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The timing of metamorphosis and growth rates of American and European eel leptocephali: A mechanism of larval segregative migration

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Abstract

Elvers of the American eel *Anguilla rostrata* (Le Sueur) and of the European eel *Anguilla anguilla* Linnaeus were collected, mostly during the 1995 fishing season, from six estuaries along the Atlantic coast of North America and from five European estuaries. The time of metamorphosis from leptocephalus to glass eel was determined from otolith daily growth increments in which the increment width and strontium:calcium ratios changed drastically. The overall mean age of European elvers was 350 days at metamorphosis (T_m) from leptocephalus to glass eel and 448 days at estuarine arrival (T_e), with 98 days between metamorphosis and estuarine arrival (T_{e-m}). These ages were all significantly greater than those of American elvers (T_m was 200 days; T_e , 255 days and T_{e-m} , 55 days) ($p < 0.001$), while growth rate of the American eel (0.21 mm per day) was greater than that of European eel (0.15 mm per day) ($p < 0.001$). The spawning season back-calculated from the daily age of elvers was March–October for the American eel and November–July for the European eel. The differences in leptocephalus stage duration and growth rate are the principal factors determining the segregation of migrating American and European eels. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Otolith; Daily growth increment; Age; Growth rate; Metamorphosis; American eel; European eel

1. Introduction

American eel (*Anguilla rostrata*) and European eel (*Anguilla anguilla*) are temperate catadromous fishes, spawning in the southwestern Sargasso Sea and growing in the inland freshwaters of eastern North America and western Europe (Schmidt, 1925; Tesch, 1977;

Kleckner et al., 1983; Kleckner and McCleave, 1988). They are distinct, genetically different species (Campanini and Rodinó, 1980; Avise et al., 1986), rather than environmentally determined, eco-phenotypic species (Tucker, 1959). After hatching, larvae (leptocephali) of American eel are transported by the North Equatorial Current and Gulf Stream to the continental shelf of North America, while European eel larvae are transported farther by the North Atlantic Current to northern European countries. The larvae metamorphose into glass eels in coastal waters. Glass eels become pigmented elvers when they enter estuaries. During the migration from the oceanic spawning

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ground to the continental shelf, the eel larvae have no orientation ability and passively drift with the oceanic current (Schmidt, 1925; Harden Jones, 1968; Kleckner et al., 1983). Both species of eel leptocephali are intermixed in spatial and temporal distribution (Kleckner and McCleave, 1985); however, in Europe and North America, the non-native species of eel is rarely found (Tesch, 1977).

Schmidt (1922, 1925) suggested a mechanism to explain the separation of the two species in continental fresh waters. He proposed that American eel larvae grow more rapidly and are ready to metamorphose off the North American coast some 12 months after hatching; while this process takes much longer for the European eel, which cannot metamorphose until they are near Europe, some three years after hatching. On the basis of the data of Schmidt (1925), Harden Jones (1968) and Tesch (1977) speculated that there was a faster growth rate in *A. rostrata*. However, after re-examining Schmidt's data, Boëtius and Harding (1985) concluded that the growth rate of *A. rostrata* (5.6 mm total length (TL) per month) is not significantly different from that of *A. anguilla* (5.3 mm TL per month). Kleckner and McCleave (1985) and Wipfelhauser et al. (1985) estimated a growth rate of 0.24 mm TL per day (7.2 mm TL per month) for *A. rostrata* by regressing total length on the numerical date of collection for a large number of specimens. Thus, the growth rates estimated by different authors were not consistent and the timing of metamorphosis of leptocephalus was still undetermined. It is still impossible to substantiate Schmidt's hypothesis that the growth rate and the timing of metamorphosis are the principal factors in determining the segregation of migrating American and European eel larvae.

The daily growth increment in otolith is one of the best methods to study the daily age, hatching date, and growth rate of larval fish (Pannella, 1971; Campana and Neilson, 1985; Jones, 1992) and to study the age of an eel at metamorphosis from leptocephalus to glass eel (Otake et al., 1994; Tzeng and Tsai, 1994; Cheng and Tzeng, 1996; Tzeng, 1996; Arai et al., 1997; Wang and Tzeng, 1998). The daily age and growth rate of American and European eels leptocephali and elvers have been studied by otolith daily growth increments (Castonguay, 1987; Lecomte-Finiger, 1992; Martin, 1995); however, the growth rate and the timing of metamorphosis of leptocephali of American and Eur-

opean eels in relation to species separation during larval migration has not been clarified.

This paper compares the timing of metamorphosis and growth rate of leptocephali for American and European eels by examining the daily growth increments and Sr/Ca ratios in elver otoliths. It also examines Schmidt's hypothesis of larval segregative migration for these species.

2. Material and method

Daily growth increments in otoliths of American and European elvers were examined using the specimens collected from six estuaries on the east coasts of Haiti, US, and Canada and from five estuaries on the west coasts of Portugal, France, UK, Ireland, and Sweden (Fig. 1). All of the elvers were collected in the peak fishing season except those from Portugal (Table 1). The elvers were preserved in 95% ethanol, with lengths measured to 0.1 mm after alcohol fixation. Pigmentation stages (the pigment distribution on body surface, which indicates the developmental stage from glass eel to elver) were assessed according to the Strubberg (1913). Newly arrived elvers in coastal waters are in stage VA, without external pigments on their body surfaces except for caudal spots. In stage VB, the eel becomes pigmented. A subsample of elvers was randomly selected and their sagittal otoliths were extracted from the vestibular apparatus and prepared for microchemistry analysis and age determination. Procedures for embedding, sectioning, polishing, coating and etching otolith followed those described by Tzeng (1990, 1996) and Tzeng and Tsai (1992, 1994).

Otolith radius and daily growth increments in otolith were measured as shown in Fig. 2. The daily age of elvers at estuarine arrival, and the daily age of leptocephalus at metamorphosis to the glass eel stage were inferred from the daily growth increments from the primordium to otolith edge, and to the position where increment width and Sr/Ca ratios dramatically changed, respectively (Cheng and Tzeng, 1996; Wang and Tzeng, 1998). The Sr/Ca ratios and daily growth increments in otoliths of the fish were measured by electron probe micro-analyzer (EPMA Model 8800) and scanning electron microscope (SEM, Hitachi S-520). Sr and Ca were measured

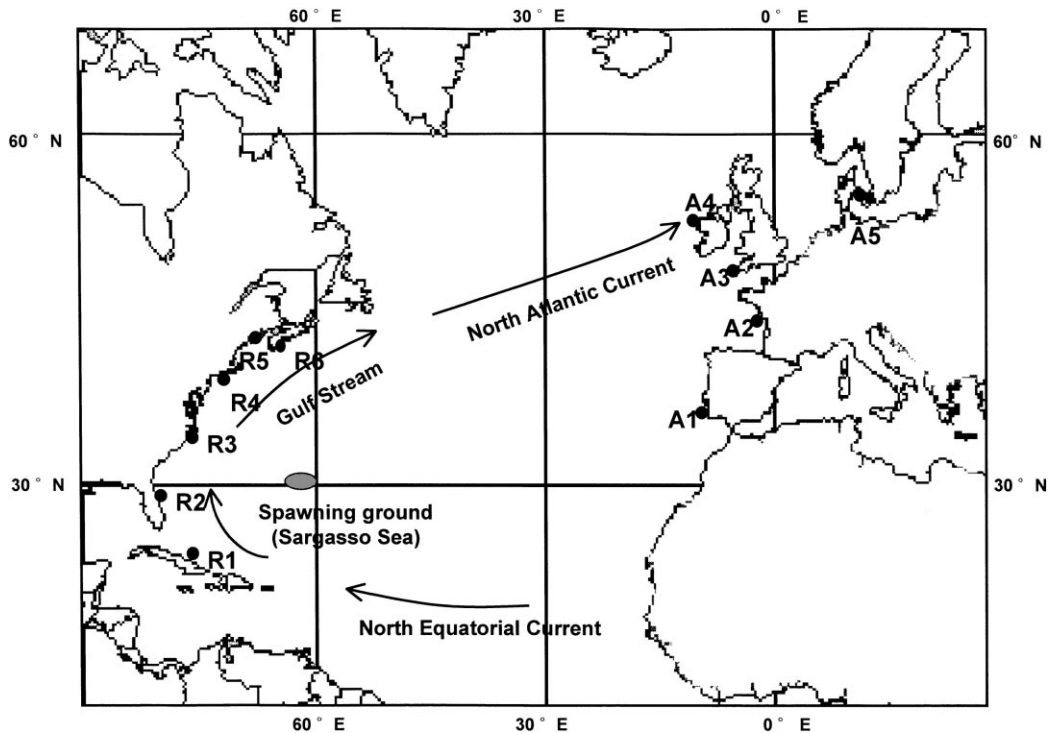


Fig. 1. Sampling sites of elvers of *A. rostrata* (R1: Haiti; R2: Florida; R3: North Carolina; R4: Rhode Island; R5: New Brunswick; R6: Nova Scotia) and *A. anguilla* (A1: Portugal; A2: France; A3: England; A4: Ireland; A5: Sweden).

along the otolith maximum axis through the primordium with a beam condition of $0.01 \mu\text{A}$ and 15 kV. At intervals of approximately $10 \mu\text{m}$, the electron beam was focused on an area approximately $5 \mu\text{m}$ in dia-

meter (Tzeng and Tsai, 1994; Tzeng, 1996; Wang and Tzeng, 1998).

The estimation of daily ages from daily growth increments and the calculation of otolith and somatic

Table 1
Sampling sites, sample sizes, sampling dates, and total length (TL) of elvers (sampling sites in Fig. 1)

| Species | Sampling site | <i>N</i> | Sampling date | Mean \pm S.D., TL |
|--------------------|--|----------|------------------|---------------------|
| <i>A. anguilla</i> | | | | |
| A1 | Minho Rio, Portugal | 50 | September 1995 | 68.61 \pm 3.02 |
| A2 | Vilaine River, France | 100 | 5 April 1995 | 66.76 \pm 3.47 |
| A3 | Severn River, UK | 170 | 1 April 1995 | 64.98 \pm 2.97 |
| A4 | Shannon River, Ireland | 57 | 9 April 1994 | 66.36 \pm 2.77 |
| A5 | Viskan River, Sweden | 63 | 13 April 1995 | 68.11 \pm 2.58 |
| <i>A. rostrata</i> | | | | |
| R1 | Haiti | 115 | 17 December 1995 | 47.79 \pm 2.33 |
| R2 | FL, USA | 4 | 28 February 1995 | 49.03 \pm 2.58 |
| | | 50 | 22 January 1997 | |
| R3 | NC, USA | 50 | 22 March 1995 | 48.19 \pm 2.87 |
| R4 | Annaquatucket River, Rhode Island, USA | 100 | 14 April 1995 | 58.52 \pm 2.83 |
| R5 | Musquash River, NB, Canada | 67 | 28 April 1995 | 59.99 \pm 3.15 |
| R6 | East River, NS, Canada | 93 | 29 May 1995 | 59.64 \pm 2.42 |

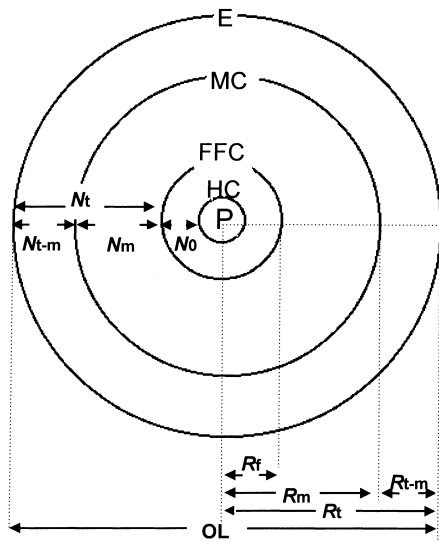


Fig. 2. A schematic diagram of measurements of radii and counts of daily growth increments in elver otoliths (P: primordium; HC: hatching check; FFC: first feeding check; MC: metamorphosis check; E: edge; R_t : radii from primordium to the first feeding check; R_m : to the metamorphosis check; R_t : radii from primordium to the otolith edge; R_{t-m} : distance from the metamorphosis check to the otolith edge; OL: otolith length; N_m , N_t and N_{t-m} : counts of daily growth increments corresponding to the radii of R_m , R_t and the section (R_{t-m}) between MC and E, respectively).

growth rates of the elvers followed those described by Wang and Tzeng (1998). Because the counting of daily growth increments was time consuming and the increments near the metamorphosis area on the otolith were often diffusive and obscure, the daily age of samples without counting daily growth increments was calculated from otolith growth rate and otolith radius. The regression of total length on pigment stage of the elvers was calculated to determine whether the elver size depends on their pigment stages. Differences in total length, daily age and growth rate between American and European elvers were tested by analysis of variance (ANOVA) (Sokal and Rohlf, 1967).

3. Results

3.1. Geographic cline in size of elvers

Mean total lengths of elvers collected from five estuaries in the European countries (range 65.0–

68.6 mm) were significantly greater than for elvers in six estuaries of the North American East Coast (range 47.8–60.0 mm) (Table 1). Multiple range analysis indicated that the mean length of American elvers increased with the distance from the spawning ground, from 47.8 to 49.0 mm in the south (R1–R3), to 58.5–60.0 mm in the north (R4–R6). The mean length of European elvers increased from 65.0 to 66.8 mm in the mid-European countries (A2–A4), to 68.6 mm in the north and 68.1 mm in the south of its geographic range (A1, A5) (Fig. 3).

The pigment development stage of elvers at estuarine arrival was mostly VB for Portugal (A1), France (A2) and Sweden (A5), but VB and VIA1 for Florida (R2) and VIA1–A3 for the other seven sites (Fig. 4). The regression of total length on pigment stage of elvers was not significant for American elvers in the south ($R^2=0.0022$, $p>0.05$) and north ($R^2=0.0002$, $p>0.05$) and European eel ($R^2=0.0346$, $p>0.05$), indicating that the geographical cline in size of elvers was independent of pigment development stage.

3.2. Changes in otolith growth increment pattern and Sr/Ca ratio

The width of otolith growth increments was wider (about twofold) and increment numbers were less in American eel elver than in European eel elver (Figs. 5 and 7). However, the patterns of growth increments and Sr/Ca ratios from the primordium to the otolith edge were similar between these two elvers (Figs. 5–7). From primordium to otolith edge, three different otolith growth increment patterns occurred, each pattern representing an ontogenetic development stage (Fig. 5). Part I, from primordium to the first feeding check (FFC), is deposited during the yolk-sac stage and no growth increment was discernible (Fig. 5). The Sr/Ca ratio was lower because the yolk-sac was of freshwater maternal origin (Fig. 6). Part II occurs from FFC to the metamorphosis check (MC) (Fig. 5), and is deposited during the leptocephalus stage. The Sr/Ca ratio in otolith of the stage increased with growth, but drastically decreased when leptocephalus starts metamorphosis (Fig. 6). MC was formed after leptocephalus complete metamorphosis. Beyond MC, otolith growth increments became wider (Fig. 7). MC occurred slightly later than the peak of Sr/Ca ratios. The time between the peak of Sr/Ca ratios and the MC

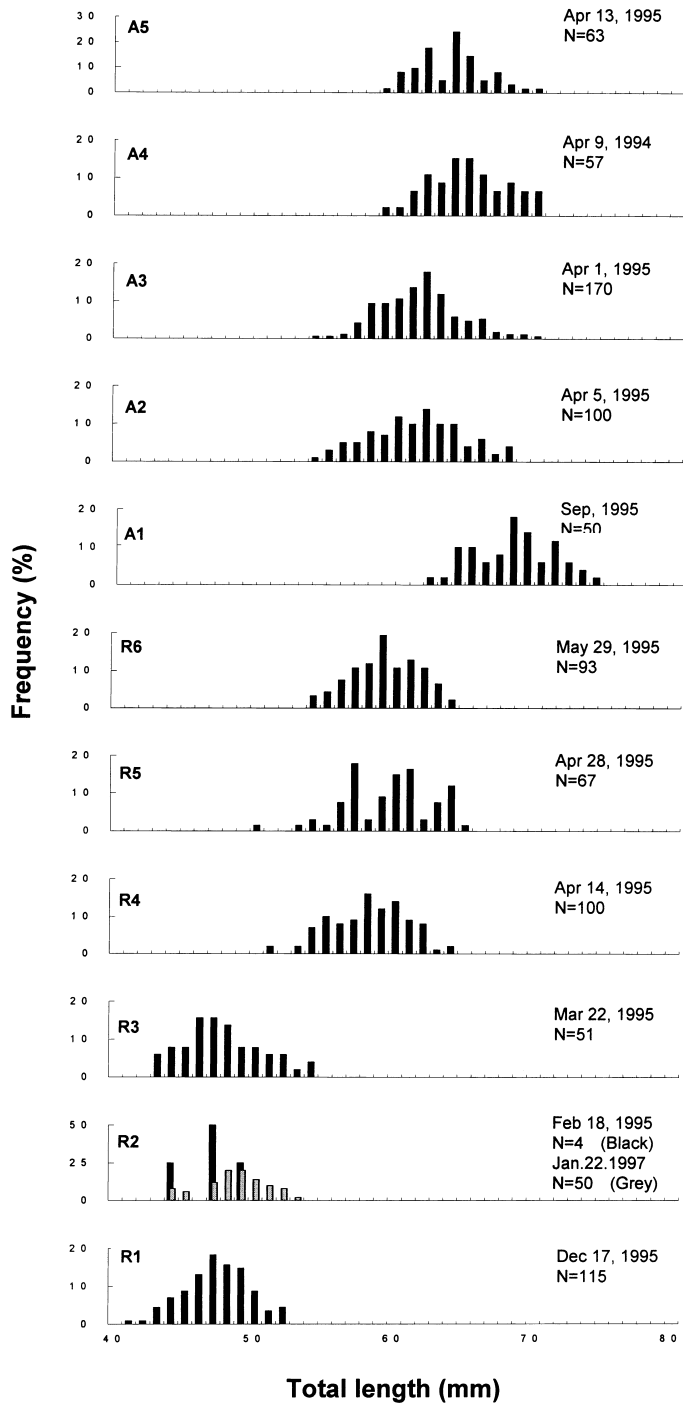


Fig. 3. Total length frequency distribution of *A. anguilla* and *A. rostrata* elvers from eleven estuaries (sites A1–A5 and R1–R6 refer to Fig. 1).

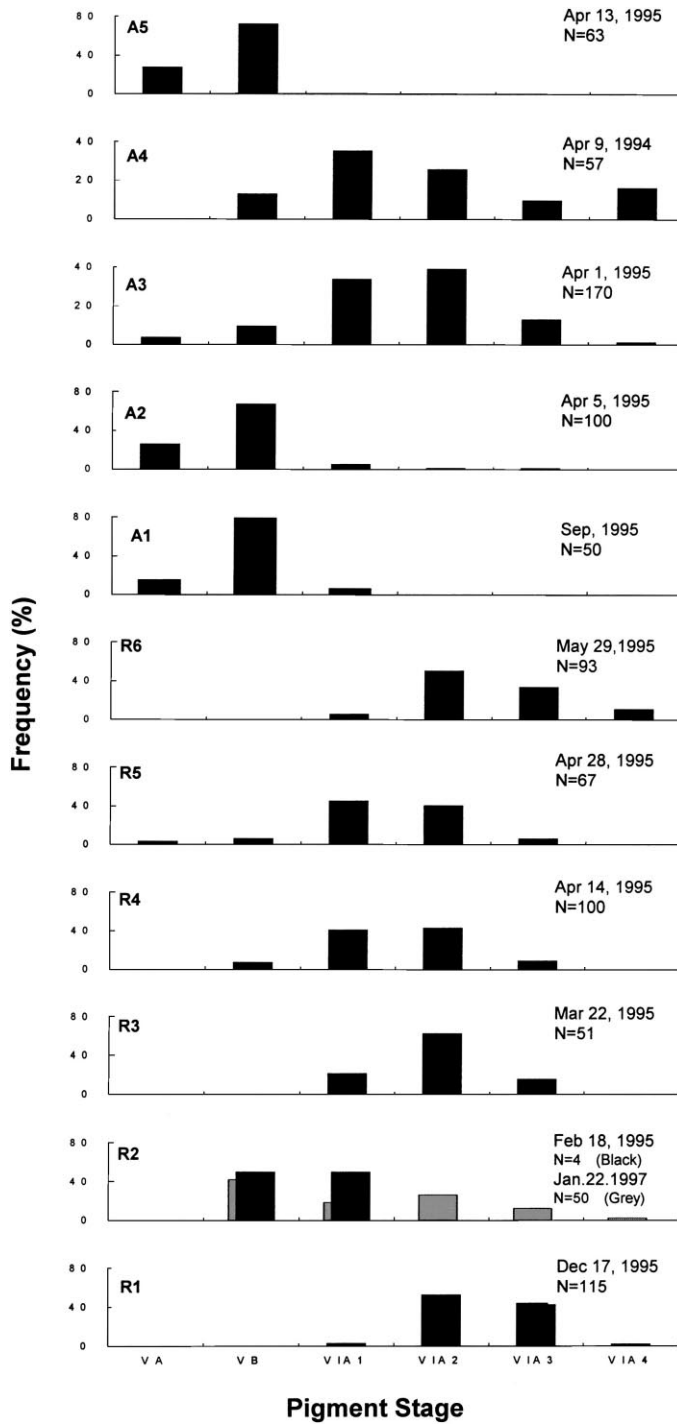


Fig. 4. Pigmentation stage frequency distribution of *A. anguilla* and *A. rostrata* elvers from 11 estuaries (sites A1–A5 and R1–R6 refer to Fig. 1).

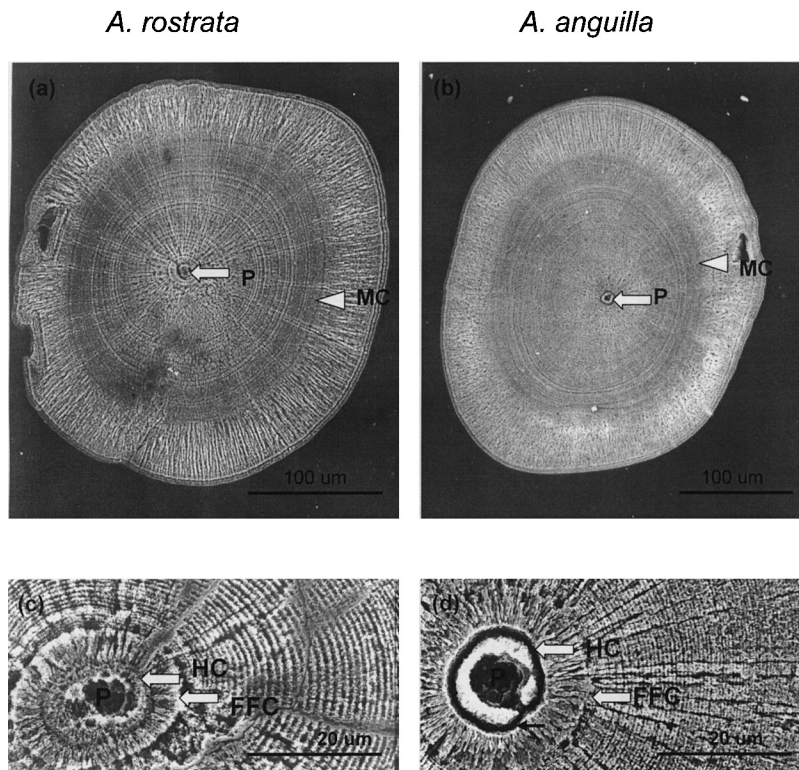


Fig. 5. SEM micrographs illustrating the daily growth increments in otoliths of elvers of *A. rostrata* from Nova Scotia (a: site R6, 47.94 mm TL) and *A. anguilla* from France (b: site A2, 68.34 mm TL). c, d: partial magnification of a, b. (P: primordium; HC: hatching check; FFC: first feeding check; MC: metamorphosis check).

corresponds to the duration of metamorphosis of the leptocephalus, it was estimated approximately one month. Part III occurs from MC to the otolith edge and has a wider growth increment and a crystalline pattern that changes from circular to radial (Figs. 5 and 7). This part was deposited in the glass eel stage during its inshore migration toward decreasing salinity and thus Sr/Ca ratios were gradually decreased (Fig. 6).

The time at metamorphosis from leptocephalus to glass eel and the otolith growth increment width varied greatly between individuals. At metamorphosis, American eel larvae were younger than European eel larvae, with approximately 150–250 growth increments versus 320–400 growth increments (Fig. 7). The age of leptocephalus at metamorphosis was determined from the number of daily growth increments between the primordium and metamorphosis check where the increment pattern and Sr/Ca ratios dramatically changed.

3.3. Comparison of otolith radius, daily age and growth rate between species

The overall mean radius of the nucleus (R_f) of the otoliths of American elvers was 9.5 μm (range 8.8–10.5 μm), and was 9.8 μm (range 9.1–10.8 μm) for European elvers (Table 2). The overall mean of R_f did not differ significantly between the two species ($p=0.08$). Similarly, the overall mean radius from the metamorphosis check to the otolith edge (R_{t-m}) was 64.7 μm (range 60.7–70.7 μm) for American elvers, and 59.5 μm (range 54.3–66.6 μm) for European elvers ($p=0.32$). In contrast, the overall mean radius of 106.1 μm from primordium to the metamorphosis check (R_m) and 165.7 μm to the otolith edge (R_t) for European elvers was significantly larger than for American elvers (92.6 and 157.3 μm) (both $p<0.001$).

The overall mean age of European elvers at metamorphosis (T_m) was 350 days (range 319–397), 448

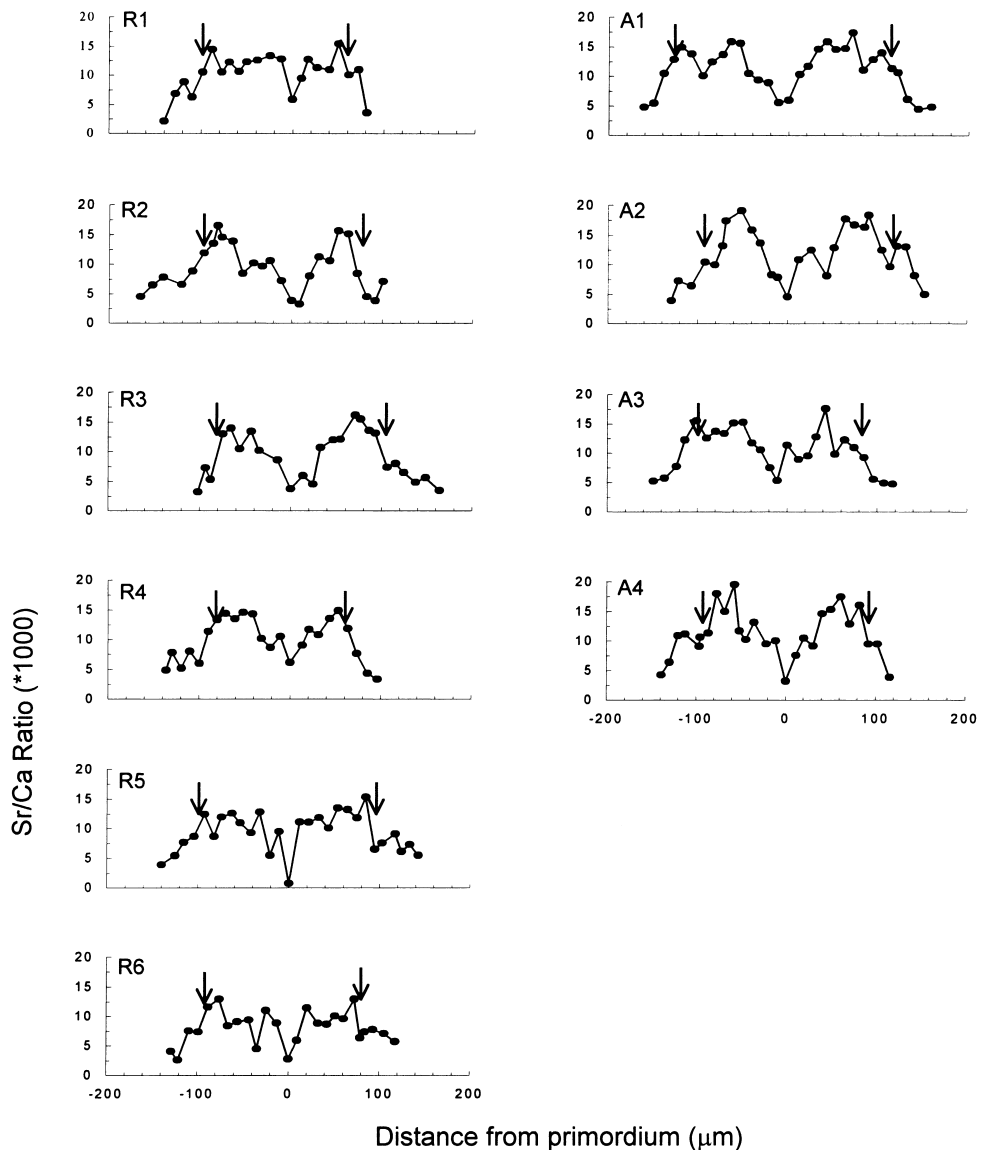


Fig. 6. The Sr/Ca concentration ratios measured along the maximum radius of the otoliths of *A. rostrata* elvers from six estuaries (sites R1–R6) and *A. anguilla* elvers from four estuaries (sites A1–A4). The primordium is denoted by zero on the X-axis. Arrows indicate locations of metamorphosis check.

(range 420–468) at estuarine arrival (T_t) and 98 (range 71–105) between metamorphosis and estuarine arrival (T_{t-m}) (Table 3). These ages were all significantly ($p < 0.001$) larger than for American elvers (T_m , 200 days (189–214 days); T_t , 255 days (220–284 days); T_{t-m} , 55 days (32–80 days)) (all $p < 0.001$). Thus, the larval duration (T_m) of European eel was longer

than that of American eel. In other words, at 200 days of age American eel larvae had metamorphosed from leptocephalus to glass eel and were ready to enter into North American coastal waters, while European eel larvae were still at the leptocephalus stage and drifting with the current in the open ocean. The difference in age at metamorphosis from leptocephalus

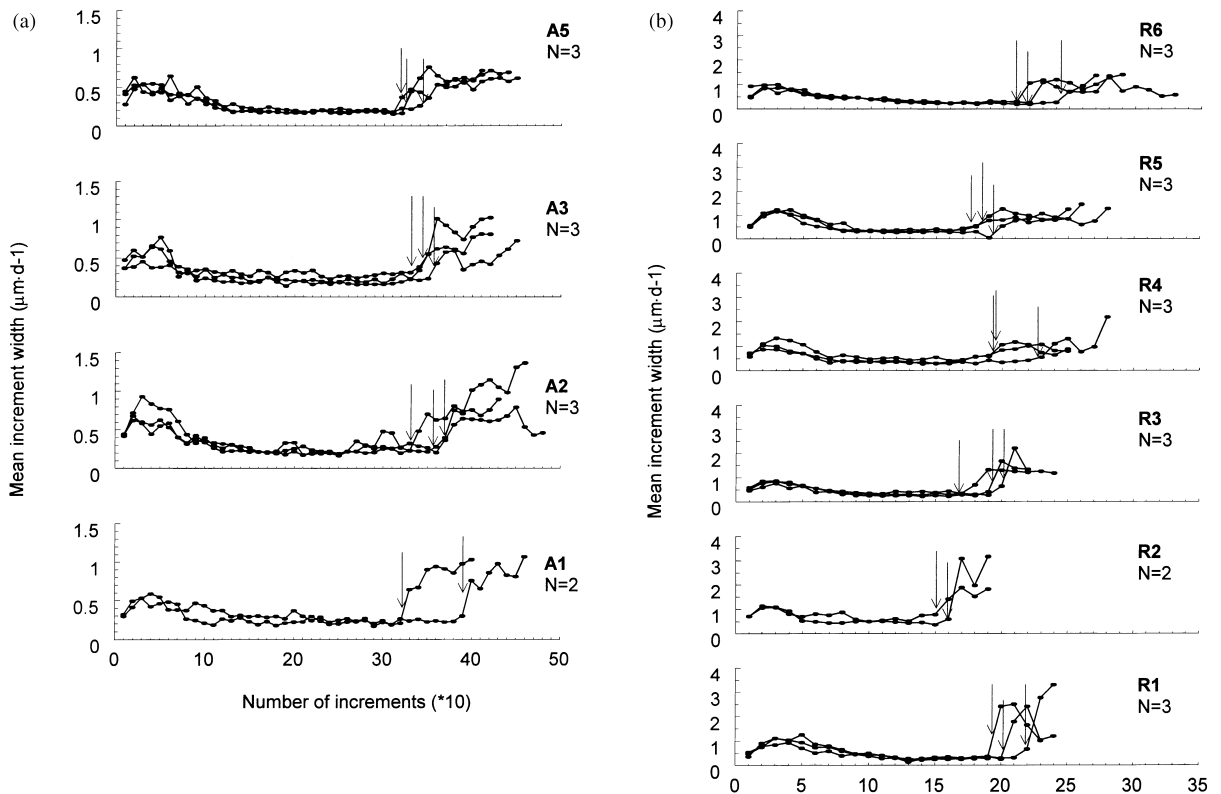


Fig. 7. Mean widths of 10 successive increments along the maximum radius from primordium to the otolith edge of *A. rostrata* and *A. anguilla* elvers (arrows indicate locations of metamorphosis check; *N*: sample size).

to glass eel between the two species was approximately 150 days.

The overall mean otolith growth rates of American elvers to metamorphosis (G_m) was $0.42 \mu\text{m}$ per day, to estuarine arrival (G_t) was $0.58 \mu\text{m}$ per day, and between metamorphosis and estuarine arrival (G_{t-m}) was $1.41 \mu\text{m}$ per day, while the somatic growth rate was 0.21 mm per day (Table 4). All American elver growth rates were significantly ($p < 0.001$) higher than those for European elvers ($G_m = 0.29 \mu\text{m}$ per day, $G_t = 0.36 \mu\text{m}$ per day, $G_{t-m} = 0.64 \mu\text{m}$ per day, somatic rate = 0.15 mm per day). American eel larvae grew approximately twice as fast, and metamorphosed and arrived at the estuary earlier than European eel larvae (Table 4).

The age of American and European elvers at estuarine arrival was inversely related to their growth rates (Fig. 8). The time at estuarine arrival decreases approximately 73 days for American eels (Fig. 8A)

and 308 days for European eel when the somatic growth rate increases 0.1 mm per day. The duration of larval life in the ocean was thus very sensitive to larval growth rate.

3.4. Hatching date

The hatching dates of American elvers, back-calculated from the sampling date and daily age of the fish at estuarine arrival, were from March to October and peaked in August (Fig. 9A). The hatching dates of European elvers were from November to July and peaked in January (Fig. 9B). The Portuguese data (European eel) was excluded because the sample was collected in September and not in the main fishing season. The spawning season of American and European eels was lengthy and segregated, with American eel spawning in summer and European eel spawning in winter.

Table 2

Otolith radii (mean±S.D.) from primordium to FFC (R_f), MC (R_m) and E (R_t), and distance from MC to E (R_{t-m}) of elvers of *A. rostrata* and *A. anguilla*

| Species site | N | Otolith radii (μm) | | | |
|------------------------------|-----|---------------------------------|------------|-----------|------------|
| | | R_f | R_m | R_{t-m} | R_t |
| <i>A. anguilla</i> | | | | | |
| A1 | 8 | 10.7±1.5 | 103.5±6.6 | 61.6±6.4 | 165.1±8.8 |
| A2 | 13 | 10.8±2.2 | 107.5±29.4 | 66.6±12.2 | 179.6±16.3 |
| A3 | 11 | 10.0±1.1 | 106.9±8.5 | 61.2±11.4 | 168.1±16.4 |
| A5 | 24 | 9.1±1.1 | 101.8±10.1 | 54.3±12.2 | 156.1±15.8 |
| Overall (μ_1) | 56 | 9.8±1.7 | 106.1±11.0 | 59.5±12.2 | 165.7±18.0 |
| <i>A. rostrata</i> | | | | | |
| R1 | 25 | 8.8±1.3 | 91.0±8.1 | 64.1±8.8 | 155.2±8.8 |
| R2 | 4 | 10.5±0.8 | 98.3±10.7 | 70.7±4.3 | 169.0±13.0 |
| R3 | 21 | 9.6±1.5 | 89.1±13.2 | 63.9±11.8 | 153.0±22.8 |
| R4 | 26 | 9.5±1.6 | 96.7±9.0 | 60.7±10.9 | 157.4±10.1 |
| R5 | 17 | 9.0±2.1 | 92.2±8.7 | 64.8±11.4 | 157.0±8.6 |
| R6 | 32 | 9.8±1.2 | 92.3±8.3 | 68.0±11.5 | 160.3±10.4 |
| Overall (μ_2) | 125 | 9.5±1.5 | 92.6±9.7 | 64.7±10.9 | 157.3±13.1 |
| Difference ($\mu_1-\mu_2$) | | 0.3 | 13.5 | -5.2 | 8.4 |
| Probability | | 0.08 | 0.00 | 0.32 | 0.00 |

4. Discussion and conclusion

The age of American eel elvers arriving along the North American Atlantic coast, has variously been

estimated as 10–12 months (Schmidt, 1922), 2 years (Liew, 1974) and 8–12 months (Kleckner and McCleave, 1985). We estimated coastal arrival in approximately 7–9 months (220–284 days), comparable

Table 3

Daily age of elvers of *A. rostrata* and *A. anguilla* at 10 estuaries (T_t), daily age at metamorphosis (T_m), and the time between metamorphosis check and arrival at estuaries (T_{t-m})

| Species sites | N | Age (days) | | |
|------------------------------|-----|-------------|-------------|-------------|
| | | T_t | T_m | T_{t-m} |
| <i>A. anguilla</i> | | | | |
| A1 | 8 | 467.7±26.66 | 397.1±26.98 | 70.6±7.30 |
| A2 | 13 | 455.4±43.93 | 350.9±37.59 | 97.8±17.89 |
| A3 | 11 | 420.0±38.25 | 318.5±27.22 | 101.5±18.91 |
| A5 | 24 | 444.6±39.09 | 346.8±36.62 | 104.5±23.55 |
| Overall (μ_1) | 56 | 447.7±41.67 | 350.2±40.43 | 97.5±22.44 |
| <i>A. rostrata</i> | | | | |
| R1 | 25 | 241.6±18.51 | 209.3±20.20 | 32.7±4.44 |
| R2 | 4 | 247.8±16.24 | 214.0±14.35 | 33.8±3.86 |
| R3 | 21 | 220.4±33.22 | 188.8±29.14 | 31.7±5.84 |
| R4 | 26 | 251.8±16.62 | 189.5±19.63 | 62.2±11.13 |
| R5 | 17 | 272.3±15.72 | 192.7±20.33 | 79.6±14.07 |
| R6 | 32 | 283.5±18.18 | 211.4±20.75 | 72.2±12.17 |
| Overall (μ_2) | 125 | 255.3±30.24 | 200.2±23.84 | 55.1±21.85 |
| Difference ($\mu_1-\mu_2$) | | 192.4 | 150.0 | 42.4 |
| Probability | | 0.00 | 0.00 | 0.00 |

Table 4

Otolith growth rate (mean±S.D.) measured from primordium to otolith edge (G_t), to metamorphosis check (G_m), and between metamorphosis check and otolith edge (G_{t-m}) and somatic growth rate of elvers of *A. rostrata* and *A. anguilla*

| Species sites | N | Otolith growth rate (μm per day) | | | Somatic growth rate (mm per day) |
|--------------------------------|----|--|-------------|-------------|----------------------------------|
| | | G_t | G_m | G_{t-m} | |
| <i>A. anguilla</i> | | | | | |
| A1 | 2 | 0.327±0.001 | 0.234±0.015 | 0.872±0.090 | 0.142±0.006 |
| A2 | 9 | 0.382±0.035 | 0.301±0.026 | 0.681±0.184 | 0.145±0.013 |
| A3 | 6 | 0.369±0.056 | 0.304±0.067 | 0.603±0.097 | 0.157±0.017 |
| A5 | 5 | 0.316±0.008 | 0.264±0.007 | 0.519±0.031 | 0.152±0.010 |
| Overall (μ_1) | 22 | 0.358±0.045 | 0.287±0.044 | 0.640±0.159 | 0.149±0.014 |
| <i>A. rostrata</i> | | | | | |
| R1 | 20 | 0.598±0.06 | 0.393±0.05 | 1.981±0.33 | 0.201±0.024 |
| R2 | 4 | 0.641±0.05 | 0.411±0.05 | 2.106±0.14 | 0.192±0.182 |
| R3 | 16 | 0.645±0.08 | 0.421±0.04 | 2.019±0.71 | 0.210±0.021 |
| R4 | 18 | 0.586±0.08 | 0.460±0.07 | 0.975±0.23 | 0.232±0.026 |
| R5 | 14 | 0.542±0.06 | 0.432±0.04 | 0.813±0.17 | 0.219±0.021 |
| R6 | 17 | 0.528±0.07 | 0.390±0.04 | 0.943±0.21 | 0.211±0.026 |
| Overall (μ_2) | 89 | 0.584±0.08 | 0.418±0.05 | 1.408±0.66 | 0.213±0.026 |
| Difference ($\mu_1 - \mu_2$) | | -0.226 | -0.131 | -0.768 | -0.064 |
| Probability | | 0.00 | 0.00 | 0.00 | 0.00 |

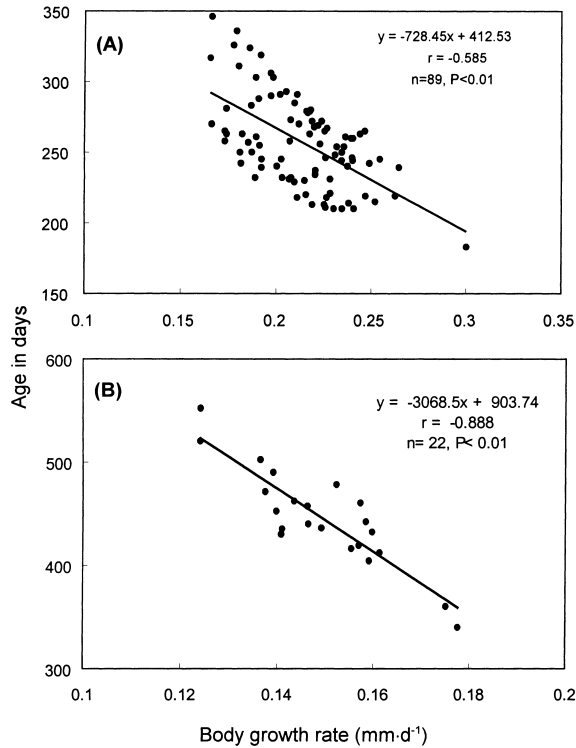


Fig. 8. Relationships between body growth rate and ages at estuarine arrival of *A. rostrata* (A) and *A. anguilla* (B) elvers.

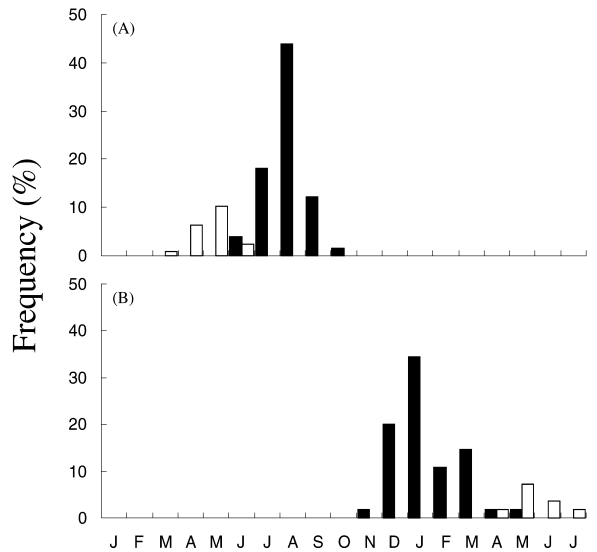


Fig. 9. Hatching dates estimated from otolith growth increments of elvers of *A. rostrata* from sites R2–R6 (solid bar: $N=102$) and R1 (open bar: $N=25$) (A); and *A. anguilla* from sites A2, A3 and A5 (solid bar: $N=47$) and A1 (open bar: $N=8$) (B).

to previous estimates except that of Liew (1974). The age of European eel elvers at coastal arrival in Europe has been estimated as 2–3 years (Schmidt, 1922, 1925), 3 years (Liew, 1974), 2–7 years (Van Utrecht and Holleboom, 1985), 11–18 months (Boëtius and Harding, 1985), and 6–9 months (Lecomte-Finiger, 1992, 1994). We estimated the age of European eel elvers at approximately 14–16 months (420–468 days), which matched only the estimate of Boëtius and Harding (1985). McCleave (1993) analyzed nine recent cruises specifically designed to sample for leptocephali of *Anguilla* and suggested that the larval duration of American eel is less than 16–17 months and that European eel leptocephalus take much longer than 12–15 months. McCleave (1993) also noted the extreme estimates of Van Utrecht and Holleboom (1985) and Lecomte-Finiger (1992, 1994). This indicated that the ages of American and European eels elvers remains open to discussion because of diverse estimates.

In order to evaluate the reliability of our estimates of the age of American eel elvers, we compared them with those of Japanese eel elvers. Although American eel occurs in the Atlantic Ocean and Japanese eel occurs in the Pacific Ocean, their spawning grounds and larval migratory routes are symmetrical and larvae drift to estuaries by similar currents, the Gulf Stream and Kuroshio Current (Schmidt, 1922; Tsukamoto, 1992; McCleave, 1993; Kimura et al., 1994; Cheng and Tzeng, 1996). Japanese eel elvers took 4–7 months to arrive along Asian coasts (Tabeta et al., 1987; Tsukamoto and Umezawa, 1990; Tzeng, 1990; Tzeng and Tsai, 1992, 1994; Cheng and Tzeng, 1996). Their spawning season was from April to October and peaked in summer (Tsukamoto, 1990; Tzeng and Tsai, 1994). The larval duration and spawning seasons of American and Japanese eels are very similar. Accordingly, we believed that the daily age of American eel elvers we estimated was reasonable.

The larval duration of European eel is controversial. Lecomte-Finiger (1992, 1994) estimated the daily age of European eel elvers at estuarine arrival to be 6–9 months (190–280 days), proposed that European eel larvae must be capable of swimming actively and thus took less than one year in transatlantic migration, and rejected Schmidt's hypothesis of a three-year migration period. We believe that the eel larvae drift with current and can not swim faster than the current as

indicated by the correspondence between estimated and actual dispersal distance for the leptocephalus of Japanese eel (Cheng and Tzeng, 1996). The estimate of Lecomte-Finiger (1992, 1994) of 6–9 months may be too small for European eel leptocephali to cross the North Atlantic Ocean. On the other hand, the migratory distance of European eel larvae from the spawning area in the southwestern Sargasso Sea to the European coast is approximately twice that for American eel larvae from the spawning area to the North American coast. If these two eel larvae migrated at the same speed and the estimated larval duration of 7–9 months for American eel was reasonable, then the estimate of Lecomte-Finiger (1992, 1994) of 6–9 months for European eel is too small, because oceanographic evidence demonstrates that floating objects need at least 10 months to drift from the Florida Strait to Great Britain (Brongersma, 1967). We believe that our estimate of 14–16 months for European eel larvae to migrate from the Sargasso Sea to European coasts is plausible.

The spawning season of American and European eels has been variously estimated to be February–April (Harden Jones, 1968; Boëtius and Harding, 1985; Wippelhauser et al., 1985), or May–June (Castonguay, 1987), and even September–October (Tsukamoto et al., 1991). All studies indicated a lengthy, overlapping spawning season for both species. Both American and European eel migrate downstream in autumn, ultimately to spawn in the Sargasso Sea. Given the different migratory distances for each species (about twice as far for European eel than for American eel), the spawning seasons should not be as similar as those reported above. The spawning season we estimated was March–October (peaking in August) for American eel and November–July (peaking in January) for European eel. In other words, the temporal segregation of the main spawning season was approximately half a year. Both species are genetically isolated; their spawning areas are overlapped (McCleave, 1993), but temporal isolation of spawning prevents interbreeding.

The timing of metamorphosis by a leptocephalus and transportation by oceanic current are considered important in determining the ultimate destination of eel (Schmidt, 1922, 1925; Tsukamoto and Umezawa, 1994; Cheng and Tzeng, 1996). The leptocephalus body shape is suitable for drifting with the current in

the open ocean. After metamorphosing, glass eels lose buoyancy and leave the strong ocean current by moving into coastal waters. The mean age of eel at metamorphosis from leptocephalus to glass eel was 200 days for American eel and 350 days for European eel, a difference of approximately 150 days. At the age of 200 days, American leptocephali have already metamorphosed and commenced recruitment to the American coast, while the European eel remains at the leptocephalus stage and will continue to drift with the current in the open ocean for approximately 150 days. Current speeds in the North Atlantic Drift were assumed to average 25 km per day (range 15–35 km per day) (Scheltema, 1971; Wegner, 1982; Lecomte-Finiger and Yahyaoui, 1989; Guerault et al., 1992). The time difference in metamorphosis of 150 days allows the North Atlantic current to disperse European eel leptocephali about 3750 km at a velocity of 25 km per day. This calculated distance is close to that between North American and European coasts (Fig. 1). Flexibility at the time of settlement and metamorphosis enables larval dispersal over great distances in order to find a suitable habitat (Scheltema and Williams, 1983; Christopher and Leggett, 1987). Differences in larval duration during oceanic transport contribute to the segregation during migration of the larvae of these two eels.

Migratory segregation can be further understood by examining larval growth rates. European eel larvae grew at 0.149 mm per day, approximately two-third the rate of American eel larvae (0.213 mm per day) and larval duration was negatively correlated with growth rate for both species (Schmidt, 1922, 1925; Tesch, 1977; Schoth and Tesch, 1982; Kleckner et al., 1983; Kleckner and McCleave, 1985, 1988). The reduced growth rate of European eel larvae prevents metamorphosis in synchrony with American eel larvae despite their overlapping spawning sites and oceanic migratory route (McCleave, 1993). The longer larval duration enables European eel to reach European waters before metamorphosis. Delayed metamorphosis with reduced larval growth was frequently found in the coral reef fish (*Thalassoma bifasciatum*) during the absence of a suitable habit for settlement (Jackson and Strathmann, 1981; Victor, 1986). Such delay may last for months in several species of invertebrates (Scheltema, 1971; Hadfield, 1978; Domanski, 1984; Pechenik et al., 1984; Richmond, 1985).

In conclusion, American eel was estimated to spawn from March to October and European eel from November to July. Larvae of the two species drift from the same spawning ground in the same current but segregate to America and European coasts according to differences in their growth rate and the timing of metamorphosis from leptocephalus to glass eel.

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