

## Growth patterns of the lanternfish *Ceratoscopelus maderensis* in the western Mediterranean Sea

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**Summary:** The age and growth patterns of the mesopelagic fish *Ceratoscopelus maderensis* (family Myctophidae) of the western Mediterranean Sea were described throughout its entire life cycle (from larvae to adult stages) using the sagittae otoliths of 59 individuals collected in December 2009. Three characteristic zones were identified along the cross-section of the sagittae (larval, metamorphic and juvenile-adult zones). Assuming growth rings as daily increments, the age of the analysed individuals (from 3.5 to 64 mm standard length [SL]) would range from 7 to 332 days. The relationship between the number of increments and the fish SL was fitted to a von Bertalanffy growth model ( $SL=70.5899 \times (1 - \exp^{-(0.0501(t+2.6705)})$ ). The growth pattern of *C. maderensis* in the western Mediterranean Sea was similar to that reported for this species in the northeast Atlantic Ocean. Though from a body size of 40-45 mm SL, growth rates declined more slowly in individuals from the western Mediterranean Sea, growth differences between these individuals and those from the northeast Atlantic Ocean were not statistically significant. This study provides new insights into the age and growth patterns of one of the most abundant mesopelagic fish species in the Mediterranean Sea that have clear implications for the study and management of marine ecosystems.

**Keywords:** daily growth, larval growth, mesopelagic fish, Myctophidae, otolith microstructure.

### Patrones de crecimiento del pez linterna *Ceratoscopelus maderensis* en el Mediterráneo occidental

**Resumen:** En el presente trabajo se describen la edad y los patrones de crecimiento desde la fase larvaria hasta la fase adulta del pez mesopelágico *Ceratoscopelus maderensis* (familia Myctophidae) del Mediterráneo occidental. Para ello, se analizó el otolito *sagitta* de 59 individuos capturados en diciembre de 2009. Se identificaron tres zonas en la *sagitta*, cada una de las cuales se corresponde con una fase del desarrollo ontogenético del pez: larvaria, metamórfica y juvenil-adulta. Asumiendo que los anillos de crecimiento son diarios, la edad de los individuos analizados (de 3.5 a 64 mm de longitud estándar [SL]) oscilaría entre 7 y 332 días. La relación entre el número de incrementos y la SL de los peces se ajustó al modelo de crecimiento de von Bertalanffy ( $SL=70.5899 \times (1 - \exp^{-(0.0501(t+2.6705)})$ ). El patrón de crecimiento de *C. maderensis* en el Mediterráneo occidental fue similar al previamente descrito para esta especie en el Noreste del Océano Atlántico. A pesar de que, a partir de 40-45 mm SL, las tasas de crecimiento disminuyeron más lentamente en los individuos del Mediterráneo occidental, las diferencias de crecimiento entre estos individuos y los del Noreste del Océano Atlántico no fueron estadísticamente significativas. Los resultados de este estudio aportan nuevos conocimientos sobre la edad y el crecimiento de una de las especies más abundantes del Mar Mediterráneo, lo cual tiene claras implicaciones de cara al estudio y la gestión de los ecosistemas marinos.

**Palabras clave:** crecimiento larvario, crecimiento diario, microestructura del otolito, Myctophidae, peces mesopelágicos.

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## INTRODUCTION

*Ceratoscopelus maderensis* (Lowe, 1839) is a lanternfish species (Myctophidae) that is generally found in mesopelagic waters at depths ranging from 200 to 1000 m between 50°N and 30°N in the North Atlantic Ocean (Hulley 1984) and throughout the Mediterranean Sea (Jonsson 1992, Cavallaro et al. 2019). Its larval stages inhabit the epipelagic layer, mostly concentrated in the first 50 m of the water column. When the transformation (metamorphic) stage is reached, individuals begin to move to the mesopelagic zone (Kendall et al. 1984, Richards 2005, Sassa et al. 2007). From this period onward, like most myctophid species, *C. maderensis* acquires a nictopelagic behaviour that implies diel vertical migrations between ca. 1000 m depth and the surface (Hulley 1984, Mytilineou et al. 2005, Olivar et al. 2012).

*Ceratoscopelus maderensis* is one of the most abundant myctophid species in the northeastern Atlantic Ocean and the Mediterranean Sea (Goodyear et al. 1972, Hulley 1981, Olivar et al. 2012). As such, this species occupies a key position in the food-web structure of the mesopelagic community feeding on zooplankton (Bernal et al. 2015), which highlights its integral role in the functioning of oceanic ecosystems as an intermediate link between primary consumers and top predators (Gjøsaeter and Kawaguchi 1980, Sassa and Takahashi 2018, Anderson et al. 2019). Despite its important ecological role, the populations of *C. maderensis* remain one of the least well-studied components of marine ecosystems at both a regional and a global scale (St. John et al. 2016). Several studies have reported growth patterns in myctophid species (e.g. Gartner 1991a, Linkowski et al. 1993, Sassa et al. 2015), but despite their wide geographical distribution, there is still a lack of information on their growth rates and lifespan.

Accurate age determinations provide basic life-history information and are imperative for describing population dynamics at the species level. Most age-determination studies on myctophids are based on the counting of daily growth increments (Brothers et al. 1976, Methot and Kramer 1981, Gjøsaeter 1987) or seasonal growth increments in sagittae otoliths (Sarmiento et al. 2018), length-based analysis (Ricker 1975 and references therein, Harvey et al. 2000) or a combination of these methods (Aguilar-Perera and Quijano-Puerto 2016, Saunders et al. 2020). Microincrements in the otoliths of myctophids appear to be equivalent to daily rings that have been validated in other myctophids directly by considering their formation over periods of 24 hours (Gartner 1991a, b, Moku et al. 2005) and indirectly by the back-calculation of birth dates from the age, date of capture and timing with their spawning season (Young et al. 1988). Therefore, most studies about the growth and age of myctophids have assumed a daily micro-increment deposition (Greely et al. 1999, Hayashi et al. 2001, Wang et al. 2018).

Linkowsky et al. (1993) investigated the growth patterns of adult individuals of *C. maderensis* from the northeast Atlantic Ocean. However, the age and

growth patterns of this species during its larval stage remained unknown so far, and no studies have been conducted in either early stages or adults from the Mediterranean Sea. The Mediterranean Sea is characterized by the near-constant water temperature below the thermocline (100m depth) at ca.13°C (Olivar et al. 2012, Houpert et al. 2015) and its relative oligotrophy (Estrada 1985, Morel and Andre 1991). This contrasts with the colder and more productive waters of the northeastern Atlantic Ocean, where temperatures range between 8°C and 18°C from 500 m depth to the surface (Emery and Meincke 1986). This could lead to dissimilar growth patterns in *C. maderensis* between the two biomes. Hulley (1984) showed that, in general, the maximum body size reached by mesopelagic fish species in the Atlantic Ocean was larger than that in the western Mediterranean Sea. However, several studies have also shown that higher temperature regimes can increase both otolith (Rountrey et al. 2014) and fish growth (Handeland et al. 2008, Silva et al. 2008). Further genetic studies on the populations of *C. maderensis* might confirm whether the species separated into two different stocks, one in the Atlantic Ocean and one in the Mediterranean Sea, with a biogeographical frontier in the Alboran Sea, as it has been demonstrated for many other fish species (Naciri et al. 1999).

The aims of the present study are i) to estimate the age and growth patterns of *C. maderensis* in the western Mediterranean Sea through the analysis of sagittae otoliths considering most of its entire lifecycle, and ii) to compare the growth patterns of this species in the western Mediterranean Sea with those reported by Linkowski et al. (1993) for this species with individuals from the northeastern Atlantic Ocean. We expect that the warmer temperatures in the Mediterranean Sea will make this species grow faster than in the northeastern Atlantic Ocean.

## METHODS

### Fish sampling

Sampling was performed on board the research vessel *Sarmiento de Gamboa* during a cruise carried out in December 2009 (late autumn). The study area was located to the northwest and southwest of Mallorca (Balearic Islands, western Mediterranean Sea, Fig. 1) at the shelf-break (>200 m depth) and the median slope (700-900 m depth). A 280 m<sup>2</sup> midwater trawl (10 mm mesh size in the cod-end) and a 3 m<sup>2</sup> (3 mm mesh size) Isaacs- Kidd Midwater Trawl (IKMT) were employed to capture adult and juvenile fish. The depth where the fishing nets operated was controlled using a SCANMAR sensor. Fishing operations were performed both near the surface (40-80 m) and near the Deep Scattering Layer (DSL) at 400 m depth, where the echosounder recorded the highest acoustic signal at 18 and 38 kHz (Olivar et al. 2012). The vessel speed was maintained at 4 knots for the large midwater trawl and 3 knots for the IKMT. After on-board fish identification using specific literature (Hulley 1981, 1984), the

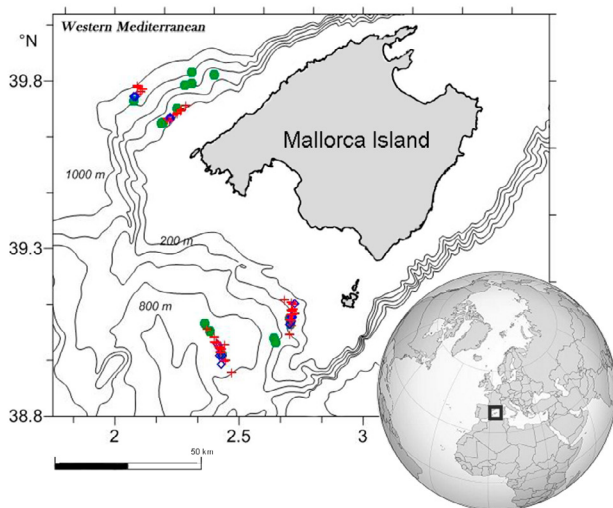


Fig. 1. – Study area where samples were collected in the northwestern and southwestern basins of Mallorca Island (Mediterranean Sea, December 2009). Sampling stations are represented according to the type of device employed: blue rhombuses correspond to Hydro-Bios MultiNet, red crosses to Isaacs-Kidd Midwater Trawl and Rectangular Midwater Trawl, and green circles to pelagic trawls; see the Methods section.

specimens were frozen and stored at  $-20^{\circ}\text{C}$  to prevent otolith damage. The water column temperature was obtained with the SBE 911plus CTD at each station.

The collection of fish larvae and transformation stages was carried out at the same stations with a  $0.25\text{ m}^2$  Hydro-Bios MultiNet with  $0.3\text{ mm}$  mesh size. Oblique tows at five discrete depths from  $200\text{ m}$  to the surface were performed during a 24-h cycle (8 in daytime and 8 at night). Ichthyoplankton samples were preserved in 5% buffered formalin and sorted once in the laboratory. The pH was maintained at *ca.* 8 to prevent otolith degradation.

Fish larvae were sorted and identified in the laboratory using relevant literature (Tåning 1918, Moser and Watson 2006). Larvae were ascribed to preflexion, flexion and postflexion stages (according to the urostyle bending), or transformation stages (according to photophore development) (Kendall et al. 1984), and were measured to  $0.1\text{ mm}$  precision under a microscope employing an ocular micrometre.

### Otolith preparation

The standard length (SL) was measured before otolith extraction for 208 individuals, of which 45 were larvae ( $<16\text{ mm SL}$ ), 49 were individuals at the transformation stage ( $17\text{--}20\text{ mm SL}$ ), and the remaining 114 were juveniles and adults ( $>20\text{ mm SL}$ ). For each individual, the left and right sagittae otoliths were extracted from the ear cavity. In the larval and transformation stages, the otolith extraction was performed using a fine needle, with the help of polarized light of the microscope for a better location of the otoliths. After drying, a drop of Cristal Bond 590™ thermolabile resin was poured over the otolith for further preservation. In the juveniles and adults, we first made a cross-sectional incision at the

back of the fish head, near the rear of the operculum. Then, the two sagittae were extracted with forceps according to Secor et al. (1991). After the extraction, both otoliths were cleaned with a 5% solution of KOH to remove the attached organic tissue and then rinsed with water. The mounting and polishing were performed according to the methods described by Morales-Nin (1992) and Stevenson and Campana (1992). An otolith of each fish was mounted on a slide to polish its sagittae section, fixing the inner face with thermolabile resin.

The otolith length was defined from maximum diameter in larvae and from rostrum to posterior margin according to Tuset et al. (2008). In the smallest larvae ( $5\text{--}7\text{ mm SL}$ ), the transparency of the otoliths allowed us to count growth increments without need for polishing. Otoliths from the transformation, juvenile and adult stages were manually polished with grinding lapping papers ( $0.1\text{--}3\text{ }\mu\text{m}$ ). In otoliths from larger specimens, the polishing process was interspersed with micrographs of the increments located in the margin of the otolith (the narrowest ones) to ensure the identification and the count of these increments and prevent any loss in the case of over-polishing. To increase transparency in thicker otoliths, the polishing process was carried out on both sides, taking care not to affect the maximum diameter of the otolith. Finally, the otoliths were ultra-polished with an abrasive consisting of a MicroCloth PSA 10/ PK 8 disc previously impregnated with an abrasive solution with  $0.05\text{ }\mu\text{m}$  of alumina. Daily increments were counted from images obtained with a digital camera mounted on an optical microscope (Zeiss Axioskop 2 Plus) and with the Image-Pro Plus v.5.0 image analysis software (magnification:  $100\times$ ,  $400\times$ ,  $630\times$  and  $1000\times$ ). Double readings were performed in the postrostrum otolith section. If the first reading was not coincident with the second one, a third reading was performed to guarantee the correct interpretation of age.

To determine whether the increment width was outside the resolution threshold of the optical microscope, some otoliths from the transformation stage ( $n=1$ ), and juvenile and adult stages ( $n=5$ ) were also examined at high resolution. Polished otoliths were immersed in a 1% HCl solution for between 60 and 300 seconds, rinsed with water and allowed to air dry for 24 hours. Finally, the otoliths were mounted, covered with gold-palladium and then observed using a scanning electron microscope (SEM).

### Growth estimation

In the Mediterranean Sea, *C. maderensis* is not sexually mature until it reaches  $\geq 40\text{ mm SL}$  (Hulley 1981, 1984). Specimens collected in this study were not sexed, so we cannot confirm whether there are size differences between sexes in individuals of *C. maderensis* from the western Mediterranean Sea. Therefore, in this study, specimens of both sexes were considered together. Linkowski et al. (1993) observed that individuals of *C. maderensis* from the northeastern Atlantic Ocean showed no significant size differences between males and females. The relationship between the fish length

and the otolith diameter was determined by linear regression to ensure that the growth of the otolith is proportional to the somatic growth of the species. As each increment is assumed to represent one-day growth, the relationship between the number of day-increments and SL was fitted by a von Bertalanffy growth curve based on Equation 1:

$$L_t = L_\infty [1 - e^{-k(t-t_0)}] \quad [1]$$

where  $L_t$  is standard length in mm,  $L_\infty$  is the asymptotic size in mm,  $k$  in days<sup>-1</sup> is the Brody growth rate coefficient, which measures the rate at which the growth rate declines, and  $t_0$  corresponds to the age at which  $L$  is 0 (von Bertalanffy 1938).

The absolute growth rate ( $g_t$ ) is given by  $g_t = k(L_\infty - L_t)$ , and when  $t=0$  ( $w$ ), the absolute growth rate is  $w = k \times L_\infty$ . Parameters  $k$  and  $L_\infty$  were fitted and estimated using R software.

Finally, a second von Bertalanffy growth curve considering adult specimens only (i.e. SL > 19 mm) was fitted in order to assess for growth differences between our specimens from the western Mediterranean Sea and from the northeastern Atlantic Ocean measured by Linkowski et al. (1993) (individuals with SL < 19 mm were not considered by these authors). The comparison of these two curves was performed without fixing parameters or fixing one, two or all three parameters using the fisheries stock-assessment method package (FSA; Ogle 2016) in R software. According to this method, when the best explanatory models are those in which most of the parameters have not been fixed, this indicates that there are differences between the curves. By contrast, when the best models are those in which most parameters have been fixed, this indicates similarities between the curves. The best models were selected using the Akaike information criterion (AIC, Burnham and Anderson 2002). Models with AIC differences  $\leq 2$  were considered equivalent (see Burnham and Anderson 2002, 2004).

**RESULTS**

A total of 208 individuals of *C. maderensis* were selected to cover the entire size range of the species in the western Mediterranean Sea. However, only 59 individuals (28%) could be successfully processed because of difficulties in the preparation process. This is mainly because the counting of increments in the otoliths of larger specimens was only possible after obtaining extremely thin and delicate sheets that broke easily during polishing or when using the hot melting resin for fixing. Despite these difficulties, the number of otoliths successfully processed was large enough to constitute a representative sample of the size range of *C. maderensis* in the western Mediterranean Sea.

Larval otoliths were round and very small (otolith diameter in larval individuals ranged between 19.96 and 218.51  $\mu\text{m}$ ) but turned into an oval shape as the fish grows (Fig. 2). The size-frequency distribution of juvenile and adult stages showed two modal size classes (20 and 50 mm respectively) (Fig. S1).

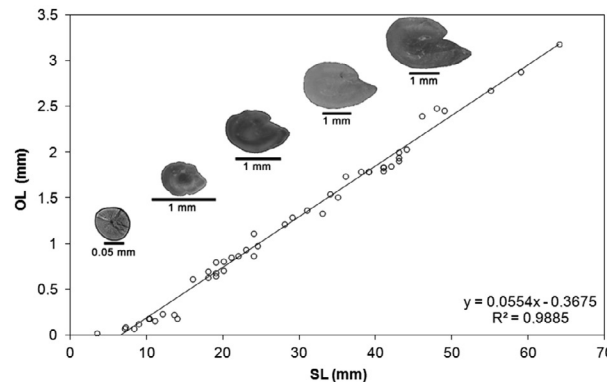


Fig. 2. – Linear regression between the maximum otolith diameter (OL) and fish length (SL) of *Ceratoscopelus maderensis* otoliths from the western Mediterranean Sea. The images show ontogenetic changes in the otolith shape with development.

**Microstructure of the otoliths**

The observation and the counting of otolith increments were feasible using both optical microscope and SEM. Three different zones were differentiated in adult specimens: larval (Fig. 3A, B), metamorphic (Fig. 3C, D), and juvenile-adult (Fig. 3E, F). Table 1 shows the SL ranges and the number of increments for each of these regions. The larval region was composed of a core (Fig. 3B) followed by a succession of an average of 27 increments ( $n=9$ ,  $\sigma=2.98$ ). The mean radius between the centre of the core and the outer part of the first increment was 2.95  $\mu\text{m}$  ( $n=3$ ,  $\sigma=0.84$ ), while the average radius of the larval zone was 125.34  $\mu\text{m}$  ( $n=19$ ,  $\sigma=30.46$ ). Within the larval region, the increment thickness increased progressively following the exponential function:

$$y = 1.2196e^{0.015x} \quad [2]$$

where  $y$  corresponds to the thickness of the increments in  $\mu\text{m}$  and  $x$  is the radius in  $\mu\text{m}$  ( $r^2=0.91$ ). The mean increment thickness in this region ranged from 1.4 to 4.2  $\mu\text{m}$  ( $n=14$ ,  $\sigma=0.88$ ). The end of the larval region was well defined by a dark band of transition between the larval and metamorphic zones (Fig. 3A). This band was 5-10  $\mu\text{m}$  wide and could also be detected using an optical microscope.

The metamorphic zone (Fig. 3C, D) extended from the external limit of the larval region (Fig. 3A) to the

Table 1. – Standard length (SL), number of increments for each developmental zone (larval, metamorphic and juvenile-adult) identified in the otoliths of N individuals of *Ceratoscopelus maderensis* from the western Mediterranean Sea.

Development phase	SL (mm)	Increments	N
Larval	≤ 14	7-43	12
Metamorphic	16-19	42-69	5
Juvenile-adult	19-64	61-332	42

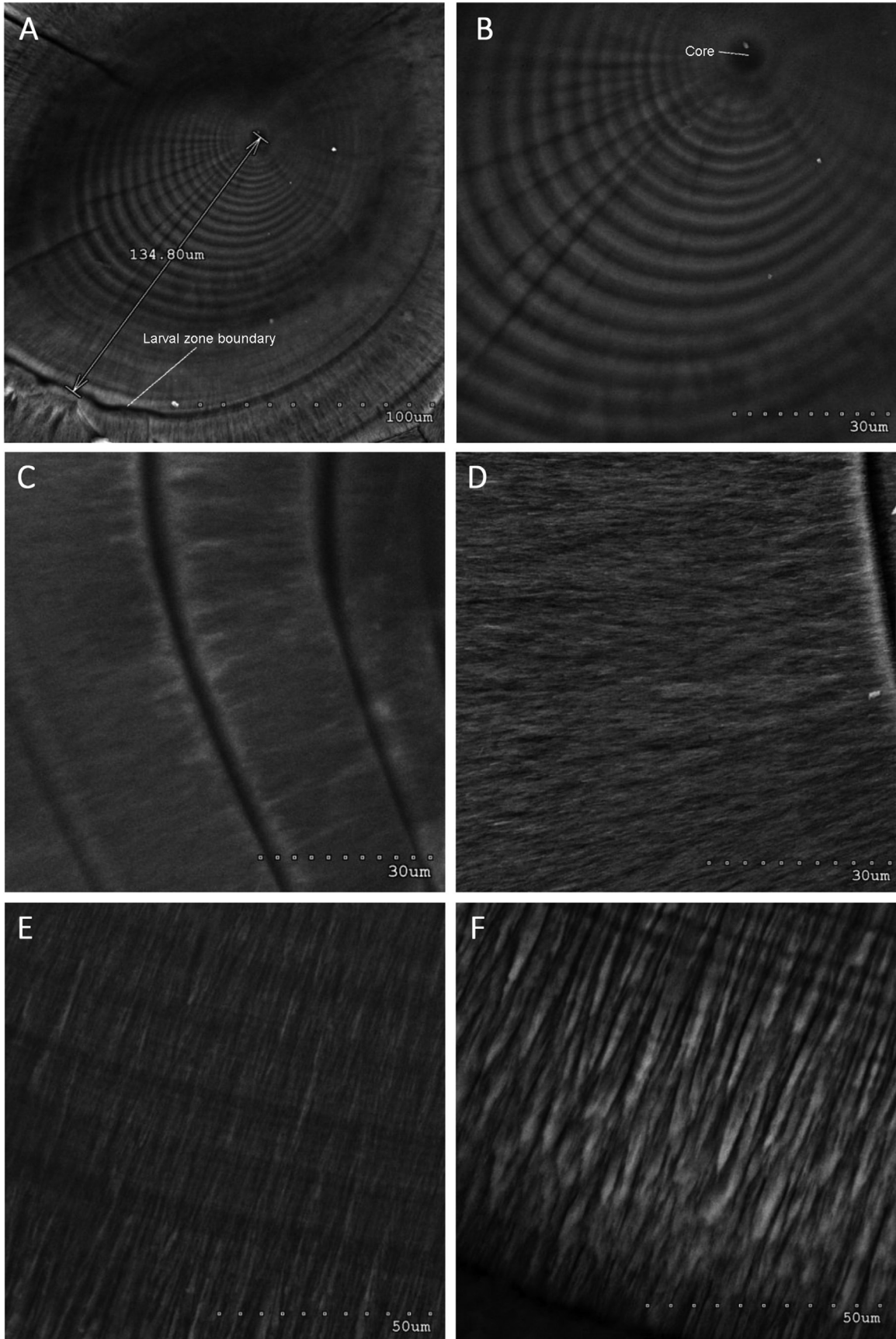


Fig. 3. – Scanning electron microphotography (SEM) of selected otoliths of *Ceratoscopelus maderensis* from the western Mediterranean Sea. (A) Larval zone: the transition between the larval and metamorphic zones is observed. (B) Detail of the central core in (A). (C), (D) Details of the metamorphic zone. (E) Increments in the juvenile-adult zone. (F) The margin of the otolith.

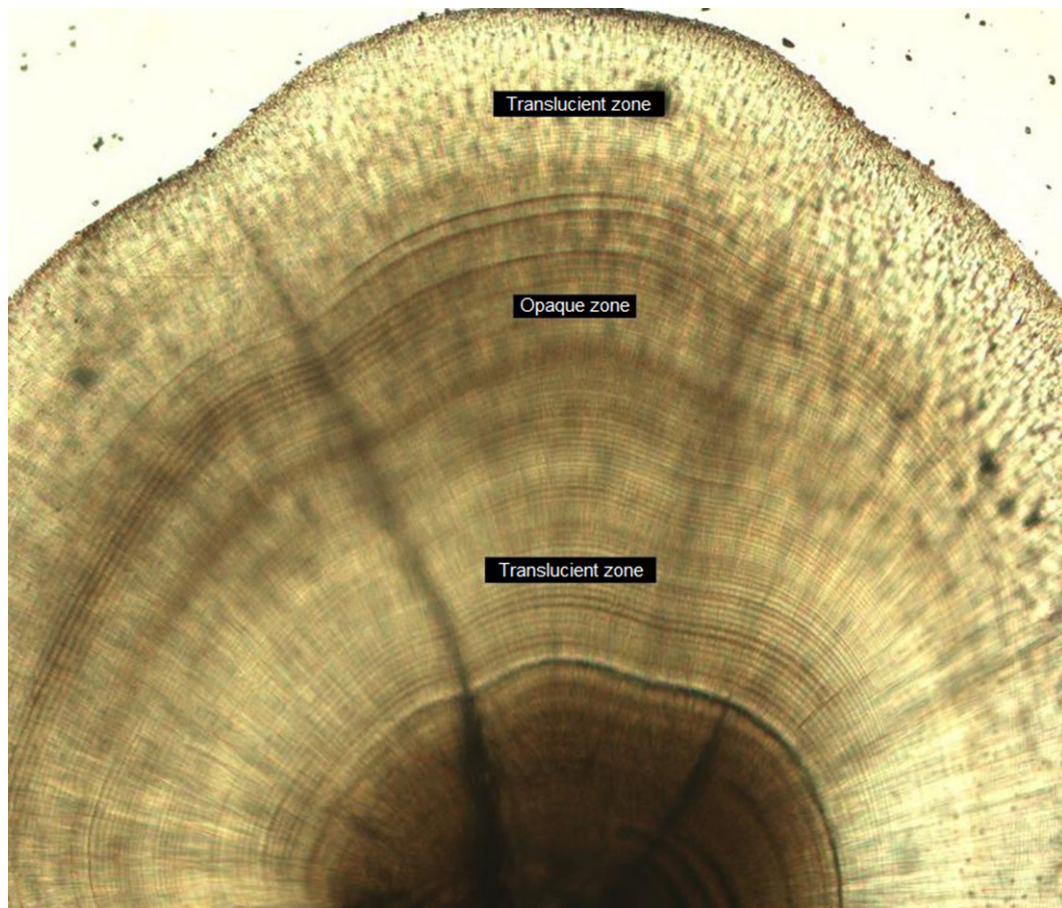


Fig. 4. – Detail (100×) of the sagittae section of the postrostrum where two translucent and one opaque zone are distinguished in *Ceratoscopelus maderensis* from the western Mediterranean Sea.

Table 2. – Calculation of the standard length (SL) from successive translucent bands in the otoliths of *Ceratoscopelus maderensis* from the western Mediterranean Sea (our study) and the Atlantic Ocean (Linkowski et al. 1993). The first translucent band (I) corresponds to the one closest to the centre of the otolith. The number of increments was estimated using the resulting von Bertalanffy model. SD, standard deviation.

Origin	Translucent zones	SL (mm)				N	Increments	Source
		Mean	SD	Range				
Western Mediterranean Sea	I	22.11	3.50	18-29	14	70	This study	
Western Mediterranean Sea	II	39.87	4.05	33-46	14	165	This study	
Western Mediterranean Sea	III	50.30	6.31	42-64	8	247	This study	
Atlantic Ocean	I	25.14	6.88	15.8-39.5	41	84	Linkowski et al. 1993	
Atlantic Ocean	II	35.27	6.25	23.9-46.1	27	130	Linkowski et al. 1993	
Atlantic Ocean	III	41.82	6.86	34.4-59.5	11	169	Linkowski et al. 1993	

beginning of the juvenile-adult region (Fig. 3E, F). Increments in this region showed no clear pattern and were sometimes even unnoticeable or incomplete and irregular. This greatly hindered counting of the number of increments in this area, so estimates for this region should be taken with caution. Additionally, it made it difficult to obtain accurate measures of the mean increment thickness in this region, which was 142.46  $\mu\text{m}$  ( $n=14$ ,  $\sigma=42.23$ ). Finally, the juvenile-adult zone (Fig. 3E, F) consisted of well-defined increments that showed

the typical radial structure and rhythmic growth patterns, as in other species. The mean increment thickness was 4.94  $\mu\text{m}$  ( $n=22$ ) and showed a decreasing trend towards the otolith edge (to  $<1\mu\text{m}$ ) (Fig. 3F). In addition to the three development regions mentioned above, from one to three translucent regions were also observed along the radial axis of the otolith of adult individuals (Fig. 4). The radius of each of these translucent regions relating to both the fish SL and the number of increments in the otolith is shown in Table 2.

## Growth

The age interpretation of the otoliths under the optical microscope with coincident readings was successful in 59 individuals between 3.5 mm and 64 mm SL (Table 1). Assuming that the frequency of increment formation in the otoliths of *C. maderensis* is daily, these individuals would be between 7 and 332 days old. The relationship between the number of increments and the SL, considering the full-size range of individuals, renders an asymptotic size of 70.59 mm and growth rates of 0.33 (for the smallest larvae) to 0.03 (for the largest adult specimen), with a growth rate decline through the development of 0.01mm (Fig. 5, Tables 3 and 4).

Table S1 shows the estimates of the parameters of the von Bertalanffy growth curves that we obtained when considering adult specimens only (SL>19mm), in order to assess growth differences between our specimens and those measured by Linkowski et al. (1993) (Fig. 6) in the northeastern Atlantic Ocean. The comparison of these two curves revealed that the best explanatory model (Model 1, Table 5) was the one in which the three parameters of the growth curve ( $L_{inf}$ ,  $k$  and  $t_0$ ) had been fixed. This indicates that growth differences between our specimens and those measured by Linkowski et al. (1993) in the northeastern Atlantic Ocean are not statistically significant. Models 1, 2, 3 and 4 (Table 5) can be considered equivalent as their  $\Delta AIC$  values were <2. For body size, von Bertalanffy models predicted a SL of 72.82 mm for the Mediterranean individuals and 77.94 mm for the Atlantic ones (Table S1). However, considering the standard error obtained, body size differences between the Mediterranean and Atlantic specimens should be considered with caution.

## DISCUSSION

This study provides for the first time the growth patterns of the lanternfish *C. maderensis* in the western Mediterranean Sea. Series of translucent bands alternating with more opaque ones were observed throughout the radius of the otolith across the ontogenetic development in agreement with observations by Linkowski et al. (1993) in Atlantic specimens. However, the age determination of *C. maderensis* had some uncertainties given the lack of clear increments during the metamorphic phase and the unknown period between hatching and the time at which the first increment is laid down. The complete reading of the number of increments in otoliths was particularly difficult in larger specimens (>40 mm SL) because the increments could not be read simultaneously across the entire otolith. In fact, only 28% of examined specimens could be successfully processed given these difficulties. While Linkowsky et al. (1993) applied the Ratke and Dean's (1982) regression model to predict the number of otolith increments in adults, in this study the preparation of the otoliths was optimized to enable the direct counting of increments from images obtained through the optical microscope. This allowed us to build a growth model using a single type of methodology to obtain all the data.

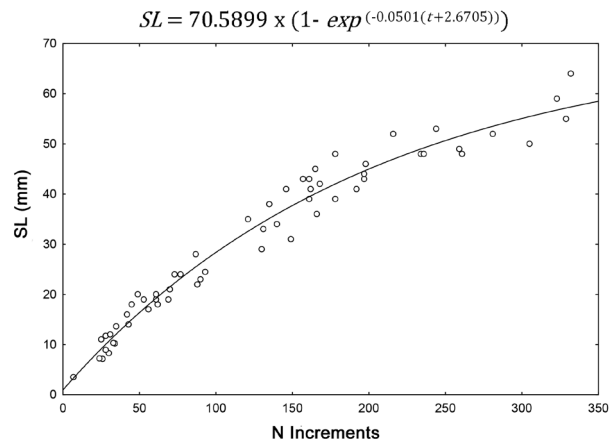


Fig. 5. – Relationship between the number of increments (N) and standard length (SL) of *Ceratoscopelus maderensis* from the western Mediterranean Sea. Data were fitted to a von Bertalanffy growth model (see Methods section).  $t$  corresponds to the time in days.

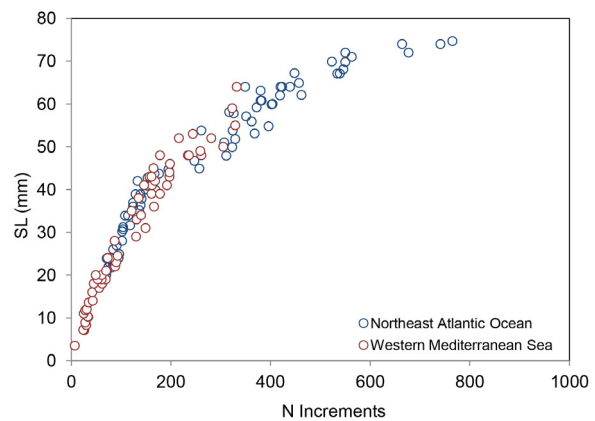


Fig. 6. – Comparison of the number of increments (N) and standard length (SL) of *Ceratoscopelus maderensis* from the western Mediterranean Sea (red circles, this study) and the North Atlantic Ocean (green circles, Linkowski et al. 1993).

Table 3. – Parameters of the von Bertalanffy growth equation for *Ceratoscopelus maderensis* using the full-size range from larvae to adults from the western Mediterranean Sea.

Parameter	CI (95%)			P
	Estimated	Lower limit	Upper limit	
$L_{\infty}$ (mm)	70.59	61.1	80.08	0.0000
$k$ (days <sup>-1</sup> )	0.01	0	0.01	0.0000
$t_0$ (days)	-2.67	-10.61	5.27	0.5032

*C. maderensis* larvae inhabit the surface layer up to 100 m depth during the day and at night (Olivar et al. 2014), but their feeding activity takes place only during daylight (Contreras et al. 2015). Thus, the photoperiod and the feeding activity of these early stages must play an important role in the deposition of calcium in the otoliths and the pattern of their increments (see Eckmann 2000, Morales-Nin 2000), which is in line with the reg-

Table 4. – Growth rates ( $g_t$ ) as a function of size for the von Bertalanffy growth model in individuals from the western Mediterranean Sea and the Atlantic Ocean. SL, standard length.

SL (mm)	Western Mediterranean Sea (this study)	Atlantic Ocean (Linkowski et al. 1993)
	$g_t$	$g_t$
5	0.33	
10	0.30	
15	0.28	
20	0.25	0.21
25	0.23	0.19
30	0.20	0.17
35	0.18	0.16
40	0.15	0.14
45	0.13	0.20
50	0.10	0.10
55	0.08	0.08
60	0.05	0.07
65	0.03	0.05
70		0.03
75		0.01
80		-0.01

ular deposition pattern that we observed in the larvae of our study. During the transformation phase, otoliths did not show such a definite deposition pattern, a finding that could probably be related to migration or feeding. This suggests that transformation individuals occur near the surface and at depths greater than 500 m, with non-defined daily feeding patterns (Contreras et al. 2015, Olivar et al. 2018). The absence of behavioural patterns during this developmental stage appears to be reflected in the otolith growth, in which the regular deposition pattern was drastically lost, as occurs in other myctophid species (e.g. Ozawa and Peñaflores 1990, Gartner et al. 1991b, Takagi et al. 2006). As in other species, the end of this phase in *C. maderensis* is determined by the recovery of regularity in the deposition of the increments (e.g. Linkowski et al. 1993).

The wide depth range associated with the habitat of *C. maderensis* encompasses major changes in seawater temperature, pressure, light and food availability. For instance, when the adult fishes migrate to near-surface layers (40-80m) at night, they are exposed to temperatures  $\sim 18^\circ\text{C}$ . In contrast, during the daytime, adults remain in mesopelagic layers (200-1000 m) where the water temperature is practically homogeneous at *ca.*  $13^\circ\text{C}$ . Considering this marked contrast in water temperature, it makes sense to assume that the specimens experience a period of adaptation during transformation, in which they do not perform the customary vertical migrations observed in adults. Therefore, during the transformation, *C. maderensis* might be experiencing gradual contact

Table 5. – Upper part: models considered to assess growth differences between our specimens of *Ceratoscopelus maderensis* from the western Mediterranean Sea (considering adult specimens only;  $SL > 19\text{mm}$ ) and those measured by Linkowski et al. (1993) in the northeastern Atlantic Ocean, deviance, Akaike information criterion (AIC) values and Akaike weights (Wi). Lower part: estimates and standard error of the parameters of the four equivalent models ( $\Delta\text{AIC} < 2$ ; Models 1, 2, 3 and 4).  $L_\infty$ , asymptotic size (mm);  $k$ , Brody growth coefficient ( $\text{days}^{-1}$ );  $t_0$ , age at which  $L$  is 0 (days).

Model	Fixed parameters	Deviance	AIC	$\Delta\text{AIC}$	Wi
1	$L_{inf}, K, t_0$	1177.060	601.828	0.000	0.335
2	$K, t_0$	1174.704	603.597	1.770	0.138
3	$L_{inf}, t_0$	1175.638	605.458	1.861	0.132
4	$L_{inf}, K$	1176.968	607.449	1.991	0.124
5	$L_{inf}$	1162.267	609.995	2.545	0.094
6	$K$	1165.683	612.878	2.883	0.079
7	$t_0$	1172.123	616.394	3.517	0.058
8		1159.323	620.648	4.254	0.040
Estimates for parameters $\pm$ SE		Model 1	Model 2	Model 3	Model 4
	$L_{inf1}$	$76.16 \pm 1.983$	$76.54 \pm 2.157$	$76.43 \pm 2.124$	$76.13 \pm 2.003$
	$L_{inf2}$		$77.16 \pm 2.872$		
	$K_1$	$0.004 \pm 0.000$	$0.004 \pm 0.000$	$0.004 \pm 0.000$	$0.004 \pm 0.000$
	$K_2$			$0.004 \pm 0.000$	
	$t_{01}$	$19.85 \pm 7.152$	$-20.83 \pm 7.432$	$-20.36 \pm 7.295$	$-19.93 \pm 7.282$
	$t_{02}$				$-19.2 \pm 7.870$



with the physicochemical conditions that the species will have to face when reaching the adult phase. Ultimately, adults exhibit diel vertical migrations to feed near the surface (Bernal et al. 2015) and remain without feeding activity in the mesopelagic zone during the light hours, as mentioned above (Hulley 1984, Olivar et al. 2012). Incremental deposition in the juvenile-adult phase involved well-defined increments, with a decreasing pattern in the increment thickness towards the otolith edge (to  $<1\mu\text{m}$ ). This decreasing pattern could also be reversed in some cases, as described in other myctophids (e.g. Greely et al. 1999, Tomás and Panfili 2000). Therefore, the increment thickness in otoliths during the juvenile-adult phase might vary among individuals, probably as a result of short-term variations in food availability.

The temperature range in the sea surface and the mesopelagic waters is higher in the Mediterranean Sea than in the northeastern Atlantic Ocean (Salat et al. 2002, Olivar et al. 2012). This is particularly interesting below the thermocline in the Mediterranean Sea, where the temperature does not drop below  $13^{\circ}\text{C}$ . In general, higher water temperature regimes speed up metabolic processes increasing growth in organisms. Furthermore, these temperature differences can be observed in the otolith microstructure (Degens et al. 1969). This may help to explain why growth rates declined more slowly from a certain body size in individuals from the western Mediterranean Sea. However, growth differences between individuals from the western Mediterranean Sea and those from the northeastern Atlantic Ocean were not statistically significant.

Many aspects of the biology and ecology of myctophids are still poorly understood and require further investigation for managing ecosystems, particularly under uncertain climate changes. This study provides further knowledge of the biology of this abundant myctophid, taking into account not only its entire life cycle but also a different geographical scenario. However, a more complete time coverage over the year and the validation of the daily periodicity of the increments are still necessary to achieve a more profound knowledge of the age and growth of the species.

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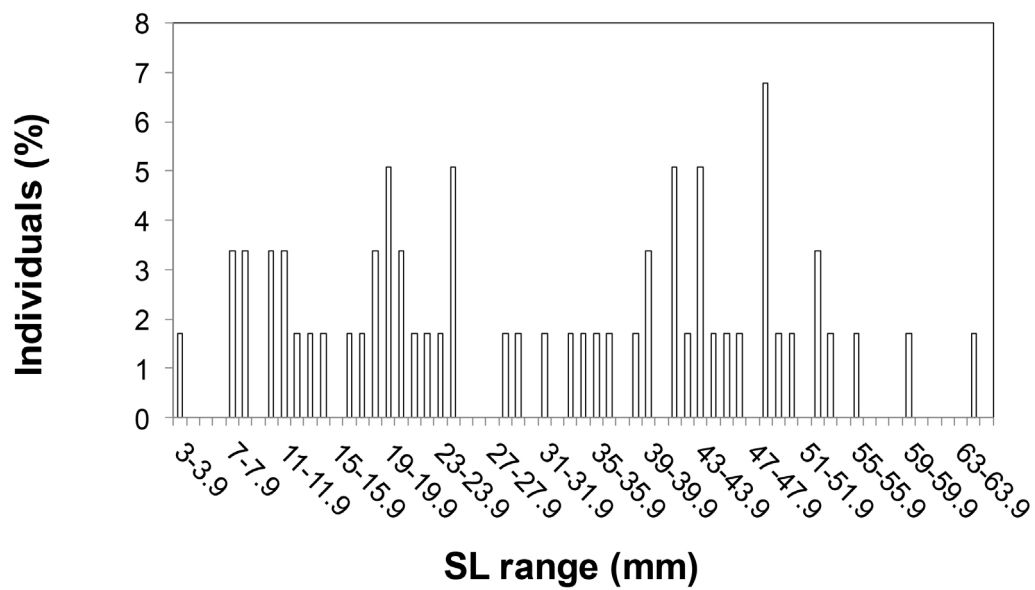
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## **Growth patterns of the lanternfish *Ceratoscopelus maderensis* in the western Mediterranean Sea**

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Supplementary material

Fig. S1. – Frequency distribution of the standard length (SL) of individuals considered in this study (N=59).

Table S1. – Estimates and standard error of the parameters of the von Bertalanffy curves obtained when comparing the growth of our adult specimens (SL>19mm) with those measured by Linkowski et al. (1993) in the northeast Atlantic Ocean.  $L_{\infty}$ : asymptotic size (mm); k: Brody's growth coefficient ( $\text{days}^{-1}$ );  $t_0$ : age at which L is 0 (days).

Parameter	Western Mediterranean Sea (this study)			Northeast Atlantic Ocean (Linkowski et al. 1993)		
	Estimate	Standard error	P	Estimate	standard error	P
$L_{\infty}$ (mm)	72.82	8.272	<0.001	77.94	2.611	<0.001
k ( $\text{days}^{-1}$ )	$4.59e^{-3}$	$1.19e^{-3}$	<0.001	$3.63e^{-3}$	$3.85e^{-4}$	<0.001
$t_0$ (days)	-8.37	13.50	>0.05	-28.59	10.10	<0.01

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