Anomalous migrations of anadromous herrings revealed with natural chemical tracers

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Abstract: Anadromous herrings of the genus *Alosa* are generally thought to leave their natal river or estuary at the end of the first growing season and return as mature adults to spawn. Nevertheless, immature yearling alosines have been observed in large numbers in the Hudson River estuary during and after the spring spawning run. I analyzed the stable isotopic ($\delta^{13}C$, $\delta^{15}N$) compositions of 26 blueback herring (*Alosa aestivalis*), eight American shad (*Alosa sapidissima*), and 10 alewife (*Alosa pseudoharengus*) collected from 55–225 km above the estuary mouth during April–July and compared them with isotopic compositions of young-of-year (resident) alosines, as well as adults (marine phase). $\delta^{13}C$ of the May-caught American shad and alewife indicated a marine origin (greater than –22.5‰); blueback herring split into both marine and freshwater ($\delta^{13}C$ less than –25.5‰) groups. June-caught fish had intermediate values. Microprobe traces of Sr in these fishes' otoliths helped further to discriminate between resident fishes and those that had migrated to sea (or brackish water) and then moved back upriver for a period of several weeks. The combination of biogeochemical tracer methods holds promise for elucidating complex life histories of fishes and helps to pose questions about plasticity of migration.

Résumé : On pense généralement que les cupléidés anadromes du genre *Alosa* quittent leur rivière ou leur estuaire natals à la fin de la première saison de croissance pour n'y revenir qu'à l'âge adulte, après avoir atteint la maturité sexuelle, afin d'y frayer. Or, on a observé des *Alosa* d'un an en grand nombre dans l'estuaire de l'Hudson durant la remonte printanière et après la fraye. J'ai analysé des compositions d'isotopes stables ($\delta^{13}C$, $\delta^{15}N$) chez 26 aloses d'été (*Alosa aestivalis*), huit aloses savoureuses (*Alosa sapidissima*) et 10 gaspareaux (*Alosa pseudoharengus*) capturés d'avril à juillet à une distance de 55–225 km en amont de l'embouchure de l'estuaire; j'ai comparé ces compositions à celles mises en évidence chez des jeunes de l'année (population résidante) et chez des adultes (phase marine). Les concentrations de $\delta^{13}C$ mesurées chez les aloses savoureuses et les gaspareaux capturés en mai dénotaient une origine marine (plus de –22,5‰); on a pu distinguer deux groupes : les aloses d'été les d'origine marine et les aloses d'été d'eau douce ($\delta^{13}C$ moins de –25,5‰). Chez les spécimens capturés en juin, les concentrations étaient intermédiaires. Par ailleurs, en utilisant une microsonde, on a décelé des traces de Sr dans les otolithes de ces poissons, ce qui nous a permis d'établir une distinction encore plus fine entre les poissons résidants et ceux qui, après avoir migré en mer (ou en eau saumâtre), étaient revenus séjourner plusieurs semaines dans les eaux d'amont. La combinaison de différents traceurs biogéochimiques est une approche prometteuse pour l'étude des poissons à cycle naturel complexe et permet d'aborder de nouveaux aspects de la plasticité de leur migration.
[Traduit par la Rédaction]

Introduction

Anadromous herrings and shads of the genus *Alosa* (Clupeidae) use estuarine and river systems as spawning and nursery habitat along both coasts of the North Atlantic. Typically, adult *Alosa* migrate in early spring from coastal marine ecosystems into fresh water to spawn; in North America, young-of-year (YOY) remain in the natal river systems through part or all of the first growing season (ASMFC 1995). YOY migrate out to the coastal ocean in the summer and fall, presumably not to return until they have recruited to the spawning population (Chittenden 1969; Richkus 1975; Leggett 1976; Limburg 1996). Relatively little is known about the behavior of these fish between the time of YOY outmigration and the return of adults to spawn, particularly in the post-YOY juvenile years (but see Milstein 1981).

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In the Hudson River, located in eastern New York State, anomalous runs of yearling blueback herring (*Alosa aestivalis*), American shad (*Alosa sapidissima*), and alewife (*Alosa pseudoharengus*) co-occur with the adult spawning runs of these species (R.E. Schmidt, Simons Rock College, personal communication; K. Hattala, New York State Department of Environmental Conservation, personal communication; K.E. Limburg, unpublished observations). Yearling fish have been collected occasionally throughout the river during the spring runs of adults up to 225 km from the mouth, defined as the southern tip of Manhattan Island, New York City. These fish are immature (as determined by gonadal development) and represent the previous year's production.

These anomalous fish are interesting from both life history and demographic perspectives. If they overwinter in the river or adjoining waters, they must overcome adverse physical conditions and may indicate that some part of the population is becoming landlocked (i.e., establishing a nonanadromous breeding population). If they are migrating in with the adults, then the question arises as to the adaptive significance of this behavior.

The purpose of the present investigation is to determine the environmental conditions, marine or freshwater, experienced by these fish to determine their migratory histories. I used two

Table 1. Date of capture, location (kilometres from mouth), and size-at-capture (total length, mm) of yearling alosines in the tidal Hudson River that were analyzed for C and N stable isotopic ratios.

Blueback herring				American shad				Alewife			
Year	Date	Location	Total length	Year	Date	Location	Total length	Year	Date	Location	Total length
1987	3 June	145		1995	23 May	183	123[a]	1995	23 May	183	138[a]
1988	16 June	200	120[b]	1995	23 May	183	129	1995	14 June	208	138
1988	12 June	225		1995	23 May	183	131	1995	28 June	201	139
1995	23 May	183	91[a]	1995	23 May	183	120	1995	28 June	201	153
1995	23 May	183	122[a]	1995	14 June	196	134[a]	1995	28 June	201	139
1995	23 May	183	125[a]	1995	14 June	208	152[a]	1996	12 May	55	112
1995	14 June	208	118	1996	21 May	97	111[a]	1996	12 May	55	92
1995	14 June	208	113	1996	30 May	97	113[a]	1996	24 Apr.	97	119
1995	14 June	208	110					1996	26 May	97	158[a]
1995	14 June	208	120					1996	26 May	97	162[a]
1995	14 June	208	123								
1995	14 June	208	120								
1995	14 June	208	112								
1995	14 June	208	112								
1995	12 July	208	139								
1995	12 July	208	144								
1995	12 July	208	145								
1995	12 July	208	137								
1995	10 July	121	140[a]								
1995	10 July	121	136[a]								
1995	10 July	121	137[a]								
1995	10 July	121	131[a]								
1995	4 Oct.	95	104[a]								
1996	12 May	55	112[a]								
1996	12 May	55	109[a]								
1996	12 May	55	97[a]								

[a]Indicates that otolith microchemical analysis was performed.
[b]Composite sample of six fish.

types of naturally occurring biogeochemical markers to determine qualitatively the extent of freshwater or seawater occupation.

First, I took advantage of the well-known freshwater–marine gradient of C stable isotopic ratios ($\delta^{13}C$) to discriminate among fish of unknown origins. (Values of δ (per mille, ‰) were computed as $(R_{sample}/R_{standard} - 1)\times 1000$ where R is the ratio of the heavier to the lighter isotope for a given element.) Freshwater ecosystems are generally depleted in the heavy (^{13}C) isotope relative to marine systems (Peterson et al. 1985; Peterson and Fry 1987). A strong gradient in $\delta^{13}C$ exists in Hudson River dissolved inorganic C (DIC) going from a marine end member ($\delta^{13}C = -2$ to 2‰ at 16 km offshore of the mouth) to freshwater values of –8 to –10‰ (Garvey 1990; N. Caraco, Institute of Ecosystem Studies, unpublished data). Generally, this will translate into algal $\delta^{13}C$ values of around –20‰ in marine and less than –28‰ in the freshwater reaches. Furthermore, N stable isotopic ratios ($\delta^{15}N$) are elevated throughout the tidal Hudson River, compared with other aquatic systems including the downstream coastal waters (Fry 1991; K.E. Limburg, unpublished data; N. Caraco, unpublished data), thus providing a second, albeit weaker, marker because N isotopic ratios are more sensitive to food chain fractionation than is true for C (Peterson and Fry 1987).

Second, I assayed the otoliths of some of the fish with an electron microprobe to determine patterns of Sr incorporation during their lifetimes because Sr:Ca ratios can discriminate between marine and freshwater phases in many diadromous fish (e.g., Casselman 1982; Kalish 1990; Secor 1992; Limburg 1995; Secor et al. 1995). Sr is roughly an order of magnitude more abundant in marine versus most eastern U.S. fresh waters (Limburg 1995), occurs in estuaries in proportion to salinity (Ingram and Sloan 1992), and so becomes incorporated into the otolith aragonite matrix roughly in proportion to its aqueous concentration (Secor et al. 1995; but see Discussion for caveats).

The purpose of this assay was to (1) confirm the results of stable isotopic analysis and (2) provide resolution of ambiguous stable isotopic signatures in some of the fish. Microprobe analysis has the advantage of providing a continuous record throughout the lifetime of an individual fish whereas stable isotope analysis provides an integrated average of the time period corresponding to fish N and C turnover.

Methods

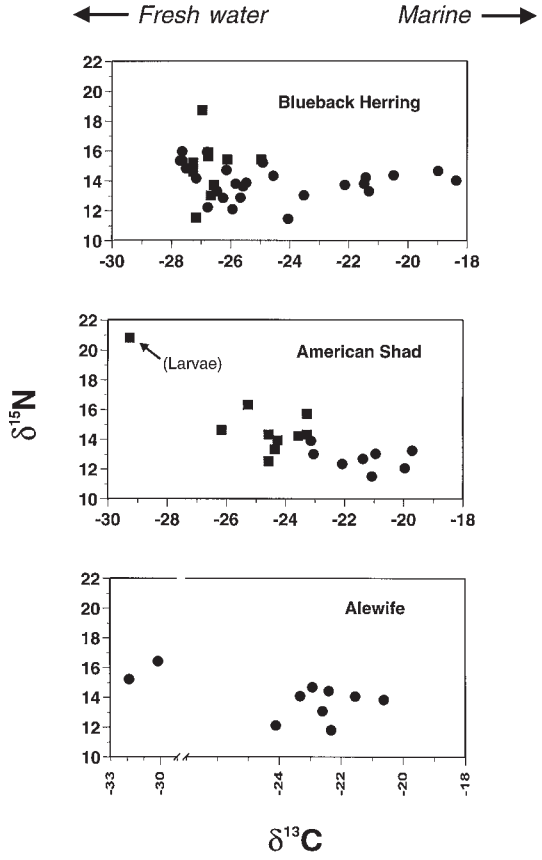
Yearling alosines (26 blueback herring, eight American shad, and 10 alewife) were collected haphazardly over a range of sites in the tidal freshwater portion of the Hudson River (Table 1). Sagittal otoliths were removed and cleaned, and fish were rinsed, dried (50°C), and homogenized whole. Samples of individual fish were analyzed by mass spectrometry ($\delta^{13}C$, $\delta^{15}N$). Replicate analyses were run at the Marine Biological Laboratory, Woods Hole, Mass. (Finnigan Delta S

isotope ratio mass spectrometer; precision ±0.1‰), at Boston University (similar instrumentation), or at the University of Alaska, Fairbanks, Alaska (Europa 20-20 continuous flow mass spectrometer; precision ±0.2‰). These were compared with composite samples (n = 5–20 whole fish) of YOY (river-resident) fish, as well as with a composite sample of five adult American shad (dorsal muscle tissue, marine endmember) and with previously collected river seston (riverine autochthonous production), terrestrial plants (allochthonous production), and food items collected from several fish stomachs. Composite samples of fish were used to hold down costs. Because several different laboratories performed the stable isotopic analyses, a blind standard (blueback herring) was used to check on consistencies among laboratories. Deviations of the standard were <0.5‰ for both isotopes from one laboratory to the next.

Yearling fish were collected from April through early July. Fish caught later in the season appeared to have a stronger river isotopic signal (i.e., depleted in ^{13}C). I hypothesized that at least some of these individuals had previously migrated in from the sea and had remained and fed in the river long enough to alter their stable isotopic composition. To test this, I assayed the otoliths of these late-caught fish with microprobe analysis of their Sr:Ca ratios. Several other fish were also assayed to test the agreement between Sr:Ca analysis and stable isotope ratios.

For this analysis, sagittal otoliths were ground in the sagittal plane to expose the core, polished (with 0.5-μm grit), and measurements of Sr and Ca made with a JEOL 733 wavelength dispersive electron microprobe at the Materials Science Center EM Facility, Cornell University, Ithaca, N.Y. Analytic details are given in Limburg (1995). Transects were made from the core of the otolith to the outer posterior edge; occasionally, a second transect from the core through the rostrum was made. Intervals between elemental analyses ranged from 50 to 85 μm. Ten to 15 analyses were conducted on each otolith. Sr:Ca molar ratios were expressed as values along the otolith transect. Due to cost constraints, not all fish were assayed for Sr:Ca (see Table 1).

Fig. 1. Stable isotope ratio "maps" plotting $\delta^{13}C$ versus $\delta^{15}N$ (‰) for YOY (squares) and yearling (circles) blueback herring, American shad, and alewife. Freshwater endmember is depleted in ^{13}C (lower $\delta^{13}C$) and marine endmember is enriched in ^{13}C.



Results

Comparison of YOY and yearlings

C stable isotopic ratios of yearling blueback herring spanned a broad range (–27.8 to –18.4‰; Fig. 1). YOY blueback herring overlapped with only part of the range (mean –26.7 ± 0.7‰ SD, range –27.3 to –25.0‰, n = 10 composite samples; Fig. 1). C isotopic ratios were different (ANOVA, $p < 0.003$) between YOY and yearling fish, but not for N ($p < 0.07$). N stable isotopic ratios of blueback herring were similar (YOY mean = 15.0 ± 1.9‰ SD, yearling mean = 14.0 ± 1.1‰ SD), although one composite sample of YOY blueback herring (collected in October 1988 at river km 90) had elevated $\delta^{15}N$ (18.8‰).

American shad yearlings differed significantly from YOY with respect to both C and N isotopic ratios (Fig. 1). Mean $\delta^{15}N$ (14.4 ± 1.1‰ SD) for juvenile YOY American shad was higher ($p < 0.004$) than for yearlings (12.8 ± 0.7‰ SD) whereas C ratios were lower ($p < 10^{-4}$; YOY = –24.4 ± 1.0‰ SD, yearlings = –21.4 ± 1.3‰ SD). A sample of larvae collected in June 1995 (river km 113) was considerably enriched in ^{15}N and depleted in ^{13}C relative to older YOY ($\delta^{15}N$ = 20.9‰, $\delta^{13}C$ = –29.3‰; Fig. 1). The composite sample of adult American shad muscle tissue was depleted in ^{15}N (11.7‰) and enriched in ^{13}C (–20.4‰) relative to YOY and to the mean values of yearlings, although some individual yearlings fell close to the adult values. YOY American shad $\delta^{13}C$ also differed from YOY blueback herring ($p < 10^{-4}$), although $\delta^{15}N$ did not ($p < 0.46$).

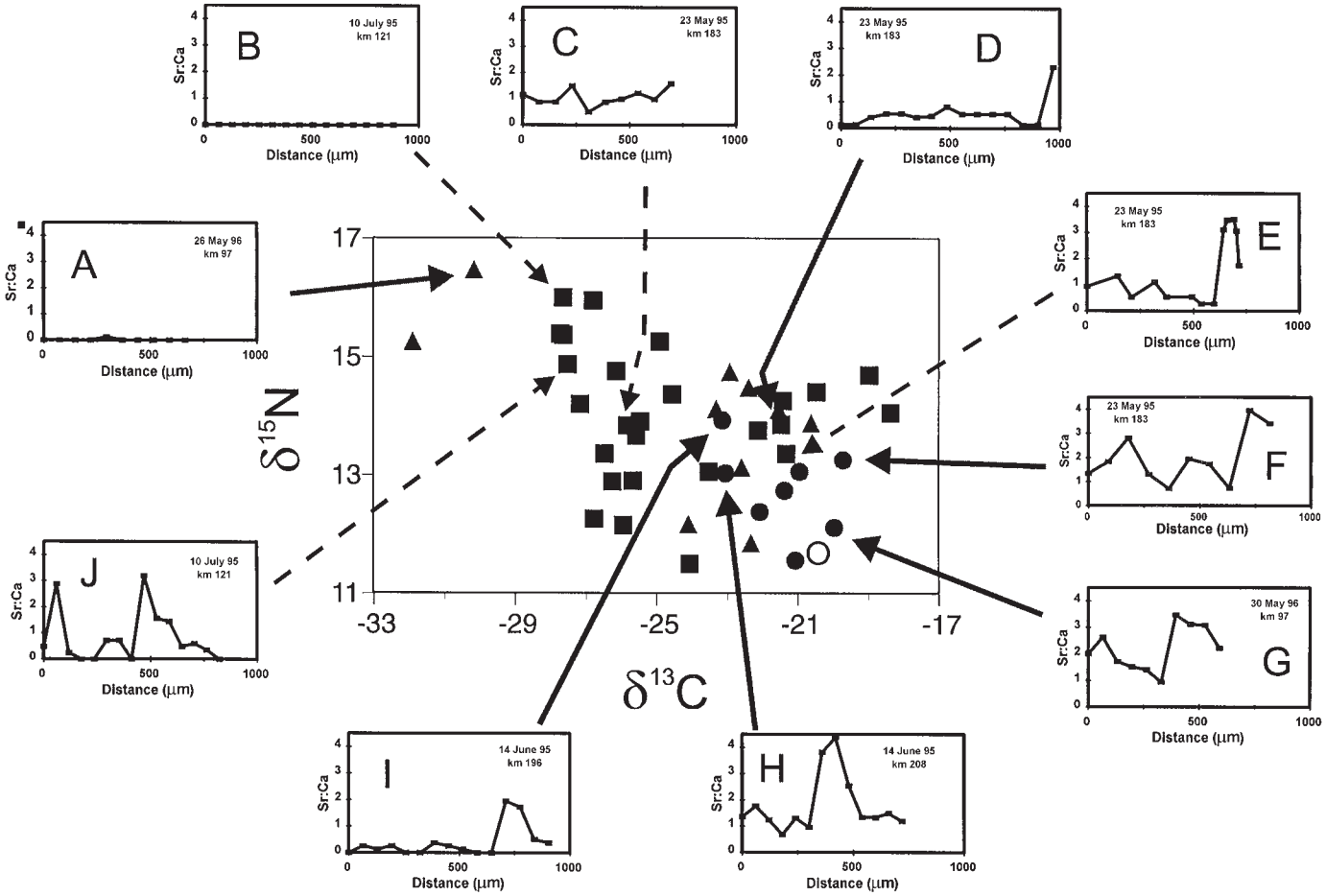
Yearling alewife appeared to split into two disparate, albeit small, groups with respect to $\delta^{13}C$ (Fig. 1), with eight fish ranging between –24.1 and –20.7‰ and two other fish having values less than –30‰. No YOY alewives were analyzed.

Comparison of stable isotope and otolith Sr:Ca analyses

Otolith Sr levels varied considerably, with some otoliths showing no detectable Sr (<300 ppm; Figs. 2A and 2B), low levels (Fig. 2C), or levels that fluctuated (Figs. 2D–2J). All yearling American shad that were assayed for Sr showed some history of elevated Sr:Ca (e.g., Figs. 2F–2I). Yearling American shad whose otolith Sr:Ca traces are shown in Figs. 2H and 2I were caught in mid-June 1995, about a month after the adult spawning run, and had stable isotopic values that were the most similar to some of the YOY American shad (Fig. 1). However, the Sr:Ca transects indicate low initial levels of Sr, followed by a spike in Sr and a subsequent decline. This is consistent with movement from fresh water to a marine or strongly estuarine environment and finally a back to fresh water.

One American shad with a moderately "marine" stable isotopic signal ($\delta^{15}N$ = 12.4‰, $\delta^{13}C$ = –22.1‰; otolith transect not shown in Fig. 2) did not show a distinct spike of Sr:Ca. Nevertheless, its lifetime mean Sr:Ca was elevated (Sr:Ca = $1.52 \times 10^{-3} \pm 0.42 \times 10^{-3}$) relative to resident YOY measured

Fig. 2. N and C stable isotope ratios (‰) for all yearling alosines (central graph). Squares, blueback herring; circles, American shad; triangles, alewife. The open circle (○) represents a composite sample from five adult female American shad. Small graphs A–J are microprobe transects of Sr:Ca ratios ($\times 10^{-3}$) from individual fish as indicated by arrows pointing to points on the central graph. Microprobe transects start at the core and proceed along the posterior axis.



in a study of the 1990 year-class (mean of 19 YOY = $0.81 \times 10^{-3} \pm 0.17 \times 10^{-3}$; Limburg 1995).

Blueback herring showed variation in Sr:Ca that was consistent either with a marine stable isotopic ratio (Fig. 2E), "freshwater" ratio (Fig. 2B), or, as in the case of late-caught American shad, past experience with elevated Sr and low levels for some time prior to capture (Fig. 2J, caught 10 July 1995). The two alewife with the most freshwater stable isotopic ratios showed undetectable levels of Sr (e.g., Fig. 2A) whereas a fish with a relatively enriched $\delta^{13}C$ isotopic ratio showed low Sr levels until the very end of the otolith transect (Fig. 2D) when Sr:Ca increased from a previous lifetime mean value of 0.42×10^{-3} to 2.31×10^{-3}, a 5.5-fold increase.

Temporal trends in stable isotopic ratios

Late-caught (June–July) yearling alosines appear to have lower $\delta^{13}C$ isotopic ratios than fish captured earlier, although the data are so sparse that strong inference can only be made for blueback herring at this time. By pooling close seasonal dates of capture (i.e., pooling 12, 14, and 16 June and pooling 10 and 12 July) to create a data set consisting of four "dates" of capture (12 and 24 May, 14 June, and 11 July), C isotopic values declined with time ($F_{3,21} = 26.7$, $p < 10^{-6}$; Fig. 3) from a mean value of –20.1 ± 1.6‰ SD on 12 May to –27.0 ± 1.0‰ SD on 11 July. The two earliest dates grouped apart from the two later dates in post hoc testing (Tukey's HSD for unequal n, $p < 0.05$). Differences ($F_{3,21} = 16.5$, $p < 10^{-4}$) were found in $\delta^{15}N$ isotopic ratios as well, although the changes were not monotonic with time. Highest values of $\delta^{15}N$ ratios occurred on 11 July; mean values of yearling blueback herring on 11 July were very close to the mean values for YOY blueback herring (Fig. 3).

Although not as many American shad and alewife yearlings were collected and analyzed, there is still a visible trend towards depleted ^{13}C over time in both species (Fig. 4) with the prominent exception of two alewife collected in May 1996 (encircled by broken line). Both of these fish were collected in Quassaick Creek, a tributary of the Hudson River located at river km 97.

Examination of the gut contents of some of the yearling blueback herring and American shad collected above river km 180 revealed that, unlike adult spawners, all had been feeding actively at the time of capture. Blueback herring fed on a dominant cladoceran (*Bosmina longirostris*) and American shad fed on emergent and terrestrial insects. An analysis of *Bosmina* collected from a blueback herring stomach on 16

Fig. 3. Shifts in mean stable isotopic ratios of yearling blueback herring as a function of time, compared with mean values (±95% confidence intervals) of marine plankton (source: Peterson et al. 1985), Hudson River seston (source: N. Caraco, Institute of Ecosystem Studies, unpublished data; K.E. Limburg, unpublished data), trees near the Hudson River (source: N. Caraco, unpublished data), and YOY blueback herring. Squares indicate mean values of yearling isotopic ratios on four dates. Error bars have been left off for clarity.

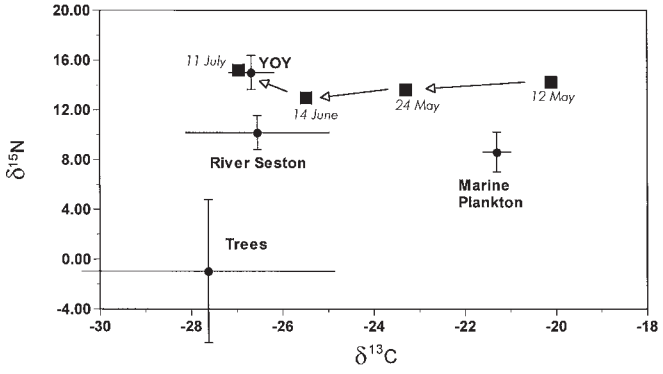
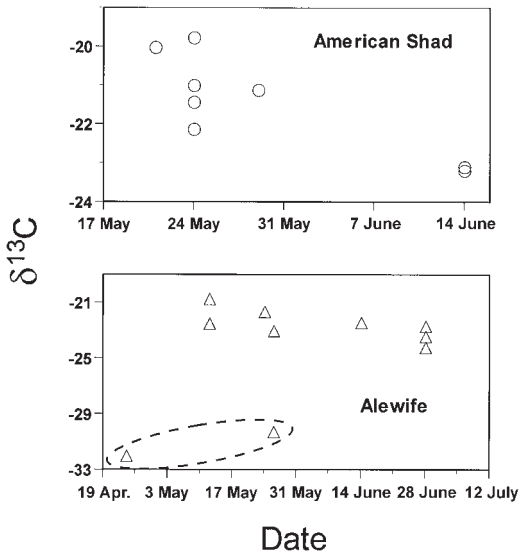


Fig. 4. Temporal trends in $\delta^{13}C$ (‰) for yearling American shad (top panel) and alewife (bottom panel). Alewife caught in a tributary creek are encircled by a broken line.



June 1988 had $\delta^{15}N = 9.9$ and $\delta^{13}C = -27.6$‰; winged insects collected from an American shad stomach on 23 May 1995 had isotopic ratios of $\delta^{15}N = 5.6$ and $\delta^{13}C = -26.7$‰.

Discussion

This may be the first report of how two independent biogeochemical markers, stable isotope ratios of tissues and Sr content of otoliths, can be used in concert to infer recent and long-term environmental histories of migratory fishes. Stable isotopic ratios of yearling alosines revealed a broad gradient of values, particularly in $\delta^{13}C$ ratios, that are consistent with fish spanning a range of habitats from fresh water to estuarine to marine. Further, patterns of Sr incorporation into otoliths confirmed the stable isotope predictions of estuarine/marine or freshwater history or, in some cases, demonstrated past experience with an elevated Sr (marine) environment followed by a decline in Sr that agreed with the stable isotopic ratios.

C and N stable isotopes turn over in tissue as a function of metabolism and growth (Peterson and Fry 1987); thus the isotopic signal of tissue is an integration of matter that was assimilated from food. In this study, yearling and YOY fish were analyzed whole to maximize the degree of integration of past dietary (and thus, environmental) histories. For recent dietary information, tissues with fast turnover (e.g., liver) would be analyzed instead. Although care should be taken not to overinterpret the results, yearling blueback herring data, when plotted sequentially over the days of the year (Fig. 3), indicate a gradual turnover. A separate analysis of YOY American shad $\delta^{13}C$ data (not shown here) indicates a rapid turnover of whole-body C (half-life = 5–6 days) observed during the ontogenetic dietary transition from zooplankton (consumed by larvae) to epibenthic invertebrates (juvenile food).

The inferences that may be drawn from this analysis, given the assumptions of mechanisms of stable isotope and Sr incorporation, are that (1) some yearling American shad, blueback herring, and alewife migrate in the springtime from marine or strongly estuarine waters up the Hudson River, concurrently with the runs of adult alosines, (2) some yearling blueback herring and alewife appear never to have left the Hudson drainage basin for marine waters, and (3) yearlings of all three species appear to remain in the upper tidal freshwater Hudson River well into the summer, feeding and growing, such that their stable isotopic composition gradually turns over and becomes similar to that of resident YOY fishes.

The fact that C stable isotopes are a better indicator of the freshwater–marine gradient than N stable isotopes is largely due to the fact that N stable isotope ratios in the Hudson River are generally elevated relative to other freshwater ecosystems (cf. Peterson and Fry 1987; Hesslein et al. 1991; Keough et al. 1996) for reasons unknown at present. Terrestrial plants and freshwater algae generally resemble the $\delta^{15}N$ in the atmosphere (0‰), at least relative to marine phytoplankton (Peterson et al. 1985; Peterson and Fry 1987). Cifuentes et al. (1988) found seasonally elevated $\delta^{15}N$ in the Delaware estuary and speculated that the elevation was due to algal assimilation when N was not limiting. In the present study, there is a general trend seen in the yearling alosines of increasing ^{15}N as ^{13}C becomes depleted (Fig. 2), but there is much scatter in the data. Some of that scatter may reflect a mix of food sources, e.g., the presence of terrestrial invertebrates in the diet of yearling American shad, with lower $\delta^{15}N$ values than river seston, may be expected to lower the $\delta^{15}N$ of American shad as it becomes assimilated into tissue.

The assumption that otolith Sr is a reliable indicator of a fish's experience with freshwater or marine environments is based largely on observations of diadromous fishes (e.g., Casselman 1982; Kalish 1990; Secor 1992; Coutant and Chen 1993; Limburg 1995). Only one experimental study has validated this relationship, and only for a single species (striped bass (*Morone saxatilis*); Secor et al. 1995). Otolith Sr content may be affected in some cases by temperature (Radtke 1989; Townsend et al. 1992), by stress (Kalish 1992), and even by growth rate (Sadovy and Severin 1992). Nevertheless,

Secor et al. (1995) found salinity to have far greater influence on otolith Sr:Ca than either temperature or growth rates. Thus, given Secor et al.'s (1995) experimental findings, in conjunction with the salinity–Sr relationship (Ingram and Sloan 1992) and other observations of diadromous fish, it is reasonable to suppose that the Sr:Ca ratios observed in this study relate to the salinity regimes experienced by individual fish.

Whereas otolith microchemistry is gaining increasing popularity to address questions of diadromy in fishes, stable isotopic ratios have been used in surprisingly few studies of migration. Fry (1983) traced fish and shrimp migrations between nearshore coastal and offshore waters in the Gulf of Mexico; diet changes have been recorded in migratory birds (Minami et al. 1995; Alexander et al. 1996), bats (Fleming et al. 1993), and whales (Best and Schell 1996). Hesslein et al. (1991) determined by S stable isotope ratios ($\delta^{34}S$) that lake whitefish (*Coregonus clupeaformis*) caught in a freshwater river had grown mainly on a marine food source. S stable isotope ratios also show a strong marine–freshwater gradient in the tidal Hudson River (K.E. Limburg, unpublished data); however, the increased potential for analytic errors and the considerably higher costs of $\delta^{34}S$ analysis discourage use of this tracer.

If the conclusions drawn above concerning movements of yearling alosines within the Hudson estuary are true, these findings raise important questions about the adaptive significance of both the apparent loss of anadromy of some blueback herring and alewife and the long-distance spring migrations to spawning grounds by immature fish that overwintered in marine or strongly brackish waters. Both alewife and blueback herring have established landlocked populations (i.e., non-anadromous spawning populations) in the Great Lakes and other lakes throughout New York State (Ihssen et al. 1992; Smith 1995; Owens et al. 1997); it is believed that a landlocked population of blueback herring has been established in the Mohawk River, the largest Hudson River tributary (J. Hasse, New York State Department of Environmental Conservation, personal communication), but there are insufficient samples to confirm this. The tidal Hudson River may be a site of mixing between stocks that are still anadromous and those that have lost the anadromous habit. Furthermore, juveniles that migrate up from the sea may be exhibiting gregarious behavior that promotes the exploration and eventual colonization of habitat or may simply become entrained in the migratory schools of adult spawners. The fraction of yearling juveniles that engage in these movements within estuaries is unknown, largely because no one has looked for this behavior. More research would help elucidate the degree of yearling anadromy in this species, and it is reasonable to assume that such gregarious migrations might be a part of the life history repertoire of other diadromous species.

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