ABSTRACT

Title of Document: INFLUENCE OF PARTIAL MIGRATION AND ENVIRONMENTAL CHANGE ON THE POPULATION DYNAMICS OF WHITE PERCH (MORONE AMERICANA) WITHIN THE HUDSON RIVER ESTUARY

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Marine Estuarine Environmental Sciences

White perch are a common estuarine fish that exhibit a complex life cycle, characterized by partial migration and sensitivity to ecosystem characteristics. Field collections, otolith microchemistry, otolith microstructure and environmental and biological monitoring data were used to investigate the prevalence of partial migration and environmental influence across life history stages of white perch within the Hudson River. Otolith strontium:calcium profiles identified a freshwater resident contingent and a migratory contingent which utilized brackish habitats. Demographic analyses indicated that migratory fish hatched earlier and experienced cooler temperatures as larvae compared to residents, and subsequently grew faster as juveniles and adults. Comparisons of early-life characteristics before (1974-1991) and after (1992-2013) the invasion of zebra mussels indicated that juvenile abundance became more sensitive to density-dependence and freshwater flow after the invasion, while growth and spatial distribution changed little. Partial migration and environmental sensitivity will shape Hudson River white perch responses to future climate change.

INFLUENCE OF PARTIAL MIGRATION AND ENVIRONMENTAL CHANGE ON THE POPULATION DYNAMICS OF WHITE PERCH (MORONE AMERICANA) WITHIN THE HUDSON RIVER ESTUARY

By

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Thesis submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Master of Science
2016

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Acknowledgements

I would like to thank my family for their never-ending support of my academic pursuits in marine science. My mom and dad have always been supportive of my unusual fascination with biology, while at the same time keeping me grounded and looking ahead. My siblings- Dan, Pat and Erin- all have unique ways of encouraging me and making me laugh, both of which have been invaluable during my time in grad school.

I feel extremely lucky to have attended Chesapeake Biological Laboratory (CBL) over the last three years. Thanks to CBL faculty and research staff for always having an open-door policy, as well as asking questions about my research and providing constructive feedback at Brown Bag Seminars and other venues. The student community at CBL has also been incredibly helpful, whether it was through help with coursework, conversations about research, or providing an outlet for social activities outside of school. Special thanks to Matt Damiano, Emily Liljestrand, Suzan Shahrestani, Cara Simpson, Andrea Sylvia and Steve Timko in this regard. Also, special thanks to members of the Secor Lab- Mike O’Brien, Matt Siskey, Alex Atkinson, Aimee Hoover and Gray Redding- who have all been great friends and helped me directly or indirectly with important aspects of my thesis, whether it was field work, processing otoliths, or data analysis.

Phil Piccoli at the University of Maryland NanoCenter, was instrumental to the success of my thesis work, and spent countless hours teaching me how to use the electron microprobe, imaging otoliths and providing methodological support. I must also thank my committee members, Jeremy Testa and Helen Bailey, who each provided unique input to my thesis work, and were excellent teachers in their respective courses, which considerably broadened my academic interests. Last but certainly not least, I would like to thank my advisor, Dave Secor. Through his patience, support, and passion for research, Dave has enhanced my scientific curiosity and understanding beyond a level that I thought possible when I arrived at CBL three years ago. I have no doubt that Dave will remain a trusted mentor and friend throughout my career.

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Thesis overview

Complex Life Cycles in Fishes

The life cycles of fishes, especially during the egg and larval period, can be considered as a series of developmental stages, separated by specific thresholds in body form and function (i.e. saltatory development; Balon 1981). Complex life cycles entail stage-specific movements to new habitats (Werner and Gilliam 1984). Here, differences in growth and dispersal capabilities between stages within a complex life cycle can influence population dynamics, but these effects tend to be modulated by the productivity and stability of each stage's habitat (Wilbur 1980). Most fish species produce very small offspring in great quantity, presumably to take advantage of highly abundant but patchily distributed planktonic prey (Winemiller and Rose 1993), which in turn generates variability in feeding efficiency, growth and survival during the larval period (Houde 1987). Thus, variability in early life conditions, through their influence on vital rates and dispersal, can carry over to the demographics and ecology of subsequent stages (Bertram and Chambers 1993, O'Connor and Cooke 2015), although there have been few detailed studies examining such carryover effects within the life cycles of fishes (see Pechenik 2006, O'Connor et al. 2014).

One pathway by which carryover effects can shape complex life cycles is through partial migration, where multiple contingents with different spatial behaviors are contained within a single population (Secor 1999). Partial migration has been observed in a wide range of fish taxa (Chapman et al. 2012a), and is generally viewed as a conditional strategy, mediated by phenotypic plasticity, where individuals select a particular migration pathway early in life based on a combination of internal (e.g. energetic status, genetic predisposition) and external (e.g. environmental conditions, predation risk) factors (Chapman et al. 2012b, Brodersen et al. 2014). By these mechanisms, environmental conditions experienced early in life can carry over to influence contingent membership. Once contingent behaviors are initiated, the divergent spatial distributions that arise can help buffer populations against local environmental disturbance (Nims and Walther 2014), and have carryover effects on the growth and bioenergetics of each contingent, especially if habitat productivity differs between contingents (Morinville and Rasmussen 2002, Gillanders et al. 2015). This interplay between growth, dispersal and the productivity and stability of natal and non-natal habitats fits Wilbur's (1980) definition of a complex life cycle, where conditional responses, such as growth-dependent migration, are considered adaptations to persist in transient environments such as temperate rivers and estuaries.

While partial migration and other forms of life history diversity are important features of complex life cycles in fishes (Schindler et al. 2010), successful transitions between adjacent stages within the life cycle are highly reliant on the availability of suitable environmental conditions and prey densities. As a result, gradual shifts in environmental conditions due to climate change and abrupt changes in ecosystem characteristics (i.e. regime shifts) can both potentially alter multiple transitions within the life cycle and have substantial impacts on recruitment dynamics and population productivity (Paulik 1973, Collie et al. 2004). Recent studies of North Sea herring have demonstrated that climate-driven increases in temperature and reduced forage availability due to a regime shift can change life-stage transitions and result in diminished recruitment (Nash and Dickey-Collas 2005, Payne et al. 2009). However, the effects and potential interactions of regime shifts and climate change on life-stage transitions remain undocumented or poorly understood in many marine and estuarine fish species exhibiting complex life cycles.

Life Cycle of White Perch

White perch (*Morone americana*) are a dominant species in estuarine fish assemblages along the east coast of North America. Estuarine white perch exhibit a complex life cycle, where adults undertake spawning migration in the spring to deposit their eggs in tidal freshwater habitats near the head of the estuary over a period of 1-2 months (Mansueti 1964, Klauda et al. 1988). After emerging from their eggs, pelagic larvae are typically retained in these natal freshwater habitats, where their growth and survival is shaped by thermal conditions and densities of pelagic zooplankton prey (Limburg et al. 1998, Kerr and Secor 2010). At an age of 40-50 days, larvae metamorphose into fully-formed juveniles and settle in littoral habitats, where their diet shifts and becomes dominated by benthic and epibenthic invertebrates (Mansueti 1964, Bath and O’Connor 1985). The environmental conditions experienced by each individual during the larval period have carryover effects on behavior during the juvenile period, where shortly after settlement, juveniles originating from earlier hatch dates tend to disperse from the natal habitat and begin utilizing brackish habitats down-estuary (migratory contingent), while the remainder stay in freshwater (resident contingent; Kraus and Secor 2004a, Kerr and Secor 2010). The migratory contingent exhibits slower growth during the larval period, but increased consumption rates and enhanced productivity in brackish water result in faster growth rates during the juvenile period compared to residents (Kerr and Secor 2009). Faster growth in the migratory contingent subsequently persists into adulthood (Kraus and Secor 2004a). Thus, the life cycle of white perch involves an ontogenetic shift from pelagic to demersal habitats (Werner and Gilliam 1984), as well as conditional movements between freshwater and more productive brackish habitats driven by partial migration, which generally conforms to the description of a complex life cycle as defined by Wilbur (1980).

Thesis Objectives

The primary purpose of my thesis research is to describe the complex life cycle of white perch within the Hudson River Estuary (HRE) in the context of partial migration and large-scale environmental change. In Chapter 1, I evaluated the carryover effects of early-life characteristics on migration behavior in juvenile white perch, as well as the subsequent carryover effects of migration behavior on growth and maturation later in life. In Chapter 2, I utilized long-term monitoring data to quantify how gradual climate-driven increases in temperature and freshwater flow and an abrupt reduction in pelagic food availability due to the invasion of zebra mussels in the HRE have influenced life-stage transitions, growth and spatial distribution of white perch.

Objective 1 (Chapter 1)

To evaluate whether Hudson River white perch exhibit discrete modes of resident and migratory behaviors (i.e. contingent structure) as juveniles and adults, I used otolith strontium:calcium (Sr:Ca) profiles to determine contingent membership. All otoliths were analyzed via wavelength-dispersive X-ray spectrometry, with each juvenile otolith analyzed via transects of equally-spaced points from the core to the edge. Similarly, adults were analyzed in transects spanning the first year of life (i.e. from the core to the first annual ring), while a subsample of adults were further analyzed to assess whether first-year migration behaviors carried over to adult migration behaviors. Kraus and Secor (2004b) determined that otolith Sr:Ca is positively related to salinity in estuarine white perch, so this analysis enabled me to obtain a longitudinal record of salinities experienced by each individual throughout various points of the life-cycle. I hypothesized that, similar to previous studies in Chesapeake Bay, white perch in the HRE can classified into a resident contingent that remains in tidal freshwater habitats throughout most of the life cycle and a migratory contingent, characterized by dispersal and consistent use of brackish water habitats (Kerr and Secor 2011).

Objective 2 (Chapter 1)

After Sr:Ca profiles were employed to classify individuals into resident or migratory contingents in two year-classes (2013 and 2014) of juvenile white perch, I compared early-life attributes between contingents each year to assess potential carryover effects of early life history on migration behavior. Hatch date distributions obtained through the examination of otolith microstructure were compared between contingents each year. Hatch dates were used to calculate the mean temperature and freshwater flow experienced by each individual during the first 50 days of life, which were subsequently compared between contingents in 2013 and 2014. In addition, the biological intercept method was used to back-calculate larval size-at-age data for each individual (Campana 1990), and compare back-calculated sizes at an age of 50 days between contingents within each year-class. The age of 50 days was chosen because this should correspond to the age at which white perch metamorphose from larvae to fully-formed juveniles and thus integrates growth throughout the larval period (Mansueti 1964). Based on previous research in the Patuxent River, I hypothesized that the migratory contingent will have significantly earlier hatch dates and reduced larval size-at-age relative to the resident contingent in each year-class of juvenile white perch (Kraus and Secor 2004a, Kerr and Secor 2010).

Objective 3 (Chapter 1)

To test whether YOY white perch exhibit different late-juvenile growth rates, I compared age-length relationships between contingents in each year-class. Differences in lifetime growth characteristics were also assessed by constructing separate von Bertalanffy growth models for each contingent, and subsequently comparing parameter estimates (L_∞ *and* k) between contingents. In accordance with previous studies, I hypothesized that the migratory contingent will exhibit faster late-juvenile growth rates after dispersal to brackish habitats (Kraus and Secor 2004a, Kerr and Secor 2009), and that migratory adults will attain a larger maximum size (L_∞) and display a faster growth rate (k) relative to residents (Kraus and Secor 2004a). Effects of observed growth differences on contingent-specific reproductive potential and per-capita productivity will be explored using previously published maturity and fecundity functions (Klauda et al. 1988) and a yield-per-recruit analysis (see Appendix), respectively.

Objective 4 (Chapter 2)

Long-term monitoring data were used to determine the influence of environmental conditions and density-dependence on white perch early life-stage transitions, growth and spatial distributions after zebra mussels invaded the HRE (1992-2013) and compare these to effects observed before the invasion (1974-1991). Utilities monitoring data were used to estimate the standing stocks of white perch eggs, yolk-sac larvae (YSL), post yolk-sac larvae (PYSL), young-of-the-year (YOY) and adults from 1992-2013, and relationships between the abundance of adjacent life-stages were estimated using linear or nonlinear regression. Over this same time period, YOY white perch length distributions were used to construct an index of first-year growth, while standing stocks for each contingent were estimated based on where YOY were collected in relation to the salt front (above = resident, below = migratory), and used to create an index of spatial distribution. The effects of environmental (temperature and freshwater flow) and density-dependent (standing stocks of various life-stages) variables on white perch life-stage transitions, growth and distribution were quantified using a series of stage-structured models and correlation analyses. Due to the diminished abundance and increased environmental sensitivity of the forage base in the HRE after the invasion of zebra mussels (Caraco et al. 1997, Pace et al. 1998, Strayer et al. 2008), I hypothesized that white perch life-stage transitions, growth and spatial distribution became more sensitive to density-dependence and environmental conditions in the post-invasion period.

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Chapter 1: Partial migration in Hudson River white perch as a series of ecological carryover effects

Introduction

Individual movements and collective migrations cause fish populations to change their spatial distribution over time in response to environmental conditions, food availability and reproductive schedules (Nathan et al. 2008, Walther et al. 2015). Historical notions of marine fish migration held that individuals within a population followed a single common migration pathway, which was selected to optimize reproductive success under the constraint of larval dispersal within dilute marine environments (Harden-Jones 1968, Sinclair 1988). However, recent evidence has indicated that many fishes exhibit partial migration, wherein multiple groups, or contingents, within a single population show distinct patterns in their spatial distribution and habitat use (Secor 1999, Chapman et al. 2012a). Partial migration in fish populations is likely maintained through tradeoffs associated with each migration behavior in a given environment, although the causes and consequences of partial migration remain poorly understood in many species (Jonsson and Jonsson 1993, Chapman et al. 2012b). Nonetheless, the ubiquity of partial migration across taxa and across aquatic environments led Secor (2015) to posit that partial migration may be a general phenomenon in fishes and may serve as a unifying concept in studies of fish movement and migration.

Partial migration is increasingly recognized as an important type of life history diversity influencing the persistence of exploited fish populations (Secor 1999, Sherwood and Grobowski 2010, Bourret et al. 2016). At the population level, studies have shown that life history diversity in fishes enhances population stability, as well as its resilience to environmental perturbations, by spreading risk across population segments with asynchronous dynamics (i.e. the portfolio effect; Secor et al. 2009, Kerr et al. 2010, Schindler et al. 2010). Moreover, preserving the buffering (i.e. variance-dampening) effects of partial migration and other forms of life history diversity is thought to be important for maintaining sustainable fisheries (Hilborn et al. 2003) and facilitating fishery recovery after depletion (Petitgas et al. 2010, Morissette et al. 2016). Thus, developing a better understanding of the causes of divergent migration behaviors and subsequently quantifying their potential influence on population dynamics is considered important in addressing fisheries management objectives (Kerr and Goethel 2013). In addition, examining the influence of environmental conditions on partial migration dynamics can provide insight into how populations displaying partial migration are likely to respond to long-term changes in temperature and precipitation as a result of climate change (Beechie et al. 2006, Finstad and Hein 2012).

The causes and consequences of partial migration can be viewed as a series of ecological carryover effects, which arise when conditions experienced during a particular life history stage alter individual physiology or behavior, which subsequently influence the phenotype or performance of the individual at a later time (Pechenik 2006, O'Connor et al. 2014). Partial migration is thought to arise through the "threshold model," which posits that individuals adopt a particular migration behavior based on whether or not a threshold size or condition level is attained early in life (Brodersen et al. 2008, Pulido 2011). This can be interpreted as a carryover effect, where early-life environmental conditions (e.g. temperature, food availability) directly influence individual growth rates, which alter size or condition distributions and consequently determine the frequency of specific migration behaviors. Such divergent migration behaviors results in groups - or contingents - which are characterized by their unique spatial distributions (e.g. a resident freshwater contingent and migratory marine contingent). While the threshold model is important in determining migration behaviors, individual decisions to disperse or remain resident early in life may also be modulated by flow conditions (Conroy et al. 2015), predation risk (Skov et al. 2011) or genetic predisposition (Brodersen et al. 2014). Regardless of the causes of divergent migration behaviors, the resulting differences in environmental conditions and food webs encountered by each contingent can carry over to influence bioenergetics, growth, and maturity characteristics later in life (Morinville and Rasmussen 2002, Kraus and Secor 2004a, Gillanders et al. 2015). These differences in life history characteristics enable each contingent to uniquely contribute to aggregate population dynamics, which may ultimately carry over to influence the productivity, stability and resilience of the population (Kerr et al. 2010, Schindler et al. 2010, Secor 2015).

White perch (*Morone americana*) is an anadromous fish species native to the eastern seaboard of the United States and Canada, ranging from South Carolina to Nova Scotia (Setzler-Hamilton 1991), although introductions have expanded its range to include many inland lakes, ponds and reservoirs (e.g. Hawes and Parrish 2003). In estuaries, white perch typically migrate upriver in the spring to spawn in tidal freshwater habitats, where eggs and larvae develop (Mansueti 1964, Klauda et al. 1988). However, previous studies in Chesapeake Bay tributaries revealed that white perch populations exhibit partial migration, characterized by two contingents within a single population

(Kerr and Secor 2011). Specifically, white perch populations contain a resident contingent, where individuals remained in their natal freshwater habitat throughout life, in addition to a migratory contingent characterized by dispersal from the natal habitat and brackish water habitat use (Kerr et al. 2009). Moreover, previous studies in the Patuxent River discovered that contingent membership was shaped by early life history, whereby hatch dates influenced subsequent temperature exposure, prey availability and growth rates; earlier hatch dates and slower growth during the larval period was associated with the migratory contingent (Kraus and Secor 2004a, Kerr and Secor 2010). After dispersal, Kerr and Secor (2009) found experimental evidence that migratory juveniles displayed a higher consumption rate and scope for growth which, coupled with higher productivity in brackish habitats, resulted in higher growth rates in migratory white perch in the late-juvenile period. The growth benefits experienced by migratory juveniles subsequently persisted into adulthood, translating to higher lifetime growth rates (Kraus and Secor 2004a). Thus, partial migration facilitates carryover effects in white perch populations, allowing conditions experienced by individuals early in life to indirectly influence adult characteristics via the adoption of different migration behaviors. Moreover, there may be substantial inter-annual variability in the numerical dominance of each contingent, which is modulated by freshwater flow in Chesapeake Bay tributaries, such that wetter years favor the migratory contingent, while residents dominate in drought conditions (Kraus and Secor 2004a, 2005).

While there is an extensive body of research supporting Chesapeake Bay white perch as a model species for studying partial migration, it is currently unknown whether white perch partial migration occurs in other estuarine systems. The Hudson River

Estuary (HRE) differs from Chesapeake Bay tributaries in its configuration (with some characteristics of fjord, salt wedge and coastal plain estuaries; Geyer and Chant 2006), nutrient status (mesotrophic to eutrophic depending on the flow regime; Fisher et al. 1988, Howarth et al. 2006), and extent of watershed connectivity (e.g. fragmented littoral habitat). Primary production in the HRE is principally controlled by light and advection, rather than nutrients, in both the brackish and tidal freshwater portions of the estuary (Malone 1977, Cole and Caraco 2006, Howarth et al. 2006). Another major difference is the invasion of zebra mussels into tidal freshwater habitats in 1991, which has altered food web structure in this portion of the HRE and had demonstrable effects on fish abundance, growth and distribution (Strayer et al. 2004; Chapter 2). Still, primary and secondary production in the HRE are thought to be strongly affected by freshwater flow patterns (Strayer et al. 2008), with high average flows typically associated with lower phytoplankton, pelagic zooplankton and benthic invertebrate densities, oftentimes leading to reduced fish abundance, including that of white perch (Strayer et al. 2004; Chapter 2). Previous studies have reported enhanced primary productivity in the brackish region of the HRE relative to the tidal freshwater portion (Gladden et al. 1988, Howarth et al. 2006), which could potentially drive growth differences between contingents, although the productivity gradient within the estuary likely exhibits seasonal and inter-annual variability.

Previous studies have identified partial migration in other diadromous fish populations within the HRE, such as striped bass (Zlokovitz et al. 2003), blueback herring (Limburg and Turner 2016) and American eels (Morrison et al. 2003). In the case of American eels, differences in habitat use between contingents resulted in substantial differences in sub-adult (i.e. yellow eel stage) growth characteristics (Morrison and Secor 2003), similar to previous studies of white perch in Chesapeake Bay (Kraus and Secor 2004a). In this study, I focused on four main objectives: 1) test whether resident and migratory contingents are present in juvenile and adult white perch in the HRE, 2) compare early-life characteristics (hatch dates and larval size-at-age) between contingents in two year-classes, 3) compare juvenile growth rates between contingents, and 4) estimate and compare von Bertalanffy (i.e. adult) growth models for each contingent. To accomplish these objectives, I collected juvenile and adult white perch in the HRE, used otolith microchemistry to assign each individual to a contingent (objective 1) and employed analyses of otolith microstructure to obtain age information that enabled comparisons of contingent attributes (objectives 2-4). In general, I expected white perch in the HRE to conform to the pattern of partial migration observed in Chesapeake Bay, with earlier hatch dates and slower larval growth rates associated with migratory behavior in juveniles, which subsequently results in faster late-juvenile and adult growth rates after dispersal to brackish habitats (Kraus and Secor 2004a, Kerr and Secor 2010).

Methods

Field Collections and Subsampling

Young-of-the-year (YOY) white perch were collected by the NY State Department of Environmental Conservation (NYSDEC) fall seine survey with a 100’·4’ (30.5m·1.2m) beach seine from September to November in 2013 and 2014. The 2014 year class was further sampled with a 50’·6’ (15.2m·1.8m) beach seine in September 2014. These collections both took place in freshwater (Coxsackie, Germantown, Staatsburg and Poughkeepsie), brackish water (Haverstraw and Tappan Zee) and transition-zone (Newburgh, near the salt front) sites in the HRE in order to obtain a representative sample of resident and migratory contingents each year (Figure 1.1). White perch yearlings (age-1) were also captured in seine samples during 2013 (n = 22) and 2014 (n = 16), and these fish were classified as adults. Adult white perch were collected using 100’·6’ (30.5m·1.8m) gillnets with 2” (5.1cm) and 3” (7.6cm) mesh panels in the spring (May) and fall (September) of 2014. Multiple mesh sizes were used to capture adult white perch across a range of sizes. Gillnets were deployed in shoal areas (< 4 m depth), with each end attached to an anchor (lead line) and a buoy (float line), and were left to soak for 30-240 minutes before being retrieved. Collections of adult white perch in spring 2014 occurred only in the transition zone (Newburgh) and freshwater (Germantown and Staatsburg) portions of the estuary, as white perch were generally expected to run upriver during the spawning season (Klauda et al. 1988), while fall collections of adults occurred in freshwater (Germantown and Staatsburg) and brackish water (Haverstraw) sites. All individuals were frozen upon capture and transported back to the laboratory for further analysis (Table 1.1).

Due to the high numbers of adult white perch that were captured (n = 722; Table 1.1), adults were subsampled based upon their total length, sample site, and season of capture and randomly selected for otolith analyses within each category. Adults were assigned to 20 mm length stanzas from 100-300 mm, and all fish > 180 mm were selected due to the rarity of large adults (n = 59 > 180 mm) and their importance for contingent comparisons (see Statistical Analyses below). As a result, the size distribution of subsampled adults was skewed slightly towards larger sizes relative to the entire adult sample (Figure 1.2). YOY captured in 2014 (n = 226; Table 1.1) were also subsampled based on their location and date of capture in order to obtain a representative sample of each contingent. In total, 124 YOY white perch otoliths (n = 67 in 2013, n = 57 in 2014) and 229 adult white perch otoliths were analyzed for age determination and Sr:Ca profiles (Table 1.1; see following sections).

Otolith Processing and Age Determination

In the laboratory, frozen white perch were thawed and measured for total length (to nearest mm) and weight (to nearest 0.1 g). Otoliths were removed via dissection, embedded in Struers EpoFix resin (Struers ApS, Ballerup, Denmark), sectioned transversely to a width of ~1 mm with a Buehler low-speed Isomet saw (Buehler, Lake Bluff, IL), mounted on a microscope slide cover and attached to glass slides using Crystalbond 509 thermoplastic glue (Ted Pella Inc., Redding, CA). Subsequently, each otolith was polished on a Crystal Master 6-Plus lapping wheel (Crystalite Corp., Lewis Center, OH) with 320, 600 and 1200 grit until the core of each otolith was clearly visible. Polishing was completed by buffing each otolith on a microcloth with wet 0.3µm alumina powder until most pits and abrasions along the aging axis were removed. Each YOY otolith was subsequently photographed under an Olympus BX51 compound microscope at 100x magnification (Figure 1.3a) and aged in Adobe Photoshop version CS6 by counting the number of increments present (representing daily age: Kraus and Secor 2004a), which was subtracted from the date of capture to obtain a hatch date.

Estimated ages for all YOY ($a_{initial}$) were subsequently corrected for the effects of temperature on the formation of the first daily increment in white perch otoliths ($a_{corrected}$) by the equation:

$$a_{corrected} = a_{initial} + (9.03 - (0.32 \times T))$$

where T is the mean daily temperature at the hatch date calculated based on $a_{initial}$ (Houde and Morin 1990). Adjustments ranged from 1-5 days. Temperature data were obtained from the IBM (International Business Machine Corporation) pumping station in Poughkeepsie located at river km 120, (USGS 2015a; http://waterdata.usgs.gov/nwis/uv?site_no=01372058). Each adult otolith was photographed under a Olympus SZX12 dissecting microscope at 40x magnification under transmitted light and aged by counting the number of annuli present (Figure 1.3b; representing annual ages: Casey et al. 1988). A correction of 0.5 years (i.e. half of the growing season) was added to the age of adults captured in the fall in order to account for their additional ~3.5 months of growth experienced relative to spring-captured adults. The biological intercept method was employed to back-calculate size-at-age data for YOY samples (Campana 1990; see Statistical Analyses below). The biological intercept method uses the proportionality between otolith radius (OR) and fish total length (TL) to reconstruct the length of each individual at any given age by the equation:

$$TL_a = TL_c + \frac{(OR_a - OR_c) \times (TL_c - TL_i)}{(OR_c - OR_i)}$$

where the subscripts *i*, *a* and *c* signify initial, at-age and at-capture values, respectively, of OR and TL. Kraus and Secor (2004a) estimated white perch OR_i and TL_i values of 3.2 µm and 3mm, respectively, which I used as inputs.

Otolith Microchemistry

After completing analyses of otolith microstructure, contingent membership was determined for each individual using otolith strontium:calcium (Sr:Ca) profiles. In a previous study of white perch in the Patuxent River, salinity was found to be positively related to ambient concentrations of Sr:Ca, which is incorporated into the otolith matrix roughly in proportion to this ambient concentration (Kraus and Secor 2004b). In addition, otolith Sr:Ca has been successfully applied to identify migration behaviors in other diadromous fishes in the HRE (Limburg 1995, Morrison et al. 2003, Zlokovitz et al. 2003), and is therefore likely to be a reliable metric to reconstruct freshwater and brackish water habitat use in HRE white perch. Otoliths were carbon-coated in a high vacuum evaporator and analyzed via wavelength-dispersive X-ray spectrometry using an electron probe micro-analyzer (EPMA; JXA-8900R SuperProbe, JEOL USA Inc., Peabody, MA) at the University of Maryland NanoCenter. Before each analysis, the EPMA was calibrated using strontianite ($SrCO_3$) and calcite ($CaCO_3$) reference standards for Sr and Ca concentrations, respectively. In each juvenile otolith, Sr:Ca was analyzed over a profile of equally-spaced points (~20µm apart) along the ventral edge of the sulcus from the core to the edge, with each point along the transect measuring an area of ~100µm^2 at the otolith surface, thus obtaining a longitudinal record of Sr:Ca for each individual (Figure 1.4a). Similarly, adult otoliths were analyzed in profiles, with ~25µm spacing, spanning the first year of life (i.e. from the core to the first annual ring; Figure

1.4b). To increase throughput and reduce sample processing time for both YOY and adults, multiple otolith sections (n = 4-8) were mounted on a single slide for electron microprobe analyses using a method adapted from Donohoe and Zimmerman (2010). In addition, lifetime Sr:Ca profiles were measured in a subsample of 49 adults to assess whether first-year migration behaviors persisted into adulthood (Figure 1.4b). For all analyses, a threshold Sr:Ca value of 2mmol/mol was used to differentiate between freshwater (below) and brackish water (above) habitat use (Kraus and Secor 2004b).

Age Precision and Sr:Ca Verification

Before the rest of the sample was aged, a subsample of YOY white perch otoliths (n = 31 in 2013, n = 25 in 2014) was analyzed in each year-class to ensure that YOY ageing techniques were consistent. Each otolith in the subsample was aged three times so that precision, bias and average percent error between readings could be estimated. I calculated the error and bias between the first and second and between the second and third readings of each otolith in each year-class. In addition, the average percent error (APE) across all three readings was estimated for each otolith and averaged within each year-class. These metrics were calculated by the formulae:

$$Error = \sum_{j=1}^{n} \left| a_{ij} - a_{(i+1)j} \right|$$

$$Bias = \sum_{j=1}^{n} a_{ij} - a_{(i+1)j}$$

$$APE_j = \frac{\sum_{i=1}^{3} \left(\frac{\left| a_{ij} - a_{mean} \right|}{a_{mean}} \right)}{3} \times 100$$

where a_{ij} and $a_{(i+1)j}$ are the estimated ages obtained from otolith j in readings i and $i+1$, respectively, and a_{mean} is the mean age of otolith j across all three readings. To determine whether bias was statistically significant, I performed paired t-tests comparing the ages from the first and second readings and the second and third readings for each year-class. Error was less than 7 days for each reading and year-class (range: 2.2 - 6.0 days), and the average percent error across individuals was 3.5% (range: 0.5 - 8.4%) and 5.6% (range: 0.8 – 12.7%) in 2013 and 2014, respectively (Table 1.2). There was a significant positive age bias ($p < 0.05$) between the first and second readings in both year classes (3.0 days in 2013; 2.6 days in 2014), but bias became non-significant ($p > 0.30$) when comparing the second and third readings (1.3 days in 2013; 0.6 days in 2014; Table 1.2). Therefore, the third reading was used to estimate ages of each individual in the subsample for all subsequent analyses (see Statistical Analyses below).

To verify the relationship between Sr:Ca and salinity, a subsample of YOY otoliths in each year class (n = 28 in 2013, n = 20 in 2014) was selected and Sr:Ca measurements were taken at four or five locations along the edge each otolith, so that the mean Sr:Ca at the edge of the otolith could be related to salinity-at-capture (after Kraus and Secor 2004b). To estimate the relationship between otolith Sr:Ca and salinity, data from both year-classes were combined and an analysis of variance (ANOVA) was performed to test whether mean Sr:Ca at the edge of the otolith was significantly different between five salinity categories (0-1ppt, 2-3ppt, 3-4ppt, 4-5ppt and 6-7ppt) and post-hoc contrasts using Tukey’s honestly significant difference (HSD) were subsequently employed to compare Sr:Ca means across salinity levels. A positive relationship was expected to exist between salinity and Sr:Ca, similar to previous observations in white perch and congeneric striped bass (Secor et al. 1995, Kraus and Secor 2004b). The ANOVA detected significant differences in mean Sr:Ca across salinity categories ($p < 0.001$), and contrasts revealed that, as expected, Sr:Ca was significantly lower at salinities < 3 ppt compared to those at higher salinities ($p < 0.001$; Figure 1.5).

Statistical Analyses

For YOY white perch, differences in hatch date distributions obtained through the examination of otolith microstructure were analyzed with a two-way analysis of variance (ANOVA) with contingent (resident and migratory), year (2013 and 2014) and their interaction as explanatory variables. Post-hoc contrasts via Tukey's HSD were subsequently employed to compare mean hatch dates across each year·contingent combination. Mean back-calculated sizes at age 50 days were compared between contingents and years using a two-way ANOVA and post-hoc contrasts with Tukey's HSD (same as hatch date analysis outlined above). The age of 50 days was chosen because this should roughly correspond to the age at which HRE white perch metamorphose from larvae to fully-formed juveniles and thus integrates growth during the whole larval period (Mansueti 1964). To test whether YOY white perch exhibit different late-juvenile growth rates, age-length relationships were compared between contingents and year-classes using an analysis of covariance (ANCOVA) with length as the dependent variable, age as a covariate and contingent and year as categorical variables. Coefficients from the ANCOVA were subsequently used to perform contrasts to test whether intercepts and slopes (i.e. growth rates) were significantly different between contingents within each year-class, and between year-classes within each contingent, such that four contrasts were tested for each intercept and slope.

To explore factors influencing observed differences in larval size at 50 days and juvenile growth rates between 2013 and 2014 (see Results), I tested for differences in dispersal characteristics, environmental conditions and YOY abundance between years. Age, date and back-calculated lengths were calculated for each microprobe point in the Sr:Ca profiles of migratory YOY in both years to determine the age, length and date of dispersal for each individual. Mean age-, length- and date-at-dispersal were calculated from the microprobe point at which each individual Sr:Ca profile increased above the 2 mmol/mol threshold, and were subsequently compared between 2013 and 2014 using two-sample t-tests assuming equal variance for each metric. The mean temperature and freshwater flow experienced by each individual in their first 50 days of life were calculated for all individuals in each year-class, and both metrics were subsequently analyzed by a two-way ANOVA with contingent, year and their interaction as explanatory variables; post-hoc contrasts using Tukey's HSD were performed to quantify differences in means. Temperature data were obtained from the IBM pumping facility in Poughkeepsie located at river km 120, (USGS 2015a), and freshwater flow data were obtained from Green Island in Troy, which is located at the head of the estuary and represents the majority of freshwater input into the HRE (Howarth et al. 2006; USGS 2015b; http://waterdata.usgs.gov/nwis/uv?site_no=01358000). Finally, YOY white perch abundance data were obtained from the NYSDEC fall seine survey (R. Adams, personal communication) and used to calculate catch per unit effort (CPUE; number of YOY caught per seine haul) for freshwater sites (salinity < 3 ppt), brackish water sites (> 3 ppt) and the entire HRE (i.e. all sites combined) in 2013 and 2014. In addition to raw CPUE estimates, catch data were natural log-transformed and the resulting CPUE (hereafter

$\log_e$CPUE) was reported to alleviate the influence of hauls with anomalously high white perch catch.

To test which factors best predicted lifetime contingent membership in adult white perch, three separate logistic regression models were constructed and compared with salinity at capture, river kilometer at capture and first-year contingent used as predictors. Each lifetime resident was coded as a 1, and each migrant as a 0, which served as the response variables (n = 49). The relative classification success of each predictor was subsequently evaluated by comparing effect sizes (Z-statistics) and deviance explained (%) among models.

von Bertalanffy growth curves were constructed separately for each contingent. Based on lifetime Sr:Ca profiles, the most reliable indicator of adult white perch contingent membership was location of capture during the fall (i.e. outside the spawning season; see Results). Therefore, adult white perch were assumed to be resident if they were captured in Germantown (freshwater, see Table 1.1; n = 112) and migrants if they were captured in Haverstraw (brackish, see Table 1.1; n = 79). The von Bertalanffy growth model is commonly used to describe lifetime age-length data in fishes and is useful for comparing growth characteristics between species, populations and population segments, by the equation:

$$L_t = L_\infty(1 - e^{-kt}) + \varepsilon$$

where L_t is the mean length at age t, L_∞ is the theoretical maximum length, k is the growth coefficient which determines how rapidly L_∞ is approached, and ε is a random error term assumed to be N $(0, \sigma^2)$. The model typically is fitted with a theoretical age at which length is zero (i.e. t_0), which was not used here and assumed to be zero (after Kraus and Secor 2004a). Parameters were estimated by minimizing the negative log-likelihood using the SOLVER add-in in Microsoft Excel, and asymptotic standard errors were obtained for each parameter. To supplement adult growth comparisons, mean total length of yearling white perch (age-1) sampled using seines (n = 38) and gillnets (n = 7; all 2" mesh) during the fall of 2013 and 2014 were compared between freshwater (salinity < 3 ppt) and brackish water (> 3 ppt) regions. To account for probable differences in size selectivity between gears, I ran a two-way ANOVA with salinity (fresh or brackish), gear (seine or gillnet) and their interaction as predictors and subsequently employed post-hoc contrasts with Tukey's HSD to compare mean yearling size across each region·gear combination.

Relative mortality between contingents was assessed retrospectively by summing the number of adults assigned to each contingent (based on first-year Sr:Ca profiles) in each year-class (birth year; range = 1999-2012; based on age determination) within the adult sample. Frequencies were used to calculate the proportion of individuals in the migratory contingent for each year-class, as well as across year-classes. Mean standing stocks of YOY white perch caught in freshwater (resident) and brackish water (migrant) portions of the HRE in seine surveys conducted by Applied Science Associates (ASA 2014) were used to calculate migrant proportions for the same set of years, by the equation:

$$Migrant\ Proportion = \frac{n_{brackish}}{n_{fresh} + n_{brackish}}$$

where $n_{brackish}$ is the mean standing stock of YOY white perch captured below the salt front from weeks 28-40 each year and n_{fresh} is the mean standing stock above the salt front for the same set of weeks (ASA 2014; see Chapter 2 for details). Contingent proportion estimates based on standing stocks were subsequently compared to estimates from retrospective analysis of white perch adults using a series of Chi-square tests, which were conducted separately for each year-class and across year-classes. This analysis implicitly assumes that 1) otolith ageing enables accurate assignment of adults to year-classes, 2) the adult white perch sample (n = 229) was a representative sample of the population, and 3) the YOY white perch standing stock estimates are not biased between freshwater and brackish regions of the HRE. Therefore, the results of this analysis should be interpreted with caution (see Discussion).

Results

Contingent Classification

Resident and migratory white perch were observed in both year-classes of YOY white perch. The resident contingent had consistently low Sr:Ca values, indicative of freshwater habitat use (Figure 1.6). Some resident individuals displayed 1-3 points in the Sr:Ca profile above the 2 mmol/mol threshold, but these were viewed as infrequent excursions related to instrumental error, as they varied substantially from profile trends. In contrast, the migratory contingent initially displayed low Sr:Ca values early in life, then exhibited a rapid increase in Sr:Ca followed by consistently high Sr:Ca values, signifying dispersal and subsequent brackish water habitat use (Figure 1.6). Of sampled YOY juveniles, the 2013 year-class was composed of 67% residents and 33% migrants, while the 2014 year-class was almost evenly split, with 51% residents and 49% migrants (Table 1.3). Both contingents were also present in the adult sample based on first-year Sr:Ca profiles (Figure 1.7a), which was dominated by residents (86% in fall 2013; 95% in spring 2014; 88% in fall 2014) and displayed very few migrants ($n = 21$ overall; Table 1.4). Most migratory individuals displayed a reduction in Sr:Ca (sometimes below the 2 mmol/mol threshold) toward the end of the first annulus, while 11% of resident individuals ($n = 26$) displayed a late increase in Sr:Ca (Figure 1.7a).

Lifetime Sr:Ca profiles indicated that first-year migration behaviors persisted to adulthood in 70% of adult white perch, while 29% of first-year migrants switched to become lifetime residents (Figure 1.7b; Table 1.5), and 31% of first-year residents became migratory later in life (Figure 1.7c; Table 1.5). Furthermore, lifetime Sr:Ca profiles suggested that location of capture during the fall was the best predictor of lifetime contingent membership, as all fish captured in Germantown (freshwater; $n = 16$) were lifetime residents, and all but one fish caught in Haverstraw (brackish; $n = 22$) were lifetime migrants (Table 1.5). This was corroborated by logistic regression models classifying lifetime contingent membership, which indicated that first-year contingent had significant predictive power (Z-statistic = 2.54; $p < 0.05$; 10% deviance explained), but was less accurate than the salinity (Z-statistic = -4.25; $p < 0.001$; 78% deviance explained) and river kilometer (Z-statistic = 3.54; $p < 0.001$; 81% deviance explained; data not shown) of the capture location. Lifetime migrants displayed occasional forays into freshwater (i.e. Sr:Ca > 2 mmol/mol), which likely represent upriver spawning migrations (Figures 1.7b and 1.7c). Out of 22 lifetime migrants, 12 individuals (55%)

dispersed as YOY (i.e. first-year migrants), 6 dispersed at age-1 (27%), 3 dispersed at age-2 (14%) and one individual dispersed at age-7 (4%; data not shown).

YOY Contingent Comparisons

ANOVA results indicated that YOY white perch hatch dates were significantly influenced by contingent and year-class (F-test: $p < 0.001$), but not their interaction ($p > 0.1$; Table 1.6). Resident white perch were exposed to warmer temperatures (t-test: $p < 0.001$), while temperatures were cooler on average in 2014 ($p < 0.01$; Figure 1.8a). A significant effect of year was observed on white perch length at 50 days (F-test: $p < 0.001$), but contingent and the year·contingent interaction were not significant ($p > 0.3$; Table 1.6). Contrasts indicated that white perch were significantly smaller at 50 days in 2013 relative to 2014 (t-test: $p < 0.001$; Figure 1.8b). As a result of differences in hatch dates, mean temperature exposure during the first 50 days of life was significantly affected by contingent and year-class (F-test: $p < 0.003$), but not their interaction ($p > 0.2$; Table 1.6). Resident white perch were exposed to warmer temperatures across both year-classes (t-test: $p < 0.001$), while temperatures were cooler on average in 2014 ($p < 0.01$; Figure 1.9a). Mean freshwater flow exposure during the first 50 days of life was significantly influenced by year (F-test: $p < 0.001$), while contingent and the year·contingent interaction had no effect ($p > 0.05$; Table 1.6). Contrasts showed that freshwater flow during this period was significantly higher in 2013 than in 2014 (t-test: $p < 0.001$; Figure 1.9b).

Comparisons of YOY white perch age-length relationships between contingents within each year-class indicated that migrants displayed a significantly lower intercept (t-test: $p < 0.01$) and a significantly faster growth rate (> 1.5x) than residents in 2013 ($p < 0.01$; Table 1.7; Figure 1.10a). In contrast, there were no significant differences in intercepts or slopes between contingents in 2014 ($p > 0.6$; Table 1.7; Figure 1.10b). Using contrasts to compare each contingent across year-classes suggested that resident white perch had a significantly lower intercept (t-test: $p < 0.03$) and a significantly faster growth rate (> 2x) in 2014 relative to 2013 ($p < 0.02$), while there were no significant differences between years for the migratory contingent ($p > 0.5$; Table 1.7; Figure 1.10).

Comparisons of dispersal characteristics between 2013 and 2014 year-classes showed that migratory YOY white perch dispersed to brackish habitats at significantly older ages ($p < 0.02$; Figure 1.11a) and later dates ($p < 0.001$; Figure 1.11c) during 2013 than in 2014. There were no significant differences in length-at-dispersal between years ($p > 0.5$; Figure 1.11b), although there was significantly more variation in 2014 than in 2013 (F-test; $p < 0.05$). Catch-per-unit effort data indicated that YOY white perch were substantially more abundant in 2014, with 81 and 714 YOY white perch caught in the same number of seine hauls in 2013 and 2014, respectively (Table 1.8). Catch data in freshwater and brackish regions of the HRE show that approximately 32% and 63% of YOY were captured in brackish water in 2013 and 2014, respectively (Table 1.8), which suggests that migratory YOY were adequately represented in samples of each year-class (33% in 2013; 49% in 2014; see Table 1.3). However, natural-log transformed catch data indicated that the migrant proportion may have been lower, especially in 2014 (27%; Table 1.8).

Adult Contingent Comparisons

Parameter estimates for von Bertalanffy growth models indicated that migratory adults grew faster ($k = 0.69$) and attained a larger maximum size ($L_\infty = 204$ mm) than the resident contingent ($k = 0.52$; $L_\infty = 194$ mm; Figure 1.12). The 95% confidence intervals for each parameter estimate did not overlap between contingents, which indicate that observed differences in adult growth characteristics were statistically significant (Table 1.9). ANOVA results comparing yearling white perch length across regions corroborated results of the von Bertalanffy growth models, as yearlings captured in brackish water (i.e. the migratory contingent) were significantly larger than those captured in freshwater (t-test: $p < 0.001$; Figure 1.13). Yearling length was significantly influenced by river region (brackish or freshwater; F-test: $p < 0.001$) and gear (seine or gillnet; $p < 0.01$), but not their interaction ($p > 0.7$). Fish captured in gillnets tended to be larger than those captured in seines (t-test: $p < 0.01$), although there was only one individual captured in freshwater using gillnets, which precluded mean comparisons across each region·gear combination (Figure 1.13).

Retrospective analysis of contingent representation based on first-year Sr:Ca profiles showed that residents were dominant in nearly all year-classes from 1999 to 2013 (Figure 1.14). The percentage of each year-class in the migratory contingent ranged from 0% to 40%, and was approximately 9% across all year-classes (Table 1.10; Figure 1.14). In contrast, seine survey data suggested that the percentage of YOY white perch in the migratory contingent each year ranged from 12% to 60%, and the overall percentage across years from 1999-2012 was 43% (Table 1.10). Chi-square tests indicated that differences in contingent proportions between retrospective and survey-based data sets were statistically significant in 6 out of 12 year-classes ($p < 0.05$), as well as across all year-classes ($p < 0.001$; Table 1.10). Thus, the representation of migratory YOY white perch was considerably lower in adult samples assessed retrospectively compared to direct estimates based on field observations.

Discussion

White perch in the HRE displayed partial migration, with resident and migratory contingents observed during the first year of life and throughout the life cycle, and the inferred causes and consequences of partial migration in HRE white perch were generally consistent with previous studies in Chesapeake Bay. Across two year-classes of YOY, earlier hatch dates and exposure to cooler temperatures during the larval period were associated with migratory behavior, significantly so in 2013. Further, migrants were exposed to higher freshwater flows than residents in 2013. Expected differences in larval size-at-age were not observed between contingents, although overall larval growth differences were observed between years. As YOY juveniles, migrants exhibited faster growth rates in 2013, but there was no difference between contingents in 2014. Although differences in YOY growth were inconsistent, migratory adults grew faster and attained a larger maximum size than residents, indicating that migratory behavior was associated with increased production over the course of the life-cycle. In addition, retrospective analyses suggested that first-year migrants were underrepresented in the adult sample compared to expectations based on survey data, which may be indicative of higher mortality rates in the migratory contingent. My analyses highlight the importance of ecological carryover effects within the life cycle of HRE white perch, as environmental conditions experienced early in life influence juvenile migration behaviors, which can persist into adulthood and significantly impact lifetime growth, maturity and possibly mortality characteristics.

Causes of Partial Migration in HRE White Perch

Previous studies of YOY white perch in the Patuxent River (a subestuary within Chesapeake Bay) identified differences in hatch dates and larval growth rates as the probable cause of divergent juvenile migration behaviors. A comprehensive study of the 2005 year-class found that the resident contingent tended to originate from later hatch dates relative to migrants, which coincided with higher temperatures and zooplankton densities during the larval period (Kerr and Secor 2010). These differences in environmental conditions experienced early in life supported previous observations by Kraus and Secor (2004a), who reported that the resident contingent tended to grow faster than migrants during the larval period. Similar associations were observed in HRE white perch, where residents tended to hatch later in the season and were subsequently exposed to warmer temperatures and lower freshwater flow, both of which are positively associated with primary and secondary productivity in the HRE (Gladden et al. 1988, Cole and Caraco 2006). These differences were much more pronounced in the 2013 year-class and were not statistically significant in the 2014 year-class, although the resident contingent in 2014 was still skewed towards later hatch dates, higher temperatures and lower flow, in accordance with expectations.

Unexpectedly, differences in hatch dates and environmental conditions experienced by each contingent during the larval period did not translate to differences in larval size-at-age in either year. During both years, the migratory contingent was slightly skewed towards smaller sizes (mean difference = -1.2 mm in 2013; mean difference = -1.9 mm in 2014), but there was substantial overlap with residents at the individual level (Figure 1.8b). Moreover, differences in larval size-at-age between contingents were nearly an order of magnitude smaller than differences between years, as white perch were over 1.5x larger at 50 days in 2014 than 2013 (mean = 20.5 mm in 2013; mean = 33.5 mm in 2014). Reduced larval growth rates in 2013 would largely explain why white perch dispersed at later ages and dates in this year-class relative to 2014, while there were no differences in length-at-dispersal (Figure 1.11).

The reduced larval growth rates observed in 2013 may have been driven by higher freshwater flow during the larval period (Table 1.6; Figure 1.9b), which was largely driven by the passing of Tropical Storm Andrea in early June. Storm events in the HRE dramatically increase freshwater flow and turbidity, which can potentially drive declines in the abundance of pelagic phytoplankton and zooplankton that persist for 1-2 months after the storm (Strayer et al. 2014a). Furthermore, Limburg et al. (1999) observed higher growth rates and energy intake in larval white perch cohorts that overlapped with seasonal blooms of copepods and cladocerans, which are preferred prey items for larvae (Limburg et al. 1997). Further evidence for the sensitivity of white perch growth to forage availability was a 10-15% decline in larval growth rates after zebra mussels invaded the HRE in 1991 (Strayer et al. 2004). If high freshwater flows suppressed the abundance of zooplankton prey in 2013, this would explain the substantial reduction in larval size-at-age observed in this year relative to 2014. Temperature is another factor which might be expected to be positively associates with larval growth rates (Klauda et al. 1988; Kerr and Secor 2009). However, higher larval growth rates in 2014 than in

2013 were not associated with higher experienced temperatures (Figure 1.9a). In a study using direct age estimates to calculate larval white perch growth rates in the HRE, Limburg et al. (1999) concluded that the effect of temperature on white perch growth was relatively weak compared to the influence of zooplankton density.

Juvenile white perch appear to adopt different migration behaviors, at least in part, as a result of individual variation in environmental conditions experienced during the larval period, which fits the definition of an ecological carryover effect (O'Connor et al. 2014). While larval growth rates were similar between contingents, significant differences in freshwater flow exposure and diminished growth in 2013 illustrate the potential importance of forage availability and suggest that individual energetic status may play a role in the adoption of different migration behaviors in HRE white perch. It is worth noting that we used a proxy for larval growth (otolith back-calculations; Campana 1990) rather than directly observing larval growth (e.g. larval size-at-age; Limburg 1999), which might have better resolved contingent growth differences. Overall, this study provides some, albeit inconsistent, evidence that growth and energetic thresholds are important determinants of migration behavior in juvenile white perch, as predicted by the threshold model (Brodersen et al. 2008, Pulido 2011). However, the carryover effects of early-life characteristics on juvenile migration behaviors in fishes are likely shaped by ecosystem productivity and inter-annual variability in environmental conditions, and the nature of this environmental influence merits further research in other systems and over longer time periods than the two year-classes examined in this study (see Chapter 3).

Consequences of Partial Migration in HRE White Perch

Although the causes of partial migration in YOY white perch were somewhat inconclusive, first-year migration behaviors persisted into adulthood in the majority (~70%) of individuals. In addition, multiple lines of evidence indicated that differences in habitat use between resident and migratory contingents carried over to influence lifetime growth characteristics (Figures 1.10, 1.12 and 1.13; discussed below). This suggests that, regardless of the cause of divergent migration behaviors, individual "decisions" to migrate or remain resident during the juvenile period have lifelong consequences in HRE white perch. On the other hand, we observed that a moderate number (31%) of first-year residents switched to become lifetime migrants later in life and vice-versa (29% of first-year migrants switched to become lifetime residents; Table 1.5). The ages at which individuals classified as lifetime migrants dispersed downriver varied, with 55%, 27% and 14% dispersing during the first, second and third year of life, respectively (see Results). These were remarkably similar to previous observations by Kerr et al. (2011) in the Patuxent River, who reported that 65%, 18% and 10% of lifetime migrants dispersed in their first, second and third year of life, respectively. In contrast, Kerr et al. (2011) found no instances of migratory individuals reverting to resident behavior. The causes of this behavioral switching in white perch remain unknown, but suggest that multiple points exist in the life cycle where individuals make decisions to maintain or reverse migration behaviors, perhaps in relation to individual energetic status and their genetic predisposition towards behavioral flexibility (Secor 1999, Brodersen et al. 2014).

Dispersal to brackish habitats in the HRE was associated with increased growth in juvenile white perch, but while migratory YOY grew over 1.5x faster than their resident counterparts in the 2013 year-class, there was no difference in growth between contingents in 2014 (Figure 1.10). This is similar to previous observations by Kraus and Secor (2004a), where seine survey data (10 years from July-September) indicated that YOY white perch captured in brackish water were significantly larger than those in freshwater during some years, but not others. Inter-annual differences in contingent growth characteristics may have been driven by variability in the productivity gradient along the brackish-freshwater axis of the estuary, which would presumably influence food availability in the littoral habitats utilized by YOY white perch (Klauda et al. 1988). For example, reduced growth in the resident contingent in 2013 compared to 2014 may have been related to lower food availability in the freshwater portion of the HRE as a result of high discharge levels (Strayer et al. 2008; Figure 1.9). Faster growth in the migratory contingent observed in 2013 might suggest that the reduction in food availability was less severe in brackish habitats, as the HRE broadens and shoals in Haverstraw Bay, which tends to reduce water velocities (Gladden et al. 1988). Alternatively, differences between year-classes may be due to bioenergetics responses. For example, Kerr and Secor (2009) found experimental evidence of compensatory growth in migratory YOY, such that slower growth in the larval period was associated with increased energy allocation towards growth during the juvenile stage, ultimately resulting in faster juvenile growth rates in the migratory contingent. If this also applies to white perch in the HRE, suppressed larval growth rates in 2013 may have elicited compensatory growth during the juvenile period, and the migratory contingent may have exhibited stronger compensation than residents due to their exposure to lower temperatures and higher flow as larvae (Kerr and Secor 2010; Figure 1.9). These differences in environmental conditions between contingents were considerably less in 2014 (Figure 1.9), which may have reduced the potential for compensatory growth in this year-class.

Although there was inter-annual variability in growth associated with migratory behavior in YOY white perch, differing spatial distributions in each contingent had strong carryover effects on growth characteristics after the first year of life. Yearlings (age-1) captured in brackish water were significantly larger than those in freshwater (Figure 1.13). In addition, comparisons of von Bertalanffy growth parameters in adult white perch indicated that the migratory contingent grew faster and reached larger sizes than residents, although there was considerable overlap in individual size-at-age between contingents, especially at older ages (Figure 1.12). Increased size-at-age in brackish habitats is consistent with previous studies of HRE white perch from 1983 to 1988, which observed that adults grew faster and were skewed towards larger sizes in the brackish portion of the estuary (LMS 1989). Similarly, Kraus and Secor (2005a) observed faster adult growth rates in migratory white perch in the Patuxent River ($k = 0.67$ for migrants; $k = 0.39$ for residents). Lifetime growth differences between contingents may be a result of higher productivity in the brackish portion of the HRE (Howarth et al. 2006), higher consumption rates and scope for growth in the migratory contingent (Kerr and Secor 2009), or some combination of both. Interestingly, white perch in the Patuxent River attained larger maximum sizes than in the HRE ($L_\infty = 217$ mm; Kraus and Secor 2005a), which may reflect higher productivity in Chesapeake Bay (Fisher et al. 1988; see Table A.2 and Figure A.5 in the Appendix), especially after the zebra mussel invasion in the HRE (Cole and Caraco 2006). Enhanced growth in the migratory contingent likely translates to faster maturation and higher fecundity (Figure A.3), as maturity and fecundity both increase with body size in HRE white perch (Klauda et al. 1988), which may potentially carry over to influence reproductive success and population dynamics (see below).

Retrospective analysis of contingent proportions across year-classes of adult white perch suggested that the migratory contingent was underrepresented compared to expectations based on seine survey data (Table 1.10). These differences might be attributed to higher morality in the migratory contingent if adult ages were accurate, seine survey data were not biased and our adult sample was representative of the population (see Methods). Counting otolith annuli to age adult white perch has previously been validated by Casey et al. (1988) through the use of tetracycline marking. The seine survey data used to calculate expected contingent proportions samples the entire spatial extent of the HRE on a bi-weekly basis (ASA 2014; see Chapter 2) and is therefore unlikely to be biased between freshwater or brackish regions. However, due to the short duration and small spatial extent of my sampling efforts for adults (8-12 gillnet deployments, within 3 regions and over a period of 3 days in both spring and fall of 2014), biased contingent representation in the adult sample cannot be ruled out. Nonetheless, the difference in the relative abundance of the migratory contingent across year-classes (9% based on adult otoliths vs. 43% based on YOY sampling) was larger than expected. If the migratory contingent does experience higher mortality rates, this may be a consequence of compensatory growth. Kerr and Secor (2009) speculated that there could potentially be a trade-off between compensatory growth and mortality in migratory white perch, and this trade-off has also been observed in many fish species and other taxa (Mangel and Stamps

2001). Alternatively, increased predation due to higher abundance of marine predators (e.g. adult bluefish and striped bass) could contribute to higher mortality rates in the migratory contingent (Limburg 2001, Heimbuch 2008).

Implications for Population Dynamics

Before drawing inferences on the potential carryover effects of partial migration on population dynamics in HRE white perch, it is important to emphasize that this study likely underrepresents life history diversity within the population. For example, recent tagging studies have shown that the fine-scale movements of adult white perch can be highly complex, exhibiting consistent diel patterns (McCauley et al. 2014) and opportunistic use of intertidal habitats (McGrath and Austin 2011). In addition, there is evidence that white perch extensively use HRE tributaries for foraging and spawning activities, but the prevalence and consequences of these behaviors are unknown at the population level (Schmidt and Lake 2006). The otolith Sr:Ca profiles that I employed to characterize migration behaviors are probably too coarse to detect these more subtle differences in habitat use, which may nonetheless represent ecologically important components of variation in the life cycle of HRE white perch.

As a result of larger size-at-age during the yearling and adult stages, it would seem likely that the migratory contingent contributes more on a per capita basis to population productivity than the resident contingent (see Table A.1 and Figure A.4 in the Appendix). However, if migratory white perch exhibit a higher mortality rate than residents, overall contributions to population production could be substantially diminished (Table A.1; Figure A.4). The dominance of first-year resident individuals in the adult sample suggests that this segment of the population has been important for maintaining overall abundance levels within the HRE, at least over the time period analyzed (1999-2013). Future modeling work (after Kerr et al. 2010; see Chapter 3) could elucidate whether the migratory contingent contributes to or diminishes overall population productivity. In other words, population modeling can help determine whether the migratory contingent acts as a source or sink in a metapopulation context.

My study also showed that seasonal and inter-annual variability in environmental conditions influence the carryover effects of early life history on partial migration in juvenile white perch, which in turn may impact population responses to climate change (Chapter 3). Freshwater flow is projected to increase in the in the US Mid-Atlantic region (including the HRE) by 10-15% over the next century (Najjar et al. 2009), which will likely have a significant impact on productivity (Strayer et al. 2014a, Chapter 2). Moreover, increased intensity or changed seasonality of flow could ultimately reduce zooplankton densities encountered by white perch larvae, which may influence the prevalence of juvenile migration behaviors, as well as the bioenergetics and growth characteristics of each contingent. Therefore, partial migration dynamics, which are largely initiated during the juvenile period in HRE white perch, will likely play an important role in determining the persistence and resilience of the population in response to expected long-term increases in precipitation and temperature due to climate change.

Conclusions

The causes and consequences of partial migration in white perch within the HRE involved a sequence of ecological carryover effects throughout the life cycle, which likely have important effects at the population level. Environmental conditions experienced during the larval period influenced the adoption of different migration behaviors as juveniles, which then had a substantial impact on growth characteristics later in life. Similar carryover effects are likely to exist in other fishes, and deserve further study. This may be especially vital in populations that are impacted by human activities such as habitat loss, eutrophication, fishing and climate change, where carryover effects have the potential to obscure individual responses to these anthropogenic impacts, which can potentially make management actions less likely to succeed (O’Connor and Cooke 2015).

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Tables

Table 1.1. Numbers of YOY and adult (yearling and older) white perch collected in each HRE sampling location and season. The number of fish used in analyses of otolith microstructure and microchemistry are displayed in parentheses. River km is distance from the mouth of the HRE.

			Fall 2013		Spring 2014	Fall 2014	
Location	**River km**	**Region**	**YOY**	**Adult**	**Adult**	**YOY**	**Adult**
Coxsackie	202	Fresh	38 (29)	1 (1)	-	16 (7)	-
Germantown	173	Fresh	-	-	120 (38)	99 (12)	296 (61)
Staatsburg	142	Fresh	-	-	70 (22)	15 (0)	6 (2)
Poughkeepsie	120	Fresh	9 (2)	11 (6)	-	-	-
Newburgh	93	Transition	31 (17)	7 (6)	122 (36)	30 (11)	-
Haverstraw	58	Brackish	24 (13)	2 (1)	-	53 (17)	86 (56)
Tappan Zee	48	Brackish	7 (5)	1 (0)	-	13 (10)	-
Total	-	-	109 (67)	22 (14)	312 (96)	226 (57)	388 (119)

Table 1.2. Age calibration results for YOY white perch from 2013 and 2014 year-classes. An asterisk (*) denotes a bias estimate that was statistically significant ($p < 0.05$) based on a paired t-test (absolute difference $\neq 0$). The sample size and mean APE (denoted by ƚ) are for all three readings in each year-class (see text).

	2013		2014	
Metric	**Reading 1-2**	**Reading 2-3**	**Reading 1-2**	**Reading 2-3**
Sample Size ƚ	25		31	
Mean APE ƚ	3.5		5.6	
Error	5.6	6.0	5.3	2.2
Bias	3.0*	1.3	2.6*	0.6

Table 1.3. Numbers of YOY white perch in each contingent from 2013 and 2014 year-classes (proportions in parentheses). The mean salinity observed at each location over the course of the sampling season (August-October) is shown for reference.

		Fall 2013			**Fall 2014**		
Location	**River km**	**Salinity**	**Residents**	**Migrants**	**Salinity**	**Residents**	**Migrants**
Coxsackie	202	0.16	29 (1.00)	0 (0.00)	0.13	7 (1.00)	0 (0.00)
Germantown	173	-	-	-	0.10	12 (1.00)	0 (0.00)
Poughkeepsie	120	0.14	2 (1.00)	0 (0.00)	-	-	-
Newburgh	93	1.26	14 (0.82)	3 (0.18)	0.15	10 (0.91)	1 (0.09)
Haverstraw	58	4.60	0 (0.00)	14 (1.00)	3.92	0 (0.00)	17 (1.00)
Tappan Zee	48	6.54	0 (0.00)	5 (1.00)	4.42	0 (0.00)	10 (1.00)
Total	-	-	45 (0.67)	22 (0.33)	-	29 (0.51)	28 (0.49)

Table 1.4. Numbers of adult white perch in each contingent based on first-year Sr:Ca profiles (see text; proportions in parentheses) from fall 2013, spring 2014 and fall 2014 samples.

		Fall 2013		**Spring 2014**		**Fall 2014**	
Location	**River km**	**First-Year Residents**	**First-Year Migrants**	**First-Year Residents**	**First-Year Migrants**	**First-Year Residents**	**First-Year Migrants**
Germantown	173	1 (1.00)	0 (0.00)	37 (0.97)	1 (0.03)	60 (0.98)	1 (0.02)
Staatsburg	142	-	-	22 (1.00)	0 (0.00)	2 (1.00)	0 (0.00)
Poughkeepsie	120	6 (1.00)	0 (0.00)	-	-	-	-
Newburgh	93	4 (0.67)	2 (0.33)	32 (0.89)	4 (0.11)	-	-
Haverstraw	58	1 (1.00)	0 (0.00)	-	-	43 (0.77)	13 (0.23)
Total	-	12 (0.86)	2 (0.14)	91 (0.95)	5 (0.05)	105 (0.88)	14 (0.12)

Table 1.5. Numbers of adult white perch in each contingent based on lifetime Sr:Ca profiles (see text; proportions in parentheses), as a function of first-year contingent (Table 1.4), sampling location and season. The mean salinity observed at each location over the course of the sampling period (September in fall, May in spring) is shown for reference.

First-Year Contingent	Location	River km	Season	Salinity	Lifetime Residents	Lifetime Migrants
Resident	Germantown	173	Fall	0.10	15 (1.00)	0 (0.00)
	Newburgh	93	Spring	0.20	6 (1.00)	0 (0.00)
	Haverstraw	58	Fall	4.13	1 (0.09)	10 (0.91)
	Total	-	-	-	22 (0.69)	10 (0.31)
Migrant	Germantown	173	Fall	0.10	1 (1.00)	0 (0.00)
	Newburgh	93	Spring	0.20	3 (1.00)	0 (0.00)
	Newburgh	93	Fall	1.26	1 (0.50)	1 (0.50)
	Haverstraw	58	Fall	4.13	0 (0.00)	11 (1.00)
	Total	-	-	-	5 (0.29)	12 (0.71)

Table 1.6. ANOVA results comparing white perch early-life characteristics between contingents and years. Temperature and flow are based on means calculated for the first 50 days of life for each individual (see text). Statistically significant p-values ($p < 0.05$) are denoted by an asterisk (*).

Response	**Predictor**	**df**	**SS**	**MS**	**F-ratio**	**p-value**
Hatch Date (ordinal day)	Contingent	1	2824	2824	16.35	<0.001*
	Year	1	6560	6560	37.98	<0.001*
	Interaction	1	327	327	1.89	0.172
	Error	120	20725	173		
Length at 50d (mm)	Contingent	1	14	14	0.72	0.399
	Year	1	5308	5308	274.94	<0.001*
	Interaction	1	4	4	0.21	0.647
	Error	120	2317	19		
Mean Temperature (°C)	Contingent	1	58.1	58.05	14.30	<0.001*
	Year	1	39.5	39.49	9.73	0.002*
	Interaction	1	6.2	6.25	1.54	0.217
	Error	120	487.2	4.06		
Mean Flow ($m^3s^{-1}d^{-1}$)	Contingent	1	17668	17668	1.17	0.280
	Year	1	1819257	1819257	120.91	<0.001*
	Interaction	1	46313	46313	3.08	0.082
	Error	120	1805498	15046		

Table 1.7. ANCOVA coefficients and contrasts comparing intercepts and slopes from white perch age-length relationships across contingents and years. Note that year contrasts are 2013 vs. 2014 and contingent contrasts are resident vs. migratory. Statistically significant p-values ($p < 0.05$) are denoted by an asterisk (*).

Year	Contingent	Intercept	SE	t-statistic	p-value	Slope	SE	t-statistic	p-value
2013	Resident	30.42	16.69	1.82	0.071	0.33	0.14	2.34	0.021*
	Migratory	-10.59	10.93	-0.97	0.335	0.67	0.09	7.33	<0.001*
	Contingent Contrast	41.00	12.61	3.25	0.002*	-0.34	0.11	-3.20	0.002*
2014	Resident	-6.32	23.14	-0.27	0.785	0.68	0.20	3.36	0.001*
	Migratory	-11.16	16.68	-0.67	0.505	0.74	0.14	5.14	<0.001*
	Contingent Contrast	4.84	16.03	0.30	0.763	-0.06	0.14	-0.42	0.672
Year Contrast	Resident	36.74	16.03	2.29	0.024*	-0.35	0.14	-2.40	0.018*
	Migratory	0.58	12.60	0.05	0.964	-0.07	0.11	-0.60	0.553

Table 1.8. Numbers caught, seine hauls and catch-per-unit effort of YOY white perch from the NYSDEC fall seine survey in 2013 and 2014 (August- early October). CPUE is estimated separately for seine hauls in freshwater (salinity < 3 ppt), and brackish water (salinity > 3 ppt; see text) regions. Natural log-transformed catch data were used to calculate $\log_e$CPUE (see text). Proportions captured in each region were calculated by dividing the number of YOY caught in freshwater and brackish water by the total, while the $\log_e$ proportion was calculated the same way using natural log-transformed catch data (see text).

Year	Region	YOY Caught (#)	Seine Hauls (#)	CPUE	$\log_e$(CPUE)	Proportion	$\log_e$ Proportion
2013	Brackish	26	6	4.3	1.3	0.32	0.29
	Fresh	55	15	3.7	1.3	0.68	0.71
	Total	81	21	3.9	1.3		
2014	Brackish	447	5	89.4	4.5	0.63	0.27
	Fresh	267	16	16.7	2.8	0.37	0.73
	Total	714	21	34.0	3.5		

Table 1.9. Parameter estimates, standard errors and 95% confidence intervals for von Bertalanffy growth models constructed for resident and migratory adult white perch. Each model was fit to data from fall-captured adults, with residents caught in Germantown, and migrants caught in Haverstraw (see text).

Contingent	n	Model R^2	Parameter	Estimate	SE	95% CI
Resident	112	0.78	k	0.52	0.02	0.48-0.56
			L_∞	194	1.35	191-196
Migratory	79	0.59	k	0.69	0.04	0.62-0.76
			L_∞	204	1.43	201-207

Table 1.10. Estimated proportions of YOY white perch in the migratory contingent based on retrospective analyses of adult white perch otoliths (see text) and seine survey data where YOY were sampled directly (ASA 2014; Chapter 2) from 1999-2012. Chi-square statistics and p-values are shown for each comparison of contingent proportions. Statistically significant p-values ($p < 0.05$) are denoted by an asterisk (*).

Year	Retrospective Proportion	Survey Proportion	χ^2	p-value
1999	0.00	0.47	0.00	0.950
2001	0.00	0.43	0.02	0.885
2003	0.40	0.35	0.05	0.816
2004	0.00	0.12	1.39	0.238
2005	0.00	0.49	9.43	0.002*
2006	0.00	0.59	3.47	0.062
2007	0.06	0.41	7.16	0.007*
2008	0.00	0.50	32.56	<0.001*
2009	0.00	0.60	32.70	<0.001*
2010	0.17	0.51	21.13	<0.001*
2011	0.21	0.16	0.10	0.757
2012	0.10	0.46	23.67	<0.001*
Total	0.09	0.43	99.06	<0.001*

Figures

Figure 1.1. Map of the Hudson River Estuary (HRE), with white perch sampling locations in freshwater (blue circles), brackish water (red circles) and transition zone (purple circles) regions.

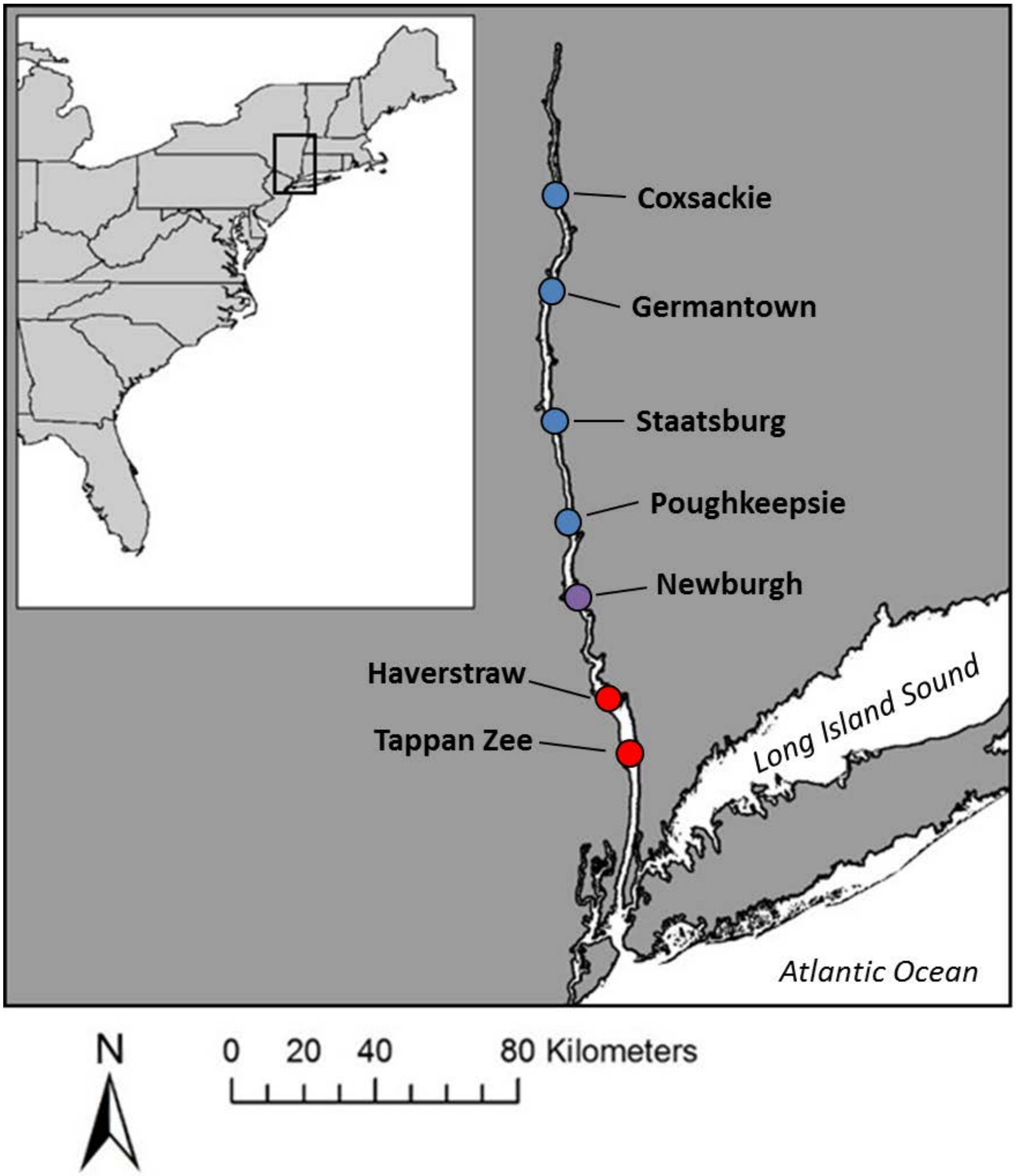


Figure 1.2. Length frequency histograms for all captured adult white perch (a; n = 722) and the subsample used in analyses of otolith microstructure and microchemistry (b; n = 229).

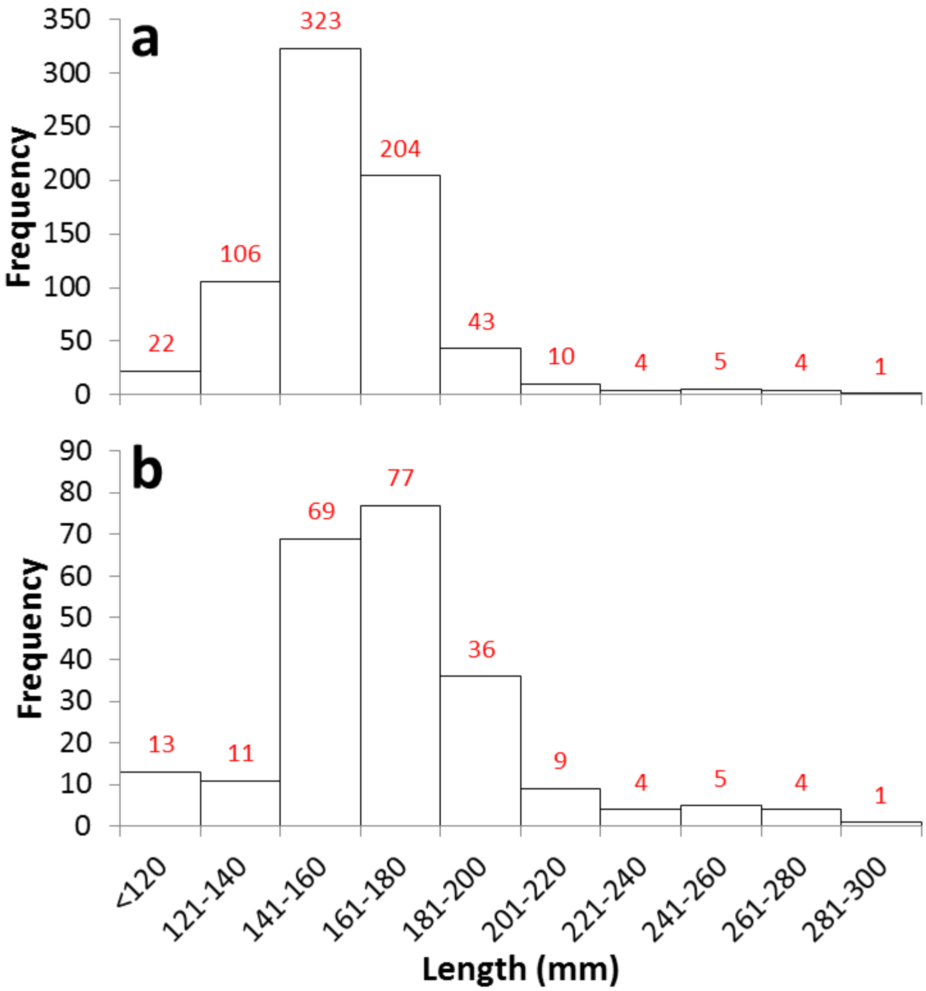


Figure 1.3. Example images of sectioned and polished otoliths from a YOY (a; photographed under a compound microscope) and adult (b; photographed under a dissecting microscope) white perch. The core and sulcul regions are noted in each otolith. YOY were aged using daily increment counts and adults were aged by counting the number of annuli (see text).

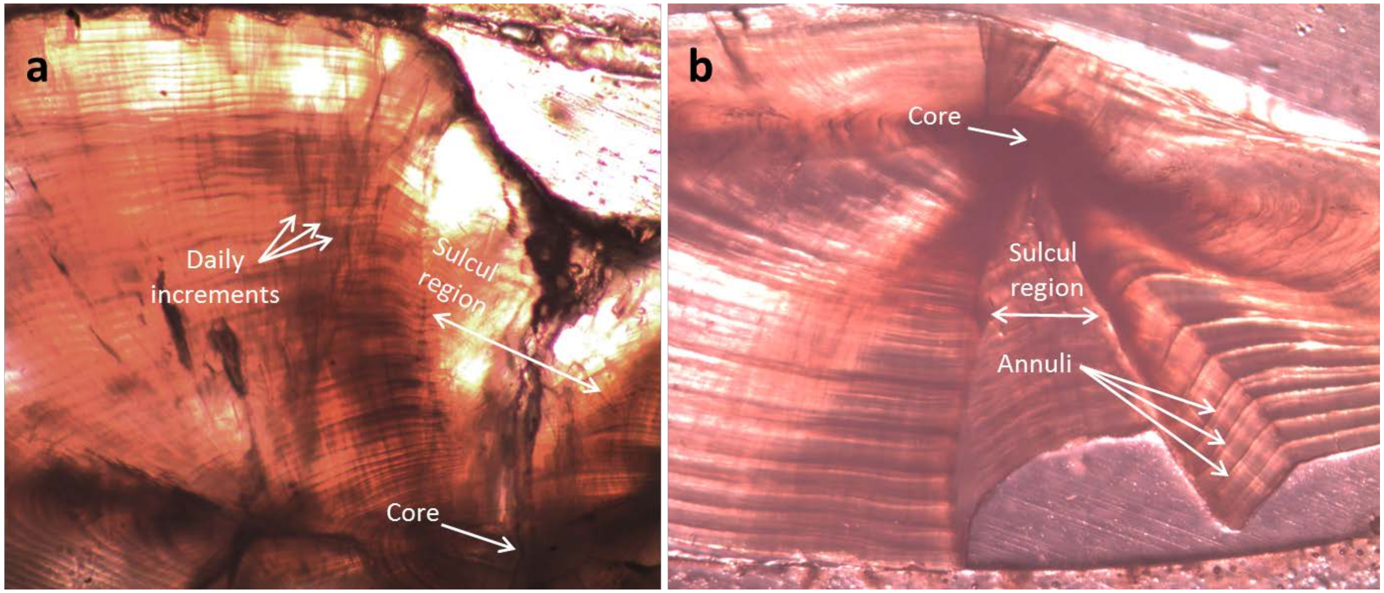


Figure 1.4. Example electron micrographs of a YOY (a) and adult (b) white perch otolith after each were analyzed for Sr:Ca profiles. The white squares in each image are microprobe points, where Sr:Ca was measured (see text). The core and sulcul regions were used as points of reference when determining the transect location in each otolith. Note the different regions used in analyses of adult Sr:Ca within the first year of life (First annulus) and after the first year of life (Lifetime).

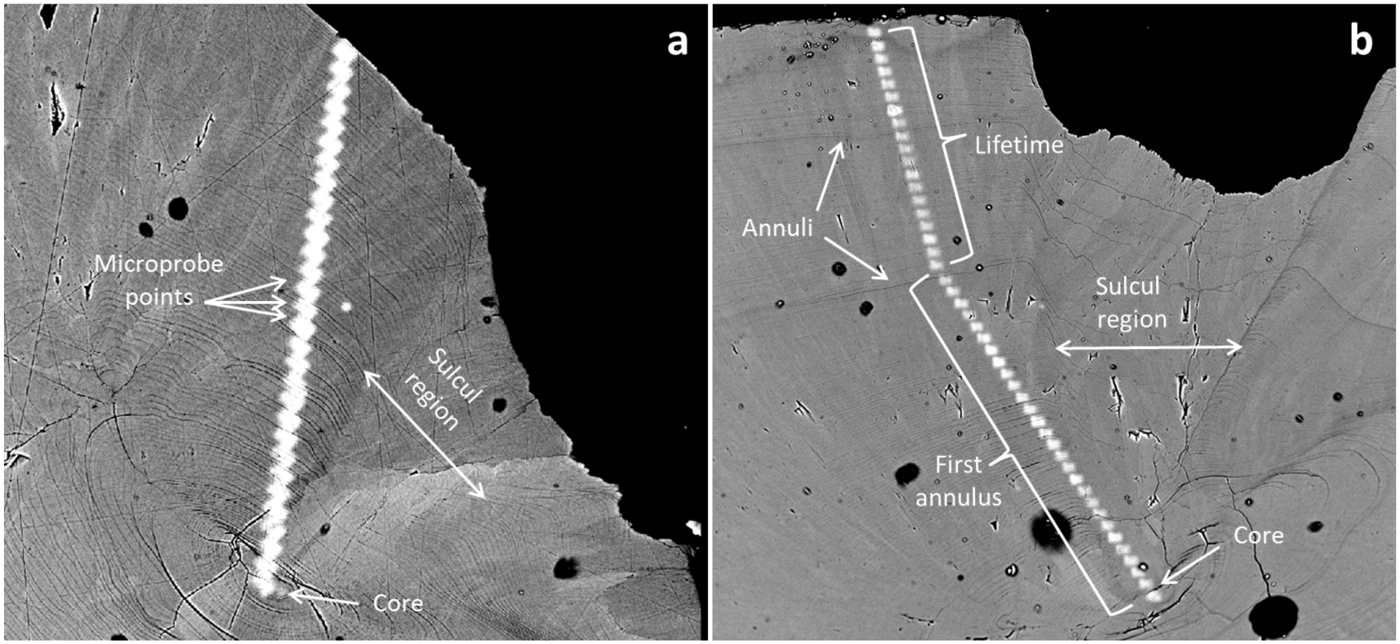


Figure 1.5. Box plots of mean Sr:Ca at the edge of YOY white perch otoliths within five salinity-at-capture bins, with sample sizes displayed for each bin. The 2 mmol/mol Sr:Ca threshold is shown for reference (dashed black line). The thick bar within each box represents the median, the edges of each box are the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the open circles are data points outside this range. The letters above each box reflect whether means in each category were significantly different based on Tukey's HSD ($p < 0.05$).

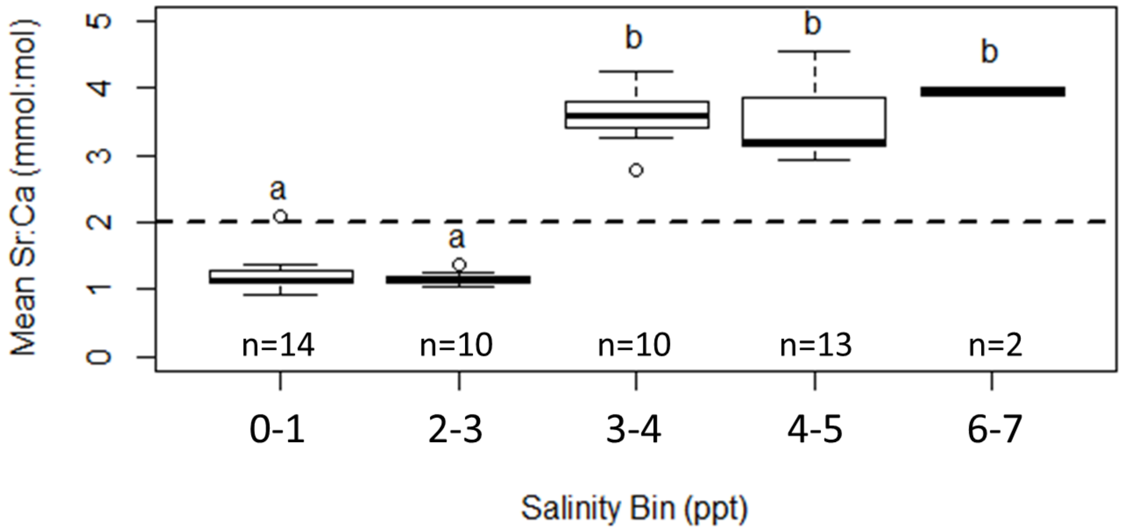


Figure 1.6. Sr:Ca profiles as a function of back-calculated total length from resident (blue) and migratory (red) YOY white perch collected in 2013 (left) and 2014 (right). The 2 mmol/mol Sr:Ca threshold is displayed for reference (thick black line).

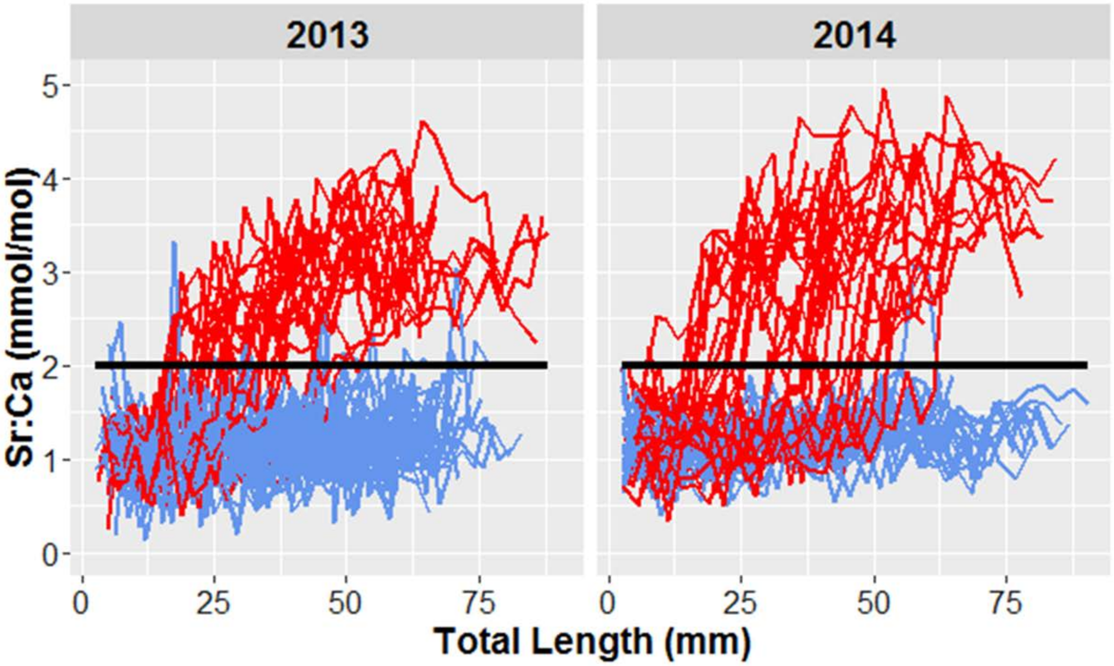


Figure 1.7. Sr:Ca profiles from migratory (red; left) and resident (blue; right) adult white perch based on first-year (a) and lifetime (b and c) transects. Lifetime profiles are grouped into first-year migrants (b) and first-year residents (c). Note the different x-axes in each plot, with (a) standardized to the proportion of the first annulus, while (b) and (c) are plotted over age with the first year excluded. The 2 mmol/mol Sr:Ca threshold is displayed for reference (thick black line).

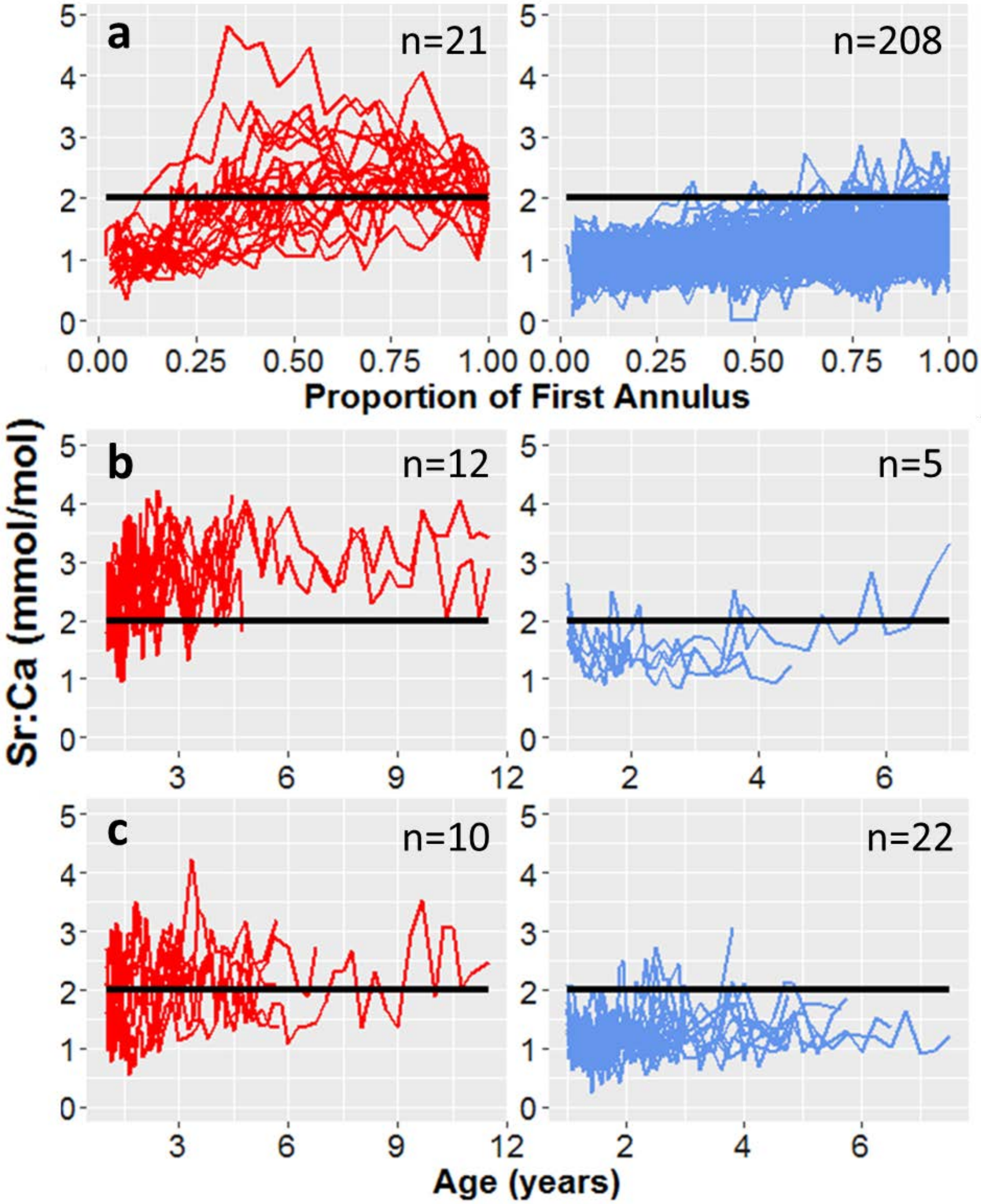


Figure 1.8. Box plots of hatch day (a) and back-calculated length at an age of 50 days (b) for resident (blue) and migratory (red) white perch in 2013 and 2014. The thick bar within each box represents the median, the edges of each box are the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the open circles are data points outside this range. The letters above each box reflect whether means in each category were significantly different based on Tukey's HSD ($p < 0.05$).

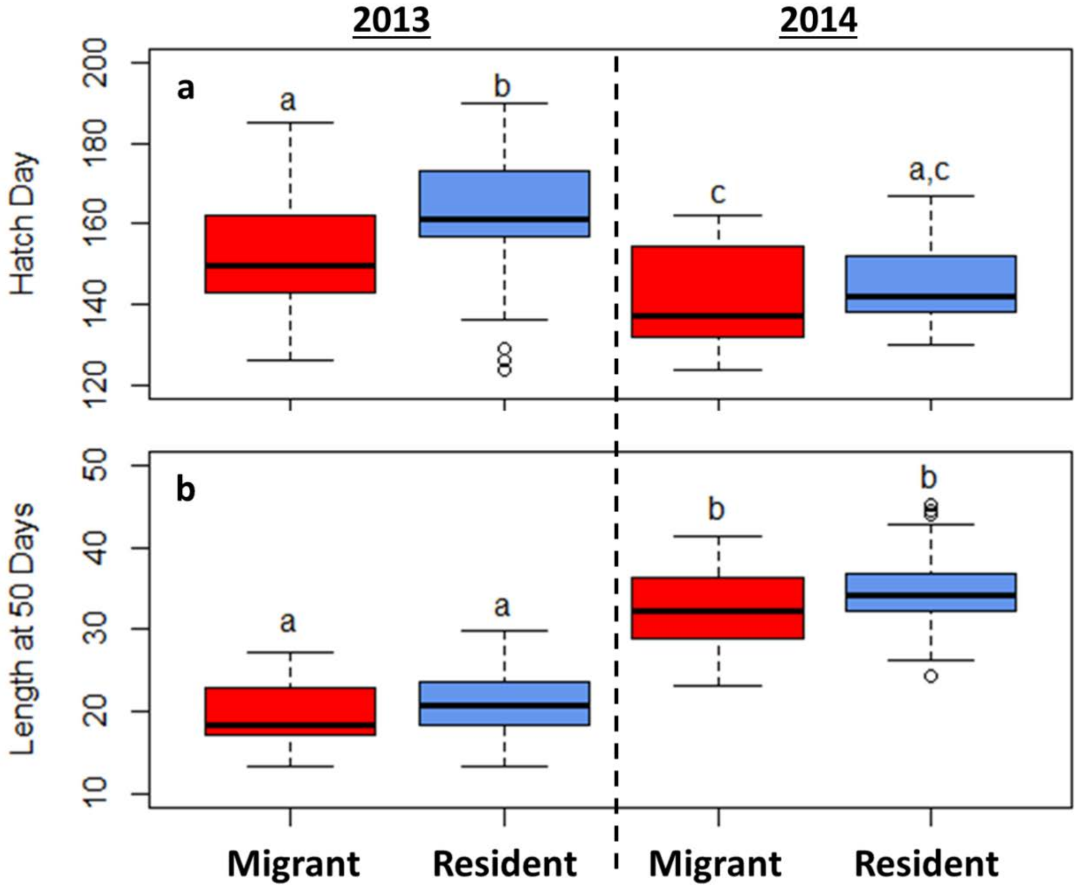


Figure 1.9. Box plots of mean temperature (a) and freshwater flow (b) experienced over 50 days post-hatch by resident (blue) and migratory (red) white perch in 2013 and 2014. The thick bar within each box represents the median, the edges of each box are the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the open circles are data points outside this range. The letters above each box reflect whether means in each category were significantly different based on Tukey's HSD ($p < 0.05$).

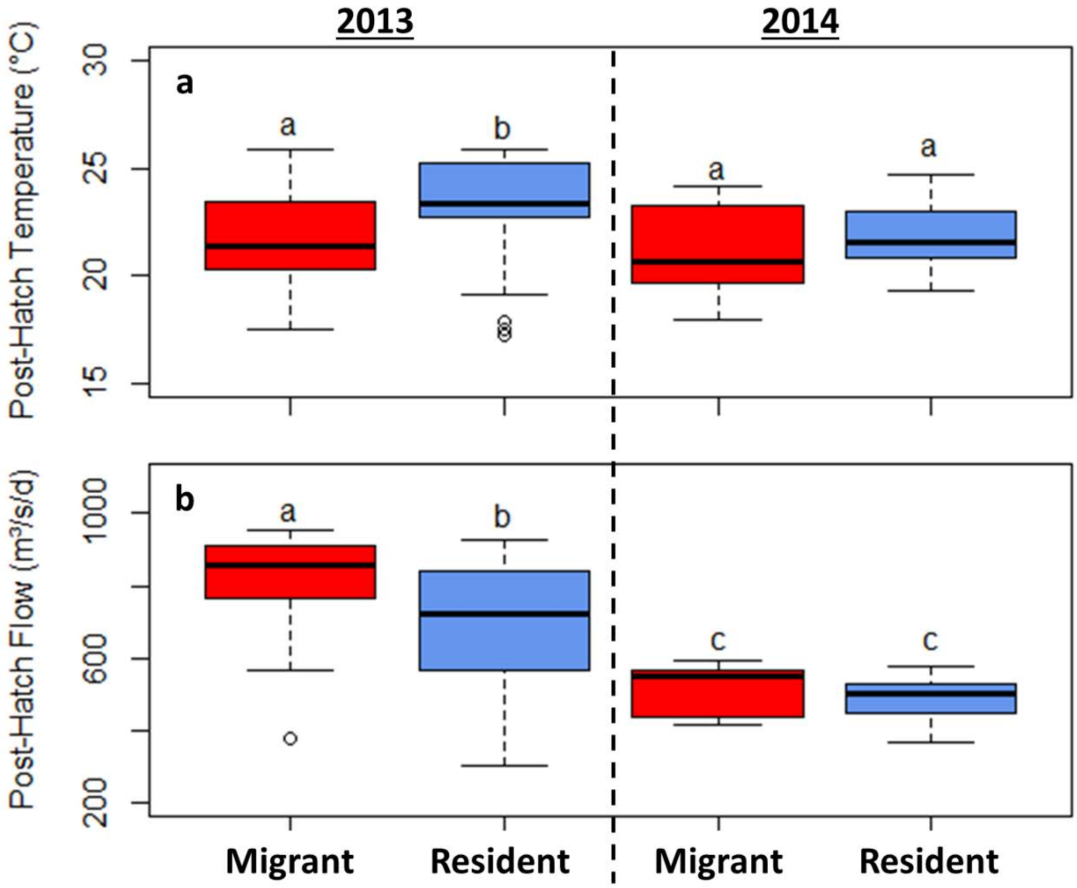


Figure 1.10. Age-length relationships plotted for resident (blue) and migratory (red) contingents of YOY white perch in 2013 (a) and 2014 (b).

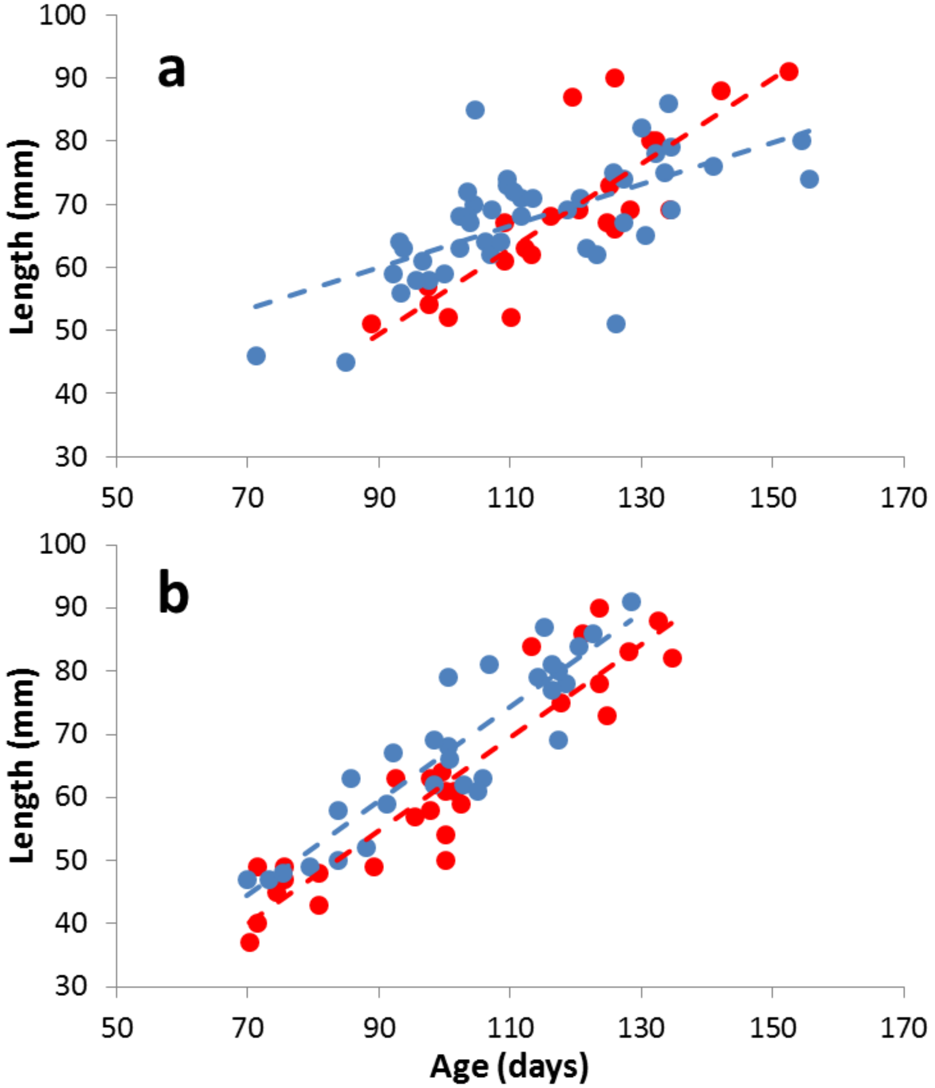


Figure 1.11. Box plots of age (a), back-calculated total length (b) and date at dispersal for migratory YOY white perch in 2013 and 2014. The thick bar within each box represents the median, the edges of each box are the 25th and 75th percentiles, and the whiskers are the 10th and 90th percentiles. The letters above each box reflect whether means in each year were significantly different based on a two sample t-test ($p < 0.05$).

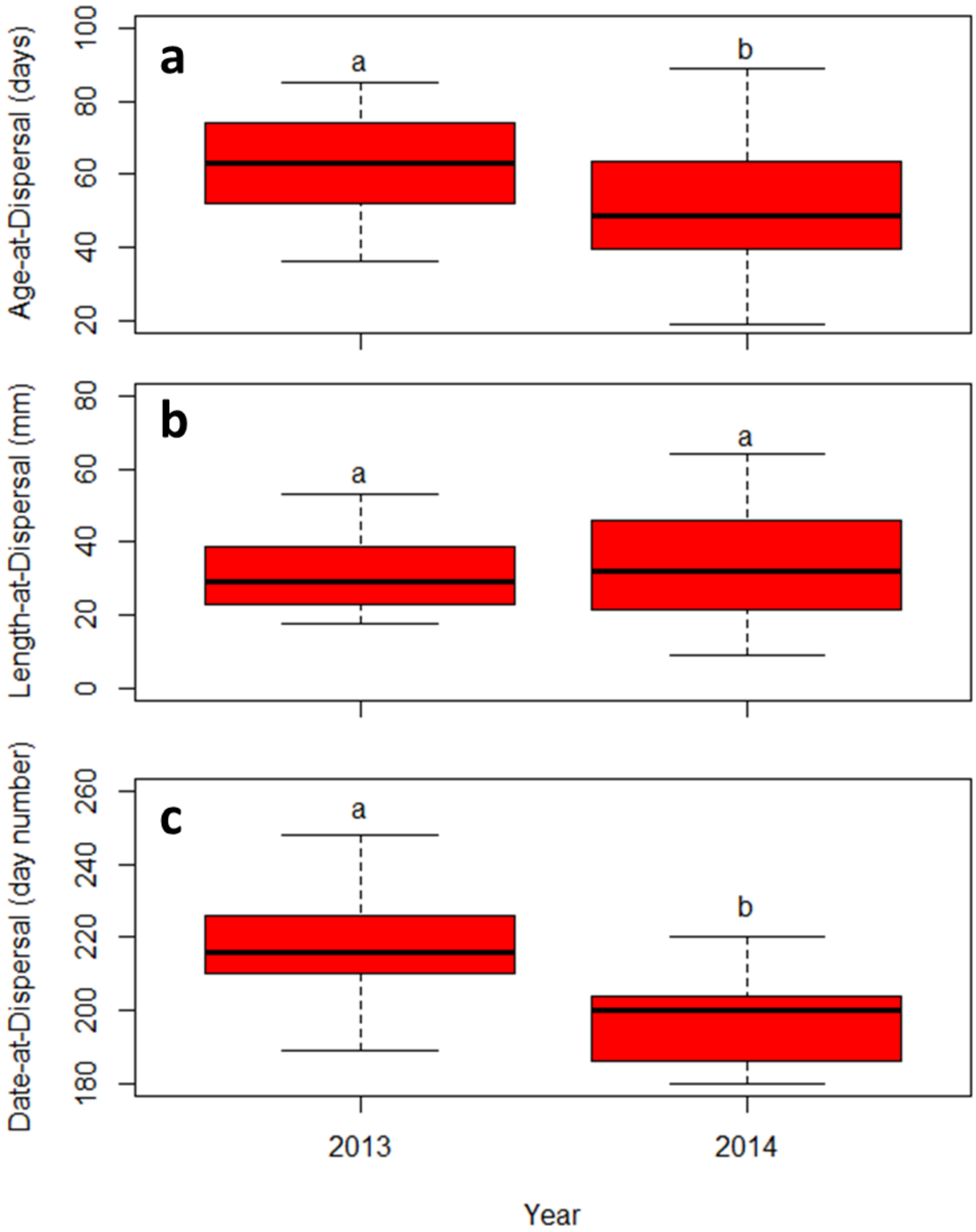


Figure 1.12. Age-length data and von Bertalanffy growth curves for resident (blue) and migratory (red) contingents of adult white perch. The dashed black line denotes a length of 190mm, when white perch in the HRE are fully mature (Klauda et al. 1988).

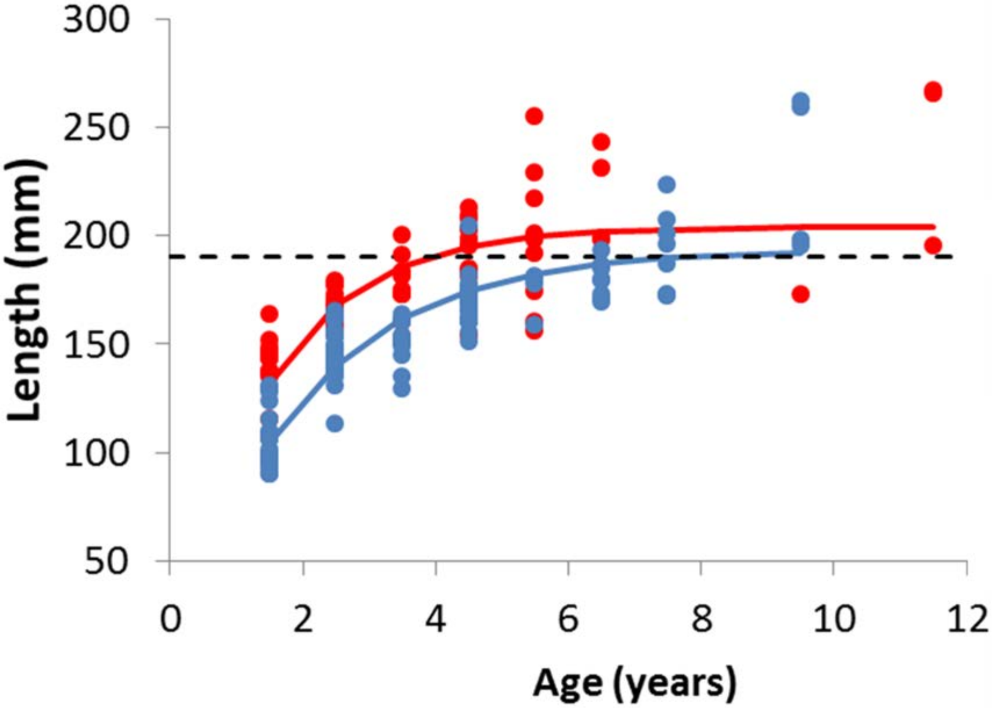


Figure 1.13. Box plots of total length of yearling white perch captured in freshwater (blue) and brackish water (red) using seines and 2" mesh gillnets, with sample sizes displayed for each category. All fish were captured during the fall in 2013 (n = 22) and 2014 (n = 23). The thick bar within each box represents the median, the edges of each box are the 25th and 75th percentiles, the whiskers are the 10th and 90th percentiles, and the open circles are data points outside this range. The letters above each box reflect whether means in each category were significantly different based on Tukey's HSD ($p < 0.05$). Note that only one individual was captured via gillnet in freshwater, so a mean could not be calculated (see Results).

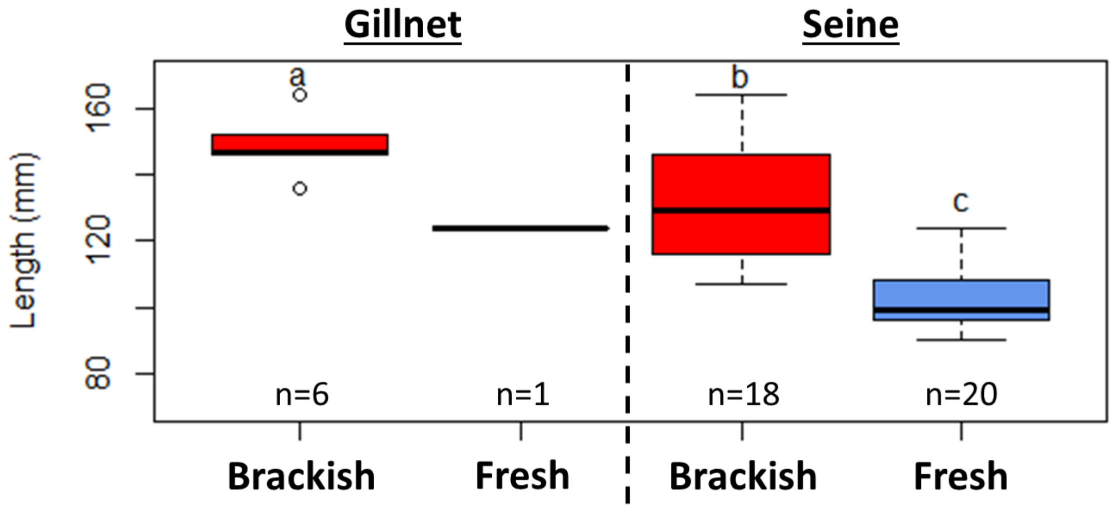
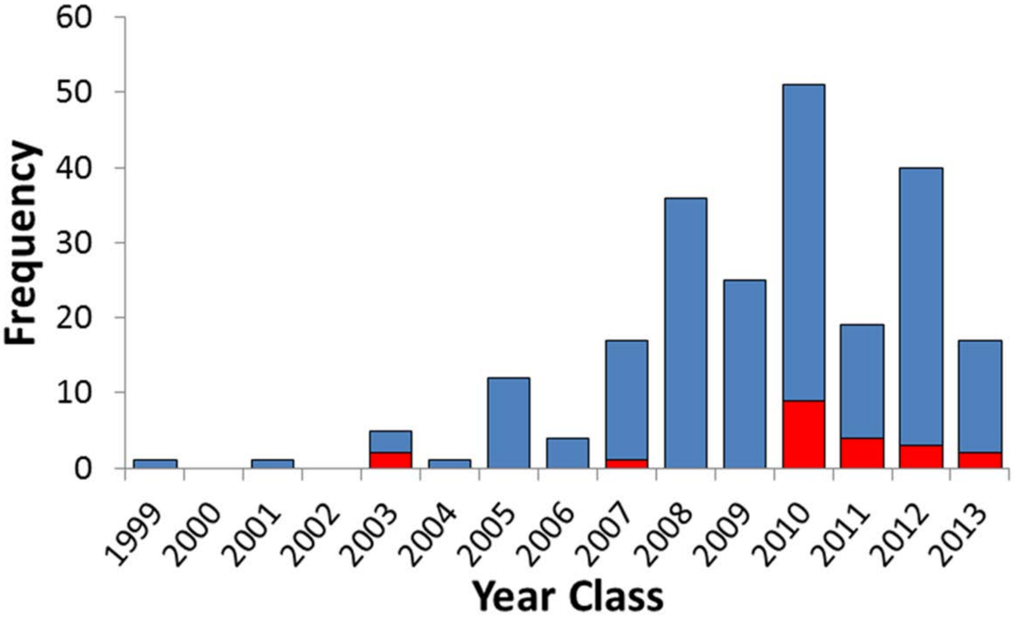


Figure 1.14. Frequencies of resident (blue) and migratory (red) contingents across year classes based on retrospective analyses of adult otoliths (see text).



Chapter 2: Interactive effects of a regime shift and climate change on the early life history of Hudson River white perch (*Morone americana*)

Introduction

Understanding how fish populations are influenced by large-scale ecosystem processes is necessary for improving their assessment and management (Sinclair and Crawford 2005), especially as many of these processes are influenced by long-term changes in climate variables such as temperature and precipitation (Najjar et al. 2010). In addition, aquatic ecosystems can be subjected to regime shifts, which alter ecosystem characteristics, species interactions, as well as the population dynamics of individual species within the system (Collie et al. 2004). Ecological regime shifts can force ecosystems into alternative stable states, which determine how populations and communities interact and respond to environmental conditions and external forcing (Strayer et al. 2008, Planque et al. 2010), and thereby confound traditional management strategies that depend on stationarity (Folke et al. 2004). Thus, examining the potential of regime shifts to intensify, dampen or reverse population responses to environmental change is an important and broadly relevant problem in fisheries research.

One important consequence of regime shifts and long-term environmental change are alterations in primary and secondary production, which influence the abundance, growth and distribution of fish populations. In particular, reductions in prey availability have the potential to increase the intensity of density-dependence in growth and recruitment processes. For example, grazing pressure from the invasive overbite clam (*Potamocorbula amurensis*) played an important role in shifting the abundance and composition of the zooplankton community in the San Francisco Estuary (Kimmerer et al. 1994), contributing to food limitation and subsequent declines in delta smelt, threadfin shad and striped bass abundance (Feyrer et al. 2007). For striped bass, these changes in the forage base were associated with a density-dependent reduction in carrying capacity, leading to long-term declines in the recruitment of striped bass to age-3 (Kimmerer et al. 2000). In addition to changing density-dependent processes, shifts in population state brought about by regime shifts, climate oscillations or fishing pressure can potentially alter how populations respond to environmental variability (Planque et al. 2010). For example, truncated age structure of Barents Sea cod due to fishing resulted in a strengthening of the correlation between temperature and recruitment (Ottersen et al. 2006). Similarly, Brander (2005) reported that recruitment across six European cod stocks from 1963-2001 was more strongly influenced by the winter North Atlantic Oscillation when spawning stock biomass was low. Thus, determining whether regime shifts alter the state of a population and, subsequently, change the responses of one or more life-stages to density-dependence or environmental conditions is a key step in incorporating species responses to climate change into assessment and management frameworks (Collie et al. 2004).

The Hudson River Estuary (HRE) is among the most intensively studied estuaries in the world. Owing to the availability of extensive long-term monitoring data that overlaps with considerable changes in the ecosystem, the HRE is an ideal system to study the effects of regime shifts and long-term environmental change on population dynamics (Strayer et al. 2014a). The HRE is a large (243 km in length), partially mixed estuary that receives most of its freshwater input from the Troy Dam at the head of the estuary (Figure 2.1; Cooper et al. 1988). Through its effects on turbidity and advection, freshwater flow strongly controls primary production in the HRE, with conditions of low flow resulting in increased water clarity and residence time and generally leading to higher rates of primary and secondary productivity (Gladden et al. 1988, Howarth et al. 2000). Freshwater flow and temperature have both generally increased in the HRE since 1950 (Seekell and Pace 2011, Strayer et al. 2014a) and are projected to continue increasing over the next century (Najjar et al. 2009). In addition to these long-term changes, the zebra mussel (*Dreissena polymorpha*) invaded the tidal freshwater portion of the HRE in 1991, which triggered rapid and extensive changes in the HRE ecosystem. Grazing pressure increased exponentially, greatly reducing the biomass of phytoplankton, pelagic zooplankton and benthic invertebrates (Caraco et al. 1997, Pace et al. 1998, Strayer and Smith 2001). As a consequence of their effects on the forage base, zebra mussels had demonstrable impacts on many fishes, with reduced abundance and growth rates for pelagic species after the invasion, as well as a downriver shift in their spatial distribution (Strayer et al. 2004). The opposite indirect effects of the zebra mussel invasion were observed on the abundance, growth and distribution of littoral fishes (Strayer et al. 2004). Importantly, the zebra mussel invasion also increased the sensitivity of the abundance of many organisms to freshwater flow. For example, the abundance of littoral benthic invertebrates and littoral fishes has developed a stronger inverse relationship with freshwater flow than was observed before the invasion (Strayer et al. 2008). However, the abundance and size of zebra mussels in the HRE have gradually decreased in the two decades since the invasion (Strayer and Malcom 2006), allowing some zooplankton and benthic invertebrate populations to recover (Pace et al. 2010, Strayer et al. 2011), and alleviating the reduction in growth rates previously observed in some fish species (Strayer et al. 2014b).

White perch (*Morone americana*) is a dominant fish species in the HRE which completes its entire life-cycle within the estuary, and is therefore likely to be sensitive to large-scale changes in the HRE ecosystem. Furthermore, because white perch larvae are pelagic, but subsequently become demersal and select littoral habitats as juveniles (Mansueti 1964), these different life-stages are likely to respond to ecosystem change in distinct ways. Importantly, the physical and biological attributes of ecosystems have been observed to influence the life history characteristics of white perch in other systems. For example, in a study of ten lakes in Maine, Tuckett et al. (2013) reported considerable differences in a suite of morphological and trophodynamic traits in white perch, which were strongly associated with measures of lake productivity. White perch recruitment in several Chesapeake Bay tributaries is positively associated with freshwater flow (Kraus and Secor 2005), likely due to a strengthening of the estuarine turbidity maximum in high flow years, which enhances larval retention and feeding success (North and Houde 2003). Similarly, first-year growth in Oneida Lake white perch is positively influenced by summer water temperatures and measures of primary and secondary productivity (VanDeValk et al. 2016). Previous studies of young-of-the year (YOY) white perch growth and recruitment in the HRE suggested that growth is unrelated to YOY abundance, but positively influenced by water temperature (Klauda et al. 1988), while recruitment to the YOY stage was unrelated to larval abundance, temperature or flow (Pace et al. 1993).

Estuarine white perch display partial migration, characterized by a resident contingent that remains in natal freshwater habitats throughout life, and a migratory contingent, which disperses from the natal habitat and primarily uses brackish water (Kraus and Secor 2004, Kerr and Secor 2011). Inter-annual variability in the numerical dominance of each contingent is modulated by freshwater flow in Chesapeake Bay tributaries, such that residents dominate in drought conditions and migrants dominate in wetter years (Kraus and Secor 2004). Evidence presented in Chapter 1 confirmed that white perch in the HRE also display partial migration (see Chapter 1) whereby the resident (freshwater) contingent is consistently more abundant, although migrant (brackish water) abundance in the HRE has previously been observed to fluctuate based upon the position of the salt front (LMS 1989). Migratory white perch in the HRE grow and mature faster than residents (see Chapter 1), and therefore may contribute disproportionately to the productivity of the population in a similar manner to Chesapeake Bay populations (Kerr et al. 2010). Although white perch recruitment, growth and migration dynamics have been well-documented in the HRE and elsewhere, the influence of density-dependence, temperature and freshwater flow on these early life characteristics may have been altered by the zebra mussel invasion. Such changes, if present, could potentially impact the status of the population in the future, as temperature and precipitation are both projected to increase (by 4°C and 7% on average, respectively) in the HRE over the next century (Najjar et al. 2009).

In a previous study detailing the effects of the zebra mussel invasion on fishes in the HRE, Strayer et al. (2004) reported declines in the abundance and growth rates of larval and juvenile white perch life-stages, but little change in their spatial distribution after the invasion. Moreover, none of these impacts, with the exception of juvenile white perch growth rates, have been reversed as zebra mussels have declined in abundance within the HRE (Strayer et al. 2014b). While these studies highlight the broader responses of white perch early life-stages to the zebra mussel invasion, it is currently unknown whether the invasion has altered the transitions between adjacent life-stages or modified the effects of environmental variables on these transitions. My objectives were to evaluate the relative influence of density-dependence and environmental conditions on the recruitment, growth, and migration dynamics of YOY white perch in the HRE. I focused on four questions: 1.) Are white perch early life-stage abundances related to the abundance and environmental conditions experienced by the previous life-stage? 2.) Is YOY white perch growth primarily influenced by density-dependence or environmental conditions? 3.) Do density-dependence and environmental factors affect the relative abundance of the migratory contingent of YOY white perch? and 4.) Have white perch life-stage transitions, growth and partial migration changed in their responses to density-dependent and environmental variables compared to observations before the zebra mussel invasion? To address these questions, I applied a series of stage-structured models and exploratory statistical analyses to an extensive set of environmental and biological monitoring data collected in the HRE from 1992-2013, after the invasion of zebra mussels (Strayer and Malcom 2006). When possible, our findings were compared to previous studies of YOY white perch recruitment (Pace et al. 1993), growth (Klauda et al. 1988, LMS 1989) and spatial distribution (LMS 1989) before the zebra mussel invasion, to test whether the regime shift brought about by the invasion has altered these early-life characteristics in white perch through changed functional relationships with abundance, flow, and other environmental variables.

Methods

Study Area

The HRE begins at the Federal Dam in Troy, NY, just south of the confluence of the Upper Hudson and Mohawk Rivers, and extends approximately 246 kilometers southward, past the tip of Manhattan, before draining into the Atlantic ocean (Figure 2.1). The HRE is a partially mixed estuary with unusually strong tidal influence compared to many estuaries, with a watershed spanning approximately 12,900 km^2 (Geyer and Chant 2006). Seasonal temperature and flow patterns in the HRE are generally similar to those in other temperate estuaries on the United States east coast, with temperature minima occurring during the winter, followed by persistent warming during spring and summer months, before cooling in the fall. Freshwater flow is moderate in the winter, preceding peak flows due to freshets during the spring, which is followed by consistent low flow in summer months and a slight increase during fall (Gladden et al. 1988). During the summer and fall, the HRE is occasionally subjected to tropical storms and hurricanes, which dramatically increase freshwater flow (sometimes exceeding 3,000 $m^3s^{-1}d^{-1}$) and turbidity, which may in turn drive sustained declines in phytoplankton and zooplankton populations (Strayer et al. 2014a). The grand mean temperature and flow in the HRE from 1951-2013 are 12.5°C and 402$m^3s^{-1}d^{-1}$, respectively, although both metrics have a positive trend over this time period, with accelerated rates of increase since 1990 (Figure 2.2). In addition, the position of the salt front in the HRE is strongly influenced by freshwater flow (Cooper et al. 1988) and can vary by 20-60 km on a seasonal basis

(Geyer and Chant 2006). The position of the salt front controls the salinity distribution within the river, which directly influences spatial variation in the abundance and composition of zooplankton, benthic invertebrate and fish communities (Ristich et al. 1977, Gladden et al. 1988, Daniels et al. 2005).

White Perch Abundance, Growth and Migration Data

Standing stock estimates were obtained from annual reports prepared by Applied Science Associates, Inc. (ASA 2014) for white perch eggs, yolk-sac larvae (YSL), post yolk-sac larvae (PYSL), young-of-the-year juveniles (YOY) and adults (yearling and older) from 1992-2013. These data are collected in “Year-class Reports” for the Hudson River Estuary Monitoring Program, an extensive survey funded by four utility companies which has been in place since 1974. Data were drawn from three separate surveys, which targeted different life history stages. Egg, YSL and PYSL standing stocks were estimated from the Longitudinal River Survey (LRS); YOY standing stock was estimated from the Utilities Beach Seine Survey (UBSS) and adult white perch standing stock was based on the Fall Juvenile Survey (FJS). Each of these surveys follows a stratified random sampling design, with shore-zone (< 3 m in depth), shoal (< 6 m), channel (water > 3 m above the river bottom in depths > 6 m) and bottom (water < 3 m above the river bottom in depths > 6 m) habitat delineations used as strata. A summary of the time-span, gear and mesh sizes used in each of the three surveys can be found in Table 2.1. The spatial and temporal resolution of each survey is relatively high and consistent (~1000 $\text{samples} \cdot \text{year}^{-1}$), with fish sampling occurring in the same 13 river sections, spanning from Albany to New York City (Figure 2.1), on weekly or bi-weekly intervals depending on the survey and time of year.

For each life stage in each survey, mean densities (number·m^{-3}) within each stratum were calculated for each river section during each sampling week. These densities are subsequently converted into standing stock estimates by multiplying the density by the stratum volume in each river section, and summing across strata (ASA 2014). River-wide standing stocks were calculated by summing standing stocks across river sections, and subsequently used to estimate annual means for each white perch life-stage from 1992-2013. I chose time periods for averaging each life-stage based upon the mean (weekly mean > 5% of the grand mean) and coefficient of variation (CV < 2) of standing stocks during each week across years. These criteria were used in order to select periods of relatively high and stable abundances, and resulted in the averaging of different time periods associated with each successive life-stage. For white perch life-stages sampled in the LRS, the time periods selected were weeks 17-25, 18-26 and 19-28 for eggs, YSL and PYSL, respectively, while weeks 28-40 and 27-41 were used in analyses of YOY (from the UBSS) and adults (from the FJS), respectively (Table 2.1). Due to likely differences in sampling efficiency (e.g. extrusion from nets) and stage duration between early life-stages, standing stocks of each life-stage should be interpreted as indices of abundance, rather than estimates of the total abundance of each stage in the HRE.

YOY white perch standing stocks were analyzed in relation to the position of the salt front to separate resident and migratory contingents during each year. Daily salt front positions in the HRE have been computed by the US Geological Survey (USGS) since 1991 (USGS 2015a; http://ny.water.usgs.gov/projects/dialer_plots/saltfront.html). Data were not available for most of 2012, and in this year daily salt front positions were estimated using the multiple regression model from Cooper et al. (1988), with lagged freshwater flow and tidal amplitude data as the independent variables. The predicted daily salt front positions from the regression model were proportional to observed values reported by the USGS from January-February in 2012 (slope = 0.97; $R^2 = 0.45$; data not shown). Based upon location relative to the weekly mean salt front position, river sections were designated as freshwater or brackish water each week. Associated freshwater and brackish water standing stocks were then averaged over weeks 28-40 (see above). The proportion of YOY that were in the migratory (i.e. brackish) contingent was calculated each year (hereafter migrant fraction) and used as an index of migratory contingent prevalence. In addition, mean YOY total length at the end of the growing season (hereafter YOY length) was calculated each year based upon the mean river-wide sizes reported during the last two sampling weeks of the UBSS (first and third weeks of October; weeks 40 and 42). These mean sizes served as an index of YOY white perch somatic growth.

In addition to standing stock estimates, I also utilized a set of annual abundance indices for white perch eggs, YSL, PYSL, YOY and yearlings reported from 1974-2013 in Year-class Reports. These indices were calculated from the same surveys as the standing stock estimates and show high correlations to the annual mean standing stocks from 1992-2013 ($R^2 > 0.90$ in all cases; data not shown). However, in order to account for differences in sampling duration between early (1974-1987) and recent (1988-2013) survey time periods, the calculation of each index utilized a different set of sampling weeks than the mean standing stocks (see above), with YOY and yearling indices drawn from weeks 33-40; while egg, YSL and PYSL indices relied on a different set of 7-week periods each year, depending on the week in which the cumulative density reached 5% of the annual sum of densities over all sampling weeks (ASA 2014). Despite these discrepancies, the strong correlation of each annual abundance index to the annual mean standing stock and the longer duration of the index data set (see above) should support quantitative comparisons of white perch life-cycle transitions before (1974-1991) and after (1992-2013) the zebra mussel invasion (see Statistical Analyses below).

Biotic and Environmental Variables

Biotic factors that may potentially influence white perch early life-stage transitions included annual measures of primary (chlorophyll-a concentration) and secondary (copepod and cladoceran densities) production in the HRE, which were obtained from the Cary Institute of Ecosystem Studies Hudson River Database (CIES 2015; http://www.caryinstitute.org/science-program/research-projects/hudson-river-ecosystem-study/hudson-river-ecosystem-study-data). Copepods and cladocerans are important prey items for larval white perch in the HRE (Limburg et al. 1997). Each metric was obtained from a bi-weekly survey conducted at a single station in the tidal freshwater portion of the HRE (Kingston; river km ~146) and averaged over the growing season (May-September) each year from 1992-2013. In addition, estimates of annual mean zebra mussel filtration rates during the growing season were received from the Cary Institute of Ecosystem Studies (D. Strayer, personal communication; see Strayer and Malcom 2006 for details) and used to examine possible effects of zebra mussels on biotic variables and white perch early life-stages.

Daily temperature and freshwater flow records were obtained respectively from the IBM pumping station in Poughkeepsie at river km 120, (USGS 2015b;

http://waterdata.usgs.gov/nwis/uv?site_no=01372058) and the Green Island facility at the head of the estuary in Troy, NY (USGS 2015c; http://waterdata.usgs.gov/nwis/uv?site_no=01358000). In addition to being the richest data set, freshwater flow at Green Island represents the majority (approximately 70%) of freshwater input into the HRE (Howarth et al. 2006). Daily temperature and flow values were averaged during winter (previous December-March), spring (April-June) and summer (July-September) months to calculate seasonal means for each year. In addition, monthly estimates of the North Atlantic Oscillation (NAO) index were accessed from the NOAA Climate Prediction Center database (NOAA 2015; http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml) and used to obtain winter averages from December-March. Descriptive statistics for all white perch early life-history, biotic and environmental variables can be found in Table 2.2.

Statistical Analyses

A life-cycle analysis was employed to model the transitions across early life-history stages of HRE white perch. Specifically, I used the methods developed by Paulik (1973) to decompose the stock-recruitment relationship of HRE white perch (in this study, the relationship between annual adult and YOY standing stocks) into a series of life-stage transitions leading up to the YOY stage. Similar life-cycle analyses have been successfully applied to describe the life-stage transitions in North Sea herring (Nash and Dickey-Collas 2005) and assess changes in these transitions over time (Payne et al. 2009). Transitions were modeled in two possible ways, depending on whether the relationship was linear or non-linear. For linear transitions, the mean standing stock of life-stage s (N_s) was modeled as a proportion of the mean standing stock of the previous life-stage (N_{s-1}) by the equation:

$$(1) \qquad N_s = \alpha(N_{s-1})$$

where α is a density-independent multiplier. I estimated α using simple linear regression with the intercept fixed at 0, and assumed this proportionality (i.e. the abundance of a life-stage is assumed to be zero if the abundance of the previous life-stage is zero) to reflect traditional assumptions in stock-recruit theory (Quinn and Deriso 1999). Similarly, non-linear transitions were modeled using a Ricker stock-recruitment function by the equation:

$$(2) \qquad N_s = \alpha(N_{s-1})e^{-\beta(N_{s-1})}$$

where α is once again the density-independent multiplier, and β is the density-dependent parameter, equal to the inverse of the value of N_{s-1} which corresponds to the maximum value of N_s (Quinn and Deriso 1999). To test for environmental effects on non-linear transitions, additional Ricker models including each combination of temperature, freshwater flow (both from the time-period over which N_{s-1} was averaged) and annual mean zebra mussel filtration rates as covariates were constructed by the equation:

$$(3) \qquad N_s = \alpha(N_{s-1})e^{-\beta(N_{s-1})-\Sigma\gamma_E(E)}$$

where Σ is a summation term for all environmental variables (E) in a given model, and γ_E represent the coefficients corresponding to each environmental variable. All models (n=7) were then compared and the best model was selected using Akaike's information criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Ricker models were linearized to the form $\log_e(N_s/N_{s-1}) = \log_e(\alpha) - \beta(N_{s-1})$ (linearized version of equation 2) or $\log_e(N_s/N_{s-1}) = \log_e(\alpha) - \beta(N_{s-1}) - \Sigma\, \gamma_E(E)$ (linearized version of equation 3) and the parameters were estimated using simple linear regression (two parameters) or multiple regression (three or more parameters).

The effects of environmental and density-dependent factors on YOY white perch growth and partial migration from 1992-2013 were explored using a Pearson correlation analysis. The response variables of interest were YOY length (a proxy for growth; see above) and the migrant fraction (an index of migratory contingent prevalence; see above), while the predictors in both analyses were the mean summer temperature and flow, annual mean zebra mussel filtration rates (environmental factors), as well as the mean standing stocks of white perch YOY and PYSL (density-dependent factors). In addition, because the availability of brackish habitat in the HRE may influence white perch growth and migration, the mean proportion of the total HRE shoal volume in the brackish portion of the estuary during the summer was calculated and used as a predictor (hereafter termed brackish shoal proportion). This proportion was calculated by assigning the 13 river sections (Figure 2.1) into freshwater and brackish regions based on the mean summer salt front position, summing the shoal volumes of all brackish sections (depth < 6 m; reported in ASA 2014) and dividing by the total shoal volume of the HRE (~345 million m^3). For comparison, correlations reported in previous studies of YOY white perch growth and spatial distribution in the 1970s and 80s (Klauda et al. 1988, LMS 1989) were compiled and compared to estimated correlations from 1992-2013. These previous studies did not adjust the p-values of their reported correlations for multiple comparisons, and I therefore selected a liberal significance level (Type-I error rate = 0.05) in the 12 correlations analyzed in the more recent time period.

I implemented a principal component analysis (PCA) to simultaneously examine relationships between 16 variables pertaining to white perch early life characteristics (the survival ratios YSL/egg, PYSL/YSL and YOY/PYSL; YOY length; and migrant fraction), related biotic factors (chlorophyll-a concentration, copepod density, cladoceran density and zebra mussel filtration rates) and environmental conditions (previous winter NAO index, and mean temperature and flow in the spring, summer and previous winter) from 1992 to 2013. White perch survival ratios, chlorophyll-a concentration, copepod density, and cladoceran density were all natural-log transformed to improve normality and alleviate the influence of extreme values. The number of meaningful principal components (PCs) was evaluated by visually assessing a scree plot (i.e. the eigenvalues of each PC) and identifying the inflection point. PCs were interpreted on the basis of loadings, and relationships among variables were assessed via plots of the loadings on each PC, with an emphasis on loadings with an absolute value > 0.25. Scores and loadings for each pair of meaningful PCs were displayed in biplots, with loadings and scores plotted on different scales for visualization purposes. Temporal trends in the scores of each meaningful PC were evaluated by calculating the correlation of each set of scores with year.

Finally, the indices of white perch egg, YSL, PYSL, YOY and yearling abundance from 1974-2013 were split into pre-invasion (1974-1991) and post-invasion (1992-2013) periods. Two-sample t-tests assuming unequal variance were performed to test for differences in the mean index of abundance for each life-stage between these two time periods. Subsequently, each life-stage transition during both time periods was modeled using the same relationships employed for the corresponding transition in the life-cycle analysis from 1992-2013 (i.e. equations 1, 2 and 3; see above) to compare transitional relationships across the two time periods. Differences in parameter estimates between pre-invasion and post-invasion periods were analyzed using analysis of covariance (ANCOVA) and post-hoc contrasts. Of particular interest were linear transitions that have changed in their steepness and non-linear transitions that have changed in their degree of density-dependence and environmental influence between the two time periods. For nonlinear transitions with environmental covariates (i.e. equation 3), the stability of the environmental effect was evaluated across each time period using a moving window analysis (after Ottersen et al. 2010), where residuals from Ricker models excluding the environmental covariate (i.e. equation 2; modeled separately for pre- and post-invasion time periods) were correlated to the environmental covariate in 5-year intervals. The relationship between the yearling (age-1) index and the YOY index from the previous year was also modeled in both time periods.

Results

Life Cycle Analysis

The stock-recruitment (adult-YOY) relationship for white perch in the HRE from 1992-2013 (top right quadrant in Figures 2.3a and 2.3b) was described by a Ricker model with freshwater flow during the PYSL period as a covariate (equation 3; $\log_e(\alpha) = 0.91$; $\beta = 5.61 \cdot 10^{-4}$; $\gamma_{flow} = 2.18 \cdot 10^{-3}$; Table 2.3). Paulik diagrams decomposing the stock-recruitment relationship into a series of life-cycle transitions (Figure 2.3) illustrated that the shape of the stock-recruitment relationship was primarily driven by the transition from PYSL to YOY (top left quadrant in Figures 2.3a and 2.3b), which was also described by a Ricker model with freshwater flow during the PYSL period as a covariate (equation 3; $\log_e(\alpha) = -4.72$; $\beta = 2.21 \cdot 10^{-6}$; $\gamma_{flow} = 1.89 \cdot 10^{-3}$; Table 2.3). Paulik diagrams also indicated that the standing stock of eggs, YSL and PYSL were proportional to the standing stock of their previous life-stages, and that each of these early life-stage transitions were best described by equation 1 (i.e., the density-independent model). Moreover, the α estimates for all early life-stage transitions were significantly positive ($p < 0.001$; Table 2.3). The standing stocks of white perch YSL and PYSL were also proportional to the adult standing stock (Table 2.3). While each α estimate was positive and statistically significant, it is important to emphasize that the standing stocks of each life-stage are indices of abundance, and therefore α estimates do not represent the actual proportionality between early life-stage abundances.

Comparisons of seven linearized Ricker model structures describing adult-YOY and PYSL-YOY relationships resulted in the selection of the model including freshwater flow during the PYSL period for both transitions (ΔAICc > 2 for all other models; Table 2.4). In addition, flow during the PYSL period had a significant negative effect on $\log_e(YOY/adult)$ and $\log_e(YOY/PYSL)$ in each model configuration where it was included ($p < 0.05$; Table 2.4), while the effects of temperature during the PYSL period and zebra mussel filtration rates were not significant ($p > 0.25$; Table 2.4). Similarly, the density-dependent term in both relationships (i.e. adult standing stock for $\log_e(YOY/adult)$ and PYSL standing stock for $\log_e(YOY/PYSL)$) had a significant negative effect on transition responses in each model tested ($p < 0.001$; Table 2.4).

Somatic Growth and Contingent Structure

For the period 1992-2013, YOY length at the end of the growth season was positively associated with mean summer water temperature ($r = 0.70$; $p < 0.01$) and negatively correlated to summer flow ($r = -0.50$; $p < 0.05$) and the PYSL standing stock ($r = -0.46$; $p < 0.05$; Table 2.5; Figure 2.4). In addition, the abundance of the migratory contingent of YOY was closely related to the abundance of the resident contingent from 1992-2013 ($R^2 = 0.81$; Figure 2.5), while the migrant fraction ranged from 0.12 to 0.60, with a mean of 0.42 (Figure 2.5). The migrant fraction was unrelated to any of the environmental or density-dependent variables analyzed ($p > 0.15$), but was positively correlated to the brackish shoal proportion from July-September ($r = 0.67$; $p < 0.01$; Table 2.5), although this trend was largely driven by two years (2004 and 2011) when the migrant fraction and brackish shoal proportion were both relatively low (Figure 2.4d).

Principal Component Analysis

Principal components 1 (PC1), 2 (PC2) and 3 (PC3) were meaningful, explaining 24%, 16% and 13% of the variance, respectively. Biplots of principal components showed strong loadings of temperature (negative) and flow (positive) during the spring and summer on PC1 (Figures 2.6 and 2.7), which was thus considered to be primarily related to environmental conditions during the growing season (i.e. April-September). YOY length and cladoceran density also exhibited strong loadings on PC1, which were positively associated with temperature and negatively related to freshwater flow during the spring and summer (Figures 2.6 and 2.7). PC2 was interpreted as a surrogate for grazing pressure and environmental conditions during the previous winter, with zebra mussel filtration rates (positive) winter flow (negative) and the winter NAO index (positive) among the strongest loadings. Loadings of the YOY migrant fraction and copepod density on PC2 were negatively associated with grazing pressure and positively affected by winter flow, while the YSL/egg survival ratio displayed the opposite pattern (Figure 2.7). Spring temperature, summer flow, copepod density and cladoceran density loaded heavily on PC3 (Figures 2.6 and 2.7), which was therefore interpreted as an indicator of environmental conditions and secondary production during the growing season. The white perch PYSL/YSL survival ratio and YOY migrant fraction were both negatively associated with spring temperature, summer flow and copepod and cladoceran densities on PC3 (Figure 2.7). There were no significant temporal trends in the scores of PC1 or PC3, while the scores of PC2 displayed a significant negative correlation with year ($r = -0.69$; $p < 0.01$; data not shown), likely due to the strong loadings of variables exhibiting significant temporal trends (e.g. zebra mussel filtration rates, summer flow and copepod density; see Table 2.2).

Pre- vs. Post-Invasion Indices of Abundance

Two sample t-tests performed on each white perch index of abundance indicated that post-invasion (1992-2013) white perch abundance was significantly lower than pre-invasion (1974-1991) abundance for eggs ($p < 0.02$), YOY ($p < 0.01$) and yearlings ($p < 0.01$; Table 2.6). In the post-invasion time period, abundances declined by approximately 50%, 40% and 60% of their pre-invasion means for eggs, YOY and yearlings, respectively (Table 2.6). Each of the four life-stage transitions differed between the two time periods, although these differences varied in magnitude (Figures 2.8 and 2.9). The egg-YSL transition exhibited a significantly steeper slope ($p < 0.001$) in the post-invasion time period (equation 1; $\alpha = 0.94$) than before the invasion ($\alpha = 0.41$; Table 2.7a). Change in the YSL-PYSL transition between the two time-periods was not statistically significant ($p > 0.15$), showing a slightly flatter slope after the invasion (equation 1; $\alpha = 5.62$) relative to the pre-invasion period ($\alpha = 6.53$; Table 2.7a). The transition from PYSL-YOY in the post-invasion period exhibited a reduced YOY maximum and increased influence of freshwater flow during the PYSL period (equation 3; $\log_e(\alpha) = 2.59$; $\beta = 0.57$; $\gamma_{\text{flow}} = 1.43 \cdot 10^{-3}$) relative to estimates before the zebra mussel invasion ($\log_e(\alpha) = 2.08$; $\beta = 0.32$; $\gamma_{\text{flow}} = 2.68 \cdot 10^{-4}$; Table 2.7b; Figure 2.7c), although contrasts performed on the linearized model coefficients indicated that none of these changes were statistically significant ($p > 0.05$). Finally, the linear relationship between the yearling index of abundance and the YOY index from the previous year exhibited a significantly flatter slope ($p < 0.05$) after the zebra mussel invasion (equation 1; $\alpha = 0.21$) than was observed during the pre-invasion time period ($\alpha = 0.32$; Table 2.7a; Figure 2.9).

Discussion

In accordance with expected effects of the zebra mussel invasion on the early life history of white perch in the HRE, life cycle analyses revealed substantial alterations in life-stage transitions after the zebra mussel invasion. Following the invasion, YOY white perch abundance became more sensitive to PYSL abundance and freshwater flow experienced during the PYSL period. In addition, reductions in yearling abundance and egg production after the zebra mussel invasion suggests that the adult population has been negatively impacted, which has not been reported in previous studies (Strayer et al. 2004). These shifts in white perch abundance and life-stage transitions are generally consistent with broader changes in the abundance and environmental sensitivity of the forage base in the HRE associated with the zebra mussel invasion (Strayer et al. 2004, 2008). In contrast, the effects of density-dependence and environmental conditions on YOY white perch growth and partial migration were generally similar before and after the zebra mussel invasion.

Environmental and Density-dependent Effects

The standing stock of white perch eggs, YSL and PYSL were directly proportional to adult abundance, while the standing stock of YOY showed density-dependence, regulated by PYSL abundance and negatively influenced by freshwater flow during the PYSL period (Figure 2.3). The reduced abundance of YOY white perch in years with high PYSL abundance is consistent with density-dependent mortality of YOY after settlement in littoral habitats. This density-dependent mortality is probably intense shortly after peak settlement, when the abundance of newly metamorphosed YOY is highest. Upon settlement, YOY white perch likely experience extremely high levels of mortality due to predation, which is in turn regulated by density and habitat type (Juanes 2007). Density-dependent prey limitation could also cause mortality either directly through starvation or indirectly by exposing juveniles to a longer period of size-dependent predation (Walters and Juanes 1993). Lower survival between the PYSL-YOY transition during higher flow years (top left quadrant in Figure 2.3) could relate to the findings of Strayer et al. (2008), who observed an inverse relationship between flow and the abundance of littoral benthic invertebrates (likely prey items for YOY white perch) in the HRE. Food availability during the PYSL stage may also be contributing to lower YOY abundances during high flow years. Densities of principal prey, copepods and cladocerans, known to affect white perch recruitment (Limburg et al. 1999) have been observed to be negatively influenced by flow (Strayer et al. 2008), which was supported by the PCA analysis (Figures 2.6 and 2.7). Contrary to this study, North and Houde (2003) reported that the stock-recruitment relationships of white perch and congeneric striped bass in the Upper Chesapeake Bay were best described when incorporating a positive effect of freshwater discharge. Interestingly, differences in the direction of the flow effect on the white perch stock-recruitment function in the Hudson River (negative) and Chesapeake Bay (positive) are generally consistent with observed effects of freshwater flow on primary and secondary production in both systems (Howarth et al. 2000, Strayer et al. 2008, Testa et al. 2008).

YOY white perch growth displayed a strong positive relationship with summer temperature, and moderate negative correlations with summer flow and PYSL abundance from 1992-2013 (Table 2.5; Figure 2.4). Environmental effects were corroborated by the PCA, where YOY length loaded positively with temperature during the growing season (i.e. spring and summer) and loaded negatively with flow on all meaningful PCs (Figures 2.6 and 2.7). The positive effect of temperature on YOY white perch growth is not surprising, and has been documented in several other systems (Kerr and Secor 2010, VanDeValk et al. 2016). The negative influence of freshwater flow on white perch growth is consistent with previous reports that low flows coincide with increased water clarity and residence times in the HRE (Gladden et al. 1988, Howarth et al. 2000), which may increase primary and secondary production, particularly in littoral habitats utilized by juvenile white perch (Strayer et al. 2008). The negative effect of the PYSL standing stock on YOY growth is more difficult to interpret, especially since growth was unrelated to YOY abundance (Table 2.5), in contrast to other studies of density-dependent growth in white perch (VanDeValk et al. 2016) and striped bass (Martino and Houde 2010). The density-dependent effect of larval abundance on YOY growth (Figure 2.4c) may be related to the density-dependent mortality reported during the PYSL-YOY transition (see above); such that competition for food in newly settled YOY may increase in years of high larval abundance, potentially reducing growth rates early in the YOY period, which carry over to influence length at the end of the growing season.

The production of YOY in the migratory contingent was proportional to the total white perch YOY abundance from 1992-2013 ($R^2 = 0.87$; Figure 2.5), with a migrant fraction of approximately 40% on average, which was positively correlated with habitat availability in the brackish portion of the HRE. While the migrant fraction was not significantly correlated with freshwater flow during the summer (r = -0.30; Table 2.5), summer flow was highly correlated with the brackish shoal proportion (r = -0.83; data not shown). Thus, in years with exceptionally high freshwater flow during the summer (2 out of the 22 years analyzed), the salt front was pushed down-estuary and subsequently restricted the availability of favorable habitat in the brackish portion of the HRE, thereby limiting the abundance of the migratory contingent. Aside from the indirect effect of summer flow, there was little evidence of environmental influence on the migrant fraction, while the relatively constant proportionality of migrant abundance and total YOY abundance implies that years with high recruitment (i.e. moderate PYSL abundance and low flow; Figure 2.3) will produce higher numbers of migrants with associated higher growth rates (see Chapter 1), which may further enhance population productivity (Kerr et al. 2010; see Table A.1 and Figure A.4 in the Appendix). In contrast, a previous study of YOY white perch in the Patuxent River observed that the resident contingent dominated in years characterized by decreased flow and low recruitment, while years with moderate to high flow favored stronger year-classes and greater prevalence (in terms of proportions) of the migratory contingent (Kraus and Secor 2004).

Impacts of the Zebra Mussel Invasion

Indices of abundance from pre-invasion (1974-1991) and post-invasion (1992-2013) time periods demonstrated, for the first time, that the abundance of white perch eggs and yearlings declined after zebra mussels invaded the HRE (Table 2.6), while also confirming the reduction of YOY standing stocks reported in previous studies (Strayer et al. 2004, 2014b). My analysis of life-stage transitions from egg to YSL to PYSL prior to the zebra mussel invasion largely mirrored previous research. Pace et al. (1993) analyzed the egg-YSL, YSL-PYSL and PYSL-YOY life-stage transitions during the pre-invasion period from 1974-1990, and found that YSL and PYSL abundances were related to the abundance of their previous life-stages in a density-independent manner, similar to our analyses of egg-YSL and YSL-PYSL transitions from 1992-2013 (Figure 2.3; Table 2.3). However, the indices of white perch abundance indicated that the slope of egg-YSL transition became steeper during the post-invasion time period (Table 2.7a), resulting in similar YSL abundance between the two time periods despite declines in egg production (Figure 2.8; Table 2.6). This pattern may suggest that a compensatory increase in hatching success and early larval survival may have occurred after the invasion.

In contrast to my findings, Pace et al. (1993) reported that the relationship between PYSL and YOY abundance was relatively flat, and unrelated to annual variations in temperature and flow, whereas the PYSL-YOY relationship reported here

(1992-2013) exhibited strong density-dependence and a significant negative effect of freshwater flow during the PYSL period (Figure 2.3; Table 2.4a). This change in the PYSL-YOY transition after the zebra mussel invasion was further corroborated by the index-based Ricker models describing the transition, which showed increases in the effect size and statistical significance of β ($\beta_{post} = 0.57$, $p < 0.001$; $\beta_{pre} = 0.32$, $p = 0.077$) and γ_{flow} ($\gamma_{post} = 1.43 \cdot 10^{-3}$, $p = 0.070$; $\gamma_{pre} = 2.68 \cdot 10^{-4}$, $p = 0.872$; Table 2.7b) during the post-invasion time-period. Although contrasts indicated that the differences between Ricker model parameters in the pre-invasion and post-invasion time periods were not statistically significant (Table 2.7b), the significant reduction in YOY abundance after the invasion and substantial differences in the shape of the YOY-PYSL relationship between time periods (Figure 2.8c) suggest that these differences are ecologically significant.

The increased sensitivity of the PYSL-YOY transition to density-dependence and freshwater flow is likely related to reductions in the food supply of white perch, and is generally consistent with riverwide declines in phytoplankton (Caraco et al. 1997), pelagic zooplankton (Pace et al. 1998) and benthic invertebrate (Strayer and Smith 2001) densities and the strong negative relationship of littoral benthic invertebrate density with flow (Strayer et al. 2008) observed in the first 10-15 years after the zebra mussel invasion. In addition, the increased sensitivity to freshwater flow has probably contributed to the diminished production of YOY observed after the zebra mussel invasion, as flow during the PYSL period (from weeks 19-28) increased at a rate of 1.9% year^{-1} in the HRE from 1992 to 2013 (Figure 2.10). The moving correlation analysis suggested that the negative effect of flow on the PYSL-YOY transition was strengthened after the zebra mussel invasion, but became weaker later in the invasion period, which may be associated with the partial or complete recovery of many zooplankton and benthic invertebrate populations in the HRE after zebra mussel mortality increased (Pace et al. 2010, Strayer et al. 2011). Therefore, the effects of density-dependence and flow on the white perch PYSL-YOY transition are non-stationary and will likely continue to change in response to the dynamics of the zebra mussel population and its impacts on the forage base in the HRE (Strayer et al. 2014a, 2014b).

White perch in the HRE begin to mature as yearlings (Klauda et al. 1988; Figure A.3a in the Appendix), which raises the possibility that the reduction in yearling abundance after the zebra mussel invasion has depleted the overall spawning stock abundance of the population. Declines in yearling abundance after the zebra mussel invasion were likely driven by reduced YOY abundance (Table 2.6) and a flattened slope in the transition between YOY and yearlings (Figure 2.9), both of which would be expected to decrease the number of individuals entering the adult population. If the diminished abundance of yearling white perch in the HRE carries over to subsequent age-classes, this would explain the significant reduction in egg production observed after the invasion (Table 2.6). Reduced post-invasion abundance of adult white perch may also provide one explanation for the negative temporal trends observed in adult, YSL and PYSL standing stocks from 1992-2013 (Table 2.2). Overall, these comparative analyses suggest that the zebra mussel invasion has forced the HRE white perch population into an alternate stable state, characterized by lower spawning stock abundance and curtailed juvenile production that is more sensitive to environmental variability, which can in turn be attributed to differences in life-cycle transitions before and after the invasion.

The strong environmental influence and moderate density-dependence observed in white perch growth from 1992-2013 are largely consistent with previous studies in the HRE. For example, Klauda et al. (1988) reported a significant positive correlation between mean water temperature in June and July and growth rates of early juvenile white perch from 1973-1979, while white perch condition (i.e. weight at a length of 70mm) was negatively associated with flow and YOY abundance (Table 2.8). Similarly, in white perch stock assessment studies from 1971-1988, LMS (1989) indicated that YOY white perch length in November was positively related to mean summer water temperature and negatively correlated to mean summer flow (Table 2.8). Using a model averaging approach, Strayer et al (2004) reported that temperature and flow had positive and negative effects, respectively on YOY white perch growth from 1974-1999, but also found evidence of reduced growth after the zebra mussel invasion, although a follow-up analysis suggested that growth rates of YOY white perch increased to their pre-invasion levels after a partial recovery of the HRE forage base in 2005 (Strayer et al. 2014b). In general, the similarity in growth responses between pre-invasion and post-invasion periods indicates that the zebra mussel invasion has not significantly altered the sensitivity of white perch growth to density-dependence and environmental factors.

After the zebra mussel invasion, I found that the migrant fraction of YOY white perch was unrelated to YOY abundance, PYSL abundance, temperature, flow or zebra mussel filtration rates, but was positively associated with the availability of shoal habitat in the brackish portion of the HRE. The importance of brackish habitat availability and the indirect effect of flow (through its influence on the salt front position) on the migratory contingent in the HRE mirror the results of previous studies of YOY white perch spatial distribution before the zebra mussel invasion. Data from 1983-1988 (LMS 1989) suggested that the location of the annual mean population center (i.e. center of abundance) of YOY white perch from late-September to November was negatively associated with freshwater flow from July-September, but unrelated to temperature or YOY abundance (Table 2.8). Similar to my analysis, LMS (1989) reported that white perch population centers evaluated on a weekly time scale in the fall from 1985-1988 were positively correlated to the position of the salt front (defined as the location of the 0.5 psu isohaline; Table 2.8). Weekly population centers of YOY white perch were typically just above the salt front (by approximately 10-50 km), which suggests that migrant fraction values were likely similar to those observed from 1992-2013 (mean = 0.42; Table 2.2). Similarly, previous studies reported that the white perch center of abundance in the HRE was not significantly altered by the zebra mussel invasion or the subsequent recovery of the forage base after 2005 (Strayer et al. 2004, 2014b). In summary, published research and analyses reported here indicate that the effects of density-dependent and environmental variables on white perch contingent dynamics have not been changed by the zebra mussel invasion.

Implications for Future Population Status

The environmental and density-dependent associations observed in white perch early life history are likely to influence how the HRE white perch population will respond to climate change. From 1946 to 2008, the HRE experienced a long-term rate of increase in flow during the white perch PYSL period (May-July) that was relatively low (~0.2% year^{-1}; Seekell and Pace 2011) compared to the observed increase in flow during this period from 1992-2013 (1.9% year^{-1}; Figure 2.10), which suggests that flow during the white perch PYSL period has been increasing at an accelerated rate over the last two decades in a similar manner to annual averages (Figure 2.2). Precipitation in the HRE watershed is projected to increase by 7% on average over the next century, which should result in a 10-15% increase in freshwater flow (Najjar et al. 2009), and this long-term change will likely be overlain by substantial decadal-scale variability that will affect the productivity of white perch and the HRE ecosystem as a whole (Strayer et al. 2014a). In addition, increases in mean freshwater flow HRE may push the average position of the salt front further downriver, restricting brackish habitat availability, and ultimately reducing the relative abundance of migratory white perch. The response of HRE white perch to long-term changes in flow will be further complicated by concurrent increases in water temperature, which Najjar et al. (2009) projected to increase by approximately 4°C on average by 2100. The effects of rising temperatures on the HRE ecosystem are likely to be modest over decadal timescales (Strayer et al. 2014a), but the increased biological rates (e.g. zooplankton productivity, white perch growth) that would accompany temperatures at the end of the century could potentially interact with higher freshwater flow (which favors lower primary production; Howarth et al. 2000) in unpredictable ways. If temperature and precipitation both increase as expected, it is possible that increased primary and secondary production due to warming will be offset by greater advective losses due to higher flows, resulting in negligible changes in the productivity of the HRE ecosystem over the next century.

Alterations in the HRE forage base as a result of the zebra mussel invasion demonstrate that the ecological impacts of other species are also important to white perch. Therefore, shifts in biotic factors in the HRE that are likely to accompany long-term changes in temperature and precipitation will continue to influence the ecological interactions (e.g. foraging, competition, predation) of white perch in the future. Previous studies have reported considerable changes in the composition of the fish community in the HRE over the last century (Daniels et al. 2005), which have been associated with the zebra mussel invasion (Strayer et al. 2004), as well as long-term changes in temperature, flow and large-scale climate forcing (O'Connor et al. 2012), all of which are likely to remain influential. Invasive species continue to colonize the HRE at a rate of ~7 species decade^{-1} (Strayer 2006), and some of these invaders may, like zebra mussels, facilitate changes in ecosystem structure which will influence white perch production and its relationships to temperature and flow.

Regime Shift-Climate Change Interactions

The HRE white perch population has been perturbed to an alternate stable state through the complex interactions of two large-scale phenomena: an abrupt regime shift and long-term increases in flow associated with climate change. The rapid increase in grazing pressure due to the zebra mussel invasion and the gradual increase in freshwater flow after the invasion had substantial impacts on the forage base, resulting in alterations in white perch life-stage transitions and subsequent declines in the abundance of eggs, juveniles and adults. While HRE white perch are an unexploited estuarine fish population (Klauda et al. 1988), the interactive effects of regime shifts and climate change are likely to be important across a range of unexploited and exploited fish stocks in freshwater, coastal and marine ecosystems. Regime shifts are typically abrupt (1-3 years), and can be triggered by overfishing (Daskalov et al. 2007), invasive species (Shiganova et al. 1998), eutrophication (Österblom et al. 2007), climate oscillations (Francis and Hare 1994), gradual changes in temperature and precipitation (Smol et al. 2005), or some combination of these factors (e.g. Weijerman et al. 2005, Möllmann et al. 2008). Regardless of the cause, abrupt regime shifts in aquatic ecosystems will inevitably lead to changes in the abundance and population dynamics of many constituent species (Collie et al. 2004). Comparisons of fish population characteristics across various stages of ecosystem disturbance and recovery in multiple systems (e.g. nutrient remediation; Kemp et al. 2009) can potentially uncover more diverse mechanisms by which populations have responded to changes in ecosystem structure in the past. Further research is warranted to develop a more comprehensive understanding of the interactive effects of regime shifts and climate change on fish populations in systems where adequate environmental and biological monitoring data are available.

Conclusions

My research highlights the importance of abrupt and long-term changes in ecosystem characteristics to the dynamics of the HRE white perch population. Alterations in the abundance and environmental sensitivity of white perch in the HRE after the zebra mussel invasion will likely influence how the population responds to long-term increases in temperature and precipitation in the HRE. In addition, despite the relatively short duration of the post-invasion period (22 years), our analyses suggested that changes in the environmental sensitivity of white perch life-stage transitions were non-stationary. Similar non-stationary changes in the shape of early life-stage transitions may be detectable in other fish species in the HRE (e.g. striped bass, river herring, centrarchids) and other marine ecosystems subjected to regime shifts, especially those characterized by intense modifications of the forage base. Improved knowledge of the causes and consequences of state shifts in fish populations, such as those highlighted here, can facilitate the implementation of stock assessment and fisheries management practices that more comprehensively account for these shifts (Collie et al. 2004).

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Tables

Table 2.1. Survey, gear and time-span descriptions for each white perch life-stage. Note that YSL and eggs were also sampled in the LRS, and thus have the same strata, gear, mesh size and sampling weeks displayed for PYSL.

Life-Stage	Survey	Strata	Gear	Mesh Size	Sampling Weeks	Weeks Averaged
Adult	FJS	Channel, Shoal and Bottom	1 m^2 Tucker Trawl (Channel), 3 m Beam Trawl (Shoal and Bottom)	3 mm (Channel), 1.3 cm (Shoal and Bottom)	27-48	27-41
YOY	UBSS	Shore zone	30.5 m x 2.4 m Seine Net	0.5 cm	24-43	28-40
PYSL	LRS	Channel, Shoal and Bottom	1 m^2 Tucker Trawl (Shoal and Channel), 1 m^2 Epibenthic Sled (Bottom)	505 µm (all strata)	11-41	19-28
YSL	LRS					18-26
Egg	LRS					17-25

Table 2.2. List of 19 primary variables analyzed in this chapter, with descriptive statistics (mean, minimum, maximum and trend (i.e. correlation coefficient with year)) for each variable from 1992-2013. Statistically significant linear trends are marked with an asterisk (*).

Variable	Units	Type	Source	Mean	Min	Max	Trend
Mean adult standing crop	Millions	White Perch	ASA (2014)	2.54	0.89	5.89	-0.30
Mean YOY standing crop	Millions	White Perch	ASA (2014)	0.71	0.05	2.35	0.13
Mean PYSL standing crop	Millions	White Perch	ASA (2014)	709	340	1529	-0.65*
Mean YSL standing crop	Millions	White Perch	ASA (2014)	105	32	257	-0.47*
Mean Egg standing crop	Millions	White Perch	ASA (2014)	123	22	351	-0.17
Proportion of migratory YOY	Unitless	White Perch	ASA (2014)	0.42	0.12	0.60	0.07
Mean YOY length in October	mm	White Perch	ASA (2014)	73.9	62.8	82.3	0.14
Mean zebra mussel filtration rate	$m^3m^{-2}day^{-1}$	Biological	CIES (2015)	3.76	0.06	8.28	-0.59*
Mean chlorophyll-a concentration	$\mu g \cdot L^{-1}$	Biological	CIES (2015)	6.3	3.7	12.2	-0.12
Mean copepod density	$number \cdot m^{-3}$	Biological	CIES (2015)	6.3	2.8	17.0	0.71*
Mean cladoceran density	$number \cdot m^{-3}$	Biological	CIES (2015)	13.9	1.9	34.7	-0.05
Mean summer salt front position	km from Battery	Environmental	USGS (2015a)	99	74	118	0.16
Mean winter temperature	°Celsius	Environmental	USGS (2015b)	1.8	0.7	4.0	0.19
Mean spring temperature	°Celsius	Environmental	USGS (2015b)	14.7	13.2	17.2	0.22
Mean summer temperature	°Celsius	Environmental	USGS (2015b)	24.5	23.2	26.4	0.32
Mean winter flow	$m^3sec^{-1}day^{-1}$	Environmental	USGS (2015c)	520	330	755	0.37
Mean spring flow	$m^3sec^{-1}day^{-1}$	Environmental	USGS (2015c)	587	181	857	-0.01
Mean summer flow	$m^3sec^{-1}day^{-1}$	Environmental	USGS (2015c)	234	98	546	0.43*
Mean winter NAO index	Unitless	Environmental	NOAA (2015)	0.28	-1.46	1.20	-0.40

Table 2.3. Parameter estimates (with standard errors in parentheses) for each white perch life-stage transition shown in Figure 2.3. The α estimates, model R^2 and p-values for Ricker models (denoted by †) are for the linearized equations, where $\alpha = \log_e(\alpha)$ (see Methods). The Adult-PYSL and egg-YSL relationships were estimated, but are not shown in Figure 2.3.

Life-Stage Transition	**α**	**β**	**γ_{flow}**	**Model R^2**	**Model p-value**
Adult-Eggs	46.40 (4.56)	-	-	0.35	<0.001
Adult-YSL	40.41 (3.19)	-	-	0.52	<0.001
Adult-PYSL	258.25 (21.59)	-	-	0.23	<0.001
Eggs-YSL	0.76 (0.08)	-	-	0.21	<0.001
Eggs-PYSL	4.87 (0.53)	-	-	0.20	<0.001
YSL-PYSL	6.07 (0.47)	-	-	0.33	<0.001
Adult-YOY†	0.91 (0.49)	$5.61\ 10^{-4}$ $(1.24\ 10^{-4})$	$2.18\ 10^{-3}$ $(8.61\ 10^{-4})$	0.59	<0.001
PYSL-YOY†	-4.72 (0.47)	$2.21\ 10^{-6}$ $(4.44\ 10^{-7})$	$1.89\ 10^{-3}$ $(8.07\ 10^{-4})$	0.62	<0.001

Table 2.4. Parameter estimates, R^2 and AICc values for seven linearized Ricker model configurations for white perch describing the relationship between YOY and PYSL (a) and between YOY and adults (b) with each combination of temperature, flow (both during the PYSL period) and zebra mussel filtration rates. Parameters that were significantly different than 0 ($p < 0.05$) are marked with an asterisk (*). Model 3 had the lowest AICc in both cases (bold italic text).

a

Model	Intercept	PYSL	Temperature	Flow	Filtration	R^2	AICc
1	-5.48*	-0.0023*	-	-	-	0.51	53.8
2	-5.41	-0.0023*	0.00	-	-	0.51	56.8
3	***-4.72****	***-0.0022****	***-***	***-0.0019****	***-***	***0.62***	***51.2***
4	-5.51*	-0.0023*	-	-	0.01	0.51	56.8
5	-1.51	-0.0024*	-0.16	-0.0022*	-	0.64	53.7
6	-4.49*	-0.0021*	-	-0.0022*	-0.06	0.64	53.9
7	-0.30	-0.0023*	-0.20	-0.0026*	-0.07	0.66	56.3

b

Model	Intercept	Adult	Temperature	Flow	Filtration	R^2	AICc
1	0.02	-0.57*	-	-	-	0.46	57.5
2	-1.95	-0.56*	0.10	-	-	0.46	60.2
3	***0.91***	***-0.56****	***-***	***-0.0022****	***-***	***0.59***	***54.1***
4	-0.03	-0.58*	-	-	0.02	0.46	60.5
5	1.68	-0.56*	-0.04	-0.0023*	-	0.59	57.5
6	1.13	-0.54*	-	-0.0024*	-0.05	0.60	57.0
7	2.90	-0.54*	-0.09	-0.0024*	-0.06	0.61	60.6

Table 2.5. Correlations between migrant fraction and YOY length and six predictor variables of interest from 1992-2013. Statistically significant ($p < 0.05$) correlations are marked with an asterisk (*).

			Response	
Predictor	**Type**	**Time Period**	**Migrant Fraction**	**YOY Length**
PYSL Standing Stock	Density-dependent	May-Jul	-0.16	-0.46*
YOY Standing Stock	Density-dependent	Jul-Sep	-0.05	0.19
Summer Temperature	Environment	Jul-Sep	0.24	0.70*
Summer Flow	Environment	Jul-Sep	-0.30	-0.50*
Zebra Mussel Filtration	Environment	May-Oct	-0.03	-0.06
Brackish Shoal Proportion	Habitat availability	Jul-Sep	0.67*	0.37

Table 2.6. Statistical comparisons of mean post-invasion (1992-2013) and pre-invasion (1974-1991) indices of abundance for white perch eggs, YSL, PYSL, YOY and yearlings. The % Difference metric is calculated as $(\text{Mean}_{post}\text{-Mean}_{pre})/\text{Mean}_{pre}$. Statistically significant p-values are denoted by an asterisk (*).

Life-Stage	Post-Invasion Mean	Pre-Invasion Mean	t-Statistic	% Difference	p-value
Egg	0.41	0.89	-2.66	-54	0.02*
YSL	0.45	0.46	-0.06	-1	0.95
PYSL	2.85	3.50	-1.30	-19	0.20
YOY	4.82	8.08	-2.83	-40	0.01*
Yearling	1.21	3.26	-3.95	-63	<0.01*

Table 2.7. Parameter estimates (with standard errors in parentheses) and p-values for linear (a) and nonlinear (b) life-stage transitions from the analysis of white perch indices of abundance shown in Figures 2.8 and 2.9. The % Difference metric is calculated as ($\text{Estimate}_{\text{post}}$-$\text{Estimate}_{\text{pre}}$)/$\text{Estimate}_{\text{pre}}$. The contrast t-statistics and p-values are for ($\text{Estimate}_{\text{post}}$-$\text{Estimate}_{\text{pre}}$) contrasts performed on each parameter using ANCOVA (estimates in b are for linearized Ricker models; see Methods). Statistically significant p-values are denoted by an asterisk (*).

a

Life-Stage Transition	Post-Invasion α	Post-Invasion p-value	Pre-Invasion α	Pre-Invasion p-value	Contrast t-Statistic	% Difference	Contrast p-value
Eggs-YSL	0.94 (0.12)	< 0.001*	0.41 (0.06)	< 0.001*	3.81	129	< 0.001*
YSL-PYSL	5.62 (0.48)	< 0.001*	6.53 (0.49)	< 0.001*	-1.31	-14	0.199
YOY-Yearling	0.21 (0.04)	< 0.001*	0.32 (0.03)	< 0.001*	-2.33	-34	0.026*

b

PYSL-YOY Parameter	Post-Invasion	Post-Invasion p-value	Pre-Invasion	Pre-Invasion p-value	Contrast t-Statistic	% Difference	Contrast p-value
$\log_e(\alpha)$	2.59 (0.46)	< 0.001*	2.08 (0.88)	0.025*	0.68	25	0.503
β	0.57 (0.10)	< 0.001*	0.32 (0.17)	0.077	1.84	78	0.074
γ_{flow}	$1.43\ 10^{-3}$ $(9.31\ 10^{-4})$	0.070	$2.68\ 10^{-4}$ $(7.18\ 10^{-4})$	0.872	0.97	508	0.340

Table 2.8. Correlations between response variables related to white perch growth and spatial distribution and a suite of environmental, density-dependent and habitat availability factors reported before the zebra mussel invasion (1971-1988). Statistically significant ($p < 0.05$) correlations are marked with an asterisk (*).

Response	Predictor	Type	Time Period	Years	Correlation	Source
Early Juvenile Growth Rate	Spring Temperature	Environment	Jun-Jul	1973-1979	0.93*	Klauda et al. 1988
Late Juvenile Growth Rate	Spring Temperature	Environment	Jun-Jul		0.12	
	Summer Flow	Environment	Aug-Sep	1975-1979	0.21	
	YOY Catch	Density-dependent	Oct-Dec	1974-1979	0.45	
Weight at 70mm	Summer Flow	Environment	Aug-Sep	1975-1979	-0.96*	
	YOY Catch	Density-dependent	Oct-Dec		-0.95*	
YOY Length in November	Summer Temperature	Environment	Jul-Sep	1971-1988	0.64*	LMS 1989
	Summer Flow	Environment	Jul-Sep		-0.52*	
	Fall YOY CPUE	Density-dependent	Oct-Dec		-0.26	
Mean Fall Population Center	Summer Temperature	Environment	Jul-Sep	1983-1988	0.79	
	Summer Flow	Environment	Jul-Sep		-0.81*	
	Fall YOY CPUE	Density-dependent	Oct-Dec		0.19	
Weekly Fall Population Center	Weekly Salt Front Position	Habitat availability	Oct-Nov	1985-1988	0.46*	

Figures

Figure 2.1. Map of the Hudson River Estuary (HRE), with the 13 river sections sampled by the Hudson River Estuary Monitoring Program outlined, and markers denoting approximate locations of monitoring stations for temperature (Poughkeepsie), flow (Troy) and biotic factors (Kingston; see text).

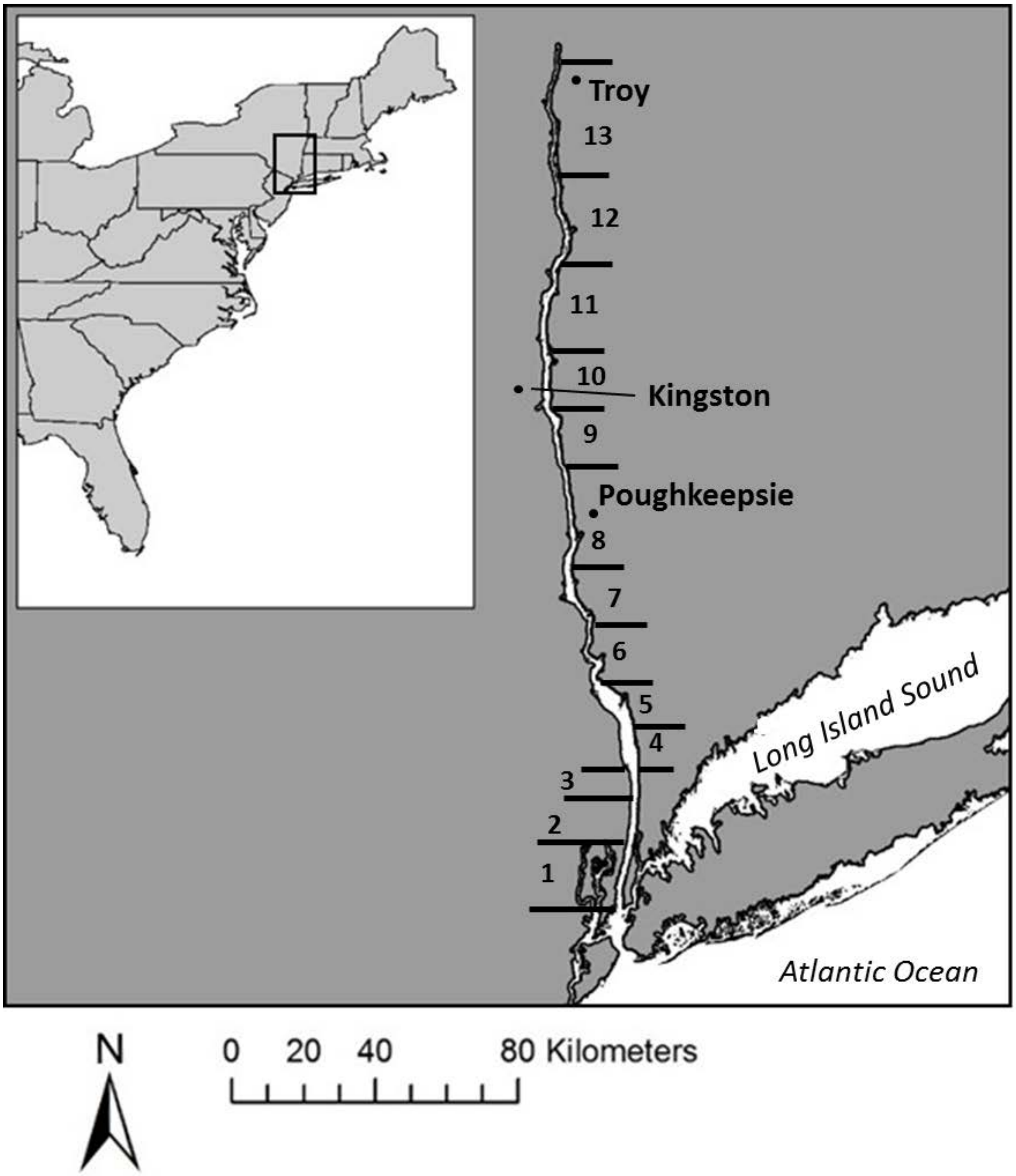


Figure 2.2. Plots of annual mean temperature (a) and freshwater flow (b) in the HRE from 1951-2013, each plotted with a locally weighted regression (thin black line; LOESS quadratic smoother with a span of 0.5) to show long-term patterns. The dashed grey lines on each plot denote the year 1991, when zebra mussels invaded the HRE (see text). Temperature data were reported in ASA (2014) and freshwater flow data were acquired from USGS (2015c).

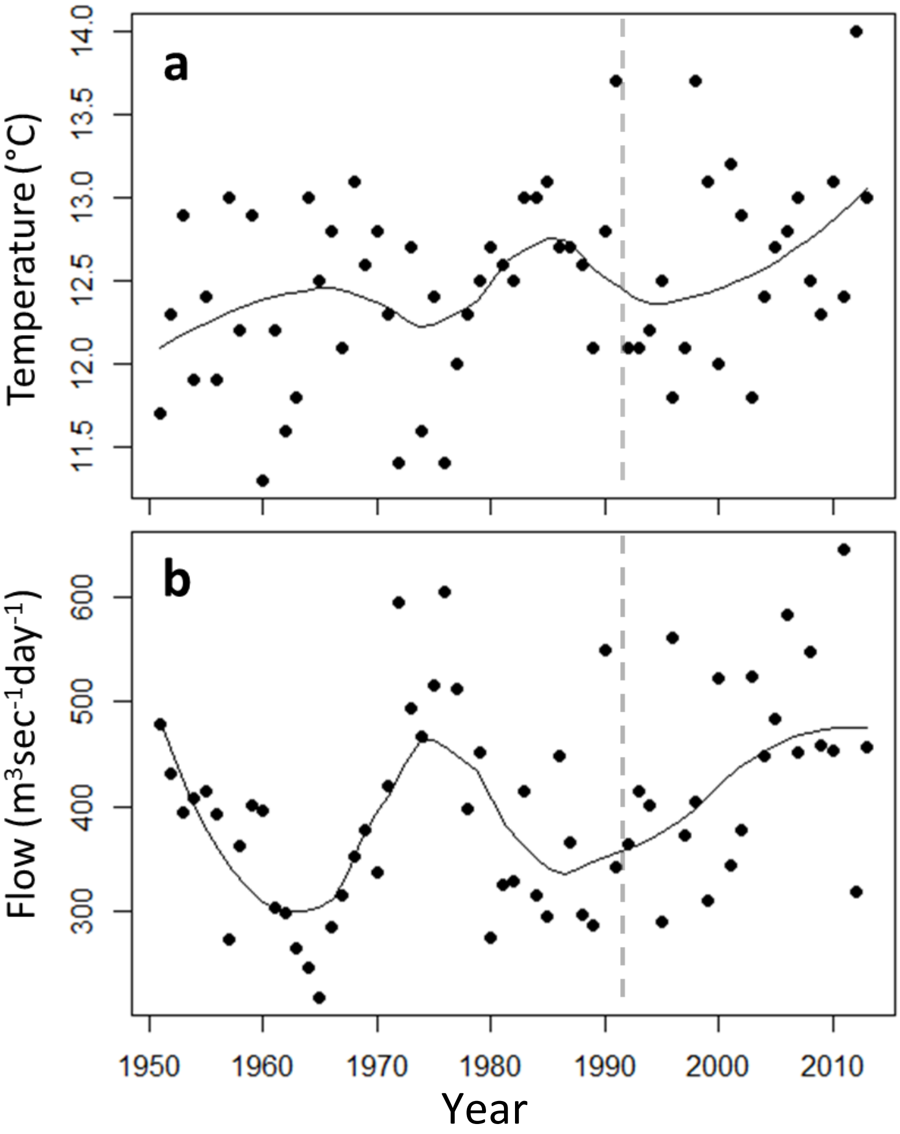


Figure 2.3. Paulik diagrams depicting relationships between annual mean standing stocks of white perch YOY, adult, YSL and PYSL (a) and YOY, adult, eggs and PYSL (b). Note that all four plots within the diagram have a common origin. Ricker models are plotted both with (dashed lines) and without (solid lines) freshwater flow as a covariate (see Methods).

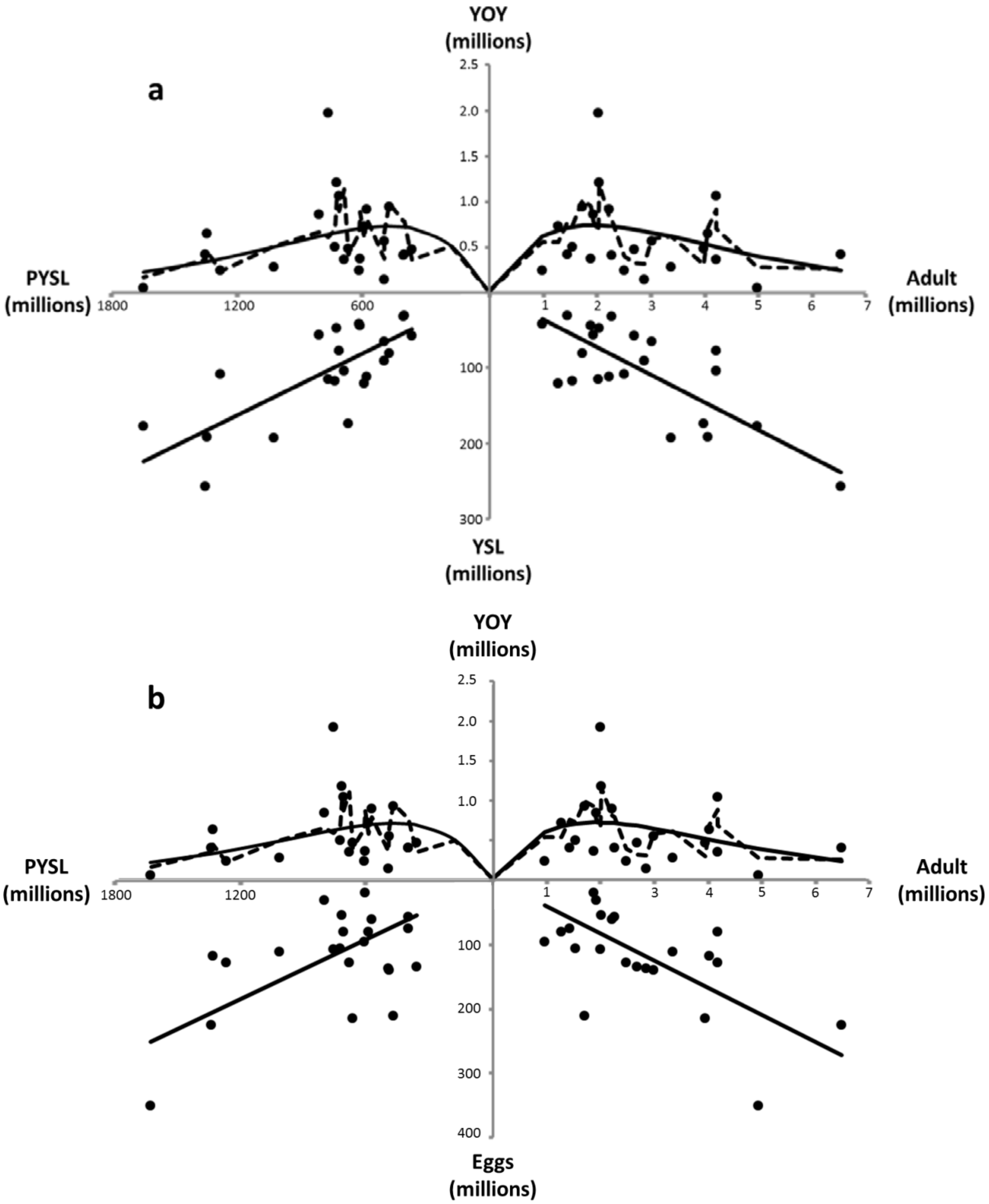


Figure 2.4. Plots of statistically significant correlations between white perch mean YOY length in October and summer temperature (a), summer flow (b) and PYSL standing stock (c) and between white perch migrant fraction and the brackish shoal proportion (d).

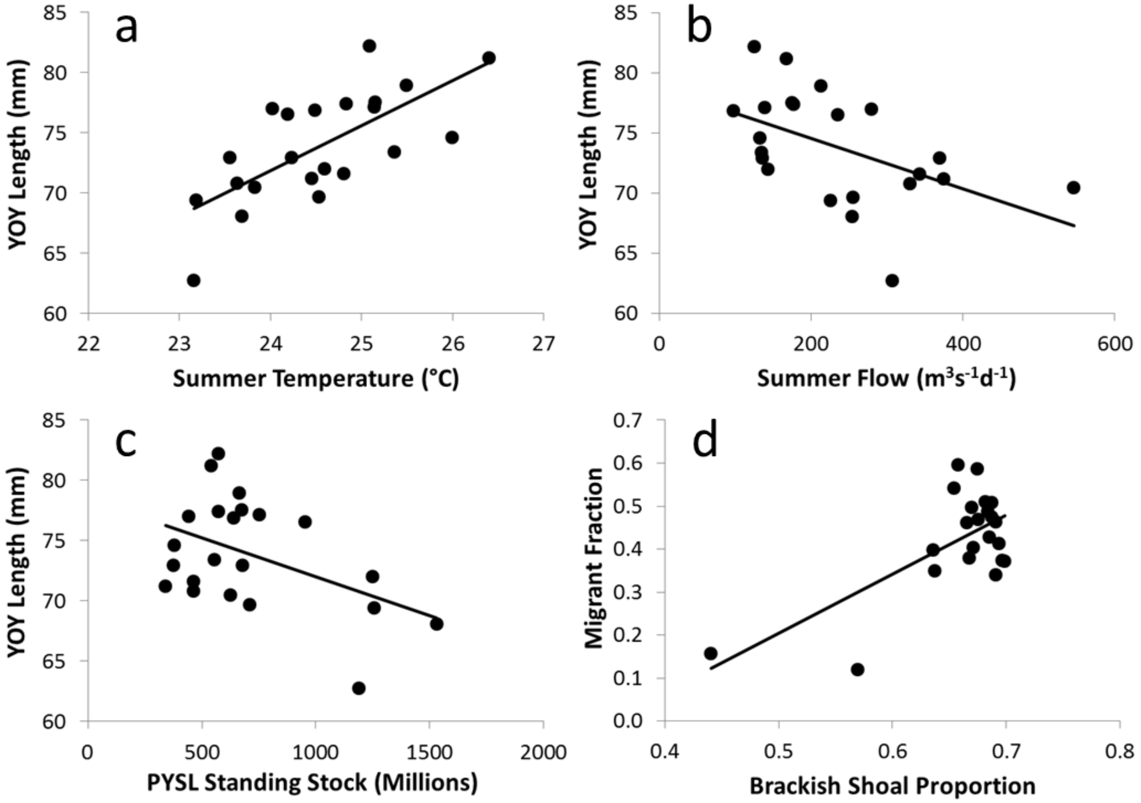


Figure 2.5. Annual mean standing stocks of resident (blue line) and migratory (red line) YOY white perch contingents from 1992-2013. The fraction of YOY in the migratory contingent each year (black line) is plotted on the secondary y-axis (right side).

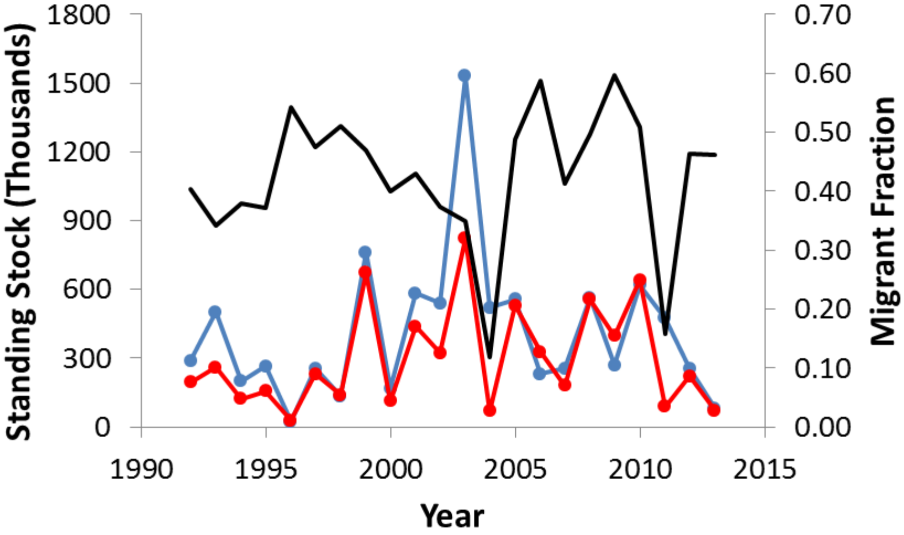


Figure 2.6. Biplots of annual scores (open circles; plotted on the primary axes) and loadings (red text and arrows; plotted on the secondary axes) for white perch life history, biotic and environmental variables shown for PC1 and PC2 (a), PC1 and PC3 (b) and PC2 and PC3 (c).

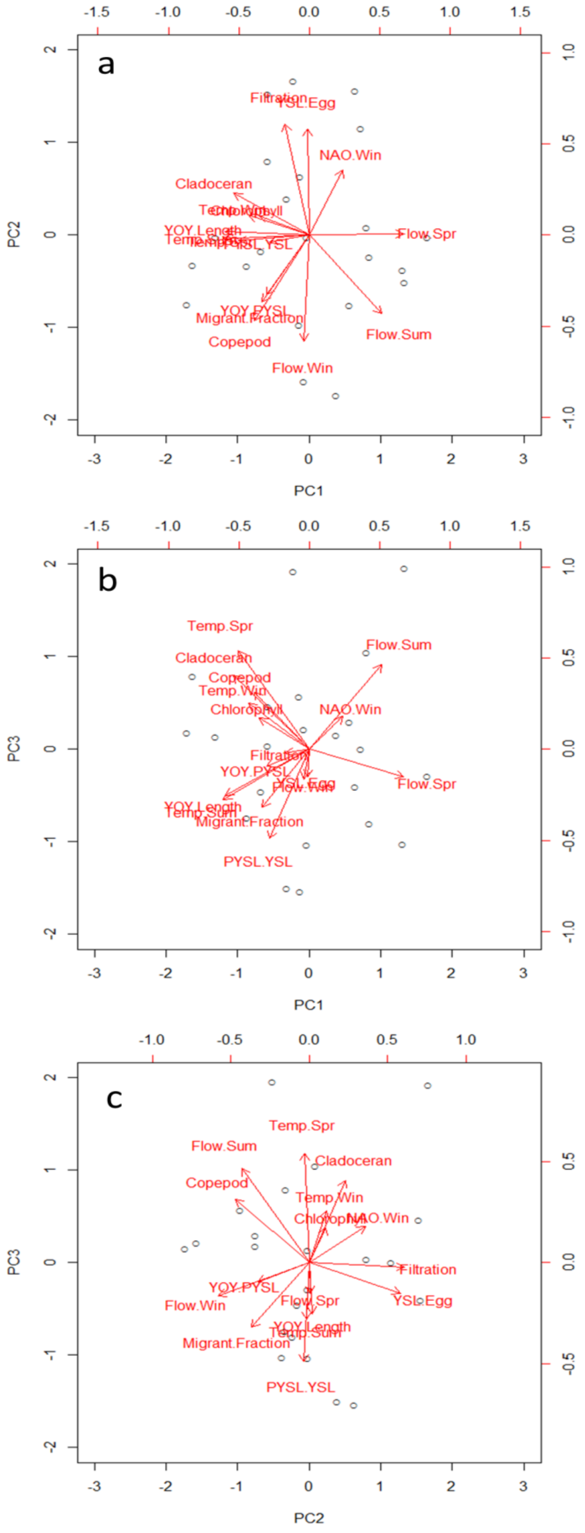


Figure 2.7. Bar plots of the unscaled loadings of each variable on Principal Components 1, 2 and 3 for white perch life history, biotic and environmental variables (see Figure 2.6). The dashed lines denote loadings of 0.25 and -0.25.

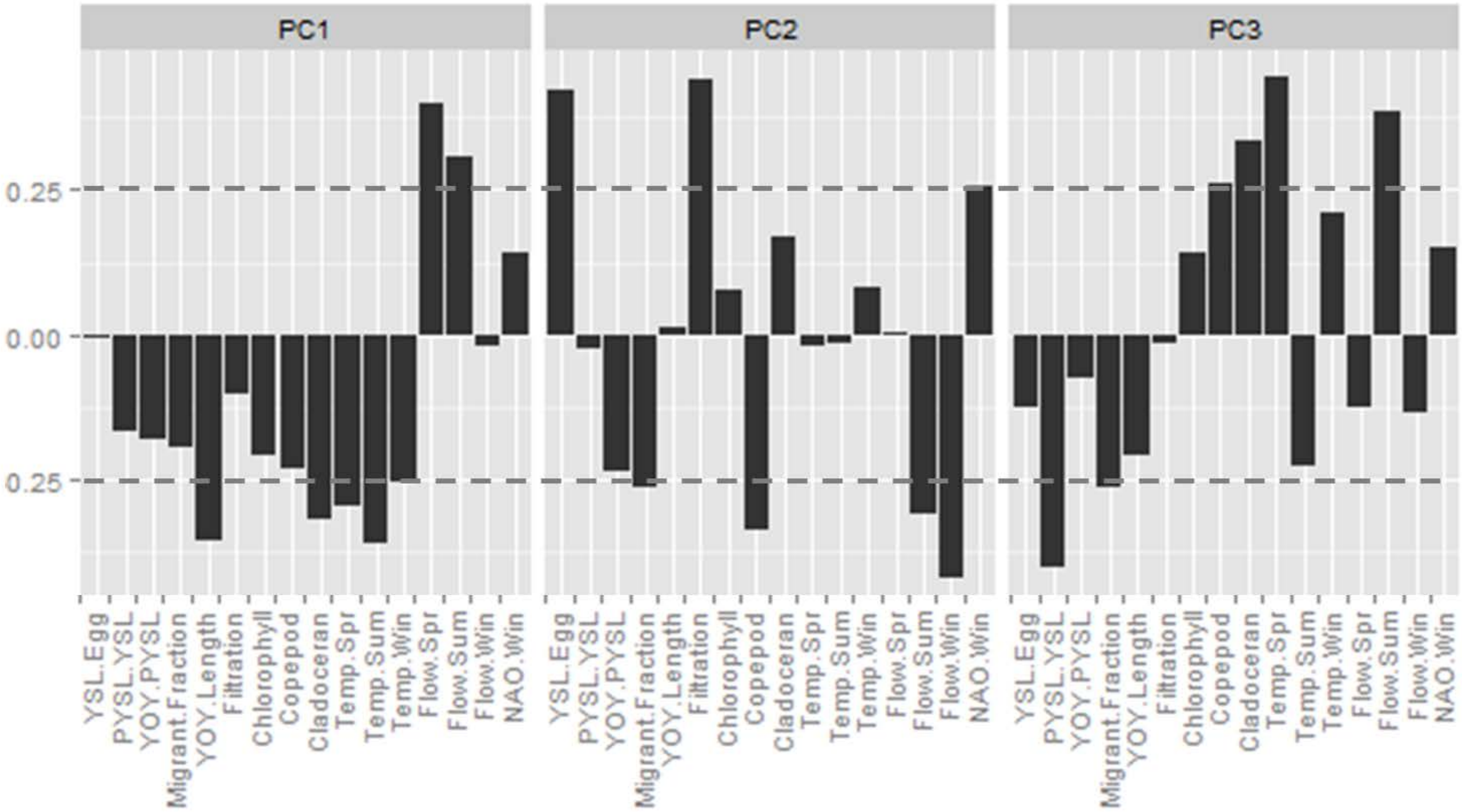


Figure 2.8. White perch life stage transitions from egg-YSL (a), YSL-PYSL (b) and PYSL-YOY (c) based on indices of abundance for each life-stage in the pre-invasion (1974-1991; black points; fitted by solid line) and post-invasion (1992-2013; white points; fitted by dashed line) time periods.

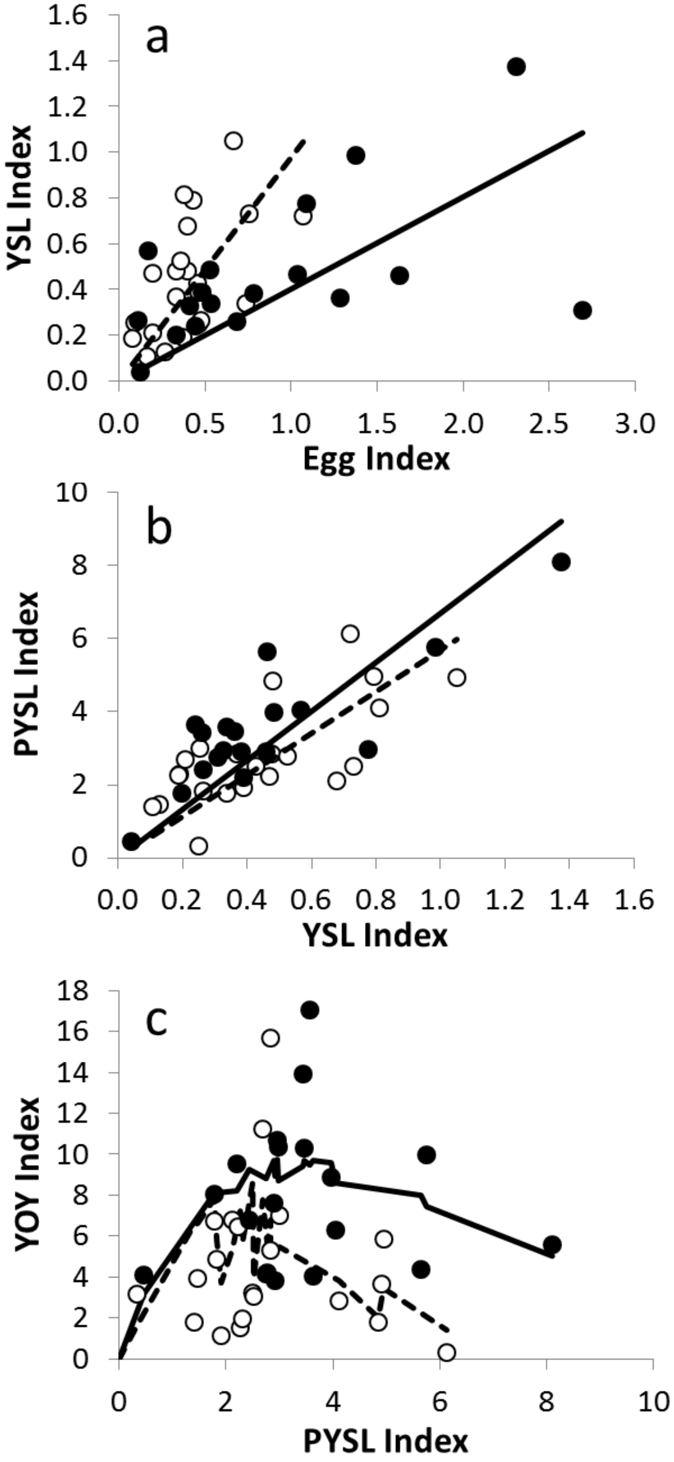


Figure 2.9. Relationship between white perch yearling abundance and YOY abundance from the previous year based upon indices of abundance for each life-stage in the pre-invasion (1974-1991; black points; fitted by solid line) and post-invasion (1992-2013; white points; fitted by dashed line) time periods.

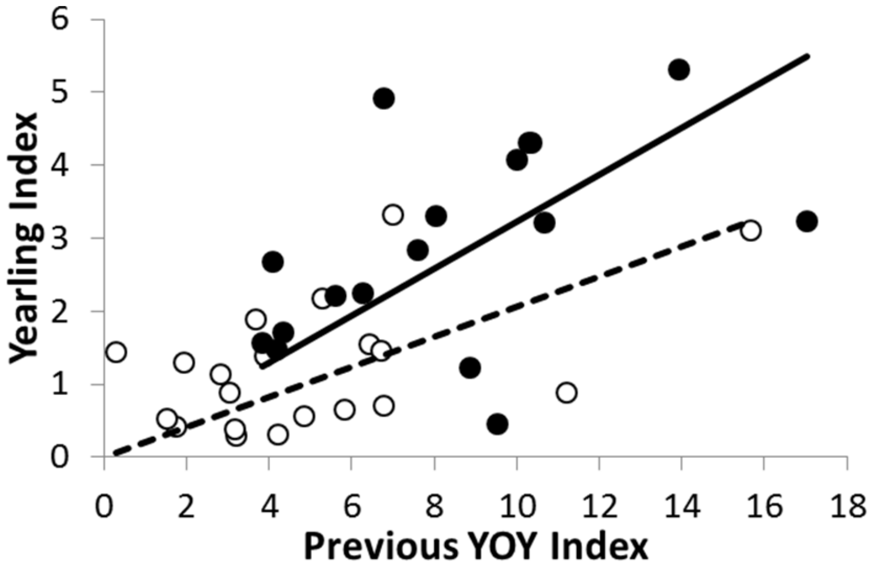


Figure 2.10. Plot of mean freshwater flow at Green Island in Troy, NY (USGS 2015c) during weeks 19-28, when white perch post yolk-sac larvae (PYSL) are most abundant, from 1992-2013. The regression equation is displayed in the top right corner, and the slope (7.99 $year^{-1}$) corresponds to an increase of 1.9% $year^{-1}$.

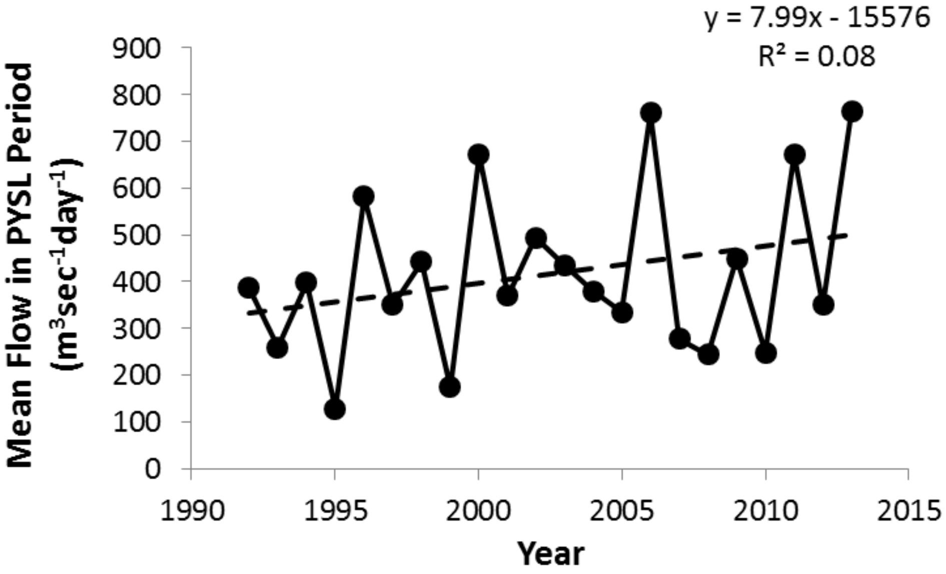
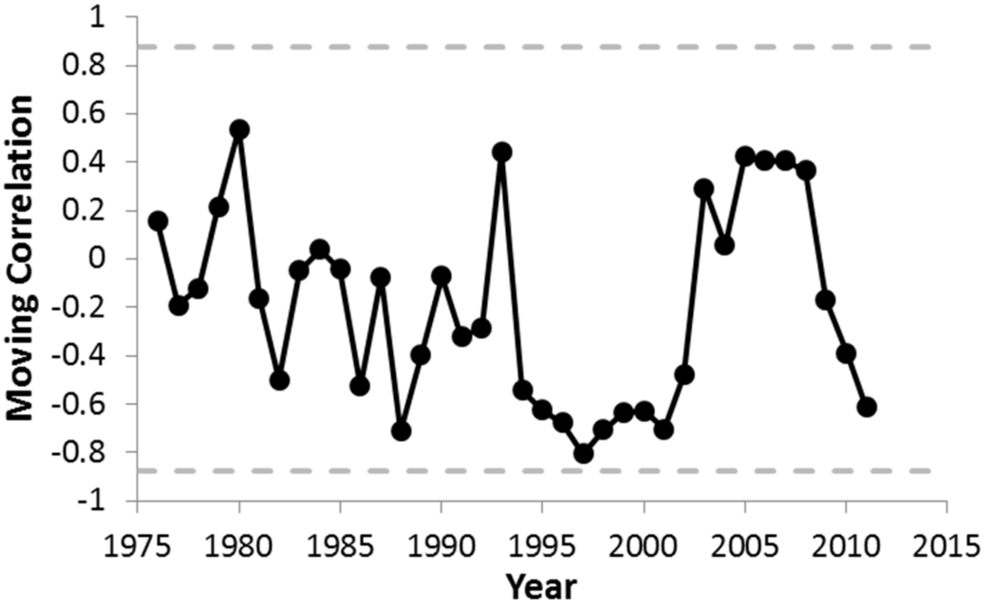


Figure 2.11. 5-year moving window correlations of linearized Ricker model residuals from the index-based PYSL-YOY relationship (pre-invasion and post-invasion periods were modeled separately without flow as a covariate) with freshwater flow during the PYSL period from 1976-2011. The gray dashed lines denote critical values for positive and negative correlations ($p < 0.05$). Note that 8 consecutive years of strong negative correlations occur after 1994, which encapsulates the years immediately after the zebra mussel invasion in the HRE (1992-1996).



Chapter 3: Future research on white perch partial migration

White perch have become a model species for studying partial migration in estuarine fishes. The causes and consequences of white perch partial migration have been rigorously studied in the Patuxent River population (Kraus and Secor 2004a, Kerr and Secor 2009, Kerr and Secor 2010), while contingent structure and adult growth characteristics have been recently evaluated in six other Chesapeake Bay tributaries (Kerr and Secor 2008, 2011). In addition, ongoing research in the Carmans River in New York has identified contingent structure in tagged adult white perch (M. Frisk, SUNY Stony Brook, personal communication). Including the current study in the Hudson River Estuary (HRE), white perch partial migration has now been documented in nine estuarine systems, which indicates that partial migration is spatially widespread and may indeed be ubiquitous in estuarine white perch populations. Data from these previous studies are potentially useful in developing a more comprehensive understanding of the population-level consequences of partial migration in white perch over expanded spatial and temporal scales.

Interannual Variability in Carryover Effects

Although I only examined two year-classes (2013 and 2014) of juvenile white perch in Chapter 1, substantial differences in environmental conditions experienced during the larval period were observed between years, which significantly altered larval growth rates. These modifications in early-life characteristics may have been partly responsible for the significant differences in late-juvenile growth between contingents observed in 2013 (lower temperature, higher flow, reduced larval growth), but not 2014.

As a result of variability in conditions during the larval period, contingent-specific bioenergetics (e.g. consumption rate, scope for growth) during the juvenile period may have differed between these two years, thereby affecting compensatory growth dynamics (Kerr and Secor 2009). Further research conducted over a longer time period (3+ years), or in systems with vastly different environmental characteristics is warranted to understand how inter-annual variability in environmental conditions shape the causes and consequences of partial migration in white perch during the first year of life. Future work quantifying bioenergetic differences between resident and migratory contingents in relation to larval growth rates (after Kerr and Secor 2009) would also help to better define compensatory growth dynamics during the juvenile period within the HRE population.

Range-Wide Drivers of Growth and Contingent Structure

Research by Tuckett et al. (2013) demonstrated that the morphology and trophic dynamics of landlocked white perch populations can change considerably over productivity gradients in lakes. Moreover, white perch exhibited smaller maximum sizes and diminished representation of the migratory contingent in the HRE compared to more productive systems in Chesapeake Bay (see Table A.2 and Figure A.5 in the Appendix). Together, these findings raise the possibility that estuarine white perch contingent structure and growth characteristics may have predictable relationships with ecosystem attributes over larger spatial scales. Response variables of interest, such as contingent proportions, von Bertalanffy growth parameters, and length-weight parameters can be compared to system-wide temperature and freshwater flow characteristics, as well as indices of primary productivity (e.g. net ecosystem production [primary production -

respiration] during the growing season) and littoral habitat availability in systems where these data are available. In addition, white perch recruitment (indexed by juvenile abundance) has been observed to be more variable in Chesapeake Bay tributaries (~70 to 100 fold; North and Houde 2001, Kraus and Secor 2005) than in the HRE (~10 to 40 fold; Klauda et al. 1988, Chapter 2). At the population level, higher recruitment variability in Chesapeake Bay may be offset by the increased representation of the migratory contingent in these systems (Table A.2), especially since the migratory contingent tends to be more productive (Figure A.4; Kraus and Secor 2004a). An index of recruitment variability (e.g. long-term maximum/minimum) may also be useful as a response variable in relation to the environmental and productivity attributes of each system. Exploration of ecosystem-scale determinants of white perch life history diversity across their native range can provide additional insight to the adaptive potential of the species in the face of long-term environmental change.

Simulating the Influence of Climate Change

Analyses in Chapter 2 uncovered a significant negative effect of annual mean freshwater flow during the post yolk-sac larval period (weeks 19-28) on the white perch stock-recruitment relationship from 1992-2013, which was largely consistent with previous research documenting the influence of flow on primary and secondary productivity within the HRE (Gladden et al. 1988, Howarth et al. 2000), especially after the zebra mussel invasion (Strayer et al. 2008). Given the importance of freshwater flow to white perch recruitment dynamics, future research should attempt to explicitly incorporate expected shifts in freshwater flow over the next century into white perch population projections. Seekell and Pace (2011) previously analyzed freshwater flow data from Green Island Dam and reported that annual mean freshwater flow increased by nearly 25% from 1946-2008, with the greatest rates of increase occurring in winter and spring months. Averages (±1 SD) of several statistically down-scaled global climate models indicated that annual mean freshwater flow in the HRE is projected to increase further by 5-25% by 2100 (Najjar et al. 2009). However, Najjar et al. (2009) emphasized the uncertainty in their flow projections and noted that increased evapotranspiration or changes in seasonality driven by warming temperatures could conceivably result in long-term decreases in freshwater flow in the HRE, especially during the spring and summer.

Simulation models are useful tools for exploring the future impacts of climate change on fish populations exhibiting environmental sensitivity and partial migration, such as HRE white perch (Kerr and Goethel 2013). A stochastic age-structured population model similar to that used by Kerr et al. (2010) has already been developed for white perch in the HRE. This model will be implemented over a 100-year period to explore 60 scenarios with each possible combination of white perch contingent structure (migrant fraction = 0, 0.2, 0.4, 0.6 or 1; similar to Kerr et al. 2010), migratory contingent mortality rate (equal to or 50% higher than the resident contingent), freshwater flow projections (25% increase, 25% decrease or no change over the next century) and environmental variability (25% increase or no change in the CV of flow over the next century). Population yield (mean spawning stock biomass), stability (coefficient of variation for spawning stock biomass) and resilience (recover time to the mean spawning stock biomass after imposing recruitment failure) will be averaged over 500 simulations for each scenario, and used to compare model outcomes across scenarios. Results from this modeling exercise should provide a holistic picture of how partial migration and climate change will likely interact to impact the population dynamics of HRE white perch over the next 100 years.

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Appendix: Per-recruit models for Hudson River white perch

Per-Recruit Model Parameterization

Klauda et al. (1988) reported mean length-at-age and maturity-at-age for male and female white perch in the Hudson River Estuary (HRE) from 1975-1977 (n = 795). Female white perch tended to be slightly larger and mature slightly later than males, but these differences were small, with overlapping standard errors (Klauda et al. 1988). In addition, differences in growth between sexes were not evaluated in the current study. Therefore, length and maturity data were averaged across sexes and years, and a logistic function was fitted to these averages to describe the proportion of white perch that were mature as a function of total length (L), by the equation:

$$\text{(1)} \qquad Proportion\ Mature = \frac{1}{1+e^{-k(L-L_{50})}}$$

where the asymptote (i.e. the numerator) was fixed at 1, L_{50} is the point at which 50% maturity was reached and k is the rate at which the asymptote was approached. Parameters were estimated by minimizing the sum of squares using the Solver add-in in Microsoft Excel. The logistic function fit the data well ($R^2 = 0.95$; Figure A.1a), and L_{50} was estimated to be 131 mm, while k was estimated at 0.08.

Juvenile and adult white perch captured in 2013 and 2014 were used to construct a length-weight relationship for the HRE population (n = 1,043) by the equation:

$$\text{(2)} \qquad W = \alpha L^{\beta}$$

where W is weight (in kg) α is the weight-length multiplier (in $kg \cdot mm^{-1}$) and β is the exponent. Parameters were once again estimated by minimizing the sum of squares using the Solver add-in in Microsoft Excel. Length explained the vast majority of the variation in weight ($R^2 = 0.98$; Figure A.1b) and α was estimated at $4.3 \cdot 10^{-9}$ kg·mm^{-1}, while β was estimated to be 3.2.

The instantaneous natural mortality rate (M) of adult white perch was estimated using a catch curve based on adult white perch captured in 2” mesh gillnets during fall 2014 (n = 216) by the regression equation:

$$log_e(N_a) = b_0 - (a \times M) \tag{3}$$

where N_a is the catch at age a, b_0 is the intercept, and a is age. Data from ages 2-11 were used, and M was estimated to be 0.27 year^{-1} (Figure A.2). Starting the catch curve at ages 3-5 yielded similar mortality estimates (range: 0.23-0.29). However, catch-at-age data were not adjusted for effort (i.e. gillnet soak time), so this mortality estimate should be viewed as preliminary.

Yield-Per-Recruit and SSB-Per-Recruit Models

Predicted length-at-age data from von Bertalanffy growth models for each contingent (Table 1.9 and Figure 1.12) were used as inputs into equations 1 and 2 to calculate the maturity-at-age and weight-at-age for resident and migratory contingents from ages 1-13 (Figure A.3). The baseline natural mortality rate was assumed to be 0.27 for both contingents. These data were used to conduct yield-per-recruit (YPR) and spawning stock biomass-per-recruit (SSBR) analyses and estimate biological reference points (BRPs) for each contingent of HRE white perch (see below).

Age-structured data were used to implement an YPR analysis, where the YPR was calculated by the equation:

$$YPR = \sum_{a=1}^{13}\left(\frac{F_a}{Z_a} \times (1 - e^{-Z_a}) \times N_a \times W_a\right) \tag{4}$$

where F_a is the fishing mortality rate at age a, Z_a is the total mortality rate (F_a plus the natural mortality rate), N_a is the abundance at age a (N_1 is assumed to be equal to 1) and W_a is the weight at age a (Figure A.3b). F_a values are typically obtained by multiplying a fixed fishing mortality rate by the age-specific selectivity (Hilborn and Walters 1992). However, there are currently no size limits on white perch caught recreationally in the HRE (NYSDEC 2016), and white perch begin to be harvested by anglers at sizes between 75 and 100 mm (Normandeau 2003). Therefore, white perch were assumed to be fully-selected (i.e. selectivity = 1) in all age-classes, similar to previous analyses of white perch in Virginia estuaries by Kerr and Secor (2008). Subsequently, the same data were used to conduct a SSBR analysis, which accounts for the maturity schedule, where SSBR was calculated by the equation:

$$SSBR = \sum_{a=1}^{13} Mat_a \times N_a \times W_a \tag{5}$$

where Mat_a is the proportion mature at age a. SSBR is calculated both with and without fishing mortality and used to calculate the spawning potential ratio (SPR), by the equation:

$$SPR = \frac{SSBR_F}{SSBR_{F=0}} \tag{6}$$

where $SSBR_F$ is the spawning stock biomass-per-recruit at a fishing mortality rate of F, and $SSBR_{F=0}$ is the spawning stock biomass-per-recruit when F is equal to 0.

Separate YPR and SSBR analyses were run for resident and migratory contingents of HRE white perch. In addition, two natural mortality scenarios were considered for the migratory contingent to explore the potential consequences of a higher mortality rate in this population segment (see Chapter 1). Specifically, the natural mortality rate of the migratory contingent was assumed to be either 0.27 (i.e. same as residents) or 0.41 (1.5x higher than residents), such that three YPR and SSBR analyses were conducted overall. YPR, SSBR and SPR were each plotted over a range of fishing mortality rates (Figure A.4). BRPs were estimated for each analysis, with F_{max} and $F_{40\%}$ reference points estimated for YPR and SSBR analyses, respectively (Hilborn and Walters 1992; Table A.1). F_{max} was estimated by maximizing YPR using the Solver add-in in Microsoft Excel, while $F_{40\%}$ was estimated by setting SPR to 0.4 using the Goal Seek function in Microsoft Excel. Fishing mortality rates exceeding F_{max} suggest that biomass is being removed faster than it can be replaced by somatic growth (i.e. growth overfishing), while $F_{40\%}$ is considered a more conservative reference point, above which individuals are removed faster than they can be replaced via recruitment processes (i.e. recruitment overfishing; Hilborn and Walters 1992). The YPR and SSBR associated with each BRP was calculated for each contingent and compared to previous estimates from Chesapeake Bay populations (Table A.1; from Kerr and Secor 2008). To aid comparisons between populations, von Bertalanffy growth parameters (L_∞ and k; from Kerr and Secor 2008) and contingent proportions based on chemical analyses of the first-annulus of adult white perch otoliths (Kraus and Secor 2004a, Kerr and Secor 2011) were tabulated along with corresponding estimates for the HRE population from this thesis (Table A.2).

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Tables

Table A.1. Contingent-specific biological reference points (BRP; F_{max} and $F_{40\%}$) for fishing mortality in HRE white perch, and corresponding spawning stock biomass-per-recruit (SSBR) and yield-per-recruit (YPR). Migratory* denotes models where a higher mortality was used for the migratory contingent (M = 0.41; see text). Previous BRP estimates for white perch populations within six Chesapeake Bay tributaries (Upper Bay, Patuxent, Potomac, Nanticoke, York and James Rivers) from Kerr and Secor (2008) are shown for comparison.

River	**Contingent**	**BRP**	**F**	**SSBR**	**YPR**
Hudson	Migratory	F_{max}	0.38	0.07	0.02
	Migratory*	F_{max}	0.51	0.04	0.02
	Resident	F_{max}	0.31	0.04	0.01
James	Combined	F_{max}	0.27	0.12	0.02
York	Combined	F_{max}	0.24	0.21	0.04
Hudson	Migratory	$F_{40\%}$	0.24	0.10	0.02
	Migratory*	$F_{40\%}$	0.31	0.06	0.02
	Resident	$F_{40\%}$	0.20	0.07	0.01
Upper Bay	Combined	$F_{40\%}$	1.65	0.08	0.03
Patuxent	Combined	$F_{40\%}$	2.35	0.12	0.04
Potomac	Combined	$F_{40\%}$	0.53	0.09	0.01
Nanticoke	Combined	$F_{40\%}$	0.82	0.15	0.04
James	Combined	$F_{40\%}$	0.21	0.13	0.02
York	Combined	$F_{40\%}$	0.19	0.22	0.04

Table A.2. Contingent proportions (M = migrant proportion; R = resident proportion; n_c = sample size) and von Bertalanffy growth parameters (n_g = sample size) for eight white perch populations. Note that the von Bertalanffy growth model for both contingents combined in the HRE included adults captured in the spring that were not used in the contingent-specific models (see Chapter 1).

		Contingent Proportions			Growth			
River	**Contingent**	**n_C**	**M**	**R**	**n_G**	**L_∞ (mm)**	**k**	**Source**
Upper Bay	Combined	75	0.31	0.69	59	240	0.46	Kerr and Secor (2008, 2012)
Choptank	Combined	78	0.55	0.45	75	225	0.48	Kerr and Secor (2008, 2012)
Potomac	Combined	45	0.35	0.65	70	258	0.26	Kerr and Secor (2008, 2012)
Nanticoke	Combined	75	0.81	0.19	88	254	0.35	Kerr and Secor (2008, 2012)
James	Combined	49	0.82	0.18	78	246	0.40	Kerr and Secor (2008, 2012)
York	Combined	75	0.68	0.32	61	269	0.35	Kerr and Secor (2008, 2012)
Patuxent	Combined	363	0.93	0.07	101	258	0.32	Kerr and Secor (2008, 2012)
	Resident	-	-	-	27	217	0.39	Kraus and Secor (2004)
	Migratory	-	-	-	336	217	0.69	Kraus and Secor (2004)
Hudson	Combined	229	0.09	0.91	263	188	0.62	Current study
	Resident	-	-	-	112	194	0.52	Current study
	Migratory	-	-	-	79	204	0.69	Current study

Figures

Figure A.1. Length-maturity information (a) from Klauda et al. (1988) averaged for both sexes of HRE white perch from 1975-1977 (open circles), fitted by a logistic function (thick black line; $R^2 = 0.95$; see text) and length-weight information (b) from juvenile and adult white perch captured in 2013 and 2014 (open circles), fitted by a power model (thick black line; $R^2 = 0.98$; see text).

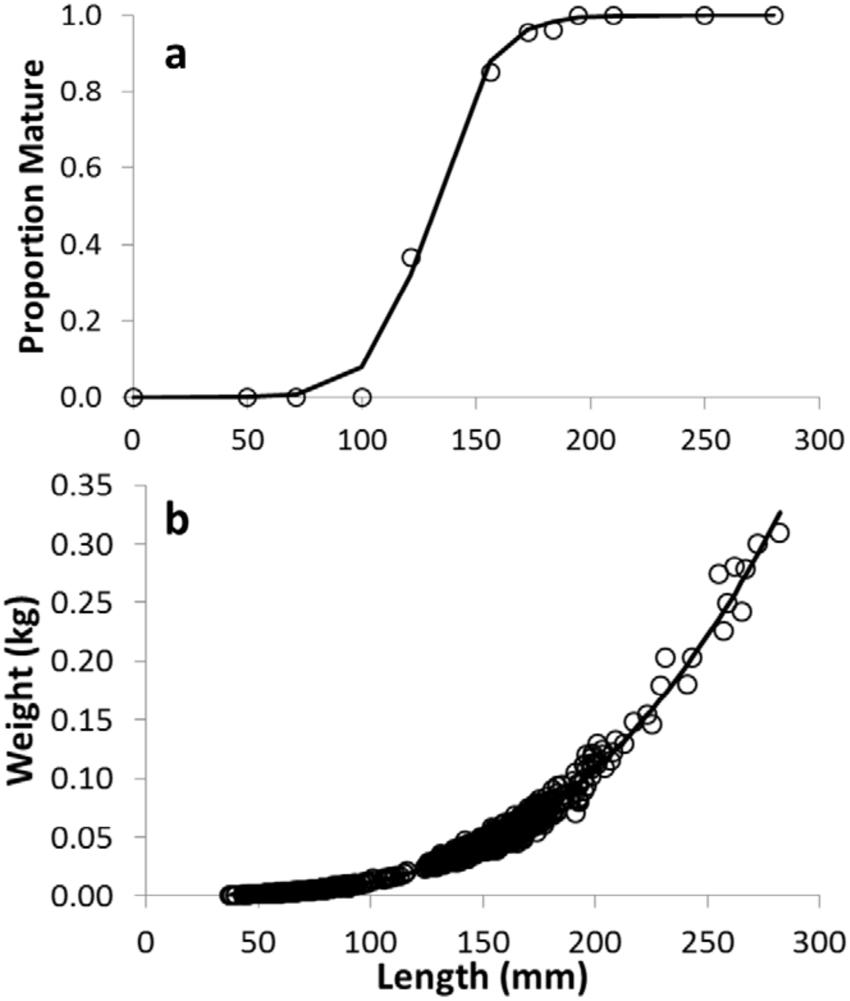


Figure A.2. Preliminary catch curve constructed for adult white perch captured in 2” gillnets during fall 2014. Catch data were natural-log transformed and plotted as a function of age. The linear regression equation and model R^2 are shown in the top right corner, where the slope represents the natural mortality rate (M).

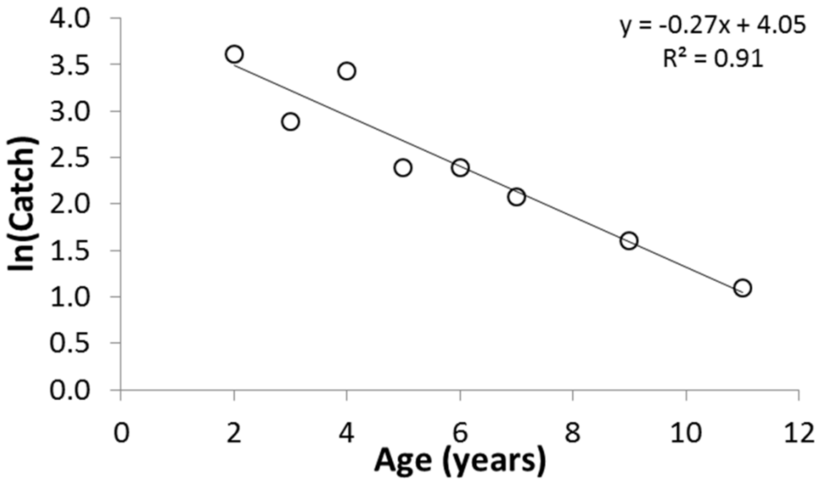


Figure A.3. Maturity-at-age (a) and weight-at-age (b) for resident (blue) and migratory (red) contingents of white perch in the HRE.

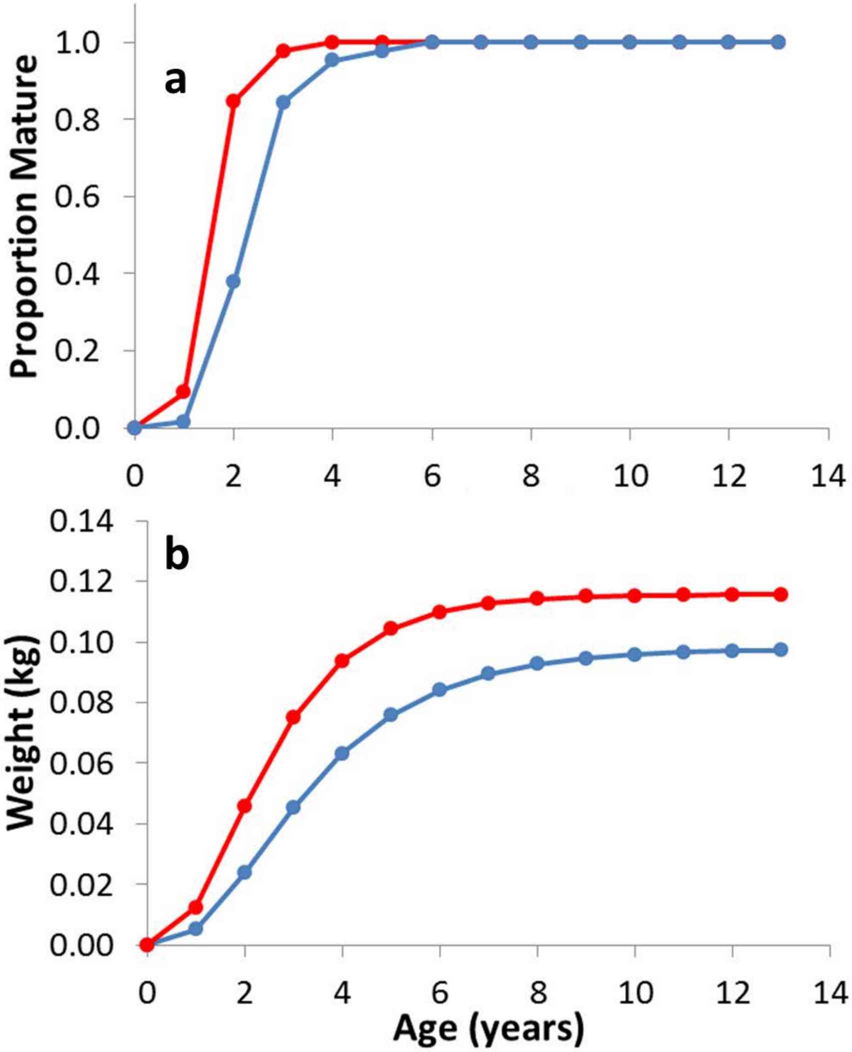


Figure A.4. Yield-per-recruit (a), spawning stock biomass-per-recruit (b) and spawning potential ratio (c) plotted as a function of fishing mortality rate for the resident contingent (blue), migratory contingent (red) and the migratory contingent with a higher mortality rate (dark red).

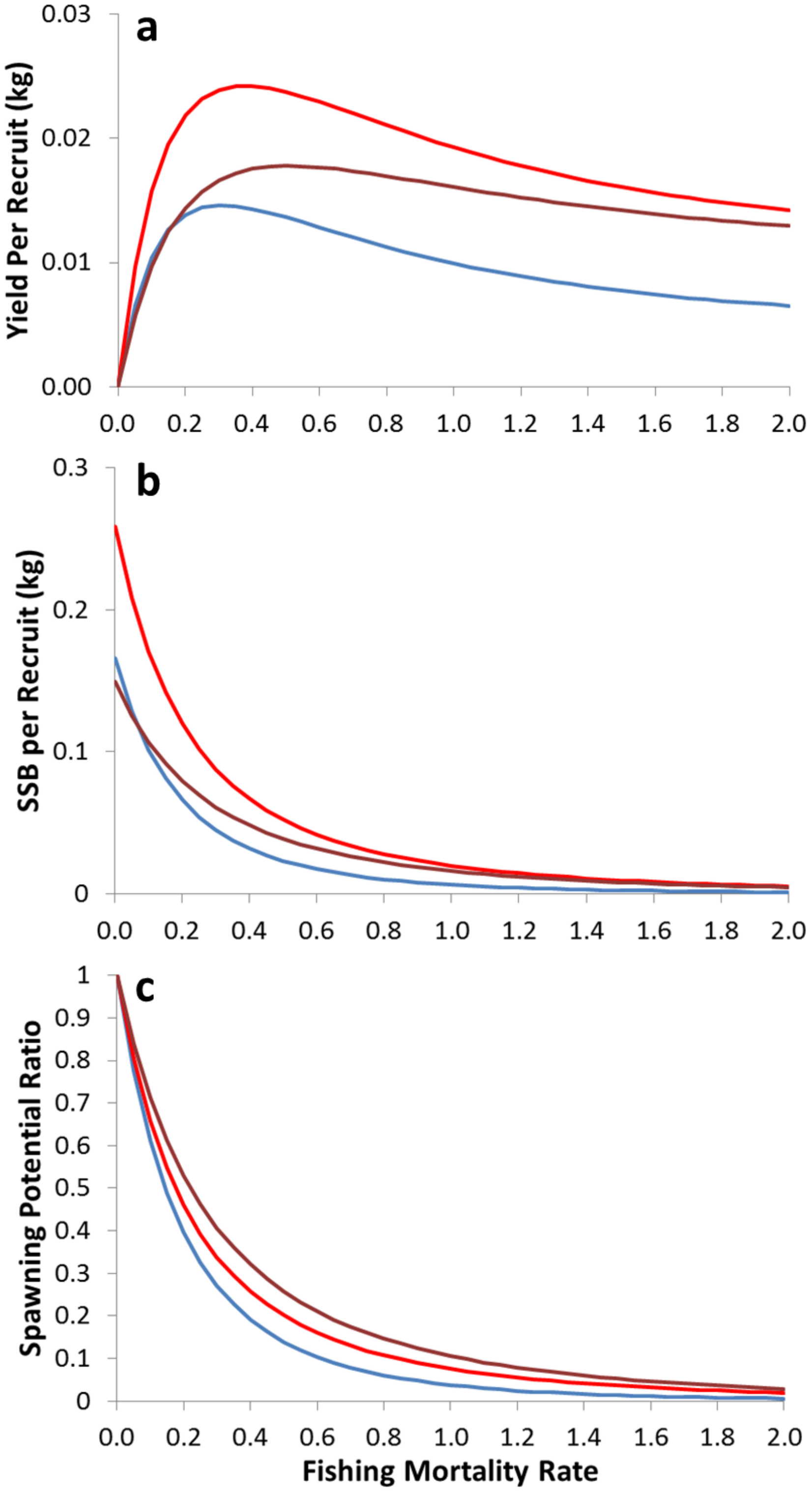
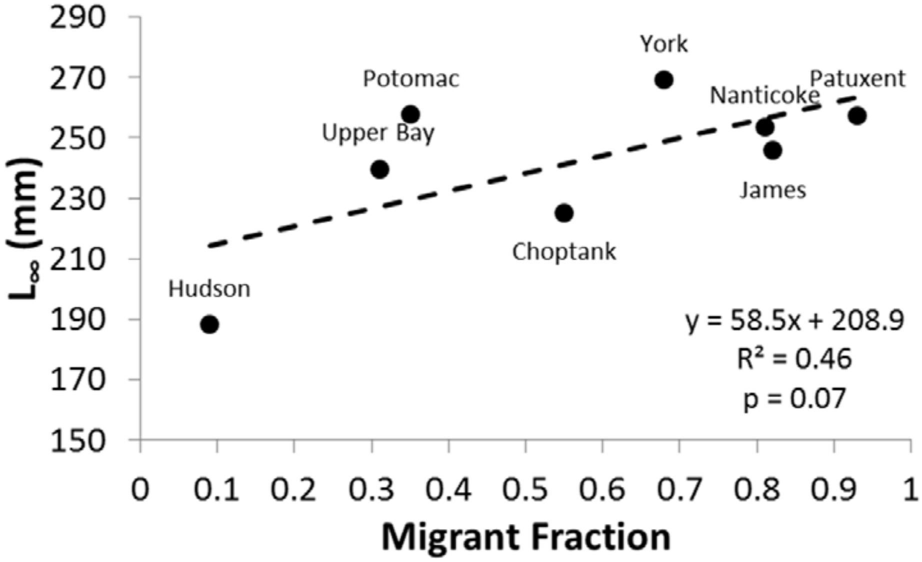


Figure A.5. Estimated L_∞ (resident and migratory contingents combined) in eight white perch populations, plotted in relation to the fraction of the adult population that was migratory during the first year of life. Data for Chesapeake Bay tributaries were from Kerr and Secor (2008, 2011). Note that the relationship is marginally non-significant, and becomes much weaker if the Hudson River is removed ($R^2 = 0.09$). Estimated k had a non-significant negative relationship with migrant fraction ($R^2 = 0.35$; $p = 0.12$; data not shown), and L_∞ estimates displayed a significant negative relationship with k estimates ($R^2 = 0.86$; $p > 0.001$; data not shown), even after removing the Hudson River.



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