Comparison of Juvenile Alewife Growth and Movement in a Large and a Small Watershed

Authors: Turner, Sara M., and Limburg, Karin E.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 4(1) : 337-345

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2012.675974

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:337–345, 2012

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2012.675974

SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

Comparison of Juvenile Alewife Growth and Movement in a Large and a Small Watershed

Sara M. Turner* and Karin E. Limburg
State University of New York, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, New York 13210, USA

Abstract

The freshwater behaviors of juvenile alewives *Alosa pseudoharengus* and the variables affecting their survival to recruitment are relatively unknown, even though recruitment to marine populations is critical to sustaining and restoring populations. Fish were collected in fall 2009 from a large watershed (the Hudson River, New York; $N = 10$) and a small watershed (the Peconic River, New York; $N = 14$), otolith chemistry was used to associate the fish to groups, and growth rates were compared both within and between rivers. Otolith Sr:Ca and Ba:Ca were measured along growth transects, and significant changes in these values were determined. In many instances, changes in these values are associated with changes in daily otolith growth increments. More variation was observed in the Ba:Ca ratios and daily growth rates of Hudson River alewives, possibly because they had more available nursery habitats. While there was variation in otolith chemistry and daily growth within Peconic River fish, fewer otolith chemistry patterns were observed in this group. Comparison of cumulative daily growth rates between the two groups showed that Hudson River alewives were smaller at younger ages but that their growth rate increased and their size at age eventually surpassed that of the Peconic River alewives. The results presented here provide the foundation for future work investigating the abiotic and biotic variables influencing juvenile alewife growth, behavior, and survival in different-size watersheds.

Alewives *Alosa pseudoharengus* (often referred to together with blueback herring *A. aestivalis* as "river herring") have been declining throughout their ranges for several decades. Despite strict harvest restrictions and moratoria imposed by many states, most populations remain depressed (Schmidt et al. 2003; Taylor et al. 2009). These fish are anadromous, spending most of their lives at sea but using coastal watersheds for spawning and nursery habitats (Fay et al. 1983). Because of the wide range of habitats they utilize, like most anadromous fishes, alewives are important links in both marine and freshwater food webs. River herring populations are impacted by alterations to inland habitats (e.g., dams, eutrophication, and invasive species), predation in rivers and the ocean, overfishing, and incidental bycatch (Limburg and Waldman 2009).

The recruitment of river herring from nursery habitats to marine populations is critical, but little is understood about their early life stages: most work to date has focused on determining emigration timing and cues and quantifying the numbers of emigrating juvenile alewives (Kosa and Mather 2001; Yako et al. 2002; Gahagan et al. 2010). Similarly, many studies have examined the growth rates of larval and juvenile fish to compare growth and recruitment among cohorts (e.g., Rutherford and Houde 1995; Limburg 1996, 2001; Baltz et al. 1998; Murt and Juanes 2009). A wide range of abiotic and biotic variables can affect juvenile growth and survival to recruitment, such as prey availability, predation risk, competition, and the availability of spatial refuges (Walters and Juanes 1993).

Subject editor: Anthony Overton, East Carolina University, Greenville, North Carolina, USA

*Corresponding author: smturner@syr.edu
Received March 21, 2011; accepted September 26, 2011

Otoliths can provide information about growth rates and past habitat usage in a wide range of fishes (Limburg 1995; Campana and Thorrold 2001; Begg et al. 2005; Elsdon et al. 2008). Otoliths are distinct from other calcified structures in that they are continually accreted, grow proportionately to somatic length, and become chemically inert on formation (Campana 1999; Campana and Thorrold 2001; Elsdon et al. 2008). The use of daily increments to age juvenile alewives was validated by Sismour (1994) by collecting eggs in the wild and rearing them in captivity. Additionally, otoliths can be used to identify past habitat occupancy because they take up some elements and isotopes in proportion to ambient water (Campana 1999). A coastwide study of the closely related American shad *A. sapidissima* used otolith chemistry to assign juveniles of known origin to their natal watershed with high accuracy (80–100%; Walther and Thorrold 2008). When a direct correlation between water and otolith chemistry has not been established, distinct patterns of otolith chemistry shifts within a population can suggest "contingents," or groups of fish with similar life history behaviors (Secor 1999; Daverat et al. 2006; Elsdon et al. 2008). Comprehensive understanding of the spatial and temporal scale of variation in water chemistry is critical to studies aimed at correlating shifts in otolith chemistry with specific habitat usage (Elsdon et al. 2008).

The use of otolith chemistry depends on the spatial variation in water chemistry signatures, which can be influenced by bedrock geology, geographic location, and terrestrial inputs. Strontium has often been used as an indicator of movement between marine and freshwater areas, as many inland waters have depleted Sr in comparison with the ocean (Limburg 1995). In large watersheds with low soil and bedrock Sr:Ca ratios, low salt intrusion, and high flow, such as the Hudson River, New York, aqueous Sr:Ca values tend to show little spatiotemporal variation (Limburg and Siegel 2006). Comprehension of small-scale habitat movements within a large watershed requires a good understanding of the spatial and temporal variability in trace elements other than strontium (e.g., Ba, Mn, Mg, and Pb) and possibly isotopes (e.g., $^{87/86}$Sr, δ^{18}O; Walther and Thorrold 2008) as well. In small, coastal catchments, tidal influence encompasses a much larger proportion of the watershed. However, if the geochemistry of freshwater above the head of tide is distinct from a marine signal, at a minimum it should be possible to detect freshwater residency and movement from freshwater into tidal estuarine and marine waters.

Previous work on American shad (Limburg 1995; Walther and Thorrold 2008) demonstrated that the ratios of strontium and barium to calcium in otoliths directly reflect environmental values. Shifts in these values thus imply movement to a new habitat or temporal changes in water signatures; therefore, individuals with similar chemistries in a given time period were probably in the same habitat. Juvenile American shad captured in the lower Hudson River estuary had increasing Sr:Ca values, which corresponds to movement from freshwater to higher-salinity environments (Limburg 1995).

Movement among different nursery areas is a key strategy used by juvenile fish to increase growth (i.e., utilize higher quality or quantity food sources) as well as the probability of survival to recruitment (i.e., to decrease predation risk). By combining the use of otolith chemistry with daily otolith growth rates, we can examine whether there is a direct relationship between movements (inferred from changes in otolith chemistry) and changes in daily growth and whether movement patterns differ in large and small watersheds. We tested the two hypotheses that (1) there is a relationship between juvenile alewife movements among nursery habitats and changes in growth rates and (2) juvenile alewives in large watersheds make more frequent, smaller-scale movements within the system than do those in small watersheds.

METHODS

Study sites.—The Hudson River watershed (Figure 1), with a drainage basin of 34,000 km^2, has a tidal estuary that extends more than 250 km and is fed by over 79 tributaries (Levinton and Waldman 2006). By convention, river kilometer (rkm) 0 marks the start of the estuary at the southern tip of Manhattan Island. Most of the estuary's freshwater flow derives from the upper Hudson River and the Mohawk River (the largest tributary of the Hudson). The Peconic River on the eastern end of Long Island is a watershed of approximately 120 km^2 that extends 28 km and flows into Peconic Bay. The bay extends for 40 km and connects to the Atlantic Ocean.

Sample collection and preparation.—Juvenile alewives were collected with a 30.5-m beach seine with a 6.35-mm mesh size; fish were stored directly in 95% ethanol. In the Hudson River, fish were collected on September 21, 2009, at Newburgh, New York (rkm 92; 41°29.082′N, 73°59.346′W). Alewives were sampled in the Peconic River on October 1, 2009, just

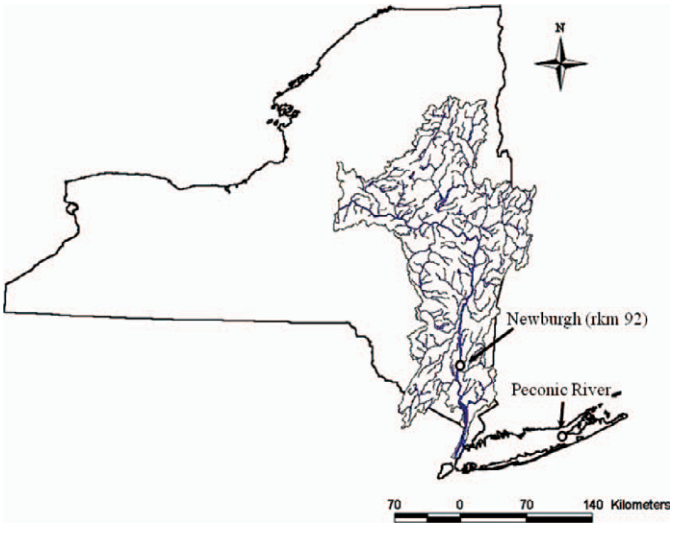

FIGURE 1. Map of the Hudson River watershed and Long Island showing the locations of the two alewife sampling sites.

below the first dam and fish ladder (i.e., just below the head of tide; 40°54.943′N, 72°39.633′W), approximately 1.25 km from Peconic Bay. Although alewives were collected in the lower reaches of both watersheds, the smaller catchment size of the Peconic River necessitated that fish be collected much closer to the Atlantic Ocean.

Within 3 months of collection, the total length (TL) of all fish was measured to the nearest millimeter; shrinkage was minimal, so lengths were not corrected. Both sagittal otoliths were removed, cleaned, dried, and sectioned in the sagittal plane by gluing them (Loc-Tite) to a 1-cm square coverslip, sulcus side down, and polished to the core. One otolith was chosen at random to be photographed for aging and microchemical analysis.

Otolith and water chemistry.—The elemental concentrations of Ca, Sr, and Ba were quantified with laser ablation inductively coupled plasma mass spectrometry (LA ICP-MS) using a PerkinElmer DRC-e ICPMS together with a UP-193 laser ablation system (Electro Scientific Industries). Strontium and barium were chosen because it has been well documented that otolith Sr:Ca and Ba:Ca are environmentally derived and highly correlated with the corresponding water values (Bath et al. 2000). For our analyses, we used a 35-μm beam size at a speed of 3 μm/s; the precisions of Ca, Sr, and Ba for NIST 610 glass were 19% (range, 6.2–56.1%), 22.7% (range, 5.9–50.1%), and 21.8% (range, 5.5–57.7%), respectively. Transects were made by running the beam from the core to the outer posterior edge (Figure 2). Data were converted to concentrations using a known-concentration, solid standard of pulverized otoliths pressed into a pellet (Limburg et al. 2011). Barium and strontium are presented in relation to calcium because they substitute readily for aragonitic calcium (Campana 1999). A five-point moving average was used to smooth the raw data.

Water samples collected in 2009 from freshwater locations throughout the Hudson River (excluding the Mohawk River, which alewives do not utilize) as well as the freshwater region of the Peconic River; both had average Sr:Ca values between 0.004 and 0.005 (by mass). The Ba:Ca values for Hudson River samples averaged between 0.001 and 0.005, while those for the Peconic River, collected just below the head of tide, ranged widely (from approximately 0.004 to 0.025) because of seawater intrusion up the estuary. Marine Sr:Ca was reported as 9.23×10^3 (Odum 1951), and Ba is negligible (Limburg and Siegel 2006). Preliminary multivariate analyses of water chemistry showed some separation among sampling locations (especially watersheds), but as not all elemental and isotopic values have been quantified for otoliths, the alewives were not assigned to specific locations for this study.

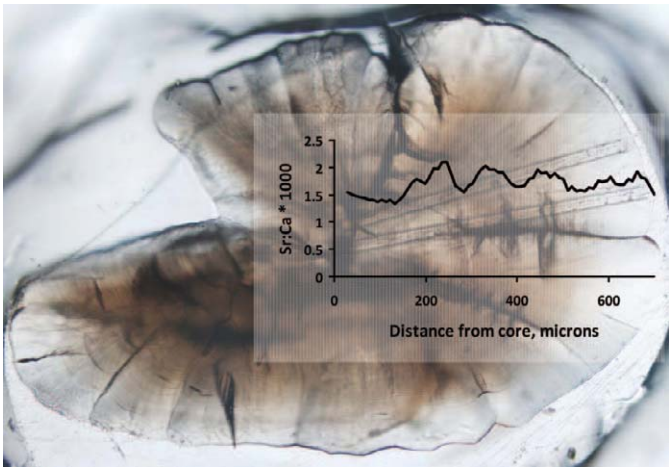

FIGURE 2. Photograph of a prepared otolith displaying laser ablation trenches from inductively coupled plasma mass spectrometry. The overlaid graph depicts the Sr:Ca ratios (weight basis) from the core to the outer edge.

A regime shift detection algorithm was used to identify significant changes in values using a sequential *F*-test, while excluding outliers (Rodionov 2004). When more than one consecutive point differed significantly (based on the variance of the data set and the *P*-value used), it was deemed a "shift" and a new moving average was applied (Rodionov 2004). The resulting data are mean values for each "regime" based on the smoothed otolith chemistry.

The mean number of shifts in the Sr:Ca and Ba:Ca ratios were quantified to determine whether juvenile alewives in the Hudson River had significantly more changes in otolith chemistry. A significant difference in the number of changes of elemental ratios would imply a greater number of movements among locations. Significance was determined using a one-tailed Mann–Whitney–Wilcoxon test, which does not assume a normal distribution.

Growth rates.—Juvenile alewives aged 80–130 d were selected from our 2009 Hudson River and Peconic River collections. Each otolith was photographed at 200× magnification using a Nikon DS-Fi1 camera attached to an Olympus BH-2 compound microscope and NIS-Elements D imaging software (Nikon 1991–2010). The distance between daily rings was measured from the core to the most distal posterior edge using the Figi image processing package (Rasband 1997–2011). Figi was also used to measure the distance from the core to the most distal posterior edge of 56 otoliths, including the 24 used for this study. The natural log of this measurement was plotted against fish TL to determine whether there was a correlation between the two. A strong correlation ($R^2 = 0.80$) was found for the relationship

$$\text{TL (mm)} = 0.01 \times \log_e(\text{otolith posterior radius [μm]}) + 5.74,$$

and thus we could use this relationship to infer somatic growth from otolith size. Daily otolith growth increments were quantified for the same alewives used for the chemical analyses. Mean daily otolith growth rates for each group were calculated over 20-d periods (i.e., days 1–20, 21–40, 41–60, 61–80, and 80+). Repeated-measures analysis of variance (ANOVA) was used to test for significant effects of time and river over time.

For this study, the chemical composition and daily growth rates as measured in sagittal otoliths were determined for 14

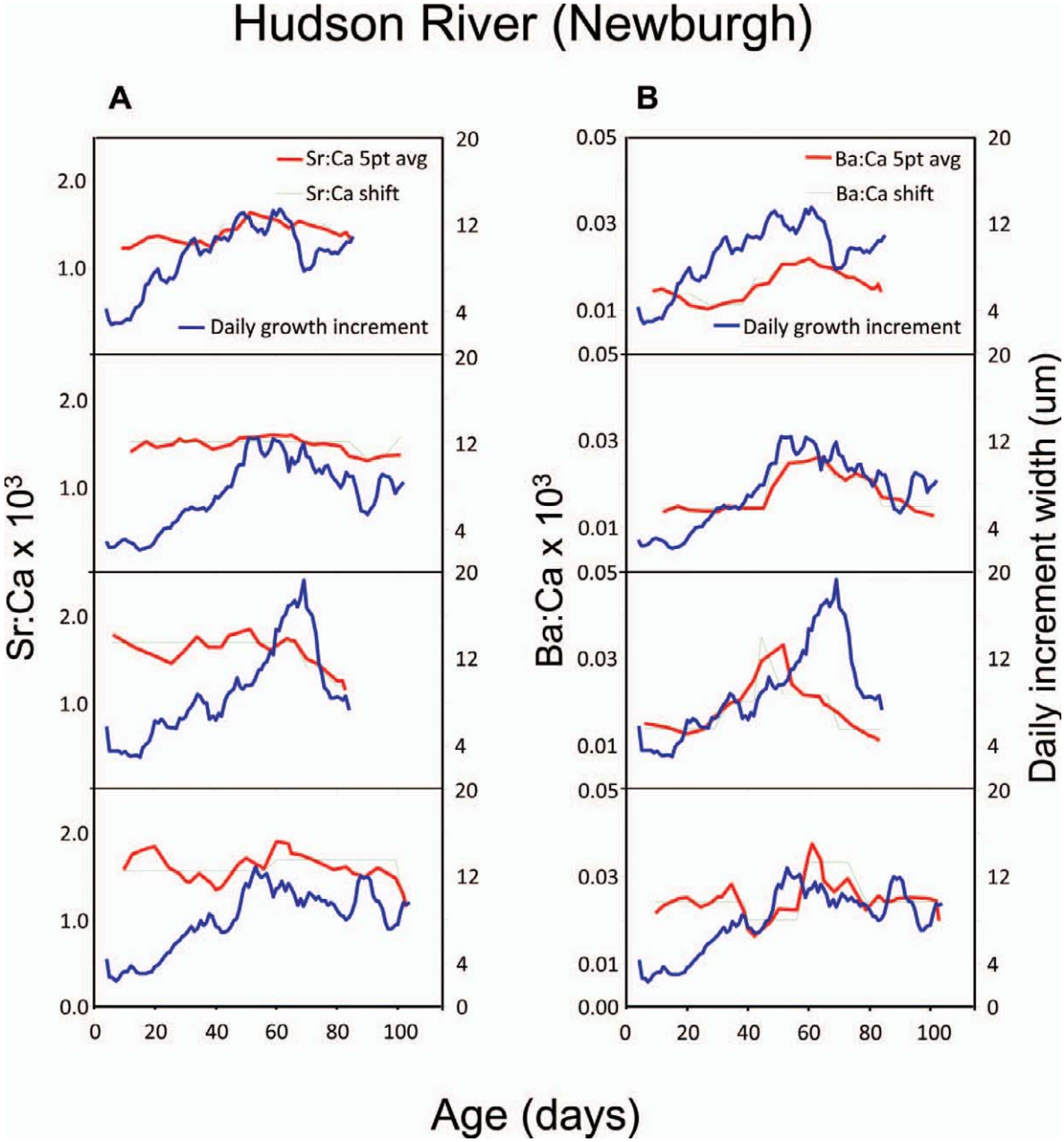

FIGURE 3. Otolith chemistry and daily otolith growth increments for four alewives collected in the Hudson River. Panel **(A)** depicts daily growth (right-hand *y*-axis) versus the Sr:Ca ratio (left-hand *y*-axis); panel **(B)** depicts daily growth versus the Ba:Ca ratio. In both graphs, the elemental ratio transects were smoothed with 5-point moving averages and regime shift analysis (Rodionov 2004) was applied to detect significant shifts away from the trends in the preceding data points.

juvenile alewives collected from the Peconic River and 10 fish collected from the Hudson River. These samples are a subset from a larger project and were chosen to test our hypotheses because they were close in age (80–130 d) at the time of collection. Despite the small sample sizes used for this study, the results are consistent with those observed in other alewives collected from these rivers.

RESULTS

Otolith Chemistry and Inferred Habitat Switching

Little to no change was observed in the Sr:Ca ratios of the otoliths from Hudson River alewives (Figure 3A). The values did vary, but over a small range relative to that observed in the otoliths of juvenile Peconic alewives (raw values:

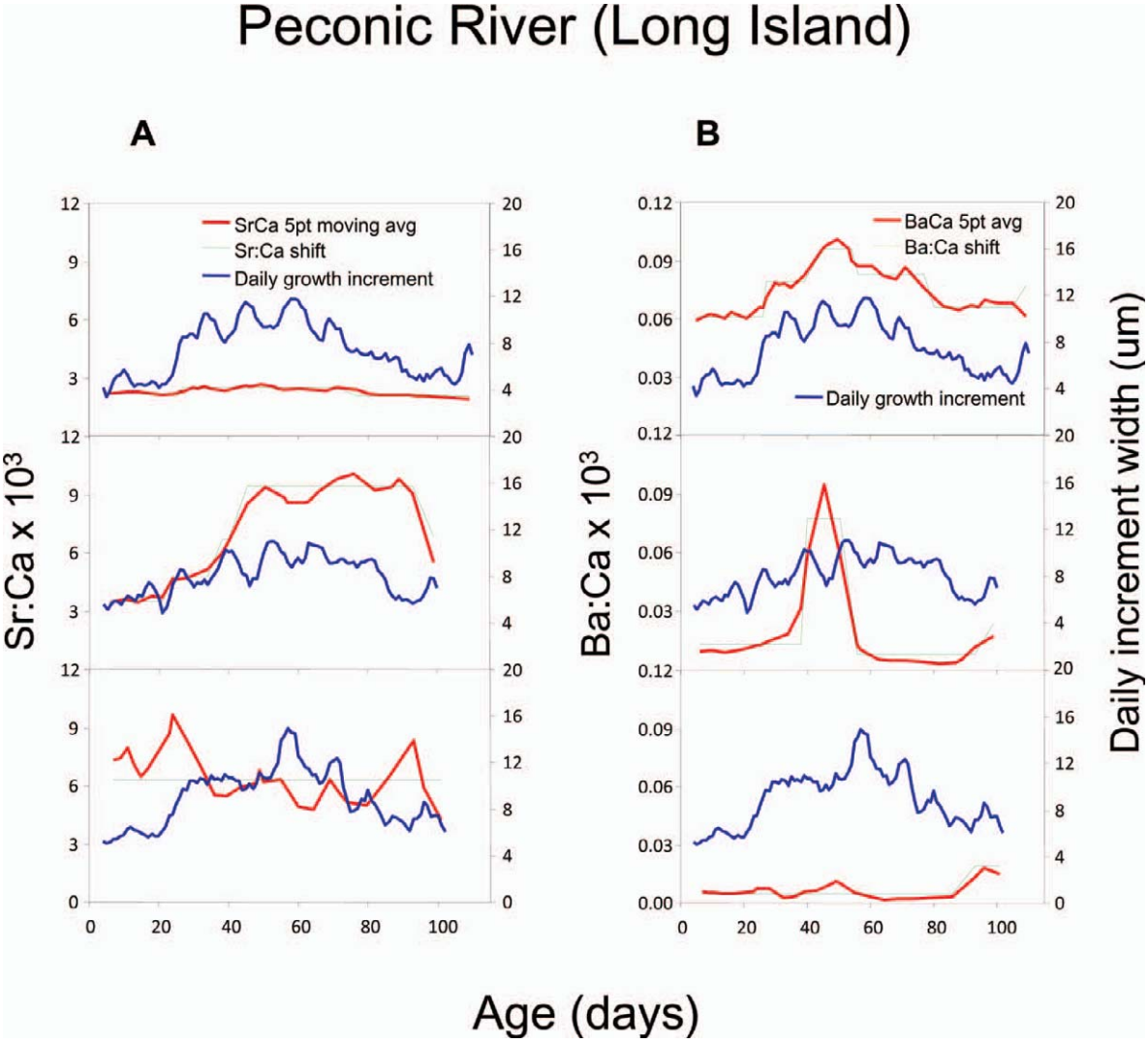

FIGURE 4. Otolith chemistry and daily otolith growth increments for three alewives collected in the Peconic River. Panel **(A)** depicts daily growth (right-hand *y*-axis) versus the Sr:Ca ratio (left-hand *y*-axis); panel **(B)** depicts daily growth versus the Ba:Ca ratio. See Figure 3 for additional information.

0.94–2.83 $\times$ 10^3; smoothed regime shift values: 1.17–2.05 $\times$ 10^3). On the other hand, substantial variation was observed in the corresponding Ba:Ca ratios (raw values: 0.006–0.053 $\times$ 10^3; smoothed regime shift values: 0.007–0.035 $\times$ 10^3; Figure 3B).

Distinct otolith chemistry patterns were observed in the Peconic River alewives (Figure 4). One pattern was characterized by constant, low Sr:Ca ratios but variable Ba:Ca ratios, which is suggestive of movement within the river (Figure 4, upper panels). Another manifested itself as a rapid shift to higher Sr:Ca ratios around age 40 d, with a corresponding rapid spike in Ba:Ca ratios followed by low Ba:Ca ratios, which is suggestive of emigration to sea (Figure 4, middle panels). A third showed moderately constant, elevated Sr:Ca and low Ba:Ca ratios, such as might be encountered in marine or strongly brackish waters (Figure 4, lower panels). The Sr:Ca ratios varied over a large scale both within and among individual otoliths (raw values: 0.94–20.31 $\times$ 10^3; smoothed regime shift values: 2.07–11.79 $\times$ 10^3; Figure 4A). The Ba:Ca ratios also varied over a wide range within and among individuals (raw values: 0.001–0.166 $\times$ 10^3; smoothed regime shift values: 0.002–0.135 $\times$ 10^3; Figure 4B).

The mean number of shifts in each elemental ratio was quantified for both groups (Table 1). The number of Sr:Ca shifts in the Hudson River was not significantly greater than that in the Peconic River (Mann–Whitney–Wilcoxon test; $P = 0.67$). There were significantly more Ba:Ca shifts in the Hudson River (Mann–Whitney–Wilcoxon test; $P = 0.024$).

TABLE 1. Mean number of regime shifts (SEs in parentheses) for otolith Sr:Ca and Ba:Ca ratios of alewives from the Hudson River ($N = 10$) and the Peconic River ($N = 14$).

Ratio	Hudson	Peconic
Sr:Ca	2.9 (0.23)	3.1 (0.35)
Ba:Ca	4.6 (0.22)	3.9 (0.23)

TABLE 2. Mean daily otolith growth (μm; SEs in parentheses) of Hudson and Peconic River alewives at different ages.

Age (d)	Hudson	Peconic
1–20	4.10 (0.29)	5.19 (0.24)
21–40	7.42 (0.73)	7.23 (0.33)
41–60	10.79 (0.65)	9.34 (0.36)
61–80	10.82 (0.63)	9.50 (0.33)
80+	7.47 (0.44)	6.40 (0.34)

Growth Rates

In Hudson River fish (Figure 3), early increments were very close together (generally <4 μm apart, i.e., growth was slow), became wider after 20 d (>7 μm apart, i.e., growth increased), remained higher than during the first 20 d, and eventually decreased in the period corresponding to cooler autumn temperatures (Figure 3; Table 2). In contrast, the earliest growth increments in Peconic River alewives were >1 μm larger that those of Hudson River fish (Figure 4; Table 2). Growth began to increase near day 20, from approximately 2–7 μm to approximately 7–12 μm, and decreased at approximately day 80 to below 7 μm (Table 2).

There were significant effects ($P < 0.006$) of time and river system × time among 20-d periods, in which Hudson River fish first exhibited slower growth (days 1–20) but eventually exhibited more rapid growth (>age 60 d; Table 2). The average cumulative daily growth rates based on otolith increments for both the Hudson and Peconic River samples were plotted from day 30 to day 80 (Figure 5). Whereas the otoliths of Hudson River juveniles were smaller than those of Peconic River fish up to age 50 d, at 50 d growth rates began to differ and from ages 60–80 d the mean otolith size at age was larger in Hudson River fish.

DISCUSSION

We observed significant differences in alewife growth and otolith chemistry between the Hudson and Peconic River watersheds that differed by over two orders of magnitude.

Otolith Chemistry

The Sr:Ca values observed in both groups of fish examined are generally within the ranges expected based on previous studies (Limburg 1995; Morrison et al. 2003; Walther and Thorrold 2008) and the chemistry of the water samples. Within the Hudson River, use of these data alone is insufficient to identify fine-scale habitat movements. In the Peconic River, Sr:Ca values vary much more over a small spatial scale, which makes sense because adult fish can pass above the head of tide to spawn and juveniles were collected below the head of tide. Alewives may remain in riverine habitats, emigrating during late summer and

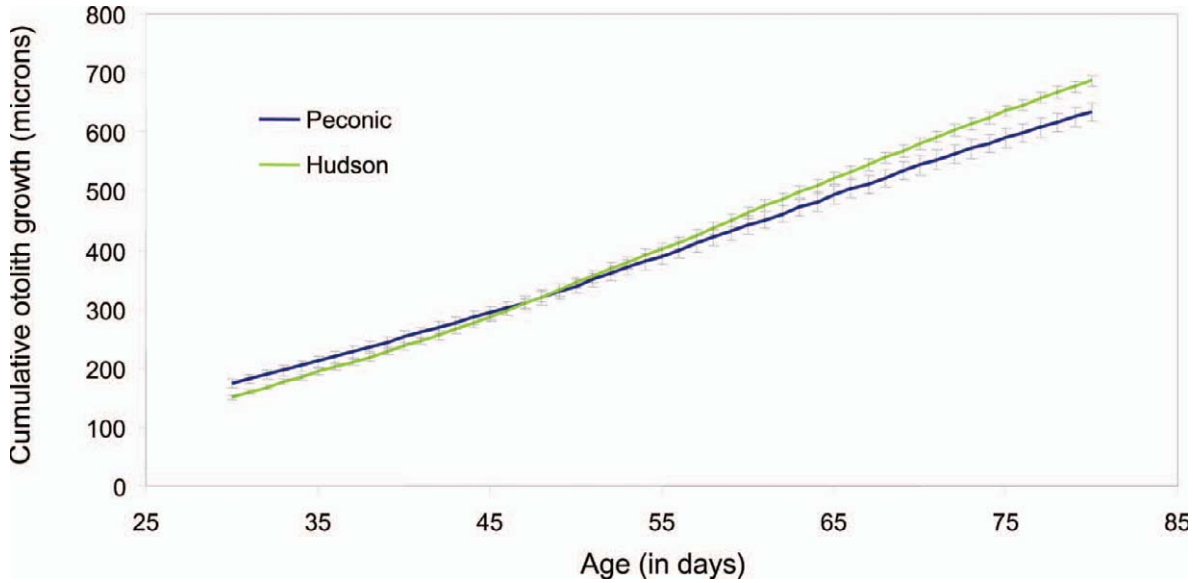

FIGURE 5. Mean cumulative daily otolith growth from day 30 to day 80 for alewives collected from the Peconic and Hudson rivers. The error bars represent SEs. The fish from the Hudson River were smaller initially, but their growth rate then increased and between days 45 and 50 they were larger at age than the Peconic River fish.

early fall (Fay et al. 1983). It was unexpected to find that significant portions of the otoliths of some of Peconic River alewives had Sr:Ca values consistent with marine values (Figure 4A), which suggests egress to the Atlantic Ocean followed by reentry into the estuary. Indeed, some fish captured in the Peconic estuary appear not to have experienced freshwater at all (see Figure 4, bottom panels); one of us has observed elevated Sr:Ca values, corresponding to nursery habitat use, in adult alewives caught in the Bronx River, a tributary to Long Island Sound (Limburg, unpublished data).

Although the number of shifts in Sr:Ca values were not significantly different, the Sr:Ca ranges were much larger in the otoliths of Peconic River alewives ($0.94–20.31 \times 10^3$ versus $0.94–2.83 \times 10^3$). The fluctuations in the Peconic River were likely driven by the large range of salinities experienced over a small spatial scale (Limburg 1995; Bath et al. 2000), while the fluctuations in the Hudson River could result from temporal variations in temperature, precipitation, and other abiotic variables (Bath et al. 2000). The magnitude of the shifts was also influenced by collection location. The alewives from the Peconic River were collected <2 km from the ocean, while those from the Hudson River were captured 92 km from the ocean; juvenile alewife behavior in the extreme lower reaches of the Hudson River has not been examined.

The Ba:Ca ratios in both water and otoliths vary enough to infer movement (or at least contingents) within both the Hudson and Peconic rivers. In the Hudson River, this, in combination with the other elements and isotopes quantified, will enable identification of movement among major habitat types (e.g., tributaries or the upper or lower portions of the river). In the Peconic River, these variations provide further evidence that juveniles display distinct movement patterns because marine habitats have substantially lower Ba:Ca ratios (Limburg and Siegel 2006). The number of shifts in Ba:Ca ratios were significantly higher in the Hudson River. This is likely the result of the many tributaries and microhabitats within the Hudson River, although temporal changes could also produce the changes observed.

Growth Rates

A wide range of factors can affect the rate at which juvenile fish grow, such as density, water temperature, and food quality and quantity (Campana 1996; Limburg 1996; Baltz et al. 1998; Jordan et al. 2000; Beamish and Mahnken 2001). Although individuals within the groups presented here displayed variation in daily growth, the overall trends in each group were distinct. Hudson River fish were smaller at younger ages, but their growth increased between 45 and 55 d, eventually resulting in greater length at age (Figure 5; Table 2). A wide range of environmental factors, especially temperature (and for Peconic River fish, emigration from the natal river), could have influenced the differences in growth.

Relationship between Chemistry and Growth

A relationship exists between growth and changes in otolith chemistry. In Peconic River alewives, chemistries generally shifted between days 20 and 40, and growth increases in this time range as well. In the Hudson River, these shifts do not appear to occur during a specific age range, but shifts in Ba:Ca ratios correspond roughly with changes in daily growth. The movement patterns appear to differ considerably in the Hudson and Peconic rivers based on the magnitude of the shifts in chemical signatures. If barium is used as a proxy for habitat, Hudson River alewives display much more variation in movements, likely due to the larger number of nurseries available (we were unable to use water signals to distinguish among sampling sites within the Hudson River). Conversely, Peconic River alewives display a few very distinct otolith chemistry patterns, potentially forming contingents (Secor 1999).

In the Northeast, juvenile alosines generally move downriver through the summer and emigrate to marine waters before their natal systems become too cold for overwinter survival (Limburg 1995; Kosa and Mather 2001; Yako et al. 2002; Gahagan et al. 2010). Such distinct behaviors in Peconic River juveniles were marked. Based on otolith chemistry, some fish spent the majority of their life in freshwater, while others moved within the lower tidal portion of the river and still others spent significant periods in full-strength seawater but returned to the estuary where they were caught.

Walters and Juanes (1993) discuss some potential biotic influences on the feeding behaviors of juvenile fish that could produce the differences seen within and between Hudson and Peconic River alewives. Food availability for juvenile alewives in the Hudson River could have decreased as a result of the invasion by zebra mussels *Dreissena polymorpha* (Strayer et al. 2004), although the population density, survivorship, and average body size of zebra mussels have decreased significantly since their initial invasion (Strayer et al. 2011) and the juvenile body lengths of *Alosa* spp. have increased since the 1990s (Limburg, unpublished observations). Decreased food quality, due to anthropogenic alterations (e.g., pollution and dams) in the Peconic River could influence growth and movements. Predation could influence the amount of time spent foraging in either watershed as well. Essentially, food availability and predatory risk are major biotic drivers of growth rate variation and movement to new nurseries. Reduced densities in the Peconic River may increase the food available for individuals, and this may be amplified if adults are spawning both above and below dams. It is likely that these biotic factors (Walters and Juanes 1993), in conjunction with a wide range of abiotic variables (Kosa and Mather 2001), influence early life history in both rivers. The insight into the variability of juvenile alewife growth and movement provided will offer a starting point for future research on the varied recruitment and survival of these fish.

Conclusion

The changes in juvenile growth rate and between-nursery movements appear to be interrelated, although our small sample sizes prevent our drawing strong conclusions at this point. However, these findings show the way forward with respect to

further analysis. One finding is clear: the movements of juvenile alewives are far more complex than indicated by the classical paradigm of anadromy. This insight supports other recent findings of unexpectedly complex diadromous movements (e.g., Limburg et al. 2001; Daverat et al. 2006; Gahagan et al. 2012, this special section).

ACKNOWLEDGMENTS

We thank Molly Payne, Natalie Scheibel, Peter Malaty, George Jackman, and the NYSDEC Hudson River Fisheries Unit for assistance in the laboratory and field. We thank Deb Driscoll for assistance in sample analyses. Special thanks to B. Gahagan, A. Overton, and two anonymous reviewers for constructive comments on earlier drafts.

REFERENCES

Baltz, D. M., J. W. Fleeger, C. F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. Environmental Biology of Fishes 53:89–103.

Bath, G. E., S. R. Thorrold, C. M. Jones, S. E. Campana, J. W. McLaren, and J. W. H. Lam. 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. Geochimica et Cosmochimica Acta 64:1705–1714.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Progress in Oceanography 49:423–437.

Begg, G. A., S. E. Campana, A. J. Fowler, and I. M. Suthers. 2005. Otolith research and application: current directions in innovation and implementation. Marine and Freshwater Research 56:477–483.

Campana, S. E. 1996. Year-class strength and growth rate in young Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 135:21–26.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.

Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences 58:30–38.

Daverat, F., K. E. Limburg, I. Thibault, J. C. Shiao, J. J. Dodson, F. Caron, W. N. Tzeng, Y. Iizuka, and H. Wickström. 2006. Phenotypic plasticity of habitat use by three temperate eel species *Anguilla anguilla*, *A. japonica*, and *A. rostrata*. Marine Ecology Progress Series 308:231–241.

Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology an Annual Review 46:297–330.

Fay, C. W., R. J. Neves, and G. B. Pardue. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic) – alewife/blueback herring. U.S. Fish and Wildlife Service Biological Services Program FWS-OBS-82/11.9, and U.S. Army Corps of Engineers, TR EL-82-4, Vicksburg, Mississippi.

Gahagan, B. I., K. E. Gherard, and E. T. Schultz. 2010. Environmental and endogenous factors influencing emigration in juvenile anadromous alewives. Transactions of the American Fisheries Society 139:1069–1082.

Gahagan, B. I., J. C. Vokoun, G. W. Whitledge, and E. T. Schultz. 2012. Evaluation of otolith microchemistry for identifying natal origin of anadromous river herring in Connecticut. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 4:358–372.

Jordan, R. C., A. M. Gospodarek, E. T. Schultz, R. K. Cowen, K. Lwiza. 2000. Spatial and temporal growth rate variation of bay anchovy (*Anchoa mitchilli*) larvae in the mid Hudson River estuary. Estuaries 23:683–689.

Kosa, J. T., and M. E. Mather. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small coastal systems. Transactions of the American Fisheries Society 130:600–619.

Levinton, J. S., and J. R. Waldman, editors. 2006. The Hudson River estuary. Cambridge University Press, New York.

Limburg, K. E. 1995. Otolith strontium traces migratory histories of juvenile American shad, *Alosa sapidissima*. Marine Ecology Progress Series 119: 25–35.

Limburg, K. E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the Hudson River estuary: otolith microstructural analysis. Canadian Journal of Fisheries and Aquatic Sciences 53:220–238.

Limburg, K. E. 2001. Through the gauntlet again: demographic restructuring of American shad by migration. Ecology 82:1584–1596.

Limburg, K. E., P. Landergren, L. Westin, M. Elfman, and P. Kristiansson. 2001. Flexible modes of anadromy in Baltic sea-trout (*Salmo trutta*): making the most of marginal spawning streams. Journal of Fish Biology 59:682–695.

Limburg, K. E., and D. I. Siegel. 2006. The hydrogeochemistry of connected waterways: the potential of linking geology to fish migrations. Northeastern Geology and Environmental Sciences 28:254–265.

Limburg, K. E., and J. R. Waldman. 2009. Dramatic declines in North Atlantic diadromous fishes. Bioscience 59:955–965.

Limburg, K. E., C. Olson, Y. Walther, D. Dale, C. P. Slomp, and H. Høie. 2011. Tracking Baltic hypoxia and cod migration over millennia with natural tags. Proceedings of the National Academy of Sciences of the USA 108:E177–E182.

Morrison, W. E., D. H. Secor, and P. M. Piccoli. 2003. Estuarine habitat use by Hudson River American eels as determined by otolith strontium:calcium ratios. Pages *in* 87–99 D. A. Dixon, editor. Biology, management, and protection of catadromous eels. American Fisheries Society, Symposium 33, Bethesda, Maryland.

Murt, J., and F. Juanes. 2009. Cohort-specific winter growth rates of YOY bluefish, *Pomatomus saltatrix*, in northeast Florida estuaries: implications for recruitment. Journal of Northwest Atlantic Fisheries Science 41:221–231.

Nikon. 1991–2010. NIS-elements D imaging software, 3.20.01 (build 685), LO. Nikon.

Odum, H. T. 1951. Notes on the strontium content of sea water, celestite *Radiolaria*, and strontianite snail shells. Science 114:211–213.

Rasband, W. S. 1997–2011. ImageJ. U.S. National Institute of Health, Bethesda, Maryland. Available: http://imagej.nih.giv/ij/. (September 2010).

Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31:1–4.

Rutherford, E. S., and E. D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass, *Morone saxatilis*, larvae in Chesapeake Bay. U.S. National Marine Fisheries Service Fishery Bulletin 93:315–332.

Schmidt, R. E., B. M. Jessop, and J. E. Hightower. 2003. Status of river herring stocks in large rivers. Pages 171–182 *in* K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.

Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fisheries Research 43:13–34.

Sismour, E. N. 1994. Contributions to the early life histories of alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*): rearing, identification, aging, and ecology. Doctoral dissertation. Virginia Institute of Marine Science, College of William and Mary, Gloucester Point.

Strayer, D. L., K. A. Hattala, and A. W. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 61:924–941.

Strayer, D. L., N. Cid, and H. M. Malcom. 2011. Long-term changes in a population of an invasive bivalve and its effects. Oecologia 165:1063–1072.

Taylor, K., M. Hendricks, C. Patterson, and S. Winslow. 2009. Review of the Atlantic States Marine Fisheries Commission fishery management plan for shad and river herring (*Alosa* spp.). Atlantic States Marine Fisheries Commission, Shad and River Herring Plan Review Team. Available:

www.asmfc.org/speciesDocuments/shad/fmpreviews/2009ShadFMPReview.pdf. (July 2011).

Walters, C. J., and F. Juanes. 1993. Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50:2058–2070.

Walther, B. D., and S. R. Thorrold. 2008. Continental-scale variation in otolith geochemistry of juvenile American shad (*Alosa sapidissima*). Canadian Journal of Fisheries and Aquatic Sciences 65:2623–2635.

Yako, L. A., M. E. Mather, and F. Juanes. 2002. Mechanisms for migration of anadromous herring: an ecological basis for effective conservation. Ecological Applications 12:521–534.