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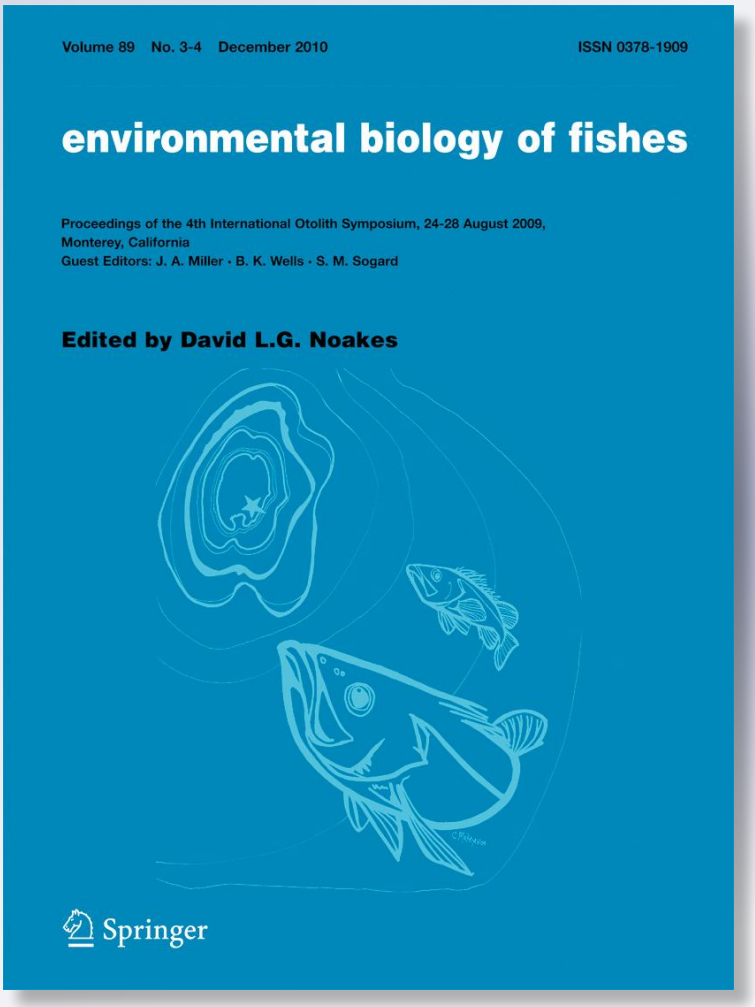

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Latent effects of early life history on partial migration for an estuarine-dependent fish

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Abstract Partial migration is the divergence of a population into migratory and resident contingents. This behavior is well documented for many diadromous species, but proximate causes of partial migration in fishes are poorly understood. Here, we tested the hypothesis that migratory and resident contingents within a population of white perch (*Morone americana*) are associated with larval growth and mortality rates, where slower growth and higher mortality was associated with migratory behavior. In addition, we examined the influence of environmental factors (temperature, zooplankton density, and freshwater flow) on larval vital rates. In 2005, an intensive field survey was conducted in the Patuxent River estuary (Chesapeake Bay, MD). Otolith microstructure analysis was used to determine vital rates of larvae and back-calculate hatch-date distributions of juveniles from resident and migratory contingents. Migratory contingent fish originated primarily from early-spawned larval cohorts, which were characterized by slower growth compared to later spawned cohorts. In contrast, resident juveniles tended to originate from later-spawned cohorts with faster growth. Zooplankton densities supported the inference that favorable larval growth conditions occurred later in the larval production period. The results support latent effects on partial migration of white perch related to spawning phenology, its interaction with temperature, and resultant larval growth rates.

Keywords Larval cohort analysis · Contingent · Otolith · Partial migration · White perch · *Morone americana*

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Introduction

Intra-population divergence in habitat use, termed contingent behavior, has been identified across taxa and in a variety of fish species [e.g., Japanese eel, *Anguilla japonica* (Tsukamoto et al. 1998); striped bass, *Morone saxatilis* (Secor 1992); bluefin tuna, *Thunnus thynnus* (Fromentin and Powers 2005)]. A specific type of contingent behavior termed "partial migration" has been studied extensively in bird (Berthold 2001) and salmonid populations (see review by Jonsson and Jonsson 1993) and was recently documented in estuarine-dependent white perch, *Morone americana* (Kerr et al. 2009). Partial migratory populations diverge into two dominant life-

cycle behaviors, migratory and resident; which exhibit demographic differences that can have population-level consequences (Kraus and Secor 2004; Kerr and Secor 2009; Kerr et al. 2010). Diversity of life history tactics within populations is increasingly recognized as a means of offsetting environmental stochasticity and in some cases may be important for the long-term persistence of populations (Secor and Kerr 2009; Kerr et al. 2010).

Partial migration is typically maintained as a conditional strategy, whereby there is a single genetic population that exhibits resident or migratory behavior based on an individual's condition relative to a genetically defined threshold, usually related to growth rate during early life (Jonsson and Jonsson 1993; Forseth et al. 1999; Bujold et al. 2004). Evidence suggests that differences in growth rate early in life may be the cause of behavioral differences within estuarine-dependent white perch (Kraus and Secor 2004; Kerr and Secor 2009). However, the proximate cause of contingent structuring in white perch remains unresolved. Across taxa, conditions experienced early in life have been shown to have latent and lifetime consequences to fitness of animals, impacting factors such as growth, survival, and fecundity (Pechenik 2006; Edeline 2007).

White perch exemplify a periodic life history pattern, favored in spatially or temporally variable environments and characterized by high fecundity, high mortality during early life history, and a late age at maturation (Winemiller and Rose 1992). In Chesapeake Bay estuaries, white perch exhibit a moderately protracted spawning period during spring (late March–June) (Secor et al. 1994; North and Houde 2001) in the tidal freshwater region of the estuary. Both the egg and larval stages develop within this region (Mansueti 1964). Divergence in habitat use within the population occurs after the transition from larval to juvenile stage (Kraus and Secor 2004) and this spatial behavior persists into adulthood (Kerr et al. 2009). Based on back-calculated larval growth rates, members of the migratory contingent were found to have significantly slower growth rates compared to the resident contingent prior to dispersal (Kraus and Secor 2004; Kerr and Secor 2009). This growth trend was reversed after dispersal, when migratory contingent members exhibited significantly faster growth rates as juveniles and adults compared to the resident contingent (Kraus and Secor 2004; Kerr and Secor 2009). We hypothesized that the moderately protracted spawning period of adult white perch results in larval cohorts that experience different environmental conditions, resulting in cohorts with different growth rates. We propose that early differences in growth rate ultimately influence an individual's contingent membership.

Larval cohort analysis provides an efficient means to examine the linkage between environmental conditions in the nursery habitat and larval vital rates (Limburg 2002). Environmental factors, including temperature, zooplankton prey density, and freshwater flow, are important determinants of larval survival and growth of white perch and striped bass (a congener of white perch) larvae in Chesapeake Bay (Houde et al. 1989; Uphoff 1989; Rutherford and Houde 1995; Secor and Houde 1995). In this past research, temperature often plays a dominant role, but density of zooplankton prey also affects cohort-specific growth and mortality rates of larvae (Limburg et al. 1999). In addition, increased precipitation and freshwater flow during the larval period have been associated with increased mortality of larval striped bass, specifically due to changes in habitat quality and sudden drops in temperature to sub-lethal and lethal levels (Houde et al. 1989; Uphoff 1989; Rutherford and Houde 1995). Increased streamflow prior to spawning (winter-early spring), however, can have a positive effect on survival of anadromous fishes due to increased nutrient delivery, an increased extent of the estuarine turbidity maximum and associated increased zooplankton production and densities (North and Houde 2003; Kimmel and Roman 2004; Shoji et al. 2005). Thus, environmental conditions during the spawning and larval period can cause differences in vital rates of larval cohorts and modify the representation of cohorts within resident and migratory contingents.

The specific objective of this study was to determine whether resident and migratory white perch were drawn at random from the population's larval hatch-date distribution or derived from specific larval cohorts that possess particular growth and mortality attributes. A secondary objective was to relate growth and mortality attributes of cohorts to temperature, zooplankton density, and freshwater flow conditions to determine how these factors might indirectly influence contingent structuring in juvenile white perch.

Methods

Juvenile fish collections and otolith preparation

Young-of-the-year white perch were collected at approximately weekly intervals from June to September in 2005 in the Patuxent River, a tributary of the Chesapeake Bay characterized as a shallow, partially mixed estuary (Fig. 1). The seine survey included 9 stations along the salinity gradient of the Patuxent River estuary (river kilometer (RK) 6, 16, 16, 33, 41, 45, 48, 53, 64, and 72; Fig. 1). Sampling was conducted using a 30.5 m × 1.24 m beach seine with 6.4 mm mesh set from shore. White perch were counted, measured and preserved in 95% ethanol at the time of collection. Water temperature and salinity were measured using a YSI-85 probe at the time of fish collections.

Juveniles were assigned to contingent based on their location of capture. Fish collected in freshwater (RK 48, 53, 64, and 72) were designated members of the resident contingent and fish collected in brackish water (RK 6, 16, 33, 41, and 45) were designated members of the migratory contingent. Analysis of the Sr:Ca profiles of adult white perch otoliths provided evidence that location of capture of juvenile fish is a good proxy for contingent membership (Kerr et al. 2009). Age was estimated from a subsample of fish from each contingent (migratory: n=33, resident: n=41); migratory fish were drawn from collections at RK 16, 33, and 45 and resident fish were drawn from collections at RK 48 and 72, based on the abundance of samples from these sites. Fish were chosen from earlier sampling dates (June and July) because age determination of older juveniles may be biased, as shown for the congeneric striped bass (Bulak et al. 1997). Sagittal otoliths from juvenile white perch were embedded in Stuers epoxy and transversely sectioned using a low speed saw equipped with diamond blades separated by a spacer (0.3 mm). Otoliths were polished using a grinding wheel with a slurry of 25 μm aluminum oxide and a felt, metallographic cloth covered with a slurry of 0.3 μm alumina powder on both sides until the primordium (core) was clearly visible. Age was estimated three times independently, and a final age was assigned based on the reader's confidence in age estimates. Daily increment formation in juvenile white perch was verified in a previous laboratory study (Kraus and Secor 2004). Hatch dates of juvenile white perch were back-calculated, and each individual was assigned to its corresponding 9-d larval cohort (cohort period is based on standard error of larval ages=4.6 days).

Ichthyoplankton collections, environmental data, and otolith preparation

Ichthyoplankton sampling occurred biweekly from April 7 to May 31 in 2005 (n=5) in the tidal freshwater region of the Patuxent River estuary. The sampling design ensured that the larval cohorts received similar sampling intensity. Thirteen fixed sampling sites were distributed along the tidal freshwater portion of the river, which was segmented into seven zones of approximately equal length with two stations sampled within each zone, with the exception of the most upriver zone (which only had one station due to difficulties with maneuverability of the boat in this area). Paired bongo nets (60 cm bongo nets with 280 μm mesh) with attached flowmeters were deployed off the research vessel Pisces (approximately 8 m in length). Oblique tows were made against the prevailing tide or wind for 5 min. Tows were depth integrated, with the net towed at bottom (within 1 m), middle, and surface depths for ~1.5 min at each depth. Water temperature (°C), salinity, conductivity (μS), and dissolved oxygen ($mg \cdot L^{-1}$) were recorded with a YSI-85 probe at the surface and at near bottom depths at each station. Continuous water quality data were also recorded at the Chesapeake Bay Program's (CBP) continuous monitoring station at Jug Bay, Maryland (RK 72; Fig. 1) and stationary temperature data loggers were deployed within the nursery area (RK 53 and 72; Fig. 1). River discharge data were obtained online from US Geological Survey (USGS), National Water Inventory Service (http://waterdata.usgs.gov/nwis) for USGS Site: Patuxent River near Bowie, MD, Site #: 01594440.

Ichthyoplankton was analyzed for at least one station per river segment for each cruise date. White perch larvae were identified to species following Waldman et al. (1999), counted and measured to 0.1 mm notochord length using an image analysis system (components include: Olympus dissecting microscope, Olympia camera, camera controller software, Image J software). A random sample of 100

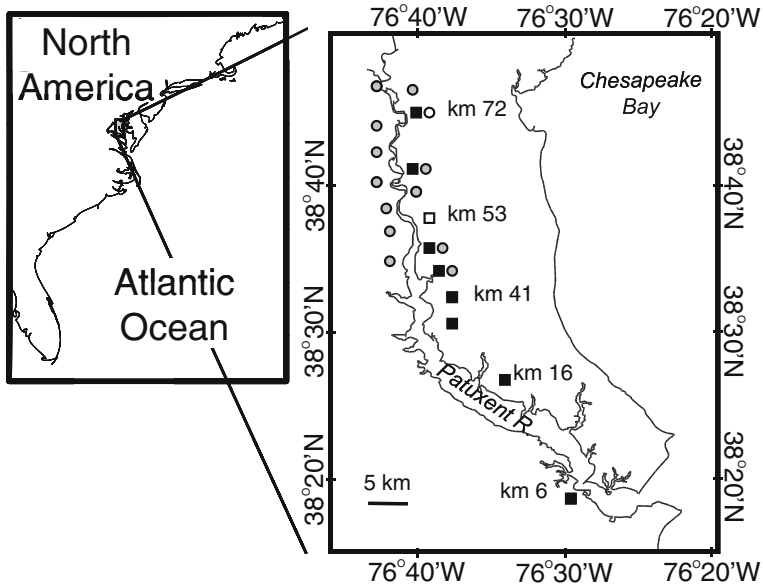

Fig. 1 Map of the Patuxent River estuary, a sub-estuary of the Chesapeake Bay (Maryland). The map illustrates stations sampled for larval (*open and filled circles*) and juvenile (*open and filled squares*) white perch during 2005. Water quality monitoring sites are indicated by open shapes (river km 53 and 72)

larvae (maximum) was measured from each site (50 yolk-sac larvae and 50 post-yolk-sac larvae). Density (number per m^3) of white perch larvae was estimated for each station based on sampling volume and corrected for daytime avoidance of the net by larger larvae (gear efficiency correction based upon analysis of striped bass larvae; Houde et al. 1988). River-segment abundance was estimated by expanding station density (mean station density was used when two stations were analyzed per segment) for each river segment to the volume of the river segment that the site represented. River area and volume measures were obtained from Cronin (1971) and Secor et al. (1994). River-wide abundance was the sum of river-segment abundances.

Sagittal otoliths were removed from a representative sub-sample of larvae (n=109) for age estimation at a daily time-step. Otoliths from larvae <12 mm SL were extracted and affixed to a microscope slide with clear lacquer. No polishing was necessary for otoliths of larvae 3–9 mm. Otoliths of larvae 9–12 mm were polished whole using a grinding wheel with a slurry of 25 μm aluminum oxide and a felt, metallographic cloth covered with a slurry of 0.3 μm alumina powder to achieve a final polish. Otoliths from larvae ≥ 12 mm SL were prepared, sectioned, polished and examined following the method previously described for juvenile white perch otoliths. Otolith microstructure was examined under a compound microscope (600 to 1000× magnification) and age (days) was estimated three times independently. Final age was assigned as the mean of the second and third reads as the counts were considered equally reliable (Campana and Jones 1992). Estimated age was corrected for the influence of temperature on the timing of first daily increment formation, following Houde and Morin's (1990) equation:

$$\text{temperature adjusted age} = \text{increment count} + (9.03 - (0.32 \times \text{T})$$

where T=temperature on the day of first increment formation. Temperature records from RK 53 and 72 were used in the calculation of temperature-adjusted ages for fish from downriver and upriver locations, respectively.

Zooplankton collection

Zooplankton was collected during each sampling cruise at one station within each of the seven sampling zones described above by pumping ambient water through a 53 μm filter. Zooplankton sampling was depth integrated; 20 L was sampled at surface, intermediate, and near bottom depths (total volume sampled=60 L), filtered and preserved in 5% formalin. Zooplankton taxa known to be important white perch prey items, including copepod nauplii, copepedites, and adults (predominantly *Eurytemora affinis*), rotifers, and cladocerans (predominantly *Bosmina*

longirostris; Setzler-Hamilton et al. 1981; Setzler-Hamilton 1991; Campfield 2004), were counted in three replicate aliquots per sample. Mean number per aliquot was scaled up to number per liter for each station and averaged across stations to estimate mean density of zooplankton taxa in the entire nursery area. Taxa were grouped into the broader categories of microzooplankton (copepod nauplii and rotifers) and macrozooplankton (copepedites, adult copepods, and cladocerans).

Data analyses

Larval length was regressed on age and the relationship was used to convert larval length-frequency distributions to age-frequency distributions (see Secor and Houde 1995). Mean age was calculated for each 0.5 mm length bin (0 to 16.5 mm). Individuals within each length bin were assigned to daily age classes based on probabilities using the calculated mean age, a standard error of 4.6 days, and assuming ages were normally distributed. In the case of the three smallest and two largest length classes, the proportion of fish at age did not sum to one (0.93 to 0.99), thus proportions at age were scaled in these bins so that they summed to one. Yolk-sac larvae (≤ 3.0 mm) were assigned a mean age of zero. Larval hatch-date distribution was back-calculated based upon capture date and individuals were grouped into 9-day cohorts. Cohort-specific growth rates were calculated using exponential growth models:

$$L_t = L_0 e^{gt}$$

where L_t=standard length (mm), L_0=estimated standard length (mm) at age 0, t=age (days after hatch), and g=instantaneous growth coefficient ($mm \cdot d^{-1}$). Cohort-specific mortality rates were calculated using an exponential mortality model:

$$N_t = N_0 e^{-Zt}$$

where N_t=estimated abundance of larvae at a specified age, N_0=estimated abundance of larvae at age zero, and Z=instantaneous daily mortality coefficient (d^{-1}). Accuracy of estimates of growth and mortality depend on the assumption that fish within the selected size range were equally susceptible to the sampling gear (Ricker 1975).

Among-cohort differences in length-specific growth and mortality rate were examined using ANCOVA with age as a covariate. Cohort-specific larval growth and mortality rates were statistically related to mean temperature and mean freshwater discharge at different stages during early life history, including the hatch period, yolk-sac period (≤ 4.0 mm), post-yolk-sac period (>4.0 mm), and the entire larval duration (period from hatch to last date cohort appears in samples) using regression analysis (model structure described in Table 2). Residual sums of squares (RSS), the corrected AIC value (AICc), AIC value of a given model relative to model with the lowest AIC (ΔAIC), and the likelihood and probability of each model were calculated. Because sample sizes were small (n=4), we relied on model probability values to compare the fit of the linear models describing the relationship between environmental conditions and vital rates during specific early life history stanzas.

Abundance at 45 days after hatch (assumed habitat transition age; Kraus and Secor 2004) was predicted for each larval cohort based upon initial observed river-wide larval abundance estimates of each cohort and cohort-specific mortality rates. These adjusted abundances were used to calculate the expected proportional contribution of each cohort to population abundance at 45 days, termed here as the "population's hatch-date distribution".

To test the hypothesis that contingent members were randomly drawn from the population's hatch-date distribution, the proportion of resident and migratory fish derived from each larval cohort (determined from back-calculated hatch dates of juvenile white perch) was compared between contingents and with the overall population using a chi-square goodness of fit test.

All statistical analyses were performed with SAS Version 8.2 (SAS Institute, Cary, NC); α=0.05 was used as a critical level of significance. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. In the case of unequal variances, identified when modeling growth across cohorts, variance was calculated for each individual cohort in PROC Mixed (SAS Version 8.2), which enables fitting of linear models in which data exhibit heterogeneous variances. Spatial differences (between grouped upriver and downriver stations) in zooplankton density were examined using ANOVA. In the case of non-normality, identi-

fied in copepedite, adult copepod, and cladocera density data, data were log transformed for statistical analyses.

Results

Hatch date analysis

Estimated ages of juvenile fish (n=74) ranged from 47 to 75 days post-hatch. Hatch dates ranged from April 13 to May 8 for the migratory contingent and April 9 to May 12 for the resident contingent. Based on hatch date, juveniles from each contingent were grouped into their corresponding larval cohorts (Table 1, Fig. 2). Members of both contingents came from larval cohorts D, E, F, and G with the highest proportion of migratory (59%) and resident contingent fish (37%) originating from cohort E. Significant differences were identified among contingents in the proportion of individuals derived from early- (cohorts D and E) and late-spawned (cohorts F and G) cohorts (chi square=4.63, d.f.=3, p=0.03). The distribution of hatch dates of the migratory contingent was centered on early-spawned cohorts with 82% of fish derived from cohorts D and E, whereas members of the resident contingent were drawn from a more even distribution of hatch dates (Fig. 2). A higher percentage of resident contingent fish came from late-spawned cohorts (41% contribution of cohorts F and G to resident contingent compared to 18% contribution to migratory contingent).

An overall population hatch date distribution (Fig. 2) was calculated from initial larval cohort abundance and cohort-specific mortality rates (mortality rates of cohorts G and H were assumed to be equal to cohort F, Table 1). There was a significant difference in the hatch dates of migratory and resident contingents and the population's distribution ($p<$ 0.01). Relative to the population's hatch-date distribution, the distribution of migratory contingent fish was skewed toward earlier spawned cohorts, whereas the distribution of resident fish was skewed toward later spawned cohorts (Fig. 2). Neither contingent exhibited representatives of the earliest (cohorts A and B) nor latest (cohorts G and H) spawned cohorts, which were present in the overall population's distribution.

Table 1 Hatch-date range, assigned hatch-date (median) for each cohort. Growth and mortality rate for each cohort. Mean environmental conditions (temperature, freshwater discharge) experienced over the early life history period (hatch period for each cohort, yolk sac period (1.5–4.0 mm), post-yolk-sac period (>4.0 mm), and the entire larval duration (period from hatch to last date cohort appears in samples)

Cohort	Hatch-Date Range		Assigned Hatch Date	Growth rate (mm d^{-1}) (SE)	Mortality rate (d^{-1}) (SE)	Mean Temperature (°C)				Mean Freshwater flow (m^3s^{-1})			
						Hatch-date	Yolk sac	Post-yolk sac	Larval duration	Hatch-date	Yolk sac	Post-yolk sac	Larval duration
A	12-Mar	20-Mar	16-Mar		0.08 (0.08)	7.5	8.3	15.2	15.4	9.1	20.4	18.2	18.2
B	21-Mar	29-Mar	25-Mar		0.08 (0.03)	8.7	9.7	16.0	16.2	37.8	45.2	13.8	19.5
C	30-Mar	7-Apr	3-Apr	0.02 (0.002)	0.06 (0.01)	11.3	13.3	16.4	16.7	48.3	37.0	11.4	16.9
D	8-Apr	16-Apr	12-Apr	0.02 (0.002)	0.05 (0.01)	14.6	15.2	16.7	17.0	13.2	11.2	11.5	11.7
E	17-Apr	25-Apr	21-Apr	0.03 (0.002)	0.05 (0.04)	15.7	15.4	17.1	17.4	10.9	10.5	11.7	11.3
F	26-Apr	4-May	30-Apr	0.04 (0.004)	0.03 (0.04)	15.1	14.9	18.0	18.3	11.7	11.1	12.1	11.5
G	5-May	13-May	9-May	0.04 (0.008)		16.9	18.9	17.2	18.1	8.3	8.2	14.8	11.5
H	14-May	22-May	18-May			17.8	15.6	19.6	18.4	15.0	16.2	9.3	12.9
I	23-May	31-May	27-May			17.6	19.2		18.7	10.8	8.9		10.8

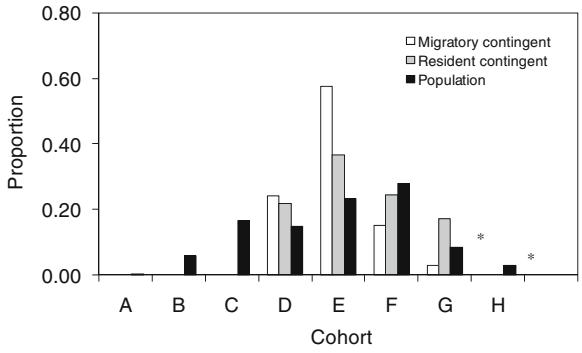

Fig. 2 Proportion of individuals within each juvenile white perch contingent (migratory and resident) and the overall population derived from each larval cohort. Asterisk indicates that these proportions were estimated based on the initial abundance of cohorts and an assumed mortality rate equal to cohort F

Larval age-length relationship

A relationship between larval age and length was established based on a representative subsample of white perch larvae (n=109; Fig. 3). Four outliers were identified based on studentized residuals (values>3), and removed (R^2 of model with outliers=0.77, R^2 of model without outliers = 0.90). The final model was Length=4.24*age-7.28 (n=105, S.D.=4.6, R^2=0.90). Using the age-length key, length frequencies of larvae were converted to age frequencies ranging from 0 to 70 days (Fig. 4). Inspection of age frequency data showed the progression of two broad seasonal cohorts with peaks in spawning occurring around April 3 and 25. Hatch dates of larvae ranged from March 12 to May 31.

Larval vital rates

Cohort-specific instantaneous growth rates (g) ranged from 0.02 mm·d^{-1} (cohort C) to 0.04 mm d^{-1} (cohort G; Table 1, Fig. 5). Growth rates were not estimated for cohorts A, B, H and I due to the low abundance of these cohorts and consequent low representation within our samples. Instantaneous growth rates of those early-spawned cohorts (D and E) represented in juvenile samples were lower than later-spawned cohorts (F and G; Table 1). A test of equality of slopes of cohort-specific age-length relationships indicated growth rates were significantly different among these cohorts (ANCOVA $F_{3,38.6}$=3.36, p=0.02). One outlier was removed from this analysis based on studentized residual value >3.

Cohorts spawned in April had the highest initial abundances (cohort C, E, F, D, respectively), whereas earlier- (cohorts A, B) and later-spawned cohorts (cohorts G, H) had low initial abundances (Fig. 4). Cohort-specific mortality rates were calculated for cohorts A-F and ranged from 0.08 d^{-1} (cohort A) to 0.03 d^{-1} (cohort F; Table 1, Fig. 6). Mortality rates could not be calculated for cohorts G-I based on the limited data available. Calculation of mortality rates for cohorts E and F were based on only a few observations over time and thus the rates should be interpreted cautiously. The earliest spawned cohorts had the highest mortality rates, with rates decreasing as the spawning season progressed. A test of equality of slopes of larval cohort abundance-at-age for cohorts represented in either resident or migratory contingents (D, E, F, and G) was not possible due to small sample size.

Influence of environmental conditions on larval growth rates

An increase in temperature was recorded within the nursery area during the period of larval production (Fig. 7). Periodic decreases in temperature of 2–3°C occurred during spring and typically coincided with spikes in freshwater discharge. The RK 53 temperature record mirrored the trends identified in the longer duration record at RK 72, albeit slightly lagged and at a higher amplitude (Fig. 7). Because the RK 72 temperature record provided a single continuous

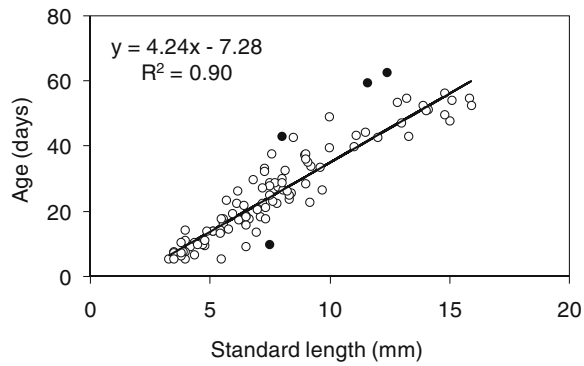

Fig. 3 Regression of otolith-based estimated age (temperature-adjusted) on standard length (n=109) for larval white perch from the Patuxent River estuary (2005). Outliers removed from regression analysis are shown as filled circles

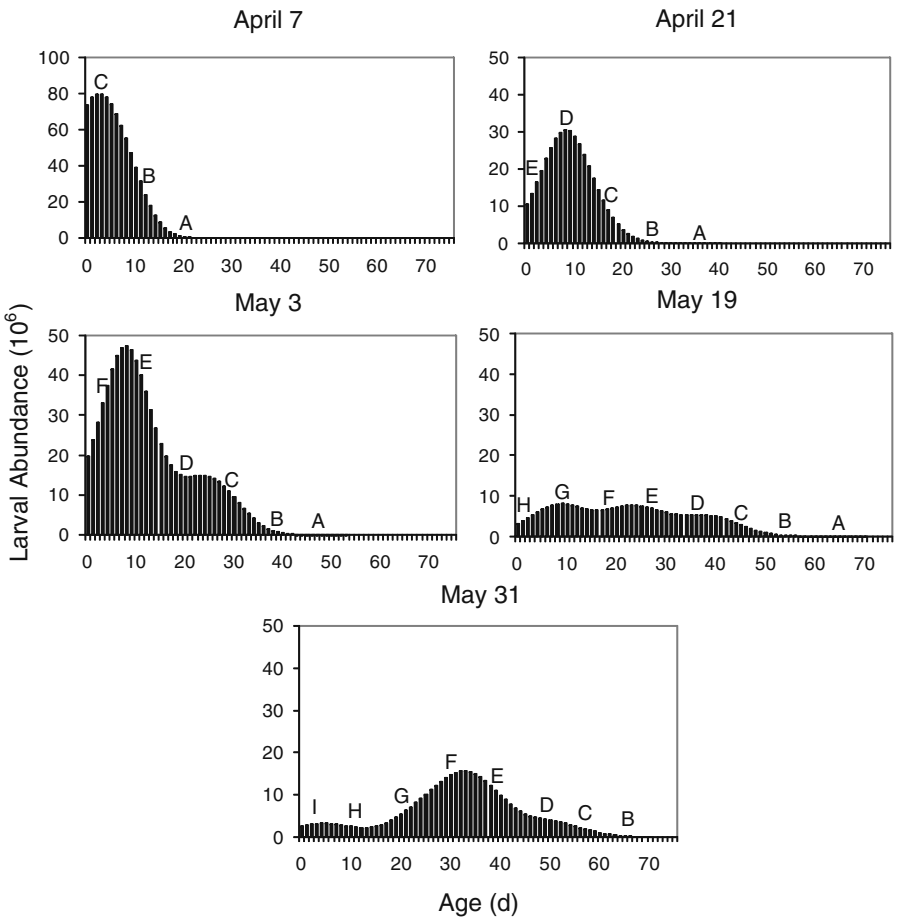

Fig. 4 Estimated riverwide abundance-at-age of larval white perch in the Patuxent River on each survey date in 2005 (April 7, April 21, May 3, May 19, and May 31). Letters denote mean age of larval cohorts at each sampling date

record, we used this data from this site in subsequent analyses. Freshwater discharge in the Patuxent River averaged 18 $m^3 \cdot s^{-1}$ from March 12 to May 31. Early in the larval production period (March 26 to April 6) periodic peaks in freshwater discharge occurred, with values as high as 128 $m^3 \cdot s^{-1}$. Later, freshwater discharge was relatively stable at less than 20 $m^3 \cdot s^{-1}$ (Fig. 7).

Temperature experienced during the entire larval period explained the most variance in larval cohort growth rate (Table 2). Temperature during the larval period of cohorts was positively correlated with growth rate (Pearson correlation coefficient=0.97, d.f.=3, p= 0.03). Freshwater flow conditions experienced during early life history phases explained very little variance in growth resulting in very low model probabilities.

Densities of zooplankton taxonomic groups (copepod nauplii, copepedites, adult copepods, cladocera, and rotifers) were similar between upriver (RK 62-75) and downriver stations (RK 44–59; p>0.05 for all groups) across sampling dates; therefore zooplankton was analyzed at the river-scale. Trends in microzooplankton and macrozooplankton densities were similar: both were relatively low during April-early May, peaked in mid-May, and returned to low densities in late May (Fig. 8). Shifts in the dominant taxa occurred over the course of the production season. The composition of zooplankton was dominated by adult copepods on April 7, copepod nauplii and copepedites on April 21 and May 3, cladocera and rotifers on May 19, and cladocera on May 31. Due to the periodicity of sampling we could not quantitatively test the influence of zooplankton density on larval growth rate.

Discussion

Through larval cohort analyses we have documented a sequence of events that link spawning phenology to

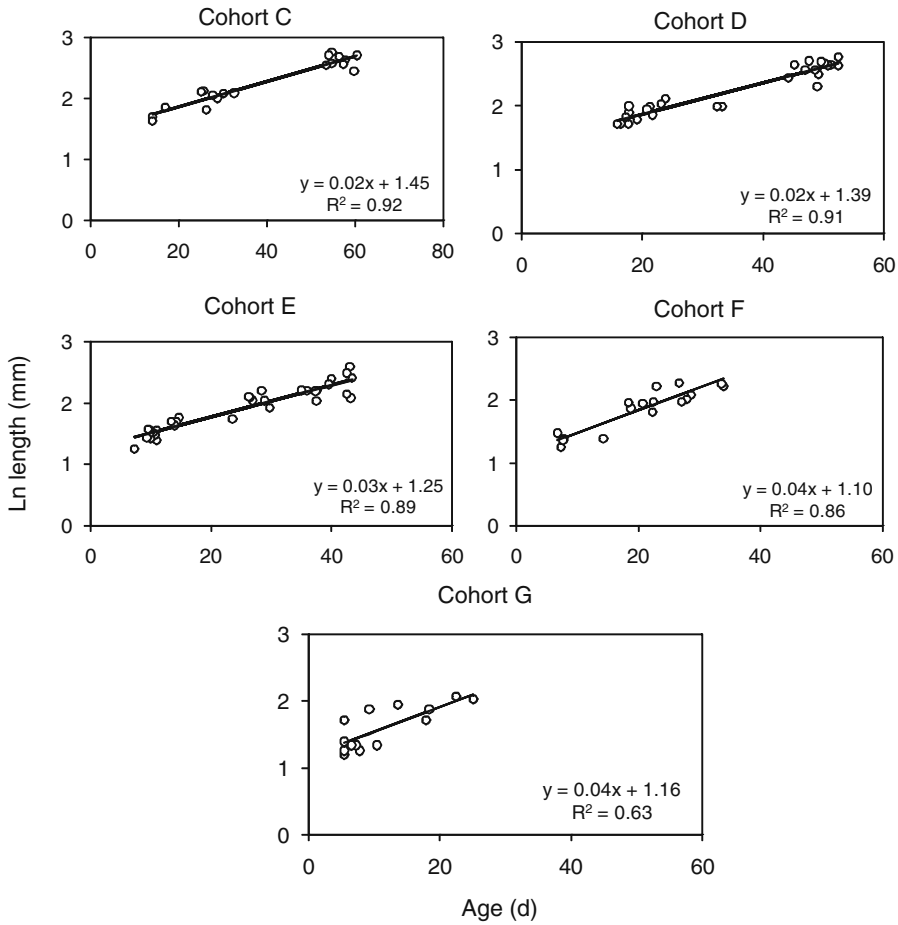

Fig. 5 Regressions of Ln (length) on age (days) for white perch cohorts (Patuxent River, 2005, cohort C, cohort D, cohort E, cohort F, cohort G)

the phenomenon of partial migration in an estuarine-dependent fish. White perch spawning, like that of congeneric striped bass, is cued by the initial rise in temperature during spring (Rutherford and Houde 1995; Secor and Houde 1995). This time period is also typically characterized by frequent precipitation events and pulsed freshwater flow into this estuary (North et al. 2005; this study). White perch continue to spawn over a wide temperature range (10 to 20°C; Funkerburk et al. 1991). Thus, variability in the environment of temperate, shallow estuaries like the Patuxent River can result in diverse thermal conditions for white perch larvae and their zooplankton prey. Consequently, within-season larval growth and survival rates can be highly variable. Growth rate of early-spawned larval cohorts represented in juvenile contingents was lower compared to later-spawned cohorts. Individuals from early-spawned cohorts contributed disproportionately to the migratory contingent. In addition to slower growth, mortality was higher for early-spawned than later-spawned cohorts, although a lack of data precluded testing of significance. A greater proportion of resident fish came from later-spawned cohorts that grew faster than early-spawned cohorts. The trends in direct estimates of larval growth are supported by back-calculated estimates of larval growth from migratory and resident juveniles, with significantly slower larval growth rates calculated for migratory compared to resident fish (Kraus and Secor 2004; Kerr and Secor 2009). Previous studies revealed that the migratory behavior initiated during the juvenile stage persists over the lifetime of individuals (Kerr et al. 2009; Kerr and Secor 2009). Thus, white perch exhibit partial migration whereby spawning time and the subsequent conditions experienced by larvae have latent effects on spatial behaviors adopted by juveniles and adults.

Our analysis revealed that contingent members were not randomly drawn from the population's larval

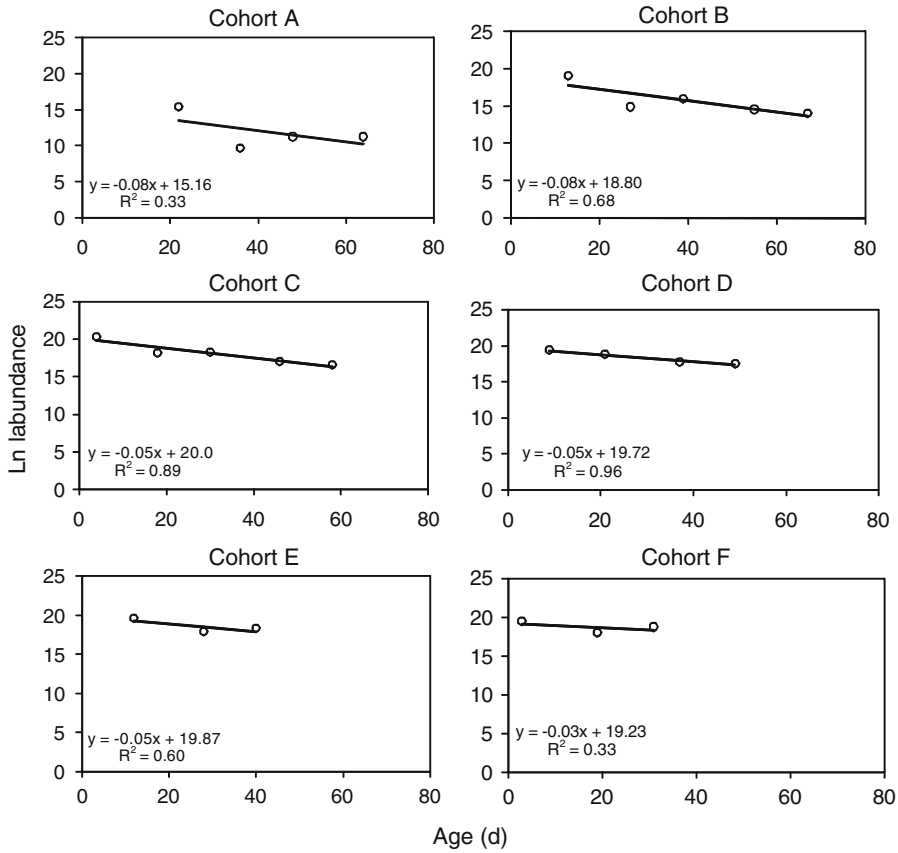

Fig. 6 Regressions of Ln (abundance) on age (days) for larval white perch cohorts (Patuxent River, 2005; cohort A, cohort B, cohort C, cohort D, cohort E, cohort F)

hatch-date distribution, rather they were derived from specific larval cohorts with particular growth attributes. Several of the larval cohorts (cohorts A, B, C, H, and I), identified through cohort analysis, were not represented in either juvenile contingent. Water temperatures below 10°C or episodic drops in temperature (2–5°C) can cause significant mortality to early life stages of white perch (Setzler-Hamilton 1991). Low temperatures in mid- to late March and periodic decreases in temperature early in the spawning season in concert with high freshwater flow were the likely cause of low initial abundance and high mortality of cohorts A and B. Cohort C was relatively well- represented in our forward projection of relative abundance of cohorts at the time of habitat transition; however, the absence of this cohort in the juvenile population may indicate that we underestimated larval-stage mortality or this cohort was subject to high mortality in the transition from the larval to juvenile stage. Because cohorts H and I were present only in our last two sampling events mortality rates were not calculated. However, these late-spawned cohorts had low initial abundance, likely due to the cessation of white perch spawning as temperatures increased above threshold levels.

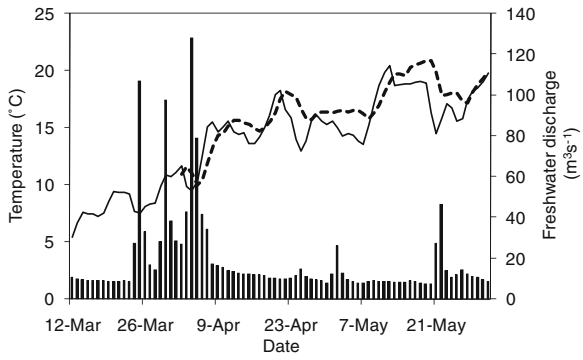

Fig. 7 Temperature (°C) recorded over the larval production season at river km 72 (*solid line*; Chesapeake Bay Program Water Monitoring Station) and river km 53 (*dashed line*) in the Patuxent River. Freshwater discharge (*solid bars*; USGS Site: Patuxent River near Bowie, MD, Site #: 01594440) is shown on the secondary y-axis

Environmental conditions experienced by white perch larval cohorts influenced growth rate. Specifi-

Table 2 Summary of model selection statistics relating growth of white perch cohorts to mean environmental conditions (temperature (temp), freshwater discharge (FW)) experienced over the early life history period (hatch period for each cohort, yolk-sac period (1.5–4.0 mm), post-yolk-sac period (>4.0 mm), and the entire larval duration (period from hatch to last date cohort appears in samples). Residual sums of squares (RSS), the corrected AIC value (AICc), the difference between model with the lowest AIC (ΔAIC), and likelihood and probability of each model are reported. Statistics for the AICc selected model are shown in bold. For all models the number of parameters was two and number of observations was 4

	Model		RSS	AICc	ΔAIC	Model likelihood	Model probability
Growth Rate	Temp	Hatch	8.56E-05	−27.01	7.50	0.02	0.02
		Yolk sac	9.43E-05	−26.62	7.88	0.02	0.02
		Post-yolk	5.49E-05	−28.79	5.72	0.06	0.05
		Larval duration	**1.32E-05**	**−34.50**	**0.00**	**1.00**	**0.82**
	FW	Hatch	7.41E-05	−27.59	6.91	0.03	0.03
		Yolk sac	8.93E-05	−26.84	7.66	0.02	0.02
		Post-yolk	6.21E-05	−28.30	6.21	0.04	0.04
		Larval duration	1.01E-04	−26.36	8.15	0.02	0.01

cally, temperature experienced by white perch larval cohorts during the entire larval period was positively associated with growth rate. Previous analysis of larval growth rates of striped bass in Chesapeake Bay estuaries showed a strong positive relationship with temperature, with early-spawned larvae experiencing lower temperatures and exhibiting lower growth rates than later-spawned larvae (Rutherford and Houde 1995; Secor and Houde 1995).

High microzooplankton density may have had a positive influence on white perch cohort growth and a negative impact on mortality rates. Trends in microzooplankton in the Patuxent River indicated high densities occurred in mid-May, coinciding with initiation of first-feeding by larvae from late season cohorts F and G. Late season cohorts exhibited the fastest growth rates and lowest mortality rate (in the case of cohort F), which may be attributable, in part, to high prey availability during early life history. Conversely, low zooplankton density during April and early May may have contributed to slower growth and higher mortality of earlier-spawned cohorts of white perch. Similar to our 2005 results, Campfield (2004) found microzooplankton (copepod nauplii and rotifers) density in the Patuxent River in 2001 peaked in early-to mid-May. Spawning occurred slightly later in 2001 and, consequently, white perch larval cohort growth rates were higher earlier in the season in 2001, coinciding with high zooplankton abundance and more optimal temperatures for growth (Campfield 2004). High concentrations of prey were also found to positively influence feeding success of first-feeding white perch larvae in the upper Chesapeake Bay (Shoji et al. 2005). Likewise, Limburg et al. (1999) identified a positive correlation between zooplankton density and larval white perch growth in the Hudson River. Thus, similar to patterns identified in other estuaries, we found an association between larvae that experienced high food availability during the first-feeding stage and enhanced growth and our analysis revealed that these individuals were more likely to remain resident in the freshwater habitat.

Across years, variation in the proportion of resident and migratory fish in the Patuxent River has been correlated with streamflow, with a high proportion of the migratory contingent in high streamflow

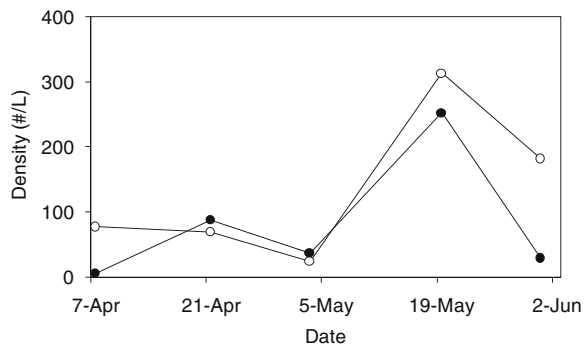

Fig. 8 Trends in riverwide microzooplankton (*closed circles*; copepod nauplii and rotifer) and macrozooplankton (*open circles*; copepedite, adult copepod, and cladocera) across sampling dates during spring 2005 in the Patuxent River

conditions (96%), lower proportion in low flow conditions (85%), and absence of the migratory contingent in drought years (Kraus and Secor 2004). The positive relationship between migratory contingent representation and streamflow could reflect a higher initial abundance of larval cohorts (i.e., higher spawning intensity) that ultimately express migratory behavior in high flow years. Alternatively, this relationship could be attributable to conditions likely to enhance survival (i.e., increased turbidity and zooplankton production; North and Houde 2003) for slower growing larval cohorts during years of higher streamflow.

The relationship between timing of spawning, environmental conditions, and spatial structure of the population indicates that the spawning behavior of white perch could play an important role in dampening both temporal and spatial recruitment variability within the population (Secor 2007). The moderately protracted spawning season of white perch may have been selected to minimize the risk of recruitment failure due to the failure of larvae to encounter appropriate nursery habitat conditions (Cushing 1975). Diversity in spawning time is hypothesized to be related to diverse size and age structure within a population, with larger, older females often spawning earlier in the season (Secor 2000; Secor 2007). Evidence from the present study suggests that a range of spawning times contribute to diverse outcomes for seasonal larval cohorts, which underlies contingent structuring. If larger fish spawn earlier, this could be a mechanism for migratory fish, which are larger-at-age compared to resident fish (Kraus and Secor 2004), to have a higher probability of spawning migratory young. Tsukamoto et al. (1987) observed a tendency for resident adults of Japanese ayu (*Plecoglossus altivelis*) to produce dispersive progeny based on their timing of spawning and vice versa. Additionally, through batch spawning a single white perch might contribute progeny to both the resident and migratory contingents within a single year-class. Observations of eggs in various stages of development in mature females indicate that individual white perch likely spawn multiple times during a single spawning season (Mansueti 1964). Thus spawning phenologies, both between and within individuals, could insure the maintenance of partial migration across successive generations.

Evidence presented here supports the idea that partial migration in white perch is maintained by a conditional strategy, wherein individuals adopt alternative life history tactics based on individual growth rate, as modified by the environment, relative to a genetically determined growth threshold. Direct and back-calculated estimates of larval growth rates indicate that fish destined to become members of the migratory contingent grow more slowly during early life history compared to resident fish (Kraus and Secor 2004; Kerr and Secor 2009). Subsequent to dispersal from the freshwater natal habitat, migratory contingent fish exhibit higher juvenile growth rates compared to resident contingent fish (Kerr and Secor 2009), and this trend continues into the adult stage (Kraus and Secor 2004). This reversal of growth trajectory is consistent with the concept of compensatory growth, with the migratory contingent compensating for slow early growth once they are established in a habitat of higher resource availability (Metcalfe and Monaghan 2001).

In this investigation, we gained insight into the unique characteristics that define resident and migratory contingent members and the controlling factors at work during early life history of fishes that define partial migratory behavior. Empirical (Kraus and Secor 2005) and modeling (Kerr et al. 2010) work shows that partial migration in Patuxent River estuary white perch dampens recruitment variability, and promotes stability and resiliency to long term climate cycles that occur in the Chesapeake Bay (Kimmel and Roman 2004). Increased understanding of the proximate cause of spatial structuring within populations can enable better management in response to climate change and other future environmental stresses. Specifically, management for increased age and size diversity within the Patuxent River population of white perch may be key in maintaining a protracted spawning period and preserving contingent structure.

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References

Berthold P (2001) Bird Migration: A General Survey. Oxford University Press, New York

Bujold V, Cunjak RA, Dietrich JP, Courtemanche DA (2004) Drifters versus residents: assessing size and age differences in Atlantic salmon (*Salmo salar*) fry. Can J Fish Aquat Sci 61(2):273–282. doi:10.1139/f03-162

Bulak JS, Crane JS, Secor DH, Dean JM (1997) Recruitment dynamics of Striped Bass in the Santee-Cooper system, South Carolina. Trans Am Fish Soc 126:133–143. doi:10.1577/1548-8659(1997)126<0133:RDOSBI>2.3.CO;2

Campana SE, Jones CM (1992) Analysis of otolith microstructure data. In: DK Stevenson and SE Campana, Editors, Otolith microstructure examination and analysis. Can Spec Publ Fish Aquat Sci 117:73–100

Campfield PA (2004) Ichthyoplankton community structure and feeding ecology in the Patuxent River estuarine transition zone. University of Maryland, College Park, MD, MS thesis

Cronin WB (1971) Volumetric, areal, and tidal statistics of the Chesapeake Bay estuary and its tributaries. Ches Bay Inst Spec Rep 20

Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, Cambridge, England

Edeline E (2007) Adaptive phenotypic plasticity of eel diadromy. Mar Ecol Prog Ser 341:229–232. doi:10.3354/meps341229

Forseth T, Naesje TF, Jonsson B, Harsaker K (1999) Juvenile migration in brown trout: a consequence of energetic state. J Anim Ecol 68(4):783–793. doi:10.1046/j.1365-2656.1999.00329.x

Fromentin JM, Powers JE (2005) Atlantic bluefin tuna: population dynamics, ecology, fisheries and management. Fish Fish 6:281–306. doi:10.1111/j.1467-2979.2005.00197.x

Funkerburk S, Jordan S, Mihursky J, Rileys D (1991) Habitat requirements for Chesapeake Bay Living Resources. Chesapeake Bay Program, Chesapeake Research Consortium, Annapolis, MD

Houde ED, Chesney EJ, Nyman RM, Rutherford ES (1988) Mortality, growth, and growth rate variability of Striped Bass larvae in Chesapeake subestuaries. Interim Report to Maryland Department of Natural Resources. Chesapeake Biological Laboratory, Solomons, Maryland, Reference No. [UMCES] CBL 88–96

Houde ED, Morin LG (1990) Temperature effects on otolith daily increment deposition in Striped Bass and white perch larvae. International Council for the Exploration of the Sea, Copenhagen, Denmark, Council Meeting 1990/M:5

Houde, ED, Nyman RM, Rutherford ES (1989) Cohort-specific growth and mortality rate variability of larvae of anadromous Striped Bass (*Morone saxatilis*) and white perch (*Morone americana*). International Council for the Exploration of the Sea, Copenhagen, Denmark, Council Meeting 1989/M:15.

Jonsson B, Jonsson N (1993) Partial migration: niche shift versus sexual maturation in fishes. Rev Fish Biol Fish 3:348–365. doi:10.1007/BF00043384

Kerr LA, Cadrin SX, Secor DH (2010) The role of spatial dynamics in the stability, resilience, and productivity of an estuarine fish population. Ecol Appl 20(2):497–507

Kerr LA, Secor DH (2009) Bioenergetic trajectories underlying partial migration in Patuxent River (Chesapeake Bay) white perch (*Morone americana*). Can J Fish Aquat Sci 66(4):602–612. doi:10.1139/F09-027

Kerr LA, Secor DH, Piccoli P (2009) Partial migration of fishes as exemplified by the estuarine-dependent white perch. Fisheries 34(3):114–123

Kraus RT, Secor DH (2004) Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA. Mar Ecol Prog Ser 279:247–259. doi:10.3354/meps279247

Kraus RT, Secor DH (2005) Connectivity in estuarine white perch populations of Chesapeake Bay: evidence from historical fisheries data. Est Coast Shelf Sci 64:108–118. doi:10.1016/j.ecss.2005.02.010

Kimmel DG, Roman MR (2004) Long-term trends in mesozooplankton abundance in Chesapeake Bay, USA: influence of freshwater input. Mar Ecol Prog Ser 267:71–83. doi:10.3354/meps267071

Limburg KE (2002) Cohort identification. In: Fuiman LA, Werner RG (eds) Fishery Science: The Unique Contributions of Early Life Stages. Blackwell Publishing, Malden, MA, pp 143–160

Limburg KE, Pace ML, Arend KK (1999) Growth, mortality, and recruitment of larval *Morone* spp. in relation to food availability and temperature in the Hudson River. Fish Bull 97:80–91

Mansueti RJ (1964) Eggs, larvae, and young of white perch, *Roccus americanus*, with comments on its ecology in the estuary. Ches Sci 5:3–45

Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? Trends Evol Ecol 16:254–260. doi:10.1016/S0169-5347(01)02124-3

North EW, Hood RR, Chao S-Y, Sanford LP (2005) The influence of episodic events on transport of Striped Bass eggs to an estuarine nursery area. Estuaries 28(1):106–121. doi:org/10.1007/BF02732758

North EW, Houde ED (2001) Retention of white perch and Striped Bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. Estuaries 24:756–769

North EW, Houde ED (2003) Linking ETM physics, zooplankton prey, and fish early-life histories to Striped Bass *Morone saxatilis* and white perch *M. americana* recruitment. Mar Ecol Prog Ser 260:219–236. doi:10.3354/meps260219

Pechenik JA (2006) Larval experience and latent effects-metamorphosis is not a new beginning. Int Comp Biol 46:323–333. doi:10.1093/icb/icj028

Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bull Fish Res Bd Can 191:1–382

Rutherford ES, Houde ED (1995) The influence of temperature on cohort-specific growth, survival, and recruitment of

Striped Bass, *Morone saxatilis*, larvae in Chesapeake Bay. Fish Bull 93:315–332

Secor DH (1992) Application of otolith microchemistry analysis to investigate anadromy in Chesapeake Bay Striped Bass Morone saxatilis. Fish Bull 90(4):798–806

Secor DH (2000) Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay Striped Bass. ICES J Mar Sci 57:403–411. doi:10.1006/jmsc.1999.0520

Secor DH (2007) The year-class phenomenon and the storage effect in marine fishes. J Sea Res 57:91–103. doi:10.1016/j.seares.2006.09.004

Secor DH, Houde ED (1995) Temperature effects on the timing of Striped Bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries 18:527–544. doi:10.1007/BF02690134

Secor, DH, Houde ED, Monteleone DM (1994) Development of otolith-marking methods to estimate survival and growth of early life stages of natural and hatchery-produced Striped Bass in the Patuxent River in 1991. Final report to Govenor's Council on the Chesapeake Bay Research Fund.

Secor, DH, Kerr LA (2009) A lexicon of life cycle diversity in diadromous and other fishes. In: Haro et al., editors. 2009. Challenges for Diadromous Fishes in a Dynamic Global Environment. American Fisheries Society Symposium 69: 537–556.

Setzler-Hamilton, E (1991) White perch, Morone americana. In: Funderbunk SL, Mihursky JA, Jordan SJ, Riley D. Habitat requirements for Chesapeake Bay living resources 2nd ed. Chesapeake Research Consortium Solomons, 12-1–12-20

Setzler-Hamilton EM, Jones PW, Martin FD, Ripple K, Mihursky JA (1981) Comparative feeding habits of white perch and Striped Bass larvae in the Potomac estuary. Proc An Meet Pot Chap Am Fish Soc 5:138–157

Shoji J, North EW, Houde ED (2005) The feeding ecology of *Morone americana* larvae in the Chesapeake Bay estuarine turbidity maximum: the influence of physical conditions and prey concentrations. J Fish Biol 66:1328–1341. doi:10.1111/j.0022-1112.2005.00685.x

Tsukamoto K, Nakai I, Tesch FW (1998) Do all freshwater eels migrate? Nature 396:635–636. doi:10.1038/25264

Tsukamoto K, Ishida R, Naka K, Kajihara T (1987) Switching of size and migratory pattern in successive generations of landlocked ayu. In: Dadswell MJ, Klauda RJ, Moffitt CM, Saunders RL, Rulifson RA, Cooper JE. Common strategies of anadromous and catadromous fishes. Am Fish Soc Symp 1, Am Fish Soc, Bethesda MD.492–506

Uphoff J (1989) Environmental effects on survival of eggs, larvae, and juveniles of Striped Bass in the Choptank River, Maryland. Trans Am Fish Soc 188:251–263. doi:10.1577/1548-8659(1989)118<0251:EEOSOE>2.3.CO;2

Waldman JR, Young JR, Lindsay BP, Schmidt RE, Andreyko H (1999) A comparison of alternative approaches to discriminate larvae of Striped Bass and white perch. North Am J Fish Manag 19:470–481, 10.1577/1548-8675(1999)019<0470:ACOAAT>2.0.CO;2

Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. Can J Fish Aquat Sci 49:2196–2218. doi:10.1139/f92-242