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Age, growth, distribution and ecological aspects of *Conger conger* leptocephali collected in the Azores, based on otolith analysis of premetamorphic specimens

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Abstract A total of 29 specimens of the anguillid leptocephali *Conger conger* were collected by the R.V. "Arquipélago", Department of Fisheries and Oceanography, University of Azores, in the waters south of the central group of the Azores Islands in October 1999. The meristic counts, morphologic features and pigmentation patterns of the leptocephali agree with the descriptions by other authors of this species. Leptocephali were found to range from 51.5 to 126.5 mm length and show a positively skewed distribution. The somatic growth rate (0.31 mm day^{-1}), estimated from the linear regression of length on age, falls within the ranges reported by several authors for other anguilliform species. Back-calculated hatching dates from the otolith microstructure suggests a long spawning season, from January to July, with one visible annual peak, occurring in summer. The analysis of our collection data in light of the current physical oceanographic knowledge of the NE Atlantic suggests that it is unlikely that the Azorean specimens came from the Mediterranean, unless the larvae were capable of very active and oriented swimming; thus the existence of another spawning place for this species somewhere near the Azores Archipelago is probable.

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Introduction

The European conger eel (*Conger conger* Linnaeus, 1758) is a marine fish widely distributed in the NE Atlantic, Mediterranean and western Black Sea (Bauchot and Saldanha 1986). However, knowledge about its early life history, such as spawning area(s) and season(s), duration of the leptocephalus phase and larval migratory route(s), is very limited, since few studies on this species have been reported.

Schmidt (1931) caught small *C. conger* leptocephali in the Sargasso Sea, Mediterranean and NE Atlantic, and proposed a similar migratory behavior to the European eel (*Anguilla anguilla* L.), i.e. spawning in the Sargasso Sea, following a larval transoceanic migration to European and North African coasts. However, Schmidt's claim that *C. conger* spawn in the Sargasso Sea is contested by McCleave and Miller (1994). These authors state that the small conger eel larvae caught in the Sargasso Sea were *C. triporiceps*, a species with an overlapping number of myomeres, which was described later by Kanazawa (1958). Nowadays, the larvae of both species are distinguished by the catch location, whereby the *C. conger* leptocephali are restricted to the central and eastern zones of the Atlantic Ocean (Strehlow et al. 1998).

The length and otolith analyses of *C. conger* leptocephali collected in the North and Central Atlantic Ocean showed that spawning occurs in the Mediterranean Sea, between July and September (Strehlow et al. 1998), supporting the existence of a spawning area in the Mediterranean for the European conger eel (Cau and Manconi 1983).

Otolith microstructure analysis provides important information about age and growth of fishes. Daily increment studies contribute to the knowledge of important events in the early life history of individual fish, such as hatching time, duration of the larval phase, growth rate and transition to another mode of life (Campana and Neilson 1985).

The present study examined the otolith record of age, growth and ontogeny in *C. conger* leptocephali, to provide a better understanding of the recruitment process of this species in the coastal habitat, and to provide further knowledge about its early life history.

Materials and methods

The leptocephali used in this study were collected during a research cruise (R.V. "Arquipélago") conducted by the Department of Oceanography and Fisheries of the Azores University in mid-October 1999, in the Central North Atlantic Ocean, near the central group of the Azores Islands. Figure 1 shows the sites where sampling took place.

Three transects (23 hauls, 18 at night and 5 during daytime) across the southern area of the Pico and Faial Isles provided 29 leptocephali of *Conger conger*. These transects were accompanied by CTD (conductivity–temperature–depth) and XBT (expendable bathythermograph) casts, which provided temperature profiles for each sampling site. The vertical profiles of temperature presented abrupt changes between 70 and 80 m deep, forming a sharp thermocline. Surface water temperature and salinity of the sampling area ranged from 20.9 to 21.7°C and 35.9 to 36.1 PSU, respectively. In Table 1 the sampling data, location, environmental oceanographic values and lengths of the collected leptocephali are presented.

All leptocephali were taken with a rectangular midwater trawl with a mouth opening of 8 m^2 (RMT8) and a 4.5 mm mesh net, mainly in the surface layers of the water (0–200 m) during the night.

After capture, the leptocephali were preserved in 4% seawater formalin and transferred in the laboratory to 70% ethanol. We identified the specimens using the criteria of D'Ancona (1931). Measurements were made to the nearest 0.1 mm, and meristic counts were done using a dissecting microscope following the method adopted by Smith (1989). Two readers made the myomere counts. The counts were repeated until a consistent value was obtained (no more than two units of difference). The shrinkage caused by the fixation and preservation methods was not corrected.

Left side sagittae were removed from 16 specimens, cleaned, mounted on cylindrical stubs, and polished with 2400 silicon carbide abrasive paper and alumina suspension (1:20) until the core was revealed. After that, they were etched for 10 s with 0.05 M HCI, sputter-coated with gold under vacuum and viewed with a scanning electron microscope (SEM; Jeol JSM 630-1 F) at 15 kV.

Following SEM analysis, core diameter (*C*), maximum otolith diameter (*D*) and maximum otolith radius (*R*) were measured from the SEM photographs (at magnifications between 300× and 2500×). The otolith radius was measured along the longest axis of the otolith. On the same axis, the total number of increments and their widths were also registered. Enumeration of otolith micro-increments was straightforward. All the increment counts were performed three times, by the same reader, between the first visible increment to the last increment near the sagitta's edge. The coefficient of variation (CV) between counts was $< 3.0\%$.

We assumed the growth increment in the larval otolith of *C. 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), *A. rostrata* (Martin 1995), *A. celebesensis* (Arai et al. 2000) and *A. marmorata* (Sugeha et al. 2001), which have been shown to have daily depositions.

In most marine fishes, the deposition of the first daily increment occurs during their first exogenous feeding, when larvae have completed yolk-sac absorption (Lough et al. 1982; McGurk 1984; Tzeng and Yu 1988). In the Japanese eel the yolk sac was completely absorbed 4–6 days post-hatching (Umezawa et al. 1989). Like other similar studies on the Japanese eel (Tzeng 1990; Cheng and Tzeng 1996; Wang and Tzeng 1998), we regarded the first distinct increment as a first feeding check (FFC) and have also added 5 days to the number of the increments on the assumption that *C. conger* begin exogenous feeding 5 days after hatching like *A. japonica* larvae.

Daily growth rates of the body (SGR, somatic growth rate) and otolith (OGR, otolith growth rate) were calculated by the ratios of total length and maximum radius of otolith to estimated age, respectively. Furthermore, the correlations between body and otolith growth rates and age were also calculated. Data are presented as mean values with standard deviations ($\pm$SD).

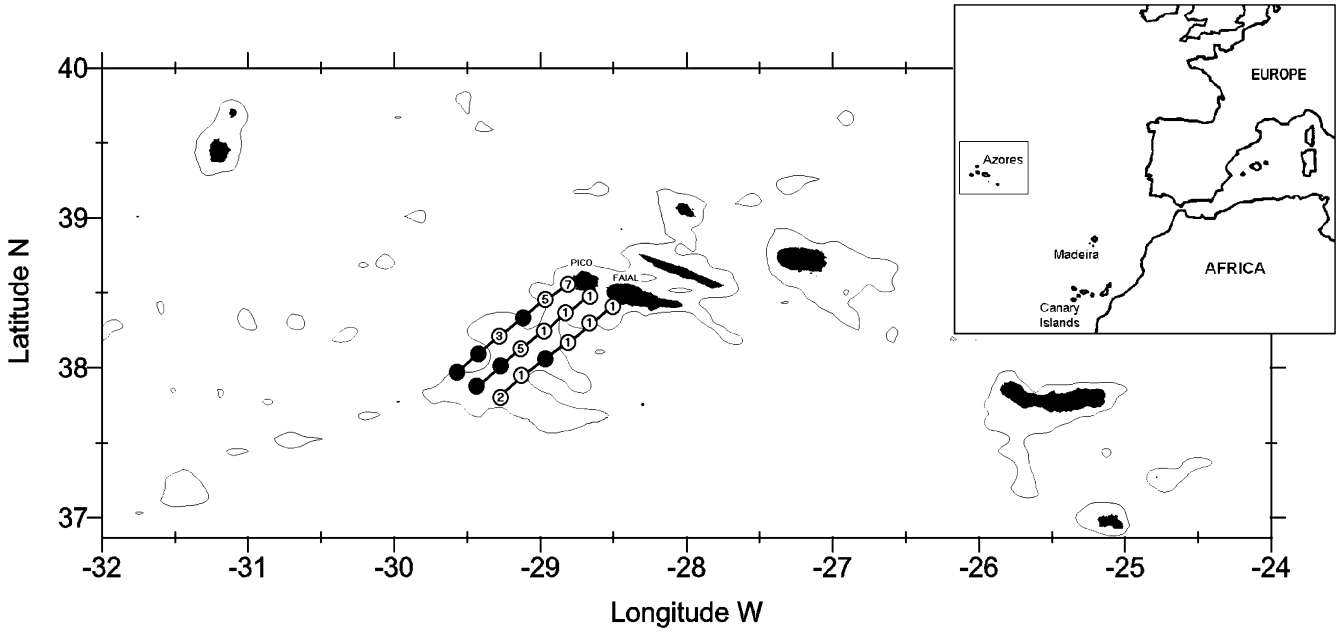

Fig. 1 *Conger conger*. Location of the Azores Archipelago in the middle of the North Atlantic Ocean (*inset*). Station locations during sampling from the R.V. "Arquipélago" (*main map*) (*lines* represent transects; *circles* indicate stations; *solid circles* are the stations without larvae; *open circles with number* indicate the stations where the conger eel larvae were collected and the respective number of specimens)

Table 1 *Conger conger*. Sampling location, date (in 1999), environmental parameters, length, age and hatching date (in 1999) of the collected leptocephali

Sampling location	Sampling date	Salinity (PSU) (Surface/Depth)	Temperature (°C) (Surface/Depth)	Depth (m)	Total length (mm)	Age (days)	Hatching date
38°33′N; 28°52′W	8 Oct	–/–	–/–	200	51.5	76	25 Jul
					68.0	114[a]	17 Jun
					80.5	122	9 Jun
	12 Oct	–/–	–/–	200	63.5	98[a]	6 Jul
					65.0	103[a]	1 Jul
					71.5	126[a]	9 Jun
					75.5	140[a]	26 May
38°26′N; 28°59′W	8 Oct	36.00/35.88	21.11/19.99	45	55.5	71[a]	29 Jul
					58.0	79[a]	22 Jul
					59.0	83[a]	18 Jul
					68.0	114[a]	17 Jun
					78.5	150[a]	12 May
38°12′N; 29°18′W	9 Oct	35.97/36.00	21.04/18.24	40	56.0	71	30 Jun
					64.5	102[a]	30 Jun
					70.5	103	29 Jun
38°28′N; 28°40′W	10 Oct	36.03/35.91	21.50/15.16	140	67.5	114	19 Jun
38°21′N; 28°50′W	10 Oct	35.99/35.99	21.18/19.83	58	57.0	76[a]	27 Jul
38°15′N; 28°58′W	10 Oct	35.89/36.01	21.06/15.66	90	75.0	115	18 Jun
38°08′N; 29°07′W	10 Oct	35.98/35.96	20.92/16.13	65	63.0	122	11 Jun
					81.0	159[a]	5 May
					82.0	182	12 Apr
					83.5	154	10 May
					104.0	224	28 Feb
38°25′N; 28°31′W	13 Oct	36.05/35.85	21.77/14.18	200	114.0	275	2 Jan
38°18′N; 28°40′W	13 Oct	36.11/35.87	21.69/14.44	200	58.5	90	16 Jul
38°11′N; 28°49′W	12 Oct	36.03/35.93	21.37/16.84	50	80.5	205	22 Mar
37°57′N; 29°07′W	10 Oct	36.06/35.83	21.22/14.22	200	126.5	246	26 Jan
37°50′N; 29°16′W	11 Oct	36.07/36.02	21.20/16.02	80	65.5	105	29 Jun
					88.5	185	10 Apr

[a]Estimated from the linear regression of length on age ($Y = 32.9 + 0.31X$)

Results

External body morphology and pigmentation

A whole body view of a premetamorphic *Conger conger* leptocephalus is presented in Fig. 2. The leptocephali had a very elongate body, compressed laterally, with ''W''-shaped myomeres and a very long simple tubular gut along the ventral margin of the body. The larvae had small heads and oval eyes, slightly elongated in a dorsoventral direction. Dorsal, caudal and anal fins were joined. The dorsal fin extends anteriorly, but does not reach half of the total length. Larvae had small pectoral fins; pelvic fins were absent.

Preserved specimens were translucent with some pigmentation. They had a few branched dots along the mediolateral line, which became sparser or disappeared alltogether anteriorly. We also observed some punctuate melanophores at the bases of the caudal and anal fin rays, but limited to the posterior region of the dorsal fin. Leptocephali also exhibited a paired row of punctuate melanophores along the ventral sides of the intestine, extending slightly beyond the anus. A crescentic patch of pigment (irido-chorioid process) was present under the eye. All the leptocephali had larval teeth in both maxillas.

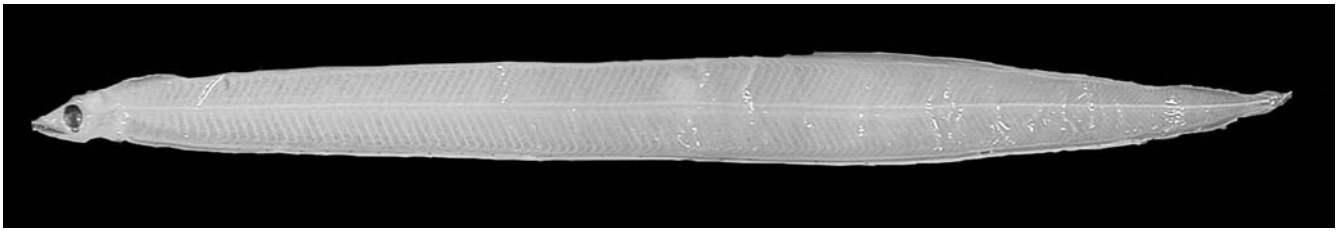

Fig. 2 *Conger conger*. Leptocephalus in a premetamorphic stage (80.5 mm in total length)

Table 2 *Conger conger*. Morphometric and meristic characters (lengths expressed in mm)

Parameter	Abbrev.	Range	Mean ± SD	Sample size
Total length	TL	51.5–126.5	73.5 ± 17.5	29
Predorsal length	PDL	33.5–78.5	48.0 ± 10.2	24
Preanal length	PAL	46.0–110.0	64.3 ± 14.9	29
Head length	HL	4.2–6.6	5.1 ± 0.6	29
Body depth	BD	4.2–11.9	6.3 ± 1.7	29
Eye diameter	ED	1.0–1.7	1.2 ± 0.2	24
Total no. myomeres	TNM	155–161	158 ± 2	28
Last vertical blood vessel	LVBV	57–62	60 ± 1	27
Predorsal myomeres	PDM	76–102	86 ± 5	24
Preanal myomeres	PAM	120–127	124 ± 2	28

Biometric and meristic data

The morphometric and meristic values obtained are in Table 2. The total number of myomeres (TNM) of *C. conger* leptocephali varied between 155 and 161. The predorsal (PDM) and preanal (PAM) myomere numbers of the premetamorphic leptocephali ranged from 76 to 102, and 120 to 127, respectively. The position of the last vertical blood vessel (LVBL) ranged between 57 and 62 myomeres.

The total length (TL) of leptocephali ranged from 51.5 to 126.5 mm, with a mean of 73.5 ± 17.5 mm. The length-frequency of *C. conger* leptocephali (Fig. 3) also suggests a positively skewed distribution, with a peak around 70 mm.

The head length (HL) ($r^2 = 0.85$, $n = 29$, $P < 0.001$) and body depth (BD) ($r^2 = 0.91$, $n = 29$, $P < 0.001$) were significantly correlated with the TL of larvae. The HL/TL is negatively related to the TL ($r^2 = 0.76$, $n = 29$, $P < 0.001$).

The preanal length/total length (PAL/TL) ratio was significantly correlated with the preanal myomeres/total number of myomeres (PAM/TNM) ratio ($r^2 = 0.48$, $n = 28$, $P < 0.001$) (Fig. 4). The mean values obtained for the PAM/TNM and PAL/TL ratios, were 0.78 ± 0.01 and 0.88 ± 0.01, respectively.

There is a weak though statistically significant relationship between the PAL/TL and the TL of larvae ($r^2 = 0.15$, $n = 29$, $P < 0.05$). However, no relationship exists between the PAL/TL index and larval age ($r^2 = 0.06$, $n = 16$, $P = 0.36$).

Sagitta microstructure and growth increment

The sagitta, characterized by a rounded shape, viewed under SEM, exhibited clear daily increments from the first feeding check (FFC) to the otolith's edge (Fig. 5A, B). However, the core, which extends from the center to the FFC, is composed of a central, amorphous primordium, surrounded by a thick ring, presumed to be the hatch check (HC), and a zone with no distinct incre-

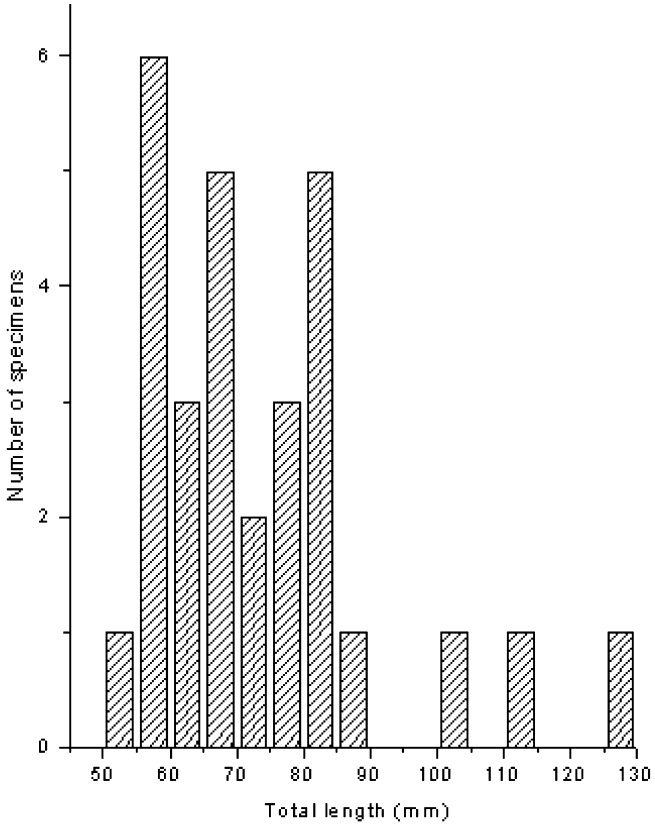

Fig. 3 *Conger conger*. Length-frequencies of the conger eel leptocephali collected during the R.V. "Arquipélago" in October 1999

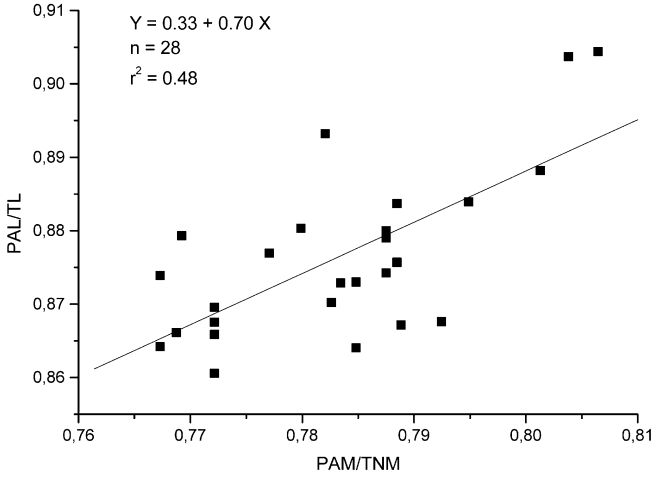

Fig. 4 *Conger conger*. Relationship between PAL/TL and PAM/TNM ratios (*line* represents a least squares fit of the linear regression, $P < 0.001$)

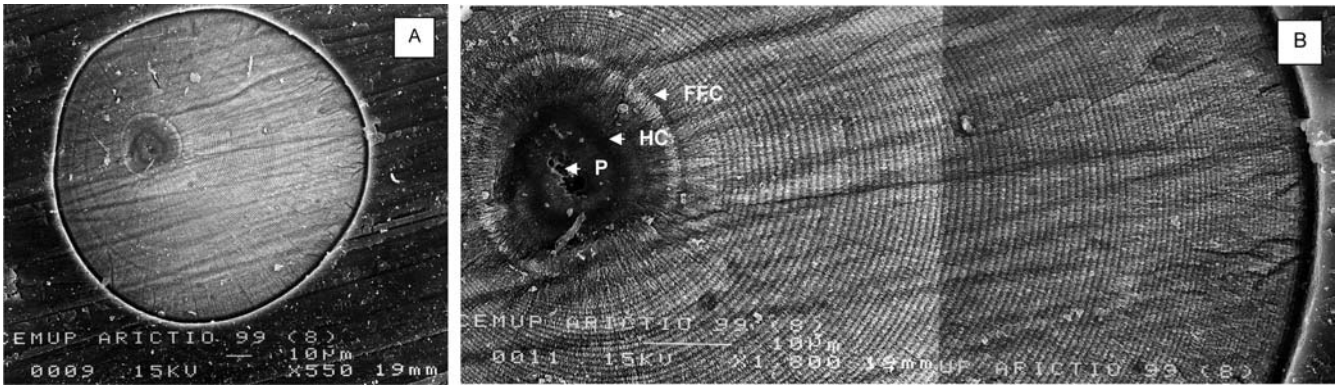

Fig. 5A, B *Conger conger*. SEM microphotographs of a sagitta of a premetamorphic leptocephalus (65.5 mm total length): **A** whole sagitta; **B** radius (*P* primordium; *HC* hatch check; *FFC* first feeding check)

ments between the HC and the FFC (i.e. during the yolk-sac stage) (Fig. 5B). These checks were postulated to be the HC and the FFC, since their morphologies were similar to those in other anguilliform fishes (Tabeta et al. 1987; Lecomte-Finiger and Yahyaoui 1989; Wang and Tzeng 1998, 2000).

The core presented an average diameter value of 24 ± 2 μm. The otolith radius (and diameter) ranged from 61 to 164 μm (101–209 μm), with a mean of 101 ± 32 μm (146 ± 38 μm).

Mean increment widths along the radius of sagittae showed a characteristic curve (Fig. 6). From the FFC to approximately 30 days afterwards, there was a pronounced increase in the increment widths (until a maximum of 0.82 μm). Then, increment widths became progressively narrow, until they reached a constant minimum value (0.38–0.42 μm) at about 160 days. After that, and only for the two largest individuals, they abruptly widened to a maximum of 0.65–0.72 μm after about 200–230 days (Fig. 7). The average width of each increment was 0.61 ± 0.17 μm (range 0.28–1.05 μm).

Increment counts ranged from 71 to 275 (Table 1), with a mean value of 149 ± 63.

The OGR was 0.71 ± 0.11 μm day^{-1}. The otolith radius is significantly correlated with the total length ($r^2 = 0.93$, $n = 16$, $P < 0.001$) and age of the leptocephali ($r^2 = 0.96$, $n = 16$, $P < 0.001$).

A very good relationship was found between the total length and the age of the leptocephali ($r^2 = 0.86$, $n = 16$, $P < 0.001$). The linear regression obtained between size and larval age (estimated from otolith daily ring increments) is displayed in Fig. 8. The slope of this regression indicates an SGR of 0.31 mm day^{-1}, and the *Y*-intercept indicates a predicted length at hatching of 32.9 mm.

Estimates of maximum SGR and OGR were 0.79 and 0.96 μm day^{-1}, respectively. The SGR ($r^2 = 0.77$, $n = 16$, $P < 0.001$) and the OGR ($r^2 = 0.65$, $n = 16$, $P < 0.001$) were negatively correlated with the age.

Age and hatching season

Hatching dates were back-calculated for 16 leptocephali. The hatching time for the remaining 13 specimens, since

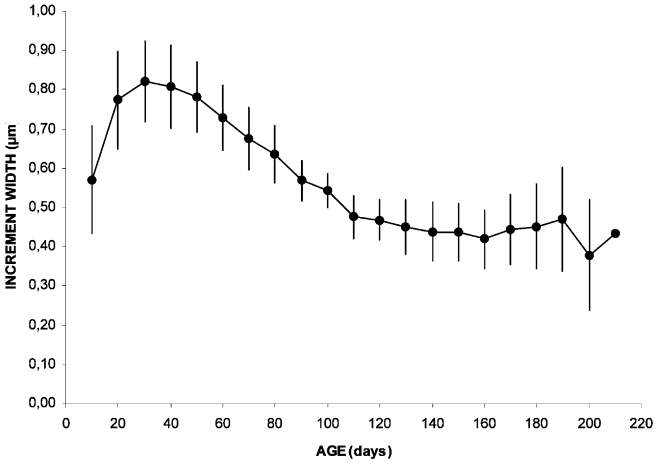

Fig. 6 *Conger conger*. Profile of otolith increment widths from ages 10–210 days. *Each data point* shows a mean value (±SD) for every ten successive increments. Number of samples for each average: 10–70 days ($n = 14$); 80 days ($n = 12$); 90–100 days ($n = 10$); 110 days ($n = 8$); 120 days ($n = 6$); 130–150 days ($n = 5$); 160–180 days ($n = 3$); 190–200 days ($n = 2$); 210 days ($n = 1$)

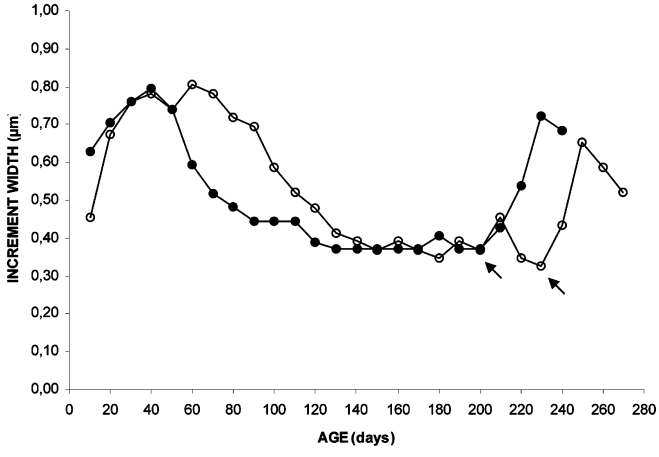

Fig. 7 *Conger conger*. Otolith increment width versus age of two individuals: 126.5 mm (●) and 114.0 mm (○) long (*arrows* sharp increases in the increment width)

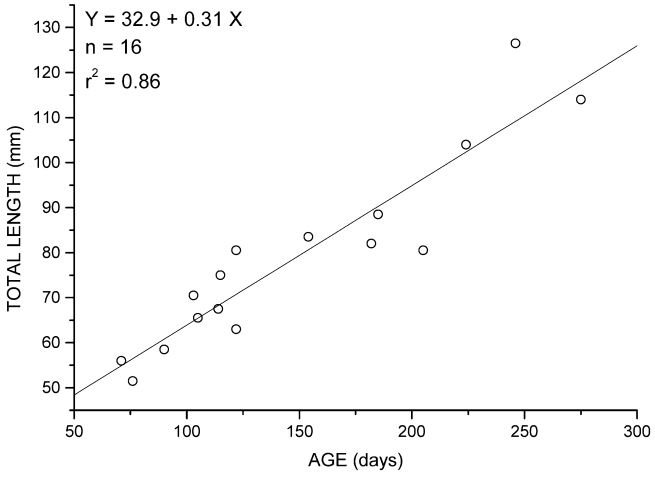

Fig. 8 *Conger conger*. Relationship between larval length and age (*line* represents a least squares fit of the linear equation, $P < 0.001$)

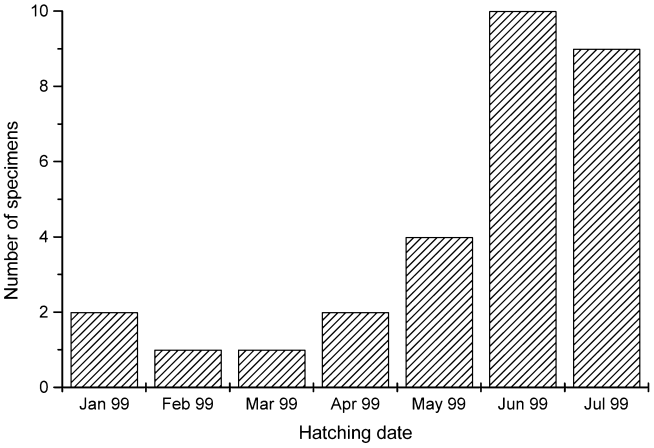

Fig. 9 *Conger conger*. Frequency distribution for eels on the estimated hatching dates

their otoliths had been damaged during the formalin-fixation process, were estimated from the equation obtained between size and age of the larvae ($TL = 32.9 + 0.31AGE$) (Table 1). Although, hatching occurred from January to July, one hatching peak is observed during the summer season (June and July) (Fig. 9).

Discussion

Conger conger leptocephali were identified by the external body morphology, pigmentation and mainly by counting myomeres. The descriptions of morphological features and pigmentation patterns of the leptocephali agree well with those made by D'Ancona (1931).

The number of myomeres (TNM, PDM, PAM and LVBV) of the leptocephali is in agreement with the data reported by several authors (D'Ancona 1931; Schmidt 1931; Castle 1970; Strehlow et al. 1998; Correia et al. 2002). However, our values appear to be more consistent than the existent data, probably because of less error in myomere counting. Differences in mean myomere counts are common in the literature. According to Vladykov and March (1975), variations between myomere frequencies could be attributed to several causes: counting technique, different numbers of specimens, variation in size of specimens and difference in collecting localities. Recent studies on American and European eels (Kleckner and McCleave 1985) and also on the European conger eel (Strehlow et al. 1998) show that there is no correlation between the myomere counts and the length of the leptocephali. The most probable cause of the literature discrepancies in myomere frequency distributions of leptocephali is the result of faulty counting techniques (Kleckner and McCleave 1985; Correia et al. 2002).

The position of the LVBV according to Smith (1979) is also a characteristic to be looked at, when identifying leptocephali. Our LVBV values are highly consistent, suggesting that this parameter, like the TNM, can be used for species identification.

The PAM/TNM ratio has been used as a criterion for the metamorphic stage (Tanaka et al. 1987; Correia et al. 2002), since it diminished drastically in the course of metamorphosis as a result of the anus beginning to move to a more anterior position in Congridae leptocephali (Otake et al. 1997; Strehlow et al. 1998). The PAM/TNM ratio obtained for this stage (0.78) is similar to the value (0.77) reported by Strehlow (1992) and nearly double the observed value (0.36) for the metamorphic stage (Correia et al. 2002). The PAM/TNM (and also the PAL/TL) ratio in *C. conger* appears to be almost constant throughout the leptocephalus (or premetamorphic) phase, but diminishes during the metamorphic stage (Correia et al. 2002). Since the PAL/TL ratio is correlated with the PAM/TNM, it has been successfully used in classifying metamorphosing stages in *C. myriaster* (Yamano et al. 1991) and in *C. conger* (Correia et al. 2002). The PAL/TL has also the advantage of being more easily obtained, namely in specimens poorly preserved (Correia et al. 2002).

The smallest PAM/TNM (PAL/TL) value for premetamorphic larvae was 0.77 (0.86), and, since the largest PAM/TNM (PAL/TL) observed value for metamorphic larvae was 0.42 (0.55) (Correia, unpublished data), these results suggest that *C. conger* leptocephali began to metamorphose at PAM/TNM (or PAL/TL) values between 0.77 and 0.42 (or 0.86 and 0.55). Lee and Byun (1996) reported, for instance, that *C. myriaster* leptocephali began to metamorphose at PAM/TNM values between 0.82 and 0.74.

The length at which the *C. conger* leptocephali undergo metamorphosis appears to be between 155 and 165 mm, based on the largest reported premetamorphic (Strehlow et al. 1998) and metamorphic leptocephali (Correia et al. 2002), with 165 and 153 mm length, respectively. About 90% of the larvae had a length between 50 and 90 mm, with an overall mean value of 73.5 mm long, suggesting that the majority of the

leptocephali in our collection are in the middle of the premetamorphic leptocephalus stage.

The length-frequency distribution of the conger eel larvae shows one peak around 70 mm, and is positively skewed as a result of the three largest individuals (104, 114, 126.5 mm). These older specimens (224, 275 and 246 days old, respectively) may have a different migration route and environmental history.

The negative correlation between the HL/TL and HL indicates that the head grows more slowly than the whole body, leading at the end of this larval stage to a typically large leptocephalus with a short head.

The relationship between larval/otolith size and age indicates that older specimens are larger and have bigger otoliths, as expected if somatic growth is correlated with otolith growth.

The otolith morphology pattern of *C. conger* leptocephali is similar to that observed by Antunes (1994) and described in other anguilliform species (Tabeta et al. 1987; Lecomte-Finiger and Yahyaoui 1989; Wang and Tzeng 1998, 2000). The majority of the specimens presented a width-increment profile identical to that reported by Antunes (1994). However, the two largest specimens presented a peripheral zone in the otoliths with wide rings, i.e. a similar pattern recently described in the countable zone of the metamorphic conger eel sagittae (Correia et al. 2002). These wide increments were unexpected since they have often been associated with the onset of metamorphosis in several anguilliform fishes, namely 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). Since these large specimens (114.0 and 126.5 mm long), based on their morphology (i.e. on PAL/TL and PAM/TNM ratios of 0.86–0.87 and 0.77–0.78, respectively), are without any doubt in the premetamorphic larval stage, these results could indicate that the internal signal, marked on the otolith surface, for the beginning of metamorphosis occurs prior to the body morphological changes. However, further studies, namely on otolith Sr:Ca ratios, are needed to validate or refute this hypothesis.

The existing growth curves for anguilliform leptocephali are based on regressions of the length on the estimated age or date of capture. However, they are usually based on few data and much speculation. The somatic growth rate estimated from the linear regression (0.31 mm day^{-1}) falls within the ranges reported by several authors for other anguilliform species: *A. rostrata*, 0.24 (Kleckner and McCleave 1985), 0.22 (Tesch 1998) and 0.19 mm day^{-1} (Boëtius and Harding 1985); *A. anguilla*, 0.15 (Tesch 1998) and 0.18 mm day^{-1} (Boëtius and Harding 1985); and *Anguilla* sp., 0.38 mm day^{-1} (Castonguay 1987). The growth rate of 0.31 mm day^{-1}, however, appears somewhat low for the following reasons. (1) The specimen sizes of the leptocephali are underestimates, since they have not been adjusted to account for shrinkage due to the fixation and preservation method, i.e. specimen shrinkage would underestimate the slope and intercept of the linear regression equation. (2) *C. conger* leptocephali undergo metamorphosis between 150 and 160 mm (Strehlow et al. 1998). A leptocephalus growing 0.31 mm day^{-1} would reach metamorphosis length in about 13 months. However, the conger eel leptocephalus time duration was recently estimated to be between 6 and 9 months (Correia et al. 2002). (3) The predicted size at hatching, 32.9 mm long (*Y*-intercept), makes no sense when compared with the reported values for related species. Observed size at hatching of experimentally reared larvae of *A. anguilla* (Bezdenezhnykh et al. 1983) and *A. japonica* (Yamamoto et al. 1975) are 2.7 and 2.9 mm, respectively. (4) Finally, the growth of the conger leptocephali probably is not linear through the entire premetamorphic phase. The growth rates of young leptocephali are comparatively higher than those of older ones, as indicated by the negative correlations between SGR (and OGR) and age. To assume a simple linear regression is probably not suitable for a leptocephali growth curve.

The larvae of *C. conger* and *C. triporiceps* are very similar in morphology and number of myomeres, in contrast to the adults of both species, which differ distinctly with regard to the number of their sensory pores and in their dentition (Strehlow et al. 1998).

The existing distinction of the American conger eel leptocephalus, *C. triporiceps*, from the European conger eel leptocephalus, *C. conger*, based on the catch locations, in the West versus the East Atlantic (McCleave and Miller 1994; Strehlow et al. 1998), is from our point of view scientifically poor. The aforementioned authors used Smith's (1989) criterion to identify both larval species; however, Smith's (1989) work only describes the western North Atlantic conger eel leptocephalus species, i.e. *C. oceanicus*, *C. esculentus*, *C. triporiceps*, and leptocephali of Congridae genus A species A, without any reference to its European congener, *C. conger*. In fact, the only study, we know of that describes the larval development of *C. conger* in detail, and which agrees well with our descriptions of the leptocephalus (present study) and the metamorphic stage (Correia et al. 2002), is the work of D'Ancona (1931). From the bibliographic descriptions available, these larvae are very similar, with one important difference: *C. triporiceps* do not have any lateral pigment (Smith 1989), in contrast to a fully developed leptocephalus of *C. conger*, which presents a series of large dots along the lateral line, from the caudal extremity to a fairly considerable distance from the head (D'Ancona 1931). According to these two descriptions the western North Atlantic species, *C. triporiceps*, can be easily distinguished from the eastern North Atlantic species, *C. conger*, based on the absence or presence of lateral pigmentation, respectively. To overcome the unequivocal systematic status of the larvae of *C. triporiceps* and *C. conger* with similar TNM, molecular biological investigations should be applied.

Interpretation of the daily increments of the leptocephali is extremely important, because the biological

oceanographic study of the early life cycle of these fishes is extremely difficult and expensive. Assuming that the micro-increments are deposited on a daily basis, although the deposition rate of the rings has not been validated directly in this species, age of the conger eel ranged between 71 and 275 days (including the additional 5 day yolk-sac period). These data indicate that hatching dates for the European conger eel varied greatly between early January and late July, with a visible peak in the summer season. This result agrees with observations made from the capture of small leptocephali in the Mediterranean Sea (Schmidt 1931) and from the temporal and spatial distribution of conger eel larvae in the NE Atlantic (Strehlow et al. 1998).

Naturally spawning conger eels have not yet been observed, and reports about the capture of maturing conger eels are restricted to the Mediterranean (Cau and Manconi 1983) and to a single female specimen in the Irish Sea (Fannon et al. 1990). It is commonly suggested, in some textbooks, that the European conger eel, *C. conger*, has several different spawning places. Lythgoe and Lythgoe (1971), Bagenal and Kenney (1973) and Wheeler (1985) found that conger eels spawn once during the summer, at great depths (3000–4000 m) in the NE Atlantic, between Gibraltar and the Azores. Spawning areas in the Mediterranean have also been reported by Wheeler (1985). However, these authors did not mention any references to sustain their assumptions. Nowadays, 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 leptocephalus 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). Recently, Strehlow et al. (1998), based on spatial and temporal distributions of conger eel leptocephali identified in oceanographic collections, 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, namely to southern Portugal and Spain, extending into the east and central zones of the Atlantic. The conger eel has a second growth period, lasting until the beginning of summer (130–150 mm to a maximum length of 165 mm), 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). The exact timing of metamorphosis, however, remains unknown, since age determination of conger eels by otoliths is difficult due to an uncountable area in the sagittae presumably structured during metamorphosis (Correia et al. 2002). In short, the premetamorphic leptocephali of *C. conger* appear to be restricted to the continental slope (Strehlow et al. 1998; present study), suggesting that the leptocephali do not enter the continental shelf and coastal waters until they have attained the metamorphosing stage, as previously suggested by Correia et al. (2002).

The leptocephali occupy a discrete depth stratum, which changes daily and ontogenetically (Schoth and Tesch 1984; Castonguay and McCleave 1987). Fishing was largely carried out in the upper 200 m of the water column, a depth range typically inhabited by leptocephali (Tesch 1980; Kracht 1982; Schoth and Tesch 1982, 1984; Kleckner and McCleave 1985; Kajihara et al. 1988; Strehlow et al. 1998), and mainly at night, since net avoidance by anguilliform fishes during daytime has been reported (Schoth and Tesch 1984; Castonguay and McCleave 1987; Tesch and Wegener 1990). As the RMT8 was not equipped with an opening–closing device, only a rough idea of the optimal fishing depth can be presented, and therefore conclusions on exact depth of capture are not possible.

The size and abundance of specimens in a collection may be influenced by gear selectivity, net avoidance, depth range sampled and trawl pattern (Kleckner and McCleave 1985). Number of catches of European conger eel leptocephali in the present study were too low to permit detailed analysis of the distribution; qualitative data between the different hauls were not fully comparable and could not be used for absolute abundance estimates. However, 62% of the larvae were caught in four hauls, suggesting the existence of aggregations. Three of these four hauls were performed at depths ranging from 40 to 60 m, i.e. well above the seasonal thermocline. There is a reported correlation between the mesh size and the length of larvae captured: 500 and 1800 μm mesh nets are appropriate for capturing leptocephali as small as 5 mm long (Wippelhauser et al. 1985) and 10 mm long (Castonguay and McCleave 1987), respectively. The net used in this work had a 4500 μm mesh, which probably does not efficiently catch conger leptocephali smaller than 50 mm long. So, negative stations at night are used only as evidence of the absence of larger leptocephali. However, since there is an overall scarcity of leptocephali, negative stations could also easily occur by chance.

As we have already mentioned, it has been suggested that around November the leptocephali of *C. conger*, with 30 mm length, leave Gibraltar and spread westward and northward (Strehlow et al. 1998). The transfer of European conger eel from the spawning area (Mediterranean), via the Strait of Gibraltar, into the Central and NE Atlantic may be partially explained as passive transport based upon known surface currents.

The warm, saline Mediterranean Water (MW) flows into the Gulf of Cadiz through the Strait of Gibraltar and descends to around 800–1200 m. This water then spreads out as the MW tongue into the North Atlantic, southward towards the Canary Islands, westward to the Azores and northward along the Iberian Peninsula (Daniault et al. 1994). Here, the Portuguese Circulation is characterized by an opposing bizonal current pattern that flows parallel to the Iberian coast, a southward coastal upwelling in summer and a northward flow of

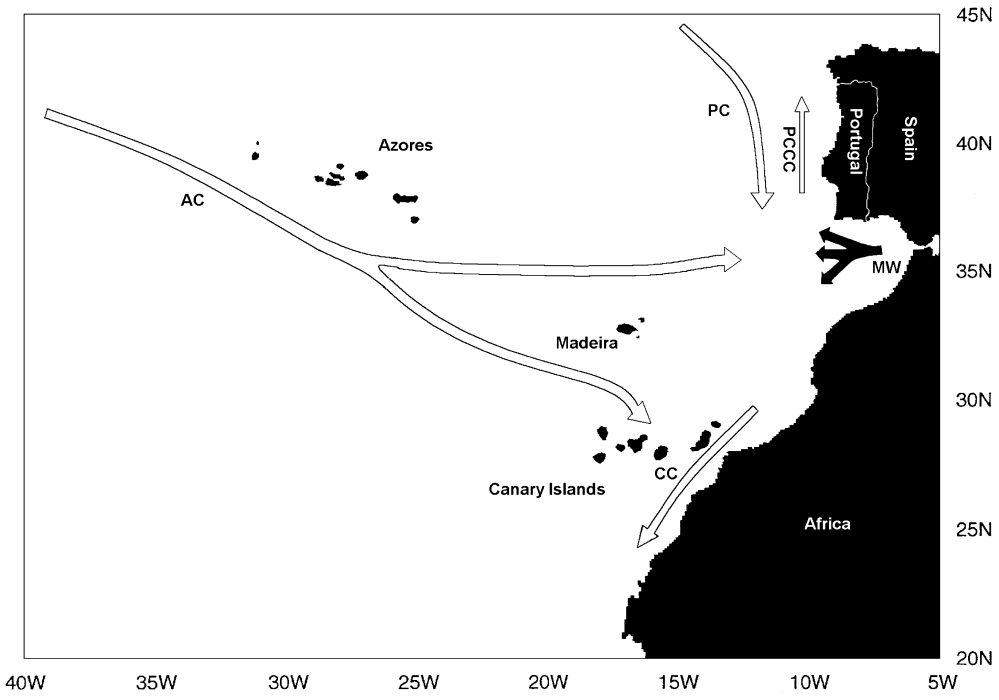

Fig. 10 *Conger conger*. Schematic diagram of the eastern North Atlantic Circulation between the Azores, the Canary Islands and the Strait of Gibraltar (*open* and *solid arrows* represent the surface and deep currents, respectively; *AC* Azores Current; *CC* Canary Current; *MW* Mediterranean Water outflow; *PC* Portuguese Current – summer season; *PCCC* Portuguese Coastal Counter Current – winter season)

the Portuguese Coastal Counter Current in winter (Fíuza 1984) (Fig. 10).

If the conger leptocephali leave the Strait of Gibraltar in November, as suggested, they could take advantage of the Portuguese Coastal Counter Current, the prevailing flow in the winter, from which larval dispersal could take place in the northwest direction. However, an unsolved question remains: must all the leptocephali leave the Mediterranean toward the continental Iberian slope, or, on the contrary, can they complete their entire larval life cycle inside the Mediterranean? So, the pathways and orientation mechanisms utilized during the larval migration are not fully understood.

In fact, it is difficult to explain how our specimens reached the Azores area from the Mediterranean based on the prevailing NE Atlantic circulation pattern (Fig. 10). The Azores Current (AC) forms from a southern branch of the Gulf Stream system and passes just south of the Azores Archipelago to the east of the Mid-Atlantic Ridge. It then splits into a northern branch along 35°N, which meanders eastward towards the Gulf of Cadiz, and a second branch, which moves southeastward towards the Canary Islands (Käse and Krauss 1996). The eastward main jet of the AC (around 32–33°N at 28°W and 33–34°N at 26°W) with a transport of 26 sv (near 28°W) and mean speed on the order of 10 cm s^{-1} (at 200 m depth) is associated further west (26°W) with adjacent westward-flowing countercurrents on each side, resulting in recirculation both north (counterclockwise circulation) and south (clockwise circulation) (Pingree 1997). Some of the water that reaches the Gulf of Cadiz is entrained in the Gibraltar outflow of MW, which spreads at depth away from the Strait of Gibraltar (Baringer and Price 1997), or contributes to a poleward-flowing upper layer of Moroccan slope (Pingree 1997). The southern branch of the AC (27°N; 27°W;) as it reaches the Canary Archipelago, joins the southward-flowing coastal Canary Current along NW Africa (Klein and Siedler 1989; Johnson and Stevens 2000). In this region water was flowing south–southwest (mean ~3 cm s^{-1}) parallel to the African coast to 25°N west of Canary Islands. This flow boundary in the east, near 20°W, marks the eastern limit of water from the southern part of the AC, extending south from Madeira (Pingree 1997). The spreading of the core of the MW from the Gulf of Cadiz under the AC at 35°N towards the Azores does not quite reach the Azores or Madeira, but south of Madeira flows nearer the African coast. However, very stable eddies that form in the Gulf of Cadiz can carry cells of MW greater distances from Gibraltar (Johnson and Stevens 2000).

We conclude that there is little chance that leptocephali, as small as 51.5 mm, leaving the known Mediterranean spawning ground might reach the Azores Archipelago. This is a distance of about 3000 km, which would have to be covered in about 2 1/2 months (estimated age of the 51.5 mm long specimen), and the known North Atlantic oceanographic currents circulate in the opposite direction. This larval migration pathway could be possible by a westerly dispersal of leptocephali, driven by localized currents generated by mesoscale eddies, but only for the oldest specimens, or if the larvae had an oriented and active swimming behavior. These data, however, suggest that the *C. conger* has another spawning area somewhere near the Azores Islands. Future research on conger eel reproductive biology must include extensive sampling of leptocephali in the Azores and Mediterranean Sea and analysis in light of current physical oceanographic knowledge, to provide new in-

sights into the spawning and larval migration of European conger eel.

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