

Salinity-linked growth in anguillid eels and the paradox of temperate-zone catadromy

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Temperate-zone anguillid eels use both saline (marine or brackish) and fresh waters during their continental phase, but use of fresh waters is paradoxical because on average these fishes grow more rapidly in saline than in fresh waters. Based on data from anguillid eels whose habitat-residency histories had been determined by Sr:Ca otolithometry, superiority of growth rates in saline water is much greater in American eels *Anguilla rostrata* in north-eastern North America (mean saline: fresh growth rate ratio 2.07) than in European *Anguilla anguilla*, Japanese *Anguilla japonica* and shortfinned *Anguilla australis* eels (range of mean ratios 1.12–1.14). Data from *A. rostrata* in the Hudson Estuary, U.S.A., and Prince Edward Island, Canada, were used to test adaptive explanations of catadromous migrations. The hypothesis that lower mortality in fresh water offsets faster growth in saline water was not supported because loss (mortality + emigration) rates did not vary between saline and fresh zones of the Hudson Estuary. Hypotheses that anguillid eels move to fresh water to escape from larger anguillid eels in saline water or to evaluate habitat quality were not supported by size and age distributions. Catadromy in temperate-zone anguillid eels increases the diversity of occupied habitats and therefore lowers fitness variance caused by environmental fluctuations. Catadromy in temperate-zone anguillid eels could be due to natural selection for maximum geometric mean fitness which is sensitive to fitness variance. Temperate-zone catadromy might also be maladaptive, at least in local areas, due to shifts over time in selective pressures or to inability of panmictic genetic systems to adapt to local conditions. © 2009 The Authors

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INTRODUCTION

Anguillid eels begin their lives in deep ocean basins, migrate as leptocephalus larvae to continental margins, metamorphose to glass eels and then elvers and then begin a yellow (growth) phase in continental waters (Aoyama, 2009). When growth is complete, yellow eels metamorphose to migrating silver eels, which return to the spawning ground where they reproduce and die.

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Young anguillid eels arriving in continental waters may either settle in the saline zone (typically inshore or sheltered salt water and brackish estuaries) or undertake catadromous migration to fresh water (Moriarty, 2003). The salinity history of individual fish can be reconstructed from strontium:calcium (Sr:Ca) ratios measured along otolith centre–edge transects (Fablet *et al.*, 2007). Recent investigations using this method show that initial habitat choice of young anguillid eels may be temporary, with some fishes shifting between salinity zones one to several times during their continental lives (Daverat *et al.*, 2006; Jessop *et al.*, 2008).

Growth rates of anguillid eels vary substantially with temperature, latitude and habitat type (Vollestad, 1992; Naismith & Knights, 1993; Yalcin-Ozdilek *et al.*, 2006). Within a particular watercourse, anguillid eels sampled in saline habitats typically have higher mean growth rates than those sampled in fresh waters [American eel *Anguilla rostrata* (Lesueur), Helfman *et al.*, 1984; Morrison & Secor, 2003; European eel *Anguilla anguilla* (L.), Acou *et al.*, 2003; Melia *et al.*, 2006; Australian long-finned eel *Anguilla reinhardtii* Steindachner, Walsh *et al.*, 2006]. Because of inter-habitat movements, however, growth rates of anguillid eels collected in a particular habitat do not necessarily reflect growth conditions of that habitat. This problem is solved by simultaneous measurement of age and residency history by otolith Sr:Ca analysis. Studies in temperate waters (latitudes *c.* 30° to 60°) in which Sr:Ca revealed habitat history have confirmed higher growth rates in saline rearing habitat than in fresh (*A. rostrata*, Morrison *et al.*, 2003; Jessop *et al.*, 2008; *A. anguilla*, Arai *et al.*, 2006; Japanese eel *Anguilla japonica* Temminck & Schlegel, Tzeng *et al.*, 2003; shortfinned eel *Anguilla australis* Richardson, Arai *et al.*, 2004).

Rapid growth enhances many fitness-related aspects of fish demographics, including quicker progression to reproductive capability and decreased vulnerability to predators (Roff, 2002; Hutchings, 2006; Edeline *et al.*, 2007). In anguillid eels sexual maturation is triggered by size, not by age (Svedang *et al.*, 1996), so rapid growth hastens the single reproductive opportunity of these semelparous fishes. Edeline (2007) termed catadromous migrations by temperate-zone anguillid eels a paradox, given the fitness penalty imposed by relatively slow growth in fresh water. The paradox is the more remarkable in that incoming glass eels which have larger energy reserves, and are thus best equipped to choose their settlement areas, actively prefer migration towards fresh water (Edeline *et al.*, 2006; Sullivan *et al.*, 2009). Proposed explanations for migration by temperate-zone anguillid eels to fresh water include avoidance of competition, agonistic interactions and cannibalism in saline waters (Daverat *et al.*, 2006; Shiao *et al.*, 2006; Edeline *et al.*, 2007), higher mortality in saline than in fresh waters (Moriarty, 2003; Daverat & Tomas, 2006), and genetic tendency for catadromy due to the genus *Anguilla*'s origin in the tropics, where productivity is said to be higher in fresh than in marine waters (Gross *et al.*, 1988; Edeline *et al.*, 2007). Helfman *et al.* (1987) suggested that female anguillid eels use fresh waters to attain a large size at maturation while incurring low mortality risk.

Two streams of ecological thinking can be applied to the question of why some anguillid eels are catadromous despite lower growth rates in fresh water. Under the paradigm that natural selection directs animal behaviour towards patterns which maximize individual fitness (Barash, 1982), fishes make migratory choices on the basis of local fitness conferred by available destination habitats (Werner & Gilliam, 1984; Jonsson & Jonsson, 1993). McCleave & Edeline (2009) proposed that newly

arrived glass eels, which lack local experience, make migratory choices based on internal energetic status, but subsequent movements are to the habitat which gives the best fitness, discounted for travel cost. Fitness in a high-quality habitat may be reduced by crowding in that habitat; hence animals are expected to distribute themselves in such a way that local fitness of individuals is similar across habitats (ideal free distribution; Fretwell & Lucas, 1970; Shepherd & Litvak, 2004). Edeline (2007) framed the choice between saline and freshwater growth areas as a conditional evolutionarily stable strategy, in which anguillid eels find different but equally adaptive solutions through varying migratory behaviours. In this model, the fitness associated with migratory choices is largely determined by the balance between predation, competition and agonistic interactions in saline habitats, and energy costs of migration and lower food availability in fresh water (McCleave & Edeline, 2009).

The second stream of thinking pertinent to anguillid eel catadromy flows from the paradigm of adaptive population resilience. Where environmental conditions fluctuate unpredictably, natural selection favours maximization of geometric mean fitness, rather than arithmetic mean fitness (Yoshimura & Jansen, 1996; Friedenberg, 2003). Because geometric mean fitness is sensitive to variance, risk-spreading behaviours which reduce fitness variance may be adaptive, even if they depress arithmetic mean fitness (Orr, 2007). Selection for maximum geometric mean fitness increases population resilience in the face of environmental perturbation. Formation of diverse migratory contingents in diadromous fishes, including anguillid eels, can thus be viewed as a mechanism that promotes population resiliency by hedging against unforeseen adverse circumstances in any one habitat (Secor & Rooker, 2005).

Temperate-zone anguillid eels have limited or no spatial genetic structure (Wirth & Bernatchez, 2003; van Ginneken & Maes, 2005; Tseng *et al.*, 2006; Pujolar *et al.*, 2009). Because genotypes cannot adapt to specific local environments, the prospect that genotypes fail to shape behaviour to maximize fitness under some local conditions becomes more plausible. Genotypes may also fail to maximize fitness if environmental conditions have been changed by human activity, so that cues used by animals to select optimal habitat are no longer valid (Battin, 2004). Catadromous migrations by temperate-zone anguillid eels might therefore be maladaptive, at least in some local areas.

This paper reviews saline: fresh growth differentials in anguillid eels, and examines adaptive and non-adaptive explanations for anguillid eel catadromy in the temperate zone. Under the paradigm of individual fitness maximization, anguillid eel catadromy could be explained if fitness-enhancing factors in fresh water counter-balance the penalty of slower growth in that habitat. Three hypotheses and tests are posited, as follows.

Jonsson & Jonsson (1993) and Moriarty (2003) suggested that fishes are subject to greater predation pressure in saline than in fresh waters. The mortality hypothesis holds that anguillid eels occupy fresh water because natural mortality is lower there, offsetting the fitness effects of slower growth. If so, natural mortality should be lower in anguillid eels occupying fresh waters than in saline waters of the same system.

Because of intraspecific dominance effects, some individual animals may be forced into inferior habitats that impose lower fitness (ideal despotic distribution; Fretwell, 1972; Calsbeek & Sinervo, 2002). Dominance in fishes is generally associated with larger relative size (Francis, 1983) and in anguillid eels may be manifested

in agonistic interactions (Knights, 1987; Bardonnet *et al.*, 2005) and cannibalism (Lookabaugh & Angermeier, 1992; Edeline & Elie, 2004). Hence for small anguillid eels catadromous migration could be advantageous if it reduces the risk of conspecific attack. The dominance hypothesis holds that anguillid eels move to fresh water to reduce the risk of agonistic interactions and cannibalism in saline waters. If so, the abundance of large anguillid eels, the size class that is most likely to attack small anguillid eels, should be lower in fresh than in saline waters.

Because animals require knowledge of the suitability of available habitats to make optimum habitat choices (Werner & Gilliam, 1984; Selonen & Hanski, 2006), anguillid eels might make exploratory visits to habitats of various salinities to guide their settlement decisions. The exploration hypothesis holds that anguillid eels visit fresh water to assess its suitability, but return to saline water after experiencing slow growth in fresh water. If this is so, then anguillid eels in fresh water should on average be younger than those in saline water.

These hypotheses are examined using data from *A. rostrata* in saline and fresh waters in north-eastern North America. Because anguillid eel growth varies with temperature (Vollestad, 1992; B. M. Jessop, pers. comm.), adjacent study areas within the same watercourse were chosen so that saline and fresh study areas are subject to similar local climates. In large rivers, movement to upstream reaches entails substantial time and energy costs due to long distances and the need to swim against current flow (Feunteun *et al.*, 2003; Edeline 2007). Because of short distances, movement between adjacent saline and fresh habitats probably involves minimal travel costs. Hypothesis tests in this paper address catadromous movements into the downstream portions of freshwater systems, thus avoiding the complicating issue of energetic costs incurred by anguillid eels which migrate far up rivers. To avoid uncertainties arising from inter-habitat migrations, growth data used in these tests were restricted to anguillid eels whose salinity histories were known from Sr:Ca otolithometry.

MATERIALS AND METHODS

This study is based on data on *Anguilla* growth and demographics, drawing particularly on *A. rostrata* studies at two locations. The Hudson Estuary, in the north-eastern U.S., is tidally influenced from its mouth at New York City to a dam at river km 255 (*i.e.* 255 km from the river mouth) (Morrison & Secor, 2003, 2004; Morrison *et al.*, 2003). Penetration of brackish water into the estuary reaches its limit in summer at river km 100. *Anguilla rostrata* have not been fished in the Hudson system since 1976 (Morrison & Secor, 2003). The major habitats for *A. rostrata* in Prince Edward Island, in Canada's Gulf of St Lawrence, are semi-enclosed saltwater bays, brackish estuaries, and freshwater ponds and streams (Cairns *et al.*, 2007). Both fresh and saline habitats on Prince Edward Island are affected by eutrophication caused by nutrients of anthropogenic origin (Cairns, 2002). *Anguilla rostrata* are fished in saline waters on the north and east coasts, but are unexploited in saline waters on the south side and in fresh waters (Cairns *et al.*, 2008). Otolith Sr:Ca studies have shown that *A. rostrata* movements between salinity zones are common in both the Hudson Estuary and Prince Edward Island (Morrison *et al.*, 2003; Cairns *et al.*, 2004; Lamson *et al.*, 2006).

Anguilla rostrata densities were estimated in the Hudson Estuary by mark–recapture analysis of those fished with baited pots (Morrison & Secor, 2004). Pots were set in waters 2–10 m deep immediately adjacent to the main channel. Densities on Prince Edward Island were estimated in freshwater ponds formed by low dams ≤ 0.5 km above head of tide, and in saline estuaries and bays downstream on the same watersheds (Fig. 1). Ponds were equipped

with low-gradient outlets or salmonid fishways that *A. rostrata* can readily transit in both directions (Lamson *et al.*, 2006). Densities were estimated from mark–recapture analysis of *A. rostrata* taken in fyke nets and by night-time transect surveys with a glass-bottom boat fitted with underwater lights (Cairns *et al.*, 2008). The same method was used in both sampling locations in each watershed. The observer on the glass-bottom boat counted only *A. rostrata* within transects. Transect width was defined by the visual angle formed by the observer’s eyes and cords mounted horizontally under each side of the boat’s viewing window. Because virtually all *A. rostrata* seen were within a few cm of the bottom, transect width was considered to be the width of the bottom that was observable within the visual angle. Transect width increased with depth, and was calculated by a formula derived from observations of calibrated rods set on the seafloor. For each transect leg, transect area was calculated as the product of transect width, determined from depths recorded every 15 s, and transect length, determined from GPS records of the vessel track. *Anguilla rostrata* densities were estimated as the number of fish counted divided by total transect area. Turbidity typically limited the view of the bottom to depths of 2.0–2.5 m. Transect segments where the bottom could not be clearly seen were excluded from analysis.

Loss rate, which combines natural mortality and emigration and immigration, was calculated for the Hudson Estuary by catch-curve analysis of *A. rostrata* age frequencies, with ages grouped in three-year bins (Morrison & Secor, 2003).

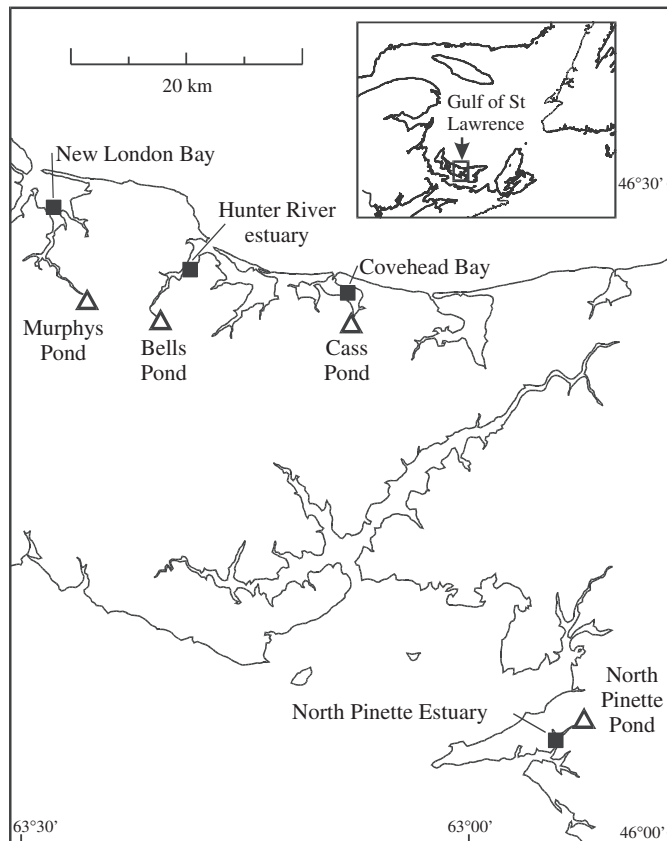


FIG. 1. Central Prince Edward Island, Canada, showing locations of saline (■) and freshwater (Δ) *Anguilla rostrata* survey sites.

Trade-offs between growth and mortality were examined in a life-table model which calculated the number of female anguillid silver eels produced per 1000 glass eels under various growth and mortality situations. The model assumes that low annual mortality in fresh water exactly compensates for rapid growth in saline waters, so that anguillid eels produced per 1000 glass eels is the same in the two habitats. Anguillid yellow eel metamorphosis to silver is triggered by size, rather than age (Svedang *et al.*, 1996). Silver eel total length (L_T) was taken as 640 mm and freshwater growth rate was taken as 56 mm year⁻¹, from means of *A. rostrata* and *A. anguilla* measurements for female silver eels sampled in fresh water (*A. rostrata*: mean L_T 655 mm, mean growth rate 41 mm year⁻¹, from 18 studies, B. M. Jessop, pers. comm.; *A. anguilla*: mean L_T 63 mm, mean growth rate 72 mm year⁻¹, from 32 studies, Vollestad, 1992). Lengths of anguillid silver eels that have grown in fresh and saline waters of the same watercourses do not show significant differences (Jessop *et al.*, 2004; Kotake *et al.*, 2005), hence the model assumed a similar size at maturation in the two habitats.

For anguillid eels in fresh water, an annual mortality rate (%) and the freshwater growth rate were applied to an initial population of 1000 glass eels, and the number alive and the L_T were calculated for each age. The population alive when the anguillid eels reached the silver L_T (640 mm) was calculated by linear interpolation between the numbers alive at the age just before, and at the age just after, attainment of the silver eel L_T . Similar model runs were applied to anguillid eels growing in saline waters, using a growth rate that was a multiple of the freshwater growth rate. Microsoft Excel Goal Seek was used to determine the annual per cent mortality in saline water runs that was required to produce the same number of silver eels per incoming glass eel as freshwater runs. Repeated model runs using a range of input mortalities allowed construction of curves relating annual mortality at freshwater growth rates to annual mortality at saline growth rates, given the same production in the two habitats of silver eels per incoming glass eel.

L_T and ages of *A. rostrata* eels on Prince Edward Island were derived from fyke nets (stretch mesh in the cone: 21 mm) set in ponds, bays and estuaries, and from electrofishing surveys in streams (Cairns *et al.*, 2007). Fyke netting probably provides reasonably unbiased samples of *A. rostrata* present because measurements of fyke netted fish and estimates of L_T during glass-bottom boat surveys produce similar L_T -frequency distributions (J. Hallett & D. Cairns, unpubl. data). Similarly, electrofishing probably provides reasonably unbiased samples because electrofishing L_T -frequencies are very similar to those based on rotary-screw trap catches in the same areas (Cairns *et al.*, 2007).

L_T were measured in a measuring trough and ages were measured by counts of otolith annuli (Cairns *et al.*, 2007, 2008). Fish were considered to be age 0 years in their year of arrival in continental waters. L_T and age data, log₁₀ transformed to reduce asymmetry of distributions, were compared among habitat types by ANOVA with Bonferroni-corrected *post-hoc* tests (Systat, 1998; www.systat.com).

RESULTS

Table I compares growth rates across salinity zones of anguillid eels whose residency history was measured by Sr:Ca analysis. Estimated growth rate in saline water, as a ratio to growth rate in fresh water, ranged from 0.95 to 2.53. Mean \pm s.d. ratios of saline to freshwater growth rate did not vary significantly between sexes at the same sites (males: 1.15 \pm 0.05; females 1.12 \pm 0.06, $n = 5$ pairs, pairwise *t*-test, $P > 0.05$). Mean \pm s.d. brackish: fresh growth rate ratios did not differ significantly from mean marine: fresh ratios in the same watercourses (brackish: fresh: 1.07 \pm 0.05; marine: fresh 1.11 \pm 0.10, $n = 5$ pairs, pairwise *t*-test $P > 0.05$). Mean \pm s.d. saline: fresh growth ratios were not significantly different among *A. anguilla* (1.14 \pm 0.23, $n = 3$), *A. japonica* (1.13 \pm 0.03, $n = 3$) and *A. australis* (1.12, $n = 1$), but these ratios differed significantly from those of *A. rostrata* (2.07 \pm 0.54,

TABLE I. Growth rates of *Anguilla* sp. whose residency histories were determined by otolith strontium:calcium analysis

Species	Site	Latitude	Sex ^a	Mean annual growth of fishes resident in								Method ^b	Source
				Fresh water		Brackish water		Salt water		N	Salt: fresh ratio		
				mm year ⁻¹	N	mm year ⁻¹	N	mm year ⁻¹	N				
<i>A. rostrata</i>	Saint-Jean River, East Quebec, Canada	49° N	mF	18.7 ^c	38	46.0 ^c	78	2.45					LAR—Thibault <i>et al.</i> (2007)
<i>A. rostrata</i>	Brackley-Covehead, Prince Edward Island, Canada	46° N	mF	45.2	27					98.2	33	2.17	BC—Lamson <i>et al.</i> (in press).
<i>A. rostrata</i>	Boughton River, Prince Edward Island, Canada	46° N	F	39.9	15	101.0	6	2.53					LCE—Cairns <i>et al.</i> (2004); D.K. Cairns unpubl. data
<i>A. rostrata</i>	East River Chester, Nova Scotia, Canada	45° N	M	19.2 ^d	17	21.8 ^e	18	1.14					BC—Jessop <i>et al.</i> (2004)
<i>A. rostrata</i>	East River Chester, Nova Scotia, Canada	45° N	F	22.7 ^d	13	27.7 ^e	13	1.22					BC—Jessop <i>et al.</i> (2004)
<i>A. rostrata</i>	East River Chester, Nova Scotia, Canada	45° N	mM	21.8 ^c	78	26.3 ^e	9	1.21					BC—Jessop <i>et al.</i> (2006)
<i>A. rostrata</i>	Hudson River, U.S.A	41–43° N	mF	26.7	16	53.7	10	2.01					LCE—Morrison <i>et al.</i> (2003)
<i>A. anguilla</i>	Galway Bay and River Corrib, Ireland	53° N	mix	30.2 ^c	14					42.0 ^c	10	1.39	LCE—Arai <i>et al.</i> (2006)
<i>A. anguilla</i>	Gironde region, France	45–46° N	mF	54.0	8	52.9	7	0.98		51.3	13	0.95	LCE—Daverat <i>et al.</i> (2004)

TABLE I. Continued

Species	Site	Latitude	Sex ^a	Mean annual growth of fishes resident in						Method ^b	Source	
				Fresh water		Brackish water		Salt water				
				mm year ⁻¹	N	mm year ⁻¹	N	mm year ⁻¹	N			
<i>A. anguilla</i>	Gironde region, France	45–46° N	mF	52.6	83	60.9 ^c	178	1.16			LCE—Daverat & Tomas (2006)	
<i>A. japonica</i>	Mikawa Bay, Japan	35° N	M	57.7	17	62.3	17	1.08	70.3	11	1.22	BC—Tzeng <i>et al.</i> (2003)
<i>A. japonica</i>	Mikawa Bay, Japan	35° N	F	79.2	6	86.2	26	1.09	89.9	10	1.14	BC—Tzeng <i>et al.</i> (2003)
<i>A. japonica</i>	Mikawa Bay, Japan	35° N	M	70.0	8	78.0	10	1.11	82.0	3	1.17	LCE—Kotake <i>et al.</i> (2005)
<i>A. japonica</i>	Mikawa Bay, Japan	35° N	F	81.0	24	89.0	74	1.10	87.0	73	1.07	LCE—Kotake <i>et al.</i> (2005)
<i>A. japonica</i>	Kaoping River, Taiwan	23° N	F	83.5	6	95.2	38	1.14				BC—Tzeng <i>et al.</i> (2002)
<i>A. australis</i>	Lake Ellesmere, New Zealand	44° S	mF	27.4	5	30.8	11	1.12				LCE—Arai <i>et al.</i> (2004)

^aM, male; mF, mostly male; F, female; mF, mostly female; mix, mix of male, female and undifferentiated. Sex categories refer to samples from all habitat types.

^bBC, growth rate from otolith backcalculation; LAR, growth rate from the slope of the length v. age regression; LCE, growth rate calculated as (length at capture–mean elver length) per continental age.

^cIncludes some fishes which moved between salinity zones.

^dResidency history > 50% fresh water.

^eResidency history < 50% fresh water.

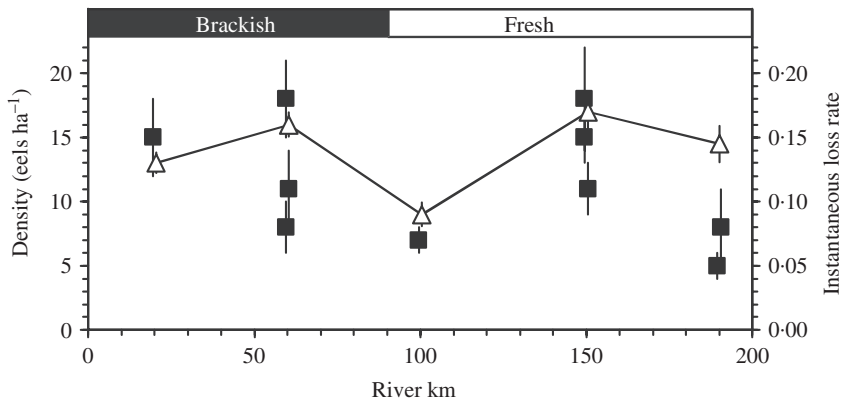


FIG. 2. Mean \pm s.e. estimated densities (■) and loss rates (mortality + emigration) (Δ) of *Anguilla rostrata* in the Hudson Estuary, U.S.A., v. km from the river mouth. Each square represents a density estimate for 1 year. Horizontal positions of points are slightly offset to avoid overlap in error bars. Data from Morrison & Secor (2003, 2004).

$n = 4$) [ANOVA least significant difference (LSD) *post-hoc* test, $P < 0.05$, based on ratios averaged across sexes and across studies within sites].

Anguilla rostrata density and loss rate (mortality + emigration) at five stations on the Hudson Estuary did not vary systematically with distance from the river mouth, and neither density nor loss rate differed significantly between the brackish and freshwater tidal zones (Fig. 2) (Morrison & Secor, 2003, 2004). Density and loss rate at the most upstream station (Albany) was not used because channelization with bankside concrete slabs at that location may have affected vital variables (Morrison & Secor, 2004). Estimated *A. rostrata* densities on Prince Edward Island ranged from 0.0 to 370.9 fish ha⁻¹ (Table II). Ratios of densities in freshwater ponds to densities of saline areas of the same watercourse had a mean of 0.9 and a range of 0.0 to 1.7.

Modelling of growth and mortality trade-offs showed that anguillid eels occupying slow-growth areas must have lower annual mortalities than fish using rapid-growth areas if they are to produce the same number of silver eels per 1000 recruits (Fig. 3). For anguillid eels in a rapid-growth saline area subject to a 20% annual mortality, whose growth rate is 1.13, 1.5, 2.0 and 2.5-fold greater than that of fish grown in fresh water, annual mortality rates in the latter population must be 17.9, 13.8, 10.4 and 8.5%, respectively, to produce the same local fitness.

Mean L_T of *A. rostrata* in unexploited waters of Prince Edward Island were greatest in freshwater ponds, followed by saline waters and streams ($P < 0.001$, all comparisons $P < 0.001$) (Table III). *Anguilla rostrata* sampled in streams (mean L_T 264 mm) were much smaller than fish from other habitat categories (range of means: 525–544 mm). Fish sampled in freshwater ponds (mean 11.4 years) were on average more than twice as old as fish sampled in saline waters (mean 5.4 years) ($P < 0.001$). In the Hudson Estuary, *A. rostrata* in fresh tidal waters were on average longer and older than those in brackish tidal waters (457 v. 440 mm, $P = 0.01$; 17.3 v. 8.6 years, $P < 0.001$; Table III).

DISCUSSION

GROWTH DIFFERENCES BETWEEN SALINE AND FRESH WATERS

This study confirms that, within the same watercourses, anguillid eels in temperate latitudes tend to grow faster in saline than in fresh water (Table I). Use of pairwise growth comparisons in saline and nearby freshwater habitats avoids interpretational problems stemming from latitudinal effects on growth (Vollestad, 1992), and use of otolith Sr:Ca ratios to indicate residency histories avoids problems stemming from inter-habitat movements. Saline: fresh growth differentials did not vary with sex, nor with the type of saline habitat. This means that anguillid eels in saline water tend to have faster growth regardless of whether they develop as males or females, or whether their habitat is marine or brackish.

Ratios of saline to freshwater growth rates were markedly greater in *A. rostrata* (mean ratio 2.07) than in *A. anguilla*, *A. japonica* and *A. australis* (overall mean 1.13, range 1.12–1.14). *Anguilla rostrata* growth was measured only in north-eastern North America, where high saline: fresh growth ratios were found for fish from a diversity of freshwater habitats (ponds, lakes, tidal and non-tidal rivers). It is unclear why the saline growth superiority measured in *A. rostrata* in north-eastern North America is much greater than that of other eel species. This region has colder winters than the northern ranges of *A. anguilla* and *A. japonica*, but the suppression of growth caused by cold winter climate cannot explain the high saline: fresh ratios, because low winter temperatures affect both estuarine and freshwater habitats. In the Gulf of St Lawrence, where saline: fresh growth ratios are the highest recorded (Table I), both fresh and estuarine waters are ice-covered in winter, and for approximately similar durations (Simpson, 1973; D. K. Cairns, pers. obs.).

Superior anguillid eel growth in saline waters at temperate latitudes is conventionally explained by the analysis of latitudinal patterns in primary productivity by Gross *et al.* (1988), which indicated that saline waters have higher productivity than fresh water at mid-latitudes, but fresh waters have higher productivity than marine habitats in the tropics (Tzeng *et al.*, 2002; McCleave & Edeline, 2009). The Gross *et al.* (1988) analysis, however, is based on mean primary productivity of latitudinal bands across oceans, including deep water beyond continental shelves (Bunt, 1975). These mean productivities are unlikely to reliably reflect conditions in estuaries and shallow bays that are used by continental-phase anguillid eels. The saline: fresh growth rate ratio of *A. japonica* in subtropical Taiwan (1.14, Table I) is similar to ratios found in *A. japonica*, *A. anguilla* and *A. australis* at higher latitudes, which suggests that superior anguillid eel growth in saline waters may not be limited to the temperate zone. Data to compare saline and freshwater growth rates are unavailable for anguillid eels occupying tropical waters.

Food supplies available to anguillid eels have not been directly measured as part of anguillid eel growth studies in saline and fresh waters. On Prince Edward Island, mean \pm s.d. chlorophyll *a* concentrations are twice as high in bays and estuaries as in freshwater ponds (bays and estuaries: $9.27 \pm 3.68 \mu\text{g l}^{-1}$, $n = 19$; ponds: $4.56 \pm 2.28 \mu\text{g l}^{-1}$, $n = 8$; Lamson *et al.*, 2009). Water-column chlorophyll *a*

TABLE II. Estimated densities of *Anguilla rostrata* in saline bays and estuaries, and freshwater ponds on their watersheds, in Prince Edward Island, Canada

Location	Saline bays and estuaries			Freshwater ponds			Fresh:saline ratio	Method ^b
	Exploitation status ^a	Density (fish ha ⁻¹)	Location	Exploitation status ^a	Density (fish ha ⁻¹)	Location		
New London Bay	E	54.5	Murphys Pond	NE	0.0		0.0	GBB
Hunter Estuary	E	222.4	Bells Pond	NE	370.9		1.7	GBB
Covehead Bay	E	76.3	Cass Pond	NE	118.0		1.5	GBB
North Pinette estuary	NE	171.2	North Pinette Pond	NE	84.4		0.5	CMR
Mean		131.1			143.3		0.9	

^aE, exploited; NE, not exploited.

^bGBB, glass bottom boat survey; CMR, capture-mark-recapture survey.

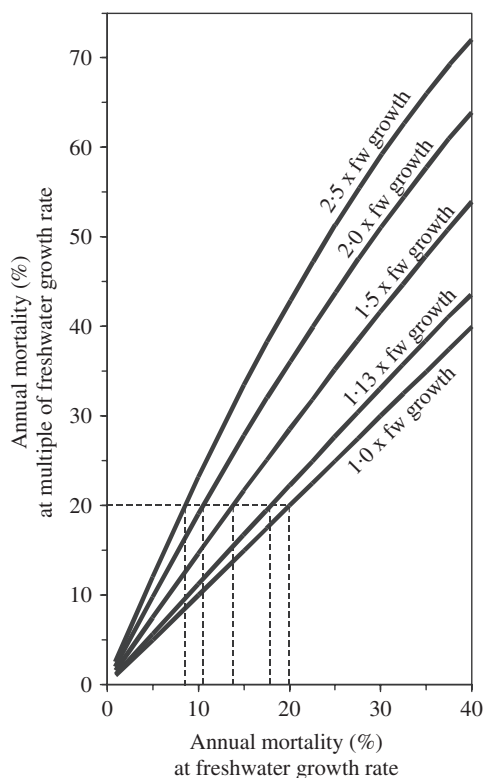


FIG. 3. Trade-offs between anguillid eel growth and mortality that produce equal numbers of silver eels per recruit. Sloped lines indicate the relation between annual per cent mortality at the freshwater (fw) growth rate and at a multiple of the freshwater growth rate, when the two growth rates produce the same number of silver eels per recruit. ---, annual mortalities for multiples of freshwater growth rates that correspond to a 20% annual mortality for anguillid eels growing in saline water. Freshwater growth rate is assumed to be 56 mm year^{-1} and size at metamorphosis from yellow to silver is assumed to be 640 mm, from reviews of *Anguilla rostrata* and *Anguilla anguilla* silver eel data (Vollestad, 1992; B. M. Jessop, pers. comm.).

concentrations, however, do not reflect productivity of macrophytes, which grow profusely in both habitats. Edeline & Elie (2004) found that *A. anguilla* glass eels reared with uniform food availability showed stronger appetites and higher growth rates in salt than in fresh water. The more rapid growth of temperate anguillid eels in saline waters may be due to differences in feeding behaviour as well as to saline-freshwater differences in food supply.

WHY DO SOME TEMPERATE-ZONE ANGUILLID EELS USE FRESHWATER GROWTH AREAS?

According to the Gross *et al.* (1988) model of latitudinal variation in diadromy, the dominance of anadromous forms among diadromous fishes in the temperate zone is due to better growth opportunities in saline than in fresh waters. Anadromous fishes in temperate waters, however, commonly form diverse migratory contingents, some

TABLE III. Mean total lengths (L_T) and ages of *Anguilla rostrata* in non-exploited waters of Prince Edward Island, Canada, and the Hudson Estuary, U.S.A.

Habitat	L_T (mm)			Age (years)		
	Mean \pm s.d.	<i>n</i>	Significance ^a	Mean \pm s.d.	<i>n</i>	Significance ^a
Prince Edward Island						
Freshwater streams	264 \pm 164	108	A			
Saline waters	525 \pm 120	1,231	B	5.4 \pm 1.7	101	A
Freshwater ponds	554 \pm 132	4,902	C	11.4 \pm 6.1	94	B
Hudson Estuary						
Brackish tidal waters	440 \pm 79	126	A	8.6 \pm 4.2	126	A
Fresh tidal waters	457 \pm 66	245	B	17.3 \pm 3.5	245	B

^aMeans with different upper case letters differ significantly ($P \leq 0.01$).

of which spend their growth periods in fresh water (Jonsson & Jonsson, 1993; Secor, 1999; Kerr *et al.*, 2009). Migration to fresh waters is also common in temperate-zone anguillid eels, and glass eels that have sufficient energy reserves actively seek fresh water as they enter the continental zone (Edeline *et al.*, 2006, 2007).

Explanations for the use of freshwater habitats for growth, when saline ones with better growth potential are available, were tested using data from the Hudson Estuary and Prince Edward Island. These tests assume that the individual fitness maximization paradigm applies to anguillid eel migratory behaviour. In both locations *A. rostrata* that had grown in saline waters grew more than twice as fast as those that had grown in adjacent fresh water (Table I; Morrison *et al.*, 2003; Cairns *et al.*, 2004; Lamson *et al.*, 2009), but average eel densities in saline water were similar to those in adjacent fresh water (Table II and Fig. 2; Morrison & Secor, 2004). The similarity of densities shown in these studies would apply only between saline waters and adjacent freshwater reaches, because anguillid eel densities in long rivers diminish with distance upstream (Naismith & Knights, 1993; Smogor *et al.*, 1995; Ibbotson *et al.*, 2002).

The mortality hypothesis proposes that high growth rates in saline waters are balanced by low mortality rates in fresh water, so that fitness is similar in the two habitats. Annual loss rate in the Hudson Estuary did not vary systematically with river km and did not differ significantly between brackish and fresh zones (Fig. 2; Morrison & Secor, 2003). Loss rate is not the same as mortality, because it also includes emigration to the spawning ground. The expectation that annual mortality in the Hudson River is higher in brackish water than in fresh water could be met if annual emigration rates are lower in saline than in fresh waters. The opposite is likely to be the case. *Anguilla rostrata* in freshwater habitats in the Hudson Estuary have a broader age distribution than those in brackish water (Morrison & Secor, 2003). This means that emigration to the spawning ground is spread over a greater range of ages in fresh water than in brackish water; hence annual emigration rate must be lower in fresh than in brackish water.

Life-table modelling showed that given a saline-water growth rate that is double that of fresh water, annual mortality in fresh water would need to be roughly half (*e.g.* 10.4% *v.* 20%) that of saline water in order to achieve the same number of silver eels per 1000 recruits (Fig. 3). The Hudson Estuary data of Morrison & Secor (2003) instead suggest similar mortality rates across salinity zones, and thus do not

support the hypothesis that low freshwater mortality explains catadromous migrations in temperate-zone anguillid eels.

Morrison & Secor's (2003) catch–curve analysis yields mortality estimates for *A. rostrata* yellow eels large enough to be caught in baited pots, but does not estimate mortality for smaller *A. rostrata*. Mortality differentials could provide an adaptive explanation for mid-latitude catadromy if young anguillid eels, newly arrived from the ocean, have higher mortalities in saline than in freshwater areas. The more intense feeding behaviour shown in laboratory studies of salt-seeking glass eels, relative to freshwater-seeking glass eels (Edeline & Elie, 2004), provides a plausible mechanism for mortality differentials because intense feeding in the wild may increase vulnerability to predation (Lankford *et al.*, 2001). If mortality in saline waters is higher than in freshwater in young anguillid eels, but not at later stages, there should be a net migration back to saline waters in subsequent years due to the fitness penalty of slow freshwater growth. Sr:Ca studies indicate that some *A. rostrata* move from fresh to brackish portions of the Hudson Estuary (Morrison *et al.*, 2003), but the greater mean age in the freshwater sector (Table III) suggests that such shifts are not the dominant movement pattern. A review of Sr:Ca studies in six *Anguilla* species at 39 locations worldwide indicates that net movements in the years following arrival from the ocean are mostly towards, rather than away from, fresh water (Lamson *et al.*, 2006).

Under the dominance hypothesis, some anguillid eels migrate to fresh water to avoid negative intraspecific interactions. Yellow-phase eels are not known to defend exclusive feeding territories and may show aggregative behaviour in tanks (Tesch, 2003). Anguillid eels in tanks, however, also show intraspecific aggression, including butting, biting, chasing and fighting with locked jaws (Knights, 1987). Anguillid eels may be cannibalistic at both the glass (Edeline & Elie, 2004) and yellow (Lookabaugh & Angermeier, 1992) stages. Because dominance is strongly influenced by relative size, small anguillid eels might be able to improve their fitness through catadromous migrations if large fishes are less abundant in freshwater areas than in saline areas (Knights, 1987; Lobon-Cervia & Iglesias, 2008). *Anguilla rostrata* sampled in non-tidal freshwater streams in the Hudson River system and in Prince Edward Island are much smaller than those sampled in nearby saline waters (Table III; Machut *et al.*, 2007). Small anguillid eels that move from saline waters into these stream habitats reduce potential contact with larger conspecifics, which is consistent with the dominance hypothesis. In the freshwater portion of the Hudson Estuary and in Prince Edward Island ponds, however, mean sizes were greater than those in saline waters (Table III). This means that small *A. rostrata* moving into these freshwater habitats would probably increase, rather than decrease, their risk of conspecific attack. Thus the dominance hypothesis can explain why anguillid eels might use streams as nursery habitats, but it cannot explain why larger anguillid eels remain in other freshwater habitats in the face of the fitness cost imposed by slow freshwater growth.

The exploration hypothesis suggests that young anguillid eels visit fresh water to gauge its suitability before making settlement decisions. After an evaluation period, these fishes could be expected to return to saline waters to avoid slow growth in fresh water. Hence anguillid eels in fresh water should be younger, on average, than those in saline waters. *Anguilla rostrata* from fresh waters of the Hudson Estuary and Prince Edward Island ponds, however, are on average more than twice as old as those in nearby saline waters (Table III; Morrison & Secor, 2003; Cairns *et al.*,

2007). Sr:Ca studies indicate that yellow eels that shift habitats usually move from saline to fresh water, and that most anguillid eels that enter fresh water remain there for the duration of the yellow phase (Lamson *et al.*, 2006).

The limits to the above tests require emphasis. Mortality estimates for anguillid eels in fresh and saline waters of the same watercourse are available only for a single system, and tests of the dominance and exploration hypotheses were based on data from two areas. Data from these sites are not necessarily representative of *A. rostrata* elsewhere, or of other anguillid species.

Sex in anguillid eels is linked to density, with high densities favouring male production and low densities favouring female production (Davey & Jellyman, 2005). Catadromous migrations to fresh water could potentially be adaptive if lower levels of crowding in fresh water engender production of females. Mean densities, however, are similar between saline and adjacent fresh waters in the Hudson Estuary and in Prince Edward Island, indicating no density differential in fresh water that would favour female production (Table II and Fig. 2). Helfman *et al.* (1987) suggested that mortality is lower in fresh than in saline waters, and that females use freshwater growth areas because they need low mortality to allow them to survive over their long period to maturity. Within freshwater systems, the proportion of females typically increases with distance from the river mouth (Lambert & Rochard, 2007). There is no consistent relation, however, between sex ratio and habitat salinity in anguillid eels. Within particular watercourses, the proportion of anguillid eels that are female in saline water has been reported to be higher than in fresh water (Bark *et al.*, 2007; Yokouchi *et al.*, 2008), lower than in fresh water (Helfman *et al.*, 1984; Walsh *et al.*, 2004), or the same as in fresh water (Jessop *et al.*, 2006; Thibault *et al.*, 2007). These observations, and the finding that saline:fresh growth ratios are similar between the sexes, suggest that differing strategies between male and female anguillid eels do not provide a basis to explain catadromy in temperate-latitude anguillid eels.

The adaptive population resilience paradigm emphasizes natural selection for maximum geometric mean fitness, and therefore also for low variance in fitness (Orr, 2007). Use of diverse habitats by a population spreads risk and decreases fitness variance, because it is unlikely that all habitats will suffer adverse conditions at the same time (Friedenberg, 2003). The population resilience engendered by use of diverse habitats may be a contributor to the widespread finding of multiple migratory contingents in diadromous fishes (Metcalf, 1998; Secor, 1999; Kerr & Secor, 2009). Temperate-zone anguillid eels could be the ultimate example of geographic risk-spreading that minimizes fitness variance, because progeny of single panmictic (or nearly panmictic) populations disperse over enormous stretches of continental coastline (Wirth & Bernatchez, 2003; van Ginneken & Maes, 2005; Tseng *et al.*, 2006; Aoyama, 2009). The use of fresh water in addition to saline habitats for growth further spreads risk and decreases variance caused by fitness failures in particular areas. In this framework, catadromous migrations of temperate-zone anguillid eels may be viewed as an adaptive response to selective pressure for low fitness variation and as a contributor to population resilience.

Battin (2004) argued that ecological traps, which occur when animals voluntarily choose poor habitats that impair population sustainability, may be common where human intervention changes the ecological context so that past cues for good habitat are no longer valid. For example, dams have greatly reduced habitat availability in many rivers, but anguillid eels entering these rivers cannot know this. Natural

selection normally corrects maladaptive habitat choice, but in temperate anguillid eels the genetic response may be slowed by the absence or near-absence of spatial genetic structure (Wirth & Bernatchez, 2003; van Ginneken & Maes, 2005; Tseng *et al.*, 2006), which precludes genetic adaptation to local conditions. It is thus possible that use of freshwater growth areas by temperate-zone anguillid eels is maladaptive. Several circumstances could lead to such an outcome. Temperate-zone anguillid eels might use freshwater habitat because of a genetic disposition that is retained from their tropical ancestors, which are thought to have developed catadromous migrations to profit from relatively higher productivity in tropical fresh waters (Tsukamoto *et al.*, 2002). Anguillid eels in the temperate zone might use fresh water if most of the species' population uses low latitude growth areas that have higher growth rates in fresh than in saline waters. Populations of *A. rostrata* in the tropical parts of the species' range (Caribbean Basin and northern South America), however, are probably small, based on low reported landings in the region (<http://www.fao.org/fishery/statistics/global-production>). Propensity for catadromous migrations could reflect adaptation to differing circumstances in the past. Archaeological and early historic records of aboriginal fisheries in the St Lawrence River (Junker-Andersen, 1988) and the Domesday Book of medieval England (Naismith & Knights, 1993) suggest very high anguillid eel abundances in pre-industrial times. Anguillid eel densities in saline habitats may have been sufficiently high to cause density-dependent mortality and growth suppression, and thus give adaptive advantage to movements to fresh water. A genetically based tendency for catadromous movements, formed by selection in earlier times, could still produce such movements in modern times. In areas where the influx of glass eels is intensely concentrated, such as the Bay of Biscay, very high densities in estuaries that force new arrivals upstream may persist (Lobon-Cervia & Iglesias, 2008).

Anguillid eels are remarkably plastic in their use of freshwater habitats, which allows them to invade and occupy most or all accessible areas of a freshwater system (Helfman *et al.*, 1987; Moriarty, 1987). Anguillid eels in non-tidal fresh waters have different growth regimes from those in marine waters (Table I) and their survival regimes may differ as well. Freshwater systems, especially large ones, should respond differently to climatic and other environmental forcing and contribute to population resiliency over generations. No other part of the anguillid eel's habitat has been as drastically affected by human activities, especially by damming, pollution and water quality degradation (Haro *et al.*, 2000; COSEWIC, 2006). Thus although anguillid eels can achieve higher growth rates in saline habitats, it seems probable that resiliency and possibly production of anguillid eel populations have been weakened by reduced quantity, quality and diversity of available freshwater habitats.

This study has shown that growth rates in saline water strongly exceed those in fresh water in *A. rostrata* in north-eastern North America, and modestly exceed freshwater growth rates in other anguillid species. On the basis of limited data, hypotheses to explain catadromy in temperate-zone anguillid eels based on individual fitness maximization were not supported. Temperate-zone catadromy may be due to selection for low fitness variance and hence geographic risk-spreading. Temperate-zone catadromy might also be maladaptive, at least in local areas, due to shifts over time in selective pressures or to inability of panmictic genetic systems to adapt to local conditions. The adaptive basis of catadromy in anguillid eels has been examined in theory (Helfman *et al.*, 1987; Tsukamoto *et al.*, 2002; McCleave & Edeline, 2009), but the

paradox addressed in this study will only be resolved when theory is rigorously evaluated by empirical tests. It is hoped that this study will encourage empirical analysis to be a central part of future explorations of life-history variation in anguillid eels.

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