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

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Running title: Limited diversity in immature fish origins

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 (Metcalfe 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

60 practice, particularly for species that travel long distances and breed in numerous discrete
61 locations (Rubenstein and Hobson 2004). Artificial tagging of adults on spawning grounds
62 cannot directly indentify natal origins at the time of recapture without assuming natal homing of
63 tagged individuals. Mitochondrial and nuclear DNA markers are only useful in identifying natal
64 origins for species with significant variability in allele frequencies among populations at the
65 spatial scale of interest. A promising alternative approach to determining natal origins employs
66 the chemical composition of tissues as a natural tag (Hobson 1999). The method requires
67 geographic variability in a chemical signature, such as an isotope ratio, that is reliably
68 incorporated into the tissue. Migratory patterns of birds and butterflies have been successfully
69 studied using natural gradients in hydrogen, carbon, and nitrogen isotope ratios that are recorded
70 in feather and wing keratin (e.g. Hobson et al. 1999, Rubenstein et al. 2002). The chemistry of
71 fish ear bones (otoliths) has been particularly useful in tracking movement patterns because
72 otoliths are metabolically inert, continuously accrete material in successive layers, and their
73 chemical composition reflects to some degree that of ambient water at the time of material
74 deposition (Campana 1999, Bath et al. 2000, Walther and Thorrold 2006). Thus if a chemically
75 distinct natal habitat signature exists, it is recorded in the core of an otolith for life, allowing
76 natal origins and movement patterns since birth to be determined retrospectively (Thorrold et al.
77 2001). In particular, natural geochemical signatures in otoliths can reveal the movements of fish
78 during their early life history stages, in which relatively small fluctuations in survival and growth
79 can have considerable influence on subsequent population dynamics (Sogard 1997).
80 Little is known about population-specific distributions of many ocean-phase anadromous
81 species. Most work has focused on identifying origins of Atlantic and Pacific salmon using a
82 variety of intrinsic and extrinsic markers. Artificial tags, genetic markers, and otolith

83 microstructure and chemical signatures have been used successfully to identifying high rates of
84 philopatry (Quinn 1993), distinguish hatchery from wild individuals (Barnett-Johnson et al.
85 2008), and to estimate mixed-stock compositions of oceanic fisheries (Seeb et al. 2004, Beacham
86 et al. 2006). Recently, analyses of coded wire tag returns and DNA markers have revealed
87 intriguing information about stock-specific distributions of juvenile and immature Pacific
88 salmonids (Trudel et al. 2009, Tucker et al. 2009, Weitkamp 2010). This work demonstrated
89 that individuals were more likely to be captured near their natal river during the first year of
90 ocean residency, and that recapture distances increased with age. However, the degree to which
91 similar stock and age-specific migration patterns apply to non-salmonid anadromous fishes has
92 rarely been addressed.
93 We used natural geochemical signatures in otoliths of American shad *Alosa sapidissima*
94 (Wilson) to determine natal origins of immature migrants in the marine environment. American
95 shad are anadromous alosine clupeids, spawning in freshwater habitats from Florida to Québec
96 (Limburg et al. 2003). These populations exhibit latitudinal gradients in life history
97 characteristics such as growth rates and fecundity (Leggett and Carscadden 1978, Limburg et al.
98 2003). Most information on oceanic distributions and migration patterns of American shad
99 populations has come from extensive mark-recapture studies on adult individuals (Talbot and
100 Sykes 1958, Leggett 1977, Dadswell et al. 1987). Adults from all populations are thought to
101 follow common migratory routes in the marine environment, with significant mixing of
102 populations on their summer feeding grounds in the Bay of Fundy (Dadswell et al. 1987).
103 Marine movements of immature fish are less well known. While some individuals remain near
104 their natal estuary after freshwater emigration (Hoffman et al. 2008), others move rapidly into
105 fully marine habitats (Limburg 2001) and have been found at locations across the continental

106 shelf during their first year (Neves and Depres 1979). Previous efforts to determine stock
107 composition of coastal migrants used both traditional tagging methods (Dadswell et al. 1987) and
108 population genetic analysis (Brown et al. 1999). Both approaches analyzed stock compositions
109 of adults, and origins of immature individuals after their emigration from fresh water have not
110 been previously identified. We thus employed geochemical tagging approaches to identify
111 origins of immature American shad captured in coastal habitats in the Gulf of Maine to
112 determine the diversity of sources present in these harvests.
113

114 ## Materials and methods

115 ### Otolith collections and analyses

116 American shad were collected in the spring along the coast of Maine and in the summer
117 in Minas Basin in the Bay of Fundy in 2005 (Fig. 1). Fish were collected in the spring by trawl
118 surveys along coastal regions of Maine that took place from May 3 to June 7, using a modified
119 shrimp net with a 1-inch stretch mesh liner that was deployed according to a stratified random
120 sampling design (Sherman et al. 2005). We retained all fish between 100-180 mm forklength to
121 restrict subsequent analyses to individuals from the 2004 year class (Leim 1924, Dadswell et al.
122 1984). Of the 104 completed tows, American shad of the specified size range were present in 20
123 tows, and all individuals from these tows were retained for analyses. Catches averaged 5 fish per
124 trawl date except for one large collection of 77 fish on 12 May (total $n = 220$). We also collected
125 fish of the same size range at a commercial herring weir on the northern shore of Minas Basin,
126 Nova Scotia during low tides from June through early August. These collections spanned the
127 entire time during which American shad of any size were present in weir catches, and all
128 individuals in the specified size range were retained. Catches in the weir averaged 10 fish per

Insert Fig. 1 here

129 day with the largest collection of 66 fish occurring on 22 July (total $n = 238$). Sagittal otoliths
130 were dissected, mounted and ground to the midplane with fine-grained lapping film. Because all
131 hatchery-produced American shad are marked with fluorescent oxytetracycline prior to release
132 (Hendricks et al. 1991), we examined sectioned otoliths under a UV light source for hatchery
133 marks. No marked fish were detected.
134 One sagittal otolith from each pair was randomly chosen for laser ablation analysis and
135 cleaned in a class 100 clean room. We used a Thermo Finnigan Neptune multiple collector
136 inductively coupled plasma mass spectrometer (ICP-MS) coupled to a 213nm laser ablation
137 system to ablate a 250 x 250 μm raster adjacent to the nucleus of each otolith. This raster
138 placement allowed us to isolate the freshwater residency period while also avoiding any
139 maternally-derived material accreted at the core. Methods including blank and mass bias
140 corrections as outlined in Walther et al. (2008) with the following modifications. During each
141 ablation pass, the instrument cycled between monitoring three sets of monitored isotopes: 1.)
142 ^{83}Kr, ^{84}Sr, ^{85}Rb, ^{86}Sr, ^{87}Sr, and ^{88}Sr were monitored simultaneously for 3 seconds, 2) ^{48}Ca was
143 monitored for 1 second, and 3.) ^{138}Ba was monitored for 1 second. By cycling through the sets
144 of monitored isotopes, we quantified ratios of Sr:Ca, Ba:Ca, and ^{87}Sr:^{86}Sr with a single ablated
145 raster on the core of each otolith. External precisions (relative standard deviations) based on
146 repeated measurements of a dissolved otolith certified reference material (CRM - Yoshinaga et
147 al. 2000) were 1.8% for Sr:Ca and 1.5% for Ba:Ca ($n = 96$). The isotope ratio ^{87}Sr:^{86}Sr was
148 calculated by correcting for interferences of ^{87}Rb on ^{87}Sr and ^{86}Kr on ^{86}Sr intensities and mass
149 bias corrections were applied (Barnett-Johnson et al. 2005, Jackson and Hart 2006). All data
150 were normalized to a CRM SRM987 ^{87}Sr:^{86}Sr value of 0.71024 based on mean ^{87}Sr:^{86}Sr values
151 measured in SRM987. The mean (± 1 SD) value of ^{87}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 $^{87}Sr:^{86}Sr$ value of 0.70918.

The second otolith from each fish was analyzed for $\delta^{18}O$ 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 ± 0.07‰ for $\delta^{18}O$ (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, $\delta^{18}O$, and $^{87}Sr:^{86}Sr$ 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 $\delta^{18}O$, $^{87}Sr:^{86}Sr$, 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

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

Insert Fig. 2 here

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

198 The second method was a Bayesian estimator explicitly formulated for use with
199 continuous multivariate otolith chemistry data (Munch and Clarke 2008). For this analysis we
200 set prior mixing proportions equal to a nearly uniform Dirichlet distribution and retained 5000
201 samples after discarding the initial 5000 draws. We assigned natal origins to individual fish
202 based on the maximum posterior classification probability, and then calculated proportional
203 representations of each source stock in the two samples.
204
205 ## Results
206 Natural geochemical signatures in otoliths revealed that more than 97% of one-year-old
207 shad in both spring and summer collections came from one of three rivers (Table 1). Based on
208 results from the Bayesian estimator, nearly 50% of the fish from spring collections in the Gulf of
209 Maine came from the Shubenacadie River, almost 42% were spawned in the Hudson River, and
210 nearly 6% were from the St. John River. Fish from origins south of the Chesapeake Bay were
211 present in negligible proportions according to both estimation methods. The Shubenacadie River
212 was even more over-represented in the summer samples from the Bay of Fundy, accounting for
213 just over 74% of the one-year-old American shad. Hudson River fish represented a further
214 ~24%, while all remaining rivers if present contributed less than 1% to the pooled summer
215 sample.
216 There was general agreement in proportional abundances of source stocks in both
217 collections as estimated by the MLE and Bayesian algorithms. The one exception was for the
218 summer samples where the MLE method suggested that 17% (approximately 40 individuals) of
219 the fish were from the Potomac River. The Bayesian estimator did not detect significant
220 numbers of Potomac River fish and instead classified those individuals as originating from the

Insert Table 1 here

221 Shubenacadie River. This result likely arose because of similarities in chemical signatures
222 between the Potomac and Shubenacadie rivers (Fig. 2).
223 Maximum posterior classification probabilities from the Bayesian estimator were higher
224 than 0.80 for 88% and 83% of fish collected from Maine and Minas Basin, respectively,
225 indicating that the majority of fish were assigned to a source river with high degrees of
226 confidence (Fig. 3). Because of the discrepancy in assignment estimates for the Potomac River
227 in the summer samples, we examined posterior probabilities of summer individuals assigned to
228 the Shubenacadie River to determine whether overall confidence was lower than other groups.
229 However, these posterior probabilities were comparably high. Over 90% of individuals were
230 assigned to the Shubenacadie River with posterior probabilities higher than 0.80, and only 16
231 individuals fell below probabilities of 0.80. Thus assignment uncertainty in the Bayesian
232 estimator could not account for the lack of Potomac River assignments.
233 By restricting our baseline to a subset of six source stocks, we calculated standard
234 deviations around mixed stock estimates for the summer samples using the HISEA program in
235 bootstrap mode. Mixed stock estimates (± 1 SD) were 24.5 ± 3.5% for the Hudson River, 52.4 ±
236 4.8% for the Shubenacadie River, 19.8 ± 3.8% for the Potomac River, 2.4 ± 3.1% for the St.
237 Lawrence River, and 0.4 ± 0.4% for the St. John River. These estimates are comparable to those
238 identified by the ISMA program, and suggested that variance around the MLE estimates was
239 relatively low.
240

Insert Fig. 3 here

241 ## Discussion

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

244 of tagging studies on adult American shad throughout the western Atlantic. Summer feeding
245 aggregations in the upper Bay of Fundy contained individuals from stocks throughout their entire
246 range, including Florida. Of adult migrants tagged in the Bay of Fundy, approximately 34%
247 were recaptured in rivers south of Cape Hatteras (Region 1), 44% were recaptured between Cape
248 Hatteras and Cape Cod (Region 2), 15% were recaptured in Bay of Fundy rivers (Region 3), and
249 7% were recaptured in the Gulf of St. Lawrence (Region 4). Dividing our composition estimates
250 into similar regions and averaging across spring and summer collections, we estimated that the
251 majority of one-year-old migrants were from Region 2 (34-47%) and from Region 3 (52-65%),
252 with precise values depending on the statistical estimation method used. All collections
253 contained less than 1% of fish from Regions 1 and 4, regardless of the estimator. Moreover,
254 Regions 2 and 3 were each overwhelmingly represented by the Hudson River and the
255 Shubenacadie River, respectively.

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

267 correlated with subsequent abundances of adult spawners from the same cohort (ASMFC 2007),
268 suggesting significant mortality and demographic restructuring during their time at sea (Limburg
269 2001). At least some of this restructuring may have already occurred prior to our collections,
270 decoupling juvenile abundance from abundances of immature migrants.

271 Southern and mid-latitude stocks were also generally absent from the mixtures, and most
272 Chesapeake Bay stocks were not present in the collections. Stocks from south of Chesapeake
273 Bay were also poorly represented in the mixtures, and no fish from Florida were detected.
274 Unfortunately, juvenile abundances are not monitored in all rivers, and data are unavailable for
275 most southern and Canadian rivers. Thus the influence of relative juvenile abundances for these
276 rivers on our composition estimates is unknown. Inadequate sampling of the fish present in the
277 Gulf of Maine and Bay of Fundy could bias the composition estimates if particular populations
278 were present in the region but consistently missed by collections. However, we believe that this
279 is unlikely given the temporal coverage of the weir collections where we collected samples
280 continuously between mid-June and early August. This corresponds to temporal abundance
281 patterns in the region, with highest abundances typically occurring around early July (Dadswell
282 et al. 1987). The Maine New Hampshire trawl survey in 2005 occupied a total of 104 stations in
283 a stratified random design covering some 13,000 km^2 and therefore we see no reason why these
284 samples would be biased (Sherman et al. 2005). Finally, with the exception of the Potomac
285 River fish, similar population compositions were detected in the Maine trawls and Minas Basin
286 weir collections, despite alternative collection methods covering different dates and locations.
287 Thus it is appears unlikely that the absence of many populations in our samples was due to
288 sampling error.

289 The Potomac River was the only significant contributor from the Chesapeake Bay region,
290 as identified by the MLE method for Minas Basin collections. While Potomac River stock
291 abundance has been low for several decades, stocking efforts have enhanced the population and
292 juvenile abundance in 2004 was the largest recorded to date by monitoring surveys (ASMFC
293 2007). However their presence in Minas Basin collections was equivocal given that the
294 population was not identified in the sample by the Bayesian estimator. This discrepancy likely
295 arose due to chemical similarities between baseline river-specific signatures, and the Bayesian
296 estimator assigned these individuals to the Shubenacadie River instead of the Potomac River.
297 Neither the Bayesian nor the MLE estimator showed evidence of high classification uncertainty,
298 as demonstrated by the distribution of maximum posterior assignment probabilities for the
299 Bayesian and small estimated variances for the MLE. Reduced classification confidence was
300 therefore not the source of the discrepancy. Instead, these two estimators confidently assigned
301 individuals with signatures falling on the boundary of two similar baselines to alternative
302 sources. This result points to the need to interpret estimates of mixed stock composition with
303 caution when baselines are similar. The use of multiple independent estimators can help confirm
304 the composition of mixed stocks and identify those sources that are equivocal.
305 Juvenile and immature American shad appear to exhibit high degrees of inter- and intra-
306 population variability in the timing and extent of their migratory movements. Freshwater
307 emigration timing can occur over a wide range of dates, with size and age playing a strong role
308 in determining downriver movements (Limburg 1996). Further, both early and late emigrants
309 can survive to spawn as returning adults (Limburg 2001), indicating juvenile migratory
310 variability does not preclude successful future reproductive contributions. Movements may be
311 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 Bain 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

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

342 There are significant management implications of American shad movements and mixing
343 in the marine environment. An assessment of mixed-stock compositions of coastal harvests off
344 Maryland and Virginia based on mitochondrial DNA variation found significant variation in the
345 contributions of individual stocks to the mixtures (Brown et al. 1999). This variation was both
346 geographical and temporal suggesting dynamic and unpredictable changes in the presence of
347 specific stocks in harvests, with many stocks represented by numbers disproportionate to their
348 population sizes. Such dynamism limits the ability to manage coastal mixed-stock fisheries
349 without allowing unsustainable mortality of the most vulnerable stocks. Our work shows that the
350 migratory habits of immature American shad are similarly complex, and managers of American
351 shad should consider the potential impact of mixed-stock fisheries on early year classes.
352 Immature fish are potentially more susceptible to harvest as bycatch in a variety of fisheries,
353 imposing further anthropogenic stress on fully exploited stocks. Increased mortality of immature
354 migrants in mixed-stock fisheries has the potential to significantly alter year-class strength,
355 restructure demographics, and further limit recovery of depleted populations. Combining results
356 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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506

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).

			Spring		Summer	
River	Code	Region	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	-	-	-	-
n			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}Sr:^{86}Sr and $\delta^{18}O$) 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

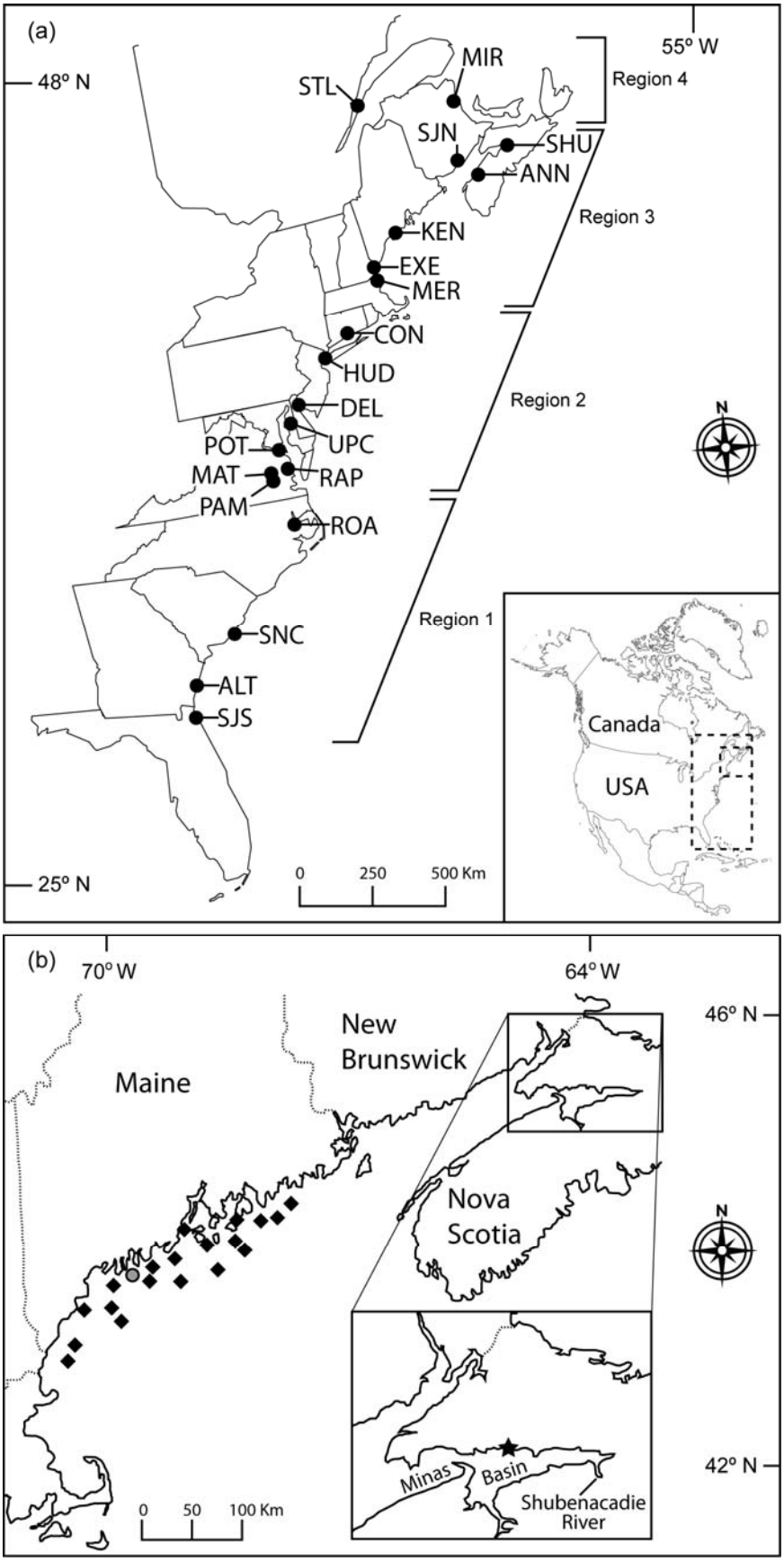
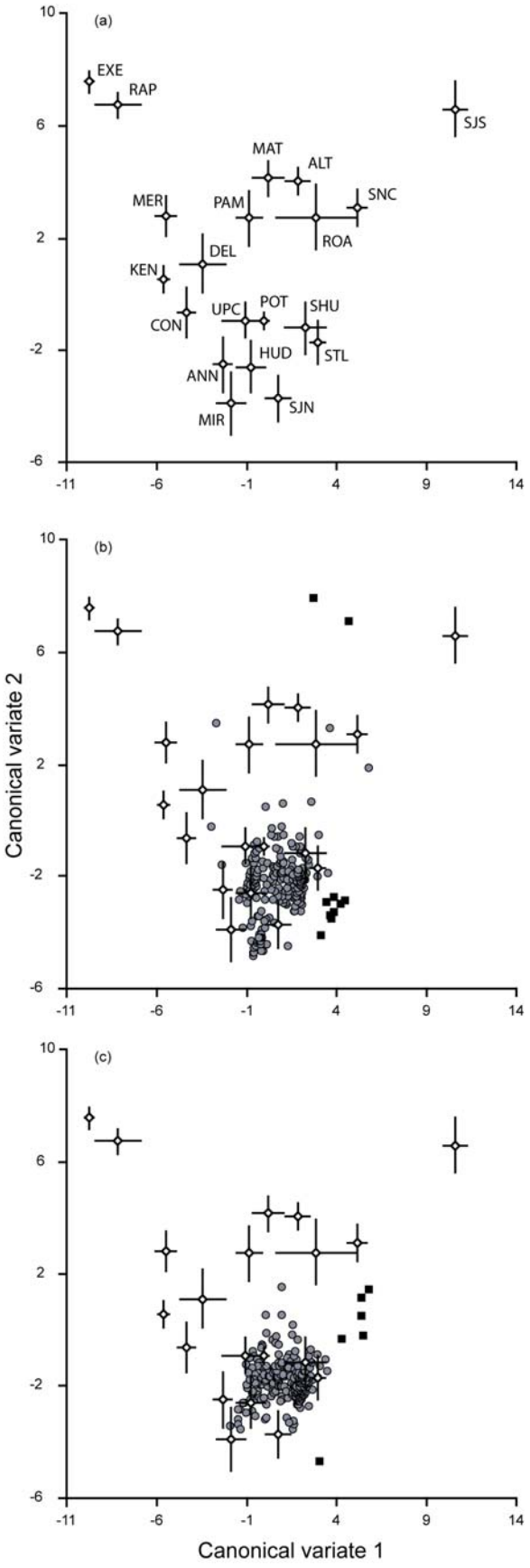

(a)
48° N
55° W
MIR
STL
Region 4
SJN
SHU
ANN
Region 3
KEN
EXE
MER
CON
HUD
Region 2
DEL
UPC
POT
MAT
RAP
PAM
ROA
Region 1
SNC
ALT
SJS
25° N
0 250 500 Km
N
Canada
USA
(b)
70° W
64° W
46° N
New Brunswick
Maine
Nova Scotia
42° N
Minas Basin
Shubenacadie River
0 50 100 Km
N

Figure 2


(a)
EXE
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ALT
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KEN
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POT
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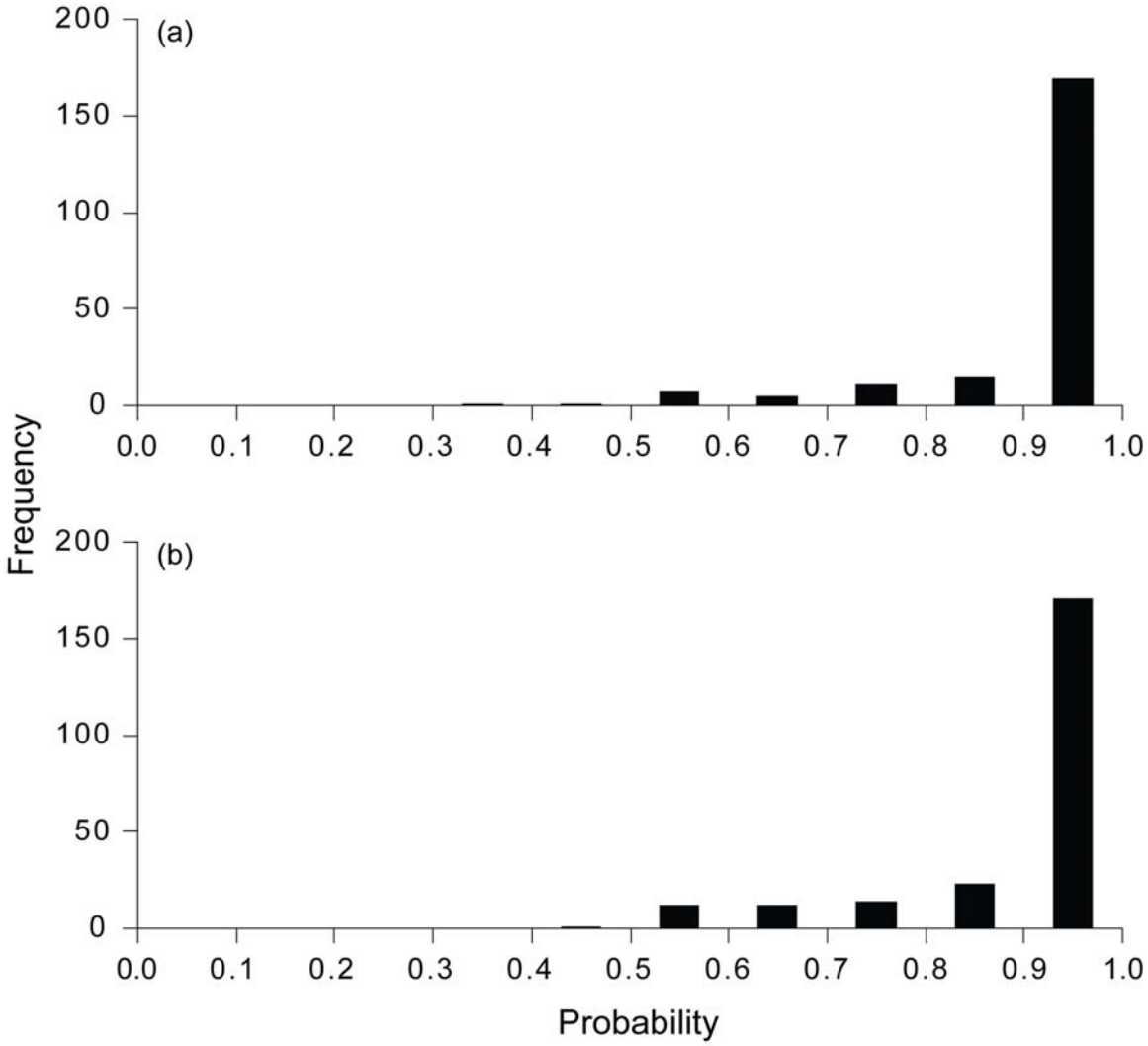
HUD
STL
ANN
SJN
MIR
(b)
(c)
Canonical variate 2
Canonical variate 1
10
6
2
-2
-6
-11
-6
-1
4
9
14

Figure 3


(a)
(b)
Frequency
Probability
200
150
100
50
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0