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Carryover effects of early growth and river flow on partial migration in striped bass *Morone saxatilis*

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ABSTRACT: High plasticity in the migrations of marine fishes can result from partial migration, where early life conditional responses to nursery conditions carryover into juvenile and adult migrations. Striped bass *Morone saxatilis* movement behaviors during the larval and early juvenile period were investigated for evidence of partial migration through otolith Sr/Ca profile analysis. Striped bass expressed expected behaviors, with contingents remaining in freshwater habitats through the early juvenile period (through 35 mm TL) or moving across the salt front to brackish water habitats (salinity ≥3); still, the range of sizes at which migration occurred was unexpectedly wide. Using a multivariate clustering analysis, 3 distinct size-based migratory contingents were identified. Two of these migrant groups dispersed following metamorphosis to the juvenile stage, while the third (and smallest) dispersed during the larval period. Both tendency to migrate and the size at which movement commenced were related to early growth, with migrants experiencing lower growth than residents. In one year, a high flow event appeared to influence the timing of migration, coinciding with the majority of dispersal events. Expected dividends for migratory juveniles in the form of improved forage (diet and stable isotope analysis), condition and growth were not detected. Partial migration within natal estuaries during ontogeny appears to be a conditional response in striped bass, possibly resulting from the interaction of liability traits and innate thresholds and influenced by environmental conditions.

KEY WORDS: Partial migration · Conditional response · Early life history · Otolith chemistry · Growth · Striped bass

INTRODUCTION

Migration is not ubiquitous within the populations of organisms that undertake this behavior; instead it is often 'partial', whereby a portion of a population refrains from the large-scale movements undertaken by their peers (Lack 1943, Secor 2015). Such partial migration is not limited to a particular taxa or scale of movement but may be the behavioral norm even in popularly recognized examples of great migrations (Chapman et al. 2011). Despite efforts focused on the causes and consequences of differential movements within populations, the dynamics underlying partial migration remain largely unknown, particularly for fishes.

Partial migration is likely widespread among fish taxa and often reflected in a diversity of juvenile-stage behaviors (Kerr & Secor 2012). The movement of young fish within and between nursery habitats is influenced by external forces they experience as well as their own inherent qualities. Due to the essential uncertainty of these influences, migration is a 'conditional strategy' (Lundberg 1988), where intrinsic characteristics, such as development and metabolic rates interact with extrinsic realities, like seasonal temperature change and forage densities. Condi-

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tional strategies operate through an early threshold, whereby an individual adopts one or another spatial behavior based on an intrinsic attribute such as condition, size, or growth (Secor 2015). Conceptualizing migration as a decision depending on individual thresholds is admittedly simplistic but provides the basis for hypotheses that can be tested in natural settings. Examples of this approach have proved useful in salmonids, where the development of migrant and resident contingents during the juvenile period is widespread and linked to early growth (Jonsson & Jonsson 1993). In Arctic charr *Salvelinus alpinus* for instance, accelerated early growth is associated with the adoption of a migratory lifestyle, while slower-growing residents form 2 distinct size-based contingents (Klemetsen et al. 2003). Outside of Salmonidae, white perch *Morone americana* (family Moronidae) separate into migratory and resident contingents in their natal estuaries seemingly based on early growth, which may in turn be influenced by timing of hatch and temporally variable forage (Kraus & Secor 2004a, Kerr & Secor 2010). Yearly differences in temperature and prey availability likely interact with growth thresholds, leading to annual variance in contingent membership (Kerr & Secor 2012). Partial migration by young fish leads to modes of nursery habitat use, which have carryover effects to population dynamics (Beck et al. 2001, Kraus & Secor 2005, Fodrie et al. 2009) and can stabilize recruitments in non-stationary marine ecosystems (Kerr & Secor 2012).

Conditional spatial behaviors during ontogeny were investigated for Chesapeake Bay striped bass *Morone saxatilis*, an anadromous population well known to exhibit variable migration behaviors later in life (Secor 1999, Secor & Piccoli 2007, Gahagan et al. 2015). As adults, most female and many male striped bass undertake oceanic migrations along the eastern seaboard of North America (Dorazio et al. 1994, Secor & Piccoli 2007, Gahagan et al. 2015). In the spring, adults make their way through coastal estuaries to fresh and near-fresh tidal reaches to spawn, prompted by environmental signals such as increasing water temperatures (Dovel & Edmunds 1971, Secor & Houde 1995). Most of the resulting larvae are retained above the salt front in portions of the estuarine turbidity maximum (ETM; North & Houde 2001). Following the early larval period, metamorphosed juveniles (i.e. young-of-the-year, YOY) disperse, occupying a large extent of available natal estuaries throughout a wide range of salinities (Robichaud-Leblanc et al. 1998). As has been demonstrated in salmonids, juvenile migratory tendencies may result as a combination of inherited traits, early experiences, and recent conditions. Thus, partial migration exhibited by adult striped bass may be influenced by conditional responses occurring during the larval and juvenile stages.

Here, we were interested in growth and environmental factors underlying the dispersal of striped bass in a Chesapeake Bay estuary during the juvenile stage in 2 successive years. The threshold model of partial migration holds that divergent migration behaviors result from the interaction of individual attributes with extrinsic factors like temperature and foraging conditions. We set out to characterize the dispersal of striped bass during the juvenile stage by reconstructing salinity-based dispersal histories estimated from otolith chemistry. Individuals were classified according to salinity profiles, which were assumed to represent modes in spatial behaviors. We evaluated the contributions of ontogenetic stage (length), growth rate, time of hatching, and environmental conditions (flow and temperature) to these early group behaviors. Further, immediate consequences of movement behaviors were evaluated as post-dispersal growth and diet. We predicted that (1) juveniles would exhibit discernable modes in their early resident or migration behaviors; (2) dispersal is a conditional response, triggered by slow early growth; and (3) migration would result in increased growth and improved foraging conditions in the non-natal habitat.

MATERIALS AND METHODS

Study system and collections

The Patuxent River (Maryland, USA) is a partially mixed tidal estuary on the western shore of the Chesapeake Bay. The 70 river-kilometer (RKM) extent of our study area (Fig. 1) consists of fresh (salinity <3) and brackish habitats (salinity ≥3). We employed a threshold surface salinity of 3, corresponding to otolith Sr/Ca = 1 mmol mol^{-1}, between freshwater and brackish water environments for otolith chemistry analyses and a spatially consistent boundary between these salinity levels located between sampling sites at RKM 44 (brackish, Eagle Harbor) and RKM 55 (fresh, Milltown Landing). A regression model supported this habitat delineation based on salinity in both years (see Supplement 1 at www.int-res.com/articles/suppl/m541p179_supp.pdf). This distinction represented a coarse resolution of the dynamic nature of surface salinity and was de-

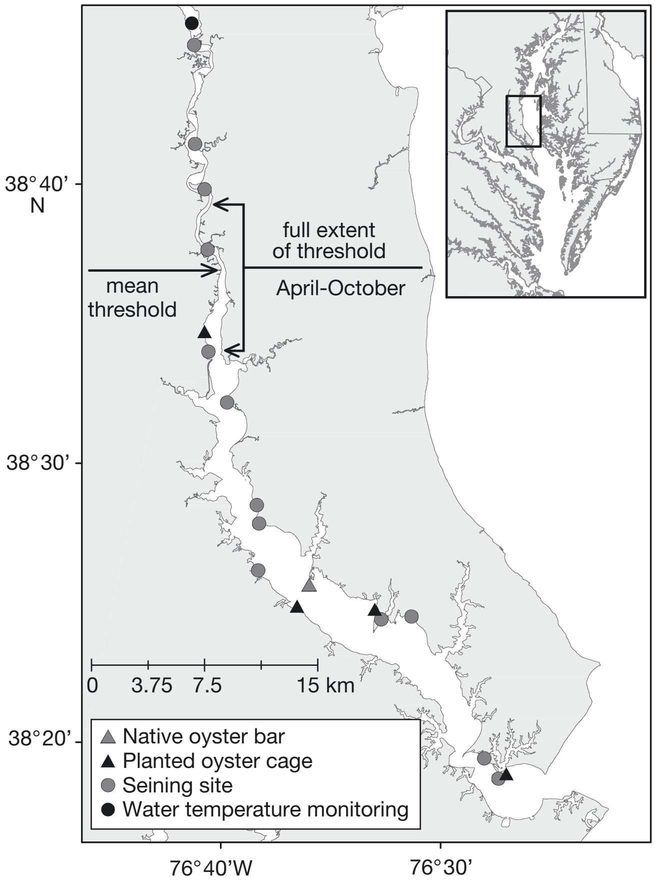

Fig. 1. Map of the Patuxent River tidal estuary, USA, showing all sample and data collection locations. The extent and mean salinity threshold (salinity = 3) between freshwater and brackish habitats are indicated by arrows

signed to support central migration inferences in this study. Striped bass *Morone saxatilis* spawn in tidal fresh habitats and predominately are retained there during the larval period, and by the juvenile stage occur throughout the river (Secor & Houde 1995). Strontium (Sr) is a conservative tracer of salinity within the Patuxent River, and its concentration in otoliths has been employed to interpret habitat-use patterns by white perch (Kraus & Secor 2004b). The salinity gradient within the Patuxent River has been relatively stable over the last 75 yr (Ritchie & Genys 1975), continuing to the present (see Fig. S1 in Supplement 1). Although otolith chemical composition may be affected by many environmental and physiological factors, as well as their interaction (Elsdon et al. 2008), the relationship between salinity and Sr uptake in juvenile striped bass otoliths has been determined experimentally, tested in the field, and parameterized as a logistic function of the environmental Sr/Ca ratio (Secor et al. 1995), salinity = $40.302 \times (1 + 56.337 \times \exp^{(-1523.3\times(Sr/Ca)-1)})$; based on these experiments, salinity explains >85% of the variance in Sr/Ca over the salinity range in the Patuxent River. In summary, the assumption that otoliths of juvenile striped bass reflected past movements from fresh to brackish water (salinity>3) was supported by (1) the relative stability of the boundary between salinity zones in the Patuxent River and (2) past otolith Sr/Ca verification studies and applications (Secor et al. 1995, 2001).

We collected juvenile striped bass in June–October 2009 and June–August 2010, sampling the same 13 sites (Fig. 1) via parallel beach seine in both years. Sampling in 2009 took place over 12 separate weeks during the summer and fall, resulting in the collection of 1034 juveniles. Sampling was more limited in 2010, primarily taking place during 2 non-contiguous weeks in June and August, resulting in the collection of 150 juveniles. To evaluate food web dependencies and trophic position using stable isotope analysis, eastern oyster *Crassostrea virginica* was used as a baseline primary consumer species (Fertig et al. 2010, Woodland et al. 2011). Oyster spat (provided by the University of Maryland Center for Environmental Science Horn Point Oyster Hatchery) were planted in mesh cages at 8 sites throughout the estuary during late May 2010 (Fig. 1) and allowed to grow and equilibrate for 118–119 d. In addition to planted oysters, native adult oysters were collected via dredge at RKM 23 in June 2010.

Otolith analyses

Otoliths from a subsample of juveniles collected in 2009 (n = 71) and 2010 (n = 34) were used in microchemical analysis of dispersal history and for growth analyses. Otolith subsamples in both years excluded efforts prior to mid-June, since the distribution of juveniles was heavily concentrated in freshwater (i.e. expected dispersals from freshwater had not yet occurred); subsamples were chosen randomly and then checked for bias to ensure similar size and temporal (i.e. date of collection) distributions (see Supplement 2 at at www.int-res.com/articles/suppl/m541p179_supp.pdf for analyses of bias in subsamples). Otoliths were embedded in epoxy resin and sectioned transversely, before being polished smooth using successively finer aluminum oxide grits. Prepared otolith sections underwent microchemical analysis at the University of Maryland's NISP Lab in the Maryland Nanocenter (College Park, MD). Sections were carbon-coated and molar proportions of calcium (precision < 1%) and Sr (precision ~8.2%) were measured by X-ray wavelength dispersive spectroscopy using a JEOL © 8900R electron probe microanalyzer, which was calibrated using calcite, $CaCO_3$ and strontianite, $SrCO_3$ standards. Microprobe analysis comprised a series of small volume (diameter 5 µm total, volume of otolith material per measurement <20 μm^3) point measurements from the first identifiable increment (adjacent to the primordium) to the edge of the otolith with measurements made at 10–18 µm intervals. Under a compound microscope, daily increments were enumerated from the primordium to the otolith edge (microstructural increments have been verified to form at a daily rate in juvenile striped bass sagittal otoliths; Secor & Dean 1989). Since the formation of the first otolith increment depends on temperature, the number of increments counted during analysis must be adjusted to accurately reflect age. To correct ages for the influence of temperature, we used the enumerated increments to identify a preliminary hatch date. The mean surface temperature (1.3 m below the surface) as measured at Jug Bay (RKM 75, above the ETM and close to the center of spawning activity) during the week of the preliminary hatch date was used in Houde & Morin's (1990) age correction: corrected age = no. of increments + 11.56 − (0.45 × temperature). Due to previous research that demonstrated a bias in older juveniles (underestimated ages; Jones & Brothers 1987, Secor & Dean 1989), we limited our age-based analyses to individuals whose original daily increment counts were <85 (n = 43 in 2009, n = 32 in 2010).

Distances along the ventral transverse axis (i.e. otolith radii, µm) from the primordium to each microprobe measurement, daily increment, and ventral edge of the otolith were measured using the image-processing program ImageJ (Rasband 2012). Each of these otolith radii were converted to back-calculated total lengths (TL, mm) using Campana's (1990) biological intercept method. Biological intercepts were determined using larvae (n = 46) collected in the Patuxent River estuary via bongo net sampling in April and May of 2009; starting at 8 d post-hatch the relationship between otolith radius (23.9 µm) and total length (6.1 mm) was found to be linear (length (mm) = 0.04 × otolith radius (µm) + 5.15; $F_{1,43} = 347.9$, $p < 0.001$, $R^2 = 0.90$). Microprobe measurements were converted into estimated total lengths, then averaged over 5 mm length stanzas for further analysis, which both standardized Sr/Ca measurements to analogous periods of development for all juveniles and accounted for the lag between environmental and otolith [Sr] (i.e. otolith material represents integration of environmental concentrations over previous week; Secor et al. 1995, Elsdon & Gillanders 2005). Back-calculated total lengths (mm) at daily increments were used to estimate instantaneous growth rates (*g*) during the larval (hatch to 15 mm TL) and early juvenile stages (15 to 35 mm TL). The regression of size-at-age was used to set the theoretical size-at-hatch (i.e. age 0) at 3.81 mm for use in growth estimates.

Feeding ecology

We used diet and stable isotope (SI) analyses to investigate the feeding ecology of resident (YOY sampled at freshwater locations) and migratory (YOY sampled at brackish water locations) individuals. By targeting habitat-at-collection instead of the contingents defined through otolith microchemistry, we were able to increase our sample sizes owing to the simple assumption that the movement behaviors of migratory contingents would lead to their occupation of brackish habitats while residents would remain in freshwater. Contents of dissected stomachs were removed from juveniles collected in 2009 (n = 56, including 15 juveniles collected in 2009 used in otolith chemical analysis) and 2010 (n = 150, including all juveniles used in otolith chemical analysis) and identified. Subsamples were chosen randomly and checked for bias to ensure similar size and temporal distributions as occurred in the entire year's sample (see Supplement 2 for analyses of bias in subsamples). Diet items were identified and placed into 1 of 15 prey item categories: amphipods, cladocerans, copepods, cumaceans, crabs and shrimp, fish larvae, fish lice, isopods, mollusks, mysids, nemerteans, polychaetes, tanaids, tunicates, and unidentified crustaceans. Frequency of prey occurrence in stomachs as proportions of all stomachs analyzed in each habitat was determined and gut fullness was estimated as the weight of gut contents relative to total gutted weight.

Stable isotope analysis was conducted based on targeted sampling and field work in 2010. White muscle tissue sections taken from a subsample of juvenile striped bass collected June–August 2010 (n = 47, including all juveniles used in otolith chemical analysis) were processed, dried, and sent to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona State University for stable isotope analysis of nitrogen and carbon, expressed in the standard δ notation as deviations in isotopic ratios of nitrogen (N; ^{15}N:^{14}N, $\delta^{15}N$) and C (^{13}C:^{12}C, $\delta^{13}C$) from international standards air and Pee Dee Belemnite. Trophic positions (TP) of striped bass juveniles (SB) were estimated through Cabana & Rasmussen's (1996) model (modified by Post 2002): TP = ($\delta^{15}N_{SB}$ – $\delta^{15}N_{pc}$)/Δ_n + λ, using δ^{15}N measured in habitat-specific oyster adductor muscle tissue as the primary consumer baseline ($\delta^{15}N_{pc}$; $\lambda = 2$) and assuming a per trophic level discrimination in δ^{15}N (Δ_n, trophic discrimination factor, TDF) of 3.4‰ (Minagawa & Wada 1984). Although there are no estimates of TDF for striped bass, discrimination in fish muscle tissue has been shown to be robust to the effects of diet and body size (Sweeting et al. 2007); Sweeting et al. (2007) suggest a slightly lower TDF (3.2‰) if a laboratory-derived value is not available for the study species, but we decided to employ the widely utilized 3.4‰. Because our samples consisted of juvenile striped bass from the same nursery system and year-class, a constant TDF was assumed to support comparisons of trophic position across habitats, assuming sufficient equilibration to local diets (Sweeting et al. 2007). Since ^{12}C is enriched in animal lipids relative to ^{13}C, the fat content of tissues must be considered when using isotope composition to estimate the trophic niches of fish (McConnaughey & McRoy 1979). However, if the lipid content of tissue (as a% of dry mass) is consistently below 5% for the organisms under study, then the chemical removal of fat from tissue (or the mathematical normalization of measured δ^{13}C) results in $\Delta\delta^{13}C < 0.5$‰ and is not necessary (Post et al. 2007). The lipid content of white muscle tissue, estimated using C:N in the linear regression developed by Post et al. (2007) for aquatic animals, never exceeded 3.5% (range 2.1–3.4%) for the juvenile striped bass analyzed in this study.

Estimates of habitat-specific trophic status of juvenile striped bass depended on 2 assumptions that required confirmation: (1) trophic baselines were known for each habitat and (2) juvenile striped bass reflected these habitats in the isotopic composition of their tissues. Since we used oysters as habitat-specific trophic baselines, both of these assumptions relied on tissue equilibration. We followed Buchheister & Latour's (2010) growth-based approach for estimating tissue turnover in fish for both species because no tissue turnover models exist. Here, anabolism, the addition of new tissue, dilutes the existing isotope composition to the point where it fully represents local nutrient sources. We conservatively assumed catabolism did not contribute to equilibration, which occurred as a result of new tissue growth. Oyster growth since deployment was determined using 4 separate *C. virginica* growth models taken from the literature; 3 of these models were developed in the Chesapeake Bay (Newcombe 1950, Harding 2007), while 1 model was developed in Tampa Bay, FL (Drexler 2011). Each model predicted new tissue generation (change in shell volume) at each location during the 118–119 d exposure period. We required a doubling in mass from all 4 models. This approach was conservative in light of recent work that indicated the sufficient equilibration of oyster adductor tissue within 120 d of planting (Fertig et al. 2010) and should ensure appropriate measurements of base trophic signatures in each of the habitats we sampled. Striped bass growth was estimated via nonlinear least squares estimation of the allometric relationship between the measured weights (g) and total lengths (mm) (weight = $a \times \text{length}^b$; Gould 1966) of juveniles collected in 2010. If mass doubled after a migrant's move to brackish habitat (i.e. the length stanza where Sr/Ca increased from <1 to ≥1 mmol mol^{-1}), it was considered equilibrated.

Statistical analyses

We adopted a multi-step process to classify migrations of juvenile striped bass within each year. Principal component (PCA) and hierarchical cluster analyses (CA) were used to identify contingents and derive classification statistics, following an approach developed by Miller et al. (2006) to predict weather patterns using autocorrelated sea level pressure data. We converted Sr/Ca profiles to multivariate formats by considering each 5 mm length stanza as a separate variable; this separated the variance in Sr/Ca values into size-specific segments, allowing the clustering procedure to define differences in the timing of changes in Sr/Ca. PCA was used to examine redundancies in Sr/Ca means among length intervals. The first 3 principal components (PCs) were retained because they explained ≥80% of the variance in both years. The corresponding PC scores of individual juveniles were used as the variables in average linkage CAs conducted for 2009 and 2010. The average linkage method includes all observations during each agglomeration step and conserves the original distributions of Euclidean distances between observations (McGarigal et al. 2000). The number of clusters derived from both analyses was determined using maxima in cubic clustering criteria (CCC; indicating the departure of the data as agglomerated from a uniform distribution; Sarle 1983) and pseudo-*F* statistics (comparing variance within and between clusters; Caliński & Harabasz 1974), and additionally assessed using the rate of changes in R^2 (variance captured by clusters; McGarigal et al. 2000). PCA and CA were conducted in the SAS statistical program. Comparisons in proportions of contingents by year were tested using Fisher's exact tests (FET).

Mixed effects models were used to both corroborate the multivariate approach described above as well as extend the analysis by directly comparing Sr/Ca measurements between contingents and length stanzas. Due to the autocorrelation of repeated Sr/Ca measurements of the same otoliths, we employed 1st order autoregressive, i.e. AR(1) covariance structure in these analyses. Because the fixed effects of contingent membership throughout life history (i.e. over successive length stanzas) on Sr/Ca were the main focus of this approach rather than the individual trajectories of Sr/Ca during the larval and juvenile stages, subject-specific Sr/Ca intercepts were designated as random effects. These analyses were limited to total lengths <40 mm to maintain large sample sizes ($n = 71$ in 2009; $n = 34$ in 2010) to maximize statistical power (e.g. increasing the length threshold to 45 mm excluded 22 juveniles across years) while still including otolith material deposited during the larval stage and the early juvenile stage following metamorphosis (14–20 mm TL; Mansueti 1958, Setzler-Hamilton et al. 1981, Grizzle et al. 1985). Following mixed model analyses, we conducted post-hoc contrasts of both contingents within length stanzas (i.e. differences in Sr/Ca between contingents at size) and successive length stanzas within contingents (i.e. changes in contingent-specific Sr/Ca during development) to identify the stage of development at which contingents moved within the estuary. Due to the number of post-hoc contrasts, we employed Benjamini & Hochberg's (1995) false discovery rate (FDR) p-value adjustment to control the familywise error rate while maintaining statistical power.

The importance of early growth on dispersal was assessed using a similar AR(1) mixed model approach to assess growth prior to and during dispersal. As before, individual growth intercepts were designated as random effects and post-hoc contrasts between contingents within stage and between successive stages within contingents were conducted. Resulting p-values were adjusted using FDR. The effect of river discharge (measured as daily mean m^3 s^{-1} at USGS Stn 01594440 at RKM 98.0, the closest main stem flow gauge within the Patuxent River system) on dispersal was evaluated using a segmented regression approach that employs a bootstrapped restarting algorithm to identify universal maximum likelihood estimations of appropriate breakpoints in linear relationships (Wood 2001). Breakpoints and their associated errors, co-occurring rates of change in population Sr/Ca (i.e. regression slopes), and weekly mean flow rates were used to further inform our interpretation of the relationship between migration and river flow. The effect of temperature on dispersal was evaluated using linear models of weekly mean surface temperature (depth 1.3 m) measured at Jug Bay (RKM 75). In addition to these analyses of specific environmental influences on migration, we also examined hatch date distributions of identified contingents using linear models to identify any temporal trends in movement behaviors. Condition was assessed using linear models of the fixed effects of contingent and habitat on weight while including total length as a covariate.

Occurrence of prey item categories was compared between habitats using FET; p-values were estimated using Monte Carlo approximations (Mehta & Patel 1986). The occurrence of vertebrate prey items (i.e. fish larvae) in diets associated with both habitats in the estuary was assessed using binomial regression (logit link function); log odds from binomial regression were converted into estimated probabilities (i.e. likelihoods) of consuming vertebrate prey items based on habitat and total length. Gut fullness was compared between habitats using *t*-tests in both years. The effects of habitat on stable isotopes of N ($\delta^{15}N$) and C ($\delta^{13}C$) measured in striped bass white muscle tissue were assessed using a multivariate fixed effects model that accounted for the effects of weight (covariate; MANCOVA). Significant effects detected in the multivariate model triggered individual fixed effects models to identify particular trophic variables that differed between habits. The effect of habitat on trophic position was tested using a *t*-test. No bias was detected in any subsample (see Supplement 2). All analyses were conducted in the R statistical program (R Core Team 2013) unless otherwise indicated.

RESULTS

Dispersal and contingent behaviors

Initial dispersal from fresh habitats occurred between 6 and 35 mm TL for most individuals in 2009 and all individuals in 2010 (Fig. 2). PC1–PC3 explained 88 and 92 % of the variance in Sr/Ca in 2009 and 2010, respectively. Cluster analysis on PC scores resulted in 4 groups in both years (Figs. 2 & 3); we

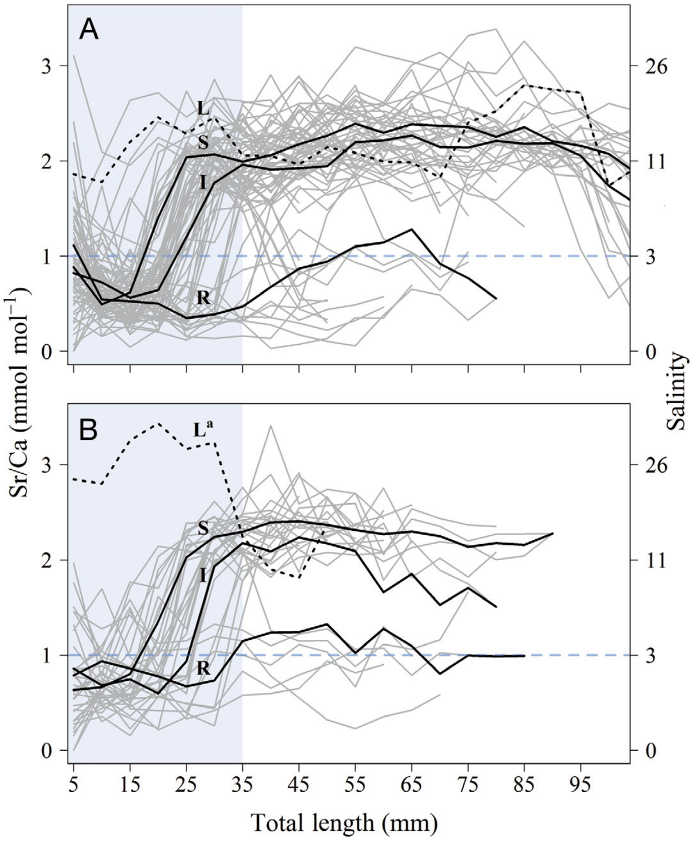

Fig. 2. Sr/Ca and experienced salinities binned by 5 mm total length increments for juvenile striped bass collected in (A) 2009 and (B) 2010. Black lines indicate mean Sr/Ca ratio and experienced salinity values of behavioral contingents identified in the multi-step classification analysis: small migrants (S), intermediate migrants (I), and residents (R); dotted black lines indicate mean Sr/Ca and experienced salinity values of larvae that may have dispersed via passive transport (i.e. non-behavioral contingents). Blue-shaded region (5–35 mm) indicates Sr/Ca values used in the multi-step classification analysis; horizontal broken blue line indicates the threshold between freshwater (Sr/Ca <1, salinity <3) and brackish water habitats (Sr/Ca ≥1, salinity ≥3). L^a: in 2010 the larval disperser contingent consisted of 1 juvenile; the broken black line represents Sr/Ca and experienced salinities for this individual. See text for a discussion of the relationship between Sr/Ca and experienced salinity

interpreted these groups as contingents exhibiting different dispersal histories (1) a combined cluster of juveniles that migrated at large sizes (>30 mm) and others that stayed resident (i.e. did not migrate at all), (2) a group that appeared to inhabit salinities >3 as larvae (<6 mm) in 2009 (a similar pattern was detected in 1 juvenile in 2010), (3) a group that migrated at small juvenile sizes (6–20 mm TL), and (4) a group that migrated at intermediate sizes (11–30 mm TL). In both years, 4 clusters resulted in

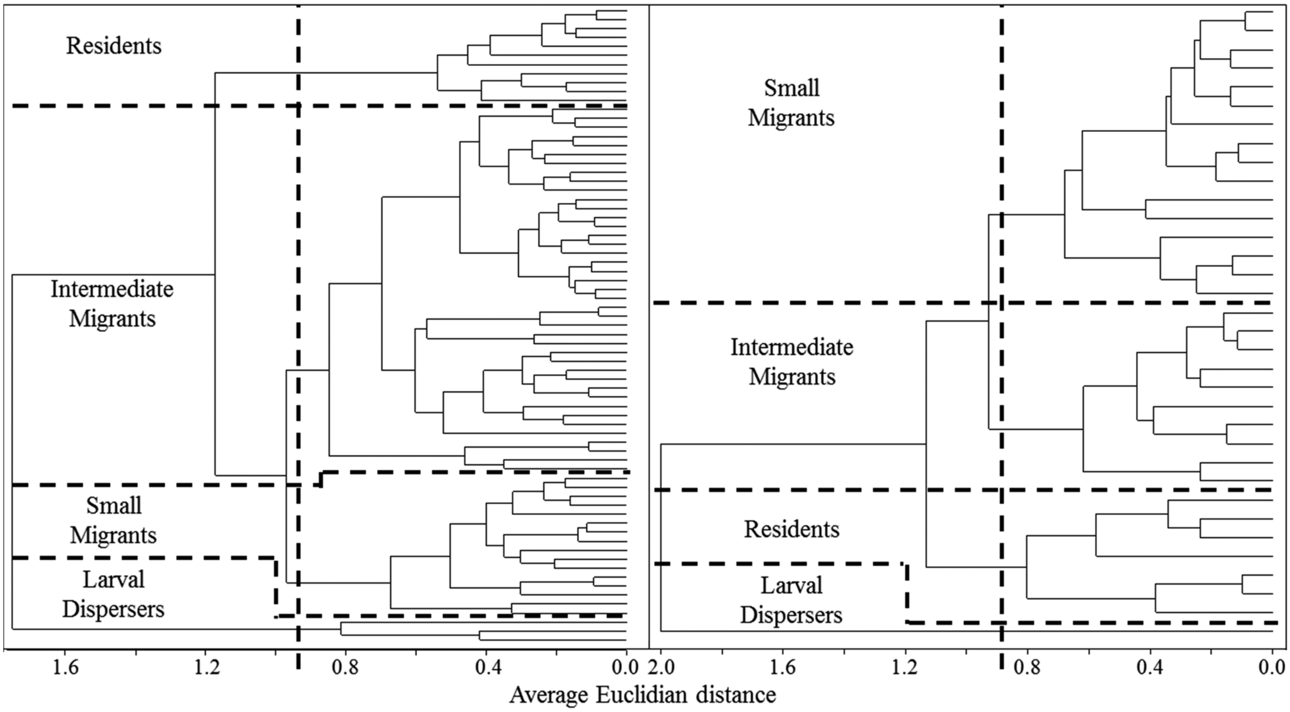

Fig. 3. Dendrograms of average-linkage cluster analysis results for 2009 (left) and 2010 (right). Vertical broken lines indicate the agglomeration step in the cluster analysis where clustering was considered complete. Horizontal broken lines indicate separation between contingents. Contingents are identified

Table 1. Number of juveniles, percent of total juveniles, and median and standard deviation of hatch dates of juveniles within each contingent and overall in 2009 and 2010

Contingent	2009				2010			
	No.	%	Hatch date median	Hatch date SD (d)	No.	%	Hatch date median	Hatch date SD (d)
Resident	11	15.5	May 5	6.6	7	20.6	May 12	6.6
Larval disperser	3	4.2	May 4	2.1	1	2.9	Apr 16	n/a[a]
Small migrant	16	22.5	May 2	5.8	16	47.1	May 1	11.9
Intermediate migrant	41	57.8	May 3	4.2	10	29.4	Apr 24	14.1
Overall	71	100	May 3	5.5	34	100	Apr 30	12.7

[a] No SD possible since contingent consists of single individual

moderately high explanatory power (R^2_{2009} = 0.67; R^2_{2010} = 0.73) as well as local maxima in CCC and pseudo-*F* statistic; in both years, ≥5 clusters resulted in small increases in explanatory power ($\Delta R^2_{2009} \leq 0.07$; $\Delta R^2_{2010} \leq 0.06$), while 3 clusters resulted in large losses of explanatory power ($\Delta R^2_{2009} = -0.21$; $\Delta R^2_{2010} = -0.24$). Significant differences were identified in contingent membership frequency between years (FET with 2000 Monte Carlo estimations, p = 0.01; Table 1). The majority, 58% of individuals, collected in 2009 were classified as intermediate migrants in contrast to 29% in 2010. In 2010, small migrants made up a much larger proportion of the sample (n = 16, 47% of sample) than in 2009 (n = 16, 23% of sample). Interpreting increases in Sr/Ca as movement from fresh to brackish habitats was supported by the observed distribution of striped bass juveniles during extensive seine sampling in June 2009. In early June (before the 15th) 90% of juveniles (TL_{mean} = 32.5 ± 2.1 mm) were collected from sampling sites in freshwater habitat; sampling during late June revealed a downriver shift in distribution as 93% of juveniles (TL_{mean} = 50.6 ± 0.8 mm) were collected at sampling sites in brackish habitats. Despite this shift in distribution as juvenile size increased, TL was not affected by the habitat from which juveniles were collected ($F_{1,67}$ = 2.67, p = 0.11 in 2009; $F_{1,43}$ = 0.73, p = 0.40 in 2010) even when time was included in the analysis (i.e. interaction of habitat and month; $F_{1,67}$ = 1.45, p = 0.23 in 2009; $F_{1,43}$ = 0.30, p = 0.59 in 2010).

Mixed effects models in both years confirmed the influence of total length and contingent on Sr/Ca (in 2009 *F* = 20.35, p < 0.001; in 2010 *F* = 15.16, p < 0.001). FDR-adjusted contrasts of sequential length bins revealed increases in Sr/Ca for the small migrants contingent between 11 and 25 mm in both 2009 and 2010 (Fig. 4). For intermediate migrants, significant Sr/Ca changes occurred between 16 and 30 mm TL in 2009 and 21 and 30 mm TL in 2010. Sr/Ca shifts were not associated with early life length stanzas for the dispersing larvae or the combined resident and large migrant group. These same contrasts also revealed decreases in Sr/Ca among intermediate migrants between hatch and 10 mm TL in both years. FDR-adjusted contrasts between contingents within length bins aligned with these results, revealing that these increases led to significantly greater Sr/Ca values for small migrants (≥16 mm in both years) and intermediate migrants (≥21 mm in 2009; ≥26 mm in 2010) when compared to the resident and large migrant contingent.

Intrinsic influences on dispersal: early growth

Growth was significantly affected by both contingent and developmental stage in both 2009 (contingent: *F* = 3.19, p = 0.03; stage: *F* = 250.29, p < 0.001) and 2010 (contingent: *F* = 7.39, p = 0.001; stage: *F* = 69.28, p < 0.001). Collected individuals grew at a higher rate during the larval period (3.8–15 mm TL) than in the early juvenile period (i.e. prior to and during dispersal, 15–35 mm TL) in both 2009 (Fig. 5) and 2010. In both years, members of the resident contingent experienced higher growth rates than members of migratory contingents (i.e. juveniles that enter brackish habitats at TL ≤35 mm). Juvenile growth rates were unaffected by contingent membership.

Extrinsic influences on dispersal: river discharge and temperature

Juvenile hatch dates did not differ between contingents in either 2009 ($F_{3,38}$ = 1.71, p = 0.18; Table 1) or 2010 ($F_{3,28}$ = 2.31, p = 0.10). Mean weekly flow, measured from April 16 through May 8 in both years, was 15.2 $m^3 s^{-1}$ (range 3.4 –41.5 $m^3 s^{-1}$; Fig. 6) in 2009 and 7.6 $m^3 s^{-1}$ (range 3.2–16.5 $m^3 s^{-1}$) in 2010. Flow in 2009 was marked by 2 major increases caused by

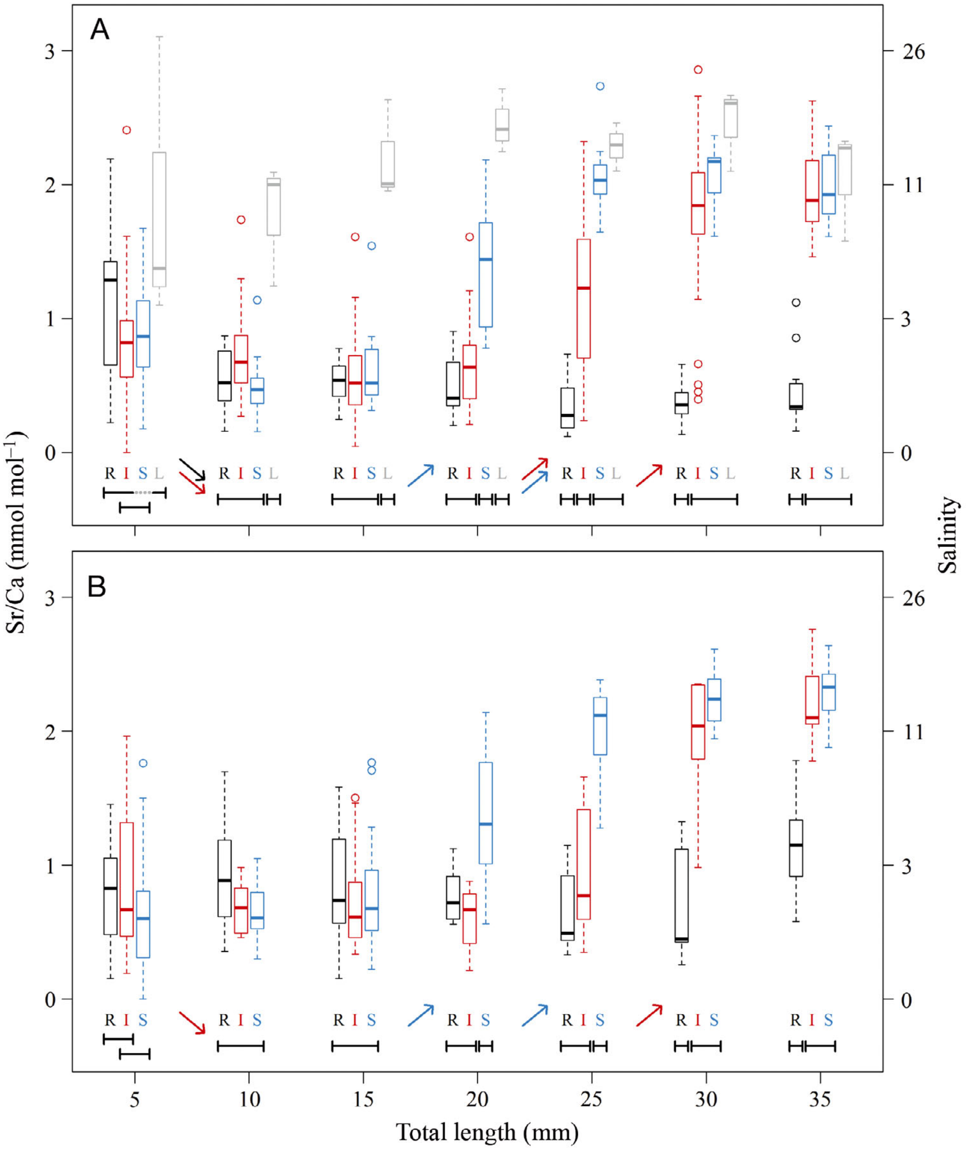

Fig. 4. Contingent-specific Sr/Ca ratios in (A) 2009 and (B) 2010, binned by 5 mm length increments. Contingents are identified by letter and color-coded (R: resident; I: intermediate migrant; S: small migrant; L: larval disperser). Separate horizontal black bars at bottom indicate significantly different Sr/Ca ratios between contingents at identical sizes, while color-coded diagonal arrows indicate significant decreases or increases within contingents as size increases. The larval disperser contingent was not included in 2010, since only 1 individual was identified via the PCA/CA procedure. In all boxplots, midlines indicate median, whiskers extend to 1.5× the interquartile range, and open dots represent outliers

weather events. The first of these increases was bracketed by the breakpoints in the rate of increase in otolith Sr/Ca: May 30, 2009 (±4 d) and June 13, 2009 (±4 d). During this event, weekly and daily mean flow rates exceeded 41 and 76 m^3 s^{-1}, respectively, and the rate of change in Sr/Ca wk^{-1} rose from slightly decreasing to rapidly increasing before stabilizing (rate of change following 2nd breakpoint was −0.02 ± 0.07 mmol mol^{-1} wk^{-1}). As in 2009, 2 breakpoints were identified in 2010, June 1 (±10 d) and June 29 (±10 d), between which weekly mean flow rates did not reach 10 m^3 s^{-1} and the rate of change in Sr/Ca wk^{-1} was dampened in comparison to that observed in 2009. Weekly mean Sr/Ca for the sampled population was positively influenced by the interaction of time (week) and flow ($F_{1,472} = 14.6$, $p < 0.001$) in 2009 and by only time ($F_{1,34} = 142.3$, $p < 0.001$) in 2010. The large shift in Sr/Ca observed in 2009 (June 4 to June 10) corresponded with the majority (55%) of classified migrants moving from

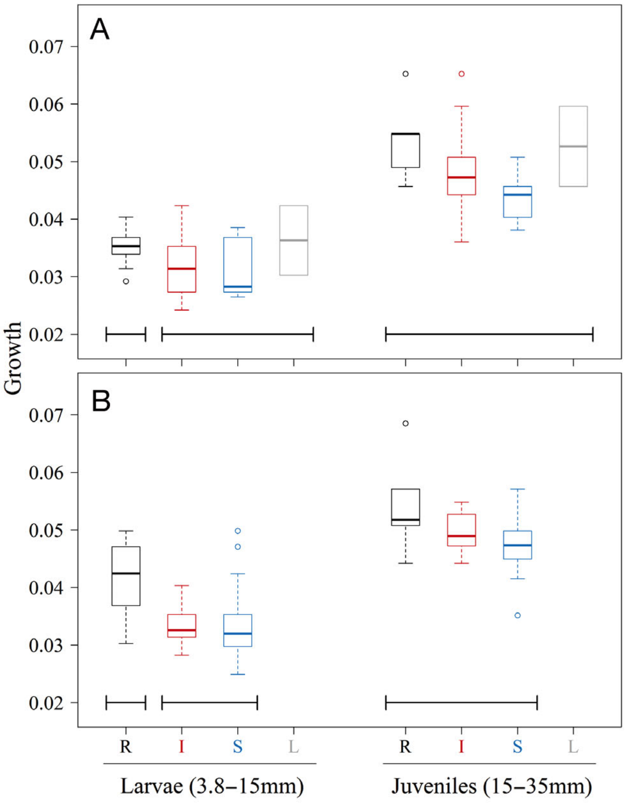

Fig. 5. Instantaneous growth rates of striped bass in (A) 2009 and (B) 2010 over the larval and early juvenile developmental stages of identified behavioral contingents: R, resident; I, intermediate migrant; S, small migrant; L, larval disperser. Separate horizontal black bars at bottom indicate significantly different growth rates within developmental stage. The larval disperser contingent was not included in 2010, since only 1 individual was identified

freshwater to brackish habitats. Migrant dispersals in 2010 were much more widely distributed in time, with no more than 18% emigrating from freshwater in any week.

Averaged otolith Sr/Ca levels were also significantly influenced by temperature and its interaction with date (week) in 2009 ($F_{1,461}$ = 13.43, $p < 0.001$) and 2010 ($F_{1,334}$ = 4.23, p = 0.04), but effects on Sr/Ca were almost imperceptible (rate of change was = 0.0138 ± 0.0038 mmol mol^{-1} wk^{-1} °C^{-1} in 2009 and 0.00644 ± 0.0031 mmol mol^{-1} wk^{-1} °C^{-1} in 2010).

Impacts of dispersal: condition and feeding ecology

The relationship between weight and length was not affected by contingent membership (2009: $F_{3,31}$ = 2.03, p = 0.13; 2010: $F_{3,28}$ = 41.1, p = 0.75). Habitat did not influence the relationship of weight and length in 2009 ($F_{1,31}$ = 0.92, p = 0.35), but habitat did influence this relationship in 2010 ($F_{1,28}$ = 4.23, p = 0.049); however, this difference was of low amplitude (the allometric scaling coefficient, b from weight = a × length^b, for juveniles collected from brackish habitats, b_{BW} = 3.09, was only 5% higher than that of freshwater, b_{FW} = 2.94).

The occurrence of prey items in diets differed between fresh and brackish water in 2010 (FET with 2000 Monte Carlo estimations, $p < 0.001$), although diets in both habitats were dominated by amphipods, appearing in 58% of freshwater and 63% of brackish water stomachs. Freshwater diets were do-

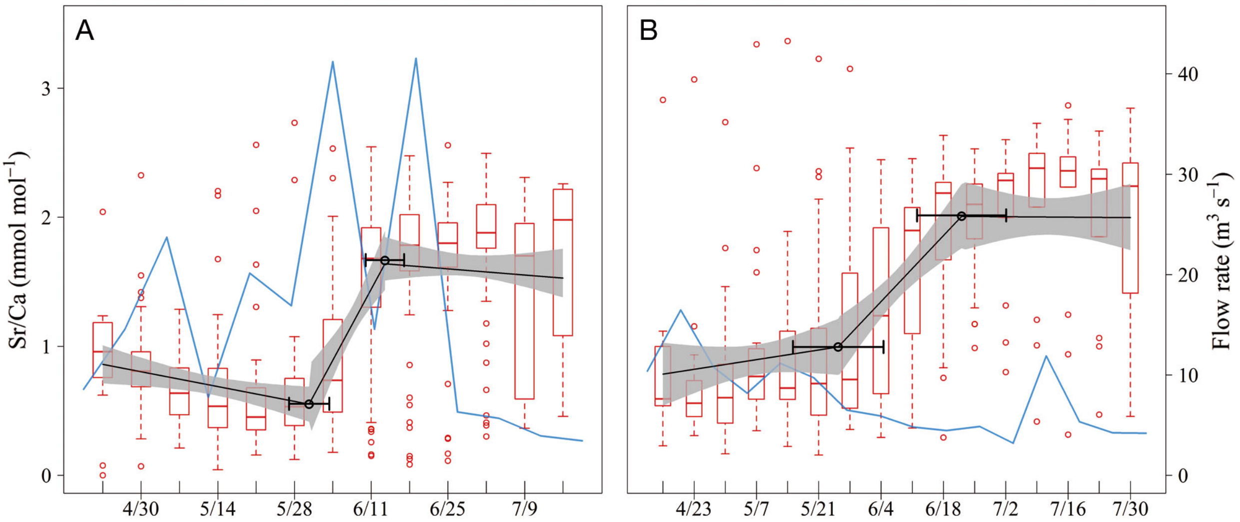

Fig. 6. Weekly (red boxes) Sr/Ca ratios for all juveniles collected in (A) 2009 and (B) 2010. Black lines, gray shading, black circles, and black horizontal whiskers indicate Sr/Ca slope, 95% CI's of slope, breakpoints, and 95% CI's of breakpoints, respectively, predicted using segmented regressions. Blue lines indicate weekly mean flow rates of the Patuxent River

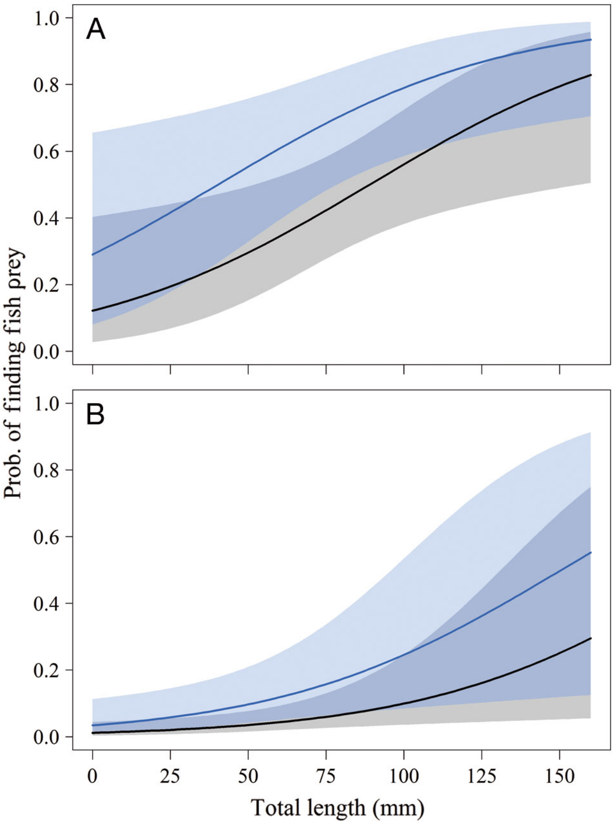

Fig. 7. Size-specific predicted probabilities of finding fish prey items in the stomachs of juveniles collected in freshwater (blue lines; 95% CI light blue shading) and brackish (black lines; 95% CI dark gray shading) habitats in (A) 2009 and (B) 2010

minated by copepods (36% of stomachs), which were not observed in brackish stomachs. Conversely, mysids composed an important part of brackish diets (26%), while only playing a minor role in freshwater diets (6%). Unlike 2010, the occurrence of prey did not differ between habitats in 2009 (FET with 2000 Monte Carlo estimations, $p = 0.73$). Vertebrate prey items (fish larvae) were more common in 2009 than in 2010. Binomial regression (likelihood ratio test of all parameters $\chi^2 = 5.10$, $p = 0.02$; Fig. 7) revealed that larval fish more likely occurred in freshwater than brackish stomachs (Wald statistic, $Z = 2.00$, $p = 0.045$), in 2009 than in 2010 ($Z = -4.83$, $p < 0.001$), and were increasingly likely to be found as fish length increased ($Z = 2.49$, $p = 0.02$). Based on *t*-tests, gut fullness (GF) did not differ between juveniles collected in freshwater ($GF_{2009} = 0.0019 \pm 0.0005$; $GF_{2010} = 0.0147 \pm 0.0044$) and brackish habitats ($GF_{2009} = 0.0040 \pm 0.0009$; $GF_{2010} = 0.0063 \pm 0.0008$) in 2009 ($t_{40} = 1.34$, $p = 0.19$) or 2010 ($t_{34} = 1.89$, $p = 0.07$).

The increase in mass of planted oysters surpassed the doubling threshold in all 4 models at all sites up to RKM 43 (Eagle Harbor; Fig. 1). At the next site upriver (RKM 49, King's Landing), 2 growth models estimated mass increases that did not reach the threshold; therefore, $\delta^{15}N$ from oysters planted in Eagle Harbor were used as baseline values for estimated trophic positions of all striped bass juveniles collected in freshwater. All migrant striped bass had experienced at least a doubling in mass since dispersal (minimum relative increase was 241%) based on the relative change in weight since dispersal estimated using allometry ($weight = a \times length^b$; $a = 7.9 \times 10^{-6}$, $t = 7.00$, $p < 0.001$; $b = 3.04$, $t = 91.13$, $p < 0.001$). As measured using stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), feeding ecology in 2010 differed based on the habitat where juveniles were collected (MANCOVA; Wilks' $\Lambda_{2,44} = 0.54$, $p < 0.001$; Fig. 8) after accounting for the effects of size (body weight; Wilks' $\Lambda_{2,44} = 0.77$, $p = 0.003$). $\delta^{13}C$ measured in the white muscle tissue of juveniles collected in freshwater was less ($\delta^{13}C_{fw} = -24.88 \pm 0.58$; $F_{1,44} = 36.99$, $p < 0.001$) and $\delta^{15}N$ ($F_{1,44} = 7.07$, $p = 0.01$; $\delta^{15}N_{fw} = 18.09 \pm 0.28$) greater than those measured in juveniles from brackish habitats ($\delta^{13}C_{bw} = -20.79 \pm 0.44$; $\delta^{15}N_{bw} = 17.31 \pm 0.17$). Instead of indicating the separation of striped bass trophic niches based on habitat, this apparent divergence likely reflects trophic baseline differences in $\delta^{15}N$. Oyster adductor muscle $\delta^{15}N$ values differed between habitats ($\delta^{15}N_{bw} = 13.87 \pm 0.14$; $\delta^{15}N_{fw} = 14.79 \pm 0.14$; $t_{18} = 2.13$, $p = 0.004$). Thus, estimated trophic position did not differ across habitats ($t_{45} = 0.24$, $p = 0.81$).

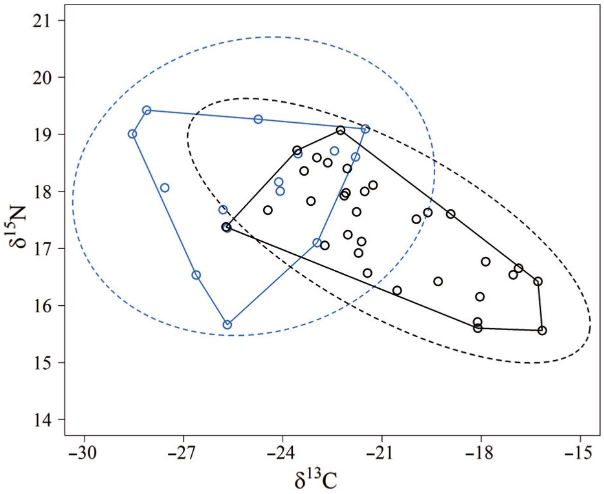

Fig. 8. Convex hulls (solid lines) and 95% ellipses (broken lines) of $\delta^{13}C$ and $\delta^{15}N$ measured in white muscle tissue of juveniles collected in 2010. Freshwater (blue) and brackish (black) habitats assigned by location of collection

DISCUSSION

Using otolith chemistry and microstructure, we uncovered multiple movement patterns by striped bass *Morone saxatilis* during the first few months of life. Early juvenile dispersal histories were separable into resident and migrant modes, typifying partial migration (Secor 2015). However, the range of sizes over which movements occurred was larger than expected in both years, reflected in the separation of migrants into multiple contingents rather than as 2 modes as had been observed in sympatric white perch *M. americana* (Kraus & Secor 2004a). Consistent modes of movement behavior undertaken at different stages of ontogeny were observed in both years of the study and suggest conditional responses that influence both when and whether juveniles migrate. In accordance with predictions, higher larval growth (i.e. growth before movement to brackish habitats) favored resident or delayed migratory behaviors. On the other hand, high flow rates appeared to influence the timing of movement. Contrary to expectations, the predicted benefits of moving to brackish water — improved diet and higher growth and condition — were not apparent in migrants.

Discrete vs. continuous thresholds

Patterns in the timing of movements were associated with growth and development. Although findings supported conditional migrations, the approaches employed entailed some limiting assumptions. For instance, the overlapping ranges of size at dispersal between the small migrant (10–25 mm TL in both years) and intermediate migrant (10–35 mm TL in 2009, 15–35 mm TL in 2010) contingents in both years could be an indication of a continuously increasing probability of movement with size, made discrete as a consequence of our analytical methodology. However, profile analyses (Fig. 2) did not support migration as a continuous series of short down-estuary movements. Rather they indicated threshold transitions between freshwater (resident) and brackish water (migratory) habitats occurring over relatively short periods during the first 2 mo of life. Further, the interaction of variable continuous traits of juvenile fish such as growth and condition (i.e. liability traits) and dynamic environmental conditions with intrinsic thresholds can trigger discretely expressed migratory modes (Pulido 2011, Dodson et al. 2013). These modes may be clearly observed during brief movement phases between habitats and allow for inferences relevant to causes and consequences of partial migration.

Onset of movement

A threshold response for migratory mode striped bass was apparent at the transition between larval and juvenile stages, which typically occurs between 14 and 20 mm TL (Mansueti 1958, Setzler-Hamilton et al. 1981, Grizzle et al. 1985). The majority of migrants moved to brackish habitats as early-stage juveniles in both years (90 %). A similar threshold has been observed in the congeneric white perch (Kraus & Secor 2004a). Although most dispersed individuals moved during the juvenile stage, a few (n = 3 in 2009 and n = 1 in 2010) showed evidence of dispersing during the larval period, a surprising result not suggested in past surveys and in a mark-recapture experiment that failed to (re)capture larvae down-estuary of the salt front (Winger & Lasier 1994, Secor et al. 1995). Interestingly, unpublished laboratory studies indicate that larvae do well in brackish water conditions if fed sufficiently (Hirai et al. 2000). Although we cannot be completely confident that apparent larval dispersers are not an artifact owing to the approach we deployed, such observations are not easily discounted. Feeding striped bass larvae can show directed movement behaviors in response to tidal flow (Bennett et al. 2002), but given the rate of flows during spring freshets, passive downstream advection could explain their early displacement.

Influences on migratory tendencies

Conditional partial migration in which resident behavior is linked to elevated pre-dispersal growth rates has been observed in a number of freshwater and coastal species, including congeneric white perch (Forseth et al. 1999, Bujold et al. 2004, Kraus & Secor 2004a). The higher growth of residents during the larval stage (defined here as 3.8–15 mm TL) when compared to members of other contingents seems to support such a conditional response in striped bass. That higher growth rates of residents preceded down-estuary movements by their compatriots in both study years strengthens the inference for a growth-mediated movement threshold. In addition to this resident-migrant contrast, the lowest early growth rates were ordered by size at dispersal: small migrants followed by intermediate migrants. We were not able to identify factors leading to early growth differences between eventual residents and migrants. A past study suggested that residents occupied areas that provided better conditions for early growth, forcing migrants to relatively lower quality locations (Mohan et al. 2015); in this scenario residents might be expected to have hatched earlier, giving them a distinct advantage to seek out and occupy favorable habitat. However, we found no evidence of this in our reconstruction of contingent hatch date distributions (Table 1); if anything, striped bass that remained in freshwater hatched slightly later than those that eventually migrated in both 2009 and 2010. In theory, later hatched striped bass could experience better larval foraging conditions, since peaks in important prey items (e.g. *Bosmina* spp.) often occur in May in the Patuxent River (Campfield 2004, Campfield & Houde 2011); this would align with the hatch dates and prey availability for the 2005 freshwater contingent of white perch in the Patuxent River (Kerr & Secor 2010). However, peaks in preferred planktonic prey vary annually (Campfield & Houde 2011), which would likely result in unpredictable 'late' larval foraging conditions and annually inconsistent growth for striped bass with later hatch dates. Ultimately, hatch date distributions of contingents overlapped substantially, suggesting influences on early growth beyond 'match-mismatch' dynamics.

If striped bass contingent dynamics mirror those of other juvenile stage fish such as brown trout *Salmo trutta* and white perch, migrants may have inherently higher metabolic rates that do not afford as much energy to be diverted to growth, which could affect early growth and trigger the search for habitats that offer greater scope for growth (Forseth et al. 1999, Kerr & Secor 2009). Unfortunately, we have no direct measure of the forage available prior to dispersal or evidence of inherent differences in resident and migrant metabolism; therefore, we are limited to speculation on the possible contributors to the lower growth among juveniles that eventually emigrate from natal freshwater habitat. Regardless of their source, the differences we measured in striped bass prior to dispersal may exemplify Dodson et al.'s (2013) model of partial migration as the interplay of liability traits and possibly conditional threshold values in early growth and developmental stages. That these trends in contingent-specific larval growth rates occurred in both years indicates a consistent mechanism triggering contingent behaviors.

High variance in size at dispersal (SD_{2009} = 13.1 mm; SD_{2010} = 6.2 mm) suggests the influence of factors in addition to size, development, or growth. That partial migration is conditioned to varying extents by environmental drivers has been established across taxa (Chapman et al. 2011). Considering dispersal from freshwater to brackish habitats is in the direction of major upper water column currents, flow is an obvious candidate for such a driver. In 2009, a 14 d period of rapidly increasing weekly mean Sr/Ca for the sampled population during which most migrants dispersed coincided with a large flow event (Fig. 6). High flow might be expected to affect the spatial distribution of juveniles based on size and development (i.e. high flow rates would disproportionately affect smaller, younger juveniles incapable of maintaining their position in the river); however, the expected pattern of hatch dates that would result from purely passive advection (i.e. small migrants hatched later than other contingents, residents hatched earlier than all other contingents) was not observed (Table 1). Evidence of fish actively using predominant water currents during migration has been documented in the early life-history stages of other species; Atlantic salmon *Salmo salar* fry in the River Tana (on the border of Finland and Norway) have been observed migrating in alternating active (i.e. swimming) and passive modes (i.e. drifting; Davidsen et al. 2005). In contrast to 2009, no more than 18% of dispersing juvenile striped bass moved to brackish water habitats during any single week in 2010, when weekly mean flow rates did not exceed 17 $m^3 s^{-1}$ and did not affect Sr/Ca during the period of the study. Davidsen et al. (2005) observed salmon fry maintaining their position by swimming into river currents in addition to passively floating and actively swimming with the current, which led to their interpretation of this passive transport as behavior rather than simple inadvertent advection. Similarly, we would expect striped bass juveniles, mostly 15–30 mm TL during this major flow event in 2009 and able to swim up to 8 km d^{-1} (based on sustained swimming speeds of 3–4 body lengths s^{-1}; Meng 1993) to be capable of maintaining their position regardless of the high flow rates.

The observed influence of flow on Sr/Ca and the majority of migrations occurring during a single week has 2 likely explanations. First, juvenile striped bass migration in the Patuxent River is largely independent of flow conditions; if this is the case, any apparent relationship between flow and Sr/Ca is due to the reduction in the time taken to transit the distance between freshwater and brackish habitats resulting from actively swimming with high currents (i.e. absolute swimming rate relative to RKM increases in high flow events). Second, juvenile striped bass migration is inherently conditional, influenced by the intrinsic status of individual fish as well as their surroundings. Under this scenario, early growth is an important liability trait whose threshold value is influenced by flow rate; as flow increases, the growth threshold triggering movement shifts, leading some juveniles to move down-river (possibly by ceasing their station-keeping behavior, or periodically switching between active and passive transport modes sensu Atlantic salmon fry; Davidsen et al. 2005). One possible outcome of this second hypothesis is that under identical early growth conditions, the number of migrants could increase in year-classes that experienced higher river flow due to the resulting change in the behavioral threshold; interestingly, juveniles that adopted migratory behaviors (i.e. did not remain resident) were relatively more frequent in 2009 (84.5% migrants) than in 2010 (79.6%). Definitive evidence supporting the importance of the interaction between early growth and flow rate will require directed study.

Consequences of migration

Higher growth and/or condition were expected to follow dispersal, as has been demonstrated in Arctic charr in northern Norway, where an immediate post migration burst of growth leads to a persistent advantage over residents (Rikardsen et al. 2000). Instead, growth did not differ between contingents, and condition was either equivalent or higher for residents in freshwater when compared to migrants in brackish habitats. We predicted improved forage awaiting migrants in brackish habitats based on previous studies of juvenile striped bass (Boynton et al. 1981), but migrant trophic niches were indistinguishable from that of residents apart from expected differences in food web bases (i.e. $\delta^{13}C$; Fig. 8), and their diets were comparatively poorer than their resident counterparts due to the lower likelihood of consuming high quality vertebrate prey in brackish habitats (Fig. 7). Although we assumed that enhanced growth or condition would have followed migration, other benefits may have accrued. In the absence of improved growth for migrant southern flounder *Paralichthys lethostigma* along the Texas coast, partial migration may persist in part due to contingent-specific preferences in prey as well as predator avoidance (Nims & Walther 2014). The reduced osmotic cost afforded by higher salinities might have provided some benefit to migrants in the form of recovered condition. Further complicating any effects of habitat on growth and condition could be the energetic costs of migrating, which may result from fish exerting themselves outside of typical optimum energy efficiency while swimming as well as forgoing foraging opportunities during movement (Bernatchez & Dodson 1987). However, the negative impacts of migration documented in other diadromous species are limited to migrations that are primarily against predominant currents (i.e. upstream; Jonsson et al. 1997; Bohlin et al. 2001) or that involve complicated physiological processes and long distances (i.e. that of European eel *Anguilla anguilla*; van Ginneken & van den Thillart 2000). Additionally, we detected no differences in foraging success (i.e. gut fullness) between the habitats in either year. Lack of change in forage and condition may simply be a relatively common outcome of partial migration. Annual variability in migration outcomes has been identified in other species (Kerr & Secor 2012, Gillanders et al. 2015) and could support the maintenance of different migratory strategies observed in juvenile striped bass.

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