

Otolith morphology and feeding ecology of an Antarctic nototheniid, *Lepidonotothen larseni*

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Abstract: This study is based on the analysis of the stomach content and the morphology and morphometry of the three pairs of otoliths (sagitta, asteriscus and lapillus) of *Lepidonotothen larseni* (Lönnberg) collected at the South Shetland Islands and Antarctic Peninsula during summer, in order to find possible relationships between ontogenetic change of sagittal otolith shape and feeding ecology. Length-weight relationship resulted in a positive allometric growth, with juveniles and adults in good nutritional condition (Le Cren condition index > 1), and with a decreasing trend from noon to late evening of the stomach repletion index. The stomach content consisted of several prey, with copepods and amphipods more frequent and abundant in juveniles, whereas euphausiids were in adults. The morphometric analysis of otoliths enabled us to relate different measurements with fish size, and those contributing mostly to separate juveniles from adults were the otolith and rostrum length and their percentage (R index). Juveniles proportionally showed a shorter and wider sagitta than adults reflected in a major E index because of a rounded shape and a minor R index because of a less developed rostrum. This pattern can be tentatively linked to the different habitat of juveniles and adults of this species, being respectively pelagic and epibenthic, as also evidenced by the ontogenetic change of feeding habits.

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Key words: feeding habitats, Nototheniidae, otoliths, Southern Ocean icefish

Introduction

Approximately 322 species of marine fishes are present in the Southern Ocean, consisting mainly of Nototheniidae, Zoarcidae and Liparidae families (Barrera-Oro 2002, Eastman 2005). The nototheniid *Lepidonotothen larseni* (Lönnberg) is an endemic species which inhabits inshore and offshore waters between 30 and 550 m depth (Gon & Heemstra 1990, Barrera-Oro 2002). It has a wide geographical distribution, including the Balleny Islands, west Antarctic Peninsula, South Shetland and South Orkney islands, Shag Rocks, South Georgia, South Sandwich, Bouvet, and Indian Ocean sector islands, such as the Prince Edward Islands and Iles Crozet (Duhamel & Pletikosic 1983, Gon & Heemstra 1990, Bushula *et al.* 2005). From an ecological point of view, *L. larseni* is an opportunistic plankton feeder able to migrate from the bottom to the surface of the water column to feed (Bushula *et al.* 2005). It feeds mainly on zooplankton such as krill, hyperid amphipods, mysids, copepods and salps, and to a lesser extent on gammarid amphipods, isopods and polychaetes (Barrera-Oro 2002).

Nototheniidae have developed a wide range of feeding strategies, which allow them to utilize food resources in a variety of habitats. The fact that species have evolved

niche difference allows the exploitation of prey in different habitats and may be a contributing factor to their dominance in fish communities (Targett 1981). The mode of feeding is a major determinant of the ecological niche of fish species, and in Nototheniidae there is a trend towards pelagization of demersal species (Klingenberg & Ekau 1996) which might be related to the food availability in the water column. Specifically, *L. larseni* undertakes vertical migrations with juveniles and adults having different distributions at horizontal and vertical scales (Frolkina *et al.* 1998). Although there are some studies on the feeding habits of *L. larseni* (Targett 1981, Barrera-Oro 2002, Bushula *et al.* 2005) and on their nutritional condition (Eastman & Sidell 2002), no comparative studies on juvenile and adult feeding ecology have been carried out so far.

In the inner ear of fishes there are complex polycrystalline structures of calcium carbonate, the otoliths (sagitta, asteriscus and lapillus), which are different in size, shape and position, conserved through the time. They are located inside sac-like structures (called respectively saccule, lagena and utricle), and connected by a thin otolithic membrane lying close to the macula, a sensory epithelium used for fish orientation (Popper & Zhongmin 2000). Because of its high specificity (Martínez Pérez *et al.* 2007), otoliths are used to determine age and growth of fishes (Campana 2001), as well as in

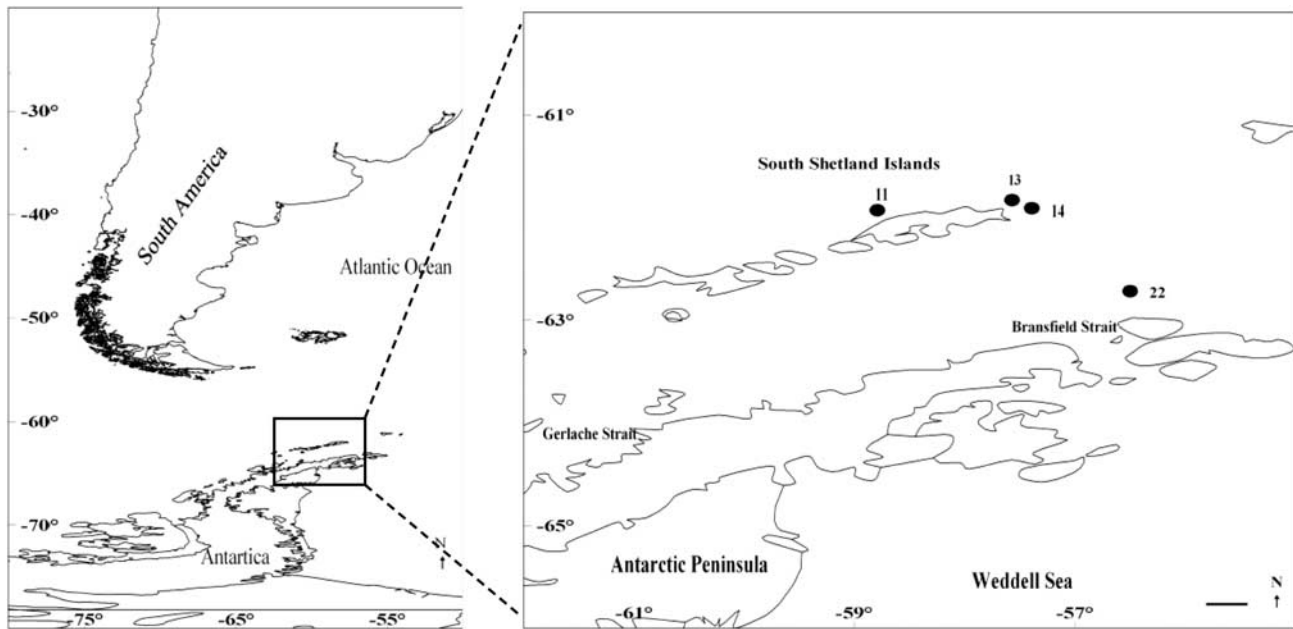


Fig. 1. Sampling stations at the South Shetland Islands and Antarctic Peninsula during the 2011 summer campaign. Surface temperature: 0.6–2.4°C. Surface salinity: 34–34.1‰. Sampled depth: 210–222 m. Scale bar: 20 km.

palaeoecology, palaeobiogeography, phylogeny and in trophic ecological studies (Koen Alonso *et al.* 2000, Assis 2003, 2005). Moreover, there is a relationship between fish ecotypes and the otolith shape because this structure shows adaptations to different environmental factors, such as depth, water temperature and substrate type (Volpedo & Echeverría 2003, Colmenero *et al.* 2010, Lombarte *et al.* 2010). For example, Volpedo & Echeverría (2003) observed an elongated otolith with a well developed rostrum in pelagic species, whereas they are rounded with a not developed rostrum in demersal species. Based on diet, otolith shape and phylogeny of Nototheniidae, Lombarte *et al.* (2010) stated that the relative size of sagitta has a great functional significance to determine the trophic niche, concluding that benthic fishes of this family have the largest sagittae in relation to body size.

The sagitta of *L. larseni* has been already morphologically described (Hecht 1987), but there are no data on morphology and morphometry of asteriscus and lapillus. The sagitta is characterized by an ovate to fusiform shape and a smooth and gently rounded external surface. The sulcus is ostial and a constricted collum separates ostium and cauda. The prominent ventral area and the rostrum are well developed in larger fishes (Radtke & Targett 1984, Volpedo *et al.* 2008).

The aims of this study are: a) to describe in more detail the morphology of asteriscus, lapillus and sagitta otoliths of *L. larseni*, obtaining useful relationships between fish size and several morphometric measurements of otoliths; b) to compare the feeding habits of juveniles and adults by their stomach contents analysis, nutritional condition and stomach repletion; and c) to analyse the relationship

between ontogenetic change of sagittal otolith shape and feeding ecology of juveniles and adults.

Materials and methods

Fifty individuals of *L. larseni* were collected at the South Shetland Islands (stations 11, 13, 14) and the Antarctic Peninsula (station 22) during the summer campaign of 2011 carried out by the ARA *Puerto Deseado* vessel (Fig. 1). Fishes were collected at noon (13h00), evening (15h30) and late evening (18h00) with demersal (25 mm mesh size) and pilot (50 mm mesh size) nets. Sampling gears were deployed at a speed of 2–3 knots and towed on the bottom (mean depth 222 m) for 15–20 minutes. In each station surface temperature and salinity data were obtained using a Seabird SBE 21 thermosalinograph. Fishes were frozen at -10°C and total length (TL, ±1 mm), standard length (SL, ±1 mm) and weight (W, ±1 g) were measured. To compare mouth sizes, the upper maxilla length (A, ±1 mm) was measured (Klingenberg & Ekau 1996). As the gonads were frequently destroyed in most samples, possibly after freezing, juveniles and adults were classified by their size, as they attain sexual maturity at 110 mm TL (Duhamel & Pletikosic 1983). Fish length-weight relationships were estimated by linear regression applied to log-transformed data.

Nutritional condition of *L. larseni* was evaluated by Le Cren condition index (LCCI) with the following equation $LCCI = W/W_{exp}$, where W is the observed weight of fish and W_{exp} is the expected weight calculated using the growth curve obtained from the regression between W and TL of the entire dataset. This index allows us to find

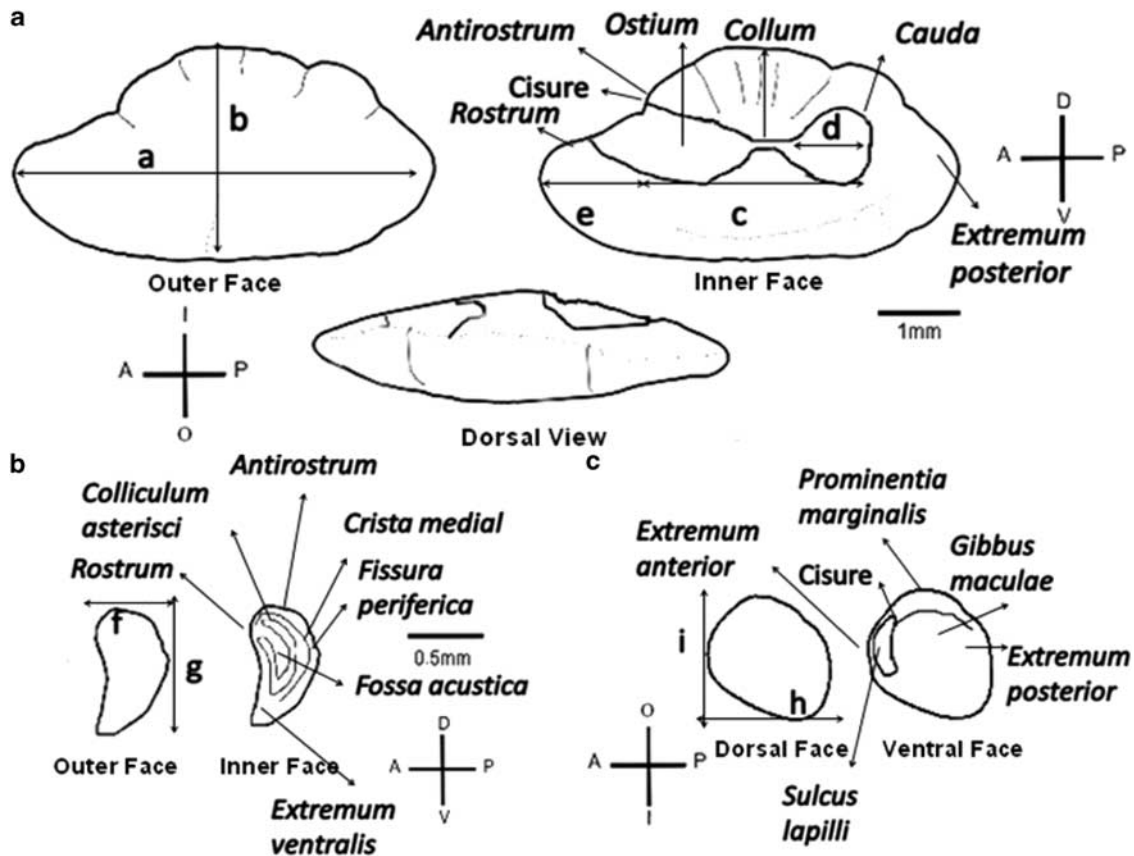


Fig. 2. Morphometric and morphological characteristics of *Lepidonotothen larseni* otoliths. **a.** Sagitta otolith (scale: 1 mm); outer face: (a) maximum length, OL, (b) maximum width, OW; inner face: (c) from cisure length, FCL (cauda base to cisure), (d) cauda length, CL, (e) rostrum length, RL. **b.** Asteriscus otolith (scale: 0.5 mm); outer face: (f) maximum length, OL, (g) maximum width, OW. **c.** Lapillus otolith (scale: 0.5 mm); dorsal face: (h) maximum length, OL, (i) maximum width, OW. Abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral, I = inner, O = outer.

out weight deviations of a certain length from the expected weight. Values higher than one indicates good nutritional condition of fishes, and lower values reflect a poor condition (Le Cren 1951). A *t*-test was applied to analyse differences between LCCI of juveniles and adults. Each stomach was excised and preserved in 70% alcohol solution. Based on the stomach fullness, three different stages were arbitrarily defined: I (empty < 25% of gut content), II (partially full 25–75%) and III (full > 75%). For each stage, the stomach repletion index was calculated by the equation $IR = (Wf/W) \times 100$, where *W* is the fish weight and *Wf* is the ingested food weight (± 0.001 g), obtained as difference between the weights of the stomach (with all the food) and the empty stomach.

The stomach contents were preserved in formaldehyde 5% for further analysis. Each zooplanktonic prey item was photographed and identified to the lowest possible taxonomic level according to Boltovskoy (1999). The frequency of occurrence (F%) was obtained by counting in which percentage of stomachs the different prey items were present, whereas the numerical abundance (N%) was

obtained by the equation $(n_p \times 100) / N_p$, where n_p is the number of each prey and N_p is the total number of prey in the stomachs. Prey size (length and width) was recorded, evaluating differences between juvenile and adult fishes, and also relating these measurements to fish mouth size.

Sagitta, asteriscus and lapillus otoliths were extracted from the otic capsule, making a transversal cut on the dorsal and posterior part of the cranium under a stereomicroscope to help with their removal. They were cleaned with a sodium hypochlorite solution for 5–8 min and stored dry to further analysis. The inner and outer faces of sagitta and asteriscus and dorsal and ventral faces of lapillus were photographed and described according to Volpedo & Echeverría (2000), Assis (2003, 2005) and Volpedo & Fuchs (2010). Maximum otolith length (OL) and maximum otolith width (OW) were measured from all otolith types, whereas rostrum length (RL), cauda length (CL) and “from cisure length” (FCL; considering from the cisure to the cauda base), were taken only on sagitta (Fig. 2). E and R indexes were calculated only for sagitta by the equations $E\% = OW/OL$ and

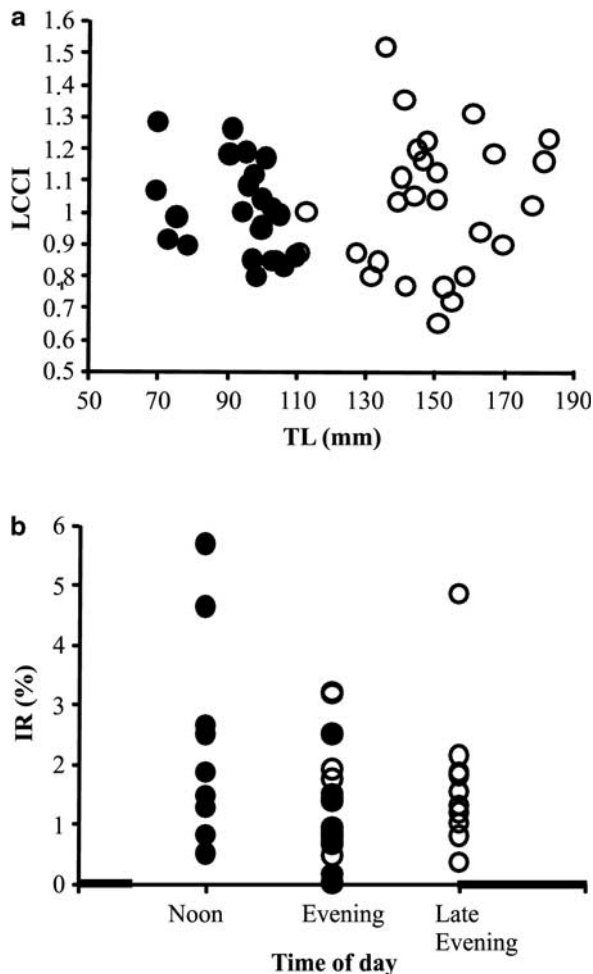


Fig. 3. **a.** Le Cren condition index (LCCI) of *Lepidonotothen larseni*, and **b.** stomach repletion index (IR) in different periods of the day: noon (13h00), evening (15h30) and late evening (18h00). Dark hours: black horizontal bars. Juveniles (filled circle) and adults (open circle).

$R\% = RL/OL$, respectively. E determines the otolith shape, while R is the percentage of the rostrum respect to otolith length (Volpedo & Echeverría 2003). Using all these variables, a multivariate discriminant analysis was carried out using the linear canonical function of Fisher (Zar 1999). For sagitta and lapillus, morphometric relationships between these variables and fish lengths were assessed by linear regression models (Zar 1999). InfoStat 2011 (Di Rienzo *et al.* 2011) was used for statistical analysis.

Results

Analysis of the nutritional condition, stomach repletion index and stomach content

Total length of fishes varied between 70 and 185 mm and total weight (W) varied between 2 and 60 g, with 46% of

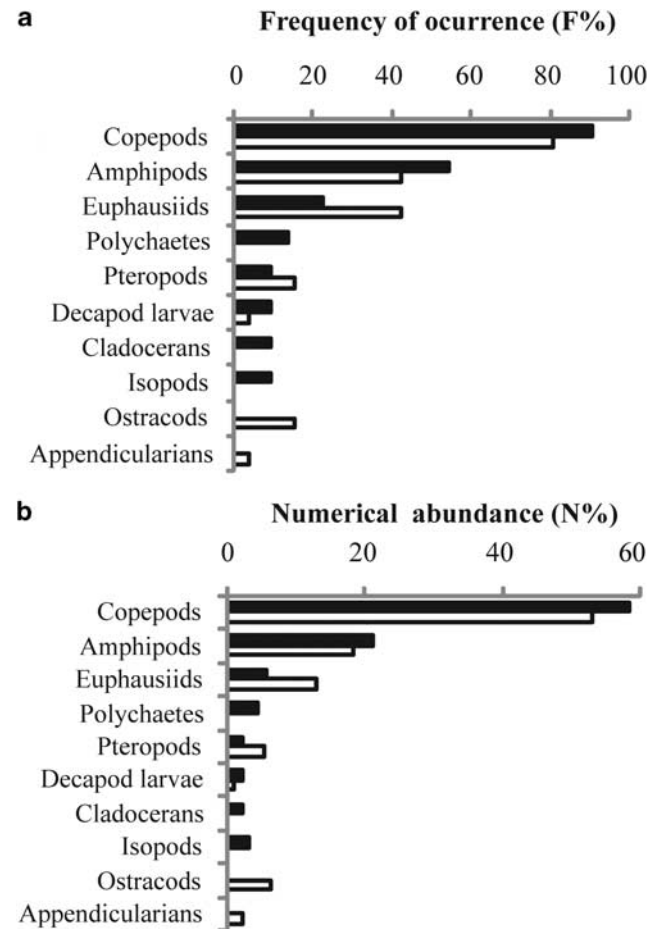


Fig. 4. **a.** Frequency of occurrence, and **b.** numerical abundance of each prey consumed by *Lepidonotothen larseni*. Juveniles (black bars) and adults (white bars).

juveniles and 54% adults. The length-weight relationship obtained for all the specimens was $W = 6.28 \times 10^{-7} TL^{3.49}$ ($r^2 = 0.96$), which indicated a positive allometric growth (b coefficient > 3). The nutritional condition of fishes estimated by LCCI ranged between 0.65 and 1.52, with a high percentage of fishes in good nutritional condition ($LCCI > 1$). No significant differences between juveniles ($LCCI$ mean = 1.007) and adults ($LCCI$ mean = 1.024) were found (Fig. 3a; $t = 0.33$, P -value = 0.745). Stomach repletion index (IR) varied between 0.01 and 5.7, with a general decreasing trend from noon to late evening (Fig. 3b). Overall, 53% of fishes presented full stomach, 36% partially full stomach and 11% empty stomach. Stomach fullness significantly changed with fish size, as 20%, 45% and 35% of juveniles and 4%, 28% and 68% of adults were at stage I, II and III, respectively. Full stomachs (stage III) were observed mainly during late evening for adults and during noon hours for juveniles.

In stomach content analysis, copepods and amphipods were more frequent and abundant in juveniles, whereas

Table I. Mean values of fish mouth size of juveniles and adults of *Lepidonotothen larseni* and mean lengths and widths of their ingested prey. Minimum and maximum values are indicated between parentheses.

Variable	Juveniles	Adults	P-value
Mouth size (mm)	7.64 (4.6–14.8)	11.52 (6.9–19.7)	< 0.0001
Length prey (mm)	4.1 (1.05–10.67)	5.6 (1.14–15.82)	< 0.001
Width prey (mm)	1.1 (0.22–3.22)	1.7 (0.42–5.33)	< 0.001

euphausiids were in adults. Polychaetes, cladocerans and isopods were only present in juveniles, while ostracods and appendicularians were only found in adults. Pteropods and decapod larvae were less frequent and abundant, but

they were present in stomach contents of both stages (Fig. 4). In a great percentage of stomachs (33.3%) inorganic material was found, mainly stones.

Prey of different sizes (in length and width) were found in stomachs of juveniles and adults, both sizes being larger in adult fishes with a bigger mouth size (Table I). Diet consisted mainly of several copepods, such as cyclopoid, calanoid (*Aetideus armatus* Boeck, *Calanus simillimus* Giesbrecht, *Metridia gerlachei* Giesbrecht, *Onchocalanus* sp. and *Rhincalanus* sp.), harpacticoid (*Microsetella norvegica* Boeck) and poecilostomatoid, both gammarid and hyperiid (*Vibilia antarctica* Stebbing) amphipods and euphausiids (*Euphausia superba* Dana). Prey consumed to a lesser extent were pteropods (Limacinidae, Pleuromodermatidae and Cavoliniidae, mainly *Clio pyramidata sulcata* Pfeffer), ostracods, polychaetes (*Vanadis* and *Travisiopsis* spp.),

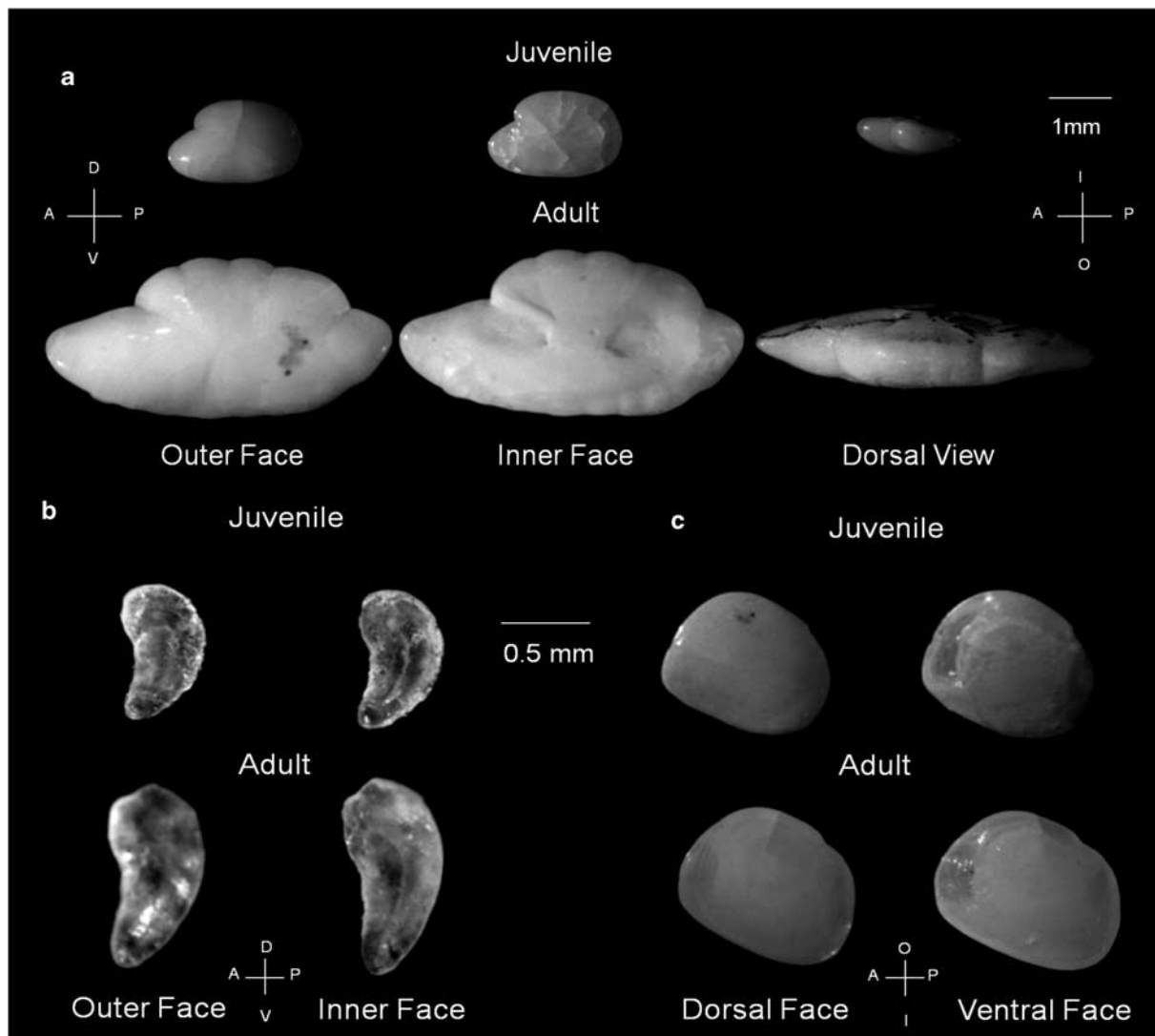


Fig. 5. a. Sagitta, b. asteriscus, and c. lapillus otoliths of juvenile and adult *Lepidonotothen larseni*. Abbreviations: A = anterior, P = posterior, D = dorsal, V = ventral, I = inner, O = outer.

Table II. Mean measurements of sagitta, asteriscus and lapillus otoliths of *Lepidonotothen larseni* (maximum otolith length (OL), maximum otolith width (OW), from cisure length (FCL), cauda length (CL), rostrum length (RL), E and R indexes. Standard deviation (SD) and coefficient of variation (CV) are indicated. Juveniles: 69.63–109.72 mm TL (total length), 62.52–97.96 mm SL (standard length). Adults: 110.67–183.00 mm TL, 97.50–164.79 mm SL. *n* = number of fishes analysed.

Otolith	Stage	Measurement	Mean	SD	CV	Minimum	Maximum
Sagitta	Adults, <i>n</i> = 27	OL	3.94	0.56	14.19	3.07	5.12
		OW	2.20	0.24	10.79	1.84	2.73
		FCL	2.29	0.39	17.02	1.89	3.14
		CL	0.96	0.25	25.80	0.44	1.51
		RL	0.90	0.20	21.92	0.57	1.40
		E	56.34	3.57	6.34	47.66	65.47
		R	22.75	2.34	10.28	18.40	29.29
	Juveniles, <i>n</i> = 23	OL	2.62	0.37	13.93	1.91	3.12
		OW	1.54	0.18	11.92	1.15	1.77
		FCL	1.57	0.22	14.24	1.16	1.93
		CL	0.62	0.13	21.45	0.38	0.86
		RL	0.56	0.10	17.56	0.31	0.69
		E	59.03	3.04	5.15	52.82	64.92
		R	21.21	2.16	10.16	16.39	24.62
Asteriscus	Adults, <i>n</i> = 6	OL	0.53	0.06	10.76	0.48	0.63
		OW	0.94	0.11	11.95	0.81	1.07
	Juveniles, <i>n</i> = 2	OL	0.46	0.02	4.03	0.44	0.47
		OW	0.71	0.02	2.98	0.7	0.73
Lapillus	Adults, <i>n</i> = 14	OL	1.05	0.09	8.50	0.93	1.20
		OW	0.87	0.07	8.0	0.79	1.02
	Juveniles, <i>n</i> = 9	OL	0.83	0.07	8.77	0.69	0.91
		OW	0.74	0.09	12.05	0.61	0.93

decapods (zoea and megalopa larvae), cladocerans, isopods and appendicularians (Oikopleuridae).

Otolith morphology and morphometry

A detailed description of the sagitta, considering both new characteristics and characteristics already mentioned in previous studies, is reported below, as well as, for the first time, those referred to the asteriscus and lapillus.

Sagitta (Fig. 5a, see also Fig. 2a)

Oval shape with a developed projection in the extremum posterior. The dorsal border is slightly scalloped and the ventral one is regular. The otolith has a slightly pronounced cisure, and well marked rostrum and antirostrum. A medium sulcus with a constricted collum which delimits ostium from cauda. The ostium is discoid and opened in the anterior margin of the otolith. The cauda is elliptic and closed far from the posterior edge. The inner and outer faces are smooth and slightly convex. In juveniles, the sagitta is more rounded with smooth borders not scalloped and the rostrum is less pronounced. Moreover, the inner face is flat and the outer one is convex.

Asteriscus (Fig. 5b, see also Fig. 2b)

Vertical otolith with a pronounced shape, and a sharp extremum ventralis. Smooth edges and inner and outer

faces are smooth and convex. Rostrum, antirostrum and major and minor cisure are not differentiated. Fossa acustica is scarcely developed and ventrally curved. Crista medial is curved to the ventral area following the fossa acustica shape, occupying almost all the otolith length.

Table III. Relationships ($Y = a + bX$) obtained between different measurements of sagitta and lapillus otoliths of *L. larseni* and fish size (TL: total length, SL: standard length). Standard errors of *a* and *b* coefficients between parentheses. See Table II for abbreviations.

Otolith	Relationship:				
	$Y = a + bX$	<i>a</i>	<i>b</i>	r^2	
Sagitta	OL vs TL	0.2804 (0.2666)	0.0247 (0.0020)	0.92	
	OW vs TL	0.4535 (0.1627)	0.0117 (0.0012)	0.88	
	RL vs TL	-0.0782 (0.1215)	0.0066 (0.0010)	0.80	
	FCL vs TL	0.2351 (0.2322)	0.0139 (0.0018)	0.83	
	CL vs TL	-0.0560 (0.1736)	0.0070 (0.0014)	0.69	
	OL vs SL	0.3696 (0.2602)	0.0270 (0.0022)	0.92	
	OW vs SL	0.4947 (1.5771)	0.0128 (0.0014)	0.88	
	RL vs SL	-0.0534 (0.1187)	0.0073 (0.0010)	0.80	
	FCL vs SL	0.2864 (0.2270)	0.0152 (0.0020)	0.83	
	CL vs SL	-0.0407 (0.1645)	0.0077 (0.0014)	0.7	
	OW vs OL	0.3297 (0.1183)	0.4711 (0.0346)	0.94	
	Lapillus	OW vs OL	0.1556 (0.0854)	0.6845 (0.0877)	0.93
		OL vs TL	0.4391 (0.0960)	0.0039 (0.0006)	0.87
		OW vs TL	0.4582 (0.0850)	0.0027 (0.0006)	0.80
OL vs SL		0.4684 (0.0987)	0.0042 (0.0008)	0.85	
OW vs SL		0.4802 (0.0869)	0.0028 (0.0006)	0.77	

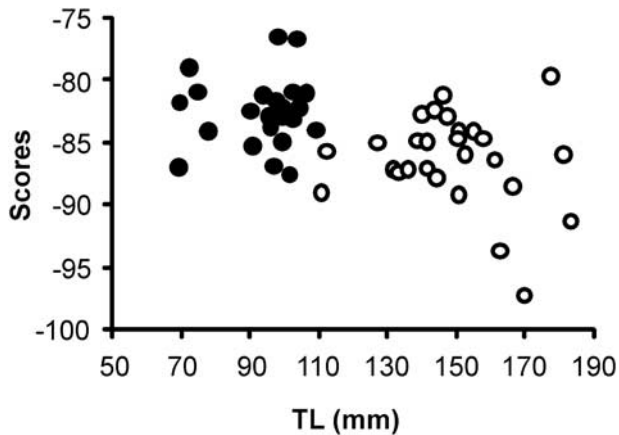


Fig. 6. Plot of scores of juveniles (total length < 110 mm) and adults (total length > 110 mm) applying the linear canonical function of the discriminant analysis ($y = 2.84615898*RL + 0.52169245*CL + 0.16328178*FCL + 0.11448414*OW - 4.017396*OL - 1.2973963*R - 0.7934913*E$). For morphometric abbreviations see Fig. 2 caption. Juveniles (filled circle) and adults (open circle).

Fissura periferica is larger than wider accompanying the crista medial length.

Lapillus (Fig. 5c, see also Fig. 2c)

Quadrangular otolith with a scarcely differentiated extremum anterior and a not distinguishable extremum posterior. Smooth edges, the ventral face is convex and the dorsal one is slightly concave. Gibbus maculae are scarcely differentiated. Sulcus lapilli is not delimited by a presulcal area (extended sulcus). Cisure is not differentiated. Prominentia marginalis conspicuous and rounded, not delimited in the profile. In juveniles the sulcus is delimited by a presulcal area (opened sulcus).

Morphometric analysis was made for the three otoliths of juvenile and adult fishes. Table II shows the mean values of maximum OL and maximum OW of sagitta, asteriscus and lapillus, and FCL, CL, RL, E and R indexes of sagitta. Cauda and rostrum lengths were the most variable measurements, while E and R were the least ones for juveniles as for adults (see coefficient of variation values in the table). Significant differences in all the morphometric variables were observed between juveniles and adults, which were reflected in a change in their otolith shape. In detail, OL ($t = -9.98$, P -value < 0.0001) and R ($t = -2.40$, P -value = 0.0202) were higher in adults, whereas E was higher in juveniles ($t = 2.84$, P -value = 0.0065). Asteriscus measurements (OL and OW) were more variable in adults than in juveniles, while in lapillus an inverse pattern was detected. All the relationships estimated between otolith measurements (sagitta and lapillus) and fish length (TL and SL) and between OW and OL were statistically significant (Table III, $P < 0.0001$ in all cases). In the case of asteriscus these relationships were not investigated owing to the small number of samples.

The discriminant analysis of sagitta allowed us to identify the best linear function of some selected otolith measurements discriminating juveniles from adults, previous assumptions verified as the homogeneity matrix of covariance was not significant (Bartlett's test, P -value = 0.9992). Starting from two groups of fishes in relation to fish size (i.e. assuming 110 mm TL as limit between juveniles and adults), one eigenvalue was obtained (3.22), being the maximum OL (-4.02), the RL (2.85) and the R index (-1.29), the best variables which separated juveniles and adults. Conversely, maximum OW (0.11), FCL (0.16), CL (0.52) and E index (-0.79) were not significant for the stages discrimination. The fifty scores obtained applying this linear canonical function was plotted in Fig. 6.

Discussion

The stomach contents analysis and the study of morphology and morphometry of sagitta, asteriscus and lapillus otoliths provided new insights on feeding behaviour and preferred habitat of the *L. larseni* population inhabiting the South Shetland Islands and the Antarctic Peninsula. Asteriscus and lapillus were described for the first time, while previous description of sagitta was improved by adding inner and outer faces descriptions including the ostium and cauda. The morphometric analysis of the sagitta and lapillus enabled us to relate different variables (OL, OW, RL, FCL and CL) in relation to fish size. Otolith morphology and morphometry are potential tools in identifying juveniles or adults of *L. larseni* in predator guts (Koen Alonso *et al.* 2000, Martínez Pérez *et al.* 2007). As otoliths can be partially deteriorated by chemical or mechanical abrasion in the stomach of predators (Granadeiro & Silva 2000), rostrum or sulcus often being eroded, we provided the FCL as well.

The sagitta showed morphological and morphometric variations during their ontogenetic development. The discriminant analysis of this otolith showed that the variables which mostly contribute to discriminate juveniles from adults were maximum OL, RL and R index. Although R index had the lowest score of these variables, it is of particular interest, as it provides evidence of an ontogenetic change of development rate of the rostrum with respect to the maximum OL (i.e. allometry). As it was expected, all other variables (RL and OL), contribute to discriminate juveniles and adults, as all increase with fish size.

The differentiation of sagittae shape could be linked to a change of fish habitat. Lombarte *et al.* (2010) observed that benthic dwellers of Nototheniidae had the largest sagittae in relation to body size, pelagic species had smaller and rounder sagittae than benthic species, and epibenthic species showed intermediate relative sizes. Particularly, they corroborated the epibenthic habitat of adults of *L. larseni* by using geometric techniques relating diet, phylogeny and otolith shape. In the present study, juveniles of *L. larseni* presented a shorter and wider sagitta than adults, resulting in a major E index because

of a rounded shape and a minor R index because of a less developed rostrum. This could indicate that juveniles live in the water column for a long time before settling, while adults could have an epibenthic habitat leaving the bottom during the night to feed in the water column (Bushula *et al.* 2005). This different distribution pattern is reflected in the type of prey consumed (indeed, more pelagic copepods were found in juvenile stomachs). In addition, the values obtained of E (56.34 ± 3.57) and R (22.75 ± 2.34) indexes for adults are similar to those reported in previous studies (Hecht 1987, Volpedo *et al.* 2008).

Lepidonotothen larseni presented a positive allometric growth ($b > 3$), as they increased in weight faster than in length. The same pattern of allometric growth was observed in *L. larseni* of 140–203 mm TL collected at the South Shetland Islands by Eastman & Sidell (2002). Interestingly, both juveniles and adults showed a good nutritional condition ($LCCI > 1$), possibly owing to the favourable environmental conditions (primarily food availability) experienced during summer season. In the sub-Antarctic Prince Edward Islands, *L. larseni* fed during all of the 24 hour cycle, but the peak of feeding activity occurred at evening when they left the bottom to feed in the water column (Bushula *et al.* 2005). An increase of feeding activity during early night and morning was confirmed elsewhere (Shandikov 1986). In our study, even though the stomach repletion presented a general decreasing trend from noon to late evening, adults exhibited a full stomach degree of fullness (stage III) during late evening, while in juveniles this peak was at noon hours. Spatial and temporal distribution varied with ontogeny, as juveniles were caught exclusively at noon and evening whereas adults were caught exclusively at evening and late evening. Probably, this pattern is related to asynchronous vertical migrations of juveniles and adults which contribute to smooth spatial and food overlap between them.

The composition and sizes of prey consumed by *L. larseni* differed between juveniles and adults. While adults fed on small and large prey (in length and width), juveniles were limited to feed on small prey because of their comparatively smaller mouth size (Duarte *et al.* 2007). The diet composition of *L. larseni* was similar to those found in previous studies (Targett 1981, Barrera-Oro & Tomo 1987, Pakhomov & Pankratov 1992, Takahashi & Iwami 1997, Frolkina *et al.* 1998, Barrera-Oro 2002, Bushula *et al.* 2005), consisting mainly of copepods, amphipods and euphausiids both in frequency of occurrence and abundance. Unlike the findings of Targett (1981), we did not find fishes or mysids in their stomach contents. In agreement with Barrera-Oro & Tomo (1987), we observed that diet changes with ontogeny, and particularly, the increase in size of *L. larseni* is related to a decrease in the consumption of copepods and an increase in that of krill. On the other hand, the presence of stones and benthic gammarid amphipods in the stomachs analysed confirmed the epibenthic habitat of adult fishes. Previous studies on other nototheniid species, such as *Lepidonotothen*

nudifrons Lönnberg, *Gobionotothen gibberifrons* Lönnberg and *Gobionotothen marionensis* (Günther), showed that they all present morphological and behavioural adaptations to different habitats to avoid food overlapping (Targett 1981, Takahashi 1983, Bushula *et al.* 2005).

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References

- ASSIS, C.A. 2003. The lagenar otoliths of teleosts: their morphology and its application in species identification, phylogeny and systematics. *Journal of Fish Biology*, **62**, 1268–1295.
- ASSIS, C.A. 2005. The utricular otoliths, *lapilli*, of teleosts: their morphology and relevance for species identification and systematics studies. *Scientia Marina*, **69**, 259–273.
- BARRERA-ORO, E. 2002. The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. *Antarctic Science*, **14**, 293–309.
- BARRERA-ORO, E.R. & TOMO, A.P. 1987. Feeding and ecology of *Notothenia larseni* Lönnberg. In EL-SAYED, S.Z., ed. *Antarctic aquatic biology*. BIOMASS Scientific Series, 7, 99–106.
- BOLTOVSKOY, D. 1999. *South Atlantic zooplankton*. Leiden: Backhuys, 1722 pp.
- BUSHULA, T., PAKHOMOV, E.A., KAEHLER, S., DAVIS, S. & KALIN, R.M. 2005. Diet and daily ration of two nototheniid fish on the shelf of the sub-Antarctic Prince Edward Islands. *Polar Biology*, **28**, 585–593.
- CAMPANA, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology*, **59**, 197–242.
- COLMENERO, A.I., AGUZZI, J., LOMBARTE, A. & BOZZANO, A. 2010. Sensory constraints in temporal segregation in two species of anglerfish, *Lophius budegassa* and *L. piscatorius*. *Marine Ecology Progress Series*, **416**, 255–265.
- DI RIENZO, J.A., CASANOVES, F., BALZARINI, M.G., GONZALEZ, L., TABLADA, M. & ROBLEDO, C.W. 2011. *InfoStat*, version 2011. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. <http://www.infostat.com.ar>.
- DUARTE, F., IBÁÑEZ, C. & CHONG, J. 2007. Changes in mouth morphometrics as related to the diet of *Thyrssites atun* (Euphrasen, 1791) from south-central Chile. *Revista Chilena de Historia Natural*, **80**, 407–417.
- DUHAMEL, G. & PLETIKOSIC, M. 1983. Données biologiques sur les Nototheniidae des Iles Crozet. *Cybium*, **7**, 43–57.
- EASTMAN, J.T. 2005. The nature of the diversity of Antarctic fishes. *Polar Biology*, **28**, 93–107.
- EASTMAN, J.T. & SIDELL, B.D. 2002. Measurements of buoyancy for some Antarctic nototheniid fishes from the South Shetland Islands. *Polar Biology*, **25**, 753–760.

- FROLKINA, G.A., KONSTANTINOVA, M.P. & TRUNOV, I.A. 1998. Composition and characteristics of ichthyofauna in pelagic waters of South Georgia (subarea 48.3). *CCAMLR Science*, **5**, 125–164.
- GON, O. & HEEMSTRA, P.C. 1990. *Fishes of the Southern Ocean*. Grahamstown, SA: JLB Smith Institute of Ichthyology, 462 pp.
- GRANADEIRO, J.P. & SILVA, M.A. 2000. The use of otoliths and vertebrae in the identification and size-estimation of fish in predator-prey studies. *Cybius*, **24**, 383–393.
- HECHT, T. 1987. A guide to the otoliths of southern ocean fishes. *South African Journal of Antarctic Research*, **17**, 1–87.
- KLINGENBERG, C.P. & EKAU, W. 1996. A combined morphometric and phylogenetic analysis of an ecomorphological trend: pelagization in Antarctic fishes (Perciformes: Nototheniidae). *Biological Journal of the Linnean Society*, **59**, 143–177.
- KOEN ALONSO, M., CRESPO, E.A., PEDRAZA, S.N. & COSCARELLA, M.A. 2000. Food habits of the South American sea lion, *Otaria flavescens*, off Patagonia, Argentina. *Fishery Bulletin*, **98**, 250–263.
- LE CREN, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch *Perca fluviatilis*. *Journal of Animal Ecology*, **20**, 201–219.
- LOMBARTE, A., PALMER, M., MATALLANAS, J., GÓMEZ-ZURITA, J. & MORALES-NIN, B. 2010. Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. *Environmental Biology of Fishes*, **89**, 607–618.
- MARTÍNEZ PÉREZ, J.A., CHAVEZ ARTEAGA, M., TELLO, J.L. & MORALES, A. 2007. Utilización de otolitos como herramienta en la determinación de especies. *Revista de Zoología*, **18**, 13–18.
- PAKHOMOV, E.A. & PANKRATOV, S.A. 1992. Bycatch, growth and feeding of Antarctic juvenile fish taken in krill (*Euphausia superba dana*) fisheries in the South Georgia area, in 1992. *CCAMLR Science*, **1**, 129–142.
- POPPER, A.N. & ZHONGMIN, L. 2000. Structure-function relationships in fish otolith organs. *Fisheries Research*, **46**, 15–25.
- RADTKE, R.L. & TARGETT, T.E. 1984. Rhythmic structural and chemical patterns in otoliths of the Antarctic fish *Notothenia larseni*: their application to age determination. *Polar Biology*, **3**, 203–210.
- SHANDIKOV, G.A. 1986. Biological characteristics of *Nototheniops tchizh* (Balushkin) (Nototheniidae) from the Ob and Lena seamounts, Indian sector of the Southern Ocean. *Proceedings of the Zoological Institute, USSR Academy of Sciences*, **153**, 91–109. [In Russian].
- TAKAHASHI, M. 1983. Trophic ecology of demersal fish communities north of South Shetland Islands, with notes on the ecological role of krill. *Memoirs of National Institute of Polar Research*, **27**, 183–192.
- TAKAHASHI, M. & IWAMI, T. 1997. The summer diet of demersal fish at the South Shetland Islands. *Antarctic Science*, **9**, 407–413.
- TARGETT, T.E. 1981. Trophic ecology and structure of coastal Antarctic fish communities. *Marine Ecology Progress Series*, **4**, 243–263.
- VOLPEDO, A.V. & ECHEVERRÍA, D.D. 2000. *Catálogo y claves de otolitos para la identificación de peces del Mar Argentino. I. Peces de importancia comercial*. Buenos Aires: Editorial Dunken, 90 pp.
- VOLPEDO, A.V. & ECHEVERRÍA, D.D. 2003. Ecomorphological patterns of the sagitta in fish on the continental shelf off Argentina. *Fisheries Research*, **60**, 551–560.
- VOLPEDO, A.V. & FUCHS, D.V. 2010. Ecomorphological patterns of the lapilli of *Paranoplatense siluriforms* (South America). *Fisheries Research*, **102**, 160–165.
- VOLPEDO, A.V., TOMBARI, A.D. & ECHEVERRÍA, D.D. 2008. Eco-morphological patterns of the sagitta of Antarctic fish. *Polar Biology*, **31**, 635–640.
- ZAR, J.H. 1999. *Biostatistical analysis*, 4th ed. New York: Prentice Hall, 929 pp.