

DISTRIBUTION, MORPHOLOGY AND ECOLOGY OF *MACROURUS WHITSONI* AND *M. CAML* (GADIFORMES, MACROURIDAE) IN THE ROSS SEA REGION

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Abstract

Samples collected in 2008 led to the identification of a new species of Southern Ocean grenadier, *Macrourus caml*, which had hitherto been identified as *M. whitsoni*. The first comparison of the distribution and ecology of the two species of *Macrourus* in the Ross Sea region is presented. The number of rays in the left pelvic fin and number of rows of teeth in the lower jaw allowed the two species to be distinguished both in the laboratory and by scientific observers at sea. The species were sympatric by depth (900–1 900 m) and by spatial area within CCAMLR Subareas 88.1 and 88.2. There was a small but significant increase in the proportion of *M. whitsoni* caught with depth. Catches of females of both species exceeded that of males (especially for *M. caml*). *Macrourus caml* grows slower, reaches a larger size, lives longer and is heavier for a given length than *M. whitsoni*. Female sexual maturity is reached at shorter length in *M. caml* than *M. whitsoni* but at a similar age (50% sexual maturity at 16 y). Gonad staging suggests extended spawning periods, beginning before December and continuing after February. Stomach and intestine contents data show both species are euryphagous predators and scavengers, with evidence of piscivory and both benthic and pelagic feeding. Amphipods were one of the main crustaceans consumed. Data tentatively suggest that *M. caml* may feed more benthically than *M. whitsoni*, but the sample size was very small. Using stable isotope analysis, trophic level was estimated at 4.4–4.5 (*M. caml*) and 4.1–4.3 (*M. whitsoni*), consistent with one or both of these species being a main prey of Antarctic toothfish.

Introduction

Fishing for Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea region of the Southern Ocean (CCAMLR Subareas 88.1 and 88.2) began in 1997 and is managed by CCAMLR with a specific requirement to minimise the effect of fishing on associated species and the overall ecosystem. Grenadiers (Gadiformes, Family Macrouridae) are the main by-catch in the toothfish fishery in the Ross Sea region, with a catch of 10 tonnes reported in 1998 which increased to 480 tonnes in 2005 (Hanchet et al., 2008a). Grenadiers are also a major prey species of Antarctic toothfish in the region (Fenaughty et al., 2003; Stevens et al., 2012). Ecosystem modelling of the Ross Sea region suggests that toothfish are the main predators of medium-sized demersal fishes (dominated by grenadiers), implying a potential for fishery-induced trophic cascades (Pinkerton et al., 2010).

Grenadier caught as by-catch and found in stomachs of Antarctic toothfish in the Ross Sea region were considered to be almost exclusively *Macrourus whitsoni* (Regan, 1913) until samples collected on New Zealand's International Polar Year Census of Antarctic Marine Life (IPY-CAML) voyage in 2008 led to the identification of a new species: *M. caml* (Smith et al., 2011; McMillan et al., 2012). Although two additional species of grenadiers, *M. carinatus* and *M. holotrachys*, occasionally occur in the region, it is likely that *M. whitsoni* and *M. caml* are the main grenadiers occurring in the Ross Sea region at depths where fishing mainly occurs (between ~500 and 2 100 m) (Hanchet et al., 2008a; McMillan et al., 2012). There has been some research on what was previously thought of as *M. whitsoni* in the Ross Sea region, including distribution, abundance (Hanchet et al., 2008a, 2008b), morphology, age, growth, staging (Marriott et al., 2003, 2006), diet and trophic position (Pinkerton et

al., 2012a). These studies probably represent a mixture of the two species *M. whitsoni* and *M. caml*.

Here, new information is presented on the relative distribution, biology and ecology of *M. whitsoni* and *M. caml* from the Ross Sea region in order to investigate to what extent the two species occupy different ecological niches. The specific objectives of this study were, for *M. whitsoni* and *M. caml* separately: (i) describe the broad-scale spatial and depth distributions in the Ross Sea region; (ii) test whether morphological characteristics provide unambiguous identification; (iii) develop length–weight relationships; (iv) estimate age and growth; (v) stage gonads; and (vi) describe diet and trophic position.

Material and methods

Sampling

This study analysed 864 samples of grenadier obtained from scientific observers on board four New Zealand autoline fishing vessels in the 2011/12 fishing season (December 2011 to February 2012): *San Aotea II*, *San Aspiring*, *Janas*, and *Antarctic Chieftain*. Scientific observers were asked to collect 10 grenadiers selected at random from one haul every second day. After this random sampling from the catch, observers made a preliminary identification of each specimen, measured and weighed them, and then returned whole fish frozen below -20°C to the laboratory for analysis. Laboratory analysis counted the number of pelvic fin rays on the left (usually) or right (if the left was damaged) sides, and number of rows of teeth in the lower jaw. The analysis was completed within six months of capture. Each specimen was identified using these meristic characters plus some qualitative characters (Table 1). Biological information on each specimen was collected, namely (where possible): total length (TL, cm); pre-anal length (PAL, cm); total wet weight (W, g); and sex.

Three strata are defined to aid discussion of broader-scale variations in biology and ecology (Figure 1). Depth of capture was taken to be the mean of the depth recorded on the fishing vessel at the start and end of setting. Depths at the start and end of setting differ (maximum difference of 606 m, median difference 169 m in this study) so this is only indicative of depth of capture.

Age and growth

Otoliths were extracted from all fish and prepared as thick sections, as recommended by Marriott et al. (2006), using a resin embedding technique (Pinkerton et al., 2012b). The sections generally exhibited a regular pattern of translucent and opaque zones; counts were made of the translucent zones. Age estimates were generated on the assumption that one opaque and one hyaline zone represent one year's growth in the otolith. Otoliths from 227 *M. whitsoni* and 628 *M. caml* were available for ageing studies. All *M. whitsoni* and 322 *M. caml* otoliths (every second block) were read. All otoliths were read without prior knowledge of the length or sex of the individual or any prior readings. Subsets of 100 otoliths per species were also read by another reader to estimate between-reader variability in attributed ages. The same otolith subsets were then reread by the first reader to obtain an estimate of the within-reader variability in attributed ages. The index of average percentage error (IAPE) (Beamish and Fournier, 1981), and mean coefficient of variation (CV) (Chang, 1982), were calculated and bias plots drawn for each test. To estimate growth parameters, von Bertalanffy curves were fitted to the resultant length-at-age data assuming a lognormal error distribution of the lengths. The population variance was assumed to be normal with constant CV over length. Analysis was carried out in R (R Development Core Team, 2011) using functions developed at the National Institute of Water and Atmospheric Research (NIWA). Due to the lack of young fish, the t_0 parameter was fixed at t_0 of -0.159 (males) and 0.159 (females) for both species (Marriott et al., 2006).

Gonad stage and age at maturity

For each fish sampled in the laboratory, the gonad stage was recorded on a five-point scale using the macroscopic characters given in the CCAMLR *Scientific Observers Manual* (CCAMLR, 2011): 1 = Immature; 2 = Maturing; 3 = Ripe; 4 = Running; 5 = Spent. For analysis of length and age at sexual maturity, fish with gonad stage of 1 were assigned as immature; fish with gonad stage 3–5 were taken as sexually mature, and fish with gonad stage of 2 were not used as it is not known whether these fish are immature and developing towards sexual maturity, or are already mature and resting.

The proportion spawning (P_s) was modelled as a function of length (L) or age (A) using a binomial distribution with logit link (Equation 1):

$$P_s = \alpha + \beta L \quad L_{50\%} = -\alpha/\beta \quad (1a)$$

$$P_s = \alpha + \beta A \quad A_{50\%} = -\alpha/\beta. \quad (1b)$$

Diet

Stomachs and intestines were removed and examined to ascertain diet. As most stomachs of grenadiers evert on capture, the degree to which useful information on diet could be obtained from examination of material in intestines (between the pyloric caeca and anus) was investigated. Prey from stomachs and intestines were obtained from the North, Slope and East strata, with a spatial distribution similar to that of other samples used in this study (see Pinkerton et al., 2012b for details). Stomach and intestine samples were taken from fish of 34–65 cm TL (*M. whitsoni*) and 37–84 cm TL (*M. caml*) covering the range of fish sizes sampled in this study. Intestinal material has previously been used for studying prey of species which tend to regurgitate during capture (Merrett and Marshall, 1981; Jones, 2008; Pinkerton et al., 2012a). Stomach and intestine contents were rinsed with water on a 500 μm steel sieve and recognisable prey items were identified under a stereoscopic microscope to the lowest taxon possible. Remains of fish digested beyond visual recognition were identified, if possible, from their otoliths using the otolith descriptions of Williams and McEldowney (1990). Each prey taxon was counted and, for material obtained from stomachs, its wet mass recorded to the nearest 0.01 g after removal of surface water by blotting paper. A nominal weight of 0.005 g was assigned to prey items from stomachs that were too small to be weighed following Pinkerton et al. (2012a). Weight of prey items in intestines was not recorded as the state of digestion varied. A fragmented prey count was based on the number of eyes, heads, mouthparts, tails, otoliths or other anatomical parts traceable to a single specimen. Rocks and shell fragments occasionally found in stomachs and intestines were excluded from analysis. Bait (primarily recently ingested arrow squid) was also excluded from the subsequent analysis. The contribution of different prey items to the diet was determined by the numerical importance (%N), frequency of occurrence (%O) and mass (%W) (Hyslop, 1980). The index of relative importance

(IRI) (Cortés, 1997) was not calculated as there were too few samples for this to be meaningful. To assess the adequacy of the stomach samples for statistical analysis of diet variations, the cumulative diversity of the categorised stomach contents measured using the Brillouin index of diversity (H) was plotted against the cumulative number of non-empty stomachs (Koen Alonso et al., 2002; Dunn, 2009).

Stable isotope

Analysis of the relative abundances of stable isotopes of carbon (^{12}C , ^{13}C) and nitrogen (^{14}N , ^{15}N) in muscle samples can complement stomach contents analysis by providing a longer-term picture of feeding and trophic position (Cherel et al., 2011). Muscle tissue was taken from the area above the lateral line close to the dorsal fin, freeze-dried and stored in a dessicator. No lipid extraction was performed because recent work suggests that the aggressive extraction of lipids from muscle samples using organic solvents at high pressure can cause changes to the $\delta^{15}\text{N}$ value of samples (NIWA, unpublished data). Because lipid synthesis strongly discriminates against the ^{13}C isotope (De Niro and Epstein, 1977, 1978), analysing tissue samples without prior extraction of lipids can lead to variations in $\delta^{13}\text{C}$ values that are independent of the organism's feeding (Rounick and Winterbourn, 1986; Logan and Lutcavage, 2006). Stable isotope measurements were made on a Delta^{Plus} (ThermoFinnigan, Bremen, Germany) continuous flow isotope ratio mass spectrometer, using CO_2 and N_2 reference gas standards (Bury, 1999; Pinkerton et al., 2012b). Internal standards (National Institute of Standards and Technology, NIST) were used to ensure consistency (precision) and international compatibility (accuracy). Stable isotope analysis of tissues from other biota was also carried out. These samples were collected from the Ross Sea region north of 74°S during the IPY-CAML research voyage to the Ross Sea region in 2008 (Hanchet et al., 2008c). Samples included near-surface phytoplankton and a variety of mesopelagic invertebrates. Trophic levels (Lindeman, 1942) were calculated using a baseline value of $\delta^{15}\text{N}$ from phytoplankton (assumed to have trophic level of 1) using a +3.2‰ change in $\delta^{15}\text{N}$ per successive trophic transfer (Sweeting et al., 2007).

Results

Spatial distribution

One fish from SSRU 881C was identified as *M. holotrachys* and is not considered further. Of the remaining 863 fish, 227 (26%) were *M. whitsoni* and 636 (74%) were *M. caml*. The sampling locations (Figure 1) include the northern extent of the Mawson Bank in SSRU 881H but did not cover areas where the greatest total by-catch of *Macrourus* spp. had been taken by the longline fishery for Antarctic toothfish, nor the areas with highest *Macrourus* spp. by-catch rates (Stevenson et al., 2012). On the broad scale (i.e. SSRUs or strata defined here), *M. whitsoni* and *M. caml* are almost completely sympatric (Figure 1; Table 2).

Length and sex distribution

Within the sample of *M. whitsoni*, 37 fish were male (16%) and 190 were female (84%); for *M. caml*, 253 fish were male (40%) and 380 were female (60%) (Figure 2). TL was 34.5–65.1 cm for *M. whitsoni* and 34.5–84 cm for *M. caml*. The length-frequency distribution for female *M. caml* caught is shifted right compared to that of *M. whitsoni* and male *M. caml*. Median lengths of fish were 45.5/51.8 cm TL (*M. whitsoni*, males/females respectively) and 52/55 cm (*M. caml*, males/females respectively). Male *M. whitsoni* in the sample were significantly smaller than the others [$t(46)$, $p < 0.001$]. Female *M. caml* were significantly larger than the others [$t(707)$, $p < 0.001$]. There was no statistically significant difference in TL between the samples of female *M. whitsoni* and male *M. caml* [$t(427)$, $p = 0.04$].

Depth distribution

Sets were allocated into 10 depth bins and the number of fish sampled by strata, species and sex counted in each bin. The proportion of *M. whitsoni* to *M. caml* randomly sampled on each set suggests that *M. caml* has a shallower distribution than *M. whitsoni* (Figure 3). Fishing was conducted at shallower depths on the continental slope, and deeper depths in the east, so effects of location and depth occur together. Depth was found to be a significant predictor for the proportion of *M. whitsoni* relative to *M. caml* on a set at the 0.1% level [$t(88)$, $p < 0.001$] whereas stratum was not. The model used was ‘number of *M. whitsoni*/total number

grenadiers ~ fishing depth + stratum’, implemented using a modified version of the R stepAIC function.

Identification and morphology

The two main morphological characters (number of rays in the left pelvic fin and the number of rows of teeth in the lower jaw) allowed the two species to be distinguished in the laboratory according to McMillan et al. (2012) (Table 3). A comparison between identifications in the laboratory and those carried out by scientific observers at sea on the four New Zealand fishing vessels in the 2011/12 season showed that the observers could also use these two main morphological characters to separate the two species. The overall agreement between identifications at sea and in the laboratory was 94.1% and only two observers fell below 90% consistency with laboratory identification.

Morphology

Two models (TL~PAL+PAL:Species:Sex+Species:Sex; PAL~TL+TL:Species:Sex+Species:Sex) implemented using a modified version of the R stepAIC function showed that there was a significant difference in the TL–PAL relationship between male *M. caml* and a combination of female *M. caml* and both sexes of *M. whitsoni* in the Ross Sea region at the 1% significance level (Table 4).

Stepwise GLM regression model (logW~logTL+logTL:Species:Sex+Species:Sex) implemented using a modified version of the R stepAIC function showed that there was a significant difference in the length–weight relationship between female *M. caml* and a combination of male *M. caml* and both sexes of *M. whitsoni* in the Ross Sea region at the 1% significance level (Table 5; Figure 4a). Based on PAL, a similar analysis (logW~logPAL+logPAL:Species:Sex+Species:Sex) showed that there was also a significant difference in the length–weight relationship between male and female *M. caml* at the 1% significance level (Table 5; Figure 4b). These regressions suggest that female *M. caml* are about 20% heavier for a given length than *M. whitsoni*.

Length of intestine

The length of intestines (between the pyloric caeca and anus) was found to be significantly

different between the two species of *Macrourus* [$t(210)$, $p < 0.001$]. Intestines of *M. whitsoni* were relatively short, narrow and robust, whereas intestines of *M. caml* were relatively long, wide and flaccid (Figure 5). This may be an additional useful characteristic to aid identification if other morphometric characters are damaged or missing.

Age and growth

In both species, otoliths displayed a transition zone where the growth changes from predominantly a dorso-ventral deposition pattern to a pattern where deposition was primarily on the proximal aspect of the otolith (see Pinkerton et al., 2012b, Marriott et al., 2003, 2006 for images). Here the zones also changed from a pattern of wide zones with many false checks to a pattern of very regularly spaced narrow zones with few false checks. The otoliths from both species of *Macrourus* were found to be difficult to interpret, with a high degree of false checks evident. The zone widths were also quite variable between fish, which made the interpretation of less clear otolith sections problematic. Consequently, within- and between-reader differences were relatively high (Figure 6). For *M. whitsoni*, ages ranging between 6 and 27 y of age were attributed, with the bulk of fish between 10 and 25 y old. For *M. whitsoni* the IAPE within readers was 6.16, the between-reader IAPE was 6.50. For *M. caml* the bulk of fish was between 13 and 38 y old. For *M. caml* the IAPE within readers was 6.43, the between-reader IAPE was 7.19.

For *M. whitsoni*, a much higher number of females of a given age were caught than males of the same age (Figure 7). For *M. caml*, females greatly outnumbered males of the same age up to an age of about 50 y. Above this age, both sexes of *M. caml* were caught in approximately the same numbers for a given age.

The von Bertalanffy growth curves for the mixture of *Macrourus* spp. from Marriott et al. (2006) seemed inconsistent with the data for both *M. whitsoni* and *M. caml* in Figures 8(a) to 8(d). The L_{inf} values from Marriott et al. (2006) were too large for *M. whitsoni*, and the k values from Marriott et al. (2006) were too large for *M. caml*. However, the age-length data obtained in the present study for the separate species of *Macrourus* poorly constrained the von Bertalanffy growth curves because of the lack of small and large fish in the sample

(Figures 8(a) to 8(d), thin solid lines). Noting that the results should be treated with caution until more complete length-at-age data are available, growth curves for both sexes of both species were obtained as follows (Figures 8(a) to 8(d), thick solid lines; Table 6). For *M. caml*, L_{inf} and t_0 were set to the values given by Marriott et al. (2006) and k was estimated by least-squares regression. The values of L_{inf} in Marriott et al. (2006) were 76.1 cm TL (males) and 92.0 cm TL (females). These compare to the maximum lengths of *M. caml* found in the present study of 74.4 cm (males) and 84.0 cm (females). For *M. caml*, L_{inf} was set to the maximum TL found in the present study for each sex (59.0 cm males; 65.1 cm females), t_0 was taken from Marriott et al. (2006) and k was fitted by least-squares regression. The initial growth rates of *M. whitsoni* were hence estimated to be 2–2.4 times higher than the initial growth rates of *M. caml* (Figure 8e).

Reproductive stage

Staging of frozen specimens of *Macrourus* spp. was found to be more difficult than staging of fresh specimens but a range of stages was present in the samples, ranging from immature to developing, ripe and spent individuals (Table 7; Figure 9). The low number of specimens available, especially for male fish, means that proportions of fish of a given stage should be considered with caution. Also, sampling started in the North stratum, moved to the Shelf and then finished in the East so that changes in gonad stage by region are confounded by changes with date over the period of sampling (1 December 2011 to 18 February 2012).

Most (84%) *M. whitsoni* and *M. caml* that were staged in this study had immature, maturing or ripe gonads; <5% had running gonads and 12% had spent gonads. For both species, males caught in this study had a higher proportion of spent gonads than females (26–32% compared to 3–6%). Otherwise, differences in gonad stages between males and females of both species were usually <10%. *Macrourus whitsoni* outside the East stratum tended to be less mature than *M. caml* at the time of sampling. For example, overall, 32% of female *M. whitsoni* but only 4% of female *M. caml* were immature (stage 1); 45% of female *M. caml* but only 26% of *M. whitsoni* had stage 3 gonads.

For *M. caml*, the proportions of fish caught with various gonad stages were similar in all strata.

However, gonads of *M. whitsoni* in the East stratum seemed generally more developed at the time of the study than gonads of *M. whitsoni* in the Slope and North strata. For *M. whitsoni*, 84% of specimens in the East stratum had gonad stages 3–5 but elsewhere only 15% of this species had these advanced gonad stages; no immature (stage 1) *M. whitsoni* were caught in the East stratum, but substantial proportions (30–51%) of *M. whitsoni* caught in the Slope and North strata had immature gonads. Fishing occurred at different depths in the different strata, but it was found that fishing depth was generally less significant in explaining the proportions of different stages caught over the study area than stratum. Significance was tested using a GLM of the form: proportion stage 1 ~ depth + stratum, implemented using a modified version of the R stepAIC function. Depth was not found to be a significant predictor of the proportion of immature *M. caml* caught when stratum was available [$t(81)$, $p > 0.1$]. Depth was also not a significant predictor of the proportion of stage 2 and 3 *M. caml* caught. However, depth was significant in explaining the proportion of spawning/post-spawn (stages 4 and 5) *M. caml* caught [$t(81)$, $p = 0.008$]. The coefficient was negative, indicating higher proportions of stage 4 and 5 *M. caml* tended to be caught at shallower depths.

The length at sexual maturity was determined from the fitted logistic form for females of both *M. whitsoni* and *M. caml* (Figure 10; Table 8). At 50% sexual maturity, female *M. whitsoni* were 52 cm TL, 18 cm PAL and aged 16 y. At 50% sexual maturity, female *M. caml* were estimated using logistic fitting to be 46 cm TL, 16 cm PAL and aged 13 y. Based on these TL values at 50% sexual maturity, the fitted von Bertalanffy growth curves for females derived in this study (Table 6) give ages at 50% sexual maturity of 16 y (*M. whitsoni*) and 17 y (*M. caml*). The length-based logistic regression for maturity of *M. caml* is better constrained than the age-based regression (i.e. Figure 10(c) is better constrained than Figure 10(d) so 17 y is likely to be a better estimate of the age at 50% sexual maturity of *M. caml* than 13 y. Age at sexual maturity could not be determined for male *M. whitsoni* or *M. caml* as there were insufficient immature (gonad stage 1) samples.

Diet and trophic position

Because stomachs of these species tend to evert on capture, only a very small number of stomach contents were available for diet analysis. Examination of 227 stomachs from *M. whitsoni* provided 10 non-empty and non-everted stomachs (4.4%) which explained 67% of the asymptotic prey diversity (Brillouin index, H); 92 stomachs are needed to explain 95% of the prey diversity. For *M. caml*, 3.5% of stomachs were useful for elucidating diet (22 out of 636 examined) (Table 9) and these explained 82% of the asymptotic prey diversity; 83 stomachs are needed to explain 95% of prey diversity. This study also obtained prey from 60 intestines from *M. whitsoni* and 93 intestines of *M. caml* which are likely to explain over 90% of the asymptotic prey diversity in terms of numbers of prey items (91% for *M. whitsoni*; 96% for *M. caml*).

In stomach samples, fish made up the greatest proportion by weight for *M. whitsoni* (68%W) but only 15%W for *M. caml*. Fish remains were found in 3 of the 10 stomachs for *M. whitsoni* but in only 10% of intestines of this species. Evidence of feeding on fish was present in 10 of the 22 stomachs of *M. caml*, and in 33% of the intestines (Table 9). Two otoliths of *Gymnoscopelus* sp. (Myctophidae) were found in stomachs of *M. caml*; no other species of fish could be identified. A variety of amphipods were found in stomachs and intestines of both species. Four amphipods from stomach samples were able to be identified as *Vibilia* sp., *Aristiopsis* sp., *Hippomedon* sp. and *Hyperietta* sp., plus two unidentified species of amphipod from the superfamily Lysianassoidea. Amphipods were found in 4 of the 10 stomachs of *M. whitsoni* and 10 of the 22 stomachs of *M. caml*. Amphipod remains were also identified in 27% of the intestines of *M. whitsoni* and 39% of the intestines of *M. caml*. Amphipods made up the largest number of prey items in both the stomachs and intestines of both species. This study recovered 130 amphipod remains from intestines of both species. In one case, the remains of 26 amphipods were found in a single intestine of *M. caml*. Remains of euphausiids were found in the stomachs and intestines of both species. Most of the euphausiids in *M. caml* stomachs (5 of 6) could be identified as *E. superba*. A wide variety of benthic and pelagic invertebrates were found in stomachs and/or intestines of the two species of *Macrourus*, including mysids (*Boreomysis* sp.), isopods, decapods (the prawn *Nematocarcinus* sp.), copepods (*Paraeuchaeta* sp.), salps, polychaetes,

chaetognaths and cephalopods. Evidence of feeding on the seabed for *M. caml* was found: fragments of coral, an echinoderm, parts of an ophiuroid and benthic polychaetes were present in the stomach and/or gut. Tanaidacea and ostracoda were also found in the intestines of *M. caml*.

In total, 38 muscle samples from *M. whitsoni* and 60 muscle samples from *M. caml* were analysed for stable isotopes of carbon and nitrogen (Table 10; Figure 11). Carbon isotopic compositions were not significantly different between the two species [$t(77)$, $p = 0.03$]. The $\delta^{15}\text{N}$ values for the two species were significantly different [$t(69)$, $p < 0.001$] implying feeding at different trophic levels. Measurements of surface phytoplankton isotopic composition in the Ross Sea region (Pinkerton et al., 2012a) were $\delta^{15}\text{N} = 1.0 \pm 0.8\text{‰}$ providing a $\delta^{15}\text{N}$ baseline. This led to estimates of trophic level of *M. whitsoni* of 4.1–4.3 and of *M. caml* of 4.4–4.5. The slightly higher trophic level of *M. caml* compared to *M. whitsoni* implies feeding on slightly higher trophic level prey on average, though the difference is small.

Discussion

Sampling

Samples were obtained from areas which did not cover the areas where the highest historical catch of *Macrourus* spp. has been taken by the fishery, nor the region of highest catch rates. It is not known whether *M. whitsoni* and *M. caml* occur outside the depth range or geographic extent of the fishery. On the broad scale however, *M. whitsoni* and *M. caml* sampled from longlines during 2011/12 were almost completely sympatric by depth (both appearing to be abundant between depths of 900 and 1 900 m) and area (both occurring throughout Subareas 88.1 and 88.2). Although there was a small but significant increase in the proportion of *M. whitsoni* relative to *M. caml* caught with increasing depth, the majority of the populations of both species seem to largely co-occur. Research to extend the geographic coverage of measurements, such as those presented here, would be useful. Scientific observers on fishing vessels seem well placed to gather more data on these important species in Subareas 88.1 and 88.2, given that identification and data quality from observers were found to be very good. All scientific observers on all New Zealand vessels in the 2011/12 season were able to use the main

morphological characters to distinguish the two species at sea with an overall success rate of 94%. Basic biological information on *Macrourus* samples (total length, pre-anal length and weight) were as accurately measured at sea as in the laboratory.

Nearly three times more *M. caml* were obtained by the fishery than *M. whitsoni*, implying either that *M. caml* is more abundant than *M. whitsoni* at the depths fished, or that the selectivity of the fishing gear is substantially greater for *M. caml* than for *M. whitsoni*. More females of both species were caught than males, especially for *M. caml* where the difference in catch between males and females was a factor of 5. Different catches of *M. whitsoni* versus *M. caml*, and males versus females, did not appear to be due to simple size-based selectivity, nor was it explained by different ages.

Length and weight

This study suggests that the maximum sizes and weights of the two species are different. *Macrourus caml* is the larger species, with the largest fish examined here 84 cm TL (compared to 89 cm in McMillan et al., 2012) and 5.4 kg in weight. In contrast, *M. whitsoni* is smaller, with the largest fish examined 65 cm TL (compared to 66 cm in McMillan et al., 2012) and 1.3 kg in weight. Although the lack of small and large fish in the sample did not allow L_{inf} for either species to be estimated, it did show that the fitted von Bertalanffy curves given in Marriott et al. (2006) were inconsistent with age-length data for either species. Species-specific von Bertalanffy growth curves were developed using L_{inf} for *M. caml* taken from Marriott et al. (2006) (76 cm and 92 cm for males and females respectively) and L_{inf} for *M. whitsoni* set to the maximum lengths in the sample (59 cm and 65 cm for males and females respectively). The resulting growth curves are plausible but more age-length data of small and large fish of both species are needed to more reliably constrain them. Relationships between TL and PAL were very similar for the two species. The spread in the relationship between TL and weight was very similar to that between PAL and weight, implying that TL is generally no less precise a measurement than PAL, even after catching by longlines, freezing and rethawing. *Macrourus caml* (females, at least) were relatively stout, being about 20% heavier than *M. whitsoni* for a given length.

Age and growth

Both of these species were found to be difficult to age with large within- and between- reader age estimate differences (details in Pinkerton et al., 2012b). These species are resident in very cold waters and the combination of low temperature and deep water means they are close to the physiological limit of fixing carbonate into skeletal elements. This environmental stress may contribute to the high degree of false checks observed in the otolith matrix (Kalish, 1992; Campana, 1999). Zone widths were quite variable in both species, suggesting that growth rates tend to vary between fish. Variability in zone spacing was more evident in *M. caml* than in *M. whitsoni* and this variable growth rate seen in the otolith sections significantly added to the difficulty in interpreting the zone structure and attributing an age estimate to any given fish. Fast growing and slow growing individuals would have accounted for the majority of the large age-estimate discrepancies observed in the age data. However, there was no systematic bias in the interpretation of the otolith sections, so the authors are content that the otoliths are being interpreted in the correct manner with the observed differences attributed to the poor clarity of the zone structure of the otoliths. The within- and between-reader precisions in the present study are a moderate improvement over the figures achieved in the Marriott et al. (2006) paper and compare favourably with similar long-lived deep-sea species (Marriott et al., 2006), though being poorer than some (e.g. van Wijk et al., 2003). There was a transition in zone spacing in the otoliths of both species as has been observed in similar species (Bergstad, 1995; Kelly et al., 1997). This transition is likely to indicate some change in life history. Marriott et al. (2003) suggested that it corresponds with the onset of maturity but this remains to be confirmed.

The two species have different early-life growth rates and seem to have different longevity: *M. whitsoni* approaches full size (80% L_{inf}) at about 17 y and can live to at least 27 y, while in *M. caml* 80% L_{inf} is attained around 35–39 y and one specimen was aged at 62 y. Estimates of initial growth rates (von Bertalanffy growth parameter k) were 0.09–0.10 y^{-1} (*M. whitsoni*) and 0.04–0.05 y^{-1} (*M. caml*), indicating more than two-fold higher initial growth rates of *M. whitsoni* than *M. caml*. Marriott et al. (2006) reported k of 0.055 y^{-1} (males) and 0.065 y^{-1} (females). These results suggest that most of the fish examined in Marriott et

al. (2006) were *M. caml* but that some *M. whitsoni* were present which increased the average growth rate in their sample. The growth rate and longevity of *M. caml* were similar to results obtained in other studies on macrourids; van Wijk et al. (2003) estimated $k = 0.069 y^{-1}$ for *M. carinatus* at Heard and McDonald Islands, with longevity of 50 y or more. Bergstad (1995) estimated that *Coryphaenoides rupestris* in the North Atlantic reached a maximum age of approximately 70 y, while Kelly et al. (1997) estimated a maximum age for males of 50 y, and 60 y for females. The relatively short lifespan (27 y perhaps) and higher initial growth rate of *M. whitsoni* seem less typical of deep-water Macrourids.

Gonad staging

The onset of sexual maturity in female *M. whitsoni* is reached at longer length than in female *M. caml*. Total length at 50% maturity (L_{50}) was 52 cm (79% L_{inf}) for female *M. whitsoni* and 46 cm (50% L_{inf}) for female *M. caml*. However, the age at 50% sexual maturity (a_{50}) was estimated to be about 16 y for both species because of the faster initial growth of *M. whitsoni*. For females of a mixture of the two species caught by research bottom trawls, Marriott et al. (2006) estimated L_{50} of 46 cm and a_{50} of 14 y, again consistent with *M. caml* dominance in the sample. Elsewhere, *M. carinatus* at Heard and McDonald Islands were reported as having L_{50} of 43 cm (61% L_{inf}) implying a_{50} of about 11 y (van Wijk et al., 2003).

The gonad stage data imply that the spawning period of both species of *Macrourus* may be quite long, starting within or before the start of the sampling period (1 December 2011) and continuing beyond the end of the sampling (18 February 2012). Sampling started in the North stratum, moved to the Shelf and then finished in the East. Fishing tends to occur deeper in the East stratum than in other areas, which confounds changes in gonad stage over the period of fishing with changes by area and depth. Fewer immature *M. caml* were caught in all strata compared to immature *M. whitsoni* but no immature (stage 1) *M. whitsoni* were caught in the East stratum at all. Fish of the size of immature *M. caml* were caught in this study, so this is not a consequence of size-selectivity of the fishing gear. The paucity of immature *Macrourus* in this sample is consistent with previous studies (e.g. McMillan et al., 2012) that suggest small individuals of both species occur at depths shallower

than those generally sampled by the longline fishery. Twelve small (probably immature) *Macrourus* spp. specimens with a total weight of about 0.4 kg were caught from four stations at depths between 402 and 760 m in the vicinity of Scott Island (McMillan et al., 2012; 2008 IPY-CAML biodiversity survey, Hanchet et al., 2008c). In the future, sampling in one area over the whole summer–autumn period (November to March) combined with histology may be useful in elucidating spawning strategies of these macrourids.

Diet and trophic position

Most methods of capture of grenadier (including bottom longline and trawl) usually result in everted stomachs due to the expansion of the gas from the swim bladder (Laptikhovskiy, 2005; Jones, 2008; Pinkerton et al., 2012b). Here, fewer than 5% of stomachs were not everted and intestinal analysis was used to augment the stomach contents data. The relatively large proportions of unidentifiable crustacea and wholly unidentifiable prey in the intestines of *M. whitsoni* (19% and 25% of prey items respectively) limit the utility of this approach. Identification of material in the intestines was easier for *M. caml* because its intestine is longer and wider and digestion seems to be slower. In *M. whitsoni*, the relatively short and narrow intestine seemed to have led to higher digestion rates, and material was much more difficult to identify. Despite relatively encouraging estimates of the proportion of the Brillouin index of prey diversity, the very low number of non-everted stomachs and difficulty of identifying prey from the intestines of *M. whitsoni* mean that diet information is indicative at a coarse taxonomic level only.

Although there are no studies on the feeding of *M. whitsoni* or *M. caml* by species, Pinkerton et al. (2012a) provides information on the diet of a mixed sample of the two species from the same region. There are also a number of studies on feeding of the related northern hemisphere species *M. berglax* (Eliassen and Jobling, 1985; Jørgensen, 1996; Román et al., 2004; Murua et al., 2005), and the southern hemisphere species *M. carinatus* (Laptikhovskiy, 2005; Pakhomov et al., 2006; Jones, 2008) and *M. holotrachys* (Dudochkin, 1988; Morley et al., 2004; Laptikhovskiy, 2005). For *M. berglax* and *M. carinatus*, amphipods and small mesopelagic fishes were typically the main food, augmented with a broad range of invertebrates,

including decapods, mysids, copepods, isopods, cephalopods and echinoderms (Jørgensen, 1996; Laptikhovskiy, 2005). Pinkerton et al. (2012a) found evidence of feeding by *Macrourus* spp. on a wide range of pelagic and benthic invertebrates, and that amphipods and fish were probably the major prey items in the Ross Sea region. The results presented here are consistent with these previous feeding studies and suggest that *M. whitsoni* and *M. caml* are euryphagous predators and scavengers. Both species are partially piscivorous and amphipods are probably one of the main crustaceans consumed. Overall, there is a suggestion that *M. caml* may feed more benthically than *M. whitsoni* (evidence of feeding on coral, ophiuroid, echinoderm, benthic polychaetes), though both species of *Macrourus* had been recently feeding on both benthic and pelagic prey. The new data are consistent with the hypothesis given in McMillan et al. (2012) that the slightly smaller and more subterminal mouth of *M. caml* suggests a more benthic diet compared to *M. whitsoni* which has a slightly larger gape, more terminal mouth and longer teeth. A difference in diet between the two species is also consistent with their having different intestines. Isotopic analysis of muscle samples from *M. whitsoni* and *M. caml* suggests that both macrourids species are feeding on prey of similar trophic levels, though these may involve different prey items. The slightly different $\delta^{15}\text{N}$ values for the two species lead to *M. caml* having an estimated trophic level of 4.4–4.5 compared to 4.1–4.3 for *M. whitsoni*. This trophic level places both *Macrourus* species below the top of the food chain in the Ross Sea region, which is occupied by Antarctic toothfish, killer whales and Weddell seals (trophic level of ~5.1; Pinkerton et al., 2010). A trophic level difference of ~1 between *Macrourus* sp. and Antarctic toothfish is consistent with their being a significant prey item for toothfish (Stevens et al., 2012).

Final comments

This study has presented a first insight into the ecology of the two main species of *Macrourus* in the Ross Sea region of the Southern Ocean (Subareas 88.1 and 88.2). *Macrourus caml* and *M. whitsoni* seem to be broadly sympatric by depth (900–1 900 m) in this region, suggesting that niche separation (if present) is achieved by more subtle ecological means. Different intestines, teeth and mouth morphology of the species hint at different diets, but regurgitation of prey during capture

meant that, although there was a suggestion in the data that *M. caml* may feed more benthically than *M. whitsoni*, differences in diet between the species could not be demonstrated. Energetically, *M. caml* grows slower, reaches a bigger size, lives longer and is sexually mature for more of its life than *M. whitsoni*. Female *M. whitsoni* seem to have L_{50} of 79% of their maximum size which requires confirmation using better length-at-age data. It is suggested that other priorities for research on *Macrourus* spp. in the Ross Sea region should be to: (i) estimate the longline by-catch of the two species of *Macrourus* separately; (ii) investigate selectivity of *M. whitsoni* and *M. caml* to baited longline fishing gear and hence estimate their relative abundances; (iii) estimate absolute biomass of both species, especially on the Ross Sea slope where fishing for Antarctic toothfish is concentrated, using stratified scientific camera and/or trawl survey(s); (iv) ascertain the relative consumption by Antarctic toothfish of *M. whitsoni* and *M. caml*. These data will help to manage and minimise the effect of fishing on associated species in the Southern Ocean ecosystem.

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Table 1: Summary of meristic and qualitative characters used to identify specimens of *Macrourus caml* and *M. whitsoni* during this study. See McMillan et al. (2012) for more detailed descriptions and illustrations.

Character	<i>M. whitsoni</i>	<i>M. caml</i>
Number pelvic fin rays	Usually 9 (rarely 10)	Usually 8 (rarely 7 or 9)
Teeth in lower jaw	1 row, enlarged, spaced	2–3 rows, small, close
Teeth in upper jaw	Outer row enlarged	Outer row not enlarged
Body colour	Pale to medium brownish	Medium–dark brownish or blackish
Intestine*	Relatively short, narrow, robust	Relatively long, wide, flaccid

* Further details on the different characteristics of intestines of the two species from the present study are given later.

Table 2: Samples by stratum, showing the mean proportion of *Macrourus whitsoni*.

	Stratum			
	North	Slope	East	All areas
<i>M. whitsoni</i>	73	104	69	246
<i>M. caml</i>	122	274	241	637
Both species	195	378	310	883
% <i>M. whitsoni</i>	37.4	27.5	22.3	27.9

Table 3: Main morphological characteristics used in identification of species in the laboratory, showing number of specimens in the present study with that trait, and the proportion of the sample with that trait in brackets.

Characteristic	Count	<i>Macrourus whitsoni</i>	<i>Macrourus caml</i>
Number of pelvic fin rays	7	0 (0.0%)	18 (2.7%)
	8	3 (1.2%)	635 (95.5%)
	9	240 (97.2%)	11 (1.7%)
	10	4 (1.6%)	0 (0.0%)
Number of teeth rows in lower jaw	1	223 (99.6%)	1 (0.2%)
	2	1 (0.4%)	613 (97.9%)
	3	0 (0.0%)	12 (1.9%)

Table 4: Total length (TL, cm) – pre-anal length (PAL, cm) relationships for *Macrourus caml* (WG2) and *M. whitsoni* (WGR) in the study area. Significance codes ('SigCode') are indicated with stars, with more stars indicating higher significance. The significance codes are shown between the bracketing values of $\Pr(>|t|)$: 0 '****' 0.001 '**' 0.01 '*' 0.05.

Relationship	PAL on TL		TL on PAL	
	t_value	$\Pr(> t)$ SigCode	t_value	$\Pr(> t)$ SigCode
SpeciesWG2:Sex1(Male)	2.983	0.002940**	-2.767	0.005783**
SpeciesWGR:Sex1	-0.470	0.638230	0.696	0.486700
SpeciesWG2:Sex2(Female)	1.429	0.153369	-2.432	0.015209*
TL(or PAL):SpeciesWG2:Sex1	-3.773	0.000172***	3.637	0.000292***
TL(or PAL):SpeciesWGR:Sex1	0.284	0.776828	-0.677	0.498568
TL(or PAL):SpeciesWG2:Sex2	-1.199	0.230782	2.471	0.013655*
<i>M. whitsoni</i> (both sexes); <i>M. caml</i> (female): $R^2 = 0.91$, $N = 606$	$PAL = 0.14 + 0.344TL$		$TL = 4.38 + 2.65PAL$	
<i>M. caml</i> (male): $R^2 = 0.89$, $N = 252$	$PAL = 1.78 + 0.302TL$		$TL = 1.91 + 2.87PAL$	

Table 5: Length–weight (W, g) relationships for *Macrourus caml* (WG2) and *M. whitsoni* (WGR) in the Ross Sea region. Total length (TL, cm). Pre-anal length (PAL, cm). Significance codes ('SigCode') are shown between the bracketing values of $\Pr(>|t|)$: 0 '****' 0.001 '**' 0.01 '*' 0.05.

Relationship	W on TL		W on PAL	
	t_value	$\Pr(> t)$ SigCode	t_value	$\Pr(> t)$ SigCode
SpeciesWG2:Sex1(Male)	-0.298	0.76544	-2.258	0.02418*
SpeciesWGR:Sex1	-1.174	0.24066	-0.498	0.61861
SpeciesWG2:Sex2(Female)	-2.679	0.00752**	-4.353	1.51e-05***
lnTL(or PAL):SpeciesWG2:Sex1	0.559	0.57659	2.881	0.00407**
lnTL(or PAL):SpeciesWGR:Sex1	1.137	0.25568	0.491	0.62369
lnTL(or PAL):SpeciesWG2:Sex2	3.259	0.00116**	5.097	4.25e-07***
<i>M. whitsoni</i> (both sexes); <i>M. caml</i> (males): $R^2 = 0.87$, $N = 478$	$W = 0.00366 TL^3.060$		NA	
<i>M. whitsoni</i> (both sexes): $R^2 = 0.87$, $N = 226$	NA		$W = 0.237 PAL^2.722$	
<i>M. caml</i> (males): $R^2 = 0.87$, $N = 252$	NA		$W = 0.124 PAL^3.016$	
<i>M. caml</i> (females): $R^2 = 0.91$, $N = 380$	$W = 0.00216 TL^3.234$		$W = 0.076 PAL^3.186$	

Table 6: Von Bertalanffy growth characteristics for *Macrourus whitsoni* and for *M. caml* based on total length (TL, cm). Standard errors (s.e.) are shown where appropriate.

Species (method)	Sex	Parameter	Value	s.e
<i>M. whitsoni</i> (L_{inf} set to the maximum TL in the sample and t_0 from Marriott et al., 2006)	Male (n = 37)	L_{inf} (cm)	59.0	...
		k (y^{-1})	0.0947	0.0043
		t_0 (y)	-0.159	0.489
	Female (n = 190)	L_{inf} (cm)	65.1	...
		k (y^{-1})	0.101	0.0025
		t_0 (y)	0.159	0.411
<i>M. caml</i> (L_{inf} and t_0 from Marriott et al., 2006)	Male (n = 129)	L_{inf} (cm)	76.1	1.93
		k (y^{-1})	0.0468	0.0010
		t_0 (y)	-0.159	0.489
	Female (n = 190)	L_{inf} (cm)	92.0	2.27
		k (y^{-1})	0.0416	0.0008
		t_0 (y)	0.159	0.411

Table 7: Gonad stage of *Macrourus whitsoni* and *M. caml* in the Ross Sea region by sex and strata.

Species	Gonad stage	Sex (all strata)		Stratum (both sexes)		
		Male	Female	North	Slope	East
<i>M. whitsoni</i>	1 (Immature)	6 (16.2%)	61 (32.1%)	20 (30.3%)	47 (51.1%)	0 (0.0%)
	2 (Maturing)	13 (35.1%)	66 (34.7%)	37 (56.1%)	31 (33.7%)	11 (15.9%)
	3 (Ripe)	6 (16.2%)	50 (26.3%)	7 (10.6%)	3 (3.3%)	46 (66.7%)
	4 (Running)	0 (0.0%)	2 (1.1%)	0 (0.0%)	0 (0.0%)	2 (2.9%)
	5 (Spent)	12 (32.4%)	11 (5.8%)	2 (3.0%)	11 (12.0%)	10 (14.5%)
<i>M. caml</i>	1 (Immature)	2 (0.8%)	15 (3.9%)	3 (2.5%)	9 (3.3%)	5 (2.1%)
	2 (Maturing)	37 (14.6%)	151 (39.7%)	30 (24.8%)	72 (26.5%)	86 (35.7%)
	3 (Ripe)	144 (56.9%)	171 (45.0%)	76 (62.8%)	126 (46.3%)	113 (46.9%)
	4 (Running)	5 (2.0%)	32 (8.4%)	1 (0.8%)	26 (9.6%)	10 (4.1%)
	5 (Spent)	65 (25.7%)	11 (2.9%)	11 (9.1%)	39 (14.3%)	27 (11.2%)

Table 8: Length (TL = total length, cm; PAL = pre-anal length, cm) and age at maturity for female *Macrourus whitsoni* and *M. caml* estimated using a fitted logistic maturity ogive, where the % value refers to the fitted proportion sexually mature. 95% confidence intervals (CI) are also shown.

Species		TL (cm)		PAL (cm)		Age (y)	
		50%	95%	50%	95%	50%	95%
<i>M. whitsoni</i> (females)	Value	51.6	56.6	17.8	20.1	16.2	23.2
	CI	50.4–52.7	55.0–59.5	17.3–18.3	19.4–21.3	15.1–17.3	21.1–27.6
<i>M. caml</i> (females)	Value	46.0	52.2	15.8	18.3	16.8*	21.4
	CI	43.3–47.7	50.4–55.4	14.9–16.4	17.6–19.5	15.4–17.7*	19.2–29.7

* Age derived from the TL logistic regression and von Bertalanffy growth curves (Table 6). There were insufficient samples to use this method for males of either species.

Table 9: Stomach and intestine contents of *Macrourus whitsoni* and *M. caml* in the Ross Sea, showing number of stomachs/intestines the prey item was found in (occurrence, O), number of individual prey items (N), and mass of prey (W). ‘Uni.’ = unidentified.

Source:	<i>Macrourus whitsoni</i>												<i>M. caml</i>				
	Intestines			Stomach			Intestines			Stomach			Intestines		Stomach		
	%O	%O	O	%N	%N	N	%W	%O	%O	O	%N	%N	N	%N	%N	N	%W
Sample size	60	10	10	81	24	24	10	93	22	22	294	54	54	22	54	22	
Fishes	10.0	30.0	3	8.6	16.7	4	67.6	33.3	18.2	4	11.9	7.4	4	15.0	4	15.0	
Amphipoda	26.7	40.0	4	23.5	20.8	5	0.9	38.7	45.5	10	37.8	24.1	13	2.6	13	2.6	
Euphausiacea	3.3	20.0	2	2.5	8.3	2	3.2	19.4	27.3	6	16.0	24.1	13	12.2	13	12.2	
Mysida	1.7	0	0	1.2	0	0	0	2.2	9.1	2	1.0	3.7	2	0.6	2	0.6	
Isopoda	0	30.0	3	0	16.7	4	4.5	9.7	22.7	5	3.7	9.3	5	5.4	5	5.4	
Decapoda	6.7	30.0	3	4.9	12.5	3	23.3	4.3	4.5	1	2.0	1.9	1	0.4	1	0.4	
Copepoda	1.7	10.0	1	2.5	4.2	1	0.04	5.4	4.5	1	1.7	1.9	1	0.02	1	0.02	
Tanaidacea	0	0	0	0	0	0	0	1.1	0	0	0.3	0	0	0	0	0	
Ostracoda	0	0	0	0	0	0	0	1.1	0	0	0.3	0	0	0	0	0	
Crustacea (uni.)	23.3	10.0	1	18.5	4.2	1	0.04	9.7	0	0	3.1	0	0	0	0	0	
Salpa	1.7	0	0	1.2	0	0	0	6.5	4.5	1	10.2	1.9	1	1.1	1	1.1	
Polychaeta	8.3	0	0	6.2	0	0	0	15.1	13.6	3	4.8	7.4	4	36.7	4	36.7	
Coral	0	0	0	0	0	0	0	0	4.5	1	0	1.9	1	0.01	1	0.01	
Chaetognatha	3.3	0	0	2.5	0	0	0	1.1	0	0	0.3	0	0	0	0	0	
Ophiuroidea	0	0	0	0	0	0	0	0	4.5	1	0	1.9	1	3.6	1	3.6	
Echinodermata	0	0	0	0	0	0	0	1.1	0	0	0.3	0	0	0	0	0	
Cephalopoda	5.0	20.0	2	3.7	16.7	4	0.5	7.5	27.3	6	2.4	13.0	7	12.3	7	12.3	
Unidentified	33.3	0	0	24.7	0	0	0	12.9	4.5	1	4.1	1.9	1	9.9	1	9.9	

Table 10: Stable isotope values of *Macrourus whitsoni* and *M. caml* in the Ross Sea region. Values shown are mean \pm standard deviation, and ‘n’ indicates number of samples.

Species		Stratum		
		North	Slope	East
<i>M. whitsoni</i>	n	10	16	12
	$\delta^{15}\text{N}$ (‰)	11.4 ± 0.4	10.9 ± 0.6	11.6 ± 0.7
	$\delta^{13}\text{C}$ (‰)	-24.8 ± 0.4	-26.5 ± 0.7	-25.3 ± 0.5
	Trophic level	4.2 ± 0.1	4.1 ± 0.2	4.3 ± 0.2
<i>M. caml</i>	n	17	24	19
	$\delta^{15}\text{N}$ (‰)	11.9 ± 0.5	11.8 ± 0.5	12.1 ± 0.6
	$\delta^{13}\text{C}$ (‰)	-24.2 ± 0.4	-25.9 ± 0.8	-25.2 ± 0.4
	Trophic level	4.4 ± 0.2	4.4 ± 0.2	4.5 ± 0.2

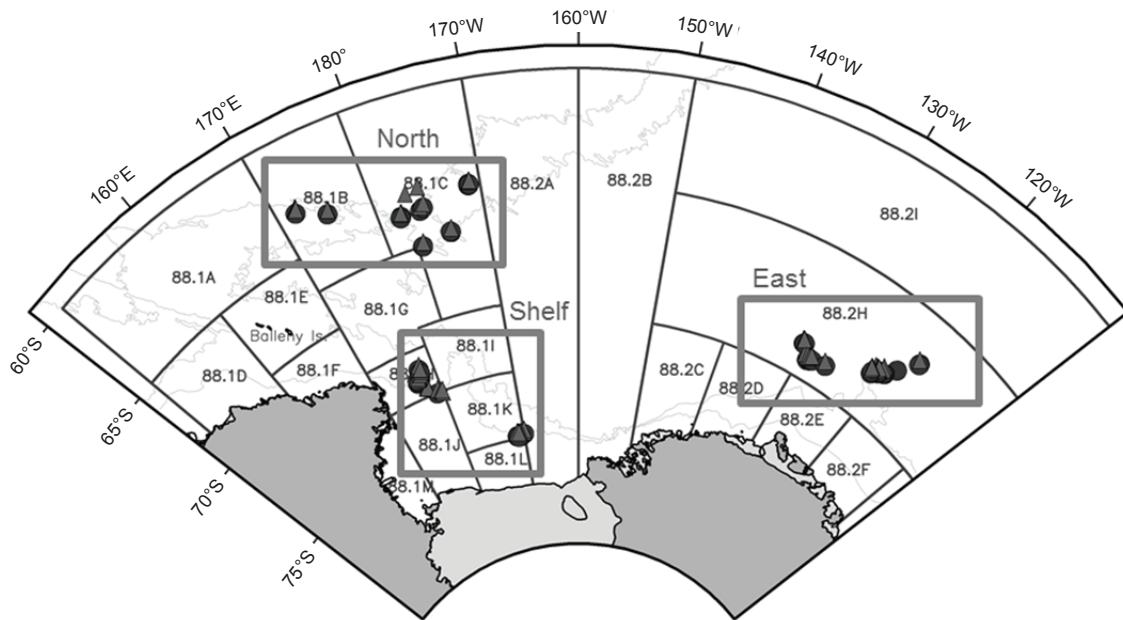


Figure 1: Locations of *Macrourus whitsoni* (circle) and *M. caml* (triangle) obtained by random sampling from the longline catch of *Macrourus* spp. by observers in the 2011/12 fishing season. Also shown are CCAMLR small-scale research units (SSRUs). Depth contours are plotted at 1 000, 2 000 and 3 000 m. Three strata used in this study are: North (SSRUs 881B, C and G); Slope (SSRUs 881H J and K); East (SSRU 882H).

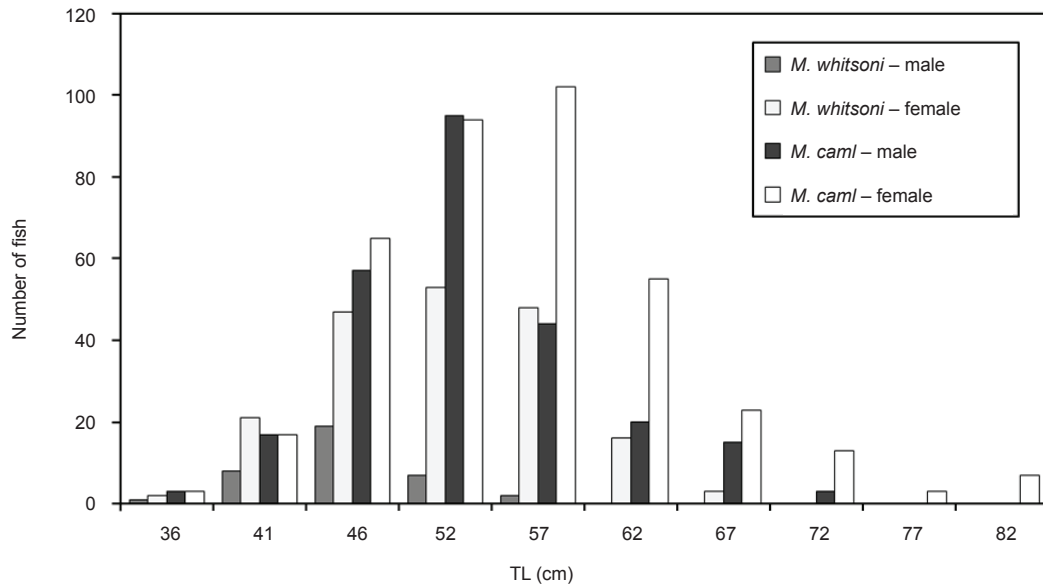


Figure 2: Total lengths (TL, cm) of fish in this study by species and sex, grouped into 10 equal-width bins (centre value of bin shown on x-axis).

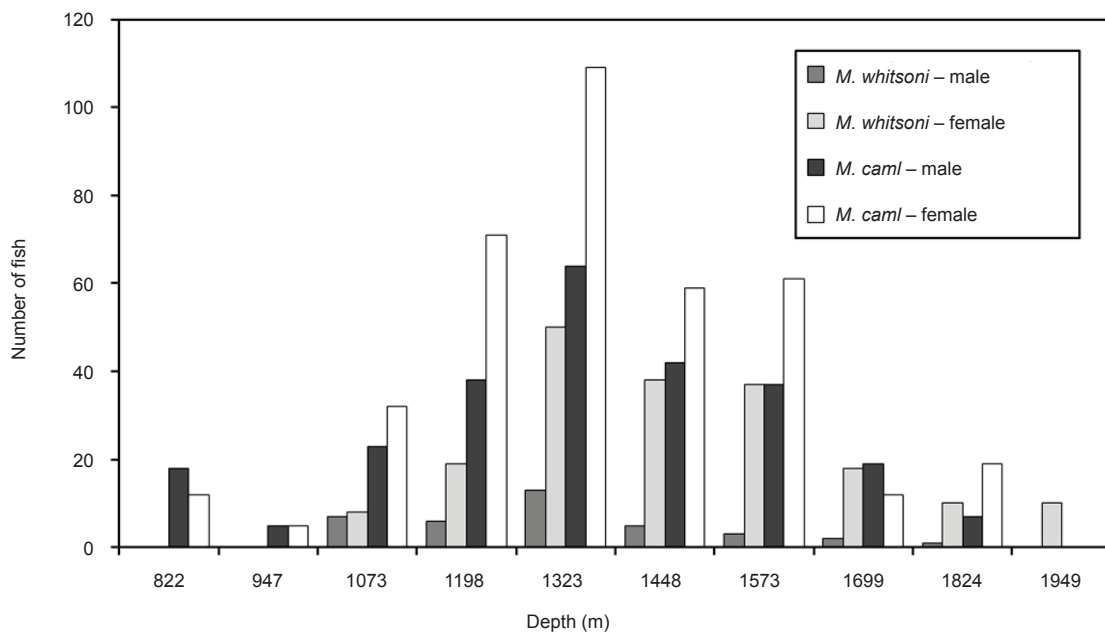


Figure 3: Depth distribution of *Macrourus whitsoni* and *M. caml*: number of samples returned from 2012 autoline catches in 10 depth bins (centre value of bin shown on x-axis). Depth of fishing is taken as the average of the start and end depths of set during setting.

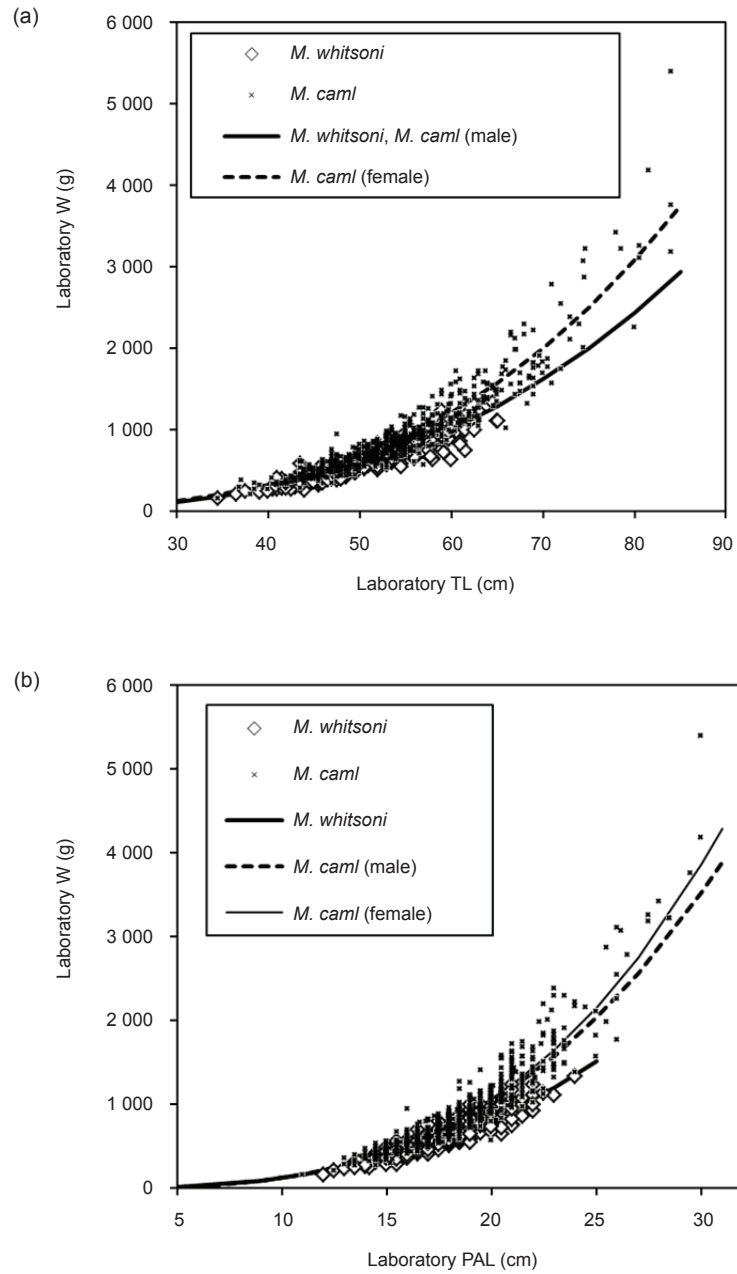


Figure 4: Relationship between weight (W) and (a) total length (TL); and (b) pre-anal length (PAL) for *Macrourus whitsoni* and *M. caml* in the Ross Sea region. See Table 5 for details of regression lines.

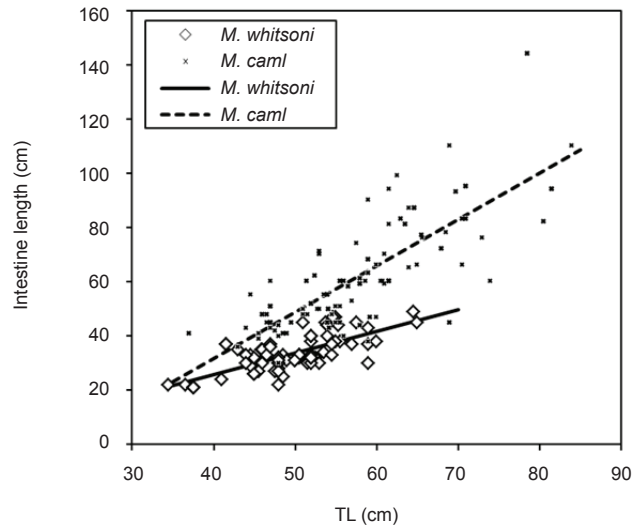


Figure 5: Relationship between total length (TL) and intestine length (pylorus to anus) for *Macrourus whitsoni* and *M. caml*.

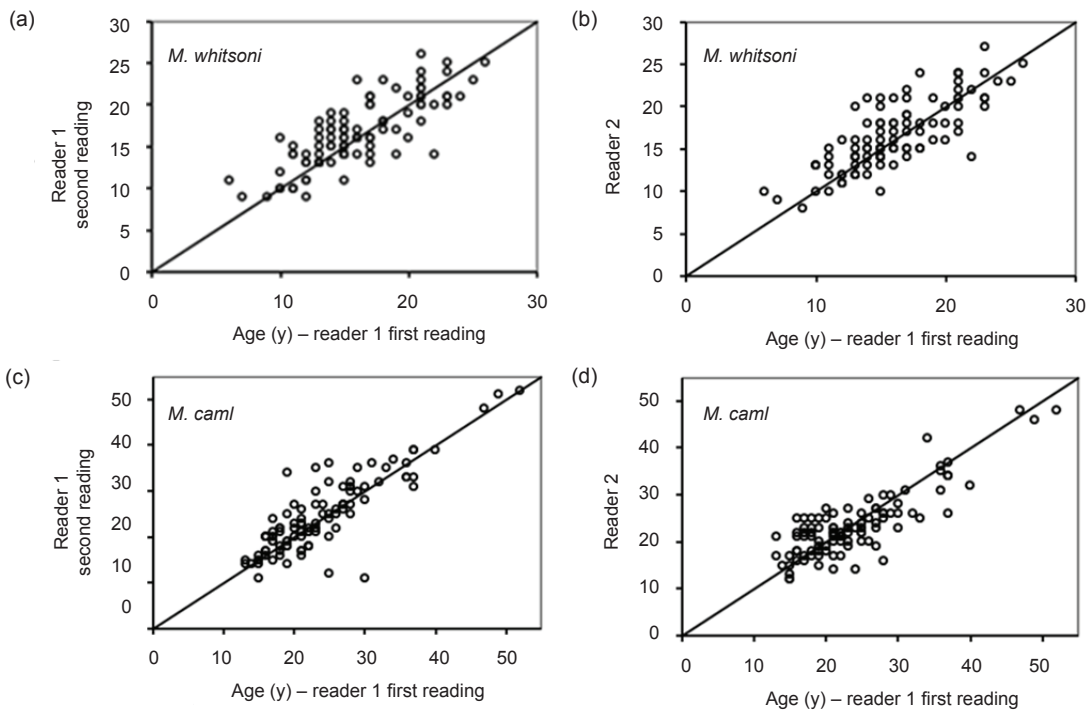


Figure 6: Age of fish (y) derived from otolith reading: within- and between-reader bias plots for *Macrourus whitsoni* (a and b) and *M. caml* (c and d).

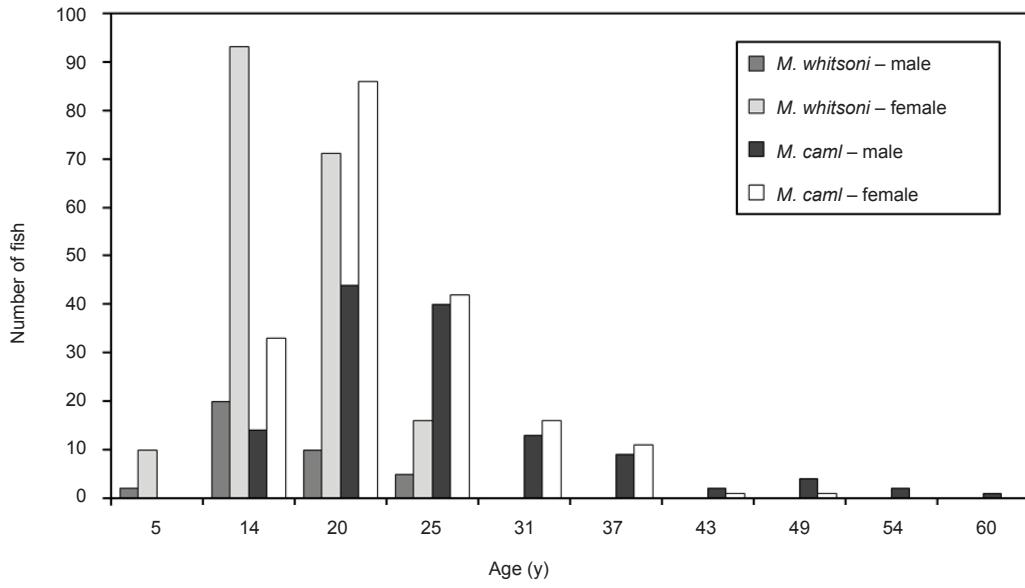


Figure 7: Age of fish in this study by species and sex, grouped into 10 equal-width bins (centre value of bin shown on x-axis).

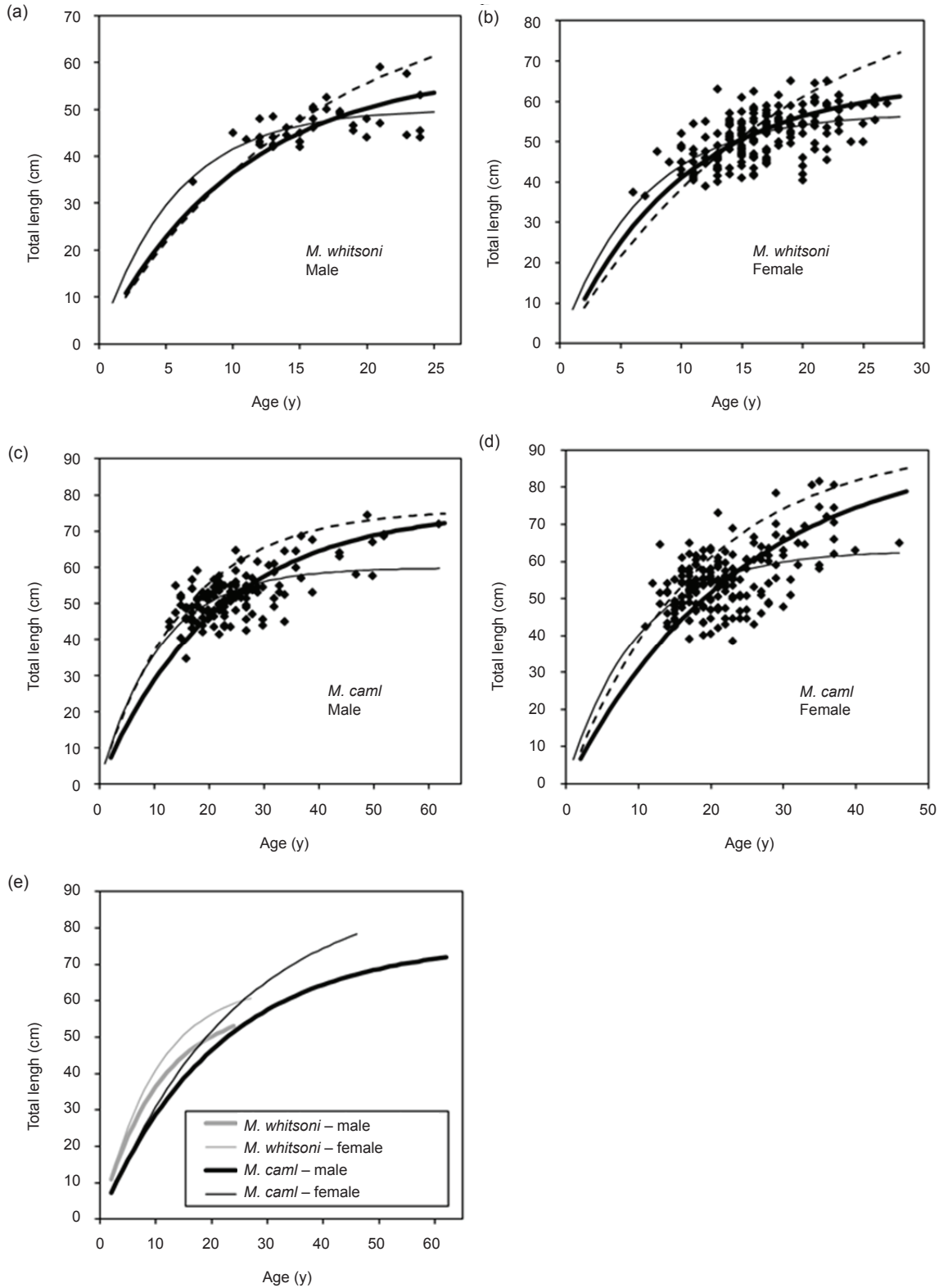


Figure 8: Von Bertalanffy growth curves for *Macrourus whitsoni* and *M. caml*. Dashed lines in panels (a) to (d) show the results of Marriott et al. (2006) (which was probably based on a mixture of the two species). Thin solid lines in panels (a) to (d) show least-squares fits to data in the present study with a nominal $t_0 = -0.1$. Thick solid lines in panels (a) and (b) show fits to data in the present study with L_{inf} taken as the maximum lengths in the present study and t_0 taken from Marriott et al. (2006). Thick solid lines in panels (c) and (d) show fits to data in the present study with both L_{inf} and t_0 taken from Marriott et al. (2006). (e) Fitted curves (thick solid lines in panels (a) to (d), and see Table 6) extending to the maximum ages recorded in this study.

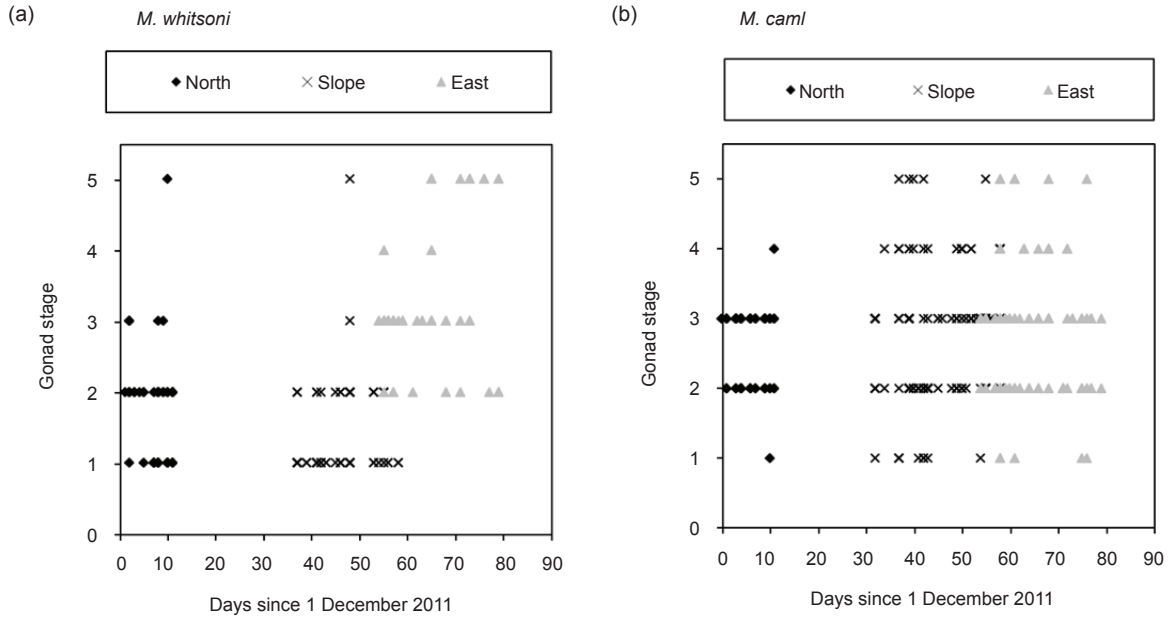


Figure 9: Changes in gonad stage of female (a) *Macrourus whitsoni*; and (b) *M. caml* in the Ross Sea region with date of sampling (days since 1 December 2011) shown by stratum.

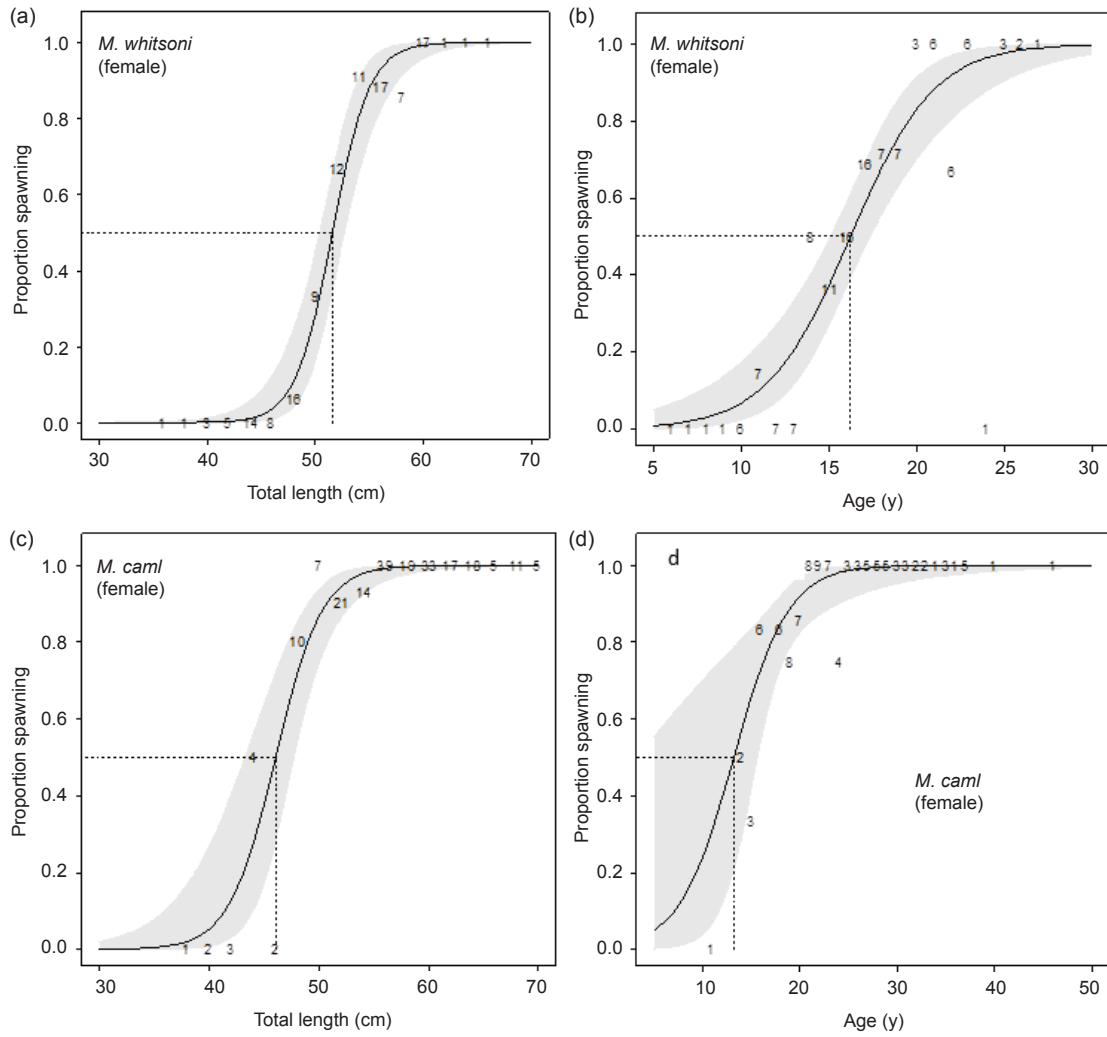


Figure 10: Total length (a and c) and age (b and d) at sexual maturity for *Macrourus whitsoni* (a and b) and *M. caml* (c and d). Females only are shown as there were insufficient males of either species for reliable logistic fitting. Numbers by the line indicate number of data points in that vicinity. Grey areas indicate CV range. Vertical and horizontal dashed lines show estimated length and age at 50% maturity.

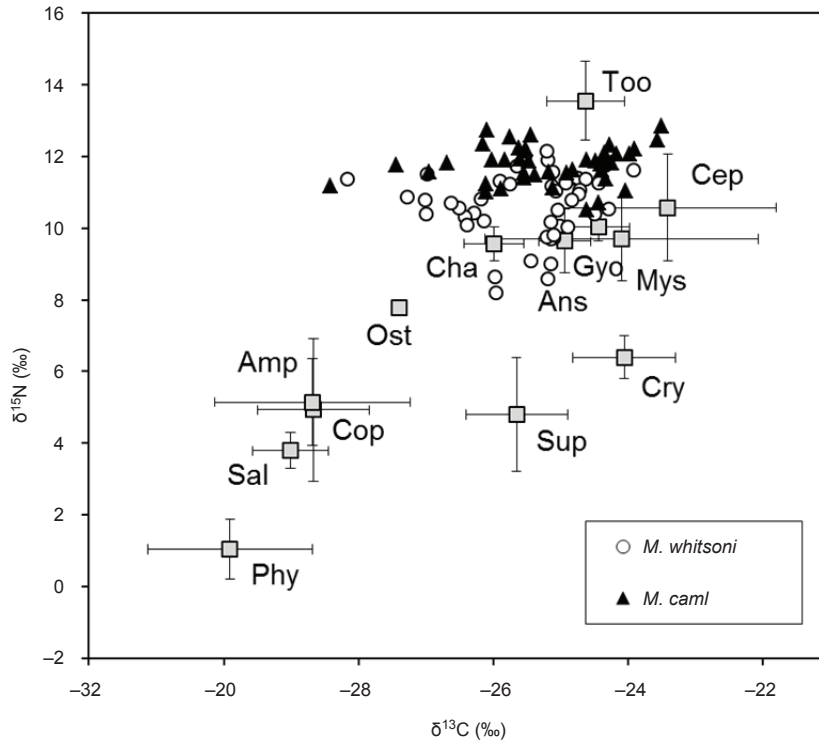


Figure 11: Carbon-nitrogen stable isotope values for *Macrourus whitsoni* (open circles) and *M. caml* (black triangles) in the North and Slope strata. Also shown are selected other biota from the Ross Sea region (mean and standard deviations): Phy = phytoplankton (near surface); Sal = salp; Cop = copepod; Amp = amphipod; Sup = *Euphausia superba*; Cry = *Euphausia crystallorophias*; Ost = ostracod; Cha = chaetognath; Mys = mysid; Ans = Antarctic silverfish (*Pleuragramma antarctica*); Gyo = lanternfish (*Gymnoscopelus opisthopterus*); Cep = cephalopod; Too = Antarctic toothfish. Prey isotope data from Pinkerton et al. (2012a); Antarctic toothfish isotope data from Bury et al. (2008).

