

Dynamics of white perch *Morone americana* population contingents in the Patuxent River estuary, Maryland, USA

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ABSTRACT: Alternative migratory pathways in the life histories of fishes can be difficult to assess but may have great importance to the dynamics of spatially structured populations. We used Sr/Ca in otoliths as a tracer of time spent in freshwater and brackish habitats to study the ontogenetic movements of white perch *Morone americana* in the Patuxent River estuary. We observed that, soon after the larvae metamorphose, juveniles either move to brackish habitats (brackish contingent) or take up residency in tidal fresh water (freshwater contingent) for the first year of life. In one intensively studied cohort of juveniles, the mean age at which individuals moved into brackish environments was 45 d (post-hatch), corresponding to the metamorphosis of larvae to juveniles and settlement in littoral habitats. Back-calculated growth rates of the freshwater contingent at this same age (median = 0.6 mm d⁻¹) were significantly higher than the brackish contingent (median = 0.5 mm d⁻¹). Strong year-class variability (>100-fold) was evident from juvenile surveys and from the age composition of adults sampled during spawning. Adult samples were dominated by the brackish contingent (93% of n = 363), which exhibited a significantly higher growth rate (von Bertalanffy, $k = 0.67 \text{ yr}^{-1}$) than the freshwater contingent ($k = 0.39 \text{ yr}^{-1}$). Combined with evidence that the relative frequency of the brackish contingent has increased in year-classes with high juvenile recruitment, these results implicate brackish environments as being important for maintaining abundance and productivity of the population. By comparison, disproportionately greater recruitment to the adult population by the freshwater contingent during years of low juvenile abundance suggested that freshwater habitats sustain a small but crucial reproductive segment of the population. Thus, both contingents appeared to have unique and complementary roles in the population dynamics of white perch.

KEY WORDS: Population contingents · Estuarine-dependency · Otolith strontium · Electron microprobe · Back-calculation

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INTRODUCTION

A common feature of many fish populations is variation in migratory pathways evidenced by the simultaneous occurrence of individuals in multiple habitats during a given life stage. Density of individuals and vital rates (e.g. growth, survival and reproduction) can vary substantially among habitats, but it is not always clear how different habitats compare with respect to their contributions to the dynamics of population abun-

dance. For example during summer, inshore areas of the western Atlantic between Cape Hatteras and Cape Cod support a high abundance of the spotfin butterflyfish *Chaetodon ocellatus*, which recruits from more southern spawning areas. Although density, growth and survival of spotfin butterflyfish would indicate that these juvenile habitats are highly important, the northern juveniles are incapable of surviving winter conditions or migrating long distances to rejoin the southern part of the population; therefore, they die before they

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can make a reproductive contribution to the population (McBride & Able 1998). This example demonstrates the importance of tracing life-long individual migratory pathways to understand the role of different habitats within a population.

A discrete segment of a population that diverges spatially along an alternative migratory pathway during the course of life history has been called a contingent. First coined by Hjort (1914) and synonymous with 'life history type' (from the salmonid literature), the term contingent provides a useful means to classify habitat connections between successive life stages. For example, Clark (1968) described 2 striped bass contingents in the Hudson River estuary: one that would migrate annually from the river to coastal habitats and another comprised of individuals that were spawned in the river and never left. Secor et al. (2001) have since observed 3 contingents in the same population, and the migration patterns of these contingents have been used to explain individual variability in PCB (polychlorinated biphenyl) contamination of striped bass in the Hudson River (Zlokovitz & Secor 1999, Ashley et al. 2000, Zlokovitz et al. 2003). Another example of population contingents is seen in Japanese eels. Whereas eels (genus *Anguilla*) are typically considered to be catadromous, Tsukamoto et al. (1998) observed that a large fraction of the oceanic population of silver (spawning stage) eels showed no evidence of fresh water occupation (see also Tsukamoto & Arai 2001 and Limburg et al. 2003). Therefore, at least 2 contingents are present in Japanese eels. There are many other examples of fishes with population contingents, and Secor (1999) postulated that contingents were polymorphisms within a population where expression of a particular migration behavior was regulated by physiological performance in the early life history (see also Thorpe et al. 1998). Despite Secor's contingent hypothesis, the processes that make contingents a regular feature of some fish populations and the consequences of contingents to population dynamics are still poorly understood.

White perch (family Moronidae, Nelson 1994) in the Patuxent River estuary, Maryland (USA), represent a model system for studying the formation of contingents and understanding the role of contingents in population dynamics. White perch *Morone americana* Gmelin is an anadromous species endemic to estuaries of the northwest Atlantic. The ecology of egg and larval stages has received intensive study (Mansueti 1964, North & Houde 2001, 2003). In the Patuxent, spawning takes place during spring in tidal fresh water via upriver migration of adults from brackish feeding areas (Mansueti 1961). Pelagic larvae metamorphose into juveniles that settle in littoral environments throughout the estuary and remain there during sum-

mer and fall. Eventually, juveniles move to deeper areas with the onset of winter and colder water temperatures (Mansueti 1961, Klauda et al. 1988, Setzler-Hamilton 1991). Though the abundance of a given year-class is believed to be established primarily during egg and larval stages, it is not clear after these stages why some juveniles remain in tidal freshwater habitats while others disperse downstream to brackish areas or what consequences this divergence might have to the population dynamics.

In addition, tidal freshwater and brackish habitats of the Patuxent River estuary have distinct characteristics that may differentially influence these divergent segments of the population. In most years, white perch range within the Patuxent River from the junction with Chesapeake Bay at the mouth of the river upstream for approximately 83 km. About one-third of this length is tidal freshwater habitat (Fig. 1). Brackish and tidal freshwater habitats are separated by an apparent eco-physiological barrier (transition zone, Fig. 1) characterized by a steep chemical gradient of ionic ratios at salinities >0 and <3 (Deaton & Greenberg 1986). This frontal region represents a species minimum zone between freshwater and estuarine-marine assemblages where species turnover rates are highest for both benthic invertebrates (Boesch 1977) and littoral fishes (Wagner 1999). The stability of the salinity gradient contributes to the geographical identity of tidal freshwater and brackish habitats in the Patuxent River (Ulanowicz & Neilson 1974), and the ecosystem processes in these discrete habitats can vary significantly (Odum 1988). Thus, there is potential for juvenile white perch to encounter considerable differences in osmotic stress, prey resources, and predators between freshwater and brackish habitats.

Here, we investigated the concurrent and protracted occurrence of juvenile white perch in both tidal freshwater and brackish habitats of the Patuxent River estuary (Fig. 1). We hypothesized that the divergence of juveniles into freshwater and brackish habitats represents population contingents, and in this paper we present a description of the ontogenetic movements of white perch in the Patuxent River estuary. We applied methods using otolith structure and chemistry to study patterns of juvenile habitat use, identify contingents, relate juvenile habitat use to adult demographics, and examine how larval growth rate may contribute to contingent structure. Due to the difficulties in using conventional tracking or mark-capture approaches to study life-long individual migration patterns, we employed a variety of alternative approaches to address 3 main objectives. (1) To understand how the density and abundance of juveniles in freshwater and brackish habitats have fluctuated historically in the Patuxent River estuary, habitat specific catch rates

(index of density) and abundances were estimated from a state monitoring data set (1983 to 2001). (2) To characterize individual movements, we measured strontium in otoliths as a natural tracer of time spent in freshwater and brackish habitats. (3) To relate movement patterns to ages and lengths of individuals, we used counts of daily and annual rings and ultrastructural measurements within otoliths of larvae, juveniles, and adults. We employed otolith-based retrospective analyses and related larval and adult vital rates to juvenile contingent classifications.

MATERIALS AND METHODS

Historical survey data. Survey data (1983 to 2001) provided information on spatial distribution and the annual abundances of juvenile white perch from freshwater and brackish habitats. The Maryland Department of Natural Resources (MD-DNR) conducts an annual seine survey of juvenile striped bass to generate an index of recruitment for fishery assessments. Since 1983, the survey has been conducted monthly during July, August, and September. In each month, fixed sites (indicated by river kilometer in Fig. 1) were sampled with a beach seine, 30.5 m long by 1.24 m in height with a 6.4 mm mesh size. White perch were enumerated and separated into 2 groups, young-of-the-year and older individuals, based on visual inspection of sizes and prior experience with length frequencies. The minimum and maximum lengths of white perch in each group were also recorded (except from 1992 to 1997). In all, 420 observations of relative abundance were available for our analyses.

We calculated juvenile catch rates as $(\text{number in catch} + 1)/(\text{area swept})$, where the area swept equaled the area of the right triangle whose adjacent sides were defined by the distance offshore to which the seine was extended and the length of the seine net (30.5 m). Although the path of the seine does not trace this ideal triangle, we considered it a reasonable approximation of the area swept. Annual catch rate estimates were calculated as the geometric mean number of juveniles per m^2 at each site over the 3 sampling months. The geometric mean was used to satisfy the assumption of normally distributed residuals.

We also calculated juvenile abundance by expanding our catch rate estimates by the area of available littoral habitat. Littoral habitat area was tabulated from Cronin & Pritchard (1975) from the shoreline (at mean low water level) to the 2 m depth contour. We calculated this area for each nautical mile of the river from the junction at the mouth of the Chesapeake Bay to 83 km upriver. Because data for the littoral habitat area were unavailable for river km 63 to 83, littoral habitat was extrapo-

lated based upon a regression of cumulative littoral habitat on river km. The amount of littoral area associated with a given site was defined upstream and downstream by either the mouth of the river, the midpoints between sites, or river km 83 (whichever was appropriate). In addition, based upon the classification criteria (outlined in the 'Introduction') for freshwater and brackish habitats, we estimated annual abundance in each habitat by summing abundances for those sites with salinities below or above 3. The annual mean salinity at river km 53 varied around 3 (other sites were strictly brackish or freshwater, see Fig. 3).

The MD-DNR survey data used to produce the abundance estimates had the limitations of a fixed site sampling design, and there was no independent way to evaluate the trends in catch rates between habitats. Still, in previous studies, the MD-DNR survey has been used successfully to study white perch population dynamics (e.g. Wood 2000, North & Houde 2001). To support our use of these data, we evaluated whether area-expanded estimates of abundance were comparable to abundance estimates of the congeneric and sympatric striped bass, obtained by mark-recapture experiments (Minkkinen et al. 1995). White perch indices of recruitment were correlated with ($R = 93\%$) and on average twice as large as those of sympatric striped bass juveniles in the MD-DNR survey (1983 to 2001). In 1993, juvenile striped bass abundance in the Patuxent was estimated at 3.5 million (Minkkinen et al. 1995), and our area-based estimate of juvenile white

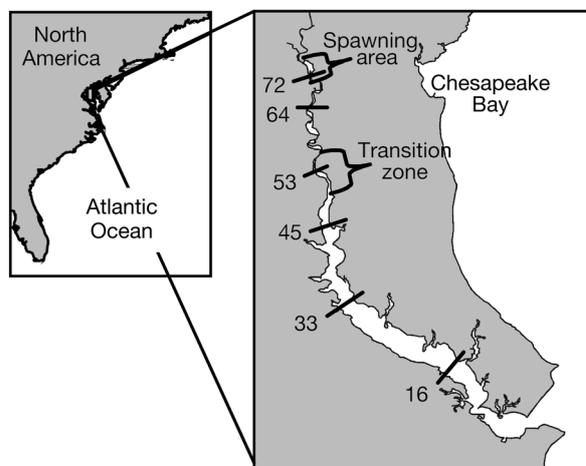


Fig. 1. The Patuxent River, a partially mixed estuary and tributary of the Chesapeake Bay. Seine survey sites used by the Maryland Department of Natural Resources are indicated by river km. The transition zone between tidal freshwater and brackish habitats is coincident with a change in geomorphology (the river widens), decreased current velocities, and the formation of a salt-front or maximum turbidity zone. The area in which spawning is concentrated is approximately between river km 71 and 75

perch abundance was 7.1 million, an approximately 2-fold difference as expected from comparison of seine survey indices. This exercise provided a coarse corroboration of our method of abundance estimation for white perch.

To facilitate analysis of inter-annual trends in abundance, a locally weighted linear regression (abbreviated here as LOWESS) smoothing algorithm was employed (Cleveland et al. 1988, Cleveland & Gross 1991). Graphical assessment of residuals was used to select a smoothing parameter, 0.3, that performed best with the available data.

Field collections. To sample littoral environments for juvenile white perch, we deployed a beach seine (same design as that used by MD-DNR in recruitment surveys) at 4 locations throughout the estuary. To maximize the potential of detecting variation in natal dispersal patterns, we sampled late in the season on 18 September 2001, before juveniles would move into deeper areas with declining water temperatures. From these collections, we randomly selected and applied our otolith assay (see following section) to 35 individuals collected at 2 freshwater sites and to 71 individuals collected at 2 brackish sites. Total length and weight was recorded for each individual. Unequal sample sizes from the different habitats reflected availability of juveniles.

White perch spawning aggregations in the Patuxent River support a small commercial fishery, from which we sampled adults caught in fyke nets. We collected all of our samples from 1 commercial fisherman who fishes throughout oligohaline and tidal freshwater habitats during the spring (B. Evans of Evans Seafood, Churchton, Maryland). We focused on 3 fyke net locations (approximately between river km 71 and 75, Fig. 1) that encompassed the focus of white perch spawning activity in the Patuxent River estuary (see also Mansueti 1961, 1964) and collected perch on 5 occasions in each of 2 consecutive years (2001: 10, 16, 24, 30 March, 5 April; 2002: 13, 21, 25 March, 1, 8 April). A similar period and duration of sampling were chosen in each year to ensure that most of the spawning season was sampled. All fish were measured (total length), sexed and otoliths removed. In a random subsample ($n \geq 40$) from each collection date, gonads were weighed and staged macroscopically, and body weight was recorded. Examination of gonads confirmed that individuals in our collections were spawning adults. For the otolith microprobe assay, individuals were randomly subsampled from our collections (2001: $n = 184$; 2002: $n = 179$), in approximately equal numbers by collection date and sex (length was random).

Otolith analyses. We examined otoliths from both juvenile and adult white perch to determine age, back-calculate length-at-age, and reconstruct environmen-

tal changes that reflected movements between freshwater and brackish habitats. The concepts and applications related to interpreting environmentally induced variability in the chemical chronologies of fish otoliths have been thoroughly reviewed (Kalish 1989, Secor et al. 1995, Campana 1999, Thresher 1999, Secor & Rooker 2000, Campana & Thorrold 2001). A principal concern is that environmental chronologies are difficult-to-impossible to interpret from periods of slow or zero growth in the otolith. Fortunately, white perch otoliths in our study area grow relatively continuously from hatching until winter (at least 8 to 9 mo), making them amenable to our application.

To infer individual movements between freshwater and brackish habitats and to characterize dispersal patterns, we constructed Sr/Ca chronologies in sectioned otoliths. For juvenile white perch in the Patuxent River estuary, we previously determined that brackish habitat use corresponded to >2 mmol Sr/mol Ca and freshwater habitat use (salinity <3) corresponded to <2 mmol Sr/mol Ca (Kraus & Secor 2004). Procedures for otolith preparation and for the electron microprobe assay of Sr/Ca were the same as those used by Kraus and Secor (2004). In transverse otolith sections, the ratio of strontium to calcium was measured at evenly spaced points along the ventral side of the sulcus, approximately perpendicular to the growth increments (Fig. 2). Each 'point' assay probed approximately $100 \mu\text{m}^2$ of the surface of the otolith section. A transect of points from the primordial region to the first annular increment (in adults) or the edge of the otolith (in juveniles) provided a chronology of Sr/Ca from which we inferred time spent in freshwater or brackish habitats during the larval and juvenile periods.

The daily age and length at which an individual moved from freshwater was estimated by counting increments from the primordium and back-calculating total length at specific locations within the chemical chronology of the otolith. These measurements allowed us to estimate larval growth rates from juvenile otoliths. To make complete increment counts, it was necessary to prepare the otolith section so that the primordium was visible. We accomplished this with consistency on juvenile samples (73%, $n = 106$, with primordium visible) but not on adult otoliths (33%, $n = 363$, with primordium visible). Consequently, we present here results of daily age from juvenile samples only. Back-calculation of total length was also limited to juvenile samples (see below).

To compare larval growth rates between all juvenile contingents, we back-calculated total length at ages of 20 and 45 d (the mean age-at-transition of the brackish contingent from fresh water to brackish water, see 'Results') by relating measurements of otolith radius to total length using the biological intercept method (Cam-

pana 1990). This method is a linear interpolation of total length from otolith radius given 2 endpoints: the otolith radius and total length at capture and the otolith radius and total length at hatching (the biological intercept). Otolith radii were measured in a straight line from the primordium to a landmark: either the growth increment of interest or the otolith margin on the ventral edge of the sulcus (see Fig. 2). With archived samples, we confirmed linear scaling and established a regression ($r^2 = 0.97$, $n = 107$) of otolith radius on total length (TL) that was constrained to pass through the observed values for the smallest individual that we measured (TL = 4.56 mm, radius = 15.2 μm). Data were available from a range of total lengths up to 63 mm, and the biological intercept parameters were estimated from the regression as a radius of 3.2 μm at TL of 3 mm at hatch. Due to issues of non-linear scaling between otolith measurements and total length in older fish (Secor & Dean 1992), we did not attempt back-calculation of transition lengths from adult samples.

To delineate characteristics of adult demography with respect to juvenile contingent membership, we assigned ages based upon annulus counts. The yearly formation of annuli has been validated for mature white perch using oxy-tetracycline marking techniques (Casey et al. 1988), and we verified annual periodicity of these marks in mature Patuxent River white perch by tracking a dominant 1996 year-class. Because different circumstances prior to maturation may influence the formation of annuli, it was also desirable to validate the formation of the first annulus (Campana 2001). We verified the periodicity of the first annulus by observing sectioned otolith samples from young-of-the-year and 1 yr old fish that were identified from length-frequency modes. We obtained these samples from MD-DNR surveys in the Patuxent River estuary. In an evaluation of aging precision, 2 readers independently interpreted annuli for each otolith, and there was perfect agreement between age assignments.

Validity of daily increments. Using samples from previous experiments with juvenile white perch (in Kraus & Secor 2004), we conducted an exercise to evaluate the accuracy of daily age estimation. Previously, daily formation of growth increments had only been evaluated in white perch larvae (<10 d post-hatch), and while the rate of increment formation was observed to be daily, the formation of the first growth increment varied by as much as 4 d, dependent upon temperatures experienced by embryos (Houde & Morin 1990). Daily increment formation has also been verified to occur for the congeneric and sympatric striped bass (Secor & Dean 1989). To verify the daily formation of growth increments in juveniles, fish were immersed in alizarin complexone to generate a mark

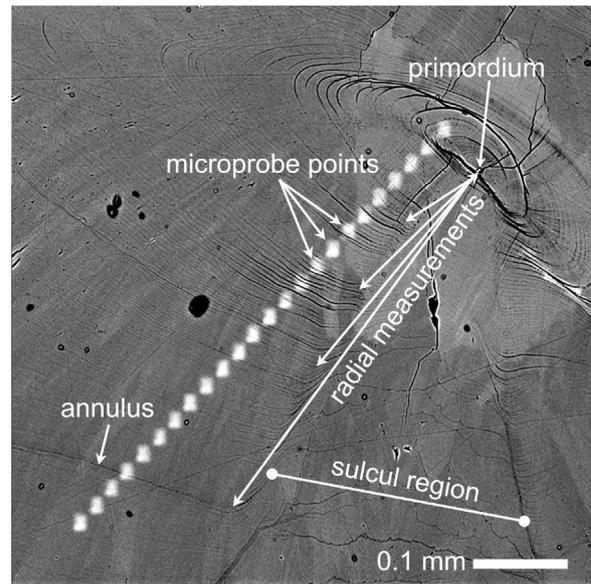


Fig. 2. Representative electron image of a transverse section of a white perch otolith. The image shows back-scattered electron density, highlighting daily, annual, and other ultra-structural features. A standard otolith radius was measured as the distance from the primordium to the appropriate growth increment along the ventral side of the sulcus. Microprobe transects were conducted along the ventral side of the sulcus to examine Sr/Ca chronologies in the first year of life. Along a transect, each 'point' assay resulted in a burn mark in the carbon coating, and these appear as white rectangles on the image

within the otolith chronology, and then placed into laboratory tanks or cages in the field (Kraus & Secor 2004). Using electron micrographs (see Fig. 2) and epifluorescent microscopy (to view the alizarin complexone mark), we found that perch that were marked and then held in our laboratory for 28 d exhibited a mean of 27 ($n = 67$, $SE = 0.22$) increments beyond the mark, and those that were marked and held in cages in the Patuxent River estuary for 29 d exhibited a mean of 28 ($n = 28$, $SE = 0.42$) increments beyond the alizarin complexone mark. Therefore, growth increments that we counted from electron microscope images (e.g. Fig. 2) provided reasonable estimates of relative (if not absolute) juvenile daily age.

Statistical analyses. Characterization of juvenile movement patterns from chemical chronologies in otoliths formed the basis of statistical comparisons. We observed 2 primary behavioral patterns with respect to change in otolith Sr/Ca before the first annulus: individuals that remained in tidal freshwater as juveniles (freshwater contingent), and those that moved to brackish habitats (brackish contingent). Growth was compared between contingents in 3 ways: (1) back-calculated estimates of early growth (prior to dispersal)

were compared with a Kolmogorov-Smirnov test (Sokal & Rohlf 1981) of the cumulative distribution functions; (2) using MD-DNR survey data, modal progressions of total lengths (juvenile growth) in either habitat type during July to September were compared with analysis of covariance (ANCOVA); and (3) parameters were compared between von Bertalanffy growth models, $L_t = L_\infty(1 - e^{-kt})$, that were fitted to adult size-at-age data using non-linear maximum likelihood estimation. L_t is length, t is age, k is a growth parameter with units of yr^{-1} , and L_∞ is an asymptote describing the theoretical maximum length. In the ANCOVA, the median value between the minimum and maximum length recorded for young-of-the-year white perch in each sample was used to estimate apparent growth rates of juveniles in freshwater and brackish habitats. These July to September growth rate estimates are apparent because they do not account for mortality.

Differences in relative survival between contingents from the juvenile to the adult period were examined on a cohort-specific basis. Annual abundance estimates were used to calculate the proportions of juveniles in freshwater and brackish habitats and these proportions were compared to the frequencies of brackish and freshwater contingents in each cohort of the adult samples with a 1-way chi-square test for specified proportions. A chi-square test of the proportions of male and female perch in each contingent was also conducted. All statistical tests were conducted using SAS[®] software, version 8.0 (SAS Institute).

RESULTS

Juveniles

Physical characteristics and spatial patterns of juvenile white perch from historical surveys demonstrated important differences between tidal freshwater and brackish habitats. In tidal fresh water, salinity was less variable, and the available littoral habitat was smaller than in brackish areas (Fig. 3). Brackish habitats were characterized by greater inter-annual variation in salinity and expansive littoral area (Fig. 3). In accordance with expectations that juvenile white perch do not tolerate salinity > 15 (Mansueti & Scheltema 1953, Setzler-Hamilton 1991), catch rates declined conspicuously at downstream sites with the highest salinities (Fig. 3). The highest variability in catch rates was observed at river km 53. Catch rates were similar but slightly lower for freshwater sites (salinity < 3) in comparison to oligohaline sites (salinity = 3 to 8), with median values between 0.5 and 1 individual per 100 m² of area swept by the seine.

Juvenile white perch abundance estimates varied over 100-fold during the period 1983 to 2002, with a maximum abundance in 1996 of over 37 million juveniles (river-wide). Smoothing by LOWESS provided a useful characterization of low (fitted values) and high (residuals) frequency variability in juvenile abundances. Whereas year-to-year fluctuations appeared stochastic (i.e. residuals were log-normally distributed and without temporal pattern), there was a trend of increasing juvenile abundance since 1983 that was evident in both the freshwater and brackish series (Fig. 4A,B). Although catch rates were often greater in tidal fresh water (Fig. 3B), overall juvenile abundances in brackish habitats far exceeded that of freshwater habitats (Fig. 4C), and this was due to the more expansive littoral habitat area in the brackish region of the estuary (Fig. 3C).

Juveniles sampled from freshwater and brackish habitats exhibited 3 distinct chronological patterns of

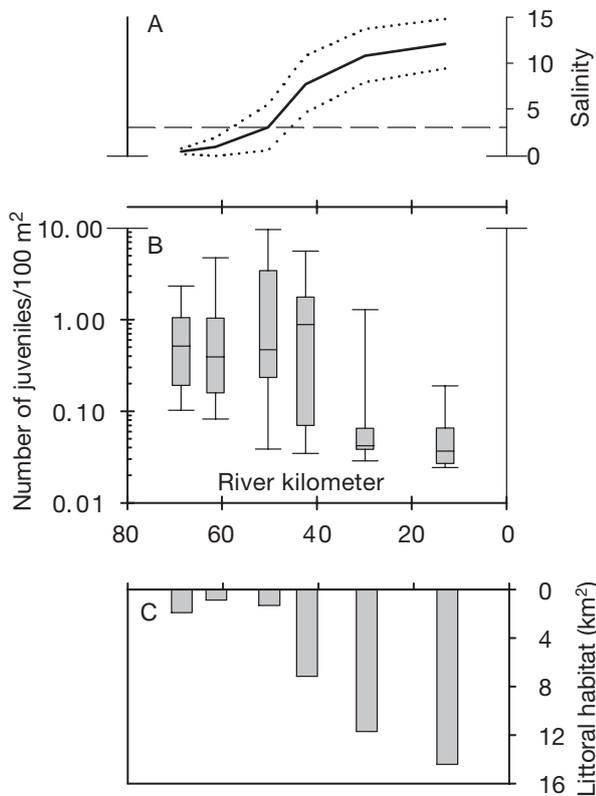


Fig. 3. (A) Salinity, (B) white perch catch rate, and (C) area of littoral habitat for 6 survey sites (see Fig. 1) within the Patuxent River estuary. At each site, the mean salinity from 1983 to 2001 (solid line) \pm 1 SD (dotted lines) is shown. A salinity criterion of 3 (dashed line) was used to categorize MD-DNR survey results as either freshwater or brackish habitats. The box-plots (logarithmic scale) show median annual white perch catch rates along with 10th, 25th, 75th, and 90th percentiles (outliers not shown)

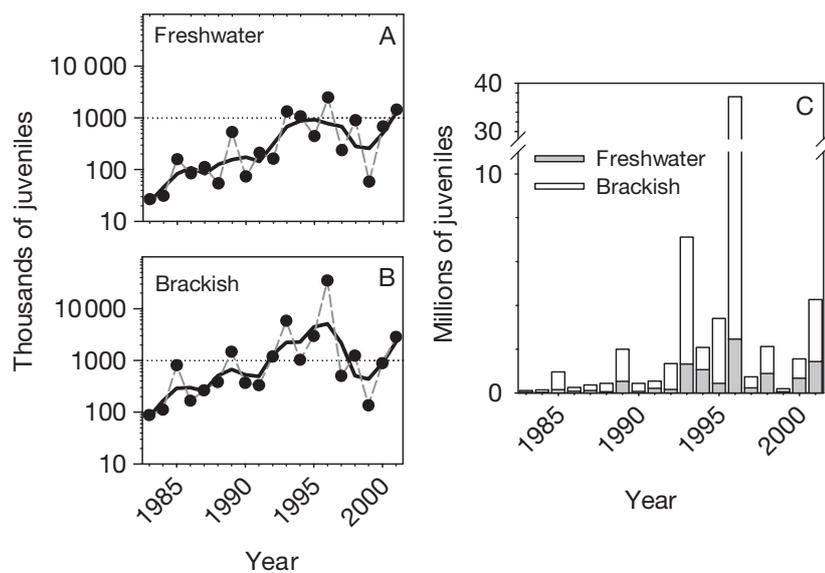


Fig. 4. Annual abundance estimates of juvenile white perch in the Patuxent River estuary. Estimates were based upon MD-DNR seine survey data collected from July to September at fixed stations. Abundances were calculated from survey catch rates (numbers per area swept) by extrapolation to the area of available littoral habitat (defined from the shoreline to a depth of 2 m, see text). Sites were classified as (A) freshwater (salinity < 3, $n = 2$ to 3) or (B) brackish (salinity > 3, $n = 3$ or 4), and the number of sites in each habitat varied due to fluctuations in mean annual salinity at one of the intermediate sites. Note that (A) and (B) have a log-scale vertical axis and the solid black line in these plots is a locally weighted regression (see text). (C) River-wide abundances on an arithmetic scale; the bars are divided according to habitat-specific abundances

otolith Sr/Ca variability (see Fig. 5): (1) all individuals sampled from brackish habitats ($n = 71$) showed a monotonic shift from low to high Sr/Ca (>2 mmol mol⁻¹) relatively early within the otolith chronology (Fig. 5A); (2) most individuals sampled from fresh water ($n = 30$) exhibited low Sr/Ca (<2 mmol mol⁻¹) throughout the otolith chronology (Fig. 5B); and (3) 5 individuals from freshwater sites had a dome shaped otolith Sr/Ca chronology (Fig. 5C). There was some unavoidable variation in starting locations of the transects near the primordia; therefore, the microprobe point number at which habitat shifts are indicated (Fig. 5) does not necessarily correspond with a particular age or otolith radius. Likewise, the last microprobe point did not correspond to the same age or otolith radius. The transitions in otolith Sr/Ca in juveniles captured in brackish habitats were indicative of a relatively rapid shift between freshwater and brackish habitats, rather than gradual movement through the transition zone. While this phenomenon appeared to be reversible (based upon the dome-shaped response in 5 individuals), residency in either freshwater or brackish habitats was established for the majority of juveniles that we examined, and this

period of residency corresponded approximately with the last 3 mo of life, July through September.

In the juveniles collected during September 2001, daily increment counts and back-calculated lengths indicated that juveniles that established residency in fresh water had accelerated larval growth between ages of 20 and 45 d when compared to the brackish contingent. Because a dome-shaped Sr/Ca chronology response was infrequent ($n = 5$) and was not observed in our adult samples, we did not consider this behavior in the following analyses. Age at transition for those juveniles moving into brackish water was estimated to be 45 d (SD = 7) after hatch, which corresponds to the age at which larvae begin to form scales, metamorphose into juveniles and settle in littoral environments (Mansueti 1964). While there was no significant difference between contingents in back-calculated growth rate at an age of 20 d, there was a significant difference in growth rates at 45 d (Kolmogorov-Smirnov test: KS test = 0.17, $p = 0.008$) (Fig. 6). In addition, estimated growth rates in both contingents fell within the range previously observed for Hudson River white perch larvae by Klauda et al. (1988).

During the July to September period of residency, juvenile growth patterns were markedly different from the back-calculated larval growth patterns in the 2001 samples. Based upon Sr/Ca chronologies that suggested residency of juveniles in either habitat during July through September, we assumed that measurements of total length from the MD-DNR survey would be independent between brackish and freshwater seine sites. While we did not detect a difference in apparent juvenile growth rate (length at date) between habitats in 2001, juveniles in brackish habitats were 5.6 mm (SE = 2.3) larger on average than those in fresh water (ANCOVA: $F_{1,10} = 5.9$, $p = 0.036$). In 2001, estimated juvenile growth from the survey data was 7.4 mm mo⁻¹. In 9 other years for which data were available, no significant difference in either growth rate or total length was detected between habitats. Significant inter-annual variation in juvenile growth rates in the Patuxent River was detected (ANCOVA: $F_{13,107} = 13.1$, $p < 0.001$), with estimates ranging from 4.8 to 13.1 mm mo⁻¹.

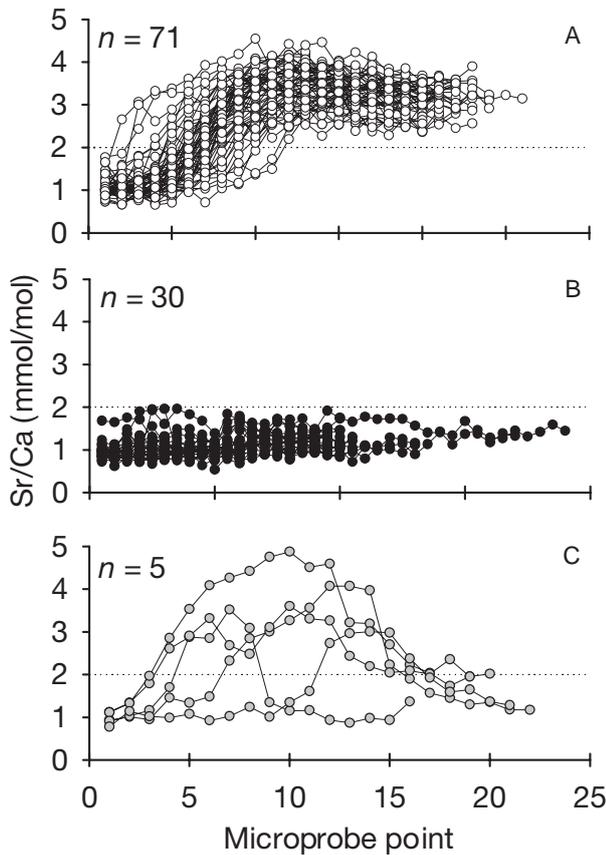


Fig. 5. Sr/Ca chronologies in the otoliths of 3 white perch contingents from the Patuxent River estuary. Shown are the microprobe results from juvenile white perch (n = 106) collected in September 2001 from (A) brackish and (B,C) freshwater sites. Microprobe points were ordered distally from the primordium and were evenly spaced at 25 μm . The horizontal dotted line in each panel represents the Sr/Ca criterion (2 mmol mol^{-1}) for distinguishing between times spent in either brackish or freshwater habitats. Note that there were some unavoidable differences between samples in starting location and transect angle; therefore, the first point in each transect does not always correspond to the larval stage

Adults

In the 363 adults that we examined, only 2 juvenile contingents were observed: those that were resident in fresh water as juveniles and those that dispersed to brackish habitats (based on Sr/Ca chronologies in otoliths). Unexpectedly, only 27 individuals (7%) were classified as freshwater residents during the juvenile stage, and the classification level was independent of sex ($\chi^2 = 0.01$, $df = 1$, $p = 0.92$). Most of the adults that we examined were between 2 and 9 yr old, but we also observed three 10 yr old and two 12 yr old individuals. There was broad overlap in sizes at ages (see also Mansueti 1961), but these dif-

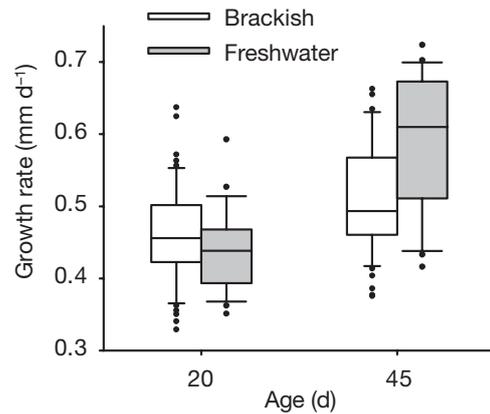


Fig. 6. Comparison of larval growth rates between freshwater (n = 23) and brackish (n = 54) contingents of juvenile white perch from the Patuxent River estuary. Growth rates were estimated with back-calculated lengths and daily otolith increment counts. The same groups of fish are compared at 2 ages (20 and 45 d). Box and whiskers show median values, and 5th, 25th, 75th, and 95th percentiles. The black filled circles are outliers

ferred with respect to contingent classification (Fig. 7). Comparison of von Bertalanffy growth curves between contingents showed that asymptotic length estimates were not significantly different (pooled $L_\infty = 217$ mm), but growth rate coefficients (k) varied sig-

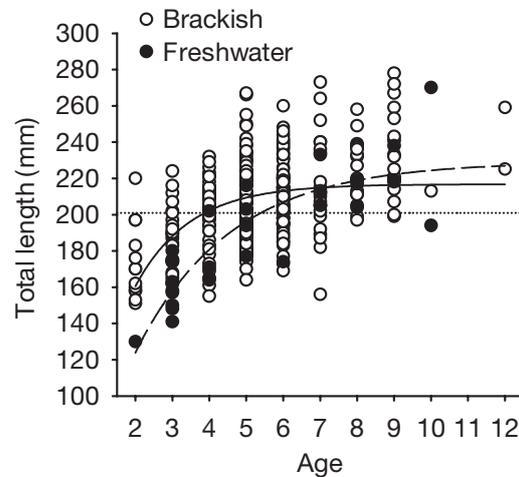


Fig. 7. Length-at-age of adult white perch sampled in 2001 (n = 184) and 2002 (n = 179) from spring spawning aggregations in the Patuxent River estuary (these numbers are combined). Individuals were classified as either brackish or freshwater contingents based upon natal dispersal behaviors inferred from Sr/Ca chronologies in otoliths. Separate von Bertalanffy growth curves were fitted to both the brackish (solid line) and freshwater (dashed line) groups. The horizontal dotted reference line indicates a minimum size limit in the commercial fishery

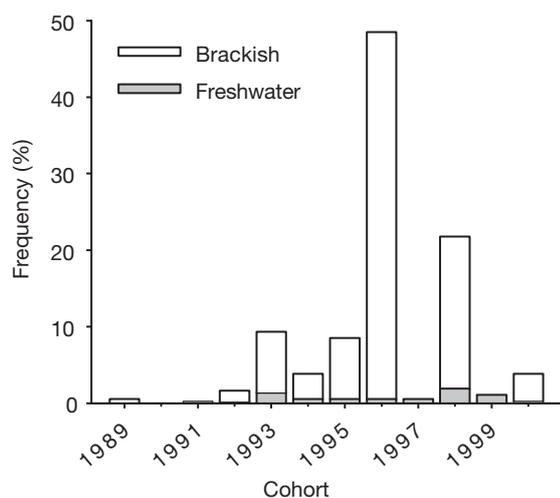


Fig. 8. Annual cohort frequencies of adult white perch sampled from spawning aggregations in 2001 and 2002 (combined, $n = 363$). The frequency is partitioned according to brackish and freshwater juvenile contingents. Cohorts were determined based upon capture year and age

nificantly (approximate $p < 0.05$). Adult white perch that dispersed from the natal habitat as juveniles grew faster ($k_{\text{brackish}} = 0.67 \text{ yr}^{-1}$, $k_{\text{freshwater}} = 0.39 \text{ yr}^{-1}$) and were larger, on average during the first 5 yr of life, than those that established residency in fresh water as juveniles (Fig. 7). Even when the single 2 yr old individual in the freshwater contingent was removed from the analysis, significant differences in growth remained and the rate did not change.

The distribution of samples with respect to cohort classification revealed the presence of at least 3 domi-

nant annual cohorts: 1993, 1996, and 1998. The 1996 cohort encompassed almost 50% of the individuals that we examined (Fig. 8) and was coincident with the highest juvenile abundance estimate (37 million; Fig. 4C). Although relative cohort strength and the proportion of contingents showed close similarity between juvenile abundances (Fig. 4) and composition of adult samples (Fig. 8), there was significant variation in contingent frequency within cohorts (see Table 1). Expressed as the proportion of total abundance in the Patuxent River, the fraction of juveniles in brackish habitats varied from 0.49 in the 1994 cohort to 0.93 in the 1996 cohort (Table 1). By comparison, the fraction of adults that were classified to the brackish juvenile contingent varied between 0.83 and 0.99 in those cohorts with >5 representative individuals (Table 1). In 4 of the cohorts (1994, 1996, 1998, and 2000), we observed a significant change between the juvenile and adult stages, and in all of these cases the relative frequency of the brackish juvenile contingent increased (Table 1). Further, in year-classes with the smallest adult representation in our samples (1989, 1991, 1997, and 1999), 7 out of the 9 adults that we examined were classified as the freshwater contingent. Though it is difficult to evaluate the oldest cohorts (1989 and 1991) because they have been exposed to the greatest life-long mortality risk, the 1997 and 1999 cohorts are relatively young and might be expected to have greater representation in the adult samples. Instead, these 6 individuals represented 22% of all adults classified to the freshwater contingent, and these cohorts exhibited relatively low overall recruitment success as indicated by juvenile abundance estimates (Fig. 4).

Table 1. Frequencies of brackish juvenile contingents within different cohorts of white perch from the Patuxent River estuary. Note that no individuals from the 1990 cohort were observed

Cohort	Binomial proportion		Chi-square (p-value) ^c	Total adults
	Juvenile survey ^a	Adult samples ^b		
1989	0.736	1.0	–	2
1991	0.612	0.0	–	1
1992	0.879	0.833 (0.152)	0.12 (0.73)	6
1993	0.814	0.853 (0.061)	0.34 (0.56)	34
1994	0.492	0.857 (0.094)	7.49 (0.006)	14
1995	0.870	0.935 (0.044)	1.17 (0.28)	31
1996	0.934	0.989 (0.008)	8.56 (0.003)	176
1997	0.678	0.0	–	2
1998	0.579	0.911 (0.032)	35.8 (<0.001)	79
1999	0.699	0.0	–	4
2000	0.565	0.929 (0.069)	7.52 (0.006)	14

^aEstimates from the juvenile survey were based on the annual abundance estimates
^bBinomial proportion estimates from the adult samples are presented with asymptotic standard errors
^cChi-square tests comparing within cohort frequencies between juvenile and adult observations were conducted when more than 5 adult samples were present

DISCUSSION

Demographic analysis coupled with otolith microanalysis showed that the behaviors of contingents are a fundamental aspect of white perch population dynamics. The dominant year-class phenomenon that we observed in white perch in the Patuxent River (typical of many temperate fishes) was structured by 2 contingents, one of which, the brackish contingent, represented the primary migratory pathway in the population. Strong year-class fluctuations (i.e. occurrence of dominant year-classes, Hjort 1914) were evidenced by 100-fold differences in juvenile abundance estimates from the MD-DNR survey data (Fig. 4) and by the dominance of the 1996 cohort in samples of adults (Table 1). In both freshwater and brackish habitats, recruitment fluctuated around a recent, 19 yr increasing trend in abundance (with a short-term decline between 1996 and 1999, Fig. 4). The phenomenon of episodic, strong year-classes has been documented for many species (see Mackenzie et al. 2003), and in white perch (as with many other species), efforts to explain year-class variability have had moderate successes (e.g. Pace et al. 1993, Limburg et al. 1999, North & Houde 2001). It appeared that once the year-class strength was established, almost all white perch from the Patuxent River that lived to reproduce followed a life history pathway in which they spent a large fraction of the juvenile stage in brackish environments (Fig. 8). This brackish contingent exhibited higher adult growth rates (Fig. 7) and higher relative survival (i.e. in 4 cohorts there was a significant increase in frequency of the brackish contingent between juvenile and adults stages; see Table 1) than the freshwater contingent. Thus, the abundance and productivity of this population are dependent upon strong year-classes, which primarily use brackish habitats during the juvenile stage.

The importance of brackish juvenile habitats to the dynamics of white perch in the Patuxent River estuary would not be immediately evident by comparison of densities (proxied here by catch rate) and vital rates between habitats. Survey catch rates of juveniles were highly variable and overlapping between sites in freshwater and brackish habitats (Fig. 3), and juvenile growth rate estimates were not significantly different between habitats. Further, evidence from back-calculated growth rates of juvenile samples from 2001 indicated that many of the individuals that moved to brackish environments exhibited poor larval growth compared to those that remained in fresh water (Fig. 6). It was not until the absolute representation of contingents was examined in terms of juvenile abundance and adult composition that the importance of brackish habitats became clear.

The processes that lead to the widespread occurrence of juvenile perch throughout the estuary appear to be involved in the dynamics of the larval and early juvenile stages. Back-calculated larval growth rates tended to be faster in individuals that remained in tidal fresh water (Fig. 6), and the age at transition in these samples was well defined at 45 d, suggesting that movement to brackish habitats occurred over a relatively short time during the early juvenile period. This result may represent developmental plasticity (*sensu* Thorpe et al. 1998), whereby failure to reach a genetically determined energy threshold evokes movement from the current habitat. Alternatively, it may simply be that faster growing larvae (freshwater contingent) can maintain their positions in tidal fresh water, while slower growing larvae are advected to brackish areas. Because of protracted spawning, growth in early life (and associated energy gain) might be substantially affected by temperature or other dynamic environmental conditions, and it would be desirable to determine hatch dates of juveniles from different habitats to gain more insight about flexible movement behaviors in white perch. Errors in counting daily increments increase with age, and beyond 65 d accuracy becomes questionable in congeneric and sympatric striped bass (Bulak et al. 1997). We did not attempt to estimate hatch dates because our samples were at least 100 d old.

Genetic differentiation could provide a mechanism for maintenance of the 2 contingents in successive generations. White perch are multiple clutch, group-synchronous spawners (Jackson & Sullivan 1995), meaning that groups of individuals spawn simultaneously several times during a season. Even though most of the adults were part of the brackish juvenile contingent, both contingents were captured together in an area well above the zone of transition between brackish and tidal freshwater habitats. Alternative hypotheses could be that either (1) the phenotypic identities of the freshwater and brackish forms are maintained by plasticity in the expression of a single genotype (reaction norm) or (2) the contingents are genetically distinct. These should be rigorously evaluated in order to better understand the evolutionary significance of population contingents in white perch. On the other hand, considering that adults of both contingents intermingle, follow the same seasonal migratory pathways (based on tagging data; Mansueti 1961), and have overlapping generations of spawners, assortive mating seems unlikely.

The demographic comparison of white perch adults based upon juvenile spatial behaviors was analogous to work on some Australian reef fishes by Gust et al. (2002), who observed that von Bertalanffy growth parameters in 4 species of reef fishes varied signifi-

cantly with position on the continental shelf. The differences were not based on genetic differentiation between the locations (Dudgeon et al. 2000). Rather, length differences between habitats were evident in the youngest individuals that were examined, and these differences propagated into the adult period. Thus, like the white perch, adult growth curve trajectories were partially established in the early life history. In addition, the adult growth curves indicated differential vulnerability of contingents to size selective fishing regulations in the commercial fishery on white perch. The brackish white perch contingent attained a mean size at Age 4 yr at which they entered the commercial fishery (fish < 203 mm are sub-legal and discarded), whereas the freshwater contingent did not reach this size until they were 5 or 6 yr old, on average (Fig. 7). Due to slower growth, the freshwater contingent experiences a delay in the effects of fishing mortality. Research is ongoing to determine whether the juvenile freshwater contingent continues to reside in fresh water as adults; preliminary evidence indicates that some, but not all, adults continue to reside in fresh water throughout their lives (D. H. Secor unpubl.).

The predominance of the brackish contingent in the Patuxent River white perch population could lead one to conclude that the freshwater contingent represents an insignificant (or anomalous) behavior and that tidal fresh water is a marginal habitat for juvenile perch. Similar to temperate butterfly fishes of the western Atlantic (McBride & Able 1998), the freshwater contingent may comprise individuals that settled in fresh water by chance and do not play a significant role in the population dynamics. Here we speculate that this is not the case, and that the freshwater contingent has an important and unique role in this population when one considers their life history strategy.

White perch have overlapping generations of adults, high fecundity (clutch sizes from 5000 to 320 000; Setzler-Hamilton 1991), low early life survival (9% d^{-1} in larvae; Houde et al. 1990), and delayed maturation (mature in second or third year of life; Mansueti 1961, Klauda et al. 1988), which are all characteristics of a periodic life history strategy (sensu Winemiller & Rose 1992). Periodic strategists tend to experience protracted episodes of poor environmental conditions that lead to low recruitment, punctuated by infrequent, high recruitment incidents (Winemiller & Rose 1992). In periodic strategists, reproduction almost always fails, in the sense that the survivors from a given annual cohort are usually insufficient to replace the adults. As an adaptation to mitigate failed recruitments, white perch spread their relatively large lifetime reproductive output across several spawning seasons (i.e. they are iteroparous with moderate longevity). Overlapping generations of spawners pro-

vide a 'storage effect' (Chesson 1984, Secor 2000) for reproductive potential, and when the infrequent (but eventual) conditions arise for successful reproduction, multiple generations can benefit (again the dominant year-class effect of Hjort 1914).

We propose that the distribution of juveniles throughout the estuary provides a similar adaptation as iteroparous spawning with a spatial (rather than temporal) 'bet-hedging' mechanism (Slatkin 1974). We observed in all years examined that at least some individuals recruited to both freshwater and brackish juvenile habitats (Fig. 4). The disproportionate changes in contingent composition (Table 1) indicated that at times both contingents represented behaviors (i.e. alternative migratory pathways) that were relatively unsuccessful or 'mis-fit' with environmental conditions (see Ulanwicz & Polgar 1980). Disproportionate changes in frequency favored the brackish contingent in some of the most abundant year-classes (Table 1 and Fig. 4). In contrast, years with relatively low juvenile abundance and low representation in the cohort composition of adult samples were disproportionately represented by the freshwater contingent. Most notable are the 1997 and 1999 cohorts in which all adults ($n = 6$) were classified to the freshwater contingent, but due to the low sample sizes these cohorts are not well defined. Despite the survey catches, the indication is that none of the brackish contingent survived to maturity in these year classes. While additional samples are needed to characterize the contingent composition of these cohorts, we suggest that the freshwater contingent may play an increasingly important role in the population dynamics of white perch in the Patuxent River estuary during periods of low recruitment. In terms of spatial bet-hedging, the freshwater contingent may be essential for maintaining a small but critical amount of reproductive potential.

When viewed in light of population contingents, the spatial dynamics of recruitment exhibited by white perch highlights a challenge for conservation-oriented habitat management. The challenge is that, even in this simplified example where a white perch population is classified according to its dependence upon 2 habitats, it is not clear how to prioritize goals between freshwater and brackish juvenile habitats. Brackish habitats contained the largest fraction of juveniles of the population, supported higher life-long growth rates, and had higher relative survival rates than freshwater habitats. If it is important to conserve the biomass production of white perch and the ecological role (impact) they have within the ecosystem (trophic level IV, Baird & Ulanowicz 1989), then management action might focus on the majority contingent and brackish environments. On the other hand, while freshwater habitats have little impact on population

dynamics, they are spatially restricted, which makes them more vulnerable to a given perturbation than brackish habitats, and they appear to be essential to sustaining reproductive potential (albeit low) during episodes of poor recruitment. Thus, if it is important to promote the viability of the population over the long term, then actions that affect minority contingent and freshwater habitats could be critical.

A partial solution to this conservation challenge is not to focus on single critical habitats, but rather to recognize the importance of habitat mosaics (e.g. Robinson et al. 2002). Fogarty (1998) demonstrated the effects of fishing on a spatially divided population of American lobster (*Homarus americanus*) that uses inshore and offshore habitats. Inshore lobster habitats supported higher biomass production and experienced higher fishing mortality than offshore habitats. Through simulating different levels of fishing mortality and larval subsidy from either habitat, Fogarty's (1998) results implied that inshore and offshore habitats made unique contributions to dynamics of the population and both habitats were necessary to sustain the population at its current abundance and fishing level. Therefore, rather than ranking habitats (as suggested by Beck et al. 2001), it is important to recognize a mosaic of habitats and the spatial behaviors that link them collectively as elements that have ecological significance.

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