Movement Patterns of American Eels in an Impounded Watercourse, as Indicated by Otolith Microchemistry

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Abstract.—Otolith Sr:Ca ratios were used to determine migrational histories of American eels *Anguilla rostrata* in an eastern Canadian coastal stream that is impounded at the head of tide. American eels sampled from the estuary were smaller (41.0 ± 9.3 cm [mean $\pm$ SD], $N = 324$) and younger (ages 1–4) than those in a freshwater pond (65.0 ± 7.5 cm, $N = 265$; ages 11–26) 2.5 km upstream of the head of tide. The Sr:Ca ratios permitted identification of three migrational contingents. In 7 of 13 (54%) American eels taken in the estuary, Sr:Ca ratios declined to $4.76 \pm 1.22 \times 10^{-3}$, indicating direct migration from the sea to estuarine settlement sites. In the 6 other American eels (46%), Sr:Ca ratios indicated an approach to freshwater soon after arrival in continental waters, followed by settlement in the estuary where ratios stabilized at $4.50 \pm 1.23 \times 10^{-3}$. In all 15 American eels sampled from the freshwater pond, Sr:Ca ratios indicated settlement in freshwater in the elver year and no subsequent change of habitat salinity (postelver ratio, $0.64 \pm 0.66 \times 10^{-3}$). The lack of evidence for postelver movements between freshwater and brackish water contrasts with literature findings that such movements are common in systems where dams do not impede access to freshwater. Dams may hamper normal American eel movements between rivers and estuaries, even in watercourses in which some American eels are able to colonize freshwaters.

Recent declines of American eels *Anguilla rostrata* and European *A. anguilla* eel have focused attention on factors that limit numbers of these species. Possible causes of the declines include changes in ocean conditions, overfishing, pollution, and dams (Richkus and Whalen 2000). Busch et al. (1998) estimated that up to 84% of riverine habitat in U.S. eastern seaboard and Lake Ontario drainages lies upstream of dams. Although natural barriers would have impeded American eel access to some of this habitat, even if dams had not been

built (Haro et al. 2000), it is clear that dams affect a substantial portion of potential eel habitat in North American fresh waters.

American eels are weak swimmers and are unable to leap over waterfalls or swim directly against strong currents. Eels ascending rivers attempt to circumvent obstacles by seeking low-current routes, usually along banks that have a rough substrate, which permits the animal to advance with a serpentine motion (Tesch 1977). Eels smaller than about 11 cm can creep up vertical walls, but larger eels require a sloping substrate (Legault 1988). Thus some obstacles impose a size-dependent barrier to migration. Although eels are known to perform remarkable feats of migra-

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tion, such as surmounting waterfalls and invading landlocked lakes (Eales 1968), the general case appears to be that physical obstacles substantially constrain upstream movements (Porcher 1982; White and Knights 1997; Feunteun et al. 1998). However, factors enabling an eel to overcome obstacles in a river have not been quantitatively investigated. This means that the effects of dams and other structures on eel ascent of a river cannot be predicted from the nature of the obstacle.

Evaluations of the effects of dams on eel populations emphasize the classic catadromous paradigm that American eels ingress into freshwater, remain in freshwater during the yellow (growth) stage, and then return to the sea as silver eels (McCleave 2001). However, eels may exhibit other migratory patterns. Secor (1999) pointed out that diadromous fish commonly show intrapopulation variation in migration, some maintaining long-term residence in one habitat, others shifting among habitats. The development of microprobe analysis of Sr:Ca ratios in fish otoliths permits determination of the migratory history of individual fish through salt, brackish, and freshwater because Sr:Ca ratios are empirically linked to ambient salinity (Secor et al. 1995; Secor and Rooker 2000). Otolith Sr:Ca ratios decline sharply during the glass eel stage because of metabolic processes unrelated to ambient habitat (Tzeng et al. 1997). For subsequent stages, laboratory validation studies have confirmed that otolith Sr:Ca ratios reflect ambient salinity, although temperature and diet also play a role (Tzeng 1996; Bath et al. 2000; Kraus and Secor 2003).

In many systems American eels exhibit seasonal migratory runs, especially in spring and fall (Smith and Saunders 1955; Medcof 1969; Jessop 1987). However, the occurrence of such runs does not necessarily mean that individual eels undertake regular seasonal movements. Application of the Sr:Ca method to American eels in an unimpounded stream in Nova Scotia showed that some individuals chose habitat of a certain salinity and then stayed there, whereas others showed irregular, often nonannual movements between the river and the estuary (Jessop et al. 2002). In the Hudson River estuary, Sr:Ca ratios of yellow American eels captured in brackish waters indicated that some animals had stayed in brackish water since their arrival as elvers, whereas others had spent varying periods in freshwater before returning to brackish water (Morrison et al. 2003). However, eels sampled in the freshwater upper reach of the estuary showed no evidence of residency in brack-

FIGURE 1.—Map of the Boughton River, Prince Edward Island, where movement patterns of American eels were examined with otolith microchemistry. Triangles indicate dams and the arrow indicates the study area.

ish water. Tzeng et al. (2003) found that the majority of Japanese eels *Anguilla japonica* sampled as silver eels in an estuary had shifted residence between freshwater and seawater, or vice versa, during their yellow eel phase. These studies suggest that movements between fresh and brackish waters are common in yellow-phase eels and that such movements are often irregular and nonannual.

Barriers to fish migration could potentially reduce American eel production in a watercourse (estuary and river) by hindering colonization of freshwater rearing areas or by suppressing movements, either annual or irregular, between river and estuary. This study uses otolith Sr:Ca ratios to determine patterns of river–estuary movements in American eels in a small system that is impounded at head of tide. These data are used to evaluate potential effects of dams on eel movements between habitats of varying salinity.

Methods

This study was conducted in the Boughton River, Prince Edward Island, Canada (Figure 1). The system is tidal from its mouth to the foot of Ross Dam, 12.5 km upstream. Water leaving Ross Pond flows through a rock channel that gradually de-

FIGURE 2.—Length-frequency distribution of American eels sampled in the Boughton River estuary and Whitlocks Pond.

scends to the natural stream bed. Whitlocks Pond, a 41-ha impoundment 2.5 km upstream from Ross Dam, has two outlets. On one there is concrete spillway with a vertical drop, and on the other the water flows through a rock channel that descends to the natural stream bed. Total stream length above Ross Dam is 8 km. Both Ross and Whitlocks dams raise water 2–3 m above the outflowing stream level. Both structures are bordered by woodland and grassy habitat.

American eels were captured in the estuary and at Whitlocks Pond in May–August 1999 via fyke nets with stretch-mesh sizes of 24 mm in the leader and 19 mm in the funnel. All eels were measured live (mm) in a V-shaped measuring trough. Eels not retained for otolith examination were released.

Otoliths from 28 American eels were embedded in Epofix resin and polished until the core was exposed on the surface. The polished otoliths were coated with a layer of carbon under a high-vacuum evaporator. The Sr and Ca concentrations from the primordium to the otolith edge were measured by an electron probe microanalyser (JXA-8900R) with a wavelength dispersive spectrometer. Quantitative analyses were conducted at an interval of approximately 10 μm , using beam conditions of 15 kiloelectron volts (keV) for the acceleration voltage, 3 nA for the current, and a beam size of $5 \times 4 \mu\text{m}^2$. The wavelength dispersive spectrum was measured for 120 s at peak positions and 20 s at background positions for Sr and at 20 s and 10 s, respectively, for Ca. The beam power density of $2.3 \text{ W} \cdot \text{m}^{-2}$ was within the range of 0.5–3.0 W

$\cdot \text{m}^{-2}$ suggested by Gunn et al. (1992), and the counting time was sufficient to ensure effective measurement. Calcite (CaCO_3 , NMNH 136321) and strontiantite (SrCO_3 , NMNH R10065) were used as standards. The weight ratio of Sr:Ca was calculated after correction with the ZAF method (Z = atomic number effect, A = absorption of X-rays within the specimen, F = fluorescence effects; Goldstein et al. 1984). After microprobe analysis, the otoliths were repolished and etched with 5% ethelenediaminetetraacetic acid to enhance the annuli (Tzeng et al. 1994). Distances were measured from the core to the metamorphosis check (transition from leptocephalus larvae to glass eel), elver check (transition from glass eel to elver), and annuli, marking age in years.

Differences between group means were tested by t -test, and heterogeneity of regression slopes was tested by analysis of covariance (ANCOVA); significance was set at $\alpha = 0.05$ in all tests.

Results

Salinities in the estuary sampling sites ranged from 3 to 15 ppt (surface) and 7 to 28 ppt (bottom), depending on tidal phase.

American eels captured in the estuary were on average much smaller than those taken in Whitlocks Pond (estuary $41.0 \pm 9.3 \text{ cm}$ [mean $\pm$ SD], $N = 324$; Whitlocks Pond $65.0 \pm 7.5 \text{ cm}$, $N = 265$; t -test, $P < 0.0001$; Figure 2). In all measured otoliths, Sr:Ca ratios were about $10\text{--}14 \times 10^{-3}$ at the metamorphosis check (Figures 3–5). Subsequent patterns of Sr:Ca ratio versus distance from the core

FIGURE 3.—For the seven American eels taken in the Boughton River estuary of Prince Edward Island that showed a saltwater–brackish water history, means and standard deviations are depicted for (A) the Sr:Ca ratios and (B) the distances of annuli from the otolith core; *N* is the number of microprobe measurements, annulus *M* is the metamorphosis check, annulus *E* is the elver check, and subsequent annuli are annual checks.

fell into three groups. In seven eels taken in the estuary, Sr:Ca ratios declined steeply between the metamorphosis and elver checks, declined slowly between the elver check and the first annulus, and then stabilized without trend at a mean of $4.76 \pm 1.22 \times 10^{-3}$ (Figure 3). These eels are inferred to have a saltwater–brackish water (SB) individual life history. In six other eels from the estuary, Sr:Ca ratios fell sharply between the elver check and the first annulus, and then descended to minimum values at ages 1–2 before rebounding to stabilize at age 2 and older at a mean of $4.50 \pm 1.23 \times 10^{-3}$ (Figure 4). These eels are inferred to have a saltwater approach to freshwater–brackish water (SAB) life history. Minimum Sr:Ca ratios between the elver check and age 2 were significantly lower for SAB eels (mean $0.51 \pm 0.40 \times 10^{-3}$) than for SB eels (mean $1.82 \pm 0.65 \times 10^{-3}$; *t*-test, *P* = 0.001). At sampling SB eels ranged from ages 1 to 4; all SAB eels were age 4.

All 15 eels sampled from Whitlocks Pond showed a steep decline in Sr:Ca ratio between the metamorphosis and elver checks (Figure 5) and were categorized as saltwater to freshwater (SF) eels. Ratios at age 1 and older were stable at a mean of $0.64 \pm 0.66 \times 10^{-3}$. Ages at sampling for Whitlock eels ranged from 11 to 26 years.

Annulus distance from the core was linearly re-

FIGURE 4.—For the six American eels taken in the Boughton River estuary of Prince Edward Island that showed a saltwater approach to freshwater–brackish water individual history, means and standard deviations are depicted for (A) the Sr:Ca ratios, (B) 9-point moving averages of the Sr:Ca ratios of individual eels, and (C) the distances of annuli from the otolith core. Annulus *M* is the metamorphosis check, annulus *E* is the elver check, and subsequent annuli are annual checks.

lated to annulus number for the period from the elver check to the fourth annulus in all movement pattern groups (Figure 6). However, regression slopes differed significantly among groups (ANCOVA, *P* < 0.0001), the SB group showing the fastest growth, followed by the SAB and SF groups.

Discussion

The Sr:Ca patterns revealed three distinct migratory contingents within the American eel population of an impounded coastal watercourse. About half (54%) of the 13 eels captured in the estuary showed otolith Sr:Ca ratios that steadily declined from the elver stage to a stable level, which is consistent with continued residency in

FIGURE 5.—For 15 American eels taken in Whitlocks Pond (Boughton River of Prince Edward Island) that showed a saltwater–freshwater individual history, means and standard deviations are depicted for (A) the Sr:Ca ratios and (B) the distances of annuli from the otolith core. Annulus *M* is the metamorphosis check, annulus *E* is the elver check, and subsequent annuli are annual checks.

brackish waters. There was no dip in ratios between the elver stage and estuarine residency, which suggests that these eels did not attempt to ascend above the estuarine settlement area. For the other half of eels caught in the estuary (46%), Sr:Ca ratios dropped to 2.1×10^{-3} or less after the elver stage before rising to a stable level. These eels apparently ascended to the upper estuary (or possibly side tributaries) within 2 years of arrival in continental waters, and subsequently fell back to establish residency in brackish waters. Both the timing and the duration of the approach to freshwater were highly variable among individuals (Figure 4B). The third group, those sampled in Whitlocks Pond, showed postelver Sr:Ca ratios that descended quickly to stabilize at levels consistent with freshwater use. These eels apparently ascended directly to freshwater in their elver year, and remained there until they were captured.

In systems where eels can enter freshwater without encountering dams, Sr:Ca patterns indicate that many eels move between marine and freshwater or vice versa during the yellow eel stage (American eel: Jessop et al. 2002; Morrison et al. 2003; Japanese eel: Tzeng et al. 2002, 2003). Tzeng et al. (2002) also sampled eels above a dam; all showed exclusively freshwater Sr:Ca patterns in

FIGURE 6.—Distances from the otolith core versus annulus counts for American eels (Boughton River of Prince Edward Island) showing saltwater–brackish water (SB), saltwater approach to freshwater–brackish water (SAB), and saltwater–freshwater (SF) movement patterns; *M* is the metamorphosis check and *E* is the elver check. Regression lines and equations are for the period from the elver check (age 0) to the 4th annulus (age 4).

the postelver period. American eels in the Boughton system showed no evidence of postelver movement between the estuary and freshwater. Some of the estuary-resident eels in the Boughton system approached freshwater but later returned to settle in the estuary. These eels may have attempted to enter freshwater, either for long-term residency or as part of an irregular excursion, but fell back because they were unable to surmount the dam at head of tide. Eels from Whitlocks Pond, all of which had entered freshwater during their elver year, may have been able to surmount the dam at the head of tide because their small size allowed them to scale vertical surfaces (Legault 1988), whereas the dam prevented passage of larger eels.

Our finding that Boughton River American eels show less movement between freshwater and brackish water than that reported for eels in unimpounded systems is consistent with literature reports that dams are a substantial impediment to eel movement, even in cases where some eels are able to surmount them (Smogor et al. 1995; White and Knights 1997; Feunteun et al. 1998).

Our data showed a nonoverlapping age distribution between American eels sampled in the Boughton estuary and Whitlocks Pond. The oldest eels in estuary samples were age 4 and the youngest eels from the pond were age 11. The absence of eels younger than age 11 in the pond could be explained by a complete barrier to migration imposed 11 years before sampling. However, no change in the nature or severity of obstacles in the

Boughton River is known for that time. Two other explanations for the divergence of ages between the two habitats are possible. Commercial fishing on Prince Edward Island is permitted in tidal waters only. Heavy exploitation of eels over the minimum size (46.0 cm up to 1997, 50.8 cm in 1998 and beyond) could have reduced the size and, therefore, the age distribution of eels in the estuary. The upper Boughton River contains an extensive network of creeks and marshes. Eels younger than age 11 may have been present in such habitats but absent from Whitlocks Pond.

Annuli in American eel otoliths from the Boughton estuary were more widely spaced than those from Whitlocks Pond, suggesting a more rapid growth rate in the estuary. In Nova Scotia, migrating silver eels with a dominant estuarine history grew more rapidly than those that had spent most of their time in freshwater (Jessop et al. 2002, unpublished data), but in Newfoundland eels grew faster in freshwater than in brackish coastal ponds (Gray and Andrews 1971). Migration contingents (Secor 1999) may show growth rates that vary among habitats. This does not necessarily mean that some habitats offer superior fitness to others because rapid growth in fishes is often accompanied by high mortality (Halpin 2000). The varying patterns of interhabitat eel movements may all have adaptive values that would be constrained by artificial barriers that prevent such movements.

Literature on the effects of dams on American eel populations emphasizes barriers to upstream colonization and turbine-induced mortality in downstream migrants (Richkus and Whalen 2000; McCleave 2001). Prince Edward Island has more than 800 dams (MacFarlane 1999) and most watercourses are impounded in one or several places. These dams do not prevent upstream colonization because eels are commonly found in impounded ponds (DKC., unpublished data); furthermore, turbine mortality does not occur because the dams are not used for water power. The findings of our study imply that dams in Prince Edward Island might negatively affect eel production by reducing the proportion of eels that are able to invade freshwater and by hindering normal migratory movements between freshwater and estuaries. However, dams could also benefit eel production by converting stream habitat, which is little used by eels on Prince Edward Island (Cairns 2002), to pond habitat, which has greater surface area and greater volume. Determination of the net effect of dams on eels requires further investigation.

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