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Aspects of the early life history of the European conger eel (*Conger conger*) inferred from the otolith microstructure of metamorphic larvae

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Abstract The life cycle of the conger eel (*Conger conger* L.) is still fairly unknown, especially its larval leptocephalus phase. The morphology, biometry and meristic characteristics of 184 metamorphosing conger eel larvae collected from the Minho River, northern Portugal, between December 1998 and April 1999 were analysed. The total number of myomeres, the general body morphology and the pigmentation pattern of leptocephali are in agreement with the corresponding data found by other authors for this species. The sagitta microstructure of 90 specimens was viewed by scanning electron microscopy. The numbers of daily increments obtained in the otolith's countable zone were between 205 and 324. The final part of the countable zone is characterised by a sharp increase in width of the daily increments (transition zone), followed by a peripheral diffuse zone. In the diffuse zone no narrow circumscribed rings are visible, which prevents an accurate estimate of the duration of metamorphosis. The data indicates that the size variation of metamorphosing leptocephali is large, suggesting that their hatching time must be variable. Our data also show that the largest larvae, in later stages of metamorphosis, arrive first to the northern Portuguese coastal waters.

Introduction

The European conger eel (*Conger conger* L.) is a marine benthic fish, commonly found along sandy and rocky shores of the Atlantic coast of Europe from Norway to the Mediterranean, and extending into the western Black Sea (Bauchot and Saldanha 1986). In spite of its relatively wide distribution, its life cycle is poorly known, especially during its leptocephalus phase.

Schmidt (1931) caught small conger eel larvae in the Sargasso Sea, Mediterranean and Northeast Atlantic, suggesting a similar migratory behaviour to the European eel (*Anguilla anguilla* L.), i.e. spawning in the Sargasso Sea, following a larval transoceanic migration to the European coast. However, the larvae caught in the Sargasso Sea and wrongly identified as *C. conger*, were indeed *C. triporiceps* (McCleave and Miller 1994). Nowadays the larvae of both species are distinguished by the catch location, being separated by a line that goes through the Canary Islands and the western zone of the Azores Islands, in a NW direction. The European conger eel leptocephali are restricted to the central and eastern zones of the Atlantic Ocean (Strehlow et al. 1998).

Different spawning places have been suggested for *C. conger*. Lythgoe and Lythgoe (1971), Bagenal and Kenney (1973) and Wheeler (1985) found that conger eel spawn only once, at great depths (3000–4000 m), during the summer, in the Northeast Atlantic between Gibraltar and the Azores. There are also spawning areas in the Mediterranean (Wheeler 1985). However, until now, the only spawning area well known for this species is in the central-east basin of the Mediterranean (Cau and Manconi 1983).

It has been suggested that the leptocephali has a long larval life (Bauchot and Saldanha 1986), taking about 1 or 2 years to drift inshore and to reach the juvenile elver form (Lythgoe and Lythgoe 1971; Wheeler 1985; Strehlow 1992). Recent studies, based on morphometric and sagitta analysis of premetamorphic larvae, showed that spawning occurs in the Mediterranean Sea between July and September. After a short growth period, the larvae (>30 mm) start migration around November, in a NW direction toward southern Portugal and Spain, extending throughout the eastern and central zones of

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the Atlantic. The conger eel has a second growth period, lasting until the beginning of the next summer (normally reaching 130–150 mm, with a maximum of 165 mm length), after which they start migration in the direction of the coastal waters of the continental slope, with a possible return to the Mediterranean. It is supposed that this coastal migration induces metamorphosis (Strehlow et al. 1998). However, the location and timing of metamorphosis is unknown.

The microstructure of the otoliths provides us with valuable information about the early life cycle of fishes. Strehlow et al. (1998) obtained a mean value of 280 days by analysis of the sagittae of premetamorphic leptocephali (between 80 and 120 mm long), using the clear daily increments from the nucleus to the otolith margin (Antunes 1994; Antunes and Tesch 1997). However, until now the sagitta microstructure of metamorphic larvae has not been described.

The present paper examines the relationships between the biometry/meristic data and the sagitta microstructural growth in *C. conger* leptocephali during metamorphosis, in an attempt to elucidate some aspects of its larval life history.

Materials and methods

The conger eel larvae (*Conger conger* L.) were obtained as by-catch from the glass eel fishery at the mouth of the Minho River in northern Portugal (Fig. 1), monthly between December 1998 and April 1999. Fishing, using a stow net, took place in the estuarine area during the night, in the period of the new moon during the flood-tide current (Antunes 1994).

After collection, the leptocephali ($n = 184$) were preserved in commercial ethanol (95%) and the general body morphology, pigmentation, morphometric and meristic characters (number of myomeres) were analysed according to the methodology described by Smith (1989). Because the preservation method induces shrinkage of the body (approximately 7.5%), the length measurements were corrected.

Both sagittae were removed from 90 specimens (randomly selected), cleaned, mounted on cylindrical stubs and polished with 2400 silicon carbide abrasive paper and aluminium paste until the core was revealed. After that, they were etched for 8 s with a 0.5% solution of HCl, sputter-coated with gold under vacuum and viewed with scanning electron microscope (SEM; Jeol JSM 630-1F) at 15 kV.

Following SEM analysis, core diameter (CD), maximum otolith diameter (D), maximum otolith radius (R), maximum width of the countable incremental zone (CZW) and maximum width of the diffuse zone (DZW) were measured from the SEM photographs (Fig. 2).

We considered the growth increment in the larval otolith of conger to be daily, although daily deposition has not been validated in this species. We base this assumption on the results of several related species, e.g. *Conger myriaster* (Mochioka et al. 1989), *Anguilla japonica* (Umezawa et al. 1989; Umezawa and Tsukamoto 1991) and *A. rostrata* (Martin 1995), which have been shown to have daily depositions.

In the countable zone (CZ), the total number and width of daily increments were registered. The average of every ten increment widths from the first feeding check to the edge of the CZ was used to measure the otolith growth rate. The maximum axis of the CZ was regarded as the otolith radius, along which increment widths were measured.

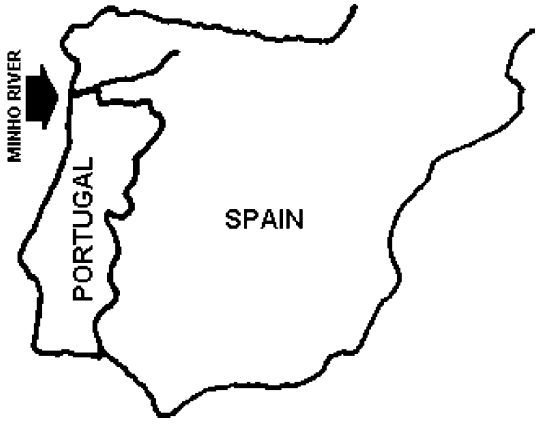

Fig. 1 *Conger conger*. Sampling location of the metamorphosing conger eel leptocephali

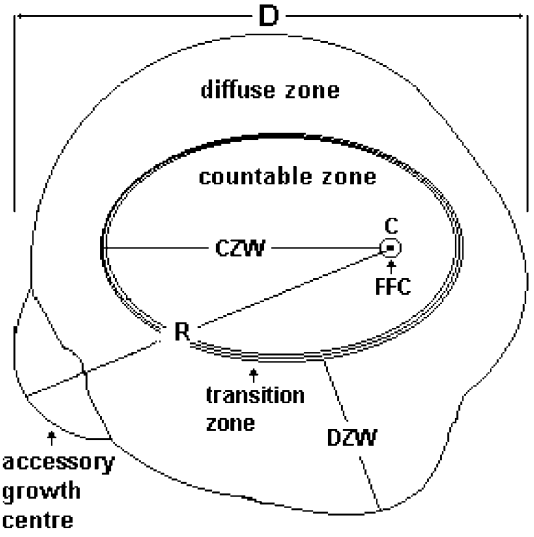

Fig. 2 *Conger conger*. Schematic diagram of the otolithometric measurements in the sagitta (*D* maximum diameter; *R* maximum radius; *CZW* maximum width of the countable zone; *DZW* maximum width of the diffuse zone; *C* core; *FFC* first feeding check)

The percentage of the area occupied by the accessory growth centres (%AGCA) of the total otolith surface was also calculated.

Statistica 5.0 was used to perform all statistical analyses. After testing for normality and homogeneity of variances, a one-way analysis of variance (ANOVA) was used to examine the differences in the relationships between morphometric and otolithometric measures among sampling periods. ANOVA was followed by a Tukey HSD-test for unequal *n* (Spjotvoll/Stoline test). Data are presented as means ± standard deviations (SD).

Results

Morphometric and meristic data

The conger eel (*Conger conger*) larvae were identified mainly by counting myomeres. Unfortunately, because some specimens were damaged from the preservation

Table 1 *Conger conger*. Morphometric and meristic counts of metamorphic conger eel larvae (*SD* standard deviation; *n* sample size; *TNM* total number of myomeres; *PDM* predorsal myomeres; *PAM* preanal myomeres; *PDL* predorsal length; *TL* total length; *PAL* preanal length; *BD* body depth; *HL* head length)

Parameter	Range	Mean ± SD	*n*
TNM	154–163		89
PDM	25–51		82
PDM/TNM	–	0.23 ± 0.04	
PAM	47–65		81
PAM/TNM	–	0.36 ± 0.03	
PDL (mm)	–	37.35 ± 5.97	146
PDL/TL	–	0.29 + 0.04	
PAL (mm)	–	55.33 ± 5.97	153
PAL/TL	–	0.43 ± 0.04	
BD (mm)	–	7.48 ± 1.35	142
HL (mm)	–	9.50 ± 0.55	184

Table 2 *Conger conger*. Body length (mm) of the conger eel leptocephali collected from December 1998 to April 1999 (*SD* standard deviation; *n* sample size; the values marked with the same *superscripted letters* are not significantly different, $P > 0.05$)

Month	Range	Mean ± SD	*n*
Dec 1998	122–149	134.5 ± 6.6^{a}	23
Jan 1999	118–153	$131.6 \pm 8.8^{a,b}$	19
Feb 1999	104–148	$128.5 \pm 8.0^{b,c}$	75
Mar 1999	115–135	$123.9 \pm 5.0^{c,d}$	15
Apr 1999	103–130	119.4 ± 5.8^{d}	52

method and/or the catch procedure, only the myomeres of a part of the collected specimens were counted. However, as the general body morphology, pigmentation and length were similar, the damaged specimens were clearly the same species. The meristic and morphometric values obtained are in Table 1.

The mean body length obtained for each month indicates a gradual decrease in larval size during the study period (Table 2; Fig. 3), although between neighbouring months the means are not significantly different ($P > 0.05$). The largest larvae (153 mm) and the smallest (103 mm) were caught, respectively, in January and April 1999.

The ratio of the number of preanal myomeres to total myomeres (PAM/TNM) and the ratio of the preanal length to total length (PAL/TL) were not significantly related to the total length (TL) ($r^2 = 0.0056$, $n = 81$, $P > 0.05$ and $r^2 = 0.0003$, $n = 153$, $P > 0.05$, respectively).

The PAL/TL index was positively and significantly correlated with the PAM/TNM ratio ($r^2 = 0.58$, $n = 81$, $P < 0.05$) (Fig. 4).

General body morphology and pigmentation

There is little information about the body morphology changes and the development of the pigmentation pattern in conger eel larvae, and the existent data is restricted to that of D'Ancona's (1931) study.

The metamorphic larvae had the body shape associated with the general and identifying features of this species (Fig. 5). They had a laterally compressed, transparent body, with W-shaped myomeres and a simple tubular gut along the ventral margin of the body. The head was of medium size and had rounded eyes. Long dorsal and anal fins were confluent with a rounded caudal fin. Larvae had small pectoral fins, and pelvic fins were absent.

Concerning the pigmentation, they possessed large dots along the lateral line, which became sparser or disappeared anteriorly. We also observed some melanophores at the bases of the caudal and anal fin rays, and limited to posterior region of the dorsal fin. They also exhibited a double ventral pigmentation on the sides of the intestine, sometimes extending slightly beyond the anus. In some specimens several spots were visible around the anus and at the mandibular angle. The crescent pigment patch under the eye (sometimes called irido-coroid process), characteristic of the premetamorphic stage, was absent.

Concerning the dentition, they had lost their larval teeth, or, as in several cases, the presence of vestigial teeth were found in both maxillas, yet with no signs of calcification. One specimen captured in February, in a more advanced stage, exhibited dorso-lateral spots in the tail zone and had well developed calcified teeth.

Sagitta microstructure

The microstructure of 90 metamorphic larval sagittae were studied by SEM. A representative scanning electron micrograph is show in Fig. 6c. From the nucleus to the periphery, the sagittae showed permanent structures like the central core (C), the increment countable zone (CZ), the diffuse zone (DZ) and the existence of one or more accessory growth centres (AGC) (Fig. 6a, c).

The core, located at the posterior side of the countable zone (usually with an amorphous primordium in the centre), was surrounded by a thick ring, presumed to be the hatch check (HC). The core had a mean diameter of 22 ± 3 μm, and no significant differences were observed between the sagittae of conger larvae captured in different months ($P > 0.05$).

During the yolk-sac stage, i.e. between the HC (when visible) and the first feeding check (FFC), no distinct daily growth was discernible. Beyond the FFC, clear daily growth increments marked the beginning of the countable zone. This check was postulated to be the FFC, since its morphology was similar to other anguilliform fishes (Tabeta et al. 1987; Lecomte-Finiger and Yahyaoui 1989; Wang and Tzeng 1998, 2000).

In the countable zone, the otolith increment width showed a characteristic curve along the sagitta radius (Fig. 7). From hatching to approximately 30 days afterwards, there was a pronounced increase of the daily ring width (until a maximum of 0.80 μm). Then, the increments became progressively narrow, until they

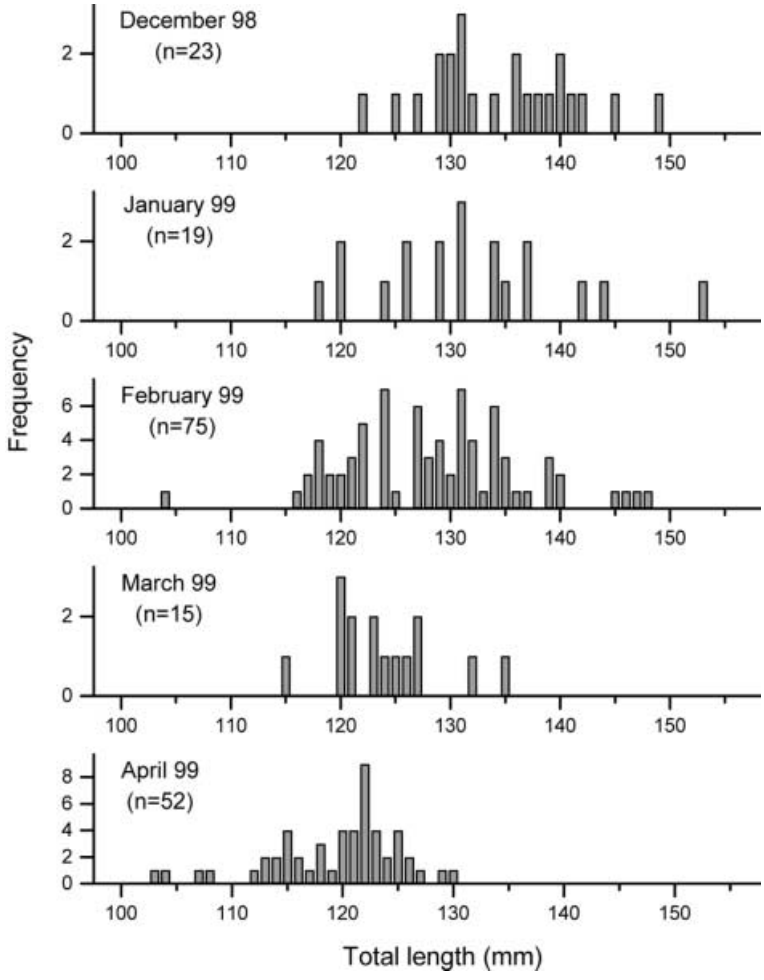

Fig. 3 *Conger conger*. Length-frequency distribution of metamorphosing conger eel leptocephali (collected from the mouth of the Minho River) between December 1998 and April 1999

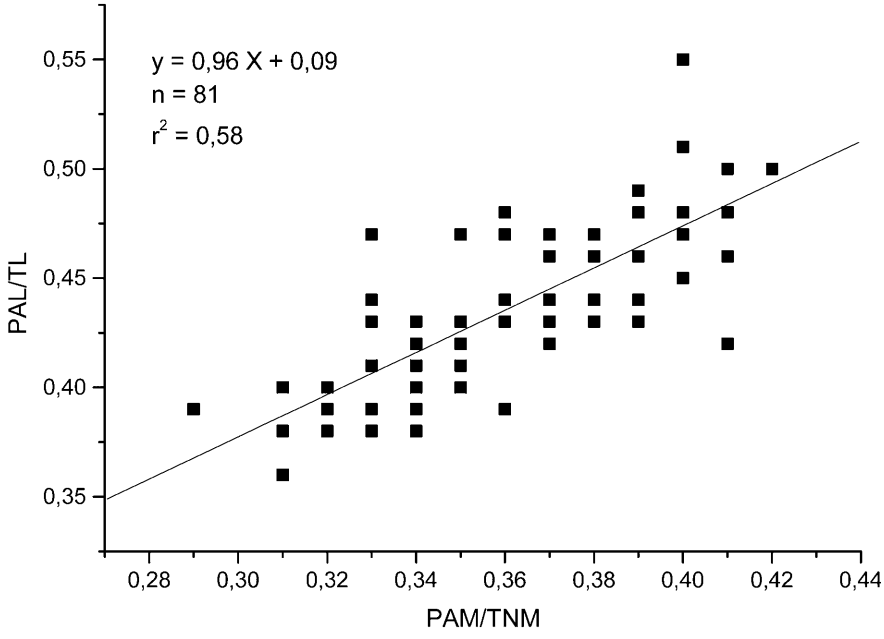

Fig. 4 *Conger conger*. Scatter diagram of PAL/TL index versus PAM/TNM ratio (the regression line represents a least squares fit of the linear equation). Abbreviations, see Table 1

reached a constant minimum value (0.35–0.45 μm) at about 160–180 days. This period of narrow rings can be quite extensive (between 170 and 280 days) depending of the specimen. After that, rings abruptly widened (to a maximum of 0.65–0.90 μm) and became less clear (transition zone), until they disappeared (Fig. 6b), which

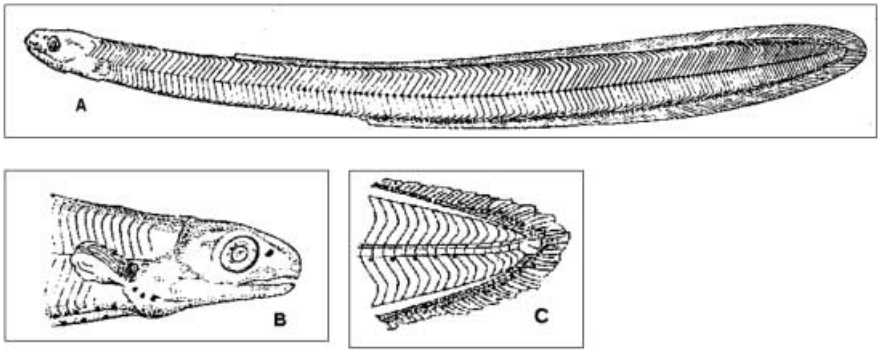

Fig. 5a–c *Conger conger*. Metamorphic leptocephalus (modified from D'Ancona 1931): **a** whole view, **b** head, **c** tail

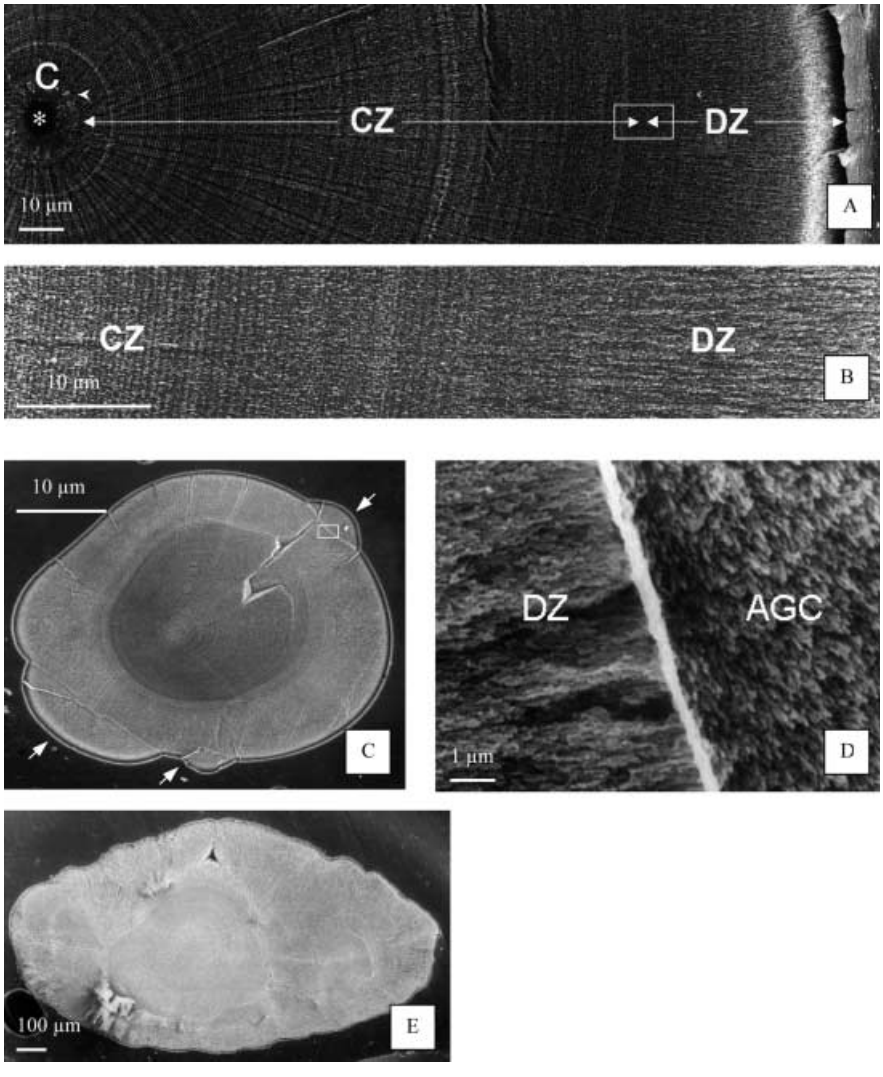

Fig. 6a–e *Conger conger*. SEM micrographs showing the sagitta microstructure pattern of metamorphic conger eel leptocephali. **a** Sequence of the different otolith zones (*C* core; *CZ* countable zone; *DZ* diffuse zone; *asterisk* primordium; *arrowhead* first feeding check). **b** Detail of the transition zone indicated by a *box* in **a**. **c** Whole view of the otolith, with accessory growth centres indicated by *arrows*. **d** Spatial arrangement of the aragonite crystals between the sagittal plane of the diffuse zone (*DZ*) and the accessory growth centre (*AGC*) (enlargement of the region indicated by a *box* in **c**). **e** Whole view of the otolith of an elver conger eel (which had successfully completed metamorphosis in an aquarium)

corresponds to the beginning of the diffuse zone, at about 205–324 days.

The mean number of increments of the total countable zone for each month of capture was not significantly different ($P > 0.05$). We obtained an overall mean of 260 ± 28 days. The exclusion of the transition zone from the total countable zone in this analysis also gave non-significant results. The overall mean was 228 ± 30 days.

As the diffuse zone (DZ) grew, one or more accessory growth centres (AGC) were formed (Fig. 6c). These structures appeared in the majority of the sagittae analysed (97%). With a different spatial arrangement of the aragonite crystals compared to the diffuse zone (Fig. 6d), the AGC are responsible for the secondary growth layers which will generate the elliptical otolith shape in adults (Fig. 6e).

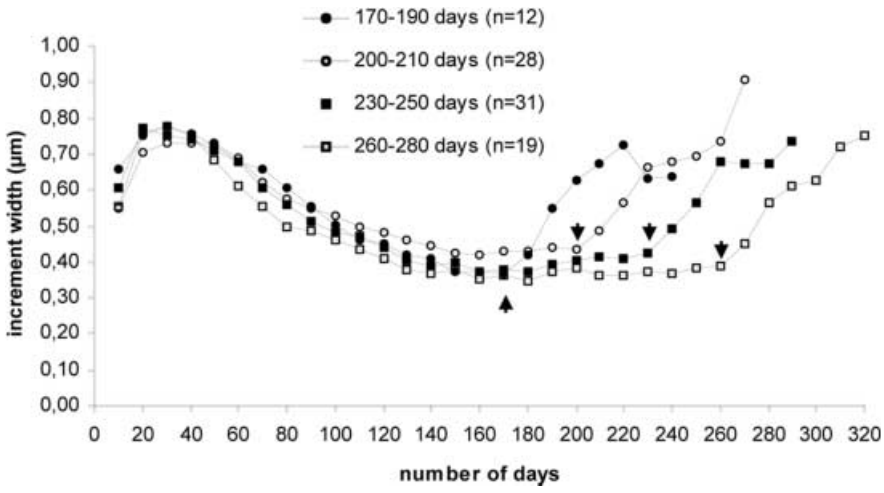

Fig. 7 *Conger conger*. Variations in mean increment width throughout the countable zone of sagittae. *Arrows* represent the points where the daily rings abruptly increase, i.e. the beginning of the transition zone (the specimens have been grouped according to the time when this happened)

Otolithometric measures

There is a very good relationship between the diameter (D) and the radius (R) of the sagitta ($r^2 = 0.88$, $n = 90$, $P < 0.05$), so either of these otolithometric measures are helpful in describing the otolith growth rate.

The sagitta size (D and R) is not significantly related to the total body length ($r^2 = 0.040$, $n = 90$, $P > 0.05$ and $r^2 = 0.033$, $n = 90$, $P > 0.05$, respectively), but is significantly correlated with the developmental stage. The diameter and the radius of the sagittae exhibited a moderate negative correlation with the PAL/TL index ($r^2 = 0.42$, $n = 81$, $P < 0.05$ and $r^2 = 0.32$, $n = 81$, $P < 0.05$, respectively). Also the DZW and the %AGCA are negatively correlated with the PAL/TL index ($r^2 = 0.27$, $n = 81$, $P < 0.05$ and $r^2 = 0.36$, $n = 76$, $P < 0.05$, respectively).

The maximum otolith diameter and radius ranged from 328 to 589 µm and from 188 to 326 µm, respectively. The width of the countable zone (CZW) was approximately constant with a mean value of 148 µm ($\pm$ 14 SD) and no significant differences between months were observed ($P > 0.05$). The width of the diffuse zone (DZW) presented a minimum value of 59 µm and a maximum of 141 µm. The otolith area occupied by the accessory growth centres (%AGCA) ranged between 0.3% and 35.0%.

So, through the study period, the majority of the otolith length differences were apparently due to the contribution of the DZW and %AGCA. Indeed, there is good correlation between sagitta length expressed as a radius ($r^2 = 0.59$, $n = 87$, $P < 0.05$) or diameter ($r^2 = 0.54$, $n = 87$, $P < 0.05$) and the %AGCA of the otolith surface. In the same manner the otolith diameter (D) and radius (R) are positively correlated with the DZW ($r^2 = 0.30$, $n = 90$, $P < 0.05$ and $r^2 = 0.49$, $n = 90$, $P < 0.05$, respectively).

In fact the R, DZW and %AGCA in the first 2 months (December/January) were significantly higher that those in the last 3 months ($P < 0.05$). The inverse situation was observed for the PAL/TL index (Fig. 8).

Discussion and conclusions

Occasionally, metamorphic conger eel larvae are caught in the Portuguese glass eel fishery (from November to April), when conducted in the mouth of the Minho River. Indeed, the entry of metamorphic conger eel larvae into the northern coastal waters of Portugal has been observed from late October until June (Correia, unpublished data). For *Conger myriaster* leptocephali this coastal water presence has been recorded between November and July, during the last developmental and metamorphic stage (Tanaka et al. 1987).

The total number of myomeres (TNM) of *Conger conger* leptocephali collected varied between 154 and 163, which is in agreement with the corresponding data found by other authors (Schmidt 1931; Strehlow et al. 1998). Nevertheless, the range of values reported can be slightly different (D'Ancona 1931; Castle 1970), probably due to errors in counting (for instance, it is extremely difficult to count the most posterior myomeres near the end of the tail), explaining, in part, some of the intraspecific variation found in the literature.

The ranges of the predorsal (PDM) and preanal (PAM) myomeres of the metamorphic larvae, 25–51 and 47–65, respectively, were, as expected, smaller than the counts obtained by Strehlow et al. (1998) for the premetamorphic stage. Indeed, during the transition to metamorphosis the anus and also the origin of the dorsal fin begin to move to a distinctly more anterior position in Congridae leptocephali (Otake et al. 1997; Strehlow et al. 1998). Thus, the PAM/TNM obtained for this stage (0.36) is less than half the reported value (0.77) for premetamorphic larvae (Strehlow 1992).

The PAM/TNM ratio has been successfully used as a criterion to describe the developmental stage of conger eel leptocephali, as stage is difficult to determine on the basis of other morphometric characteristics (Tanaka et al. 1987). However, since the PAL/TL index is correlated with the PAM/TNM ratio, it was decided to preferentially use this index as a developmental stage

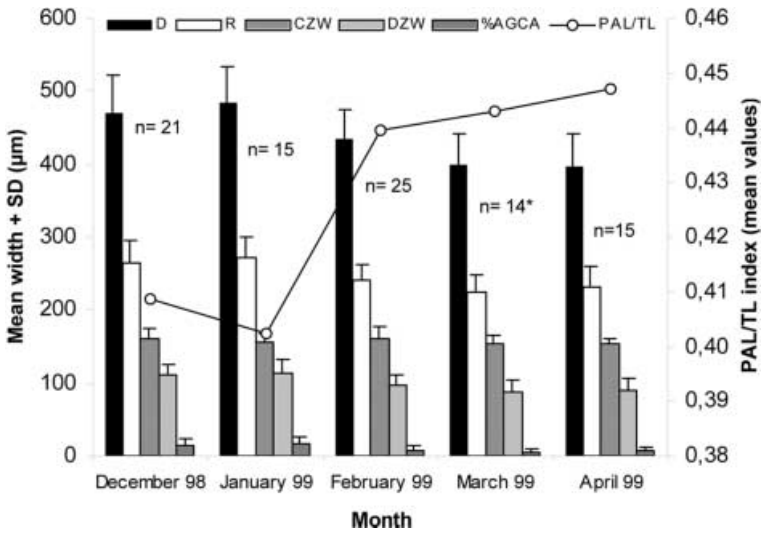

Fig. 8 *Conger conger*. Monthly variation of the otolithometric data (*, for AGC only 12 specimens presented this structure) and the PAL/TL index of the larvae captured during the study period. For the R, DZW and %AGCA, the values for the first 2 months are significantly higher than the values for other months ($P < 0.05$). The inverse situation is observed for the PAL/TL index (*D* maximum diameter; *R* maximum radius; *CZW* maximum width of the countable zone; *DZW* maximum width of the diffuse zone; *%AGCA* percent area occupied by accessory growth centres; *PAL/TL* preanal length/total length)

indicator, as it is easier to measure, especially in poorly preserved specimens. Indeed the PAL/TL index was successfully used in classifying three different metamorphosing stages in *C. myriaster* (Yamano et al. 1991).

The lack of a relationship between the PAM/TNM ratio (or the PAL/TL index) and the total length indicates that the size variation in the metamorphosing leptocephali (and possibly the full-grown leptocephali) is large, suggesting that they belong to different hatching populations. Data also show (TL and PAL/TL index) that early migrating leptocephali are large in size and of advanced metamorphic stage.

There is no relationship between body size and otolith size, although an inverse correlation between them would be expected for a population in which somatic growth is correlated with otolithic growth. However, the sagitta size is significantly related with the PAL/TL index, a useful indicator of developmental stage.

The monthly variation in otolith size is supported by the PAL/TL index. The largest larvae in late stages of metamorphosis that were caught during the first 2 months (December 1998 and January 1999) have the largest R, DZW and %AGCA, suggesting that they are older in spite of the total age remaining unknown. Furthermore, if early migrating leptocephali are older than late migrating ones, their hatching times must be quite different, as previously suggested by the variation in body size.

All morphological features and pigmentation patterns of the collected leptocephali are in agreement with the descriptions of D'Ancona (1931). Our specimens appear to belong to a single developmental stage. In the future, it would be useful to establish a criterion, based on pigmentation, for differentiation of the developmental stages occurring during metamorphosis.

The otolith morphology of the European conger eel is similar to that observed in the Japanese conger eel (Lee and Byun 1996); however, the opaque zone is replaced by a diffuse zone in this species.

In the countable zone, the width of the increments presented the same pattern when compared with the sagittae of premetamorphic stages (Antunes 1994), with the exception of the relatively wide increments at the periphery of the countable incremental zone (transition zone). These wide rings appears to be a metamorphosis check, since this particular increment pattern is associated with a drastic change in the otolith strontium:calcium ratios in *C. myriaster* (Mochioka et al. 1989; Lee and Byun 1996; Otake et al. 1997), *Anguilla japonica* (Otake et al. 1994; Arai et al. 1997), *A. rostrata* (Wang and Tzeng 1998, 2000) and *A. anguilla* (Wang and Tzeng 2000).

The different thicknesses of the increments along the sagitta radius are probably associated with both endogenous and exogenous factors. The seasonal variations in seawater temperature as well as photoperiod should be two of the most important environmental factors. In fact, previous studies on growth of herring larvae have shown the major influence of the environment (temperature, photoperiod and food abundance) on the deposition of increments in otoliths (Lough et al. 1982; Pavlov et al. 2000).

If we consider that the countable zone without the transition zone of the sagittae corresponds to the premetamorphic larval stage, as has been described in other anguilliform species, our results suggest that the larvae of the European conger eel take about 6–9 months from hatching to the onset of metamorphosis. These estimates shorten the hypothesised 15 months (1 1/4 years) proposed by Strehlow et al. (1998). Furthermore, since the mean increment number in the otolith countable zone is almost constant among the recruitment seasons, it suggests that early migrating individuals metamorphose at the same age as late migrating ones.

However, the transition zone and also a part of the diffuse zone can be present in the late premetamorphic larvae, representing additional time for this larval phase. For instance, Otake et al. (1997) considered that the onset of metamorphosis for *C. myriaster* occurs early, approximately in the fourth month.

At this point, assuming that: (1) the peak of the hatching season occurs in summer (Schmidt 1931; Strehlow et al. 1998), (2) the leptocephalus stage lasts about 6–9 months and (3) the latest larvae captured (in June 1999) were not yet at the end of the metamorphic process, we can estimate that the duration of metamorphosis is at least 1 year, and probably occurs on the continental shelf and in coastal waters. This estimate gives a total larval phase of about 2 years before the juvenile elver stage is reached in the European conger eel.

Asano et al. (1978) reported that, in the laboratory, the metamorphosis of *C. myriaster* leptocephali takes about 22 days, at temperatures of 18–22°C. Lee and Byun (1996), based on sagitta analysis of specimens collected from the wild, estimated the duration of metamorphosis to be 53–75 days (10–16°C). However, the temperature effect is not the only parameter to be taken into account. The difficulty and ambiguity in identifying the beginning and completion of metamorphosis of reared leptocephali may also result in inaccurate estimation of the duration of the metamorphic stage (Otake et al. 1997). It is also plausible that captive specimens may accelerate metamorphosis (Butler et al. 1996). In fact, metamorphic conger eels captured in the Minho River in June 1999 and 2000 and reared in aquaria at two different temperatures (26°C and 16°C, respectively) completed metamorphosis at a final length of 70–80 mm, in about 1 1/2 months (Correia, unpublished data).

Whether metamorphosis is triggered by some environmental stimulus or occurs spontaneously at a certain age or size is unknown (Smith 1989). For some species we know that metamorphosis is initiated when pelagic leptocephali migrate to inshore waters, suggesting that the shallow, near-shore environment is somehow involved in the triggering mechanism (Pfeiler et al. 1990). However, metamorphosis in some species takes place in the open ocean, indicating that factors other than proximity to shore are involved (Pfeiler 1999).

In contrast to the sagitta rings of premetamorphic conger eel larvae, which are easily countable (Antunes 1994), the existence of a diffuse zone and several accessory growth centres in the metamorphic specimens hinders an accurate estimate of the duration of metamorphosis.

Although larvae did not feed and body length diminished during metamorphosis, otoliths continued to grow, since a diffuse zone was formed outside the countable zone, which was associated with a clear change in the otolith growth direction.

This diffuse zone, non-existent in the premetamorphic larvae up to 133 mm of total length (Strehlow et al. 1998), has also been described in European eel larvae; however, in this species, the diffuse zone is already present before the onset of metamorphosis (Antunes and Tesch 1997). Since the growth rate of otoliths often changes during transitive periods of fishes, in glass eel otoliths, this diffuse zone has been suggested to mark a period of very slow growth and to be made up of many daily growth increments that are so narrow they cannot be distinguished (Antunes and Tesch 1997). Despite the favourable external factors, namely the high temperatures of the end of summer and early autumn, the diffuse zone could represent a decrease in increment width and may be due to the nearly-completed growth of the larvae before metamorphosis starts. According to a new theory, this zone is formed during a period when the vertical rhythmic movements (i.e. diurnal vertical migration) of the leptocephali cease (Williamson et al. 1999).

The fact that the Japanese conger eel *C. myriaster* has a continuous series of daily growth rings and no "diffuse zone" (Tanaka et al. 1987; Mochioka et al. 1989; Lee and Byun 1996), as do the Japanese eel *A. japonica* (Arai et al. 1997) and the American eel *A. rostrata* (Wang and Tzeng 1998), suggests a different manner of larval development from European eels (*Conger*, *Anguilla*). Although American and Japanese eels occur in the Atlantic and Pacific Oceans, respectively, their spawning grounds and larval migratory routes are symmetrical, and larvae drift to estuaries by similar currents (Wang and Tzeng 2000).

The high incidence of AGCs indicates that they are universal structures in metamorphic conger eel sagittae, appearing in a late stage of metamorphosis. The same morphological features have been observed in *C. myriaster* (Lee and Byun 1996). The cause behind the formation of these structures is not yet completely understood. However, in other species their formation is often associated with life-history transitions such as metamorphosis (Secor et al. 1995). They represent an extra period of growth, which is difficult to estimate, and are probably produced during a significant habitat change, for example, the entry into less saline coastal waters.

Otolith growth appears to progress in three stages: stage 1 corresponds to the countable zone, stage 2 to the diffuse zone and stage 3 corresponds to the formation of the accessory growth centres. The transition between these zones is probably triggered by internal signals, but the rate of deposition of aragonite in the sagitta's distinctive parts could be modulated by external factors.

This study indicates that the growth pattern of otoliths of conger eel leptocephali may be similar between eel species, although some differences exist between European and Japanese/American species, probably due to differences in their life cycles, namely in the distance of their larval migratory routes.

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