# Decadal-Scale Change in a Large-River Ecosystem

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Like many large-river ecosystems, the Hudson River has been changing rapidly, chiefly as a result of human activities. Many of these changes take place on a decadal timescale, longer than the duration of most ecological studies. We use long-term studies of the Hudson to describe decadal-scale change in this ecosystem. Major impacts on the Hudson in the last few decades include biological invasions, climate change and extreme weather events, and changes in harvests of fishes. The effects of these impacts may be manifested at even longer timescales because of slow ecological responses and rapid evolution. Similar changes are occurring in large rivers around the world. We propose a framework based on the abruptness, severity, duration, and novelty of the drivers and responses to organize and understand these highly varied decadal-scale changes. Tracking and managing these rapidly changing ecosystems require an active program of scientific research and monitoring.

Keywords: biological invasions, climate change, disturbance, long-term studies, recovery

Few ecosystems are as conspicuously variable as rivers. Since Heraclitus noted 2500 years ago that "it is not possible to step twice into the same river," temporal variability has guided the human use and management of rivers (e.g., flood protection, irrigation, power production, seasonal navigation, fisheries) and, more recently, has been an important theme in river ecology. Variability in rivers arises from both natural and anthropogenic drivers and is expressed on multiple timescales (figure 1), from seconds (ephemeral eddies) to millennia or longer (glacial–interglacial cycles, tectonism). Events occurring on timescales of days to a year or two, including seasonal variation, have been well studied by river ecologists, and high-frequency events (seconds to days) are beginning to be well documented by sensor networks now in place on many rivers.

In contrast, multiyear to millennial processes, which can be understood through direct long-term studies and through retrospective studies (e.g., paleoecology) and models, have received less attention, in part because of the logistic difficulties associated with maintaining long-term studies (Dodds et al. 2012). We focus here on ecological variability occurring on timescales of decades (i.e., 3–30 years), which we argue is important in determining the ecological character of large-river ecosystems and is highly relevant to management. Examples of decadal-scale variability include many processes that change slowly (e.g., climate change, whether natural or anthropogenic; land-use change in the catchment; chronic pollution and recovery from such pollution; and overharvest of biological populations). Decadal-scale
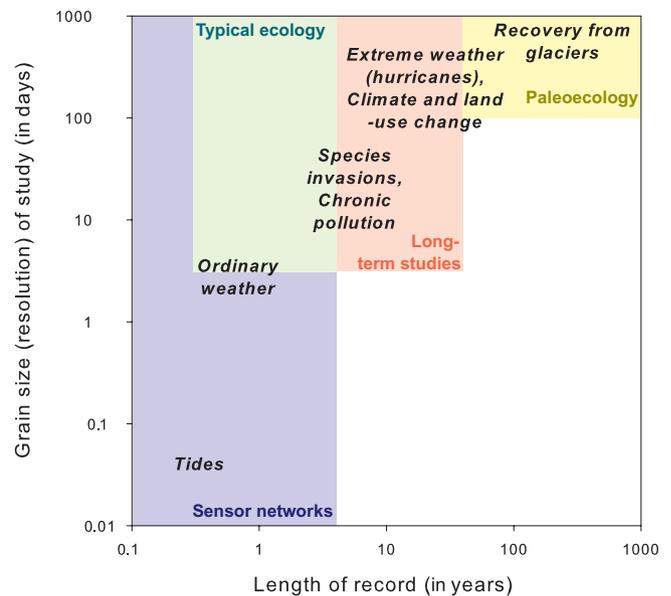
Figure 1. Some important kinds of temporal variability in rivers (not meant to be an exhaustive list of drivers of temporal change), along with scientific tools that are most useful in different domains. This list of tools is also intended to be illustrative rather than exhaustive, and the domains shown are only approximate.

variability also includes rare events with long return times (e.g., extreme weather events; morphological change to the channel and floodplain of the river, such as dams, levees,

dredging and filling, and shoreline hardening; extreme chemical events, whether natural or anthropogenic [e.g., spills]; and invasions of new nonnative species).

Here, we describe long-term change in the Hudson River, a well-studied river in eastern New York, as a way of introducing the general phenomenon of decadal-scale variability in rivers. We argue that such variability is pervasive, strong, and varied in rivers around the world today and is centrally important to understanding and managing large-river ecosystems such as the Hudson. We also propose a general framework for organizing and understanding the apparently disparate drivers and responses that underlie decadal-scale variability in rivers.

A case study of decadal-scale change in the Hudson River ecosystem

The freshwater tidal portion of the Hudson River includes a 150-kilometer (km)–long section of this large river (drainage area, 34,615 square kilometers; mean annual discharge, 592 cubic meters per second) in eastern New York. The annual hydrograph is dominated by spring snowmelt and has not been heavily altered by dams. Most of the channel in this part of the Hudson is from 0.5–4 km wide and 5–20 meters (m) deep, although there are extensive wetlands and shallow areas less than 1 m deep at low tide. The entire study area is subject to tides of 0.8–1.6 m in range, and strong tidal currents reverse in direction every 6 hours and prevent stratification. Because its channel was glacially deepened and is maintained by tidal flows that are much larger than mean freshwater flows, the Hudson does not have a large floodplain like those of many alluvial rivers. The Hudson freezes over during most winters, reaches from 26 degrees Celsius (°C) to 28°C during most summers, and is turbid and rich in nutrients. The food web is supported by a mixture of allochthonous inputs and autochthonous production by phytoplankton, attached algae, and rooted plants. Production by heterotrophic bacteria exceeds phytoplankton production. The dominant species in the freshwater tidal Hudson include diatoms and cyanobacteria in the phytoplankton; wild celery (*Vallisneria americana*), water chestnut (*Trapa natans*), and cattail (*Typha angustifolia*) in the shallows and wetlands; *Bosmina freyi* and various copepods and rotifers in the zooplankton; bivalves, tubificoid oligochaetes, chironomids, and amphipods in the zoobenthos; and young of the year of anadromous species (especially *Alosa* spp. and *Morone* spp.) in the fish community. This account was summarized from Levinton and Waldman (2006), which provides more detail.

The Hudson has been unusually well studied since the 1970s by consultants working for the electric utilities (e.g., Klauda et al. 1988, Smith CL 1992), biologists at the New York State Department of Environmental Conservation, various academic ecologists (e.g., Levinton and Waldman 2006), and our group at the Cary Institute of Ecosystem Studies and our collaborators. We focus here on the 25-year period from 1987 to 2012, during which the Cary group conducted intensive studies of the ecology of the freshwater tidal portion of the Hudson. We also draw on data collected on the Hudson by other researchers and include key findings from the brackish parts of the tidal Hudson.

Species invasions. Like many rivers, estuaries, and lakes around the world (e.g., Cohen and Carlton 1998, Ruiz et al. 1999, Ricciardi 2006, Jackson and Grey 2013), the Hudson has been heavily invaded (Strayer 2006) and now contains dozens of nonnative species. Some of these species have large ecological effects. In particular, the zebra mussel invasion was probably the most prominent ecological change in the Hudson since 1987. Zebra mussels (*Dreissena polymorpha*) first appeared in the freshwater tidal Hudson in 1991 and, by the end of 1992, constituted more than half of the heterotrophic biomass in the ecosystem. Since 1993, growing season filtration rates by the zebra mussel population have typically been 10%–100% of the volume of the river per day (Strayer et al. 2011)—much higher than the aggregate filtration rate of all suspension feeders in the Hudson before zebra mussels arrived (which was approximately 3% per day). In response to these high filtration rates, populations of phytoplankton and small zooplankton (protozoans, rotifers, and copepod nauplii) declined severely in the early years of the invasion (figure 2). Many other parts of the ecosystem that were connected to the phytoplankton also changed, and many of these changes were large (figure 2; see also Caraco et al. 1997, 2006, Findlay et al. 1998, Pace et al. 1998, Strayer and Smith 2001, Strayer et al. 2004).

But the zebra mussel population in the Hudson and its impacts have been changing. The demography of the zebra mussel population has changed since the early 1990s, with greatly increased mortality rates and an increased dominance of small, young animals (Strayer et al. 2011). Consequently, the filtration rate of the zebra mussel population has fallen by approximately 80% (but is still substantial). Presumably in response to these changes in the zebra mussel population, parts of the Hudson's ecosystem have begun to recover toward preinvasion conditions—in some cases, fully recovering to preinvasion conditions (figure 2; see also Pace et al. 2010, Strayer et al. 2011, 2014, Strayer and Malcom 2014). In contrast, we detected no recovery in other parts of the ecosystem, including phytoplankton biomass, littoral zoobenthos, and fish abundance and distribution (Strayer et al. 2014). Therefore, the initially severe effects of the zebra mussel invasion have partially moderated.

We do not yet understand all of the mechanisms behind these recent changes, nor can we confidently predict the future trajectory of the zebra mussel population and its effects. The increase in the mortality rates of zebra mussels resulted partly from increased predation from blue crabs (*Callinectes sapidus*, which migrate into the freshwater tidal Hudson during the summer) and partly from other causes (Carlsson et al. 2011). The recovery of some parts of the ecosystem may have resulted as much from the shift in the size structure of the zebra mussel population as from
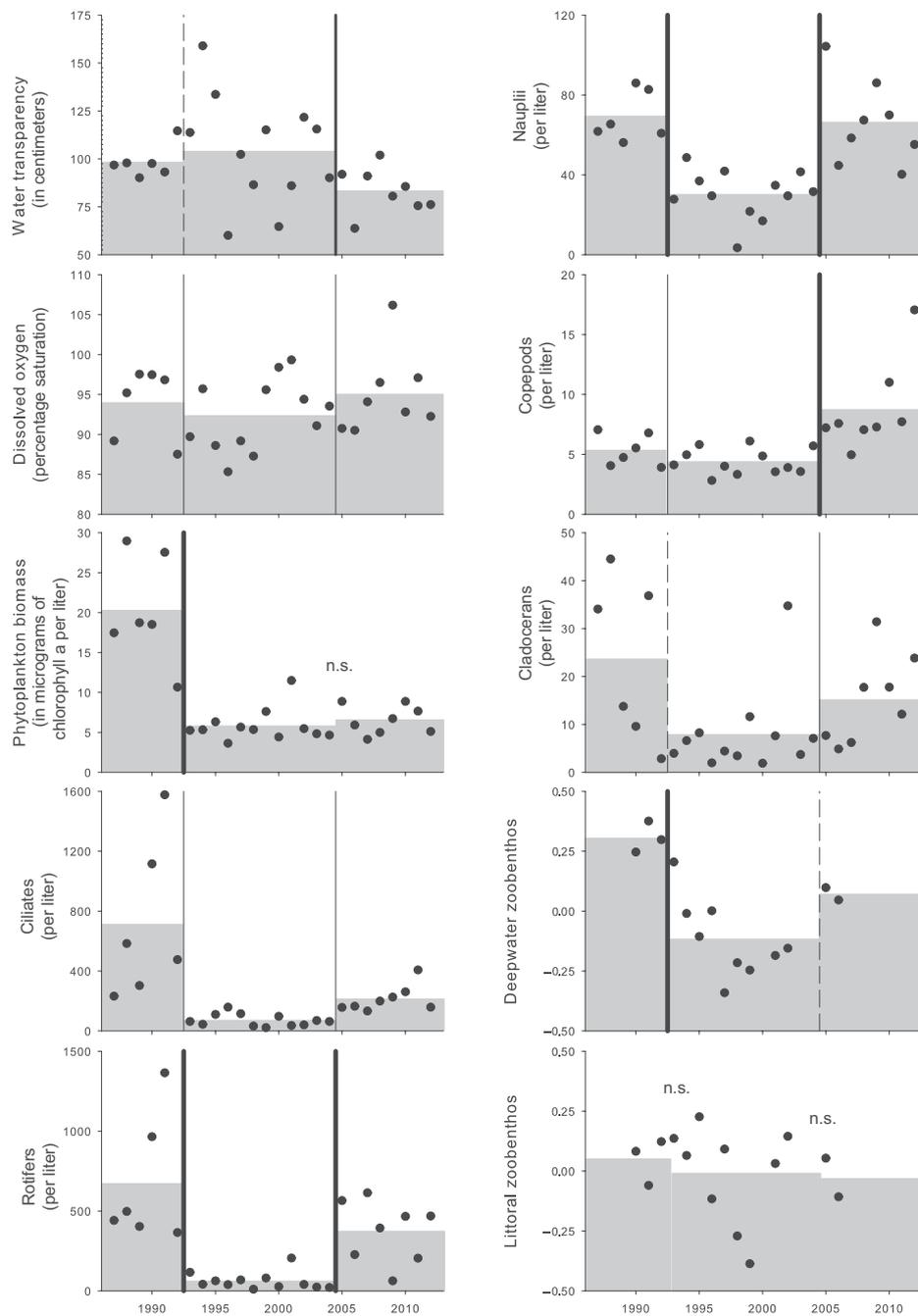
Figure 2. Initial effects of the zebra mussel invasion on selected ecological variables and recent recovery from those initial effects. The data points show annual means from the growing season (May–September) or single annual measurements (for the zoobenthos). The gray bars show the arithmetic means for three time periods: preinvasion (1987–1992), early invasion (1993–2004), and recovery (2005–2012). We chose 2005 as the beginning of the recovery period, because that is when large zebra mussels almost disappeared from the Hudson as a result of increased mortality (Pace et al. 2010). The vertical lines separating these time periods show the statistical significance of differences between adjacent time periods: No line and n.s. mean that the probability level (p) was greater than 0.1; the dashed line indicates that .1 > p > .05; the thin solid line shows .05 > p > .01; the medium solid line shows .01 > p > .001; and the heavy solid line shows p < .001. Except for zoobenthos, for which we used t-tests, the statistical tests were based on time-series analyses of biweekly samples, with interventions at 1 September 1992 and 4 May 2005 and freshwater flow as a covariate. The data were log transformed or interpolated as needed. To remove large spatial variation from the zoobenthic data, we normalized all densities to the long-term mean density at each station by log₁₀ transforming the data and calculating the density in a given year at a station as the residual from the long-term mean density at that station. Therefore, the y-axes for zoobenthic density are $\log_{10}$ scaled (see Strayer et al. 2011 for further details). The significance tests were one tailed (because hypotheses about effects are directional), except for littoral zoobenthos.
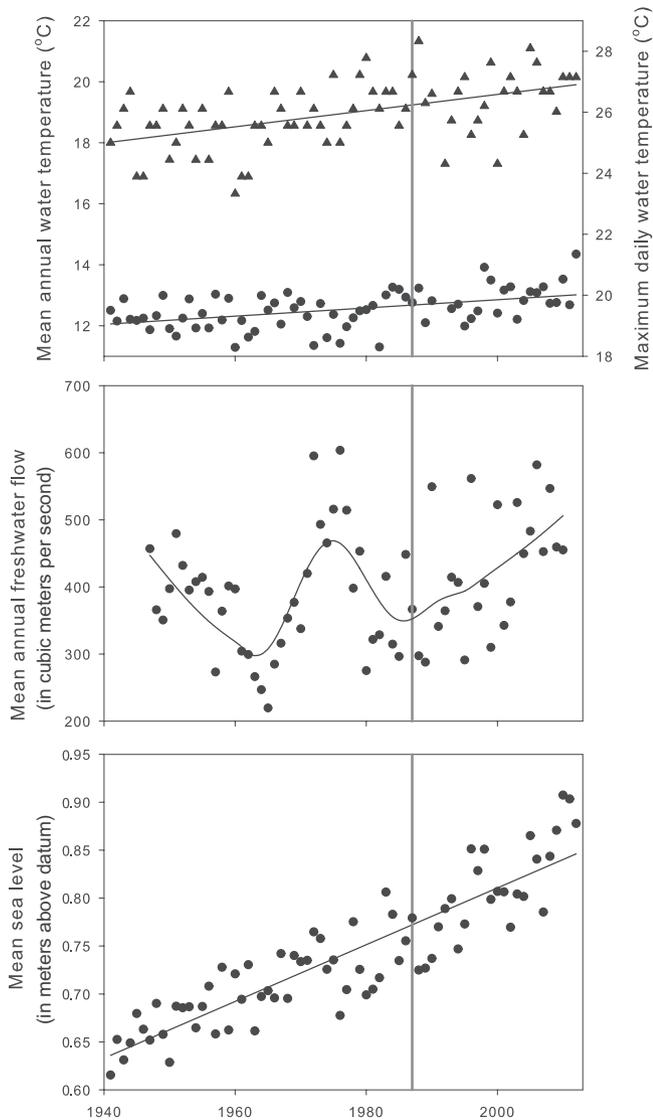
Figure 3. Recent trends (1940–2012) in water temperature, freshwater flow, and mean sea level in the Hudson River. The vertical line shows the year 1987, when our long-term studies began. The temperature data are from the Poughkeepsie Water Treatment Plant and the US Geological Survey (see Seekell and Pace 2011 for details), the flow data are for Green Island at the head of the estuary from the US Geological Survey (http://io.aibs.org/greenisland), and the sea level data are for the Battery in New York City (http://io.aibs. org/battery). The linear regressions for the mean and maximum daily water temperatures were both significant (p < .0001); their slopes are 0.013 degrees Celsius (°C) per year and 0.027 °C per year, respectively; and their coefficients of determination were $r^2 = .22$ and $r^2 = .26$, respectively. Flow was fitted with a locally estimated scatterplot smoothing regression with α = .5, $r^2 = .44$. The mean sea level has been rising at a mean rate of 2.96 millimeters per year ($r^2 = .80$, p < .0001).

reduced overall filtration rates (Pace et al. 2010, Strayer and Malcom 2014). Whatever the precise mechanisms of this recovery, the effects of zebra mussels on the Hudson are still changing substantially 20 years after the initial invasion and are driving large temporal variation in the ecosystem.

The zebra mussel is not the only nonnative species in the Hudson (Strayer 2006). Other nonnative species that have appeared or irrupted since 1987 include the Asian clam (*Corbicula fluminea*), the quagga mussel (*Dreissena rostriformis bugensis*), the Chinese mitten crab (*Eriocheir sinensis*), the freshwater drum (*Aplodinotus grunniens*), and the channel catfish (*Ictalurus punctatus*). All of these species are capable of producing strong ecological effects, although these effects have not been studied in the Hudson. As in many other aquatic ecosystems (e.g., Cohen and Carlton 1998, Ruiz et al. 1999, Ricciardi 2006, Jackson and Grey 2013), invasion rates in the Hudson remain high (Strayer 2006), and new invaders continue to appear. As a result of these new invasions and the changing effects of established invaders such as the zebra mussel, nonnative species will continue to cause large changes in the Hudson ecosystem over the coming decades.

Climate change. As is the case around the world, regional climate change has affected the Hudson (figure 3), and climate change is expected to accelerate in the coming decades (NYCPCC 2013). Three aspects of climate change are especially important to the Hudson ecosystem: temperature, freshwater flow, and sea level. The mean water temperature in the Hudson has been rising since the 1930s (Seekell and Pace 2011) and has risen approximately 0.33°C since our intensive studies began in 1987 (figure 3). Since 1987, precipitation and freshwater flow in the Hudson have risen by more than 40%, and the sea level at the mouth of the Hudson rose by 74 millimeters. The temperature and sea level are projected to continue to rise substantially in the future, whereas the mean freshwater flow is predicted to remain near twentieth-century levels or to rise slightly (Milly et al. 2005, Matonse et al. 2013). We can use long-term data from the Hudson to explore three kinds of responses to this changing climate: the effects of changes in mean conditions, the effects of changes in extreme conditions, and changes in phenology.

Because changes in the mean temperature and sea level up to this point have been modest, ecological responses in the Hudson (to the extent that they have been studied) also appear to be modest. Models of interannual variability in temperature and fish populations (Strayer et al. 2004, 2014) suggest that interannual variations in water temperature have had undetectable or small effects on the numbers and distribution of young fishes and the growth rates of juvenile fishes (figure 4). The growth rate of post-yolk-sac fish larvae was the only ecological variable analyzed that was consistently correlated with warm temperatures (figure 4). If the Q_{10} temperature coefficient is 2, a 0.33°C rise in mean
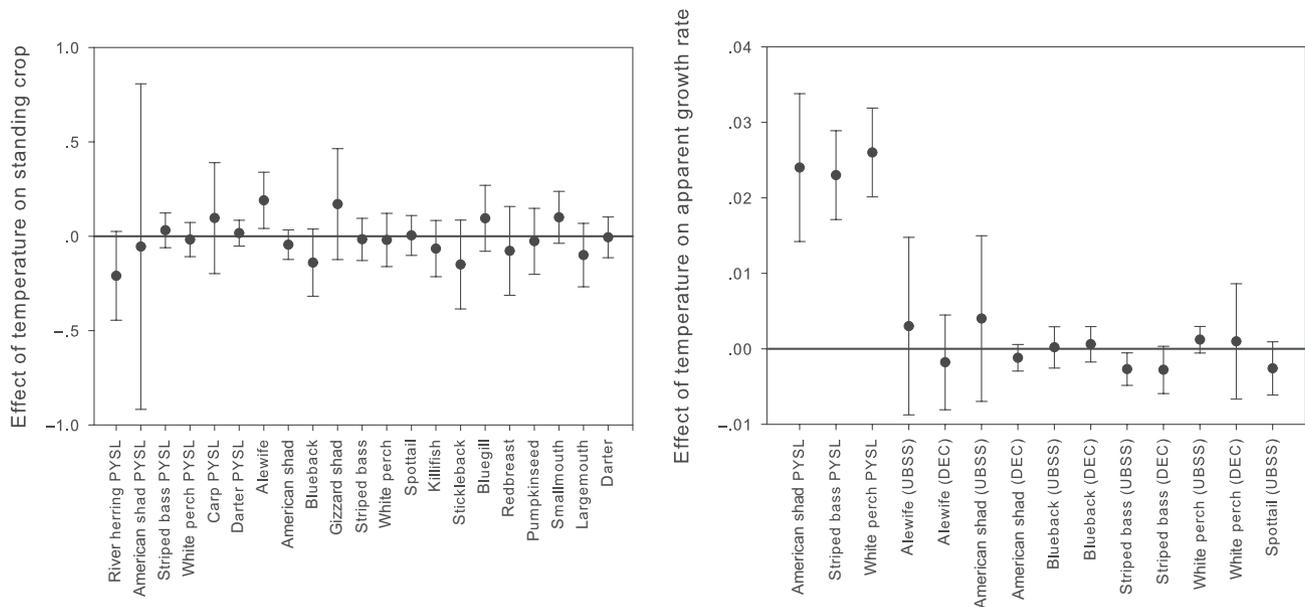
Figure 4. Effects of water temperature on the abundance and growth rates of fishes in the Hudson River, based on Strayer and colleagues (2004). The units are changes in log₁₀-transformed abundance per degree Celsius and changes in growth rate (per week) per degree Celsius. The abundance data are from the utilities beach seine survey of juveniles; the growth analysis includes both post-yolk-sac larvae (PYSL) and juveniles, from two independent data sets. See Strayer and colleagues (2004) for details. The error bars represent the 95% confidence intervals. Abbreviations: DEC, New York State Department of Conservation survey; UBSS, utilities beach survey.

temperature would produce only a 2% increase in biological rates, so these modest changes are not surprising. A change in the mean temperature and sea level may become more important as these changes become larger in coming decades. In the case of sea level rise, if substratum elevations in wetlands and vegetated shallows do not accrete fast enough to keep up with the rising sea level, rooted vegetation in these areas may shift in composition or disappear altogether, which would lead to large ecological changes, with ramifications throughout the ecosystem. This problem is receiving increasing attention from estuarine and coastal ecologists (Kirwan and Megonigal 2013) but may also affect the lower courses of rivers that feed into inland waters whose water levels are affected by climate change.

In contrast to the modest effects of the rising temperature and sea level over the past few decades, changes in mean freshwater flow since 1987 have had large, measurable effects on the character of the ecosystem. Plankton populations are more poorly developed in wet years than in dry years, growth rates of young-of-the-year fish are reduced, and fish populations are centered farther downriver (figure 5; Strayer et al. 2004). It appears that interannual variation in freshwater flow has been responsible for much of the recent interannual variation in the Hudson ecosystem (Strayer et al. 2008), so the more-than-40% increase in mean freshwater flows since 1987 has caused important changes in the Hudson. Climate models (Milly et al. 2005, Matonse et al. 2013) suggest that mean flows in the region will not increase or decrease dramatically in the future, although decadal-scale

variation such as that shown in figure 3 will continue to affect the ecosystem.

Changes in extreme conditions may also drive important changes in ecosystem structure and function. Examples include high summer temperatures, high freshwater flows associated with hurricanes or other storms, and high storm surges on top of rising sea levels. Because of their importance, we discuss hurricane-related floods separately below. The summer maximum temperatures in the Hudson have been rising about twice as fast as the mean annual temperature (figure 3) and are thought to be responsible for the disappearance or decline in coolwater fishes, such as rainbow smelt (*Osmerus mordax*) and tomcod (*Microgadus tomcod*), in the Hudson in the last few decades (Daniels et al. 2005). Fernald and colleagues (2007) also found that the dominance of planktonic cyanobacteria was strongly correlated with high summer temperatures, perhaps as a result of changes in ephemeral stratification of the water column. Consequently, blooms of cyanobacteria, many of which are toxic or unsightly, may become more frequent and severe as the Hudson warms. The ecological effects of storm surges associated with hurricanes such as Sandy (Hsu 2013) have not received much attention in the Hudson, but these large surges (3.9 m high along the coast for Sandy) must affect shallow-water, wetland, and riparian habitats (e.g., Blanchette et al. 2009). Therefore, as others have observed (e.g., Smith MD 2011), changes in extreme events, as well as changes in mean conditions, can be important in driving ecological change.
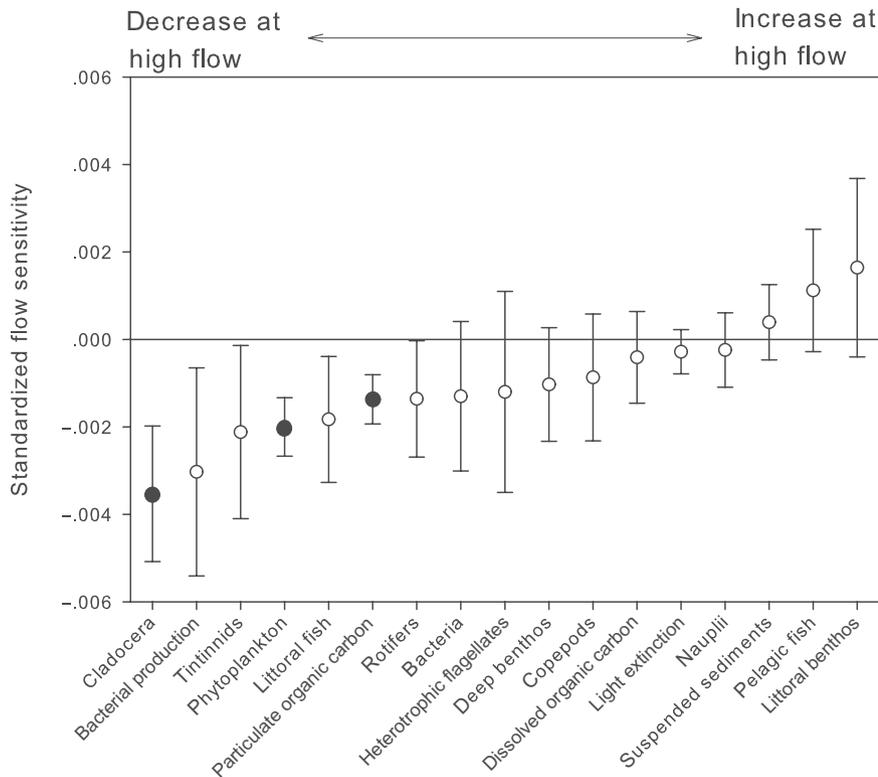
Figure 5. Ecological effects of freshwater flow in the Hudson River based on multiple regressions using freshwater flow and the presence of zebra mussels as independent variables (Strayer et al. 2008). The data are partial regression coefficients, standardized to their preinvasion means, and the error bars represent standard errors. That is, a slope of −0.002 means that the variable declined by 0.2% of its mean before the zebra mussel invasion for every cubic-meter-per-second increase in freshwater flow. The black data points are significantly different from 0 at α < .05, and the white points are not significant at α > .2. Except for bacterial production, all of the biological variables are abundances of the biota. Tintinnids are the dominant planktonic ciliates in the Hudson.

Climate warming has led to phenological shifts in many ecosystems, so that events occur earlier in the spring (e.g., Parmesan and Yohe 2003, Thackeray et al. 2010). We found only slight evidence for phenological shifts in the spring population peaks of cladoceran zooplankton and young fish in the Hudson in recent years (figure 6). Only the larvae of white perch and striped bass have tended to appear a little (1–2 weeks) earlier in the season in recent years, and even this shift is small compared with interannual variation in the timing of population development. The insensitivity of phenology to recent climate change in the Hudson appears to be a result of the opposing effects of rising temperature and rising freshwater flows. The timing of seasonal events is advanced in warm years and retarded in wet years (table 1), and these two effects have nearly canceled each other out in the last few decades. Table 1 suggests that different members of the Hudson's food web may be differentially sensitive to changes in temperature and freshwater flow, which may lead to phenological mismatches (e.g., between the times when

zooplankton and larval fish appear) as the climate continues to change (cf. Thackeray et al. 2010). However, these differences are small compared with existing interannual variation in phenological matching (figure 7). Because the future climate is supposed to be substantially warmer but not substantially wetter on average, we expect to see springtime events such as the population peaks of cladocerans and young fishes arrive earlier in future years.

Hurricanes. We observed the effects of two tropical storms and a hurricane on the Hudson: Hurricane Floyd, in 1999, and Tropical Storms Irene and Lee, which occurred less than 2 weeks apart in 2011 and which we therefore consider a single storm event. These storms had large, long-lasting impacts on physical, chemical, and biological variables in the Hudson (figure 8). Both storm events greatly increased freshwater flow, increased concentrations of suspended inorganic and organic particles, decreased water transparency, and decreased plankton populations. For these variables, Floyd had effects smaller than but similar to those of Irene and Lee. Neither storm event had much of a sustained impact on dissolved oxygen or dissolved organic carbon concentrations. In contrast, the two storm events had different consequences for dissolved inorganic nitrogen and phosphorus. The concentrations of these nutrients changed little after Irene and Lee but nearly doubled after Floyd. It is clear that the effects of different storms on the Hudson differ both quantitatively and qualitatively.

The effects of hurricanes may extend into the next year or beyond through the population dynamics of long-lived organisms such as fish and perennial plants. Populations of submersed plants may be diminished for a year or more after severe storms (figure 9; Orth and Moore 1984). Although the longer-term impacts of storms on the Hudson's fishes have not been investigated, large storms have either increased or decreased fish recruitment in other systems (e.g., Lake et al. 2006, Dodds et al. 2012).

Changes in harvests. Historically, the Hudson supported large fisheries for several species of finfish (e.g., the American shad, Atlantic sturgeon, striped bass) and shellfish (the Eastern oyster and the blue crab) (Limburg et al. 2006). These fisheries diminished in size as a result of population collapse and contamination (figure 10) so that only American shad and blue
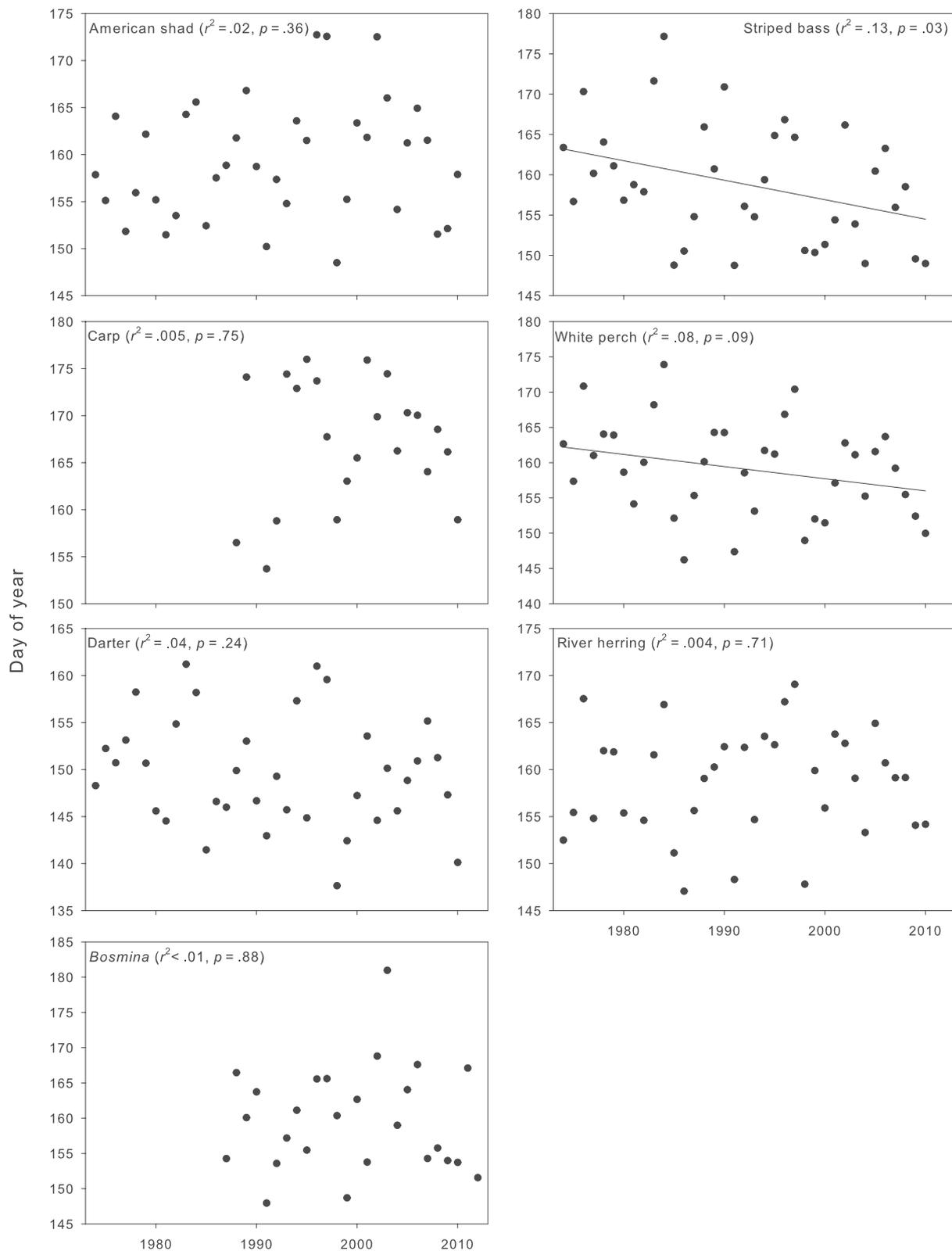
Figure 6. Tests for simple phenological shifts in the appearance of post-yolk-sac larvae of Hudson River fishes and early summer bloom of the zooplankter Bosmina. *The* y-*axis shows the average date at which the fish populations develop (population center of gravity; cf. Thackeray et al. 2008), calculated from data from 6 April to 11 August, or the average date at which* Bosmina *blooms develop (population center of gravity, calculated from data obtained between 1 May and 1 July). The data are from the utilities' long river ichthyoplankton survey and the Cary Institute.* River herring *refers to blueback herring and alewife, whose post-yolk-sac larvae are indistinguishable.*

Table 1. *Multiple regression models to predict interannual variation in the timing of population phenologies (population center of gravity, cf. Thackeray et al. 2008) of an abundant zooplankter and post-yolk-sac larvae of several fish species from temperature and freshwater flow means for the period of 1 May to 1 July.*

Species	Model R^2	Slope of flow effect (in days per cubic meter per second)	Slope of temperature effect (in days per degree Celsius)
Bosmina	.39**	0.02*	−1.59
American shad	.41***	0.014*	−1.77**
Common carp	.56***	0.00098	−4.93***
Tessellated darter	.24*	0.012†	−1.03†
River herring	.44***	0.004	−2.72***
Striped bass	.19*	0.018*	−0.36
White perch	.27**	0.014*	−1.21†

Note: *River herring* includes blueback herring and alewife (the post-yolk-sac larvae of these two species are indistinguishable).   †($p < .2$).
*($p < .05$).   **($p < .01$).   ***($p < .001$).
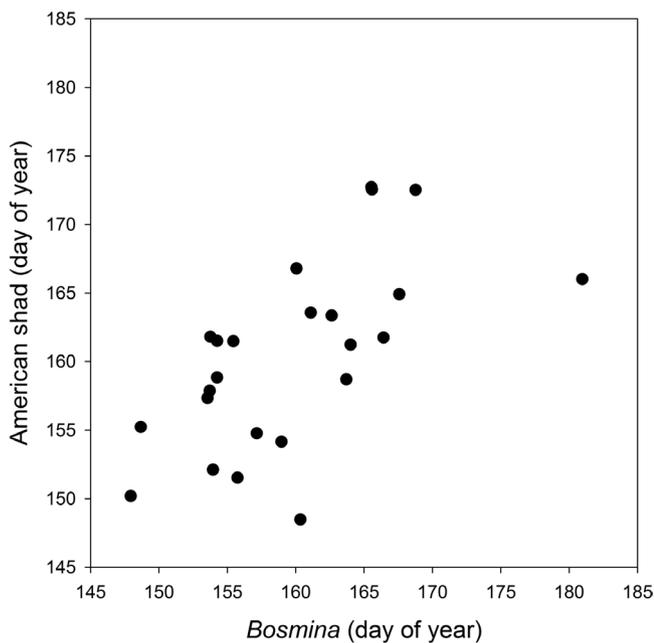
Figure 7. Phenological matching between population development (center of gravity, Thackeray et al. 2008) of post-yolk-sac larvae of American shad and the early summer bloom of Bosmina*, one of its principal prey species. The reduced-major-axis slope is 0.93, with r^2 = .39 and p = .001, but note the considerable interannual variation in phenological matching.*

crabs were commercially harvested during the past 25 years, and shad landings were a small fraction of historical catches. Increasingly stringent harvest regulations have been imposed in an attempt to allow fish populations to recover, including several measures during the past 25 years. A moratorium was placed on Atlantic sturgeon fisheries in the Hudson in 1996, and the New York Bight stock of this species (including the Hudson) was designated *endangered* by the National Oceanic and Atmospheric Administration in 2012. New York closed all commercial and recreational fisheries for the American

shad starting in 2010 and imposed new, strict regulations on catches of blueback herring and alewife in 2012.

Early, poorly regulated fisheries in the Hudson are thought to have caused large changes in the population size and body size of the target species and probably had large, cascading effects on other parts of the ecosystem. These cascading effects have not been well studied in the Hudson, but on the basis of our understanding of other ecosystems (e.g., Pace et al. 1999), they were probably large and far reaching. If fish populations recover in response to new regulations (as did the striped bass population in the late twentieth century; see below), these cascading effects may be reimposed over a period of decades. It is too early to know how effective the new regulations will be in restoring fish populations and their ecosystem roles in the Hudson.

Changes of unknown cause. Finally, we observed some large, important ecological changes over the past 25 years in the Hudson whose causes are obscure (figure 11). As Findlay (2005) noted, concentrations of dissolved organic carbon in the Hudson have been rising markedly. Recent increases in dissolved organic carbon in surface waters are generally attributed to a recovery from acidification (higher pH yields greater solubility of the major organic acids), but other plausible mechanisms include climate change and nitrogen fertilization (Findlay 2005, Monteith et al. 2014). Even more remarkably, concentrations of nitrate in the river have fallen by approximately 50% over the past 25 years. This decline did not appear in any of the seven Hudson tributaries for which long-term data are available (*http://io.aibs.org/cary*, *http://io.aibs.org/nwis*) and is chiefly due to losses during summer months, so it appears to be a result of some unknown process (perhaps biological) within the Hudson itself. Although denitrification rates are high in beds of water chestnut (Tall et al. 2011), the overall area covered by water chestnut in the Hudson has not increased in recent years (Findlay et al. 2014), and increases in the size of the largest bed in the Hudson could account for only about 10%–20% of the observed nitrate loss.
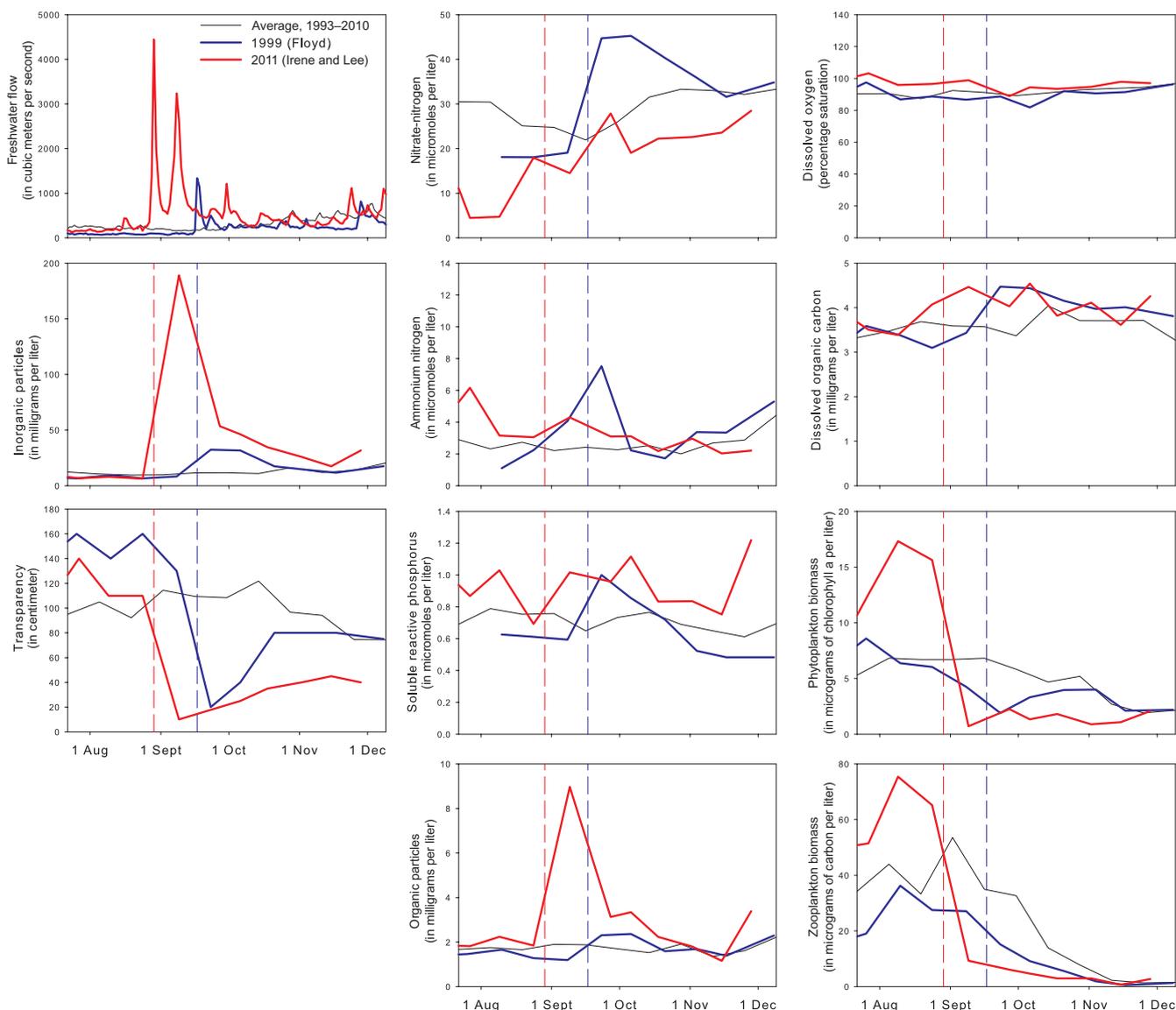
Figure 8. Effects of Hurricane Floyd (blue) and Tropical Storms Irene and Lee (red) on the Hudson River ecosystem. The black lines show the averages for 1993–2012 (i.e., post–zebra mussel period), excluding the years in which hurricanes occurred (1999 and 2011), and the vertical dashed blue and red lines show the dates of peak flows of the two storm events. The flow data are from the US Geological Survey; all of the other data are from the Cary Institute.

Past and future changes in the Hudson. Of course, the last 25 years is only a small part of the period during which humans have strongly influenced the Hudson River ecosystem. If we had studied some other 25-year period during this history, we would have noticed different driving variables—sewage pollution and a subsequent recovery from that pollution, the overharvest of oysters or finfishes, dredging and filling of aquatic habitats, deforestation of the catchment (Henshaw 2011)—but we would have always concluded that the ecosystem was undergoing substantial change and that many of the most important changes were occurring on decadal timescales.

We expect decadal-scale change to continue to be important in the Hudson in the future. The water temperature and

sea level will continue to rise, species invasions will continue, extreme climatic events will occur and perhaps intensify, persistent emerging contaminants will accumulate, and land use in the catchment will continue to change. In addition, ecological restoration has begun to pick up speed in the Hudson (Miller 2013) and may have long-lasting positive effects on the river's ecosystem.

Slow ecological responses to changes in the Hudson. Ecological responses to disturbances and stresses are not always instantaneous. Indeed, many ecological responses to decadal change in drivers themselves take decades to play out, further lengthening the timescale of change in river ecosystems. We can think of these responses as the long echoes of past events.
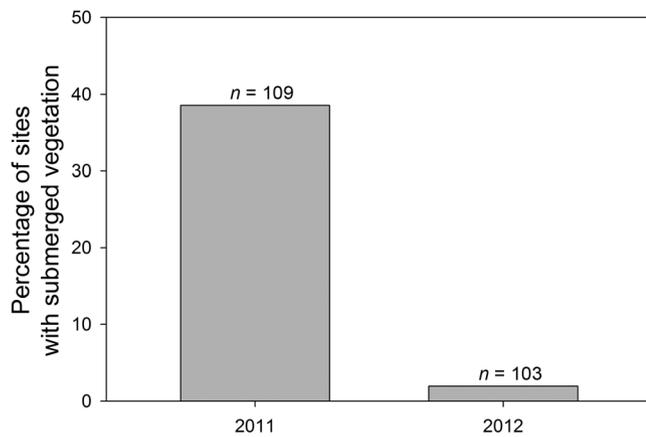
Figure 9. *The loss of vegetation at long-term monitoring sites in the littoral zone of the freshwater tidal Hudson River before (2011) and after (2012) the large storms Irene and Lee.*
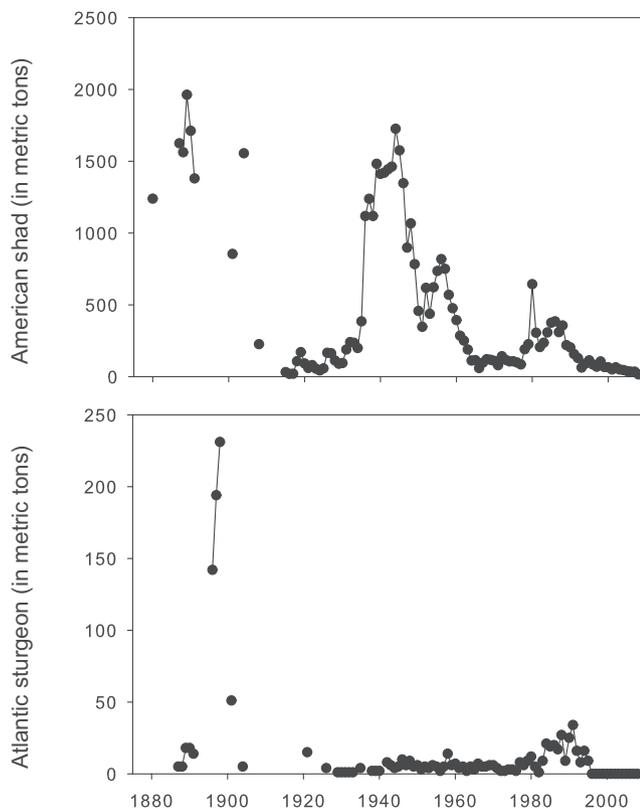
Figure 10. *Landings of two important fish species in the Hudson River (sturgeon landings are for all of New York State, of which the Hudson is the most important fishery). Note the large differences in scale between the panels. The unconnected points indicate gaps in the record. The data are from the Atlantic States Marine Fisheries Commission (www.asmfc.org).*

Examples include the accumulation or depletion of materials in slow pools (e.g., sediment-bound contaminants, structures built by ecosystem engineers); the demographic responses of

long-lived species; the rapid evolution of biological populations; and, if we consider humans as part of the ecosystem, the social and engineering responses of humans and their institutions (e.g., the adoption of new laws and regulations, the design and construction of new engineering projects). All of these kinds of slow responses have been important in the Hudson and will be important in the future.

Long-lived pollutants offer a good example of pools with slow dynamics. Like many large rivers in industrialized countries, the Hudson has a long history of contamination by persistent pollutants. In the Hudson, contamination by polychlorinated biphenyls (PCBs), metals, and polycyclic aromatic hydrocarbons is widespread and has had strong ecological effects (Levinton et al. 2003, Bopp et al. 2006, Levinton and Waldman 2006, Wirgin et al. 2006, 2011). The gradual accumulation of these long-lived pollutants took place over years to decades of industrial activity, and the recovery of the river after inputs of these pollutants were controlled (largely by the 1970s) likewise took place at decadal timescales. Recovery in the Hudson has occurred through the burial and export of pollutants (Bopp et al. 2006), microbial degradation of some organic pollutants (Williams and May 1997), and human intervention. For example, large amounts of nickel and cadmium were removed from Foundry Cove (USEPA 2011), and a very large-scale dredging project is now under way to remove PCBs from the upper Hudson (*www.epa.gov/hudson*). The result of all of these processes has been a marked reduction in the levels of these contaminants in the Hudson. These reductions should continue during the coming decades, at the same time that the long-term accumulation of poorly controlled emerging contaminants is increasing (e.g., Lara-Martin et al. 2010).

Populations of long-lived species may take years to decades to fully respond to a change in driving variables. Many important species in the Hudson (e.g., the finfish, perennial plants of wetlands and shallows, freshwater mussels) have life spans ranging from several years to several decades. The adults of these species can persist for many years after conditions become unsuitable for the recruitment of young, and the recovery of such populations may take multiple life spans to accomplish. Therefore, the population of striped bass in the Hudson continued to grow for 10–20 years after new harvest regulations were imposed after 1981 (Strayer et al. 2004, Limburg et al. 2006), the response of native freshwater mussels to the zebra mussel invasion is still incomplete after 20 years (Strayer and Malcom 2014), it is taking decades for nonnative genotypes of common reed (*Phragmites australis*) to replace cattails (*Typha* spp.) in Hudson River wetlands (Winograd and Kiviat 1997), and the moratorium on the harvest of Atlantic sturgeon is planned to last for 40 years (two to five generations) to allow sufficient time for the population to recover (Limburg et al. 2006).

Although evolution is often thought of as slow, ecologically significant evolution can take place on decadal timescales (Thompson 2013). Two striking examples show that such decadal-scale evolution has been important in the
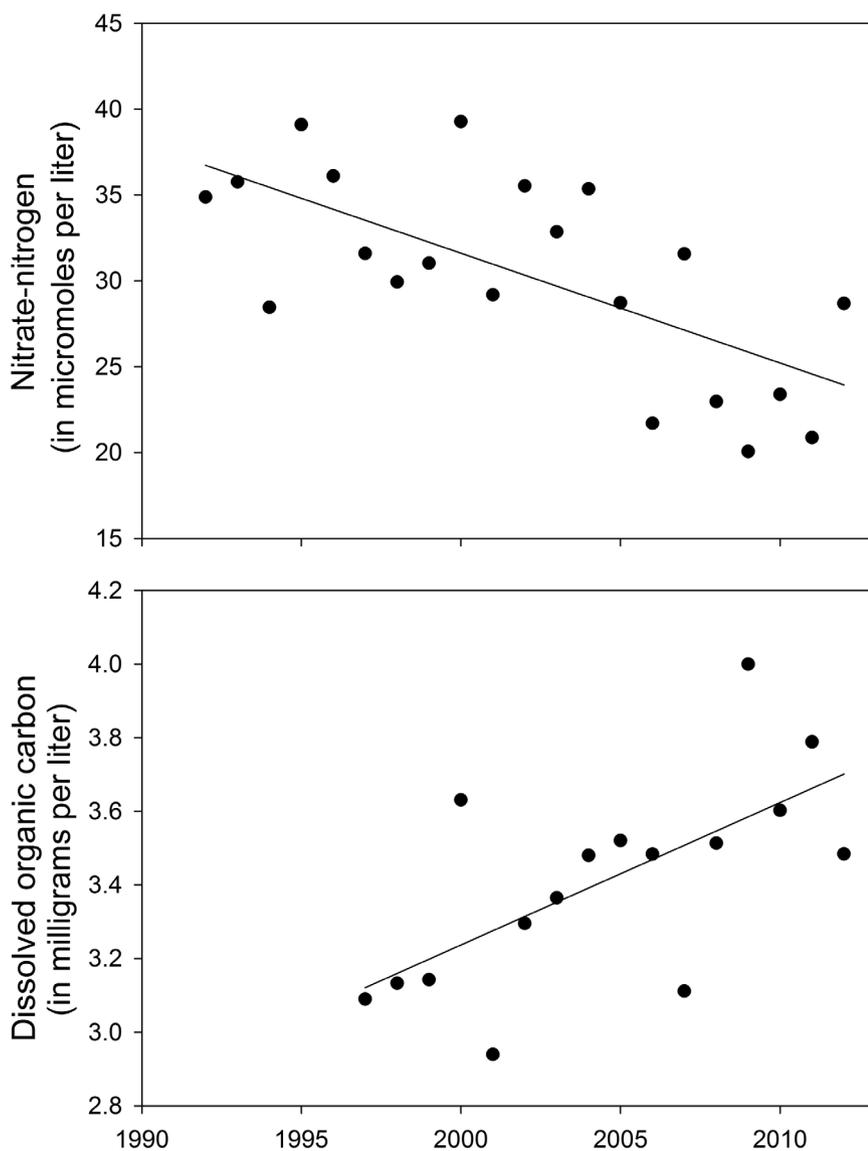
Figure 11. Examples of decadal-scale changes in the Hudson River ecosystem whose underlying causes are unknown or poorly understood. The data are growing-season means from our main monitoring station at Kingston, New York. For nitrate, $r^2 = .46$, $p = .0007$; for dissolved organic carbon, $r^2 = .43$, $p = .006$.

Hudson. Tomcod in the Hudson are afflicted by extraordinarily high rates of liver cancer (more than 90% of 2-year-old fish have cancerous or precancerous lesions on the liver) and rarely live longer than 3 years as a result of contamination by halogenated aromatic hydrocarbons (Wirgin et al. 2006). Presumably as a consequence of this high mortality rate, most Hudson River tomcod now carry an allele that makes them approximately 100 times less sensitive to these contaminants than the tomcod in nearby, less contaminated waters (Wirgin et al. 2011). This shift in gene frequencies must have taken place since halogenated aromatic hydrocarbons became abundant in the Hudson in the middle of

the twentieth century. The second well-documented case of decadal-scale evolution in the Hudson occurred in Foundry Cove, a bay that was spectacularly contaminated in the middle of the twentieth century with cadmium and nickel from a battery factory. Despite the contamination, the cove supported a dense population of the oligochaete *Limnodrilus hoffmeisteri*, which proved to have a high genetic resistance to metal toxicity. After the contamination was removed in 1993 and 1994, metal resistance in the oligochaetes rapidly vanished (Levinton et al. 2003). The development and loss of this resistance both took place within a few decades. Similar rapid (i.e., decadal-scale) evolution has presumably occurred in response to other powerful drivers (e.g., species invasions) in the Hudson, although it has not been studied. Therefore, several ecological and evolutionary responses to disturbance and stress have time constants on the order of decades, which provides further mechanisms for decadal-scale change.

Change in large-river ecosystems

Is the Hudson typical of the world's rivers? It might seem from this account that the Hudson has been subjected to unusually severe stresses and disturbances and has therefore been exceptionally dynamic over the past 25 years. The Hudson *has* been dynamic, but many other river ecosystems have been comparably dynamic during at least the last century or two. Rivers around the world are under high and increasing pressure from changes to hydrology (including water withdrawals); the construction of dams and other barriers; extensive land-use change in their catchments; repeated biological invasions; habitat change in the channel and riparian zone (e.g., dredging, levees); increased loading of nutrients and toxins; the overharvest of biological populations; and climate change (e.g., Dudgeon et al. 2006, Vörösmarty et al. 2010, Carpenter et al. 2011). The Hudson has been more severely affected than has the typical river by some of these drivers. For instance, the effects of recent biological invasions (especially that of the zebra mussel) in the Hudson have been more severe than in most of the world's rivers (but many rivers have been heavily invaded and highly altered by invasions; e.g., Leprieur et al. 2008). However, the Hudson has largely escaped radical changes to its flow regime, large water withdrawals, and

dams on the lower mainstem that have so seriously affected many of the world's rivers (Nilsson et al. 2005), to the point that migratory fishes have been eliminated from many rivers (Gustafson et al. 2007, Limburg and Waldman 2009), and channels have even been entirely dewatered at times (Postel 2000). Few of the world's rivers have altogether escaped strong impacts from humans (Vörösmarty et al. 2010), and even these rivers will soon be affected by climate change and other human-driven impacts, such as new hydroelectric dams (e.g., Stone 2011, Castello et al. 2013). Most of the human impacts listed above have strong dynamics at the decadal timescale, although they may also have faster or slower dynamics, as well. Although the details about the changes that we observed in the Hudson are to some extent unique to the Hudson, we can conclude that the Hudson is typical of the world's rivers in that it has experienced strong dynamics at the decadal scale, largely (but not entirely) as the result of multiple human impacts.

Understanding decadal-scale dynamics of large-river ecosystems. Is there a useful way to organize and generalize across these highly various drivers and responses of decadal-scale change in river ecosystems? Traditionally, ecologists have distinguished *pulse* (short-lived) from *press* (long-lived) disturbances. Therefore, we might separate pulse disturbances such as hurricanes from press disturbances such as a changed hydrology resulting from a dam. However, as Pickett and Cadenasso (2013) pointed out, the attributes of drivers other than their duration may be important, so the pulse–press dichotomy, although it is useful, is insufficient. They suggested categorizing disturbances and stresses according to the abruptness of their onset and release, as well as their duration. The ecological responses to these drivers may also vary in the immediacy of the response (instantaneous versus lagged), the duration (short lived versus long lived or permanent), and the abruptness of the onset and release or recovery (Pickett and Cadenasso 2013). We suggest extending Pickett and Cadenasso's (2013) framework by adding two more attributes of stresses and disturbances. First, the severity of a disturbance or stress distinguishes mild events, such as a 1% change in freshwater flow or the establishment of an uncommon, weakly interacting non-native species, from severe events, such as a total drying of a formerly perennial river or the establishment of very abundant, strongly interacting invader such as the zebra mussel. Second, disturbances and stresses vary in novelty. For instance, the introduction of a predatory fish may have much greater effects in a formerly fishless system than in one in which several species of predatory fish already occur (e.g., Simon and Townsend 2003).

We offer the framework of table 2 as one way to organize and understand decadal-scale change in river ecosystems (as well as in other kinds of ecosystems) and postulate that drivers with similar attributes will have similar effects on ecosystems. Each of the attributes in table 2 affects the way that the ecosystem responds. For instance, system responses

may be more or less in equilibrium with gradual changes in drivers but lag far behind abrupt changes in drivers, which results in long-lasting disequilibria. Furthermore, the biota may cope with gradual changes in drivers through adaptation or migration but may fail to do so for abrupt changes, which could lead to irreversible changes (e.g., local or global extinction) in the system. Brief changes in drivers will cause only small changes in the accumulation or depletion of materials and may simply be tolerated by long-lived biota, which can recover when drivers return to their former values. In contrast, long-lasting changes in drivers may lead to large changes in the cumulative pools of materials and may exceed the ability of the biota to tolerate, adjust, or adapt, which would, again, lead to losses of species from the system. We have already explained how the severity and novelty of changes in driving variables should affect system responses. Therefore, the attributes of change in the driving variables constrain the kinds of possible responses by the ecosystem. Likewise, the kinds of responses of the system can, themselves, be organized by a small number of functional attributes (table 2; Pickett and Cadenasso 2013).

Implications for managing large-river ecosystems. It is easy to think of ecosystems as stationary—not necessarily constant, but dynamic within some limited range that does not change over time. According to this worldview, increased research and management experience improve our understanding of the system over time until we understand it well enough to manage it satisfactorily. At this point, there is no pressing need for further research, unless our management needs change so that we need to refine our understanding of the system. This is not to say that ecosystems such as the Hudson are simple to understand and manage even when they are stationary, but there is at least the theoretical likelihood that understanding increases monotonically over time.

In contrast, ecosystems such as the Hudson and many of the world's large rivers are clearly nonstationary; the past is not necessarily a reliable guide to the future. Milly and colleagues (2008) pointed out that stationarity can no longer be assumed for hydrology and water resource management. Our work on the Hudson emphasizes that this nonstationarity applies to many other aspects of large-river ecology, including physical structure, chemistry, and biology. Not only are these systems changing, but they are changing rapidly—on a timescale of decades. Even if we had achieved a very thorough understanding of the Hudson ecosystem by 1987, we know that the Hudson of 2013 was different from the Hudson of 1987, in terms of its species composition, the genetic and functional traits of its species, its food web structure, the mortality from harvest and other agents, the climate in which it is embedded, the levels and composition of pollutants that it contains, and so on. The scientific understanding of 1987, although it was undoubtedly valuable in understanding and managing today's Hudson, is already out of date, describing an ecosystem that has morphed out of existence.

Table 2. Key attributes of the drivers (disturbances and stresses) and responses that lead to decadal-scale change in river ecosystems.

Driver			Response		
Attribute	**Alternatives**	**Examples**	**Attribute**	**Alternatives**	**Examples**
Onset	Abrupt versus gradual	Closing of a dam (abrupt), land-use change in the catchment (gradual)	Onset	Abrupt versus gradual; instantaneous versus lagged	Washout of plankton during a flood (abrupt, instantaneous); delays in routing of sediments and other materials to the river in response to changes in the catchment (gradual, lagged)
Duration	Brief versus long	Storm flows (short), imposition of levees (long)	Duration	Short versus long	Recovery of a microbial population following storm flows (short); extirpation of a local population (long)
Release	Slow versus fast; small versus large	Reestablishment of native vegetation following abandonment of agriculture (slow), reestablishment of base flow hydrology and chemistry after a storm (fast), small decline in abundance in nonnative species as it accumulates enemies (small), complete return to base flow hydrology and chemistry after a storm (large)	Recovery	Slow versus fast; small versus large	Demographic responses of sturgeon populations (slow) or microbial populations (fast); recovery of cladocerans (small) versus rotifers (large) from the zebra mussel invasion in the Hudson
Severity	Mild versus severe	Establishment of nonnative species that are uncommon (mild) or abundant (severe)			
Novelty	Novel versus familiar	Establishment of nonnative species that are functionally distinctive (novel) or functionally redundant with existing species (familiar)			

Note: Although they are presented here as dichotomies, the attributes can be treated as continuous. *Source:* Adapted from Pickett and Cadenasso (2013).

In this nonstationary worldview, scientific research, monitoring, and management experience must constantly be pursued to follow the rapidly changing ecosystem (Dodds et al. 2012). This same point was made by Hilborn and Ludwig (1993), who wrote, "The key question is whether we can design research programs that will learn about a system faster than the system changes" (p. 551). If we are to realize the substantial benefits that nonstationary and often understudied (e.g., Tank et al. 2008) large-river ecosystems can provide, we must commit to a vigorous ongoing program of research and monitoring.

Acknowledgments

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