Interpretation of geographic variation in size of American eel *Anguilla rostrata* elvers on the Atlantic coast of North America using their life history and otolith ageing

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ABSTRACT: Elvers of the American eel *Anguilla rostrata* (LeSueur) were collected from 6 estuaries ranging in location from Haiti to the U.S. Atlantic coast and north to Canada during the fishing season in 1995. 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. Mean age of the leptocephalus at metamorphosis (T_m) was 189 to 214 d, while age upon arrival at the estuaries (T_t) was 220 to 284 d. Time from metamorphosis to arrival at the estuaries (T_{t-m}) was 32 to 80 d. Faster-growing and earlier-metamorphosing leptocephali migrate to the mid-point of the sampling range, but slower-growing and delayed-metamorphosis leptocephali occur in both the southern and northern ranges. Duration of the glass eel phase was longer in the north than in the south, while glass eels grew faster in the south than in the north. Mean total length of elvers at entry to the estuaries increased significantly from 48 mm in the south to 60 mm in the north. Geographic variation in elver length was due to duration of the glass eel phase rather than timing of metamorphosis from leptocephalus to glass eel, because elver length was significantly positively correlated with T_{t-m} (r = 0.79, p < 0.01) but not significantly correlated with T_m (p > 0.05). Duration of the glass eel phase was influenced by the coastal oceanographic conditions.

KEY WORDS: Otolith microchemistry · Aging · Early life history · Geographic variation in size · Elvers · American eel

INTRODUCTION

The American eel *Anguilla rostrata* (LeSueur) is a temperate catadromous fish, widely distributed in the rivers of eastern North and Central America (Schmidt 1909). Developmental stages of the American eel are similar to those of *Anguilla anguilla* and include: leptocephalus, glass eel, elver, yellow eel and silver eel (Bertin 1956). The American eel has a panmictic population (Avise et al. 1986) which spawns in the Sargasso Sea in the southwestern North Atlantic Ocean (Schmidt 1925, Kleckner et al. 1983, Kleckner & McCleave

1988). After a long-distance oceanic migration, the leptocephali metamorphose to glass eels on the continental shelf, and then become elvers in the estuaries (Bertin 1956, Tesch 1977). Due to their wide distribution in the open ocean and difficulty in collection, the biology of leptocephali is poorly known (Kleckner & McCleave 1982, 1985, Schoth & Tesch 1982, Castonguay & McCleave 1987, Miller & McCleave 1994). The size of elvers at entry to the estuary tends to increase with increasing distance from the spawning area (Vladykov 1966, Smith 1968, Haro & Krueger 1988). This phenomenon was initially explained by a sex/size hypothesis that the female grows faster than the male and that the female predominates more in the north than in the south (Vladykov 1966). Haro & Krueger

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(1988) rejected Vladykov's hypotheses and proposed that the geographic trend in elver length may be due to the variation in the timing of metamorphosis of lepto-cephali to the glass eel stage. However, until now there have been no studies on the age determination of leptocephalus at metamorphosis to substantiate this speculation.

Daily growth increments in otoliths (Pannella 1971) have been widely used to determine the daily age (Campana & Neilson 1985), growth rate (Volk et al. 1984), life history and change of habit of fish (Campana 1984). The age of Japan-ese eel *Anguilla japonica* elvers at meta-morphosis and entry to various estuaries has been extensively studied (Tsukamoto & Umezawa 1990, 1994, Tzeng 1990, 1996, Otake et al. 1994, Tzeng & Tsai 1994, Cheng & Tzeng 1996). These studies con-clude that a visible metamorphosis check is deposited in the otolith at metamorphosis. Strontium concentra-tion in the otolith decreases dramatically during meta-morphosis. Since growth increments in otoliths of American eel elvers are deposited daily (Martin 1995), the age of the leptocephalus at metamorphosis and the age of the elver at entry to the estuary can be deter-mined from daily growth increments and the strontium content of the otolith.

This study investigates the causes of the geographic variation in size of American eel elvers on the east coasts of North America and Haiti by using the microstructure and microchemistry of otoliths.

MATERIALS AND METHODS

American eel elvers were collected from 6 estuaries on the Atlantic coasts of Haiti, the USA and Canada (Table 1, Fig. 1). All samples were collected in 1995, with 1 additional sample collected in 1997 from Florida because the corresponding sample size in 1995 was small. The elvers were collected with a dip net during their upstream migration on a night-time flood tide (Usui 1991) and were preserved in 95% alcohol. Total lengths to 0.1 mm were measured after alcohol fixa-tion. Pigmentation stages, which indicate the develop-mental stage from glass eel to elver, were assessed according to pigment distribution on the body surface (Strubberg 1913). Sagittal otoliths of the elvers were extracted from the vestibular apparatus and prepared for microchemistry analysis and age determination as described by Tzeng (1990, 1996) and Tzeng & Tsai (1994).
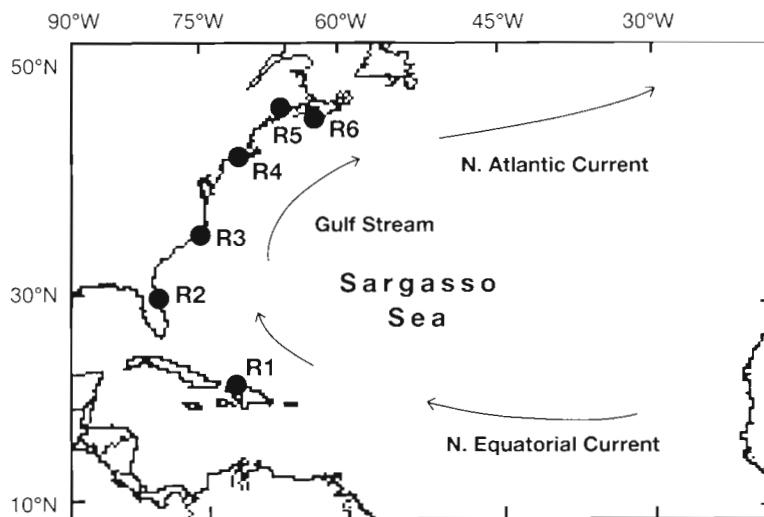

Fig. 1 Sampling sites of *Anguilla rostrata* elvers (R1. Haiti; R2: Florida; R3: North Carolina; R4: Rhode Island; R5: New Brunswick; R6: Nova Scotia)

EPMA (Electron Probe Microanalysis; EPMA Model 8800) was used to analyze the weight ratio (wt ‰) of strontium (Sr) to calcium (Ca) in eel otoliths. $SrTiO_3$ and $CaCO_3$ were used as standards for Sr and Ca, respectively. Sr and Ca were measured along the oto-lith maximum axis through the primordium with a beam condition of 0.01 μA and 15 kV. At intervals of approximately 10 μm, the electron beam was focused on an area approximately 5 μm in diameter. The energy dispersive strength of Ca and Sr was evaluated using four 5 s scanning periods. After ZAF (Z, atomic number effect; A, absorption factor; F, fluorescence effects) correction (Goldstein et al. 1984), the weight ratio of Sr and Ca was calculated using a constant CO_2 of 43.87% (Chen & Tung 1984). The metamorphosis check at which the leptocephalus metamorphosed to the glass eel stage was inferred from the point at which the Sr/Ca ratio changed (Tzeng & Tsai 1994, Tzeng 1996). To link the time series change of Sr/Ca ratio with otolith growth increment, the otolith was washed

Table 1. Sampling sites (shown in Fig. 1) and dates and sample sizes of *Anguilla rostrata* elvers

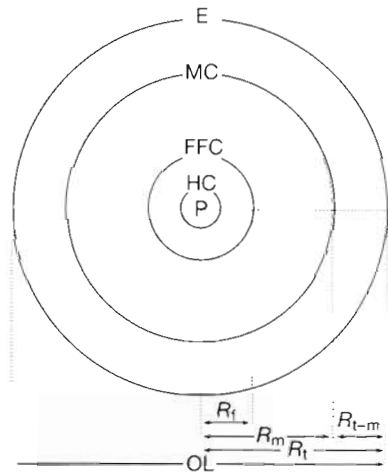| Site		Date	N
R1	Haiti	Dec 17, 1995	115
R2	Florida, USA	Feb 28, 1995	4
		Jan 22, 1997	50
R3	North Carolina, U.S.A.	Mar 22, 1995	50
R4	Annaquatucket River,		
	Rhode Island, USA	Apr 14, 1995	100
R5	Musquash River,		
	New Brunswick, Canada	Apr 28, 1995	67
R6	East River, Nova Scotia, Canada	May 29, 1995	93

Fig. 2. A schematic diagram of radii measurements in elver otoliths. P: primordium; HC: hatching check; FFC: first feeding check; MC: metamorphosis check; E: edge. Radii were measured from the primordium to the first feeding check (R_f), to the first feeding check (R_m) metamorphosis check, and to the otolith edge (R_t); R_{t-m}: distance from the metamorphosis check to the otolith edge; OL: otolith length

and obscure, the daily age of samples without counting daily growth increment was calculated from otolith growth rate and otolith radius:

$$T_m = \frac{R_m - R_f}{G_m} + N_0 \qquad (4)$$

$$T_{t-m} = \frac{R_{t-m}}{G_{t-m}} \qquad (5)$$

$$T_t = T_m + T_{t-m} \qquad (6)$$

where G_m and G_{t-m} were obtained from Eqs. (2) & (3), and N_0 is the adjustment factor (5 d) for yolk-sac stage duration. Otolith growth rate of the elvers in the 6 estuaries was site-specific; the rate was calculated at each sampling site to estimate daily ages.

The homogeneity of mean total length, various daily ages $(T_t, T_m,$ and $T_{t-m})$ and otolith growth rates $(G_t, G_m,$ and $G_{t-m})$ among the 6 estuaries was tested with Scheffe's multiple range analysis (Sokal & Rohlf 1969). Correlations between total length and T_t, T_m and T_{t-m} for the elvers were calculated.

with acetone to take off the carbon coating after EPMA analysis and was then prepared for age determination using an SEM (scanning electron microscope, Hitachi S-520) (Tzeng 1996).

Otolith radii from the primordium to the first feeding check (R_f), to the metamorphosis check (R_m) and to the otolith edge (R_t) and the distance from the metamorphosis check to the otolith edge (R_{t-m}) were measured using an SEM photograph taken at 300× magnification along the longest sagittal axis of the otolith (Fig. 2). The growth increments $(N_m, N_{t-m},$ and $N_t)$ on the radii of $R_m, R_{t-m},$ and R_t were counted on SEM photographs at 1200× magnification. Because increments are not deposited in the core of the otolith for the 5 d of the yolk-sac stage (Yamamoto & Yamauchi 1974, Yamauchi et al. 1976, Tzeng 1990, Tzeng & Tsai 1994), 5 d (N_0) were added to the number of growth increments to estimate the daily age of elvers at metamorphosis $(T_m = N_m + N_0)$ and the daily age at estuarine arrival $(T_t = N_t + N_0)$. The time between metamorphosis and arrival at the estuary (T_{t-m}) equals N_{t-m}. Daily growth increments were counted for 89 otoliths.

Three kinds of otolith growth rate estimates were made:

Overall growth rate of otolith, $G_t = R_t/T_t$ (1)
Early growth rate of otolith, $G_m = R_m/T_m$ (2)
Estuarine growth rate of otolith, $G_{t-m} = R_{t-m}/T_{t-m}$ (3)

Because the counting of daily growth increments was time consuming and the increments near the metamorphosis area on the otolith were often diffusive

RESULTS

Total length and pigment stage

Total lengths of the elvers collected from the 6 estuaries on the Atlantic coasts of Haiti and North America ranged between 41 and 65 mm. Two different length groups were identified: mean length of the northern group [Nova Scotia (R6), New Brunswick (R5) and Rhode Island (R4)] was significantly greater than that of the southern group [North Carolina (R3), Florida (R2) and Haiti (R1)]. Mean lengths ranged from 47.8 to 49.0 mm for the southern group and from 58.5 to 60.0 mm for the northern group, with a difference in mean length of approximately 12 mm (Fig. 3).

The pigment development stage of elvers at estuarine arrival was mostly VB and VIA1 for R2, but VIA1 and VIA2 for the other 5 sites. This may indicate that the immigration of elvers in Florida occurred at an earlier stage than for the other sites. In addition, the trend of mean total length of elvers from different sampling sites was similar among pigmentation stages, indicating that the difference in mean length between northern and southern groups was independent of elver pigmentation stage (Fig. 4).

Otolith microstructure and microchemistry

The primordium of the elver otoliths was amorphous. Between the hatching check (HC) and the first feeding
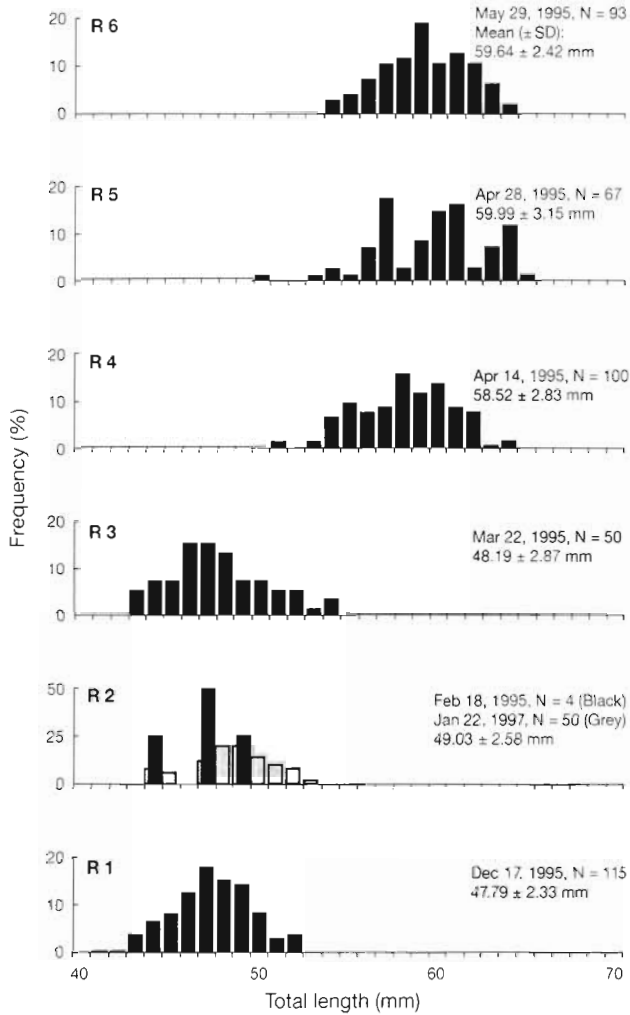
Fig. 3. *Anguilla rostrata.* Length frequency distribution of elvers collected from 6 estuaries in Haiti and North America (Sites R1 to R6 in Fig. 1). Mean ± SD of each distribution is also indicated

check (FFC), no distinct daily growth was discernible. Beyond the FFC, there were distinct daily growth increments. The shape of the otolith crystalline arrangement changed from a circular to a radial form at approximately $\frac{2}{3}$ of the total radius distance from the primordium. Also, the increment widths at the transition boundary become very narrow. The changes in both crystalline pattern and increment width yielded a distinct check, which was interpreted as the metamorphosis check (MC) (Fig. 5).

Changes in crystalline arrangement and increment width in the otolith reflect different developmental stages of the fish. The nucleus from the primordium to the FFC, which is deposited before the yolk-sac stage, has no discernible daily growth increments. The mean nucleus radius ranged between 9.5 and 15.0 μm. The zone from the FFC to the MC was deposited during the

leptocephalus stage. Daily growth increments were wide and clear in the beginning of the stage, but became indistinct and almost uncountable across the MC check. This indicated that the growth of the leptocephalus was fast in the early stage and then gradually slow. From the MC to the otolith edge, the crystalline arrangement became radial in form and had wide increments, indicating that growth became fast after metamorphosis (Fig. 5). Daily growth increments from the MC to the otolith edge were wider in the southern grap than in the northern group of elvers, i.e. the daily growth of glass eel in the period after metamorphosis was faster in the southern group than in the northern group.

Sr/Ca ratio in otoliths was approximately 5×10^{-3} in the nucleus and increased with otolith growth, reaching a maximum ranging between 1.4 and 2.0×10^{-2} at the MC. Beyond the check, the Sr/Ca ratio sharply decreased (Fig. 6). The dramatic changes in Sr/Ca

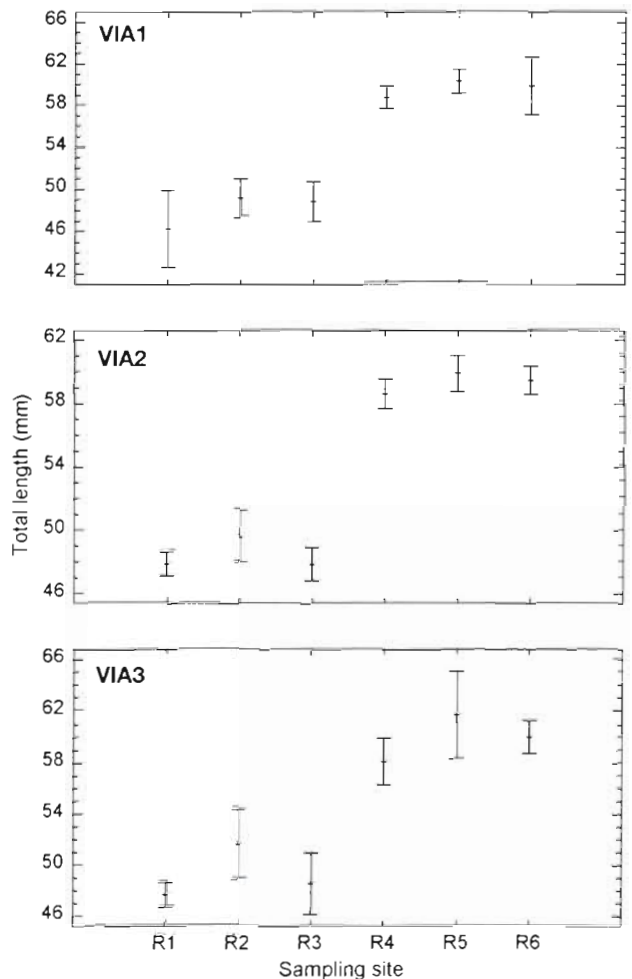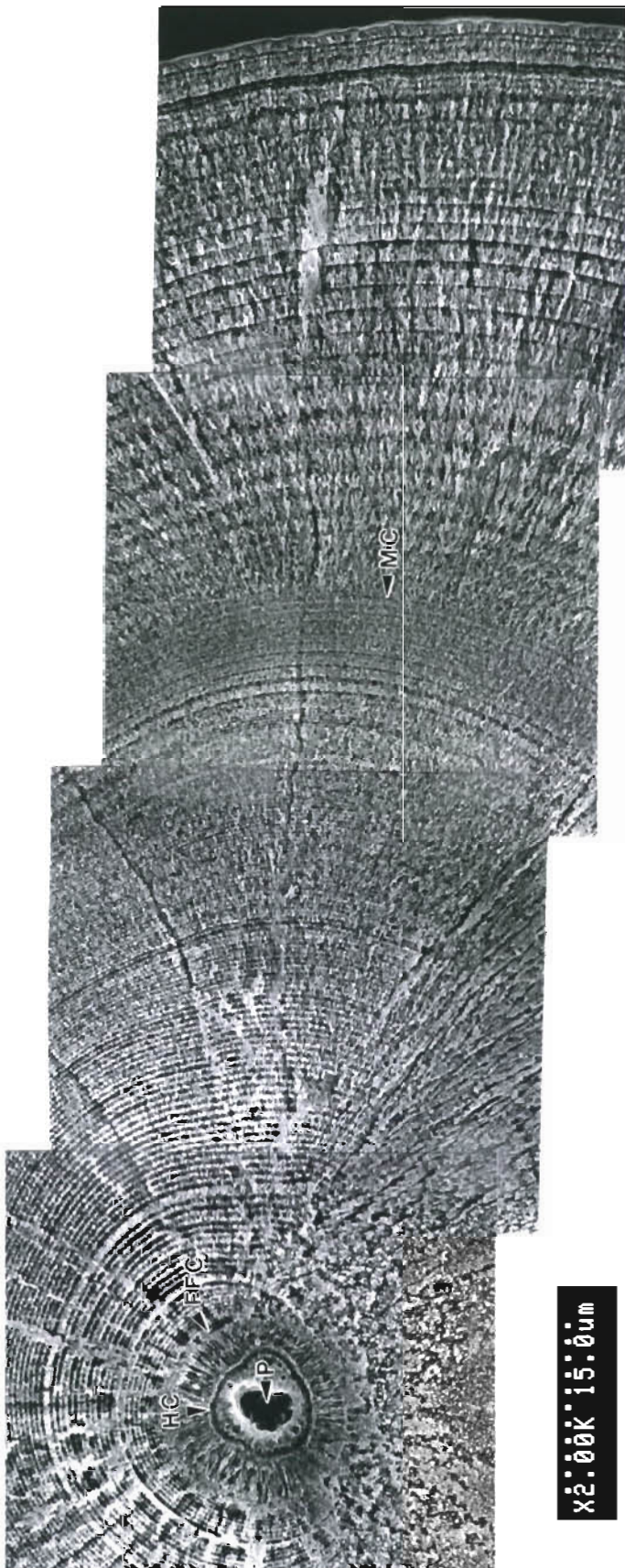Fig. 4. *Anguilla rostrata.* Mean (± 95% confidence intervals) total length by pigmentation stage (VIA1, VIA2 and VIA3) of elvers collected from 6 estuaries in Haiti and North America

Fig. 5. *Anguilla rostrata*. Daily growth increment of an elver (49.35 mm) otolith collected from Haiti (Site R1). FFC: first feeding check; HC: hatching check; MC: metamorphosis check; P: primordium. Scale bar = 15 μm

ratios in the otolith has been proposed to correspond to both the time of metamorphosis from leptocephalus to glass eel and the time of migration from oceanic to coastal waters in *Anguilla japonica* (Otake et al. 1994, Tzeng & Tsai 1994, Arai et al. 1997).

Geographic trend in otolith growth rate

The geographic trend in mean growth rate of the elver otoliths at the 6 sampling sites differed in the period before metamorphosis (G_m) and in the period from metamorphosis to estuarine arrival (G_{t-m}) (Table 2). G_m was larger at the mid-point (R4) of the 6 sampling sites than at the southward and northward sites (R1 and R6) (Table 2). Conversely, the estuarine growth rate (G_{t-m}) was larger in the southern group (R1 to R3) than in the northern group (R4 to R6) (Table 2). The geographic trend in G_t roughly paralleled that of G_{t-m} because the variance of G_{t-m} was larger than G_m (Table 2).

Timing of metamorphosis and estuarine arrival

The mean ages of the elvers at the 6 sampling sites ranged from 220 to 284 d at estuarine arrival (T_t) and from 189 to 214 d at metamorphosis (T_m), with 32 to 80 d between metamorphosis and estuarine arrival (T_{t-m}). An analysis of variance (ANOVA) indicated that T_t, T_m and T_{t-m} differed significantly among sampling sites (Table 3).

T_m was shortest at the mid-point (R3) of the 6 sampling sites, and increased toward the south (R1 and R2) and north (R4 to R6) (Table 3). On the other hand, T_{t-m} was larger in the northern group (R4 to R6) than the southern group (R1 to R3) (Table 3), consistent with the geographic trend of elver length (Fig. 3). The geographic trend in T_t roughly paralleled that of T_{t-m} because the variance of T_{t-m} is larger than T_m (Table 3). The geographic trends in T_m and T_{t-m} were inversely related to G_m and G_{t-m} (Table 2).

Relationship between total length and T_t, T_m and T_{t-m}

The total length of American eel elvers at estuarine arrival was not significantly correlated with T_m (r =
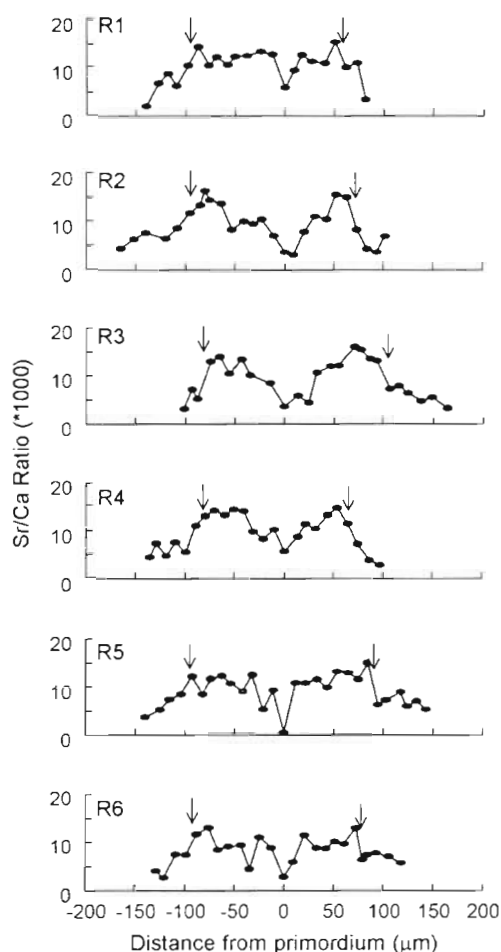
Fig. 6. *Anguilla rostrata*. Sr/Ca concentration ratios measured along the maximum axis through the primordium of elver otoliths collected from 6 estuaries in Haiti and North America. Arrows indicate position of the metamorphosis check

0.00, p > 0.05), but was significantly positively corre-lated with T_{t-m} (r = 0.79, p < 0.01) and also with T_t (r = 0.55, p < 0.01) (Fig. 7). Thus, the size of elvers at estuarine arrival increased with the duration from metamorphosis to estuarine arrival, but was indepen-dent of the age at metamorphosis.

DISCUSSION AND CONCLUSION

The mean total length of elvers at entry to 6 estuaries on the Atlantic coasts of Haiti, USA and Canada dif-fered significantly between northern and southern groups. Factors which have the potential to influence elver length include pigmentation stage of the elver in the estuary (Tzeng 1985), seasonal decline in length of elvers at entry to the estuary (Strubberg 1913, Matsui 1952, Jellyman 1979, Tzeng 1985) and annual vari-ability in elver characteristics at entry to the estuary

Table 2. *Anguilla rostrata*. Homogeneity tests for otolith growth rate (mean ± SD, µm d^{-1}) in elvers in Haiti and North America measured from the primordium to the otolith edge (G_t), to the metamorphosis check (G_m), and between the metamorphosis check and the otolith edge (G_{t-m})

	Site	N	Mean ± SD	Homogeneous groups
G_t	R6	17	0.528 ± 0.07	A
	R5	14	0.542 ± 0.06	A
	R4	18	0.586 ± 0.08	AB
	R1	20	0.598 ± 0.06	AB
	R2	4	0.641 ± 0.05	AB
	R3	16	0.645 ± 0.08	B
	Total	89	0.584 ± 0.08	
G_m	R6	17	0.390 ± 0.04	A
	R1	20	0.393 ± 0.05	A
	R2	4	0.411 ± 0.05	AB
	R3	16	0.421 ± 0.04	AB
	R5	14	0.432 ± 0.04	AB
	R4	18	0.460 ± 0.07	B
	Total	89	0.418 ± 0.05	
G_{t-m}	R5	14	0.813 ± 0.17	A
	R6	17	0.943 ± 0.21	A
	R4	18	0.975 ± 0.23	A
	R1	20	1.981 ± 0.33	B
	R3	16	2.019 ± 0.71	B
	R2	4	2.106 ± 0.14	B
	Total	89	1.408 ± 0.66	

Table 3. *Anguilla rostrata*. Homogeneity test for daily age (mean ± SD) of elvers from estuaries in Haiti and North America (T_t), for daily age at metamorphosis (T_m), and for the time between metamorphosis and arrival at the estuary (T_{t-m})

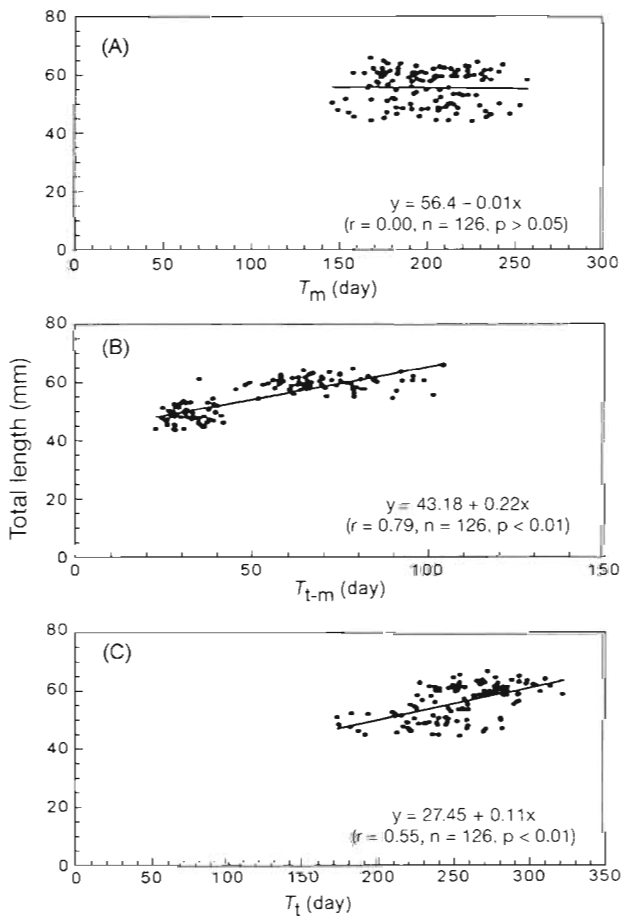|	Site	N	Mean ± SD	Homogeneous groups
T_t	R3	21	220.4 ± 33.22	A
	R1	25	241.6 ± 18.51	B
	R2	4	247.8 ± 16.24	BC
	R4	26	251.8 ± 16.62	BCD
	R5	17	272.3 ± 15.72	CDE
	R6	32	283.5 ± 18.18	E
	Total	125	255.3 ± 30.24	
T_m	R3	21	188.8 ± 29.14	A
	R4	26	189.5 ± 19.63	A
	R5	17	192.7 ± 20.33	AB
	R1	25	209.3 ± 20.20	AB
	R6	32	211.4 ± 20.75	B
	R2	4	214.0 ± 14.35	B
	Total	125	200.2 ± 23.84	
T_{t-m}	R3	21	31.7 ± 5.84	A
	R1	25	32.7 ± 4.44	A
	R2	4	33.8 ± 3.86	A
	R4	26	62.2 ± 11.13	B
	R6	32	72.2 ± 12.17	C
	R5	17	79.6 ± 14.07	C
	Total	125	55.1 ± 21.85	

Fig. 7. *Anguilla rostrata*. Relationships between total length of elvers and (A) age of leptocephali at metamorphosis (T_m), (B) time between metamorphosis and arrival at the estuaries (T_{t-m}) and (C) age at estuarine arrival (T_t)

(Haro & Krueger 1988). Pigmentation stage was found to have no effect on the elver length at estuarine arrival. Annual variability was negligible because the elvers from all estuaries were collected during 1995. Also, the elvers collected from Florida in 1995 and 1997 had similar length distributions. Within an estuary, elver length tends to decline through the run (Tzeng 1985). Run timing is earlier in the southern than in the northern portions of the range and elver length increases from south to north (Vladykov 1966, Haro & Krueger 1988). The observed size difference of 12 mm between the mean lengths of elvers from Haiti and Canada was larger than the seasonal decline, which is usually less than 6% in American eel (Haro & Krueger 1988). The geographic difference in elver length of American eel was not due to differences in sampling date.

Haro & Krueger (1988) proposed that the geographic trend in elver length may be due to the variation in the timing of metamorphosis of leptocephali to the glass

eel stage. However, we found that the correlation between the age at metamorphosis and the length of elvers at estuarine entry was not significant, although the correlation between elver length and the time between metamorphosis and entry to estuaries was significant. This indicated that the geographic difference in elver length along the east coast of North America was correlated with the difference in the duration of the glass eel stage in coastal waters. In coastal waters, the glass eel phase in the northern part of the range lasted approximately 62 to 80 d, which is 2 to 3 times longer than in the southern part of the range (32 to 34 d). Thus, higher elver length at northern sites in comparison to southern sites may be due to the longer duration of the glass eel phase in coastal waters. The early life history, described in the following, of the elver contributes to the further understanding of this relationship.

The early life history of the American eel *Anguilla rostrata* is similar to that of the Japanese eel *Anguilla japonica* (Tsukamoto 1990, 1992, Tsukamoto & Umezawa 1990, 1994), with 2 distinct stages: the leptocephalus in the open ocean and the glass eel and elver in coastal waters. American eels spawn in the southwestern Sargasso Sea, after which the leptocephalus drifts with the Florida Current and Gulf Stream, then metamorphoses into a glass eel as it approaches the continental shelf and becomes an elver at entry to the estuary. The geographic trend in the mean daily ages of the leptocephalus (T_m) and the time from metamorphosis to arrival at the estuary (T_{t-m}) differed among the 6 estuaries sampled. T_m was smallest at the midpoint of the 6 sampling sites (North Carolina) and increased towards the southern sites (Haiti and Florida) and northern sites (New Brunswick and Nova Scotia). On the other hand, T_{t-m} was smaller in the south (Haiti to North Carolina) than in the north (Rhode Island to Nova Scotia). This suggests that the migration and dispersal patterns differ between the leptocephalus and glass eel stages. In addition, there was an inverse geographic trend between growth rate and leptocephalus age at metamorphosis. This indicates that faster-growing and earlier-metamorphosing leptocephali entered the middle of the sampling range, while slower-growing, delayed-metamorphosis leptocephali dispersed southward and northward. This result is consistent with leptocephali entering the Gulf Stream system directly from the Sargasso Sea, as postulated by Kleckner & McCleave (1982), rather than by a more southern route through the Bahamas.

However, when the eel metamorphoses from leptocephalus to glass eel and enters coastal waters, geographic trends in age (T_{t-m}) and growth rate (G_{t-m}) differed completely from that of the leptocephalus in the open ocean. T_{t-m} was smaller in the southern part

of the sampling range (Haiti to North Carolina) than in the northern part (Rhode Island to Nova Scotia), but G_{t-m} was the opposite, being smaller in the north than in the south. Thus, glass eels grew faster, but stayed in coastal waters a shorter time, in the south than in the north. The duration of the glass eel phase in coastal waters may be regulated by coastal oceanographic conditions. The coastal waters off the southern sampling sites (Haiti to North Carolina) are influenced by the warm Gulf Stream, but the northern waters (Rhode Island to Nova Scotia) are influenced by the cold Labrador Current (Lalli & Parsons 1993). Higher temperatures in the south will accelerate the development of the glass eel, producing faster glass eel growth, more rapid elver development and earlier immigration to the estuary in the south than in the north. Although growth of the elver in the glass eel phase was faster in the south, their duration in coastal waters was shorter, which may lead to a smaller total length of elvers at entry to the estuary in the south than in the north.

In conclusion, the American eel *Anguilla rostrata* elvers are smaller in the southern than in the northern estuaries of the Atlantic coast of North America because the duration of the glass eel phase in the coastal waters is shorter in the southern than in the northern part of their range and not because of differences in the timing of metamorphosis from leptocephalus to glass eel.

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