

**ARE SPAWNERS THE FIRST TO GO? RETROSPECTIVE  
ANALYSIS OF EARLY MIGRATORY HISTORIES OF  
ADULT AMERICAN SHAD COLLECTED DURING THE  
SPAWNING RUN**

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## Abstract

The processes of juvenile outmigration and ultimate recruitment to the spawning population were studied in American shad (*Alosa sapidissima*), an anadromous herring of the western Atlantic. Adults were collected on or near the spawning grounds in the Hudson River, New York, in spring 1995. Retrospective analysis of their early life histories was carried out by measuring strontium and calcium concentrations and Sr:Ca ratios in the inner portions of their otoliths, which were deposited when the fish were young-of-year (YOY). Sudden elevations of Sr:Ca were interpreted as seaward migration events. The physical location of these elevations on the otolith could be related to the age and size at which the YOY fish migrated from fresh water to the sea.

The major findings were:

1. Recruited adults showed patterns of first outmigration that were bimodal with respect to size and age, and these patterns were repeated in the 1988, 1989, and 1991 year classes;
2. In years where YOY data were available (1989 and 1990), the size distributions of apparent outmigration of YOY do not agree with the distributions of returning adults from the same year classes. Most of the losses of 1989 were from cohorts that appear to have left the Hudson from mid-August through September, and in 1990, from cohorts that migrated before October.
3. The 1990 year class shows strong evidence of at least two major recruitment bottlenecks: one affecting larvae hatched in early cohorts, and the second affecting juveniles hatched from late cohorts;
4. There are no strong relationships in the size or age at outmigration with the timing at which adults return in the spring to spawn for either sex;
5. Age at first outmigration is somewhat younger in females than in males, but both sexes showed bimodal distributions of age and size at outmigration.

Potential causes of differential mortality on emigrating YOY include the presence of large predators outside of the Hudson, as well as the presence of hypoxic waters into which the fish may have entered, perhaps while evading predators. This study demonstrates that post-egress mortality can be a strong factor that can restructure the demography within a year class of fish.

## Introduction

The recruitment of individual fish to viable populations may be viewed as a series of “bottlenecks” or “gauntlets” through which the individual must survive. A number of definitions of “recruited” exist: e.g., in fisheries, a recruit is often defined as having reached a size that is vulnerable to a particular gear. In an evolutionary sense, the ultimate successful recruit is one that reproduces, and thereby contributes its genes to the next generation. In light of tremendous early mortality in many fish species, information about the early life history of successful spawner recruits would shed light on what factors lead to survival. For instance, do certain behaviors or actions promote long-term survival, or is everything merely due to chance?

Recent advances in otolith research (Secor et al. 1995a) have enabled investigators to pose questions not only about the age and growth of individual fish, but increasingly, to study aspects of life history that are recorded either structurally or chemically in otoliths. One of the most powerful techniques employed is to measure the concentrations of strontium (Sr) relative to calcium, along transects of the otolith that correspond to different times in the life of the fish. Although the Sr:Ca ratio may be affected by temperature (Radtke 1989), stress (Kalish 1992), or growth rates (Sadovy and Severin 1992), the large gradient of Sr from fresh to sea water (Ingram and Sloan 1992) provides an even stronger contrast in diadromous fish as they move across the freshwater-seawater boundary (Secor et al. 1995b, Casselman 1982, Radtke et al. 1996). Using this technique, I have been able to document unusual migrations in juvenile American shad, *Alosa sapidissima*, as well as in alewife (*A. pseudoharengus*) and blueback herring (*A. aestivalis*) in the Hudson River (Limburg 1995, 1998).

The present study decomposes the 1995 spawning run of American shad in the Hudson River. Specifically, male and female fish were collected at various times during the spawning run. Their otoliths were removed and prepared for microscopic analyses. “Life-history transects” of Sr:Ca, obtained with a wavelength dispersive spectroscopic microprobe, can pinpoint when in the first growing season juvenile shad leave the nursery of the tidal freshwater Hudson; corresponding microstructural analysis provides an estimate of the age and growth history of the fish prior to leaving the river. Thus, it is possible to test life history hypotheses about optimal timing of habitat switching (Limburg 1994, 1996a). Are the ultimately successful recruits those individuals that exited the Hudson early in the season? Or is a critical threshold size necessary to reach before successful outmigration?

Further, are there different strategies for males and females? Are size and age at juvenile outmigration related to the timing of spawning (e.g., is there a genetic basis for both)?

## Methods

Fish (whole or heads only) were obtained from commercial fishermen during the spring of 1995. Originally I had intended to make three collections (early, mid, and late run), but was presented with an opportunity to make a collection at the very end of the run as well, in conjunction with the Susquehanna River shad restoration program. Table 1 details the numbers of fish and in which part of the run they were collected. Collections took place from River Mile 25 (km 40) to RM 113.5 (km 183). Although most spawning occurs above Kingston (RM 90), I assumed that all fish collected had entered the river only recently and therefore represented the cohorts that entered at different times in the spawning run. This is a reasonable assumption, given that shad can easily reach the spawning grounds in a few days (Glebe and Leggett 1981).

**Table 1. Numbers of spawning American shad collected for the study, spring 1995, by sex and stage of the spawning run.**

Spawning Status	Males	Females	Remarks
Early Run (2 - 13 April)	38	39	
Mid Run (18 Apr - 3 May)	34	35	Lost length data on one female
Late Run (10-14 May)	37	49	Lost length data on 8 females
Very Late Run (23 - 24 May)	20	6	
Totals	129	129	258 total, of which 242 had otoliths prepared

Total lengths (TL, mm) were measured when whole fish were available. When only heads were available, TL was estimated by the following regression:

$$\text{Fish TL} = 122.9 + 4.24 (\text{OL}) + 7.40 (\text{Sex}), \quad r^2 = 0.85, \quad N = 135$$

where OL = operculum length (tip of snout to the outer edge of the operculum), mm and sex was coded as -1 for males and 1 for females.

Sagittal otoliths were extracted, cleaned, and stored with code numbers. Later, ages (in years) were determined by counting annuli (indicated as paired opaque and clear zones). Counts were done several times and averaged. Immersion of the otoliths in water, together with oblique illumination under a stereomicroscope, facilitated the readings. In addition, scales of twenty fish were collected and aged by K. Hattala, New York State Department of Environmental Conservation, and myself. These scale-based ages were compared to otolith estimates. In all but two cases, age estimates agreed or differed by one year.

For each fish, one otolith was embedded sulcus-side down in Spurr's resin, and when available, the second was retained as a backup. Prior to embedding, gentle planing of the anti-sulcus side was done to thin the section and improve readability. The embedded otoliths were subsequently cut, ground in the sagittal plane, and polished to 0.5  $\mu\text{m}$ , and coated with a thin carbon layer to prevent charging in the microprobe. Because adult shad otoliths tend to become curved in the sagittal plane as compared to juvenile otoliths, special care was needed to ensure good exposure of the innermost layers (laid down when the fish were YOY). This meant that sometimes otoliths were partially destroyed in the process of getting a good transect in a particular area. This did not impede the subsequent analysis.

Microprobe analyses were initiated at Cornell University's Materials Science Center, but were discontinued due to a loss of sensitivity of the probe. Most of the analyses were carried out at the Department of Geology, University of Uppsala, Sweden, with a Cameca SX-50 microprobe. The parameters for operation were: accelerating voltage, 20 kV; current, 20nA; electron beam diameter, 15 microns. Strontium was counted for 40 s on the peak and 40 s on the background (only on one side, to avoid the strong interference from a second order Ca K- $\alpha$  peak). Calcium was counted until a precision of at least 0.1% was reached (usually < 20 s), and background was counted for 10 s on each side of the peak. Strontianite ( $\text{SrCO}_3$ ) and calcite ( $\text{CaCO}_3$ ) were used as calibration standards. The detection limits were  $0.03 \pm 0.004$  weight percent for both elements.

Multi-point measurements were made along a transect (approx. 1000  $\mu\text{m}$ ) in the posterior portion of the otolith. This distance covers the increment deposition over the entire first year of the fish's life. Typically 10 initial points were made to locate crudely the "jump" in strontium concentration, indicating a move from fresh to salt water. Point measurements were then made at closer intervals (10-30  $\mu\text{m}$ ) better to resolve the location on the otolith of elevated Sr. The transition from low to elevated Sr:Ca ratios usually occurred over a short distance (Figure 1). In cases where the daily increment widths approached the

beam diameter size, it could be seen that transitions from low to high Sr:Ca (fresh water to marine water) occurred in as little as two days.

Occasionally, poor preparation left too much overburden above the otolith core and innermost regions. This could be confirmed optically on the microprobe, as the distance between the otolith core and the sample surface could be measured in the Z axis. When this occurred, erroneously high Sr measurements were made. Depending on the particular preparation, this problem sometimes occurred just near the core, so that just a few data points were elevated. In that case, the innermost data points were noted but not interpreted as a migration event. If overburden was extensive, the specimen was either re-ground or rejected. A total of 182 fish were successfully probed.

The distance on the transect from the core to the Sr:Ca “jump” was used to estimate the size at first outmigration from the natal river (presumably the Hudson). An otolith size-body size relationship was fitted to data collected on YOY American shad (Figure 2a; Limburg, unpublished). The best fit was obtained by square-root transformation of the body size (TL) data ( $r^2 = 0.93$ ,  $p < 10^{-4}$ ,  $n = 1340$ ). Microprobe data were graphed (as in Fig. 2b) to locate visually the elevation in Sr:Ca, and this distance (the X variable) was used to estimate size at outmigration.

Age at first outmigration was estimated by mounting the otolith under a compound microscope, shining reflected light on it to reveal the burn marks from the microprobe beam, locating the point at which the Sr:Ca elevation occurred, and then using transmitted light to count daily increments from that point back to the core. Counts were made 2-3 times per otolith and averaged.

Finally, the mean widths of the first ten daily increments were measured with an optical micrometer at 400X magnification.

All statistical analyses were carried out with STATISTICA (Statsoft, Inc., 1997).

## **Results**

### Characteristics of the Adults in the Sample.

In spite of the limited size and age distribution obtained by sampling with commercial fishing gear<sup>1</sup>, eight year-classes from 1986-1993 are represented (Figure 3). Males tended to be younger with the largest percentage (41%) being assigned to the 1990 year-class, with high numbers representing the 1989 and 1991 classes as well. Females were dominated (39%) by the 1989 year-class, with another 33% in the 1990 class.

The spawning migration appears to have been size-biased (Figure 4) particularly with respect to male spawners. Larger fish tended to be caught earlier in the spawning run, and smaller fish later. There were significant ( $p < 0.01$ ) effects of time, sex, and their interaction (Figure 5).

Growth rates (TL-7 mm [size at hatch]  $\div$  Age [yr]) declined significantly ( $p < 0.01$ ) with age; there was a non-significant tendency for female growth rate to exceed that of males (Figure 6). It is interesting to note that log-linear extrapolation of growth rates back to Age 1 suggests a first year growth rate of approximately 180 mm. Young-of-year juveniles caught in the Hudson at the end of their riverine stay rarely exceed 100 mm (based on examination of Hudson River Utilities' data sets, NYSDEC data sets, and my own collections). To explain the discrepancy, fish must either make up the difference (some 70-120 mm) at sea, or a selection for faster-growing individuals may occur as a result of size-selective mortality. Alternatively, the model does a poor job at estimating growth rates at young ages. Given the mean size of 7 yearling shad collected haphazardly in spring spawning surveys ( $126.6 \pm 13.1$  mm; see Limburg 1998 for details on these fish), the last seems a clear possibility.

#### Size and Age at First Outmigration.

Both male and female spawners, in the aggregate, show a surprising pattern of size and age at their first departure from the Hudson (Figure 7). Both sexes show distinctly bimodal distributions: that is, there is one "clump" of younger, smaller outmigrants, and a second "clump" of older, larger ones. Furthermore, the relative sizes of the size/age clusters differ for males and females. Males tended to migrate somewhat later in age and at larger sizes, whereas females left the river earlier and at smaller sizes (Table 2). Both sexes show the same pattern of size at age when migrating out (Figure 8 a,b), that is, a linear increase in size at age between 40-100 days, followed by a deceleration in growth. This is consistent

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<sup>1</sup> With the exception of the last sample, collected 24 May by Everett Nack and the Wyatt Group (Lancaster,

with patterns of growth I observed in individual YOY fish otoliths, which can be characterized by Gompertz (S-shaped) growth curves. (Note that the sample of adults did not contain any individuals which had migrated at extremely small sizes; hence the “lower tail” of the Gompertz curve is not present.)

**Table 2. Percentages of fish in first egress, by sex, age, and size.**

Age	Male	Female
≤ 80 days	45 %	61.4 %
> 100 days	41.8 %	31.2 %
Size		
≤ 80 mm	47.2 %	52.5 %
> 80 mm	52.8 %	47.5 %

### Effects of the Time of Spawning

Is the timing of juvenile egress from the natal river linked to the time they return to spawn as adults? For instance, do early-season YOY outmigrants become early-season adult spawners? The evidence does not appear to support such links. Neither age (Figure 9) nor size at outmigration (Figure 11) shows distinct patterns with respect to sex or the time of occurrence in the spawning run. Male ages at outmigration tend to be more uniformly distributed than female ages, and even when the ages are log-transformed (Figure 10), only one group (early spawning females) is normally distributed. All spawning run-sex categories display two modes in sizes at outmigration (Figure 11), and log-transformation of the sizes does not normalize the distributions (Figure 12).

### Differences by Year Class

The bimodal patterns of age and size at outmigration (Figure 7) could simply be the serendipitous result of adding together different year classes of fish, and individual year classes may show different patterns altogether. Four year classes were sampled in large

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PA). In this case, a 600-ft, 2-inch mesh haul seine was deployed.

enough numbers to examine this issue: 1988 (N = 25), 1989 (N = 54), 1990 (N = 64), and 1991 (N = 26). Relative frequencies of size at outmigration show bimodal distributions in at least three of the four years (Figure 13), with modes in the 50-59 mm and 90-99 mm size categories. The 1990 year class is characterized by a large mode in the 90-99 mm category, with other size groups more evenly represented. The relative frequency distributions for 1989 and 1991 are virtually identical.

Frequency distributions of age at outmigration (Figure 14) are more variable from one year to the next, although in each year class, the largest age group is the youngest (< 60 days old). In the 1991 year class, nearly half the outmigrants were less than two months old. Also, all year classes show some sort of separation into two broad categories, i.e. young outmigrants and old ones.

An important question to ask is: given that the bimodal patterns (particularly size at outmigration) recur in different year classes, does this reflect the manner in which each year class of YOY shad actually emigrated from the Hudson, or is it the result of differential mortality? And if the latter, what mechanisms might be responsible?

In large, open systems like the Hudson River, the detection of anadromous migration as it occurs is difficult, particularly the active outmigration of juveniles from the nursery grounds to the sea. However, if we assume that the occurrence of YOY in the lower part of the estuary reflects migration out (i.e., that the fish caught there are in the act of migrating), and if sample sizes are large enough to get reasonable estimates of size distributions, then comparisons between YOY and adults of the same year class are possible for the years 1989 and 1990. The first assumption – that YOY caught in the lower estuary are migrating out – seems reasonable on the basis of the Sr:Ca changes in otoliths. Sr:Ca generally shifts rapidly in the transition from freshwater to seawater, and appears to occur over just a few days.

Extensive collections of YOY American shad were made in 1989 and 1990 for otolith-based cohort analyses of growth and migration. The 1990 material was worked up and published (Limburg 1996b), but the 1989 data were not. In both years, juvenile YOY were collected from July-November in the upper, middle, and lower portions of the tidal Hudson. The lower Hudson collections were carried out by New York Department of Environmental Conservation (DEC) personnel and consisted of beach seine collections in the Tappan Zee and mid-water trawls conducted in Haverstraw Bay. Sampling effort was more

even in 1989, so I will discuss mainly that year. In each sample, up to 100 individuals were collected.

The size frequencies of YOY in the lower Hudson in 1989 (presumably migrating out) differ markedly from the pattern seen in the adults who survived to the 1995 spawning season (Figure 15). In particular, the YOY size distribution is unimodal, with a maximum in the 70-79 mm size class, whereas the returning adults show a bimodal distribution with maxima in the 50-59 mm and 90-99 mm size classes. Compared with the YOY, the adults who first left the Hudson in the 70-89 mm size range are strongly underrepresented and those who left at 90 mm or larger are strongly over-represented. The 60-69 mm class is underrepresented in the adults (by about 20% compared to the YOY), but the 40-59 mm fish are slightly over-represented. Very few fish < 40 mm TL were observed in 1989 in the lower Hudson samples, and none were observed in the adult sample.

The discrepancies in the YOY and adult retrospective size distributions suggest that differential mortality occurred, with disproportionately high mortality on the 70-89 mm fish and disproportionately low mortality on larger fish as well as on fish in the 40-59 mm range. This appears to be a function of *when* the fish migrated (Figure 16). The smallest fish (< 60 mm) were seen in the lower Hudson in July only; fish 90 mm or larger were observed almost exclusively in October and November. Fish in the intermediate size range were collected mostly in August, September, and early October. Of fish in the 70-79 mm range (the most underrepresented group in the adults), 83% were caught from 22 August to 23 September.

Comparison of presumed outmigrating YOY in 1990 (N = 514) with survivors that appeared in the 1995 spawning run again reveals differential recruitment (Figure 17), with highest survival in the fish that migrated at sizes  $\geq 90$  mm. YOY 90 mm and larger were observed in the lower Hudson only in October and November that year. Fish in the 50-59 mm range were seen in mid-July to mid-August, as was the case for about 90% of the 60-69 mm fish. Fish in this size range were strongly underrepresented in the returning adults. Also, fish under 50 mm composed 1% of the YOY collected in 1990 in the lower Hudson, but made up over 10% of the total survivors in the 1995 spawning run sample (Figure 17).

#### Comparison of Larval Growth Rates Within the 1990 Year Class

Growth in the larval phase is often considered a critical factor affecting survival (Houde 1987; Rothschild 1986). Because otolith growth corresponds well with somatic growth in larval and juvenile American shad (Figure 2), the widths of otolith increments

deposited in the first 10 days serve as good retrospective indicators of larval growth rates. I was able to compare mean increment widths from days 1-10 in juveniles from the 1990 YOY with the same mean widths in adults that had recruited from that year class, and which were sampled in the 1995 spawning run.

In my intensive study of the 1990 YOY (Limburg 1996b), fish were collected from the Albany (KM 235), Poughkeepsie (KM 121), and Tappan Zee (KM 30-50) vicinities with 30 m (100 ft) beach seines, and in Haverstraw Bay (KM 51-65) with a mid-water trawl. Otoliths were used to determine the ages of these fish, and daily otolith growth rates were digitized and measured on up to 20 fish per sample.

The distributions of average 10-d larval growth rates are shown in Figure 18. All of the distributions show a central tendency, with highest growth rates in the Albany fish. Albany and Poughkeepsie YOY had significantly (Tukey's HSD post hoc test,  $p < 0.001$ ) higher growth rates than Tappan Zee and Haverstraw YOY (Figure 19). Adult spawners from the 1990 year class had larval growth rates indistinguishable from Tappan Zee and Haverstraw YOY. Because larval growth rates in 1990 generally increased with time (Figure 20), it is possible to extrapolate, by regressing 1990 juvenile hatch dates on their larval otolith growth rates, the most likely time period in which the adults would have been born. The mean 10-d larval otolith growth rate in 1990 adults was  $4.2 \text{ microns d}^{-1}$ , and this corresponds to birth dates around early to mid June (Figure 21).

## **Discussion**

### Interpretation of Retrospective Analyses

Adult shad returning to the spawning grounds, years after their original departure, tell in the aggregate a different story about migration and survival than is possible to observe with young-of-the-year fish still in the Hudson. Where possible, comparisons of YOY patterns with retrospective patterns in the adult population give powerful insights to the processes affecting recruitment.

In this analysis, I have interpreted the "jump" in otolith strontium:calcium ratios as an indicator of movement out of the Hudson and into coastal marine waters. An alternative interpretation, for instance of the Sr:Ca signal in early outmigrants, is that marine water entered the lower Hudson and influenced the Sr:Ca in fishes residing there. There are two

lines of evidence suggesting this interpretation is largely untrue. First, in most cases, once the Sr:Ca concentrations became elevated, they tended to remain high through at least the first winter. Second, in those instances where adjacent daily rings were probed, the transition from low to high Sr:Ca showed a monotonic increasing pattern over a 2-4 day interval. The pattern suggests a directed movement toward an area of higher salinity. This is not to say that some movements within the estuary were not detected prior to outmigration; but the appearance of higher strontium in the otolith tended to be abrupt.

The bimodal distribution of juvenile egress from the spawning and nursery habitats to the sea is a most striking observation, and one that was not expected at the outset of this study. This pattern, especially clear with respect to size at first outmigration but also evident with age at egress, is obvious in three of the year classes sampled in sufficient numbers (1988, 1989, and 1991), whereas the 1990 year class was dominated by older, larger outmigrants. In 1989 and 1990, years for which extensive data on YOY were available, the size distributions of YOY observed in the lower Hudson (postulated to be in the act of migrating out) do not match the size-at-egress distributions of returning adults.

The cause of this pattern of differential mortality is unlikely to be stress by temperature. First, water temperatures in the Hudson and adjacent coastal waters do not approach the upper lethal bound (ca. 32-33 °C; Limburg, unpublished observations). Neither is low temperature stress (lower lethal temperature 4 °C; Chittenden 1972) likely to be a problem. Although it is not possible to estimate hatch dates for any of the adults except the 1990 year class, comparisons of 1989 and 1990 YOY and adults suggest that fish with highest differential mortality left well before the onset of cool water temperatures. Furthermore, high differential survival was observed in fish that left the river at TLs of 90 mm or more. For most of these individuals, daily growth increments at the time of departure (and often for a month or so before) were highly compressed, indicating very slow growth rates corresponding to the cooling end of the growing season (see Limburg 1996, Figures 10 and 11, for typical otolith growth patterns across the growing season ).

Physiological stress due to low dissolved oxygen (DO) levels potentially could be a problem if fish migrated into areas of very low DO. Although American shad can tolerate lower DO than many fish (down to 3 ppm before loss of equilibrium; Chittenden 1969), oxygen concentrations < 1 ppm cause rapid death (Chittenden 1969). Low DO has long been a widespread problem in the East River and western Long Island Sound due to heavy

organic pollution (Parker and O'Reilly 1991), worsening in the years 1987-1993 (Welsh et al. 1994). In 1989, more than 40% of Long Island Sound (the western end, closest to the Hudson River) had less than 3 ppm DO in water below the pycnocline; the worst conditions are reported for late summer (EPA 1994). The situation in New York Harbor and New Jersey coastal waters adjacent to the Hudson is similar. If outmigrating juvenile shad encountered a mass of hypoxic water, extensive mortality could occur. However, this presupposes that the fish would have no means to avoid entering the water mass.

Predation is a third, plausible source of differential mortality. Juvenile anadromous fish exiting the Hudson River run a predatory gauntlet that very likely varies in species composition, size distributions, and intensity over the course of the summer and fall as well as year to year. The role of one of the major predators, young-of-year bluefish (*Pomatomus saltatrix*), has been elucidated in the lower Hudson. These fish enter the Hudson at sizes of 40-60 mm fork length (Juanes et al. 1993; Hare and Cowan 1996), vigorously pursue and consume prey (Juanes et al. 1993; Buckel and Conover 1997), and grow at rates similar to tropical piscivores (Juanes and Conover 1994). However, field studies of bluefish piscivory in the Hudson (Scharf et al. 1997) showed that shad YOY were mostly consumed at relatively small sizes (median 45 mm TL, range 35-60 mm); also, shad are usually a minor component of the bluefish menu, compared to striped bass, bay anchovy, Atlantic silversides, and Atlantic tomcod (Juanes et al. 1993; Buckel and Conover 1997). Thus, predation by "snappers" in the Hudson itself does not appear to be the leading source of differential mortality observed in returning adult shad, although they may be responsible in part for the loss of smaller size classes in 1990.

On the other hand, many predators spanning a range of sizes occur in coastal waters near the Hudson. For instance, striped bass age 2+ and above are found off Manhattan (J. Waldman, Hudson River Foundation, personal communication), and various predatory flounders, spotted sea trout, drum, etc. are present in New York Harbor and New York Bight. Predator:prey size ratios generally range from 3- to 5-fold for successful prey capture (Miller et al. 1988; Luecke et al. 1990). Thus, for the 1989 differential mortality on the 70-89 mm YOY shad, predation most likely would have been by fish  $\geq 200$  mm long. If they were removing YOY shad as they left the Hudson, this would have occurred in late August and September that year.

It is also possible that some combination of predation and encountering hypoxic water masses could be responsible for the patterns of differential mortality observed; for example, YOY emigrants might have inadvertently entered hypoxic waters while avoiding predators. Alternatively, YOY emigrants might have been trapped with predators, unable to move into the low DO waters.

#### Evidence for Two-Stage Differential Recruitment in the 1990 Year Class

1990 in the Hudson was a year characterized by a warming period in April-early May, followed by a strong front that brought heavy rain, increased river discharges, and lowered the water temperature in mid-late May (Lawler, Matusky and Skelly Engineers 1992). This weather event appears to have been responsible for removal of a large part of the year class in the egg or larval stage (Limburg 1996b). Eighty-two percent of the yolk-sac larvae were observed in May, but hatch dates estimated from juvenile otoliths showed that only 13.8% of juvenile recruits were born before 1 June. Spring weather events can be an important source of egg and larval mortality for other species as well (e.g., striped bass, *Morone saxatilis* (Rutherford and Houde 1995)).

Hatch dates of recruited juveniles corresponded well to otolith growth rates during the first ten days post-hatch in 1990 (Figure 20). This is likely due to the combined influence of a warming trend in June and increased food availability (Limburg 1996b). By using this relationship, I estimated the hatch dates of adults recruited from that year class and found evidence of differential recruitment once again, this time preferentially from cohorts hatched in early to mid-June (Figure 21). That very few adults were estimated to have May birthdays (N = 4, and the earliest was 29 May) corroborates the observation of poor recruitment of April and May cohorts into the population. In the river in 1990, nearly half (49%) of the juveniles observed were hatched after mid-June. The absence of cohorts hatched after mid-June among the recruited adults suggests a second strong source of mortality exerted on the population sometime after exiting the river.

Although this comparison can only be made for 1990, when hatch dates and growth rates were determined on YOY fish, there is no significant difference in early larval growth rates among the year classes represented in the adult spawners sampled in 1995.

#### Life History Implications of Early-Season Outmigration

Perhaps as striking as the observation of bimodal size- and age-at-egress distributions is the fact that so many of the successful spawner recruits had actually left the nursery at low sizes and ages. Not only does this finding confirm my previous observation of a few early outmigrants who wandered back into the Hudson as YOY (Limburg 1995), but it also lends support to Chittenden's observation that "...the young shad seem to move towards the sea from the earliest stages of life..." in the Delaware River (Chittenden 1969, p. 378). It is at odds with observations by O'Leary and Kynard (1986) that shad YOY in the Connecticut River wait until an autumnal drop in water temperatures to exit the nursery river. However, their study may not have begun early enough in the season to observe early outmigration, or else conditions may be sufficiently different in the Connecticut River to promote another migratory pattern.

It is tempting to speculate on the predominance of females among the early outmigrants (Table 2). Over all years, 61% of the females left the natal system younger than 80 days of age (11 weeks old). This number is based in large part on the 1989 and 1990 year classes, in which 70% of the females left before they reached 80 days.

Ontogenetic niche shift theory (Werner and Gilliam 1984) predicts that organisms switch habitats when the expected benefits of the move (in terms of future reproductive success) outweigh the expected costs (in terms of mortality risk). If female American shad behave according to this theory, then the added benefit of leaving the natal river at younger ages (and therefore, getting out sooner to feed and grow in the marine environment) may outweigh the increased risks of predation. Female American shad fecundity at any given latitude is directly related to body size (Leggett and Carscadden 1978). If migration out at younger ages were advantageous to females, one would predict that (1) early outmigrating females grow faster than older exiters, thereby reaching maturity younger, and (2) that size at first spawning would be greater than for females which waited longer to leave the nursery. This could be tested by collecting both otoliths and scales of female adult shad and comparing the timing of first egress and the age (and presumably size) at first reproduction.

On the other hand, there is no evidence in this study for seasonal determination of sex. For the 1990 year class, the only year for which hatch dates can be estimated, there is no difference between when males and females were born (male mean:  $33032.2 \pm 4.9$  days,  $N = 36$ ; females:  $33033 \pm 3.5$  days,  $N = 27$  (Julian Day 33032 = 8 June 1990);  $F_{1,61} = 0.45$ ,  $p < 0.50$ ). Atlantic silverside (*Menidia menidia*) larvae exposed experimentally to low water

temperatures become female (Conover and Fleisher 1986). However, Conover was later able to show that this trait predominates at lower latitudes and is unimportant at higher latitudes (Lagomarsion and Conover 1993). As for silverside, sex determination in American shad may be under little or no temperature control in mid-latitude populations; experiments would be needed to test this.

#### Possible Environmental Implications of Early vs. Late Outmigration

One of the potential sources of differential mortality affecting outmigrating YOY American shad may be hypoxia created by eutrophication of New York Harbor and western Long Island Sound. Although a conjecture with respect to Hudson River fish, this kind of mortality risk was posed in the Delaware River in the 1960s and 1970s, when sewage loading between Trenton and Philadelphia caused an “anoxia block” within the river for long distances and over a period of weeks to months in the summer. Blockage could occur periodically in the spring and fall as well (Chittenden 1969). Fish entering the “block” would die; so that, if timing of outmigration has some genetic determinant, summertime anoxia would be expected to restructure the genetic composition of the population. If the Delaware stock has rebuilt itself solely from its original members, it should be possible to investigate whether the patterns of outmigration have been altered by past history of summertime anoxia.

Future trends in climate are expected to warm both inland and coastal waters several degrees (EPA 1997). If this occurs, water will hold less dissolved oxygen, and if eutrophication continues, this will exacerbate problems of hypoxia. Thus, in addition to the many foreseen problems associated with climate change, increased warming and eutrophication could alter patterns of juvenile-to-adult recruitment in shad and probably other anadromous species.

## **Conclusions**

Sr:Ca ratios in otoliths can be used as a powerful means to trace migration, and subsequently to pose questions about the changing structure of fish populations. In this study, the main important findings were:

1. Recruited adults showed patterns of first outmigration that were bimodal with respect to size and age, and these patterns were repeated in the 1988, 1989, and 1991 year classes;

2. In years where YOY data were available (1989 and 1990), the size distributions of apparent outmigration of YOY do not agree with the distributions of returning adults from the same year classes. Most of the losses of 1989 were from cohorts that appear to have left the Hudson from mid-August through September, and in 1990, from cohorts that migrated before October.
3. The 1990 year class shows strong evidence of at least two major recruitment bottlenecks: one affecting larvae hatched in early cohorts, and the second affecting juveniles hatched from late cohorts;
4. There are no strong relationships in the size or age at outmigration with the timing at which adults return in the spring to spawn for either sex;
5. Age at first outmigration is somewhat younger in females than in males, but both sexes showed bimodal distributions of age and size at outmigration.

Whereas larval mortality long has been recognized as a key factor affecting year class strength, juvenile mortality is gaining attention now as a second, major gauntlet (Sogard 1997; Chambers and Trippel 1997). Diadromous fishes, which make large-scale migrations into habitats that differ greatly from the spawning and nursery areas, are very likely to be susceptible to predation and environmental stresses as they switch habitats. Larvae are most susceptible to size-dependent predation, food limitation (which can slow growth rates and make them more vulnerable to predators), and temperature excursions. Juveniles are vulnerable to predators generally 3X longer or more, but are less susceptible to starvation, as their somatic reserves tend to be larger than in larvae. However, strong environmental forcing (hypoxic or thermal shock events) may also be important in structuring recruitment, either solely or in conjunction with biotic pressures.

The results of this study indicate that post-egress mortality is important in determining which age and size classes of outmigrants ultimately do contribute to the spawning stock. Further, two important sources of mortality – large predators and hypoxic water – warrant further investigation.

Finally, the answer to the original question. “Are spawners the first to go?” appears to be “Yes!”; however, late-season outmigration is a highly successful tactic, as well.

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