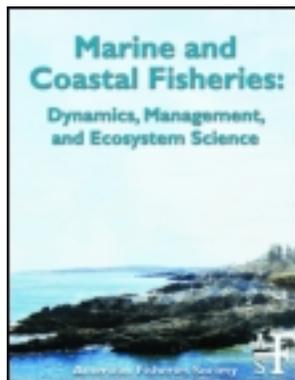


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Findings on American Shad and Striped Bass in the Hudson River Estuary: A Fish Community Study of the Long-Term Effects of Local Hydrology and Regional Climate Change

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SPECIAL SECTION: AMERICAN SHAD AND RIVER HERRING

Findings on American Shad and Striped Bass in the Hudson River Estuary: A Fish Community Study of the Long-Term Effects of Local Hydrology and Regional Climate Change

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Abstract

It has been hypothesized that climate change is an underlying factor in determining fish abundances in the Hudson River estuary (HRE). To study the effects of hydrology and climate on the HRE fish community, we applied multivariate statistical methods to data on 20 species–life history stages collected from 1974 to 2005. We confirm that the HRE fish community has changed over this period. These changes are correlated with local hydrology (freshwater flow and water temperature) and regional climate (the Atlantic Multidecadal Oscillation [AMO] and North Atlantic Oscillation). We found that the abundances of striped bass *Morone saxatilis* larval stages are positively correlated with high freshwater flows and those of juvenile American shad *Alosa sapidissima* negatively correlated with the AMO or warmer sea surface temperatures. Our findings suggest that climate-related variability affects HRE juvenile shad abundances and that management strategies for this declining species should include the implications of climate change.

In the complex web of environmental variables to which fish respond, regional climate is perhaps the least well understood and probably the least studied. There are documented correlations among both fish abundances and distributions and climate signals, but most studies concern fish populations in open-ocean settings such as the North Sea, the Bering Sea, the Northeast Atlantic and the Northwest Pacific (e.g., Brander 2007; Brunel and Boucher 2007). Recently, however, there has been a focus on the effects of climate change on coastal fish populations in the eastern United States. For example, Condrón et al. (2005) found that the abundance of North American Atlantic salmon *Salmo salar* fluctuates with a sea surface temperature–based climate index reflecting the Atlantic Multidecadal Oscillation (AMO).

They concluded that continued warming near the Grand Banks of Newfoundland will negatively impact the already depleted salmon stock regardless of the reduction in commercial fishing. Similarly, Hare and Able (2007) found that large-scale variability in the abundance of Atlantic croaker *Micropogonias undulatus* along the East Coast of the United States is also driven by climatic processes, with increases in abundance or larger year-classes being correlated with the warm winters associated with the positive phase of the North Atlantic Oscillation (NAO; Hurrell et al. 2003).

The effects of climate are not linear, and complex relationships between climate indices and abiotic factors such as discharge and streamflow have been identified in some aquatic

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systems in the eastern United States. Specifically, the AMO has been linked to rainfall and streamflow variability in Florida, with the inflow to Lake Okeechobee varying by 40% between the warm and cool phases of the oscillation (Enfield et al. 2001). Similarly, Bradbury et al. (2002) found that the NAO and the Pacific North American oscillation are positively correlated with streamflow variability in several New England streams. Lastly, much evidence suggests that fish abundances and distributions are affected by streamflow (Poff and Ward 1989; Puckridge et al. 1998; Juanes et al. 2004; Doyle et al. 2005; Gillette et al. 2006).

The Hudson River estuary (HRE) fish community is ideal for testing how local hydrology (e.g., water temperature and streamflow) and regional climate influence fish abundance patterns over time. It has relatively long data records for both fish abundance and abiotic factors. A long-term decline in the diversity and stability of this community has been identified in nearshore fish assemblages by Daniels (1995) and Hurst et al. (2004). Also, there is strong evidence that an exotic species, the zebra mussel *Dreissena polymorpha*, has altered the fish communities in the upper HRE since its invasion in 1991 (Strayer et al. 2004). Although historical fish abundances and distributions are changing or shifting in the HRE, the mechanisms responsible for these shifts remain unclear (Pace et al. 1993b).

Regional climate change is broadly considered to be an underlying factor in determining fish abundances in the HRE, but a quantified relationship between climate phenomena and the observed variations within the fish community has not yet been established (Waldman et al. 2006). For example, Daniels et al. (2005) state that the fish assemblages in the HRE are changing, note that the causes for these changes are varied, and speculate that global warming caused the disappearance of rainbow smelt *Osmerus mordax* in the HRE.

The purpose of this study was to examine the effects of local hydrology and regional climate on the HRE fish community. Identifying possible correlations among climate indices, freshwater flow, water temperature, and fish abundances over time allows us to examine the effects of climate at both local and regional scales. Our first objective was to confirm that the HRE fish community changed significantly over the 32 years from 1974 to 2005. Our second objective was to examine how the HRE fish community responded to changes in climate and hydrological variables over this period through constrained ordination analysis. Our third and final objective was to evaluate the relative importance of the environmental variables (regional climate and local hydrology) on HRE fish community abundance patterns.

METHODS

Study area.—The Hudson River extends 507 km from its source, Lake Tear of the Clouds in the Adirondack Mountains, to New York Harbor (Figure 1). It is tidally influenced up to a dam located near Troy, New York (250 river kilometers [rkm] from the mouth). The New York Department of State has des-

ignated large portions of the Hudson River estuary as a Significant Coastal Fish and Wildlife Habitat (USFWS 1997). Four coastal wetlands within the HRE are designated by the National Oceanic and Atmospheric Agency (NOAA) as National Estuarine Research Reserve System sites. The estuarine portion of the Hudson River is composed of a diverse assemblage of marine, freshwater, and estuarine fishes. Beebe and Savidge (1988) report that 140 species have been collected in the Hudson River estuary and that approximately one dozen of these species are diadromous (Waldman 2006).

After examining studies of the spatiotemporal fish abundance trends in nearshore areas (Daniels 1995; Hurst et al. 2004) and the entire HRE (Pace et al. 1993b; Strayer et al. 2004; ASAAC 2007), we decided to focus this study on the entire HRE, defined as extending from the Battery (rkm 0) to Troy (rkm 248) (Figure 1).

Fish community data.—There has been an intensive multi-species survey in the HRE every year since 1974, when year-class reports were first prepared for the electric utility generating stations. The goal of these reports is to determine the environmental impact that these electric utility generating stations are having on the HRE fish populations. The utilities' survey consists of three annual surveys, the Long River Survey (LRS), designed to assess egg and larval densities; the Fall Juvenile Survey (FJS) to assess juvenile densities offshore; and the Beach Seine Survey (BSS) to assess nearshore fish communities and abundance. The survey begins at the Battery and ends in Albany (ASAAC 2007). Over 30 years of spatiotemporal fish abundance data are available due to this survey. The utilities' fish survey data have been subjected to a full quality assurance–quality control procedure and have been used in numerous analyses (e.g., Pace et al. 1993a; Strayer et al. 2004; Dunning et al. 2006).

Our analyses were conducted using the fish abundance indices calculated in the annual utilities' survey report for the period 1974–2005 (Table 1). Full details of the abundance index calculation can be found in Chapter 2 and Appendix D of the 2005 Year-Class Report (ASAAC 2007) and are only briefly summarized here. The numbers of fish collected in the survey each year were converted to an index representing the number caught under a standardized sampling effort. The indices are based on fish densities for the LRS and FJS and bycatch per unit effort (CPUE) for the BSS and are calculated for the entire estuary. To allow comparisons of data across years, only data from samples that were collected from common weeks or consistently sampled over the period 1974–2005 for each survey were used for the index calculations.

A variety of resident marine, freshwater, and anadromous fish species were chosen to represent the HRE community (Table 1). The fish species and life history stages were selected based on recommendations in the 2005 Year-Class Report because some fish species are selectively sampled during these surveys owing to gear design and sampling location. That is, the sampling gear is biased for the chosen species. The utility companies selected these species based on the New York State Department

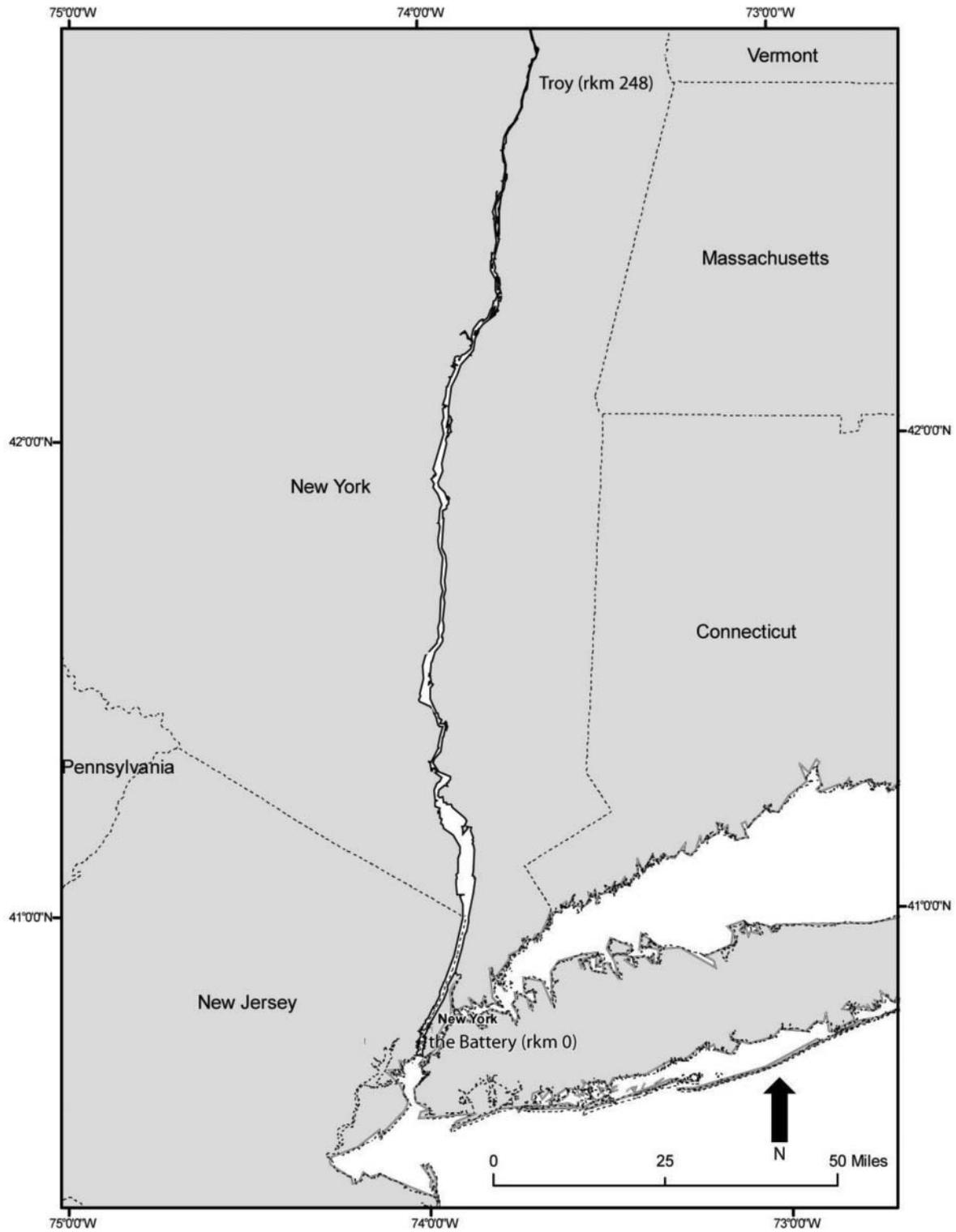


FIGURE 1. Map of the Hudson River estuary. The study area extended from the Battery to Troy.

TABLE 1. Fish abundance indices from 1974 to 2005 that were used in the multivariate analyses.

Species	Species code	Life history stage ^a	Survey ^b
American shad <i>Alosa sapidissima</i>	SH	Egg, ysl, pysl Juv	LRS BSS
Striped bass <i>Morone saxatilis</i>	SB	Egg, ysl, pysl juv	LRS BSS
White perch <i>Morone americana</i>	WP	Egg, ysl, pysl Juv, yearling	BSS LRS
Bluefish <i>Pomatomus saltatrix</i>	BL	Juv	BSS
White catfish <i>Ameiurus catus</i>	WC	Yearling and older	BSS
Hogchoker <i>Trinectes maculatus</i>	HC	Juv	FJS
Rainbow smelt <i>Osmerus mordax</i>	RS	Juv	LRS
Atlantic tomcod <i>Microgadus tomcod</i>	AT	Pysl and juv	LRS
Spottail shiner <i>Notropis hudsonius</i>	SS	Juv	BSS

^a Ysl = yolk-sac life history stage, pysl = post-yolk-sac life history stage, and juv = juvenile life history stage.

^b LRS = Long River Survey, BSS = Beach Seine Survey, FJS = Fall Juvenile Survey (see text for details).

of Environmental Conservation's concern about the ecological effects of the utilities' practices.

Our fish community data set was a matrix containing 32 years (rows) and 20 species–life history stages (columns; Table 1). In many ecological data sets, especially community data sets involving species abundances, it is often quite useful to standardize (or relativize) the data before conducting analyses. Based on the recommendations of Legendre and Gallagher (2001), we used a row total standardization to adjust for differences in absolute fish abundances among years (rows) and place the emphasis on the relative abundance profiles within years. We evaluated other row standardizations as recommended by Legendre and Gallagher (2001), and the results were consistent.

Climate indices.—We used two climate indices in this study: the AMO and the NAO. The AMO is a climate index based on a multidecadal oscillation in North Atlantic sea surface temperatures (SSTs) that were first recognized by Schlesinger and Ramankutty (1994). It is thought to be closely tied to ocean thermohaline circulation (Delworth and Mann 2000; Kerr 2000; Sutton and Hodson 2005). Over the last ~150 years, the observed annual, mean, basin-averaged North Atlantic SST data show a statistically significant warm–cold oscillation, with overall warm periods in the late 19th century, 1931–1960, and 1991 to the present and overall cold periods in 1905–1925 and 1965–1990 (Sutton and Hodson 2005; Enfield et al. 2001). The AMO climate index used in this report is an unsmoothed time se-

ries of monthly SST anomaly data for the North Atlantic region (Enfield et al. 2001) taken from the Kaplan SST version 2 global data set (www.cdc.noaa.gov). These data cover the period from 1856 to the present and consist mainly of ship observations and buoy data coupled with remote sensing data from 1981 on. The data set is a 5° × 5° set of SST anomalies with a base period of 1951–1980. We specify the AMO in this paper as the unsmoothed, detrended time series of area-weighted SST anomaly data in the North Atlantic basin from the equator to 70°N covering the period from 1974 to 2005.

The NAO is the predominant mode of climate variability in the northern Atlantic Ocean region on annual to decadal time scales (Hurrell et al. 2003). The NAO is a quasi-periodic oscillation in the winter atmospheric pressure difference in the North Atlantic region between the subtropical high (the “Bermuda” or “Azores” high) and the subpolar low (the “Icelandic” low). In the positive phase of the NAO, this pressure difference is great, mid-latitude winds are stronger than normal, the Northwest Atlantic regions receive cold Canadian winds, and trans-Atlantic storms tend toward northern Europe as they make landfall; in the negative phase, the pressure difference is less and the reverse conditions occur (Visbeck 2002; Hurrell et al. 2003; Visbeck et al. 2003). The NAO climate index that we used is the time series corresponding to one of ten leading atmospheric “teleconnection patterns,” or recurring large-scale patterns of low-frequency (long-time-scale) variability in the atmospheric pressure and circulation fields for the Northern Hemisphere, identified by researchers at NOAA's Climate Prediction Center.

For both the AMO and the NAO, we used the monthly value from each year with the highest magnitude, that is, the “extreme” value. In other words, the “AMO extreme” and “NAO extreme” for each year were chosen as the single monthly data point with the greatest absolute value. We assumed that the highest negative or positive monthly value from each year would have the greatest chance of influencing fish behavior and distribution.

Hydrological variables.—Yearly maxima of water temperature and freshwater flow in the HRE were assembled from various sources. Freshwater flow from 1974 to 2005 was measured by the U.S. Geological Survey at the federal dam gauge at Green Island, New York. This gauge is typically used to represent freshwater flow into the HRE (Abood et al. 1992). We quantified freshwater flow as the maximum monthly mean net discharge per year. We did not use maximum annual peak flows because they can be unduly influenced by regulation or diversion. We obtained daily recorded water temperatures and used the maximum annual temperature for each year (1974 to 2005) from the Poughkeepsie Water Works (rkm 122).

Data analysis.—We used multivariate statistical methods to assess the changes in fish assemblage abundance profiles over the period 1974–2005 in relation to hydrology and climate change. First, we constructed a Mantel correlogram to examine the changes in fish assemblage profiles over time. In this context, the Mantel correlogram measures how the strength of correlation between fish assemblage profiles in different years varies

as the number of years between profiles increases. The Mantel test operates on distance matrices. We transformed the fish community data set into a distance matrix using the Euclidean measure of dissimilarity, whereby each entry represented the dissimilarity in fish assemblage profiles between two different years of the survey. We assessed the statistical significance of the Mantel test statistic for each time lag based on a Monte Carlo randomization procedure with 1,000 permutations.

Next, we used redundancy analysis (RDA) to examine fish community abundance profiles in relation to environmental and climate variables. Redundancy analysis is a constrained ordination technique that seeks to find the major axes of variation in the dependent variable set (fish data set) that can be explained by linear constraints in the independent variable set (environmental data set) (Legendre and Legendre 1998). We sought to determine how much of the variance in the fish community data set could be explained by the variation in the climate indices (AMO and NAO), freshwater flow, and water temperature. We judged the efficacy of the ordination by the percent of inertia (variance) in the overall fish community and in each species–stage explained by the environmental constraints. To gain insight into the species–environment relationships expressed by the RDA, we scaled the plotting symbol for each year by the abundance of a selected fish species–stage and used generalized additive models (GAMs) to fit the surfaces of the explanatory variables to the ordination plot for the selected species–stage.

We also used variance partitioning to decompose the constrained ordination into the independent and joint effects of local hydrology (freshwater flow and water temperature) and regional climate (AMO and NAO indices) (Legendre and Legendre 1998). Specifically, we used variance partitioning to determine how much of the variation in the fish community over time could be explained by (1) local hydrology alone, after accounting for regional climate effects, (2) regional climate alone, after accounting for local hydrology effects, and (3) the joint, or confounded, effects of local hydrology and regional climate.

Finally, we used cross-correlation functions (CCFs), a time series approach (Crawley 2007), to examine how the AMO affected juvenile American shad. Specifically, we looked at whether the changes in juvenile shad from 1974 to 2005 lagged the AMO changes. We used CCFs to analyze two stationary time series, juvenile shad abundance indices and the AMO from 1974 to 2005, to indicate any direct or delayed dependence between them.

All statistical analyses were conducted using R (R Development Core Team 2008), including functions in the vegan library and programs written by the authors.

RESULTS

The HRE fish community has changed gradually from 1974 to 2005, as inferred from the Mantel correlogram (Figure 2). The pattern of steadily decreasing correlation (Mantel r)

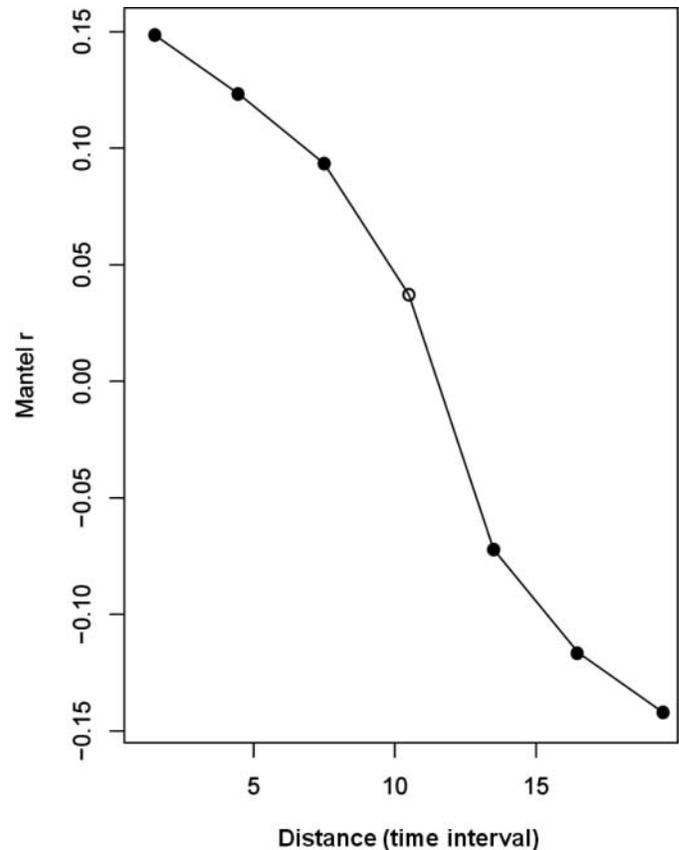


FIGURE 2. Mantel correlogram showing the correlations in fish community structure in relation to the time (years) between observations (represented by the distance class); solid circles represent significant correlations. The monotonically decreasing correlation over time indicates that fish community similarity decreases steadily over time.

with increasing distance in time (number of years between surveys) indicates a long-term trend in the fish community structure.

Based on RDA, the variation in the HRE fish community over time was significantly explained by the linear environmental constraints of freshwater flow, water temperature, and AMO. Specifically, over 46% of the total inertia in the fish community was explained by the environmental constraints. Three species–stages were fit well by the ordination based on the percentage of their inertia explained by the environmental constraints, including post-yolk-sac larval (PYSL) striped bass (73%), juvenile American shad (69%), and yolk-sac larval striped bass (49%). The ordination triplot in Figure 3 shows the first two constrained ordination axes, each of which explained a significant ($P < 0.01$) amount of the variation in the fish assemblage data. The triplot depicts the species–stages and environmental variables as vectors representing the magnitude (vector length) and direction (vector angle) of the greatest linear rate of change in the corresponding variables. For example, larval striped bass show a strong positive relationship with high freshwater flows,

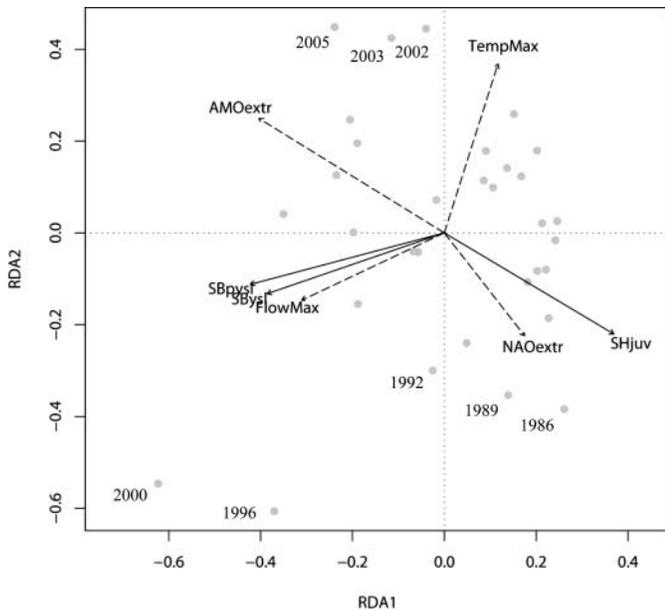


FIGURE 3. Constrained ordination triplot based on redundancy analysis (RDA) showing the first and second axes ($P < 0.01$). The lengths and directions of the vectors reveal the strengths and directions of the maximum rates of change in the corresponding variables. Environmental variables are depicted by dashed vectors and species–stage variables by solid vectors. Species codes and stages are listed in Table 1. The codes AMOextr and NAOextr denote the extreme values of the yearly climate indices associated with the Atlantic Multidecadal Oscillation and the North Atlantic Oscillation, respectively; the codes FlowMax and TempMax denote the maximum yearly values of freshwater flow and water temperature in the Hudson River estuary.

indicating an increase in relative abundance during years with high flows.

Similarly, juvenile shad show a strong inverse relationship to AMO, indicating that juvenile shad decreased in relative abundance during years in the extreme positive phase of the AMO. The strong linear relationship between juvenile shad and the AMO was even more evident in the enhanced ordination plot in Figure 4. In contrast, nonlinear configurations in the water temperature and freshwater flow GAM surfaces (not shown) indicate a more complex relationship with juvenile shad.

Partitioning of the explained variance in the constrained ordination indicated that both local hydrology (freshwater flow and water temperature) and regional climate (AMO and NAO) had strong and independent abilities to explain the variation in the fish community. Of the 46.4% of the inertia in the fish community explained by the environmental constraints, all but 2% was explained uniquely by either local hydrology or regional climate. Local hydrology independently (i.e., after accounting for that due to regional climate) explained 21.1% of the variation in the fish community; regional climate independently explained 23.5% of the species inertia.

The CCF revealed a significant negative correlation between the AMO and juvenile shad abundances in the HRE at a 3-year positive lag. Thus, there is a delayed dependence between the

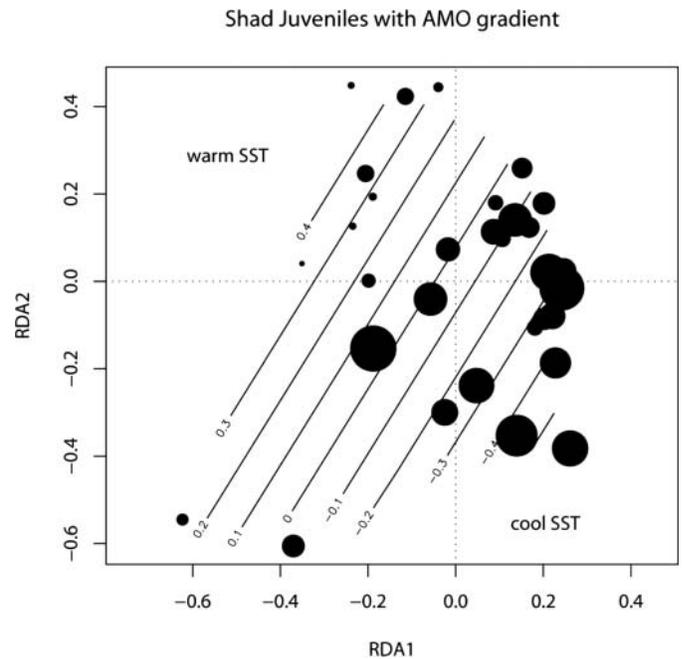


FIGURE 4. Enhanced ordination plot depicting the relative abundance of juvenile American shad each year between 1974 and 2005. The solid circles represent years; the size of each circle is proportional to the relative abundance of juvenile shad in that year. Superimposed on the ordination plot is a fitted surface of the Atlantic Multidecadal Oscillation (AMO) based on a generalized additive model. The regular and straight contours indicate that a linear model was optimal; the contour labels represent the predicted values of the AMO.

abundance of juvenile shad and the AMO, the latter negatively affecting the former 3 years later.

DISCUSSION

There was a significant long-term trend in the selected species–stage abundances from 1974 to 2005, indicating that the HRE fish community has changed significantly over this period. This finding is consistent with the findings from other estuaries. For example, Collie et al. (2008) observed a similar shift in assemblage structure in Narragansett Bay and adjacent Rhode Island Sound from 1959 to 2005, where they documented a decrease in demersal species and an increase in warmwater fish and invertebrates. Within the HRE, Strayer et al. (2004) discovered a shift in the fish assemblage caused by the invasion of the zebra mussel during the early 1990s. Specifically, they found a decrease in open-water fish (e.g., *Alosa* spp.) and an increase in littoral fish (e.g., centrarchids). Daniels et al. (2005) also documented temporal shifts in the HRE fish assemblage; they did not quantitatively assess the factors associated with the long-term trend, however, only speculating on the importance of biotic and abiotic factors.

We found a remarkably strong relationship between abiotic factors and the shift in fish community abundance profiles over time. Specifically, freshwater flow, water temperature, and the AMO explained 46% of the total inertia or variance in the

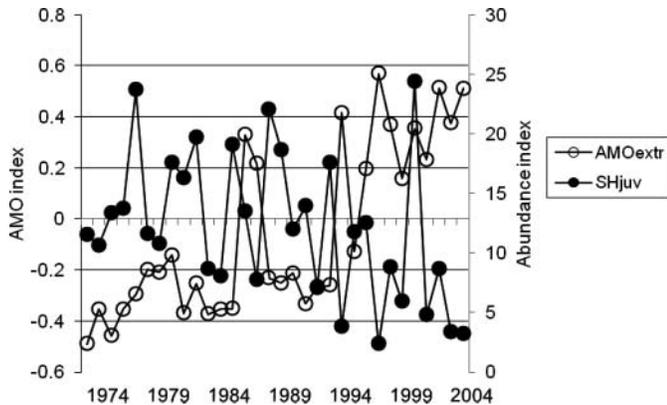


FIGURE 5. Time series plot depicting the relative abundance of juvenile American shad for each year between 1974 and 2005 and the AMO extreme values used in the redundancy analysis.

species–stage abundance patterns. Moreover, these abiotic factors were mostly independent (i.e., not confounded) in their ability to explain the species' inertia. Of the 20 species–stages we analyzed, only juvenile American shad and larval striped bass were well fit by the constrained ordination, suggesting that they are the only species–stages that are highly influenced by local hydrology and regional climate in the same manner as the entire community. After conducting a Monte Carlo randomization procedure to assess statistical significance, we confirm that these results are not due to chance and that the other species–stages were not well fit by the RDA. Additional individual species–stage statistical models would be required to examine whether other species–stages are uniquely influenced by these abiotic factors.

Our results, however, provide different conclusions about the relative importance of local and regional climate on the two most abundant anadromous species in the HRE. Juvenile American shad abundances are affected by regional climate, as indicated by their strong negative correlation with the AMO (Figures 3–5), whereas larval striped bass respond to local hydrology, as indicated by their strong positive correlation with freshwater flow (Figures 3, 6). Currently, American shad abundances are decreasing and striped bass abundances are increasing in the HRE (ASMFC 2007). The differential population trajectories for these two species may be a function of their differing life histories.

Both American shad and striped bass are anadromous, with the adults entering the estuary in early spring to spawn (Waldman 2006). Adult shad and striped bass may overlap spatially and temporally in their spawning patterns, causing competition and predation among the larval and juvenile stages (Bilkovic et al. 2002). However, juvenile striped bass typically spend at least 2 years in the HRE, whereas juvenile shad leave the estuary during the fall of their first year. Although both ocean-phase shad and striped bass can undergo extensive seasonal ocean migrations from Nova Scotia to North Carolina (Dadswell et al. 1987; Waldman et al. 1990), many HRE adult

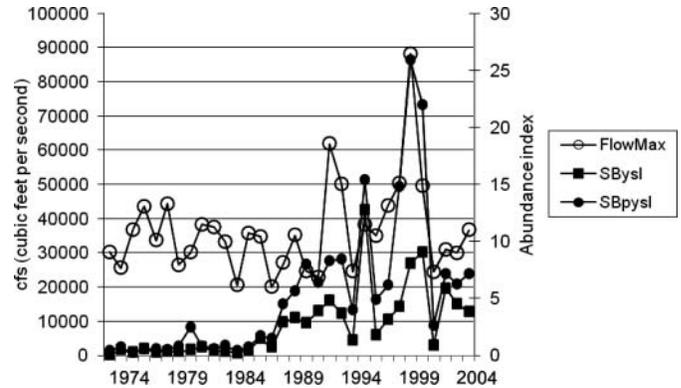


FIGURE 6. Time series plot depicting the relative abundances of yolk-sac and post-yolk-sac larval striped bass for each year between 1974 and 2005 and the maximum freshwater flow used in the redundancy analysis.

striped bass remain residents of the estuary, New York Harbor, and western Long Island Sound (Secor 1999). In general, striped bass are inshore fish and do not usually occur more than 6–8 km offshore (Collette and Klein-MacPhee 2002). In contrast, in late fall and winter, shad often move to deeper waters and have been caught up to 175 km offshore (Dadswell et al. 1987). Shad's seasonal migrations also include both short coastal migrations and more extensive offshore migrations along the continental shelf at depths up to 200 m (Neves and Depres 1979). Unfortunately, most of the data available on shad movements are fishery dependent, and because the fishery is conducted inshore catch data are of limited use in determining offshore migration patterns (Neves and Depres 1979).

Because the AMO index calculation is based on North Atlantic SST values, our results suggest that increases in juvenile shad abundances are negatively correlated with North Atlantic SSTs. During a negative (positive) AMO phase shad populations are high (low) because of cooler (warmer) SSTs (Figures 4, 5). Changes in juvenile abundances are due to direct mortality (Limburg 2001) and probably oceanic phase as well, as shad are influenced by the climate-related factors experienced during their ocean migration. Climate change, and temperature in particular, can have both direct and indirect impacts on fish. The direct effects act on their physiology and behavior and alter their growth, development, reproductive capacity, mortality, and distribution. The indirect effects alter the productivity, structure, and composition of the ecosystem (Brander 2007). Although shad move seasonally within preferred isotherms and their migration patterns are controlled by temperature (Leggett and Whitney 1972; Neves and Depres 1979), they also cross these thermal barriers when they migrate inshore (Dadswell et al. 1987). Hobson et al. (2008) found that summer isotherms are now reaching their northern limit more frequently in the North Atlantic. Warm SSTs are thus occurring further north more often in the summer months, implying that shad are also experiencing warmer temperatures more often. Similarly, Condon et al. (2005) demonstrated this causal link spatially and

graphically with North American Atlantic salmon, the AMO, and North Atlantic SSTs. They found that salmon abundances fluctuate with the AMO and were able to link survival with temperature changes in the Grand Banks (a known overwintering area for salmon) and concluded that continued warming near the Grand Banks will further reduce stock numbers. Future work should further investigate the effects of the AMO and North Atlantic SSTs on migrating oceanic-phase American shad.

Local hydrology also affects the HRE fish community. In particular, our results show that larval striped bass abundances are positively correlated with freshwater flow, with increases in relative abundance during years with high freshwater flows (Figure 6). In contrast, Pace et al. (1993a) found that variability in water temperature and freshwater flow in the HRE explained little of the interannual variation in larval striped bass abundances from 1974 to 1990. However, in a more recent analysis, Dunning et al. (2006) showed that the abundance of PYSL striped bass in the Battery region from 1999 to 2002 was higher when the freshwater flow in the estuary during May and early June was higher. They concluded that freshwater flow strongly affects the abundance of striped bass larvae in the lower HRE, a finding that is similar to ours. This result has also been documented in the upper Chesapeake Bay estuary. While studying striped bass recruitment, North and Houde (2003) found that abundances of striped bass PYSL in the upper Chesapeake Bay estuary are lower during years with low freshwater flow. They concluded that annual changes in freshwater flow could control larval survival and recruitment by modifying the physical and biological characteristics of the estuarine turbidity maximum region.

Although within-river biotic and abiotic conditions clearly affect the abundances of juvenile American shad, our results indicate that ocean climate, or North Atlantic SSTs, also strongly affects juvenile shad abundances within the river. Limburg (2001) suggests that predation and hypoxia negatively affect the juvenile shad migrating from the Hudson River and thus shape year-class strength. Similarly, Strayer et al. (2004), while studying the effects of zebra mussels in the HRE, found that populations of open-water species (e.g., *Alosa* spp.) had shifted downriver away from the zebra mussel populations and decreased in abundance. Even without considering biotic factors, robust climate patterns are evident, further highlighting the importance of regional climate on HRE juvenile shad abundances. Furthermore, the relative importance of local hydrology and regional climate in driving changes in fish abundance patterns in the HRE from 1974 to 2005 has varied, and our research shows that these factors behave independently in this system and can influence the fish community in different ways.

In particular, the significant 3-year lag found between shad abundance and the AMO time series is the minimum duration that shad spend at sea before returning to spawn in the HRE (ASMFC 2007). The lag could indicate the effects of climate, specifically SSTs, on the physiology or reproductive biology or characteristics of ocean-migrating shad (Walther et al. 2002). Geographic variations in the life history of American shad and

climate change could be another link between shad and SSTs. Leggett and Carscadden (1978) found a correlation between latitude and population variation in American shad reproductive strategies. American shad populations are semelparous south of Cape Hatteras, North Carolina, and iteroparous north of Cape Hatteras. Leggett and Carscadden (1978) also found that the degree of iteroparity or percent repeat spawning increases in American shad populations from North Carolina to Canada. This gradient demonstrates an adaptive strategy driven by the thermal regime of their natal rivers (Leggett and Carscadden 1978). Climate change, including more warm years recently, may be affecting iteroparity in the rivers north of Cape Hatteras. Additional research could include reexamining the differences in the proportion of repeat spawners among the iteroparous American shad populations in light of the changing thermal regimes in many riverine systems.

The effects of climate change are a central contemporary issue that is at the forefront of many ecological research endeavors (Walther et al. 2002). Addressing these effects will provide guidance for managing our resources now and in the future. We are currently experiencing the warmest global temperatures in recorded history. Changes due to warming cause variations in AMO and SST patterns (Enfield et al. 2001) and may affect HRE fish abundances and distributions. Quantifying the effects of fluctuations in these patterns with regard to fish population dynamics could help Hudson River fisheries managers better manage the resource in light of future climate scenarios. Climate change is not listed as a potential cause of the decline in HRE shad in the latest American shad assessment and recovery plan (ASFMC 2007; NYSDEC 2008). Our results, however, provide clear evidence for climate-related variability in the abundances of juvenile shad populations in this estuary.

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REFERENCES

- Abood, K. A., G. A. Apicella, and A. W. Wells. 1992. General evaluation of Hudson River freshwater flow trends. Pages 3–28 in C. L. Smith, editor. Estuarine research in the 1980s. State University of New York Press, Albany.
- ASAAC (ASA Analysis and Communication, Inc.). 2007. 2005 year class report for the Hudson River Estuary Monitoring Program. Prepared for Dynege Roseton, LLC, Entergy Nuclear Indian Point 2, LLC, and Mirant Bowline, LLC, Washingtonville, New York.
- ASMFC (Atlantic States Marine Fisheries Commission). 2007. Stock assessment report of the Atlantic States Marine Fisheries Commission. American shad stock assessment report for peer review, volume I. ASMFC, Report 07-01, Washington, D.C.

- Beebe, C. A., and I. R. Savidge. 1988. Historical perspective on fish species composition and distribution in the Hudson River estuary. Pages 25–36 in L. W. Barnhouse, R. J. Klauda, D. S. Vaughan and R. L. Kendall, editors. Science, law, and Hudson River power: a case study in environmental assessment. American Fisheries Society, Monograph 4, Bethesda, Maryland.
- Bilkovic, D. M., J. E. Olney, and C. H. Hershner. 2002. Spawning of American shad and striped bass in the Mattaponi and Pamunky rivers, Virginia. U.S. National Marine Fisheries Service Fishery Bulletin 100:632–640.
- Bradbury, J. A., Dingman, S. L., and Keim, B. D. 2002. New England drought and relations with large scale atmospheric circulation patterns. Journal of the American Water Resources Association 38:1287–1299.
- Brander, K. M. 2007. Global fish production and climate change. Proceedings of the National Academy of Sciences of the USA 104:19709–19714.
- Brunel, T., and J. Boucher. 2007. Long-term trends in fish recruitment in the north-east Atlantic related to climate change. Fisheries Oceanography 16:336–349.
- Collette, B. B., and G. Klein-MacPhee. 2002. Striped bass. Pages 377–389 in B. B. Collette and G. Klein-MacPhee, editors. Bigelow and Schroeder's fishes of the Gulf of Maine. Smithsonian Institution Press, Washington, D.C.
- Collie, J. S., A. D. Wood, and H. P. Jeffries. 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65:1352–1365.
- Condron, A., R. DeConto, R. S. Bradley, and F. Juanes. 2005. Multidecadal North Atlantic climate variability and its effect on North American salmon abundance. Geophysical Research Letters 32:L23703.
- Crawley, M. J. 2007. The R book. Wiley, West Sussex, UK.
- Dadswell, M. J., G. D. Melvin, P. J. Williams, and D. E. Themelis. 1987. Influences of origin, life history, and chance on the Atlantic coast migration of American shad. Pages 313–330 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Daniels, R. A. 1995. Long-term change in the near shore fish assemblage of the tidal Hudson River. Pages 260–263 in E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals and ecosystems. U.S. Department of the Interior, National Biological Service, Washington, D.C.
- Daniels, R. A., K. E. Limburg, R. E. Schmidt, D. L. Strayer, and C. Chambers. 2005. Changes in fish assemblages in the tidal Hudson River, New York. Pages 471–503 in J. N. Rinne, R. M. Hughes, and B. Calamusso, editors. Historical changes in large river fish assemblages of the Americas. American Fisheries Society, Symposium 45, Bethesda, Maryland.
- Delworth, T. L., and M. E. Mann. 2000. Observed and simulated multidecadal variability in the Northern Hemisphere. Climate Dynamics 16:661–676.
- Doyle, M. W., E. H. Stanley, D. L. Strayer, R. B. Jacobson, and J. C. Smith. 2005. Effective discharge analysis of ecological processes in streams. Water Resources Research 41:11411.
- Dunning, D. J., Q. E. Ross, A. F. Blumberg, and D. G. Heimbuch. 2006. Transport of striped bass larvae out of the lower Hudson River estuary. Pages 273–286 in J. Waldman, K. Limburg, and D. Strayer, editors. Hudson River fishes and their environment. American Fisheries Society, Symposium 51, Bethesda, Maryland.
- Enfield, D. B., A. M. Mestas-Nunez, and P. J. Trimble. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U.S. Geophysical Research Letters 28:2077–2080.
- Gillette, D. P., J. S. Tiemann, D. R. Edds, and M. L. Wildhaber. 2006. Habitat use by a midwestern USA riverine fish assemblage: effects of season, water temperature and river discharge. Journal of Fish Biology 68:1494–1512.
- Hare, J. A., and K. W. Able. 2007. Mechanistic links between climate and fisheries along the East Coast of the United States: explaining population outbursts of Atlantic croaker (*Micropogonias undulatus*). Fisheries Oceanography 16:31–45.
- Hobson, V. J., C. R. McMahon, A. Richardson, and G. C. Hays. 2008. Ocean surface warming: the north Atlantic remains within the envelope of previous recorded conditions. Deep-Sea Research 55:155–162.
- Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck. 2003. An overview of the North Atlantic oscillation. Pages 1–35 in J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, editors. The north Atlantic oscillation: climatic significance and environmental impact. American Geophysical Union, Washington, D.C.
- Hurst, T. P., K. A. McKown, and D. O. Conover. 2004. Interannual and long-term variation in the nearshore fish community of the mesohaline Hudson River estuary. Estuaries 27:659–669.
- Juanes, F., S. Gephard, and K. F. Beland. 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. Canadian Journal of Fisheries Aquatic Sciences 61:2392–2400.
- Kerr, R. A. 2000. A North Atlantic climate pacemaker for the centuries. Science 288:1984–1985.
- Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.
- Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam.
- Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35:1469–1478.
- Leggett, W. C., and R. R. Whitney. 1972. Water temperature and the migrations of American shad. U.S. National Marine Fisheries Service Fishery Bulletin 70:659–670.
- Limburg, K. E. 2001. Through the gauntlet again: demographic restructuring of American shad by migration. Ecology 82:1584–1596.
- Neves, R. J., and L. Depres. 1979. The oceanic migration of American shad, *Alosa sapidissima*, along the Atlantic coast. U.S. National Marine Fisheries Service Fishery Bulletin 77:199–212.
- North, E. W., and E. D. Houde. 2003. Linking ETM physics, zooplankton prey, and fish early-life histories to striped bass *Morone saxatilis* and white perch *M. americana* recruitment. Marine Ecology Progress Series 260:219–236.
- NYSDEC (New York State Department of Conservation). 2008. Hudson River American Shad an ecosystem-based plan for recovery. NYSDEC, Hudson River Fisheries Unit, New Paltz.
- Pace, M. L., S. Baines, H. Cyr, and J. A. Downing. 1993a. Relationship among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 50:1976–1983.
- Pace, M. L., J. A. Downing, H. Cyr, S. Baines, and S. Lalond, S. 1993b. Analysis of Hudson River fish populations from the utilities monitoring program. Final Report to the Hudson River Foundation, New York.
- Poff, N. L., and J. V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805–1817.
- Puckridge, J. T., F. Sheldon, K. F. Walker, and A. J. Boulton. 1998. Flow variability and the ecology of large rivers. Marine and Freshwater Research 49:55–72.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Schlesinger, M. E., and N. Ramankutty. 1994. An oscillation in the global climate system of period 65–70 years. Nature 367:723–726.
- Secor, D. H. 1999. Specifying divergent migrations in the concept of stock: the contingent hypothesis. Fisheries Research 43:13–34.
- Strayer, D. L., K. Hattala, and A. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 61:924–941.
- Sutton, R. T., and D. L. R. Hodson. 2005. Atlantic Ocean forcing of North American and European summer climate. Science 309:115–118.

- USFWS (U.S. Fish and Wildlife Service). 1997. Significant habitats and habitat complexes of the New York Bight watershed. USFWS, Charlestown, Rhode Island. Available: <http://library.fws.gov/pub5/begin.htm>. (April 2012).
- Visbeck, M. 2002. The ocean's role in Atlantic climate variability. *Science* 297:2223–2224.
- Visbeck, M., E. P. Chassignet, R. G. Curry, T. L. Delworth, R. R. Dickson, and G. Krahnmann. 2003. The ocean's response to North Atlantic Oscillation variability. Pages 113–145 in J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, editors. *The North Atlantic oscillation: climatic significance and environmental impact*. American Geophysical Union, Washington, D.C.
- Waldman, J. R. 2006. The diadromous fish fauna of the Hudson River: life histories, conservation concerns, and research avenues. Pages 171–188 in J. S. Levinton and J. R. Waldman, editors. *The Hudson River estuary*. Cambridge University Press, New York.
- Waldman, J. R., K. E. Limburg, and D. L. Strayer. 2006. The Hudson River environment and its dynamic fish community. Pages 1–7 in J. R. Waldman, K. E. Limburg, and D. L. Strayer, editors. *Hudson River fishes and their environment*. American Fisheries Society, Symposium 51, Bethesda, Maryland.
- Waldman, J. R., D. J. Dunning, Q. E. Ross, and M. T. Mattson. 1990. Range dynamics of Hudson River striped bass along the Atlantic Coast. *Transactions of the American Fisheries Society* 119:910–919.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.