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Growth and age validation in high-Antarctic fish

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Abstract The growth of three demersal species dominant in biomass and abundance in the Weddell Sea, *Chionodraco myersi* (channichthyid), *Trematomus eulepidotus* (nototheniid) and *Dolloidraco longedorsalis* (artedidraconid), was studied on specimens caught in summer. Ages were determined using ground and polished otolith sections and an image analysis system to measure the otolith radius and distances of each growth increment to the otolith core. Ageing precision and accuracy have been estimated. Indirect validation methods, based on the increment growth pattern, were applied to support the annual periodicity of the increments. Due to the lack of some age classes, back-calculated age-length keys were determined and used to fit the von Bertalanffy growth parameters by sex and species. The determined values showed sexual dimorphism, with females having faster growth rates, except in *D. longedorsalis*. The growth performance index was between 1 and 2, as in other high-Antarctic fish. For *T. eulepidotus*, age and growth data were available, but this is the first report for *C. myersi* and *D. longedorsalis*. Moreover, this is the first time that accuracy and precision have been estimated for high-Antarctic fish age determination.

Introduction

The Antarctic marine environment is characterised by low but stable temperatures, and a markedly seasonal

production cycle mediated by the seasonal changes in day length and the shading effects of sea ice (White 1991). In this environment, events such as growth and reproduction have been shown to be seasonal (White 1977; Clarke 1983; Everson 1984; Kock 1985). The development of extensive commercial-scale fisheries and the scientific interest arising from international research initiatives have stimulated a series of investigations to develop reliable methods for determining the age of Antarctic fish (Everson 1980). Otoliths have been considered the preferred ageing structures (White 1991). However, few ageing studies are available from high-Antarctic waters where the seasonality is more marked and the field work is seriously limited due to ice cover.

The fish fauna of the Weddell Sea is characterised by a series of assemblages related to water depths. The most common demersal species are the nototheniids, *Trematomus lepidorhinus*, *T. eulepidotus* and *T. scotti*, the artedidraconid, *Dolloidraco longedorsalis* and the channichthyid, *Chionodraco myersi* (Ekau 1988; Balguerías and Morales-Nin 1997). The behaviour of these species ranges from sluggish, e.g. *D. longedorsalis*, which preys on advected epibenthos, to the ichthyophage and active *C. myersi*, while *T. eulepidotus* is an active benthopelagic fish, feeding on euphausiids (Ekau 1991; Hubold 1991; Eastman 1993). Weddell Sea fish have a slow growth; trophic niche and life history strategy seem to be more important factors in the control of growth than temperature (Hubold 1992).

In this paper we report the growth of *T. eulepidotus* Regan, 1914, *D. longedorsalis* Roule, 1913 and *C. myersi* (Dewitt and Tyler, 1960). The age was determined by means of otolith interpretation, and ageing precision and accuracy were determined. The back-calculated age-length relationships were used to fit by sex the growth parameters of these dominant fish species in the Weddell Sea. Validation of ages is discussed in the light of the Antarctic characteristics.

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Materials and methods

On the EASIZ I cruise of RV "Polarstern" in February/March 1996, two sampling areas in the Weddell Sea were selected: southwest of Vestkapp (ca. 73°S, 19°W) and Kapp Norvegia (ca. 72°S, 12°W). In both areas, a series of bottom trawls were made using an Agassiz trawl with an opening of 3 × 1 m and 10 mm mesh size in the cod-end, or a bottom trawl (GSN) with an opening of 22 × 3 m and mesh size of 20 mm in the cod-end. The Agassiz was towed at 1 knot for 5–35 min, and 13 hauls were made between 170 and 2334 m. Ten hauls with the GSN were carried out at 3 knots; each haul was between 14 and 26 min duration and in 227–889 m water depth. The sea temperature ranged between –1.95 and 0 °C and the salinity was between 34.32 and 34.6.

The fish were sorted from the catch and identified to species level according to FAO identification sheets (Fischer and Hureau 1985). The total length of each fish was determined to the nearest lower millimetre and fishes were sexed. Sagittal otoliths were extracted and preserved dry for further study.

Antarctic fish otoliths usually have a dense calcareous structure and are opaque, requiring sectioning to observe the internal structure (White 1991). The right sagittae were glued to glass slides

and were ground until a frontal section with clear growth structures was reached. They were then polished using decreasing grade lapping films to obtain a surface without polishing scratches. Before observation, the otolith surface was moistened with a 50% mixture of alcohol and glycerol. The otoliths ($N = 160$ for *T. eulepidotus*, $N = 90$ for *C. myersi*, $N = 131$ for *D. longedorsalis*) were read using a compound microscope coupled to a high-resolution TV camera connected to a PC. The alternate opaque and translucent increments were considered as annuli following the definition of Everson (1980). The translucent rings appeared as dark narrow bands followed by a check. All otolith readings were carried out along the core-anti-rostrum axis (Fig. 1). The otolith radius and the distance from the core to each translucent ring were measured with a modified OPTIMAS software.

The precision of the ages estimated was determined by repeated reading of a sub-sample of otoliths of each species and applying the index of average percent error (Beamish and Fournier 1981).

The accuracy of the ages could not be determined directly due to the limitations of the sampling. Thus, the annual nature of the annulus was indirectly supported by assessing: (1) the decreasing exponential annulus width with age (i.e. fish length), and (2) the regularity of the ring pattern in the sample by plotting all the ring-to-core distances and testing the normality of the distributions by

Fig. 1 Micrographs of sagittal otoliths: **a** from a 22-cm *Trematomus eulepidotus* aged 8 years, showing the increments (*R*) used for age determination and the measurement radius (the question mark indicates the increment considered as laid down in the initial development stages), **b** and **d** from 12.5-cm and 31.8-cm fish length *Chionodraco myersi*, aged 2 years and 12 years, respectively, **c** from a 10.1-cm-length *Dolloidraco longedorsalis* aged 12 years. Scale bar: **a** 0.29 cm, **b** 0.22 cm, **c** 0.27 cm, **d** 0.28 cm

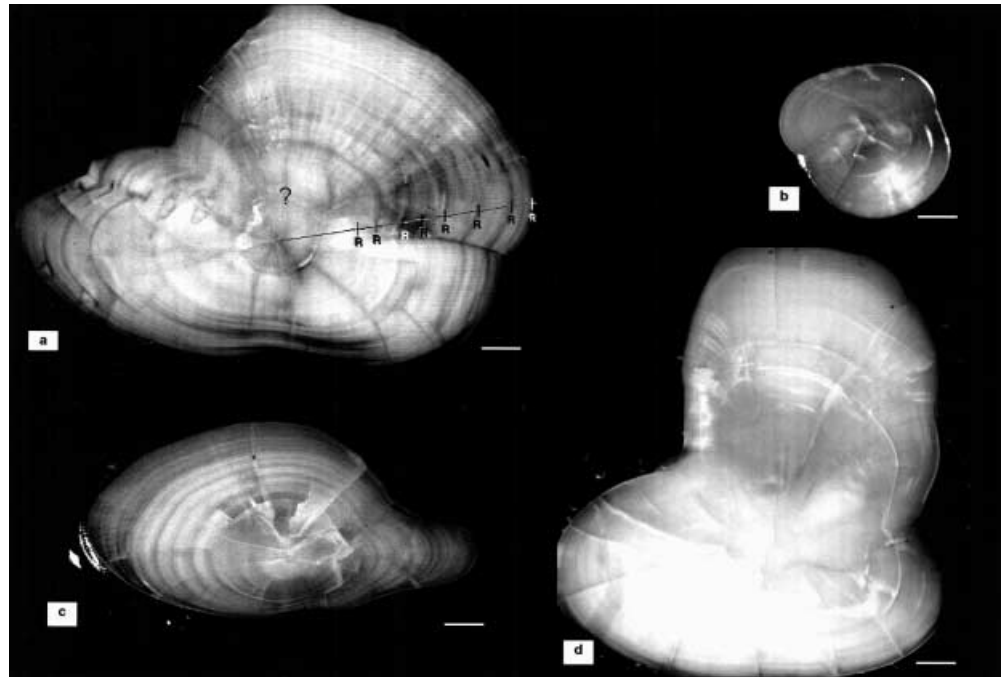
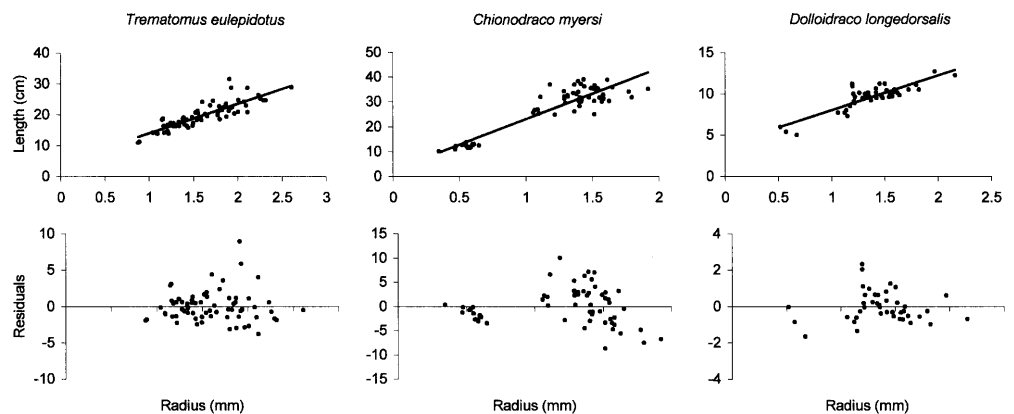


Fig. 2 Fish length-otolith radius relationships (*top*) and plot of the regression residuals (*bottom*) for the three studied species



means of a Kolmogorov-Smirnov test. The ages obtained were thus based on the count of presumptive annuli, because we only validated their annual nature indirectly (Morales-Nin 1992).

As the birth date was not known, we estimated the number of increments as the age in years.

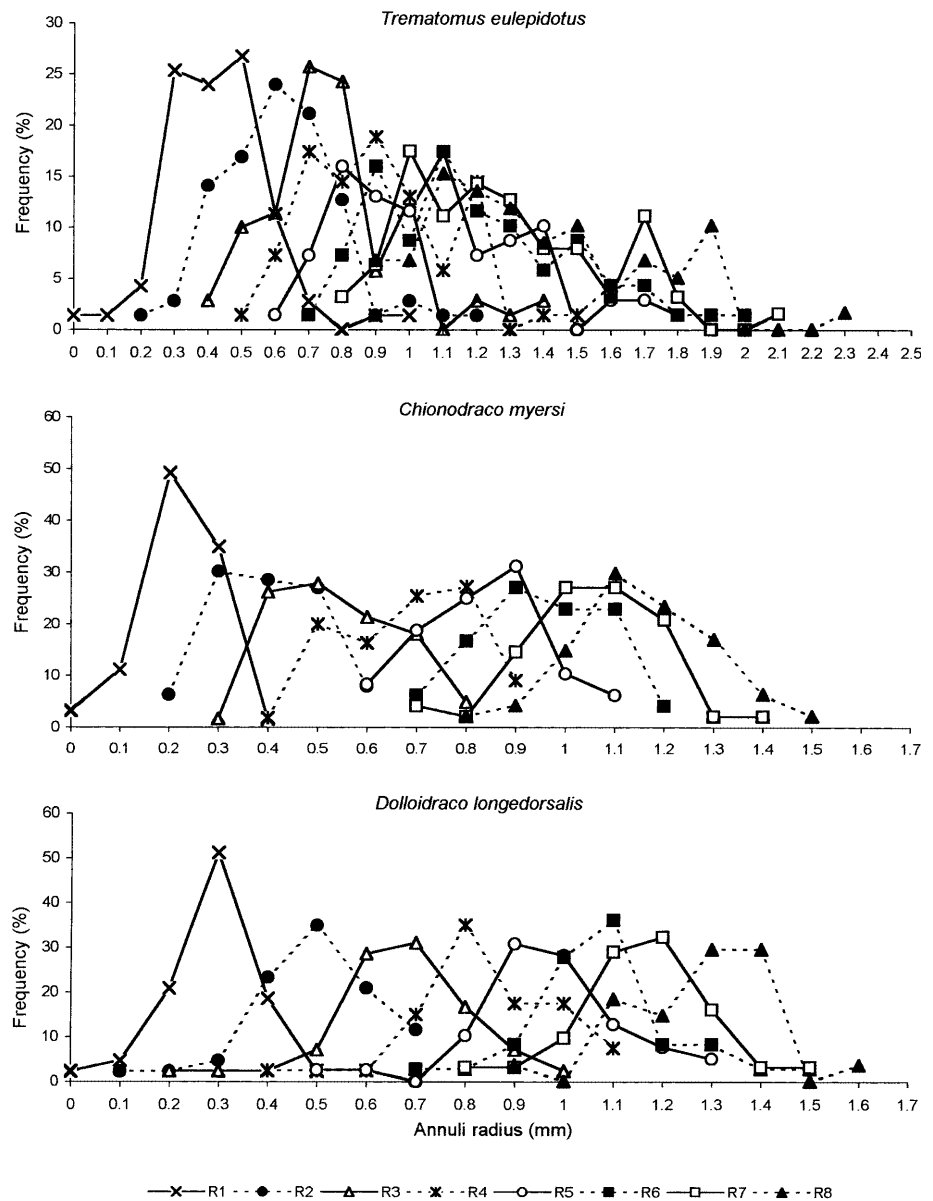
Linear relationships were used to determine fish length (TL)-otolith radius (OR) relationships for each species and sex. The

hypothesis of isometric growth was tested with a *t*-test. Once the TL-OR relationship was determined, the modified Fraser-Lee back-calculation procedure (Campana 1990) was applied. This method estimates TL at a previous age (*a*) through insertion of the measured radius of the otolith at age *a* into the OR-TL regression and by considering the fish length (TL_c) and otolith radius (OR_c) at capture:

Table 1 Regression parameters of the otolith radius-fish length relationship determined for the total of the population and by sex for each species (*n* number of specimens)

Species	a	b	r ²	P	n
<i>Trematomus eulepidotus</i>	4.5273	9.4459	0.7412	<0.01	169
Females	5.5672	8.9436	0.7096	<0.05	106
Males	3.0402	9.9605	0.8930	<0.05	59
<i>Chionodraco myersi</i>	2.6593	20.4323	0.8354	<0.01	121
Females	0.9969	22.3618	0.8719	<0.05	64
Males	2.9076	18.9675	0.9099	<0.05	44
<i>Dolloidraco longedorsalis</i>	3.8557	4.1787	0.7178	<0.01	170
Females	3.7179	4.2689	0.7683	<0.05	87
Males	3.0815	4.7045	0.7683	<0.05	63

Fig. 3 Plot of the frequency of occurrence of the increment-to-core distances for the first eight growth increments considered as annuli for the three studied species



$$TL_a = d + (TL_c - d)OR_c^{-1}OR_a$$

where d is the intercept of the OR-TL regression.

Other more accurate methods, such as the biological intercept (Campana 1990), were not feasible due to the lack of data on the early stages of these species.

To evaluate growth, individually estimated lengths-at-age comprising both direct readings and back-calculated values, were fitted to the von Bertalanffy growth function by using a non-linear regression (Statistica 4.5 program). The individuals with indeterminate sex were added to the data from males and from females for the calculations ($N = 4$ for *T. eulepidotus*, $N = 13$ for *C. myersi*, $N = 20$ for *D. longedorsalis*). As L_∞ and k are inversely correlated, they were compared using the growth performance index ($\Phi = 2 \cdot \log L_\infty + \log k$) (Munro and Pauly 1983).

Results

The fish length-otolith radius relationship showed a significant correlation in the three species (Fig. 2). The fit of the line to the points was good without any significant trend (Fig. 2 residuals), except in *C. myersi* where the lack of the size between 14 and 22 cm might have influenced the relationship. Also, some dispersion was found in the largest *T. eulepidotus*, probably due to errors in the measurement or to inherent otolith variability with growth (Fig. 2). The values of the TL-OR for each sex and species are included in Table 1.

The sagittal otoliths of the three species showed wide opaque increments and narrow translucent zones with a check or discontinuity before a new opaque zone was initiated (Fig. 1). The spacing of the rings and their continuity around the otolith were the criteria used to differentiate the increments from false rings, which were numerous in the first development stages. The plot of increment to core distances (Fig. 3) for the first eight increments in the three species showed a regular ring pattern and normal distributions ($P > 0.5$). The accumulative graph of the increment widths followed the decreasing trend characteristic for fish otoliths, except for the old *C. myersi* and *D. longedorsalis*, probably due to the low otolith number examined for the age interval (Fig. 4).

The index of average percent error was relatively small (APE% = 6.5 in average for the three species), and thus the precision of the age estimates was considered satisfactory, although it was not possible to compare this value with other Antarctic studies because this is the first measure of precision on Antarctic fish age determination.

Thus, the ageing procedure was considered as precise and indirectly validated. The increments were considered as annuli and the age-length relationships were determined (Tables 2, 3, 4, 5, 6, 7). There were no fish younger than 2 years old in any of the three species. Moreover, *C. myersi* also lacked medium-sized fish.

There was a considerable overlap between ages, corresponding to slow-growing fish. When the back-calculated data were incorporated into the age-length

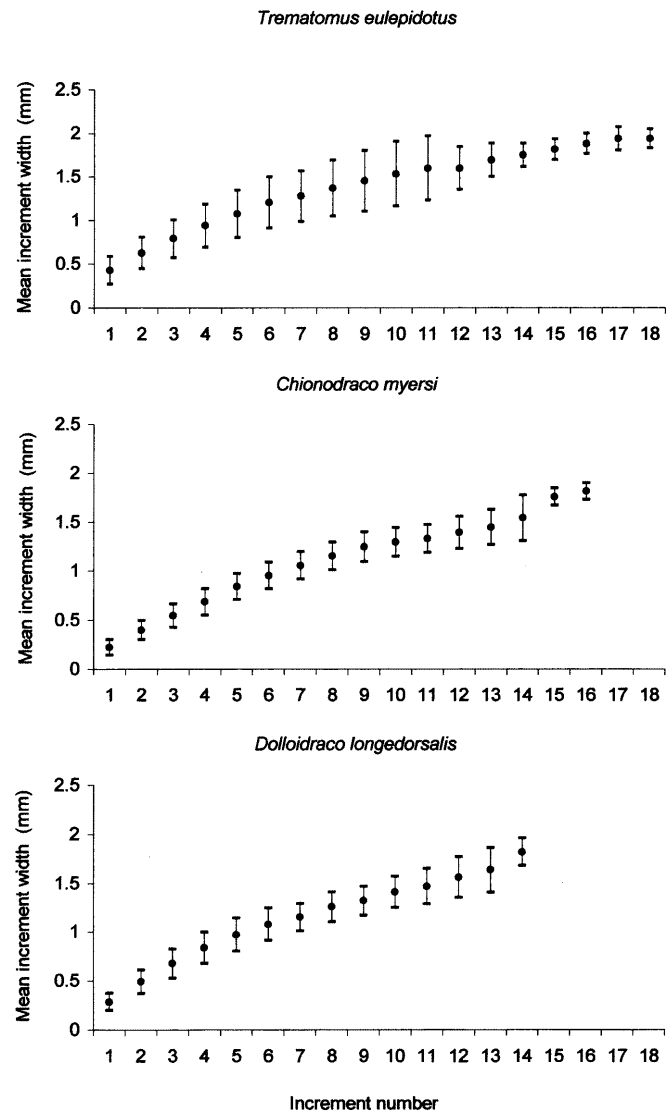


Fig. 4 Cumulative mean width (dots) and standard deviation (bars) of the otolith annuli for the three studied species

relationships, the von Bertalanffy growth pattern appeared more clearly (Fig. 5).

The females showed a higher growth rate than males, except for *D. longedorsalis* (Table 8), as described for other nototheniid fish (La Mesa et al. 1996). Among the three species, *C. myersi* had the highest growth index and *D. longedorsalis* the lowest index, although the growth parameter k was similar in the three species.

The spread of sizes with age was notable, specially for *T. eulepidotus* (Tables 2, 3). However, this spread was similar in younger (<19 years) *T. bernacchii* for Terra Nova Bay (La Mesa et al. 1996). The spread was somewhat reduced in the other species but was more pronounced for females (Tables 4, 5, 6, 7). Although *D. longedorsalis* had smaller values, the spread was similar in respect to the maximum TL (Tables 6, 7). Sexual growth dimorphism was found in the three

species, females having a higher growth performance index than males except for *D. longedorsalis* (Table 8). The higher growth rate of females has been reported for nototheniid fish (La Mesa et al. 1996), where in some species, like *C. myersi*, the differences are also in external characters such as the dorsal fin size (Iwami and Abe 1981).

Discussion

The recognition that ageing error is important has stimulated an interest in the validation of age determination methods. The validation should prove that the ageing structure has a consistent interpretable pattern of

Table 2 Age-length relationship for males of *Trematomus eulepidotus* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli																
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Males length (cm)																	
10	1																
11		1															
12							1										
13						1	1		2								
14							1	1			1						
15										1		1					
16					2	1	1	2	1	1	1		1				
17						1				1	3						
18									2			1	1				
19				2			2						1	1	1	1	
20							1	2									
21				1	1				1	2		1					
22					1		1	1					1	1			
23					1		1	1	1			1					
24									1		1						
<i>n</i>	1	1		3	5	3	9	7	8	6	5	4	4	2		1	
μ	10.9	11.2		20.2	19.9	15.8	17.8	19.0	18.7	17.8	18.4	19.7	19.3	21.1		19.6	
<i>SD</i>				1.5	3.3	1.8	3.9	3.5	4.1	2.9	3.4	3.3	2.5	2.6			

Table 3 Age-length relationship for females of *Trematomus eulepidotus* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli																	
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
Females length (cm)																		
10	1																	
11		1																
12																		
13						1	1											
14							1	2										
15						1		1	1									
16							3	5	1									
17							1		2	2	2							
18			1				1		3	2	1	1		1	1			
19					1			1			2							
20					1		1		2	1		2	1	1			1	
21					1				1				3				1	
22							1	1	1	1	1		1		2		1	
23								1	1	1		1		2	1	1		
24						1		2	5						1			
25							2		2	3								
26									1	1		1	2		1			
27											2							
28										1	2	3	1					
29																1		
30																		
31								1										
<i>n</i>	1	1	1		3	3	11	14	20	11	10	8	8	4	6	2	3	
μ	10.9	11.2	17.2		20.4	17.9	18.8	19.4	21.5	22.4	22.7	24.4	23.6	21.3	22.9	26.5	21.4	
<i>SD</i>					0.6	5.6	4.2	5.1	3.4	4.0	4.7	4.2	2.9	2.5	2.6	4.8	0.9	

increments (i.e. precision) and that these increments are laid down with a periodicity attributable to a regular time scale (i.e. accuracy) (Beamish and MacFarlane 1983). The precision is generally measured as an index of repeatability of age interpretation; in our study the use of a semi-automatic image analysis system detecting the increments based on the luminosity index decreased the subjectivity and the degree of agreement was very high.

Accuracy can be proven or estimated; estimates of accuracy are less valuable, but in some cases only an estimate is possible. This is the present case and a common feature in Antarctic fish where validated ages are very scarce (White 1991). This author classified the published validation studies on the following categories: (1) use of otoliths and scales from larval and juvenile fish to determine the dimensions of the nucleus (Slosarczyk 1987; North 1988); (2) detailed comparison

Table 4 Age-length relationship for males of *Chionodraco myersi* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli															
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
Males length (cm)																
10	1															
11		1	2													
12	1	8	2													
13		1	2													
24							1									
25					1	2			1							
26					1						1					
27																
28									1							
29									1	1						
30								2		2	1	1				
31								1	1	1	1	2				
32										1	1			1		
33																
34																
35															1	
<i>n</i>	2	10	6		2	2	1	3	4	5	4	3	1		1	
μ	11.2	12.6	12.5		25.9	25.5	24.8	30.6	28.7	30.8	30.1	31.4	32.0		35.2	
<i>SD</i>	1.5	0.3	0.8		1.2	0.3		0.6	2.4	1.1	2.7	0.7				

Table 5 Age-length relationship for females of *Chionodraco myersi* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli																
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Females length (cm)																	
10	1																
11		3	2														
12	2	7	1														
13		1	3														
24												1					
25											1			1			
26																	
27								1									
28							1										
29																	
30									1		2	1					
31								3	1								
32										2	2						
33									2		1	3					
34									1			3					
35										1	2	4					
36								1	1			1	2			1	
37								1									
38												1	1				
39										1							
<i>n</i>	3	11	6				1	6	6	4	8	14	4			1	
μ	11.6	12.3	12.6				28.7	32.8	33.2	34.9	31.9	33.9	34.3			36.2	
<i>SD</i>	1.3	0.6	0.9					3.8	2.2	3.2	3.4	3.2	6.1				

of readings derived from scales and otoliths sampled from the same individual fish (Freitag 1980; Coggan et al. 1990); (3) the examination of time series samples to demonstrate the period when the seasonal increments are deposited (North 1988; Barrera-Oro 1989; Ashford and White 1993); (4) the use of chemical markers to time-mark otoliths and scales (Radtke 1987); (5) the exchange of materials used for determining age among specialists. Other studies have used length-frequency analysis to support the otolith age-length relationships (Kock 1980, 1981; Pankhurst 1990). From these studies only categories 3 and 4 provide direct age validation, while category 1 and length-frequency analysis provide indirect validation. The other methods only improve accuracy.

In our study the precision has been estimated using approaches common for temperate-water fish but new for Antarctic fish. To validate the temporal meaning of the growth increments, we could only use indirect validation methods, like the monotonously decreasing interval between increments, which forms the basis of age estimation using rings (Gauldie 1988). Moreover, if the ring formation responds to a major environmental

event, their formation should be synchronous in the population. The regularity of the ring pattern was shown by plotting all the ring-to-focus, showing that the first increments are laid down following the same pattern in each species. These methods are widely used when direct validation is not feasible (Morales-Nin et al. 1998).

The studied species had a complex and variable ring pattern in the central otolith area, which made difficult the interpretation of a common growth pattern for each species. As in temperate species, these rings might reflect changes in habitat or life strategy (Morales-Nin et al. 1998). A crucial point in the age determination of Antarctic fish is the localisation of the first annulus. Larval Antarctic fish may grow slowly during their development, laying down very narrow micro-increments in their otoliths (Ruzicka and Radtke 1995). Thus, the diameter of the first ring might be quite small. The presence of these rings and the difficulty of locating the first ring, due to the scarcity of juvenile fish in the samples, have caused some authors to consider their ages as relative (Vacchi et al. 1992). In our study, the first ring considered as annuli showed a clear distribution and size in the three species, suggesting that it

Table 6 Age-length relationship for males of *Dolloidraco longedorsalis* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli												
	2	3	4	5	6	7	8	9	10	11	12	13	
Males length (cm)													
5	2												
6		1											
7		1	1		3								
8			1	1	2	3							
9				4	4	3	6	1	2	1	1	1	
10					1	2	3	4	3		4		
11						1	1	1	3				
12									1	1			
<i>n</i>	2	2	2	5	10	9	10	6	9	2	5	1	
μ	5.2	6.5	8.1	9.2	8.9	9.6	10.1	10.6	10.7	10.9	10.4	9.6	
<i>SD</i>	0.3	0.7	0.6	0.3	1.0	0.9	0.8	0.6	0.9	1.8	0.4		

Table 7 Age-length relationship for females of *Dolloidraco longedorsalis* (*n* number of specimens, μ mean length, *SD* standard deviation)

	Annuli													
	2	3	4	5	6	7	8	9	10	11	12	13	14	19
Females length (cm)														
5	2													
6		1												
7		1	1		2									
8				2	1	4								
9				1	3	2	3	1	5	1		1		
10					1	2	6	4	5	2	1	3		
11						3	3	9	1		1	4	1	
12							1		1	1		1	1	1
13							1	1	1			1		
<i>n</i>	2	2	1	3	7	11	14	15	13	4	2	10	2	1
μ	5.2	6.5	7.7	8.8	9.0	9.9	10.8	11.1	10.5	10.7	11.0	11.1	12.1	12.2
<i>SD</i>	0.3	0.7		0.8	1.0	1.3	1.2	0.9	1.1	1.2	0.8	1.0	0.9	

corresponded to a major event such as the winter. *D. longedorsalis* and *T. eulepidotus* show later summer spawning, while *C. myersi* spawns in winter/early spring (Duhamel et al. 1993). These species have a long pelagic development (North and Kellermann 1989), and thus the first annuli might correspond to the second winter and the ages might be biased. Future studies should try to assess this.

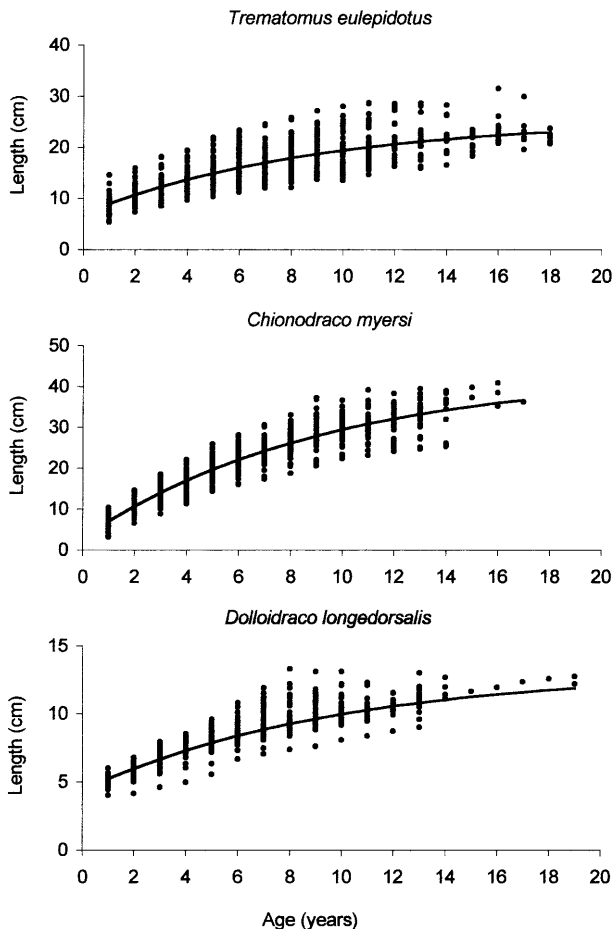


Fig. 5 Von Bertalanffy growth curve fitted to the estimated and back-calculated age-length relationships for the three studied species

Table 8 Von Bertalanffy growth parameters determined for the total of the population and by sex for each species. Parameters' standard error in brackets. The correlation and the percent of variance explained (%var.ex.) are also given. N is the number of

Species	L_{∞} (cm)	k (years ⁻¹)	t_0 (years)	r	%var.ex.	N	Φ
<i>Trematomus eulepidotus</i>	24.7501 (5.9672)	0.1151 (0.8082)	-2.9356 (2.0179)	0.8193	67.132	734 (81.646%)	1.8482
Females	26.5077 (3.4395)	0.1072 (0.4020)	-3.0211 (1.1430)	0.8228	67.693	487 (82.124%)	1.8769
Males	21.0043 (4.323)	0.1642 (0.1157)	-1.6545 (1.6387)	0.7885	62.170	247 (80.718%)	1.8600
<i>Chionodraco myersi</i>	43.0974 (2.8492)	0.1080 (0.1515)	-0.6328 (0.2044)	0.9477	89.810	627 (85.422%)	2.2983
Females	43.3551 (2.7260)	0.1187 (0.1596)	-0.1257 (0.1712)	0.9519	90.603	365 (85.081%)	2.3485
Males	43.4349 (6.5208)	0.0929 (0.0271)	-0.8624 (0.3976)	0.9516	90.525	262 (85.901%)	2.2437
<i>Dolloidraco longedorsalis</i>	13.1741 (1.1673)	0.1010 (0.0561)	-3.9812 (0.4018)	0.9351	87.445	304 (67.256%)	1.2438
Females	14.1321 (1.3515)	0.0821 (0.0188)	-4.4404 (0.7274)	0.9362	87.639	201 (69.550%)	1.2148
Males	10.1572 (0.6738)	0.2038 (0.0489)	-1.7413 (0.5416)	0.8819	77.691	103 (61.677%)	1.3227

The lack of several age classes in the studied population was compensated for through back-calculated age-length relationships from otolith measurements. However, the results might have some error due to the relatively low correlation of otolith size and fish length, mainly in *T. eulepidotus*. This is a common feature in nototheniid fish, where individual morphometric variability in otolith size has been described (Williams and McEldowey 1990). This variability was probably related to sexual dimorphism, because the correlation between TL and OR improved when the regression was calculated for each sex (Table 1).

The growth performance index of all three species was between 1 and 2, as proposed for the high-Antarctic zone by Hubold (1991). Few data are available for a comparison of these species. The K von Bertalanffy growth parameter value determined by sexes for *T. eulepidotus* by Ekau (1988), although corresponding to a different age and size structure, was similar to the values obtained in this study ($K = 0.09$ years⁻¹ for females, $K = 0.15$ years⁻¹ for males). Nevertheless, the growth performance index was lower in our study and with less difference between sexes ($\Phi = 1.95$ for females and $\Phi = 1.91$ for males, Ekau 1988, $\Phi = 1.87$ for females and $\Phi = 1.86$ for males, this study).

Age and growth studies on high-Antarctic fish are difficult due to the accessibility limitations that hinder sampling regularly over a year and conducting validation studies. Moreover, the species' life-cycle, with long pelagic development and with size ranges not accessible to the sampling gear, also limit the available information. Bearing in mind these shortcomings, we propose to apply the methodology used in other areas to determine the accuracy and precision of the age estimates, to give a more sound assessment of the age composition and growth of these little-studied species.

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back-calculated length at age; their percentage in respect to the total age-length relationships is given in brackets. The Munro and Pauly (1983) growth coefficient Φ is included

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