Migration of juvenile American eels *Anguilla rostrata* between freshwater and estuary, as revealed by otolith microchemistry

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ABSTRACT: The temporal patterns in the otolith Sr:Ca ratios of yellow-phase American eels *Anguilla rostrata* from the East River, Chester, on the Atlantic coast of Nova Scotia, Canada, indicated variable patterns of migration between river and estuarine/marine waters. About 29% of yellow eels (n = 107) had a history of migration between river and estuary other than their initial entry. Male and sexually undifferentiated eels, potentially mostly male, comprised 96% of the sample and females comprised 4%, but the proportions of migratory and non-migratory eels did not vary by sex or development stage. Most migrants (81%) made only 1 round trip, while 19% made 2 round trips. Yellow eels with a migratory history were patchily distributed, with most (84%) concentrated 9.4 km upriver. About 36% of yellow eels showed a check (false annulus) corresponding with a habitat transition from estuary to river, while for 16% of yellow eels the check occurred during the initial freshwater entry as an elver. Otolith checks not associated with a habitat transition occurred for 22% of yellow eels, primarily at intermediate ages. Mean lengths-at-age were higher for eels with a history of primarily estuarine growth than for eels of primarily freshwater growth, as were annual growth rates (26.6 versus 21.7 mm yr^{-1}).

KEY WORDS: *Anguilla rostrata* · American eel · Strontium:calcium ratios · Growth rate · Migratory history · Otolith check

INTRODUCTION

Periodic seasonal migrations between fresh and estuarine or marine waters have been reported for several species of anguillid eels, such as American eels *Anguilla rostrata* (Smith & Saunders 1955, Medcof 1969, Jessop et al. 2002, 2004, Morrison & Secor 2003, Morrison et al. 2003), European eels *A. anguilla* (Tzeng et al. 1997, 2000) and Japanese eels *A. japonica* (Tsukamoto & Arai 2001, Tzeng et al. 2002, Arai et al. 2003). The early observational studies have more recently been extended by studies of otolith microchemistry that have been used to reconstruct the history of fish migration between marine, estuarine, and fresh waters via the relationship between habitat salinity (and Sr:Ca ratio) and otolith Sr:Ca ratios, with high otolith Sr:Ca ratios reflecting high salinity (Campana 1999, Elsdon & Gillanders 2003). The major anguillid species are now considered facultatively rather than obligatorily catadromous in their migratory behaviour (Tsukamoto & Arai 2001). Several migratory groups have been identified for individual species based on their residency and degree of migratory behaviour between marine/estuarine and fresh waters, and have been termed ecophenotypes by Tsukamoto & Arai (2001) and contingents by Jessop et al. (2002, 2004) and Morrison et al. (2003).

The recent discovery of American eel contingents with varying inter-habitat migratory behaviours underlines the shallowness of our understanding of eel migration in fresh and coastal waters. Little is known about the extent of such migratory behaviour, both quantitatively and geographically. Jessop et al. (2002, 2004) found that about 64% of downstream migrating, sexually maturing silver-phase (silver) eels in the East River, Chester, Nova Scotia, Canada, had a history of previous movement as yellow-phase (yellow) juvenile eels between fresh and brackish waters. Morrison et al. (2003) reported that about 65% of the yellow eels sampled in the brackish lower reach of the Hudson River estuary (New York, USA) had first entered freshwater as elvers and remained there for a variable number of years until returning to brackish water. Migrations from estuary to river by yellow eels are well-known (Smith & Saunders 1955, Jessop 2003a), and autumnal estuarine-to-freshwater migrations and spring freshwater-to-estuary migrations may also occur (Medcof 1969). Such migrations are generally unquantified, but Jessop (2003a) reported a spring upriver migration of 1202 juvenile eels or about 1.5% of the concurrent run of $791\,200 \pm 17\,250$ (95% CI) elvers. The frequency of annual migrations by individual yellow eels and the proportion of such migrants in the stock are unknown, as is the potential influence of age and length on migration activity. Yellow eels from the East River are expected to show a pattern of migration history similar to that of silver eels (Jessop et al. 2002), but differing in detail due to their younger age composition.

Eel density typically decreases and age composition increases with distance upstream, and the energetic cost of upstream migration increases with distance (Smogor et al. 1995, Feunteun et al. 2003). Eel migratory behaviour may change with ontogenetic development or as population density or environmental conditions change within habitats or the ecosystem (Feunteun et al. 2003). The distribution within the river of eels that periodically migrate between river and estuary is unknown.

Eel growth rates vary among habitats within river systems (Tesch 1977) and between freshwater and estuarine habitats (Helfman et al. 1987). Significantly lower historical growth rates, as determined by the analysis of otolith Sr:Ca ratio patterns, occurred in migratory silver eels with a largely freshwater residence history than in eels with an estuarine residence history (Jessop et al. 2004), while Morrison et al. (2003) found that yellow eels grew faster in brackish water than in freshwater. Differences in growth rate are predicted among yellow eels with a history of freshwater and estuarine residency consistent with growth rates found for silver eels of comparable residence history from the East River.

Distinguishing annuli from supernumerary checks (false annuli) in anguillid eel otoliths has been a long-standing problem (Moriarty & Steinmetz 1979, Michaud et al. 1988, Panfili & Ximénès 1994). Stresses, such as water temperature changes, starvation, handling, and normal migratory events, may induce changes in otolith increment periodicity, width, and optical density (Liew 1974, Volk et al. 1999). Matching the pattern of Sr:Ca ratios along a transect from otolith core to edge with that of annuli and checks or stress zones may permit evaluation of whether a freshwater–estuarine transition coincides with an otolith check.

Both the East River, Chester, and the Hudson River are in the northern 30% of the continental distribution of American eels (Tesch 1977), and may be supportive of the hypothesis by Tsukamoto & Arai (2001) and Tsukamoto et al. (2002) that marine/estuarine residency of *Anguilla* spp. should occur more frequently at high latitudes where freshwater productivity may be lower than that of adjacent coastal regions. Jessop et al. (2004) suggested that the latitudinal distribution of marine/estuarine resident eels should be considered relative to the geographic distribution of each species and not on a strictly latitudinal basis and that the frequency of marine/estuarine residence would decline near the northern limit of their geographic range.

Although a comprehensive analysis of yellow eel movement between fresh and brackish/marine waters would include samples from both river and estuarine/coastal habitats, we used samples from a river habitat to evaluate, via the analysis of otolith Sr:Ca ratios, the following hypotheses: (1) that the proportion of yellow eels in freshwater showing freshwater–estuarine migration will be low to moderate; (2) that the proportion of yellow eels migrating between fresh and brackish/marine waters decreases with distance upstream; (3) that the proportion of yellow eels with a migratory history increases with age and length; (4) that most yellow eels with a migratory history will show evidence of only 1 migration, with multiple migrations being uncommon; (5) that the occurrence of predominantly estuarine or freshwater residency by yellow eels would be detectable in their annual growth rate; and (6) that the periodic transition from fresh to estuarine waters may create a stress mark visible in the otolith.

MATERIALS AND METHODS

Study area. The East River (latitude $44°\,35'\,16''\,N$) drains a watershed of 134 km², of which 10.5% is lake surface, into Mahone Bay, which is located slightly south of the mid-point along the Atlantic coast of Nova Scotia, Canada (Fig. 1). The main branch of the East River (East Branch) contains about 53% of the total

watershed lake area, while the main tributary, the Canaan River, and the much smaller Barry's Brook tributary contain about 47% of the watershed lake area. American eels *Anguilla rostrata* occur widely (Barker 1997), probably throughout the river system, and are the most abundant fish species by a factor of at least 4 (Watt et al. 1997). River discharge ranges from <5 m^3 s^{-1} during the summer to about 35 m^3 s^{-1} during the spring flood. River pH ranges from 4.7 to 5.0, and conductivity averages 24 µmho cm^{-1} (Watt et al. 1995). Summer water temperatures range from 23 to 25°C, while winter temperatures reach 1 to 2°C. The Sr:Ca ratio of the river water at a site 1.3 km upriver of the mouth was measured at 5.6 × 10^{-3} (wt%) in April 2001, and it was measured at 4.1 × 10^{-3} in July 2001 at a site just upriver of the junction of the East Branch and the Canaan River (Jessop et al. 2002). A small falls (0.6 m) exists at the river mouth, about 11 m upstream from the high-tide mark (located just upstream or downstream of the Highway 3 bridge, depending upon river discharge; maximum saltwater penetration is just downstream of the bridge), creating a sharp transition between river and estuary (essentially the East River basin at the upper end of the East River Bay). Additional details and maps of the watershed may be found in Jessop (2000a) and Jessop et al. (2002).

In Mahone Bay, about 2 km from the river mouth, the salinity varies seasonally and with depth from ~27 to 31.5 ppt (M. Dadswell, Acadia University, Wolfville, Nova Scotia, pers. comm.). Surface (0 to 60 m) salinities in the coastal zone are generally about 31 to 32 ppt during winter and 30 to 31 ppt during summer. Water temperatures in the East River estuary are about –1 to 2°C during winter, rising to about 18 to 20°C during the summer, but are often in the range of 12 to 17°C. The estuary is well mixed, with a maximum tidal range of ~2 m and an average range of 1.5 m.

Sample collection. Yellow (juvenile) eels were collected by electrofishing on 17 July 2001 from 5 sites at various distances upstream from the river mouth (kilometres along the course of the river: Site 1 = 1.3 rkm, Site 2 = 3.0 rkm, Site 3 = 6.3 rkm, Site 4 = 9.4 rkm, Site 5 = 11.0 rkm; Fig. 1), anaesthetised with clove oil, then bagged and placed on ice until they could be frozen for later processing. At each site, up to 3 fish per 10 cm length interval were collected, with fewer fish available at larger sizes. After thawing, length (to
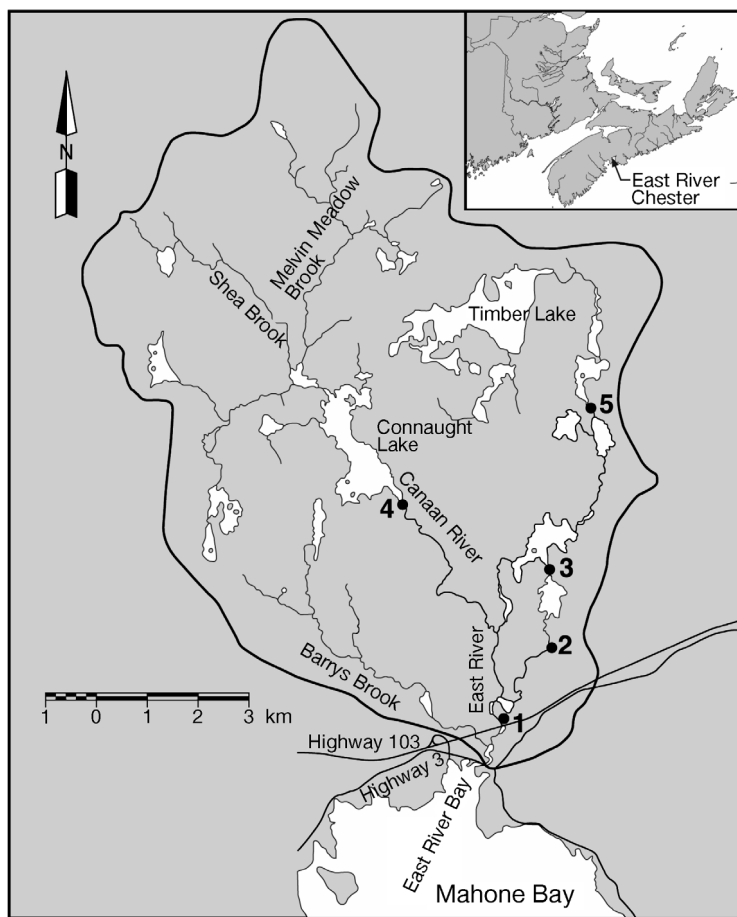

Fig. 1. The East River (Chester, Nova Scotia, Canada). Locations along the Atlantic coast of Nova Scotia, tributary rivers and yellow eel sampling sites (1 to 5) are shown

1.0 mm), weight (to 0.1 g), skin pigmentation stage (yellow, silver) and sex, evaluated by gonad tissue smears (Krueger & Oliveira 1997), were taken (Table 1). The heads were then removed and preserved in 95% ethanol for later extraction of the otoliths. American eels of about 300 mm length shrink by about 9% in length (W. Morrison, Chesapeake Bay Biological Laboratory, pers. comm.) and 12% in weight (D. Cairns, Dept. of Fisheries and Oceans, pers. comm.) after freezing and thawing, and were adjusted using the following equations: for length, $Y = (X + 0.7478)/0.9855$, r^2 = 0.99, and for weight, $Y = (X - 4.3311)/1.0310$, r^2 = 0.99, where Y represents fresh and X represents thawed measurements. Preservation methods, such as freezing and ethanol immersion, have little effect on the otolith Ca concentration, and variability in the Sr/Ca ratio is due largely to variation in the Sr concentration (Proctor & Thresher 1998).

Otolith preparation and Sr and Ca measurement. After removal, sagittal otoliths were prepared for electron probe microanalysis of the Sr and Ca concentra-

tions along a transect of the sagittal plane of the otolith from the primordium to the otolith edge, as described by Tzeng et al. (1997), while Jessop et al. (2002) describe the electron microprobe instrumentation and procedures. The temporal pattern of Sr:Ca ratios(wt%) along the otolith transect was used to evaluate the environmental history of each eel, under the assumption that the temporal pattern reflects habitat salinity (Tzeng 1996, Kawakami et al. 1998, Secor & Rooker 2000, Kraus & Secor 2004). Ratios of Sr:Ca of $\leq 4.0 \times 10^{-3}$ were considered to indicate freshwater residence, and values $>5.0 \times 10^{-3}$, to indicate estuarine or marine residence, with intermediate values representing a change in habitat (Jessop et al. 2002, 2004).

Migratory classification. Each eel was classified, based on the pattern and value of the Sr:Ca ratio measurements in relation to life-stage markers, e.g. metamorphosis check at the transition from leptocephalus to glass eel and elver check at the transition from glass eel to elver stage, and based on annuli, into 1 of 4 migratory groups following Jessop et al. (2002, 2004) (Fig. 2).
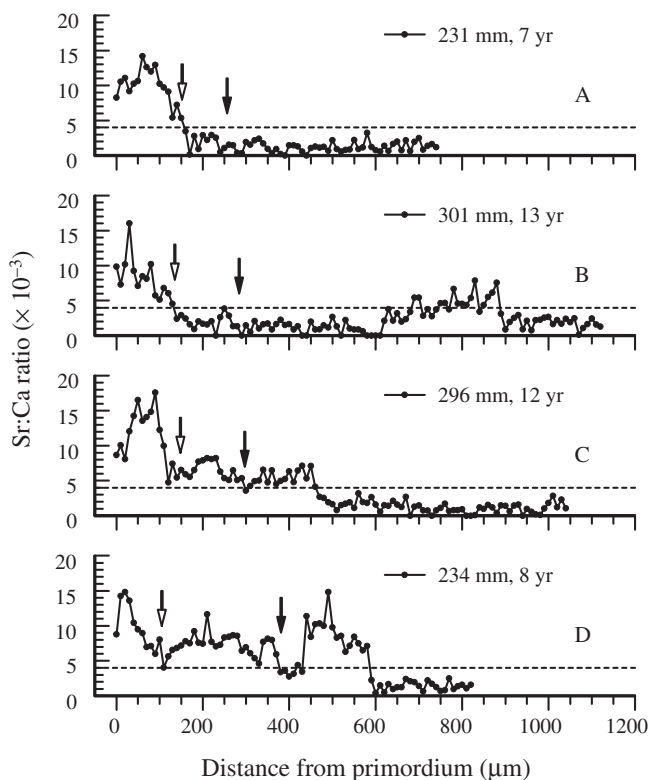

Fig. 2. *Anguilla rostrata*. Sr:Ca ratio transects along the otolith radius from the core to the edge illustrating various patterns of migratory movement and residence, classified into Migratory Groups 1 to 4 (A to D), by yellow eels from the East River, Nova Scotia. The horizontal dashed line at a Sr:Ca ratio of 4×10^{-3} represents the transition between fresh and saline waters, while the arrows indicate the elver check (white arrow) and first annulus (black arrow)

Group 1: Entrance to freshwater as an elver and remaining in freshwater until capture as a juvenile (yellow) eel (Fig. 2A).

Group 2: Entrance to freshwater as an elver and remaining in the river for a variable number of years before returning to the estuary for a variable number of years and finally returning to the river before capture (Fig. 2B).

Group 3: Entrance to freshwater as a juvenile after ≥ 1 yr in the estuary, then remaining in the river until capture (Fig. 2C).

Group 4: Entrance to freshwater as a juvenile after ≥ 1 yr in the estuary, then remaining in the river for a variable number of years before returning to the estuary for a variable number of years and finally returning to the river before capture (Fig. 2D).

Migration groups can be further combined, with Groups 1 and 3 combined designated as non-migratory eels and Groups 2 and 4 designated as migratory eels. These classifications ignore the possibility of continual estuarine residence or a failure to return to freshwater prior to undertaking the spawning migration because such information is unavailable from eels sampled in freshwater.

For Migration Groups 1 and 2 (entered river as elvers), the percentage of freshwater growth, after initial river entrance, was based on the percent of Sr:Ca measurement values that were $\leq 4.0 \times 10^{-3}$, as measured from the first Sr:Ca value of the first pair of values $\leq 4.0 \times 10^{-3}$ to the otolith edge. For Migration Groups 3 and 4 (entered river as juveniles), the freshwater growth period was estimated as the percentage of Sr:Ca values that were $\leq 4.0 \times 10^{-3}$ from the elver check to the otolith edge. Mean freshwater percentages for various groupings were estimated from the Sr:Ca data for individual eels with the improved transformation by Freeman & Tukey (1950) and then back-transformation of the transformed means.

Otolith back-calculation procedures. After microprobe analysis, the otoliths were re-polished and etched with 5% EDTA to enhance the annuli (Tzeng et al. 1994). All otoliths analysed for Sr:Ca ratio were aged from photographs of the otoliths, at known calibrations, by counting the annuli (translucent zones under reflected light) and the distances measured from the core to each life-stage marker, e.g. metamorphosis check and elver check, and the annuli marking the age in years after the elver stage to the otolith edge. Annuli were distinguished from supernumerary checks (false annuli) primarily on the basis of their width, optical density, relative positions and degree of continuity around the otolith circumference (Panfili & Ximénès 1994, Oliveira 1996, Graynoth 1999). Distances were measured (to 0.001 mm) along the Sr:Ca transect (100 of 107 eels) by image analysis software and on an adjacent transect (7 of 107 eels) when the re-polishing

process had removed the Sr:Ca transect. Oliveira (1996) confirmed by tetracycline marking the annual formation of otolith rings by yellow American eels from a river in the north-eastern United States.

The body length–otolith radius relation for the yellow (juvenile) eels was compared by ANCOVA (analysis of covariance) with that for the silver eels given in Jessop et al. (2004); the regression slopes were homogeneous (p = 0.64; statistical significance was accepted at $\alpha = 0.05$). Thus, the yellow eels were combined with the juvenile and silver eels used by Jessop et al. (2004) for estimating the relationship between total length (TL, mm) and otolith radius (OR, mm), appropriate to the BPH (body proportional hypothesis) back-calculation model (Francis 1990, 1995) (Fig. 3). The BPH model was selected based on the results in Jessop et al. (2004) and because mean back-calculated Lengths-at-ages 1 (66 mm) and 2 (89 mm) compared favourably with observed lengths of juvenile eels (60 to 85 mm) of assumed Ages 1 to 2 during mid-June to early August at a site 1.3 km upstream of the river mouth (Jessop 2003a). The regression coefficients of the TL–OR relation ($\log_{10}$ TL [mm] = $1.1349 \times \log_{10}$ OR + 2.4681) were used to define the following back-calculation equation:

$$\mathrm{Log}_{10} L_i = [(c + d\log_{10} O_i)/(c + d\log_{10} O_c)]\log_{10} L_c$$

where L_i is the back-calculated eel body length at Age i, O_i is the otolith radius at Annulus i, O_c is the otolith radius from core to edge, L_c is the eel body length at capture, c is the intercept and d is the slope from the regression of body TL on OR. Mathematically, L_i is a geometric estimate; it was adjusted to an arithmetic estimate following Ricker (1975, p. 275). Back-calculated lengths-at-age without the adjustment to the geometric mean averaged <0.7% (<1 to 2.3 mm) less than the adjusted lengths-at-age.

Growth analysis. The growth analysis primarily follows that of Jessop et al. (2004). Eel growth rates were calculated beginning with the first annulus (Age 1). Annual growth was estimated as the difference between the lengths at Age $t + 1$ and Age t. Few yellow eels older than Age 15 occurred (maximum Age 22), requiring the length-at-age and annual growth analyses to be restricted to Ages 1 to 11 for subdivision into habitat growth groups. This reduced potential biases from the natural migratory loss of faster growing eels (Oliveira & McCleave 2002).

The migratory groups were pooled and re-categorised on the basis of the degree of freshwater growth after the glass eel stage. Three habitat growth groups were defined based on the percentage of freshwater growth: 75 to 100, 50 to 74.9 and <50%. Although a continuum occurs in the degree of freshwater growth, an estuarine habitat group was defined as those eels

for which >50% of the Sr/Ca values were >4.0×10^{-3} along the otolith transect from the elver check or first pair of values $\leq 4.0 \times 10^{-3}$.

Although the proportion of otolith (and fish) growth in various habitats (fresh, estuarine, marine waters) has sometimes been assumed equivalent to the proportion of time spent in each habitat (Jessop et al. 2004), this is not true for fish that have resided for varying times in different habitats when growth rates differ markedly between habitats. Growth and time are distinct, if related, concepts. By definition, otolith growth period equals habitat residency period for eels that have resided entirely in a fresh, estuarine or marine habitat. The difference between proportion of growth and proportion of residence time increases with increasing difference between the growth rates in each habitat. Small differences may have no significant consequences, but large differences may.

Repeated-measures procedures are required for analysis of the multiple, sequential measures of otolith radius length that correspond to different ages from individual fish, because the assumption of independence among observations is not met (Chambers & Miller 1995, Oliveira & McCleave 2002). For a given fish, each year of age provides 1 growth interval and all growth intervals were considered equally without regard to the age at capture of an eel. After a process of model selection, a mixed-effects linear model with an autoregressive error structure was used to analyse the longitudinal data on eel length-at-age and annual growth (Bowen et al. 1992, Pinheiro & Bates 2000). The length-at-age data was best fitted with a linear model that assumes a common intercept and separate slopes, and the growth data was best fitted with a model that assumes a common slope and separate intercepts. Age
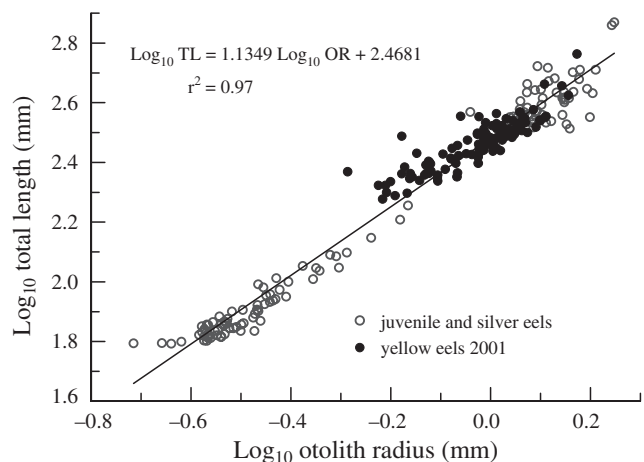

Fig. 3. *Anguilla rostrata*. Relationship between the total length (TL, mm) and otolith radius (OR, mm) appropriate to the BPH (body proportional hypothesis) back-calculation model for small- and medium-sized yellow (juvenile) and silver eels from Nova Scotia

was considered a within-subject effect and percent freshwater residency was considered a between-subjects effect. Residual plots indicated that the length-at-age and annual growth rate values were approximately normally distributed with homogeneous variances and no major outliers. S-Plus 6.2 (Insightful) was used to analyse the mixed-effects models.

Sex was not included as an effect for analysis because 41.1% of 107 eels were classified as undifferentiated, 55.1% as male and 3.7% as female. Most undifferentiated eels remaining resident in a small northern stream habitat may develop into males, given that males may predominate in riverine habitats relative to lacustrine habitats in small northern streams (Oliveira & McCleave 2000, Oliveira et al. 2001). The low proportion of lacustrine habitat in the river system and the inverse relation between the proportion of males and the proportion of lacustrine habitat (Oliveira et al. 2001) imply that males will predominate in the river system, consistent with the 57% male silver eels reported by Jessop et al. (2002).

Migratory history. The migratory history and distribution within the river of the yellow eels were examined by r × c contingency tables of the number of eels classified according to the percent freshwater (FW) growth group and distance upstream. The growth groups were 75 to 100% FW (mean = 99.9%, range = 80.0 to 100%), 50 to 75% FW (mean = 67%, range = 50.0 to 72.9%) and <50% FW (mean = 38%, range = 17.8 to 48.2%), based on the distribution of growth percentages and sample size considerations. The mean percent freshwater growth in each group, as a proportion, was used as an ordering score. The distance upstream (site) groups were 1.3, 3.0, 6.3, 9.4 and 11.0 rkm. The linear-by-linear test for ordered categorical data was used to examine the hypothesis of no row by column interaction (Agresti et al. 1990). For eels classified according to migration history (non-migratory = Migration Groups 1 + 3, migratory = Migration Groups 2 + 4), the relations with distance upstream, percent freshwater growth group and length and age groups (with mean lengths and ages used as ordering scores for each group) were analysed by an ANOVA (analysis of variance) with arbitrary scores test. The Chi-squared goodness-of-fit test was used to examine differences in cell values within the migratory and non-migratory groups. StatXact 6 (Cytel Software) was used to calculate exact p-values.

The number of otolith growth checks attributable to a transition between fresh and salt water habitats was evaluated by comparing the pattern of Sr:Ca ratios along a transect from otolith core to edge with that of annular and other growth checks. A growth check was considered a habitat transition check when the position of the check and the Sr:Ca change were separated by <35% of the distance between bracketing annuli. Thus, the distance between elver otolith transition checks and the Sr:Ca transition across the 4.0×10^{-3} boundary averaged 12.9% (range: –9.2 to 31.5%) of the distance between the elver check and the Age 1 annulus. Also, if the annual growth period is considered to be from about 1 May to 31 October, then division into 3 equal categories results in spring (May to June), summer (July to August) and autumn (September to October) groups and the season of check deposition can be determined from its relative position between bracketing annuli.

Transects of otolith Sr:Ca values sometimes contain singleton values varying from near to substantially different from the prevailing trend, e.g. a low or high spiking value in a series of high or low values that crosses the 4.0×10^{-3} threshold value separating fresh and estuarine waters, e.g. Fig. 2B,C during the estuarine residence period and Fig. 4B during the freshwater period. We have chosen not to interpret singleton values as a migratory movement.

RESULTS

Lengths and weights by site, sex and migratory group

The mean lengths and weights (base 10 logarithm transformed) of yellow American eels *Anguilla rostrata* from the East River (Table 1) differed significantly among sites (lengths: $F = 3.34$, df = 4, 102, p = 0.013; weights: $F = 3.62$, df = 4, 102, p = 0.008). However, Tukey's multiple comparison test indicated no significant differences in mean lengths in pair-wise comparisons among sites, most likely due to the heterogeneous variances among sites and small sample size for Site 2 and consequent low test power (Day & Quinn 1989). Logarithmic transformation was less successful for lengths than for weights in normalising variable distribution and reducing variance heterogeneity

Table 1. *Anguilla rostrata.* Sample data (n = 107) for microchemistry analysis of otoliths of American eels collected from the East River, Nova Scotia, Canada

Site	n	Age (yr)	Length (mm) (mean ± SD)	Range (mm)	Weight (g) (mean ± SD)	Range (g)
1	20	6–18	295.4 ± 35.87	215.6–349.5	43.5 ± 15.75	16.5–69.4
2	13	5–14	253.3 ± 58.76	174.0–342.4	28.9 ± 16.68	9.5–58.4
3	21	5–22	259.8 ± 80.88	195.3–561.6	45.1 ± 86.17	13.7–416.1
4	29	5–19	275.8 ± 57.15	195.3–442.9	42.4 ± 30.16	13.0–168.5
5	24	7–20	297.1 ± 51.41	230.8–436.8	51.4 ± 31.02	20.2–142.9

within sites resulting from the systematic selection of eels by length group and differences in eel size distribution among sites. The mean weight at Site 5 was greater than that for Sites 2 and 3, while the mean weights did not differ among Sites 1 to 4 (Tukey's test). An ANCOVA of the weight–length regressions among sites proved uninteresting because the homogeneity of slopes requirement was not met and there were undesirable significant differences in the mean lengths (covariate) among sites even after the data were logarithmically transformed.

Yellow eel mean lengths differed significantly among sex groups ($F = 18.0$, df = 2, 104, p < 0.0001), with female yellow eels (461.7 mm) significantly longer than males (275.8 mm), which did not differ significantly from sexually undifferentiated eels (265.6 mm) (Tukey's test). Mean weights differed significantly among sex groups ($F = 21.2$, df = 2, 104, p < 0.0001) in a manner similar to that for lengths, with female eel mean weights (213.1 g) significantly heavier than those of males (38.5 g), which did not differ significantly from those of sexually undifferentiated eels (35.2 g).

Yellow eel mean lengths and weights did not differ significantly among migration history groups (length: $F = 0.63$, df = 3, 103, p = 0.60; weight: $F = 0.76$, df = 3, 103, p = 0.52) or among percent freshwater history groups (length: $F = 0.27$, df = 2, 104, p = 0.76; weight: $F = 0.32$, df = 2, 104, p = 0.73).
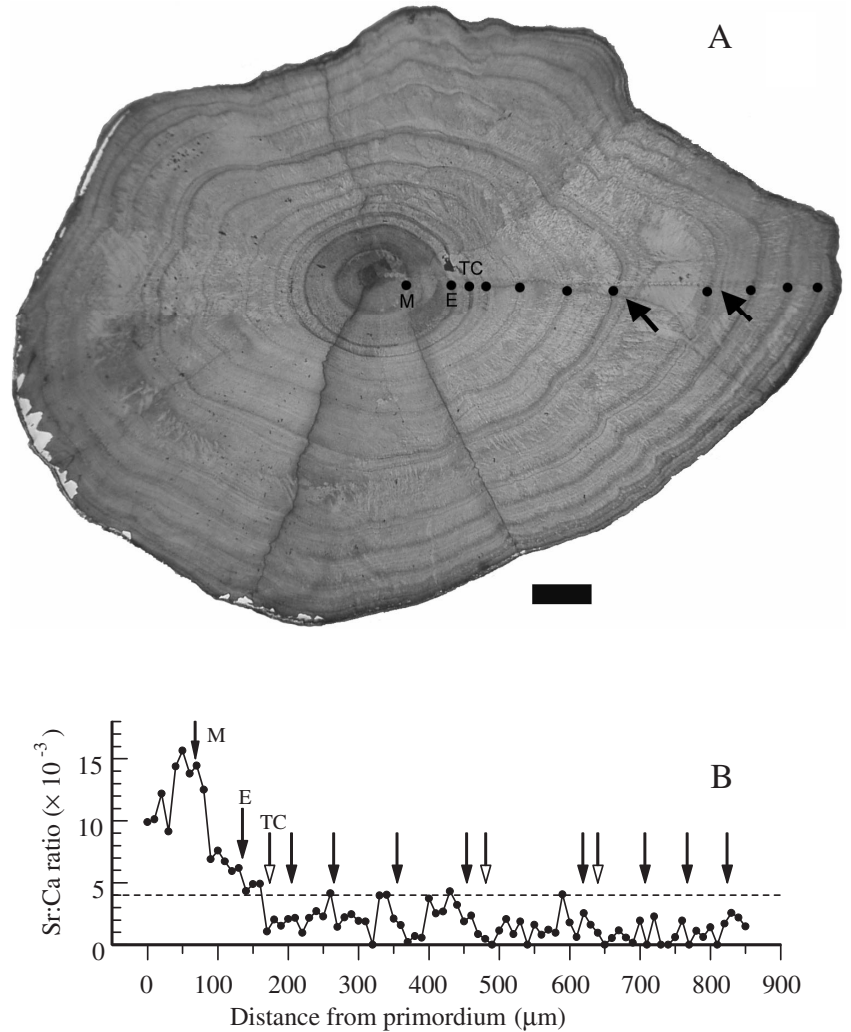

Fig. 4. *Anguilla rostrata*. (A) Otolith of yellow eel (Eel 2-66, 232 mm TL, Age 8 yr) showing metamorphosis check (M), elver check (E), habitat transition check (TC) and annuli (remaining dots) and other checks (arrows) along the transect measured for Sr:Ca ratio data. Scale bar = 0.1 mm. (B) Plot of Sr:Ca ratio data indicating metamorphosis, elver and habitat transition checks and annuli (black arrows) and other checks (white arrows)

Age interpretation and Sr:Ca data

The otoliths of 50% of 107 yellow eels had, in addition to annuli, what appeared to be checks (false or supernumerary annuli) based on their appearance (width, optical density and closeness to putative annuli) (Fig. 4A). When the measured positions of these otolith checks and putative annuli along the Sr/Ca transects were overlaid on the Sr:Ca values, 36% of yellow eels (72% of eels with otolith checks) had checks that closely corresponded with a sharp decrease in Sr:Ca values from $>5 \times 10^{-3}$ to $<4 \times 10^{-3}$, indicating a transition from the estuary to the river (Fig. 4B) and 22% of eels had checks with no evidence of a habitat transition. About 38% of the habitat transi-

tion checks occurred between the elver check and the first annulus. Thus, a habitat transition check occurred for 16% of the yellow eels first entering the river as elvers. The remaining habitat transition checks occurred at older ages for juvenile migrant eels (Migration Groups 2 and 4). Most (88%) otolith checks not associated with a habitat transition occurred for juvenile eels. A few (6%) eels showed 2 habitat transition checks. The percentages for different otolith categories may not sum to 100% because otoliths of individual eels may show several checks that are of different types.

The mean otolith distance between the elver check and habitat transition check depended upon when the eel entered the river. Most (65%) elvers showing an

otolith habitat transition check entered during the summer, when the mean distance to the check was 49.8 µm (Table 2). Most (68%) juvenile eels showing an otolith habitat transition check entered the river during spring (mean distance = 19.6 µm), as did juveniles with otolith checks caused by other than a habitat transition (46%, mean distance = 17.5 µm). The definition of the seasonal (spring, summer, autumn) migration groups implies that the mean distances between elver check (or annulus) and a transition check will be comparable among seasonal migration groups, as was observed. The fewest otolith checks (≤18%) occurred in autumn.

Further support for the interpretation of the check between the elver check and putative first annulus as a habitat transition check rather than an annulus is provided by back-calculation estimates of length-at-age. If the check is interpreted as the first annulus, the length at Age 1 estimate may be smaller, e.g. 43 to 48 mm, than the observed size of the smallest elvers (>47 mm, Jessop 2003b). If regarded as a check, the length at Age 1 at the putative first annulus then falls within the observed lengths at Age 1 for juvenile eels aged by otoliths (Jessop et al. 2004) and of the length-frequency distribution of juveniles in the next length mode beyond the elver stage (Jessop 2003a). Recognition of the habitat transition check was sufficient to eliminate most, but not all (3 of 26 cases), unusually low estimates of back-calculated lengths at Age 1.

Table 2. *Anguilla rostrata*. Season of deposition and location between annuli of growth checks in the otoliths of yellow eels from the East River, Nova Scotia. Individual eels may be represented in >1 category — 77 checks were observed in 53 eels. Measurements to growth checks were made for most, but not all eels. For elvers: the % distance represents the distance between elver check and first annulus; for juveniles, it represents the distance between annuli

Growth check	Season	n	% Group	Distance (µm) Mean	SD	%
Elver, transition	Spring	4	24	32.3	8.62	23
	Summer	11	65	49.8	13.06	43
	Autumn	2	12	88.0		68
Elver, non-transition	Summer	4	100	80.8	10.84	62
Juvenile, transition	Spring	19	68	19.6	6.87	22
	Summer	5	18	27.0	10.79	42
	Autumn	4	14	49.0	20.83	77
Juvenile, non-transition	Spring	13	46	17.5	4.75	21
	Summer	10	36	41.0	19.44	57
	Autumn	5	18	65.0	14.50	74
Juvenile, combined	Spring	32	57	18.8	6.10	22
	Summer	15	27	36.3	17.97	52
	Autumn	9	16	57.9	18.43	75

Migration history

Most yellow eels initially entered the river as elvers (88% of 107 eels), while 12% entered as juveniles, ranging in age from 1 to 6 yr old. Most yellow eels (71%) had a non-migratory history, 29% had a history of migration between fresh and saline waters other than the initial migration into freshwater as elvers (Table 3). Of the 31 migratory history eels, most (81%) showed evidence of only 1 round trip to the estuary and back, but 19% made 2 round trips. Also, 45% of the migrant eels had re-entered the river in the year of capture, and all were captured at Site 4 (Fig. 1). One in 4 (25%) female eels had a migratory history, as did 19 of 59 males (32%) and 11 of 44 sexually undifferentiated eels (25%). The proportions of migratory and non-migratory eels did not vary by sex or development stage (Chi-squared test = 0.67, df = 2, p = 0.79).

Yellow eels with migratory and non-migratory histories varied significantly in geographic distribution within the East River (ANOVA with arbitrary scores test statistic = 11.3, df = 1, p = 0.0007). The percentage of yellow eels with a migratory history varied markedly among sites and within sites (Table 3). Most (84%) migrant eels were found at Site 4 (9.4 km upriver), where they comprised 90% of all eels caught at that site. Few migrants occurred at Sites 1 and 5, and none, at Sites 2 and 3. This suggests a patchy distribution. The significance of the differences in number of migratory eels among sites is obvious. The number of non-migrant eels also varied significantly by site (Chi-squared test = 15.6, df = 4, p = 0.0036), with Site 4 having fewer eels than the other sites, which had similar numbers.

Migration history (non-migratory, migratory) varied significantly with percent freshwater (FW) growth history (<50, 50 to 75 and 75 to 100% FW; Table 4) (ANOVA with arbitrary scores test statistic = 55.5, df = 1, p < 0.0001). As expected, yellow eels with a non-migratory history, that is continued residence in the river, were much more likely to have a high percentage of freshwater growth (75 to 100% FW), while migratory eels had a higher percentage of estuarine growth. The mean lengths of yellow eels with non-

Table 3. *Anguilla rostrata*. Migration history and distance upriver of capture of yellow eels from the East River, Nova Scotia

	Distance upriver (km) 1.3	3.0	6.3	9.4	11.0	Total (%)
Non-migratory	17	13	21	3	22	76 (71)
Migratory	3	0	0	26	2	31 (29)
% among sites	10	0	0	84	6	
% within sites	15	0	0	90	8	
Total	20	13	21	29	24	107 (100)

Table 4. *Anguilla rostrata*. Migration history and percent freshwater (FW) habitat growth of yellow eels from the East River, Nova Scotia

	<50% FW	50–75% FW	75–100% FW	Total
Non-migratory	0	5	71	76
Migratory	9	15	7	31
Total	9	20	78	107

Table 6. *Anguilla rostrata*. Percent freshwater (FW) growth and length distribution of yellow eels from the East River, Nova Scotia

	Length (mm)				
	100–199	200–299	300–399	400+	Total
<50% FW	0	5	4	0	9
50–75% FW	0	12	7	1	20
75–100% FW	6	49	20	3	78
Total	6	66	31	4	107

migrating and migrating histories did not differ significantly ($F = 0.63$, df = 1, 105, p = 0.43).

The percent of freshwater growth was significantly negatively correlated with distance upstream (linear-by-linear association test statistic = -2.30, 1-sided p < 0.0001) (Table 5). Thus, the proportion of eels with a low freshwater and high estuarine growth history (migrant eels) tended to increase upstream. Yellow eel mean lengths did not differ significantly among percent freshwater growth groups ($F = 1.09$, df = 2, 104, p = 0.34), largely due to the high variability of the lengths of the <50% FW group. Dividing the lengths into 4 length groups, e.g. 100 to 199 mm with the mean length used as a weighting factor, also resulted in a non-significant negative correlation between percent freshwater growth group and length group (linear-by-linear association test statistic = -1.02, 1-sided p = 0.15). Thus, percent estuarine growth did not vary with increasing length (Table 6). If the fish in the 400+ mm group (all female) are omitted from consideration, the result remains the same (linear-by-linear association test statistic = -1.38, 1-sided p = 0.11). There was no significant association between percent freshwater group and age group (Age Groups 5 to 9, 10 to 14 and 15+ yr) (linear-by-linear association test statistic = 0.48, 1-sided p = 0.33).

Length and growth differences among habitat residence groups

The mixed-effects linear model for yellow eel length-at-age found significant differences among habitat growth (% FW) groups in the slopes of their regres-

sions of length-at-age on age (Table 7, Fig. 5). Linear contrasts to test the differences between the slopes for each habitat growth group indicated that the lengths-at-age of the <50% FW group differed significantly ($t = 3.72$, df = 1, 910, p = 0.0002) from those of the 75 to 100% FW group, but not from those of the 50 to 75% FW group ($t = 1.73$, df = 1, 910, p = 0.084). The lengths-at-age of the 50 to 75% FW group differed significantly from those for the 75 to 100% FW group ($t = 2.52$, df = 1, 910, p = 0.012). Mean lengths-at-age began to differ significantly between the <50% FW group and the 75 to 100% FW group at about Age 5 (Fig. 5), as inferred from the non-overlap of the 95% CIs (confidence intervals).

A mixed-effects linear model for yellow eel annual growth indicated that annual growth was negatively correlated with age ($t = -2.55$, df = 1, 838, p = 0.011) and that the intercepts were significant for each habitat growth group (p < 0.0001; Table 8, Fig. 6). Although a linear growth model fit the data well, the change in growth rate with age appears non-linear, increasing then decreasing, particularly for the <50% FW habitat growth group in which the sample size is small (n = 9). The intercepts (and adjusted means) of the regressions of annual growth on age differed significantly between the <50 and 75 to 100% FW habitat growth groups ($t = -3.04$, df = 1, 104, p = 0.003), but did not differ significantly between the <50 and 50 to 75% FW groups ($t = -1.52$, df = 1, 104, p = 0.132). The intercept of the 50 to 75% FW group was marginally not significantly differ-

Table 5. *Anguilla rostrata*. Percent freshwater (FW) growth and distance upriver of capture of yellow eels from the East River, Nova Scotia

	Distance upriver (km)					
	1.3	3.0	6.3	9.4	11.0	Total
<50% FW	1	0	0	7	1	9
50–75% FW	3	1	0	15	1	20
75–100% FW	16	12	21	7	22	78
Total	20	13	21	29	24	107

Table 7. *Anguilla rostrata*. Mixed-effects linear model results of length-at-age on age, by habitat (percent freshwater, % FW) growth group for yellow eels (n = 107, 1020 length-at-age observations) from the East River, Nova Scotia

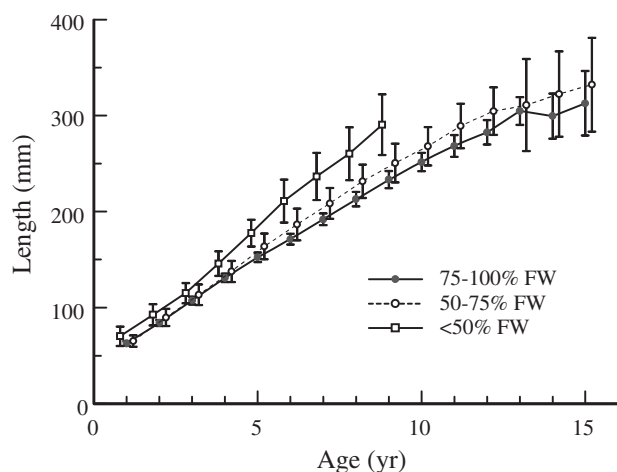| Parameter	df	Value	SE	t	p
Intercept					
Length	910	41.8 mm	1.53	27.3	<0.0001
Slopes					
75–100% FW	910	21.7 mm yr^{-1}	0.45	48.1	<0.0001
50–75% FW	910	24.0 mm yr^{-1}	0.84	28.5	<0.0001
<50% FW	910	26.6 mm yr^{-1}	1.26	21.0	<0.0001

Fig. 5. *Anguilla rostrata*. Mean back-calculated lengths-at-age (mm) with 95% CIs, by percent freshwater (% FW) growth, of yellow eels from the East River, Nova Scotia. Group sample sizes: 75 to 100% FW, n = 78; 50 to 75% FW, n = 20; <50% FW, n = 9

Table 8. *Anguilla rostrata*. Mixed-effects linear model results for annual growth on age, by habitat (percent freshwater, % FW) growth group, for yellow eels (n = 107 945 growth observations) from the East River, Nova Scotia

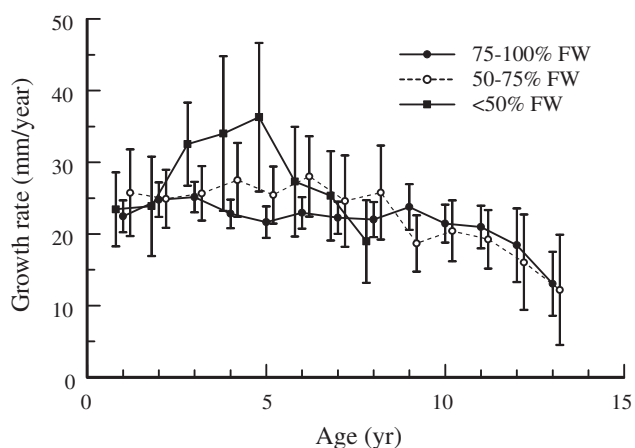| Parameter	df	Value	SE	t	p
Slope					
Age	838	−0.3 mm yr⁻¹	0.13	−2.6	0.011
Intercepts					
75–100% FW	104	23.2 mm	0.81	28.6	<0.0001
50–75% FW	104	25.0 mm	1.09	22.8	<0.0001
<50% FW	104	27.2 mm	1.51	18.0	<0.0001

Fig. 6. *Anguilla rostrata*. Mean annual growth (mm yr⁻¹) with 95% CIs, by percent freshwater (% FW) growth of yellow eels from the East River, Nova Scotia. Group sample sizes: 75 to 100% FW, n = 78; 50 to 75% FW, n = 20; <50% FW, n = 9

ent from that of the 75 to 100% FW group (t = 1.97, df = 1, 104, p = 0.051). The mean annual growth, over all ages, was 21.8 mm yr⁻¹ (SD = 4.08) for the 75 to 100% FW group and was 26.3 mm yr⁻¹ (SD = 4.62) for the <50% FW group. The grand mean of individual eel growth rates was 22.7 mm yr⁻¹ (SD = 4.45) to Age 12 and 22.5 mm yr⁻¹ (SD = 4.50) for all ages.

DISCUSSION

Length and weight by site and migratory group

The variability among some sites in mean lengths and weights resulted from differences in the size distributions among sites, with a few longer eels at some sites, abetted by the systematic selection of eels by length group, greatly influencing the mean and variance. The similarities among migration history and habitat growth (percent freshwater) groups in mean lengths and weights may reflect the limited (relative to silver eels) size and age distributions of the yellow eels, the high natural variability in eel lengths, weights and ages, and the small sample sizes in some migration history and habitat growth groups.

Age interpretation with Sr:Ca ratio assistance

As hypothesised, the detection of annuli and false annuli (supernumerary checks) may be assisted by otolith Sr:Ca analysis along a radius and by knowledge of the position of the elver check. The transition from estuarine to fresh waters produced a check in the otolith between the elver check and first annulus, resulting in a distinctive, closely spaced, double-band pattern for about 16% of the yellow eels from the East River. Double-ring patterns consisting of an annulus and check (false annulus) are common in temperate eel species (Liew 1974, Tzeng et al. 1994, Oliveira 1996, Graynoth 1999), particularly at intermediate ages when the annual growth rate is relatively high. They are less common at older ages.

The distinctive elver check was previously thought to mark the transition from salt- to freshwater (Michaud et al. 1988, Lecomte-Finiger 1992) and to be formed during the first 3 to 4 wk of residence in a river estuary (Michaud et al. 1988), and was, thus, also termed the freshwater check. Recent studies (Lecomte-Finiger 1994, Cieri & McCleave 2001) confirm no relationship with the entrance to freshwater for this 'transition check or elver mark'. The 'freshwater entry' explanation does not account for the presence of an elver check before the first annulus in juvenile eels that have spent a month or more after arrival before conditions are suit-

able for upstream migration (Haro & Krueger 1988, Dutil et al. 1989, Jessop 2000b), or that have spent an extended time in the estuary before migrating upstream during the summer or autumn, or that first entered the river after a period of several years in the estuary (Jessop et al. 2002, present study). The transition from salt- to freshwater may, but often does not, produce an otolith check. The observation by Michaud et al. (1988) that the percentage of elvers with an elver check increases with pigmentation stage and its presence in estuarine-resident juvenile eels suggests an ontogenetic phenomenon relating to the transition from glass eel to pigmented elver. Graynoth (1999) concluded that the mark after the 'freshwater check' in a double-ring pattern in otoliths of *Anguilla dieffenbachia* was a supernumerary check, possibly caused by entry into freshwater. The otolith Sr:Ca ratio analysis of American eel otoliths confirms that such a check may be produced by the quick transition from estuary to river. Sudden water temperature changes of only a few degrees Celsius for more than several hours, such as would occur in the relatively abrupt transition from estuary to river (temperature increase of 3 to 4°C in the East River [Jessop 2003c]), may produce distinct marks in fish otoliths (Volk et al. 1999).

The freshwater transition check, when present, averaged 32% of the distance between the elver check and the first annulus, which compares well with the observations of Graynoth (1999) for *Anguilla dieffenbachia* (<40%). Misidentification of the first habitat transition check as an annulus results in back-calculated lengths at Age 1 that are often less than the observed lengths for elvers let alone for Age 1 juveniles. Consequently, the observation of such unusually short lengths at Age 1 should be cause for re-examination of the age interpretation.

Checks in the otoliths of juvenile American eels occurred throughout the growth period, as observed by Oliveira (1996), and their frequency generally declined from spring through autumn, whether caused by habitat transitions or other environmental factors. Otolith interpretation and observation (Jessop 2003a) both agree that juvenile eels mostly enter the river during spring. However, most (65%) yellow eels showing an otolith habitat transition check as an elver enter during the early summer (July to August), yet >95% of American eel elvers enter the East River during the spring (May to June), although elver runs may continue until late July or August (Jessop 2003b). Some biological basis may exist for the possibility that elvers entering the river later in the run have a higher survival rate than do earlier entrants (Jessop 1998). The assumption that slow-growing, late-recruiting elvers are more vulnerable to predation or other mortality factors and may have poor recruitment is unverified (Tzeng 1990), but

the survival of early migrants is higher in aquaculture (Tabeta & Mochioka 2003). The seasonal pattern, if any, in elver mortality is unknown. Perhaps habitat transition checks are, for some physiological reason, more likely to occur later in the elver run.

Not all checks in the zone between the elver check and putative first annulus were clearly identified as habitat transition checks because of positional mismatching between the Sr:Ca values and distance measurements along the otolith transect. Positional mismatching may be due to measurement differences between methods (microprobe Sr:Ca transect and manual image measurements for back-calculation), particularly when the radius measured may not be the longest available, or may be real and indicate a different timing and another cause for the check.

Supernumerary checks sometimes appeared closer to the following annulus than to the preceding annulus. Thus, the elver may have entered the river in spring and later encountered river conditions, e.g. water temperature change, or a starvation episode during the summer or autumn that produced the check (Liew 1974, Volk et al. 1999). Spring and autumn positional checks that occurred at intermediate ages tended not to be associated with a transition between river and estuarine habitats and must have been caused by other environmental conditions. The occasional group of 2 to 3 closely spaced rings was more difficult to interpret because, as noted by Graynoth (1999), they may consist of a single annulus and associated checks or several annuli separated by narrow summer growth zones. Whatever their origin, misidentified checks result in the overestimation of age and underestimation of growth rate.

Migration history

Most, if not all, eels are believed to recruit to the river as elvers (Tesch 1977, Feunteun et al. 2003), but substantial numbers may recruit as juveniles. This study, as determined by the analysis of otolith Sr.Ca patterns, indicated that 88% of yellow eels from the East River recruited as elvers, while a similar analysis of silver eels found that 75% had recruited as elvers (Jessop et al. 2002). About 12% of yellow eels recruited as juveniles (present study) as compared with 25% of silver eels (Jessop et al. 2002), values that are of comparable magnitude given the expected variability within and among study sampling methods (electrofishing resident eels versus fyke netting of downstream migrants). Eels recruiting from the estuary to the river as juveniles may contribute significantly to the production of downstream-migrant silver eels (Jessop et al. 2002).

Seasonal migrations of juvenile American eels are known to occur between river and estuary (Smith &

Saunders 1955, Medcof 1969, Jessop et al. 2002, Morrison et al. 2003), but the proportion of the eel stock engaging in and the frequency of such migration is generally unknown. This study supported the hypothesis that the proportion of yellow eels in the East River having a history of freshwater–estuarine migration would be low to moderate (29% observed) and the hypothesis that most (81% observed) yellow eels would have undertaken only 1 migration between estuary and river. About 19% of eels made 2 round trips. These values underestimate total migration activity in that they do not include eels that have migrated to, and remain in, the estuary. In comparison, of the 64% of silver eels (n = 41) reported by Jessop et al. (2002) to migrate between river and estuarine habitats, 46% were assessed as having made 1 round trip, 32% as making 2 round trips and 22% as making 3 round trips (B. M. Jessop unpubl. data). A lower proportion of between-habitat migrations for yellow eels than for silver eels is consistent with the younger age composition of the yellow eels. Silver eels provide the most complete evaluation of migratory history. We know of no comparative data for other rivers.

Although male and sexually undifferentiated eels, potentially mostly male, comprised 96% of the sample and females only 4%, the proportions of migratory and non-migratory eels did not vary by sex or development stage. The degree to which male and female eels differ in inter-habitat migration is uncertain, but Jessop et al. (2004) found similar proportions of male and female silver eels in different habitat growth groups.

The interpretation of the migratory history of an individual eel may not always be clear. Habitat transitions were assessed based on the range, extent and position of the fluctuation zone relative to the overall pattern of transect Sr:Ca values. The origin of singleton high or low Sr:Ca values in a series of low or high values is uncertain (habitat movement, seasonal change in Sr:Ca deposition, analysis artefact, etc.). The decision not to interpret singleton values as a migratory movement may result in underestimation of the frequency of movements between habitats, particularly in the few cases where Sr:Ca values spiked to $<3.0 \times 10^{-3}$ or $>5.0 \times 10^{-3}$. Most habitat transitions were quite obvious, but interpretive difficulties included patterns in otolith Sr:Ca values that were suggestive of estuarine-resident eels repeatedly entering and leaving the freshwater mixing zone of the estuary rather than actually migrating a distance upriver, such as when a series of fluctuating values, including singleton Sr:Ca values, occurred constrained near the 4×10^{-3} Sr:Ca value defining the transition between fresh and saline waters. Such fluctuations in Sr:Ca values may occur between annuli or across several annuli.

Ambient freshwater Sr:Ca ratios of 4.1 to 5.6×10^{-3} are unlikely to have created difficulties in interpreting otolith Sr:Ca ratios because of their relatively low value and the non-linear discrimination between element concentrations in the ambient water and the otolith (Rieman et al. 1994, Elsdon & Gilanders 2003).

The hypothesis that the proportion of yellow eels with a migratory history decreases with distance upstream was not supported; instead, the proportion varied markedly among sites and tended to be patchily distributed, with most migratory eels being found at 1 upstream site. The observation that 45% of yellow eels with a migrant history had entered the river in the year of capture and that all were found well upstream (Site 4) suggests that migrant eels enter the river in annually varying numbers, can move rapidly upstream and may do so in groups. Non-migratory yellow eels were more evenly distributed throughout the river. As expected, non-migratory eels showed a higher proportion of freshwater growth than did migrant eels. Given that the East River is a relatively short river, the conclusion that the proportion of yellow eels with a migratory history decreases with distance upstream may not apply to longer rivers where the proportion of freshwater resident eels is highest at inland sites (Tzeng et al. 2002, Shiao et al. 2003). Although the energy cost of migrating increases with distance upstream, other factors such as density-dependent migration and variable habitat quality can influence the geographic distribution of eels within the river (Feunteun et al. 2003).

Hypotheses that the proportion of yellow eels with a migratory history (low percent freshwater growth) increases with length and age were not supported, perhaps because of the limited length range due to sampling mostly male and sexually undifferentiated eels and high variability in the relations between age and length (positive) and age and growth rate (negative) (Oliveira & McCleave 2002, Jessop et al. 2004, present study). Longer, older silver eels from the East River with a higher proportion of females had a higher percentage of migratory history (64%, Jessop et al. 2002) than did the yellow eels (29%) of this study.

Length and growth differences among habitat residence groups

As hypothesised, yellow American eels with a largely estuarine growth history, as evaluated by otolith Sr:Ca ratio data, were longer at a given age and grew faster than those with a largely freshwater growth history, similar to the findings for silver-phase eels (Jessop et al. 2004). Annual growth rates were roughly similar for yellow and silver (Jessop et al. 2004) eels with a history of estuarine growth (yellow eel 26 mm yr^{-1}, silver

eel [male] 22 mm yr^{-1}) and of freshwater growth (yellow eel 22 mm yr^{-1}, silver eel [male] 19 mm yr^{-1}). Thus, yellow eels grew about 1.2 times faster in the estuary than in freshwater. Yellow eels from brackish-water sites in the lower reaches of the more southerly Hudson River also grew more rapidly (55 mm yr^{-1} mean lifetime growth rate based on length and age at capture) than did those from freshwater sites (28 mm yr^{-1}) (Morrison & Secor 2003), as did those from the Cooper River (South Carolina, USA) (freshwater 89 to 96 mm yr^{-1}, Harrel & Loyacano [1982]; estuary 111 mm yr^{-1}, Hansen & Eversole [1984]). The exception to this pattern occurred in Newfoundland, where freshwater growth was slightly greater (66 to 67 mm yr^{-1}) than in brackish-water coastal ponds (62 to 65 mm yr^{-1}) (Gray & Andrews 1971). Thus, although a negative latitudinal cline exists in annual growth rates, irrespective of sex, for silver American eels (and by inference for yellow eels), with northern stocks growing more slowly than southern stocks (Oliveira 1999), within a river–estuarine system the growth rates of estuarine-resident eels are generally higher than those of freshwater-resident eels. The Newfoundland exception may arise because of its latitude near the northern limit of the species range, resulting in a cooler microclimate and shorter growing season in the coastal brackish-water ponds than in more inland streams. This growth rate observation is consistent with the suggestion by Jessop et al. (2004) that the hypothesis proposed by Tsukamoto & Arai (2001) of a higher proportion of marine eels at higher latitudes, with the implication of higher marine/estuarine growth rates, may not apply near the northern limit of the eel's geographic range.

The periodic migration by juvenile American eels between freshwater and estuarine habitats presumably increases the fitness and reproductive success of individual eels and enhances stock survival. Inter-habitat migration by diadromous fishes has been attributed to differences in food availability among habitats (Gross 1987, Gross et al. 1988), although this hypothesis may be somewhat simplistic (Dodson 1997). Faster growth rates in marine/estuarine waters than in freshwater (Jessop et al. 2004, present study) are consistent with the higher productivity of marine/estuarine waters than of freshwater in temperate latitudes (Gross et al. 1988). Higher eel growth rates in the estuary may minimise the time to achieve the size and fitness required for sexual maturation (Oliveira 1999) for a portion of the eel stock. The relatively small proportion of yellow eels that undertake inter-habitat migration may reflect a bet-hedging strategy to minimise the effects of factors such as the high environmental variability in the northern part of the American eel distribution, the relative availability of suitable estuarine and freshwater habitat, or even differential

predation risk, which may be higher in the estuary than in the river, where larger eels are the most abundant fish predator (Watt et al. 1997). Differences among migratory contingents in growth rates and age at maturity, and any geographic cline in the proportions of migratory groups have implications for the evolution of migration. An analysis of lifetime fitness among different migratory contingents of American eels in relation to the validity of evolutionary models in explaining variations in migratory pattern and life-history traits (Dodson 1997) remains to be done.

The use of otolith Sr/Ca ratio data has confirmed the historic observations of seasonal migration by yellow American eels between river and estuary in small rivers of the Atlantic coast of the Maritime Provinces of Canada (Smith & Saunders 1955, Medcof 1969). The extent to which such migratory behaviour occurs over the range of the American eel remains to be determined, as does its relation to the abundance of estuarine and coastal resident eels.

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