



Spatial distribution and population structure of juvenile Antarctic toothfish (*Dissostichus mawsoni*) in the South Shetland Islands

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Abstract

As most of biological and ecological features of the Antarctic toothfish have been provided almost exclusively by the recent fishery exploitation in the Ross Sea targeting adult fishes, the early life history of this species is fragmentary and still needs to be fully addressed. Aiming to fill this gap, we provide new insights on the spatial distribution and population structure of juvenile *D. mawsoni* caught during bottom trawl surveys on the shelves around the South Shetland Islands (CCAMLR Subarea 48.1). Juveniles were relatively evenly distributed on the northern shelf of the South Shetlands and all around Elephant Island, with a few specimens caught in the Bransfield Strait. Although the specimens were caught in all depth strata surveyed, they were most abundant between 100 and 300 m depth, with an evident shift towards deeper waters with ontogeny. The sampled population consisted of 150 juveniles measuring between 22 and 78 cm TL, equally distributed between sexes, most of them with gonads at an immature stage of maturity. Both sexes showed a positive allometric body growth, indicating healthy body condition. Based on counts of annual growth increments from sagittal otolith sections, age estimates ranged between 2 and 7 years in males and between 2 and 8 years in females, respectively. Annual growth rate was estimated from the age-length keys, spanning from 5 to 10 cm TL. Integrating population structure with early life history of juvenile *D. mawsoni*, we provide some indication on connectivity between the investigated nursery area and potential neighbouring spawning areas.

Introduction

The Antarctic toothfish (*Dissostichus mawsoni*) is a large nototheniid fish endemic to the Southern Ocean, with a circumpolar distribution at latitudes south of the Antarctic Convergence (DeWitt et al. 1990). It has a wide depth distribution increasing throughout the ontogeny, and can be found from the sea surface to over 2000 m (Eastman 2017). Although there remain several uncertainties, the life cycle of *D. mawsoni* has been tentatively inferred on the basis of the spatial distribution of different stages of development, drift of eggs and larvae through oceanic circulation models and tag-release studies (Hanchet et al. 2008). As with several

other nototheniid species, early juveniles of *D. mawsoni* up to 12 cm total length (TL) are pelagic and generally found inshore, where they feed on adult euphausiids and fish larvae (Pakhomov and Pankratov 1992). From 18 cm TL onwards, juveniles are distributed over the continental shelf in waters as deep as 300–500 m, acquiring a benthopelagic lifestyle (Eastman and DeVries 2000). As adults, *D. mawsoni* achieve neutral buoyancy and descend to deeper waters along the shelf slope (Near et al. 2003). At sexual maturity, adults migrate offshore to more oceanic waters located between the shelf break and the Antarctic Convergence to spawn (Hanchet et al. 2015). Females produce pelagic eggs, which have been collected in the upper 200 m depth using a plankton net (Stevens et al. 2016). Eggs are relatively large (up to 3.9 mm) and spherical in shape, showing a transparent chorion, a smooth surface and a small perivitelline space (Ghigliotti et al. 2018).

Within the CCAMLR Subarea 48.1, the South Shetland Islands may represent an important nursery area, as documented by the presence of juvenile *D. mawsoni* during the austral summer (Söffker et al. 2018 and references therein). Nevertheless, an exploratory fishery for *Dissostichus* spp. using longlines carried out in summer 1998 yielded very

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Fig. 1 Sagittal otolith section of juvenile *D. mawsoni* aged 7+ years old (female, 70 cm TL), resulting from the number of translucent zones (black dots) plus one year

low catches, which did not warrant a fishery targeting these species in this area (Arana and Vega 1999). Multiple bottom trawl surveys conducted on the continental shelf areas around the South Shetlands during the last three decades (1981–2012) recorded juveniles ranging from 11 to 70 cm in size at depths between 100 and 500 m (Kock 1998; Söffker et al. 2018). Smaller juveniles ranging from 2 to 12 cm were also occasionally caught at depths between 10 and 100 m as

bycatch during pelagic trawls targeting krill. The location of catches was relatively consistent with the predicted habitat suitability map, recently provided for *D. mawsoni* in the Weddell Sea and neighbouring areas (Teschke et al. 2017).

The methodological approach for ageing *D. mawsoni* is currently well established, consisting of baking, embedding in resin and further sectioning of sagittal otoliths (Sutton and Horn 2010; Nowara et al. 2017). Transverse sections of sagittal otoliths have generally been used to determine age in both adult and juvenile specimens of *D. mawsoni*, by counting alternating opaque and translucent zones forming annual growth-bands (*annuli*) (Burchett et al. 1984; Horn 2002; Horn et al. 2003). Annual periodicity of growth-band formation has been demonstrated by marking otoliths of tagged fish with oxytetracycline (Horn et al. 2003), and the lead-radium dating technique has been applied to validate the age estimation criteria and the accuracy of age estimates in this species (Brooks et al. 2011). Furthermore, timing and position of the first annulus has been assessed by counting the presumed daily increments in early juveniles of *D. mawsoni* collected off the South Shetland Islands (La Mesa 2007).

Studies on age and growth of *D. mawsoni* have been carried out primarily on large, adult specimens from the Ross Sea, coming from commercial longline catches targeting larger fish in offshore waters (Horn 2002; Brooks et al. 2011). Similarly, stock assessment models were developed in the Ross Sea by incorporating fishery catch-at-age and multi-year mark-recapture data (e.g. Mormede et al. 2014).

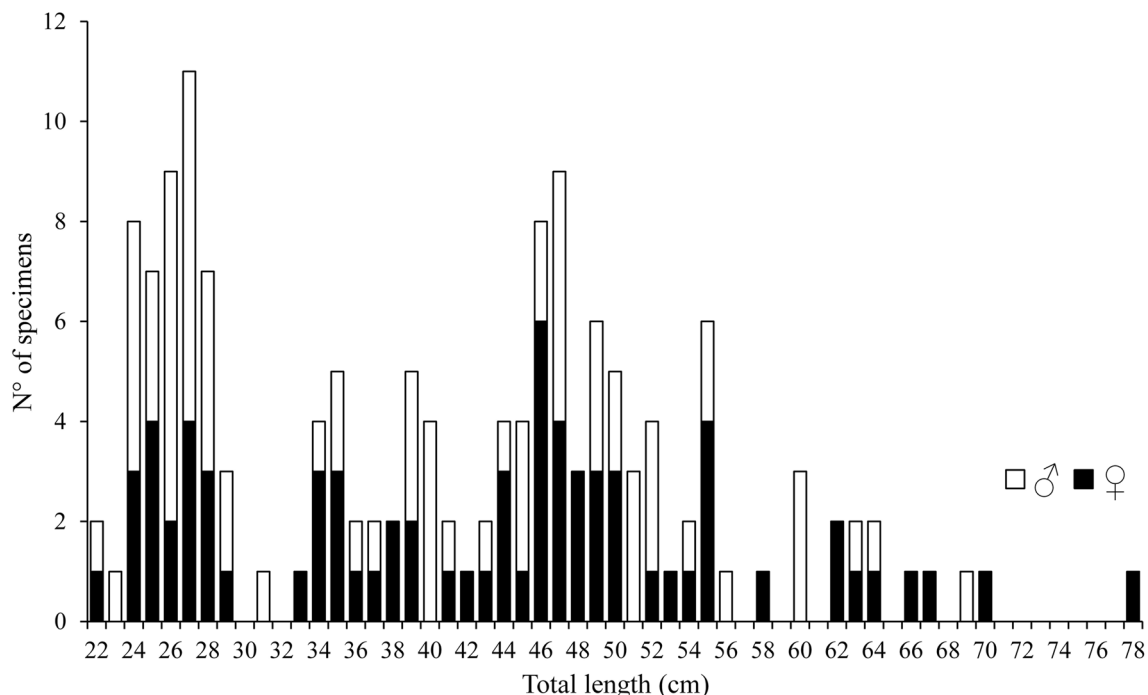
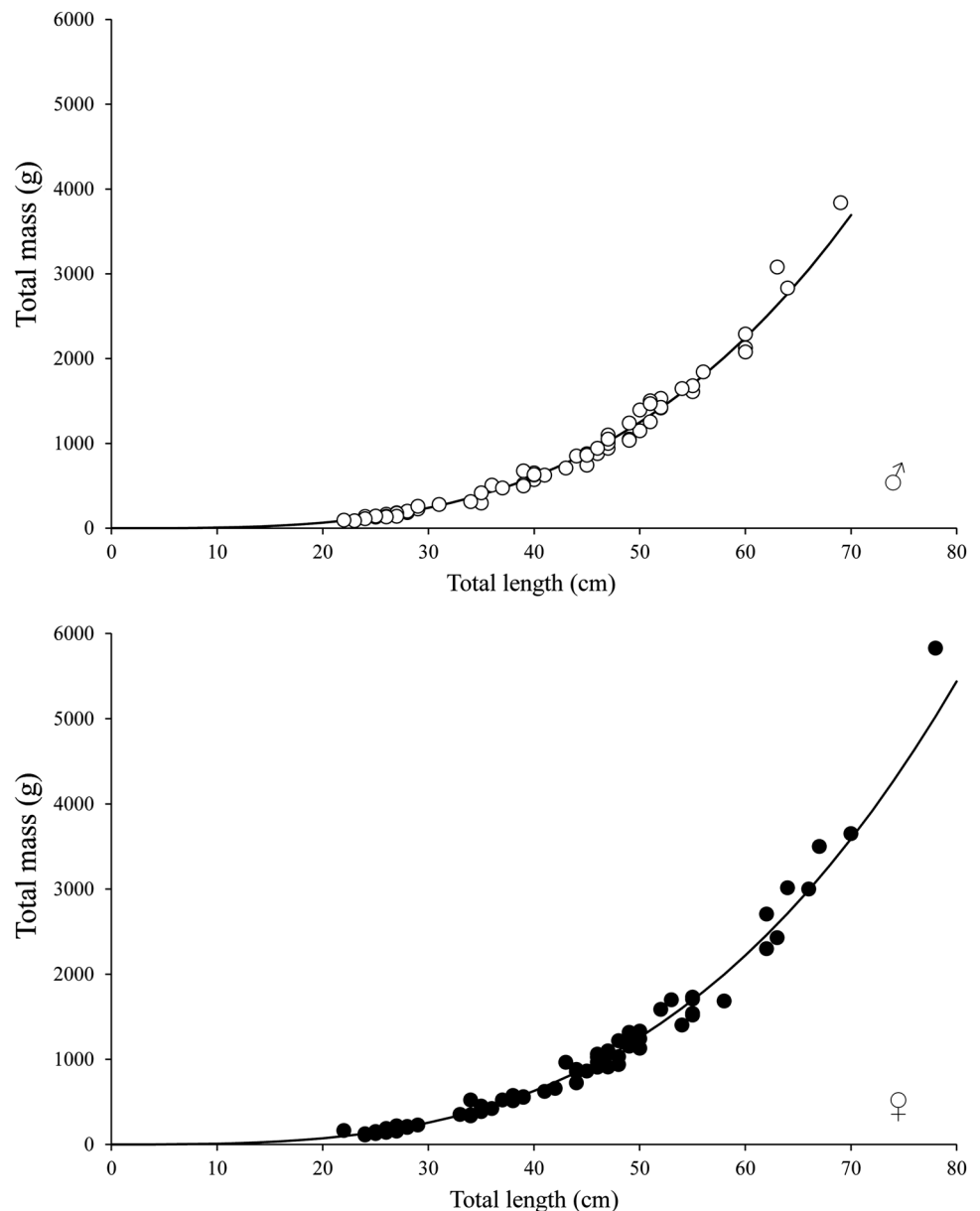


Fig. 2 Length frequency distribution of juvenile *D. mawsoni* collected from the CCAMLR Subarea 48.1

Fig. 3 Fish body length–mass relationships of juvenile *D. mawsoni* collected from the CCAMLR Subarea 48.1



As a consequence, the age composition and growth rate of this species during early life remain poorly known (Horn et al. 2003).

In the present study, we aim to investigate the spatial distribution of *D. mawsoni* juveniles caught in several trawl surveys conducted near the South Shetland Islands, providing data on the local population structure in terms of size, sex and age, assessed through the microscopic analysis of annulation pattern in sagittal otolith sections.

Materials and methods

Samples of juvenile *D. mawsoni* were collected during three U.S. Antarctic Marine Living Resources (AMLR) cruises conducted aboard the RV *Yuzhmorgeologiya* in March 2001, 2003 and February–March 2006, and during two German cruises carried out aboard the RV *Polarstern* in January–February 2002 (ANT-XIX/3) and December 2006–January 2007 (ANT-XXIII/8). All cruises surveyed roughly the same geographic area, including the continental shelf around Elephant Island, the northern shelf of the lower South Shetland Islands (King George to Livingston Islands), and in 2006, the Bransfield Strait adjacent to the Antarctic Peninsula. The sampling strategy of all bottom trawl surveys was based on a random depth-stratified survey

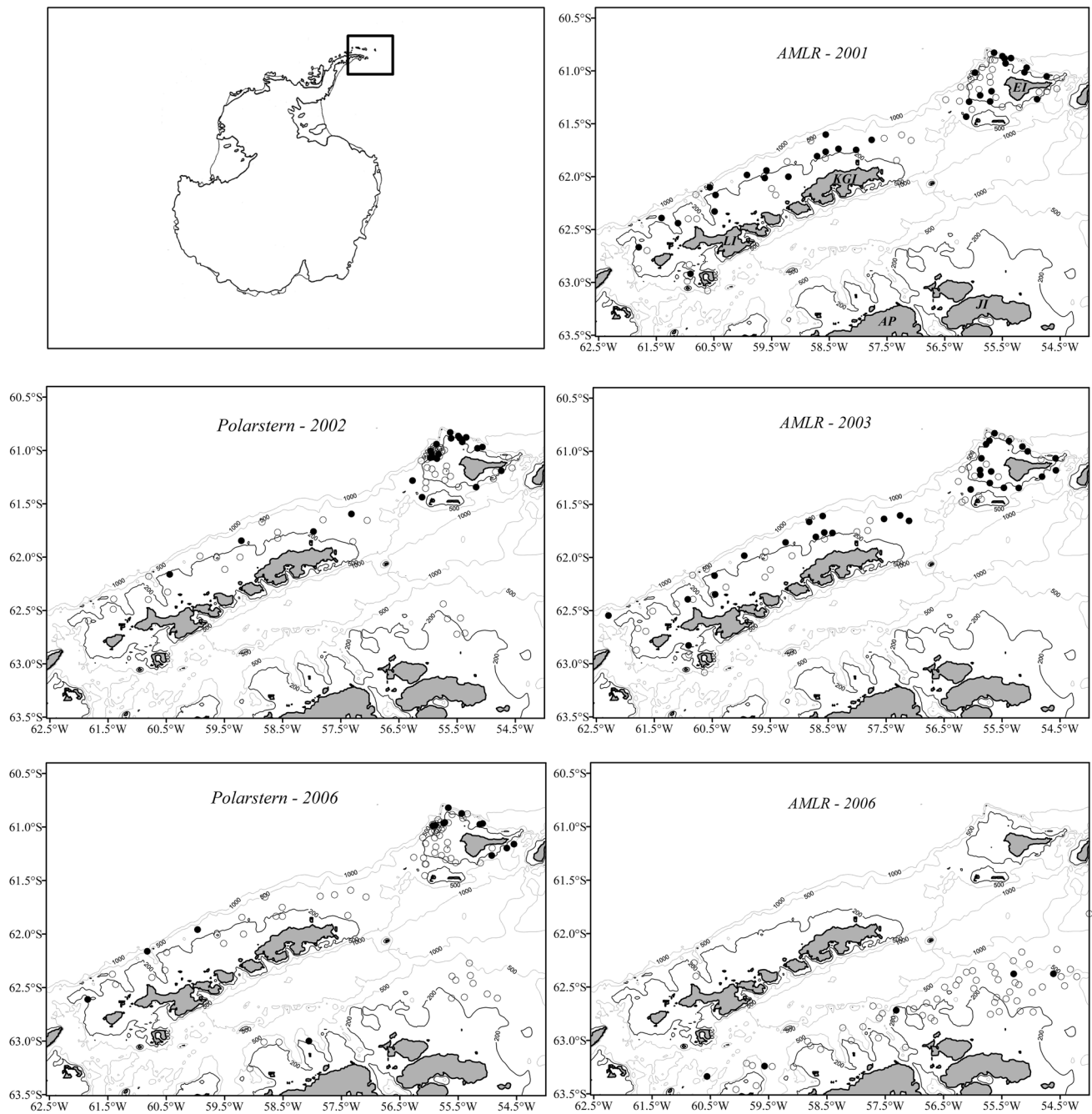


Fig. 4 Spatial distribution of juvenile *D. mawsoni* in the surveyed area, showing all sampling stations (empty circles=no catch). AP Antarctic Peninsula, JI Joinville Island, LI Livingston Island, KGI King George Island, EI, Elephant Island

design, with five depth strata set at 50–100 m, 100–200 m, 200–300 m, 300–400 m, 400–500 m. Sampling was carried out using a four-panel Hard Bottom Snapper Trawl (Net Systems Inc.) and a two-panel 140' bottom trawl, both with a codend mesh size of 40 mm. Trawl nets were generally towed on the bottom at about 2–2.5 knots for 30 min during daylight hours only. Further data on trawling operations

and catch compositions are reported elsewhere (Jones et al. 2001, 2003, 2006; Kock et al. 2003, 2008).

After each tow, fish were individually measured to the nearest cm below (total length, TL), weighed to g (total mass, TM) and sexed. Gonad stage of maturity was assessed according to the five-point scale widely adopted for nototheniids (Kock and Kellermann 1991). Sagittal otolith pairs

Fig. 5 Catches frequency distribution in relation to sampling depth of juvenile *D. mawsoni* from the CCAMLR Subarea 48.1

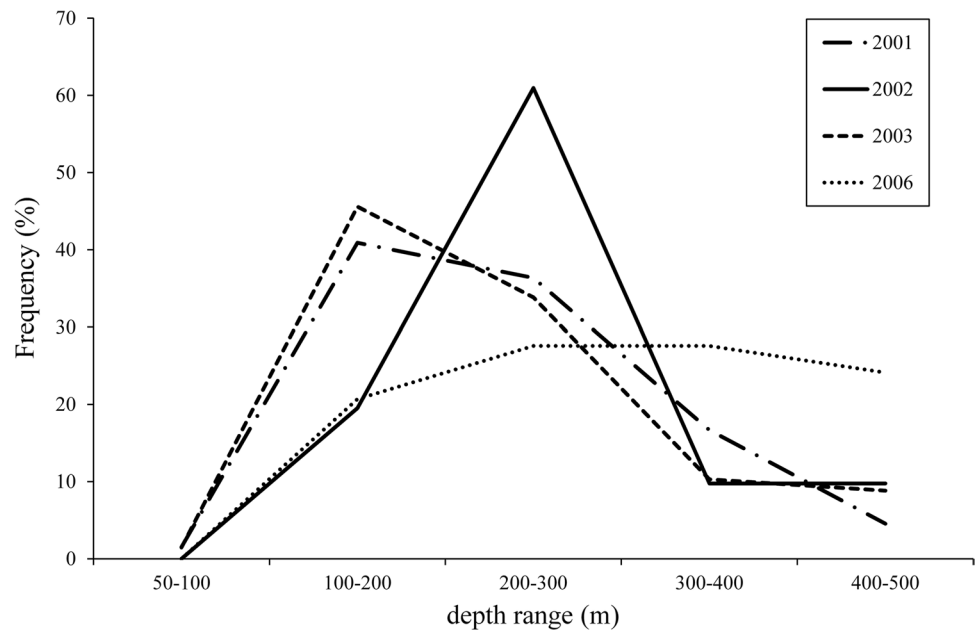
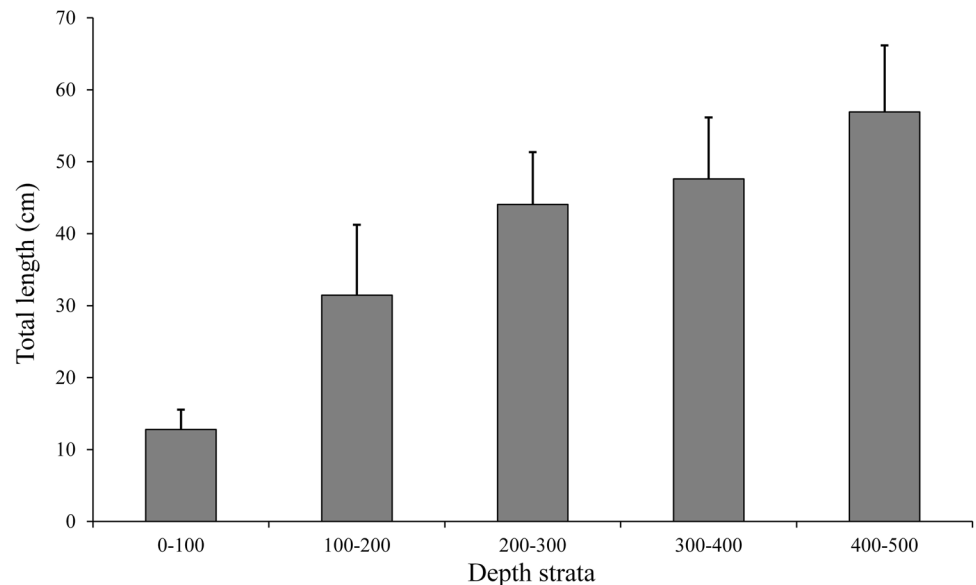


Fig. 6 Mean size of juveniles *D. mawsoni* recorded in sampling depth strata. Bars represent standard deviation



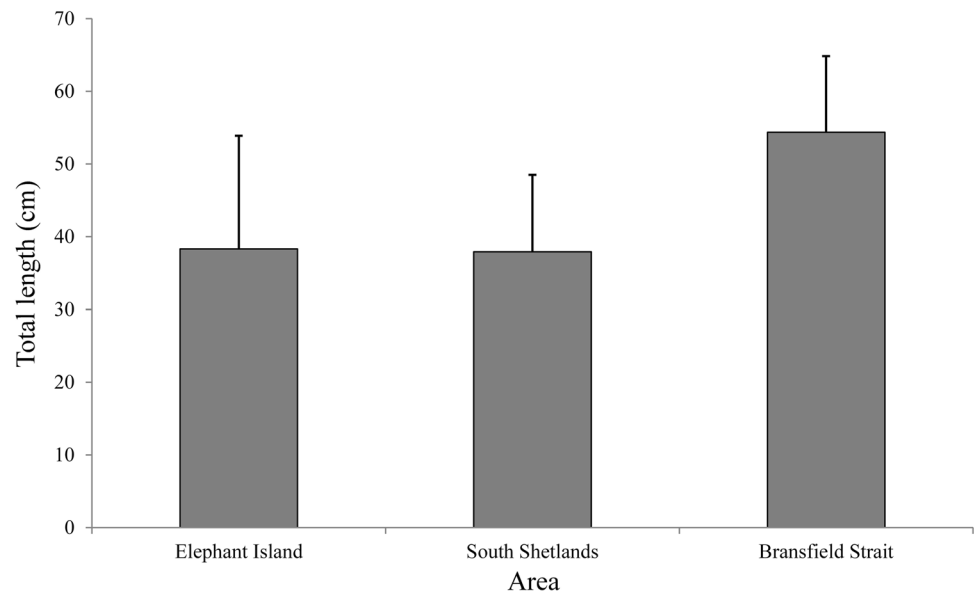
were removed from each individual, cleaned of adhering tissues and stored dry in labelled vials. A single otolith was randomly selected from each individual and weighed to the nearest mg (otolith mass, OM).

As commonly found in other notothenioids (e.g. White 1991), sagittal otoliths of *D. mawsoni* have a dense calcareous structure and are opaque, requiring sectioning and grinding to reveal the inner structure. The randomly selected otoliths were baked whole in an oven at 350 °C for a few minutes until they reached a light amber colour, which

enhanced the contrast between neighbouring growth zones, facilitating their counting. They were then embedded in resin (Crystalbond 509 Amber, Aremo products Inc.), ground using abrasive paper and polished on lapping films with 0.05 µm alumina powder. Once transverse sections revealing the primordium surrounded by the nucleus were obtained, they were fixed on glass slides and examined using reflected light with a stereomicroscope at ×25 to ×40 magnification.

Otoliths were read according to criteria established in the manual for age determination of Antarctic toothfish (Sutton and Horn 2010). An annulus consists of a wide opaque zone and a contiguous relatively narrow translucent zone, which under reflected light appears as a light

Fig. 7 Mean size of juveniles *D. mawsoni* recorded in sampling areas. Bars represent standard deviation



and a dark ring, respectively. The count path showing the most unambiguous annulation pattern was from the nucleus along the dorsal–ventral axis and then towards the proximal side of the otolith section (Fig. 1). As a rule of thumb, rings that did not persist along either side of the count path or were inconsistent in appearance were considered as false checks, and not counted. Assuming that annuli were laid down annually, the individual age was estimated by counting all translucent zones plus one year, based on previous results characterizing the age and hatching time of early juveniles (La Mesa 2007). The final age estimate was conventionally followed by plus (+), as all catches were obtained 2–3 months later than larval hatching.

Otoliths were read twice by the same reader (MLM) two weeks apart, without any ancillary data on fish size. To estimate ageing precision, representing the reproducibility or consistency between readings (Campana 2001), the index of average percent error (APE) (Beamish and Fournier 1981) and the mean coefficient of variation (CV) (Chang 1982) were calculated for the whole data set.

The length–frequency distributions of sexes were compared by applying a Kolmogorov–Smirnov two-sample test. Departure from the expected 1:1 sex ratio was tested using a χ^2 goodness-of-fit test. The body length–mass relationship was estimated for each sex through the exponential function $TM = aTL^b$, where TM is the total body mass (g) and TL is the total length (cm). Departure from isometric growth (i.e. $b=3$) was tested using a t test applied to the equation $t = (b - 3) SE^{-1}$, where SE is the standard error of b . The allometric indices (b) calculated for each sex were compared by applying an F test. The relationship between fish age estimates and otolith mass (OM) was

determined by simple linear regression analysis (Hanson and Stafford 2017). All statistical analyses were performed with STATISTICA 8 software (StatSoft, Inc., Tulsa, OK, USA). Mean values are reported with standard deviations (SD).

Results

A total of 77 males ranging from 22 to 69 cm and from 88 to 3840 g and 73 females ranging from 22 to 78 cm and from 112 to 5830 g were investigated, pooling together otoliths from all catches. The length–frequency distribution consisted of multiple modes (Fig. 2), with no statistical difference between sexes (Kolmogorov–Smirnov test, $D=0.16$, $p>0.05$). Sex ratio departure from the proportion 1:1 was not statistically significant ($\chi^2=0.06$, $df=1$, $p=0.74$). Fish body length–mass relationships were described by the following equations (Fig. 3):

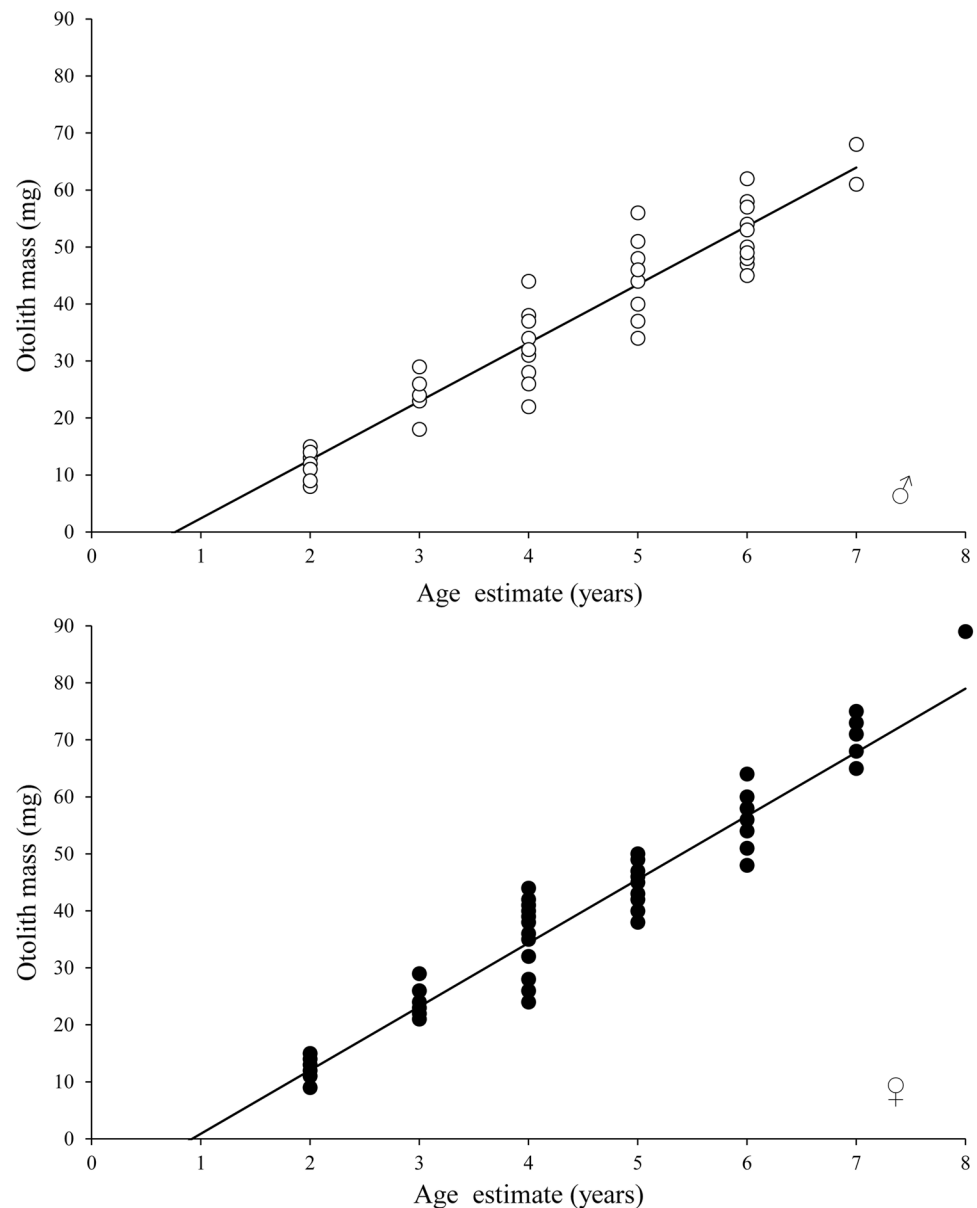
$$TL = 0.00416 TM^{3.22} \quad n = 77 \quad r^2 = 0.99 \quad \text{♂}$$

$$TL = 0.00643 TM^{3.11} \quad n = 73 \quad r^2 = 0.98 \quad \text{♀}$$

Body growth was positively allometric ($b>3$) in both sexes ($t=7.15$, $df=75$, $p<0.01$ for males; $t=2.65$, $df=71$, $p<0.01$ for females), differing significantly between them ($F=4.30$, $df=1$, 146, $p<0.05$). In relation to gonad maturity, most specimens were immature (stage 1), or occasionally at maturing virgin or developing stage (stage 2).

The spatial distributions of juvenile *D. mawsoni* catches are summarized in Fig. 4. During the AMLR cruises

Fig. 8 Linear relationships between fish age estimate and otolith mass of juvenile *D. mawsoni* collected from the CCAMLR Subarea 48.1



conducted in 2001 and 2003, catches were mainly distributed on the shelf at 200 m depth around Elephant Island and north of King George and Livingston Islands. During the AMLR cruise 2006, the few specimens caught were collected across the Bransfield Strait, off the tip of the Antarctic Peninsula and off Joinville Island. During the German cruises 2002 and 2006, most of catches were recorded to northwest of Elephant Island, and occasionally north of King George and Livingston Islands. The spatial distribution across the depth strata indicate that most catches were in the 100–200 and 200–300 m depth strata, largely decreasing in deeper waters except for the cruises during 2006 (Fig. 5). A positive linear relationship was found between fish size and sampling depth ($r=0.55$, $n=231$, $p<0.001$), with an evident shift towards deeper

waters during the ontogeny (Fig. 6). On the other hand, mean size of juveniles was similar between samples collected around Elephant Island and off the South Shetlands, whereas the few specimens (11) caught in the Bransfield Strait appeared to be larger than the previous ones (Fig. 7).

The sagittal otolith morphology of juvenile *D. mawsoni* was characterized by the square shape, the ostial sulcus acusticus and the rostrum shaped as a distinctly separated projection from the anterior margin (Hecht 1987). The linear relationships between individual age estimates and otolith mass (OM, mg) are summarized in the following equations:

$$OM = -7.85 + 10.26 \text{ age} \quad n = 75 \quad r^2 = 0.93 \quad \text{♂}$$

Table 1 Age-length keys for juvenile *D. mawsoni* collected from the CCAMLR Subarea 48.1

| TL (cm) | Age (years) | | | | | | | | | | | | | |
|---------|-------------|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♀ | | | | | | | ♂ | | | | | | |
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 2 | 3 | 4 | 5 | 6 | 7 | |
| 22 | 1 | | | | | | | 1 | | | | | | |
| 23 | | | | | | | | 1 | | | | | | |
| 24 | 3 | | | | | | | 5 | | | | | | |
| 25 | 4 | | | | | | | 3 | | | | | | |
| 26 | 2 | | | | | | | 7 | | | | | | |
| 27 | 4 | | | | | | | 7 | | | | | | |
| 28 | 3 | | | | | | | 4 | | | | | | |
| 29 | 1 | | | | | | | 2 | | | | | | |
| 30 | | | | | | | | | | | | | | |
| 31 | | | | | | | | | 1 | | | | | |
| 32 | | | | | | | | | | | | | | |
| 33 | | 1 | | | | | | | | | | | | |
| 34 | | 2 | 1 | | | | | | | 1 | | | | |
| 35 | | 3 | | | | | | | 2 | | | | | |
| 36 | | 1 | | | | | | | 1 | | | | | |
| 37 | | | 1 | | | | | | 1 | | | | | |
| 38 | | 1 | 1 | | | | | | | | | | | |
| 39 | | 1 | 1 | | | | | | 3 | | | | | |
| 40 | | | | | | | | | | 4 | | | | |
| 41 | | | 1 | | | | | | | 1 | | | | |
| 42 | | | 1 | | | | | | | | | | | |
| 43 | | | 1 | | | | | | | 1 | | | | |
| 44 | | | 3 | | | | | | | 1 | | | | |
| 45 | | | 1 | | | | | | | 2 | 1 | | | |
| 46 | | | 1 | 5 | | | | | | 1 | 1 | | | |
| 47 | | | 2 | 2 | | | | | | 2 | 2 | 1 | | |
| 48 | | | 1 | 2 | | | | | | | | | | |
| 49 | | | | 2 | 1 | | | | | | 3 | | | |
| 50 | | | | 2 | 1 | | | | | | 1 | 1 | | |
| 51 | | | | | | | | | | | 1 | 2 | | |
| 52 | | | | 1 | | | | | | | 2 | 1 | | |
| 53 | | | | | 1 | | | | | | | | | |
| 54 | | | | 1 | | | | | | | | 1 | | |
| 55 | | | | | 4 | | | | | | 1 | 1 | | |
| 56 | | | | | | | | | | | | 1 | | |
| 57 | | | | | | | | | | | | | | |
| 58 | | | | | 1 | | | | | | | | | |
| 59 | | | | | | | | | | | | | | |
| 60 | | | | | | | | | | | | 3 | | |
| 61 | | | | | | | | | | | | | | |
| 62 | | | | | 1 | 1 | | | | | | | | |
| 63 | | | | | | 1 | | | | | | 1 | | |
| 64 | | | | | 1 | | | | | | | | | 1 |
| 65 | | | | | | | | | | | | | | |
| 66 | | | | | | 1 | | | | | | | | |
| 67 | | | | | | 1 | | | | | | | | |
| 68 | | | | | | | | | | | | | | |
| 69 | | | | | | | | | | | | | | 1 |

Table 1 (continued)

| TL (cm) | Age (years) | | | | | | | | | | | | |
|----------|-------------|------|------|------|------|------|----|------|------|------|------|------|------|
| | ♀ | | | | | | | ♂ | | | | | |
| | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 2 | 3 | 4 | 5 | 6 | 7 |
| 70 | | | | | | 1 | | | | | | | |
| 78 | | | | | | | 1 | | | | | | |
| <i>n</i> | 18 | 9 | 15 | 15 | 10 | 5 | 1 | 30 | 8 | 13 | 12 | 12 | 2 |
| Mean | 25.9 | 35.4 | 42.6 | 48.3 | 55.6 | 65.6 | 78 | 26.0 | 36.4 | 42.5 | 49.3 | 54.9 | 66.5 |
| SD | 1.8 | 1.9 | 4.1 | 2.4 | 4.7 | 3.2 | 0 | 1.7 | 2.8 | 3.7 | 2.9 | 5.0 | 3.5 |

$$OM = -10.26 + 11.16 \text{ age} \quad n = 73 \quad r^2 = 0.94 \quad \text{♀}$$

Comparing otolith mass among age classes, there was a marked overlap between them, except for the 2+ and 3+ year-old fish (Fig. 8). Using age as covariate, no significant difference in the relationships was found between sexes (one-way ANCOVA, $F=4.0$, $p>0.05$).

All juveniles caught were successfully aged. Based on the annulation pattern revealed from the sagittal otolith sections, age-length keys were computed separately for each sex (Table 1). Age ranged between 2+ and 7+ years in males and between 2+ and 8+ years in females. The majority of fish within the sample (80%) were estimated to be between 2+ and 5+ years old. As a measure of ageing precision, the average percentage error (APE) and the mean coefficient of variation (CV) were both less than 5%, which represents a reference point for species of moderate longevity and reading complexity, supporting the reliability of the ageing procedure adopted.

Discussion

The continental shelf waters between 100 and 500 m depth around the South Shetland Islands and off the tip of the Antarctic Peninsula host a well-structured population of juvenile *D. mawsoni*. Although they are less abundant than other fin-fish species in the area, the relatively low number of specimens was relatively evenly caught throughout the stations, encompassing a wide geographic area around the South Shetland Islands. The local sex-balanced population of *D. mawsoni* consisted of one-year-old small juveniles ranging from 11 to 13 cm (La Mesa 2007), as well as of 2–8 year-old juveniles ranging approximately from 20 to 70 cm (present data). All juveniles were caught near the seafloor, indicating they were bottom dwellers residing close to the substrate, as reported elsewhere (Eastman et al. 2013). However, juveniles smaller than 12 mm likely inhabit the upper layers of water column at less than 100 m depth, having been caught by vessels targeting krill (Söffker et al. 2018).

In agreement with previous studies (e.g. Hanchet et al. 2008), we found an evident shift of juveniles *D. mawsoni*

towards deeper waters with ontogeny, associated with a shift towards neutral buoyancy achieved in adulthood through the accumulation of subcutaneous lipid deposits (Near et al. 2003). Comparing the populations of *D. mawsoni* sampled around Elephant Island and north of the South Shetland Islands, which represented the two main sampling areas surveyed during the cruises, the mean fish size did not differ from each other, whereas juveniles caught in the Bransfield Strait were of larger size (though in small number).

Despite the Bransfield Strait and adjacent waters representing one of the most important areas of larval retention off the Antarctic Peninsula for several notothenioids (e.g. La Mesa et al. 2016), neither eggs nor larvae of *D. mawsoni* have been caught. The spawning grounds of this species are likely ridges and banks generally located further north in oceanic waters (Hanchet et al. 2015). Based on biological data (i.e. gonad stage) recorded for adults, a series of potential spawning areas have been hypothesized all around Antarctica. In particular, three main spawning areas were located in the Lazarev Sea and Bellingshausen Seas, respectively east and west of the Antarctic Peninsula (Dunn et al. 2012). Taking into account the patterns of larval dispersion for *D. mawsoni* obtained through the HiGEM circumpolar oceanographic model (Dunn et al. 2012), the presence of one-year-old juveniles around the South Shetland Islands would be consistent with the time required to reach the area from a spawning site located upstream in the Bellingshausen Sea, driven by the Southern Antarctic Circumpolar Current Front (e.g. Ashford et al. 2008). On the other hand, older juveniles of *D. mawsoni* could be transported from Lazarev Sea to the Antarctic Peninsula through the Antarctic Slope Current (ASC), which flows westward along the continental shelf slope forming the southern limb of the Weddell gyre (Söffker et al. 2018).

The use of baked sagittal otolith sections was confirmed to be a valid method for ageing juveniles of *D. mawsoni*. As reported in previous studies (Horn 2002; Sutton and Horn 2010), the interpretation of annual growth rings in juveniles was often complicated by the presence of false rings or split zones (see Fig. 1), although more present in the dorsal portion of sections. Age-frequency distributions

estimated in the present study closely resembled those reported from the same area by Horn et al. (2003), by adding a year to the previous data as discussed in the methods section. The first three age classes, 1+ (from La Mesa 2007), 2+ and 3+ were well separated from each other, matching closely the relevant modal size groups. Conversely, older juveniles overlapped considerably, in agreement with the polymodal distribution of fish size.

Derived from the mean length at age reported in the age-length keys, annual growth rates of juveniles of *D. mawsoni* decreased roughly between 10 and 5 cm TL. Growth rates for juveniles were consistent with the annual growth rates estimated for adult fishes aged from 8 to 25 years, which ranged from 5 to 2 cm TL (Horn 2002). Juveniles of *D. mawsoni* exhibited a positive allometric body growth and healthy body condition, likely assured by an energy-rich food intake, consisting mainly of fish (70–75%) and krill (25–30%), as well as by the high feeding rate inferred by the low number of empty stomachs (14–18%) at this stage of development (Jones et al. 2001, 2003).

In relation to gonad maturity, the majority of juveniles (85%) were staged as immature (stage 1), whereas a few remaining specimens were macroscopically staged as maturing virgin females or developing males (stage 2). Adult of larger size (90–168 cm TL) of *D. mawsoni* were collected during a past exploratory fishing survey conducted in the same area in waters as deep as 600–2500 m, but they were at an early stage of gonad maturity as well (Arana and Vega 1999). Bearing in mind the habitat requirements of the spawning grounds of this species reported elsewhere (Hanchet et al. 2008), we can hypothesize that the larger adults living in the Subarea 48.1 move north-eastward throughout the lower Scotia Arc, to reach the winter spawning population located east of the South Sandwich Islands (Söffker et al. 2018).

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Compliance with ethical standards

Conflicts of interest The authors declare to have no conflicts of interest and that all applicable institutional, national or international guidelines for the use and care of animals have been strictly followed in the study.

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