed for 30 min from the surface to a maximum depth of 25 m. The tows were conducted in an approximately north to south direction over water depths of ~ 25 m, and the volume of water filtered was calculated from the swept area of the net estimated from GPS-derived vessel speed and trawl duration data. *Krefftichthys anderssoni* represented approximately 37 % of the fish larvae collected in 35 % of the net hauls (Belchier and Lawson 2013). For each sampled month, a maximum of 200 *K. anderssoni* larvae were measured, with standard length (SL) ranging between 2 and 19 mm. Further details about the larval fish surveys and sampling procedures are described in Belchier and Lawson (2013). Variability amongst sampling years and sampling months was analysed with type III ANOVA for unbalanced samples. The mean larval month was then determined by calculating the average length of the mean length obtained in each month sampled.

Diet analysis

Following Shreeve et al. (2009), prey species were identified to the highest level that the state of digestion would allow using standard zooplankton identification guides (Boltovskoy 1999). Individual prey items were then counted and weighed. If the prey was highly disaggregated, the weights of component species were estimated as a proportion of the weight of total contents.

Krefftichthys anderssoni diet was expressed using percentage mass (%M), percentage frequency of occurrence (%F), percentage number (%N) and an index of relative importance (%IRI, Cortés 1997). Percentage mass was based on the weight of prey found in the stomach and not on estimated original mass. The %IRI was calculated for

prey specimens and the % IRI_{DC} for key diet categories (hereafter DC) (Main et al. 2009; Shreeve et al. 2009). The %IRI was calculated as:

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

Diet categories were selected for the prey taxa comprising >1 % IRI of the diet: *Themisto gaudichaudii* (thm), *Thysanoessa* spp. (thy), *Calanoides acutus* (cac), *Calanus simillimus* (cas), *Metridia* spp. (met) and *Rhincalanus gigas* (rcg). The $\%IRI_{DC}$ was calculated with data aggregated by region, season and size class (Table 1). The fish size class categories, termed small (<32 mm SL), medium (32–60 mm SL) and large (>60 mm SL), were derived from the length-frequency analyses. The 95 % confidence limits for the mean %IRI of each DC were calculated using a bootstrapping technique, whereby each species dataset (individual stomachs) was re-sampled with replacement 1000 times following Main et al. (2009).

Results

Oceanographic conditions

Krefftichthys anderssoni was mainly captured in regions north of the Southern Boundary of the Antarctic Circumpolar Current (SB-ACC), so only oceanographic conditions in the northern Scotia Sea are described here. Stations in the WSS and MSS lay between SB-ACC and South Antarctic Circumpolar Current Front (SACCF), where mean temperatures and Chl *a* concentration in the Antarctic surface waters (AASW) ranged from −0.2 to 2.1 °C and 0.2–2.6 mg m^{-3}, respectively. Stations in the NSS and GB were situated between SACCF and the 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^{-3}). The APF stations were situated in waters close to the southern Antarctic Polar Front (S-PF) on the summer and autumn surveys, whilst these stations (JR161) lay north of S-PF in spring. Surface waters in around the APF had a mean temperature >4 °C during all surveys with mean Chl *a* concentrations ranging between 0.2 and 0.6 mg m^{-3}. Winter water (WW; 100–200 m) and Circumpolar Deep Water (CDW; >200 m) were evident at all stations located between SB-ACC and APF. Mean temperatures in the WW ranged between 0.2 and 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. More detailed descriptions of the oceanographic conditions can be found in Venables et al. (2012) and Whitehouse et al. (2012).

Distribution and density

A total of 143 station net hauls were conducted during the three surveys (Table 2). All stations were sampled repeatedly to a varying degree during the study period except the WSS, where sampling was confined to the spring survey. *Krefftichthys anderssoni* density and biomass were variable; however, the distribution pattern was consistent between sampling years, with species being predominantly distributed in the northern Scotia Sea (NSS, GB and PF) and seldom occurring in the sea-ice zone (SSS, $n = 4$). The highest overall densities and biomass were found in spring (0.12 ind. 1000 m^{-3}; 0.20 g 1000 m^{-3}), and the lowest densities and biomass occurred in summer (0.04 ind. 1000 m^{-3}; 0.05 g 1000 m^{-3}; Table 2). The species was most abundant in spring around the GB (0.22 ind. 1000 m^{-3} and 0.25 g 1000 m^{-3}) and least abundant in the MSS regions in autumn (<0.02 ind. 1000 m^{-3} and <0.04 g 1000 m^{-3}; Table 2).

Krefftichthys anderssoni was most abundant at depths greater than 400 m during daytime, although the species was caught at the surface layers (0–200 m) during this time, suggesting daylight surface schooling of part of the population (Fig. 2). During the night-time, the species was distributed higher in the water column, with peaks in density situated around 201–400 m, indicative of some DVM (Fig. 2). There was also evidence of seasonal variation in the species' depth distribution. Peaks in both night-time density and biomass occurred at depths 201–400 m during the spring, but occurred progressively deeper in summer (401–700 m) and autumn (701–1000 m; Fig. 2). The data showed an increasing dominance of larger specimens in the deepest regions of the water column during summer and autumn, as the mean size of specimens between 700 and 1000 m was at least 15 mm larger than that observed at depths higher up the water column (e.g. 34 mm at 401–700 m compared to 49 mm at 700–1000 m in autumn). Such size stratification was not apparent in spring.

Life history and length-frequency structure

The larval mean length varied of larvae varied both with sampling year ($F = 196.50$, $p < 0.0001$) and sampling month ($F = 150.74$, $p < 0.0001$) and with the interaction of the two factors ($F = 151.00$, $p < 0.0001$). The smallest larvae (mean SL = 5.71 mm ± 0.73, SD) were captured in June, whilst the largest larvae were captured in March (mean SL = 14.25 mm ± 1.46, SD; Fig. 3). These results indicate that the species is most likely a winter spawner, and therefore, individuals are considered as belonging to a

Table 2 Rhombic lanternfish *Krefftichthys anderssoni* mean density (individuals per 1000 m³) and mean biomass (g per 1000 m³⁾ of in the Scotia Sea

| | N | Spring 2006 (JR161) | | N | Summer 2008 (JR177) | | N | Autumn 2009 (JR200) | |
		Abundance (Min−Max)	Biomass (Min−Max)		Abundance (Min−Max)	Biomass (Min−Max)		Abundance (Min−Max)	Biomass (Min−Max)
PF	8	0.18 (0.01–0.34)	0.23 (0.05–0.56)	10	0.01 (0.00–0.02)	0.01 (0.00–0.02)	8	0.10 (0.00–0.04	0.08 (0.00–0.09)
GB	5	0.22 (0.00–0.63)	0.25 (0.00–1.00)	10	0.08 (0.00–0.34)	0.07 (0.00–0.25)	2	0.26 (0.26–0.27)	0.24 (0.00–0.47)
NSS	8	0.15 (0.00–0.63)	0.24 (0.00–0.79)	8	0.04 (0.0–0.21	0.08 (0.00–0.35)	4	0.07 0.00–0.18)	0.06 (0.19–0.29)
MSS	4	0.17 (0.00–0.69)	0.42 (0.00–1.71)	9	0.02 (0.00–0.16)	0.04 (0.00–0.40)	12	0.01 (0.00–0.04)	0.01 (0.00–0.09)
WSS	8	0.02 (0.00–0.11)	0.025 (0.00–0.17)	0	0.00	0.00	0	0.00	0.00
SSS	17	0.00	0.00	19	0.00	0.00	10	0.00	0.00
All	50	0.12 (0.00–0.67)	0.20 (0.00–1.71)	56	0.04 (0.00–0.34)	0.05 (0.00–0.40)	36	0.06 (0.00–0.42)	0.06 (0.00–0.47)

N indicates the number of net hauls per season and region, *SSS* southern Scotia Sea, *WSS* western Scotia Sea, *MSS* mid-Scotia Sea, *NSS* northern Scotia Sea, *GB* George Basin, *PF* Polar Front

Fig. 2 Mean vertical distribution of the lanternfish *Krefftichthys anderssoni* density (individuals 1000 m⁻³) and biomass (g 1000 m⁻³) across the Scotia Sea during the day and night. No net hauls were collected during the daytime in autumn 2009 (JR200)
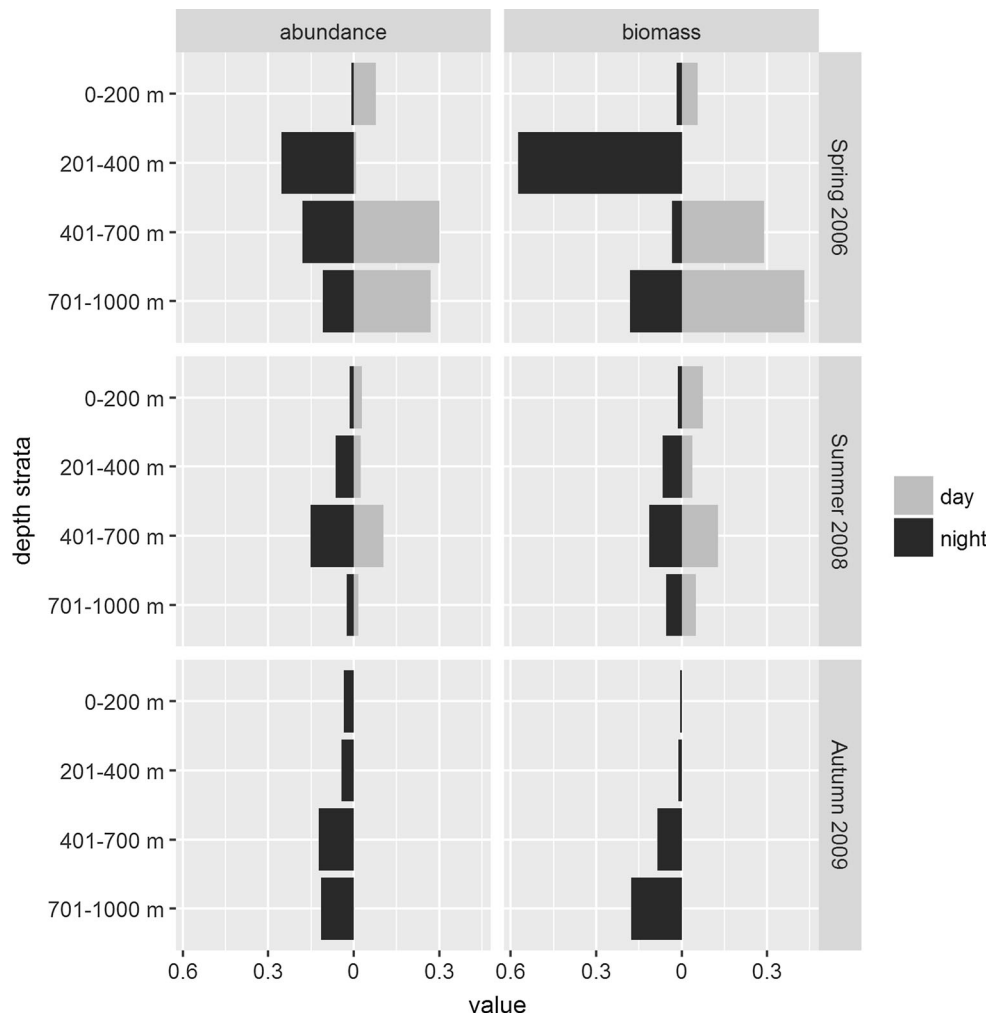
0-group from the time of hatching until the 31 July of the following year, to a group I from the 1 August to the 31 July of the next year and so on.

The overall size range of *K. anderssoni* post-larval stages was 15–75 mm SL, and the series of Kolmorov–Smirnov tests between seasons, regions and depth strata did
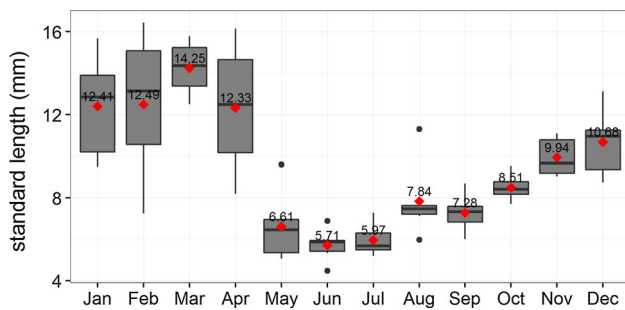
Fig. 3 Lanternfish *Krefftichthys anderssoni* larvae mean standard length by month. The *red dot* indicates the mean SL, whilst the *box* limits indicate the 25, 50 and 75 % quartiles. (Color figure online)

not show significant differences between frequency distributions (for all pairwise comparisons $p > 0.05$). Overall, length-frequency analyses suggested that the species had a post-larval life cycle of ~ 2 years (Fig. 4, Table 3). Although the data were not collected in consecutive seasons, the overall seasonal pattern in population structure appeared to be as follows. The spring population contained two size/age classes, the I-group (more than 1-year-old specimens, mode: 35 mm), composed by fishes hatched in the previous year winter, and II-group (more than 2-year-old specimens, mode: 60 mm). There was only little growth evident for these two cohorts in summer, with
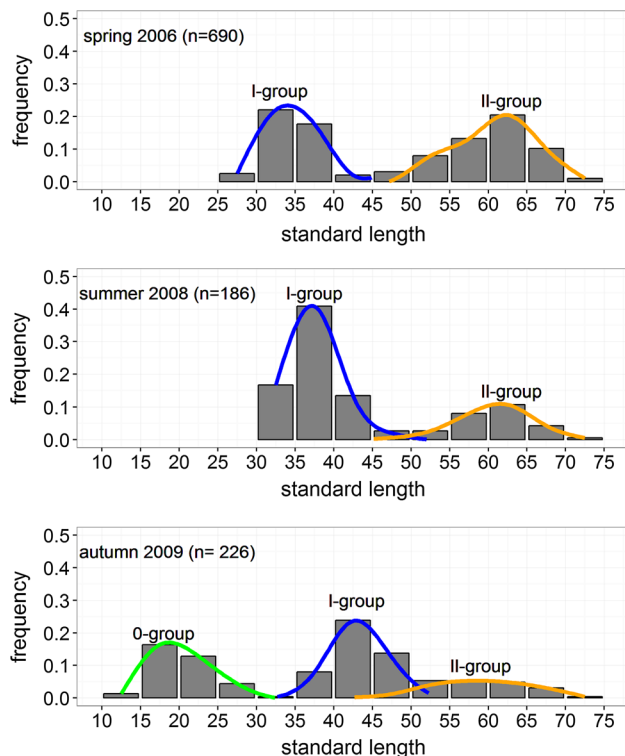

Fig. 4 Lanternfish *Krefftichthys anderssoni* standard length-frequency (mm, SL) distribution in the Scotia Sea by season. Mixture distributions (*solid lines*) were determined using Mixdist package in R

spreading of the II-group distribution as a result of a decrease in the population growth rate. Larvae hatched during the previous winter were first evident as the 0-group (specimens in the end of first year of life, mode: 20 mm) in the population in autumn. Both the I-group (mode: 43 mm) and remnants of the II-group (mode: 59 mm) were also evident at this time, suggesting a relatively high rate of summer growth for the I-group. The autumn groups 0 and I would presumably overwinter and recruit into the new I- and II-groups, respectively, the following July/August. Although Kolmorov–Smirnov tests did not reveal significant ($p > 0.05$) spatial variation in the population structure of *K. anderssoni* across the Scotia Sea, the length-frequency distributions showed important differences (Fig. 5). Three cohorts were present in the population at the PF, the 0-group (mode: 20 mm), I-group (mode: 39 mm) and II-group (mode: 57 mm), indicating that recruitment and growth had occurred in this region. By contrast, the 0-group was notably absent in open-ocean regions south of the APF in the Scotia Sea, with only I-group and II-group specimens present in the population in the northern sector (GB and NSS), and mostly II-group specimens present at the southernmost limit to the species core distribution around the MSS. This suggests that the species does not recruit in the oceanic regions of the Scotia Sea and that populations become dominated by older and larger specimens with increasing latitude into colder waters. The analyses also showed that the species' population structure varied with depth, as the 0-group was predominantly confined to the surface waters (0–200 m) and only I- and II-group specimens were present in the deeper layers (>200 m; Fig. 5, Table 3).

Diet analysis

A total of 374 stomachs were examined during the analysis, of which 97 (24 %) were found to be empty. The diet of *K. anderssoni* was mainly composed of copepods (80 % $IRI_{Copepoda}$), notably the species *Rhincalanus gigas* (59 %IRI), *Calanoides acutus* (14 %IRI) and *Calanus simillimus* (7 %IRI). Euphausiacea (10 %$IRI_{Euphausiacea}$), represented mostly by *Thysanoessa* spp. (14 %IRI), were the second most important prey group consumed. The species also consumed the amphipod *Themisto gaudichaudii*, but it only comprised a relatively minor part of the diet (1 %IRI) (Table 4).

Based on the %IRI_{DC}, seasonal, spatial and ontogenetic differences in the diet of *K. anderssoni* were apparent. Whilst the copepods *R. gigas* (spring: 61 %IRI; summer: 72 %IRI) and *C. acutus* (spring: 10 %IRI; summer: 24 %IRI) dominated the diet in spring and summer, there was a clear switch to *Thysanoessa* spp. in the autumn

Table 3 Age groups mean standard length by season, region and gender for the lanternfish *Krefftichthys anderssoni* across the Scotia Sea

	Mean SL ± SD (mm)			χ^2	df	p
	0-group	I-group	II-group			
Season						
Spring 2006		34.63 ± 3.05	60.10 ± 5.73	24.57	5	<0.0001
Summer 2008		37.48 ± 3.51	60.65 ± 4.85	2.98	3	0.394
Autumn 2009	20.45 ± 3.56	43.21 ± 3.50	58.83 ± 6.28	5.10	4	0.277
Region						
WSS & MSS		42.74 ± 14.33	61.06 ± 4.41	1.90	3	0.594
NSS		33.76 ± 5.83	61.42 ± 4.58	17.83	7	0.013
GB		36.36 ± 5.39	60.42 ± 5.79	83.46	7	<0.0001
PF	19.55 ± 2.19	39.40 ± 5.45	57.28 ± 6.84	3.89	4	0.421
Sex						
Females		37.81 ± 3.59	60.57 ± 5.76	18.79	5	0.002
Males		41.36 ± 6.16	60.24 ± 4.55	18.51	6	0.005

SL standard length (mm), *SL* standard length, *SD* standard deviation, *df* degrees of freedom, *WSS* western Scotia Sea, *MSS* mid-Scotia Sea, *NSS* northern Scotia Sea, *GB* George Basin, *PF* Polar Front

(78 %IRI; Fig. 6a). *Krefftichthys anderssoni* consumed mostly the copepods *Calanoides acutus* (30–40 %IRI), *Metridia spp.* (18 %IRI) and *Calanus simillimus* (14 %IRI) in the MSS and NSS, but further north its diet was dominated by *R. gigas* (59 %IRI) and *Thysanoessa* spp. (27 %IRI) in the GB and by *R. gigas* at the PF (73 %IRI) (Fig. 6b). Although the diet of all *K. anderssoni* size classes was dominated by the copepod *R. gigas*, size-related variations in diet were still apparent, as there was a progressive increase in *Thysanoessa* spp. consumption with increasing fish size (26 %IRI in larger fish), whilst smaller/younger individuals preyed more on *C. acutus* (29 %IRI) (Fig. 6c).

Discussion

Krefftichthys anderssoni is one of the most important myctophid species in the Scotia Sea, being an abundant, key prey species for a wide range of Southern Ocean marine predators (Guinet et al. 1996; Waluda et al. 2010). However, to our knowledge, this study is the first to detail information about the species distribution, life cycle, population structure and feeding ecology in different seasons at the ocean-basin scale in any region of the Southern Ocean. Myctophid fish are difficult to sample in this region and exhibit a relatively high degree of patchiness in their distribution patterns and population dynamics. Since data were collected in different years, and therefore possible inter-annual effects cannot be accounted for, such variation should be taken into consideration when interpreting the results.

Distribution patterns

During this study, *K. anderssoni* was caught between the APF and SACCF, which is consistent with other studies of this broadly Antarctic species in the region (Hulley 1981; McGinnis 1982; Duhamel et al. 2014). The species was most abundant in the northern regions of the Scotia Sea, particularly around the NSS and GB often attaining a greater density and biomass than some of the other larger myctophid species, such as *E. antarctica* and *G. braueri* (Saunders et al. 2014, 2015a). Although previous studies have hypothesized a close association between *K. anderssoni* and the APF (e.g. Koubbi et al. 2001), the present data support the concept that it also occurs in high density south of this front in the northern Scotia Sea (Piatkowski et al. 1994; Collins et al. 2008).

Vertical distribution

Krefftichthys anderssoni occurred predominantly below 200 m in circumpolar deep water (CDW) (Venables et al. 2012). Consistent with other studies in the region, there was evidence of DVM within this water mass, with individuals moving from below 400 m during the day to depths between 201 and 400 m at night (Piatkowski et al. 1994; Collins et al. 2008). Daytime net avoidance in the upper regions of the water column has been reported widely for many Southern Ocean myctophids (Collins et al. 2008), but part of the *K. anderssoni* population was caught in the surface layers (0–200 m) during daylight hours in our study. Daytime surface aggregations have been reported previously for this species off the Kerguelen Islands

Fig. 5 Lanternfish
Krefftichthys anderssoni length-frequency (mm, SL) distribution in the Scotia Sea by sampling region (*bar* diagrams in the *left column*) and by depth strata (*bar diagrams* in the *right column*). *PF* polar front, *GB* Georgia Basin, *NSS* northern Scotia Sea, *MSS* mid-Scotia Sea and *WSS* western Scotia sea. The curves indicate the normal distribution of the three age groups identified based on the mixture of distributions analysis. The *green line* represents the age group 0 (0-group); the *blue line* represents the age group 1 (I-group), and the *orange line* indicates the age group 2 (II-group). (Color figure online)
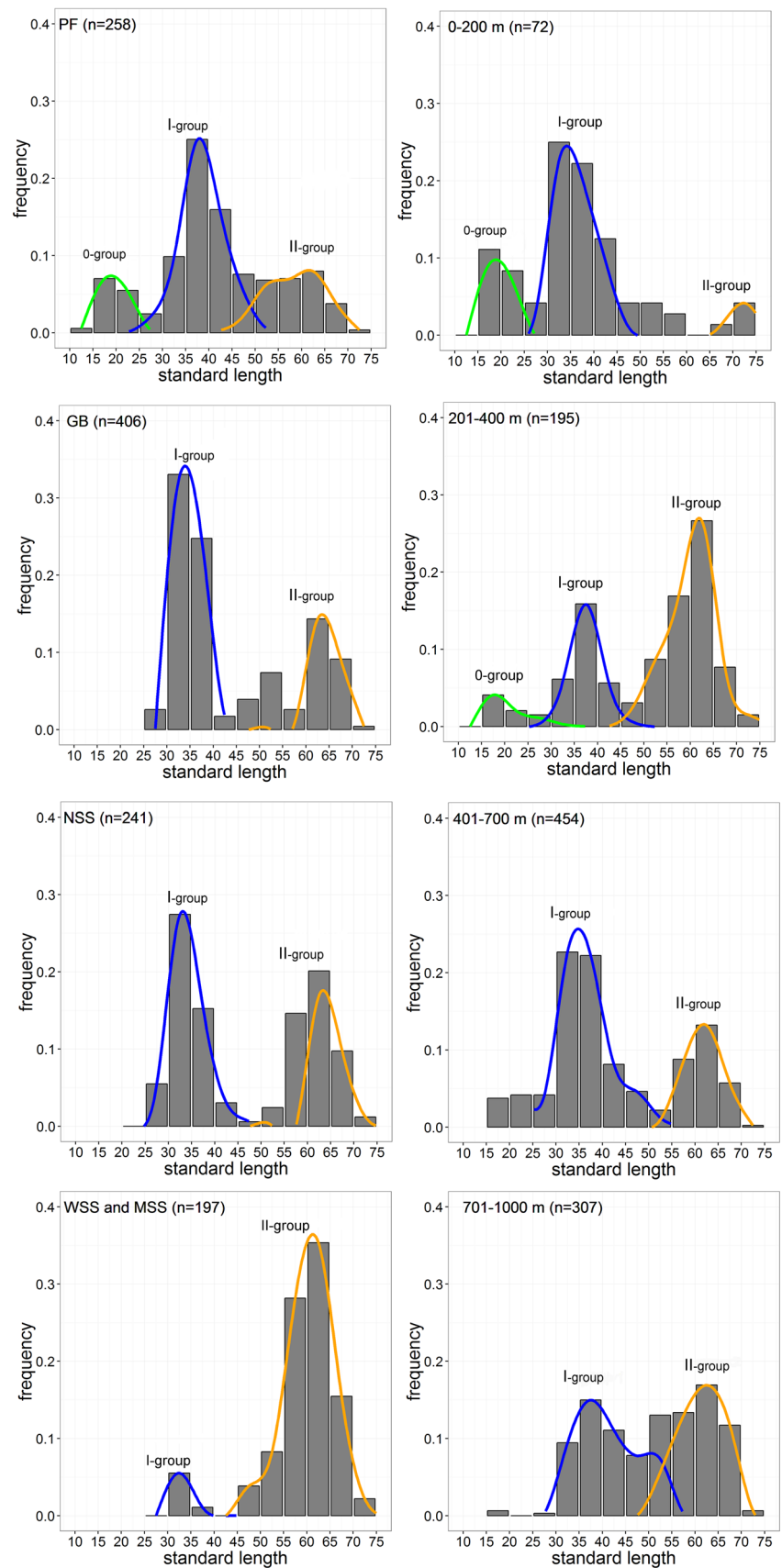
Table 4 Lanternfish *Krefftichthys anderssoni* diet composition by season and total sample

Prey	Spring (JR161)				Summer (JR177)				Autumn (JR200)				All seasons			
	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	%IRI	%N	%M	%F	% IRI
Amphipoda	4.79	6.99	15.20	1.43	0.78	1.08	10.77	0.13	0.45	0.99	4.65	0.09	3.34	4.99	12.54	0.88
Primno macropa	0.08	0.57	1.75	0.02	0.24	0.86	4.62	0.05	0.00	0.00	0.00	0.00	0.12	0.58	2.15	0.03
Themisto gaudichaudii	4.61	6.02	12.87	2.51	0.54	0.23	6.15	0.04	0.45	0.99	4.65	0.10	3.15	4.15	10.04	1.31
Vibilia antarctica	0.08	0.36	1.75	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.24	1.08	0.01
Unidentified amphipoda	0.03	0.04	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.03	0.36	0.00
Copepoda	86.71	57.41	77.19	88.71	96.28	84.45	86.15	97.21	66.59	17.16	20.93	24.06	87.88	59.40	70.61	87.72
Calanoides acutus	24.39	11.61	15.20	10.05	46.97	23.06	36.92	24.31	0.90	0.39	6.98	0.14	28.96	13.07	19.00	14.27
Calanus propinquus	1.52	2.06	7.02	0.46	0.06	0.13	1.54	0.00	0.00	0.00	0.00	0.00	0.99	1.40	4.66	0.20
Calanus simillimus	8.17	5.80	21.05	5.39	10.03	2.62	18.46	2.20	64.80	16.56	13.95	17.18	12.95	6.20	19.35	6.62
Clausocalanus spp.	0.26	0.07	4.09	0.02	0.78	0.13	6.15	0.05	0.00	0.00	0.00	0.00	0.39	0.08	3.94	0.03
Ctenocalanus spp.	1.33	0.23	1.75	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.86	0.15	1.08	0.02
Drepanopus spp.	3.95	0.07	0.58	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.55	0.05	0.36	0.02
Eucalanus spp.	0.55	0.77	3.51	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	0.51	2.15	0.03
Euchaeta spp.	0.34	0.61	3.51	0.06	0.12	0.10	1.54	0.00	0.00	0.00	0.00	0.00	0.25	0.43	2.51	0.03
Metridia spp.	9.06	2.35	25.73	5.39	0.54	0.23	12.31	0.09	0.67	0.17	6.98	0.09	6.04	1.63	19.71	2.70
Microcalanus spp.	0.03	0.01	0.58	0.00	0.00	0.00	0.00	0.00	0.22	0.06	2.33	0.01	0.03	0.01	0.72	<0.01
Pleuromamma robusta	0.26	0.25	2.92	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.16	1.79	0.01
Rhincalanus gigas	31.25	31.04	53.22	60.83	37.54	57.84	80.00	71.75	0.00	0.00	0.00	0.00	30.66	33.95	51.25	59.18
Unidentified copepoda	5.60	2.54	8.77	1.31	0.24	0.35	3.08	0.02	0.00	0.00	0.00	0.00	3.67	1.76	6.09	0.59
Euphausiacea	5.84	31.92	30.41	9.16	2.52	13.08	26.15	2.55	29.15	76.90	48.84	71.09	6.66	32.33	32.26	10.61
Thysanoessa spp.	5.39	28.04	20.47	12.56	1.38	11.95	7.69	0.96	29.15	76.90	48.84	78.39	6.05	29.49	21.86	13.89
Unidentified euphausiids	0.44	3.88	9.94	0.79	1.14	1.13	18.46	0.39	0.00	0.00	0.00	0.00	0.61	2.83	10.39	0.64
Ostracoda	2.17	0.95	2.92	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.40	0.63	1.79	0.06
Unidentified fish	0.03	0.01	0.58	<0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01	0.36	<0.01
salps	0.05	1.05	1.17	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.70	0.72	0.01
Unidentified Crustacea	0.26	1.24	5.85	0.16	0.06	0.30	1.54	0.01	0.45	0.72	4.65	0.08	0.22	0.97	4.66	0.10

Percentage number (%N), percentage mass (%M), frequency of occurrence (%F) and index of relative importance (%IRI) of items of each prey species are given with sums for prey categories
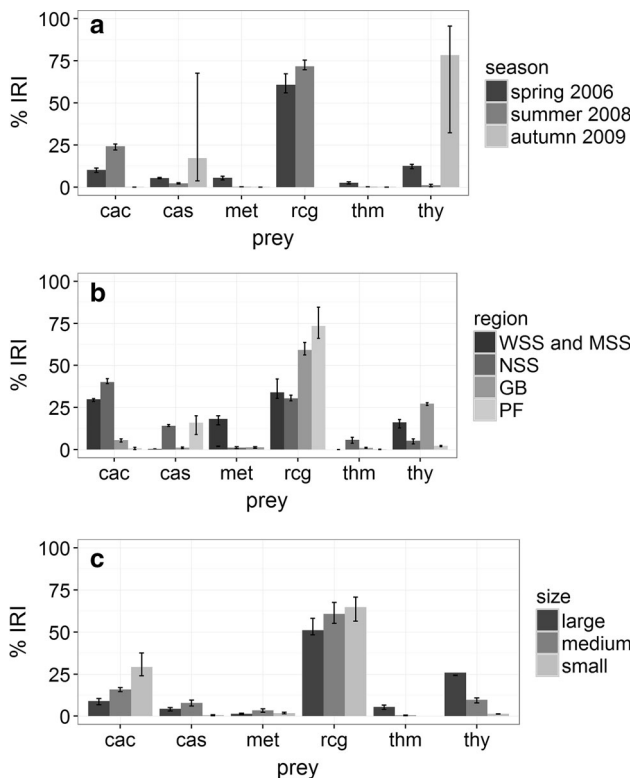
Fig. 6 Variations in the lanternfish *Krefftichthys anderssoni* diet in the Scotia Sea by **a** season, **b** region and **c** size. Diet is expressed as mean %IRI of the dominant prey categories (%IRI$_{DC}$) with 95 % confidence intervals. *cac Calanoides acutus*, *cas Calanus simillimus*, *rcg Rhincalanus gigas*, *met Metridia* spp., *thm Themisto gaudichaudii*, *thy Thysanoessa* spp.

(Indian sector of the Southern Ocean), which is consistent with both acoustic studies of myctophid schools at South Georgia (Saunders et al. 2013) and foraging studies of higher predators, such as King Penguins, in the northern Scotia Sea (Scheffer et al. 2010). Similar behaviour has also been reported for myctophids of the *Protomyctophum* genus in this region (Saunders et al. 2015b). Our data suggest that the daytime surface aggregations were attributable to specimens from 0-group and I-group, possibly reflecting extended surface feeding by juveniles in the warmer and more food-rich layers of the water column following DVM (Venables et al. 2012; Ward et al. 2012a).

There was clear seasonal variation in the depth distribution of *K. anderssoni*, with relatively high concentrations of specimens moving progressively to deeper layers of the water column between spring and autumn. Such behaviour is similar to that of other myctophids in the region, such as *Electrona carlsbergi*, *Gymnoscopelus fraseri* and *G. nicholsi*, although these species tend to be distributed higher in the water column (above 400 m) than *K. anderssoni* during all seasons (Saunders et al. 2014; 2015a). A seasonal deepening of mesopelagic fish populations is generally assumed to be a response to the winter deepening

of food resources within the deep scattering layers (DSL), such as overwintering copepods (Atkinson 1998; Dypvik et al. 2012; Pepin 2013). To a certain extent, our observations are in accordance with this hypothesis, as there was a seasonal deepening of the overwinter stages of the copepods *R. gigas* and *C. acutus* in the region (Ward et al. 2012a). However, these copepods, particularly *R. gigas*, occurred predominantly in regions above 400 m, as did the euphausiids *Thysanoessa* spp., which were the other main prey group consumed by *K. anderssoni*. The data further indicated that the seasonal migration was age specific, suggesting that factors other than predation on the DSL might also be important in driving this behaviour. For example, the aggregation of large, mature adults at depth in autumn may reflect mating behaviour prior to spawning in winter.

Population dynamics

Krefftichthys anderssoni had a life cycle of around 3 years (approximately 1 year as larva and 2 years post-metamorphosis), with seasonal growth apparent for all cohorts and clear spatial variation in population structure across the Scotia Sea (Hulley 1981; McGinnis 1982; Collins et al. 2008). Length-frequency analyses indicated that spawning and recruitment were predominantly confined to regions around the APF in oceanic waters and that the population became increasingly dominated by larger and older specimens with increasing latitude. This trend, which is also apparent for several other myctophids in the region (Saunders et al. 2014, 2015a), is indicative of an oceanic expatriate proportion of the population in the Scotia Sea that could be related to temperature following oceanic transportation of individuals from regions further north. For example, recruitment of this typically sub-Antarctic species may be inhibited in the cold oceanic waters of the Scotia Sea with only the larger specimens, being able to tolerate the colder temperatures at increased latitudes. Ontogenetic feeding/spawning migrations have also been suggested for myctophids in this region (Hulley 1981; McGinnis 1982; Zasel'sliy et al. 1985; Collins et al. 2008), although the adaptive advantage of such behaviour between regions of comparable food availability is unclear (Atkinson 1998; Ward et al. 2002, 2012a).

Small *K. anderssoni* specimens appeared in June and July, suggesting the species as winter spawner. Our data support the notion that the shelf waters around South Georgia are an important region for spawning and recruitment of *K. anderssoni* south of the APF (Collins et al. 2008; Belchier and Lawson 2013). Other studies have reported that the species has a life cycle and distribution pattern that is closely coupled with waters of the APF (Piatkowski et al. 1994; Koubbi et al. 2001, 2011), possibly

due to the warmer water temperatures and food availability associated with this region. Similarly, environmental conditions around the South Georgia shelf may be suitable for spawning, growth and recruitment of the species (Atkinson et al. 2001), enabling it to form a self-sustaining population in the northern Scotia Sea, a region south of its core distributional range. Interestingly, *K. anderssoni* could be one of the few biomass-dominant species that recruits successfully in the Scotia Sea south of the APF, as 0-group specimens and larvae are notably absent in population studies of all other common species in the region, including *E. carlsbergi*, *G. braueri*, *G. nicholsi* and *Protomyctophum bolini* (Rowedder 1979; Linkowski 1985; Piatkowski et al. 1994; Greely et al. 1999; Pusch et al. 2004; Collins et al. 2008; Donnelly and Torres 2008; Belchier and Lawson 2013; Saunders et al. 2014, 2015a). Larvae stages of *Electrona antarctica* were also absent in the Scotia Sea during these studies, although they have been reported south of the APF in regions elsewhere (Flores et al. 2008). Eggs of these other species have been reported in the Scotia Sea, although most appear to be associated with regions of the APF (Efremenko 1986), suggesting that recruitment may be confined to warmer waters further north.

Diet patterns

Krefftichthys anderssoni preyed on the most abundant species of the Southern Ocean zooplankton community (Boltovskoy, 1999; Ward et al. 2012a), particularly copepods and small euphausiids. The most important species consumed were the copepods *R. gigas*, *C. acutus* and *C. simillimus* and the euphausiids *Thysanoessa* spp., which became of greater importance in the diet during autumn. The results are broadly consistent with the spatially and temporally limited observations in the Scotia Sea and elsewhere (Pakhomov et al. 1996; Gaskett et al. 2001; Shreeve et al. 2009) and suggest that the diet of *K. anderssoni* depends on the seasonality and depth of zooplankton abundance (Atkinson et al. 2001). *Calanoides acutus*, *C. simillimus* and *R. gigas* are amongst the most abundant copepods of the Southern Ocean in the upper 400 m of the water column, with a depth distribution that changes throughout the year (Ward et al. 2012a). Our data showed a relatively high overlap between the vertical distribution patterns of *K. anderssoni* and these prey species in each season, suggesting that the species feeds on both diel and seasonally migrating copepods following DVM to regions higher in the water column at night (Ward et al. 2006, 2012a). There was also high overlap in the horizontal distribution patterns of *K. anderssoni* and these prey species across the Scotia Sea that may explain the southernmost extent of its broad-scale distribution pattern. For instance, there was a marked decrease in the abundance of the main copepods, particularly *R. gigas*, *C. acutus* and *C. simillimus*, in regions south of the SACCF,

which constituted the approximate boundary to this myctophids' southern range in the Scotia Sea (Ward et al. 2012a). This suggests that the species survival at these increased latitudes may be inhibited by both low water temperatures and insufficient availability of its main food source. Whilst the spring and summer diet of *K. anderssoni* was dominated by the copepods *R. gigas* and *C. acutus*, the species' diet shifted to euphausiids in the autumn, with *Thysanoessa* spp. being present in 77 % of the stomachs analysed. This change in prey was broadly consistent to changes in the abundance and biomass of the prey field. During spring and summer, the copepods *R. gigas* and *C. acutus* aggregated between 400 and 600 m (Ward et al. 2012a), which overlapped with the depth distribution of *K. anderssoni*. During autumn, the euphausiids *Thysanoessa* spp. became relatively more abundant in the prey field above the 400 m (Piatkowski et al. 1994; Ward et al. 2012a) even though far less abundant than copepods in the same region (Ward et al. 2012a). Shreeve et al. (2009) also identified the importance of small euphausiids in the diet of *K. anderssoni* during autumn. In the Arctic, species of the genus *Thysanoessa* are known to form swarms and to conduct DVM during autumn (Cottier et al. 2006). It is possible that the Antarctic species perform the same behaviour and could be consumed when moving to deeper waters where large *K. anderssoni* aggregate during autumn. The diet preference of *K. anderssoni* also changed with ontogeny. For example, whilst the smaller (<32 mm SL) and medium (32–60 mm SL) groups fed preferentially on copepods, the large and older animals (>60 mm SL) fed preferentially on *Thysanoessa* spp. Such changes in prey with predator size may be related to increased gape and swimming speed with predator size (Karpouzi and Stergiou 2003).

Our results suggest that *K. anderssoni* is a selective predator. Previous studies comparing the fatty acids signature of myctophids with their potential prey off the Kerguelen Plateau indicate that copepods of the genus *Oncaea* can contribute as much as 19 % of the diet of *K. anderssoni* (Connan et al. 2010). However, our results show that, in the Scotia Sea *K. anderssoni* do not feed directly on these copepods, even though being, along with *Oithona* spp. the most abundant copepods in Scotia Sea (Ward et al. 2012a). Also, only in the Mid Scotia region does the genus *Metridia* (mean sized and abundant copepods) feature substantially in *K. anderssoni* diet (18 %IRI). In contrast, *Protomyctophum bolini*, an equally small myctophid (20–70 mm SL), feeds mostly on *Metridia* spp. (Saunders et al. 2015b). Other evidence that suggests a high degree of prey selectivity in the *K. anderssoni* feeding behaviour is, as explained above, their preference of feeding on *Thysanoessa spp.* an apparently less abundant species when compared with copepods (Piatkowski et al. 1994; Shreeve et al. 2009). The selective predation seems to be common to several myctophid species in the Scotia

Sea. In their study, Saunders et al. (2015c) showed that several myctophid feed preferentially on the most nutritive prey as the copepodite older stages and on the euphausiid *Thysanoessa* spp., rather than the most abundant copepods as *Oithona* spp. and *Oncaea* spp.

Niche separation between coexisting myctophids

Krefftichthys anderssoni coexists with several other myctophid species in the Scotia Sea (Collins et al. 2008; Collins et al. 2012; Saunders et al. 2014, 2015a, b). Of the common species within this community, *P. bolini*, *E. carlsbergi* and *G. fraseri* have ostensibly similar distribution patterns or feeding habits to *K. anderssoni*. These species are indeed warmer water and cosmopolitan species that help to define the bioregion north of the SACCF (Ward et al. 2012b). However, a general examination of the life cycle strategies, diet, population dynamics and vertical distribution patterns of the four species suggests a degree of niches separation that may reduce interspecific completion and enable coexistence in the region (Barange 1990). *Krefftichthys anderssoni* (10–70 mm SL) and *P. bolini* (20–70 mm SL) are the smallest myctophid species found in the Scotia Sea with similar lifespan of 2 years (Saunders et al. 2015a). However, *P. bolini* seems to be less abundant than *K. anderssoni* and its vertical distribution is limited to 400 m, performing DVM to shallower waters (0–200 m) in spring and summer (Push et al. 2004; Saunders et al. 2015b). *Krefftichthys anderssoni* had a wider vertical distribution with density maxima between the 400 and 700 m. Its vertical distribution is also ontogenetically driven, with the bigger and older individuals being more abundant in the deeper waters, particularly below the 700 m. This is particularly relevant when both species seem to share at least one important prey, the copepod *R. gigas* (Saunders et al. 2015a). The larger DVM performed by *K. anderssoni* and the limited depth range of *P. bolini* suggest that whilst *K. anderssoni* feeds mainly during the night when it ascends to the shallower layers, *P. bolini* feeds constantly on the most common copepods around 400 m. *Krefftichthys anderssoni* also shows greater dietary diversity, with *Calanus acutus* and *C. simillimus* being common prey to the species.

Electrona carlsbergi adults were particularly abundant in NSS during spring, apparently competing with the *K. anderssoni* for prey (mainly *R. gigas* and *Metridia* spp.) (Shreeve et al. 2009; Saunders et al. 2014). However, *E. carlsbergi* attains significantly large sizes and has a larger lifespan (75–85 mm SL within 5 years, Linkowsky 1985) exhibiting a different life cycle strategy. Moreover, *E. carlsbergi* has a patchy distribution limited by depth, season and area to the upper strata of the water column (0–200 m) in NSS during spring. During spring, *K.*

anderssoni is more abundant in GB area along the entire water column performing large DVM. This means that although feeding on the same main prey (*R. gigas*) during spring, both these myctophid species do not seem to compete directly for space and prey.

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

The differences found between the four species growth rates, diet, spatial and vertical distribution appear sufficient to avoid direct competition for food and space in the northern Scotia Sea region. Indeed, previous studies on isotopic niches of myctophids of Kerguelen region (Cherel et al. 2010) and in the oceanic waters off Adélie land (Cherel et al. 2011) showed that the differences found in the nitrogen stable isotope ratio (^{15}N/^{14}N, δ^{15}N) and in the carbon stable isotope ratio (^{13}C/^{12}C, δ^{13}C) signatures revealed a strong niche segregation between the myctophid genera *Gymnoscopelus*, *Electona* and *Protomyctphum*. When comparing the stable isotope signatures of these species groups with *K. anderssoni*, in both studies the results show that the later present a significantly low δ^{15}N signature in the muscle, most probably due to the species small size and due to its diet dominated by herbivorous and omnivorous copepods (Ward et al. 1996; Atkinson 1998) that have a lower δ^{15}N signature (Stowasser et al. 2012). The apparent *K. anderssoni* specialization to feed on *Thysanoessa* spp. during autumn also contributes to the niche separation between these and the other myctophid species (Shreeve et al. 2009).

Conclusion

This study provides new insight into the ecology and trophodynamics of one of the most abundant myctophid species in the Scotia Sea, which is important for understanding the structure and dynamics of the Southern Ocean

food web and ecosystem. These data also contribute to resolving the biology, adaptations and dynamics of the global mesopelagic fish community, which is an essential prerequisite for understanding the functioning of the global open-ocean ecosystem and its biogeochemical cycles.

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