ABSTRACT

Title of Document: CAUSE, CONSEQUENCE, AND PREVALENCE OF SPATIAL STRUCTURE OF WHITE PERCH (*MORONE AMERICANA*) POPULATIONS IN THE CHESAPEAKE BAY.

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Partial migration defines the simultaneous occurrence of migratory and resident groups within populations. Using otolith chemistry (strontium:calcium measures), I documented partial migration for an estuarine-dependent white perch (*Morone americana*) population in the Patuxent River estuary (Chesapeake Bay, MD). Previous research indicated that as juveniles, a portion of the population remained resident in freshwater natal habitats and another portion dispersed down-estuary into brackish water habitats. I established these behaviors are alternative life history tactics that persist over the lifetime of individuals. Through back-calculation of hatch-dates, juvenile contingents were associated with their respective larval cohorts, indicating that spatial structuring was influenced by time of spawning, and temperature and prey conditions experienced during early life history. Dispersive individuals originated primarily from earlier spawned larval

cohorts, characterized by slower growth and higher mortality rates compared to later spawned cohorts, which contributed disproportionately to the resident contingent. Laboratory experiments revealed that partial migration was associated with varying energetic tactics, with dispersive contingent fish exhibiting higher consumption and faster growth rates subsequent to migration. The prevalence of contingent behavior within other white perch populations in Chesapeake Bay was explored using otolith stable isotope ($\delta^{18}O$) values, which had a positive relationship with salinity and together with otolith $\delta^{13}C$ serve as a proxy for regional habitats distributed along an estuarine salinity gradient. Resident contingent fish dominated Upper Bay and Potomac River populations, whereas the dispersive contingent dominated within the Choptank, Nanticoke, James, and York Rivers. The consequences of spatial structuring to productivity (spawning stock biomass), stability (variance in spawning stock biomass), and resilience (years to rebuild the population) of white perch populations were examined using an age-structured simulation model. Increased representation of migratory fish resulted in increased population productivity and resilience, whereas presence of the resident contingent within the population contributed to stability. Increased population stability and productivity also occurred when the abundance of the two contingents varied inversely to one another over time (i.e., asynchronous dynamics). The different roles contingents play in mediating population dynamics and long-term persistence highlights the importance of managing for conservation of spatial structure within fish populations.

CAUSE, CONSEQUENCE, AND PREVALENCE OF SPATIAL STRUCTURE OF WHITE PERCH (*MORONE AMERICANA*) POPULATIONS IN THE CHESAPEAKE BAY.

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Dissertation 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
Doctor of Philosophy
2008

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ACKNOWLEDGEMENTS

I would like to acknowledge the National Science Foundation for their support of this research under Grant No. OCE-032485. I am also grateful to the the Chesapeake Biological Laboratory Graduate Education Committee, American Fisheries Society, and the University of Maryland Graduate School for travel support to present this research at scientific meetings.

I sincerely thank my committee members for their help throughout my tenure as a graduate student at the Chesapeake Biological Laboratory. In particular, I am grateful to Dr. Dave Secor, my advisor, for his guidance and support throughout my time at CBL. Thank you very much to my committee members, Dr. Ed Houde, Dr. Rodger Harvey, Dr. Mike Roman, Dr. Steve Cadrin, for their insightful comments and recommendations during my dissertation process. A special thanks to my past and present lab-mates, Rebecca Wingate, Ryan Woodland, Deanna McQuarrie, Kari Fenske, Bob Murphy, Brandon Puckett, and Jody Callihan, for their camaraderie and assistance on many aspects of this research. I am grateful to Eric Durrell and the Maryland Department of Natural Resources and Hank Brooks and the Virginia Institute of Marine Science for their help in obtaining fish samples. I acknowledge Phil Piccoli (University of Maryland), and Chris Eastoe and David Dettman (University of Arizona Isotope Geochemistry Laboratory) for their technical assistance. Many individuals at the Chesapeake Biological Laboratory deserve thanks for provided support in various forms, including: Mike Wilberg, Tom Miller, Chris Rowe, Lizzy Jenny, Lynton Beaven, Steve Fenske, Bud Milsaps, Adam Peer, Adriana Hashinga, Ed Martino, Bill Connolly, Carlos Lozano, Janet

Nye, and Phil Sandstrom. I would like to thank my REU students Lisa Guy and Matt Lusk for all their hardwork on summer research projects. My gratitude goes to the staff and administration at CBL for their assistance over the years and many thanks to all the students and faculty who have made my experience at the lab so enjoyable. Finally, I am grateful to Ramiro and my family for their love and support.

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 5

LIST OF FIGURES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 7

Chapter 1: OVERVIEW

The concept of the "unit stock", wherein a population is considered a single unit with one shared fate, has been a fundamental principle of fisheries science for many years. This view is reflected in the simplified vision of regional population dynamics assumed by many assessment models, in which populations are considered to be homogeneous, with all individuals behaving similarly and consequently having equal birth, growth, and mortality rates (Hilborn and Walters 1992, Gotelli 2001). It is increasingly recognized that inclusion of demographic complexity is necessary to more accurately characterize a population. Age-related differences in vital rates have long been recognized as having a significant impact on population-level dynamics and have been incorporated into the framework of age-structured population models (Quinn and Deriso 1999). Only recently, however, has the role of spatial structure within populations received increased attention for its impact on vital rates and its potential role in determining population-level dynamics (Secor 2005, Secor 2007, Cadrin and Secor *In Press*). For some species, incorporation of the spatial structure within populations may enhance our ability to assess, manage, and forecast changes in the population.

Contingent structure describes a type of spatial structuring in populations whereby portions of the population exhibit divergent migration behaviors or habitat use (Clark 1968, Secor 1999). The presence of this type of life cycle diversity within populations has been identified across taxa (e.g. insects, mammals, birds), and within fish populations, extensively documented in salmonids and increasingly recognized in marine and estuarine populations (Dingle 1996, Jonsson and Jonsson 1993, Secor and Kerr *In Press*). Theory underlying life cycle diversity in fishes has borrowed heavily from the

avian literature, particularly from the concept of partial migration (Berthold 2001). Partial migration is a type of contingent structuring wherein one portion of a population is migratory and another portion is sedentary, remaining resident on the breeding or spawning ground over its lifetime (Lack 1943; Berthold 2001). The scientific consensus is that partial migration is under both environmental and genetic control, and the degree of migratory behavior expressed in a population relates to the interaction of environmental factors with a genetic control mechanism or threshold, typically related to individual fitness (Berthold 2001). The concept of portions of a population exhibiting divergent habitat use is not new (Hjort 1914, Gilbert 1914, Clark 1968), and I contend that this behavior is more widespread than previously realized, particularly in marine and estuarine fish populations. Traditional techniques, such as direct observations of distributions, are oftentimes not effective at resolving diversity of habitat use within a population; however, with the development of new tools, such as electronic tagging and otolith chemistry techniques, the identification of contingent behavior in fish populations has become more prevalent (Secor and Kerr *In Press*). Spatial patterns consistent with contingent behavior have recently been identified across several species of marine and estuarine fish, including striped bass *Morone saxatilis* (Secor et al. 2001), Atlantic cod *Gadus morhua* (Smedbol and Wroblewski 2002, Ames 2004), Atlantic bluefin tuna *Thunnus thynnus* (NRC 1994), black bream *Acanthopagrus butcheri* (Elsdon and Gillanders 2005), and winter flounder *Pleuronectes americanus* (DeCelles and Cadrin 2007). Identification of spatial structure may prove important for effective and sustainable management of these populations.

Contingent structuring can have consequences to both within- and between-population dynamics. Because local conditions will influence the growth, maturity, fecundity, and survival of contingents, spatial structure can affect the overall productivity of a population (Hayes et al. 1996). Spatial structure may also affect population stability if contingents exhibit differential responses to the environment, a situation that potentially can dampen recruitment variability (Secor 2007). Furthermore, contingent behavior may play an important role in metapopulation dynamics, with migratory contingent fish maintaining connectivity between populations. Contingent structure also has bearing on a population's response to habitat degradation and exposure to pollution, as contingents will be differentially impacted by localized anthropogenic stressors (Zoklovitz and Secor 1999, Nelson et al. 2002). The concept of the "unit stock" in fisheries does not account for fine-scale spatial patterns, such as contingent structuring, despite the potential impact on vital rates and population dynamics (Secor 1999).

The aim of my dissertation research was to advance knowledge of the spatial ecology of fishes and to explore the causes, consequences, and prevalence of spatial structuring in an estuarine fish population. My research focused on white perch populations in the Chesapeake Bay, a semi-anadromous species for which contingent behavior was previously identified during the first year of life (Kraus and Secor 2004a). My research contributes to the understanding of 1) the lifetime persistence of resident and dispersive behavior identified in juvenile-stage white perch, 2) the role of environmental conditions experienced early in life in determining contingent membership of white perch, 3) the differences in energetic tactics between contingents, 4) the application of otolith tracers to reconstruct habitat use of estuarine fishes, and 5) the prevalence of

contingent structuring in white perch populations. In addition, contingent dynamics were incorporated into a modeling framework to examine the role of contingent structure on population productivity, stability, and resilience. This detailed examination of contingent behavior has enabled evaluation of spatially-explicit processes regulating the dynamics and persistence of this estuarine fish population.

In Chapter 2, I examined the life-time migration histories of adult white perch using otolith strontium:calcium profile analysis. In this study, I documented the persistence of alternative life history tactics initiated during the juvenile stage. I present a detailed description of this type of contingent structuring, termed partial migration, wherein a portion of the population remains resident in the natal habitat and another portion exhibits denatant migration. In addition, a review of the recent literature is provided to show evidence that partial migration is more widespread among fishes than previously recognized.

The aim of Chapter 3 was to investigate the proximate cause of partial migration in fishes by examining whether dispersive and resident contingents are derived from specific larval cohorts that possess particular growth and mortality attributes. I hypothesized that dispersive contingent fish were associated with cohorts that exhibited slower growth and lower survival rates. In addition, I examined the influence of environmental factors, including temperature, freshwater flow, and zooplankton density, on cohort-specific vital rates. I found that dispersive contingent white perch originated primarily from early-spawned larval cohorts, which were characterized by slower growth and higher mortality rates compared to cohorts spawned later in the production season, conforming to my hypothesis. The hatch-date distribution of resident fish was centered

on later spawned cohorts characterized by faster growth and lower mortality rates. Results indicate that the cause of contingent structuring in this population is related to the timing of spawning or hatch, its interaction with temperature and prey availability, and the impact on larval growth and mortality rate.

In Chapter 4, I evaluated whether bioenergetic differences exist between contingents and whether these differences are a consequence of habitat differences (i.e., salinity) or intrinsic factors related to the proximate cause of contingent structure. I conducted a randomized factorial experiment with two contingent types and two salinity treatments (1 and 8) over a 30-day period. I found that juvenile white perch contingents exhibited differing growth and metabolic trajectories, independent of salinity, with the dispersive contingent exhibiting higher consumption and growth rates. This research indicated that contingent membership and the related phenomenon of partial migration in this population are associated with varying energetic tactics that significantly influence the scope for growth.

Chapter 5 describes an evaluation of the utility of otolith tracers ($\delta^{13}C$, $\delta^{18}O$, and Sr/Ca) as proxies for salinity of nursery habitat of juvenile white perch. Analysis of both water samples and otolith material from young-of-the-year white perch in the Patuxent River estuary revealed a positive relationship between salinity and otolith $\delta^{13}C$, $\delta^{18}O$, and Sr/Ca values. In assigning fish to their known salinity habitat, $\delta^{18}O$ and Sr/Ca were moderately accurate tracers, and $\delta^{13}C$ provided near complete discrimination between habitats. Overall, the results indicate that resolution and reliability of salinity histories of juvenile white perch will be improved through the application of stable isotopes as tracers of salinity history.

In Chapter 6, I examined the prevalence of contingent structuring across sub-estuary populations of white perch in the Chesapeake Bay. A random sub-sample of otoliths from adult white perch collected from the Upper Bay, Potomac, Choptank, Nanticoke, James, and York Rivers (2005-2006) were analyzed for stable isotope ratios. Based on river-specific water isotopic ($\delta^{18}O$) mixing models, nursery habitat of adult fish was reconstructed and adults were classified as either resident or dispersive contingent members. Most populations were comprised primarily of dispersive contingent fish (Choptank, Nanticoke, James, and York Rivers), with the exception of the Upper Bay and Potomac River systems which were dominated by resident fish. This study suggests contingent structuring is prevalent across white perch populations in the Chesapeake Bay region.

The goal of Chapter 7 was to examine the role spatial structure plays in population productivity and long-term persistence. Here, spatial dynamics and environmental forcing similar to those in the Patuxent River system were incorporated into a population model of white perch to examine the consequences to population stability, resilience, and productivity. Two linked age-structured models incorporating contingent-specific vital rates were used to model population dynamics of white perch. Simulations revealed that the dynamics of the population was most sensitive to the proportion of individuals within each contingent. Increased levels of dispersal within the population resulted in increased productivity and resilience, but a decrease in stability. Overall, this research indicated that contingent structure is important in maintaining population persistence and highlights the need to conserve spatial structuring within

populations and to think in terms of spatial management of populations through area-specific regulations.

Chapter 2: PARTIAL MIGRATION IN AN ESTUARINE FISH

ABSTRACT

Partial migration defines the pattern of intra-population modalities of migratory and resident behavior. In avian ecology, partial migration is a fundamental behavior that underlies the evolution of migration in general. Among fish taxa it historically has been narrowly reserved for salmon ecophenotypes, but is likely more widespread. Here, I document partial migration for the estuarine-dependent white perch (*Morone americana*), in the Patuxent River estuary (Chesapeake Bay, MD), wherein a portion of the population resides in freshwater natal habitats and another portion disperses down-estuary to reside in brackish water (salinities > 3) habitats. Life-time migration histories were examined using otolith strontium:calcium profile analysis. Alternative life history tactics, initiated during the juvenile period in response to individual status, persisted over the lifetime of the individual and had population-level consequences, including differences in growth rate and productivity. Based upon a review of recent literature, I argue that partial migration is more widespread among fishes than previously recognized, and such population structure has important implications for population dynamics and persistence.

INTRODUCTION

The high capacity for dispersal of birds, insects, and fishes has led to theory that seeks to generalize sedentary and migratory behaviors among and within species. In the study of bird populations, partial migration (also referenced as obligate partial migration)

is a central idea wherein one portion of a population is migratory and another portion is sedentary, remaining resident on the breeding ground over its lifetime (Lack 1943, Berthold 2001). By comparison, fish ecology contains few organizing theories related to intra-population diversity in life cycles. Indeed, a central idea (member-vagrant hypothesis; Sinclair 1988) argues against selection for divergent migrations within populations of marine fishes, despite evidence that life cycle diversity is common (McQuinn 1997, Secor 1999, Fromentin and Powers 2005). The concept of partial migration has been adopted from the avian literature to describe salmon ecophenotypes (phenotypes expressed in response to environmental conditions; see review by Jonsson and Jonsson 1993), but has not been widely applied outside this family (Kitamura et al. 2006, Brodersen et al. 2008). I propose that partial migration is a widely applicable and useful concept for understanding life cycle diversity of fishes, because it provides a mechanistic understanding of the evolution, control, and adaptability of migratory behavior (Berthold 2001).

Theory associated with partial migration could underlie much of the diversity in migration behaviors in fishes, which either has been ignored due to emphasis on closed population assumptions that are required in traditional stock assessment (Secor 1999; Cadrin and Secor *In press*), or obscured by the use of multiple terms to describe the phenomenon (Secor and Kerr *In press*). Proposed mechanisms for the maintenance of partial migration within bird and salmon populations include 1) a conditional strategy, whereby individual's genetic makeup allows for the adoption of resident or migratory behavior based on an interaction between individual condition and the environment (Gross 1996, Gross and Repka 1998a, Lundberg 1988), 2) frequency-dependent selection

of the migratory tactic (i.e., an evolutionary stable strategy; Lundberg 1988, Gross 1996), and 3) genetic polymorphism, whereby the two morphs represent reproductively isolated sub-populations (Lundberg 1988, Verspoor and Cole 1989).

The most widely accepted mechanism for partial migration across taxa is a conditional strategy, a concept rooted in the ideas of individual fitness and life history tradeoffs. The preponderance of evidence from salmonid population studies supports the idea of partial migration as a conditional strategy, with the degree of migratory behavior expressed within the population based on the interaction of a genetically-defined threshold with environmental factors (Jonsson and Jonsson 1993). Specifically, within brown trout (*Salmo trutta*; Forseth et al. 1999, Cucherousset et al. 2005) and Atlantic salmon populations (*Salmo salar*; Metcalfe et al. 1995, Bujold et al. 2004) growth rate (or metabolism) early in life has been identified as the developmental threshold that triggers migratory behavior.

Theory on the evolution of partial migration in birds can enhance our understanding of the expression of migratory behavior across fish populations. Experimental evidence in bird populations, such as blackcaps, indicates that shifts from partially migratory to fully migratory or sedentary populations were possible in only a few generations through selection (Berthold 1999). In the wild, the degree of migratoriness expressed within a population is specific to the regional selection regime (Berthold 1999). This flexibility in the expression of migratoriness allows partial migration to be a widespread, highly adaptable, and successful behavioral strategy among birds. I speculate that, similar to birds, partial migration is common across fish species as a behavioral strategy, but to date is only described in populations wherein it is

morphologically expressed in convenient observational systems (i.e., salmonid populations).

The white perch (*Morone americana*) is a dominant estuarine species that completes its life cycle in fresh and brackish tidal waters. Adults migrate to freshwater habitats in the spring to spawn and eggs and larvae develop in this environment (Figure 1; Mansueti 1964). Chemical tracers in otoliths of white perch in the Patuxent River estuary identified divergent habitat use during the first year of life, with a portion of the population remaining resident in the natal freshwater region and a second portion of the population dispersing into brackish water (salinities >3) environments (Kraus and Secor 2004a); however little is known regarding the permanence of freshwater residency. Evidence supports the idea that initiation of migratory behavior is regulated by a growth threshold early in life history, whereby slower larval growth rates were associated with subsequent dispersive behavior by juveniles (Chapter 3, Kraus and Secor 2004a, Kerr and Secor *In press*). Here, I provide evidence that early patterns of divergent behaviors have lifetime consequences on migratory patterns, a principal tenet in demonstrating partial migration. A review of the recent literature is presented to support the contention that partial migration is likely a widespread phenomenon in fishes. Additionally, I address the impact partial migration may have on the dynamics and long-term persistence of populations, making recognition of this behavior important for achieving management and conservation goals.

METHODS

Sample Collection

Adult white perch were collected by fyke net in the tidal freshwater portion of the Patuxent River estuary where adults in the population were aggregated for spawning in the spring of 2001 and 2002 (Figure 2, Figure 3). A collection of adult otoliths (N=363) was previously classified by juvenile habitat use (freshwater or brackish) based on strontium:calcium (Sr/Ca) measurements during the year-1 period of growth in the otolith (Kraus and Secor 2004a). I used these same prepared otoliths for age estimation and to conduct profile analyses of Sr:Ca (terminology after Elsdon et al. 2008) during the late juvenile and adult phases of life history. Annual growth zone formation of mature white perch otoliths was previously validated by oxytetracycline injection (Casey et al. 1988).

Otolith Analysis

Sixty otoliths were sub-sampled from this collection. All fish characterized as freshwater residents during the first year of life (n=27), and a random sub-sample of fish that dispersed (n=33) during year-1 were selected for Sr/Ca profile analysis according to Kraus and Secor (2004a). Points were measured for Sr/Ca at 25 μm intervals along a transect from the first opaque zone (year 1) to the otolith edge. Backscatter electron micrographs were taken after microprobe analysis to assign the location of points to annual growth increments. Mean Sr/Ca values were calculated for each year of growth in the otolith. Width of annual growth increments was measured along the ventral side of the sulcal ridge from photos using ImageJ software (Rasband, W.S., ImageJ, U. S.

National Institutes of Health, Bethesda, Maryland, USA, http://rsb.info.nih.gov/ij/, 1997-2007).

Statistical Analysis

Individuals were classified as migratory or resident based on mean annual Sr/Ca values. Previous experimental work (Kraus and Secor 2004b) showed that brackish water habitat use corresponded to Sr/Ca values >2 mmol mol^{-1} and freshwater habitat use (salinity <3) corresponded to Sr/Ca values <2 mmol mol^{-1}. Mean fish age, mean length at age, and sex ratio were compared between contingents with a Wilcoxon rank sum test: (age, a non-parametric test used due to non-normality of the data), two-sample t-test (length at age), and chi-square (sex ratio). Growth rate was estimated using back-calculated fish length at age from the widths of otolith growth increments using the Biological Intercept Method (Campana 1990). The biological intercept of 3.2 μm at 3 mm TL was used (Kraus and Secor 2004a). Mean back-calculated length was compared between resident and migratory fish at age 1, 2, and 3 years. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. Statistical analyses were performed with SAS Version 8.2 (SAS Institute, Cary, NC); $\alpha = 0.05$ was used as a critical level of significance.

Generalized estimating equations were used to analyze otolith Sr/Ca values, because mean Sr/Ca values were autocorrelated across annuli of individuals and the assumption of a normal distribution was not reasonable for this data (Liang and Zeger 1986). Data were analyzed using the GENMOD procedure in SAS Version 8.2 (SAS Institute, Cary, NC). The distribution of the data was specified as binomial and fit with a logistic link function. Repeated measures analysis was used to test whether lifetime

patterns of habitat use, based on mean annual Sr/Ca values, were dependent on age, sex of the fish, or the age by sex interaction. This analysis was constrained to ages 1–7 years based on the representation of ages in the sample and concerns of potential bias due to low representation of older age classes. The deviance ratio, a goodness of fit measure, was examined to assess model adequacy.

RESULTS

Fish that exhibited lifetime residence in freshwater habitat were classified as residents (mean Sr/Ca: 1.0 ± 0.2 mmol mol^{-1}), whereas fish with elevated Sr/Ca indicative of brackish water residence were classified as migratory individuals (mean Sr/Ca: 2.9 ± 0.8 mmol mol^{-1}). Individuals classified as resident exhibited similar mean Sr/Ca values during the juvenile (years < 3) and adult (years 3+) period (juvenile: 1.0 ± 0.2 mmol mol^{-1}, adult: 1.1 ± 0.3 mmol mol^{-1}). Mean Sr/Ca values of migratory contingent fish were slightly elevated during the adult period (juvenile: 2.7 ± 0.9 mmol mol^{-1}, adult: 3.1 ± 0.5 mmol mol^{-1}). Otolith Sr/Ca values increased with age in migratory contingent fish, but remained stable in resident fish (Figure 4). The majority of the subsample of fish examined in this study were classified as migratory (85%) and the minority, resident (15%). Because the sample represented a sub-sample from a larger collection (N = 363) of fish; the sample-weighted representation within the overall population (across age-classes) equates to 97% migratory and 3% resident fish.

Mean age of fish was similar between contingents (age range 2 to 10; Wilcoxon rank sum test: $Z = -1.83$, $p = 0.07$). Significantly larger length at age was observed in migratory fish at age 2 and 3, but not at age 1 (t-tests: age 1: d.f. = 58, t-test statistic =

-1.43, p = 0.16; age 2: d.f. = 58, t-test statistic = -2.26, p = 0.03; age 3: d.f. = 54, t-test statistic -2.30, p = 0.03; Figure 5). There was a tendency for migratory individuals to be female (55%) and the resident individuals to be male (78%), but the sex ratio for resident and migratory contingents was not significantly different from the 50:50 ratio of the overall sample (chi-square tests: $p \geq 0.1$). Repeated measures analysis revealed a significant effect of age on migratory behavior, specifically individual status at age 1 and age 2 significantly affected the life history tactic (resident or migratory) of white perch (age 1: p = 0.01; age 2: p = 0.03; Table 1). There was no evidence that life history tactic was sex-dependent, as female and male white perch exhibited a similar mean and range of Sr/Ca values (Table 1). The interaction of individual status at age and sex was also not significant (Table 1). The deviance ratio value calculated for the model confirmed a good model fit.

Examination of Sr/Ca profiles showed that individuals that dispersed from the freshwater natal habitat did so primarily at age 1 (63%), and to a lesser extent at age 2 (18%), 3 (12%), and 4 (6%), with one individual dispersing at age 7. Thus, contingent behavior was generally initiated during the juvenile period (100% sexual maturity is reached by age 2 (males) and age 4 (females); Mansueti 1961) and persisted over the lifetime of individuals (Figure 6). There were a few cases of resident individuals (n = 3) becoming migratory later in life (after age at 100% maturity for the respective sex). Profiles of migratory individuals exhibited periodic decreases in Sr/Ca indicative of recurring movements into low salinity environments for short periods of time, but once a migratory tactic was initiated, no permanent reversion to resident behavior was detected (Figure 6).

DISCUSSION

Based on microchemical analysis of otoliths, I determined that white perch exhibit partial migration, with a portion of the population remaining in the natal habitat (resident contingent) and another portion exhibiting denatant migration (migratory contingent). The majority of individuals were migratory, moving into brackish waters during the juvenile stage, remaining in this environment into the adult stage, and returning to freshwater to spawn. Still, a substantial minority of individuals remained in their natural freshwater habitat throughout their lifetime (Figure 6).

The question of which fish within a population migrate has been examined in several salmonid populations. Overall, males tend to dominate the composition of resident fish, whereas females are more likely to migrate (Jonsson and Jonsson 1993). The tendency for females to migrate is linked to the growth advantage conferred to migrants within these populations and its consequences to reproductive success, such that larger females produce more eggs and thus have higher fitness (Fleming and Gross 1990, Jonsson and Jonsson 1993). No significant trend in females exhibiting migratory, rather than resident behavior was observed in the Patuxent River white perch population.

Growth rate early in life has been linked to the expression of migratory behavior, with faster growing fish initiating migration earlier than slow growing fish in some populations (e.g., Atlantic salmon, Metcalfe and Thorpe 1992; brown trout, Forseth et al. 1999; brook charr *Salvelinus fontinalis*, Thériault and Dodson 2003). Faster growing fish may disperse because they have the energy reserves necessary to migrate or in response to limited food availability relative to their high energetic needs (Jonsson and Jonsson

1993). Alternatively, in some populations slow growing individuals initiate migration in response to low food availability or high population density that limits them from growing at an optimal or threshold level (Jonsson and Jonsson 1993). Conditions experienced early in life appear to trigger migration in the white perch population, which occurred primarily in year-1 and secondarily in year-2 of life. Examination of the physiological basis of migratory behavior in this white perch population indicated that migratory fish grew slower early in life (larval period) compared to resident fish and, subsequent to dispersal, juveniles had higher growth rates (Kraus and Secor 2004a, Kerr and Secor *In Press*). Evidence supports the hypothesis that the conditions experienced by white perch early in their life history (e.g., temperature and prey density) have consequences to individual growth rates, and are the proximate factor determining migratory or resident behavior of white perch (Chapter 3).

Within partially migratory bird and fish populations, individuals can shift between resident and migratory behavior within their lifetime; this behavioral change is thought to be related to individual fitness (Lundberg 1985, Dingel 1996, Zimmerman and Reeves 2002). Mid-life shifts between migratory and resident behavior have been documented in Arctic charr (Radtke et al. 1996) and striped bass (Zlokovitz et al. 2003). Evidence of switching life history strategies supports the hypothesis that this phenomenon is not genetically programmed, but represents alternative phenotypes. There was no evidence within the white perch population of migrants becoming residents later in life. Thus, it appears that the benefit of a migratory lifestyle outweighs advantages associated with remaining resident. I did, however; find evidence of resident fish initiating migratory

behavior later in life. I hypothesize that, for these individuals, conditions in the freshwater habitat became less advantageous to individual fitness later in life.

The flexibility in life history identified in white perch is consistent with obligate partial migration and is similar to that identified in several species of Salmonidae (e.g., Arctic char *Salvelinus alpinus*, Nordeng 1983; brown trout, Jonsson 1985; Atlantic salmon, Thorpe 1989). The maintenance of alternative life history tactics is thought to be governed by tradeoffs between the costs of migration (e.g., increased predation, physiological costs) balanced against the benefits of migration (e.g., higher food availability, increased growth potential; Jonsson and Jonsson 1993, Metcalfe 1998, Mangel and Stamps 2001). Over a lifetime, resident contingent fish exhibit slower growth (Kraus and Secor 2004a; this study), and are expected to have lower reproductive rates and fitness compared to the migratory portion of the population. Although not tested in this study, evidence from other studies indicates that the benefits of migration into higher salinity waters may be offset by greater predation risk in these deeper estuarine environments (Ruiz et al. 1993, Miltner et al. 1995, Paterson and Whitfield 2000). Additionally, faster juvenile growth rates exhibited by migratory individuals may be offset by physiological costs of accelerated growth such as reduced predator evasion (Metcalfe 1998, Billerbeck al 2001, Mangel and Stamps 2001).

Because of the causative link between environmental conditions experienced during early life history and migratory behavior (Chapter 3), inter-annual variation in the environment will likely lead to inter-annual differences in the expression of life history tactics within a population (Mangel 1994). For white perch, recruitment to the migratory contingent dominates in high flow years, with the resident contingent increasingly

represented in low flow years, and exclusively present during drought years (Kraus and Secor 2004a). A corollary to this idea is that anthropogenic perturbation of the environment will have a significant effect on the expression of partial migration through its influence on both individual condition (e.g., growth rate) and the environment (e.g., productivity). For instance, eutrophication within freshwater habitats may promote increased residency due to high productivity (Gross 1987). Similarly, increased water temperature may increase energetic demands by white perch, potentially increasing the migratory portion of the population. Partial migration also has consequences to pollution ecology. For example, striped bass (*Morone saxatilis*) classified as freshwater residents had greater levels of PCBs than migrants (Zoklovitz and Secor 1999). King et al. (2004) identified a positive association between PCBs in white perch and the level of development in the Chesapeake Bay watershed. Because urbanization and development in the Chesapeake Bay watershed is centered in freshwater regions of the estuary, I would expect this relationship would translate to high PCB levels in resident fish inhabiting freshwater environments.

Partial migration can also play a role in population dynamics, in some instances facilitating population growth and stability. Years of high flow are related to high recruitment and greater production of migratory juveniles and adults; the resident contingent, although less productive, may be important to the stability of the population during successive years of low flow, when its production is favored (Kraus and Secor 2004a). The different roles contingents play in mediating population dynamics and persistence highlights the potential importance of managing for conservation of partial migration within fish populations.

Partial migration could be widespread across fish taxa but is insufficiently recognized due to lack of ecophenotypes associated with migratory and resident tactics, as they are in salmonids. Further, the current language of fish migration (e.g., anadromous, catadromous, amphidromous) generalizes migratory behavior of populations and tends to be taxa-specific, obscuring the general recognition of partial migration as a central phenomenon in describing complex life cycles. In a review of the recent literature Secor and Kerr (*In press*) observed that increased application of approaches that hind-cast individual's spatial history and reconstruct migration patterns (e.g., otolith microchemistry and electronic tagging) has resulted in a geometric increase in papers describing life cycle diversity. Importantly, although a large set of terms was used to describe this diversity, many of the terms centered on a pattern of resident versus migratory behavior, consistent with our expectation that partial migration could be widespread (Table 2). For example, resident and migratory components have been recognized in the Atlantic bluefin tuna (*Thunnus thynnus*) population whereby a portion of the population completes its life cycle within the Mediterranean Sea and others migrate into the western Atlantic (Rooker et al. 2007). Additionally, Gulf of Maine cod (*Gadus morhua*) exhibit resident and migratory morphs (Wroblewski et al. 1994) that may be structured through partial migration.

Migratory behavior has evolved independently many times and there appears to be commonalities governing expression of migratory behavior across taxa (Dingle 1996). The developments in avian literature on expression of migratory behavior both among and within populations can inform our understanding of the genetic and environmental factors regulating migration thresholds of fish. As there is a potential for rapid change in

the expression of migratory behavior within populations in response to environmental change, a mechanistic understanding of migration could improve forecasts of behavioral responses to future climate variability. Notably, partial migration points to the idea that individuals exhibiting minority behaviors—in the past discounted as strays or vagrants—can play an important role in population dynamics.

TABLES

Table 1. Generalized estimating equations parameter estimates.

Parameter		Estimate	Standard Error	Z score	P
	Intercept	1.86	0.61	3.03	0.00
Annuli	1	-1.59	0.57	-2.77	0.01
	2	-1.16	0.55	-2.12	0.03
	3	-1.00	0.52	-1.93	0.05
	4	-0.26	0.34	-0.76	0.45
	5	-0.08	0.24	-0.33	0.74
	6	0.01	0.13	0.11	0.91
	7	0	0	.	.
	Sex	1.05	1.56	0.67	0.50
Sex*annuli	sex*1	-1.31	1.54	-0.85	0.39
	sex*2	-1.05	1.51	-0.69	0.49
	sex*3	-0.03	1.44	-0.02	0.98
	sex*4	-0.45	1.35	-0.34	0.74
	sex*5	-0.69	1.33	-0.52	0.60
	sex*6	-0.86	1.31	-0.66	0.51
	sex*7	0	0	.	.

Table 2. Lexicon of terms and phrases used to describe life cycle diversity within species and populations. Terms and phrases that apply to alternate life cycles were searched using Cambridge Scientific Abstracts © Aquatic Sciences and Fisheries Abstract (Adopted from Secor and Kerr *In press*). Usage indicates the overall number of times a term was used. Usage is further broken down by taxonomic family and the ecosystems connected by migration (number in parentheses indicates usage when >5 citations).

Mode	Term	Usage	Families	Ecosystem
Dispersive modes (4)	Stray(s)	70	Salmonid (60), Acipenserid, Clupeid, Cyprinid, Gadid, Moronid, Scombrid	River-Coast (57), Coast, River, River-Lake
	Ocean type(s)	35	Salmonid (34), Gadid	River-Coast (34), Coast
	Sea type(s)	4	Salmonid	River-Coast
	Dispersers	1	Gadid	Coast
Retentive modes (15)	Non-anadromous	30	Salmonid (29), Coregonid	River-Coast (29), River
	Non-migratory	21	Salmonid (14), Anguillid, Clupeid, Cyprinid, Osmerid, Sparid	River-Coast (15), Coast, River-Coast, River-Lake
	Sedentary	16	Anguillid, Centrarchid, Cottid, Cyprinid, Ecosid, Engraulid, Gadid, Osmerid, Salmonid	River (8), Coast, Lake-Coast, River-Coast, River-Lake

Mode	Term	Usage	Families	Ecosystem
Retentive modes (15)	Resident form(s)	12	Salmonid (10), Osmerid	River-Coast (9), River-Lake
	Stream type(s)	8	Salmonid (8)	River, River-Coast
	Freshwater type(s)	5	Osmerid, Gasterosteid	River-Coast
	Resident type(s)	4	Gasterosteid, Salmonid, Anguillid	River-Coast, River-Estuary
	River type(s)	4	Salmonid, Plecoglossid	River-Coast, River-Lake
	Lake type(s)	3	Salmonid	River-Coast, River-Lake
	Resident behavior(s)	2	Moronid, Salmonid	River-Coast
	Non-amphidromous	2	Gobiid, Plecoglossid	River-Lake, Estuary-Coast
	Non-catadromous	1	Anguillid	River-Coast
	Non-diadromous	1	Eleotrid	River-Estuary
	Resident ecotype	1	Salmonid	River-Lake
	Retentive	1	Review	Review

FIGURES

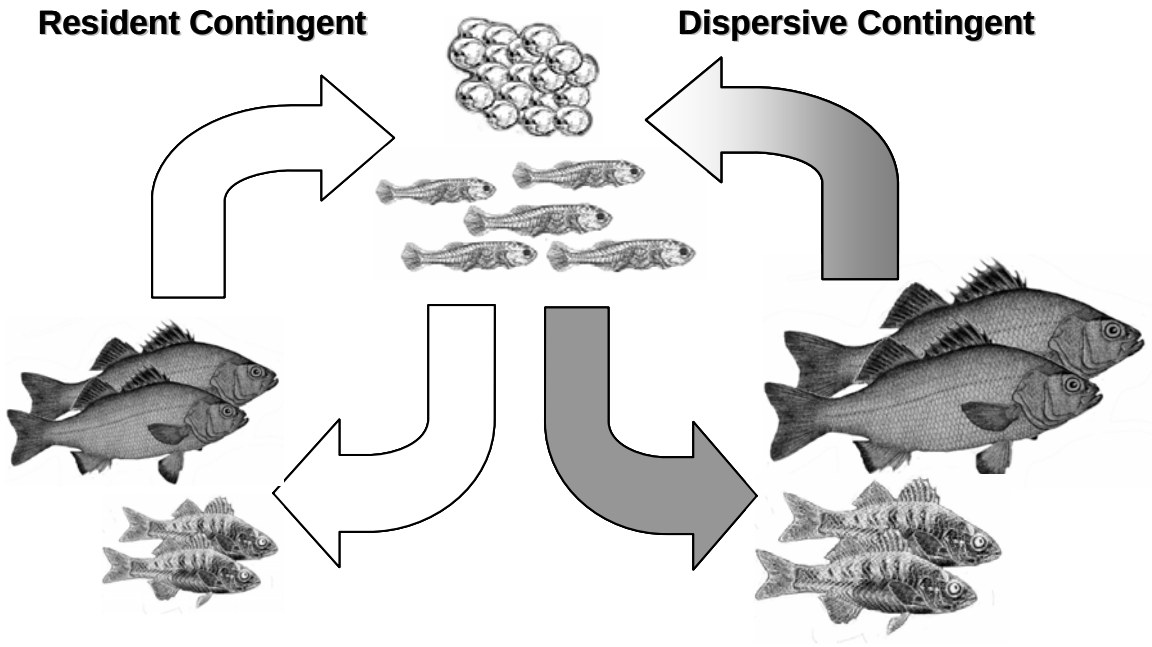


Figure 1. Illustration of the life cycle of white perch. Gray arrows represent movement into brackish water and white arrows represent residence in freshwater.

Figure 2. Collection of adult white perch by fyke net in the Patuxent River estuary by local waterman Bob Evans (photo: Richard Kraus).

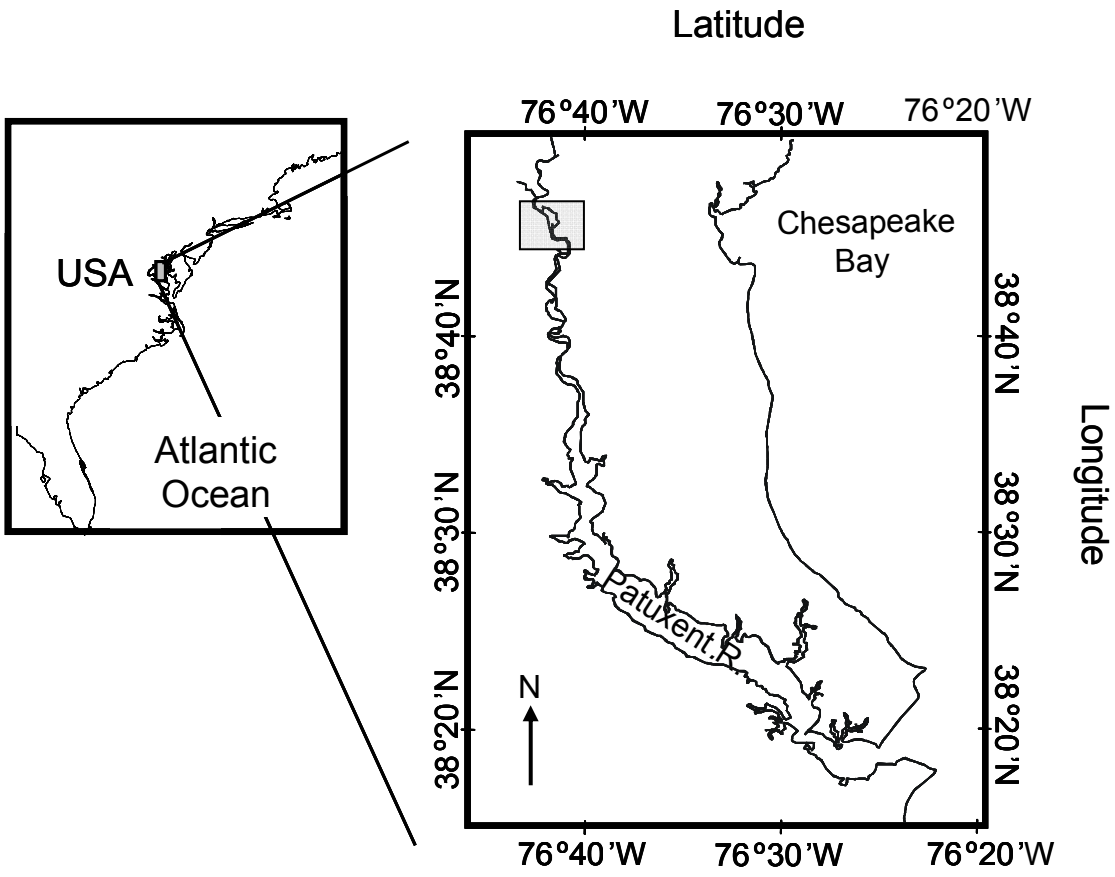


Figure 3. Map of the Patuxent River estuary. Shaded box illustrates the location of freshwater habitat wherein adult fish were collected.

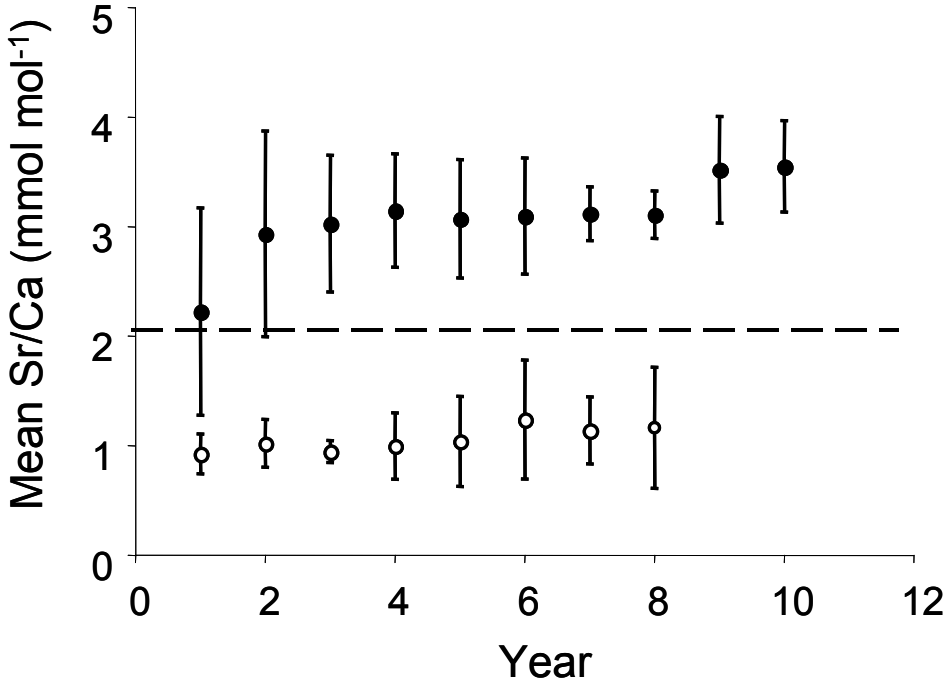


Figure 4. Mean annual Sr/Ca (mmol mol^{-1}) of adult white perch otoliths grouped based on contingent classification (open circles = resident contingent, closed circles = migratory contingent). Error bars represent standard deviations. The black hatched line delineates brackish water habitat use corresponded to Sr/Ca values >2 mmol mol^{-1} and freshwater habitat use (salinity <3) corresponded to Sr/Ca values <2 mmol mol^{-1}).

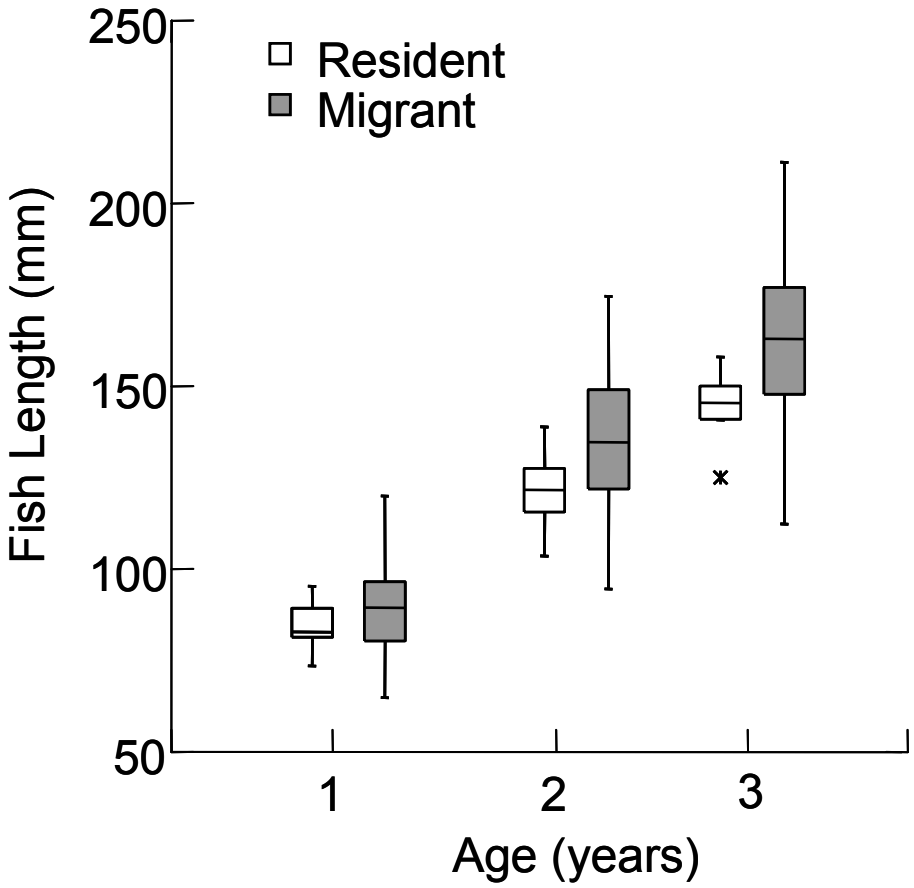


Figure 5. Back-calculated length at age (age 1 to 3) of white perch contingents (resident and migratory). The center vertical line marks the median, the length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles. Asterisks are datapoints outside this range

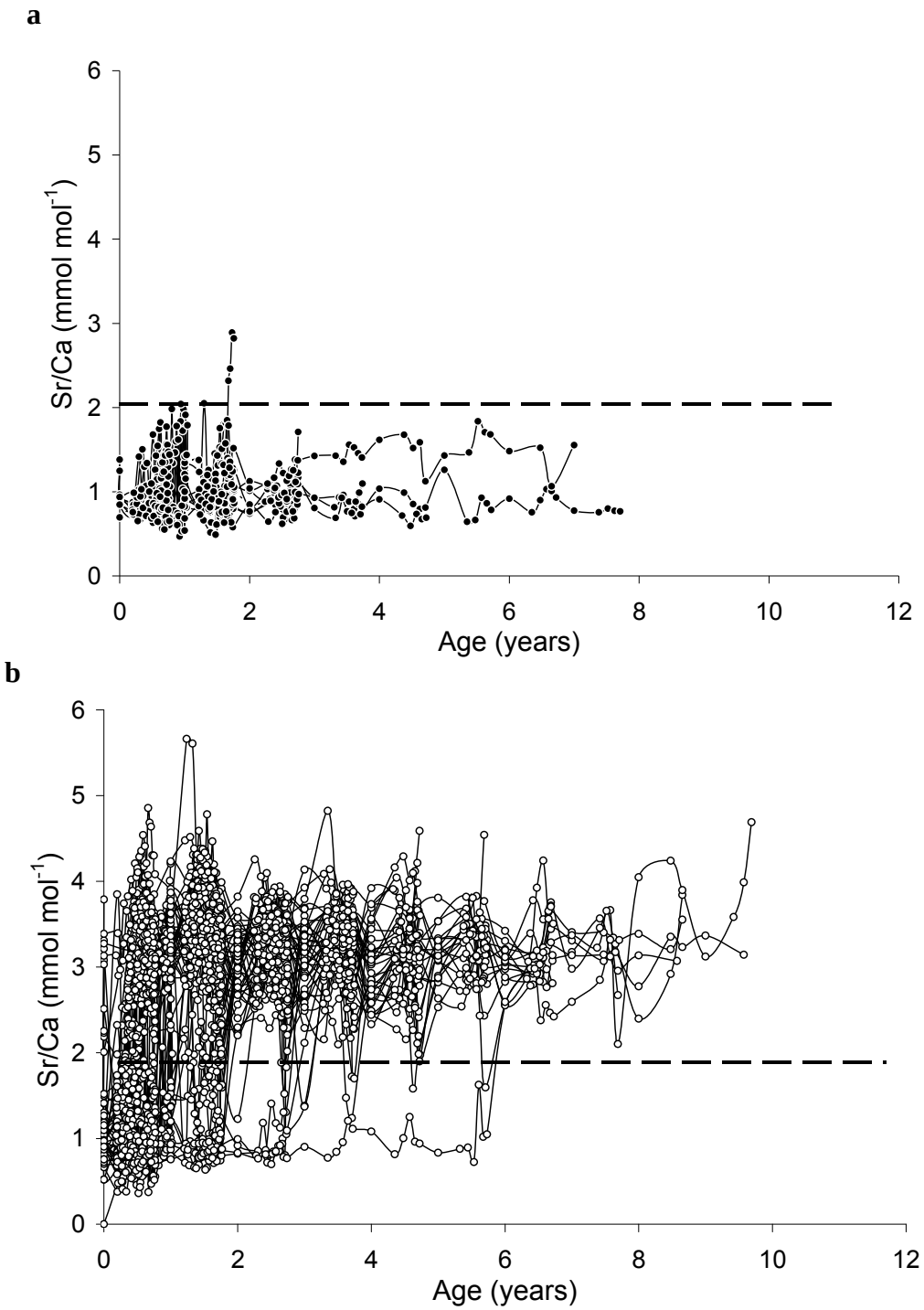


Figure 6. Time series of Sr/Ca (mmol mol^{-1}) values sampled across the growth zones of adult white perch otoliths. Individuals are grouped based on lifetime habitat use and classified as (a) resident or (b) migratory contingent members. The black hatched line delineates the threshold between brackish water habitat use corresponded to Sr/Ca values >2 mmol mol^{-1} and freshwater habitat use (salinity <3) corresponded to Sr/Ca values <2 mmol mol^{-1}).

Chapter 3: PROXIMATE CAUSES OF PARTIAL MIGRATION IN THE ESTUARINE-DEPENDENT WHITE PERCH *MORONE AMERICANA*.

ABSTRACT

Partial migration is the divergence of a population into migratory and resident contingents. This behavior has been documented in many diadromous species and can result in population-level consequences; however, the proximate cause of partial migration in fishes has not been well studied. Here, I tested the hypothesis that dispersive and resident contingents within a partial migratory population of white perch are derived from specific larval cohorts that possess particular growth and mortality attributes, where faster growth and greater survival was associated with resident behavior. In addition, I examined the influence of environmental factors (temperature, zooplankton density, and freshwater flow) on cohort-specific vital rates. In 2005, an intensive field survey was conducted in the Patuxent River estuary (Chesapeake Bay, MD). Otolith analysis was used to determine vital rates of larvae and back-calculate hatch-date distributions of resident and dispersed juvenile contingents. Dispersive contingent fish originated primarily from early-spawned larval cohorts, which were characterized by slower growth and higher mortality rates compared to cohorts spawned later in the production season, supporting my hypothesis. Compared to the dispersive contingent, the hatch-date distribution of resident fish was characterized by higher representation of later-spawned cohorts with faster growth and lower mortality rates.

Zooplankton densities supported the inference of favorable larval growth conditions in later spring. The results support an important role in the phenology of spawning, its interaction with temperature, and larval growth and mortality rates for contingent structuring in this population.

INTRODUCTION

Intra-population divergence in habitat use, termed contingent behavior, has been identified across taxa and in a variety of fish species (e.g., Japanese eel, Tsukamoto et al. 1998; striped bass, Secor 1992; bluefin tuna, Fromentin and Powers 2005). A specific type of contingent behavior termed "partial migration" has been studied extensively in bird (Berthold 2001) and salmonid populations (see review by Jonsson and Jonsson 1993) and was recently identified in the estuarine-dependent white perch (Chapter 2). Partial migratory populations diverge into two dominant life-cycle behaviors, migratory and resident, that typically exhibit demographic differences with population-level consequences (Kraus and Secor 2004a; Chapters 4 & 7). Diversity of life history tactics within populations is increasingly recognized as a means of offsetting environmental stochasticity and in some cases is determined to be important for the long-term persistence of populations (Secor 2007, Secor and Kerr *In Press*; Chapter 7).

Partial migration is typically maintained as a conditional strategy, whereby there is a single genetic population that exhibits resident or migratory behavior based on an individual's condition relative to a genetically defined threshold, usually related to growth rate during early life history (Jonsson and Jonsson 1993, Forseth et al 1999, Bujold et al. 2004). Evidence suggests that differences in growth rate early in life may be

the cause of contingent structuring within estuarine-dependent white perch (Kraus and Secor 2004a; Kerr and Secor *In Press*). However, the proximate cause of contingent structuring in the white perch population remains unresolved. Here, I explore the idea that individual growth rate during the larval period is the determinant of contingent behavior and examine the role environmental control plays in establishing generational modalities in juvenile and adult migratory behavior.

White perch exemplify a periodic life history pattern which is favored in spatially or temporally variable environments and characterized by high fecundity, high mortality during early life history, and a late age at maturation (Winemiller and Rose 1992). In Chesapeake Bay estuaries, white perch exhibit a moderately protracted spawning period during spring months (late March-June; Secor et al. 1994, North and Houde 2001) in the tidal freshwater region of the estuary where both the egg and larval stages develop (Mansueti 1964). Divergence in habitat use within the population occurs after the transition from larval to juvenile stage (mean age of 45 ± 7 days, Kraus and Secor 2004a) and this spatial behavior persists into adulthood (Chapter 2). Based on back-calculated larval growth rates, members of the dispersive contingent were found to have significantly slower growth rates compared to the resident contingent prior to dispersal (Kraus and Secor 2004a, Kerr and Secor *In Press*). This growth trend was reversed after dispersal, when dispersive contingent members exhibited significantly faster growth rates as juveniles and adults compared to the resident contingent (Kraus and Secor 2004a, Kerr and Secor *In press*). I hypothesized that the moderately protracted spawning period of adult white perch results in larval cohorts that experience different environmental

conditions and as a consequence exhibit differences in growth and survival rates that determine individual's contingent membership.

Larval cohort analysis enables examination of the linkage between environmental conditions in nursery habitat and cohort-specific vital rates. Environmental factors, including temperature, zooplankton prey density, and freshwater flow, are known to be important determinants of larval survival and growth of moronid larvae in Chesapeake Bay (Uphoff 1989, Houde et al. 1989, Rutherford and Houde 1995, Secor and Houde 1995). Temperature is one of the principal factors affecting larval growth and mortality rates, across taxa an estimated increase of 0.01 in instantaneous daily weight-specific growth and mortality rates was found per ºC increase in temperature (Houde 1989a). Density of zooplankton prey also affects cohort-specific growth and mortality rates of larvae, with a positive correlation identified between white perch growth rate and prey abundance in the Hudson River (Limburg et al. 1999). In addition, increased precipitation and freshwater flow during the larval period have been associated with increased mortality of larval striped bass (*Morone saxatilis*), specifically due to changes in habitat quality and sudden drops in temperature (Uphoff 1989, Houde et al. 1989, Rutherford and Houde 1995). Increased streamflow during the winter-early spring, however, can have a positive effect on survival of anadromous fishes due to increased nutrient delivery, availability of freshwater habitat, and consequently increased zooplankton production (Kimmel and Roman 2004). Thus, environmental conditions during the spawning period can cause differences in vital rates of larval cohorts and modify the representation of cohorts within resident and dispersive contingents.

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

METHODS

Sample Collection and Analysis

Ichthyoplankton collections and otolith preparation

Ichthyoplankton sampling was conducted biweekly from April 7 to May 31 in 2005 in the tidal freshwater region of the Patuxent River estuary. The Patuxent River, a tributary of the Chesapeake Bay, is a shallow, partially mixed estuary (Figure 1). The sampling design ensured that the larval cohorts would receive similar sampling intensity. Thirteen fixed sampling sites were distributed along the tidal freshwater portion of the river, which was segmented into seven approximately equal length zones with two stations sampled within each zone, with the exception of the most upriver zone (Figure 1). Paired bongo nets (60 cm bongo nets with 280 μm mesh) with attached flowmeters were deployed off the 25 ft. R/V Pisces. Oblique tows were conducted against the prevailing tide or wind for five minutes. Tows were depth integrated, towing the net at bottom (within 1 m), middle, and surface depths for ~1.5 min. at each depth. Latitude, longitude, and flowmeter readings were recorded at the start and end of each tow period. Upon retrieval of the nets, the contents of cod ends were collected on a 280 μm mesh

filter and preserved in 95% ethanol. Water quality measures (temperature (°C), salinity, conductivity (μS), and dissolved oxygen (mg/L)) were recorded at the surface and at depth at each station. Continuous water quality data was also recorded at the Chesapeake Bay Program's (CBP) continuous monitoring station at Jug Bay, Maryland (river km (RK) 72; Figure 1) and stationary temperature data loggers were deployed within the nursery area (Kings Landing (RK 53) and Jug Bay; Figure 1) to log temperature continuously throughout the larval production season. River discharge data was obtained online from US Geological Survey (USGS), National Water Inventory Service (http://waterdata.usgs.gov/nwis) for USGS Site: Patuxent River near Bowie, MD, Site #: 01594440.

In the laboratory, ichthyoplankton was identified and sorted to family under a stereo-microscope. Ichthyoplankton was analyzed in at least one station per river segment for each cruise date. Moronid larvae were identified to species following Waldman et al. (1999). White perch larvae were enumerated and measured to 0.1 mm notochord length using an image analysis system. A maximum of 100 larvae were measured from each site (50 yolk-sac larvae and 50 post-yolk-sac larvae). Densities (number per m^3) of white perch larvae were estimated for each station based on sampling volume (estimated from flowmeter readings) and corrected for daytime avoidance of the net by larger larvae (correction estimated for striped bass in the Potomac River; Houde et al. 1988). River-segment abundance was estimated based on expanding average station densities to the volume of the river segment that the site represents. River area and volume measures were obtained from Cronin (1971) and Secor et al. (1994). River-wide abundance was estimated by summing river segment abundances.

Sagittal otoliths were removed from a representative sub-sample of larvae (n = 116) for age estimation at a daily time-step. Otoliths from larvae < 12 mm SL were extracted and affixed to a microscope slide with clear lacquer. Otoliths of larvae 9-12 mm were polished whole using a grinding wheel with a slurry of 25 μm aluminum oxide and a felt, metallographic cloth covered with a slurry of 0.3 μm alumina powder to achieve a final polish. Otoliths from larvae $\geq$ 12 mm SL were embedded in Stuers epoxy and transversely sectioned using a low speed saw equipped with diamond blades separated by a spacer (0.3 mm). Otoliths were polished as described above on both sides until the primordium (core) was clearly visible. Otolith microstructure was examined under a compound microscope (600 to 1000x magnification) and age (days) was estimated three times independently. Final age was assigned as the mean of the second and third otolith reads. Daily formation of increments in larval white perch otoliths was previously verified (Houde and Morin 1990, Kraus and Secor 2004a). Estimated age was corrected for the influence of temperature on the timing of first daily increment formation, following Houde and Morin (1990). The equation to adjust age estimates was:

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

where T = temperature on the day of first increment formation, assuming there was little change in temperature back to hatch-date. Kings Landing and Jug Bay temperature records were used in the calculation of temperature-adjusted ages from downriver and upriver locations, respectively.

Larval length was regressed on age and the relationship was used to convert larval length-frequency distributions to age-frequency distributions. Mean age was calculated for each 0.5 mm length bin (0 to 16.5 mm). Assuming a normal distribution and using

the standard error of the regression (4.6 days), the probability larvae within each length bin were in a particular age class was calculated. In the case of the three smallest and two largest length classes, the proportion of fish at age did not sum to one (0.93 to 0.99), thus proportions at age were scaled accordingly to equal one. Yolk-sac larvae ($\leq$ 3.0 mm) were not aged directly, but assigned a mean age of zero. Larval hatch-date distribution was back-calculated and larvae were grouped into 9-day cohorts.

Individuals with otolith-derived age information were assigned to cohorts based on hatch-date and used in the calculation of larval growth rates. Cohort-specific growth rates were calculated using exponential growth models:

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

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

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

where N_t = estimate abundance of larvae at a specified age, N_0 = estimated abundance of larvae at age zero, Z = instantaneous daily mortality coefficient (d^{-1}), t = age (days after hatch). It should be noted that the accuracy of estimates of growth and mortality depend on the assumption that fish within the selected size range were equally susceptible to the sampling gear (Ricker 1975). The ratio of instantaneous growth (weight-specific growth rate was used in this calculation) to mortality rate (G:Z) was calculated as a relative index of a cohort's recruitment potential (Houde 1989b, Rutherford and Houde 1997). Weights were estimated from lengths using a length-weight relationship for moronid larvae (Houde and Lubbers 1986, Limburg et al. 1997):

$$W = 3.763 \times 10^{-4} \times L^{(4.2879)}$$

where W = mg wet weight, and L = length in mm. Weight-specific growth rates were estimated as:

$$W_t = W_0 e^{Gt}$$

where W_t = weight (mg) at specified age, W_0 = weight (mg) at age 0, t = age (days after hatch), G = instantaneous growth coefficient (d^{-1}).

Among-cohort differences in length-specific growth and mortality rate were examined using ANCOVA with age as a covariate. Cohort-specific larval growth and mortality rates were statistically related to mean temperature and freshwater flow conditions at different stages during early life history, including the hatch period for each cohort, yolk-sac period ($\leq$ 4.0 mm), post-yolk-sac period (>4.0 mm), and the entire larval duration (period from hatch to last date cohort appears in samples) using regression analysis. The goodness of fit of models relating variation in vital rates to each environmental factor was examined using corrected Akaike's Information Criterion (AIC_c):

$$AIC_c = n \ln(\frac{RSS}{n}) + 2K + \frac{2K(K+1)}{n - K - 1}$$

where RSS = the residual sums of squares, n = the number of observations, and K = the number of parameters in the model. The relative likelihood and probability of each model were calculated and compared.

Abundance at 45 days after hatch (habitat transition age) was predicted for each larval cohort based upon initial river-wide abundance estimates and cohort-specific mortality rates. These adjusted abundances were used to calculate the expected

proportional contribution of each cohort to population abundance at 45 days, or what I termed the population's hatch-date distribution.

Zooplankton Collection

Zooplankton was collected during each sampling cruise at one station within each of the seven sampling zones described above. Zooplankton was collected by pumping ambient water through a 53 μm filter, the mesh size was selected to collect the appropriate size range of prey items for white perch. Zooplankton sampling was depth integrated; 20 L of water was sampled at surface, intermediate, and near bottom depths (total volume sampled = 60 L) and combined in a single sample for each station. Zooplankton samples were preserved in 5 % formalin. Counts of zooplankton taxa known to be important white perch prey items, including copepod nauplii, copepedites, adult copepods, rotifers, and cladocerans (Setzler-Hamilton et al. 1981, Setzler-Hamilton 1991, Campfield 2004), were enumerated in three replicate 1 mL aliquots per sample. Mean number per aliquot was scaled up to number per liter for each station and averaged across stations to estimate mean density of zooplankton taxa in the tidal freshwater portion of the river. Taxa were also grouped into the broader categories of microzooplankton (copepod nauplii and rotifers) and macrozooplankton (copepedites, adult copepods, and cladocerans). Correlation in the trends of microzooplankton and macrozooplankton were examined using the Pearson correlation coefficient and spatial differences (between grouped upriver and downriver stations) in zooplankton were examined using ANOVA.

Juvenile fish collections and otolith preparation

Juvenile stage white perch were collected at approximately weekly intervals from July-September in 2005 by beach seine. The seine survey included 9 stations stratified along the salinity gradient of the Patuxent River estuary (river km 6, 16, 33, 41, 45, 48, 53, 64, and 72, Figure 1). Sampling was conducted using a 30.5 m x 1.24 m bag-less beach seine with 6.4 mm mesh size set from shore. White perch were counted, measured and preserved in 95 % ethanol at the time of collection. Water quality data, including temperature and salinity, was measured at the time of fish collections.

Juveniles were assigned to contingent based on their location of capture (freshwater: RK 48, 53, 64, and 72 vs. brackish water: RK 6, 16, 33, 41, and 45). Sr:Ca profile analysis of juvenile white perch otoliths provided evidence that location salinity, which is relatively stable in the Patuxent River throughout the summer months, is a proxy for contingent membership (Kraus and Secor 2004a, Chapter 2). Age was estimated from a subsample of fish from each habitat (dispersive: n = 33, resident: n = 41); dispersive fish were drawn from collections at RK 16, 33, and 45 and resident fish were drawn from collections at RK 48 and 72, based on the abundance of samples from these sites. Fish were drawn predominantly from June and July sampling because ageing of older juveniles is suspect based on reduced accuracy of ageing congeneric striped bass > 65 days (Bulak et al. 1997). Sagittal otoliths from juvenile white perch were extracted, rinsed, cleaned of adhering tissue, and dried for at least 24 hours. Otoliths were sectioned and polished as described above for larval otoliths (SL>12 mm). Otolith microstructure was examined under a compound microscope (600 x magnification). I estimated daily age 3 times independently, and a final age was assigned based on my confidence in age

estimates. Daily increment formation in juvenile white perch was verified in a laboratory study (Kraus and Secor 2004a).

Hatch dates of juvenile white perch were back-calculated, and each individual was assigned to its corresponding larval cohort. To test the hypothesis that contingent members were randomly drawn from the population's hatch-date distribution, the proportion of individuals derived from each larval cohort was compared between each contingent and the overall population using a chi-squared test for specified proportions. In addition, differences in the proportional contribution of early- and late-spawned larval cohorts to resident and dispersive contingents were examined using a contingency table and chi-square statistic.

Statistical Analyses

All statistical analyses were performed with SAS Version 8.2 (SAS Institute, Cary, NC); $\alpha = 0.05$ was used as a critical level of significance. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. In the case of unequal variances, identified when modeling growth across cohorts, variance was calculated for each individual cohort in PROC mixed (SAS Version 8.2). In the case of non-normality, identified in copepedite, adult copepod, and cladocera density data, a log transformation of data was employed for statistical analyses. In the test of equality of mortality rates across larval cohorts, untranformed abundance was used due to non-normality of model residuals using ln(abundance).

RESULTS

Environmental Conditions

Temperature records from the CBP water monitoring station at Jug Bay and the stationary temperature data logger at Kings Landing recorded an overall increase in temperature within the nursery area over the larval production season (Figure 2). Periodic decreases in temperature of 2-3°C occurred during the spring months and typically were concordant with spikes in freshwater discharge. The Kings Landing temperature record mirrored the trends identified in the longer duration record at Jug Bay, albeit slightly lagged and at a higher amplitude (Figure 2). Because the Jug Bay temperature record provided a single continuous temperature record that encompassed the entire larval production season, I relied on this record to characterize temperature experienced by larval cohorts over the course of the larval production season. Freshwater discharge in the Patuxent River averaged 18 m^3s^{-1} from March 12 to May 31. Early in the larval production period (March 26 to April 6) periodic peaks in freshwater discharge occurred, with values as high as 128 m^3s^{-1}. Later, freshwater discharge was relatively stable at less than 20 m^3s^{-1} (Figure 2).

Densities of zooplankton taxonomic groups (copepod nauplii, copepedite, adult, cladocera, and rotifer) were similar between upriver (RK 62-75) and downriver stations (RK 44-59; $p > 0.05$ for all groups) across sampling dates; thus I characterized zooplankton at the river-scale. Mean river-wide microzooplankton and macrozooplankton densities were positively correlated, although the relationship was not significant (Pearson correlation coefficient = 0.80; d.f. = 3, $p = 0.11$). Zooplankton densities were relatively low during the first three cruise dates (April 7, April 21, and

May 3), peaked on May 19, and returned to low densities on May 31 (Figure 3). Shifts in the dominant taxa occurred over the course of the production season. The composition of zooplankton was dominated by adult copepods on April 7, copepod nauplii and copepedites on April 21 and May 3, cladocera and rotifers on May 19, and cladocera on May 31 (Appendix 1, Table 1).

Larval Abundance

The nursery area for white perch extended from RK 45 to 75, with the salt-front (defined as the first station down-estuary with conductivity >800 μS) typically located between RK 45 and 48 on a particular sampling date. The highest abundance of yolk-sac larvae occurred on the first sampling date at upriver stations (RK 72-74); on subsequent sampling dates abundance of yolk-sac larvae was highest at sites further downriver (RK 51 (May 19, May 31), RK 59 (May 3), and RK 64 (April 21)). Based on the presence of yolk-sac larvae on the first sampling date it appears that some spawning occurred shortly before the first sampling cruise (Figure 4). In addition, a small number of yolk-sac larvae were present on the last sampling date and consequently I was unable to track this cohort. Despite this, evidence suggests the temporal coverage of the spawning season was sufficient to characterize the dominant cohort structure. No post-yolk-sac larvae were collected on April 7. However, on subsequent sampling dates abundance of feeding larvae was highest at downriver stations (RK 48 (April 21) and RK 51 (May 3, May 19, May 31)), in the vicinity and slightly up-river of the salt-front. Across sampling dates the highest riverwide abundance of post-yolk-sac larvae occurred on May 3 (Figure 4). The relatively low abundance of larvae at the most down-estuary and up-estuary stations

indicated that sampling adequately encompassed the geographic extent of the nursery habitat. (Appendix 1, Table 2)

Age-Length Relationship

A relationship between temperature-adjusted larval age and length was established based on a representative subsample of white perch larvae (n = 116; Figure 5). Four outliers were identified based on studentized residuals (values > 3), removal of these data points improved the linear model fit considerably (R^2 of model with outliers = 0.77, R^2 of model without outliers = 0.90), thus they were omitted from the final model: Length = 4.24*age-7.28 (S.D. = 4.6, R^2 = 0.90). Comparisons made between a linear and log-linear fit to the data using AIC and the associated model probability, indicated that the data were better fit with a linear model. Using the age-length key, length frequencies of larvae collected on each sampling date were converted to age frequencies (ranging from 0 to 70 days; Figure 6) and used to calculate the hatch-date distribution of larvae. The hatch dates of white perch larvae ranged from March 12 to May 31. Nine 9-day cohorts were identified (Cohorts A-I, Table 1).

Larval Vital Rates

Cohort-specific instantaneous growth rates (g) ranged from 0.021 d^{-1} (cohort C) to 0.037 d^{-1} (cohort G; Table 1, Figure 7). Growth rates were not estimated for cohorts A, B, H and I due to the low abundance of these cohorts and consequent low representation within our samples. Cohort-specific growth rates of early-spawned cohorts were lower than later-spawned cohorts (Table 1). However, a test of equality of slopes of cohort-specific age-length relationships indicated growth rates were not significantly different

across cohorts (ANCOVA $F_{5,103} = 1.45$, $p = 0.45$). Mean absolute growth rates during the first 45 days after hatch were calculated for each cohort to compare rates with published values for white perch and ranged from 0.10 to 0.29 mm d^{-1} (Table 1).

Cohorts spawned in April had the highest initial abundances (cohort C, E, F, D, respectively), whereas earlier- (cohorts A, B) and later-spawned cohorts (cohorts G, H) had low initial abundances. Cohort-specific mortality rates were calculated for cohorts A-F and ranged from 0.08 d^{-1} (cohort A) to 0.03 d^{-1} (cohort F; Table 1, Figure 8). Mortality rates could not be calculated for cohorts G-I based on the limited data available. The earliest spawned cohorts had the highest mortality rates, with rates decreasing as the spawning season progressed. A test of equality of slopes of larval cohort abundance-at-age revealed no significant difference in mortality rate across cohorts (ANCOVA $F_{5,12} = 1.2$, $p = 0.37$).

The ratio of G:Z reflected the combined effect of cohort-specific differences in weight-specific growth and mortality rate. Ratios were calculated for cohorts C-F and estimated for G (assuming a mortality rate equal to cohort F). The ratio of G:Z increased over the course of the larval production period, with cohorts F and G having the highest ratios (>5; Table 1).

Environmental Effects

I compared environmental conditions (temperature and freshwater flow) experienced over different stanzas during early life history (hatch, yolk-sac, post-yolk-sac, and larval duration periods). Due to the low sample size and consequently low power of these models the significance level is not reported, rather I have relied on model

probability values derived from AIC values to compare the fit of models describing the relationship between environmental conditions during specific periods in early life history and vital rates. Temperature experienced during the post-yolk-sac period explained the most variance in growth rate and the G:Z ratio (Table 2). Temperature during the post-yolk-sac and the entire larval period explained nearly equal variance in cohort mortality rate, however, the probability of these models was low (Table 2). Temperature experienced during the post-yolk-sac period was positively correlated with growth rate (Pearson correlation coefficient = 0.85, d.f. = 3, p = 0.08) and the G:Z ratio (Pearson correlation coefficient = 0.84, d.f. = 3, p = 0.08) and negatively correlated with mortality (Pearson correlation coefficient = -0.95, d.f. = 4, p = 0.06).

Juvenile Fish

Temperature-adjusted ages of juvenile fish ranged from 47 to 75 days post-hatch. Hatch dates ranged from April 13 to May 8 for the dispersive contingent and April 9 to May 12 for the resident contingent. Based on hatch date, juveniles from each contingent were grouped into their corresponding larval cohorts (Figure 9). Members of both contingents came from larval cohorts D, E, F, and G with the highest proportion of dispersive (59%) and resident contingent fish (37%) originating from cohort E. Significant differences were identified among contingents in the percent of individuals derived from early- (cohorts D and E) and late-spawned (cohorts F and G) cohorts (chi square = 4.63, d.f. = 3, p = 0.03). The distribution of hatch dates of the dispersive contingent was centered on early-spawned cohorts with 82% of fish derived from cohorts D and E, whereas members of the resident contingent were drawn from a more evenly

distributed hatch-date distribution (Figure 9). However, compared to the dispersive contingent, a higher percentage of resident contingent fish came from late-spawned cohorts (41% contribution of cohorts F and G to resident contingent compared to 18% contribution to dispersive contingent; Figure 9).

The population's hatch-date distribution was comprised of cohorts A-H (Figure 9). Calculated from initial cohort abundance and cohort-specific mortality rates, mortality rates of cohorts G and H were assumed to be equal to cohort F in order to estimate the contribution of later spawned cohorts to the overall population distribution. The highest contributions to the population distribution came from cohort E and F, with lower contributions from cohorts D and C, and little contribution from cohorts A, B, G, and H. There was a significant difference in the percent of individuals derived from early- and late-spawned contingents and the population's distribution ($p < 0.01$). Relative to the population's hatch-date distribution, the distribution of dispersive contingent fish was skewed toward earlier spawned contingents, whereas the distribution of resident fish was skewed toward later spawned cohorts (Figure 9). Neither contingent exhibited representatives of the earliest (cohorts A and B) nor latest (cohorts G and H) spawned cohorts present in the population's distribution.

DISCUSSION

Characterization of larval cohorts and "hind-casting" the hatch-date distribution of juvenile contingents within the same year-class provided evidence in support of the hypothesized proximate cause of contingent structuring in this white perch population. Juveniles from each contingent were derived from specific larval cohorts that possessed

particular growth and mortality attributes, rather than drawn at random from the population's hatch-date distribution. Dispersive contingent fish originated predominantly from earlier spawned cohorts, characterized by slower growth rates, higher mortality rates, and lower G/Z ratios compared to cohorts spawned late in the production season. A greater proportion of resident fish came from later spawned cohorts, exhibiting higher growth rate, lower mortality rate, and high G/Z ratios. Overall, timing of spawning and the conditions experienced by white perch early in their life history were found to have consequences at the individual-level (i.e., vital rates) which affected spatial structuring at the population-level (contingent structure).

Timing of spawning and contemporaneous environmental conditions influenced cohort-specific vital rates, which may ultimately trigger initiation of contingent behavior within the white perch population. Based on the distribution of hatch dates, white perch spawned from mid-March through the end of May in 2005, with peak spawning occurring in early to mid-April concomitant with the initial rise of water temperatures above 10°C. White perch spawn over a wide temperature range (10 to 20°C; Funderburk et al. 1991), with optimal hatching temperatures ranging from 12 to 14°C (Setzler-Hamilton 1991). Water temperatures below 10°C or episodic drops in temperature (2-5°C) can cause significant egg mortality (Setzler-Hamilton 1991). Mortality rates for white perch cohorts ranged from 0.03 to 0.08 d^{-1} and were lower than those estimated for white perch in the Potomac River (0.08 to 0.11 d^{-1}; Houde et al. 1989) and Hudson River (0.04 to 0.80 d^{-1}; Limburg et al 1999). Cohort-specific mortality rates were highest in the earliest-spawned cohorts and decreased as the spawning season progressed. Low temperatures in mid- to late March and periodic decreases in temperature early in the spawning season in

concert with high freshwater flow were the likely cause of high mortality in cohorts A and B. Mortality rates were not calculated for cohorts H and I; however, the low initial abundances of these late-spawned cohorts are likely due to the cessation of white perch spawning as temperatures increased above optimal levels. For several cohorts, calculation of mortality rates are based on only a few observations over time and thus should be viewed cautiously.

Growth rates calculated for white perch larvae in the Patuxent River estuary were similar to previous estimates. Depending on food and temperature conditions, white perch larvae grew from 0.01 to 0.28 mm d^{-1} in laboratory experiments (Margulies 1988), while field growth rates of white perch cohorts ranged from 0.13 to 0.36 mm d^{-1} in the Patuxent River (2000 and 2001, Campfield 2004), 0.29 to 0.69 mm d^{-1} in the Potomac River (1987; Houde et al. 1989) and 0.13 to 0.38 d^{-1} in the Hudson River (1994; Limburg et al. 1999). Previous analysis of larval growth rates of striped bass in Chesapeake Bay estuaries showed a strong positive relationship with temperature, with early-spawned larvae experiencing lower temperatures and consequently exhibiting lower growth rates than later spawned larvae (Rutherford and Houde 1995, Secor and Houde 1995). Similarly, a positive correlation was identified between temperature (during the post-yolk-sac period) and growth rate of white perch. Temporal differences in cohort-specific growth rates observed in my study followed trends identified in striped bass, but were not significantly different among cohorts. In addition, cohort-specific G:Z ratios increased over the course of the production season, indicating enhanced growth and/or survival conditions for larvae spawned later in the production season. Late-spawned cohorts (F

and G) had the highest G:Z ratios, indicating that conditions were optimal for growth and/or survival for these cohorts.

The lack of temporal resolution in zooplankton density measures limited my ability to quantitatively test the influence of prey availability on cohort-specific growth, mortality, and G:Z ratios. High concentrations of prey were found to positively influence feeding success of first-feeding white perch larvae in the upper Chesapeake Bay (Shoji et al. 2005). In addition, Limburg et al. (1999) identified a positive correlation between zooplankton density and larval white perch growth and G:Z ratio in the Hudson River, and a similar relationship may exist in the Patuxent River. Trends in microzooplankton in the Patuxent River indicated high densities occurred in mid-May, coinciding with initiation of first-feeding by larvae from cohorts F and G. Cohorts F and G exhibited the fastest growth rates and highest G:Z ratios which may be attributable, in part, to high prey availability during early life history. Conversely, low zooplankton density during April and early May may have contributed to slower growth rates of earlier-spawned cohorts of white perch.

The relationship between timing of spawning, contemporaneous environmental conditions, and spatial structure indicates that the spawning behavior of white perch could play an important role in dampening both temporal and spatial recruitment variability within the population (Secor 2007). The moderately protracted spawning season of white perch likely represents behavior selected to minimize the risk of recruitment failure due to the mismatch of appropriate nursery habitat conditions and the presence of larvae (Cushing 1975, Secor 2007). Diversity in spawning time is hypothesized to be related to diverse size and age structure within a population, with

larger, older females often spawning earlier in the season (Secor 2000, Secor 2007). Evidence from the present study suggests that diverse spawning times contribute to diversity in cohort structure, forming the basis for contingent structuring. Interestingly, if larger fish spawn earlier, this could be a mechanism for dispersive fish, which are larger-at-age compared to resident fish, to have a higher probability of spawning dispersive young. Furthermore, because resident fish inhabit the spawning environment, whereas dispersive contingent fish reside down-estuary and respond to external cues that dictate the timing of up-river migration for spawning, this may facilitate resident spawning at more opportune times, such that larval growth and survival is enhanced. Thus, a possible positive feedback may exist in which spatial structure contributes to diversity in spawning times.

Additionally, a single white perch may contribute progeny to both the resident and dispersive contingents within a single year-class. Observations of eggs in various stages of development in mature females support the hypothesis that individual white perch likely spawn multiple times during a single spawning season (Mansueti 1964). Thus, diversity in spawning time, both within and between individuals, likely contributes to the spatial structure within the population. Evidence of the potential importance of this behavioral adaptation in dampening recruitment variability and enhancing resilience of the population (Chapter 7) highlights the need for preservation of biocomplexity, such as diverse age structure and spawning behavior, within populations.

This research, in concert with evidence accumulated from prior studies on Patuxent River white perch, has contributed to our understanding of the mechanism of contingent structuring. Evidence presented here supports the idea that contingent

structuring is maintained by a conditional strategy, wherein individuals adopt alternative life history tactics based on individual growth rate, as modified by the environment, relative to a genetically determined growth threshold. Direct and back-calculated estimates of larval growth rates indicate that fish destined to become members of the dispersive contingent exhibit slower growth during early life history compared to resident fish (Kraus and Secor 2004a, Kerr and Secor *In Press*). Subsequent to dispersal, dispersive contingent fish exhibit higher juvenile growth rates compared to resident contingent fish (Kerr and Secor *In press*), and this trend continues into the adult stage (Kraus and Secor 2004a). This reversal of growth trajectory is consistent with the concept of compensatory growth, with the dispersive contingent compensating for slow growth experienced early in life once established in a habitat of higher resource availability (Metcalfe and Monaghan 2001). The magnitude of contingent representation in a given year is likely determined by mortality rates of specific larval cohorts. Interannual variation in representation of white perch contingents in the Patuxent River has been correlated with streamflow, with high representation of the dispersive contingent in high streamflow conditions (96%), lower representation in low flow conditions (85%), and absence of the dispersive contingent in drought years (Kraus and Secor 2004a). The positive relationship between dispersive contingent representation and streamflow suggests enhanced survival conditions (i.e., increased zooplankton production; North and Houde 2003) for slower growing larval cohorts during years of higher streamflow. This scenario could be typical of cool, wet years wherein low temperatures result in a greater representation of slow growing cohorts that have high survival.

It is important to note that the conclusions drawn in this study are based on one year of data from the Patuxent River and therefore must be considered cautiously. In this study I identified environmental factors (temperature and zooplankton density) that appear to be important determinants of cohort vital rates and consequently contingent membership. Because physical and biological conditions (e.g., climate, weather, and prey density) operate simultaneously in a system and interact in a complex manner, it is difficult to conclusively determine how important each factor is independently. Conclusions regarding the dominant contribution of slow-growing and fast-growing larvae to specific contingents, however, are supported by back-calculated growth rates of resident and dispersive white perch in 2001 (Kraus and Secor 2004a). Interannual variability in timing of spawning and concomitant environmental conditions may result in interannual differences in the relative contribution of early- and late-spawned larval cohorts to specific contingents. For example, both 2001 and 2005 were average streamflow years in the Patuxent River and, similar to 2005, Campfield (2004) found microzooplankton (copepod nauplii and rotifers) density in the Patuxent River in 2001 peaked in early- to mid-May. Spawning occured slightly later in 2001 and, consequently, white perch larval cohort growth rates were higher earlier in the season in 2001, coinciding with high zooplankton abundance and more optimal temperatures for growth (Campfield 2004).

In addition to the influence of the temporal distribution of larvae during the spawning season, I cannot discount the role that the spatial distribution of larvae may play in determining spatial structure in the population. Those larvae that actively move or experience passive advection down-estuary toward the salt-front may subsequently

settle in more down-estuary habitats as juveniles. Larval growth is typically enhanced for fish residing in the vicinity of the salt-front/estuarine turbidity maximum (ETM) due to high prey concentrations (North and Houde 2003). The impact of larval spatial dynamics on contingent membership of white perch was not explicitly examined in this study, however, the fact that the dispersive contingent is comprised predominantly of slow-growing larvae does not support the idea that fish distributed in the vicinity of the ETM necessarily comprise the dispersive contingent.

Based on a combined approach of larval cohort analysis and back-calculation of hatch-date distribution of juvenile contingent members, I gained insight into the unique characteristics that define resident and dispersive contingent members and the controlling factors at work during early life history of fishes that define population structure. Because contingent structuring within populations may have implications with respect to the way populations respond to environmental change, there is a need to manage fished populations with spatial structure in mind. Increased understanding of the proximate cause of spatial structuring within populations can enable better management in a changing environment. Specifically, management for increased age and size diversity within the Patuxent River population of white perch may be key in maintaining a protracted spawning period and preserving contingent structure (Secor 2007).

TABLES

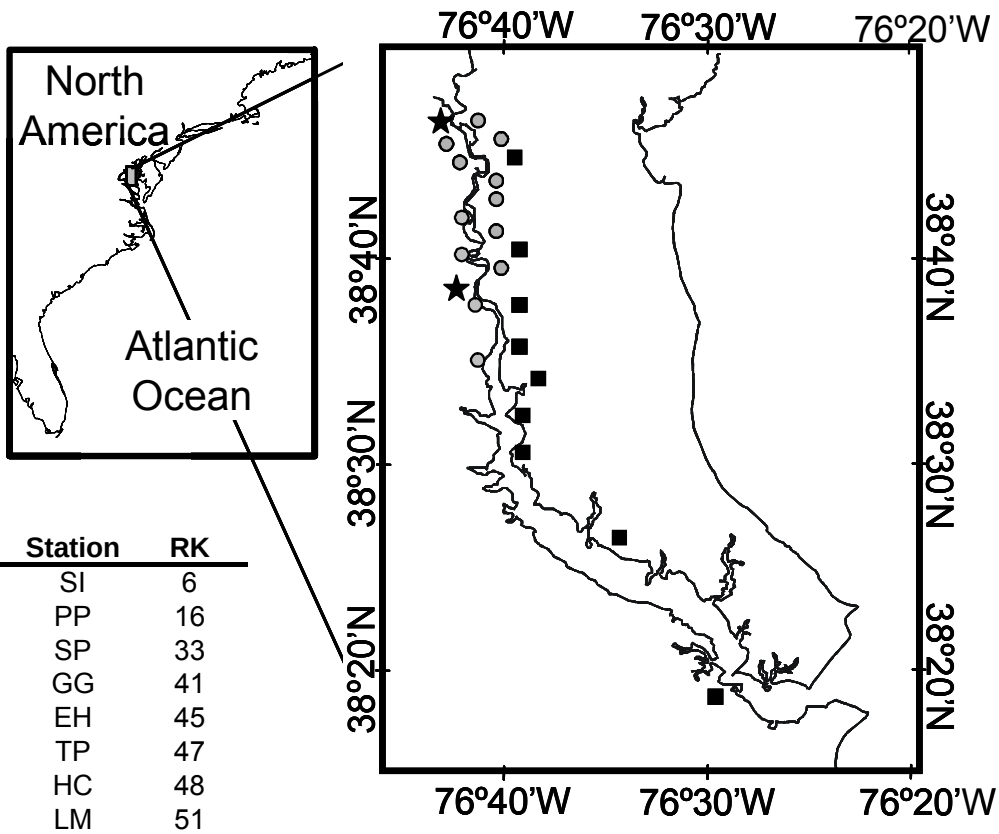
Table 1. Hatch-date range and the assigned hatch-date (median) for larval cohorts of white perch (Patuxent River, 2005). Growth and mortality rate and G/Z ratio for each cohort are reported. Mean environmental conditions (temperature, freshwater discharge) experienced over the early life history period (hatch period for each cohort, yolk-sac period (1.5-4.0 mm), post-yolk-sac period (>4.0 mm), and the entire larval duration (period from hatch to last date cohort appears in samples).

								Mean Temperature (°C)				Mean Freshwater flow (m^3s^{-1})			
Cohort	Hatch-Date Range		Assigned Hatch Date	Length-specific growth rate (d^{-1})	Weight-specific growth rate (d^{-1})	Mortality rate (d^{-1})	G/Z	Hatch-date	Yolk sac	Post-yolk sac	Larval duration	Hatch-date	Yolk sac	Post-yolk sac	Larval duration
A	12-Mar	20-Mar	16-Mar			0.08		7.5	8.3	15.2	15.4	9.1	20.4	18.2	18.2
B	21-Mar	29-Mar	25-Mar			0.08		8.7	9.7	16.0	16.2	37.8	45.2	13.8	19.5
C	30-Mar	7-Apr	3-Apr	0.02	0.09	0.06	1.38	11.3	13.3	16.4	16.7	48.3	37.0	11.4	16.9
D	8-Apr	16-Apr	12-Apr	0.02	0.10	0.05	2.12	14.6	15.2	16.7	17.0	13.2	11.2	11.5	11.7
E	17-Apr	25-Apr	21-Apr	0.03	0.11	0.05	2.35	15.7	15.4	17.1	17.4	10.9	10.5	11.7	11.3
F	26-Apr	4-May	30-Apr	0.04	0.16	0.03	5.16	15.1	14.9	18.0	18.3	11.7	11.1	12.1	11.5
G	5-May	13-May	9-May	0.04	0.16	0.03*	5.30	16.9	18.9	17.2	18.1	8.3	8.2	14.8	11.4
H	14-May	22-May	18-May					17.8	15.6	19.6	18.4	15.0	16.2	9.3	12.9
I	23-May	31-May	27-May					17.6	19.2		18.7	10.8	8.9		10.8

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

		Model	RSS	P	N	AICc	ΔAIC	Model likelihood	Model probability
Growth Rate	Temp	Hatch	8.15E-05	2	5	-45.12	17.59	0.00	0.00
		Yolk-sac	1.05E-04	2	5	-43.87	18.83	0.00	0.00
		Post-yolk	**2.42E-06**	**2**	**5**	**-62.71**	**0.00**	**1.00**	**0.60**
		Larval duration	3.09E-06	2	5	-61.48	1.22	0.54	0.33
	FW	Hatch	8.07E-05	2	5	-45.17	17.53	0.00	0.00
		Yolk-sac	8.33E-05	2	5	-45.01	17.69	0.00	0.00
		Post-yolk	5.84E-06	2	5	-58.30	4.40	0.11	0.07
		Larval duration	8.08E-05	2	5	-45.16	17.54	0.00	0.00
		Model	RSS	P	N	AICc	ΔAIC	Model likelihood	Model probability
Mortality Rate	Temp	Hatch	2.43E-04	2	4	-22.83	5.79	0.06	0.02
		Yolk-sac	3.50E-04	2	4	-21.37	7.25	0.03	0.01
		Post-yolk	5.87E-05	2	4	-28.52	0.10	0.95	0.32
		Larval duration	**5.72E-05**	**2**	**4**	**-28.62**	**0.00**	**1.00**	**0.34**
	FW	Hatch	2.23E-04	2	4	-23.18	5.44	0.07	0.02
		Yolk-sac	2.33E-04	2	4	-23.01	5.61	0.06	0.02
		Post-yolk	6.81E-05	2	4	-27.92	0.70	0.71	0.24
		Larval duration	2.23E-04	2	4	-23.17	5.45	0.07	0.02

		Model	RSS	P	N	AICc	ΔAIC	Model likelihood	Model probability
G/Z index	Temp	Hatch	5.79	2	5	10.73	13.49	0.00	0.00
		Yolk-sac	7.12	2	5	11.77	14.52	0.00	0.00
		Post-yolk	0.39	**2**	**5**	**-2.75**	**0.00**	**1.00**	**0.53**
		Larval duration	0.46	2	5	-1.89	0.87	0.65	0.35
	FW	Hatch	5.64	2	5	10.60	13.35	0.00	0.00
		Yolk-sac	5.78	2	5	10.73	13.48	0.00	0.00
		Post-yolk	0.72	2	5	0.29	3.04	0.22	0.12
		Larval duration	5.64	2	5	10.61	13.36	0.00	0.00



Station Name	Station	RK
Solomons Island	SI	6
Peterson Point	PP	16
Sheridan Point	SP	33
God's Grace Point	GG	41
Eagle Harbor	EH	45
Truman's Point	TP	47
Holland Cliff	HC	48
Lower Malborough	LM	51
Miltown Landing	ML	53
White's Landing	WL	59
Chaineyville Road	CH	60
Spice Creek	SC	62
Nottingham	N	64
Ferrey Landing	FL	66
Lyons Creek	LC	70
Jug Bay	JB	72
Patuxent River Park	PX	74
Western flow	WF	75

Figure 1. Map of the Patuxent River estuary, a sub-estuary of the Chesapeake Bay (Maryland; Kraus and Secor 2004a). The map illustrates stations sampled for larval white perch (grey circles) and the location of juvenile white perch collections (black squares) during 2005 in the Patuxent River estuary. Sites of water quality monitoring are indicated by black stars (Jug Bay and Kings Landing, MD).

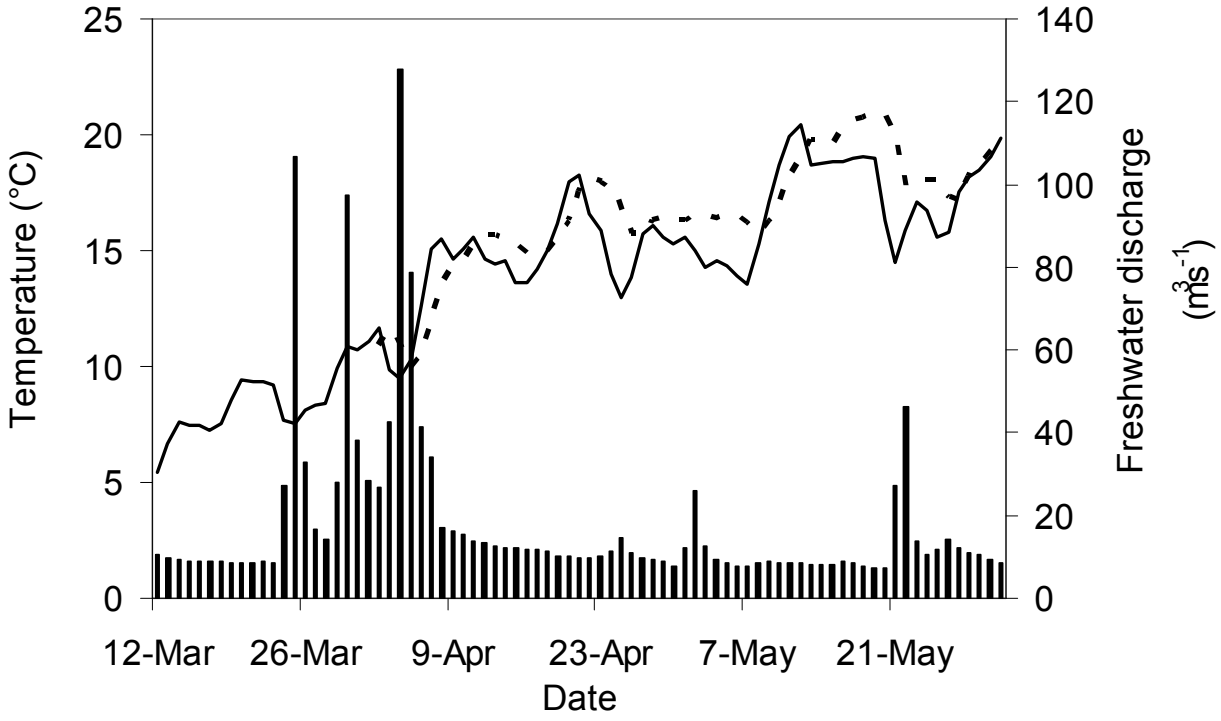


Figure 2. Temperature (°C) recorded over the larval production season at Jug Bay (solid line; Chesapeake Bay Program Water Monitoring Station) and Kings Landing (dashed line) in the Patuxent River. Freshwater discharge (solid bars; USGS Site: Patuxent River near Bowie, MD, Site #: 01594440) is shown on the secondary y-axis.

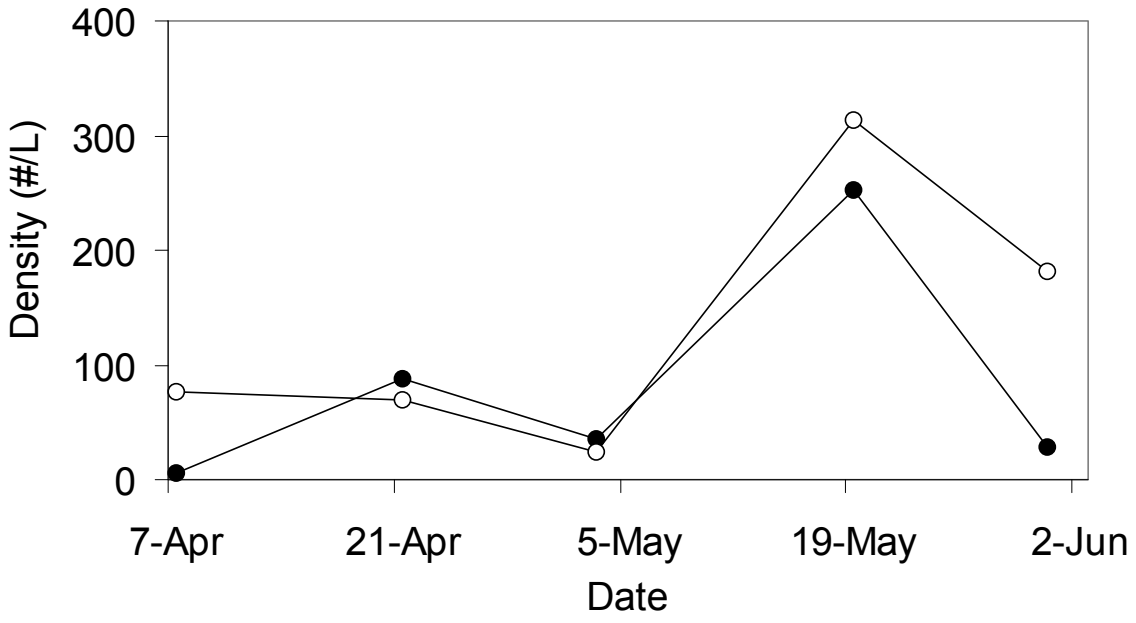


Figure 3. Trends in mean riverwide microzooplankton (closed circles; copepod nauplii and rotifer) and macrozooplankton (open circles; copepedite, adult copepod, and cladocera) across sampling dates during spring 2005 in the Patuxent River.

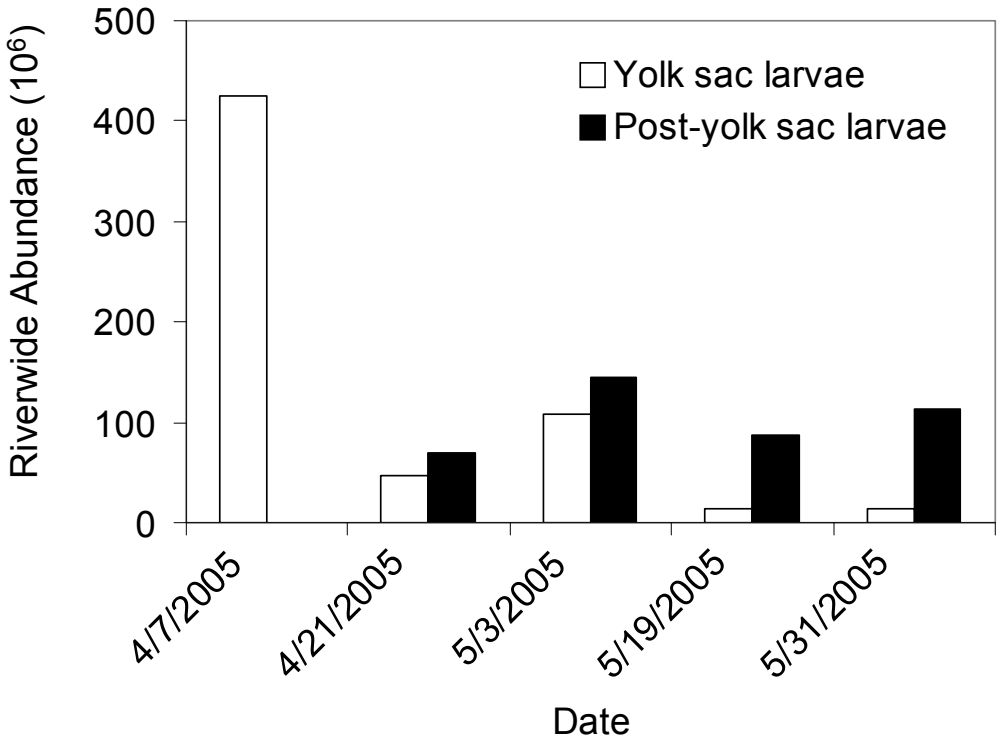


Figure 4. Riverwide abundance of white perch yolk-sac (open bars) and post-yolk-sac larvae (solid bars) in the Patuxent River across sampling dates during the larval production season (2005).

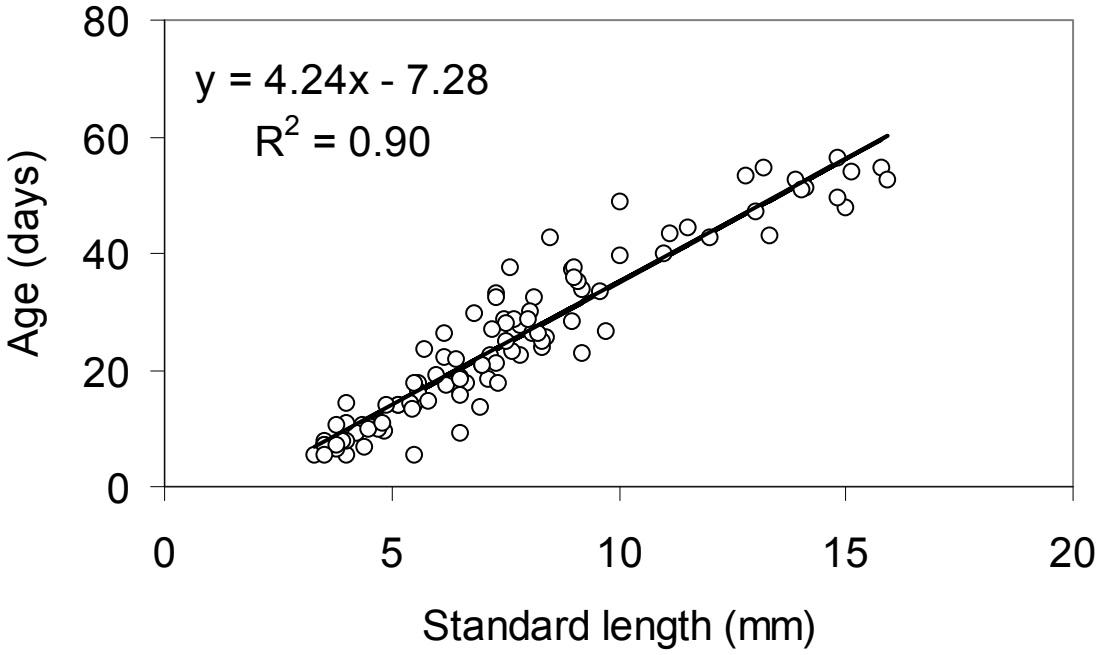
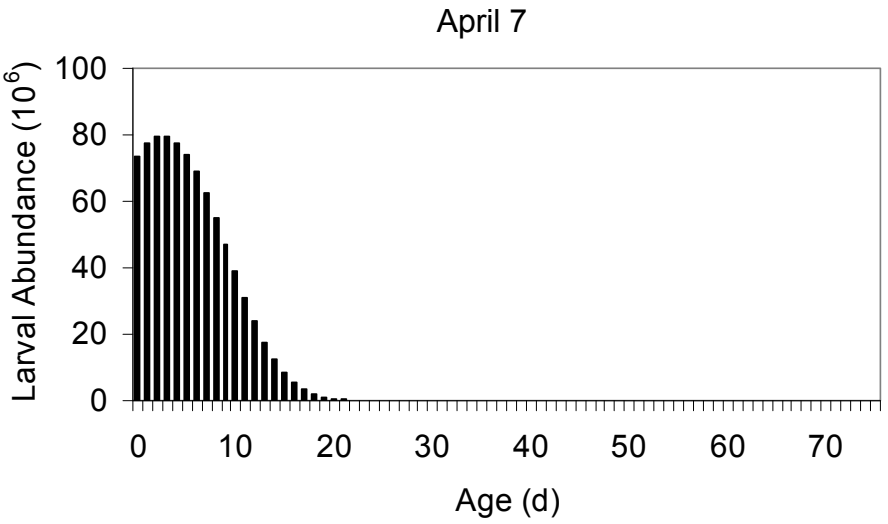
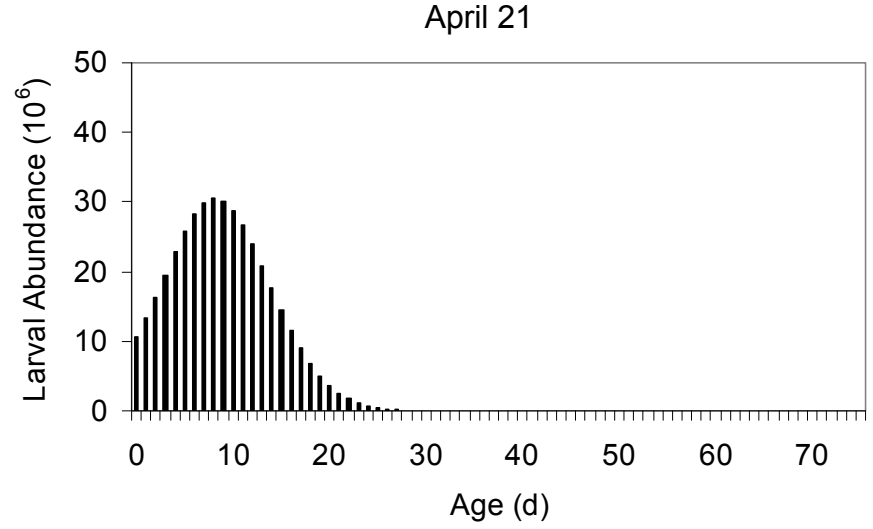
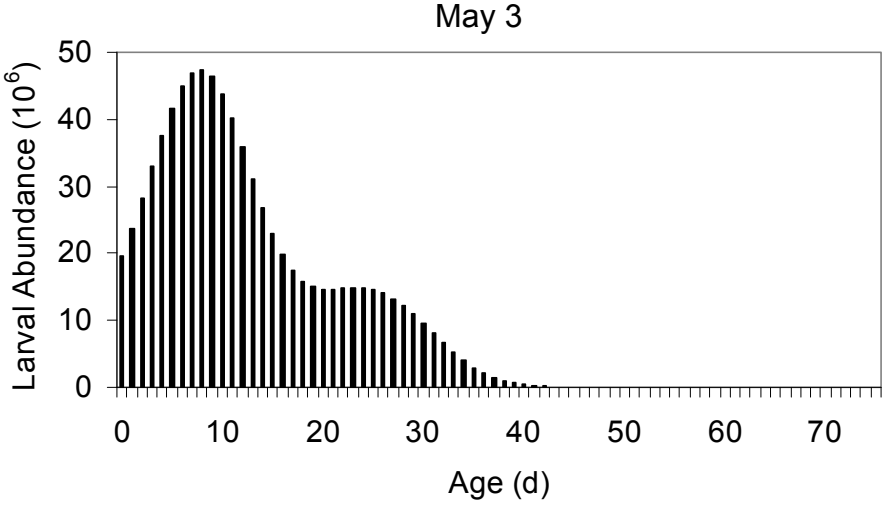


Figure 5. Regression of otolith-based estimated age (temperature-adjusted) on standard length (n = 116) for larval white perch from the Patuxent River estuary (2005).


April 7
Larval Abundance (10^6)
100
80
60
40
20
0
0
10
20
30
40
50
60
70
Age (d)


April 21
Larval Abundance (10^6)
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Age (d)


May 3
Larval Abundance (10^6)
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Age (d)

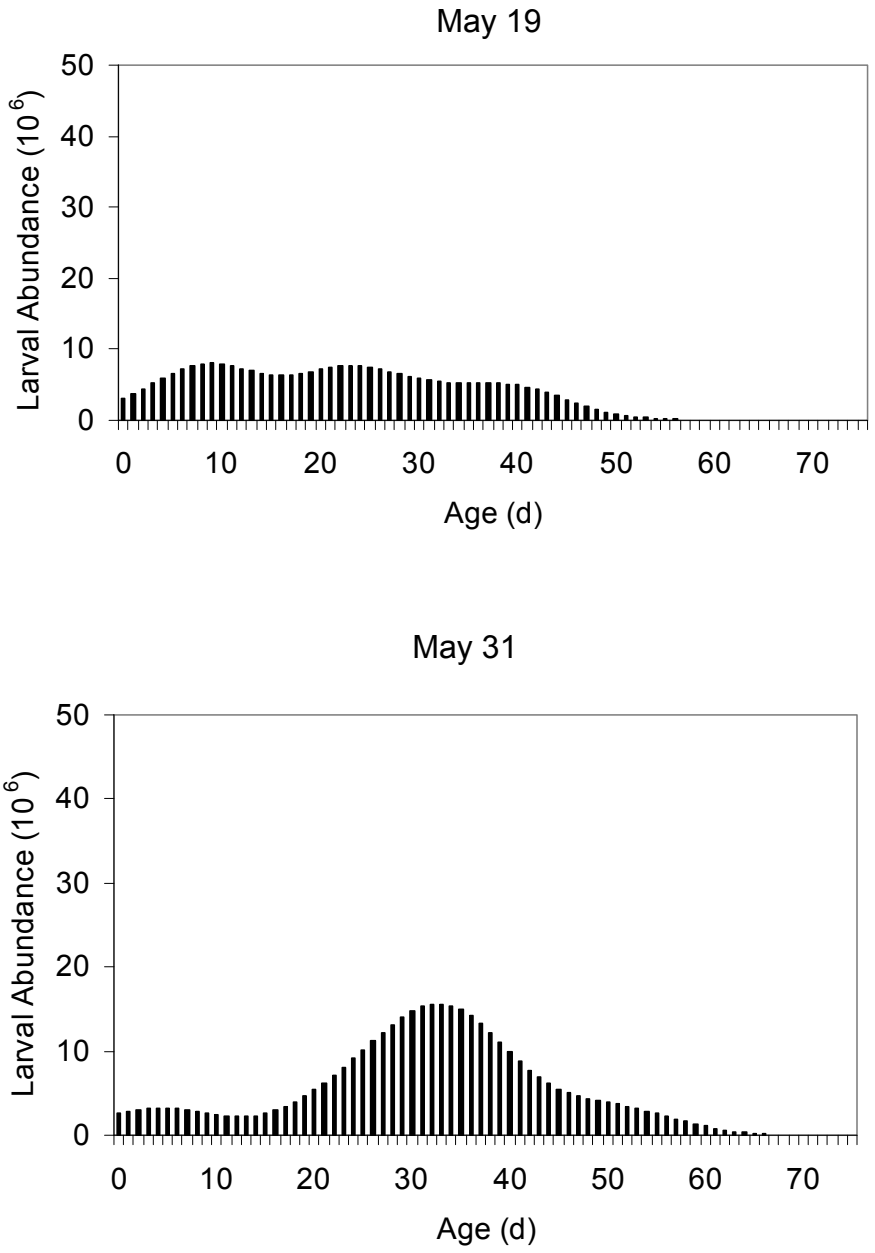


Figure 6. Estimated riverwide abundance-at-age of larval white perch in the Patuxent River on each survey date in 2005 (April 7, April 21, May 3, May 19, and May 31).

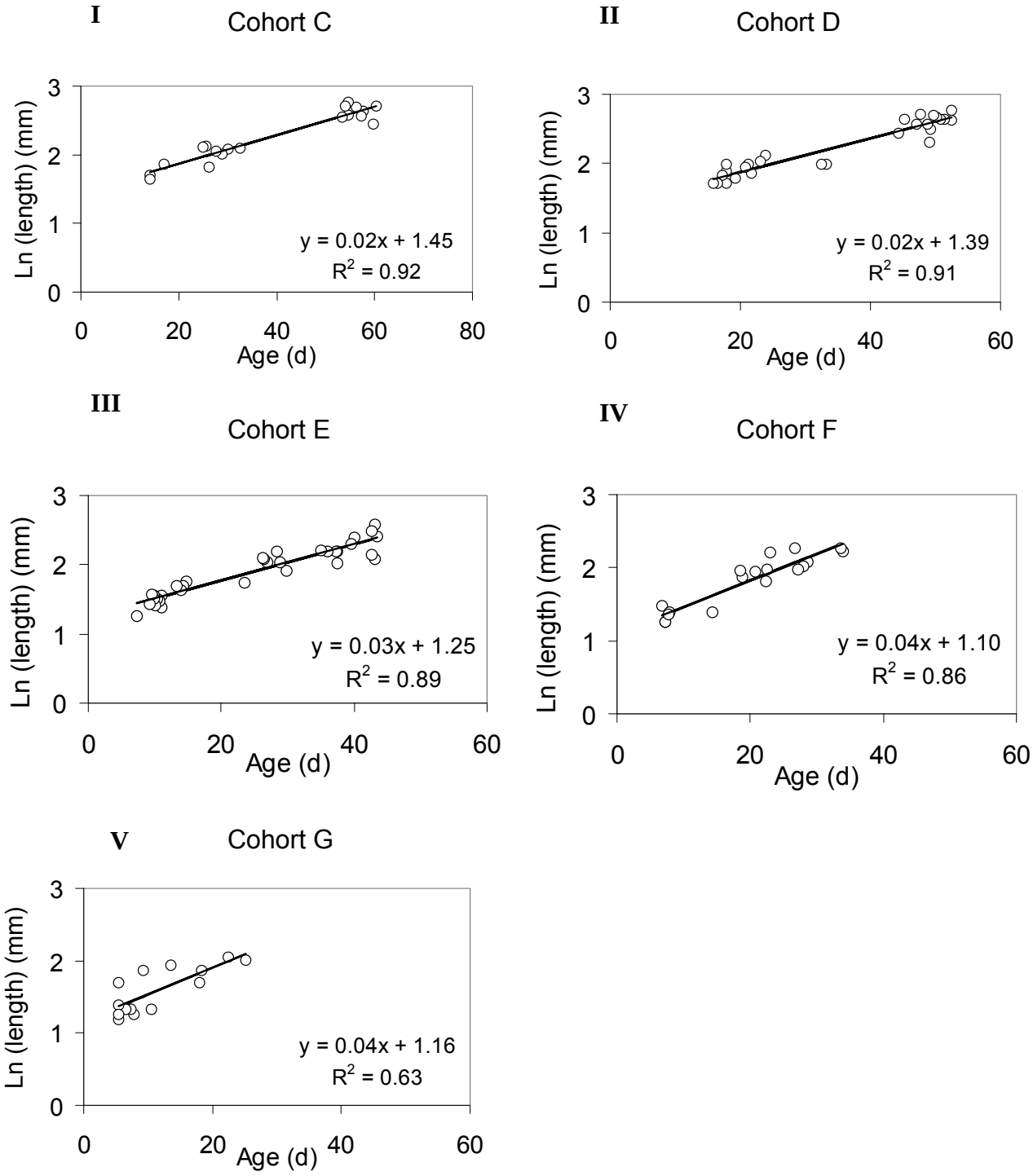


Figure 7. Regressions of Ln(length) on age (days) for white perch cohorts (Patuxent River, 2005, I: cohort C, II: cohort D, III: cohort E, IV: cohort F, V: cohort G).

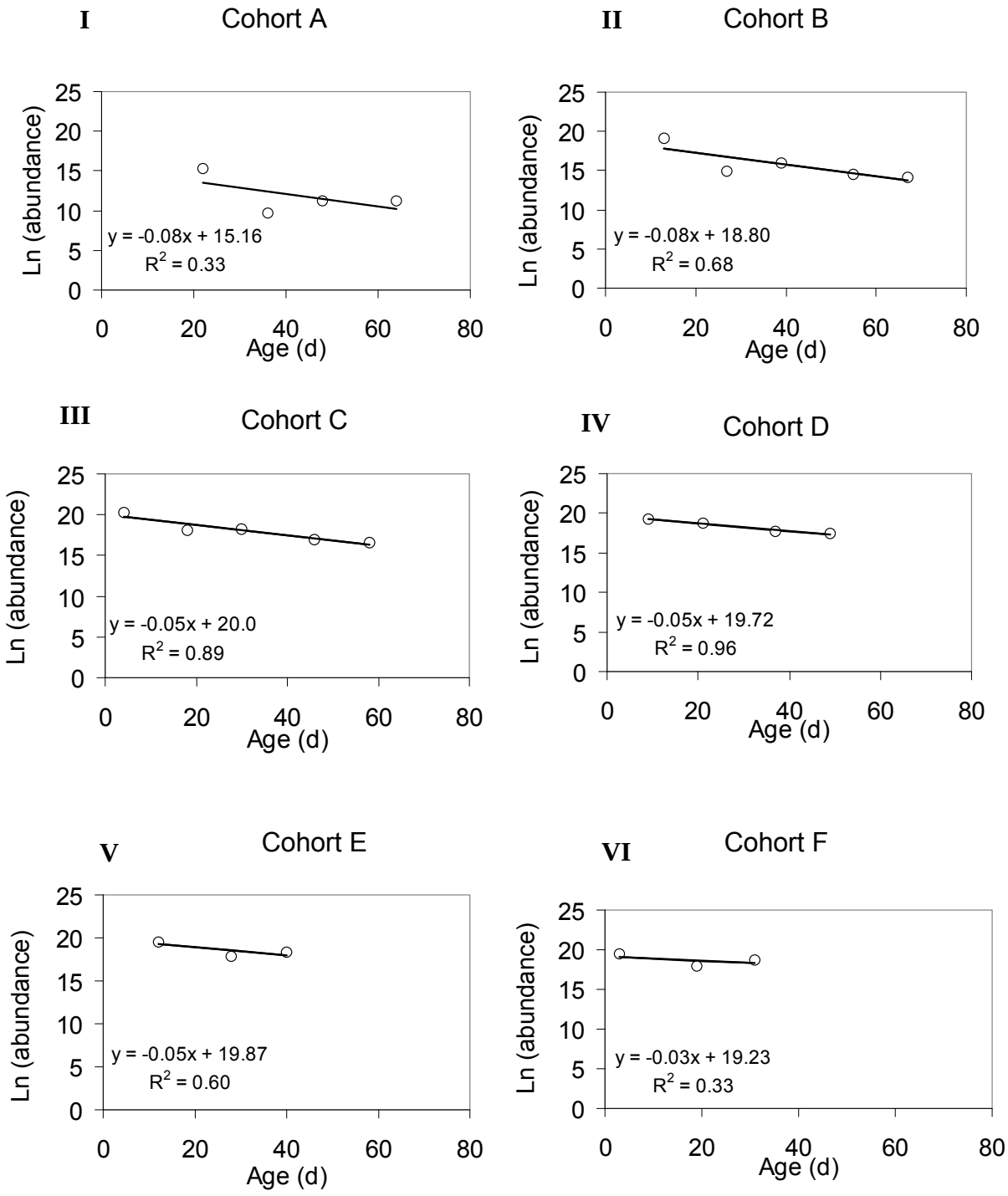


Figure 8. Regressions of Ln(abundance) on age (days) for larval white perch cohorts (Patuxent River, 2005; I: cohort A, II: cohort B, III: cohort C, IV: cohort D, V: cohort E, VI: cohort F).

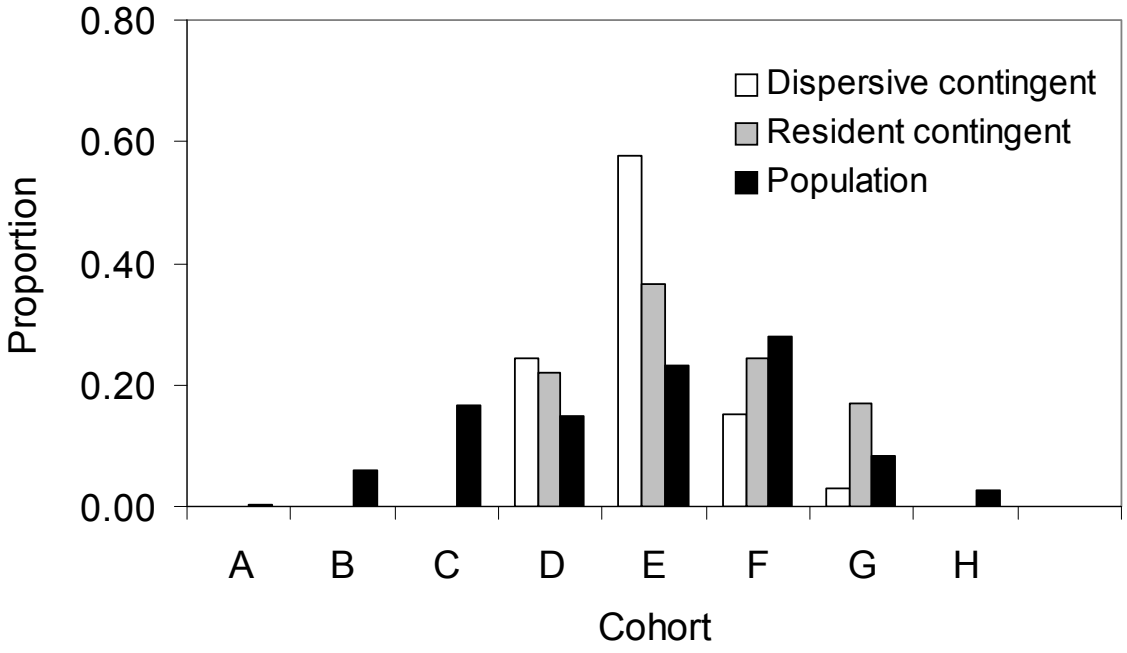


Figure 9. Proportion of individuals within each juvenile white perch contingent (dispersive and resident) and the overall population derived from each larval cohort.

Chapter 4: BIOENERGETIC TRAJECTORIES UNDERLYING PARTIAL MIGRATION IN PATUXENT RIVER (CHESAPEAKE BAY) WHITE PERCH *MORONE AMERICANA*.

ABSTRACT

Partial migration—the coexistence of resident and migratory individuals within the same population—may be common in fish populations. A proposed mechanism underlying partial migration is differing dispersive responses to early growth conditions, but few studies have explicitly tested this. During their first year of life, white perch in the Patuxent River exhibit either residency in freshwater natal habitats (resident contingent) or disperse down-estuary into brackish habitats (dispersive contingent). I tested whether white perch (*Morone americana*) juveniles exhibited differing growth and metabolic trajectories based on contingent membership or in response to salinity. A randomized factorial experiment with two contingent types and two salinity treatments (1 and 8) was conducted over a 30-day period. The experiments supported a contingent effect, with the dispersive contingent exhibiting higher consumption rates and a higher scope for growth. In addition, I identified a weak salinity effect with evidence of increased consumption and routine metabolism in mesohaline conditions. Juvenile growth rates calculated from individuals in the field supported laboratory results, with dispersive contingent members exhibiting higher growth rates. I conclude that contingent membership and the related phenomenon of partial migration in this population is associated with varying energetic tactics that significantly influence the scope for growth.

INTRODUCTION

Partial migration, or the presence of resident and migratory forms within a population, has been identified in several diadromous (Secor et al. 2001, Tsukamoto and Arai 2001, Kraus and Secor 2004a) and marine fish populations (Able et al. 2003, Fromentin and Powers 2005, Elsdon and Gillanders 2006). The coexistence of resident and migratory individuals within a single population is hypothesized to be related to differences in the behavioral response of individuals to tradeoffs associated with migration versus residence (Jonsson and Jonsson 1993). Benefits of migration have been documented in many anadromous populations, with migrants typically having increased growth potential and achieving a larger size than resident fish due to increased feeding opportunities and osmoregulatory benefits associated with higher salinity waters (Gross 1987, Metcalf and Thorpe 1990, Jonsson and Jonsson 1993). Increased predation risk and disease are among the costs of migration, contributing to higher mortality rates of migratory individuals (Jonsson and Jonsson 1993).

While the ultimate cause of movement out of a habitat is likely related to food availability and predation risk (Werner and Gilliam 1984), the proximate cause of this behavior continues to be debated. Despite some evidence that contingents can occur as reproductively isolated sub-populations (e.g., Verspoor and Cole 1989), the preponderance of evidence supports partial migration as an expression of a conditional strategy leading to polyphenic responses within populations. In a single genetic population, the adoption of resident or migratory tactics relates to an individual's condition relative to a threshold, most likely related to growth (Lundberg 1988, Gross and Repka 1998a,b). Differences in growth between residents and migrants are

hypothesized to be established early in life and have been attributed to factors such as timing of spawning, social status, feeding hierarchies, density, and sex-specific differences (Jonsson and Jonsson 1993, Secor 1999). Investigations of growth thresholds as a cue to initiate migration (or reinforce retention) have documented migrants within a population to be either faster growing (Jonsson 1985, Forseth et al. 1999, Thériault and Dodson 2003) or slower growing than residents at the time of dispersal (Bujold et al. 2004, Kraus and Secor 2004a). In some populations, slow growers benefit more from migration out of an environment that does not meet their energetic needs to a new habitat with potential higher food availability, whereas in others migration may be limited to larger/faster growing fish that have the energy reserves necessary to migrate (Jonsson and Jonsson 1993, Thériault and Dodson 2003). Thus, migration within a population is condition-dependent in relation to habitat-specific predation risk and potential growth rate benefits, with individual habitat use reflecting the tactic that achieves maximum individual fitness (Jonsson and Jonsson 1993, Brodersen 2008). Understanding the bioenergetic differences associated with resident and migratory life history strategies can enhance our understanding of partial migration within fish populations.

During their first year of life, estuarine-dependent white perch (*Morone americana*) in the Patuxent River estuary (Maryland) persist as juveniles in freshwater natal habitats (resident contingent), or disperse down-estuary into brackish water habitats (dispersive contingent). Otolith microchemical analysis indicates that these two behaviors are discrete (Kraus and Secor 2004a) with patterns of divergent habitat use initiated shortly after the larval-juvenile transition (Kraus and Secor 2004a) and predominantly persisting into adulthood (Chapter 2). Thus, this population can be

characterized as exhibiting partial migration. Adult growth rates were higher for migratory fish than residents in the Patuxent river estuary (Kraus and Secor 2004a). Similarly, juveniles that dispersed from natal habitats were larger at the end of their summer growth season, than those that were resident, despite beginning their juvenile period at a smaller size. This led Kraus and Secor (2004a) to speculate that post-dispersal growth or size-dependent mortality must be higher in the dispersive contingent. I hypothesized that juveniles in brackish water habitats might achieve higher growth rates due to salinity conditions, underlying energetic differences between contingents, or the interaction of these two factors.

Habitat-related differences in salinity are known to influence fish energetics by affecting scope for growth and metabolism (Fry 1971, Boef and Payan 2001, Kestemont and Baras 2001). Metabolic influences of salinity on fish are attributable to the cost of osmoregulation, changes in ion transport, and the impact of salinity stress (Morgan and Iwama 1991, Kirschner 1995). A commonly observed phenomenon is that of higher growth rates in mesohaline salinities (salinities of 5-18), which are often attributed to decreased osmoregulatory costs associated with isotonic (salinities of 9-12) environments (Morgan and Iwama 1991, Boef and Payan 2001). In addition, food intake is influenced by salinity, with consumption inhibited at both high and low salinities and maximized at optimal salinities (Kestemont and Baras 2001, Niklitschek and Secor 2005).

Higher growth rate and/or growth efficiency have been associated with mesohaline salinities for several juvenile fishes that utilize estuaries, including two congeners of white perch, the striped bass (*Morone saxatilis*, Otwell and Merriner 1975, Secor et al. 2000) and white bass (*Morone chrysops*; Heyward et al. 1995). Secor et al.

(2000) documented a significant effect of salinity on growth of young-of-the-year (YOY) striped bass, where growth rates were highest at an intermediate salinity of 7 compared to freshwater and salinity of 15. Similarly, growth of white bass was highest in intermediate salinity treatments (4 and 8), compared to freshwater and higher salinities (12, 16, and 20; Heyward et al. 1995). Thus, one alternative hypothesis is that lower routine metabolism and higher food intake in mesohaline waters could lead to increased scope for growth in juvenile white perch (Jobling 1995, Boeuf and Payan 2001). The second alternative hypothesis is that intrinsic energetic differences may exist between resident and dispersive contingents.

There has been limited evaluation of the proximate cause of life cycle diversity from an energetic perspective, with most investigations focused on salmonid populations (e.g., Forseth et al. 1999, Cutts et al. 2002, Morinville and Rasmussen 2003). In this study I investigate energy intake and allocation by resident and migratory forms of the estuarine-dependent white perch. I tested if differences in energy intake and allocation between contingents are intrinsic (i.e., related to the proximate causes of contingent behavior), or are extrinsically driven by habitat differences in salinity. I used laboratory studies to compare ecophysiological responses, including growth, consumption, and routine metabolism, between juvenile contingents and salinity levels. Additionally, I examined larval and juvenile growth rates of field-collected individuals from both contingents. I specifically tested the hypotheses: 1) contingent membership is associated with specific energetic tactics, with the dispersive contingent exhibiting higher consumption, growth, and routine metabolism relative to the resident contingent, and 2) regardless of contingent membership, fish reared in mesohaline conditions exhibit higher

consumption, growth, and lower routine metabolism relative to fish reared in freshwater conditions**.**

METHODS

Laboratory Experiment

Fish Collection and Acclimation

Juvenile white perch were collected in the Patuxent River estuary on July 25, 2005 using a 30.5 m x 1.24 m bagless beach seine with 6.4 mm mesh size set from shore. Samples of the resident contingent were collected from a tidal freshwater site (river km 72) and samples of the dispersive contingent were collected from a brackish water site (river km 25; Figure 1). Juvenile fish were transported in ambient water equipped with aeration pumps to a holding tank at the Chesapeake Biological Laboratory (Solomons, Maryland). Fish were maintained in water conditions similar to that at capture for 5 days to acclimate them to laboratory conditions. During this period well water was mixed with ambient seawater (Patuxent River estuary) to maintain the resident contingent at a salinity of 1 and the dispersive contingent at a salinity of 8. Resident fish were held at a salinity of 1 in the laboratory experiment, although they can survive in freshwater in the field, due to low survival in 100% well water in the laboratory related to very low hardness levels. Both contingents were maintained at a temperature ~25°C, a temperature representative of summer water temperatures in the Patuxent River estuary. Fish were treated with antibiotics (Kanamycin sulfate), and an antibacterial (Aquarium Pharmaceuticals Melafix) and antifungal (Aquarium Pharmaceuticals Pimafix) bath was administered for seven days to reduce infections and possible associated mortality.

Juvenile white perch were fed Chironomid larvae (San Franciso Bay Brand frozen bloodworms) *ad libitum* twice daily during the acclimation period. The feeding regime was selected based on results that indicated *ad libitum* feeding of young-of-the-year striped bass, a congener of white perch, in the laboratory was not significantly different when fish were fed 2-4 times daily (Hartman and Brandt 1995). Prior to the start of the experiment, fish underwent acclimation to experimental conditions over the course of 10 days in which case salinity was maintained at the same level or was changed at a rate of $1 \bullet d^{-1}$ until the desired salinity treatment was reached.

Experimental Design and Methods

The experimental design was a randomized factorial design with salinity treatments 1 and 8, two contingent types (resident and dispersive), four replicate tanks per treatment, and 5 fish per tank. Replicate tank was the experimental unit of study. Treatments (n = 4) included all possible crosses between contingent and salinity levels. Prior to initiation of the experiment, fish were weighed in water and transferred to experimental tanks. Fish were held in 60 liter tanks held within a recirculating heated water bath to maintain temperature at 25°C. Salinity treatments were static with a 50% water change every two days. Water was tempered and aerated in heated baths for 24 hours before water changes. Photoperiod was identical for all treatments and timed to mirror ambient daylight cycles in August (13 hours light, 11 hours dark). Fish were fed Chironomid larvae to satiation twice daily throughout the experiments. Water quality data (water temperature, salinity, dissolved oxygen, conductivity, and pH) were recorded daily for each tank using a YSI-85 probe.

Growth rate was measured in a 20-day experiment. Initial wet weight of fish was measured after fish were fasted for 24 hours (Hartman and Brandt 1995). Final wet weight of fish was measured on day 20 after a 24 hour period of fasting. Six fish from each treatment were freeze dried at the end of the experiment and a wet/dry weight (g) conversion was calculated using linear regression. Daily specific growth rate (% body wt•d^{-1}) was calculated as:

$$SGR = \frac{\ln(W_f) - \ln(W_i)}{t} \times 100$$

where W_f is final weight (g; dry weight basis) of each replicate tank and W_i is initial weight (g) and t is time (days).

Consumption was measured twice daily during the last 7 day period of the growth experiment. Wet weight of Chironomid larvae was determined prior to feeding and food not consumed 1 hour after introduction was removed from the tank, drained of excess water, and weighed wet. Dry weight of the recovered food was determined after drying in an oven (60°C) for 24 hours. A dry/wet weight conversion was calculated for Chironomid larvae using linear regression.

Daily specific feeding rate (% body wt•d^{-1}) was calculated based on 7-day experimental duration:

$$SFR = \left(\sum_{t=0}^{t=7} C_t W_t^{-1} \right) 7^{-1} \times 100$$

where C_t is the total weight of food consumed on day t (g; dry weight basis) and W_t is the total weight of fish per replicate tank on day t (g; dry weight basis). Daily weight of fish in each tank was estimated assuming exponential growth:

$$W_t = W_0 e^{Gt}$$

where W_0 is the initial weight of fish in the tank (g), t is time (days), and G is the instantaneous growth coefficient

$$G = \frac{\ln(W_f) - \ln(W_i)}{t}$$

Gross growth efficiency (%) was calculated over the same 7-day period as feeding rate as:

$$K_1 = FI^{-1} \times 100$$

where F is total fish growth (g; dry weight basis) per replicate tank and I is total consumption (g; dry weight basis) over the 7-day period.

Routine metabolism measures were conducted on fish from each treatment after growth and consumption experiments were completed. Routine metabolic rates of two juvenile white perch from each replicate of each of the four experimental treatments were estimated based on oxygen consumption rates measured over a 24 hr period in a computer-controlled, closed-circuit microrespirometer (Micro Oxymax ©, Columbus Instruments). Individual fish were placed in 1-L experimental Fernback flasks containing water from their corresponding treatment. Flasks were housed in a controlled temperature unit maintained at 25°C. The micro-respirometer measured oxygen depletion over time at 1.5 hour intervals from the flasks' head space. Fish were starved for 24 hours prior to the respiration measurement to minimize the impact of feeding metabolism on the measure of routine metabolism. In addition to experimental flasks, a flask without fish was run as a control and a flask containing a medical battery with a known oxygen depletion level was run to evaluate the accuracy of the Oxymax sensors. Oxygen consumption was reported on a per replicate tank basis as mean mg $O_2 \bullet g^{-1} \bullet d^{-1}$ (dry weight basis).

Energy budgets (Winberg 1956) were constructed for each treatment to compare relative differences in energy allocation. The energy budget included experimentally measured values for total energy consumed and energy of production/growth calculated over the same 7-day period, and energy devoted to routine metabolism. In addition, values of specific dynamic action (SDA), energy of feces and excretory products were modeled and included in the energy budget. Scope for growth of white perch was calculated for each treatment as the difference between energy consumed and the energy devoted to egestion, excretion, SDA, and routine metabolism.

Energy density was determined for Chironomid prey and six fish per treatment on a per g dry weight basis through bomb calorimetry. Fish and Chironomid larvae were freeze-dried and ground to a powder. Powdered samples were submitted for bomb calorimetry analysis to the Central Analytical Lab at the Center of Excellence for Poultry Science at the University of Arkansas. Growth, consumption, and routine metabolism measures were converted to kJ per day. Mean energy density of fish in each treatment was used to convert g fish growth to kJ. Mean energy density of Chironomid larvae (9.7 $kJ \bullet g^{-1}$, SD = 1.5) was used to convert g food consumed to kJ and an oxycalorific conversion factor (0.014 $kJ \bullet mg^{-1}$ O_2 consumed) was used to convert oxygen consumed to kJ (Schmidt-Nielsen 1990).

Energy devoted to egestion, excretion and specific dynamic action was not directly measured in this study, but estimated as the proportion of energy consumed or assimilated based on values determined for young-of-the-year striped bass (Hartman and Brandt 1995). It is important to note that use of bioenergetic values of a congener may not represent absolute values for white perch. This approach assumed that the proportion

of energy allocated to these functions did not differ between contingents or salinity treatments. Specific dynamic action and excretion were modeled as constant proportions of assimilated energy (0.172 and 0.068, respectively); egestion was a constant proportion of energy consumed (0.104; Hartman and Brandt 1995). Energy not accounted for by measured and modeled parameters relative to the total amount of energy consumed was classified as "other" and most likely represents energy attributable to the active metabolism of the fish.

Statistical Analyses

All calculations, unless otherwise specified, are reported in terms of dry weight. This measure was taken as a means of standardization due to the high water content of Chironomid larvae relative to fish and the difficulty in blotting food dry in a consistent manner for accurate measurement of wet weight. Two-way analysis of variance was employed to test the significance of the effects of contingent-membership and salinity on each response variable. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. Statistical analyses were conducted with SAS Version 8.2 (SAS Institute 1999-2001, Cary, NC); $\alpha = 0.05$ was used as a critical level of significance.

Field Data

Fish Collection

Juvenile white perch were collected in the Patuxent River estuary at monthly intervals from June-August in 2005 by beach seine (same specifications as described above). The seine survey included freshwater sites (river km 50, 53, 64 and 72) and brackish water sites (river km 16 and 45) in close proximity to the sites where

experimental fish were collected (Figure 1). Total lengths of white perch (mm) were measured at the time of collection.

Age Estimation Methods

A random subsample (n = 55) of juveniles collected on June 21 and 28, 2005 from each habitat (freshwater (n = 28) vs. brackish water (n = 27)) were selected for age estimation at a daily time step. Sagittal otoliths were extracted, rinsed, cleaned of adhering tissue, and dried for at least 24 hours. One otolith from the pair was embedded in Stuers epoxy and transversely sectioned using a low speed saw and two diamond blades separated by a 0.3 mm spacer. Otoliths were polished on both sides until the primordium (core) was clearly visible using a grinding wheel with a slurry of 25 μm aluminum oxide and a felt, metallographic cloth covered with a slurry of 0.3 μm alumina powder to achieve a final polish. Otolith microstructure was examined under a compound microscope (200–600 x magnification) and daily age estimated by one reader (3 independent reads). Daily increment formation in juvenile white perch was previously verified in a laboratory study (Kraus and Secor 2004a). Otolith radius was measured along the ventral side of the sulcal ridge from the primordium to growth increments at specific time intervals (days 20, 45, and 60).

Growth Rate Analysis

Larval growth rates were back-calculated using the biological intercept method. This method assumes a linear relationship between fish length and otolith radius and uses a biological intercept that is determined from the mean size of the fish and the otolith at the smallest larval stage (Campana 1990). Fish length was calculated as:

$$L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$$

where: L_a is length of fish at some previous age a, L_c is fish length at capture, O_a is otolith radius at age a, O_c is otolith radius at capture, L_o is fish length at biological intercept, and O_o is otolith radius at biological intercept. The biological intercept of 3.2 μm at 3 mm TL was used (Kraus and Secor 2004a). Back-calculated larval growth rates were compared between contingents across growth stanzas during early life history (0–20 days, 20–45 days, and 45–60 days) using t-tests to analyze growth rate data from 0–20 days and 45–60 days and a Kolmogorov-Smirnov test to analyze growth rate data from 20-45 days due to unequal variance and non-normality of this data.

Median length (mm) of juvenile white perch from the resident (river km 72) and dispersive contingent (river km 45) was determined on each date of collection June 28, July 7, and August 18. Mean salinity at the location of resident fish collections was 0.1 (mean temperature = 28°C) and 8.4 at the collection location of the dispersive contingent (mean temperature = 29°C). Because the trend in YOY white perch growth over this time period was a linear function of time, juvenile white perch growth rate was calculated as the mean daily linear growth rate (GR):

$$GR = \frac{L_2 - L_1}{t}$$

where L_2 is median length (mm) at the second time step, L_1 is median length at the initial time step, and t is time (days). Assuming independence of samples at each collection date, contingent differences in median length at each collection date were examined using Wilcoxon rank sum tests.

RESULTS

Laboratory Experiment

Young-of-the year white perch collected in July 2005 ranged in wet weight from 1.41 to 3.38 g at the initiation of the laboratory experiments. Total fish weight per treatment did not differ significantly at the inception of the experiment ($F_{3,12} = 0.2$, $p = 0.87$). Mean wet weight of the resident contingent fish (2.10 ± 0.45 g) was similar to dispersive contingent fish (2.09 ± 0.39 g; $t = -0.1$, d.f. = 78, $p = 0.90$). The dry/wet weight conversion for white perch was described by the linear regression equation: $y = 0.29x - 0.12$ ($r^2 = 0.99$), where y = dry weight and x = wet weight. Similarly, a dry/wet weight conversion was calculated for Chironomid larvae: *Day 1-5*: $y = 0.07x + 5E^{-05}$ ($r^2 = 0.89$); *Day 6-7*: $y = 0.12x + 0.004$ ($r^2 = 0.84$). Two regression equations were calculated due to differences in the size and dry/wet weight relationship of Chironomid larvae from two commercially purchased batches from the same manufacturer.

Fish energy density ($kJ \bullet g^{-1}$) was not significantly different between contingent ($F_{1,20} = 0.7$, $p = 0.43$) or salinity ($F_{1,20} = 0.4$, $p = 0.51$) treatments, but the interaction of the terms was significant ($F_{1,20} = 13.0$, $p < 0.01$). Mean fish energy density was highest for dispersive fish reared in freshwater and resident fish reared in brackish water (resident-freshwater = 18.4 $kJ \bullet g^{-1}$ (SD = 0.6), resident-brackish=19.8 $kJ \bullet g^{-1}$ (SD = 0.8), dispersive-freshwater = 19.9 $kJ \bullet g^{-1}$ (SD = 0.8), dispersive-brackish = 18.9 $kJ \bullet g^{-1}$ (SD = 1.1)). However, the differences between energy density of fish reared in transposed salinities compared to fish reared in their corresponding salinity were small (less than 10%).

Overall, mean specific growth rate was 60% higher for dispersive contingent treatments compared to resident contingent treatments (Figure 2a). This was reflected in the mean specific growth rate, reported in terms of dry weight (resident-freshwater = 0.30% body wt•d^{-1} (SD = 0.12), resident-brackish = 0.43% body wt•d^{-1} (SD = 0.20), dispersive-freshwater = 0.59% body wt•d^{-1} (SD = 0.11), dispersive-brackish = 0.58% body•wt·d^{-1} (SD = 0.11; Figure 2a). Two way analysis of variance indicated a significant effect of contingent ($F_{1,12} = 9.7$, $p < 0.01$) on daily specific growth rate, but no significant effect of salinity ($F_{1,12} = 0.8$, $p = 0.39$) or the interaction of the terms ($F_{1,12} = 1.0$, $p = 0.34$).

Overall, specific feeding rate was 13% higher in dispersive contingent treatments compared to resident contingent and 8% higher in brackish water treatments compared to freshwater treatments (Figure 2b). The effect of both contingent and salinity is evident in mean specific feeding rates, reported in terms of dry weight (resident-freshwater = 11.7% body wt•d^{-1} (SD = 1.1), resident-brackish = 14.5% body wt•d^{-1} (SD = 0.4), dispersive-freshwater = 14.3% body wt·d^{-1} (SD = 1.7), dispersive-brackish = 15.7% body wt·d^{-1} (SD = 0.7); Figure 2b). Two-way analysis of variance indicated a significant effect of contingent ($F_{1,12} = 10.4$, $p < 0.01$) and salinity ($F_{1,12} = 12.3$, $p < 0.01$), but no significant effect of the interaction of the two terms ($F_{1,12} = 1.2$, $p = 0.30$) on specific feeding rate.

There was no evidence of changed growth efficiency due to contingent-specific attributes or alternate salinity conditions. Gross growth efficiency ranged from 6.8 to 15.9% for the resident contingent and 7.2 to 15.2% for the dispersive contingent (Figure 2c). Gross growth efficiency was not significantly different based on contingent ($F_{1,11} =$

1.6, p = 0.23), salinity ($F_{1,11}$ = 0.2, p = 0.71), or the interaction of the two terms ($F_{1,11}$ = 0.2, p = 0.65).

Contrary to our expectations that less energy would be required for fish maintained in mesohaline conditions, mean routine metabolism was higher for both contingents reared in brackish water than in freshwater (Figure 2d). The range of daily oxygen consumption rate was 11.4 to 20.6 mg•O_2 g^{-1}•d^{-1} for resident contingent treatments and 14.0 to 21.0 mg•O_2 g^{-1}•d^{-1} for dispersive contingent treatments (Figure 2d). Two-way analysis of variance indicated a significant effect of salinity ($F_{1,12}$ = 4.9, p = 0.05), but no significant effect of contingent ($F_{1,12}$ = 0.04, p = 0.84) or the interaction of the two terms ($F_{1,12}$ = 0.04, p = 0.84) on routine metabolism. Based on studentized residual values, one outlier was identified in the dataset (resident contingent individual in freshwater: 11.4 mg O^2•g^{-1}•d^{-1}). Removal of this outlying value did not, however, significantly alter the outcome of the two-way analysis of variance and thus was not removed from the final analysis.

Two way analysis of variance indicated a significant effect of contingent ($F_{1,12}$ = 10.0, p < 0.01) on scope for growth, but no significant effect of salinity ($F_{1,12}$ = 1.6, p = 0.23) or the interaction of the terms ($F_{1,12}$ = 4.1, p = 0.07). Overall, the mean scope for growth was 29 % higher for the dispersive contingent treatments compared to the resident contingent (dispersive contingent: 3.0 kJ•d^{-1} (SD = 0.4), resident contingent: 2.3 kJ•d^{-1} (SD = 0.6); Figure 3a). Measured differences in growth between contingents indicated the total potential energy available for growth was not utilized for either contingent and the realized growth differences between contingents were greater than expected, with the dispersive contingent allocating 63 % more energy to growth (1.4 kJ•d^{-1}, SD = 0.4)

compared to the resident contingent (0.8 kJ•d^{-1}, SD = 0.3; Figure 3a). There was no significant difference in percent allocation of energy to growth or routine metabolism between contingents, salinity treatments, or the interaction of the terms ($p > 0.5$ for all terms, Figure 3b).

Field Data

Larval Growth Rate

Back-calculated larval growth rates of juvenile resident contingent fish were consistently higher across growth stanzas compared to dispersive contingent fish (Figure 4a). Significantly higher growth rates were observed in resident contingent fish from day 45 to 60 ($t = -2.38$, d.f. = 35, $p = 0.02$). Growth rates were not significantly different in earlier growth stanzas (*0-20 days*: $t = -1.96$, d.f. =53, $p = 0.06$ and *20-45 days*: KS = 0.2, d.f. = 52, $p = 0.70$). It is important to note, however, that backcalculated growth rates are calculated from fish that survived to the juvenile stage and thus may give a biased representation of larval growth.

Juvenile Growth Rate

Length of fish from both resident and dispersive contingents increased linearly over the summer collection period (Figure 4b). Juvenile growth rate was higher for dispersive contingent individuals (0.20 mm•d^{-1}) compared to resident contingent (0.16 mm•d^{-1}). Median length at time of collection was not significantly different between contingents for June (Wilcoxon rank sum test: $Z = 1.59$, $p = 0.11$) and July ($Z = -0.04$, $p = 0.97$) collection dates. Median length was significantly different in August ($Z = -2.18$, $p = 0.03$), when the dispersive contingent was 5% larger than the resident contingent (Figure 4b).

DISCUSSION

Contingent Effect

Laboratory experiments revealed a significant effect of contingent membership and, to a lesser degree, an effect of salinity on juvenile white perch energetics. The higher daily specific feeding rate of dispersive contingent members, regardless of the salinity environment, resulted in a higher energy budget and higher growth compared to resident contingent fish. Field collected data reflected the trend in growth rate observed in the laboratory with dispersive contingent fish exhibiting higher juvenile growth rates compared to resident contingent fish. Laboratory results support the idea that apparent growth differences between resident and dispersive contingents identified in the field are not solely the result of differences in size-dependent mortality. In addition, despite ample food availability within the laboratory setting, resident contingent fish did not consume as much as dispersive contingent fish, indicating food limitation is not the sole cause of lower juvenile growth rates of resident contingent individuals.

This study provides evidence that partial migration in this white perch population has an underlying bioenergetic basis. Larval and juvenile growth rates determined from juveniles collected in the wild indicated that migratory individuals exhibited accelerated growth during the juvenile stage relative to the slow growth exhibited during the larval period. In 2005 growth of dispersive fish remained slower than resident fish through a mean age of 60 days. Following dispersal, accelerated growth of dispersive fish was evident based on equal median length between contingents collected on June 28 and significantly higher median length of dispersive fish collected on August 18. Kraus and

Secor (2004a) identified similar patterns in growth rate of white perch collected in 2001. In 2001, back-calculated growth rates of dispersive individuals remained lower than resident fish through age 45 days, whereas subsequently to dispersal dispersive contingent fish were larger on average than resident fish. Slow growth of white perch during early life history appears to be linked to expression of migratory behavior during the juvenile stage. We speculate that the timing of dispersal, and thus the reversal in the growth trajectory, could shift from year to year in relation to environmental conditions.

The reversal of growth trajectory for the dispersive contingent from relatively slow growth during the larval period to relatively fast growth during the early juvenile period may indicate compensatory growth (Metcalfe and Monaghan 2001). Compensatory growth typically involves increased consumption rates, documented here for white perch, as a means of accelerating growth rate. Thus, while factors such as environmental conditions that influence larval growth rate may be the proximate cause of contingent structure, the energetic needs of the individual are likely the ultimate cause of dispersal from the natal freshwater habitat. Here, freshwater habitats do not meet the energetic needs of the dispersive contingent. Their dispersal and the subsequent accelerated growth suggests their energetic needs are met in the brackish water environment.

Habitat transition of dispersive contingent fish appears to occur in early summer when fish first transition to the juvenile stage. Temporal trends in zooplankton (copepedites, adult copepods, and *Bosmina* cladocerans) abundance in the Patuxent River estuary typically peak in early- to mid-May and subsequently decline through the summer and fall months (Herman et al. 1968, Campfield 2004, Chapter 3). Decreased abundance

of forage zooplankton in late spring, such as *Eurytemora* and *Acartia* calanoid copepods (St-Hilaire et al. 2002, Campfield 2004), may serve as the trigger that initiates migration in individuals that are growing below their optimum level. Within the Patuxent River estuary, an increasing trend in the biomass of adult copepods with salinity was documented in average streamflow years (Reaugh et al. 2007). Thus, it appears that temporal and spatial trends in productivity within the Patuxent River estuary are consistent with the idea that the brackish water habitat presents greater feeding opportunities for white perch than the freshwater habitat.

Evidence of higher consumption and growth rates for dispersive contingent members prompts the question of what favors the persistence of the resident life history tactic. Life history tradeoffs, specifically the costs of compensatory growth to the dispersive contingent, likely play a role in the maintenance of the resident contingent. Ultimately, the long-term tradeoff of accelerated growth in individuals is lower fitness, and consequently lower survival (Mangel and Stamp 2001, Munch and Conover 2003). Specific costs associated with compensatory growth in fish include adverse affects on physical processes (e.g., bone ossification rate, growth rate, age at sexual maturation, muscle lesions; Metcalfe et al. 2002) that have consequences to swimming performance, feeding ability, and defense against predators (Arendt and Wilson 2000; Billerbeck et al. 2001). In addition, decreased abundance of piscivore predators with decreasing salinity or/depth has been documented within estuaries (Miller et al. 1985, Miltner et al. 1995, Paterson and Whitfield 2000). Although trends in predator abundance have not been studied directly within the Patuxent River estuary, I speculate that this phenomenon could contribute to increased direct mortality with movement into higher salinity waters.

An alternative cause of energetic differences between contingents identified in the laboratory is underlying genetic structure. Temporal or spatial isolation of contingent spawning (assortive mating) would be required for genetic separation of contingents. Examination of variation in mitochondrial DNA of white perch from eight sub-estuaries in the Chesapeake Bay identified three genetically-distinct populations of white perch, with the Patuxent River grouped into a population that included the Upper Bay, Choptank, and Nanticoke Rivers (Mulligan and Chapman 1989). Although hypothesis testing of genetic differences between contingents was not the objective of that study, genetic dimorphism was not evident within the Patuxent River estuary. Additionally, the collection of gravid adult white perch from both contingents in the freshwater region of the Patuxent River, as determined by retrospective analysis of habitat use based on otolith chemistry (Kraus and Secor 2004a), suggests significant mixing between contingents during the springtime spawning period. These observations do not support the idea of assortive mating.

Salinity Effect

Overall, the influence of salinity on juvenile white perch physiology was less than that of contingent membership. Evidence for an effect of salinity on white perch physiology included higher consumption rate and routine metabolism of individuals reared in brackish water. There was no significant effect of salinity on scope for growth, measured growth, or gross growth efficiency. Thus, despite higher consumption rates in brackish water, this energy was not converted to somatic growth.

The higher consumption rates of white perch in brackish water compared to freshwater were expected and were similar to the response reported in other species,

including coho salmon (*Oncorynchus kisutch*, Otto 1971, Kestemont and Baras 2001). Contrary to expectations based on studies of white perch congeners, I documented higher routine metabolism of yoy white perch reared in brackish water compared to freshwater treatments. Across species, the relationship between fish metabolism and salinity appears to be inconsistent, with the impact on osmoregulatory costs (10 to >50% of the total energy budget; Kirschner 1993, Morgan and Iwama 1991, Boef and Payan 2001) associated with rearing fish in isotonic conditions compared to freshwater ranging widely. Oxygen consumption has been documented to both increase (*Onchorynchus mykiss*: ~ +14%, *Onchorhynchus tshawytscha*: ~ +10%, Morgan and Iwama 1991) and decrease (*Onchorynchus mykiss*: -16%, Rao 1968; *Mugil curema*: -31%, Fanta-Feofiloff et al. 1986; *Centropomus undecimalis*: -39%, Perez-Pinzon and Lutz 1991) with movement from freshwater to isotonic conditions. In a literature review, Morgan and Iwama (1991) identified several fish for which there was no change in metabolic rate over a wide range of salinities and classified this response as typical of euryhaline fish. Thus, the influence of increased salinity on osmoregulatory costs of the euryhaline white perch may have been minimal (i.e., too small to be detected against individual variation). I speculate that interacting effects of salinity on other processes, such as feeding rate (i.e., increased routine metabolism in fish feeding at higher rates; Madenjian and O'Connor 1999), may have contributed to the higher routine metabolism in brackish water treatments.

There were no significant interactions of contingent and salinity effects identified except with respect to fish energy density. Dispersive and resident fish had higher energy content when reared in transposed salinities rather than in their respective salinities. This

interaction defies easy explanation based upon expectations for the effects of growth and salinity on energy density. Still, relatively small differences in energy content (5-7% between contingent and 5-8% between salinity) were observed, particularly relative to the magnitude of energetic responses (e.g., growth rate, feeding rate, and routine metabolism) to the main effects of salinity and contingent, indicating that the changes in energy density among crossed treatments did not confound overall results of contingent and salinity effects on metabolism and growth trajectories.

Partial Migration

In this study I moved beyond describing patterns in fish life history to gain an understanding of the ecophysiological basis underlying the behavior. I concluded that contingent membership and the related phenomenon of partial migration in this white perch population is associated with varying energetic tactics that significantly influence the scope for growth. Similar to populations of brown trout (*Salmo trutta*; Forseth et al. 1999) and Atlantic salmon (*Salmo salar*; Metcalfe et al. 1995, Metcalf 1998; Bujold et al. 2004), growth performance of white perch during early life history appears to determine contingent behavior. Identification of growth differences between resident and migratory individuals has improved our understanding of the mechanisms governing partial migration and the potential consequences of partial migration to population productivity. The concept of partial migration has been adopted from the avian literature to describe diversity in life history tactics in salmonid populations (Jonsson and Jonsson 1993), but may be widely applicable to fish populations in general. I hypothesize that, similar to avian populations, partial migration may be a fundamental behavior pattern in fish

populations and associated theory could form the basis of a comprehensive theory of fish migration.

FIGURES

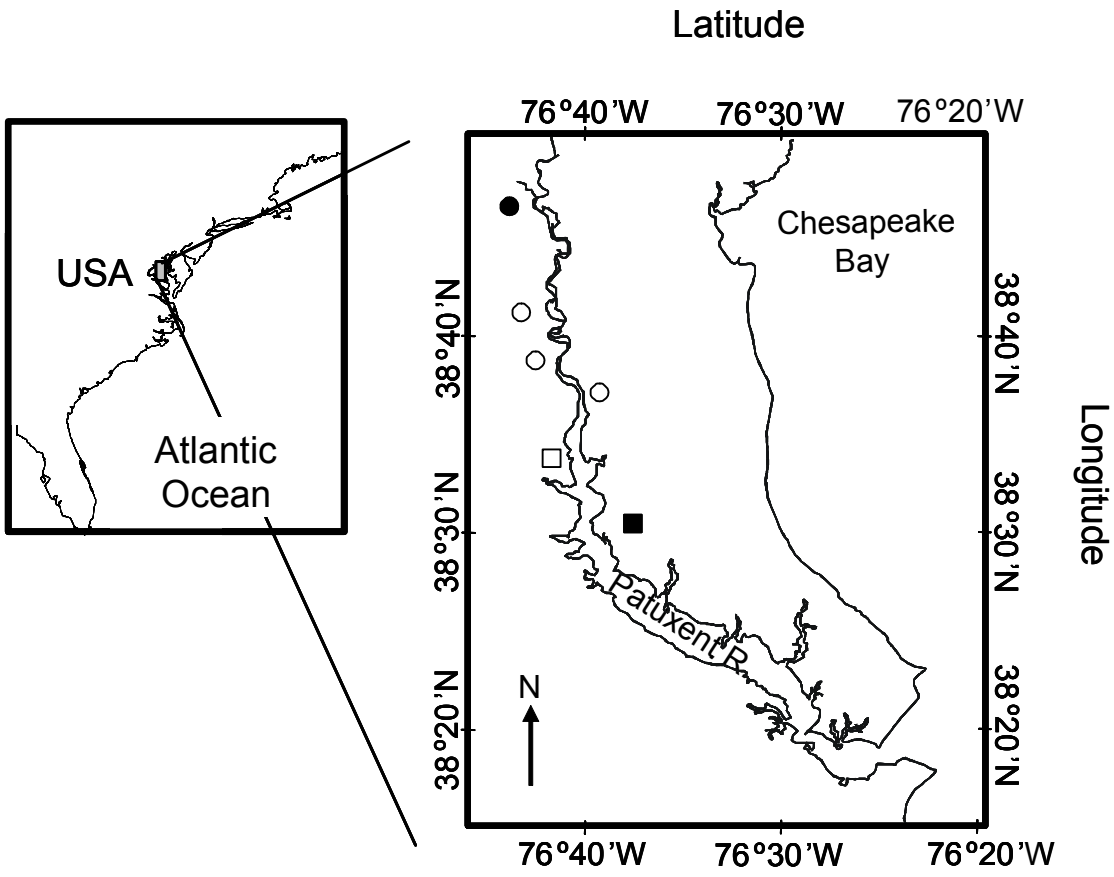


Figure 1. Map of the Patuxent River estuary, a sub-estuary of the Chesapeake Bay (Maryland; Kraus and Secor 2004a). The map illustrates locations of collection of resident (river km 72; black circle) and dispersive contingent (river km 25; black square) white perch used in laboratory study and locations of collection of resident (river km 50, 53, 64, and 72; open and black circles) and dispersive contingent fish (river km 16 and 45; open squares) used in field growth rate analysis.

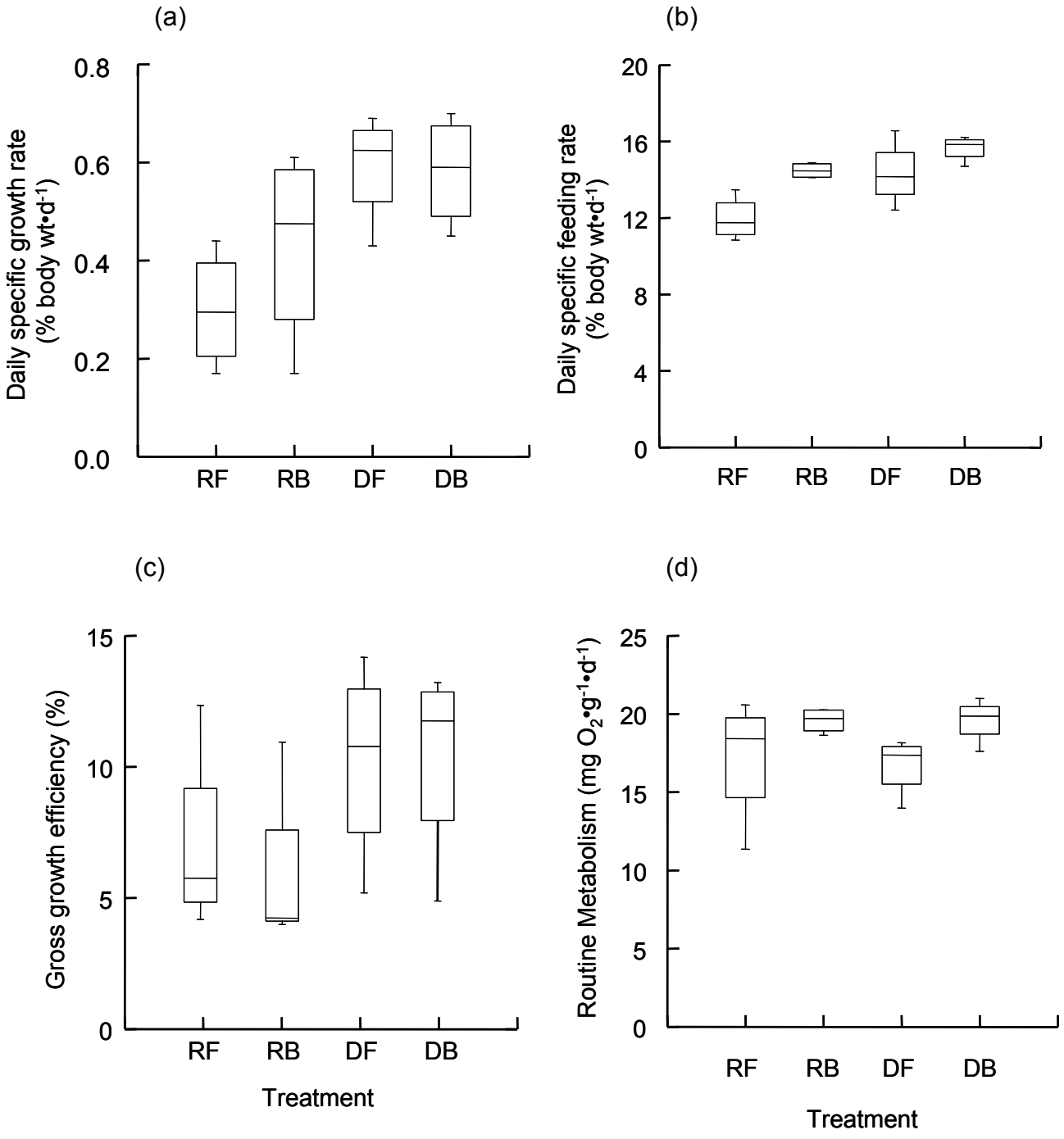


Figure 2. (a) Daily specific growth rate (% body wt•d^{-1}), (b) daily specific feeding rate (% body wt•d^{-1}), (c) gross growth efficiency (%), and (d) routine metabolism (mg O_2•g^{-1}•d^{-1}) of juvenile white perch across experimental treatments. Treatments include resident fish reared in freshwater (RF), resident fish reared in brackish water (RB), dispersive fish reared in freshwater (DF), and dispersive fish reared in brackish water (DB).

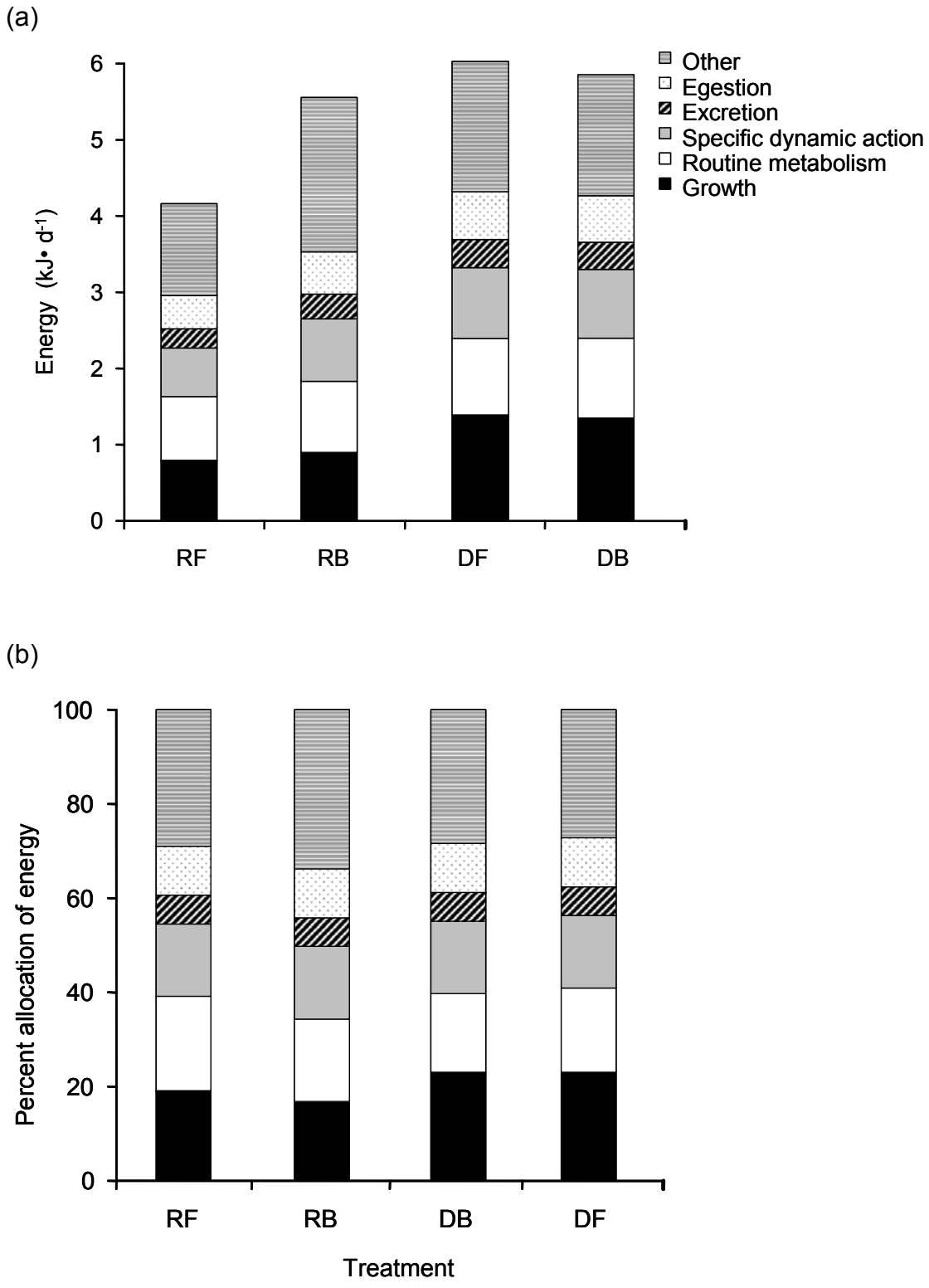


Figure 3. (a) Energy budget (kJ•d^{-1}) and (b) percent allocation of energy (%) for resident fish reared in freshwater (RF), resident fish reared in brackish water (RB), dispersive fish reared in freshwater (DF), and dispersive fish reared in brackish water (DB).

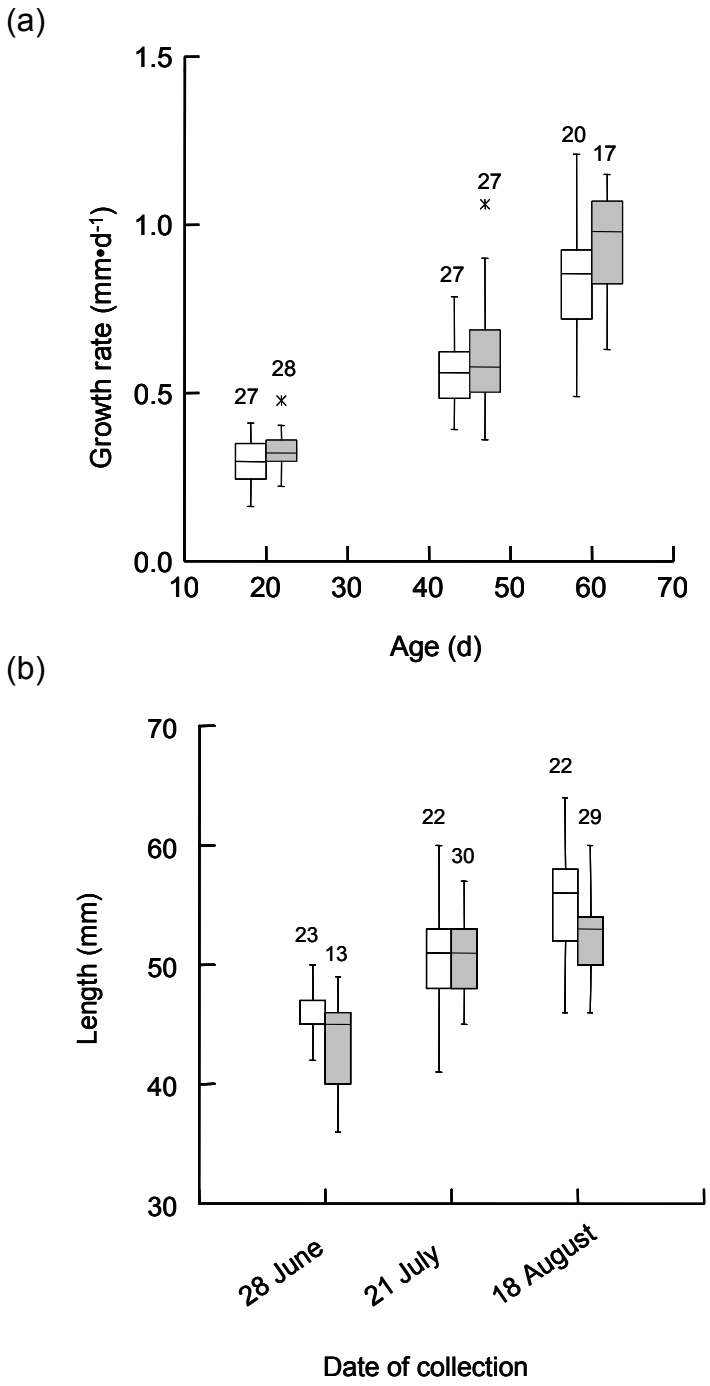


Figure 4. (a) Back-calculated larval growth rates (mm•d^{-1}) of white perch from dispersive (open bars) and resident contingents (grey bars) across growth stanzas during early life history (0-20 days, 20-45 days, and 45-60 days. (b) Lengths (mm) of juvenile white perch from dispersive (open bars) and resident contingents (grey bars) during the summer months (June, July, and August) of 2005 in the Patuxent River estuary. Numbers above each box indicate sample size**.** The center vertical line marks the median, the length of each box shows the range within which the central 50% of the values fall, with the box edges at the first and third quartiles**.** Asterisks are datapoints outside this range.

Chapter 5: STABLE ISOTOPE ($\delta^{13}C$ and $\delta^{18}O$) AND SR/CA COMPOSITION OF OTOLITHS AS PROXIES FOR ENVIRONMENTAL SALINITY EXPERIENCED BY AN ESTUARINE FISH

ABSTRACT

The ability to identify past patterns of salinity habitat use in coastal fishes is viewed as a critical development in evaluating nursery habitats and their role in population dynamics. The utility of otolith tracers ($\delta^{13}C$, $\delta^{18}O$, and Sr/Ca) as proxies for environmental salinity was tested for the estuarine-dependent juvenile white perch *Morone americana*. Analysis of water samples revealed a positive relationship between the salinity gradient and $\delta^{18}O_{water}$, $\delta^{13}C_{DIC,}$ and Sr/Ca_{water} values in the Patuxent River estuary. Similarly, analysis of otolith material from young-of-the-year white perch (2001, 2004, 2005) revealed a positive relationship between salinity and otolith $\delta^{13}C$, $\delta^{18}O$, and Sr/Ca values. In assigning fish to their known salinity habitat, $\delta^{18}O$ and Sr/Ca were moderately accurate tracers (68% (± 22%) and 75% (± 23%) correct classification, respectively), and $\delta^{13}C$ provided near complete discrimination between habitats (98% (± 7%) correct classification). Further, $\delta^{13}C$ exhibited the lowest inter-annual variability and the largest range of response across salinity habitats. Thus, across estuaries, it is expected that resolution and reliability of salinity histories of juvenile white perch will be improved through the application of stable isotopes as tracers of salinity history.

INTRODUCTION

Identification of nursery and lifetime habitat use is critical to understanding fish population dynamics as the spatial distribution of a population influences its growth, survival, reproduction, and recruitment (Secor 1999, Beck et al. 2001). Habitat use also affects a population's response to environmental changes and fishing pressure. For example, spatial partitioning of fish in different habitats can distribute the mortality risk within a population and ultimately promote long-term persistence (Secor 2007). Otolith chemistry is a useful approach for classifying spatial behaviors of fishes at the population-level, sub-population-level, and finer spatial scales (Campana 1999, Thresher 1999, Campana and Thorrold 2001).

Within estuarine environments, the salinity gradient can be used as a proxy for habitat use and several otolith chemistry tracers have been identified as proxies for salinity. Sr/Ca ratios have proved useful tracers of salinity history of many estuarine species (Secor and Rooker 2000). However the variable nature of Sr/Ca values in freshwater sources and the uniform Sr/Ca value of oceanic sources has raised concern about the general reliability of this tracer (Kraus and Secor 2004b). Stable isotope ratios ($\delta^{18}O$ and $\delta^{13}C$) provide an alternative tracer of salinity history for species that use estuarine habitats. A number of studies indicate that $\delta^{18}O$ and $\delta^{13}C$ can serve as proxies for salinity (e.g. Lloyd 1964, Spiker 1980, Ingram et al. 1996, Fry 2002), but thus far the temporal and spatial variability of otolith stable isotope signatures has not been evaluated across the salinity gradient of an estuary.

Otolith stable isotope ratios are a function of water chemistry and isotopic fractionation that occurs during the transport of dissolved substances from water to the

region of precipitation of the otolith (Campana 1999). Water chemistry is regulated by physical, chemical, and biological processes resulting in freshwater having a unique $\delta^{18}O$ and $\delta^{13}C$ signature from that of seawater. Estuaries that exhibit conservative mixing of two dominant end-members exhibit a gradient in water chemistry that is correlated with the salinity gradient (Fry 2002).

The overall goal of this study was to evaluate Sr/Ca, $\delta^{18}O$, and $\delta^{13}C$ as tracers of the environmental salinity experienced by an estuarine fish. The objectives were to: (1) evaluate the relationship between stable isotope values ($\delta^{18}O$ and $\delta^{13}C$) and the salinity gradient in the Patuxent River estuary as measured in water and otolith samples, (2) compare the accuracy of salinity habitat classifications based on $\delta^{18}O_{otolith}$, $\delta^{13}C_{otolith}$, and $Sr/Ca_{otolith}$, and (3) compare the temporal stability of stable isotope tracers of salinity habitats based on white perch (*Morone americana*) collected over three years.

METHODS

Sample Collection

Species and Study Area

The white perch is semi-anadromous and one of the most abundant fish in the Chesapeake Bay (Jung and Houde 2003). As young-of-the-year (YOY) juveniles, white perch use inshore estuarine areas as nursery grounds (Wang and Kernehan 1979, Setzler-Hamilton 1991), typically inhabiting waters ranging from freshwater to salinities of 13 (Stanley and Danie 1983).

The Patuxent River is a shallow, partially mixed estuary with distinct zones of brackish and tidal freshwater (Figure 1). The water in the river is a mixture of freshwater

derived from precipitation and watershed runoff and saltwater from the main stem of the Chesapeake Bay. The salinity gradient of the Patuxent River ranges from freshwater (0) at the river head to mesohaline (mean salinity range of 10 to 16) conditions at the mouth (Ritchie and Genys 1975). The salinity gradient across the estuary is relatively stable and predictable for a given season (Ritchie and Genys 1975), with the largest deviations in salinity during spring driven by snow melt and major precipitation events.

Environmental Data Sources

Mean habitat-specific salinity and temperature (°C) were calculated based on monthly water quality data collected by Maryland Department of Natural Resources (MDDNR) in 2001 and by MDDNR and this study's sampling efforts in 2004 and 2005. Water quality data (water temperature (°C), salinity, dissolved oxygen (mg l^{-1}), and conductivity (μS)) were collected using a handheld YSI Model 85 Instrument. Stream flow data (ft^3 sec^{-1}) collected by United States Geological Survey (USGS) at the Bowie, MD site (USGS code: 01594440) were used to characterize the monthly mean fluctuations in river discharge for the Patuxent River estuary in 2001, 2004, and 2005. Using an estimated median freshwater residence time of 68 days (Hagy et al. 2000), stream flow data was averaged over the time period sampled within the otolith plus 68 days prior, encompassing a period from March 25 to September 30.

Water Sample Collection

Water samples were collected at sites along the Patuxent River estuary from May to September 2005. Grab samples of water were taken from littoral areas in freshwater, oligohaline, and mesohaline habitats in the vicinity of fish collection sites. Water samples were filtered through a 0.45 μm glass fiber filter using a hand vacuum pump.

Vacuum filtration has the potential to subtly alter isotopic signatures in low carbonate systems. However, because DIC is assumed to be predominantly present as HCO_3^- in the Patuxent River (based on pH conditions of 7.0-8.0; MDDNR) filtration was not deemed to significantly affect the isotopic values of water samples. Samples were transferred to ICHEM borosilicate glass vials (20 ml), fixed with $HgCl_2$ on site, and kept chilled on ice. Samples were refrigerated (~4°C) until the time of analysis.

Fish Collection

Juvenile white perch were collected in August and September of 2001, 2004, and 2005 using a 1.2 m x 30.5 m beach seine deployed at sites along the salinity gradient. Collections occurred in freshwater (FW = salinity 0-1), oligohaline (OH = salinity >1-3), and mesohaline habitats (MH = salinity 6-8; Figure 1). All white perch were counted, measured, and preserved in ethanol or frozen at the time of capture. Sagittal otoliths from juvenile white perch were extracted, rinsed, cleaned of adhering tissue, and dried for at least 24 hours.

Water and Otolith Sample Analysis

Water samples were submitted to the University of Arizona Isotope Geochemistry Laboratory (http://www.geo.arizona.edu/research/iso_geoch_lab.htm) for stable isotope analysis. Water samples were equilibrated with CO_2 gas at approximately 15°C in an automated equilibration device and analyzed for $\delta^{18}O$ using a gas-source isotope ratio mass spectrometer (Finnigan Delta S). To measure the isotopic signature of DIC, CO_2 was generated from water samples via acidification and $\delta^{13}C$ was measured on a continuous-flow gas-ratio mass spectrometer (ThermoQuest Finnigan Delta PlusXL). Values were reported as per mil (‰) relative to a standard ($\delta^{13}C_{DIC}$: Vienna Pee Dee

Belemnite (VPDB) using international standards NBS-19 and NBS-18, and $\delta^{18}O_{water}$: Vienna Standard Mean Ocean Water (VSMOW)). Analytical precision of the mass spectrometers for $\delta^{18}O_{water}$ and $\delta^{13}C_{DIC}$ was 0.08‰ and 0.3‰ respectively, based on the standard deviation of repeated measures of the standard.

Otoliths from individuals collected in FW, OH, and MH habitats in 2001 were analyzed for $\delta^{18}O_{otolith}$, $\delta^{13}C_{otolith}$, and $Sr/Ca_{otolith}$ and otoliths from individuals collected in 2004 and 2005 were analyzed for $\delta^{18}O_{otolith}$ and $\delta^{13}C_{otolith}$ (Table 2). The $Sr/Ca_{otolith}$ data was originally presented in Kraus and Secor (2004a), which was an analysis of divergent patterns of juvenile habitat use. Here, we used a sub-sample (N=20) of that data that included 6-7 otoliths collected from three salinity habitats to directly compare Sr/Ca and stable isotope tracers in 2001. In the Kraus and Secor (2004a) analysis, one otolith from each individual was transversely sectioned and analyzed for $Sr/Ca_{otolith}$ by electron microprobe wavelength dispersive X-ray spectroscopy at a series of points in a transect across the otolith section. In the present analysis, the other otolith of the pair from 2001 collected fish and one randomly selected otolith from each of the 2004 and 2005 collected fish were analyzed for $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$. Whole otoliths were adhered to glass microscope slides with acrylic resin and polished to a flat surface using 800 and 600 mm grit polishing paper. YOY white perch in the Patuxent River transition to the juvenile period and persist in either freshwater or disperse to brackish water habitats from approximately 45 days (SD = 7 days, Kraus and Secor 2004a) onward. Otolith length at time of transition (45 days + 2 SD) was calculated on a habitat-specific basis due to observed differences in fish growth between salinity habitats and was used as a guideline in sampling otoliths. The portion of the otolith > 45 days was excised using a New

Wave® micro-milling machine with a fine-tipped mill (6 μm). The resultant sample consisted of 2 solid peripheral pieces of calcium carbonate removed from the rostrum and post-rostrum regions of the otolith.

Otolith samples were submitted to the University of Arizona Isotope Geochemistry Laboratory for analysis. Otolith carbonate was dissolved with 100% phosphoric acid to generate carbon dioxide (CO_2). The resultant CO_2 was analyzed for $\delta^{18}O_{otolith}$ and $\delta^{13}C_{otolith}$ by continuous-flow gas-ratio mass spectrometer (ThermoQuest Finnigan Delta PlusXL) and reported as per mil relative to a standard (Vienna Pee Dee Belemnite (VPDB) using international standards NBS-19 and NBS-18). Analytical precision of the mass spectrometer for $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ was 0.04‰ and 0.1‰ respectively and based on the standard deviation of repeated measures of the standard.

Statistical Analysis

Univariate analysis of variance (ANOVA) tested the null hypothesis of no significant difference in $\delta^{13}C_{DIC}$, $\delta^{18}O_{water}$, and $Sr/Ca_{otolith}$ across salinity habitats (FW, OH, and MH). Two way ANOVA tested the null hypothesis of no significant difference in $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ across salinity habitats (FW, OH, and MH) and within habitat between years (2001, 2004, and 2005). Tukey's test identified significant between-habitat differences. The accuracy with which individuals were classified to salinity habitat was evaluated on a yearly basis using linear discriminant function analysis with jackknife resampling (a 'leave-one-out' cross-validation procedure) to determine the accuracy of using all three tracers ($Sr/Ca_{otolith}$, $\delta^{13}C_{otolith}$, and $\delta^{18}O_{otolith}$), and combinations there of, as predictors. Diagnostics were employed to test for normality, homogeneity of variance and covariance, and influential observations for $\delta^{13}C_{DIC}$, $\delta^{18}O_{water}$, $\delta^{13}C_{otolith}$,

$\delta^{18}O_{otolith}$, and $Sr/Ca_{otolith}$. One otolith value from a fish collected in the mesohaline habitat was identified as an outlier with respect to both $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ values (-12.42 ‰ and -6.94 ‰ respectively); this case was removed from all statistical analyses of $\delta^{13}C$ and $\delta^{18}O$ values. Statistical analyses were performed with Systat software version 8.0 (SPSS 1998) or SAS Version 8.2 (SAS Institute 1999); $p = 0.05$ was used as a critical level of significance.

RESULTS

Young-of-the year white perch collected in 2001, 2004, and 2005 ranged in length from 49 to 88 mm TL. Mean fish length (TL) increased with increasing salinity (FW = 61.1 mm (SD = 9.0), OH = 66.6 mm (SD = 6.1), and MH = 72.5 mm (SD = 10.0)). Significant differences in fish length (and consequently otolith weight) were identified between sites (ANOVA, $F_{2,17} = 10.69$, $p < 0.01$) and years. Still, because all three tracers showed no significant correlation with fish length over the three years of collection (ANCOVA, $p \geq 0.05$ for all tracers in all years), there was no need to detrend the tracer data to remove the effect of fish length in these analyses (Campana et al. 2000).

Over the June-September period corresponding to the timing of juvenile otolith growth sampled, mean salinity differed across sites, but within each site only varied slightly across years (Table 1). Temperature changed over the period of otolith precipitation, typically increasing from June to July, and subsequently decreasing into September. Temperature change was similar across sites, with a maximum difference of 1.6ºC between sites on any particular collection date. Stream flow data was not site specific; however monthly trends across years showed the highest streamflow occurring

in March or April, and flow rate declining into September. Overall monthly mean stream flow was lowest in 2001 compared to 2004 and 2005 (Table 1).

Strontium/Calcium Analyses

A positive and significant relationship has been previously reported between Sr/Ca_{water} values and the salinity gradient in the Patuxent River estuary (Kraus and Secor 2004b). Mean $Sr/Ca_{otolith}$ values in 2001 collected fish exhibited an increasing trend for fish inhabiting increasingly saline environments (Table 2, Figure 2). Mean $Sr/Ca_{otolith}$ values were significantly different across salinity habitats ($F_{2,17}$= 170.51, $p < 0.001$). Significant between habitat differences were identified between FW and OH and FW and MH ($p < 0.001$), but no significant difference was identified between MH and OH sites ($p = 0.05$).

Stable Carbon Isotope Analyses

Measures of $\delta^{13}C_{DIC}$ across the salinity gradient of the Patuxent River estuary over the period from May 31 to September 20, 2005 exhibited a positive and significant relationship (Figure 3a). The overall mixing curve of aqueous $\delta^{13}C_{DIC}$ across the salinity gradient for all dates sampled was estimated with a power curve ($y = -9.74 + 2.59x^{0.46}$; $r^2 = 0.97$). Mean $\delta^{13}C_{DIC}$ values aggregated over time were significantly different across salinity habitats ($F_{2,23}$= 17.35, $p < 0.001$). Significant differences were detected between all salinity habitats based on $\delta^{13}C_{DIC}$ values ($p < 0.001$ for all pairwise comparisons).

Across all years, $\delta^{13}C_{otolith}$ values were positively correlated with salinity (Pearson Correlation Coefficient: $r = 0.95$, $n = 48$; Table 2; Figure 4). Two way ANOVA indicated fish $\delta^{13}C_{otolith}$ values were significantly different across salinity habitats ($F_{2,39}$ =

239.12, $p < 0.001$) and years ($F_{2,39}= 9.04$, $p < 0.001$), but there was no significant difference within habitat across years ($F_{4,39}= 0.91$, $p = 0.47$). Significant differences were found between all sites for all years based on $\delta^{13}C_{otolith}$ values ($p < 0.01$ for all pairwise comparisons).

Stable Oxygen Isotope Analyses

A positive and significant relationship was identified between $\delta^{18}O_{water}$ values and the salinity gradient (Figure 3b). The mixing curve for aqueous $\delta^{18}O_{water}$ was estimated with a linear fit ($y = -6.45 + 0.18x$; $r^2 = 0.82$). Mean $\delta^{18}O_{water}$ values aggregated over time were significantly different across salinity habitat ($F_{2,23}= 24.62$, $p <0.001$). Significant differences were detected between FW and OH ($p = 0.01$) and FW and MH ($p < 0.001$) sites, but no significant differences were observed between OH and MH sites ($p = 0.10$).

Mean $\delta^{18}O_{otolith}$ values exhibited an increasing trend for fish inhabiting FW, OH, and MH environments (Table 2, Figure 5). Across years sampled, $\delta^{18}O_{otolith}$ values were positively correlated with salinity (Pearson Correlation Coefficient: $r = 0.49$, $n = 48$). Two way ANOVA indicated significant differences in $\delta^{18}O_{otolith}$ of fish collected across salinity habitats ($F_{2,39} = 21.05$ $p < 0.001$) and years ($F_{2,39}= 49.22$, $p < 0.001$), but no difference within habitats across years ($F_{4,39}= 2.05$, $p = 0.11$). Significant differences were identified between FW and MH, and MH and OH habitats (both at $p < 0.01$), but there was no significant difference between FW and OH habitats ($p = 0.69$).

The overall trend in $\delta^{18}O_{otolith}$ values across habitats indicated 2005 values were lower than 2001 and 2004 values (Figure 5). This trend was driven by the two lowest

$\delta^{18}O_{otolith}$ values for the freshwater and oligohaline habitats. Across the three years sampled, fish were primarily collected in September, however, due to a low sample size of fish from freshwater and oligohaline regions during fall 2005, I supplemented September seine samples with two individuals captured in August from each of these salinity habitats.

Multivariate Analyses

A strong correlation was detected between $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ from fish collected in 2001, 2004, and 2005 (Figure 6). Across years I observed similar groupings based on $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ values by salinity habitat.

Using all three tracers, discriminant analysis revealed 100% correct classification of individuals collected in 2001 to known FW, OH, and MH habitat (Table 3). Analysis of various combinations of individual tracers revealed that $\delta^{13}C_{otolith}$ alone provided better discrimination of salinity (100%), than either $Sr/Ca_{otolith}$ (75%), or $\delta^{18}O_{otolith}$ (79%). In 2004, classification was improved using $\delta^{13}C_{otolith}$ alone (100%), compared to $\delta^{13}C_{otolith}$ and $\delta^{18}O_{otolith}$ (92%; Table 3). Similarly, classification of individuals collected in 2005 was improved using $\delta^{13}C_{otolith}$ alone (93%), compared to using both $\delta^{13}C$ and $\delta^{18}O$ (87%) as predictors. Pillia's trace test indicated all combinations of tracers contributed significantly in all years ($p < 0.006$), with the exception of $\delta^{18}O$ as a single predictor in 2005 ($p = 0.11$).

DISCUSSION

Utility of Otolith Tracers

Quantification of the spatial and temporal variation of otolith tracers is essential to establishing the reliability of these tools for reconstruction of the environmental history of fishes. Both $\delta^{18}O_{otolith}$ and $\delta^{13}C_{otolith}$ showed significant spatial variation across the estuarine salinity gradient and limited temporal variation. Thus, otolith stable isotope chemistry proved to be an effective tracer of salinity habitat use by juvenile white perch within the Patuxent River estuary across years. In particular, $\delta^{13}C_{otolith}$ showed the highest degree of accuracy in classifying individuals to habitat and the lowest interannual variability in the isotopic signatures of each salinity habitat. The efficacy of stable isotopes as tracers of salinity in the estuarine environment indicates distinct isotopic signatures of freshwater and saltwater end-members and relative stability (within season and among years) in the mixing ratios of these two water masses within the estuary. Despite expected deviations due to natural processes (e.g. plankton productivity, benthic respiration, atmospheric exchange, and evaporation-precipitation) and anthropogenic input (e.g. waste water discharge), the mixing of end-members appears to dominate and approach conservative mixing in this system (Spiker 1980, Taft et al. 1980, Criss 1999). Because end-members will differ across estuaries there may be some estuaries where riverine $\delta^{13}C_{DIC}$ more closely resembles oceanic $\delta^{13}C_{DIC}$, and in these cases, $\delta^{13}C$ would not be as effective a tracer. Initial analysis of end-members should provide insight as to whether this tracer will prove useful in a local estuarine system.

Otolith Sr/Ca also proved useful in classifying habitat use of juvenile white perch in the Patuxent River estuary due to the distinct Sr/Ca signature of the freshwater end-

member and the stability of the estuarine salinity gradient (Kraus and Secor 2004b). However, recent studies have shown that the relationship between Sr concentration and salinity is not consistent due to variation in Sr/Ca values (ranging from <1 to >19 mmol mol^{-1}) in freshwater end-members that can approach and exceed the relatively uniform value of seawater (Kraus and Secor 2004b). In this study, the freshwater Sr/Ca end-member value in the Patuxent River estuary was in the low range, typical of most freshwater values (Kraus and Secor 2004b). Still, the use of otolith Sr/Ca values resulted in low resolution discrimination across salinity habitats and lack of detectable difference between oligohaline and mesohaline habitats. This was due to a seawater end-member that dominates even at very low salinities (salinities < 3). Because the relationship between Sr/Ca and salinity is curvilinear and the majority of variation in this otolith tracer occurred only at low salinities in the Patuxent River estuary, this tracer is of limited utility in distinguishing habitat use in higher salinity habitats.

Variability in Water Chemistry

Water samples provided periodic snapshots of the isotopic composition across the salinity gradient of the Patuxent River estuary and thus were more variable than the time-integrated stable isotope values (~ 3 months) measured in fish otoliths. The physical, chemical, and biological processes that define $\delta^{18}O_{water}$ and $\delta^{13}C_{DIC}$ in freshwater and seawater sources differ (Degens 1969, Mook and Tan 1991, Criss 1999). I identified an increasing trend over time in $\delta^{18}O_{water}$ values from May to September 2005, whereas a temporal trend in $\delta^{13}C_{DIC}$ values was not evident (Figure 3a,b). The seasonal trend in enrichment of water in the heavier isotope of oxygen was most likely attributable to increased evaporation as waters warmed over the summer months. Similarly, Fairbanks

(1982) reported a 2‰ enrichment in $\delta^{18}O_{water}$ during the summer months in 12 east coast rivers. The small scale variability in $\delta^{13}C_{DIC}$ values likely reflects changes in precipitation and freshwater flow (terrestrial input) in the river.

Variability in Otolith Chemistry

Interannual variability within habitat was greater for white perch $\delta^{18}O_{otolith}$ values compared to $\delta^{13}C_{otolith}$ values. The overall lower trend in $\delta^{18}O_{otolith}$ values in 2005 collected fish was attributed to the influence of four fish collected one month earlier (August) than the remaining fish analyzed in this study. The more negative $\delta^{18}O_{otolith}$ values in August-collected fish follows the observed increasing seasonal trend in $\delta^{18}O_{water}$ values with the highest values encountered in September. Furthermore, high 2001 $\delta^{18}O_{otolith}$ values may be related to changes in the isotopic composition of the seawater end-member. Because the mouth of the Patuxent River estuary is located north of the entrance of the Chesapeake Bay and south of the Susquehanna River, which contributes ~60% of the freshwater flow to the Bay (MDDNR), the freshwater flow out of this tributary affects the signature of the seawater end-member of the Patuxent River estuary. Freshwater flow from the Susquehanna River was below the long-term (1985-2000) average for 2001 (MDDNR), these drought conditions resulted in salinities that exceeded long-term averages and a seawater end-member $\delta^{18}O_{water}$ signature that was elevated compared to 2004 and 2005.

Estimating Isotopic Disequilibria

In addition to understanding the underlying water chemistry, it is important to quantify the isotopic disequilibria between water and otoliths to accurately interpret

$\delta^{18}O_{otolith}$ and $\delta^{13}C_{otolith}$ values (Thorrold et al. 1997). Mean habitat-specific differences between stable isotope values in the otolith and water of the estuary allowed for a coarse estimate of isotopic fractionation, recognizing that a laboratory-derived estimate would be more rigorous. Field data indicated that white perch $\delta^{13}C_{otolith}$ values were deposited in disequilibrium with $\delta^{13}C_{DIC}$ values, whereas $\delta^{18}O$ values in otoliths were deposited at near equilibrium with $\delta^{18}O_{water}$ values (Figure 4 and 5). Otoliths were depleted in $\delta^{13}C$ by 4.65‰ (SD = 0.84) and $\delta^{18}O$ by 1.16‰ (SD = 0.46) relative to water values. The magnitude of isotopic depletion was in the range of reported values for fish otoliths in the literature ($\delta^{13}C$: -6.29, SD = 2.97 and $\delta^{18}O$: -0.87, SD = 1.01; Campana 1999).

The slight depletion of $\delta^{18}O_{otolith}$ values compared to $\delta^{18}O_{water}$ values may be attributable to temperature-dependent kinetic fractionation during otolith precipitation (Thorrold et al 1997, Elsdon and Gillanders 2002, Høie et al. 2004). Due to the simultaneous trend of increasing temperature with increasing salinity across the Patuxent River estuary (Table 1), the effect of temperature (depletion of $\delta^{18}O$ with increasing temperature) may have also counteracted the expected influence of salinity (enrichment in $\delta^{18}O$ with increasing salinity) on $\delta^{18}O_{otolith}$ values. Although the magnitude of the influence of temperature (-0.2‰/ºC increase; Høie et al. 2004) and salinity (+0.23‰/1 salinity increase) on the $\delta^{18}O_{otolith}$ signature are similar, their effects are opposite. Due to the scale at which each factor changed across the estuary during a single year, the influence of temperature is likely minimal (maximum temperature difference of 1.3ºC between FW and MH habitats) compared to the expected dominant effect of salinity (maximum salinity difference of 7.1 between FW and MH habitats).

Disequilibria between $\delta^{13}C_{otolith}$ and $\delta^{13}C_{DIC}$ values are primarily attributed to the incorporation of metabolically derived isotopes into the otolith (Kalish 1991a,b, Schwarcz et al 1998, Thorrold et al. 1997). In the case of carbon, the majority input to the otolith originates as DIC (65 to 80%) with a minority derived from metabolic origin (20-35%; Kalish 1991a, Weidman and Millner 2000, Høie et al. 2003). Thus, a small contribution of an isotopically depleted metabolic source to the otolith is expected to result in $\delta^{13}C_{otolith}$ values that are more negative than $\delta^{13}C_{DIC}$ (McConnaughey 1989, Kalish 1991a,b, Thorrold et al. 1997). Direct measure of the isotopic composition of white perch diet was not made, however, $\delta^{13}C$ values for white perch tissue are reported to range from -20 to -28‰ (Delaware Bay; Litvin and Weinstein 2003; Hackensack River, New Jersey; Weis 2005). Mass balance calculations support the idea that the average fractionation of white perch $\delta^{13}C_{otolith}$ could be produced by the contribution of 30% carbon from a metabolic source with a $\delta^{13}C$ value of -25.5‰ (average tissue value (-24‰) – trophic enrichment factor (1.5 ‰) = -25.5‰) or by a smaller percent contribution of a more negative metabolic source.

Differences in the metabolism of fish or the diet/food web between salinity habitats could potentially influence otolith stable isotope values (Kalish 1991a,b, Thorrold et al. 1997, Høie et al. 2003). Recent laboratory experiments have documented increased growth and feeding rates of white perch that disperse into brackish water habitats (Chapter 4). Increased metabolism has been negatively correlated with $\delta^{13}C_{otolith}$ values (Kalish 1991b, Schartz et al. 1998, Høie et al. 2003) and thus would have an effect opposite to salinity. The relationship between fish metabolism and $\delta^{13}C_{oto}$, however, remains equivocal (Thorrold et al 1997). Because $\delta^{13}C_{otolith}$ values mirror the increasing

trend of $\delta^{13}C_{DIC}$ across the salinity gradient, I hypothesize that differences between habitats are driven by the salinity gradient rather than potential metabolic differences between fish in each habitat. Additionally, differences in the isotopic signature of organic matter at the base of the food web (% autocthonous vs. % allocthonous material) between freshwater and brackish water environments, if incorporated in the diet of white perch, could account for variability in the isotopic signature of the otolith.

Conclusions

Estuaries play an important role in early life history of many commercially important coastal fishes. Across estuaries and year classes, I expect the resolution of salinity histories of juvenile white perch will be improved through the application of stable isotopes, particularly $\delta^{13}C$, as tracers. Empirical studies examining the underlying water chemistry, uptake pathways, and the fractionation of stable isotope signatures in otoliths (Kalish 1991a,b, Thorrold et al 1997, Høie et al 2004, this study) and estuarine isotopic mixing models (Fry 2002) support the application of stable isotopes as tracers of salinity habitat. As I further develop our ability to accurately reconstruct past habitat use on a finer-scale using otolith chemistry, these tracers will enable evaluation of the importance of the spatial distribution of juveniles within estuaries with respect to population-level dynamics and conservation objectives.

TABLES

Table 1. Mean environmental variables for the freshwater (FW), oligohaline (OH), and mesohaline (MH) habitats in the Patuxent River estuary in 2001, 2004, and 2005. River km is measured as the distance from river mouth. Mean salinity and temperature are averages for the June-September period for each year and mean monthly streamflow is average over March 25-Septemer 30 based on estimated residence time of freshwater in the estuary.

			Salinity		Temperature (°C)		Monthly stream flow (ft^3/sec)	
Year	River Km	Habitat	Mean	SD	Mean	SD	Mean	SD
2001	64	FW	0.2	0.1	26	1	390	217
	53	OH	2.2	1.9	27	1		
	41	MH	7.3	3.2	27	1		
2004	64	FW	0.2	0.2	25	2	402	137
	53	OH	1.7	1.7	26	2		
	45	MH	6.5	1.7	27	2		
2005	64	FW	0.5	0.8	29	2	512	400
	53	OH	2.4	2.9	29	2		
	45	MH	7.0	3.5	29	1		

Table 2. Mean otolith stable isotope ($\delta^{13}C_{otolith}$ & $\delta^{18}O_{otolith}$) and Sr/Ca values for the freshwater (FW), oligohaline (OH), and mesohaline (MH) habitats in the Patuxent River estuary in 2001, 2004, and 2005.

		$\delta^{13}C_{otolith}$ (‰)		$\delta^{18}O_{otolith}$ (‰)		$Sr/Ca_{otolith}$ (mmol mol^{-1})	
Year	Habitat	Mean	SD	Mean	SD	Mean	SD
2001	FW	-13.40	0.42	-7.07	0.13	1.26	0.27
	OH	-11.82	0.59	-6.89	0.16	3.09	0.21
	MH	-9.03	0.66	-6.33	0.23	3.39	0.18
2004	FW	-13.77	0.50	-7.48	0.02		
	OH	-12.49	0.34	-7.16	0.02		
	MH	-9.36	0.71	-7.29	0.02		
2005	FW	-13.95	0.84	-7.83	0.02		
	OH	-12.26	0.26	-7.58	0.02		
	MH	-9.66	0.31	-7.26	0.01		

Table 3. Summary of results of linear discriminant function analysis with jackknife resampling (a 'leave-one-out' cross-validation procedure) to determine the accuracy of using all three tracers ($Sr/Ca_{otolith}$, $\delta^{13}C_{otolith}$, and $\delta^{18}O_{otolith}$), and combinations there of, as predictors. The percent correct classification of fish to salinity habitat (FW=freshwater, OH=oligohaline, MH=mesohaline) is reported for each year and discriminant model.

	Habitat	Sr/Ca, $\delta^{13}C$ & $\delta^{18}O$	$\delta^{13}C$ & $\delta^{18}O$	$\delta^{13}C$	$\delta^{18}O$	Sr/Ca	$\delta^{13}C$ & Sr/Ca	$\delta^{18}O$ & Sr/Ca
2001	FW	100	100	100	67	100	100	100
	OH	100	86	100	71	57	100	100
	MH	100	100	100	100	67	100	83
	Total	100	95	100	79	75	100	94
2004	FW		75	100	75			
	OH		100	100	80			
	MH		100	100	60			
	Total		92	100	72			
2005	FW		80	80	60			
	OH		80	100	20			
	MH		100	100	80			
	Total		87	93	53			

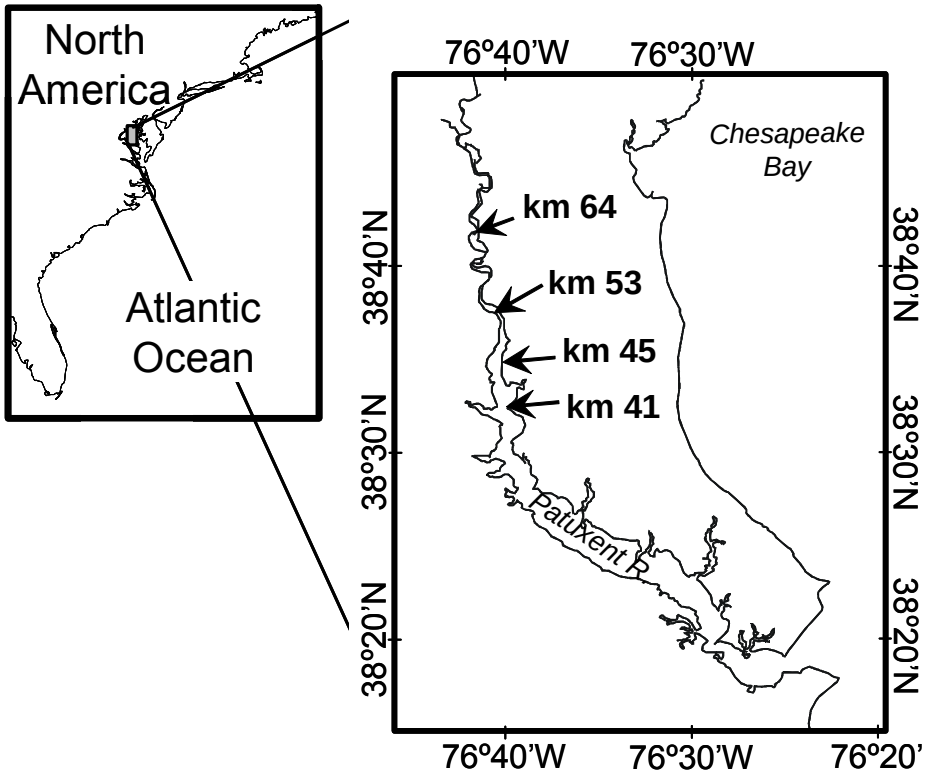


Figure 1. Map of the Patuxent River estuary, a subestuary of the Chesapeake Bay (Maryland; Kraus and Secor 2004a). The map illustrates the location of fish collections in freshwater (river km 64), oligohaline (river km 53), and mesohaline (river km 41 and 45) regions of the estuary.

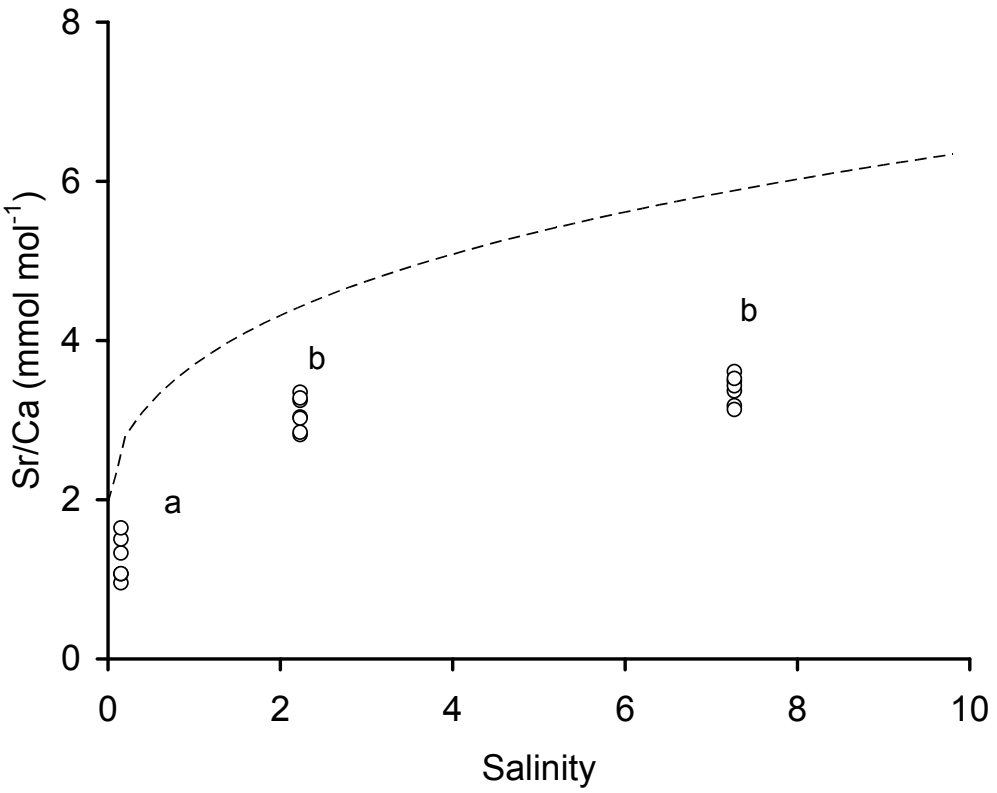


Figure 2. Otolith Sr/Ca values from fish collected in freshwater, oligohaline, and mesohaline habitats in the Patuxent River estuary in 2001 (open circles). Significant pairwise differences are denoted by different lowercase letters. Dashed trendlines indicate the relationship between Sr/Ca_{water} and the salinity gradient.

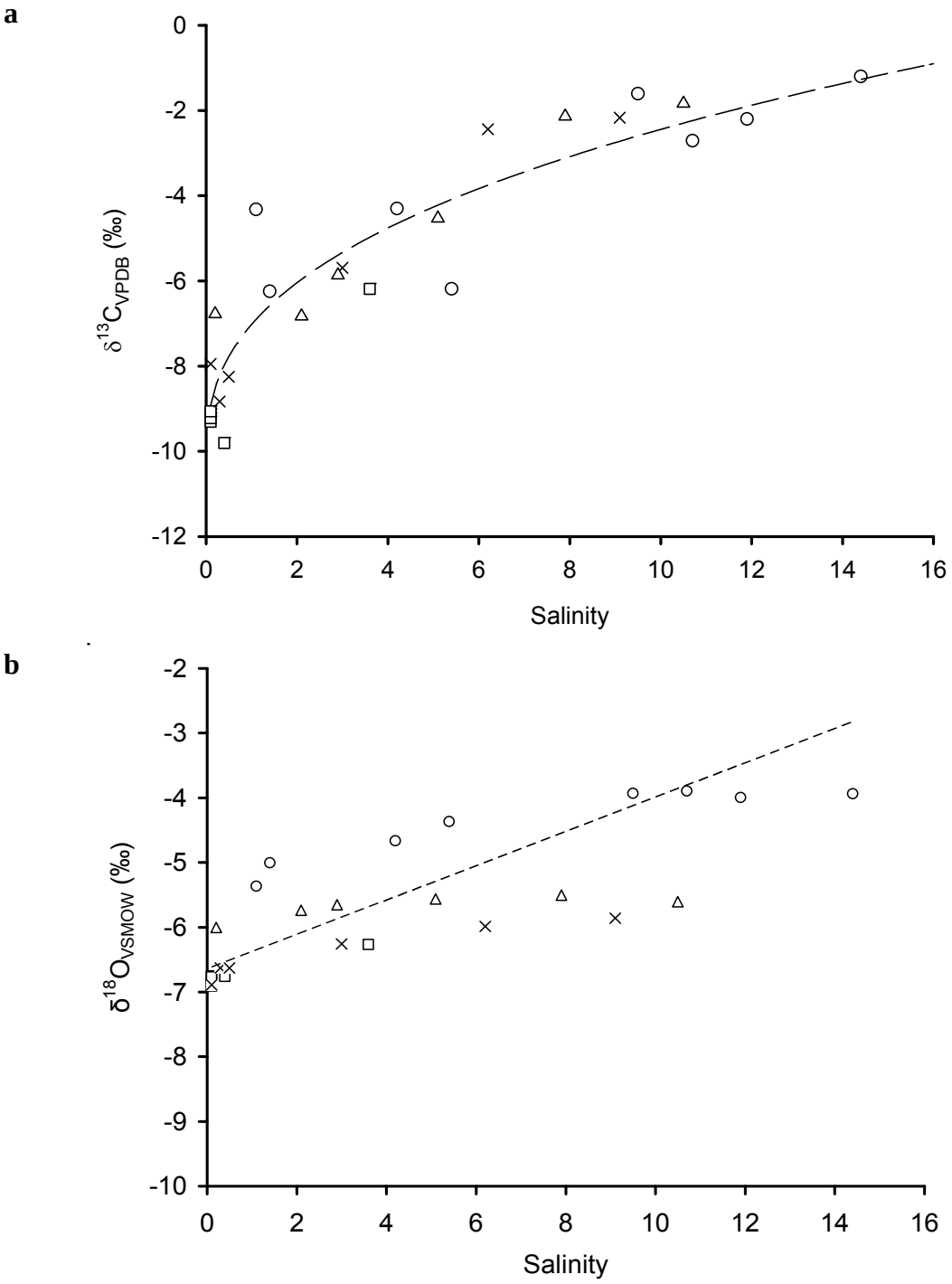


Figure 3. (a) $\delta^{13}C$ and (b) $\delta^{18}O$ values of water samples collected at sites stratified along the salinity gradient of the Patuxent River estuary in 2005 (May to September). Data were aggregated and fit with a power function (dashed line) in the case of $\delta^{13}C$ and a linear function (dashed line) for $\delta^{18}O$. Collection date is indicated by symbols: May 31 (open squares), June 6 (crosses), June 28 (open triangles), and September 20 (open circles). Values were reported relative to a standard ($\delta^{13}C_{DIC}$: VPDB using international standards NBS-19 and NBS-18, and $\delta^{18}O_{water}$: Vienna Standard Mean Ocean Water).

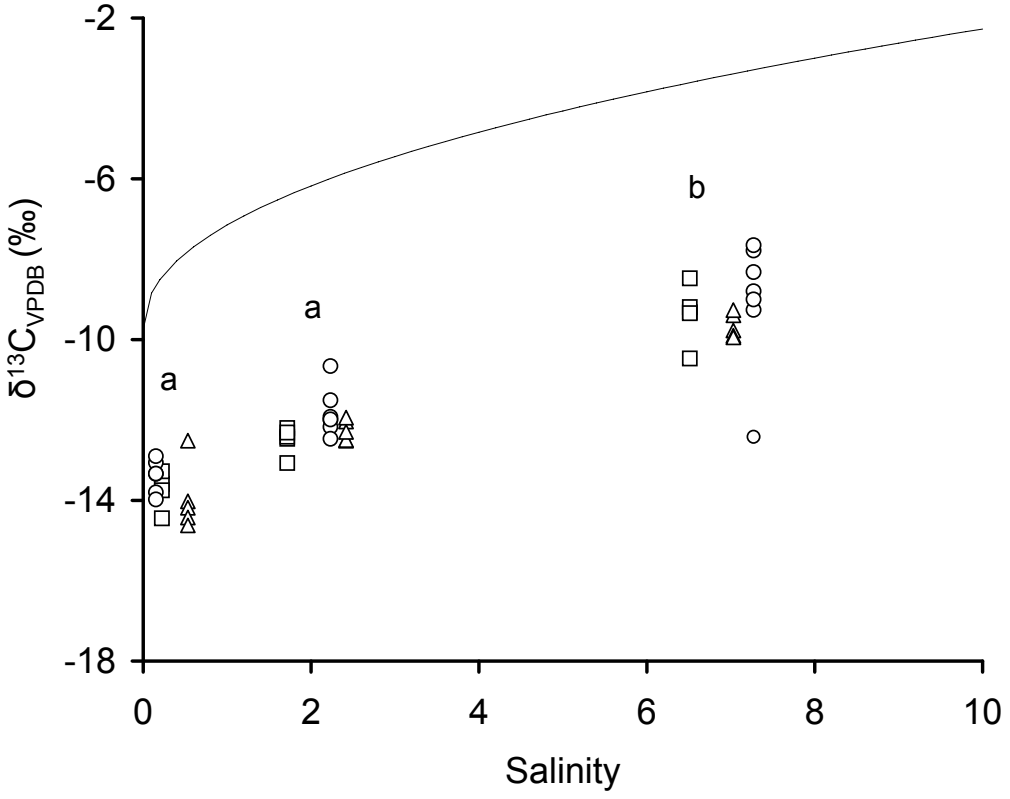


Figure 4. Otolith stable carbon ($\delta^{13}C$) values from fish collected in freshwater, oligohaline, and mesohaline habitats in the Patuxent River estuary in 2001 (open circles), 2004 (open squares), and 2005 (open triangles). Significant pairwise differences are denoted by different lowercase letters. Dashed trendlines indicate the relationship between $\delta^{13}C_{DIC}$ and the salinity gradient. Trendlines are included to illustrate the isotopic disequilibria between water and otolith tracer chemistry.

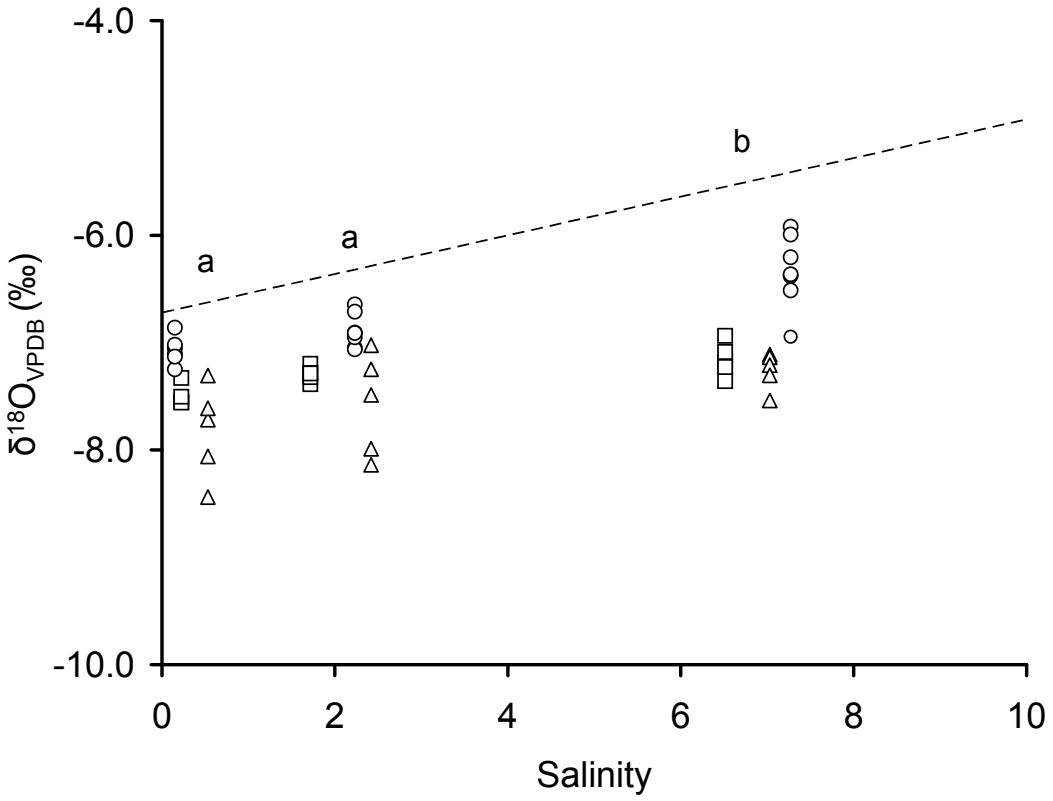


Figure 5. Otolith stable oxygen ($\delta^{18}O$) values from fish collected in freshwater, oligohaline, and mesohaline habitats in the Patuxent River estuary in 2001 (open circles), 2004 (open squares), and 2005 (open triangles). Significant pairwise differences are denoted by different lowercase letters. Dashed trendlines indicate the relationship between $\delta^{18}O_{water}$ (corrected to a VPBP scale) and the salinity gradient. Trendlines are included to illustrate the isotopic disequilibria between water and otolith tracer chemistry.

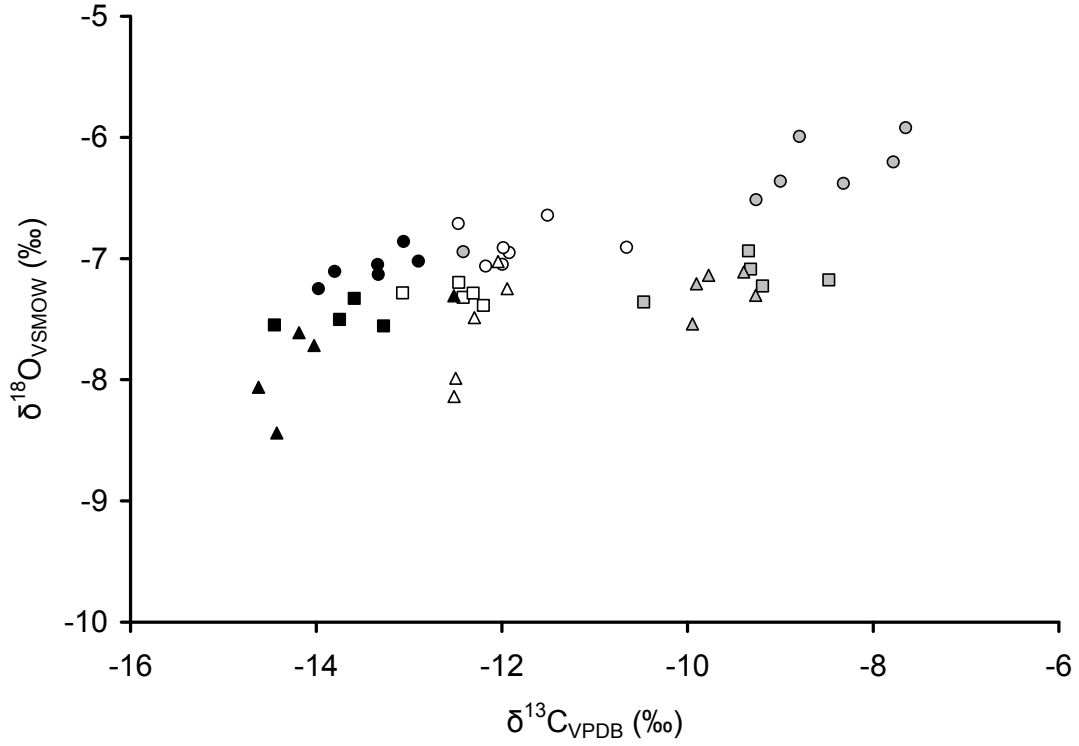


Figure 6. Dual isotope plot with $\delta^{18}O_{otolith}$ plotted against $\delta^{13}C_{otolith}$ values from fish collected in freshwater (black), oligohaline (white), and mesohaline (gray) habitats in the Patuxent River estuary in 2001 (circles), 2004 (squares), and 2005 (triangles). Note that the absolute values of salinity vary across years for each habitat.

Chapter 6: PREVALENCE OF SPATIAL STRUCTURING IN POPULATIONS OF WHITE PERCH (*MORONE AMERICANA*) IN THE CHESAPEAKE BAY

ABSTRACT

Spatial heterogeneity in habitats used by juvenile fishes in coastal environments may be associated with early life modalities of sedentary and dispersive behaviors. Prior research identified two contingents (freshwater resident and brackish water dispersive) of juvenile white perch in the Patuxent River. I examined whether contingent structuring is present in other sub-estuaries of the Chesapeake Bay. A sample of adult white perch otoliths was collected from the Upper Bay, Potomac, Choptank, Nanticoke, James, and York Rivers (2005-2006) and analyzed for stable isotope ratios ($\delta^{18}O$ and $\delta^{13}C$). Based on analysis of white perch otolith $\delta^{18}O$ values, I investigated the generality of contingent behavior across populations of white perch in the Chesapeake Bay. Contingent-membership of individuals was estimated from otolith $\delta^{18}O$ values using river-specific isotopic mixing models ($\delta^{18}O$ of water) to characterize the isotopic signature of the natal habitat. The majority of adults within the Upper Bay and Potomac River populations were residents, recruited from the freshwater natal habitat, whereas the majority of individuals from the Choptank, Nanticoke, James, and York were dispersive fish, recruited from brackish waters. Interannual variability in the relative contributions of nursery habitat to adult populations was identified. Population-specific patterns in habitat

values suggest that contingent structuring could play an important role in regulating population and metapopulation dynamics.

INTRODUCTION

The importance of estuaries as critical nursery habitat for the juvenile stage of many commercially and recreationally important fishes has long been recognized and has served as a basis for protection of essential fish habitat (EFH; Hildebrand and Schroeder 1928, Gunter 1967, Boesch and Turner 1984). Recently, there has been an increased focus on refining the definition of nursery habitat for the purpose of prioritizing management, restoration, and conservation goals within estuaries (Beck et al. 2001, Dahlgren et al. 2006). The numerous methods used to rank the importance of nursery habitat, however, often produce conflicting results. Historically, juvenile presence, abundance, and density within a region were used as indicators of the importance of a specific area as nursery habitat. More recently, the focus has shifted to linking juvenile habitat use to adult production and evaluation of the realized contribution of nursery habitat to population productivity (Beck et al. 2001, Kraus and Secor 2005a, Dalgren et al. 2006, Fodrie and Levin 2008). Beck et al. (2001) determined the relative importance of nursery habitat based on the number of fish that recruit to the adult population from a specific region of the estuary on a per-unit-area basis. This approach enables identification of high quality nursery habitats in the short term, but fails to recognize the importance of minority behaviors and their contribution to long-term population persistence (Kraus and Secor 2005a). Dahlgren et al. (2006) subsequently proposed prioritizing those nursery habitats that contribute a greater proportion of individuals to the

adult population in absolute numbers, regardless of areal coverage. This index is termed the effective juvenile habitat (EJH; Dalgren et al. 2006). EJH identifies the habitats most important to sustaining overall population productivity. However, this approach fails to recognize the importance of complex temporal dynamics in nursery habitat value. I contend that characterization of nursery habitat should include evaluation of the contribution of habitat to both population productivity (habitat contribution averaged over time) and stability (interannual variation in habitat contribution).

Spatial heterogeneity in the habitats used by juvenile fish within a population may be associated with early life modalities of resident and migratory behaviors (i.e., partial migration; Chapter 2). These modalities, termed contingents, may contribute differentially to population productivity and stability as one or the other modes is favored under varying climate regimes or prey conditions (Hilborn et al. 2003; Kraus and Secor 2005 a,b, Secor 2007, Chapter 7). Heterogeneous response to a changing environment at the species or population-level is the hallmark of community and metapopulation dynamics that allows for persistence over long time scales (Hanksi 1999, Doak et al. 1998). Population dynamics may function similarly, whereby differing contingent-specific responses to the environment promotes stability and consequently long-term population persistence (Chapter 7). Anthropogenic activities, such as habitat destruction in a particular region, can compromise population persistence through loss of a contingent, resulting in increased recruitment variability. Thus, identification of contingents and evaluation of contingent-specific habitat utilization is important to understanding the dynamics of populations.

The sub-estuaries of the Chesapeake Bay provide important nursery habitat for juvenile white perch populations. White perch inhabit littoral areas of estuaries, ranging in salinities from 0 to 18 (Mansueti 1961). Contingent structuring has been documented within one sub-estuary population, the Patuxent River estuary, of the Chesapeake Bay and it is likely that it occurs in other estuarine systems (Kraus and Secor 2005b). In the Patuxent River estuary, the dominant spatial behavior by juveniles was dispersive (>90%); these fish moved down-estuary to inhabit brackish water habitat. A minority of juveniles exhibited freshwater residency (Kraus and Secor 2005a). Despite the low abundance of juveniles residing in freshwater, this contingent was hypothesized to contribute to the long term persistence of the white perch population, important to recruitment during periods of drought, whereas the brackish water contingent contributed most and drove fluctuations in adult abundance, dominating during periods of high freshwater flow (Kraus and Secor 2005a).

Retrospective analysis of past nursery habitat use by adult fish populations enables us to establish the contribution of specific habitats to population dynamics. Otolith stable isotope values ($\delta^{18}O$ and $\delta^{13}C$) have proven useful in estimating paleosalinity from biogenic carbonates (Ingram et al. 1996; Cronin et al. 2005) and in modern reconstruction of salinity habitat use by estuarine-dependent fishes (Kerr et al. 2007). Here, I have focused my analysis on the stable isotopes of oxygen because of the availability of baseline $\delta^{18}O$ water data in the Chesapeake Bay. Otoliths incorporate the $\delta^{18}O$ signature of ambient water with some degree of temperature-dependent fractionation (Thorrold et al. 1997, Høie et al. 2004). Because many estuaries exhibit a gradient in water $\delta^{18}O$ values that is correlated with salinity, and because $\delta^{18}O$ of otoliths

is deposited in near equilibrium with water, otolith $\delta^{18}O$ values can be a useful proxy for reconstructing habitat salinity of fish (Kerr et al. 2007). Differences in water $\delta^{18}O$ values across the salinity gradient of estuaries are driven by the hydrologic cycle of evaporation and precipitation, termed Raleigh fractionation (Mook and Tan 1991). During evaporation, the lighter isotope of oxygen (^{16}O) reacts faster and is turned into water vapor, leaving surface waters relatively enriched in the heavier isotope (^{18}O), and precipitation that falls back to land enriched in the light isotope. The $\delta^{18}O$ value of seawater is considered to be stable ($\delta^{18}O = 0 \pm 1‰$), whereas typical freshwater riverine values are wider ranging ($\delta^{18}O$ = -10 to -6‰ in the mid-Atlantic region; Kendall and Coplen 2001).

In this study, I investigated contingent structuring in white perch populations across sub-estuaries of the Chesapeake Bay, including the Upper Bay, and Potomac, Choptank, Nanticoke, York, and James Rivers (Figure 1). Similar to the Patuxent River estuary, these sub-estuaries of the Bay are partially mixed estuaries (Day et al. 1989), but exhibit considerable variation in their size and available freshwater habitat (Cronin and Pritchard 1975, Kraus and Secor 2005b). Levels of $\delta^{18}O$, measured in the year-1 growth of adult white perch otoliths, were used to resolve contingent membership, as this behavioral phenomenon is predominantly established in the first year of life (Chapter 2). In addition, I tested the hypothesis that estimates of the relative contribution of contingents to adult production within each river, as determined from otolith chemistry, would be equivalent to the relative abundance of juveniles within the freshwater and brackish water nursery habitats as determined from seine survey data.

METHODS

Juvenile Index of Nursery Habitat Importance

The Maryland Department of Natural Resources (MDDNR) and Virginia Institute of Marine Science (VIMS) conduct an annual seine survey within the Chesapeake Bay (including stations within the Upper Bay, and the Potomac, Choptank, Nanticoke (MDDNR), James and York Rivers (VIMS)) to monitor trends in abundance of young-of-the year (yoy) striped bass (*Morone saxatilis*). In addition to striped bass, other fish species are monitored, including white perch. Within Maryland waters examined in this study, the seine survey included 27 stations (17 in freshwater and 10 in brackish water habitat) sampled at approximately monthly intervals from July to September. Within Virginia waters examined in this study, the seine survey included 19 stations (16 in freshwater and 3 in brackish water habitat) sampled biweekly from July to mid-September. A 30.5 m x 1.24 m (1.22 m in VA) bagless beach seine with 6.4 mm mesh size was used in the seine survey. Data collected included catch numbers per seine haul for yoy white perch and associated water quality, including water temperature (°C) and salinity.

The natal habitat of white perch is defined here as salinities 0 to 3, this salinity zone of the estuary is typically a center of distribution for the overlap of white perch larvae and their potential prey (North and Houde 2003). The highest densities of white perch occur in the vicinity of the salt front and the associated estuarine turbidity maximum, with the distribution of larvae extending into slightly higher and lower salinities (Chapter 3, Campfield 2004, North and Houde 2003). The salinity range 0 to 3 is presumed to represent a boundary of suitable natal conditions for egg and larval

development of white perch, based on studies of the sympatric striped bass (*M. saxatilis*, Winger and Lasier 1994; Jassby et al. 1995; Secor and Houde 1995). Juvenile abundance within the natal habitat (0-3), termed freshwater habitat here, and outside the natal habitat in brackish water habitat (salinities > 3) was calculated by expanding densities of yoy fish (calculated as the geometric mean of catch rates for July, August, and September) to the area of available littoral habitat in each river segment (0 to 2 m depth contour; Cronin and Pritchard 1975) and summing segments to get an estimate of abundance within each habitat (following Kraus and Secor 2005b). EJH was calculated as the habitat that contributed >50% of individuals on average (i.e., across year classes) to the adult population (following Dahlgren et al 2006). The data used in this analysis was restricted to the years corresponding to year-classes of fish analyzed for otolith chemistry. Additionally, nursery value, or the % of individuals contributed to the adult population from freshwater and brackish water habitat on a per-unit-area basis (Beck et al. 2001) was calculated for each river. Expansion of densities of yoy white perch was limited to the 0-2 m contour as sampling by MDDNR and the VIMS seine survey was constrained to this depth contour.

Otolith-based Reconstruction of Nursery Habitat Importance

Adult fish collection

Adult white perch were collected from spring months fisheries in the Upper Bay, and the Potomac, Choptank, Nanticoke, James, and York Rivers in 2005 and 2006 (Table 2, Figure 1). Fish were collected in freshwater to oligohaline regions of these rivers by pound, trawl, and fyke net when aggregated for spawning in spring (March – May).

Total length and weight of fish were measured and maturity stage was determined visually. Otoliths were removed, cleaned of adhering tissue, and stored dry.

Otolith preparation and stable isotope analysis

A random sub-sample of 45-75 otoliths from adult fish collections made in each sub-estuary was analyzed for $\delta^{18}O$ and $\delta^{13}C$ (Table 2). Sagittal otoliths (one per individual) were affixed to glass microscope slides with thermoplastic glue and transversely sectioned using a Buehler© low speed saw with diamond blades to 0.5 mm thickness. Otolith sections were adhered with thermoplastic glue to microscope slides and polished using wet-dry sandpaper (600-800 grit) and alumina powder (0.3 μm). Otolith thin-sections were viewed under a stereo-microscope with transmitted light and age was estimated based on counts of growth band pairs (one opaque and one translucent band). Otoliths were aged three times independently and assigned a final age based on confidence in age estimates.

A portion of the otolith representing growth during the first year of life (referred to here as year-1 growth) was removed from otolith thin-sections using a New Wave® micro-milling machine with a fine-tipped end mill (0.6 μm). Based on measurements of the dimensions of year-1 growth deposition in white perch otoliths (length = 2.7 mm, height = 0.9 mm, depth= 0. 5 mm), a rectangular area was removed (length = 1.3 mm, height = 0.9 mm, depth= 0.5 mm). This sampling method was not designed to remove all year-1 otolith growth, but rather to target a consistent portion of the otolith for removal that was representative of this period of growth within the otolith.

Powdered otolith samples were submitted to the University of Arizona Isotope Geochemistry Laboratory for analysis. $\delta^{18}O$ and $\delta^{13}C$ were measured using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252). Powdered otolith carbonate samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. The resultant CO_2 was analyzed for $\delta^{18}O$ and $\delta^{13}C$, and values were reported as per mil (‰) relative to a standard (Vienna Pee Dee Belemnite [VPDB] using international standards NBS-19 and NBS-18). Analytical precision measures of the mass spectrometer for $\delta^{13}C$ and $\delta^{18}O$ were 0.06 and 0.1‰, respectively, and based on the standard deviation of repeated measures of the standard.

River-specific mixing models

River-specific isotopic mixing models ($\delta^{18}O$) were developed to estimate a $\delta^{18}O$ threshold that defined the natal habitat of white perch within each estuary. This approach assumed a linear relationship between water $\delta^{18}O$ values and the salinity gradient within each estuary (i.e. conservative mixing of freshwater and seawater end-members in a 1:1 mixing ratio; Mook and Tan 1991, Fry 2002). The isotopic value of the freshwater end-member (freshwater source) was estimated for each river from freshwater $\delta^{18}O$ values sampled at approximately bi-monthly intervals over three years in the Upper Bay, Potomac, Choptank, and James Rivers (1985-1987; Coplen and Kendall 2000) and more recent water sampling in the Nanticoke and York Rivers (Walthers *In Review*; present study). Mean annual freshwater values were calculated over the growth season of the otolith (April-October; as estimated from striped bass (*Morone saxatilis*); Zlokovitz et al. 2003). Chesapeake Bay polyhaline water (Cronin et al. 2005) and Atlantic Shelf water

(Chapman et al. 1986; Khim and Krantz 1996) $\delta^{18}O$ values were used as the proximate and ultimate saltwater end-member values for each river-specific mixing model. A conversion was used to re-scale water values ($\delta^{18}O_{VSMOW}$) to a carbonate reference scale ($\delta^{18}O_{VPDB}$; Coplen et al. 1983). Linear regression analysis was used to estimate the relationship between salinity and water $\delta^{18}O$ within each river. These regression relationships were then used to estimate a $\delta^{18}O$ threshold ($\delta^{18}O$ value at salinity of 3) that enabled classification of white perch as either residents within their natal habitat or dispersive fish, based on their otolith $\delta^{18}O$ values adjusted for temperature-dependent fractionation. Temperature-dependent fractionation between otoliths and water was estimated based on the relationship: $\delta^{18}O_{otolith}$-$\delta^{18}O_{water}$ = 3.90 (T°C) - 0.20 (Høie et al. 2004) and the corresponding mean annual temperature during the otolith growth season (April-October; Chesapeake Bay Program Water Monitoring data) within each river. Based on an individual's otolith $\delta^{18}O$ value (adjusted for fractionation) relative to the river-specific $\delta^{18}O$ threshold, fish were classified as either freshwater residents (salinity 0-3) or dispersive contingent fish, inhabiting brackish water (salinity >3) during their first year of life.

EJH was calculated as the habitat/contingent that contributed >50% of individuals on average (i.e., across year classes) to the adult population (following Dahlgren et al 2006). Interannual variation in EJH within each river was examined for those year-classes with $\geq$ 5 individuals. The relationship between annual contribution of habitats to the adult population and recruitment level (total abundance) was examined. In addition, the influence of environmental conditions (mean river discharge and temperature) during the spring production season (March-May) on representation of contingents was

examined. Mean river discharge and temperature were determined for each river system following Kraus and Secor (2005b). River discharge data was not available for the Nanticoke River. Additionally, nursery value was calculated based on otolith-derived nursery habitat classifications for each river. Area used in the calculation of nursery value was limited to the 0-2 m contour because one objective of this research was to compare tracer-based estimates of the relative importance of nursery habitat to seine survey estimates, which are constrained to this depth contour.

Juvenile fish collections

Young-of-the-year white perch (n = 8-16, Table 2) were collected by beach seine (as described above) in the freshwater habitat within each river system in 2006 and 2007 (with the exception of the James River for which fish were sampled in a slightly higher salinity of 4). Otoliths were analyzed whole for $\delta^{18}O$ (as described previously) as a means of verifying estimated freshwater end-member values.

Statistical Analyses

Mean freshwater end-member $\delta^{18}O$ values were compared across river systems using analysis of variance (ANOVA) and the slopes of river-specific isotopic mixing models were compared using analysis of covariance (ANCOVA). Otolith $\delta^{18}O$ values of juvenile fish were examined in two ways: 1) a two-way ANOVA was employed to test the significance of the effects of river, year, and the interaction of these factors on yoy white perch otolith $\delta^{18}O$ values, and 2) two-sample t-tests were used to compare freshwater end-member $\delta^{18}O$ values and yoy white perch otolith $\delta^{18}O$ values (after correction for temperature-dependent fractionation). Adult otolith $\delta^{18}O$ values were compared across river systems using ANOVA, with a Tukey's test employed to identify

significant between-river differences. In addition, the relationship between annual representation of contingents in adult populations and possible explanatory factors, including total abundance of juvenile recruits, mean spring river discharge and mean spring water temperature, were examined using Pearson correlation analysis. Comparisons between the estimated contribution of freshwater nursery habitat based on juvenile seine survey data and the contribution of freshwater habitat to the adult populations estimated from otolith chemistry were conducted using chi-square analysis. ANOVA was used to examine differences in $\delta^{18}O$ of fish otoliths across year-classes within each river, due to non-normality of data in the Choptank and Potomac Rivers a Kruskal Wallis test was used in these systems. A two-way ANOVA was used to examine the influence of location, sex, and the interactions of these factors on mean $\delta^{18}O$ of fish otoliths within each river and to examine the length-at-age relationship between contingents (length was log-transformed for this analysis due to non-normality).

Statistical analyses were performed with SAS Version 9.0 (SAS Institute 1999, Cary, NC); $\alpha = 0.05$ was used as a critical level of significance. Diagnostics were employed to test for univariate normality, equal variance, and influential observations. In the case of unequal variance in otolith $\delta^{18}O$ values observed across rivers, variance was calculated for each group in PROC mixed (SAS Version 9.0). Unequal variance observed between water and juvenile $\delta^{18}O$ values in the James River was treated using Welch-Satterthwaite t-test.

RESULTS

Geographic Differences in $\delta^{18}O$

Mean $\delta^{18}O$ values of freshwater end-members ranged from -8.5 (Upper Bay) to -5.6‰ (Nanticoke River; Table 1) and were significantly different across river systems ($F_{5,8} = 38.08$, $p < 0.01$). The $\delta^{18}O$ signature of freshwater was most depleted in the Upper Bay and Potomac Rivers and relatively enriched in the James, York, Choptank, and Nanticoke Rivers (Table 1). Differences in the isotopic signature of freshwater end-members translated to significant differences in the slopes of mixing models across river systems ($F_{5, 339}=11.52$, $p = <0.01$, Table 1, Figure 2).

Otolith $\delta^{18}O$ values of yoy white perch sampled within the freshwater nursery habitat of each river system river were significantly different across year ($F_{4,13.6} = 43.29$, $p = <0.01$) and river ($F_{4,10.5} = 103.74$, $p = <0.01$), but within each river there were not significant differences between years ($F_{4,10.5} = 2.91$, $p = 0.08$). Geographic patterns in mean yoy otolith $\delta^{18}O$ values paralleled trends identified in water isotope values. Juvenile otolith $\delta^{18}O$ values were most depleted in the Upper Bay and Potomac and relatively enriched in down-Bay river systems (James and York Rivers, Table 1, Figure 3a). Otolith $\delta^{18}O$ values from juvenile fish collected in the freshwater nursery habitat (and corrected for fractionation) were not significantly different from mean annual freshwater values within the Upper Bay, Potomac, and Choptank rivers (t-test $p > 0.05$ for these rivers). Agreement between water values and yoy otolith values supported the characterization of the freshwater end-members within these river systems. Otolith and water values were significantly different in the James River (t-test d.f. = 9.31, t-test statistic = 3.7, $p < 0.01$); however, fish measured within this system were collected at

slightly higher salinities (mean salinity 3.9), which corresponded with the observed elevated $\delta^{18}O$ values of otoliths compared to water. Comparisons could not be made between yoy otolith and freshwater $\delta^{18}O$ values for the Nanticoke or York Rivers because only one year of water data was available.

Across river systems, $\delta^{18}O$ values of year-1 growth within adult white perch otoliths ranged from -2.4 to -9.8‰. Mean otolith $\delta^{18}O$ values were significantly different across rivers ($F_{5,112} = 66.70$, $p < 0.01$), with significant pair-wise differences between all rivers with the exception of the Choptank and James Rivers ($p = 0.87$; Figure 3). Otolith $\delta^{18}O$ values were most depleted in the Upper Bay and Potomac Rivers, slightly elevated in the Choptank and James Rivers, and most elevated in the Nanticoke and York Rivers (Figure 3b). Variance in otolith $\delta^{18}O$ values differed across river systems with the Nanticoke River having the highest and the York River having the lowest variation in otolith $\delta^{18}O$ values (Figure 3b). Overall, a broad geographic pattern in otolith $\delta^{18}O$ values was evident, with otolith $\delta^{18}O$ values becoming more positive moving from up- to down-Bay estuaries.

Nursery Habitat Use

Fish were classified as either residents in the natal freshwater habitat (salinities 0 to 3) or dispersive fish, residing in brackish water (salinities >3), based on otolith $\delta^{18}O$ and threshold values determined for each river-system (Table 1). The percent contribution from natal freshwater and brackish water habitats to the adult population varied across rivers (contribution from freshwater habitat: 18 to 69%, contribution from brackish water habitat: 31 to 82%; Table 2). On average (i.e., across year classes), the Upper Bay and Potomac Rivers were predominantly comprised of freshwater resident

fish, whereas the Choptank, James, Nanticoke, and York Rivers were dominated by brackish water dispersive contingent fish (Table 2).

Interannual differences in the contribution of freshwater nursery habitat to the adult population were observed (Figure 5). The coefficient of variation of freshwater nursery habitat's contribution to the adult population was high (>98%) for the James, York, and Nanticoke Rivers, somewhat lower for the Choptank (83%), and lowest in the Potomac River (57%) and Upper Bay (43%). In most river systems, the 1998, 2000, and 2003 year-classes exhibited high representation of resident fish originating from freshwater habitat. Across river systems there was a pattern of positive correlation between the percent contribution of freshwater habitat to the adult population and river discharge. However, only three positive correlations were significant (Potomac River: Pearson correlation coefficient = 0.81, d.f. = 5, $p = 0.03$; James River: Pearson correlation coefficient = 0.98, d.f. = 2, $p = 0.02$; York River: Pearson correlation coefficient = 0.98, d.f. = 2, $p = 0.03$). One significant negative correlation with temperature and freshwater resident contingent representation was identified in the York River (Pearson correlation coefficient = -0.98, d.f. = 2, $p = 0.02$), and a positive correlation with recruitment was identified in the Upper Bay (Pearson correlation coefficient = 0.97, d.f. = 2, $p = 0.04$). Otherwise, no significant correlations between contingent representation and temperature or recruitment level were observed.

No significant differences between the juvenile index (based on seine survey data) and hindcast (based on otolith chemistry) estimates of the contribution of freshwater residents were identified in the Upper Bay, Potomac, and Nanticoke ($p > 0.11$; Figure 6). However, differences in the juvenile index and hindcast contribution of freshwater and

brackish water nursery habitats were identified in the Choptank, York, and James Rivers ($p < 0.01$; Figure 6). Based on seine survey data, freshwater habitat was expected to be more important with respect to recruitment to the adult population across rivers, with the exception of the Choptank River (Table 2, Figure 6). In the James and York Rivers the estimated abundance of juveniles in freshwater habitat was higher than the proportional contribution of this habitat to adult production as determined from otolith analysis, the opposite was true in the Choptank River.

The rivers examined in the study vary in the amount of freshwater and brackish water habitat available to juvenile stage fish (Table 3). Proportionally, the Upper Bay has the highest amount freshwater habitat (78% of total area within 0-2 m contour), whereas the Nanticoke has the lowest freshwater area (7% of total area within 0-2 m contour). The contribution of freshwater nursery habitat to the adult population on a per-unit-area basis (sensu Beck et al. 2001) based on otolith chemistry ranged from 0.4 to 8.1% fish km^{2-1} across river systems (Table 3). Otolith-based estimates of the nursery value of brackish water ranged from 0.5 to 6.3% (Table 3). In the Upper Bay, James, and York Rivers nursery value estimates based on otolith chemistry were highest in brackish waters, whereas in the Potomac, Choptank, and Nanticoke Rivers nursery value was highest in freshwater habitat. Nursery habitat value estimates based on juvenile seine survey data were in agreement with otolith-based estimates for the Upper Bay, Potomac, and Nanticoke, however, the seine survey revealed an opposite trend in nursery value in the Choptank, James and York Rivers (Table 3).

Demographic Characteristics of Contingents

Across rivers, adult fish ranged from 2 to 13 years of age. Year classes represented included 1993 to 2004, with the dominant year class, 2001, comprising 31% of the overall sample. The 2001 year class also dominated the sampled population within each river, with the exception of the Potomac which was dominated by the 1996 year class. Significant differences in $\delta^{18}O$ across year-class were identified in all river systems (Upper Bay: $F_{3,31} = 5.34$, $p < 0.01$, Potomac River: chi-square = 42.85, d.f. = 6, $p < 0.01$, Choptank River: chi-square = 35.11, d.f. = 4, $p < 0.1$, Nanticoke River: $F_{5,65}$: 5.27, $p < 0.01$, James River: $F_{4,63}$: 15.17, $p < 0.01$, and York River: $F_{3,38} = 21.21$, $p < 0.01$. In most river systems the sample was dominated by female fish, with the exception of the Choptank River. There was, however, no significant difference in $\delta^{18}O$ by sex ($F_{1,262} = 2.94$, $p = 0.09$) or the interaction of sex and location ($F_{5,125} = 0.73$, $p = 0.60$). There was not sufficient sample sizes within each river system to examine growth differences between contingents; however, I examined growth differences between contingents by pooling individuals across river systems. No significant differences in size at age were found between contingents ($F_{1,357} = 0.5$, $p = 0.48$).

DISCUSSION

Geographic Differences in $\delta^{18}O$

Geographic differences in oxygen isotopic signatures across rivers may reflect larger patterns of $\delta^{18}O$ with latitude. On the east coast, $\delta^{18}O$ values of water become more depleted north of the equator (Kendall and Coplen 2001). This pattern is driven by

the movement of prevailing weather patterns from the equator northward and the precipitation of heavier, more easily condensed ^{18}O before ^{16}O, leading to depletion in $\delta^{18}O$ in a northward direction (Rohling and Cooke 1999). This trend has been identified in rivers, wherein higher latitude rivers typically import freshwater with generally lower $\delta^{18}O$ values compared to lower latitude rivers (Rohling and Cooke 1999). Within the Chesapeake Bay, we find this same trend, but on a much smaller scale. Based on an established relationship between water $\delta^{18}O$ values and latitude on the east coast (Kendall and Coplen 2001), the amplitude of change within the latitudinal range of the Chesapeake Bay is expected to be on the order of a 1‰, with lower values in the north (Susquehanna River) compared to the south (James River). The identified difference in the mean $\delta^{18}O$ of freshwater end-members of the most northern and southern estuaries examined in this study was 1.6 ‰.

Nursery Habitat Use

Based on analysis of white perch otolith $\delta^{18}O$ values, I observed a pattern of habitat use consistent with contingent structuring across Chesapeake Bay sub-estuaries. In addition to identifying diversity in nursery habitat use, differences in the productivity of freshwater and brackish water nursery habitats were identified across spatial and temporal scales. The effective juvenile habitat (EJH), or source of the majority of recruits to the adult population, identified by otolith analysis was the freshwater habitat within the Upper Bay and Potomac River populations and the brackish water habitat in the Choptank, Nanticoke, James, and York Rivers. On a per-unit-area basis otolith chemistry revealed brackish water habitat was of higher nursery value in the Potomac,

Choptank, Nanticoke, and James Rivers and freshwater habitat was estimated to be of higher value in the Upper Bay and York Rivers. Quantification of the importance of nursery habitats can be a powerful tool in the identification of essential fish habitat and prioritization of habitat for conservation, particularly as juvenile fish in freshwater and brackish water regions of these estuaries may be differentially impacted by anthropogenic stresses.

The EJH (Dahlgren et al. 2006) and nursery value (Beck et al 2001) methods in ranking nursery habitat have utility, but both approaches have limitations and should be used judiciously with consideration of the objective (e.g., population management or habitat conservation) and the complexity not captured in these approaches (Sheaves et al 2006). The main drawback of the per-unit-area approach is that it does not account for the ultimate impact a habitat has on population dynamics. For instance, freshwater habitat had a relatively low nursery value in the Upper Bay. However, because 78% of the total habitat in the estuary is freshwater this habitat is dominant in its role on productivity. Likewise, a high nursery value for a habitat that is small in area (such as freshwater habitat in the Nanticoke River) may overemphasize the importance of this habitat to the population. The more simplistic EJH approach accounts for this problem, but also has drawbacks as is does not represent the interannual variation in the productivity of nursery habitat. Temporal variation in the relative importance of nursery habitat may be large due to complex temporal dynamics and should be accounted for in the characterization of nursery habitats. For example, in white perch populations temporal variability in the representation of the freshwater residents within rivers was greater than spatial variability in representation between rivers. Thus, measures of

nursery contribution to population sustainability need to be examined on both the appropriate spatial and temporal scales. This requirement necessitates significantly more knowledge about a population, but ignoring temporal dynamics can lead to erroneous conclusions regarding the importance of minority habitats that may contribute to long-term persistence.

Population-specific patterns in nursery habitat use may be a consequence of differences in local conditions, such as water temperature and prey availability within each river system. Recent examination of the proximate cause of partial migration within the Patuxent River population of white perch revealed this behavior is the expression of phenotypic plasticity, whereby individual growth rate, as affected by environmental conditions experienced during early life history, relative to a growth threshold, determine the life history tactic of an individual (Chapter 3). Evidence suggests that all white perch populations examined within the Chesapeake Bay may be partial migratory, exhibiting flexibility in life histories, a trait adapted for persistence in a stochastic environment. Thus, differences in the representation of contingents spatially (across estuaries) and temporally are likely related to environmental variables that influence growth and mortality rates of individuals in these populations.

Alternatively, the role of density-dependent regulation in structuring the distribution of white perch in freshwater and brackish water habitats cannot be discounted (MacCall 1990, Post et al. 1997). Density-dependent habitat selection assumes that individuals first inhabit the most suitable habitat, but as the density of the population increases, the suitability of the habitat decreases and individuals will utilize habitat that was originally considered less suitable (MacCall 1990). It is difficult to disprove the

influence of density dependence on habitat selection of white perch, however, cumulative evidence derived from a more in-depth study of contingent structuring within the Patuxent River estuary suggests that this is not likely the primary cause of divergent habitat use within this population (Kraus and Secor 2004a). First, dispersive contingent fish were present within a particular year-class, regardless of whether the freshwater habitat was at carrying capacity (~2 million fish), suggesting this phenomenon is not exclusively a consequence of density dependence (Kraus and Secor 2004a). In addition, the timing of movement down-estuary, shortly after the transition from larval to juvenile stage, would require that density of late-stage larvae mediates habitat use. Most evidence suggests, however, that density-independent factors are the dominant influence on vital rates during the larval stage (Houde 1989b). Additionally, the higher growth rate of dispersive contingent fish reported in my thesis (Chapter 4) does not indicate that brackish water habitat is sub-optimal for juvenile white perch.

Rankings of the relative importance of nursery habitat to adult production in the Upper Bay, Potomac, and Nanticoke Rivers by seine survey data and otolith chemistry showed agreement. However, differences in assessment of the importance of nursery habitat to adult numbers by these two methods were identified in the Choptank, James, and York Rivers. Retrospective analysis revealed a greater than expected contribution of brackish water habitat to adult productivity within the James and York Rivers, whereas the contribution of the freshwater habitat was estimated to be greater than expected in the Choptank River. These differences may be attributable to uncertainty associated with estimating contingent-membership of fish (discussed in more detail below) or may

represent real differences in the expected (based on the juvenile seine survey) vs. reconstructed (based on otolith chemistry) contribution of nursery habitat.

There are potential problems with relying exclusively on juvenile abundance (habitat-specific densities) as a proxy for the importance of nursery habitat, particularly when there is spatial structuring within the population that is initiated during the juvenile stage. Both the timing and spatial coverage of the seine survey may have biased the estimated abundance of juveniles within each habitat. If the timing of the seine survey (July-September) occurs before expression of dispersive behavior and settlement into nursery habitat, then the abundance of juveniles in freshwater may be overestimated. Within the Patuxent River the majority of individuals initiate dispersal during their first year of life shortly after the transition from larval to juvenile stage (at an estimated mean age: 45 ±7 days; Kraus and Secor 2004a). However, we cannot be sure the timing of migration is similar across sites, or years (Chapter 4), as it is likely expressed in response to local conditions. Alternatively, differences in the expected and reconstructed contribution of nursery habitats may stem from the spatial distribution of seine sites. Seine sites are focused primarily within the freshwater region in the James and York Rivers (ratio of FW: BR seine sites: James: 7:1, York: 9:2), likely resulting in better characterization of yoy white perch abundance in the freshwater environment and potentially contributing to overestimation of the importance of this nursery habitat. The same may be true in the Choptank River where seine sites are weighted toward brackish water habitat (ratio of FW: BR seine sites: 1:3) and the expected brackish water contribution was higher than back-calculated estimates. Finally, selective recruitment of individuals (i.e., habitat-specific differences in natural mortality) from brackish water

habitats in the James and York Rivers and freshwater in the Choptank to the adult population could be responsible for the departure of seine survey data from otolith chemistry estimates of nursery habitat value. It is important to note that an implicit assumption in this analysis is that there is equal survival between contingents. Differences in survival between contingents in these rivers may have affected this comparison.

River-specific mixing models constructed from water $\delta^{18}O$ values enabled determination of a threshold value that characterized the upper boundary of the natal habitat. Use of a threshold to define the natal habitat was effective in the classification of fish that remained resident within this habitat and those that exhibited denatant migration into higher salinity waters. However, there was uncertainty associated with this approach. Characterization of year to year variation in the freshwater oxygen signature is particularly important in constructing estuarine mixing models because the $\delta^{18}O$ value of freshwater end-members within estuaries is more highly variable than the saltwater end-member (Criss 1999). Sampling of water concomitant with otolith sampling is preferable; however, this requirement prevents reconstructive analysis of a random sample of the adult population (which comes from many year-classes of juveniles) unless water sampling is ongoing several years prior to sampling of the adult population. Here, I have taken advantage of published stable isotope values to gain broad spatial and temporal coverage, allowing for better characterization of the $\delta^{18}O$ of freshwater end-members and the degree of interannual variation in the signature. Agreement between freshwater and yoy white perch otolith $\delta^{18}O$ values provided independent verification of my characterization of freshwater end-members in most rivers. By classifying fish to

broad salinity zones indicative of their behavior (resident and dispersive) I aimed to minimize problems associated with classifying fish to their absolute nursery habitat salinity.

Temperature-dependent fractionation is another potential source of error. If fractionation was not well constrained by my analytical approach, this may have confounded the prediction of contingent from otolith oxygen isotope ratios. A sensitivity analysis revealed that contingent classification was relatively insensitive to fractionation, with a 25% increase in fractionation eliciting a 6% misclassification of fish to salinity class. Mean temperature-dependent fractionation estimated for white perch otoliths (-0.62 ‰, S.D. = 0.23) was in the range of reported fractionation values for fish otoliths in the literature (-0.87 ‰, SD=1.01; Campana 1999). Estimated values were slightly lower than field-based estimates of fractionation in white perch otoliths (-1.43 ‰,SD = 0.46). However, these estimates were made during summer months characterized by higher average temperature and thus higher average fractionation values (Kerr et al. 2007).

It is important to note that criteria for classifying a fish's nursery habitat undoubtedly influence the outcome of nursery habitat metrics. For example, calculation of the relative importance of each contingent to population productivity was influenced by my classification of natal habit as ranging from salinities 0-3. As there was no evidence of a bimodal distribution of otolith $\delta^{18}O$ values in most rivers, variation in the upper salinity boundary of the natal habitat would have a large impact on contingent classification. Additionally, the area-based calculations of nursery value are sensitive to both the salinity threshold and depth threshold (0-2 m) used to define white perch habitat. Thus, characterization of the importance of nursery habitat should be viewed cautiously

and in the context of the research question examined, as these calculations are dependent on the definition of nursery habitats.

Contingent Structure

The presence of contingent structuring within white perch populations has potential consequences to both within- and between-population dynamics. The consequences of contingent structure to within population dynamics are discussed in Chapter 7 and are not discussed further here. The presence of dispersive individuals within each sub-estuary could provide a means of connectivity between populations of white perch in the Chesapeake Bay. Based on grouping by genetic distances, three genetically-distinct populations of white perch were identified in the Chesapeake Bay using mtDNA: 1) the northern and eastern sub-estuaries (Upper Bay and Patuxent, Choptank, and Nanticoke Rivers), 2) the Potomac River, and 3) the southern sub-estuaries (York and James Rivers; Mulligan and Chapman, 1989). Connectivity between sub-estuaries is likely maintained by the dispersive contingent, with the degree of exchange mediated by the salinity structure of the Chesapeake Bay. Adult white perch typically reside in salinities ranging from 5-13, with a maximum tolerance presumed to be 18 based upon their distribution (Mansueti 1961). Hence, the relatively stable salinity structure within the Bay has likely enabled a high degree of mixing between some sub-estuaries and limited connectivity between others (Mulligan and Chapman 1989). White perch populations in the Patuxent, Choptank, and Nanticoke River are dominated by dispersive contingent fish. Despite the low representation of the dispersive contingent within the Upper Bay, when scaled to total abundance this river produces nearly 50 times the number of migratory fish of the Patuxent, Choptank, and Nanticoke Rivers combined.

Thus, I hypothesize that connectivity in the northern and eastern sub-estuaries of the Bay may be maintained through emigration of fish from the Upper Bay into smaller more southerly systems. The genetic isolation of the Potomac River population is supported by the relatively low abundance of the dispersive contingent in this system and the salinity structure of this river. The high representation of dispersive contingent fish in the James and York Rivers could support population connectivity between these rivers when the salinity structure permits (i.e., storm events). Judging by the comparatively low abundance of white perch in the York River (mean total abundance calculated from seine survey data: James = 79,057,996, York = 1,244,317), the James River may serve as a source to this decidedly smaller population. The distribution of populations and their degree of connectivity can be important in the long-term persistence of individual populations, particularly in the case of source-sink population dynamics (Hanski 1999, Crowder et al. 2000). Removal of migratory portions of populations, through fishing pressure or habitat degradation, which preserve connectivity between local populations, could lead to declines in the regional population.

Evidence of contingent structuring across populations and its potential impact on within- and between-population dynamics highlights the need to consider contingent structure in population assessment (e.g., location of seine survey sites) and management. The presence of fish that remain resident in their natal habitat across river systems, a habitat which in some years is wholly responsible for recruitment success to the adult population, indicates that freshwater habitat (salinity < 3) serves an important role as nursery habitat for white perch. Overall, EJH and nursery value approaches produced different rankings of the importance of habitat to adult production within rivers. While

these approaches are useful in certain management contexts, they take a simplistic and deterministic approach. By not evaluating stochasticity in habitat productivity among years, these approaches may overlook an important minority habitat component contributing to the persistence of the population. The stochasticity of nursery habitat productivity makes assignment of a value or rank to a particular habitat difficult and supports the preservation of a both dominant and sub-ordinate rank habitats, rather than conservation of a single most productive habitat.

TABLES

Table 1. River-specific mixing models as estimated from linear regression (x=salinity and y=$\delta^{18}O$) and associated R^2 values. $\delta^{18}O$ thresholds are estimated values that denote the upper limit of $\delta^{18}O$ in the natal freshwater habitat within each river. Mean (S.D.) $\delta^{18}O$ (‰) of 1-3 years of freshwater end-member values (seasonal means) in each river and yoy white perch otoliths from freshwater habitat within each river system are reported.

				Freshwater end-member		Juvenile otoliths	
River	Mixing Model	R^2	$\delta^{18}O$ threshold	Mean (S.D.)	Years (n)	Mean (S.D.)	n
Upper Bay	y = 0.22x - 7.46	0.94	-6.8	-8.23 (0.83)	3	-9.28 (0.85)	16
Potomac R.	y = 0.21x - 7.01	0.96	-6.4	-7.46 (0.30)	3	-7.52 (0.35)	10
Choptank R.	y = 0.18x - 6.35	0.96	-5.8	-6.33 (0.23)	3	-6.42 (0.25)	10
Nanticoke R.	y = 0.17x - 6.15	0.92	-5.6	-5.62	1	-6.97 (0.37)	10
York R.	y = 0.18x - 6.50	0.95	-5.9	-6.60	1	-5.33 (0.86)	8
James R.	y = 0.19x - 6.56	0.96	-6.0	-6.68 (0.04)	3	-6.02 (0.55)	10

Table 2. Mean (S.D.) δ18O values of year-1 otolith growth of a sub-sample (n) of adult white perch (N) collected across rivers. The proportional representation of contingents (FW: resident in freshwater, BR: dispersive fish in brackish water), or effective juvenile habitat, was estimated based on otolith chemstry and seine survey data.

			Effective Juveile Habitat			
		$\delta^{18}O_{VPDB}$	Otolith Chemistry		Seine Survey	
River	n (N)	Mean (SD)	BR	FW	BR	FW
Upper Bay	75 (612)	-7.91 (0.91)	0.31	0.69	0.28	0.72
Potomac R.	45 (588)	-7.36 (0.90)	0.35	0.65	0.46	0.54
Choptank R.	78 (551)	-6.42 (0.84)	0.55	0.45	0.89	0.11
Nanicoke R.	75 (627)	-4.92 (1.29)	0.81	0.19	0.83	0.17
York R.	75 (165)	-5.75 (0.83)	0.68	0.32	0.35	0.65
James R.	49 (139)	-6.44 (0.89)	0.82	0.18	0.21	0.79

Table 3. Areal coverage (km^2) and proportional areal coverage of freshwater (FW) and brackish water (BR) habitat across rivers. Percent of white perch contributed to the adult population on a per unit area basis (individuals/km^2).

	Areal coverage (km^2)			Proportional areal coverage		Otolith Chemistry		Seine Survey	
River	FW	BR	Total	FW	BR	BR	FW	BR	FW
Upper Bay	90.7	26	116.7	0.78	0.22	0.76	1.20	0.79	1.07
Potomac R.	46.8	65.3	112.1	0.42	0.58	1.40	0.53	1.15	0.71
Choptank R.	11.5	19.2	30.7	0.37	0.63	3.94	2.85	1.00	4.61
Nanticoke R.	2.3	32.2	34.5	0.07	0.93	8.12	2.53	7.38	2.58
York R.	11.5	12.9	24.4	0.47	0.53	0.43	1.13	0.86	0.59
James R.	74.8	60.3	135.1	0.55	0.45	1.60	6.33	6.91	1.59

FIGURES

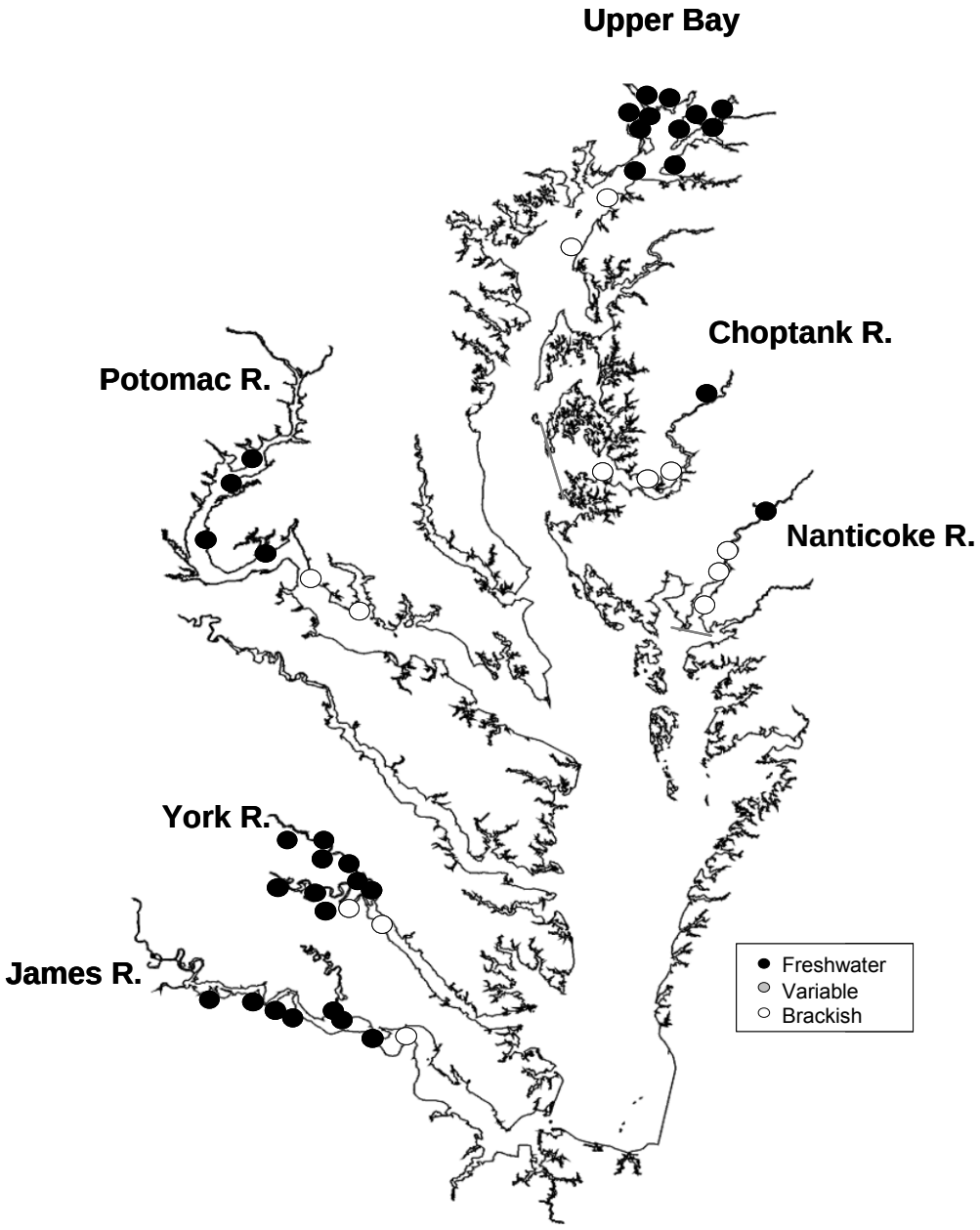


Figure 1. Map of Chesapeake Bay subestuaries, including Upper Bay, and the Potomac, Choptank, Nanticoke, James, and York Rivers where samples of adults collected for otolith chemistry analysis. Location of juvenile seine survey sites within brackish and freshwater habitat are shown.

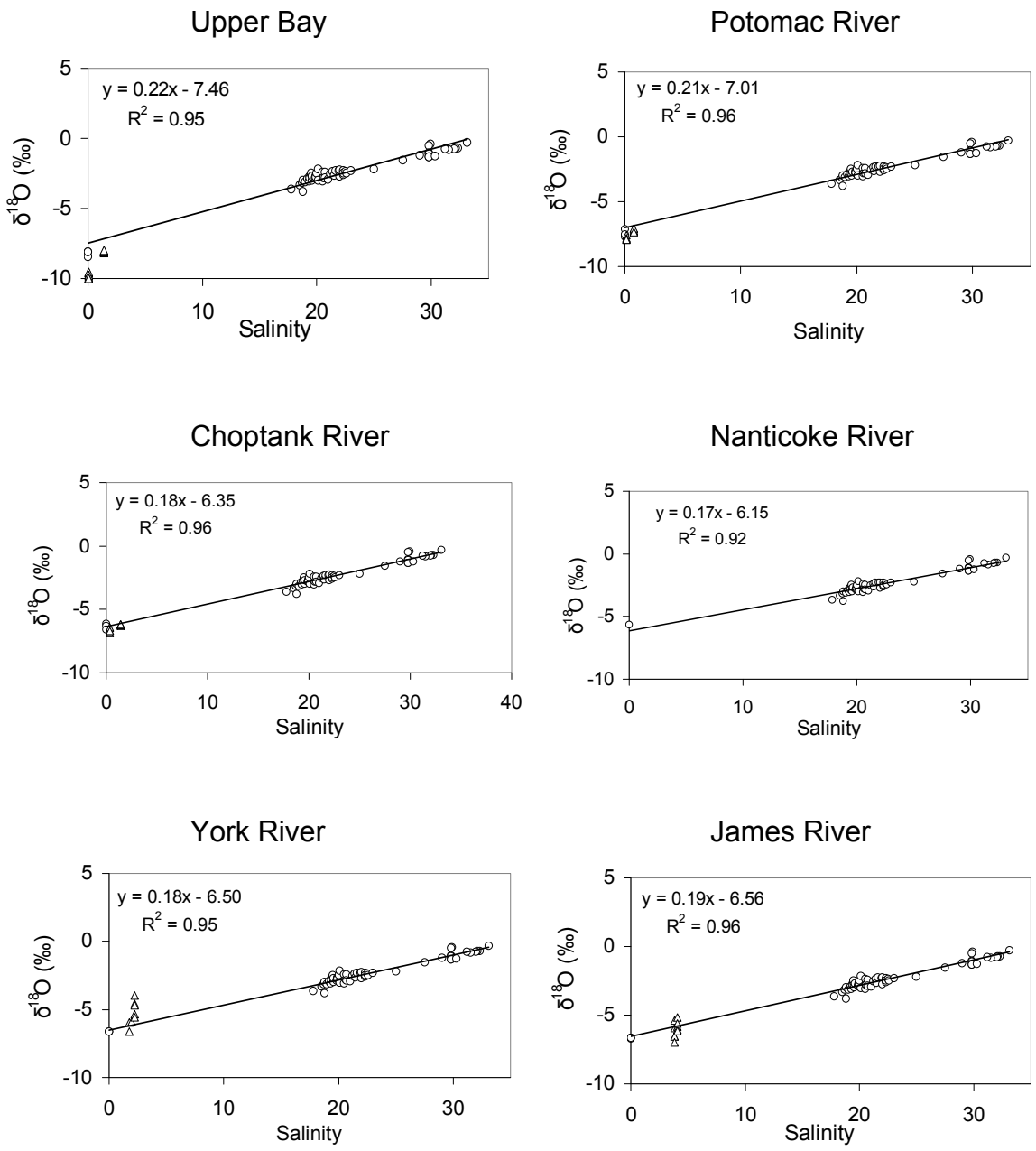


Figure 2. Mixing models of $\delta^{18}O$ across the salinity gradient within each river system. Open circles are water $\delta^{18}O$ values (freshwater (1985-1987; Coplen and Kendall 2000; Chesapeake Bay polyhaline water (Cronin et al. 2005) and Atlantic Shelf Water (Chapman et al. 1986; Khim and Krantz 1996)). Open triangles are otolith $\delta^{18}O$ values of yoy white perch collected in the freshwater habitat within each river-system (2006 and 2007) and analyzed for $\delta^{18}O$ to validate estimated freshwater end-member values. James River otoliths were collected in higher salinity waters (4). Water values were converted to Vienna Pee Dee Belemnite (VPDB) scale.

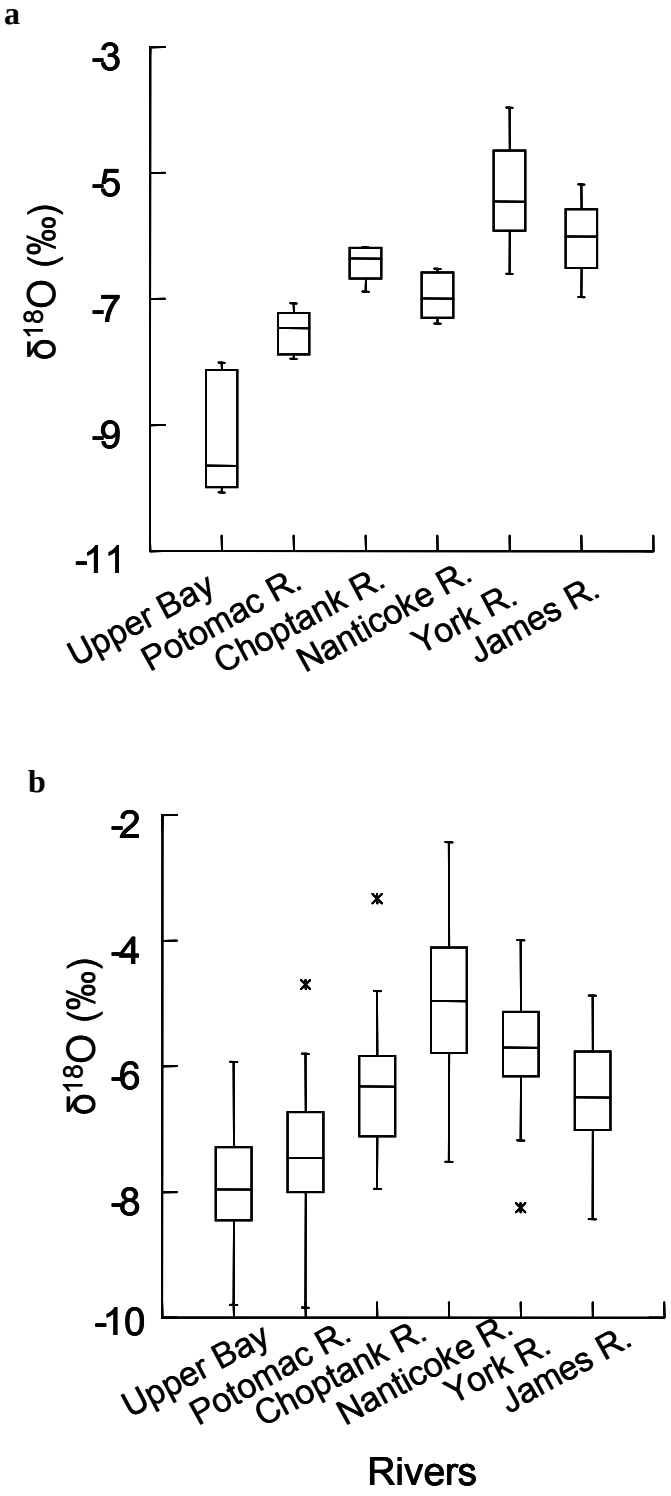


Figure 3. a) Geographic trends in otolith $\delta^{18}O$ values measured in yoy white perch and the b) juvenile period within adult white perch otoliths across estuaries in the Chesapeake Bay. Values were reported relative to a standard (Vienna Pee Dee Belemnite (VPDB) using international standards NBS-19 and NBS-18).

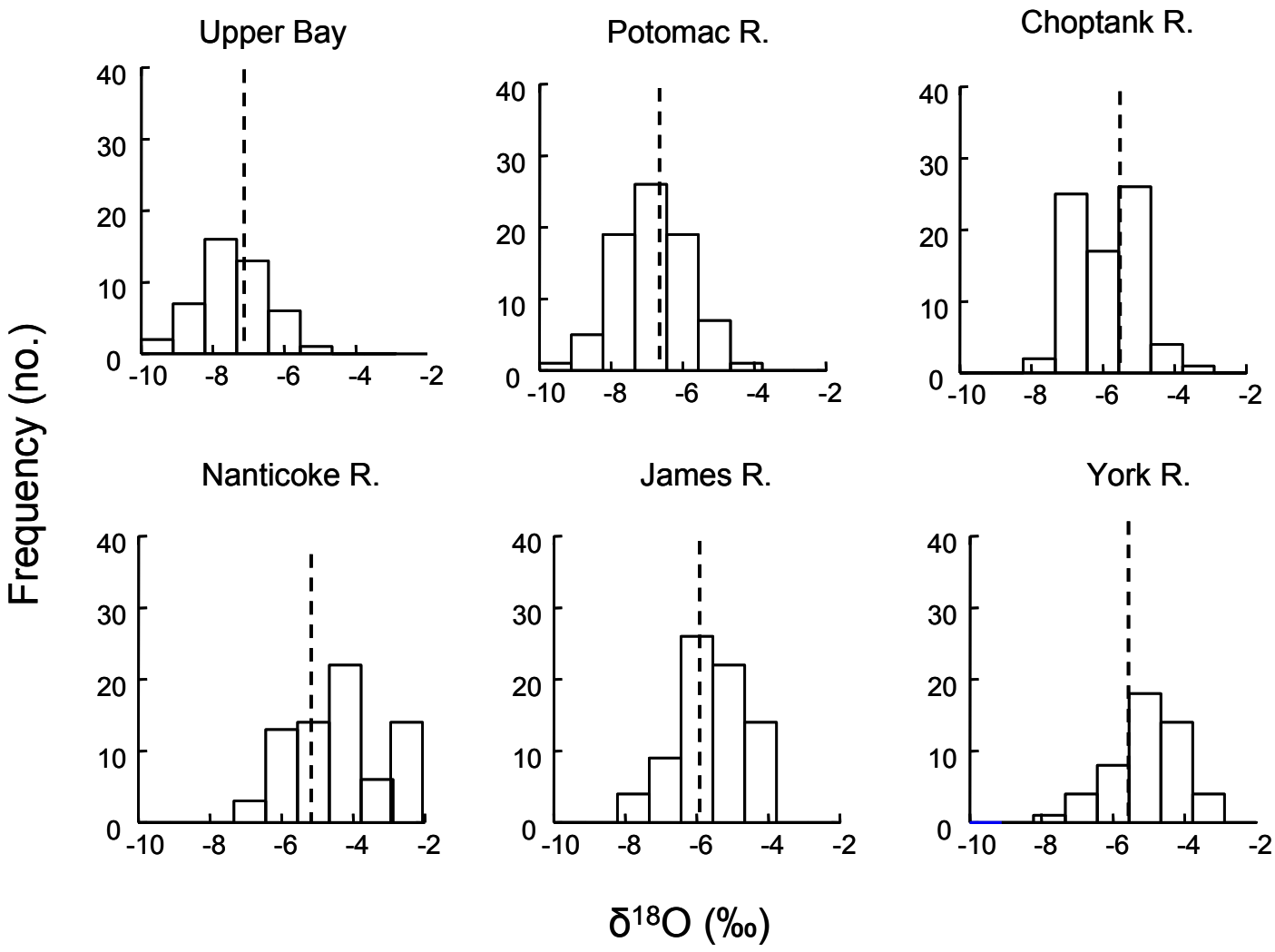


Figure 4. Frequency distribution of $\delta^{18}O$ (‰) values of year-1 growth in adult white perch otoliths within each river. Values were reported relative to a standard (Vienna Pee Dee Belemnite (VPDB) using international standards NBS-19 and NBS-18). The hatched line indicates the $\delta^{18}O$ threshold of the freshwater natal habitat within each river system.

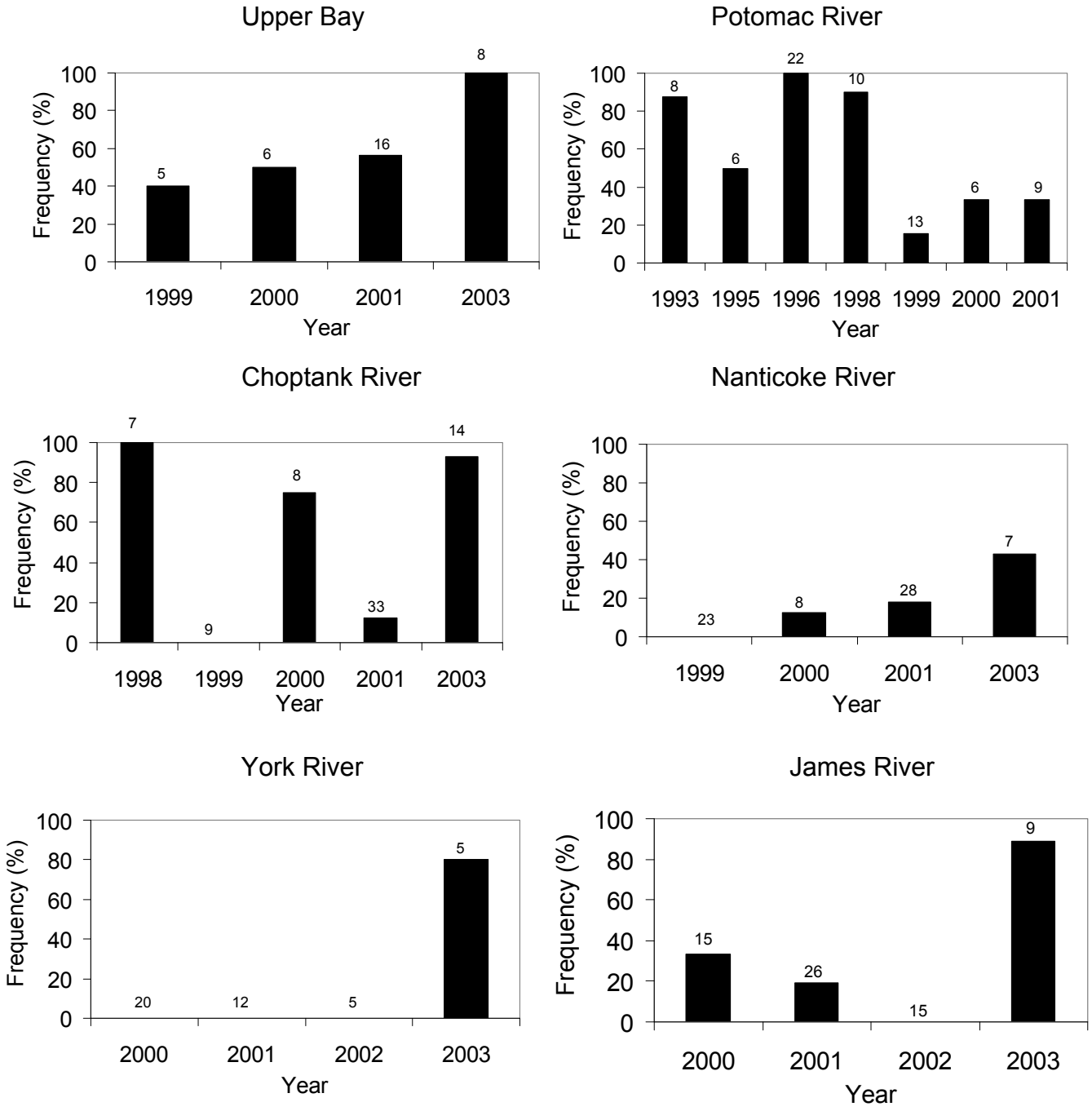


Figure 5. Interannual differences in the estimated contribution of freshwater habitat to white perch populations across sub-estuaries of the Chesapeake Bay Years shown are those for which there were $\geq$ 5 individuals in the year-class. Numbers above bars indicate sample size for each year-class.

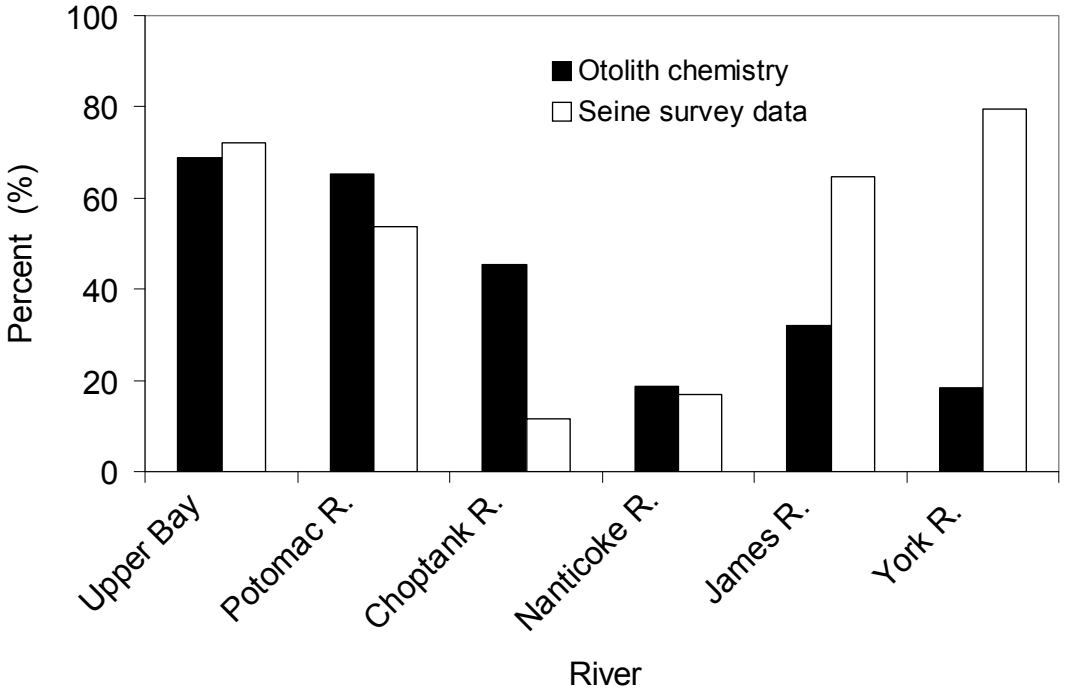


Figure 6. Estimated contribution of freshwater nursery habitat to adult populations of white perch in Chesapeake Bay estuaries based on seine survey data (open bars) and otolith chemistry (solid bars).

Chapter 7: THE ROLE OF SPATIAL DYNAMICS IN THE STABILITY, RESILIENCE, AND PRODUCTIVITY OF AN ESTUARINE FISH POPULATION.

ABSTRACT

Understanding mechanisms supporting long-term persistence of populations and sustainability of productive fisheries is a priority in fisheries management. Complex spatial dynamics is increasingly viewed as a plastic behavioral response that can contribute to population stability and resilience. Here, spatial dynamics and environmental forcing were incorporated in interacting local population models to examine the consequences to population stability (coefficient of variation of spawning stock biomass), resilience (time to recover from disturbance), and productivity (spawning stock biomass). White perch served as a model species that exhibits generalized resident and dispersive spatial life histories. The role that contingents, portions of a population exhibiting divergent spatial life histories, play in mitigating population responses to unfavorable environmental conditions was evaluated. Age-structured models incorporating contingent-specific vital rates were used to simulate population dynamics of white perch in a sub-estuary of Chesapeake Bay. The effect of contingent structure on the dynamics of the population was most sensitive to the proportion of individuals within each contingent, and to a lesser degree to level of correlated response by contingent to the environment. Increased levels of dispersive contingent representation within the population resulted in increased productivity and resilience, but decreased stability.

Negative correlation in the response of contingents to the environment resulted in increased stability and productivity, with little effect on resilience. Contingent structure is important in maintaining population persistence, highlighting the need to conserve spatial structuring within populations and to plan for spatial management of populations that includes habitat-specific regulations.

INTRODUCTION

In the past, the extensive range, abundance, and fecundity of many fish species had been thought to ensure that few populations were at risk of localized depletion or extinction (Huxley 1884). Today, the increased prevalence of stock collapse (e.g. Canadian stocks of Atlantic cod *Gadus morhua*) and long recovery time of exploited populations (e.g., select *Sebastes* populations; Jacobson and Cadrin 2002, MacCall and He 2002) indicates that features of these populations that contribute stability and resilience may be compromised. Stability is the ability of a population to maintain its integrity and persist despite disturbance, and resilience is the ability of a population to return to an equilibrium state after disturbance (adopted from McCann 2000). Management to mitigate the effects of environmental change and exploitation will require conservation of characteristics that promote the long-term persistence of populations. Increasingly, spatial structure within populations is viewed as a mechanism that can contribute to population stability and resilience by buffering population-level responses to unfavorable environmental conditions and preventing recruitment failure (Berkeley et al. 2004; Hilborn et al. 2003; Ruzzante et al. 2006; Bradbury et al. 2008).

Contingent structure is a type of spatial structuring whereby portions of a population exhibit divergent spatial tactics (e.g., resident and migratory behavior; Secor 1999). Spatial structure within populations can affect overall dynamics, because the distribution of individuals in space and time impacts their abundance, growth, reproduction, maturity, recruitment, and survival (Hayes et al. 1996). Additionally, intrinsic differences may exist between contingents based on the proximate cause (i.e., differences in growth rate; Chapter 3, Kerr and Secor *In Press*). Habitat-related or intrinsic differences in vital rates and productivity of contingents will have consequences to the contingent's response to the environment; as such each contingent carries its own risk of recruitment failure. Thus, divergent habitat use within a population may have the consequence of spreading out the risk of extinction in a population (Secor 2007). This type of phenotypic plasticity is underlain by genotypic flexibility and is thought to evolve in stochastic environments wherein it decreases the variance in individual fitness and increases geometric mean fitness (long-term fitness) across generations (Hopper 1999).

An important mechanism of community stability is the differential response of populations to environmental conditions (Doak et al. 1998, McCann 2000). The link made between asynchronous dynamics and stability has also influenced metapopulation theory, which focuses on the impact of spatial structuring of local populations on regional population persistence (Hanksi 1999). In fish populations, life history diversity was found to have a stabilizing effect on metapopulations due to differential responses of phenotypes to environmental fluctuations (e.g., differential response of spawning populations of sockeye salmon to environmental fluctuations; Hilborn et al. 2003). Thus, life history diversity, or biocomplexity is viewed as important to the sustainability of fish

stock complexes (collections of discrete spawning populations; Hilborn et al. 2003, Ruzzante et al. 2006). In this study, I argue that these same ideas extend to intra-population dynamics with divergent spatial tactics within a population contributing to its overall stability.

Depending on contingent-specific demographics and recruitment variability, contingent structure may have a positive or negative impact on productivity and resilience. Drawning from economic theory on investment strategy, consolidation of investment in high risk stocks may increase chances of catastrophic loss, but potentially can produce more rapid and higher earnings, compared to diversification of investments which reduces risk at the expense of profit. Likewise, diversification of a population into contingents potentially may decrease productivity and result in a longer time to recover after disturbance. Alternatively, if a population that is relatively stable, but not highly productive is diversified to include an episodically high yield contingent, then contingent structure within populations may enhance resiliency through a phenomenon termed the "storage effect", whereby potential for strong recruitments is essentially stored in the adult population (Secor 2007). Spatial structuring may confer a storage effect based on contingent-specific differences in recruitment, with episodic high recruitment of a single highly productive contingent promoting rapid recovery when appropriate environmental conditions are present.

The goal of this research was to incorporate complex spatial dynamics into a local population model and examine the consequences of spatial structuring to stability (measured as variance in spawning stock biomass), resilience (time to recover from disturbance), and productivity (long-term average spawning stock biomass) of the

population. Using white perch (*Morone americana*), a model species that exhibits life-cycle diversity, I illustrated the role that contingents, portions of a population with discrete spatial tactics, play in buffering population-level responses against unfavorable environmental conditions and recruitment failure.

The white perch (*Morone americana*) is an abundant fish in the Chesapeake Bay. Adults spawn in the tidal freshwater portions of estuaries in the spring, where eggs and larvae develop (Mansueti 1964). The white perch population in the Patuxent River estuary is a partial migratory population, with a portion of the population remaining resident in natal freshwater environments (resident contingent) and the other portion dispersing down-estuary to inhabit brackish water habitats (dispersive contingent; Kraus and Secor 2004a, Chapter 2). Based on otolith Sr/Ca profile analysis, divergence in spatial behaviors occurred during the juvenile stage, predominantly after the transition from larval to juvenile stage (Kraus and Secor 2004a, Chapter 2). Contingent structuring affected growth and recruitment rates (Kraus and Secor 2004a, Kerr and Secor *In Press*). During later juvenile and adult stages, growth rates of resident fish were lower than dispersive fish (Kraus and Secor 2004a, Kerr and Secor *In Press*). Recruitment rates of the dispersive contingent were correlated with the strength of the spring freshet in the Patuxent River (Kraus and Secor 2004a). The percentage of white perch recruits that were dispersive within a particular year-class ranged from 0 in drought years, 85% in low flow years, to 96% in high flow years (Kraus and Secor 2004a). Thus, the dispersive contingent dominated the composition of the year-class in both high and low flow years, the freshwater contingent was presented at low levels in high flow years, increasingly represented in low flow years, and exclusively present during drought years (Kraus and

Secor 2004a). These findings led to the hypothesis that the resident contingent behavior contributes to long term persistence, whereas the dispersive contingent contributes to population productivity and resilience (Kraus and Secor 2004a).

METHODS

Age-structured Model

Population dynamics of white perch in the Patuxent river estuary was modeled as two linked, contingent-specific, fully age-structured models. The parameters of age-structured models were derived from analysis of adult white perch otoliths from fish collections during the 2005 and 2006 springtime spawning season in the Patuxent River estuary and previously reported literature values (Table 1).

Age structured models included 13 age groups (age-0 to age 12). Recruitment or abundance at age-0 (N_0) was calculated by

$$\text{Age-0: } N_0 = \frac{B_1 * SSB}{B_2 + SSB} + error^{\varepsilon}$$

where SSB is the spawning stock biomass, B_1 is the maximum number of recruits produced and B_2 controls the rate at which the asymptote, or maximum recruits/spawner is reached (Table 1; Beverton and Holt 1957). The error term was modeled as the log-normal deviation associated with SSB.

Spawning stock biomass was calculated as a function of the number at age, weight at age, and fecundity at age of white perch

$$SSB_{(t)} = \sum_{a=1}^{a=12} N_{t,a} W_a P_a$$

where W_a is the average spawning weight (kg) of an age-*a* fish, P_a is the average fraction of age-*a* fish that are mature, and $N_{t,a}$ is the average number of fish of age-*a* at time *t* (Brodziak et al. 1998). A length-weight relationship was used to estimate weight at age (W_a, Table 2)

$$W_a = \alpha L_a^{\beta}$$

where L_a is length at age, α is a proportionality constant and β is the exponent. Length at age was estimated from contingent-specific von Bertalanffy growth equations (Kraus and Secor 2004a, Table 1 and 2).

$$L_a = L_\infty \left[1 - e^{-k(t-t_0)}\right]$$

where L_∞ is the asymptotic size, k defines the rate at which the curve approaches the asymptote, and t_0 is the hypothetical time at which the size of the fish is zero. The proportion of fish mature at age was assigned based on mean standard length at age (Mansueti 1961; Table 2).

Contingent dynamics were initiated at age-1 and contingent-specific population abundance at age-1 was calculated by

$$\underline{\text{Resident}}: \; N_{1(t+1),r} = N_0(1-D)e^{-Z_{l,r}}$$

$$\underline{\text{Dispersive}}: \; N_{1(t+1),d} = N_0(D)e^{-Z_{l,d}}$$

where N_0 = initial population size, D = the proportion of the year-class that is dispersive (i.e., disperses from the freshwater natal habitat), and Z_l = contingent-specific larval mortality (r = resident, d = dispersive). These formulations assume the probability of becoming a dispersive fish is not heritable. Larval mortality was modeled as a function

of streamflow, with the dispersive contingent having specific values for high flow (daily instantaneous mortality rate = 0.04 d^{-1}) and low flow years (daily instantaneous mortality rate = 0.11 d^{-1}), and no recruitment occurring in drought years (Table 1). Daily instantaneous larval mortality rate of the resident contingent was 0.13 d^{-1} in low flow years and ranged from 0.04 to 0.13 d^{-1} in high flow years (Table 1). Total larval mortality rates (dispersive contingent: high flow = 0.50, low flow = 1.54; resident contingent: high flow = 0.50 to 1.54, low flow = 1.54) were calculated using stage-duration estimates based on contingent-specific larval growth rates (dispersive = 0.5 mm d^{-1}, resident = 0.6 mm d^{-1}; Chapter 4: back-calculated contingent-specific growth rates 0-60 days). Levels of dispersive contingent representation (D) were varied to explore a range of realistic scenarios (see *Simulation*s description below). Abundance-at-age for ages 2 to 12 (N_2 to N_{12}) was calculated by

$$N_{a+1(t+1)} = N_{a(t)} e^{-Z_a}$$

where N_a = age-specific abundance, and Z_a = total adult annual mortality. Adult annual mortality rate (Mansueti 1961) was held constant at 0.56 across sex and contingent (Table1).

Environmental Stochasticity

Stochasticity was included in age-structured models as variability around the average percentage of the population that disperses (D) from the freshwater natal environment each year (variability ranged from 0 to 12%) in the Patuxent River estuary (Kraus and Secor 2004a). Additionally, drought years, in which there are no dispersive recruits within the population, were simulated at a rate of 20% (based on observations

from Kraus and Secor 2004a). Stochasticity also entered into stock-recruitment relationship as variation in number of recruits, calculated as inverse of the normal cumulative distribution for specified mean number of recruits and standard deviation (±10%).

Simulations

A series of 500 stochastic model runs, each conducted over a 150-year time period were performed for each model simulation (only the last 100 years were used in analyses to allow model to reach equilibrium). Simulations evaluated the impact of contingent representation in the population and correlation in contingent responses to the environment on the productivity, stability, and resilience of the overall population. To examine the consequence of changes in mean dispersal (D) within the population, three simulations were constructed with differing degrees of contingent structure (25, 50, and 75% dispersal). Additionally, two simulations were generated in which the white perch population was modeled without contingent structure, a model in which all fish were dispersive (D = 100%) and a model with only resident fish (D = 0).

To explore the impact of recruitment synchrony in contingent responses to the environment, differing levels of positive and negative correlation were explored. Correlation in year-1 recruitment between contingents was linked to the high/low flow response in larval mortality for the resident contingent. Values were varied to achieve the desired level of correlation between contingents (Table 1), ranging from positive (ρ = 0.90) to negative (ρ = - 0.85) correlation in recruitment.

Mean SSB was calculated as a metric of population productivity. Mean coefficient of variation (CV = SD/μ*100) of SSB was calculated as a measure of instability. Resilience was quantified as the number of years to rebuild the populations above mean SSB after a sequence of poor recruitment years. Poor recruitment years were incorporated in the model as a series of five years during which recruitment was 10% of maximum number of recruits (B_1 from the stock-recruit model). Additionally, simulations that encompass all pairwise combinations of dispersal and correlation levels were run to produce surface plots of productivity, instability, and resilience.

RESULTS

Contingent Representation Simulations (ρ = 0)

The overall productivity of the white perch population was sensitive to the relative abundance of contingents within the population. Mean productivity increased as levels of dispersal of age-1 white perch increased (Figure 1a). Across contingent representation simulations, ranging from 0 (entire population was resident in freshwater natal region) to 100% (entire populations was dispersive), mean SSB of the population ranged from 50,626 kg (D = 0%) to 120,966 kg (D = 100% dispersive). The modeled SSB of the fully resident population was only 42% of a fully dispersive population.

The population became more unstable with increased representation of the dispersive contingent (CV = 4 % at D = 0%; CV = 38% at D = 100%; Figure 1b). At high levels of dispersive contingent representation (D = 50 and 75%), relative variation in overall population SSB was high (27 and 34%, respectively), although there was a dampening effect (11 and 4 %, respectively) conferred from contingent structure. At low

levels of dispersive contingent representation (D = 25%) the CV was dampened by as much as 21%. Contingent structure, through increased representation of the resident contingent, had a positive effect on stability of the population. Mean instability of the fully resident population was about 10% of instability in a fully dispersive population.

Increased representation of the dispersive contingent decreased the number of years to rebuild the population. Across dispersal scenarios, the number of years to rebuild the population to average SSB after perturbation ranged from 10.8 (D = 100%) to 16.9 years (D = 0%; Figure 1c). Rebuilding time of the fully resident population was 57% longer than a fully dispersive population. Overall, the trend in resilience with respect to dispersal levels tracked closely with the trend in productivity of the overall population.

Correlation Simulations (D = 0.5)

The highest overall population productivity occurred in simulations with the highest level of negative correlation between contingents (ρ = -0.85, -0.75; Figure 2a). Productivity was also high in the simulation with the highest positive (ρ = 0.90) correlation. Simulations wherein contingents were slightly negatively to positively correlated (ρ = -0.25, 0.25, 0.50, 0.75) had lower productivity.

High negative correlation between contingents dampened the CV in the overall population and CV increased with increasing positive correlation between contingents (Figure 2b). A high negative correlation (ρ = -0.85) between contingents had a large effect on dampening variance in population fluctuations (12% decrease in CV relative to ρ = 0), whereas high levels of positive correlation (ρ = 0.90) increased CV of the

population (4% increase in CV relative to $\rho = 0$). Overall, changes in the degree of correlation between contingents did not have a large effect on resilience of the population (Figure 2c).

Dispersal-Correlation Pairwise Combinations

The response surface for productivity increased linearly with increased representation of the dispersive contingent within the population and showed a concave response to changes in correlation between contingents, particularly at low dispersal fractions (Figure 3a). The highest productivity occurred at combinations of high dispersive contingent representation and high negative correlation between contingents. The response surface of instability was steeper for contingent representation within the population compared to correlation levels, which exhibited an s-shaped response (Figure 3b). The highest levels of instability occurred at high levels of dispersive contingent representation and high positive correlation between contingents. Overall, the response surface for resilience was relatively flat, with the exception of a peak in rebuilding time at 0 dispersive contingent representation and dynamics that represents a high negative correlation between contingents (total larval mortality = 1.54 (high flow year), 0.5 (low flow year)) if contingent structure had been present (Figure 3c). Overall, the relative higher steepness of productivity and instability response surfaces to contingent representation, compared to correlation between contingents indicated higher sensitivity of both population productivity and stability to the relative abundance of contingents.

DISCUSSION

The basic structure and parameter estimates of simulation models were informed by in-depth research of the white perch population in the Patuxent River estuary of the Chesapeake Bay. The dynamics of each contingent in isolation reflected the patterns observed in the Patuxent River estuary. The dispersive contingent was specified as the more productive (i.e., higher growth rates, higher levels of recruitment), but more highly variable contingent, with occasional recruitment failure due to environmental conditions (i.e., drought). The resident contingent had lower productivity, but relatively stable recruitment over time. Model simulations revealed that recent estimates of high dispersive contingent representation (D = 85%, Kraus and Secor 2004a) and high positive correlation (ρ = 0.82 to 0.94; Kraus and Secor 2005b) between contingents, engender the white perch population in the Patuxent river with relatively high productivity, high resilience, and high instability, albeit a slightly dampened spawning stock biomass CV compared to a fully dispersive population. Because dynamics of the population are sensitive to relative abundance of contingents, and contingent representation is highly correlated with streamflow, it is easy to envision how changes in climate regime (i.e., periodicity of drought, high and low flow years) could dramatically alter the dynamics of Patuxent River population of white perch. Shifting the relative abundance of each contingent (i.e., the dispersal fraction) and the degree of independence in the contingent-response to the environment (ρ) enabled full evaluation of the roles each contingent plays in regulating population dynamics.

Simulations revealed that the response of the three population metrics examined (instability, resilience, and productivity) were most sensitive to shifts in the proportion of

the white perch population that dispersed from the freshwater natal habitat (D) and, to a lesser degree, the level of correlated response (ρ) of contingents to environmental factors (i.e., streamflow). Increased representation of the dispersive contingent within the population resulted in increased productivity and resilience, but decreased stability. Negative correlation in the response of contingents to the environment resulted in increased stability and productivity, with little effect on resilience. Overall, the freshwater resident contingent contributed to the stability of the population, reducing interannual variability in recruitment, whereas the contingent that dispersed into brackish water contributed to productivity and resilience of the population. The periodic high recruitment and higher productivity of the dispersive contingent contributed disproportionately to potential for rebuilding the overall population. These simulations provide evidence that contingent structure may contribute to population persistence.

Contingent representation and correlation simulations were designed to cover a range of possible population conditions that are biologically significant, encompassing the relative abundance of contingents and correlation scenarios identified in other white perch populations within sub-estuaries of the Chesapeake Bay. Stable isotope ($\delta^{18}O$) analysis of adult white perch otoliths from the Upper Bay, Potomac, Choptank, Nanticoke, James, and York Rivers (2005-2006) revealed evidence of contingent structure across estuaries, with varying levels of contingent representation (dispersive contingent comprised 31 to 82% of Chesapeake Bay white perch populations across year classes; Chapter 6). High levels of interannual variation in contingent representation were identified within these systems and are likely driven by environmental variability, thus shifts in climate could result in rapid and dramatic shifts in the contingent

representation within these populations (Chapter 6). Correlations in juvenile abundance between freshwater and brackish water habitat also ranged across and within systems (ρ = 0.21 to 0.96; Kraus and Secor 2005b). Thus, these simulations will inform our understanding of white perch population dynamics across sub-estuary populations within Chesapeake Bay.

Management strategies to promote population stability, productivity, or resilience through conservation of contingent structure within populations would require management of either the relative abundance of, or level of correlation, between contingents. Although it is difficult to envision managing the correlation between contingents because correlation dynamics are structured during early life history in response to the environment, we can potentially manage the relative abundance of each contingent through habitat or other conservation efforts aimed at a specific contingent or spatial management of exploitation in the fishery (i.e., focused fishing effort on more productive contingent). An important issue, however, will be how to rank performance indicators of productivity, instability, and resilience. Undoubtedly, different interest groups will give divergent weights to these performance indicators. Steele (2006) addressed this same problem in the context of weighting the importance of ecosystem metrics, suggesting that "we must accept that there is a societal or nonscientific element in assigning these weights — and work out a way to do this equitably". For white perch populations, the best management practice could be a balance in conserving contingent structure that would support both population growth and stability.

In this study, I examined the consequences of intra-population spatial structure to the persistence of an estuarine fish population. Spatial structuring within populations has

been documented extensively within diadromous fish populations (i.e., Salmonidae and Anguillidae). More recently, the importance of spatial structuring has been recognized in several marine fish populations (e.g. Atlantic cod, Smedbol and Wroblewski 2002, Ames 2004; Atlantic herring, McQuinn 1997; Atlantic bluefin tuna, NRC 1994) and I contend that it is more widespread than previously recognized in marine and estuarine species (Secor and Kerr *In Press*, Chapter 2). The degree to which the results of the white perch model can be generalized to other fish populations will be explored in future work through tailoring the model structure and parameters to other fish populations that exhibit spatial structure.

Overall, the results of this modeling exercise suggest the need to consider finer-scale management of fish populations and to reevaluate the concept of population integrity (i.e., the "unit stock", Harden Jones 1968, Cushing 1975). Partial migration has been accounted for in management of some salmonid populations (e.g. Pacific salmon, Knudsen et al. 1999). However, management for contingent structure has lagged in estuarine and marine fish populations. The importance of persistent representation of resident and migratory phenotypes, without genetic differentiation, as an evolutionary adaptation to a heterogeneous environment needs to be recognized within these populations and conserved. Including contingent structure in population assessments and fishery management plans may require higher resolution spatial surveys and more sophisticated population models. Despite the increased costs of these efforts, benefits to management will include more explicit performance indicators related to stability and resilience and increased efficiency of spatial management of fisheries, such as protection of essential fish habitat (EFH; Cadrin and Secor *In Press*). Additionally, increased

understanding of intra-population spatial structure may have ecological benefits, such as preventing extinction of unique life history patterns whose loss may have unexpected consequences to population dynamics.

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TABLES

Table 1. Parameter estimates used in age-structured models of white perch and their sources.

Parameter	Definition	Value	Source
B_1	Maximum number of recruits produced	1,985,000	Rothchild et al. 1992
B_2	Controls rate at which B-H reaches asymptote	1000	This study, estimated Beverton Holt parameter
Z_l	Total mortality over the larval period (total mortality was calculated from instantaneous mortality rates and stage-duration estimates. Contingent-specific larval growth rates were used to estimate duration of larval period based size at transformation).	Resident: 1.54 (dry yr.), 1.54 to 0.50 (wet yr.) Dispersive: 1.54 (dry yr.), 0.50 (wet yr.)	Chapter 3, Houde et al. 1989
Za	Mean total adult mortality (mortality held equal for both contingents and sexes)	0.56	Mansueti 1961
L_{inf}	Asymptote (mm)	217	
k (yr^{-1})	Rate at which the growth model approaches the asymptote	Resident: 0.39, Dispersive: 0.69	Kraus and Secor 2004a
t_0	Length at age-0	0	
α	Length-weight parameter	6.42E-06	Calculated from 2005 and 2006 Patuxent river adult white perch collections
β	Length-weight parameter	3.28	

Table 2. Length at age, weight at age, and proportion mature of female white perch from the resident and dispersive contigents.

Contingent	Age	Length (mm)	Weight (kg)	Proportion Mature
Resident	0	0.00	0.00	0.00
	1	70.08	0.01	0.00
	2	117.53	0.04	0.73
	3	149.65	0.09	0.98
	4	171.40	0.14	1.00
	5	186.13	0.18	1.00
	6	196.10	0.21	1.00
	7	202.85	0.24	1.00
	8	207.42	0.25	1.00
	9	210.51	0.27	1.00
	10	212.61	0.28	1.00
	11	214.03	0.28	1.00
	12	214.99	0.29	1.00
Dispersive	0	0.00	0.00	0.00
	1	108.16	0.03	0.00
	2	162.41	0.11	0.73
	3	189.62	0.19	0.98
	4	203.27	0.24	1.00
	5	210.11	0.26	1.00
	6	213.54	0.28	1.00
	7	215.27	0.29	1.00
	8	216.13	0.29	1.00
	9	216.56	0.29	1.00
	10	216.78	0.29	1.00
	11	216.89	0.29	1.00
	12	216.94	0.29	1.00

FIGURES

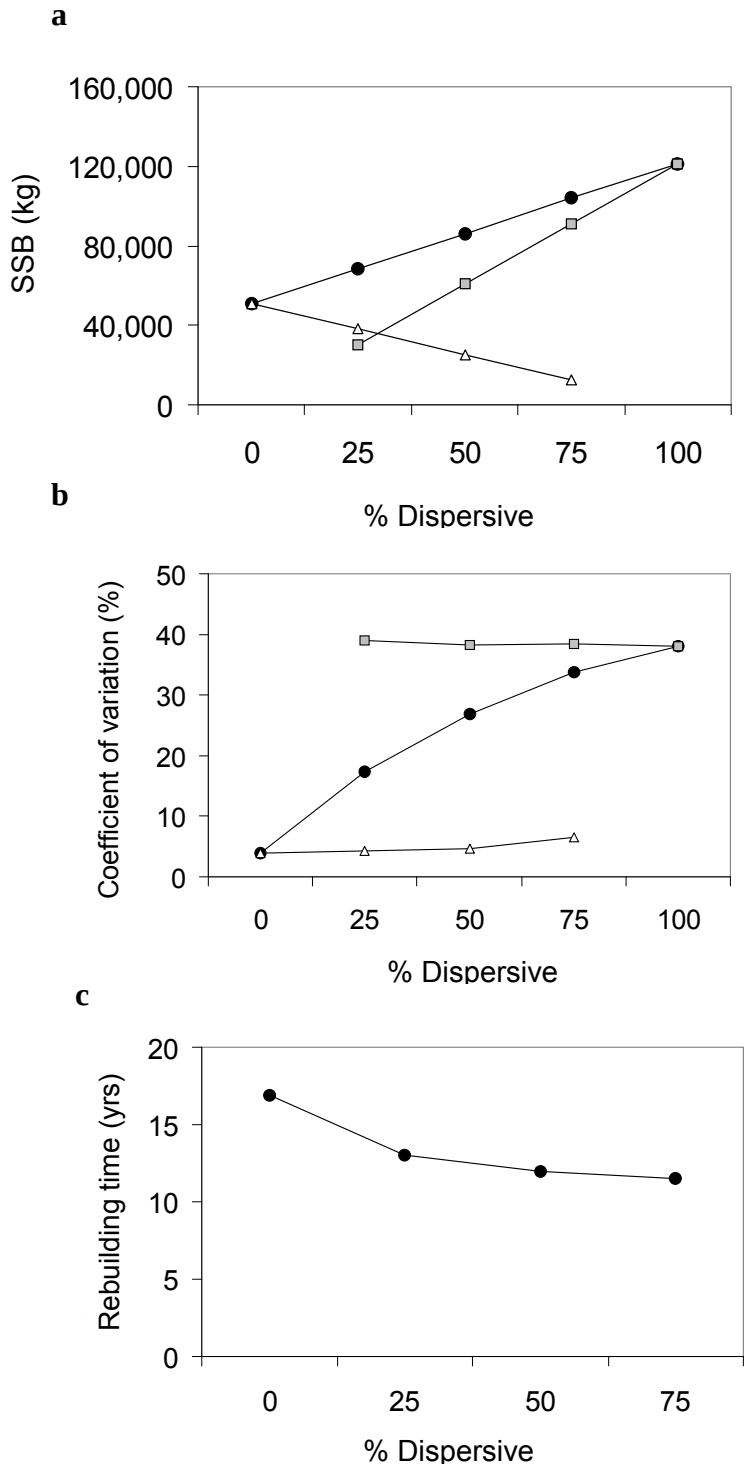

Figure 1. a) Spawning stock biomass and its b) coefficient of variation (%) of the resident (open triangle) and dispersive contingent (filled square) and overall white perch population (filled circle) across contingent representation scenarios (% of population that is dispersive, $\rho = 0$). c) Rebuilding time (years) for spawning stock biomass (c) of the white perch population across dispersal scenarios ($\rho = 0$).

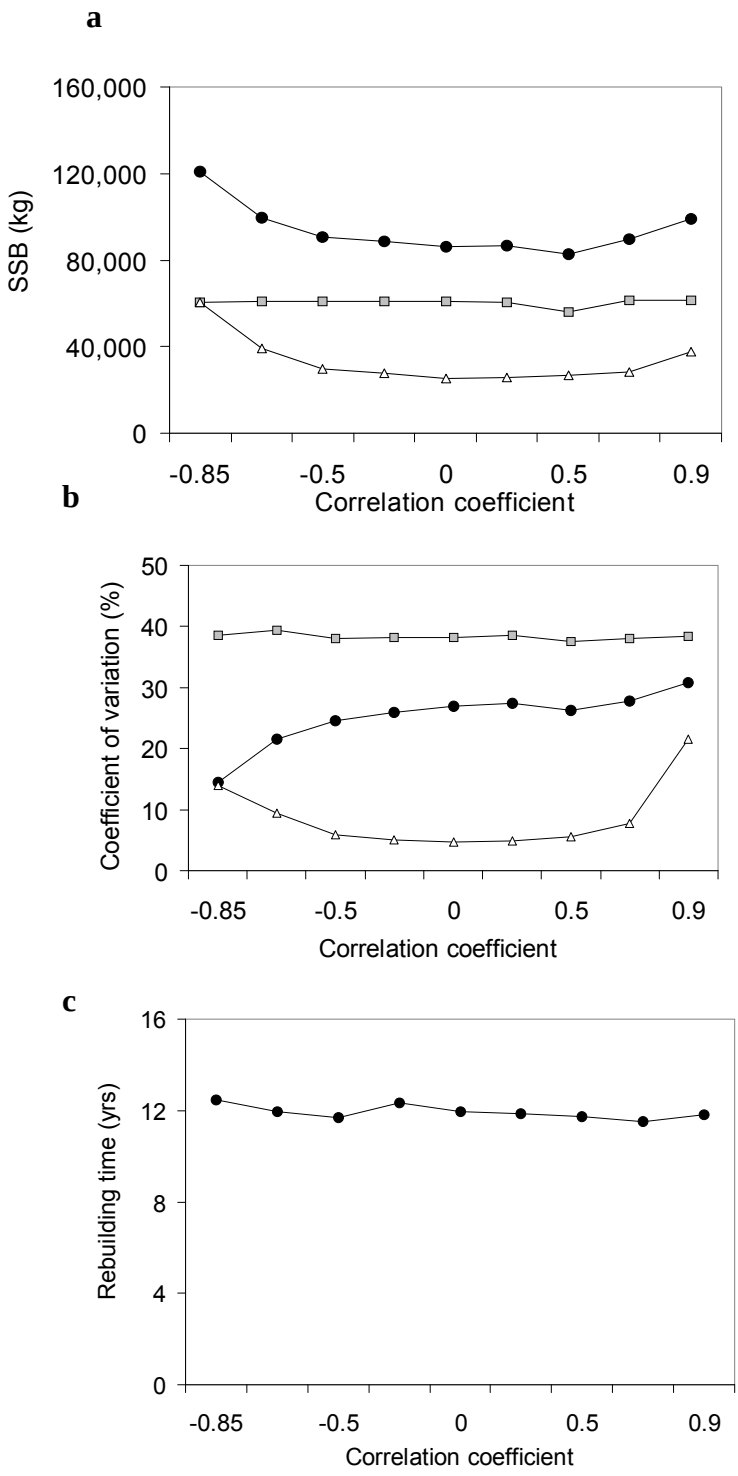

Figure 2. a) Spawning stock biomass and its b) coefficient of variation of the resident (open triangle) and dispersive contingent (filled square) and overall white perch population (filled circle) across a range of scenarios for recruitment synchrony (correlation; D = 50%). c) Rebuilding time (years) for spawning stock biomass (c) of the white perch population across a range of scenarios for recruitment synchrony (correlation; D = 50%).

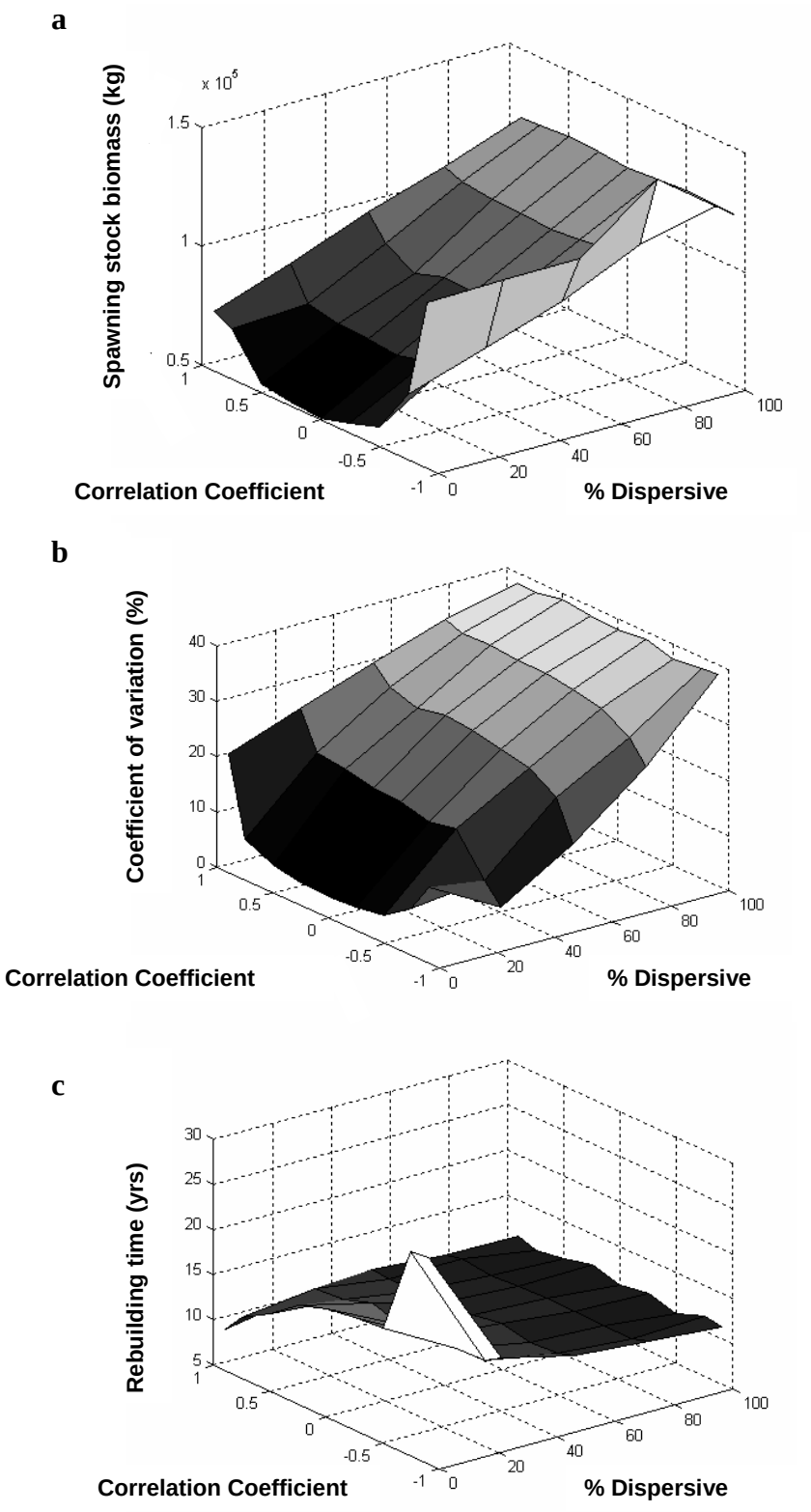

Figure 3. a) Surface plots of productivity, b) instability, and c) resilience across all pairwise combinations of dispersal and recruitment synchrony (correlation) between contingents.

APPENDIX 1: SUPPLEMENTAL RESULTS FROM CHAPTER 3

Table 1. Density (#/L) of zooplankton taxa known to be important white perch prey items (copepod nauplii, copepedites, adult copepods, rotifers, and cladocerans) across station and sampling date in the Patuxent River in 2005.

Date	Station	RK	Copepod Nauplii	Copepedite	Adult Copepod	Rotifers	Cladocera	Total
7-Apr	EH	45	5.6	72.2	398.9	0.0	1.1	477.8
	HC	48	3.3	5.8	5.3	1.5	2.4	18.3
	WL	59	0.0	1.0	2.4	0.0	0.7	4.0
	SC	62	3.6	7.2	7.8	0.0	5.3	23.9
	FL	66	4.3	5.3	6.1	1.7	3.5	20.8
	JB	72	6.7	4.6	2.5	0.8	2.2	16.8
	WF	75	7.5	2.5	0.6	3.5	3.3	17.4
21-Apr	EH	45	149.4	35.0	25.8	0.0	0.3	210.6
	HC	48	10.7	47.8	10.1	0.1	1.0	69.7
	WL	59	22.8	33.2	3.1	0.1	0.7	59.9
	SC	62	46.0	52.5	5.1	2.1	0.4	106.1
	FL	66	57.8	68.6	16.7	2.8	0.6	146.4
	JB	72	297.5	142.5	19.2	9.2	0.0	468.3
	WF	75	9.9	17.1	6.7	6.4	1.1	41.1
3-May	EH	45	93.3	70.6	8.9	0.0	0.6	173.3
	HC	48	10.3	11.4	0.3	0.0	2.2	24.2
	WL	59	8.1	4.4	0.0	0.3	2.2	15.0
	SC	62	42.5	12.2	0.3	0.3	8.1	63.3
	FL	66	32.2	8.1	0.0	1.1	5.0	46.4
	JB	72	48.6	18.3	0.0	1.7	6.9	75.6
	WF	75	12.6	5.3	0.4	1.9	2.5	22.8
19-May	EH	45	128.9	18.9	0.3	0.0	0.6	148.6

Date	Station	RK	Copepod Nauplii	Copepedite	Adult Copepod	Rotifers	Cladocera	Total
	HC	48	32.2	100.8	1.9	27.5	45.8	208.3
	WL	59	87.8	25.6	3.3	251.1	464.4	832.2
	SC	62	100.0	33.3	0.0	638.9	647.2	1419.4
	FL	66	10.0	53.3	0.0	1.7	286.7	351.7
	JB	72	33.3	66.7	0.0	427.8	369.4	897.2
	WF	75	13.3	21.7	12.8	16.7	41.7	106.1
31-May	EH	45	88.9	29.2	0.0	0.0	0.0	118.1
	HC	48	23.3	34.4	0.0	0.0	0.0	57.8
	WL	59	5.4	28.3	2.1	0.0	27.9	63.8
	SC	62	5.8	26.3	1.7	0.0	35.8	69.6
	FL	66	10.0	40.6	1.7	2.2	275.0	329.4
	JB	72	29.2	79.9	0.0	3.5	409.0	521.5
	WF	75	33.3	59.2	0.0	0.8	223.3	316.7

Table 2. Station, river segment, and river-wide abundance of yolk-sac larvae and feeding larvae sampled in 2005 in the Patuxent River estuary.

			Station		River Segment		River	
Date	Station	RK	Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)	Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)	Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)
4/7/2005	EH	45	4.67	0.00	6.55	0.00	425.27	0.00
	TP	47	1.87	0.00				
	HC	48	1.43	0.00	6.65	0.00		
	LM	51	5.22	0.00				
	WL	59	5.77	0.00	11.36	0.00		
	CH	60	5.59	0.00				
	SC	62	4.42	0.00	38.08	0.00		
	N	64	33.66	0.00				
	FL	66	9.72	0.00	59.98	0.00		
	LC	70	50.25	0.00				
	JB	72	133.41	0.00	278.67	0.00		
	PX	74	145.26	0.00				
	WF	75	23.99	0.00	23.99	0.00		
4/21/2005	EH	45	6.80	0.14	10.47	4.92	47.37	68.94
	TP	47	3.67	4.78				
	HC	48	5.56	23.79	12.95	45.96		
	LM	51	7.39	22.17				
	WL	59	2.30	6.31	5.12	12.90		
	CH	60	2.82	6.59				
	SC	62	5.49	1.81	13.58	5.00		
	N	64	8.09	3.19				
	FL	66	1.00	0.13	1.94	0.15		
	LC	70	0.94	0.01				

Date	Station	RK	Station Yolk-sac larvae (no. x 10^6)	River Segment Feeding larvae (no. x 10^6)	River Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)	Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)
	JB	72	0.89	0.01	1.76	0.01		
	PX	74	0.87	0.00				
	WF	75	1.55	0.00	1.55	0.00		
5/3/2005	EH	45	14.65	0.22	26.13	0.50	107.97	144.50
	TP	47	11.48	0.28				
	HC	48	2.77	6.11	23.02	57.39		
	LM	51	20.25	51.29				
	WL	59	24.53	31.31	34.16	43.60		
	CH	60	9.63	12.29				
	SC	62	7.08	13.54	15.75	35.95		
	N	64	8.68	22.41				
	FL	66	1.26	2.18	3.12	5.41		
	LC	70	1.86	3.23				
	JB	72	3.09	1.57	4.35	1.64		
	PX	74	1.26	0.07				
	WF	75	1.44	0.00	1.44	0.00		
5/19/2005	EH	45	0.24	0.00	2.14	0.68	14.43	86.67
	TP	47	1.90	0.68				
	HC	48	1.61	1.76	8.18	26.90		
	LM	51	6.57	25.14				
	WL	59	0.72	21.79	1.00	30.35		
	CH	60	0.28	8.55				
	SC	62	2.12	15.66	2.91	21.45		
	N	64	0.78	5.79				
	FL	66	0.00	4.62	0.00	6.33		

Date	Station	RK	Station Yolk-sac larvae (no. x 10^6)	River Segment Feeding larvae (no. x 10^6)	River Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)	Yolk-sac larvae (no. x 10^6)	Feeding larvae (no. x 10^6)
	LC	70	0.00	1.71				
	JB	72	0.03	0.53	0.05	0.97		
	PX	74	0.02	0.43				
	WF	75	0.14	0.00	0.14	0.00		
5/31/2005	EH	45	0.08	0.00	0.11	0.00	14.01	113.78
	TP	47	0.03	0.00				
	HC	48	0.78	6.59	3.75	31.57		
	LM	51	2.97	24.98				
	WL	59	0.65	16.62	0.91	23.14		
	CH	60	0.26	6.52				
	SC	62	1.42	14.36	3.53	35.59		
	N	64	2.10	21.23				
	FL	66	0.74	8.98	1.84	22.27		
	LC	70	1.10	13.29				
	JB	72	0.65	0.62	1.16	1.12		
	PX	74	0.52	0.50				
	WF	75	2.71	0.09	2.71	0.09		

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