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Intensified environmental and density-dependent regulation of white perch recruitment after an ecosystem shift in the Hudson River Estuary

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Abstract

Long-term monitoring data were used to test whether the invasion of zebra mussels in the Hudson River Estuary (HRE) in 1991 altered the influence of density-dependence and environmental conditions on life-stage transitions, growth and partial migration in white perch (*Morone americana*). During the post-invasion period (1992-2013), we estimated standing stocks of white perch eggs, yolk-sac larvae (YSL), post yolk-sac larvae (PYSL), young-of-the-year (YOY) and adults, as well as indices of YOY growth and spatial distribution. A series of linear and nonlinear functions were employed to model life-stage transitions, while the effects of six environmental and density-dependent variables on YOY growth and partial migration were quantified. Comparisons to pre-invasion observations (1974-1991), indicated that egg-YSL, PYSL-YOY and YOY-yearling transitions changed significantly after the invasion, while PYSL abundance developed a stronger negative effect on YOY growth. The PYSL-YOY transition became more sensitive to density-dependence and freshwater flow from 1992-2013, which is consistent with diminished abundance and increased environmental sensitivity of the forage base in the HRE reported after the zebra mussel invasion.

Introduction

Examining the potential of ecosystem shifts to intensify, dampen or reverse population responses to long-term environmental change is an important and broadly relevant problem in fisheries research. Shifts in aquatic ecosystems are characterized by altered food web structure, species interactions, and population dynamics of individual species within the system (Hare and Mantua 2000; Collie et al. 2004). Threshold changes can drive ecosystems into alternative stable states, which control how populations and communities interact and respond to environmental conditions and external forcing (Strayer et al. 2008; Planque et al. 2010), thereby confounding traditional management strategies that depend on stationarity (Folke et al. 2004).

Important consequences of abrupt ecosystem shifts and long-term environmental change (i.e. gradual, but persistent trends) include alterations in primary and secondary production, which influence the productivity and spatial distribution of fish populations. In particular, reductions in prey availability have the potential to intensify density-dependence in growth and recruitment. For example, grazing pressure from the invasive overbite clam (*Potamocorbula amurensis*) played an important role in shifting the abundance and composition of the zooplankton community in the San Francisco Estuary (Kimmerer et al. 1994), which contributed to food limitation and subsequent density-dependent reductions in carrying capacity for delta smelt (*Hypomesus transpacificus*), threadfin shad (*Dorosoma petenense*) and striped bass (*Morone saxatilis*; Kimmerer et al. 2000; Feyrer et al. 2007). In addition to changing density-dependent processes, shifts in population state brought about by ecosystem shifts, climate oscillations or fishing pressure can potentially alter how populations respond to long-term temperature increases (Ottersen et al. 2006; Planque et al. 2010). Thus, determining whether ecosystem shifts alter the state of a population and, subsequently, change the responses of one or more life-stages to density-dependence or environmental conditions is a key step in incorporating species responses to climate change into assessment and management frameworks (Collie et al. 2004).

The availability of extensive long-term monitoring data that overlaps with considerable changes in the ecosystem makes the Hudson River Estuary (HRE) a model system to study the ecological consequences of abrupt ecosystem shifts and long-term environmental change (Strayer et al. 2014a). The HRE is a large (243 km in length) estuary that receives most of its freshwater input from the Troy Dam at the head of the estuary (Figure 1; Cooper et al. 1988). Through its effects on turbidity and advection, freshwater flow strongly controls primary and secondary production in the HRE, with conditions of low flow resulting in increased water clarity and residence time and generally leading to enhanced productivity (Gladden et al. 1988; Howarth et al. 2000). Freshwater flow and temperature have both increased in the HRE since 1950 (Seekell and Pace 2011; Strayer et al. 2014a) and are projected to continue increasing over the next century (Najjar et al. 2009). In addition to these long-term changes, the zebra mussel (*Dreissena polymorpha*) invaded the tidal freshwater portion of the HRE in 1991, became highly abundant in 1992, then triggered a rapid and extensive ecosystem shift (see reviews by Strayer et al. 2008; 2014a). Grazing pressure increased exponentially, greatly reducing the biomass of phytoplankton, pelagic zooplankton and benthic invertebrates (Caraco et al. 1997; Pace et al. 1998; Strayer and Smith 2001). As a consequence of their role in reducing the forage base, zebra mussels had demonstrable impacts on many fishes, with pelagic species generally displaying reduced abundance and growth rates after the invasion, as well as downriver shifts in their spatial distribution (for details, see Strayer et al. 2004). However, increased water clarity after the invasion enhanced primary and secondary production in littoral habitats, resulting in increased abundance, higher growth rates and upriver distributional shifts in many littoral fishes (e.g. centrarchids; Strayer et al. 2004). Importantly, the zebra mussel invasion also made the abundance of many organisms more sensitive to freshwater flow. For example, the abundance of littoral benthic invertebrates and littoral fishes has developed a stronger inverse relationship with freshwater flow than was observed before the invasion (Strayer et al. 2008). More recently, the abundance and size of zebra mussels in the HRE have decreased (Strayer and Malcom 2006), allowing some recovery of zooplankton, benthic invertebrate and fish stocks (Pace et al. 2010; Strayer et al. 2011; Strayer et al. 2014b).

White perch (*Morone americana*) is a dominant estuarine fish species in North America which completes its entire life-cycle within the estuary, and is therefore likely to be sensitive to ecosystem shifts and long-term environmental change within these systems. Adult white perch undertake spring spawning migrations into tidal freshwater, where eggs develop into pelagic larvae and subsequently metamorphose into fully-formed juveniles that select littoral habitats (Mansueti 1964; Klauda et al. 1988). Thus, different life-stages may respond to large-scale ecosystem change in distinct ways. In addition, white perch life history characteristics are sensitive to ecosystem attributes (e.g. Tuckett et al. 2013). For example, recruitment in several Chesapeake Bay tributaries is positively associated with freshwater flow (Kraus and Secor 2005), likely due to a strengthening of the estuarine turbidity maximum in high flow years, which enhances larval retention and feeding success (North and Houde 2003). Similarly, first-year growth in Oneida Lake white perch is positively influenced by summer water temperatures and measures of primary and secondary productivity (VanDeValk et al. 2016). Before the zebra mussel invasion, studies of young-of-the year (YOY) white perch growth and recruitment in the HRE suggested that growth was unrelated to YOY abundance, but positively influenced by water temperature (Klauda et al. 1988), while recruitment was unrelated to larval abundance, temperature or flow (Pace et al. 1993).

Estuarine white perch display partial migration, characterized by a resident contingent that remains in natal freshwater habitats throughout life, and a migratory contingent, which exhibits active dispersal from the natal habitat and subsequently uses brackish water (Kraus and Secor 2004; Kerr and Secor 2011). Inter-annual variability in the numerical dominance of each contingent is modulated by freshwater flow in Chesapeake Bay tributaries (Kraus and Secor 2004). White perch in the HRE also display partial migration, with a numerically dominant freshwater resident contingent (Gallagher 2016). Likely owing to higher productivity in the brackish portion of the HRE (Howarth et al. 2006), migratory white perch grow and mature faster than residents (Gallagher 2016), and therefore may contribute disproportionately to the productivity of the population (Kerr et al. 2010). Although white perch recruitment, growth and partial migration dynamics have been well-documented in the HRE and elsewhere, the influence of density-dependence, temperature and freshwater flow on these early-life characteristics may have been altered by the zebra mussel invasion. Such changes, if present, could potentially affect future population dynamics, as temperature and precipitation are both projected to increase (by 4°C and 7% on average, respectively) in the HRE over the next century (Najjar et al. 2009).

Our objective was to evaluate whether the zebra mussel invasion modified the relative influence of density-dependence and environmental conditions on the recruitment, growth, and migration dynamics of YOY white perch in the HRE. Due to the reduced abundance and increased environmental sensitivity of the forage base (Strayer et al. 2008), we hypothesized that, following the zebra mussel invasion: 1.) recruitment to the YOY stage became more sensitive to density-dependence and environmental conditions 2.) YOY growth developed stronger density-dependence and 3.) partial migration became more strongly density-dependent, such that high YOY abundance produces a larger fraction of YOY in the migratory contingent. To test these hypotheses, we applied a series of stage-structured models and exploratory statistical analyses to an extensive set of monitoring data collected after the invasion of zebra mussels (1992-2013). These findings were then compared to previous studies of YOY white perch recruitment, growth and spatial distribution before the zebra mussel invasion (1971-1991), to test whether the ecosystem shift brought about by the invasion has altered these important processes through changed functional relationships with abundance, flow, and other environmental variables.

Methods

Study area

The HRE is a large, partially mixed estuary characterized by unusually low sinuosity and strong tidal influence compared to many estuaries, with a watershed spanning approximately 12,900 km^2 (Figure 1; Geyer and Chant 2006). Annual mean temperature and flow in the HRE from 1951-2013 have positive, non-linear trends over this time period, with accelerated rates of increase since 1990 (Figure 2). In addition, the position of the salt front in the HRE is strongly influenced by freshwater flow (Cooper et al. 1988) and can vary by 20-60 km on a seasonal basis (Geyer and Chant 2006). The position of the salt front controls the salinity distribution within the river, which directly influences spatial variation in the abundance and composition of zooplankton, benthic invertebrate and fish communities (Gladden et al. 1988; Strayer and Smith 2001; Daniels et al. 2005).

Data availability

This analysis was shaped by data availability, which differed between pre-invasion (1974-1991) and post-invasion (1992-2013) periods. Daily temperatures and salt front positions in the HRE are only available during the post-invasion period since 1992 and 1991, respectively. We also lacked white perch growth and spatial distribution data before the zebra mussel invasion (1974-1991) and therefore used relationships reported in previous studies by Klauda et al. (1988) and Lawler, Matusky and Skelly Engineers (1989). Finally, two types of abundance data were used. Standing stock estimates with high spatial and temporal resolution were only available for the post-invasion period, and were thus preferred when describing life-stage transitions and spatial distribution indices during this period. A second set of annual abundance indices were less resolved, but spanned the pre-invasion and post-invasion periods (1974-2013), and were used to perform statistical comparisons of life-stage transitions before and after the invasion.

White perch abundance, growth and migration data

Standing stock abundance estimates were obtained from annual reports prepared by Applied Science Associates (2014) for white perch eggs, yolk-sac larvae (YSL), post yolk-sac larvae (PYSL), young-of-the-year juveniles (YOY) and adults (age-1 yearlings and older). These data are collected in “Year-class Reports” for the Hudson River Estuary Monitoring Program, an extensive survey funded by four utility companies which has been in place since 1974. Data were drawn from three separate surveys, which targeted different life-stages. Egg, YSL and PYSL standing stocks were estimated from the Longitudinal River Survey; YOY standing stock was estimated from the Utilities Beach Seine Survey (seine survey hereafter) and adult white perch standing stock was based on the Fall Juvenile Survey. Early life-stages are differentiated using standardized laboratory protocols based upon developmental traits (e.g. yolk-sac absorption). Each of these surveys follows a random sampling design, stratified by depth zones. A summary of the depth strata, time-span, gear and mesh sizes used in each of the three surveys can be found in Table S.1. The spatial and temporal resolution of each survey is relatively high and consistent

(~1000 samples year^{-1}), with fish sampling occurring in the same 13 river sections, spanning from Albany to Manhattan (Figure 1), on weekly or bi-weekly intervals depending on the survey and time of year.

For each life-stage in each survey, mean densities (number m^{-3}) within each stratum and river section were calculated each sampling week. These densities were subsequently converted into river-wide standing stock estimates by multiplying the density by the stratum volume in each river section, and summing across strata and river sections (Applied Science Associates 2014). Standing stocks were subsequently averaged over a different set of weeks for each life-stage in order to obtain annual means from 1992-2013. Weeks were selected if the life-stage of interest was consistently present in the river and vulnerable to the sampling gear across the majority of years in our data set. For white perch early life-stages, the time periods selected were weeks 17-25, 18-26 and 19-28 for eggs, YSL and PYSL, respectively, while weeks 28-40 and 27-41 were used in analyses of YOY and adults, respectively (Table S.1). The same set of weeks was also used to calculate the mean temperature and freshwater flow experienced by each life-stage during each year for use in subsequent analyses (see Statistical Analyses). The Longitudinal River Survey tows the sampling gear against the prevailing current at 0.9-1.0 m s^{-1}, so evasion of white perch YSL and PYSL (maximum swim speed ~0.1 m s^{-1}) is unlikely. However, due to likely differences in sampling efficiency (e.g. size-selective sampling of larvae) and stage duration between life-stages, standing stocks should be interpreted as indices of abundance, rather than estimates of the absolute abundance of each stage in the HRE.

YOY white perch standing stocks were analyzed in relation to the position of the salt front to separate resident and migratory contingents during each year. Daily salt front positions in the HRE have been computed by the US Geological Survey (USGS) since 1991 (USGS

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

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

Environmental and biological variables

Daily temperature and freshwater flow records were obtained respectively from a pumping station in Poughkeepsie at river km 120, (USGS 2015b; http://waterdata.usgs.gov/nwis/uv?site_no=01372058) and the Green Island monitoring site at the head of the estuary in Troy, NY (USGS 2015c; http://waterdata.usgs.gov/nwis/uv?site_no=01358000). In addition to being the richest data set, freshwater flow at Green Island represents approximately 70% of freshwater input into the HRE (Howarth et al. 2006). Daily temperature and flow values were averaged during spring (April-June) and summer (July-September) months to calculate seasonal means for each year. In addition, estimates of annual mean zebra mussel filtration rates during the growing season (May-September) from 1992-2013 were obtained from the Cary Institute of Ecosystem Studies (D. Strayer, personal communication; see Strayer and Malcom 2006 for details) and used to examine possible effects of zebra mussels on white perch early life-stages. Descriptive statistics for all white perch early life-history, biological and environmental variables can be found in Table 1.

Statistical analyses

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

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

where α is a density-independent multiplier. We estimated α using simple linear regression with the intercept fixed at 0, reflecting traditional assumptions in stock-recruit theory (Quinn and Deriso 1999). Preliminary analyses indicated that environmental variables had negligible impacts on linear transitions (data not shown), and were therefore not included. Similarly, non-linear transitions were modeled using a Ricker stock-recruitment function by the equation:

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

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

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

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

The effects of environmental and density-dependent factors on YOY white perch growth and partial migration from 1992-2013 were explored using a Pearson correlation analysis. The response variables of interest were YOY length and the migrant fraction, while the predictors in both analyses were the mean summer temperature and flow, annual mean zebra mussel filtration rates (environmental factors), as well as the mean standing stocks of white perch YOY and PYSL (density-dependent factors). In addition, because the availability of brackish habitat in the HRE may influence white perch growth and migration, the mean proportion of the total HRE shoal volume in the brackish portion of the estuary during the summer was calculated and used as a predictor (hereafter termed brackish shoal proportion). This proportion was calculated by assigning the 13 river sections (Figure 1) into freshwater and brackish regions based on the mean summer salt front position, summing the shoal volumes of all brackish sections (depth < 6 m) and dividing by the total shoal volume of the HRE (~345 million m^3). For comparison, correlations reported in previous studies of YOY white perch growth and spatial distribution in the 1970s and 80s (Klauda et al. 1988; Lawler, Matusky and Skelly Engineers 1989) were compiled and compared to estimated correlations from 1992-2013. These previous studies selected a Type-I error rate of 0.05 and did not adjust p-values of their correlations for multiple comparisons. However, for the 12 correlations analyzed in the more recent period, we applied a Bonferroni correction ($0.05 \times 12^{-1} = 4.17 \times 10^{-3}$) to adjust the Type-I error rate.

Indices of white perch egg, YSL, PYSL, YOY and yearling abundance were compared between pre-invasion (1974-1991) and post-invasion (1992-2013) periods. Two-sample t-tests assuming unequal variance were performed to test for differences in the mean index of abundance between these two time periods. Subsequently, life-stage transitions during each time period were modeled using the functional relationships described previously (equations 1, 2 and 3). Differences in parameter estimates (α, β, γ) between pre-invasion and post-invasion periods were analyzed using analysis of covariance (ANCOVA) and post-hoc contrasts, with invasion period (pre- or post-invasion) used as a categorical variable. The relationships between the egg index and the YOY index, as well as the yearling index and the YOY index from the previous year were also modeled for both periods.

Results

Life cycle analysis

Based on standing stock data, the stock-recruitment (adult-YOY) relationship for white perch in the HRE from 1992-2013 (Figure 3) was described by a Ricker model with freshwater flow during the PYSL period as a covariate ($\log_e(\alpha) = 0.91$; $\beta = 5.61 \times 10^{-4}$; $\gamma_{flow} = 2.18 \times 10^{-3}$; Table 2). Paulik diagrams decomposing the stock-recruitment relationship into a series of life-cycle transitions (Figure 3) illustrated that the shape of the stock-recruitment relationship was primarily driven by the transition from PYSL to YOY (Figure 3; $\log_e(\alpha) = -4.72$; $\beta = 2.21 \times 10^{-6}$; $\gamma_{flow} = 1.89 \times 10^{-3}$; Table 2). The standing stock of eggs, YSL and PYSL were proportional to the standing stock of their previous life-stages in a density-independent manner ($p < 0.001$; Table 2). The standing stocks of white perch YSL and PYSL were also proportional to the adult standing stock. While each α estimate for linear transitions was positive and statistically significant, it is important to emphasize that the standing stocks of each life-stage are indices of abundance, and therefore α estimates do not represent the actual proportionality between life-stage abundances.

Comparisons of seven linearized Ricker model structures describing adult-YOY and PYSL-YOY relationships from 1992-2013 indicated that the most likely model included freshwater flow during the PYSL period for both transitions (ΔAICc > 2 for all other models; Table 3). Flow during the PYSL period had a strong negative effect on $log_e(YOY \times adult^{-1})$ and $log_e(YOY \times PYSL^{-1})$, which was consistent across models ($p < 0.05$; Table 3), while the effects of temperature during the PYSL period and zebra mussel filtration rates were comparatively weak ($p > 0.25$; Table 3). Similarly, the density-dependent term in both relationships (i.e. adult standing stock for $log_e(YOY \times adult^{-1})$ and PYSL standing stock for $log_e(YOY \times PYSL^{-1})$ consistently had a strong negative effect on transition responses in each model ($p < 0.001$; Table 3).

Somatic growth and contingent structure

For the period 1992-2013, YOY length at the end of the growth season was positively associated with mean summer water temperature ($r = 0.70$; $p < 0.01$) and negatively correlated to summer flow ($r = -0.50$; $p < 0.05$) and the PYSL standing stock ($r = -0.46$; $p < 0.05$; Table 4;

Figure 4). In addition, the abundance of the migratory contingent of YOY was closely related to the abundance of the resident contingent from 1992-2013 ($R^2 = 0.81$), with the migrant fraction ranging from 0.12 to 0.60, (mean = 0.42; Table 1). The migrant fraction was unrelated to any of the environmental or density-dependent variables analyzed ($p > 0.15$), but was positively correlated to the brackish shoal proportion from July-September ($r = 0.67$; $p < 0.01$; Table 4), although this trend was largely driven by two years (2004 and 2011) when the migrant fraction and brackish shoal proportion were both relatively low (Figure 4d). However, after applying a Bonferroni correction for multiple comparisons, the post-invasion correlations between YOY length and summer flow and PYSL abundance, as well as between migrant fraction and brackish shoal proportion became non-significant ($p > 0.01$; Table 4). The effects of temperature, flow and salt front position on YOY white perch growth and partial migration were generally similar to correlations reported prior to the zebra mussel invasion, although the effect of PYSL abundance on YOY growth was weaker during this period (Table S.2).

Pre- vs. post-invasion indices of abundance

Post-invasion (1992-2013) indices of white perch abundance were significantly lower than pre-invasion (1974-1991) indices for eggs ($p < 0.02$), YOY ($p < 0.01$) and yearlings ($p < 0.01$; Table 5). In the post-invasion time period, abundance indices for eggs, YOY and yearlings declined by approximately 50%, 40% and 60%, respectively, of their pre-invasion means (Table 5). Each life-stage transition differed between the two time periods, although differences varied in magnitude (Figures 5 and 6). The egg-YSL transition exhibited a significantly steeper slope ($p < 0.001$) in the post-invasion time period ($\alpha = 0.94$) than before the invasion ($\alpha = 0.41$) (Table 6). Change in the YSL-PYSL transition between the two time-periods was not statistically significant ($p > 0.15$), but showed a slightly flatter slope after the invasion ($\alpha = 5.62$) relative to the pre-invasion period ($\alpha = 6.53$) (Table 6). The PYSL-YOY transition during the post-invasion period exhibited a reduced YOY maximum and increased influence of freshwater flow during the PYSL period ($log_e(\alpha) = 2.59$; $\beta = 0.57$; $\gamma_{flow} = 1.43 \times 10^{-3}$) relative to estimates before the zebra mussel invasion ($log_e(\alpha) = 2.08$; $\beta = 0.32$; $\gamma_{flow} = 2.68 \times 10^{-4}$) (Table 6; Figure 5), although contrasts performed on the linearized model coefficients indicated that none of these changes were statistically significant ($p > 0.05$). Similarly, contrasts indicated that the egg-YOY transition showed significantly enhanced density-dependence after the invasion ($\beta_{post} = 3.61$; $\beta_{pre} = 1.34$; $p > 0.001$), as well as a strong, but non-significant, increase in the effect of freshwater flow ($\gamma_{post} = 1.57 \times 10^{-3}$; $\gamma_{pre} = -4.86 \times 10^{-4}$; $p = 0.097$) (Table 6). Finally, the linear relationship between the yearling index of abundance and the YOY index from the previous year exhibited a significantly flatter slope ($p < 0.05$) after the zebra mussel invasion ($\alpha = 0.21$) than was observed during the pre-invasion time period ($\alpha = 0.32$) (Table 6; Figure 6).

Discussion

In accordance with expected effects of the zebra mussel invasion on the early life history of white perch in the HRE, our analyses revealed substantial alterations in life-stage transitions after the zebra mussel invasion. Following the invasion, the PYSL-YOY transition became more sensitive to PYSL abundance (i.e. density-dependence) and freshwater flow experienced during the PYSL period. In addition, declines in yearling abundance and egg production after the zebra mussel invasion suggest that the adult population has been negatively impacted, which has not been reported in previous studies (Strayer et al. 2004). These shifts in white perch abundance and life-stage transitions are generally consistent with broader changes in the abundance and flow sensitivity of the forage base in the HRE after the zebra mussel invasion (Strayer et al. 2004;

2008). In contrast, similar patterns in pre-invasion and post-invasion correlations suggested that the effects of density-dependence and environmental conditions on YOY white perch growth and partial migration changed little after the zebra mussel invasion.

Environmental and density-dependent effects

The reduced abundance of YOY white perch observed in years with high PYSL abundance (Figure 3) is consistent with density-dependent mortality of YOY after settlement in littoral habitats. This density-dependent mortality is probably most intense shortly after peak settlement, when the abundance of newly metamorphosed YOY is highest. Upon settlement, YOY white perch likely experience high levels of mortality due to predation, which is in turn regulated by density and habitat type (Juanes 2007). Density-dependent prey limitation could also cause mortality either directly through starvation or indirectly by exposing juveniles to a prolonged period of size-dependent predation (Walters and Juanes 1993). Lower survival between the PYSL-YOY transition during high flow years could relate to the findings of Strayer et al. (2008), who observed an inverse relationship between flow and the abundance of littoral benthic invertebrates (prey items for YOY white perch) in the HRE. Reduced pelagic forage availability during the PYSL stage may also be contributing to lower YOY abundances during high flow years. Densities of principal zooplankton prey are known to affect white perch recruitment (Limburg et al. 1999), while cladocerans and (to a lesser degree) copepods have been observed to be negatively influenced by flow (Strayer et al. 2008). Contrary to this study, North and Houde (2003) reported that the stock-recruitment relationships of white perch and congeneric striped bass in the Upper Chesapeake Bay were best described when incorporating a positive effect of freshwater discharge. Interestingly, differences in the direction of the flow effect on the white perch stock-recruitment function in the Hudson River (negative) and

Chesapeake Bay (positive) generally match the effects of freshwater flow on primary and secondary production in these contrasting systems (Howarth et al. 2000; Strayer et al. 2008; Testa et al. 2008).

The positive effect of temperature on YOY white perch growth is not surprising, and has been observed in other freshwater and estuarine systems (Kerr and Secor 2010; VanDeValk et al. 2016). The negative influence of freshwater flow on white perch growth is consistent with previous reports that low flows coincide with increased water clarity and residence times in the HRE (Gladden et al. 1988, Howarth et al. 2000), which may increase primary and secondary production, particularly in littoral habitats used by juvenile white perch (Strayer et al. 2008). The negative effect of the PYSL standing stock on YOY growth is more difficult to interpret, especially since growth was not significantly related to YOY abundance, in contrast to other studies that have documented density-dependent growth in white perch (VanDeValk et al. 2016) and striped bass (Martino and Houde 2010). The effect of larval abundance on YOY growth (Figure 4c) may be related to the density-dependent mortality observed during the PYSL-YOY transition (see above); such that competition for food in newly settled YOY may increase in years of high larval abundance, potentially reducing growth rates early in the YOY period, which carry over to influence length at the end of the growing season. In addition, the relatively constant proportionality between migrant abundance and total YOY abundance implies that years with high recruitment (i.e. moderate PYSL abundance and low flow; Figure 3) will produce higher numbers of migrants with associated higher growth rates (Gallagher 2016), which may further enhance population productivity (Kerr et al. 2010).

Impacts of the zebra mussel invasion

Indices of abundance from pre-invasion (1974-1991) and post-invasion (1992-2013) time periods demonstrated, for the first time, that the abundance of white perch eggs and yearlings declined after zebra mussels invaded the HRE (Table 5), while also confirming the reduction of YOY standing stocks reported in previous studies (Strayer et al. 2004, 2014b). Our analysis of life-stage transitions from egg to YSL to PYSL prior to the zebra mussel invasion largely mirrored previous research. Pace et al. (1993) analyzed the egg-YSL, YSL-PYSL and PYSL-YOY life-stage transitions during the pre-invasion period from 1974-1990, and found that YSL and PYSL abundances were related to the abundance of their previous life-stages in a density-independent manner, similar to our analyses of the egg-YSL and YSL-PYSL transitions from 1992-2013 (Figure 3; Table 2). However, our analysis indicated that the slope of egg-YSL transition became steeper during the post-invasion time period (Table 6), resulting in a similar range of YSL abundance between the two time periods despite declines in egg production (Figure 5; Table 5). This pattern suggests that a compensatory increase in hatching success and early larval survival may have occurred after the invasion.

In contrast to our findings, Pace et al. (1993) reported that the relationship between PYSL and YOY abundance was relatively flat, and unrelated to annual variations in temperature and flow, whereas the PYSL-YOY relationship reported here (1992-2013) exhibited strong density-dependence and a significant negative effect of freshwater flow during the PYSL period (Figure 3; Table 3a). This change in the PYSL-YOY transition after the zebra mussel invasion was corroborated to an extent by the index-based Ricker models describing the transition, which showed a 1.7-fold and 5-fold increase in β ($\beta_{post} = 0.57$; $\beta_{pre} = 0.32$) and γ_{flow} ($\gamma_{post} = 1.43 \times 10^{-3}$; $\gamma_{pre} = 2.68 \times 10^{-4}$), respectively, during the post-invasion time-period. Although contrasts indicated that the differences between Ricker model parameters in the pre-invasion and post-invasion time periods were not statistically significant, we argue that the significant reduction in YOY abundance after the invasion, the consistent negative effect of flow on the post-invasion adult-YOY and PYSL-YOY transitions, and substantial differences in the shape of the Egg-YOY and PYSL-YOY relationships between time periods suggest that these differences are ecologically significant.

The increased sensitivity of the PYSL-YOY transition to density-dependence and freshwater flow may be related to reductions in the food supply for white perch. This change is generally consistent with riverwide declines in phytoplankton (Caraco et al. 1997), pelagic zooplankton (Pace et al. 1998) and benthic invertebrate (Strayer and Smith 2001) densities, as well as the strong negative relationship of littoral benthic invertebrate density with flow that Strayer et al. (2008) observed in the first 10-15 years after the zebra mussel invasion. In addition, the increased sensitivity to freshwater flow has probably contributed to the diminished post-invasion production of YOY, as flow during the PYSL period (from weeks 19-28) increased at a rate of 1.9% year^{-1} on average in the HRE from 1992 to 2013 (Figure 7). The mechanistic basis for intensified density-dependence observed after the zebra mussel invasion in the HRE merits further research in white perch and other fishes that reside in rivers, lakes and estuaries affected by invasive bivalves (Kimmerer et al. 2000; Higgins and Vander Zanden 2010).

White perch in the HRE begin to mature as yearlings (Klauda et al. 1988), which suggests that reduced yearling abundance after the zebra mussel invasion may have depleted the overall spawning stock abundance of the population. Declines in yearling abundance after the zebra mussel invasion were likely driven by reduced YOY abundance and a flattened slope in the transition between YOY and yearlings, both of which would be expected to decrease the number of yearlings. If the diminished abundance of yearling white perch in the HRE carries over to subsequent age-classes, this would explain the significant reduction in post-invasion egg production (Table 5), and provides one explanation for the negative temporal trends observed in adult, YSL and PYSL standing stocks from 1992-2013 (Table 1). Overall, these comparative analyses suggest that the zebra mussel invasion has forced the HRE white perch population into an alternate state, characterized by lower spawning stock abundance and reduced juvenile production that is more sensitive to environmental variation, which can in turn be attributed to differences in life-stage transitions before and after the invasion.

Interactions between ecosystem shifts and climate change

While our study was correlative in nature, the weight of evidence suggests the HRE white perch population has been perturbed to an alternate state through the complex interactions of two large-scale phenomena: an abrupt ecosystem shift due to the invasion of zebra mussels (Strayer et al. 2008) and long-term increases in flow associated with climate change (Seekell and Pace 2011). Precipitation in the HRE watershed is projected to increase by 7% on average over the next century, which should result in a 10-15% increase in freshwater flow (Najjar et al. 2009), and this long-term change will likely be overlain by decadal-scale variability that will affect the productivity of white perch and the HRE ecosystem (Strayer et al. 2014a). The response of HRE white perch to long-term changes in flow will be further complicated by concurrent increases in water temperature, which Najjar et al. (2009) projected to increase by approximately 4°C on average by 2100. The effects of rising temperatures on the HRE ecosystem are likely to be modest over decadal timescales (Strayer et al. 2014a), but the increased biological rates (e.g. zooplankton productivity, white perch growth) that would accompany temperatures at the end of the century could potentially interact with higher freshwater flow (which favors lower primary production; Howarth et al. 2000) in unpredictable ways.

Where adequate environmental and biological monitoring data are available, careful assessment of temporal shifts in life-history transitions may generate a better understanding of the interactive effects of ecosystem shifts and climate change on fish populations, and the diversity of environmental drivers involved. Ecosystem shifts are typically abrupt (1-3 years), and can be triggered by overfishing (Daskalov et al. 2007), invasive species (Shiganova et al. 1998), eutrophication (Österblom et al. 2007), climate oscillations (Francis and Hare 1994), gradual changes in temperature and precipitation (Smol et al. 2005), or some combination of these factors (e.g. Weijerman et al. 2005; Möllmann et al. 2008). Regardless of the cause, abrupt aquatic ecosystem shifts will lead to changes in the abundance and population dynamics of many constituent species (Collie et al. 2004). Further comparisons of fish population characteristics across various stages of ecosystem disturbance and recovery in multiple systems (e.g. nutrient remediation; Kemp et al. 2009) can potentially uncover more diverse mechanisms by which populations have responded to changes in ecosystem structure in the past.

This research highlights the importance of abrupt and long-term changes in ecosystem characteristics to the dynamics of the HRE white perch population. Alterations in the abundance and environmental sensitivity of white perch in the HRE after the zebra mussel invasion will likely influence how the population responds to long-term increases in temperature and precipitation in the HRE. Similar changes in the shape of early life-stage transitions may be detectable in other fish species in the HRE (e.g. striped bass, river herring, centrarchids) and other areas subjected to ecosystem shifts, especially those characterized by intense modifications of the forage base. Improved knowledge of the causes and consequences of state shifts in fish populations, such as those highlighted here, can enhance efforts to adequately detect and account for such changes in conservation and fisheries management practices.

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Tables

Table 1. List of 13 primary variables analyzed in this study, with descriptive statistics (mean, minimum, maximum and correlation coefficient with year) for each variable from 1992-2013. Statistically significant temporal correlations ($p < 0.05$) are marked with an asterisk (*). Sources are abbreviated as ASA (Applied Science Associates) and USGS (United States Geological Survey).

Variable	Units	Type	Source	Mean	Min	Max	r_{year}
Mean adult standing stock	Millions	White Perch	ASA (2014)	2.54	0.89	5.89	-0.30
Mean YOY standing stock	Millions	White Perch	ASA (2014)	0.71	0.05	2.35	0.13
Mean PYSL standing stock	Millions	White Perch	ASA (2014)	709	340	1529	-0.65*
Mean YSL standing stock	Millions	White Perch	ASA (2014)	105	32	257	-0.47*
Mean Egg standing stock	Millions	White Perch	ASA (2014)	123	22	351	-0.17
Proportion of migratory YOY	Unitless	White Perch	ASA (2014)	0.42	0.12	0.60	0.07
Mean YOY length in October	mm	White Perch	ASA (2014)	73.9	62.8	82.3	0.14
Mean zebra mussel filtration rate	$m^3m^{-2}day^{-1}$	Biological	D. Strayer	3.76	0.06	8.28	-0.59*
Mean summer salt front position	km from Battery	Environmental	USGS (2015a)	99	74	118	0.16
Mean spring temperature	°Celsius	Environmental	USGS (2015b)	14.7	13.2	17.2	0.22
Mean summer temperature	°Celsius	Environmental	USGS (2015b)	24.5	23.2	26.4	0.32
Mean spring flow	m^3sec^{-1}	Environmental	USGS (2015c)	587	181	857	-0.01
Mean summer flow	m^3sec^{-1}	Environmental	USGS (2015c)	234	98	546	0.43*

Table 2. Parameter estimates (with standard errors in parentheses) for each white perch life-stage transition based on mean standing stocks during the post-invasion period (1992-2013). The α estimates, model R^2 and p-values for Ricker models (denoted by ǂ) are for the linearized equations, where $\alpha = \log_e(\alpha)$ (see Methods).

Life-Stage Transition	**α**	**β**	**γ_{flow}**	**Model R^2**	**Model p-value**
Adult-Egg	46.40 (4.56)	-	-	0.38	<0.001
Adult-YSL	40.41 (3.19)	-	-	0.53	<0.001
Adult-PYSL	258.25 (21.59)	-	-	0.39	<0.001
Egg-YSL	0.76 (0.08)	-	-	0.36	<0.001
Egg-PYSL	4.87 (0.53)	-	-	0.28	<0.001
YSL-PYSL	6.07 (0.47)	-	-	0.55	<0.001
Adult-YOYǂ	0.91 (0.49)	$5.61\ 10^{-4}$ $(1.24\ 10^{-4})$	$2.18\ 10^{-3}$ $(8.61\ 10^{-4})$	0.59	<0.001
PYSL-YOYǂ	-4.72 (0.47)	$2.21\ 10^{-6}$ $(4.44\ 10^{-7})$	$1.89\ 10^{-3}$ $(8.07\ 10^{-4})$	0.62	<0.001

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

a

Model	Intercept	Adult	Temperature	Flow	Filtration	R-square	AICc	ΔAICc
1	0.02	-0.57*	-	-	-	0.46	57.5	3.4
2	-1.95	-0.56*	0.10	-	-	0.46	60.2	6.1
3	***0.91***	***-0.56****	***-***	***-2.19 10^{-3}****	***-***	***0.59***	***54.1***	***0.0***
4	-0.03	-0.58*	-	-	0.02	0.46	60.5	6.3
5	1.68	-0.56*	-0.04	-2.26 10^{-3}*	-	0.59	57.5	3.3
6	1.13	-0.54*	-	-2.40 10^{-3}*	-0.05	0.60	57.0	2.9
7	2.90	-0.54*	-0.09	-2.40 10^{-3}*	-0.06	0.61	60.6	6.5

b

Model	Intercept	PYSL	Temperature	Flow	Filtration	R-square	AICc	ΔAICc
1	-5.48*	-2.29 10^{-3}*	-	-	-	0.51	53.8	2.6
2	-5.41	-2.28 10^{-3}*	0.00	-	-	0.51	56.8	5.6
3	***-4.72****	***-2.20 10^{-3}****	***-***	***-1.91 10^{-3}****	***-***	***0.62***	***51.2***	***0.0***
4	-5.51*	-2.31 10^{-3}*	-	-	0.01	0.51	56.8	5.6
5	-1.51	-2.39 10^{-3}*	-0.16	-2.15 10^{-3}*	-	0.64	53.7	2.5
6	-4.49*	-2.11 10^{-3}*	-	-2.15 10^{-3}*	-0.06	0.64	53.9	2.7
7	-0.30	-2.30 10^{-3}*	-0.20	-2.58 10^{-3}*	-0.07	0.66	56.3	5.0

Table 4. Correlations between white perch migrant fraction and YOY length and six predictor variables of interest from the post-invasion period (1992-2013). Correlations that were statistically significant ($p < 0.05$) before multiple comparison adjustment are marked with an asterisk (*), and those that remained significant after applying a Bonferroni correction ($p < 4.17 \times 10^{-3}$) are marked with two asterisks (**).

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

Table 5. Statistical comparisons of mean post-invasion (1992-2013) and pre-invasion (1974-1991) indices of abundance for white perch eggs, YSL, PYSL, YOY and yearlings (age-1). The % Difference metric is calculated as (Mean$_{post}$-Mean$_{pre}$) × Mean$_{pre}^{-1}$ × 100. Statistically significant ($p < 0.05$) p-values are denoted by an asterisk (*).

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

Table 6. Parameter estimates (with standard errors in parentheses) and p-values for life-stage transitions based on white perch indices of abundance shown in Figures 6 and 7. The % Difference metric is calculated as $(\text{Estimate}_{\text{post}}-\text{Estimate}_{\text{pre}}) \times \text{Estimate}_{\text{pre}}^{-1} \times 100$. The contrast t-statistics and p-values are for $(\text{Estimate}_{\text{post}}-\text{Estimate}_{\text{pre}})$ contrasts performed on each parameter using ANCOVA (estimates for PYSL-YOY and egg-YOY transitions are from linearized Ricker models where $\log_e(N_s \times N_{s-1}^{-1}) = \log_e(\alpha) - \beta(N_{s-1}) - \gamma_{flow}(flow)$; see Methods). Statistically significant ($p < 0.05$) p-values are denoted by an asterisk (*).

Life-Stage Transition	Parameter	Post-Invasion Estimate	Post-Invasion p-value	Pre-Invasion Estimate	Pre-Invasion p-value	Contrast t-Statistic	% Difference	Contrast p-value
Egg-YSL	α	0.94 (0.12)	< 0.001*	0.41 (0.06)	< 0.001*	3.81	129	< 0.001*
YSL-PYSL	α	5.62 (0.48)	< 0.001*	6.53 (0.49)	< 0.001*	-1.31	-14	0.199
YOY-Yearling	α	0.21 (0.04)	< 0.001*	0.32 (0.03)	< 0.001*	-2.33	-34	0.026*
PYSL-YOY	$\log_e(\alpha)$	2.59 (0.46)	< 0.001*	2.08 (0.88)	0.025*	0.68	25	0.503
	β	0.57 (0.10)	< 0.001*	0.32 (0.17)	0.077	1.84	78	0.074
	γ_{flow}	1.43 10^{-3} (9.31 10^{-4})	0.070	2.68 10^{-4} (7.18 10^{-4})	0.872	0.97	508	0.34
Egg-YOY	$\log_e(\alpha)$	4.47 (0.35)	< 0.001*	3.49 (0.37)	< 0.001*	1.88	28	0.069
	β	3.61 (0.60)	< 0.001*	1.34 (0.20)	< 0.001*	3.60	169	< 0.001*
	γ_{flow}	1.57 10^{-3} (7.94 10^{-4})	0.056	-4.86 10^{-4} (9.08 10^{-4})	0.596	1.71	-423	0.097

Figures

Figure 1. Map of the Hudson River Estuary (HRE), with the 13 river sections sampled by the Hudson River Estuary Monitoring Program outlined by river kilometer (rkm), and markers denoting approximate locations of monitoring stations for temperature (Poughkeepsie) and freshwater flow (Troy; see text). Manhattan and Albany are shown for reference. Shape files for the map were obtained from the New York State Department of Environmental Conservation GIS Clearinghouse (NYSDEC 2016).

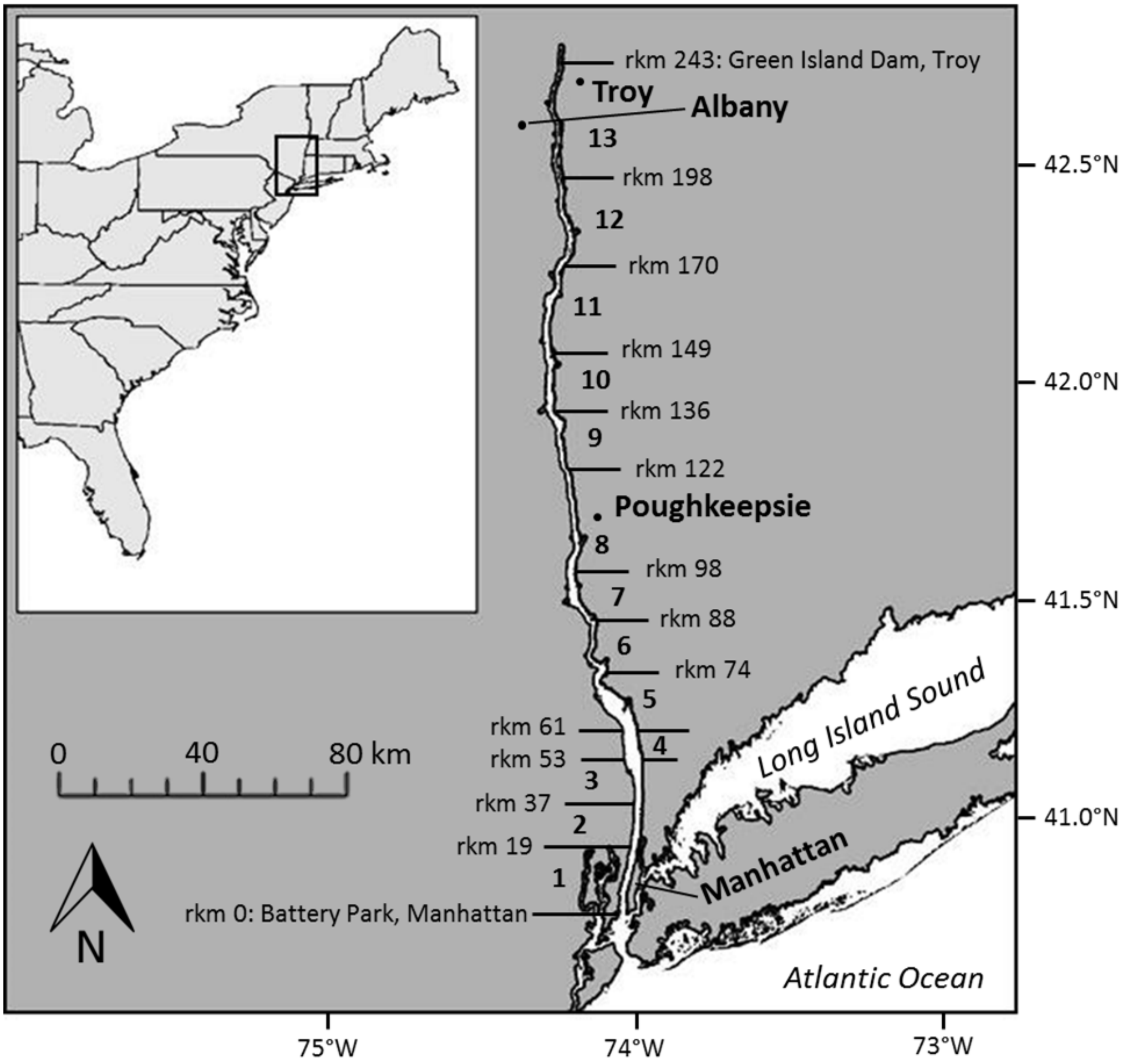

Figure 2. Plots of annual mean temperature (a) and freshwater flow (b) in the HRE from 1951-2013, each plotted with a locally weighted regression (thin black line; LOESS quadratic smoother with a span of 0.5) to show long-term patterns. The dashed grey lines on each plot denote the year 1991, when zebra mussels first appeared in the HRE (see text). Temperature data were reported in Applied Science Associates (2014) and freshwater flow data were acquired from USGS (2015c).

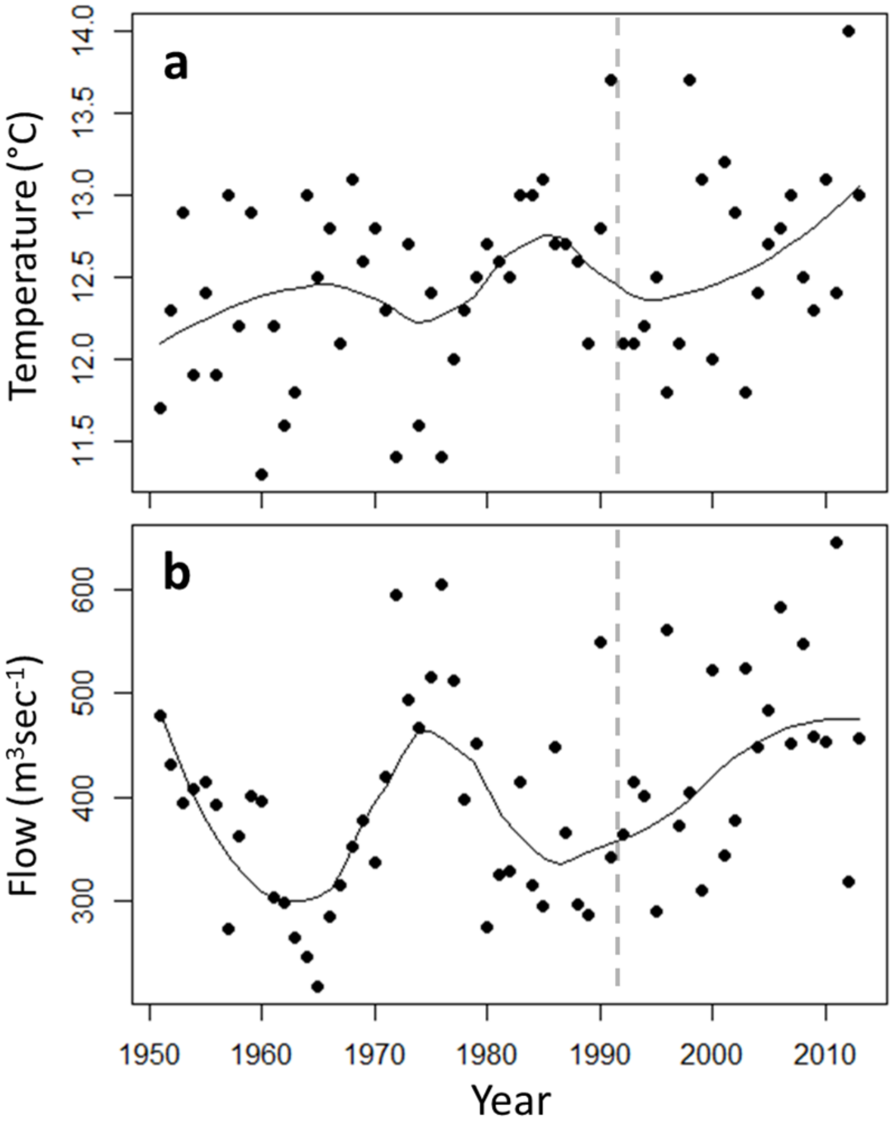

Figure 3. Paulik diagram depicting (clockwise from top right) adult-YOY, adult-YSL, YSL-PYSL and PYSL-YOY life-stage transitions based on mean standing stocks during the post-invasion period (1992-2013). Note that all four plots within the diagram have a common origin. Ricker models are plotted both with (dashed lines) and without (solid lines) freshwater flow during the PYSL period as a covariate (see Methods).

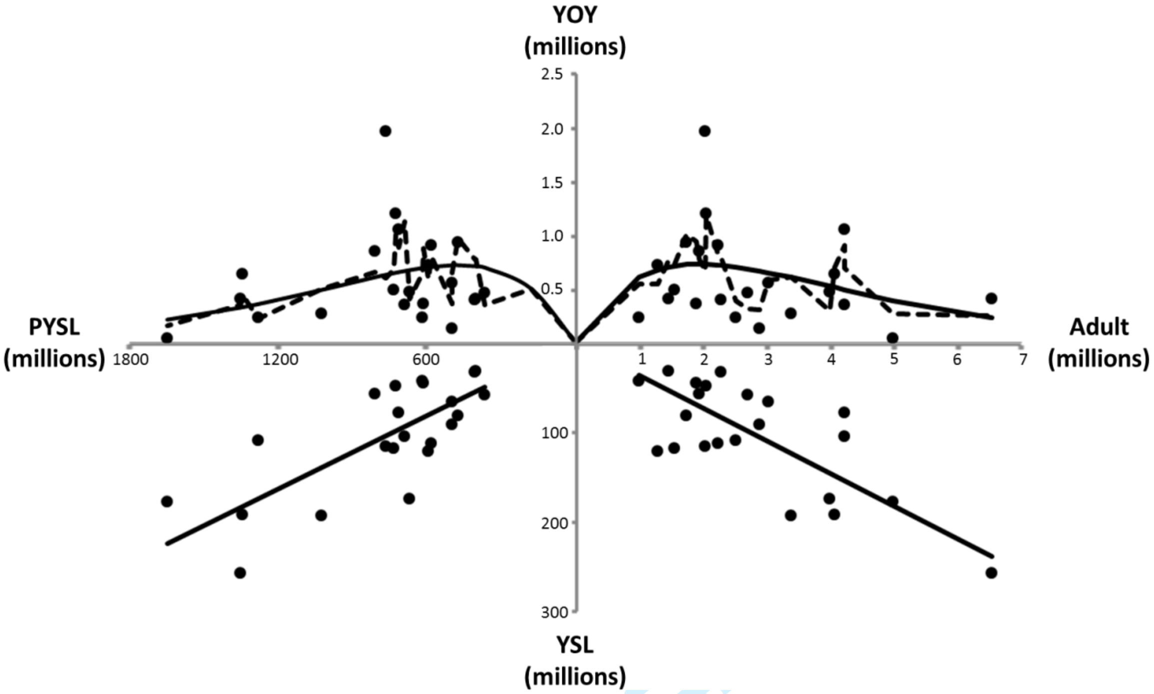

Figure 4. Scatter plots and regression lines for the four strongest post-invasion correlations (1992-2013; $p < 0.05$ before multiple comparison adjustments) between YOY white perch mean length in October and summer temperature (a), summer flow (b) and PYSL standing stock (c) and between migrant fraction and the brackish shoal proportion (d). Note that relationships in b, c and d were no longer statistically significant after applying a Bonferroni correction for multiple comparisons ($p > 4.17 \times 10^{-3}$).

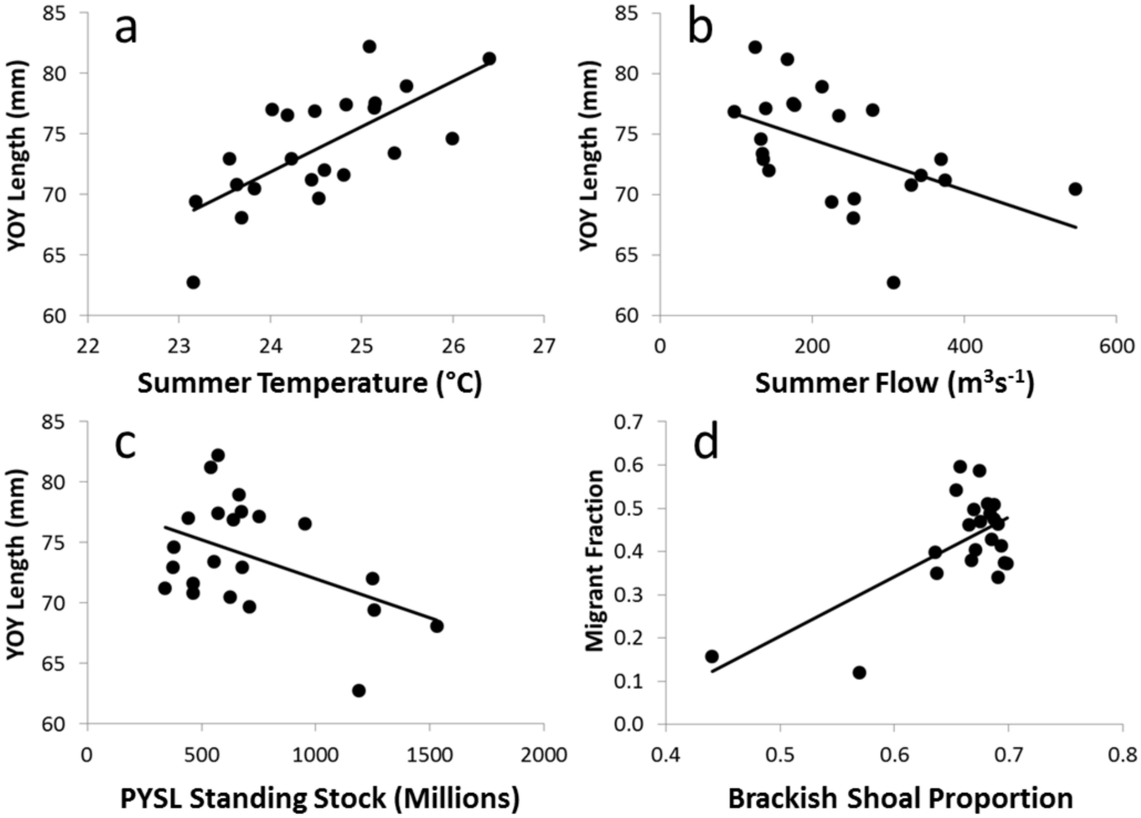

Figure 5. Paulik diagram depicting (clockwise from top right) egg-YOY, egg-YSL, YSL-PYSL and PYSL-YOY life-stage transitions based on indices of abundance during pre-invasion (1974-1991; black points; fitted by solid lines) and post-invasion (1992-2013; white points; fitted by dashed lines) time periods. Note that all four plots within the diagram have a common origin. The egg-YOY and PYSL-YOY relationships are plotted with freshwater flow during the PYSL period as a covariate (see Methods).

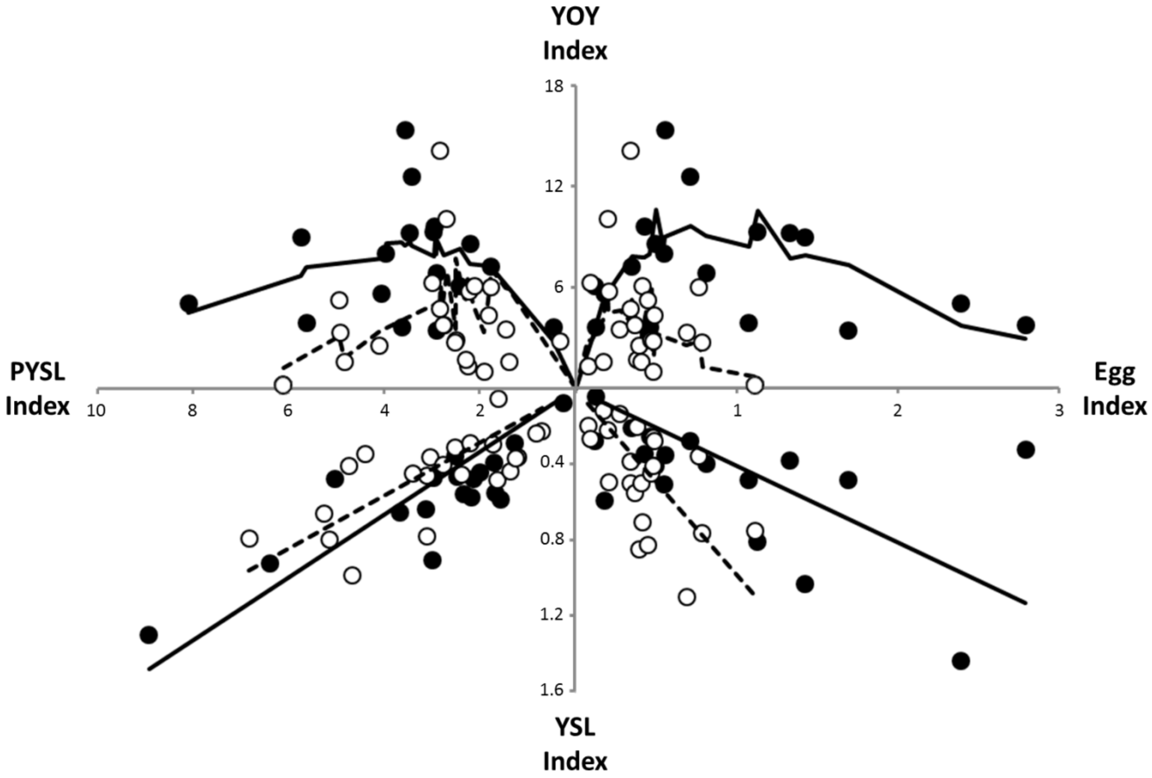

Figure 6. Relationship between white perch yearling (age-1) abundance and YOY abundance from the previous year based on indices of abundance for each life-stage during pre-invasion (1974-1991; black points; fitted by solid line) and post-invasion (1992-2013; white points; fitted by dashed line) time periods.

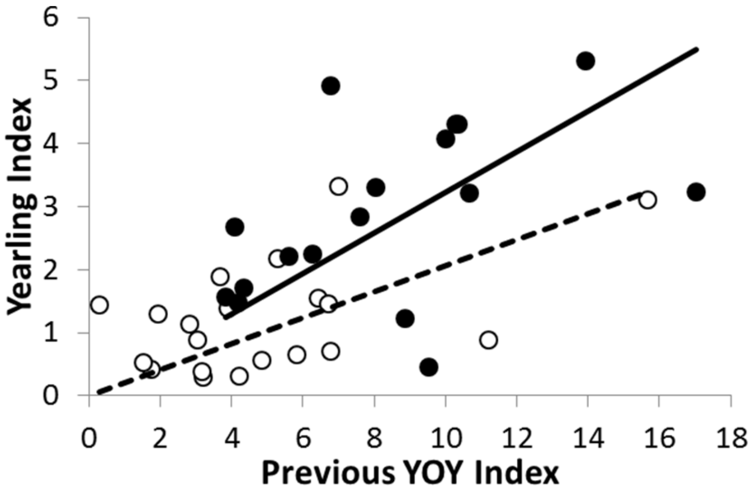

Figure 7. Plot of mean freshwater flow at Green Island in Troy, NY (USGS 2015c) during weeks 19-28, when white perch post yolk-sac larvae (PYSL) are most abundant, from 1992-2013. The regression equation is displayed in the top right corner, and the slope (7.99 year^{-1}) corresponds to an increase of 1.9% year^{-1}.