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RESEARCH ARTICLE

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Early life history of the American conger eel (*Conger oceanicus*) as revealed by otolith microstructure and microchemistry of metamorphosing leptocephali

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Abstract The early life history of the American conger eel, *Conger oceanicus*, was studied using otolith microstructure and chemical composition in metamorphosing leptocephali collected from New Jersey estuarine waters. The age of leptocephali was estimated by counting daily growth increments. Age of early metamorphosing leptocephali at recruitment to the estuary ranged from 155 to 183 days, indicating that migration of conger eel leptocephali from their oceanic spawning ground to the estuary requires 5–6 months. Back-calculated hatching dates suggest that the spawning season lasted 3 months, from late October to mid-December. However, in the late metamorphic leptocephali, the presence of an unclear peripheral zone in the otolith prevents the accurate estimation of the larval stage duration. The calcium content was almost constant throughout the otoliths. Both strontium and Sr:Ca ratios increased with age, but dramatically decreased at age 70–120 days. The otolith increment width also showed a marked increase at the same ages, indicating the onset of metamorphosis. A negative correlation between age at metamorphosis and otolith growth rate indicates that faster growing leptocephali arrive at the estuary earlier than slower growing ones. A close relationship was also found between age at recruitment and age at metamorphosis, suggesting that individuals that metamorphosed earlier were recruited to the estuary at a younger age. This larval migration pattern appears to be similar among anguilliform fishes.

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Introduction

The American conger eel, *Conger oceanicus* (Mitchill, 1818), is a bottom-dwelling fish frequently found along the east coast of North America, from the Gulf of Maine to northern Florida, and extends into the north-eastern Gulf of Mexico (Smith 1989; Collette and Klein-MacPhee 2002). This species occurs from shallow coastal waters, occasionally entering estuaries and bays, to the edge of the continental shelf at depths up 577 m, and is usually associated with structured habitats such as piers, wrecks, jetties, reefs, or burrows shared with tilefish, *Lopholatilus chamaeleonticeps* (Able and Fahay 1998; Collette and Klein-MacPhee 2002).

There is little information available on the early life history of *C. oceanicus*. Schmidt (1931) found small leptocephali in the Sargasso Sea and concluded that this area was the breeding place of this species, but he provided no details on the number and distribution of these larvae. No adult conger eels have been observed spawning in the Sargasso Sea, and eggs have not been reported (Able and Fahay 1998). Early stage leptocephali collected in the Sargasso Sea, east and northeast of the Bahamas Islands (Castonguay and McCleave 1987; McCleave 1993; McCleave and Miller 1994; Miller 1995), and larger leptocephali (up to 85 mm) collected from the Florida Current and Gulf Stream, south of Cape Hatteras, North Carolina (McCleave and Miller 1994), showed that Schmidt (1931) was clearly correct in stating that conger eel spawns in the western North Atlantic.

Bigelow and Schroeder (1953) suggested that *C. oceanicus* matures during summer and then moves offshore, but they gave no evidence for this pattern. The absence of ripe and spent female conger eels in the

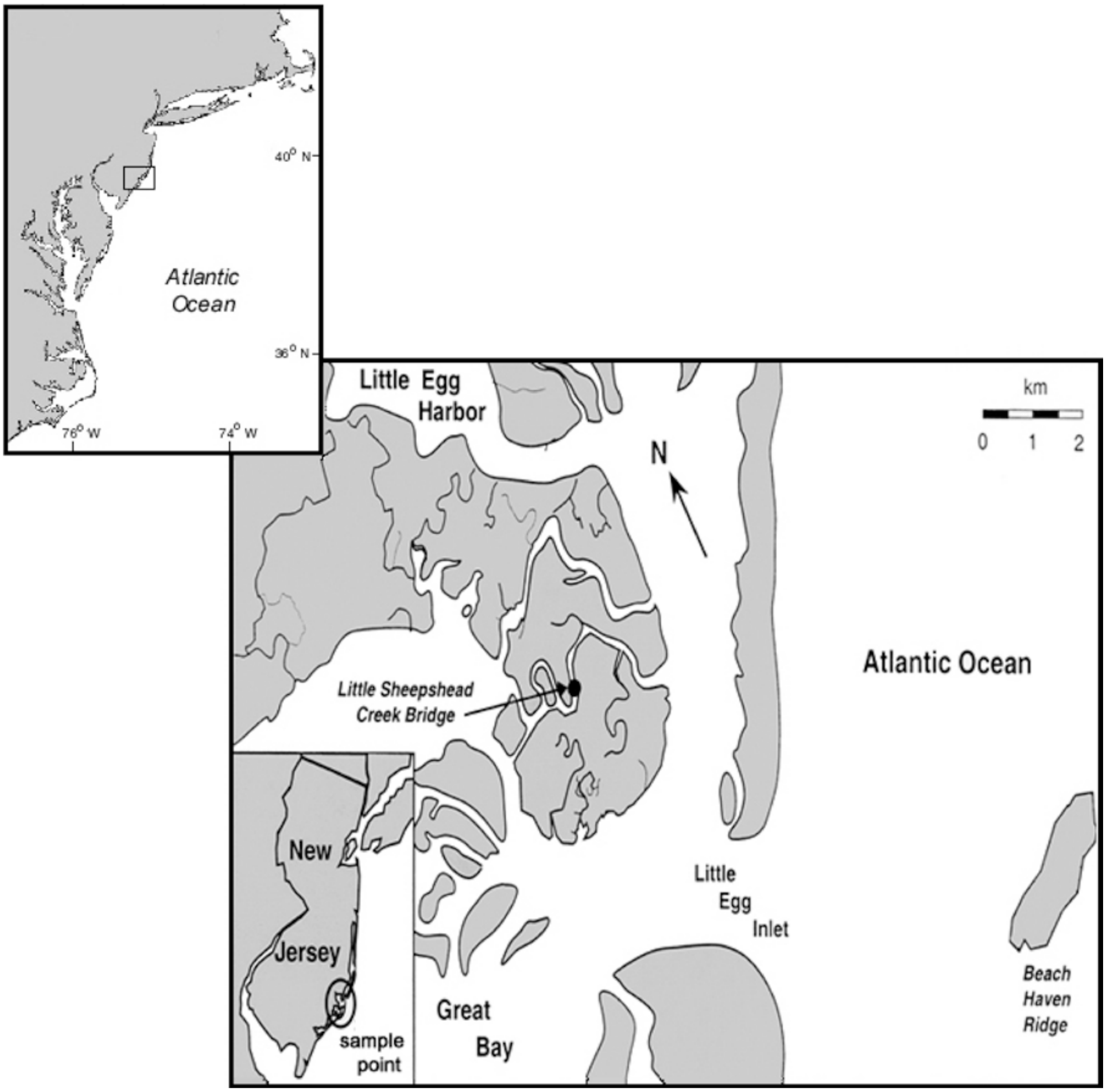

Fig. 1 *Conger oceanicus*. Catch location of the metamorphosing leptocephali in New Jersey, USA

inshore waters of the Mid-Atlantic Bight and early signs of maturation in females in late spring and early summer (Hood et al. 1988; Eklund and Targett 1990) suggest that they leave the region to spawn off-shore, probably in the Sargasso Sea (Able and Fahay 1998). The spawning season is apparently long, perhaps from late summer through the winter (McCleave and Miller 1994). The mechanisms used by the leptocephali to exit the Gulf Stream and cross the continental shelf to colonise juvenile habitats are not well understood (McCleave 1993; McCleave and Miller 1994; Bell et al. 2003). The duration of the conger eel larval period is not known.

The examination of otolith microstructure and microchemistry has been used to reconstruct the early life history (e.g. spawning area and season, duration of the leptocephalus phase and distribution and larval migratory route) of several anguilliform fishes, including some other species of conger eels (Otake et al. 1997; Correia et al. 2003).

The present paper examines, for the first time, the otolith microstructural growth and the changes in otolith Sr:Ca ratios in *C. oceanicus* leptocephali during the metamorphic stage, in an attempt to elucidate some aspects of the early life history of this species.

Materials and methods

The 20 metamorphosing conger eel (*Conger oceanicus*) leptocephali used in this study were collected as part of a long-term ichthyoplankton sampling programme (Able and Fahay 1998; Witting et al. 1999). Fishing took place in the estuary, at night, using a 1-m diameter, 1-mm mesh plankton net, off of a bridge in Little Sheepshead Creek (Great Bay, southern New Jersey) (Fig. 1), in May 2001, April 2002 and May 2002 (Table 1). Three half-hour tows were performed with the net at a mid-

Table 1 *Conger oceanicus*. Collection date, length (*TL*), developing stage (preanal length to total length; *PAL/TL*), age at recruitment to the estuary and hatching date of the metamorphosing leptocephali

No.	Collect. date	TL (mm)	PAL/TL	Age (days)	Hatching date
CO5	14 May 2001	97.0	0.74	168	28 Nov 2000
CO4		96.0	0.63	179	18 Nov 2000
CO2	24 May 2001	94.0	0.52	–	–
CO10	30 May 2001	93.0	0.58	–	–
CO6		84.0	0.58	–	–
CO8		97.0	0.55	–	–
CO9		90.0	0.53	–	–
CO7		88.0	0.53	–	–
CO3		91.0	0.51	–	–
CO11		89.0	0.47	–	–
CO12	4 Apr 2002	99.0	0.71	156	31 Oct 2001
CO15	1 May 2002	104.0	0.68	155	28 Nov 2001
CO13		100.0	0.63	182	30 Oct 2001
CO14		85.0	0.67	183	31 Oct 2001
CO16	8 May 2002	99.0	0.70	171	19 Nov 2001
CO19		101.0	0.67	167	23 Nov 2001
CO17		87.0	0.66	149	11 Dec 2001
CO21		99.0	0.61	–	–
CO20		93.0	0.60	–	–
CO18		98.0	0.58	–	–

water depth (approximately 2 m). Temperature and salinity were recorded at the beginning and at the end of sampling, using a field thermometer and a hand-held refractometer, respectively. Water temperature and salinity of the sampling area ranged from 8°C to 17°C and from 26 to 30 psu, respectively.

After capture the leptocephali were preserved in 95% ethanol, and the general body morphology, pigmentation, morphometric and meristic characters were analysed following the methodology described by Smith (1989). Measurements were made to the nearest 0.1 mm, and myomere counts were done using a dissecting microscope. There was no correction for shrinkage caused by preservation.

Otoliths were prepared for the examination of microstructure and microchemistry, as described in Correia et al. (2003). Otoliths were embedded in epoxy resin, ground to expose the core with a series of graded silicon carbide papers (600, 1200 and 2400 grit), and further polished with diamond pastes (6, 3 and 1 µm) and alumina solution (1:20). Finally, they were cleaned in an ultrasonic bath, rinsed with deionised water and given a gold coating by high vacuum evaporation. Sr and Ca concentrations (% dry weight) were measured along the longest axis of the otolith using a wavelength dispersive X-ray electron microprobe (CAMEBAX SX 50). Apatite [$Ca_5(PO_4)_3$] and celestite ($SrSO_4$) were used as standards. Accelerating voltage and beam current were 15 kV and 10 nA, respectively. The electron beam was focused on a point about 2 µm in diameter, spacing measurements at 5-µm intervals. The microprobe measurement points, which were seen as burn depressions on the otolith surface, were assigned to otolith growth increments. The averages of successive data for Sr and Ca concentrations pooled for every ten successive growth increments were used for the life-history transect analysis. The results are presented as the amount of Sr divided by the amount of Ca times 1000. Otolith Ca content obtained in this study was about 10% less than that found in other previously published studies. Since Ca (and also Sr) could be measured with considerable accuracy and precision by wavelength dispersive electron microprobes (Campana et al. 1997), the reason for the low Ca content in otoliths was probably the 2 years of ethanol preservation prior to elemental composition analysis; in at least one study, a decline of this element in otoliths has been reported as a result of this preservation method (Proctor and Thresher 1998). However, the overall results are still valid, since our purpose was not to analyse the absolute values of Ca and Sr, but to examine the variation of Sr:Ca ratios (although these values could be overestimated) along the otolith growth sequence, in order to reconstruct the ontogenic history of the individual fishes. Following microprobe analysis, the otolith surface was repolished with alumina solution (1:20), etched for 15 s with 0.05 M HCl and vacuum coated with gold for scanning electron microscope observation (SEM, Jeol JSM 630–1F) at 15 kV. Core diameter, maximum otolith diameter and maximum otolith radius were measured from the SEM photographs (at magnifications between ×300 and ×2500) according to the procedures of Correia et al. (2002a). The otolith radius and increment width were measured along the maximum otolith radius. The averages of every ten successive increment widths from the hatch check to the end of the increment countable zone were used for otolith growth analysis.

We assumed 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 anguilliform species, e.g. *Conger myriaster* (Mochioka et al. 1989), *Anguilla japonica* (Tsukamoto 1989; Umezawa et al. 1989; Umezawa and Tsukamoto 1991), *A. rostrata* (Martin 1995; Cieri and McCleave 2001), *A. celebesensis* (Arai et al. 2000a) and *A. marmorata* (Sugeha et al.

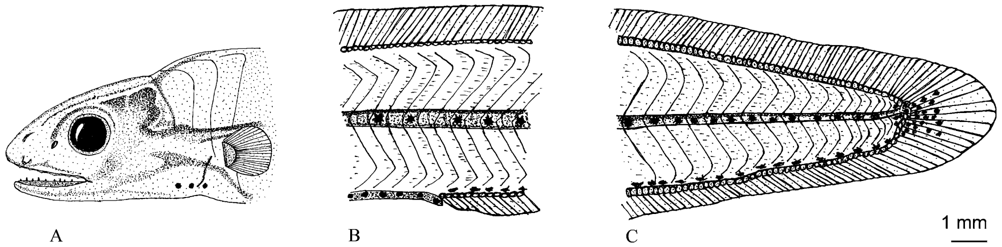

Fig. 2A–C *Conger oceanicus*. Illustration of the head (**A**), anal region (**B**) and caudal fin (**C**) of a metamorphosing leptocephalus (total length: 84.0 mm; preanal length/total length: 0.58)

2001), which have been shown to deposit increments daily. Based on previous studies on otolith microstructure and microchemistry of fishes that have a leptocephalus larval stage (see "Discussion"), the age at which increments showed a rapid increase in width simultaneous with a marked decrease in Sr:Ca ratios was regarded as the onset of metamorphosis for this species. Since all the individuals captured were still in metamorphosis, the duration of this stage could not be determined. For the early metamorphic leptocephali (preanal length/total length, PAL/TL≥0.63), the number of increments between the hatch check and the otolith edge was regarded as the age at recruitment. Unfortunately, for late metamorphic leptocephali (PAL/TL < 0.63), the age at recruitment (and also the timing between the onset of metamorphosis and the time of capture) could not be established directly from the otoliths, because there was a peripheral diffuse zone with unclear increments.

Statistical analyses were performed using Statistica 5.5. Significance of the correlation coefficient and regression slope were tested, respectively, by a Fisher's Z-transformation and by an ANOVA (Zar 1996). We used a level of significance (α) of 0.05. Data are presented as ranges and mean values (± standard deviations).

Results

Morphology, pigmentation and dentition

The metamorphosing leptocephali of *Conger oceanicus* were elongate, laterally compressed, with "W"-shaped myomeres and a simple tubular gut along the ventral margin of the body (Fig. 2). The head was of medium size, with rounded eyes, lips and nasal tubes. The dorsal fin was extended anteriorly, but did not reach half of the total length. They had large melanophores along the midlateral line, which became sparser or disappeared altogether anteriorly. Additional smaller melanophores appeared near the tail region. They had two prominent melanophores near the anus and three melanophores at an angle with the lower jaw, around the heart. The crescent-shaped patch of pigment under the eye, which is characteristic of the developing leptocephalus stage, was absent. Some of the leptocephali had small vestigial euryodontic teeth in both maxillas; however, the majority had lost their larval dentition.

Biometric and meristic values

The total length (TL) of leptocephali ranged from 84.0 to 104.0 mm, with a mean of 94.2 ± 5.7 mm (Table 2). The developmental stage indicator, preanal length/total length (PAL/TL), ranged from 0.47 to 0.74, with a mean value of 0.61 ± 0.08. The total number of myomeres (TNM), predorsal myomeres (PDM) and preanal myomeres (PAM) ranged from 141 to 147, from 44 to 52 and from 58 to 76, respectively. The PAL/TL ratio was positively and significantly correlated with the PAM/TNM ratio ($r^2 = 0.86$, $n = 20$, $P < 0.05$).

Otolith growth pattern

Otoliths in the metamorphosing leptocephali were oval (Figs. 3A, 4A) and showed the same concentric ring pattern, except for the margin. Depending on the larval developmental stage, the otolith showed some permanent structures, like a central core (C), the increment countable zone (ICZ), the diffuse zone (DZ) and the existence of one or more accessory growth centres (AGC). The core, located on the posterior side of the otolith, is composed of an amorphous primordium surrounded and delimited by the innermost discontinuous zone, presumed to be the hatch check (HC) (Fig. 3B). The core had a mean diameter of 19 ± 1 µm. Beyond the HC, clear daily growth increments marked the beginning of the ICZ. In this zone, the otolith increment width showed a characteristic curve along the radius (Fig. 5). Otolith increment widths increased (to a maximum of 1.10 µm) between the HC and age 30–50 days (phase I); thereafter, they gradually decreased,

Table 2 *Conger oceanicus*. Morphometric and meristic characters of the 20 metamorphosing conger eel leptocephali

Parameter	Range	Mean ± Standard deviation	Mode
Total length (mm)	84.0–104.0	94.2. ± 5.7	
Predorsal length (mm)	30.0–52.0	40.8 ± 6.0	
Preanal length (mm)	42.0–71.0	57.4 ± 8.8	
Head length (mm)	6.0 –7.5	6.8 ± 0.4	
Body depth (mm)	6.3–10.0	8.3 ± 1.1	
Eye diameter (mm)	1.5–1.6	1.5 ± 0.0	
Total number of myomeres	141–147		145
Predorsal myomeres	44–52		44
Preanal myomeres	58–76		65

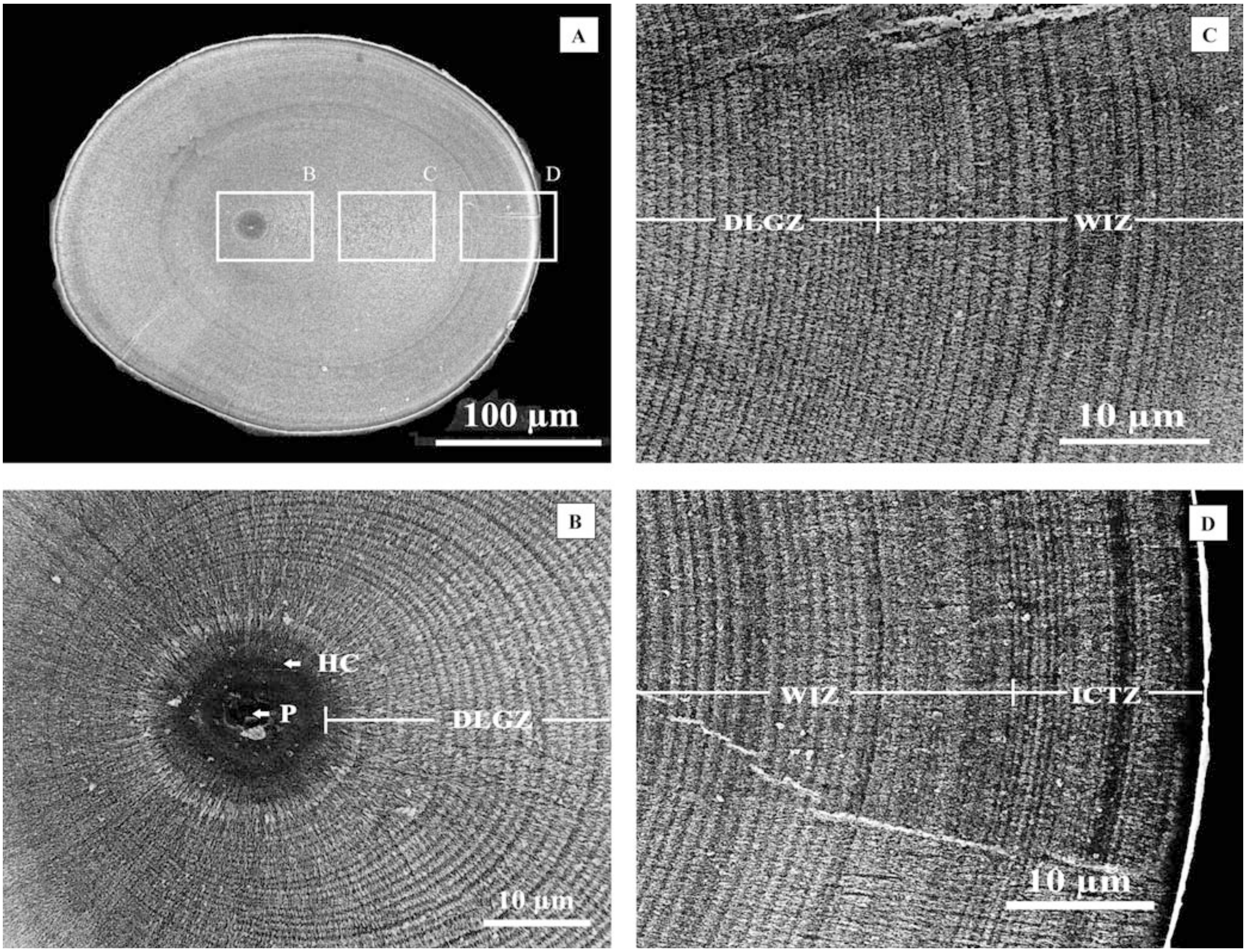

Fig. 3A–D *Conger oceanicus*. SEM micrographs showing the otolith microstructure of an early metamorphosing conger eel leptocephalus (total length: 96.0 mm; preanal length/total length: 0.63): **A** whole view (*boxes with letters* correspond, respectively, to panels B, C and D); **B** otolith core and surrounding zone; **C** boundary between the developing leptocephalus growth and metamorphic zones; **D** otolith edge (*P* primordium; *HC* hatch check; *DLGZ* developing leptocephalus growth zone; *WIZ* wide increment zone; *ICTZ* increment countable terminal zone)

until a relatively constant minimum value (0.65 µm) was reached, at about 80 days (phase II). This inner portion of the otolith's ICZ, which includes phases I and II, is named the developing leptocephalus growth zone (DLGZ) (Fig. 3C). In a third phase, the increments widen abruptly (to a maximum of 1.20–1.50 µm); this phase, depending on the specimen, could occur between 70 and 120 days. This wide increment zone (WIZ) occurred over about 20–40 days, after that the increment width decreased (increment countable terminal zone, ICTZ) (phase IV) (Fig. 3C, D). In the late metamorphic leptocephali ($PAL/TL < 0.63$), the increments of the peripheral zone became less clear and disappeared, which corresponds to the onset of the DZ (phase V). However, clear marks sometimes appeared in the marginal region. As the DZ increased, AGCs were formed (phase VI), giving the otolith a fan-like form (Fig. 4A). In these structures the aragonite needles were arranged at an angle relative to the sagittal plane (Fig. 4B).

There is a good correlation between the diameter (D) and the radius (R) of the otolith ($r^2 = 0.76$, $n = 20$, $P < 0.05$). The R and D of the otoliths ranged from 142 to 212 µm and from 250 to 376 µm, with a mean of 173 ± 17 µm and 301 ± 38 µm, respectively. The otolith size (D and R) was not significantly related to total body length, TL ($r^2 = 0.16$, $n = 20$, $P = 0.08$ and $r^2 = 0.19$, $n = 20$, $P = 0.06$), but it was significantly related to head length, HL ($r^2 = 0.42$, $n = 20$, $P < 0.05$ and $r^2 = 0.39$, $n = 20$, $P < 0.05$), and to the PAL/TL ratio ($r^2 = 0.57$, $n = 20$, $P < 0.05$ and $r^2 = 0.70$, $n = 20$, $P < 0.05$). The number of increments in the ICZ ranged from 143 to 202, with a mean of 180 ± 18. The width of the DZ ranged from 14 to 52 µm (28 ± 11 µm).

Otolith Sr:Ca ratios

Strontium (Sr) concentrations dramatically changed along the life-history transect. Sr content in the otoliths

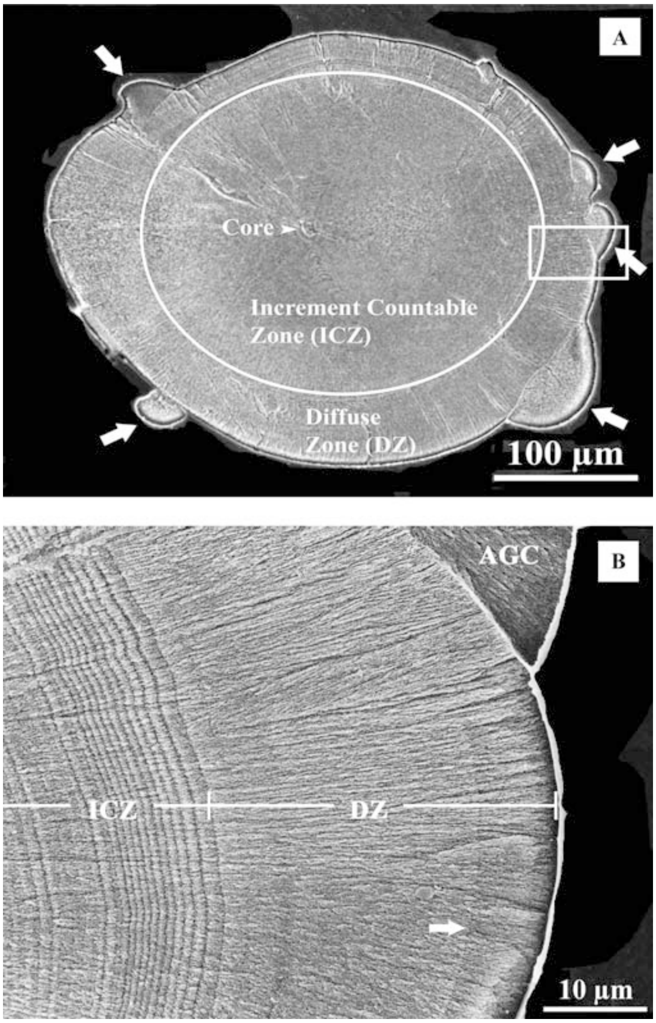

Fig. 4A, B *Conger oceanicus*. SEM micrographs showing the otolith microstructure of a late metamorphosing conger eel leptocephalus (total length: 88.0 mm, preanal length/total length: 0.53); **A** whole view of the otolith with accessory growth centres (*arrows*); **B** marginal region of the otolith (detail of the region indicated by a *box in panel A*) showing the disturbed arrangement of the peripheral rings (*AGC* accessory growth centres; *ICZ* increment countable zone; *DZ* diffuse zone; *arrow in panel B* clear mark)

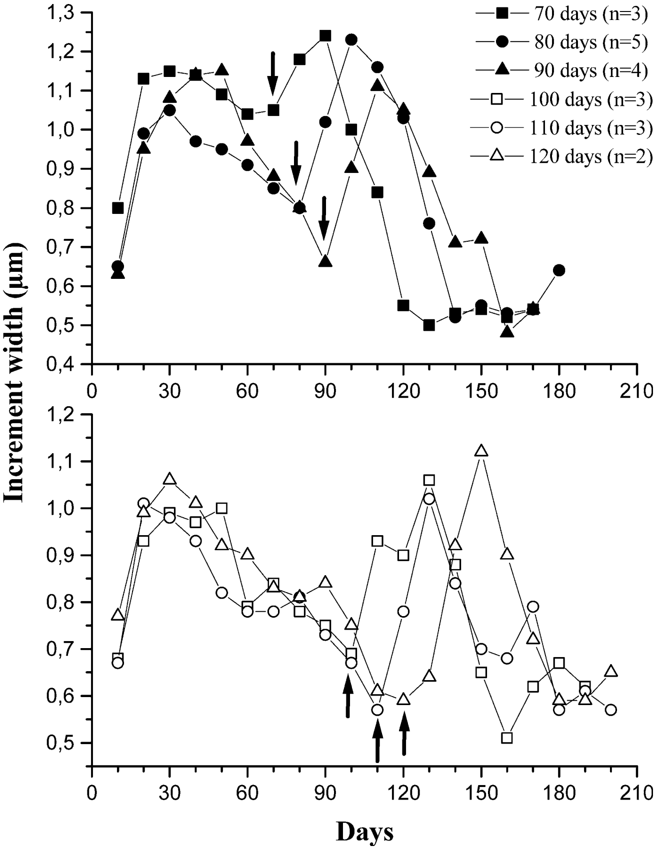

Fig. 5 *Conger oceanicus*. Profiles of the mean increment width throughout the otolith's increment countable zone. Specimens were grouped by the time when the width of daily rings abruptly increased (see *arrows*)

averaged 0.25 ± 0.08% in the core and increased outwards to a maximum level of about 0.39 ± 0.06%, at ages 70–120 days. Subsequently Sr content decreased rapidly to about 0.28 ± 0.03% at the outermost regions. Calcium (Ca) content was almost constant (26.2 ± 1.8%) throughout the otolith, except for the core region, which recorded a low value (25.9 ± 1.8%). Sr:Ca ratios changed in a similar manner to Sr content (Fig. 6) and averaged 8.5×10^{-3} (1.0×10^{-3} SD) in the core and rapidly increased soon after hatching. The ratios reached a maximum level of about 15.4×10^{-3} (1.8×10^{-3} SD), some 70–120 days after hatching, i.e. at the end of DLGZ formation. Subsequently, the ratios sharply decreased and maintained a stable minimum value of 11.9×10^{-3} (0.9×10^{-3} SD) outwards to the otolith edge (Fig. 7). The sudden increase in otolith increment width (WIZ), at ages 70–120 days, coincided with the rapid drop in otolith Sr content and Sr:Ca ratios, and marked the onset of metamorphosis (see "Discussion") (Fig. 8).

Age and hatching time

The ages at recruitment of the leptocephali to the estuary, while still in an early developmental stage (PAL/TL≥0.63), and thus without a DZ in the otolith, ranged from 149 to 183 days (Table 1). Hatching dates, back-calculated from these daily estimates, indicated that the spawning season lasted about 3 months, from late October to mid-December.

Age at metamorphosis

The duration of the developing leptocephalus stage (i.e. the number of increments in the DLGZ) ranged between 70 and 120 days, with a mean value of 92 ± 16 days. The age at metamorphosis was negatively correlated with the mean increment widths of the DLGZ ($r^2=0.62$, $n=20$, $P<0.05$) (Fig. 9). A close linear relationship was also

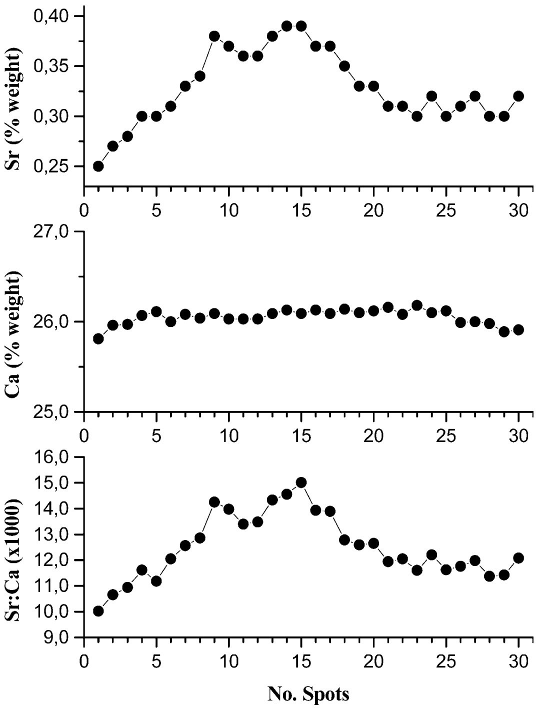

Fig. 6 *Conger oceanicus*. Profile of the mean values for Sr and Ca contents and Sr:Ca ratios, from the core to the edge of otoliths, determined by wave-length dispersive electron micropobe analysis (sample size: 10 specimens)

apparent between the age at recruitment and age at metamorphosis for the early metamorphic leptocephali ($r^2 = 0.85$, $n = 9$, $P < 0.05$) (Fig. 10). For these specimens, metamorphosis started 59–83 days (67 ± 8 SD) before the arrival in estuarine waters.

Discussion

Conger oceanicus arrive in coastal waters while they are undergoing metamorphosis (Able and Fahay 1998; Bell et al. 2003). Metamorphosing leptocephali collected in this study ranged from 84.0 to 104.0 mm TL and covered the length range (70–110 mm) reported by Bell et al. (2003). The total number of myomeres, the principal species identification criterion, ranged between 141 and 147, which is in agreement with the values reported by other authors (Schmidt 1931: 140–149; Smith 1989: 140–148; McCleave and Miller 1994: 137–148). The ranges of the predorsal and preanal myomeres, 44–52 and 58–76, of our specimens were, as expected, smaller than the counts obtained by Smith (1989) for the developing stage (PDM: 67–81; PAM: 113–124), since during metamorphosis the anus and the dorsal fin begin to move anteriorly in congrid leptocephali (Otake et al. 1997; Strehlow et al. 1998; Bell et al. 2003). The use of the PAL/TL, instead of the usual PAM/TNM, as an indicator of the development stage in several studies of eels (Yamano et al. 1991; Otake et al. 1997; Correia et al. 2002a, 2002b, 2003; Bell et al. 2003) has the advantage of being more easily obtainable and less affected by measurement errors (Correia et al. 2002a). In our study the PAL/TL was highly correlated with the PAM/TNM ratio and ranged between 0.47 and 0.74. These values are similar to the ranges recorded recently by Bell et al. (2003) on other transforming leptocephali collected at this location (0.45–0.60).

The metamorphosing leptocephali had the body shape associated with the general and identifying features of this species. Based on morphology, pigmentation and dentition these metamorphosing leptocephali correspond to developmental stage M1, described by Bell et al. (2003). The body is laterally compressed, with the formation of the lips and the straightening of the dorsal profile of the head. Body depth decreases, and the anus and dorsal fin move anteriorly. These leptocephali have large distinct melanophores along the midlateral line and small melanophores along the top of the gut; additional smaller melanophores may appear near the tail region. Some leptocephali may have vestigial teeth, but they disappear before the end of this stage. Stage M1 individuals are usually caught in coastal areas and estuaries, in pelagic and demersal habitats (Bell et al. 2003).

The otolith growth pattern of *C. oceanicus* metamorphosing leptocephali is similar to that recorded by Lee and Byun (1996) and Correia et al. (2002a, 2003) for *C. myriaster* and *C. conger*, respectively. The profile of the otolith growth increments could be divided into five phases. From hatch check to about 30–50 days, the growth increments became wide (phase I). This inflection in otolith growth might be related to favourable somatic growth, after successfully switching their nutritional source from yolk material to exogenous feeding (Arai et al. 2001). After this peak, the increment width diminished gradually and maintained a low value to an age of about 80 days (phase II). Thereafter, the increments abruptly widened during the following 20–40 days (phase III), and started to decrease in width at the outer margin of the increment countable zone (phase IV). Later in metamorphosis, the otolith continued to grow after increment resolution was lost, at about 180 days, resulting in the appearance of a peripheral diffuse zone (phase V). The first three phases of the otolith increment width profile were similar in the three above-mentioned conger species, although the fourth and fifth phases were absent, respectively, in *C. conger* (Correia et al. 2002a, 2003) and *C. myriaster* (Lee and Byun 1996). The biological relationship between otolith growth and morphological and ecological events is not fully understood.

The otoliths of *C. oceanicus* developed a peripheral diffuse zone in the metamorphosing specimens, as has already been recorded in *C. conger* (Correia et al. 2002a, 2003; Antunes and Correia 2003). Several authors have described the otolith microstructure of *C. myriaster* during metamorphosis, but they never identified the existence of a peripheral diffuse zone, although they reported several problems. Tanaka et al. (1987), for instance, recorded a disturbance of the ring arrangement in the marginal region of the otoliths and assumed it to

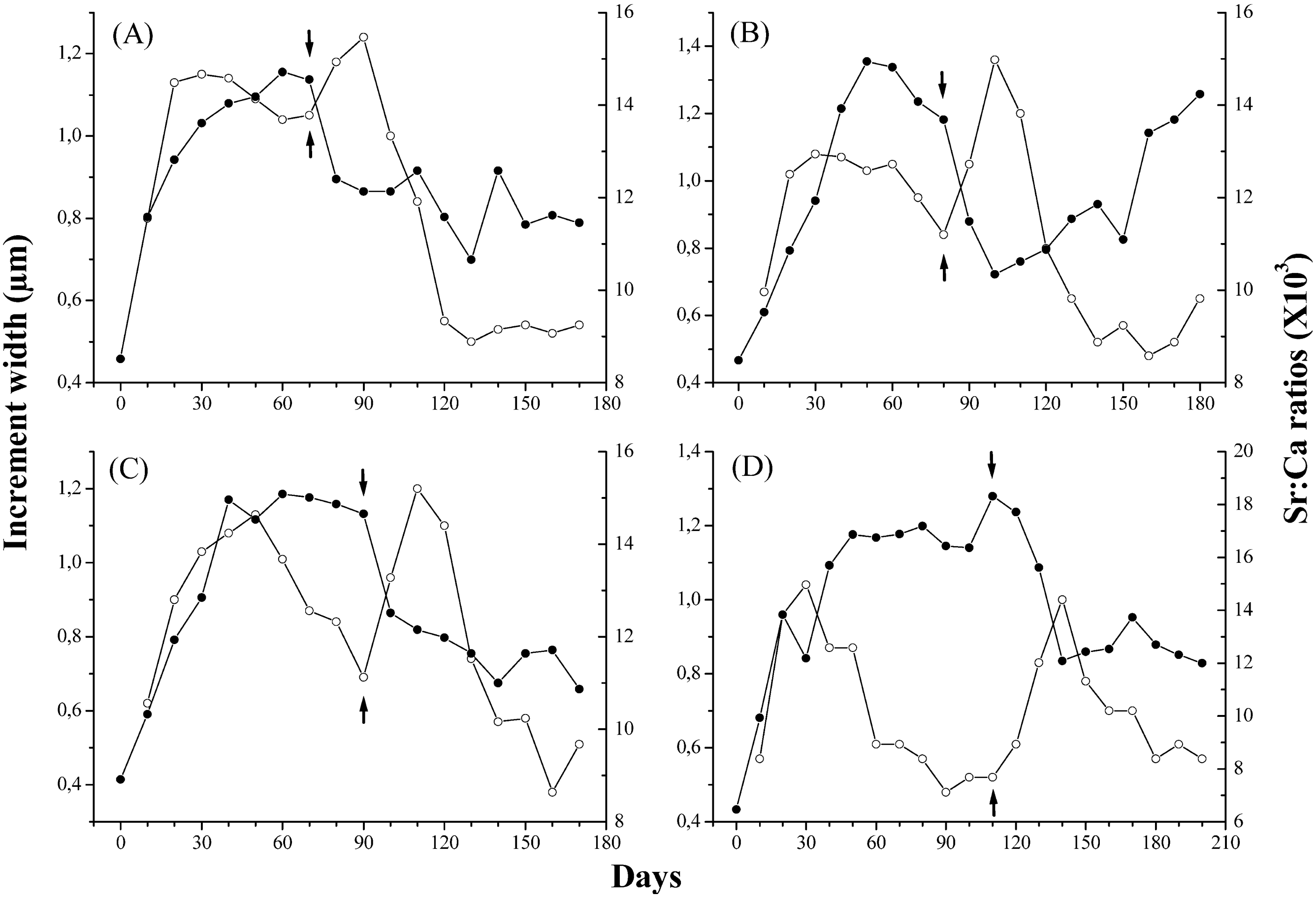

Fig. 7A–D *Conger oceanicus*. Profiles of otolith increment width (*open circles*) and Sr:Ca concentration ratios (*solid circles*), measured from the core (age 0) to the end of the increment countable zone. Specimens were grouped by the time when coincidental changes in increment width and Sr:Ca ratios occurred (**A**: 70 days, $n=3$; **B**: 80 days $n=2$; **C**: 90 days, $n=3$; **D**: 110 days, $n=2$). *Black arrows* represent the time when the width of daily rings abruptly increased

be an anomalous, non-permanent structure. Mochioka et al. (1989) also reported some irregularities on the outer surface of the otoliths, while Lee and Byun (1996) observed a peripheral opaque zone in the otoliths, where the increments were difficult to identify under light and scanning electron microscopy. Finally, Otake et al. (1997) related some technical problems in consistently etching all rings from the core to the edge of the otolith. This unclear increment area, previously observed in the European eel *A. anguilla* (Antunes and Tesch 1997), could represent a period of very slow growth made up of several daily rings that are too thin to be distinguished and counted (Williamson et al. 1999), or a process of calcium resorption in the marginal portion of the otolith during metamorphosis (Cieri and McCleave 2000), or even poor otolith preparation, e.g. overetching (Arai et al. 2000a). This unreadable marginal otolith diffuse zone, the meaning of which remains unknown, prevents the accurate estimate of the total age of the late metamorphosing individuals from our collections.

The occurrence of accessory growth centres in some otoliths of *C. oceanicus* appears to be in common with other congrid eels during metamorphosis (Lee and Byun 1996; Correia et al. 2002a, 2003). These structures are responsible for the secondary growth layers, which will generate the elliptical otolith shape in adults (Correia et al. 2002a). The mechanism resulting in such structures is not fully understood; however, it has been suggested that the AGCs reported in flatfish otoliths are related to a change in habitat and behaviour (Sogard 1991; Modin et al. 1996; Neuman et al. 2001). A transforming otolith, which will result in an adult-like form, may also be necessary to navigate through different environments to pursue prey and detect approaching predators (Brown et al. 2001).

Patterns of Sr/Ca ratios of otoliths have been used to reconstruct a chronology of environmental conditions related to the age and life stage of fishes, particularly the habitat use and seasonal migration of various anguilliform fishes, including *Anguilla* spp. (Otake et al. 1994; Tzeng 1995; Cheng and Tzeng 1996; Arai et al. 1997, 1999, 2000b, 2002; Tzeng et al. 1997) and *Conger* spp. (Otake et al. 1997; Correia et al. 2003). In these fishes changes in otolith Sr:Ca ratios have been considered to be related to shifts in temperature and water chemistry along possible migratory routes (Tzeng 1994; Tzeng et al. 1997; Tsukamoto et al. 1998; Tsukamoto and Arai 2001; Jessop et al. 2002), as well to ontogenetic varia-

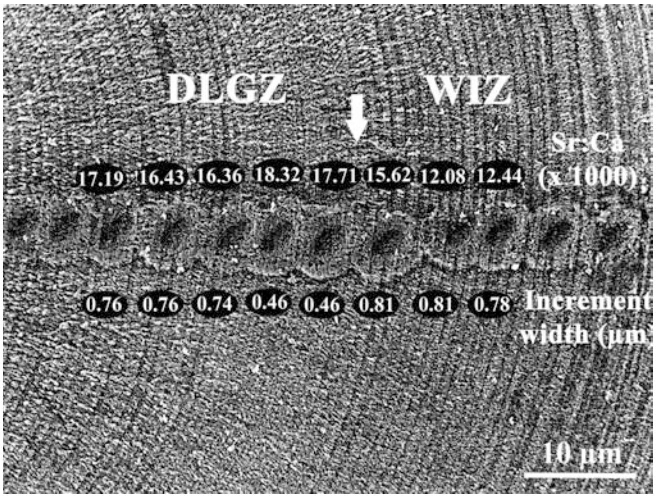

Fig. 8 *Conger oceanicus*. SEM micrograph showing the Sr:Ca ratios and increment width values, in an otolith of a metamorphosing conger eel leptocephalus (total length: 101.0; preanal length/total length: 0.67) (*DLGZ* developing leptocephalus growth zone; *WIZ* wide increment zone; *arrow* onset of metamorphosis)

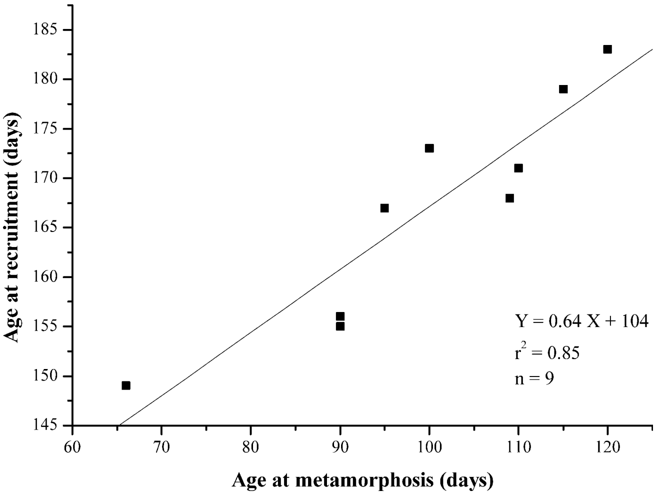

Fig. 10 *Conger oceanicus*. Metamorphosing leptocephali. Relationship between age at recruitment to the estuary and age at metamorphosis. Regression line represents a least square fit of the linear equation ($P < 0.05$)

tions in otolith elemental composition (Otake et al. 1997).

The pattern of Sr:Ca ratios along the otolith transect in the metamorphosing *C. oceanicus* leptocephali was consistent with the values reported in other anguilliform species (*C. myriaster*: Otake et al. 1997; *C. conger*: Correia et al. 2003). Sr:Ca ratios were lowest in the primordium and at the edge of the otolith. It has been suggested that the low Sr content observed in the otolith primordium of eels is probably due to the maternal or freshwater origin of the oocyte (Tzeng and Tsai 1994; Wang and Tzeng 2000). However, the results obtained by Otake et al. (1997) and by Correia et al. (2003) respectively for *C. myriaster* and *C. conger* two strictly marine species, showed that this feature could not be associated with a change in salinity and probably reflects the organic chemical composition of the otolith core (Correia et al. 2003). The rapid decrease in the Sr:Ca ratio and the simultaneous increase in otolith increment width appear to occur during metamorphosis and have been observed in several species of anguilliform fishes, including *A. japonica* (Otake et al. 1994; Cheng and Tzeng 1996; Arai et al. 1997), *A. anguilla* and *A. rostrata* (Arai et al. 2000b; Wang and Tzeng 2000), *A. australis*, *A. celebesensis* and *A. dieffenbachii* (Marui et al. 2001), *A. bicolor pacifica* (Arai et al. 1999; Marui et al. 2001), *A. marmorata* (Marui et al. 2001; Arai et al. 2002), *C. myriaster* (Otake et al. 1997) and *C. conger* (Correia et al. 2003). Tzeng and Tsai (1994) and Wang and Tzeng (2000) proposed that the drop in the Sr:Ca ratio in the eel otolith after metamorphosis reflects the sudden change in ambient salinity associated with the migratory behaviour of the eel, i.e. the entry into freshwater habitats less rich in Sr. However, since *C. oceanicus* individuals in our collections were often taken at nearly full salinities (approximately 28 psu) (Martino and Able 2003), this likely would not result in a change in Sr:Ca ratios. This phenomenon probably represents the mobilisation of body minerals for the rapid bone development that occurs during late metamorphosis in leptocephalus fishes (Otake et al. 1997). The same author proposed that the rapid drop in Sr:Ca ratios might be associated with decreasing Sr levels in the body as a result of catabolism of Sr-rich sulphated glycosaminoglycans during metamorphosis. Campana (1999) suggested that the elevated Sr:Ca ratios in eel leptocephalus otoliths, namely the peak in the Sr:Ca ratio at the time of metamorphosis from the larval stage, is due to the extremely low growth rates, even at high temperatures, since metamorphosis is a life-history stage with markedly curtailed growth (Pfeiler 1999). These findings suggest that such changes are a common feature

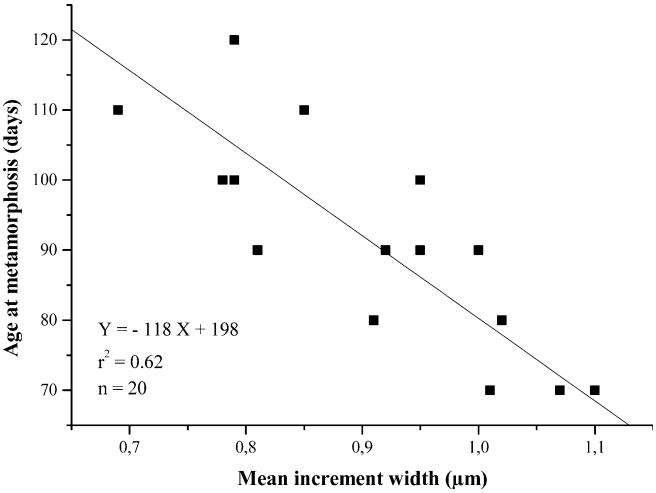

Fig. 9 *Conger oceanicus*. Metamorphosing leptocephali. Scatter diagram of age at metamorphosis versus mean otolith increment width. Regression line represents a least square fit of the linear equation ($P < 0.05$)

in leptocephalus larvae and may be associated with the remarkable morphological and physiological transformations that occur during development.

The close relationship between the diameter and radius of the otolith indicates that both measures are helpful in describing otolith growth. As already observed for *C. myriaster* (Lee and Byun 1996) and *C. conger* (Correia et al. 2002a, 2003), somatic and otolith growth became uncoupled during the metamorphic stage. However, otolith size was significantly related to head length, suggesting that the head and otolith continue to grow, although fish length decreased during metamorphosis. Assuming that the formation of the first growth increment coincided with hatching and that increments are deposited on a daily basis, the ages of the early metamorphosing leptocephali, which did not have the unclear diffuse zone, were estimated as 149–183 days after hatching. These results should be interpreted with caution because of the small sample size. The hatching dates, back-calculated from sampling dates and estimated ages, ranged from late October to mid-December and agree with the proposed spawning period based on the collection of small larvae (McCleave and Miller 1994). These dates also suggest a short spawning period during the winter season. However, the presence of small leptocephali (<30 mm long) of *C. oceanicus* over deep water in the south-western Sargasso Sea in autumn and winter implies a protracted spawning period there (McCleave and Miller 1994). Back-calculated hatching dates from the otoliths of developing leptocephali of *C. conger* also indicate a long spawning season, from December to July, with one consistent annual peak, occurring in the beginning of summer (Correia et al. 2002b, 2003). Lee and Byun (1996) estimated hatching dates from September through February by analysis of the otolith microstructure of *C. myriaster* leptocephali. An extended spawning period has also been reported for *Anguilla japonica* (Tabeta et al. 1987; Tsukamoto 1990; Tsukamoto and Umezawa 1990), and it has been proposed that this might be due to multiple populations of adult *A. japonica* prolonging the duration of the spawning season (Tsukamoto 1990).

The duration of the developing leptocephalus stage, i.e. the number of daily increments from the hatch check to the onset of the wide increment zone, indicates that *C. oceanicus* takes about 2–4 months from hatching to reach metamorphosis. Correia et al. (2002a, 2003) reported a duration of 6–9 months for the developing leptocephalus stage of *C. conger*, and Lee and Byun (1996) noted 4–8 months in the case of *C. myriaster*. The differences observed in the duration of the developing leptocephalus stage between these *Conger* species may be related to the different distances from the spawning ground to the juvenile coastal area and/or to the dynamics of the ocean currents in the various areas. *C. conger*, for example, spawns in the open ocean at least 3000 km from the coast (Correia et al. 2002b, 2003). Takai (1959) proposed a single spawning site for *C. myriaster* at the edge of the continental slope in the East China Sea, but there is also a possibility of multiple spawning sites in the East Asia region (Mochioka et al. 1988). However, these hypotheses concerning the exact location of the spawning site for this species are not based on any substantial data relating to the population structure or the distribution of larvae and eggs. Spawning of *C. oceanicus* in the Sargasso Sea indicates that adults cross the Florida Current–Gulf Stream and that successful leptocephali might cross the current in the opposite direction to colonise juvenile habitat on the continental shelf, a migratory pattern similar to that of the American eel, *Anguilla rostrata* (McCleave and Miller 1994). It is also conceivable that leptocephali use deeper countercurrents under the Gulf Stream, which apparently occur in this area (Able and Fahay 1998), to recruit to juvenile habitats. Apparently the Japanese eel, *A. japonica*, spawns in an analogous location with respect to the western boundary current of the North Pacific Ocean, i.e. the Kuroshio Current (Tsukamoto 1992). The size distributions of leptocephali suggest that gyres in the south-western Sargasso Sea, an Antilles Current, and the Florida Current north of the Bahamas are routes of exit for anguillid and congrid eels (McCleave 1993). Most *C. oceanicus* appear to enter the Florida Current north of the Bahamas (McCleave and Miller 1994), but there are few data on the distribution of leptocephali or early juveniles between the current and the shelf in relation to physical features (McCleave 1993). The mechanisms used by these leptocephali to exit the Gulf Stream and cross the continental shelf are still poorly understood (Able and Fahay 1998). Our data suggest, however, that the migration of leptocephali from their oceanic spawning ground to the estuary requires 5–6 months. The lengthy duration of metamorphosis and the timing of metamorphosis are important factors determining the long-distance dispersal of the eels (Cheng and Tzeng 1996), and might be responsible for the segregation of the migrating *A. rostrata* and *A. anguilla* (Wang and Tzeng 2000). A short duration of the leptocephalus stage might favour oceanic retention, while a long duration might favour emigration (McCleave 1993). The onset of metamorphosis to the juvenile phase may be delayed until appropriate physical conditions are meet (Tzeng 1990), as has been suggested for *C. oceanicus* (Bell et al. 2003). Larvae with long pelagic phases may be more susceptible to being carried by different currents and to being exposed to different growth conditions (Benoît et al. 2000).

The age at metamorphosis is inversely related to the growth rate, suggesting that more slowly growing fish apparently metamorphosed later. This phenomenon was also found in *Pseudopleuronectes americanus* (Chambers and Leggett 1987), in *A. japonica* (Tzeng 1990), in *Megalops cyprinoides* (Tzeng et al. 1998) and in *C. conger* (Correia et al. 2003). Although *C. oceanicus* is not usually considered an estuarine species, rare, single occurrences of young stages in estuaries have been reported throughout the Mid-Atlantic Bight (Hauser 1975; Moring and Moring 1986; Able and

Fahay 1998). The ingression of *C. oceanicus* leptocephali into estuaries occurs regularly from May to July (Able and Fahay 1998), at the mean age of 168 ± 12 days (present study), and co-occurs with metamorphosis and settlement to bottom habitats (Bell et al. 2003). Metamorphosis appears to have started several days (68 ± 8) before arriving in the estuary. The positive relationship between the age at recruitment and the age at metamorphosis suggests that *C. oceanicus* that metamorphosed at an earlier stage tended to recruit to estuaries at younger ages, indicating that early metamorphosing larvae are recruited earlier. Several authors (Tsukamoto 1990; Tsukamoto and Umezawa 1990; Wang and Tzeng 1998; Arai et al. 1999, 2000b, 2001; Marui et al. 2001) found the same phenomenon in temperate and tropical eels. This relationship between the timing of metamorphosis and the inshore migration of leptocephali seems to be typical for anguillid and congrid eels. However, there is a need for further studies of this critical stage, in order to elucidate the mechanisms used by *C. oceanicus* to optimise recruitment to coastal areas.

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