

# Connectivity in estuarine white perch populations of Chesapeake Bay: evidence from historical fisheries data

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## Abstract

The role of complex life cycles in patterns of estuarine habitat use can be evaluated by studying stage-specific changes in abundances between principal habitats. Here, we evaluated how two primary habitats, tidal freshwater (salinity <3) and brackish water (salinity 3–15), structured juvenile white perch (*Morone americana*) abundance for eight sub-estuaries of the Chesapeake Bay. In addition, abundances of juveniles in the two primary habitats were related to indices of overall sub-estuary (population) adult abundance. Smaller sub-estuaries (e.g., Patuxent, Nanticoke, Rappahannock) showed higher juvenile abundances in brackish habitats whereas larger systems (e.g., Head of Bay, Potomac, and James) exhibited higher juvenile abundances in freshwater. Within each sub-estuary, we observed strong and positive correlations between freshwater and brackish juvenile abundances. Though adult abundance indices were poor predictors of juvenile abundance in either habitat, a significant amount of variability in adult abundance was explained by juvenile abundances in prior years for most sub-estuaries. The strength of the association varied by sub-estuary and habitat and suggested that juvenile habitats may make disproportionate contributions to the adult population, dependent upon sub-estuary. There were also significant correlations in juvenile abundance between sub-estuaries, indicating inter-annual synchrony in recruitment among populations. Within sub-estuaries, river discharge did not provide a direct indication of recruitment variability, and currently there is no clear explanation for correlation in juvenile abundances between sub-estuaries. Still, a positive association between correlations in river discharge and significant correlations in juvenile abundances supported previous hypotheses that freshwater flow may be an important factor influencing juvenile abundance, but it is likely that other environmental factors are also driving synchronous fluctuations in juveniles within and between Chesapeake Bay white perch populations.

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## 1. Introduction

Direct study of connectivity in the life histories of fish entails tracing individual ontogenetic movements at local (between habitats) and broad (between ecosystems) spatial scales. Quantitative knowledge of the movements from juvenile to adult habitats is important to support

conservation of nursery habitats (Beck et al., 2001) and to better understand the role of different habitats in spatially structured population dynamics. Unfortunately, in many fishes, the conventional mark-recapture approaches that provide such information can be difficult for larvae and young juveniles and impractical for life-long tracking of individuals (Secor, 1999; Thorrold et al., 2002). This situation has prompted studies that use natural tags such as otolith chemistry (e.g., Thorrold et al., 2000; Gillanders and Kingsford, 2003), but this

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novel approach has provided information on connectivity for relatively few species. Most studies that have elucidated aspects of connectivity in fish populations have done so indirectly through simulation modeling (e.g., Cowen et al., 2000), or with data on temporal changes in distribution that are related to abundance and size (Gillanders et al., 2003).

In an analysis of white perch from the Patuxent River estuary, one sub-estuary of Chesapeake Bay, otolith chemistry revealed differences in the relative contributions (“connectivity”, Gillanders et al., 2003) of juveniles from freshwater and brackish habitats to the adult population (Kraus and Secor, 2004). In this white perch population, most individuals that survived to reproduce utilized brackish habitats as juveniles. Currently, there are no otolith chemistry data from white perch populations in Chesapeake Bay apart from the Patuxent estuary (Kraus and Secor, 2004), and it is unknown to what extent juvenile habitat use may affect adult demographics in these other systems. In addition, tagging data, genetic evidence, and salinity preferences indicates that there is little mixing between white perch populations in the many sub-estuaries of Chesapeake Bay (Mansueti and Scheltema, 1953; Mansueti, 1961; Mulligan and Chapman, 1989; Setzler-Hamilton, 1991). Thus, sub-estuaries in the Chesapeake Bay each represent separate populations or sub-populations of white perch. Because data were available on juvenile distribution and abundance from fisheries monitoring series (Maryland Department of Natural Resources, MD-DNR, and Virginia Institute of Marine Science, VIMS, seine surveys), commercial fishery landings (MD-DNR), and environmental variables (Chesapeake Bay Program and United States Geological Survey monitoring), we viewed this as an opportunity to explore fluctuations in juvenile and adult abundances in several relatively isolated populations of white perch that were in close proximity.

Our primary objective was to characterize the variability in abundances of juvenile and adult white perch in multiple sub-estuaries of Chesapeake Bay. We compared spatial recruitment dynamics across sub-estuaries by quantifying associations between adult population size and abundances of juveniles in tidal freshwater and brackish habitats. Though this effort represents a basic descriptive analysis of Chesapeake Bay white perch population dynamics, we evaluated the results with respect to hypotheses about connectivity in the life cycle of white perch. First, we postulated that within a given sub-estuary, there would be a stronger association between juvenile abundance in brackish waters and adult abundance, indicating a greater dependency of the adult population on recruitment from that habitat. This represents an indirect study of connectivity because we were not able to determine the juvenile habitats used by adult white perch. Second, we

were interested in the processes that influence annual changes in juvenile abundance, as these processes (i.e., freshwater flow, temperature, and climate pattern) might provide insight to the associations between juvenile habitats and the adult population. We hypothesized that due to the limited mixing between populations (Mulligan and Chapman, 1989), juvenile abundances would fluctuate independently across sub-estuaries, but we accepted that sub-estuaries that were close in proximity might have similar environmental fluctuations that could result in inter-population correlations in juvenile abundances (the so called *Moran effect*, see Moran, 1953).

## 2. Methods

Several data sources were identified as relevant to evaluate juvenile and adult abundances in eight major sub-estuaries within Chesapeake Bay. These sub-estuaries were the Head of Bay, and the Choptank, Nanticoke, Patuxent, Potomac, Rappahannock, York and James Rivers (Fig. 1). White perch populations in these sub-estuaries are typically isolated by high salinities (>15) that are believed to represent a barrier to movement (Mansueti and Scheltema, 1953; Mulligan and Chapman, 1989; Setzler-Hamilton, 1991). The Head of bay sub-estuary is a conglomerate of several minor adjacent tributaries, including the Patapsco River, Gunpowder River, Elk River, Sassafras River, and others, but Head of bay is most influenced hydrologically by freshwater flow from the Susquehanna River tributary. Because a high degree of mixing between tributaries in Head of bay was expected based upon genetic similarity (Mulligan and Chapman, 1989), these tributaries were treated as a single group (Head of bay). Due to lack of data, other major sub-estuaries, the Chester, Pocomoke and Wicomico Rivers, were not characterized in this analysis.

### 2.1. Juvenile abundances

To characterize the dynamics of recruitment in each sub-estuary, juvenile abundances were estimated by area expansion of catch rates from seine surveys conducted by the Maryland Department of Natural Resources (MD-DNR) and the Virginia Institute of Marine Science (VIMS). We considered that catch rates were often equivalent between sub-estuaries; therefore, the catch rates alone did not account for differences in size between sub-estuaries or the absolute number of juveniles produced annually by each population. Moreover, our preliminary examination of the seine data revealed strong inter-annual expansions and contractions of the range of juveniles within brackish waters of the sub-estuary. Because available habitat (littoral area; defined from the shoreline to the 2 m depth contour) varied greatly between different parts of the

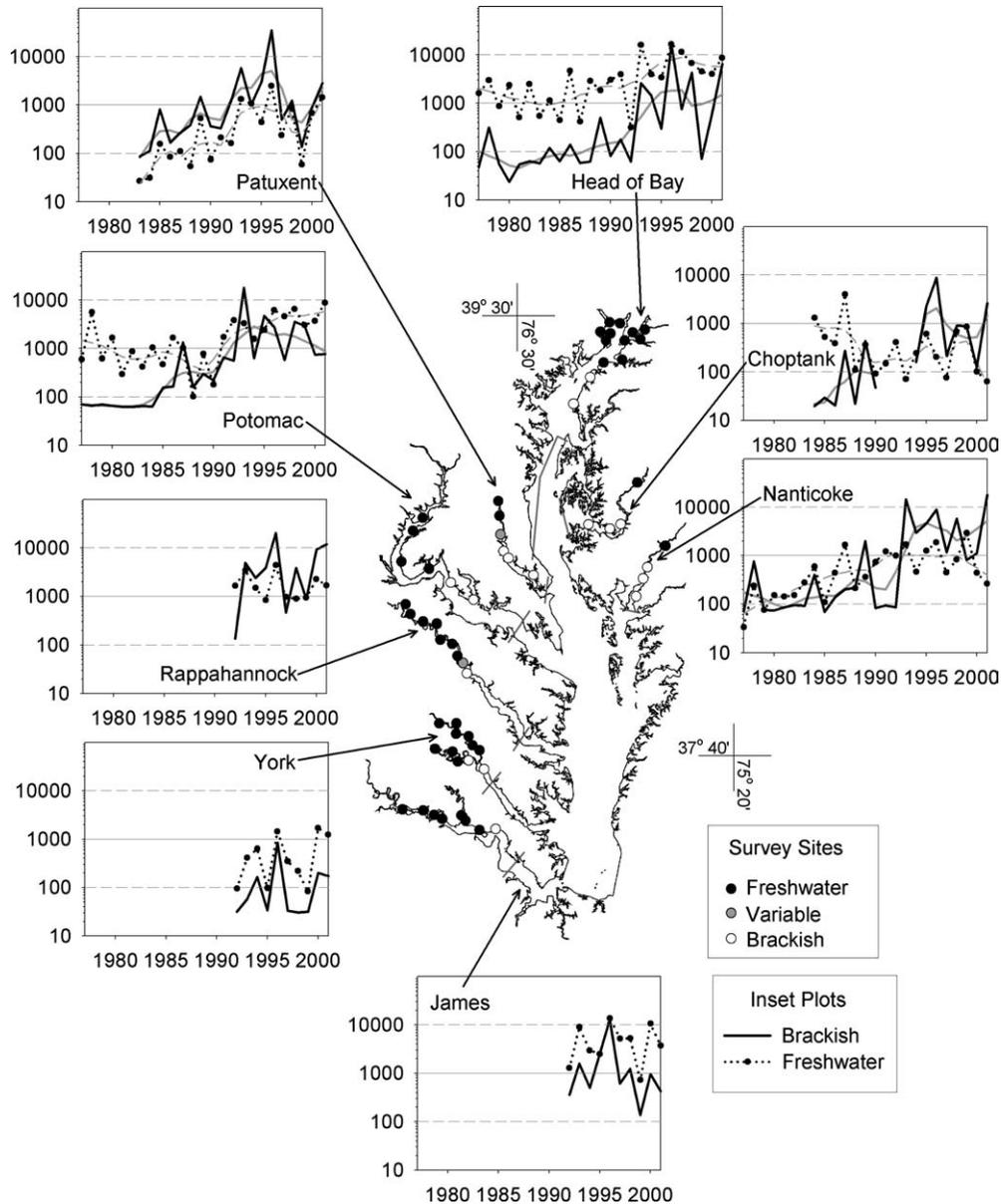


Fig. 1. Sampling distribution and habitat-specific white perch juvenile abundance (vertical axis=thousands of individuals) trends in major sub-estuaries of Chesapeake Bay. Seine survey sites are indicated on the map with dots representing classification according to mean annual salinity (see key; freshwater=salinity <3; brackish=salinity 3 to 15). Note that habitat classification varied at two sites, one each in the Patuxent and Rappahannock Rivers. The approximate position of the salinity=15 isohaline is also indicated on the map by a gray line. Estimated annual mean abundances of juvenile white perch are shown in the smaller time-series panels. In the Maryland sub-estuaries, LOWESS smoothed trends are shown for the brackish (solid gray line) and freshwater (dashed gray line) time-series.

estuary, catch rates alone were inadequate for understanding annual changes in abundance. No alternate means were available (e.g., mark-recapture studies) to estimate abundance; therefore, area expansion of catch rates was used to estimate juvenile abundance by sub-estuary and habitat type. On each survey, catch rates were calculated as the number of juveniles (+1) per area swept by the seine (see King, 1995, and Rueda and Defeo, 2001). Juveniles were rarely less than 30 mm total length and were easily distinguished from sympatric *M. saxatilis* (see Olney et al., 1989, and Murdy et al., 1997).

Seines were 30.5 m long by 1.2 m high with a 6.4 mm mesh size, and were deployed from shore. Area swept was calculated as 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. Because distance offshore was not recorded in early years of monitoring, estimates were only available since 1977 in Maryland and since 1992 in Virginia. Within years, 28 sites in Virginia and 33 sites in Maryland were sampled monthly from July to September, when juveniles were expected to be fully accessible to the

gear. Note that in Maryland estimates were made in all years between 1977 and 2001, except for the Patuxent and the Choptank. In the Patuxent, the series began in 1983, and in the Choptank the series began in 1984 (with missing data for freshwater in the Choptank from 1991 to 1993).

Annual abundance estimates for freshwater (salinity <3) and brackish (salinity 3–15) habitats in each sub-estuary were calculated as follows. At each seine site, the mean log-transformed catch rate for three sampling months of the survey was multiplied by the available littoral habitat (Table 1). For a given site, the available littoral habitat (taken from Cronin and Pritchard, 1975) had boundaries upstream and downstream that were defined either as the mid-point between two stations or as the long-term mean position of the salinity=15 isohaline (Fig. 1), the proposed limit of salinity tolerance for juvenile white perch (Mansueti and Scheltema, 1953; Setzler-Hamilton, 1991). Upstream boundaries of the freshwater habitat were defined by the upstream extent of tidal influence (Cronin and Pritchard, 1975). Site abundances were then summed within each habitat (freshwater or brackish) in each sub-estuary. Whether a site was classified as freshwater or brackish was determined based upon the mean annual salinity at that site. Except for one transitional site each in the Rappahannock and the Patuxent (denoted by “variable” in Fig. 1), site classification was invariant across years. In Head of bay, freshwater sites were distributed in close proximity and it was unclear how to estimate habitat area on a per site basis. Therefore, the mean catch rate from all Head of bay freshwater sites across the three sampling months was expanded by a single habitat area estimate.

Across the multi-year survey, correlations were estimated for juvenile abundances between habitats and sub-estuaries. Because inter-annual trends were evident, it was necessary to decompose abundance variability into low and high frequency patterns prior to correlation analysis; therefore, locally weighted linear regression (abbreviated here as LOWESS) smoothing algorithm was employed (Cleveland et al., 1988; Cleveland and Gross, 1991). The LOWESS approach is a local regression method, where a smoothing parameter defines a subset (local neighborhood) of observations that are weighted according to a function that declines with distance from the center of the neighborhood. The smoothing parameter specifies a proportion of the data and was selected at 0.3 for Maryland data. Graphical assessment of residuals was used to select the smoothing parameters that performed best with the available data. The fitted values were smoothed a second time (using the same parameters), and the residuals from this second pass were inspected to see whether large residuals or temporal patterns were present (indicative of a poor fit). LOWESS provided a useful characterization of Maryland data, with no temporal trends in the residuals. Diagnostic evaluation with a second LOWESS pass showed that the fitted values adequately represented the low frequency trends in these data. The smoothed values were used to represent the low-frequency long-term trends in the series and the residuals were considered representative of high frequency inter-annual variation. In Virginia sub-estuaries, the series were short (10 years) and relatively stationary (residuals of the mean had no temporal pattern); therefore, LOWESS smoothing was not performed on these data. Instead, data from Virginia were analyzed as

Table 1

Summary of ancillary data used to characterize temporal patterns of juvenile abundance, adult abundance, and environmental conditions in white perch populations of different sub-estuaries of Chesapeake Bay

Sub-estuary	Surface Area <sup>a</sup>			USGS Code <sup>b</sup> for River Discharge	Site Code <sup>c</sup> for Water Temperature
	Freshwater <sup>d</sup>	Brackish <sup>d</sup>	Total <sup>e</sup>		
Head of Bay	90.7	26	650	01578310	CB1.0
Choptank	11.5	19.2	244	01491000	ET5.1
Nanticoke	2.3	32.2	68	01489000 <sup>f</sup>	ET6.1
Patuxent <sup>g</sup>	2.8, 4.1	34.6, 33.3	97	01594440	TF1.5
Potomac	46.8	65.3	628	01646500	TF2.2
Rappahannock <sup>g</sup>	23.8, 32.2	72.0, 63.6	222	01668000	TF3.2
York	11.5	12.9	71	01674500 <sup>h</sup> , 01673000 <sup>i</sup>	TF4.2 <sup>h</sup> , TF4.4 <sup>i</sup>
James	74.8	60.3	266	02037500	TF5.6

<sup>a</sup> Estimated from Cronin and Pritchard (1975) in km<sup>2</sup>.

<sup>b</sup> Data obtained from USGS website (<http://waterdata.usgs.gov/nwis>).

<sup>c</sup> Data obtained from Chesapeake Bay Program website (<http://www.chesapeakebay.net/data/index.htm>).

<sup>d</sup> Littoral area from shoreline to depth of 2 m at mean low water.

<sup>e</sup> Inclusive of all depths at mean low water.

<sup>f</sup> Period of record for river discharge ended in 1991, the longest continuous series available in the Nanticoke.

<sup>g</sup> Fluctuations in mean annual salinity at some sites resulted in variable surface area estimates.

<sup>h</sup> Mattaponi River tributary of York River.

<sup>i</sup> Pamunkey River tributary of York River.

a high frequency variability time series only. Correlation analyses between habitats and between sub-estuaries were conducted with standardized values (i.e., *Z*-scores).

A sub-set of juvenile abundance series was selected for analysis of recruitment fluctuations between rivers based upon sampling distribution. It was observed in some rivers that one habitat tended to be under sampled with respect to the other (Fig. 1). For example, brackish trends in the Choptank, Nanticoke, and James were characterized by a single site. In addition, across years there were typically high correlations between habitats (Table 2). Therefore, a representative series of juvenile abundances from one habitat was selected for each sub-estuary. Freshwater juvenile abundances were selected for the Head of bay, Potomac, Rappahannock, York, and James, and brackish juvenile abundances were selected to represent the Patuxent, Choptank and Nanticoke. Correlation analysis between rivers was limited to patterns of inter-annual variability in juvenile abundance. This analysis consisted of 26 correlations, and we chose a liberal significance level at  $\alpha=0.05$  (without adjustment for multiple comparisons) in order to facilitate exploration of patterns.

## 2.2. Indices of adult abundances

To develop a catch-per-unit-effort (CPUE) index of adult abundance, commercial records of landings and effort were obtained from Maryland Department of Natural Resources (Annapolis) and Virginia Marine

Resources Commission (Newport News). Data were available from 1993 to 2001 in Virginia, and for Maryland the series began in 1980 with missing data from 1985 to 1989 and in 1991. The landings data were classified by the area from which the catch was made (numbered commercial fishing areas – NOAA codes), representing between 2 and 15 distinct areas per sub-estuary. This level of spatial resolution allowed a separate adult CPUE to be estimated for each sub-estuary.

The majority of annual landings (from 50 to 80% depending on the sub-estuary) were reported from the months of January through March in Virginia and February through April in Maryland. Accordingly, adult CPUE was calculated for these periods. The only regulation on these fisheries has been a minimum length of 8-inches (20 cm) in Maryland, and white perch above this length are sexually mature. In addition, during these periods, white perch have moved towards tidal freshwater to spawn and are highly aggregated. Thus, there was a high expectation that commercial data during these periods should represent discrete spawning populations within each sub-estuary.

For purposes in this study, effort was expressed as the amount of gear per total area (km<sup>2</sup>; Table 1, 4th column) of the sub-estuary. There were four principal commercial gear types (fyke net, gill net, pound net, and fish pot), and the predominance of one gear type over another varied between sub-estuaries. Within each system, reported monthly effort was summed across areas and months in terms of total number of nets, pots,

Table 2

Summary of correlation and regression analyses of white perch populations in different sub-estuaries (NK = Nanticoke, CK = Choptank, HB = Head of bay, PX = Patuxent, PO = Potomac, RA = Rappahannock, YK = York, and JA = James) of Chesapeake Bay

	HB	CK	NK	PX	PO	RA	YK	JA
<i>Juvenile abundance correlations<sup>a</sup></i>								
Low frequency	0.51 <sup>†</sup>	0.82 <sup>†</sup>	0.27	0.82 <sup>†</sup>	0.21	–	–	–
High frequency	0.96 <sup>†</sup>	0.94 <sup>†</sup>	0.68 <sup>†</sup>	0.94 <sup>†</sup>	0.73 <sup>†</sup>	0.49	0.86 <sup>†</sup>	0.74 <sup>†</sup>
<i>Fyke net adult CPUE<sup>b</sup></i>								
Freshwater regression								
Recruitment lags <sup>c</sup>	3,4	2,3	2,4	5	4	–	–	–
Adjusted <i>r</i> <sup>2</sup>	0.44	0.62 <sup>†</sup>	0.17	0.55 <sup>†</sup>	0.01	–	–	–
Brackish regression								
Recruitment lags <sup>c</sup>	3,4	4	3	3,4,5	5	–	–	–
Adjusted <i>r</i> <sup>2</sup>	0.49 <sup>†</sup>	0.34	0.13	0.76 <sup>†</sup>	<0.01	–	–	–
<i>Gill net adult CPUE<sup>b</sup></i>								
Freshwater regression								
Recruitment lags <sup>c</sup>	3,4	4	2	2,5	3,4	–	–	–
Adjusted <i>r</i> <sup>2</sup>	0.35	0.14	0.36 <sup>†</sup>	0.29	<0.01	–	–	–
Brackish regression								
Recruitment lags <sup>c</sup>	3	2,4,5	3,4,5	2,5	4,5	–	–	–
Adjusted <i>r</i> <sup>2</sup>	0.27 <sup>†</sup>	0.88	0.87 <sup>†</sup>	0.26	0.27	–	–	–

– = no data.

<sup>a</sup> Pearson correlation coefficients between freshwater and brackish juvenile abundances.

<sup>b</sup> Response variable in regression was the adult stock indexed by adult CPUE.

<sup>c</sup> Explanatory variables included in the final model: juvenile abundances *n*-years prior.

<sup>†</sup> *P* < 0.05.

or total length of gill net. Patterns of effort varied by gear and by sub-estuary, and not all gears were used consistently in every sub-estuary. Only fyke net and gill net effort were reported consistently, and these gears were selected for estimating adult CPUE in different sub-estuaries. Associated landings were divided by the effort value and log-transformed into the familiar population size index, catch-per-unit-effort or CPUE (Fabrizio and Richards, 1996, give a synopsis of using CPUE from fisheries data to describe populations). Because this value was scaled by area, adult CPUE was directly comparable between sub-estuaries. The primary underlying assumption in using adult CPUE as an index of population size is that the fraction of the population that is taken by a single unit of effort (the catchability) is always constant. Note that no independent evaluation could be made for this assumption.

We explored associations between adult CPUE and juvenile abundances using correlation and regression. Pearson correlations were estimated between annual measurements of adult CPUE and juvenile abundance, and a regression analysis of adult CPUE using lagged juveniles abundances as explanatory variables was conducted. One difficulty in these analyses was that abundance (numbers of juveniles) was compared directly with biomass (adult CPUE). Commercial data on numbers of white perch caught were not available. The regression approach was similar to Goodyear's (1985) analysis of striped bass *Morone saxatilis*, except that age-specific data on individual cohorts were unavailable. Regression analyses were only conducted with Maryland data because Virginia adult CPUE series were discontinuous and too short to support the approach. Based upon the life span of white perch and the limited series of recruitment, no time lags greater than five years were considered. A regression model selection approach was used where models with all possible combinations of explanatory variables were compared. Out of a subset of significant models ( $\alpha=0.05$ ), the one with the highest adjusted  $r^2$  was chosen.

### 2.3. Environmental correlates

We explored correlations between juvenile abundance and environmental variables of presumed importance: freshwater flow (North and Houde, 2001), temperature (Limburg et al., 1999), and climate pattern (Wood, 2000). Summed monthly river discharge in spring months (March through May) indexed freshwater flow (North and Houde, 2001), and mean spring water temperature in tidal freshwater was estimated from values at representative monitoring sites (Table 1). Monitoring sites were chosen that represented the main river body and that were less likely to be influenced by higher variability expected in shallow or small tributary environments. Spring months are considered crucial to establish

gravitational circulation patterns that lead to successful white perch recruitment (see North and Houde, 2001). In the York, which has two main tributaries in tidal freshwater, river discharge and temperature data were represented by one site each in the Pamunkey and Mattaponi Rivers. The summed monthly river discharges and mean spring water temperatures were examined for trends and standardized for correlation analyses.

As a proxy for winter-spring meteorological pattern, an index of the NAO (North Atlantic Oscillation) was obtained from the Climate Analysis Section, NCAR, Boulder, USA (<http://www.ldeo.columbia.edu/NAO/>) and applied to each sub-estuary for correlation analyses. The NAO has been used as an indicator of environmental forcing on fish populations in the north eastern Atlantic (Ottersen et al., 2001; Attrill and Power, 2002), and in North America it has been shown that NAO anomalies describe mild versus severe winter conditions (Hurrell, 1995).

## 3. Results

### 3.1. Juvenile abundance trends

In most of the selected series, juvenile abundances exhibited prominent low and high frequency fluctuations (Fig. 1). Habitat specific abundances ranged from 20,000 to 35,000,000 across all sub-estuaries. The highest abundances were observed in the most recent halves of the series, and river-wide abundances (not plotted) tended to be highest in the largest sub-estuaries (by area, Table 1): the Head of bay, Potomac, and to some extent the James. Within sub-estuaries, abundances of juveniles varied between habitats. Higher abundances were generally observed in brackish habitats of the Nanticoke, Patuxent and Rappahannock. By comparison, higher juvenile abundances were observed in freshwater habitats of the Head of bay, Potomac, York and James sub-estuaries. In Maryland sub-estuaries, brackish juvenile abundances increased over the time series (Fig. 1). The most prominent trends were in the Choptank, Nanticoke, and Patuxent, where brackish juvenile abundances increased over a hundred-fold during the period 1977–2002 (Fig. 1). Changes in freshwater juvenile abundances were generally less extreme (ten-fold changes over the entire series), and for short periods trends were opposite to brackish juvenile abundances, declining in the Potomac (1977–1985) and Choptank (1984–1989). Inter-annual fluctuations in juvenile abundance about the LOWESS-smoothed trends were also high in both habitats, with ten-fold differences between years common in all sub-estuaries (Fig. 1).

### 3.2. Adult abundance trends

Adult CPUE series for fyke and gill nets showed two prominent patterns (Fig. 2). First, most of the variability

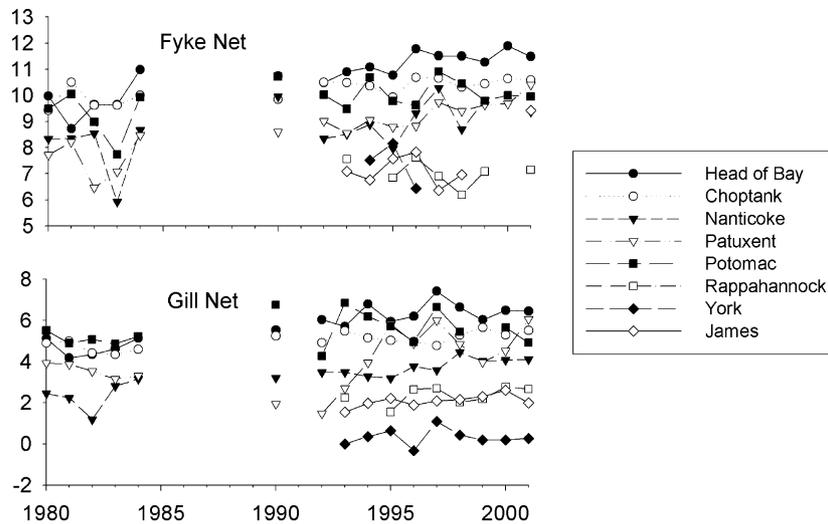


Fig. 2. Trends in catch per unit effort (adult CPUE) from commercial fisheries data on adult white perch in major sub-estuaries of Chesapeake Bay (symbols defined in the key). Adult CPUE was calculated as the log of the ratio of landings to effort (gear amount per km<sup>2</sup>). Estimates from two principal gears are shown: fyke net (upper) and gill net (lower). Gaps in the series are due to missing data.

occurred between sub-estuaries, and for the most part the ranking of the sub-estuaries with respect to adult CPUE was the same for either gear since 1992. The highest adult CPUE values were observed in the Head of bay, followed closely by the Choptank and the Potomac (Fig. 2). Intermediate abundances occurred in the Patuxent and the Nanticoke. The lowest adult CPUE values were observed in Virginia sub-estuaries, and this was true for both gears. Secondly, most sub-estuaries exhibited constant, gradual increases in adult CPUE (for either gear). These trends were especially evident between 1992 and 2001, where adult CPUE levels increased 1–30% across sub-estuaries. Notable exceptions to this trend were seen in the Patuxent, which exhibited a more marked increase in fyke and gill net CPUE (21 and 120%, respectively) during this period.

### 3.3. Environmental variables

With the exception of the Patuxent, we observed no clear trends in spring river discharge and water temperature (plots are not presented here but can be found in Kraus, 2003). In the Patuxent there was an indication of a long-term oscillation in temperature, declining since 1984 and then increasing from 1993 with below average temperatures between 1988 and 1998. Anomalous high temperature in 1991 disrupted this trend in the Patuxent. Only three significant correlations were observed between environmental variables and juvenile abundance: river discharge and high frequency juvenile abundance variability in freshwater were positively correlated in the Head of bay ( $r=0.51$ ,  $P=0.009$ ) and Nanticoke ( $r=0.62$ ,  $P=0.0013$ ), and temperature and brackish juvenile abundance were positively correlated in the York ( $r=0.77$ ,  $P=0.010$ ).

No correlations were observed between the NAO and juvenile abundances. The only consistent (though non-significant) pattern among sub-estuaries and habitats was positive correlations between river discharge and high frequency recruitment variability (inclusive of Virginia data).

### 3.4. Within river comparisons

Positive correlations in juvenile abundance between habitats were observed in all sub-estuaries (Table 2). In Maryland where comparisons were possible, correlations in the high frequency inter-annual variability in juvenile abundance were always higher than correlations in the low frequency trends between habitats (Table 2). The strongest correlations between freshwater and brackish habitats were with the high frequency recruitment patterns in the Head of bay, Choptank, and Patuxent (Table 2).

Graphical exploration of the relationships between adult CPUE and habitat specific juvenile catch rates indicated bivariate normal associations. Further, significant correlations between adult and juvenile abundances were only observed in the Head of bay and Nanticoke. The coefficients were all positive and ranged between 0.61 to 0.71 in the Head of bay (both gear types and habitats) and between 0.63 (freshwater recruitment) and 0.65 (brackish recruitment) in the Nanticoke (gill net adult CPUE only).

In regression analyses to predict adult abundances (indexed by adult CPUE) from prior years of juvenile abundances, separate analyses were conducted for each juvenile habitat, freshwater and brackish. This was necessary due to high correlation in juvenile abundances between habitats, and hence confounding of variables in

the model. In the final models, all the coefficients were positive, and the adjusted- $r^2$  values ranged from 0.27 in the Head of Bay to 0.87 in the Nanticoke (Table 2). Despite strong correlation in juvenile abundances between habitats within the same sub-estuary, there were notable differences between habitats in the amount of variability in adult CPUE that lagged juvenile abundances could explain (Table 2). For example, in Head of bay, Choptank, and Patuxent sub-estuaries both low and high frequency recruitment patterns were significantly correlated between habitats. In the Head of bay, only brackish juvenile abundances explained a significant amount of variability in CPUE (both fyke and gill net adult CPUE, Table 2). In the Choptank, the adjusted  $r^2$  value was twice as large in the model with freshwater juvenile abundances as with brackish juvenile abundances (fyke net adult CPUE only, Table 2). Still, only a single site represented freshwater abundances, possibly biasing this result. Finally, in the fyke net regression models in the Patuxent, variability in CPUE was more strongly associated with juvenile abundances from brackish habitats (Table 2). Similar differences were also evident in the Nanticoke, but the juvenile abundances were not strongly correlated between habitats (Table 2). In the Potomac, there were no significant regression models, and none of models based upon gill net adult CPUE were significant in the Choptank or Patuxent.

### 3.5. Between river comparisons

Significant juvenile abundance correlations between sub-estuaries tended to occur between sub-estuaries that were close in geographical proximity (13 out of 26 correlations were significant; Fig. 3). Significant correlations were observed between sub-estuaries of the mid-bay region (Nanticoke, Patuxent and Potomac) and between Virginia sub-estuaries (Fig. 3). Exceptions to this pattern were significant correlations between the Head of bay and the Nanticoke ( $r=0.47$ ,  $P=0.017$ ), the Head of bay and the James ( $r=0.64$ ,  $P=0.046$ ), and a nearly significant correlation between the James and the Patuxent ( $r=0.63$ ,  $P=0.051$ ).

Because positive correlations between river discharge and juvenile abundance were observed in all sub-estuaries, correlations in river discharge between sub-estuaries were compared to juvenile abundance correlations (Fig. 3). Correlations in river discharge between sub-estuaries were moderate to high (0.57 to 0.97), always positive, and significant in all cases except between the Choptank and James. Two patterns were observed in the comparison of juvenile abundance and river discharge correlations between sub-estuaries. First, none of the abundance correlations exceeded the river discharge correlations (Fig. 3). Second, those juvenile abundance correlations that were significant tended to

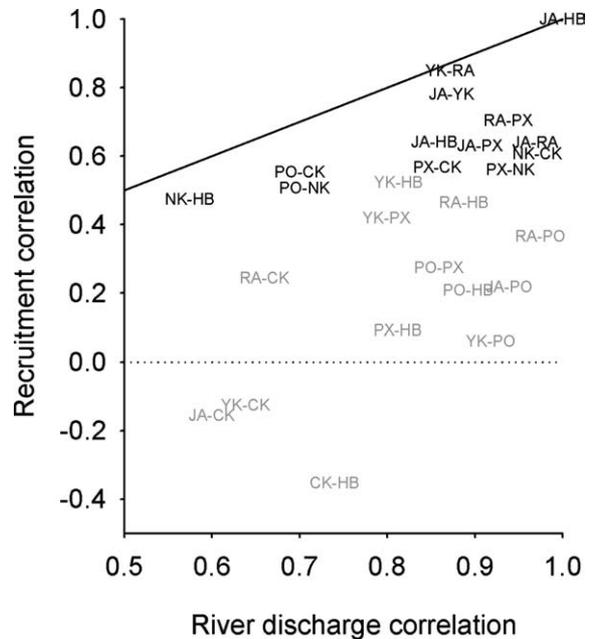


Fig. 3. Comparison of Pearson correlation coefficients for white perch juvenile abundances and annual spring river discharge between major sub-estuaries of Chesapeake Bay. Recruitment (juvenile abundance) correlation was estimated for the high frequency variability in juvenile abundances between sub-estuaries. River discharge correlations were estimated using standardized values of river discharge. Symbols are paired abbreviations of the sub-estuaries (NK=Nanticoke, CK=Choptank, HB=Head of bay, PX=Patuxent, PO=Potomac, RA=Rappahannock, YK=York, and JA=James). Black symbols designate significant ( $P<0.05$ ) correlations in recruitment, whereas non-significant correlations are gray symbols. A one-to-one relationship line is also plotted.

be more similar to the correlations in river discharge than abundance correlations that were not significant.

## 4. Discussion

There was high variability in juvenile abundance across the ~20 year data set and a general inability to detect an effect of adult CPUE on juvenile abundance. Recruitment variability (both low and high frequency) was approximately two orders of magnitude within sub-estuaries and over three orders of magnitude across sub-estuaries. This type of pattern with higher recruitment variability between (two to eight orders of magnitude) than within populations has been observed in other species such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*) and plaice (*Pleuronectes platessa*) (MacKenzie et al., 2003). MacKenzie et al. (2003) proposed that while the spawner-recruit relationships were functionally similar, the inter-population differences in recruitment between populations of the same species reflected different carrying capacities. Similar statements about white perch populations are not warranted because of the lack of apparent influence of adult CPUE on juvenile

abundances (excepting significant and moderate correlations in the Head of bay and Nanticoke). In addition, one of the smallest sub-estuaries, respective of littoral habitat (the brackish portion of the Patuxent, Table 1), yielded the highest estimates of juvenile abundance (Fig. 1), and the recent increasing trends in recruitment and larger sizes of other sub-estuaries suggested that much higher abundances of juveniles might be possible. The lack of correlation between adult CPUE and juvenile abundance is puzzling. There is certainly a low level of spawning abundance where recruitment declines, but this level may not have been observed in recent times. This in turn would suggest that the fishery is not driving Chesapeake Bay populations to low spawner abundance and low recruitment levels.

While juvenile catch rates appeared to be independent of adult CPUE in most sub-estuaries, fluctuations in adult CPUE were significantly affected by progression of prior year-classes into the adult stock and fishery (Table 2). This result was consistent with the age composition of fyke net catches in the Patuxent, which showed the presence of strong and weak year-classes (Kraus and Secor, 2004). Of all the adults that were aged in that study, a single annual cohort from 1996 comprised 50% of the samples in the Patuxent. There were also some year-classes (1997 and 1999) that appeared to be recruitment failures, representing 0.5 to 1% of samples, respectively. Individuals from a particular year-class are not all expected to recruit to the fishery in the same year due to varying growth rates. Based upon the lagged explanatory variables in the regression models, age-at-entry into the fishery varied between 2 and 5 years old. This is consistent with the range of ages observed for the minimum legal size limit in the Maryland fishery (Mansueti, 1961; Wallace, 1971; St. Pierre and Davis, 1972; Casey et al., 1986) and accounts for models with multiple lagged juvenile abundances. The differences between regressions with lagged freshwater and lagged brackish juvenile abundances as explanatory variables indicated that brackish habitats are more closely tied to variations in adult abundance in Patuxent and Nanticoke whereas freshwater habitats may have more importance in the Choptank. Overall, freshwater and brackish habitats appeared to have a disproportionate influence on the dynamics of the adult CPUE, indicating that the relative production of adults from different juvenile habitats varies between sub-estuaries.

Though white perch populations defined in this analysis were expected to be relatively isolated (Mulligan and Chapman, 1989), juvenile abundances were significantly correlated between many of the sub-estuaries. The smoothed recruitment trends indicated that, during the past two decades, the mean level of recruitment has increased in every sub-estuary (except in freshwater in the Choptank), but these increases were not precisely synchronous. For example, mean recruitment in Patuxent

steadily increased by almost two orders of magnitude from 1983 to 1996, whereas the increasing recruitment pattern in the Head of bay was from 1985 to 1997 and was not as pronounced in magnitude (Fig. 1). Further, many of the high frequency inter-annual recruitment correlations were significant (Fig. 3).

The imprecise but coincident variability in white perch recruitments suggested that a common factor was affecting all sub-estuaries. Correlated recruitment series between populations of several fish species in the North Atlantic have been observed previously (Templeman, 1972; Garrod and Colebrook, 1978). Similarly in Chesapeake Bay, Wood (2000) showed that the bay-wide recruitments of all anadromous species (including white perch) were strongly correlated over the long-term. Myers et al. (1995) found that the portion of the data in which there were correlations between fish populations in the North Atlantic (Templeman, 1972; Garrod and Colebrook, 1978) was coincident with a strong decline in spawning stock biomass due to large removals by fishing. When an additional 20 years of observations were added to the analysis, the correlations in recruitment disappeared (Myers et al., 1995). Because the observed juvenile white perch abundances were generally independent of adult CPUE, the increases in landings of adult white perch in recent years do not provide a satisfactory explanation for the correlations between white perch recruitment. Instead, the low-frequency trend in white perch juvenile abundances may be due to decadal-scale climatic changes, as Wood (2000) has proposed.

In the present analysis, none of the density-independent factors that were examined (temperature, NAO, river discharge) provided an indication of a common environmental (climatic) influence on low frequency white perch recruitment variability across sub-estuaries. Pace et al. (1993) encountered a similar lack of association for white perch in the Hudson River. The only consistent pattern observed across sub-estuaries was a weak-to-moderate positive correlation between river discharge and inter-annual (high frequency) variability in juvenile abundances. This result was consistent with the hypothesis developed by North and Houde (2001) for the Head of bay sub-estuary. North and Houde (2001) hypothesized that freshwater flow exerts an organizing influence during the larval life history stage of white perch, in that river discharge controls gravitational circulation patterns at the estuarine turbidity maximum, which in turn enhance larval feeding opportunities, ultimately resulting in high recruitment of juveniles. Comparison of between estuary correlations in river discharge with inter-annual recruitment correlations supports this hypothesis. The correlations in juvenile abundance between sub-estuaries were always equal to or less than correlations in river discharge (Fig. 3). In addition, significant recruitment

correlations tended to be oriented parallel to the one-to-one line (Fig. 3). If river discharge were a perfect indicator of recruitment, then correlations in juvenile abundance would be equivalent to correlations in river discharge between estuaries. While the apparent limitation by the one-to-one line in this comparison suggested that river discharge may be an important variable, it is likely that additional factors or processes may be needed to account for the deviation of some correlations pairs from the one-to-one line. As Limburg et al. (1999) noted, there might be a continuum between several extrinsic variables (rather than a single factor) that is important to white perch recruitment. For instance, biotic controls on recruitment may be less important in sub-estuaries that have high physical energy (Limburg et al., 1999; North and Houde, 2001). Biotic correlates (e.g., food and predators) could not be examined here, but these have been shown to be important during earlier life stages (Limburg et al., 1999). Although the inter-river correlation analysis does not indicate connectivity between life stages of white perch, it does suggest that these correlations may provide a better understanding of the factors that influence production of juveniles in freshwater and brackish habitats.

Problems that complicate interpretation of patterns of spatial recruitment of white perch populations in Chesapeake Bay are under-sampled juvenile habitats in different sub-estuaries, and lack of validation of juvenile abundance estimates and adult CPUE as an index of spawning adult abundance. For the juvenile survey data, this problem is most apparent where only a single site is available to characterize a particular habitat. In the fishery data, trends in effort and associations between adult CPUE and effort were also examined, but probably due to the short length of the series, the range of observed fishing effort was not sufficient to demonstrate that as effort increased stock size (indexed by CPUE) declined. Though this result could be consistent with a population that is not fully exploited by the fishery, it is equally possible that the CPUE is simply a poor indicator of population size (e.g., this is expected in the Patuxent where gill nets are of minor importance). Still, these analyses represent an important starting point for understanding population dynamics of white perch in Chesapeake Bay, and we suggest that it will be necessary to study connectivity more directly (e.g., through natural tags) to understand spatial recruitment dynamics in white perch populations of Chesapeake Bay.

In summary, white perch recruitment may vary by several orders of magnitude between years and between habitats. Our analysis indicates that adult population dynamics are influenced to varying degrees by annual recruitment differences between freshwater and brackish habitats, and that these recruitment differences vary substantially across sub-estuaries. Recruitment variability may be controlled to a small but significant degree by

freshwater flow, and the relative importance of biotic controls needs investigation. Although these conclusions are tentative because juvenile abundance estimates and adult CPUE remain unvalidated, long-term fisheries monitoring data can provide an important resource for conducting exploratory analyses of connectivity among populations and sub-populations of estuarine fishes.

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