REGULAR PAPER

Age and growth of Brauer's lanternfish *Gymnoscopelus braueri* and rhombic lanternfish *Krefftichthys anderssoni* (Family Myctophidae) in the Scotia Sea, Southern Ocean

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ABSTRACT

This study examines age and growth of Brauer's lanternfish *Gymnoscopelus braueri* and rhombic lanternfish *Krefftichthys anderssoni* from the Scotia Sea in the Southern Ocean, through the analysis of annual growth increments deposited on sagittal otoliths. Otolith pairs from 177 *G. braueri* and 118 *K. anderssoni* were collected in different seasons from the region between 2004 and 2009. Otolith-edge analysis suggested a seasonal change in opaque and hyaline depositions, indicative of an annual growth pattern, although variation within the populations of both species was apparent. Age estimates varied from 1 to 6 years for *G. braueri* (40 to 139 mm standard length; L_S) and from 0 to 2 years for *K. anderssoni* (26 to 70 mm L_S). Length-at-age data were broadly consistent with population cohort parameters identified in concurrent length-frequency data from the region for both species. The estimated values of von Bertalanffy growth curves for *G. braueri* were $L_\infty = 133.22$ mm, $k = 0.29$ year^{-1} and $t_0 = -0.21$ year and the values for *K. anderssoni* were $L_\infty = 68.60$ mm, $k = 0.71$ year^{-1} and $t_0 = -0.49$ years. There were no significant ($P > 0.05$) differences in growth between sexes for either species, suggesting that males and females have similar growth and development trajectories in the Scotia Sea. A positive allometric relationship between L_S and wet mass was found for each species, as well as a significant ($P < 0.0001$) linear relationship between otolith size and L_S. Growth performance (Φ') was similar between the two species and congruent with other myctophid species across the Southern Ocean. This study provides important parameters for future Southern Ocean ecosystem studies in a resource management context.

KEYWORDS

body size, growth, morphology, Myctophidae, otoliths, Southern Ocean

1 | INTRODUCTION

Mesopelagic fishes represent a vast biomass in the world's oceans and are integral in the operation of oceanic ecosystems (Gjøsaeter & Kawaguchi, 1980; Pakhomov *et al.*, 1996; Irigoien *et al.*, 2014; Anderson *et al.*, 2019). However, they remain one of the least well-studied components of marine ecosystems, both globally and regionally (St. John *et al.*, 2016). The most common mesopelagic fishes are the lanternfish (family Myctophidae), comprising *c.* 245 species in 33 genera and occur throughout most of the world's oceans (Gjøsaeter & Kawaguchi, 1980; Catul *et al.*, 2011). In the Southern Ocean, myctophids are the most abundant and speciose fish group, with 35 species and an estimated biomass of between 70 and 200 million tonnes (Hulley, 1981; Lubimova *et al.*, 1987; Duhamel *et al.*, 2014). They are an integral part of the Southern Ocean food web, being both prey for many higher predators, including seals, sea birds, squid and large predatory fish (Rodhouse *et al.*, 1992; Reid & Arnould, 1996; Olsson & North, 1997; Cherel *et al.*, 2002; Collins *et al.*, 2007) and major consumers of zooplankton, including Antarctic krill *Euphausia superba* (Pakhomov *et al.*, 1996; Pusch *et al.*, 2004; Shreeve *et al.*, 2009; Saunders *et al.*, 2018). Myctophids also play an important role in Southern Ocean bio-geochemical cycles, as they provide a pathway for the substantial export of carbon between the sea surface and the deep ocean through their extensive vertical migrations (Pakhomov *et al.*, 1996). Despite their ecological importance, there is a paucity of information on their growth and life history (Rowedder, 1979; Linkowski, 1985; Greely *et al.*, 1999; Saunders *et al.*, 2017). This, in turn, has limited the representation of myctophids in Southern Ocean ecosystem models and confounded our understanding of how ecosystem-level processes, such as food web dynamics and biogeochemical cycles, operate in the region (Smetacek *et al.*, 2004; Hill *et al.*, 2007; Murphy *et al.*, 2007; Kock *et al.*, 2012).

The lack of data on Southern Ocean myctophids exists mostly because they have seldom been fished commercially, which has negated the need for their routine stock assessment and monitoring. They are also challenging to sample with trawl nets at the appropriate spatial and temporal scales. Aging methods, such as the analysis of growth increments deposited in sagittal otoliths, are difficult and often confounded for mesopelagic fish (Rowedder, 1979; Greely *et al.*, 1999; Campana, 2001; García-Seoane *et al.*, 2014), which has further limited studies to just a few species in the region. Most age-related studies of Southern Ocean myctophids are based on ages determined from annual rhythmic depositions (so called seasonal rings) in otoliths that are considered to represent time marks. Linkowski (1985) used this approach to estimate age, growth and preliminary mortality rates of Nichol's lanternfish *ymnoscopelus nicholsi* (Gilbert 1911) in the Scotia Sea and western South Atlantic Ocean. Similarly, age and growth were also estimated for both electron subantarctic lanternfish *Electrona carlsbergi* (Tåning 1932) and *Electrona antarctica* (Günther 1878), mostly in the south-west Atlantic Ocean, although the results remain inconclusive and debatable for the latter species (Rowedder, 1979; Zasel'sliy *et al.*, 1985; Konstantinova, 1987; Linkowski, 1987). Greely *et al*. (1999) further described age and growth in *E. antarctica* based on observations of primary growth increments that were assumed to represent daily growth depositions, albeit sample sizes were relatively small (*n* = 31) and validation was not accomplished, highlighting the need for further studies on Southern Ocean myctophids using both conventional and microstructural techniques.

Brauer’s lanternfish *Gymnoscopelus braueri* (Lönnberg 1905) and rhombic lanternfish *refftichthys anderssoni* (Lönnberg 1905) are two of the most common myctophids in the Southern Ocean, including the Scotia Sea (Atlantic sector; Collins *et al.*, 2008; Collins *et al.*, 2012; Duhamel *et al.*, 2014; Saunders *et al.*, 2015; Lourenço *et al.*, 2017), which is one of the most productive regions in the Southern Ocean (Holm-Hansen *et al.*, 2004). Recent studies in this region have cast new light on seasonal patterns of distribution, abundance, population dynamics and feeding ecology of these two species (Saunders *et al.*, 2015; Lourenço *et al.*, 2017). Both species are broadly Antarctic types that have a circumpolar distribution pattern and principally consume copepods and small euphausiids (Hulley, 1981; Saunders *et al.*, 2018). *Gymnoscopelus braueri* is a relatively large species, attaining a maximum size of around 162 mm standard length (L_S) and has an estimated life span of at least 4 years (Saunders *et al.*, 2015).

The species occurs throughout the Scotia Sea at depths between 0 and 1000 m, with the greatest concentrations occurring predominantly in waters < 400 m deep and some evidence of both seasonal and diel vertical migration (DVM) behaviour (Collins *et al.*, 2008; Saunders *et al.*, 2015). Vertical segregation in size classes and size-related sexual dimorphism are also apparent for this species in the region. In contrast, *K. anderssoni* is one of the smallest species in the Scotia Sea (*c.* 75 mm L_S maximum), with an estimated life span of *c.* 2 years (Lourenço *et al.*, 2017). The species is confined to the northern Scotia Sea (southernmost boundary at *c.* 56° S; Figure 1) and is predominantly deep-dwelling in waters below 400 m (Collins *et al.*, 2008; Lourenço *et al.*, 2017). However, there is evidence to suggest that it partially occupies shallower waters to feed, either through DVM behaviour or possibly foray-type vertical migrations (Scheffer *et al.*, 2010; Saunders *et al.*, 2018). Unlike *G. braueri*, *K. anderssoni* appears to recruit in the Scotia Sea, with spawning evident in the waters around the South Georgian shelf-break in the austral winter (July–August; Belchier & Lawson, 2013). Saunders *et al.* (2015) and Lourenço *et al.* (2017) describe the seasonal abundance, distribution patterns, population dynamics. In brief, *G. braueri* had an overall mean abundance ranging from 0.07 to 0.17 ind. 1000 m^{-3} in their survey area and the species was distributed throughout the Scotia Sea in all seasons. The species occurred at depths between 0 and 1000 m at night, with the greatest concentrations in the upper 400 m of the water column. *Krefftichthys anderssoni* attained an overall mean abundance between 0.04 and 0.12 ind. 1000 m^{-3}. However, the species was predominantly confined to the northern Scotia Sea in all seasons and seldom occurred at stations south of the Southern Antarctic Circumpolar Current Front (Figure 1). Its depth distribution ranged between 0 and 1000 m at night, but the greatest concentrations occurred predominantly at depths below 400 m.

Despite these recent advances in the ecology of these two species, there remain uncertainties regarding their growth patterns and life spans due to the issues that are inherent with length-frequency based cohort analysis (Campana, 2001). In this study, we examine the age and growth of *G. braueri* and *K. anderssoni* in the Scotia Sea through the analysis of sagittal otoliths collected as part of the most comprehensive myctophid fish surveys in the region to date (Collins *et al.*, 2012). We also examine otolith and body size relationships for these two species and compare their growth performance with that of populations of other myctophid species in the Southern Ocean. Our study provides important parameters for new food web, resource management and ecosystem studies in the Southern Ocean.

2 | MATERIALS AND METHODS

As required by the Antarctic Treaty (www.ats.aq), all research was conducted after a preliminary environmental assessment and under permits issued by the UK Foreign and Commonwealth Office and the Government of South Georgia and South Sandwich Islands. Fishes were collected as part of faunal surveys and no animal experiments were conducted. Therefore, no ethical approval was required.

2.1 | Study site

Four research cruises were conducted in the Scotia Sea (south-west Atlantic Ocean, *c.* 57° S, 40° W; Figure 1) onboard RRS *James Clark Ross* during March–April 2004 (research cruise JR100), October–December 2006 (JR161), January–February 2008 (JR177) and March–April 2009 (JR200). The 2004 survey was conducted in waters to the north-west of South Georgia (Collins *et al.* 2008), whilst surveys between 2006 and 2009 covered the region from the ice-edge to the Antarctic Polar Front (APF), with sampling stations spread across the predominant water masses and frontal zones in the region (Collins *et al*. 2012).

2.2 | Sample collection and processing

Mesopelagic fish were collected using two 25 m^2 rectangular mid-water trawl nets (with 5 mm mesh at the cod end) that can be opened and closed sequentially *via* an electronic down-wire unit (RMT25; Piatkowski *et al.*, 1994). The net was towed obliquely at *c*. 4.6 km h^{-1} for 30–60 min in each depth zone and each deployment was monitored in real-time using a custom-built net monitoring system that also logged depth and temperature. At each station, depth-stratified hauls were undertaken at 0–200, 200–400, 400–700 and 700–1000 m. These zones were sampled by day and night in spring 2006 (JR161), summer 2008 (JR177) and autumn 2004 (JR100), but sampling was conducted only during hours of darkness in autumn 2009 (JR200). Additional net hauls were also undertaken opportunistically on acoustically detected mesopelagic fish aggregations during each survey. In total, 283 hauls were conducted during the study period.

Net samples were sorted onboard to the lowest taxonomic level possible (Hulley, 1990). Total catch mass per species were recorded using a motion-compensated balance. All fish standard length (L_S, mm) were measured and frozen at –20 °C for subsequent analysis. At the laboratory, otoliths were dissected from a random sub-sample of 10–25 fish per haul or from each fish where catches were small. Prior to otolith extraction, fish were re-measured and weighed to the nearest 0.01 g. Sex and maturity status was also recorded, where possible, as described in Saunders *et al.* (2017). Additional length–mass data were obtained from random sub-samples that were processed concurrently for mesopelagic fish dietary studies.

2.3 | Age and growth analyses

Age determination by the observation of growth increments in the otoliths was attempted for *G. braueri* and *K. anderssoni*, with 177 and 118 undamaged otolith pairs selected at random for each species, respectively. Following Panfili *et al.* (2002), otoliths were immersed in 96% ethanol and their lateral face was viewed under a microscope over a dark-background under reflected light. Growth rings were counted across the posterior dorsal radius from the nucleus to the otolith edge (Figures 2, 3). Following previous studies of Southern Ocean and high latitude myctophids, it was assumed that one annual growth ring consisted of one opaque and one translucent band while allowing for the presence of many split increments (Smoker & Pearcy, 1970; Gjøsaeter, 1973; Linkowski, 1985; Konstantinova, 1987; Linkowski, 1987). Otoliths were examined independently by two readers. During instances when there were differences in age, otoliths were re-examined by both readers until a consensus was reached. Data were subsequently omitted where no consensus was possible (< 3% of records per species). The type of otolith edge (either opaque or hyaline) was also recorded.

As well as a temporal otolith edge analysis (Campana, 2001), length-at-age data were compared with concurrent length-frequency data to partially substantiate the aging criteria. Both length-frequency and length-at-age data were selected from periods when all discernible cohorts were present and presumably recruiting in their respective populations (summer and autumn for *G. braueri* and *K. anderssoni*, respectively; Saunders *et al.*, 2015; Lourenço *et al.*, 2017). Component-fitting software (CMIX; de la Mare, 1994) was used to fit normal distributions to composite length-frequency data and identify cohort modes following the procedure detailed in Saunders *et al.* (2007). In brief, a series of runs were performed during the analysis based on the presence of one to four cohorts in the data. The best component fit to the observed data was determined using a χ^2-test. No constraints were placed on the mean length, variance or proportions expected within each component when fitting the mixed distributions.

Growth curves were calculated by fitting the von Bertalanffy growth model (VBGM) to the observed data (Essington *et al.*, 2001): $L_t = L_\infty\,[1 - e^{-k(t-t_0)}]$, where L_t refers to the average L_S (mm) at age t, k is the growth coefficient (year^{-1}), L_∞ is the asymptotic average L_S and t_0 is the notional average age at length zero. Initial parameters for the growth model were estimated using the Ford-Walford plot method prior to fitting the VBGM using least-squared non-linear regression (Walford, 1946). Approximate ± 95% confidence intervals for the growth models were calculated using a bootstrapping technique, whereby growth parameter residuals were re-sampled to generate multiple datasets (1000 iterations with replacement), from which multiple model fits were obtained. Percentiles of the predicted values from the many model fits were then used to represent the confidence intervals of the non-linear VBGM (Zuur *et al.*, 2007). Likelihood-ratio tests were used to compare VBGM curves between sexes (Kimura, 1980), where possible and the growth performance index (Φ') was estimated for each species to facilitate comparisons of growth between other species in the Southern Ocean (Pauly, 1979; Pauly & Munro, 1984): $\Phi' = 2 \log L_\infty + \log k$

2.4 | Otolith measurements

The relationships between L_S and otolith length and width were examined for *G. braueri* and *K. anderssoni* using linear-regression analysis (Zuur *et al.*, 2007). The relationship between fish age and otolith size was also examined for the two species. Measures of both otolith length (L_O) and width (W_O) were taken to the nearest 0.001 mm using a microscope and a calibrated eyepiece graticule following Williams and McEldowney (1990). L_O was defined as the greatest distance from the anterior tip to the posterior edge and W_O was defined as the greatest distance between the otolith dorsal and ventral margins. Where possible, both otoliths from each pair were measured and a Wilcoxon signed-rank test was conducted to test for differences between relationships for measurements derived from left and right otoliths. Differences between sexes were not examined here, primarily due to insufficient sex-resolved data.

2.5 | Length-mass relationships

Standard length (L_S) to total mass (M) relationships were examined through the simple non-linear regression model: $M = aL_S^b$, where a and b are constants of the regression. Differences between length-mass relationships for males and females were examined using an analysis of covariance (ANCOVA). For this procedure, length and mass data were log (ln) transformed and relationships for each sex and both sexes combined were fitted using linear regression. This enabled an examination of ANOVA probability values from the interaction of L_S on W by sex and a comparison of the slope coefficients for each sex in the linear regressions.

3 | RESULTS

3.1 | Age and growth analysis

3.1.1 | *Gymnoscopelus braueri*

A total of 177 undamaged otolith pairs were examined from *G. braueri*, with specimens in the otolith sub-sample ranging between 40 and 139 mm L_S. Distinct hyaline and opaque zones were apparent in the otoliths of this species (Figure 2) and consensus in age readings was established for 171 otolith pairs between the two observers. Like its congener *G. nicholsi*, a faint narrow hyaline ring was present around the small opaque zone around the nucleus(Figure 2), which was regarded as an auxiliary larval ring and therefore disregarded during the counting process (Linkowski, 1985).

Determination of the nature of the otolith edge was difficult in *G. braueri*, particularly in the older age groups where the newly formed narrow opaque zones were difficult to separate from a previous hyaline zone. We found that only < 16% of otoliths from specimens older than 3 years had a discernible opaque edge, regardless of season. However, newly formed opaque zones were more distinguishable in otoliths from specimens < 3 years old and there was evidence of a seasonal pattern in the type of otolith edge in this group. In spring, most otoliths (80%) were characterised by a narrow hyaline edge, whilst most otoliths (65%) had an opaque edge during summer and autumn. However, the temporal pattern in otolith edge formation across the whole population also appears complex at the broad spatiotemporal scale of the study, as a relatively high proportion of otoliths had hyaline edges during the main productive season. Based on the assumption that the observed sets of alternating hyaline and opaque represented annual growth marks, *G. braueri* attained a maximum age of *c.* 6

years. Specimens < 1 year old were absent in the region, which was not attributable to the net mesh size (Saunders *et al.*, 2017).

Relatively high variation in body size was apparent for age classes between 2 and 5 years, with a difference in size of *c.* 60 mm L_S between the smallest and largest specimens per age class (Figure 4a). However, comparisons of the estimated means, modes and 25–75th percentiles showed that there was consistent overlap in the overall size distributions of the identified age and length-frequency based year (and putative age) classes for specimens between 1 and 3 year (Figure 4a). The exact timing of spawning in *G. braueri* remains unknown, although there is evidence to suggest that hatching is timed to coincide with the main phytoplankton bloom in spring (September–October; Hulley, 1981; Efremenko, 1986). Following Saunders *et al.* (2015), we assumed that hatching and recruitment occurs in October, such that age 1+ year specimens sampled in spring, summer and autumn would be around 13, 15 and 18 months old, respectively. Similarly, 2+ year specimens would be 25, 27 and 30 months old in these respective seasons, whilst 3+ year specimens would be 37, 39 and 42 months and so on for the subsequent year classes. In this way, an approximation of seasonally resolved age-at-length data was derived and the estimated VBGM parameters for the sample population were L_∞ = 133.22 mm (95% CI = 113.76–231.67, t = 7.63, $P < 0.001$) k = 0.29 (95% CI = 0.09–0.50, t = 2.55, $P < 0.01$) and t_0 = –0.21 (95% CI = –1.96 to 0.50, t = –0.49, $P > 0.05$; Figure 5a). Growth curves were not significantly different between males and females from the available data ($P > 0.05$). The growth performance index for *G. braueri* was 3.71.

3.1.2 | *Krefftichthys anderssoni*

A total of 118 undamaged otolith pairs were examined for *K. anderssoni* ranging between 26 and 70 mm L_S, but only 15 specimens were < 35 mm L_S. Otoliths of this species were characterised by narrow opaque bands followed by broad hyaline, presumable reflecting seasonal differences in growth (Figure 3). The nature of the otolith edge was most clear in specimens < 2 years old, with some evidence of seasonal changes in the sequence of hyaline and opaque edges. We found that 56% of otoliths were characterised by a hyaline edge in spring and 69% had an opaque edge in summer and autumn. However, the temporal pattern in otolith edge formation across the population appears complex in this species at a broad spatiotemporal scale. Assuming the deposition patterns to be annual growth increments, *K. anderssoni* attained a maximum age of *c.* 2 years, with consensus in age readings established for all samples between the two observers.

There was relatively high variation in the size range of specimens for each age class, particularly in the 1+ year class (37–67 mm L_S), but there was broadly consistent overlap in the overall size distributions of 1 and 2 year old age classes identified from both otolith and length-frequency based cohort analyses (Figure 4b). Robust size comparisons between the length-at-age and length-frequency data were not possible for the 0 year group, as there were too few otoliths taken from specimens < 35 mm L_S and the data were therefore not fully representative of the size range of this cohort. However, the available data support the assumption that the defined annuli criteria for *K. anderssoni* otoliths represented annual growth, since the majority of 0 year class individuals fell below the 25th percentile of the size distribution for the subsequent 1 year age group–1 year class (Figure 4b).

Based on published data, we assumed that hatching and recruitment in *K. anderssoni* commences from late autumn (April–May), such that 0 year specimens sampled in autumn, spring and summer would be around 0, 6 and 8 months old, respectively (Belchier & Lawson, 2013; Lourenço *et al.*, 2017). Similarly, 1 year specimens collected in autumn, spring and summer would be *c.* 12, 18 and 20 months old, respectively, whilst 2 year specimens would be *c.* 24, 30 and 32 months old in these respective seasons. VBGM parameters for *K. anderssoni* were L_∞ = 68.60 mm (95% CI = 61.53–105.41, t = 11.26, $P <$ 0.001), k = 0.71 (95% CI = 0.23–1.18, t = 2.85, $P < 0.01$) and t_0 = –0.49 (95% CI = –1.48 to –0.12, t = –1.76, $P > 0.05$) based on this approximation model (Figure 5b). Likelihood ratio tests revealed no significant differences in growth between sexes based on the available data ($P > 0.05$). The growth performance index for *K. anderssoni* was 3.52.

3.2 | Length-mass relationships

3.2.1 | *Gymnoscopelus braueri*

The relationship between L_S and wet mass (M) was examined for a total of 888 *G. braueri* specimens collected across the Scotia Sea between 2006 and 2009. Of the *G. braueri* specimens analysed, 33% were female, 23% were male and 44% were immature–juvenile. The size of *G. braueri* females ranged from 59 to 140 mm L_S and their mass from 1.26 to

19.49 g. Male *G. braueri* were smaller in size, ranging from 41 to 128 mm L_S and 1.05 to 19.52 g. Immature–juvenile specimens ranged from 34 to 95 mm L_S and 0.25 to 6.55 g. The length-mass relationship showed positive allometric growth, regardless of sex (Figure 6a). Linear regression of the log transformed data was used to compare the relationship between sexes and there was no significant difference ($F_{1, 494} = 0.2482$, $P > 0.05$) in the relationships of L_S to M between males (slope $b = 2.84$) and females (slope $b = 2.90$).

3.2.2 | *Krefftichthys anderssoni*

A total of 671 *K. anderssoni* specimens were collected in the northern Scotia Sea between 2006 and 2009 for the length-mass relationship analysis. The sample set comprised 39% females, 24% males and 37% immature–juvenile specimens. Both *K. anderssoni* males and females ranged from 31 to 74 mm L_S, with females having slightly greater mean size than males (mean ± SD female = 56.31 ± 11.13 mm compared with male = 51.67 ± 11.43 mm). The mass of females ranged from 0.21 to 4.16 g and from 0.28 to 3.94 g for males. Immature–juvenile specimens were between 27 and 67 mm L_S and between 0.14 and 3.30 g M. The length-mass relationship showed positive allometric growth for the species (Figure 6b). Linear regression analysis of log transformed data showed that there was no significant difference ($F_{1, 422} = 1.5301$, $P > 0.05$) in the relationship of L_S to M for males (slope $b = 2.86$), or females (slope $b = 2.93$).

3.3 | Otolith morphometrics

Analyses showed no significant differences in size between left and right otoliths for either species examined (W_O = 14126 μm, $P > 0.05$ for *G. braueri* and W_O = 13380 μm, $P > 0.05$ for *K. anderssoni*), so mean values for each otolith pair were calculated for examining the relationship between L_S and otolith size. Significant linear relationships between L_S and L_O ($F_{1,\,490}$ = 2875.04, $P < 0.001$) and W_O ($F_{1,\,490}$ = 3742.25, $P < 0.001$) were observed for *G. braueri* (Figure 7a). Otolith width was the best predictor of body size based on the R^2 values of the regression fits. Significant linear relationships between L_S and L_O (L_O; $F_{1,\,229}$ = 975.06, P<0.001) and otolith width W_O ($F_{1,\,229}$ = 1397.17, P<0.001) were also observed for *K. anderssoni*, with the latter being the best predictor of body size based on the R^2 values of the regression fits (Figure 7b).

4 | DISCUSSION

4.1 | Sampling considerations

This study provides estimates of age and growth of *G. braueri* and *K. anderssoni* in the Southern Ocean using otolith-based aging methods. Sampling mesopelagic fish in the remote Southern Ocean at a comprehensive temporal and spatial resolution is challenging and, consequently, there are several caveats that need to be considered with the data. For instance, our growth analyses were based on sample sizes of < 180 otoliths per species, with a relatively low number of replicate observations per individual length class across the size ranges of each species. Our data were also pooled across samples collected over a large spatial scale in both different seasons and years, so possible spatial and temporal effects cannot be accounted for. These factors are likely to have contributed substantially to the relatively high level of variation observed in the length-at-age data and our otolith edge analysis, as there is relatively high spatial heterogeneity in mesopelagic fish distribution patterns, population dynamics and behaviour associated with the dynamic oceanographic processes in the region. Our study therefore highlights the complexity in determining age and growth of myctophid fish in the region. However, our results are broadly consistent with studies of other Southern Ocean myctophids (Linkowski, 1983, 1987) and with mesopelagic fish in other temperate and high latitude regions (Smoker & Pearcy, 1970; Gjøsaeter, 1973). Despite all of these issues, we believe that our data are the best that is available to date and our parameters provide an step forward for future food web, ecosystem management and biogeochemical modelling studies in the Southern Ocean.

4.2 | Methodolical and validation issues

Interpretation of the deposition patterns in the otolith structures of Southern Ocean myctophids is complex (Greely *et al.*, 1999). Conventional age determination in teleosts is usually implemented by counting the sequence of opaque and translucent zones on sagittal otoliths that are presumed to be deposited annually. In temperate waters, the formation of translucent zones is considered to occur during winter, whereas opaque zones are formed during more rapid periods of growth in summer (Campana, 2001). These differences in fish otolith bio-mineralisation are linked to temporal fluctuations in metabolism, food intake and ambient temperature (Høie *et al.*, 2008; Neat *et al.*, 2008). However, it has been suggested that interpretation of these seasonal patterns is confounded in fish species that reside at high latitudes where annual periodicity in hydrographic conditions, particularly temperature, are less pronounced (Radtke, 1987; Radtke *et al.*, 1989; Greely *et al.*, 1999). Nevertheless, seasonality in the composition, abundance and behaviour of the zooplankton prey is apparent across the mesopelagic zone at high latitudes, which is also likely to have a large influence on metabolism and growth and hence biomineralization patterns in otoliths (Mackas *et al.*, 2012; Ward *et al.*, 2012). Our study further demonstrates the complexity in interpreting myctophid otolith deposition patterns, as we found that, although most *G. braueri* and *K. anderssoni* otoliths were characterised by opaque edges in summer and hyaline edges in spring, this seasonal pattern was not uniform across all individuals within the respective populations at the resolution of our data. Definitive validation of annual growth depositions in otoliths therefore remains a major challenge for myctophids in this remote oceanic region, where it is difficult to sample congruent populations appropriately at the temporal resolution (*e.g.*, monthly) required for the application of the most feasible validation methods, such as marginal increment analysis (MIA). Furthermore, the technical and methodological difficulties that have further hindered the application of robust MIA in any Southern Ocean myctophid study to date are detailed in Campana (2001).

Microstructural analysis methods using scanning electron microscopy (SEM) are being increasing applied to mesopelagic fish species around the globe, particularly larval stages and are considered to represent an improvement over conventional aging methods

(Gjøsæter, 1987; Gartner, 1991; Linkowski *et al.*, 1993; Linkowski, 1996; Moku *et al.*, 2005; Bystydzienska *et al.*, 2010; Campana *et al.*, 2016). The SEM approach determines growth from presumed daily (as well as other periods, such as lunar episodes) increments in otoliths, which, in some instances, have been validated for some species, through MIA (Morales-Nin *et al.*, 2000; Dwyer *et al.*, 2003; Moku *et al.*, 2005; Campana *et al.*, 2016). However, these methods are complex, time consuming and costly, which has limited their use for routine stock assessments of many commercial target species and restricted their utility for mesopelagic species that are both practically and logistically challenging to sample. As with conventional methods, definitive validation also remains challenging with the SEM approach (Gjøsaeter, 1981, 1987; Linkowski *et al.*, 1993; Greely *et al.*, 1999). To date, only one SEM study has focused on any Southern Ocean species quantitatively (*E. antarctica*), which highlights the need for further studies to substantiate the applicability of both SEM and conventional techniques for aging Southern Ocean myctophids (Greely *et al.*, 1999).

4.3 | *Gymnoscopelus braueri*

In this study, we found a clear and consistent contrast between translucent and opaque zones in *G. braueri* otoliths that appeared to represent an annual growth pattern, as has been observed for its congener, *G. nicholsi* (Linkowski, 1985). Although comprehensive validation was not possible in this study, there was a broad overlap in the size distributions of cohorts identified through otolith-based and length-frequency-based methods, providing a degree of confidence in our analytical criteria, at least for the early year classes in the population (1–3 year old). This partial validation is consistent with the otolith-based aging criteria devised for *G. nicholsi* by Linkowski (1985). Our results indicate that *G. braueri* attains a maximum age of around 6 years in the Scotia Sea region. Our data highlight the problems associated with length-frequency based population analyses of this species, as such methods are unable to resolve ages classes older than 4 years due to specimens between 4 and 6 years old being indiscernible in size (Saunders *et al.*, 2015). This effect has also been reported widely for many oceanic fish species, including *G. nicholsi* in the Scotia Sea (Linkowski, 1985, 1987; Campana, 2001). As a consequence, a substantial component of the population is likely to be underrepresented using length-frequency based methods, which has implications for effective representation of *G. braueri* population dynamics in Southern Ocean food web, biogeochemical and ecosystem models. The study therefore demonstrates that otolith-based aging is necessary for future *G. braueri* population studies.

Our analyses suggest that, although *G. braueri* females attain a larger size than males, they have similar growth trajectories in the Scotia Sea. This was supported by our analysis of length-mass relationships in the species, which appeared not to be sex-specific. Sex-specific growth patterns have been found in several mesopelagic fishes, including Southern Ocean *Electrona* spp., which are considered to reflect differences in growth and maturation strategies between males and females (Linkowski, 1985, 1987; Greely *et al.*, 1999). Our results suggest similar strategies in growth and development between *G. braueri* sexes in the region, which may be indicative that the females of this species experience reduced reproductive development relative to growth in the region, thus restricting their potential to attain reproductive capacity. The possibility that *G. braueri* forms non-reproducing sink populations in waters south of the Antarctic Polar Front, as shown by the consistent absence of 0 group specimens (< 40 mm L_S) across seasons, was hypothesised by Saunders *et al.* (2017), who further suggested that the species may not reach full reproductive condition and spawn successfully in the region due to the cold water temperatures (Oven *et al.*, 1990). However, more sex-resolved otolith data collected across the full-size range of the species and across its full distributional range, are required to substantiate this fully.

A further consequence of the possibility that *G. braueri* is only an expatriate migrant in the Scotia Sea, is that our parameters of growth in this colder region is not fully representative of growth across its distributional range. Although Belcher *et al.* (2019) found little evidence of regional variation in the species' respiration rates across the *c.* –1 to +4°C temperature range of the Scotia Sea, populations of *G. braueri* appear to be centred at sub-Antarctic and temperate latitudes, where growth, recruitment and metabolic process take place in much warmer conditions (Hulley, 1981; McGinnis, 1982), raising the possibility of regional differences in life cycle strategies. Higher rates of growth at lower latitudes, together with variations in the timing of fish migrating, or being advected, southwards into the Scotia Sea may therefore explain some of the observed variability in our length-at-age data for this species. Additionally, our growth data were only applicable to age classes > 1 year old, as younger components of the population were consistently absent from populations in regions south of the APF. Our VBGM parameters are therefore potentially unrepresentative for the early life stages (< 1 year and *c.* 40 mm L_S) of this species and estimates of larval growth remain unknown. Sampling in regions at lower latitudes is clearly required to investigate the growth patterns across the full lifecycle of this species, as well as to substantiate possible regional differences in growth patterns as a function of differences in underlying temperature regimes.

4.4 | *Krefftichthys anderssoni*

Our study found clear translucent and opaque zones in *K. anderssoni* otoliths that appeared to represent a distinct annual growth pattern in most specimens. Congruent with length-frequency based analysis, the species had a lifespan of *c.* 2 years (Lourenço *et al.*, 2017). The presence and absence of apparent annual growth depositions in the otoliths of this predominantly deep-dwelling species, is interesting given that Scotia Sea population appears to reside predominantly in the thermally stable circumpolar deep water throughout the year, where seasonality effects in environmental conditions, particularly temperature, would be expected to be less pronounced. The species also appears to occupy only a narrow thermal range throughout the Scotia Sea, which is centred around *c.* 2 °C (Saunders & Tarling, 2018). However, recent studies in the region have found relatively small proportions of *K. anderssoni* in the surface layers, both at night and during the day, suggesting foray-type vertical migration behaviour that would expose some parts of the population to distinct seasonality in temperature regimes in the upper 200 m of the water column (Collins *et al.*, 2008; Lourenço *et al.*, 2017). Trophodynamics studies of *K. anderssoni* in the Scotia Sea also show that, although the species resides predominantly at depths below 400 m across seasons, its diet is largely comprised of copepods, small euphausiids and amphipods that are found in the upper 200 m of the water column, suggesting surface feeding through foray type vertical migrations. Therefore, different components of the population may be subjected differently to the effects of marked seasonal variations in temperature, productivity and prey field abundance and composition (Venables *et al.*, 2012; Ward *et al.*, 2012) throughout the lifecycle across its distributional range, which may partially explain the apparent annual nature of the growth depositions in some otoliths, but not others.

Growth in *K. anderssoni* was previously examined by Belchier and Lawson (2013) and Lourenço *et al.* (2017) in the coastal waters around South Georgia. These studies reported growth rates of the early life stages (< 16 mm L_S) of the species that were slower than would be expected from our growth model. However, comparisons of the results from these studies are confounded, since the ichthyoplankton surveys conducted in the South Georgian coastal waters only sampled to a maximum depth of 25 m, which may have missed the larger sized larval specimens residing deeper in the water column. Distinct vertical separation in size-classes in fish larvae are commonly observed, whereby depth distribution increases progressively with increasing size and ontogeny (Sassa & Kawaguchi, 2005). Also, our growth model was largely confined to post-larval stages > 35 mm L_S, as *K. anderssoni* appear to be absent in the oceanic waters of the Scotia Sea, which further biases comparisons with previous growth studies in the region. As with *G. braueri*, further data collected at a finer temporal resolution across the entire distributional range of *K. anderssoni* are required to substantiate the growth patterns of this predominantly sub-Antarctic species and investigate possible regional variations in growth and life cycle processes under different environmental regimes (Hulley, 1981).

4.5 | Comparisons of Southern Ocean myctophid growth

Comparisons of the available growth curves for Southern Ocean myctophids indicate that there is considerable inter-specific variation in growth and hence life cycle characteristics (Figure 8a). For example, *G. braueri* attains a much greater size and longevity than *K. anderssoni* and appears to have a greater rate of growth over comparable age classes. Linkowski (1987) compared growth curves for Southern Ocean *Electrona* spp. and hypothesised that differences in growth parameters for Antarctic and sub-Antarctic–temperate species were consistent with their broad-scale distribution patterns, as species solely occupying waters south of the APF (*E. antarctica*) through the life cycle had slower growth rates than their more northern counterparts, *E. carlsbergi* and flaccid lanternfish *Metelectrona ventralis* (Becker 1963). This notion was supported by Greely *et al.* (1999), although rates of growth and longevity of *E. antarctica* were considered to be lower than previously observed. However, Pauly (1979) highlighted the difficulties inherent with comparing the growth curves of different organisms and taxa and hypotheses regarding inter-specific variations in Southern Ocean myctophid growth, therefore, remain unsubstantiated. To address this, we complied VBGM parameters from the available studies on Southern Ocean myctophid growth in the published scientific literature and, following Pauly (1979), used the index of growth performance to examine differences in growth between myctophid species in the region (Figure 8b). Our analysis showed that, although there is some variation in growth performance between species, Southern Ocean myctophids generally have Φ' values clustered between *c.* 3.5 and 4.0, suggesting relatively similar patterns in growth performance. A Kruskal-Wallis test further showed that there were no significant differences in growth performance between populations of species residing in Southern Ocean ($H_{(6)}$ = 7.67, $P > 0.05$). This suggests that, although populations of Southern Ocean myctophids occupy different thermal environments and have different life cycle characteristics, they are broadly adapted to optimise their growth and physiology in relation to the underlying environmental conditions such that species produce similar growth performance strategies across the Southern Ocean.

In conclusion, we provide estimates of the growth patterns of two biomass-dominant species in the Scotia Sea, *G. braueri* and *K. anderssoni*. We found that *g*rowth curves did not differ between sexes for either species, suggesting that males and females have similar growth and development trajectories in the Scotia Sea. Also, growth performance (Φ') was similar between the two species and congruent with other myctophid species in the Southern Ocean. Recent studies have revealed that the Scotia Sea is undergoing broad-scale environmental change that may be affecting myctophid populations (Freer *et al.*, 2019) and may have an adverse effect on food-web stability and ecosystem processes (Atkinson *et al.*, 2004; Murphy *et al.*, 2007; Flores *et al.*, 2012; Atkinson *et al.*, 2019). Given that there are few baseline data on the ecology of Southern Ocean myctophids to ascertain how they may respond to sustained environmental change and the resulting consequences for local food-web stability, our study comprises important life-cycle parameters for future ecosystem studies in the region in a climate change and resource management context.

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CONTRIBUTIONS

R.A.S. analysed the data, with assistance from S.L. and wrote the manuscript. M.A.C. collected the samples and S.L. and R.P.V. conducted the lab work. J.C.X. and C.A. supervised the lab work and assisted with the concept design. All authors contributed to manuscript writing.

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FIGURES LEGEND

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FIGURE 1 Map of the Scotia Sea showing the locations of the RMT25 net hauls for each survey: JR 100, March–April 2004; JR161, October–December 2006; JT177, January–February 2008; JR200, March–April 2009. ([thin curved black line], the principle fronts (N-PF, northern Antarctic Polar Front; S-PF, southern Antarctic Polar Front), Southern Antarctic Circumpolar Current Front (SACCF) and southern boundary of the Antarctic Circumpolar Current (SB-ACC), after Venables *et al.* (2012). . ([thick curved black line], position of the 15% ice-edge cover at 24/10/2006.

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1 Delete S and W from lat and long values.

2

FIGURE 2 Otoliths from *Gymnoscopelus braueri*: (a) immature specimen 1-year old, 48 mm standard length (L_S) caught in the northern Scotia Sea in spring 2006; (b) 2 year old female 80 mm L_S caught in the northern Scotia Sea in spring 2006; (c) 3 years old (a 95 mm L_S female caught around South Georgia in autumn 2004) and (D) 4 year old female 116 mm L_S caught in the Southern Scotia Sea in spring 2006. ★, The otolith core; ●, the opaque and translucent band-pair forming each annulus. Images show the lateral face of (a), (d) left otoliths and (b), (c) the right otoliths.

FIGURE 3 Otoliths from *Krefftichthys anderssoni*: (a) immature specimen < 1 year old with no distinct annulus, 34 mm standard length (L_S) caught in the northern Scotia Sea in spring 2006; (b) 1 year old male 46 mm L_S caught in the northern Scotia Sea in spring 2006; (c) 2 year old female 71 mm L_S caught in the northern Scotia Sea in spring 2006. ★, The otolith core; ●, the opaque and translucent band-pair forming each annulus. Images show the lateral face of right otoliths (a), (c) or (b) left otoliths.

FIGURE 4 Box plots of the age-at-length data (|, median; □, interquartile range; |– –|, 95% range; ●, outliers) in relation to population cohorts identified in concurrent length-frequency data for (a) *Gymnoscopelus braueri* and (b) *Krefftichthys anderssoni* in the Scotia Sea. Year classes are: 0, 0 group; I, I group; II, II group; III, III group; IV+, IV+ group.

Typesetter

1 Delete x-axis label, but not numerical values from (a).

2 Change x-axis label of (b) to read Standard length (mm)

3 Replace 2x Frequency with single centred Frequency

4 Replace 2x Age group (yr) with single centred Age group (years)

FIGURE 5 Von Bertalanffy growth curves for (a) *Gymnoscopelus braueri* collected between the Scotia Sea Antarctic Polar Front and the sea ice zone and (b) *Krefftichthys anderssoni* collected in the northern Scotia Sea during March–April 2004, October–December 2006, January–February 2008 and March–April 2009. —, Model fit; —, bootstrapped *c.* 95% CI; —, 95% prediction intervals.

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1 Replace 2x Age (yr) with single centred Age (years)

2 Delete y-axis label, but not numerical values, from (b)

3

FIGURE 6 Relationship between standard length and wet mass for (a) *Gymnoscopelus braueri* ($y = 4.3272E^{6}x^{3.123}$, $R^2 = 0.9517$, $P < 0.001$) and (b) *Krefftichthys anderssoni* ($y = 1.0472E^{5}x^{2.9843}$, $R^2 = 0.9643$, $P < 0.001$)in the Scotia Sea: ●, juveniles; ●, females; O, males; —, the regression fit; —,95% confidence intervals; —, 95% confidence intervals.

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1 Replace 2x x-axis labels with single centred label.

2 Delete y-axis label, but not numerical values, from (b)

3 Replace y-axis label of (a) with Wet mass (g)

4 Delete numerical data from top of panels.

5 Delete 

FIGURE 7 Relationship between *Gymnoscopelus braueri* standard length (L_S) and (a) otolith length (L_O; $y = 2.2476 + 49.7598x$, $R^2 = 0.8544$, $P < 0.001$) and (b) otolith width (W_O; $y = –17.6812 + 59.6263x$, $R^2 = 0.8840$, $P < 0.001$). (c) Relationship between *Krefftichthys anderssoni braueri* L_S and L_O ($y = –19.0045 + 52.62928x$, $R^2 = 0.8098$, $P < 0.001$) and L_S *v.* W_O (W_O, $y = –28.0017 + 67.3415x$, $R^2 = 0.8592$, $P < 0.001$) in the Scotia Sea. **—**, Regression fits to the observations; **—**,95% CI of the regression; **—**,95% CI of the observations.

Typesetter

1 DISCARD TWO-PANEL FIGURE SUBMITTED; NEW FOUR-PANEL FIGURE SUPPLIED
2 Delete species names and otolith labelling from above each panel
3 Delete x-axis labels, but not numerical values, from (a) and (b)
4 Delete y-axis labels, but not numerical values, from (b) and (d)
5 Replace 2x x-axis labels with single centred label below (c)-(d).
6 Replace 2x y-axis labels with single centred label to left of (a)-(c).

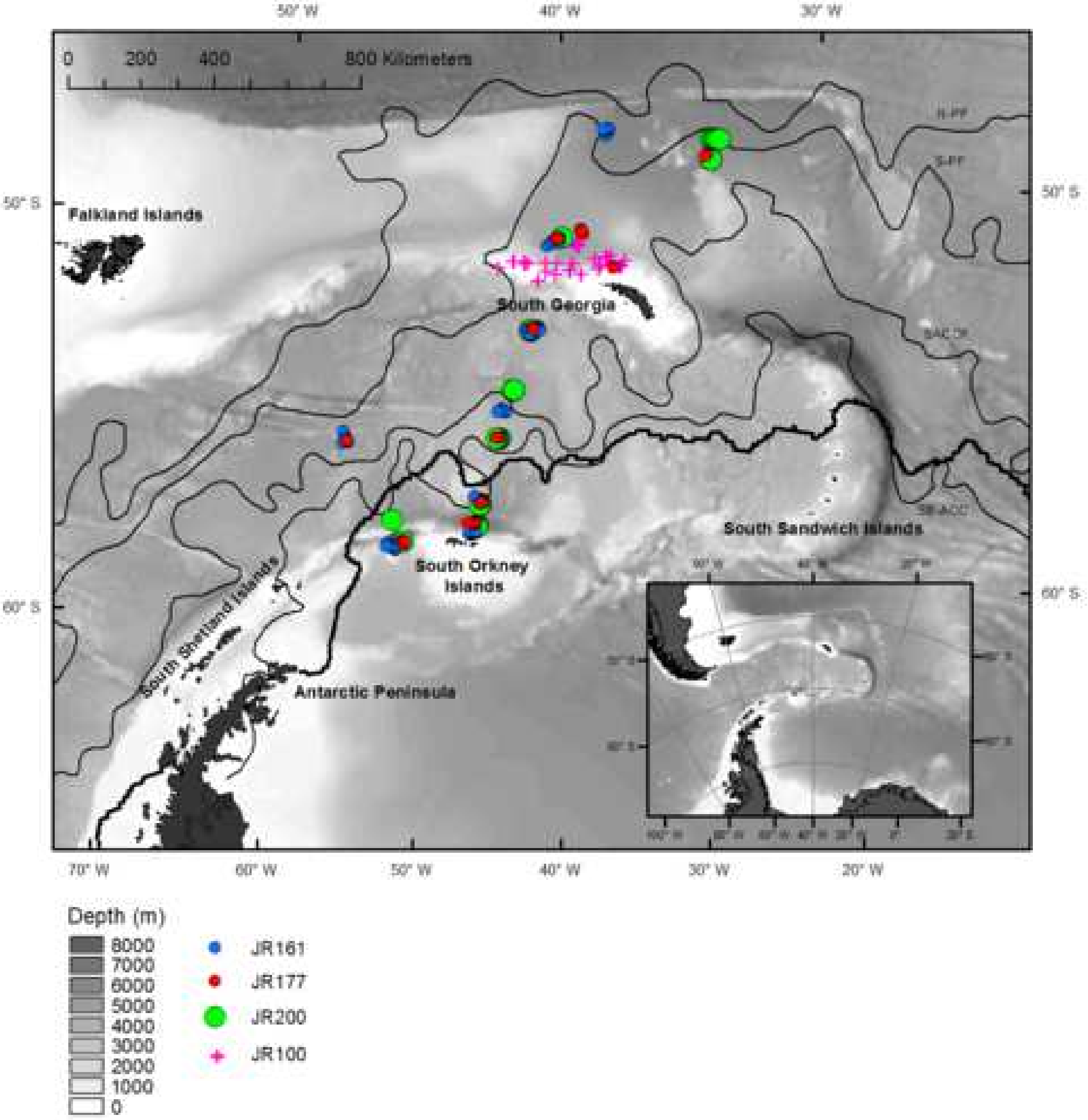
FIGURE 8 (a) Comparison of the estimated standard length (L_S) growth curves of Southern Ocean myctophids and (b) the growth performance of their populations, as summarised in the auximetric grid (Pauly, 1979): ELC, *Electrona carlsbergi*; ELN, *Electrona antarctica*, conventional aging methods; MLV, *Metelectrona ventralis* (Linkowski, 1987); ELA, *Electrona antarctica*, microstructural aging methods (Greely *et al.*, 1999); GYN, *Gymnoscopelus nicholsi* (Linkowski, 1985); ELC*, *Electrona carlsbergi* and GYN*, *Gymnoscopelus nicholsi* (Konstantinova, 1987); GYR, *Gymnoscopelus braueri* () and KRA, *Krefftichthys anderssoni* present study.

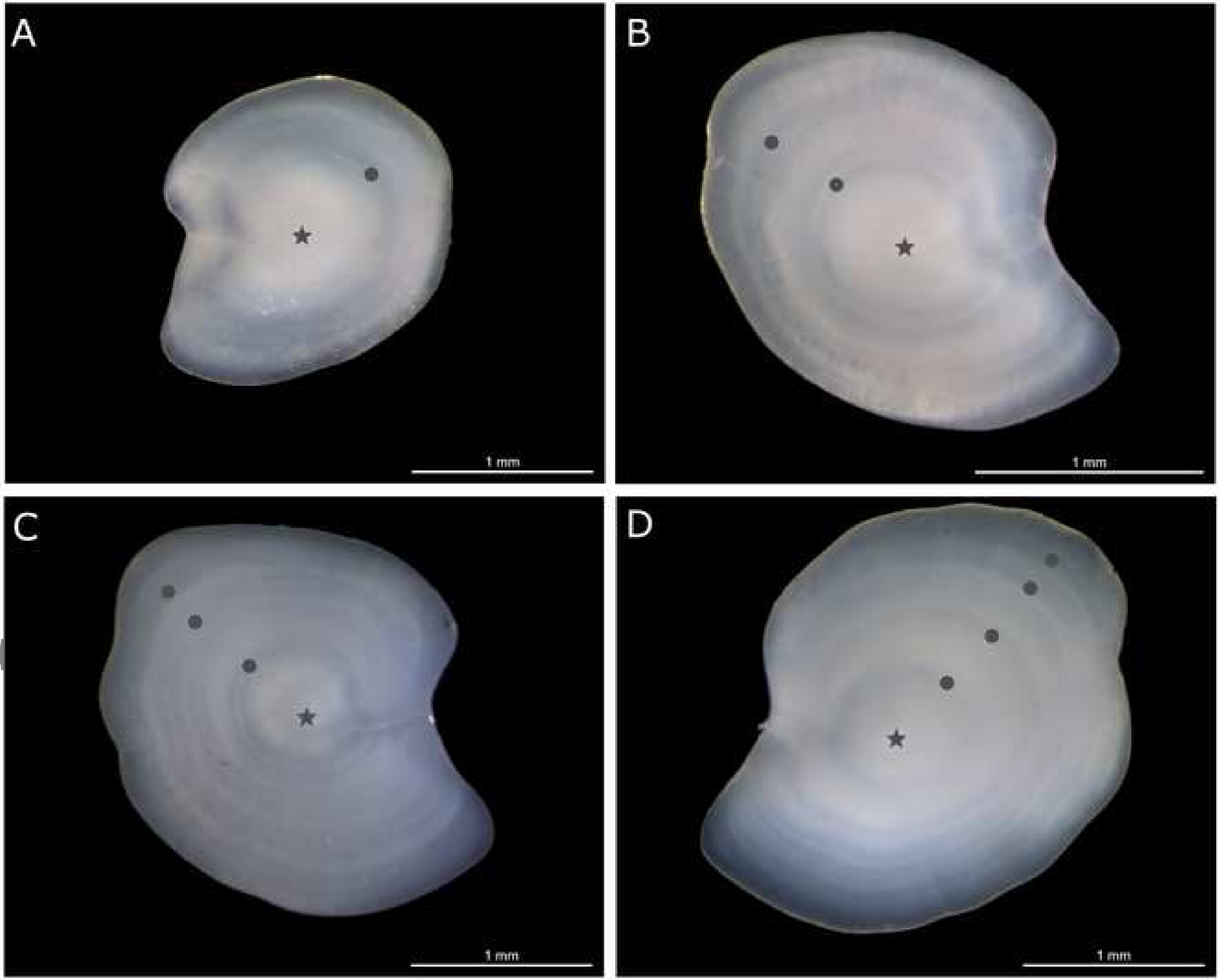
Typesetter

1 Replace Age (yr) with Age (years).

2 Replace LogL_{infinity} with log$L_{S\infty}$.

3 Replace Log$k$ (yr^{-1}) with log$k$ (year^{-1})


50° W
40° W
30° W
0
200
400
800 Kilometers
N-PF
S-PF
50° S
50° S
Falkland Islands
South Georgia
SACCF
SB-ACC
South Sandwich Islands
South Orkney Islands
South Shetland Islands
Antarctic Peninsula
60° S
60° S
70° W
60° W
50° W
40° W
30° W
20° W
Depth (m)
8000
7000
6000
5000
4000
3000
2000
1000
0
JR161
JR177
JR200
JR100


A
1 mm
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C
1 mm
D
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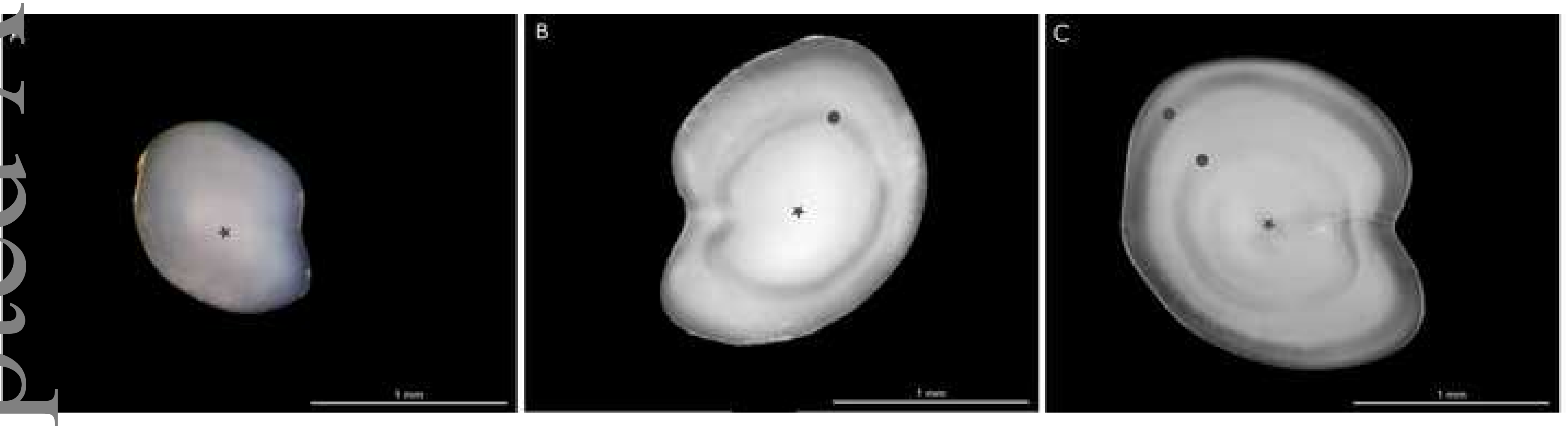
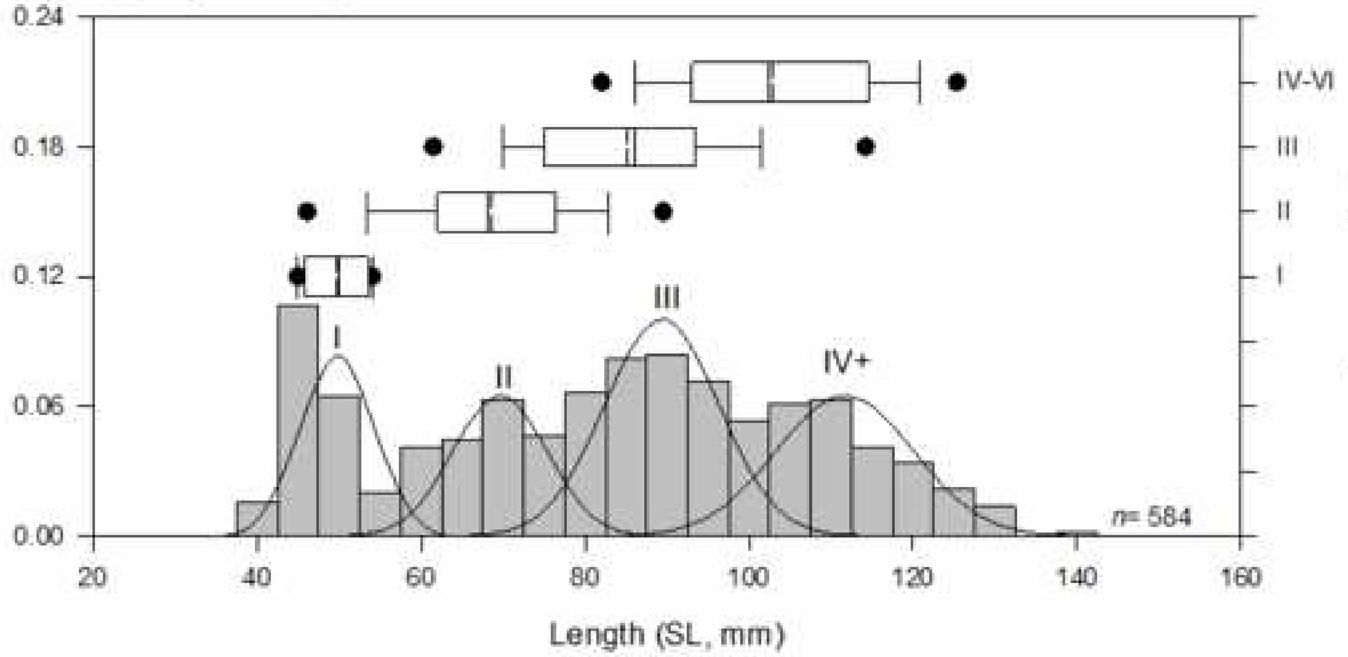
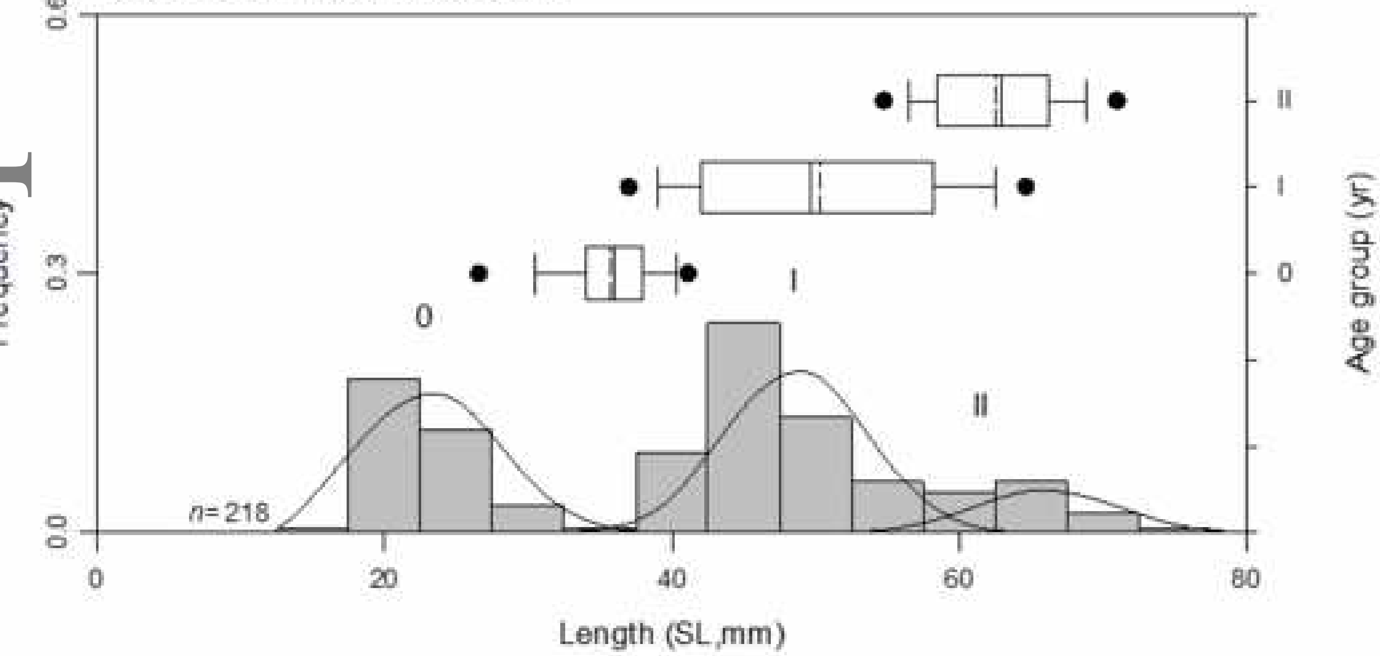
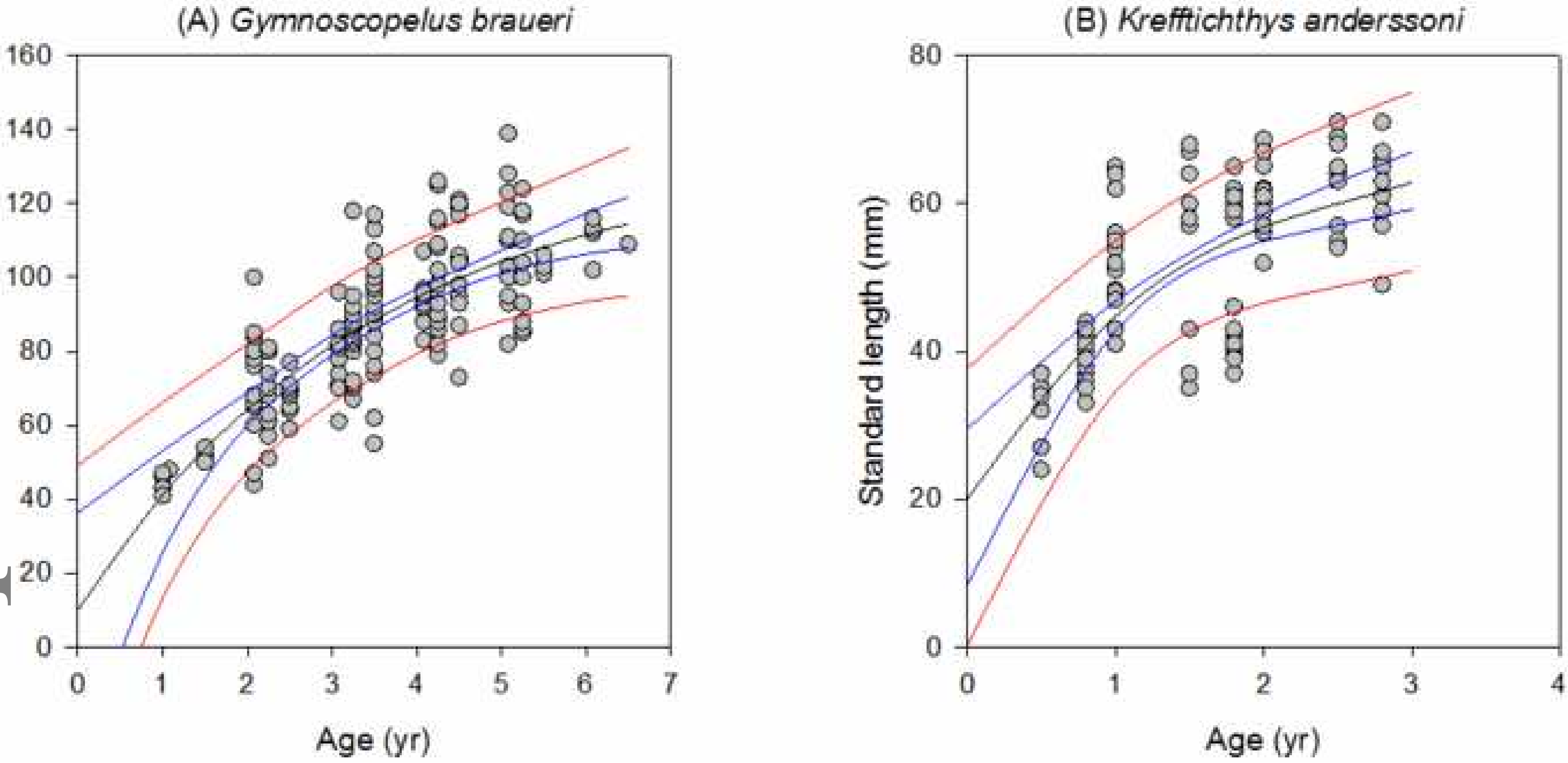

A
1 mm
B
1 mm
C
1 mm

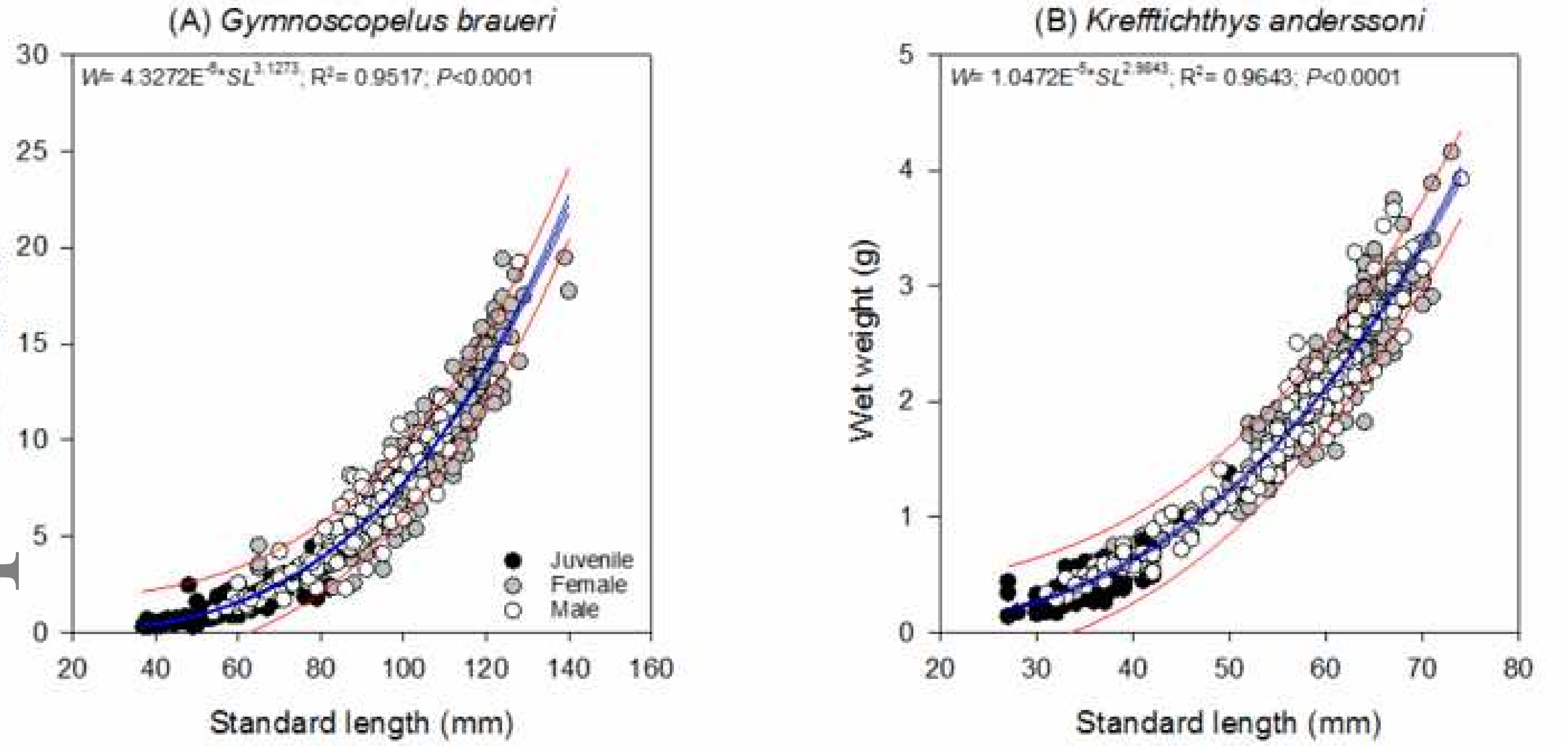
(A) *Gymnoscopelus braueri*

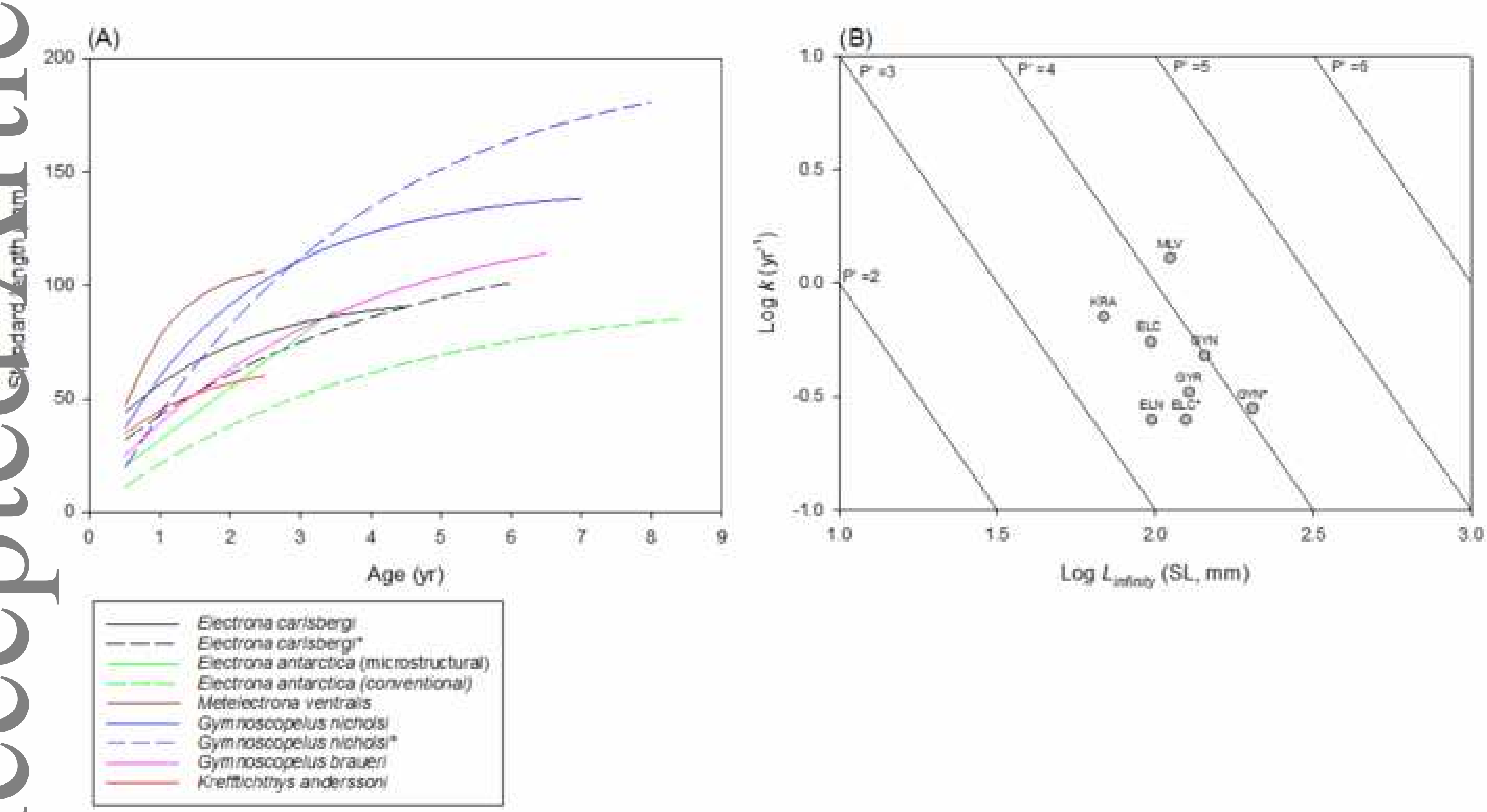


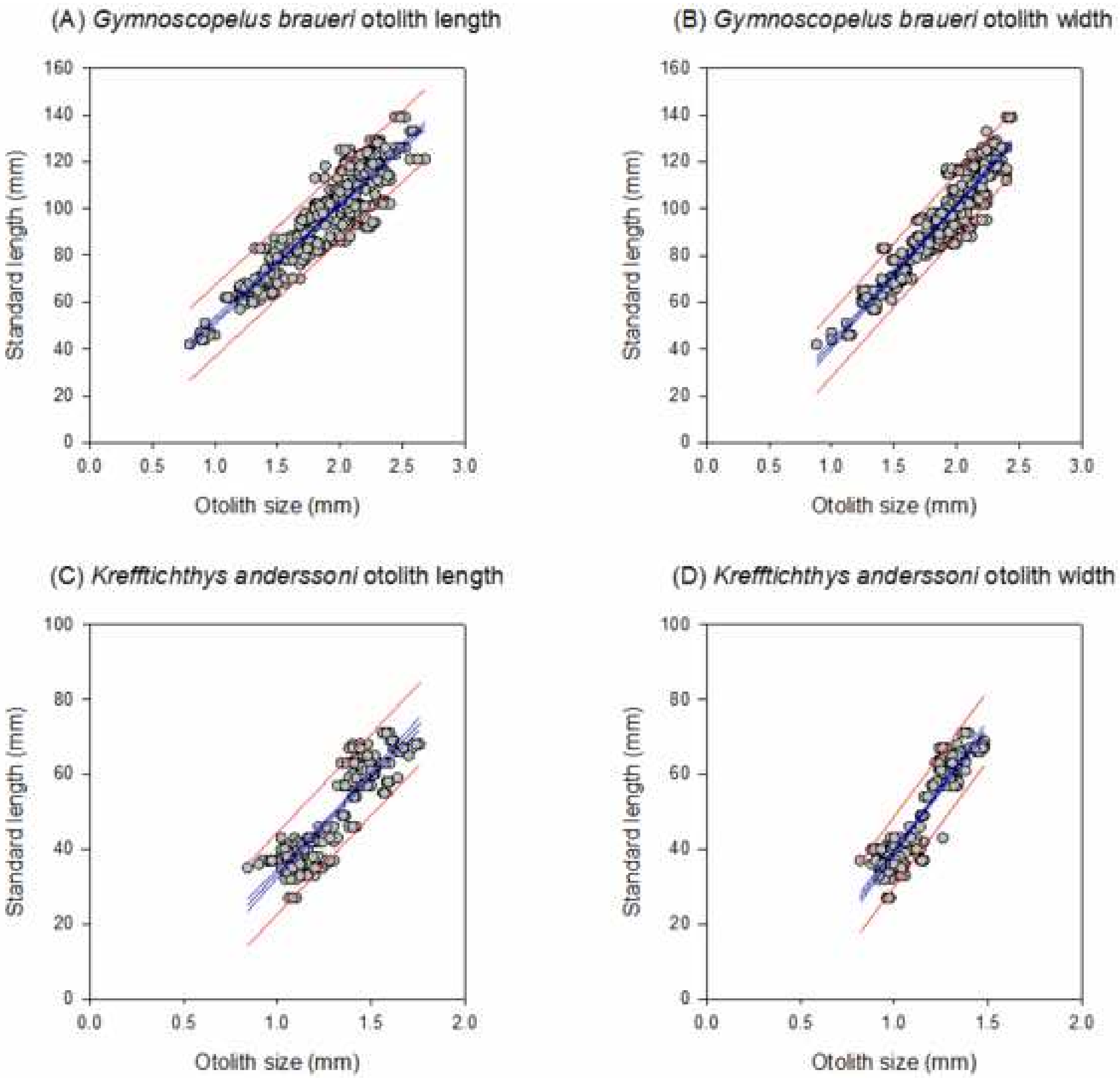
(B) *Krefftichthys anderssoni*




(A) *Gymnoscopelus braueri*
Standard length (mm)
0
20
40
60
80
100
120
140
160
0
1
2
3
4
5
6
7
Age (yr)
(B) *Krefftichthys anderssoni*
Standard length (mm)
0
20
40
60
80
0
1
2
3
4
Age (yr)


(A) *Gymnoscopelus braueri*
$W = 4.3272E^{-6} * SL^{3.1273}$; $R^2 = 0.9517$; $P < 0.0001$
30
25
20
15
10
5
0
Wet weight (g)
20
40
60
80
100
120
140
160
Standard length (mm)
● Juvenile
● Female
○ Male
(B) *Krefftichthys anderssoni*
$W = 1.0472E^{-5} * SL^{2.9643}$; $R^2 = 0.9643$; $P < 0.0001$
5
4
3
2
1
0
Wet weight (g)
20
30
40
50
60
70
80
Standard length (mm)


(A)
Standard length (mm)
200
150
100
50
0
0
1
2
3
4
5
6
7
8
9
Age (yr)
Electrona carlsbergi
Electrona carlsbergi*
Electrona antarctica (microstructural)
Electrona antarctica (conventional)
Metelectrona ventralis
Gymnoscopelus nicholsi
Gymnoscopelus nicholsi*
Gymnoscopelus braueri
Krefftichthys anderssoni
(B)
Log k (yr⁻¹)
1.0
0.5
0.0
-0.5
-1.0
P' =3
P' =4
P' =5
P' =6
P' =2
MLV
KRA
ELC
GYN
GYR
ELN
ELC*
GYN*
1.0
1.5
2.0
2.5
3.0
Log L infinity (SL, mm)


(A) Gymnoscopelus braueri otolith length
(B) Gymnoscopelus braueri otolith width
(C) Krefftichthys anderssoni otolith length
(D) Krefftichthys anderssoni otolith width
Standard length (mm)
Otolith size (mm)
0
20
40
60
80
100
120
140
160
0.0
0.5
1.0
1.5
2.0
2.5
3.0