Limited diversity in natal origins of immature anadromous fish during ocean residency

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Abstract

Variable migration patterns can play a significant role in promoting diverse life history traits among populations. However, population and stage specific movement patterns are generally unknown yet crucial aspects of life history strategies in many highly migratory species. We used a natural tag approach using geochemical signatures in otoliths to identify natal origins of one-year-old anadromous American shad (*Alosa sapidissima*) during ocean residency. Otolith signatures of migrants were compared to a database of baseline signatures from 20 source populations throughout their spawning range. Samples were dominated by fish from only two rivers, while all other potential source populations were nearly or completely absent. These data support the hypothesis that American shad exhibit diverse migratory behaviors and immature individuals from populations throughout the native range do not all mix on northern summer feeding grounds. Rather, our results suggest populations of anadromous fish are distributed heterogeneously at sea in the first year of life and thus may encounter different ocean conditions at a critical early life history stage.

Keywords: anadromy, otoliths, natal origins, mixed-stock analysis, geochemistry

Introduction

Migratory behavior is a taxonomically widespread phenomenon that allows individuals to exploit diverse habitats and resources over the course of their lifetime (Dingle 2006). These movements are often seasonally timed to ensure individuals move to those regions more favorable to survival and growth (Dingle 1996, Roff 2002). Migratory routes thus reflect behavioral decisions to optimize trade-offs between energetic costs and mortality risks associated with traveling long distances and the fitness benefits of moving to a potentially more favorable habitat (Baker 1978, Dodson 1997). These trade-offs have direct consequences on future reproductive performance and can significantly influence life history traits including semelparity (Bell 1980, Hutchings 1993). While variation in migratory behavior is common (Ketterson and Nolan 1983, Quinn and Brodeur 1991), the degree to which individuals from each population follow common migratory routes at a given time is often unknown. However, life history characteristics such as mean growth rates, maturation schedules, and reproductive output among populations often vary and migratory behaviors may be similarly diverse, reflecting population-specific requirements and tradeoffs. Such variable behavior may expose individuals from different populations to divergent environmental conditions during their migratory movements, with important implications for growth and survival (Metcalf 2006). Alternatively, populations that consistently follow common migratory routes may exhibit differential survival in poor ocean conditions, leading to selective mortality. Understanding population-specific migratory behavior and geographic distributions at a given life history stage is necessary to assess the interplay between environmental conditions and the future performance of each population.

A basic problem when studying migratory species is the identification of natal origins (Webster et al. 2002). This apparently straightforward question can be difficult to answer in

practice, particularly for species that travel long distances and breed in numerous discrete locations (Rubenstein and Hobson 2004). Artificial tagging of adults on spawning grounds cannot directly indentify natal origins at the time of recapture without assuming natal homing of tagged individuals. Mitochondrial and nuclear DNA markers are only useful in identifying natal origins for species with significant variability in allele frequencies among populations at the spatial scale of interest. A promising alternative approach to determining natal origins employs the chemical composition of tissues as a natural tag (Hobson 1999). The method requires geographic variability in a chemical signature, such as an isotope ratio, that is reliably incorporated into the tissue. Migratory patterns of birds and butterflies have been successfully studied using natural gradients in hydrogen, carbon, and nitrogen isotope ratios that are recorded in feather and wing keratin (e.g. Hobson et al. 1999, Rubenstein et al. 2002). The chemistry of fish ear bones (otoliths) has been particularly useful in tracking movement patterns because otoliths are metabolically inert, continuously accrete material in successive layers, and their chemical composition reflects to some degree that of ambient water at the time of material deposition (Campana 1999, Bath et al. 2000, Walther and Thorrold 2006). Thus if a chemically distinct natal habitat signature exists, it is recorded in the core of an otolith for life, allowing natal origins and movement patterns since birth to be determined retrospectively (Thorrold et al. 2001). In particular, natural geochemical signatures in otoliths can reveal the movements of fish during their early life history stages, in which relatively small fluctuations in survival and growth can have considerable influence on subsequent population dynamics (Sogard 1997).

Little is known about population-specific distributions of many ocean-phase anadromous species. Most work has focused on identifying origins of Atlantic and Pacific salmon using a variety of intrinsic and extrinsic markers. Artificial tags, genetic markers, and otolith

microstructure and chemical signatures have been used successfully to identifying high rates of philopatry (Quinn 1993), distinguish hatchery from wild individuals (Barnett-Johnson et al. 2008), and to estimate mixed-stock compositions of oceanic fisheries (Seeb et al. 2004, Beacham et al. 2006). Recently, analyses of coded wire tag returns and DNA markers have revealed intriguing information about stock-specific distributions of juvenile and immature Pacific salmonids (Trudel et al. 2009, Tucker et al. 2009, Weitkamp 2010). This work demonstrated that individuals were more likely to be captured near their natal river during the first year of ocean residency, and that recapture distances increased with age. However, the degree to which similar stock and age-specific migration patterns apply to non-salmonid anadromous fishes has rarely been addressed.

We used natural geochemical signatures in otoliths of American shad *Alosa sapidissima* (Wilson) to determine natal origins of immature migrants in the marine environment. American shad are anadromous alosine clupeids, spawning in freshwater habitats from Florida to Québec (Limburg et al. 2003). These populations exhibit latitudinal gradients in life history characteristics such as growth rates and fecundity (Leggett and Carscadden 1978, Limburg et al. 2003). Most information on oceanic distributions and migration patterns of American shad populations has come from extensive mark-recapture studies on adult individuals (Talbot and Sykes 1958, Leggett 1977, Dadswell et al. 1987). Adults from all populations are thought to follow common migratory routes in the marine environment, with significant mixing of populations on their summer feeding grounds in the Bay of Fundy (Dadswell et al. 1987). Marine movements of immature fish are less well known. While some individuals remain near their natal estuary after freshwater emigration (Hoffman et al. 2008), others move rapidly into fully marine habitats (Limburg 2001) and have been found at locations across the continental

shelf during their first year (Neves and Depres 1979). Previous efforts to determine stock composition of coastal migrants used both traditional tagging methods (Dadswell et al. 1987) and population genetic analysis (Brown et al. 1999). Both approaches analyzed stock compositions of adults, and origins of immature individuals after their emigration from fresh water have not been previously identified. We thus employed geochemical tagging approaches to identify origins of immature American shad captured in coastal habitats in the Gulf of Maine to determine the diversity of sources present in these harvests.

Materials and methods

Otolith collections and analyses

American shad were collected in the spring along the coast of Maine and in the summer in Minas Basin in the Bay of Fundy in 2005 (Fig. 1). Fish were collected in the spring by trawl surveys along coastal regions of Maine that took place from May 3 to June 7, using a modified shrimp net with a 1-inch stretch mesh liner that was deployed according to a stratified random sampling design (Sherman et al. 2005). We retained all fish between 100-180 mm forklength to restrict subsequent analyses to individuals from the 2004 year class (Leim 1924, Dadswell et al. 1984). Of the 104 completed tows, American shad of the specified size range were present in 20 tows, and all individuals from these tows were retained for analyses. Catches averaged 5 fish per trawl date except for one large collection of 77 fish on 12 May (total $n = 220$). We also collected fish of the same size range at a commercial herring weir on the northern shore of Minas Basin, Nova Scotia during low tides from June through early August. These collections spanned the entire time during which American shad of any size were present in weir catches, and all individuals in the specified size range were retained. Catches in the weir averaged 10 fish per

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day with the largest collection of 66 fish occurring on 22 July (total $n = 238$). Sagittal otoliths were dissected, mounted and ground to the midplane with fine-grained lapping film. Because all hatchery-produced American shad are marked with fluorescent oxytetracycline prior to release (Hendricks et al. 1991), we examined sectioned otoliths under a UV light source for hatchery marks. No marked fish were detected.

One sagittal otolith from each pair was randomly chosen for laser ablation analysis and cleaned in a class 100 clean room. We used a Thermo Finnigan Neptune multiple collector inductively coupled plasma mass spectrometer (ICP-MS) coupled to a 213nm laser ablation system to ablate a 250 x 250 μm raster adjacent to the nucleus of each otolith. This raster placement allowed us to isolate the freshwater residency period while also avoiding any maternally-derived material accreted at the core. Methods including blank and mass bias corrections as outlined in Walther et al. (2008) with the following modifications. During each ablation pass, the instrument cycled between monitoring three sets of monitored isotopes: 1.) ^{83}Kr , ^{84}Sr , ^{85}Rb , ^{86}Sr , ^{87}Sr , and ^{88}Sr were monitored simultaneously for 3 seconds, 2) ^{48}Ca was monitored for 1 second, and 3.) ^{138}Ba was monitored for 1 second. By cycling through the sets of monitored isotopes, we quantified ratios of Sr:Ca, Ba:Ca, and $^{87}\text{Sr}:$ ^{86}Sr with a single ablated raster on the core of each otolith. External precisions (relative standard deviations) based on repeated measurements of a dissolved otolith certified reference material (CRM - Yoshinaga et al. 2000) were 1.8% for Sr:Ca and 1.5% for Ba:Ca ($n = 96$). The isotope ratio $^{87}\text{Sr}:$ ^{86}Sr was calculated by correcting for interferences of ^{87}Rb on ^{87}Sr and ^{86}Kr on ^{86}Sr intensities and mass bias corrections were applied (Barnett-Johnson et al. 2005, Jackson and Hart 2006). All data were normalized to a CRM SRM987 $^{87}\text{Sr}:$ ^{86}Sr value of 0.71024 based on mean $^{87}\text{Sr}:$ ^{86}Sr values measured in SRM987. The mean (± 1 SD) value of $^{87}\text{Sr}:$ ^{86}Sr values in the SRM987 ($n = 40$) run

throughout the analyses was 0.71026 ± 0.00003 , which is within 1 standard deviation of the true value of SRM987 (0.71024). Periodic measurements of an aragonitic marine sclerosponge ($n = 9$) yielded a mean (± 1 SD) value of 0.70916 ± 0.00001 that was close to the global marine $^{87}\text{Sr}:^{86}\text{Sr}$ value of 0.70918.

The second otolith from each fish was analyzed for $\delta^{18}\text{O}$ ratios using isotope ratio monitoring mass spectrometry (irm-MS). A computer-controlled micromill removed a 400 x 400 μm raster in the same region ablated on the first otolith. Samples were analyzed on a Thermo Finnigan MAT253 equipped with a Kiel III carbonate device following methods outlined by Ostermann and Curry (2000). The long-term precision estimate of the mass spectrometer based on analyses of the NBS19 standard is $\pm 0.07\text{‰}$ for $\delta^{18}\text{O}$ (Ostermann and Curry 2000).

Statistical analyses

Geochemical signatures in otoliths of one-year-old migrants were compared with signatures from known-origin juveniles and water samples collected the previous year from 20 rivers along the Atlantic coast (Walther and Thorrold 2008). River-specific signatures based on Sr:Ca, Ba:Ca, $\delta^{18}\text{O}$, and $^{87}\text{Sr}:^{86}\text{Sr}$ ratios were highly distinct, with an average cross-validated classification accuracy of 93%. The 20 stocks in the juvenile database represent the majority of extant spawning biomass, including all stocks that are most likely to be present in the mixed sample.

We visualized differences in otolith $\delta^{18}\text{O}$, $^{87}\text{Sr}:^{86}\text{Sr}$, Sr:Ca and Ba:Ca ratios by plotting signatures in multivariate space using canonical discriminate plots (Fig. 2.). Signatures from otoliths of one-year-old migrants captured in the Maine trawl surveys and Minas Basin were plotted over those from known-origin juveniles (Fig. 2). The majority of core signatures from

immature migrants were within the ranges of values defined by the ground-truthed juvenile signatures. A few signatures fell outside these ranges and likely originated from sources not included in the juvenile database. These fish were excluded from estimates of migrant stock compositions to reduce potential estimation biases. These unclassified fish represented only 5% ($n = 11$) and 2.5% ($n = 6$) of spring and summer collections, respectively. Untransformed data were used in all analyses, as normal probability plots showed only moderate departures from normality and transformations did not alter residual distributions. Stock compositions were analyzed separately for fish collected from the spring Maine trawl surveys ($n = 209$) and the summer weir collections in Minas Basin ($n = 232$).

Stock compositions were assessed using two different types of assignment methods. For all assignment methods we used $\delta^{18}\text{O}$, $^{87}\text{Sr}/^{86}\text{Sr}$, $\text{Sr}:\text{Ca}$ and $\text{Ba}:\text{Ca}$ ratios for each fish as a multivariate signature. The first assignment method was the maximum-likelihood estimation (MLE) program Integrated Stock Mixture Analysis (ISMA) (Campana et al. 1999). This algorithm estimates proportions of unknown mixtures that derive from stocks parameterized by a reference data set and does not identify origins of individual fish (Millar 1987). The ISMA program was used because it allowed inclusion of all 20 potential source rivers, unlike an alternative MLE program HISEA (Millar 1990), which allows only a maximum of 8 contributing sources. However, the ISMA program does not estimate variance around mixture proportions. In order to explore the magnitude of variance around mixture proportions, we restricted our contributing sources to the six most abundant estimated sources (St. Lawrence, Shubenacadie, St. John, Hudson, and Potomac rivers). Using these six sources as a baseline, we calculated stock mixtures and associated standard deviations for the summer samples using the HISEA program in bootstrap mode by resampling the mixed stock data 1000 times with replacement.

The second method was a Bayesian estimator explicitly formulated for use with continuous multivariate otolith chemistry data (Munch and Clarke 2008). For this analysis we set prior mixing proportions equal to a nearly uniform Dirichlet distribution and retained 5000 samples after discarding the initial 5000 draws. We assigned natal origins to individual fish based on the maximum posterior classification probability, and then calculated proportional representations of each source stock in the two samples.

Results

Natural geochemical signatures in otoliths revealed that more than 97% of one-year-old shad in both spring and summer collections came from one of three rivers (Table 1). Based on results from the Bayesian estimator, nearly 50% of the fish from spring collections in the Gulf of Maine came from the Shubenacadie River, almost 42% were spawned in the Hudson River, and nearly 6% were from the St. John River. Fish from origins south of the Chesapeake Bay were present in negligible proportions according to both estimation methods. The Shubenacadie River was even more over-represented in the summer samples from the Bay of Fundy, accounting for just over 74% of the one-year-old American shad. Hudson River fish represented a further ~24%, while all remaining rivers if present contributed less than 1% to the pooled summer sample.

There was general agreement in proportional abundances of source stocks in both collections as estimated by the MLE and Bayesian algorithms. The one exception was for the summer samples where the MLE method suggested that 17% (approximately 40 individuals) of the fish were from the Potomac River. The Bayesian estimator did not detect significant numbers of Potomac River fish and instead classified those individuals as originating from the

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Shubenacadie River. This result likely arose because of similarities in chemical signatures between the Potomac and Shubenacadie rivers (Fig. 2).

Maximum posterior classification probabilities from the Bayesian estimator were higher than 0.80 for 88% and 83% of fish collected from Maine and Minas Basin, respectively, indicating that the majority of fish were assigned to a source river with high degrees of confidence (Fig. 3). Because of the discrepancy in assignment estimates for the Potomac River in the summer samples, we examined posterior probabilities of summer individuals assigned to the Shubenacadie River to determine whether overall confidence was lower than other groups. However, these posterior probabilities were comparably high. Over 90% of individuals were assigned to the Shubenacadie River with posterior probabilities higher than 0.80, and only 16 individuals fell below probabilities of 0.80. Thus assignment uncertainty in the Bayesian estimator could not account for the lack of Potomac River assignments.

By restricting our baseline to a subset of six source stocks, we calculated standard deviations around mixed stock estimates for the summer samples using the HISEA program in bootstrap mode. Mixed stock estimates (± 1 SD) were $24.5 \pm 3.5\%$ for the Hudson River, $52.4 \pm 4.8\%$ for the Shubenacadie River, $19.8 \pm 3.8\%$ for the Potomac River, $2.4 \pm 3.1\%$ for the St. Lawrence River, and $0.4 \pm 0.4\%$ for the St. John River. These estimates are comparable to those identified by the ISMA program, and suggested that variance around the MLE estimates was relatively low.

Discussion

The stock compositions of immature migrants in Minas Basin differed substantially from those reported for older age classes. Dadswell et al. (1987) compiled data from several decades

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of tagging studies on adult American shad throughout the western Atlantic. Summer feeding aggregations in the upper Bay of Fundy contained individuals from stocks throughout their entire range, including Florida. Of adult migrants tagged in the Bay of Fundy, approximately 34% were recaptured in rivers south of Cape Hatteras (Region 1), 44% were recaptured between Cape Hatteras and Cape Cod (Region 2), 15% were recaptured in Bay of Fundy rivers (Region 3), and 7% were recaptured in the Gulf of St. Lawrence (Region 4). Dividing our composition estimates into similar regions and averaging across spring and summer collections, we estimated that the majority of one-year-old migrants were from Region 2 (34-47%) and from Region 3 (52-65%), with precise values depending on the statistical estimation method used. All collections contained less than 1% of fish from Regions 1 and 4, regardless of the estimator. Moreover, Regions 2 and 3 were each overwhelmingly represented by the Hudson River and the Shubenacadie River, respectively.

Several large northern populations of American shad were effectively absent from both the spring and summer samples. Fish from all extant Canadian stocks aside from the Shubenacadie River were either present in small numbers or were not detected. In addition, most rivers in the northeast United States contributed little to the samples. The lack of fish from these northern rivers was unexpected given their large historic population sizes. One possible explanation for their absences is the observation that many northern rivers including the Connecticut have experienced recent declines in year-class strength (ASMFC 2007). However, the Hudson River has experienced comparable drops in abundance indices to the Connecticut River (ASMFC 2007), and yet contributed a substantial number of fish to the assemblages here. Year class strength therefore does not appear to account entirely for different proportions of northern stocks in the mixtures. In addition, juvenile abundance indices are generally poorly

correlated with subsequent abundances of adult spawners from the same cohort (ASMFC 2007), suggesting significant mortality and demographic restructuring during their time at sea (Limburg 2001). At least some of this restructuring may have already occurred prior to our collections, decoupling juvenile abundance from abundances of immature migrants.

Southern and mid-latitude stocks were also generally absent from the mixtures, and most Chesapeake Bay stocks were not present in the collections. Stocks from south of Chesapeake Bay were also poorly represented in the mixtures, and no fish from Florida were detected. Unfortunately, juvenile abundances are not monitored in all rivers, and data are unavailable for most southern and Canadian rivers. Thus the influence of relative juvenile abundances for these rivers on our composition estimates is unknown. Inadequate sampling of the fish present in the Gulf of Maine and Bay of Fundy could bias the composition estimates if particular populations were present in the region but consistently missed by collections. However, we believe that this is unlikely given the temporal coverage of the weir collections where we collected samples continuously between mid-June and early August. This corresponds to temporal abundance patterns in the region, with highest abundances typically occurring around early July (Dadswell et al. 1987). The Maine New Hampshire trawl survey in 2005 occupied a total of 104 stations in a stratified random design covering some 13,000 km² and therefore we see no reason why these samples would be biased (Sherman et al. 2005). Finally, with the exception of the Potomac River fish, similar population compositions were detected in the Maine trawls and Minas Basin weir collections, despite alternative collection methods covering different dates and locations. Thus it appears unlikely that the absence of many populations in our samples was due to sampling error.

The Potomac River was the only significant contributor from the Chesapeake Bay region, as identified by the MLE method for Minas Basin collections. While Potomac River stock abundance has been low for several decades, stocking efforts have enhanced the population and juvenile abundance in 2004 was the largest recorded to date by monitoring surveys (ASMFC 2007). However their presence in Minas Basin collections was equivocal given that the population was not identified in the sample by the Bayesian estimator. This discrepancy likely arose due to chemical similarities between baseline river-specific signatures, and the Bayesian estimator assigned these individuals to the Shubenacadie River instead of the Potomac River. Neither the Bayesian nor the MLE estimator showed evidence of high classification uncertainty, as demonstrated by the distribution of maximum posterior assignment probabilities for the Bayesian and small estimated variances for the MLE. Reduced classification confidence was therefore not the source of the discrepancy. Instead, these two estimators confidently assigned individuals with signatures falling on the boundary of two similar baselines to alternative sources. This result points to the need to interpret estimates of mixed stock composition with caution when baselines are similar. The use of multiple independent estimators can help confirm the composition of mixed stocks and identify those sources that are equivocal.

Juvenile and immature American shad appear to exhibit high degrees of inter- and intra-population variability in the timing and extent of their migratory movements. Freshwater emigration timing can occur over a wide range of dates, with size and age playing a strong role in determining downriver movements (Limburg 1996). Further, both early and late emigrants can survive to spawn as returning adults (Limburg 2001), indicating juvenile migratory variability does not preclude successful future reproductive contributions. Movements may be similarly diverse after transitioning to coastal habitats. Juvenile emigrants have long been

312 known to overwinter in nearshore estuarine environments (Hildebrand and Schroeder 1927,
313 Milstein 1981, Hoffman et al. 2008). Others move more rapidly through estuaries to fully
314 marine environments (Limburg 2001) and both subadults and adults have been captured across
315 the shelf between 39°N and 41°N at depths of 50-100 m during winter months (Neves and
316 Depres 1979). Finally, yearling American shad have been observed to make non-spawning
317 movements into fresh water alongside spawning adults (Limburg 1998), further suggesting that
318 some individuals remain in estuarine habitats and do not participate in coastal migrations during
319 this immature life history stage. Our results support the hypothesis that American shad exhibit a
320 diverse suite of migratory movements during the first year of life. Some individuals originated
321 from nearby rivers (e.g. the Shubenacadie in Minas Basin collections), indicating minimal
322 movement after freshwater emigration. Others derived from more distant sources (e.g. the
323 Hudson), suggesting not all populations remain near their natal estuary during their first year.
324 The current study was focused on collections made in coastal habitats of the Gulf of Maine, and
325 the identity of individuals collected from offshore environments remains to be determined.
326 However, this work represents the first step in unraveling population-specific distributions of this
327 highly migratory species during the immature life history stage.

328 Dadswell et al. (1987) described patterns of adult American shad migrations along the
329 eastern coast of North America whereby individuals from all populations throughout their range
330 moved through the upper Bay of Fundy to capitalize on high local summer productivity and food
331 availability. While Dadswell and co-workers observed this pattern for mature fish, our results
332 showed a very different compositional pattern for immature migrants. Processes such as
333 environmental variability, year class strength, and stock-specific behavior may collectively
334 influence the composition of mixed-stock assemblages collected at any location and at any point

in time. Inter-annual variability in assemblage composition was not addressed by this study, but temporal and ontogenetic changes in migratory behavior are certainly possible. Importantly, our data showed natal origin may play a role in determining the marine distributions of immature American shad. This variable behavior implies divergent exposure to suites of environmental stress, energetic costs, food availability, and predation pressure. The influence of population-specific marine distributions on latitudinal clines in life history traits in American shad is as yet unexplored.

There are significant management implications of American shad movements and mixing in the marine environment. An assessment of mixed-stock compositions of coastal harvests off Maryland and Virginia based on mitochondrial DNA variation found significant variation in the contributions of individual stocks to the mixtures (Brown et al. 1999). This variation was both geographical and temporal suggesting dynamic and unpredictable changes in the presence of specific stocks in harvests, with many stocks represented by numbers disproportionate to their population sizes. Such dynamism limits the ability to manage coastal mixed-stock fisheries without allowing unsustainable mortality of the most vulnerable stocks. Our work shows that the migratory habits of immature American shad are similarly complex, and managers of American shad should consider the potential impact of mixed-stock fisheries on early year classes.

Immature fish are potentially more susceptible to harvest as bycatch in a variety of fisheries, imposing further anthropogenic stress on fully exploited stocks. Increased mortality of immature migrants in mixed-stock fisheries has the potential to significantly alter year-class strength, restructure demographics, and further limit recovery of depleted populations. Combining results from studies employing traditional tags, morphometrics, DNA analysis, and now natural

chemical tags in otoliths reveals the complex nature of American shad migrations in the marine environment.

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References

- ASMFC. 2007. American shad stock assessment report for peer review., Atlantic States Marine Fisheries Commission, Bethesda, MD. Stock Assess. Rep. No. 07-01 (Suppl.)
- Baker, R.R. 1978. The evolutionary ecology of animal migration. Holmes & Meier Publishers, Inc., New York, NY.
- Barnett-Johnson, R., Pearson, T.E., and Ramos, F.C. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. *Limnol. Oceanogr.* **53**(4): 1633-1642.
- Barnett-Johnson, R., Ramos, F.C., Grimes, C.B., and MacFarlane, R.B. 2005. Validation of Sr isotopes in otoliths by laser ablation multicollector inductively coupled plasma mass spectrometry (LA-MC-ICPMS): opening avenues in fisheries science applications. *Can. J. Fish. Aquat. Sci.* **62**(11): 2425-2430.
- Bath, G.E., Thorrold, S.R., Jones, C.M., Campana, S.E., McLaren, J.W., and Lam, J.W.H. 2000. Strontium and barium uptake in aragonitic otoliths of marine fish. *Geochim. Cosmochim. Acta* **64**(10): 1705-1714.
- Beacham, T.D., Candy, J.R., Jonsen, K.L., Supernault, J., Wetklo, M., Deng, L.T., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2006. Estimation of stock composition and individual identification of Chinook salmon across the Pacific Rim by use of microsatellite variation. *Trans. Am. Fish. Soc.* **135**(4): 861-888.
- Bell, G. 1980. The costs of reproduction and their consequences. *Am. Nat.* **116**(1): 45-76.

390 Brown, B.L., Smouse, P.E., Epifanio, J.M., and Kobak, C.J. 1999. Mitochondrial DNA mixed-
 391 stock analysis of American shad: coastal harvests are dynamic and variable. Trans. Am.
 392 Fish. Soc. **128**(6): 977-994.

393 Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and
 394 applications. Mar. Ecol. Prog. Ser. **188**: 263-297.

395 Campana, S.E., Chouinard, G.A., Hanson, J.M., and Frechet, A. 1999. Mixing and migration of
 396 overwintering Atlantic cod (*Gadus morhua*) stocks near the mouth of the Gulf of St.
 397 Lawrence. Can. J. Fish. Aquat. Sci. **56**(10): 1873-1881.

398 Dadswell, M.J., Melvin, G.D., Williams, P.J., and Themelis, D.E. 1987. Influences of origin, life
 399 history, and chance on the Atlantic coast migration of American shad. Am. Fish. Soc.
 400 Symp. **1**: 313-330.

401 Dadswell, M.J., Bradford, R., Leim, A.H., Scarratt, D.J., Melvin, G.D., and Appy, R.G. 1984. A
 402 review of research on fishes and fisheries in the Bay of Fundy between 1976 and 1983
 403 with particular reference to its upper reaches. Can. Tech. Rep. Fish. Aquat. Sci. **1256**:
 404 163-294.

405 Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Oxford.

406 Dingle, H. 2006. Animal migration: is there a common migratory syndrome? J. Ornithol. **147**(2):
 407 212-220.

408 Dodson, J.J. 1997. Fish migration: an evolutionary perspective. *In* Behavioural ecology of teleost
 409 fishes. Edited by J.J. Godin. Oxford University Press, Oxford. pp. 10-36.

410 Hendricks, M.L., Bender, T.R., and Mudrak, V.A. 1991. Multiple marking of American shad
 411 otoliths with tetracycline antibiotics. *N. Am. J. Fish. Manag.* **11**(2): 212-219.
 412 doi:10.1577/1548-8675(1991)011<0212:MMOASO>2.3.CO;2

413 Hildebrand, S.F., and Schroeder, W.C. 1927. Fishes of the Chesapeake Bay. *Bull. US Bur. Fish.*
 414 **43**(1): 93-100.

415 Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review.
 416 *Oecologia* **120**(3): 314-326.

417 Hobson, K.A., Wassenaar, L.I., and Taylor, O.R. 1999. Stable isotopes (δD and $\delta^{13}C$) are
 418 geographic indicators of natal origins of monarch butterflies in eastern North America.
 419 *Oecologia* **120**(3): 397-404.

420 Hoffman, J.C., Limburg, K.E., Bronk, D.A., and Olney, J.E. 2008. Overwintering habits of
 421 migratory juvenile American shad in Chesapeake Bay. *Environ. Biol. Fishes* **81**(3): 329-
 422 345.

423 Hutchings, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate.
 424 *Ecology* **74**(3): 673-684.

425 Jackson, M.G., and Hart, S.R. 2006. Strontium isotopes in melt inclusions from Samoan basalts:
 426 implications for heterogeneity in the Samoan plume. *Earth Planet. Sci. Lett.* **245**(1-2):
 427 260-277.

428 Ketterson, E.D., and Nolan, V., Jr. 1983. The evolution of differential bird migration. *In* Current
 429 Ornithology, Vol. 1. *Edited by* R.F. Johnston. Plenum Press, New York, NY. pp. 357-
 430 402.

431 Leggett, W.C. 1977. Ocean migration rates of American shad (*Alosa sapidissima*). J. Fish. Res.
 432 Board Can. **34**(9): 1422-1427.

433 Leggett, W.C., and Carscadden, J.E. 1978. Latitudinal variation in reproductive characteristics of
 434 American shad (*Alosa sapidissima*): evidence for population specific life history
 435 strategies in fish. J. Fish. Res. Board Can. **35**(11): 1469-1478.

436 Leim, A.H. 1924. The life history of the shad (*Alosa sapidissima* (Wilson)) with special
 437 reference to the factors limiting its abundance. Contrib. Can. Bio. **2**(11): 161-284.

438 Limburg, K.E. 1996. Growth and migration of 0-year American shad (*Alosa sapidissima*) in the
 439 Hudson River estuary: otolith microstructural analysis. Can. J. Fish. Aquat. Sci. **53**(1):
 440 220-238.

441 Limburg, K.E. 1998. Anomalous migrations of anadromous herrings revealed with natural
 442 chemical tracers. Can. J. Fish. Aquat. Sci. **55**(2): 431-437.

443 Limburg, K.E. 2001. Through the gauntlet again: demographic restructuring of American shad
 444 by migration. Ecology **82**(6): 1584-1596.

445 Limburg, K.E., Hattala, K.A., and Kahnle, A. 2003. American shad in its native range. Am. Fish.
 446 Soc. Symp. **35**: 125-140.

447 Metcalfe, J.D. 2006. Fish population structuring in the North Sea: understanding processes and
 448 mechanisms from studies of the movements of adults. J. Fish. Biol. **69** (Supp. C): 48-65.

449 Millar, R.B. 1987. Maximum likelihood estimation of mixed stock fishery composition. Can. J.
 450 Fish. Aquat. Sci. **44**(3): 583-590.

451 Millar, R.B. 1990. A versatile computer program for mixed stock fishery composition
 452 estimation. Can. Tech. Rep. Fish. Aquat. Sci. **1753**: iii + 29p.

453 Milstein, C.B. 1981. Abundance and distribution of juvenile *Alosa* species off southern New
 454 Jersey. Trans. Am. Fish. Soc. **110**(2): 306-309.

455 Munch, S.B., and Clarke, L.M. 2008. A Bayesian approach to identifying mixtures from otolith
 456 chemistry data. Can. J. Fish. Aquat. Sci. **65**(12): 2742-2751.

457 Neves, R.J., and Depres, L. 1979. The oceanic migration of American shad, *Alosa sapidissima*,
 458 along the Atlantic coast. Fish. Bull. **77**(1): 199-212.

459 Ostermann, D.R., and Curry, W.B. 2000. Calibration of stable isotopic data: an enriched delta O-
 460 18 standard used for source gas mixing detection and correction. Paleoceanography
 461 **15**(3): 353-360.

462 Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish.
 463 Res. **18**(1-2): 29.

464 Quinn, T.P., and Brodeur, R.D. 1991. Intra-specific variations in the movement patterns of
 465 marine animals. Am. Zool. **31**(1): 231-241.

466 Roff, D.A. 2002. Life history evolution. Sinauer Associates, Inc., Sunderland, MA.

467 Rubenstein, D.R., and Hobson, K.A. 2004. From birds to butterflies: animal movement patterns
 468 and stable isotopes. *Trends Ecol. Evol.* **19**(5): 256-263.

469 Rubenstein, D.R., Chamberlain, C.P., Holmes, R.T., Ayres, M.P., Waldbauer, J.R., Graves, G.R.,
 470 and Tuross, N.C. 2002. Linking breeding and wintering ranges of a migratory songbird
 471 using stable isotopes. *Science* **295**(5557): 1062-1065.

472 Seeb, L.W., Crane, P.A., Kondzela, C.M., Wilmot, R.L., Urawa, S., Varnavskaya, N.V., and
 473 Seeb, J.E. 2004. Migration of Pacific Rim chum salmon on the high seas: insights from
 474 genetic data. *Environ. Biol. Fishes* **69**(1-4): 21-36.

475 Sherman, S.A., Stepanek, K., and Sowles, J. 2005. Maine - New Hampshire inshore groundfish
 476 trawl survey: procedures and protocols [online]. Available from
 477 <http://www.maine.gov/dmr/rm/trawl/reports.htm> [accessed 17 March 2010].

478 Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull.*
 479 *Mar. Sci.* **60**(3): 1129-1157.

480 Talbot, G.B., and Sykes, J.E. 1958. Atlantic coast migrations of American shad. *Fish. Bull.*
 481 **58**(142): 473-490.

482 Thorrold, S.R., Latkoczy, C., Swart, P.K., and Jones, C.M. 2001. Natal homing in a marine fish
 483 metapopulation. *Science* **291**(5502): 297-299.

484 Trudel, M., Fisher, J., Orsi, J.A., Morris, J.F.T., Thiess, M.E., Sweeting, R.M., Hinton, S.,
 485 Fergusson, E.A., and Welch, D.W. 2009. Distribution and migration of juvenile Chinook

486 salmon derived from coded wire tag recoveries along the continental shelf of western
 487 North America. Trans. Am. Fish. Soc. **138**(6): 1369-1391. doi:10.1577/T08-181.1

488 Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E., Wallace, C.,
 489 Teel, D.J., Crawford, W., Farley, E.V., and Beacham, T.D. 2009. Seasonal stock-specific
 490 migrations of juvenile sockeye salmon along the west coast of North America:
 491 implications for growth. Trans. Am. Fish. Soc. **138**(6): 1458-1480. doi:10.1577/T08-
 492 211.1

493 Walther, B.D., and Thorrold, S.R. 2006. Water, not food, contributes the majority of strontium
 494 and barium deposited in the otoliths of a marine fish. Mar. Ecol. Prog. Ser. **311**: 125-130.

495 Walther, B.D., and Thorrold, S.R. 2008. Continental-scale variation in otolith geochemistry of
 496 juvenile American shad (*Alosa sapidissima*). Can. J. Fish. Aquat. Sci. **65**(12): 2623-2635.

497 Walther, B.D., Thorrold, S.R., and Olney, J.E. 2008. Geochemical signatures in otoliths record
 498 natal origins of American shad. Trans. Am. Fish. Soc. **137**(1): 57-69.

499 Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., and Holmes, R.T. 2002. Links between
 500 worlds: unraveling migratory connectivity. Trends Ecol. Evol. **17**(2): 76-83.

501 Weitkamp, L.A. 2010. Marine distributions of Chinook salmon from the west coast of North
 502 America determined by coded wire tag recoveries. Trans. Am. Fish. Soc. **139**(1): 147-
 503 170. doi:10.1577/T08-225.1

504 Yoshinaga, J., Nakama, A., Morita, M., and Edmonds, J.S. 2000. Fish otolith reference material
 505 for quality assurance of chemical analyses. Mar. Chem. **69**(1-2): 91-97.

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507

508 Table 1. Percent composition from each source river in mixtures of immature migrant American
509 shad from spring Maine trawl surveys and summer Minas Basin weir collections as estimated by
510 both the MLE and Bayesian methods. Recapture regions as defined by Dadswell et al. (1987)
511 are indicated. Rivers are ordered from north (top) to south (bottom).

River	Code	Region	Spring		Summer	
			MLE	Bayesian	MLE	Bayesian
Miramichi	MIR	4	-	-	-	-
St. Lawrence	STL	4	0.3	-	0.3	-
Shubenacadie	SHU	3	41.3	49.8	56.4	74.1
St. John	SJN	3	5.4	5.7	0.3	0.4
Annapolis	ANN	3	-	-	-	-
Kennebec	KEN	3	-	-	-	-
Exeter	EXE	3	-	-	-	-
Merrimack	MER	3	0.5	-	-	-
Connecticut	CON	2	0.1	-	-	-
Hudson	HUD	2	44.2	41.6	25.4	24.1
Delaware	DEL	2	-	-	-	-
Upper Chesapeake	UPC	2	1.7	1.0	-	0.4
Potomac	POT	2	5.6	-	17.7	0.9
Rappahannock	RAP	2	-	-	-	-
Mattaponi	MAT	2	-	-	-	-
Pamunkey	PAM	2	-	1.0	-	-
Roanoke	ROA	1	-	1.0	-	-
Santee-Cooper	SNC	1	1.0	-	-	-
Altamaha	ALT	1	-	-	-	-
St. Johns	SJS	1	-	-	-	-
<i>n</i>			209	209	232	232

Figure captions

Fig. 1. (a) Map of rivers where otoliths and water samples were collected to parameterize source-specific multivariate otolith signatures, as described by Walther & Thorrold (2008). Abbreviated river codes follow those given in Table 1. Rivers are grouped into regions following Dadswell et al. (1987).

(b) Collection locations of American shad sampled in 2004. Trawl surveys (diamonds) collected fish along the coast of Maine in the spring. The largest trawl collection (gray circle) of 77 fish occurred on 12 May. Summer collections were made at a weir (star) in Minas Basin in the Bay of Fundy.

Fig. 2.

(a) Canonical discriminant plot of isotope ($^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{18}\text{O}$) and elemental (Sr:Ca and Ba:Ca) signatures from juvenile otoliths or water samples collected from 20 rivers in 2004 (Walther and Thorrold 2008). Open diamonds are means (± 1 SD) of canonical scores for each river. Abbreviated river codes follow those given in Table 1.

(b) Canonical discriminant plot of natal geochemical signatures from otoliths in individual immature fish (shaded circles) collected in spring Maine trawl surveys along with mean (± 1 SD) canonical scores for each source river (open diamonds). Filled squares are otolith signatures from fish that were excluded from composition analyses.

(c) Canonical discriminant plot of natal geochemical signatures from otoliths of individual immature fish (shaded circles) from summer Minas Basin weir collections along with mean (± 1 SD) canonical scores for each source river (open diamonds). Filled squares are otolith signatures from fish that were excluded from composition analyses.

Fig. 3. Frequency distribution of maximum posterior classification probabilities for individual fish as determined by a Bayesian estimator (Munch and Clarke 2008). Results are shown for fish collected in (a) spring Maine trawls and (b) summer Minas Basin weir collections.

Figure 1

Figure 2

Figure 3