

August 28, 2014

Dr. Dennis Suszkowski
Hudson River Foundation
17 Battery Place, Suite 915
New York, NY 10004

Dr. Suszkowski,

Attached with this cover letter is the final Technical Report for the project entitled “Recovery of the Hudson River fish community from the zebra mussel invasion”. The HRF grant information is as follows:

Title: Recovery of the Hudson River fish community from the zebra mussel invasion
Grant No: 010/11A
Investigators: David L. Strayer, Cary Institute of Ecosystem Studies
Kathryn Hattala, New York State Department of Environmental Conservation
Andrew Kahnle, New York State Department of Environmental Conservation
Grant period: 4/5/2011 - 5/21/2014

Also attached is a recent publication directly related to this work (Strayer, D.L., K.A. Hattala, A.W. Kahnle, and R.D. Adams. 2014. Has the Hudson River fish community recovered from the zebra mussel invasion along with its forage base? *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1146-1157). No original data was collected for this project, thus no electronic data files are being submitted with this final technical report.

We are thankful for the Hudson River Foundation’s continued support and partnership in our Hudson River research program. Please contact me if you have any questions or require any further documentation.

Sincerely,



Brandt R. Burgess, Ph.D.
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Enclosed: Strayer Final Technical Report
Peer-reviewed Journal Article





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Dr. Dennis Suszkowski
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27 Aug 2014

Dear Dennis:

This is the final report for the project “Recovery of the Hudson River fish community from the zebra mussel invasion”(HRF 010/11A; Cary #3166). The goal of this project was “to re-examine long-term records of Hudson River fishes to test whether fish populations are recovering from the zebra mussel invasion as a result of the observed recovery of populations of their food items.” I worked with my Co-PIs, Kathryn Hattala and Andrew Kahnle (now retired) of the New York State Department of Environmental Conservation, and their colleague Robert Adams, as well as biologists and data managers from ASA to analyze long-term records of Hudson River fishes collected by the electric generating utilities, their contractors, and the NYSDEC. We found clear evidence that growth rate, but not abundance or geographic distribution, of Hudson River fishes has recovered in recent years in accord with recent recovery of the forage base (zooplankton and macroinvertebrates). We published these findings in a widely respected, peer-reviewed scientific journal (Strayer, D.L., K.A. Hattala, A.W. Kahnle, and R.D. Adams. 2014. Has the Hudson River fish community recovered from the zebra mussel invasion along with its forage base? *Canadian Journal of Fisheries and Aquatic Sciences* 71: 1146-1157), and presented our findings at two international scientific meetings (“Recovery of the Hudson River fish community from the zebra mussel invasion”, contributed talk, Annual Meeting of the Society for Freshwater Science, Jacksonville, FL, May 2013; “Recovery of the Hudson River fish community from the zebra mussel invasion”, contributed talk at the triennial meeting of the International Association of Limnology, Budapest, Hungary, August 2013). I previously sent you a copy of our paper from the *Canadian Journal of Fisheries and Aquatic Sciences*, and will attach one to the email by which I convey this report.

In addition, I have included pieces of this analysis as part of broader papers and talks about the Hudson and how it has been changing in recent years, as follows: Strayer, D.L., J.J. Cole, S.E.G. Findlay, D.T. Fischer, J.A. Gephart, H.M. Malcom, M.L. Pace, and E.J. Rosi-Marshall. 2014. Decadal-scale change in a large-river ecosystem. *BioScience* 64: 496-510; “Effects of tropical storms Irene and Lee on fish distributions in the Hudson River estuary: a

preliminary analysis”, invited talk, Hudson River Environmental Society, 19 September 2012; “Effects of the zebra mussel invasion on aquatic ecosystems: the Hudson River and beyond”, invited seminar, University of Nebraska, March 2013; “Long-term change in the Hudson River ecosystem”, invited talk, Hudson River Environmental Society, New Paltz, NY 24 April 2013; “Twenty-five years of ecological change in the Hudson River: lessons for the world’s rivers”, invited seminar, University of Toledo, OH, January 2014; “Twenty-five years of ecological change in the Hudson River: lessons for the world’s rivers”, G.W. Minshall Lecture, Idaho State University, Pocatello, ID, April 2014. Thus, the results of our analysis have been widely disseminated to the regional and international scientific community.

Although the overall expenses for the project were as budgeted, there were some line-by-line deviations from the original budget. The largest of these was a shift in labor used to perform the work. We had projected that ASA and research support specialists would do much of the data handling, but in the end for efficiency and simplicity I ended up doing much of this work myself. As a result, my salary line was over budget, while these other lines were correspondingly under budget.

As always, I am very grateful to the Hudson River Foundation for their financial support of and continuing interest in our research. Please don’t hesitate to contact me if you have any questions about this project.

Sincerely,

A handwritten signature in black ink that reads "David Stray". The signature is written in a cursive style with a long, sweeping underline that extends to the right.

Has the Hudson River fish community recovered from the zebra mussel invasion along with its forage base?

David L. Strayer, Kathryn A. Hattala, Andrew W. Kahnle, and Robert D. Adams

Abstract: In the first decade after zebra mussels (*Dreissena polymorpha*) appeared in the Hudson River, the biomass of zooplankton and deepwater macrobenthos fell by ~50%, while the biomass of littoral macrobenthos rose by >10%. These changes in the forage base were associated with large, differential changes in the abundance, geographic distribution, and growth rates of openwater and littoral fish. In recent years, populations of zooplankton and deepwater macrobenthos have risen towards pre-invasion levels, while littoral macrobenthos remained unchanged. We therefore hypothesized that the abundance, distribution, and growth rates of openwater fish species would shift back towards pre-invasion levels, while littoral fish species would not change. Our analysis of large data sets for young-of-year fishes found no systematic change in the abundance or geographic distribution of either group of fish in the Hudson. We did find a marked increase in growth rates of openwater fish, but no change in growth rates of littoral fish, in support of our hypothesis. Our study shows that the ecological effects of a biological invasion may change over time.

Résumé : Dans la décennie qui a suivi l'apparition de la moule zébrée (*Dreissena polymorpha*) dans le fleuve Hudson, la biomasse de zooplancton et de macrobenthos d'eau profonde a connu une baisse de ~50 %, alors que la biomasse de macrobenthos littoral a augmenté de >10 %. Ces modifications de la base de la pyramide alimentaire étaient associées à d'importantes variations différentielles de l'abondance, de la répartition géographique et des taux de croissance des poissons littoraux et d'eau libre. Ces dernières années, les populations de zooplancton et de macrobenthos d'eau profonde ont augmenté pour s'approcher de leurs niveaux pré-invasion, alors que le macrobenthos littoral est demeuré inchangé. Nous avons donc émis l'hypothèse que l'abondance, la répartition et les taux de croissance des espèces de poissons d'eau libre se rapprocheraient de leurs niveaux pré-invasion, alors que ceux d'espèces de poissons littoraux ne changeraient pas. Notre analyse de grands ensembles de données pour des poissons jeunes de l'année n'a révélé aucune variation systématique de l'abondance ou de la répartition géographique de l'un ou l'autre des groupes de poissons dans le fleuve Hudson. Nous avons toutefois noté une augmentation marquée des taux de croissance des poissons d'eau libre, mais aucun changement des taux de croissance des poissons littoraux, ce qui appuie notre hypothèse. L'étude démontre que les effets écologiques d'une invasion biologique peuvent varier dans le temps. [Traduit par la Rédaction]

Introduction

Many studies have now shown that biological invasions can have strong and far-reaching ecological effects, especially in fresh waters (see reviews by Davis 2009; Strayer 2010; Lockwood et al. 2013). Nevertheless, the long-term effects of biological invasions are still poorly known. Several mechanisms ought to change the ecological effects of an invasion through time (Strayer et al. 2006; Ricciardi et al. 2013). The invader could evolve to better match the new environment and community in which it finds itself, the species or genetic composition or traits of the invaded community could shift to resist or use the invader, materials can be accumulated in or depleted from slow pools, or the invader can interact with rare events such as storms or fires. Although all of these mechanisms are presumably common in ecosystems, the size, timing, and ultimate importance of long-term changes have received little study (Strayer et al. 2006; Strayer 2012), in part because direct, long-term studies of invaders and their effects are rare.

Previous studies have reported a wide range of important mechanisms and directions of change in impacts on native species. Some studies found that invaders became less abundant, allowing

for recovery of the native biota (e.g., Dostál et al. 2013). Others found that the initial invader declined over time, but it was succeeded chiefly by other non-native species rather than natives (e.g., Yelenik and D'Antonio 2013). Still others (e.g., Mitchell et al. 2011) reported that the effects of a non-native species rose through time as cumulative impacts increased. Unsurprisingly, some studies (e.g., van Hengstum et al. 2014) have been unable to detect any systematic temporal variation in impacts. At this point, all we can say is that the impacts of non-native species may change substantially over time, that a wide range of changes occur, and that we do not know whether any general patterns apply across a range of ecosystems.

Invasions of dreissenid mussels (*Dreissena* spp.) and other bivalves (e.g., *Corbicula* spp., *Limnoperna fortunei*) have had strong effects on the food webs, water chemistry, and physical structure of freshwater ecosystems around the world (e.g., Sousa et al. 2008, 2013; Boltovskoy et al. 2009; Strayer 2009; Higgins and Vander Zanden 2010). The effects of the zebra mussel (*Dreissena polymorpha*) on the Hudson River ecosystem have been especially well studied. In the first decade after zebra mussels appeared in the Hudson in 1991, biomass of phytoplankton and small zooplankton fell by

Received 16 October 2013. Accepted 7 April 2014.

Paper handled by Associate Editor Aaron Fisk.

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more than 80% (Pace et al. 1998; Caraco et al. 2006), and populations of native bivalves and other zoobenthos that depend on plankton fell by 50% or more (Strayer and Smith 1996, 2001). As pelagic and deepwater populations decreased, littoral populations increased in response to clearer water. Areal primary production by submersed macrophytes increased (Caraco et al. 2000), and the size of macrophyte beds and the biomass of littoral macroinvertebrates probably increased (Strayer and Smith 2001; Strayer et al. 2004).

These changes in the food web were reflected in fish populations in the Hudson (Strayer et al. 2004). In the first decade after zebra mussels arrived, young-of-year openwater fishes such as *Alosa* spp. and *Morone* spp. became less abundant, grew more slowly, and shifted their distributions downriver away from where zebra mussels live in the Hudson, consistent with the loss of their openwater food resources. In contrast, littoral fishes such as centrarchids became more abundant, grew more quickly, and shifted their distributions upriver into the area in which zebra mussels were abundant, again consistent with an increase in food in the littoral zone.

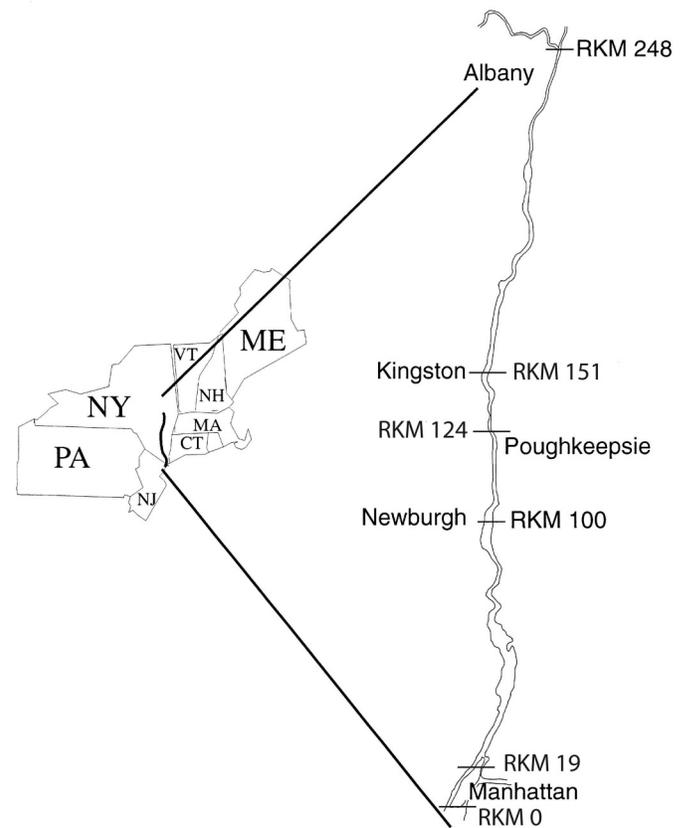
Like other biological invasions, the long-term effects of bivalve invasions on freshwater ecosystems are not well understood. The two meta-analyses that looked for evidence that the effects of zebra mussels changed through time (Ward and Ricciardi 2007; Higgins et al. 2011) found no evidence that effects on macroinvertebrates or phytoplankton changed with time over the first few years after invasion. However, the effects of the zebra mussel invasion on the Hudson River ecosystem have been changing. Though the species remains abundant in the Hudson, the size-structure and mortality rates of the zebra mussel population have changed dramatically (Carlsson et al. 2011; Strayer et al. 2011). Populations of the zooplankton and deepwater zoobenthos that serve as food for most of the fish in the Hudson have recovered to or nearly to pre-invasion levels (Pace et al. 2010; Strayer et al. 2011, 2014). In contrast, phytoplankton biomass (and presumably water clarity) has not recovered, and remains ~80% below pre-invasion levels (Pace et al. 2010; Strayer et al. 2014). We therefore hypothesized that some fish populations in the Hudson may also have recovered towards pre-invasion levels. Specifically, we hypothesized that initial effects of the zebra mussel invasion on the abundance, distribution, and growth of openwater fishes would have reversed as their forage base recovered. In contrast, because phytoplankton has not recovered, we hypothesized that littoral production would not have returned to pre-invasion levels (we saw no recent declines in littoral macrobenthos — Strayer et al. 2011, 2014) and initial effects of the zebra mussel invasion on the abundance, distribution, and growth of littoral fishes would be unchanged.

Materials and methods

Study area

The study area is the tidal Hudson River (Fig. 1), extending 229 km from the George Washington Bridge (RKM 19; i.e., 19 km upriver of the Battery at the downriver end of Manhattan) to the dam at Troy (RKM 248). The entire study area is subject to tides (daily tidal range = 0.8–1.5 m) and strong tidal currents, but sea salt typically is not present upriver of RKM 100. Most of the channel is 1–4 km wide and 5–20 m deep, although extensive shallow areas supporting beds of submerged vegetation and wetlands exist. The water is warm (maximum temperature 26–28 °C), turbid (Secchi transparency ~1 m), hard (pH = 7–8; Ca = 25–30 mg·L⁻¹), and nutrient-rich ((PO₄-P > 10 µg·L⁻¹, NO₃-N ~ 0.4 mg·L⁻¹). The Hudson's zooplankton is dominated by the cladoceran *Bosmina freyi* and various copepods and rotifers, and its macrozoobenthos is dominated by bivalves, oligochaetes, chironomids, and amphipods. The fish community contains many warmwater species, but

Fig. 1. The study area. RKM, river kilometre (kilometres upriver from the Battery in New York City).

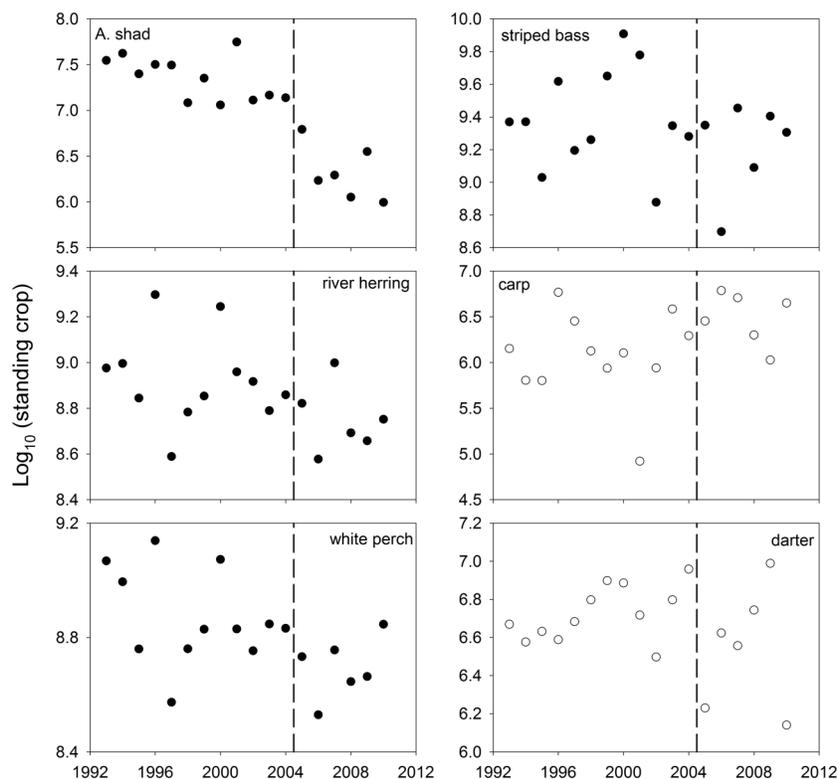


it is numerically dominated by young-of-year of anadromous species such as *Alosa* spp. and *Morone* spp. The food web is supported by both allochthonous and autochthonous sources (Cole and Solomon 2012).

Data sources

The sources of data and analytical methods closely follow those used in our earlier study of zebra mussel effects on Hudson River fishes (Strayer et al. 2004), from which the following account of methods is summarized. We used three data sets: the utilities' long-river ichthyoplankton survey (LRS), the utilities' beach seine survey (UBSS), and the New York State Department of Environmental Conservation's beach seine survey (DECBSS) (the utilities surveys are conducted by contractors of the electric generating companies, which monitor fish populations in the Hudson as a condition for withdrawing cooling water). Utilities data sets were available for 1993–2010, and DECBSS data were available for 1993–2011. The LRS was described by Klauda et al. (1988), Heimbuch et al. (1992), and Young et al. (1992). Samples were taken biweekly beginning in March, weekly from April through June, then biweekly until late September. The river between the Battery (RKM 0) and Troy (RKM 248) was divided into 13 sections and several habitat strata (channel, bottom, shoal, and shore), from which samples were taken in a stratified random design. At least two samples were taken from each stratum in each sampling period, resulting in ~2400 samples·year⁻¹. Samples were taken with a Tucker trawl or an epibenthic sled having an aperture of 1 m² and mesh of 505 µm, resulting in a typical sample volume of ~300 m³. Species and life stages (egg, yolk-sac larva, post-yolk-sac larva, or 0+ juvenile) were identified and counted, and lengths of selected species (alewife, American shad, blueback herring, white perch, striped bass, and spottail shiner) were measured. We analyzed the abundance of post-yolk-sac larvae (PYSL) from this data set, excluding

Fig. 2. Riverwide standing crops of post-yolk-sac larvae of selected fish species in the Hudson River, 1993–2010 (closed circles, openwater species; open circles, littoral species). The vertical dashed line separates the early invasion and late invasion periods. Note the log scale on the y axes.



data from region 0 (RKM 0–19). PYSL of blueback herring and alewife are treated together as “river herring” in our analysis because they cannot be readily distinguished.

The utilities’ beach seine survey was riverwide, with samples taken biweekly from mid-June until October. Approximately 1000 samples were taken each year, in a stratified random design based on the river sections described above, using a 30.5 m beach seine. Fish were identified to species and life stage (YOY or older) and counted, and lengths of selected species (as for the ichthyoplankton survey) were measured. We analyzed data for YOY (i.e., 0+ juveniles) only.

The goal of the DECBSS was to estimate relative abundance of juvenile *Alosa* spp. Samples were taken biweekly (generally alternating with the utilities’ beach seine survey) from late June–October at 28 fixed sites near Newburgh Bay, Poughkeepsie, Coxsackie, and Albany. Samples were taken with a 0.64 cm mesh beach seine with 12.2 m × 3.05 m wings and a 6.1 m × 3.7 m bag. Fish were identified and counted, and lengths of selected species (alewife, American shad, blueback herring, striped bass, largemouth bass, smallmouth bass, and other sport fish) were measured. We analyzed data for YOY (i.e., 0+ juveniles) only.

Statistical methods

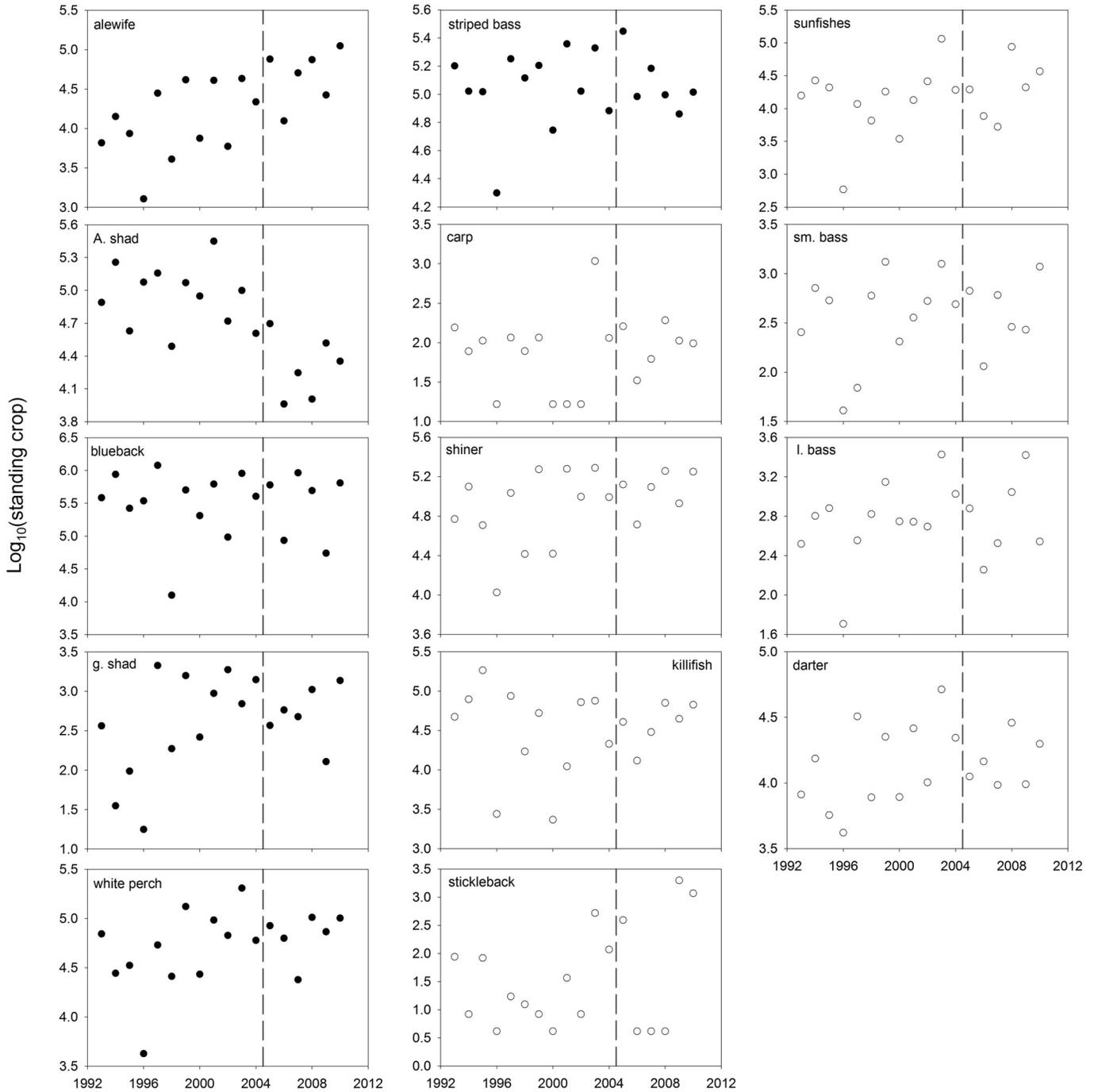
Our basic approach was to test for differences in attributes of Hudson River fishes between the early invasion years (1993–2004) and the late invasion years (2005–2011). We delimited the late invasion period based on observed recovery of zooplankton and deepwater zoobenthos in the Hudson (Pace et al. 2010; Strayer et al. 2011). While it would have been desirable to use a continuous variable (year-to-year variation in the actual size of the forage base) rather than a categorical variable (early invasion vs. late invasion) to assess zebra mussel impacts, data on zoobenthic biomass in the Hudson are not available for every year. Because most

of the Hudson’s fish species rely heavily on benthic animals as well as plankton (Strayer and Smith 2001), we were not able to construct a satisfactory continuous index of prey availability in the Hudson. Therefore, we chose to treat time as a categorical variable.

Following the logic explained by Strayer et al. (2004), we defined openwater species as alewife (*Alosa pseudoharengus*), American shad (*Alosa sapidissima*), blueback herring (*Alosa aestivalis*), gizzard shad (*Dorosoma cepedianum*), Atlantic menhaden (*Brevoortia tyrannus*), white perch (*Morone americana*), and striped bass (*Morone saxatilis*); and littoral species as brown bullhead (*Ameiurus nebulosus*), common carp (*Cyprinus carpio*), spottail shiner (*Notropis hudsonius*), banded killifish (*Fundulus diaphanus*), fourspine stickleback (*Apeltes quadracus*), sunfishes (*Lepomis* spp.), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), and tessellated darter (*Etheostoma olmstedii*). These are species that were well represented in the data sets and whose biology in the Hudson is reasonably well known. Because they are relatively scarce, we combined bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibbosus*), redbreast sunfish (*Lepomis auritus*), and unidentified centrarchids as “sunfishes” instead of considering them as individual taxa, in contrast to our previous analysis (Strayer et al. 2004).

For openwater species, the hypotheses are clearly directional (populations should increase and shift back upriver, and growth rates should increase in the late invasion period), so statistical tests are one-tailed. For the littoral species, opposing mechanisms (recovery of zooplankton prey, possible loss of littoral production — see Strayer and Smith 2001; Strayer et al. 2004, 2011) could cause fish populations to change in either direction, so statistical tests are two-tailed. When we test hypotheses or calculate confidence intervals, we use two levels of statistical significance ($\alpha = 0.05$ and

Fig. 3. Riverwide standing crops of juveniles of selected species in the Hudson River, 1993–2010 (closed circles, openwater species; open circles, littoral species). The vertical dashed line separates the early invasion and late invasion periods. Note the log scale on the y axes.



$\alpha = 0.2$). We included the higher level of α as part of our analysis because Type II errors have serious consequences here (concluding that the effects of the invasion have not changed when they actually have changed). However, we use several criteria to assess our results, and our conclusions do not depend on adopting $\alpha = 0.2$ as the standard for statistical significance.

We examined three attributes of Hudson River fishes: population size, geographic distribution within the river, and apparent growth rates. We tested for recovery of the estimated riverwide population of fish (riverwide standing crop) using the LRS of PYSL and the UBSS of 0+ juveniles. In the LRS, we calculated the mean

number of PYSL over the time period in which each species usually was present and samples were taken throughout the river (samples were not always taken above RKM 124 after week 27). Specifically, we used the following time periods: American shad (weeks 19–27), river herring (weeks 18–27), white perch (weeks 18–27), striped bass (weeks 20–27), carp (weeks 21–27), and tessellated darter (weeks 19–27). For the UBSS, the dependent variable was the mean riverwide standing crop over weeks 32–40, as in Strayer et al. (2004).

We modeled \log_{10} -transformed abundance using multiple regression with the following independent variables: mean water

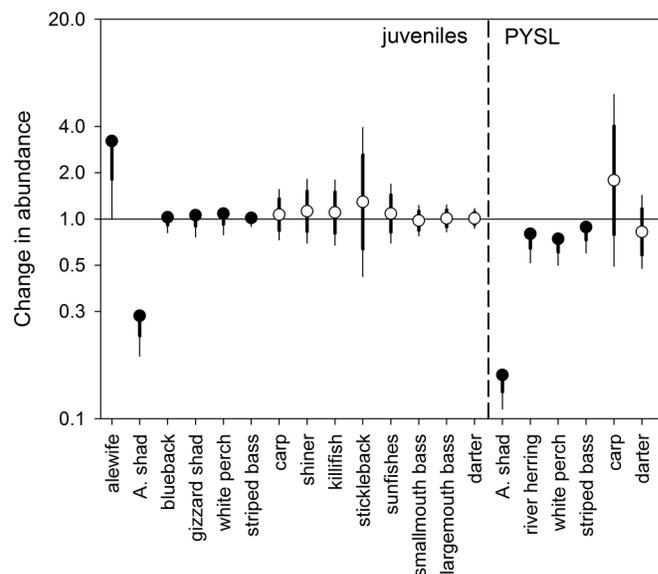
Table 1. Statistical models to predict log₁₀-transformed abundance of selected age-classes of fish in the Hudson River.

Species	Flow ($\times 10^{-5}$, m ³ ·s ⁻¹)	Temperature (°C)	Invasion period
Post-yolk-sac larvae			
Blueback herring + alewife	0.215 6 (12)	0.319 -0.022 (0.037)	0.572 -0.097 (0.108)
American shad	0.414 -27 (40)	0.502 -0.073 (0.090)	1.00 -1.02 (0.127)
White perch	0.169 1 (5)	0.213 -0.008 (0.017)	0.744 -0.13 (0.098)
Striped bass	0.194 -4 (12)	0.177 -0.002 (0.17)	0.309 -0.053 (0.096)
Common carp	0.177 4 (16)	0.186 -0.010 (0.032)	0.602 0.252 (0.264)
Tessellated darter	0.212 5 (12)	0.171 -0.0002 (0.011)	0.473 -0.084 (0.112)
0+ juveniles			
Alewife	0.315 -46 (80)	0.323 0.068 (0.115)	0.845 0.507 (0.288)
American shad	0.263 -21 (41)	0.154 0.001 (0.017)	0.995 -0.631 (0.150)
Blueback herring	0.598 -141 (149)	0.176 0.001 (0.034)	0.175 0.011 (0.057)
Gizzard shad	0.180 -6 (33)	0.284 0.058 (0.111)	0.190 0.024 (0.081)
White perch	0.177 1 (19)	0.286 0.038 (0.073)	0.228 0.034 (0.079)
Striped bass	0.381 -36 (56)	0.501 0.073 (0.091)	0.179 0.007 (0.032)
Spottail shiner	0.236 -19 (41)	0.538 0.110 (0.129)	0.265 0.050 (0.098)
Banded killifish	0.188 5 (19)	0.192 0.008 (0.027)	0.179 0.003 (0.030)
Fourspine stickleback	0.178 -33 (80)	0.179 0.010 (0.065)	0.257 0.111 (0.228)
<i>Lepomis</i> spp.	0.185 -8 (33)	0.307 0.060 (0.109)	0.208 0.035 (0.090)
Smallmouth bass	0.191 -12 (32)	0.802 0.242 (0.157)	0.174 -0.010 (0.047)
Largemouth bass	0.178 -1 (20)	0.188 0.009 (0.035)	0.178 0.004 (0.041)
Tessellated darter	0.188 5 (19)	0.192 0.008 (0.027)	0.179 0.003 (0.030)

Note: Table shows the summed Akaike weight for each variable (upper number) along with the model-averaged slope and standard error (lower numbers) for each variable.

temperature and freshwater flow during the period of analysis and the stage of the zebra mussel invasion (coded as 0 for 1993–2004 and 1 for 2005–2010). If the data set contained zeroes, we substituted a $\log(X + c)$ transformation, where c is the minimum nonzero value observed for that species. We ran all possible subsets of regression models and present model-averaged estimates of parameters (Burnham and Anderson 2002). We present two measures of the importance of the independent variables in predicting fish abundance. First, we present the sum of Akaike weights (w_i) for all models containing a given variable, which is the likelihood that the most appropriate model to describe the data includes that variable. Higher values of w_i provide stronger evidence for the importance of that variable. Second, we present the model-averaged estimates of the slopes (β_i) for each variable, along with their standard errors. There are two ways by which to calculate these model-averaged slopes: averaging over only models in which the variable actually appears and averaging over all possible models, including those in which the variable does not

appear (see Burnham and Anderson 2002, pp. 151–152 for a discussion of this point). In contrast to our earlier analysis (Strayer et al. 2004), we present the latter estimate. Slope estimates for just the models in which the variable appears can be calculated by dividing the slopes that we present by the Akaike weight.



appear (see Burnham and Anderson 2002, pp. 151–152 for a discussion of this point). In contrast to our earlier analysis (Strayer et al. 2004), we present the latter estimate. Slope estimates for just the models in which the variable appears can be calculated by dividing the slopes that we present by the Akaike weight.

To assess geographic distribution of fish within the Hudson, we compared the number of fish of each species in the freshwater estuary, which was strongly affected by the zebra mussel invasion, to that in the brackish estuary, which was little affected by zebra mussels. We chose RKM 100 as a breakpoint because zebra mussel impacts on plankton appear to disappear near this point (Caraco et al. 1997, 2000; Pace et al. 1998). We calculated the mean standing crop of each species above and below RKM 100 for the same time periods used for the analysis of abundance (above). Then, we calculated an index of distribution

$$D = \frac{\log_{10}(\text{standing crop above RKM 100})}{\text{standing crop below RKM 100}}$$

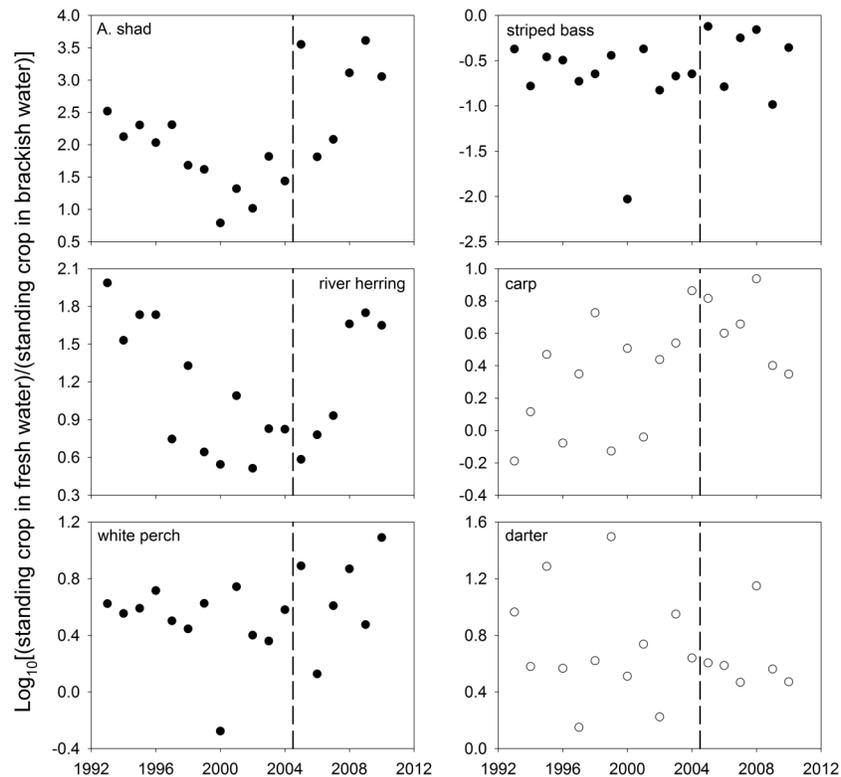
where positive values of D indicate that most of the population was upriver of RKM 100 and negative values indicate that most of the population was downriver of RKM 100. If the data set contained zeroes, we substituted a $\log(X + c)$ transformation, where c was the minimum nonzero value observed in that data set. We modeled D using the same procedures as those used to model abundance.

We analyzed trends in apparent growth rates of YOY fish in the IRS, UBSS, and DECBSS. Apparent growth rate (g) is the rate of change in mean fish size between two successive sampling dates

$$g = \ln(L_{t+1}/L_t)/t$$

where L_{t+1} and L_t are mean total lengths at two successive sampling times separated by t weeks of time. Mean total lengths were calculated for each week and river region separately (see below).

Fig. 5. Geographic distribution of post-yolk-sac larvae of selected fish species in the Hudson River, 1993–2010 (closed circles, openwater species; open circles, littoral species). The vertical dashed line separates the early invasion and late invasion periods.



We estimated apparent growth rates only if $n \geq 30$ fish were measured in each week (we relaxed this requirement to $n \geq 10$ fish for alewife in the DECBSS data and American shad in the LRS data). We modeled growth by multiple regression, using the following independent variables: mean freshwater discharge and water temperature (during the two weeks in which growth was estimated), mean body length of fish, and stage of the invasion (early invasion vs. late invasion). Body length was included in all models.

Only one littoral zone species (spottail shiner) was caught in sufficient numbers to support a complete statistical analysis of apparent growth. We added a simpler, less formal procedure to include information on some of the less abundant littoral species. Using the DECBSS data set, we calculated the mean length of each species of fish for each week (regardless of year) in each of the early invasion and late invasion periods. That is, we pooled the data for 1993–2004 and 2005–2011 for each species. We made this calculation for every week and species for which at least five fish were measured in each of the two time periods. We then simply compared whether mean length was larger for each week in the early invasion or late invasion period.

For estimating confidence intervals around model-averaged slopes in graphs, we assumed 16 degrees of freedom for abundance and distribution and 60 degrees of freedom for apparent growth (it is not straightforward to estimate the exactly correct degrees of freedom in model-averaging — see p. 164 of Burnham and Anderson (2002)). This arbitrary decision has little practical effect on the size of confidence intervals, because t values are relatively insensitive to degrees of freedom over these ranges.

Results

Abundance

The time courses of fish abundance in the river (Figs. 2 and 3) show no obvious evidence of systematic changes in fish abun-

dance during the late invasion period (2005–2011). Furthermore, the statistical analysis (Table 1; Fig. 4) did not reveal any systematic change in abundance of either openwater or littoral species during the late invasion period. Populations of a few openwater fishes changed between the early invasion and the late invasion period, but these changes were inconsistent in direction or weak. Abundance of both PYSL and juveniles of American shad fell sharply, abundance of PYSL (but not juveniles) of white perch fell, and abundance of juveniles of alewife (but not PYSL of river herring, which tended to fall — Table 1) rose significantly. Only the increase in juvenile alewives was consistent with our hypothesis of recovery. None of the littoral species showed significant ($p < 0.2$) changes in abundance (Fig. 3), although PYSL of common carp tended to increase (Table 1), so there is no evidence for a systematic change in the abundance of littoral species during the late invasion period.

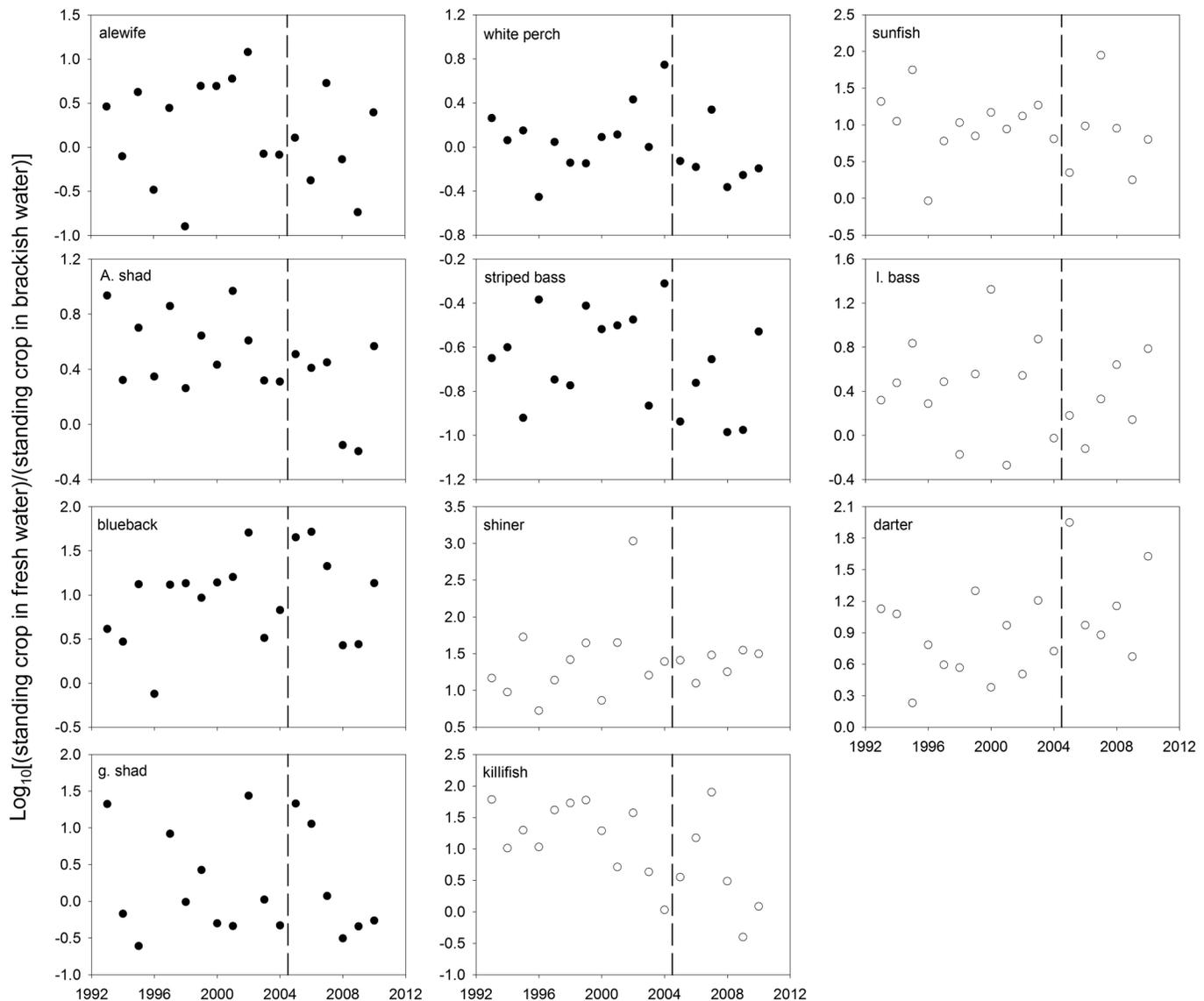
Freshwater flow had weak, inconsistent effects on fish abundance (Table 1). Temperature also generally had weak effects on fish abundance, but the direction of the effect was consistently negative for PYSL and positive for juveniles (Table 1).

Distribution

Neither the simple time courses of fish distribution in the river (Figs. 5 and 6) nor the statistical analysis (Table 2; Fig. 7) showed any evidence of systematic changes in fish distribution in the Hudson during the late invasion period. Of all of the openwater and littoral fish species, only the PYSL of the American shad (but not the juveniles) shifted significantly ($p < 0.05$) during the late invasion period.

The distribution of many fish species shifted downriver in years of high freshwater flow (Table 2), as observed by Strayer et al. (2004). In contrast, the effects of water temperature on fish distribution were weak and inconsistent (Table 2).

Fig. 6. Geographic distribution of juveniles of selected fish species in the Hudson River, 1993–2010 (closed circles, openwater species; open circles, littoral species). The vertical dashed line separates the early invasion and late invasion periods.



Apparent growth

The growth curves (Figs. 8 and 9) show that juveniles (but not PYSL) of openwater species were consistently larger at a given time of the year during the late invasion period than during the early invasion period. The single littoral species for which data are available (spottail shiner juveniles) did not show any apparent change between the two time periods. The statistical analysis of apparent growth rates (Table 3; Fig. 10) likewise found no difference between the early invasion and late invasion periods for PYSL of any species or for juveniles of a littoral species (spottail shiner). However, we found general increases in the late invasion period for apparent growth rates of juveniles of openwater species (Table 3; Fig. 10). Both the growth curves and the statistical models of apparent growth suggested that responses of striped bass were less pronounced than those of other openwater species.

Differences in fish size and apparent growth rates between the early invasion and late invasion periods were large. For example, by week 39–40 (i.e., near the end of the growing season), American shad were 21% longer in the late invasion period than in the early invasion period (Fig. 9). Assuming that

body mass is proportional to the cube of body length, this corresponds to an 78% increase in body mass. Likewise, the estimated changes in apparent growth rate of openwater species (increase $\sim 0.01/\text{week}$, Fig. 10) are large compared with the baseline growth rates ($\sim 0.04/\text{week}$).

As expected, apparent growth rates declined with increasing body size (Table 3). They tended to decline with increasing freshwater flow and rise with increasing temperature (Table 3).

The less formal analysis of growth rates (Table 4) also provided strong evidence for increases in body length of openwater species but no such evidence for littoral species. Again, among the abundant openwater species, striped bass showed the weakest evidence for larger sizes during the late invasion period. A rarer openwater species, the Atlantic menhaden, also did not show any evidence of increased growth.

Discussion

We found mixed evidence that fish in the Hudson River have recovered from the initial effects of the zebra mussel invasion. Apparent growth rates of juvenile openwater fish rose substan-

Table 2. Statistical models to predict distribution of selected age-classes of fish in the Hudson River.

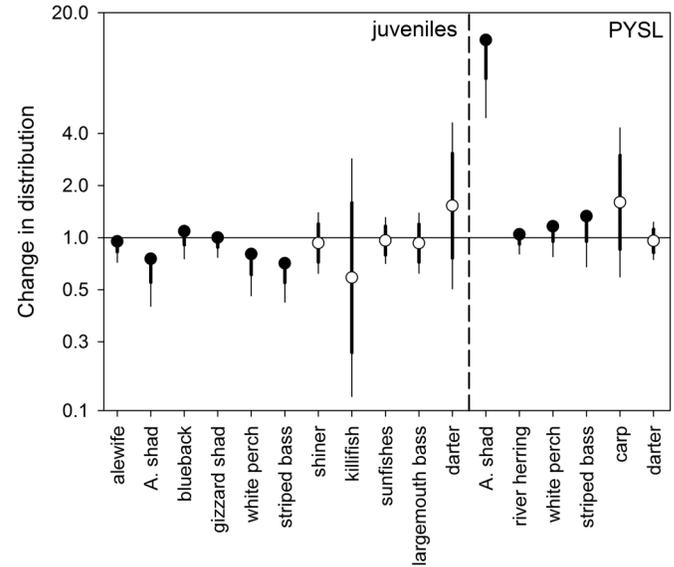
Species	Flow ($\times 10^{-5}$, $m^3 \cdot s^{-1}$)	Temperature ($^{\circ}C$)	Invasion period
Post-yolk-sac larvae			
Blueback herring + alewife	0.368 -39 (62)	0.208 -0.017 (0.052)	0.183 0.018 (0.065)
American shad	0.939 -230 (96)	0.536 -0.162 (0.190)	0.997 1.142 (0.257)
White perch	0.931 -105 (41)	0.190 0.012 (0.029)	0.379 0.065 (0.100)
Striped bass	0.945 -137 (51)	0.172 0.011 (0.031)	0.454 -0.123 (0.167)
Common carp	0.221 9 (20)	0.184 0.008 (0.025)	0.625 0.204 (0.203)
Tessellated darter	0.682 -66 (58)	0.227 0.018 (0.043)	0.191 -0.019 (0.051)
0+ juveniles			
Alewife	0.898 -308 (144)	0.165 0.005 (0.036)	0.175 -0.022 (0.069)
American shad	0.744 -122 (92)	0.183 0.004 (0.025)	0.490 -0.123 (0.157)
Blueback herring	0.184 5 (30)	0.530 0.149 (0.179)	0.209 0.037 (0.091)
Gizzard shad	0.175 -7 (40)	0.204 0.030 (0.080)	0.171 0.0001 (0.065)
White perch	0.206 -10 (26)	0.184 -0.008 (0.027)	0.428 -0.096 (0.138)
Striped bass	0.180 3 (13)	0.169 0.001 (0.013)	0.692 -0.149 (0.129)
Spottail shiner	0.191 -13 (38)	0.742 0.252 (0.192)	0.205 -0.032 (0.082)
Banded killifish	0.528 -155 (186)	0.181 -0.001 (0.047)	0.439 -0.232 (0.324)
<i>Lepomis</i> spp.	0.408 -71 (106)	0.181 -0.006 (0.037)	0.184 -0.017 (0.062)
Largemouth bass	0.327 -43 (74)	0.237 -0.028 (0.062)	0.187 -0.032 (0.082)
Tessellated darter	0.182 1 (24)	0.690 0.196 (0.169)	0.510 0.184 (0.226)

Note: Table shows the summed Akaike weight for each variable (upper number) along with the model-averaged slope and standard error (lower numbers) for each variable.

tially in recent years (Fig. 11), as we hypothesized would occur in response to recent recovery of their forage base. Littoral species, in contrast, showed no increase in apparent growth between 1993–2004 and 2005–2011, again as hypothesized. On the other hand, we found no evidence that the abundance or distribution of either openwater or littoral fish in the Hudson recovered towards pre-invasion conditions. Indeed, distributions of openwater fish species have continued to move further downriver in recent years (Fig. 11).

Several nonexclusive explanations could account for the discrepancy between the strong recovery in apparent growth rates and the absence of any detectable recovery in abundance or distribution of fish. First, we suggested in our earlier paper (Strayer et al. 2004) that we might have more statistical power to detect a change in growth rate, because fish body size can be estimated more precisely than fish population size or geographic distribution. However, in the present study, confidence intervals around estimates of changes in fish abundance and distribution were about the same size as those around estimates of changes in growth rates (Figs. 4, 7, and 10), so this explanation seems unlikely to account for the absence of significant effects on fish abundance

Fig. 7. Model-averaged estimates of proportional change in fish distributions in the Hudson River (ratio of standing crop in freshwater section of the river to standing crop in the brackish section of the river) between 1993–2004 and 2005–2010 (closed circles, openwater species; open circles, littoral species). We give 80% confidence limits (one-tailed for openwater species, two-tailed for littoral species) as thick lines and 95% confidence limits as thin lines. For one-tailed tests, significant results are indicated if the confidence limit is above the horizontal line.



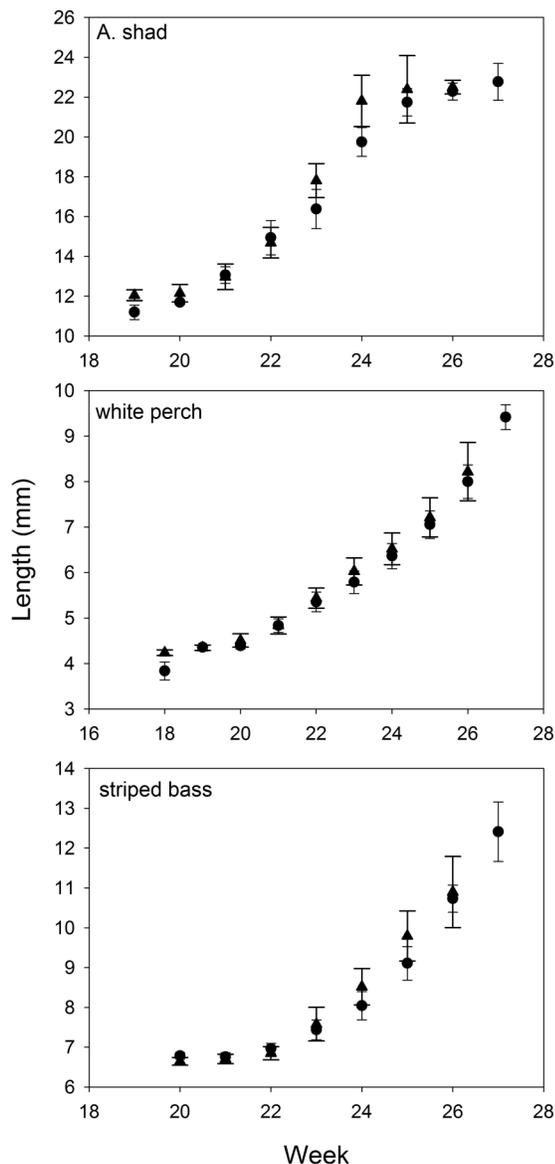
and distribution. Second, growth rates might be ecologically more sensitive than abundance of distribution to changes in the forage base. For example, growth rates might respond measurably to smaller changes in the forage base than do abundance and distribution, or have a larger response to a given change in food availability. Third, there may be longer time lags in demographic responses like fish abundance and distribution than in somatic responses like growth rates. While it is reasonable to expect growth rates to respond instantaneously to change in food availability, population size and distribution may require a generation or more to respond. Thus, it may simply be too soon to see the full response of fish abundance and distribution to recovery of the forage base in the Hudson.

Other influences on fish abundance, distribution, and growth in the Hudson in recent years include interannual variation in freshwater flow and water temperature, and changes in spawning locations. High freshwater flow often was correlated with downriver distributions and slow growth rates of fish, and high water temperatures often were correlated with low abundances of PYSL, high abundances of juveniles, and fast growth rates of both life stages. However, these environmental factors typically had weak effects in our models. The marked recent shift upriver in PYSL of American shad (Fig. 7) presumably was caused by the recent shift in spawning by this species to upriver sites in recent years, which in turn may be related to harvests at formerly important spawning sites near Kingston (RKM 151) (New York State Department of Environmental Conservation, unpublished data). We do not think that zebra mussels had anything to do with this shift in distribution of PYSL of American shad. Whatever its cause, it is interesting to note that this distributional shift did not persist into the juvenile stage.

Long-term invasion dynamics

Our results serve as another reminder that the long-term effects of an invasion may be different than its transient short-term

Fig. 8. Growth curves for post-yolk-sac larvae of selected fish species in the Hudson River during the early invasion (1993–2004, circles) and late invasions (2005–2010, triangles) periods. Error bars show 1 SE.



effects (Strayer et al. 2006). Growth rates of openwater fishes in the Hudson River, substantially reduced in the early years of the zebra mussel invasion, have now substantially recovered, presumably in response to the recovery of the zooplankton (Pace et al. 2010) and macrobenthos (Strayer et al. 2011) upon which they feed. It remains to be seen whether this recovery in growth rates are themselves transitory or permanent, and whether abundance and distribution of Hudson River fishes eventually will recover to pre-invasion levels.

Most discussion about how the impacts of a non-native species might diminish over time focuses on declines in its population density (e.g., Strayer et al. 2006; Ricciardi et al. 2013). However, increased mortality on an invader might result in changes in its traits (especially body size) in addition to or instead of changes in population density. In the Hudson, it appears that a large increase in mortality on zebra mussels led to important changes in size structure, but minimal changes in

population density, and that these changes in body size have largely been responsible for partial recovery of the ecosystem (Pace et al. 2010; Carlsson et al. 2011; Strayer et al. 2011; Strayer and Malcom 2014). Such temporal changes in body size as a result of increased mortality could occur in any non-native species with plastic body size or indeterminate growth, including vascular plants as well as many animals, and could, therefore, be a common mechanism of temporal change in the effects of an invader.

It is striking and perhaps meaningful that studies of individual ecosystems often report temporal changes in invasion effects (e.g., this and other studies on the Hudson; Lankau et al. 2009; Mitchell et al. 2011; Yelenik and D'Antonio 2013), whereas broader meta-analyses of invasion effects (e.g., Ward and Ricciardi 2007; Higgins et al. 2011; van Hengstum et al. 2014) have tended not to report significant effects of time since invasion. A wide range of mechanisms exist by which invasion effects can be modulated through time, each with its own time course and likely context dependence (Strayer et al. 2006; Strayer 2012; Ricciardi et al. 2013). Thus, it seems possible that meta-analyses that simply use time since invasion as an independent variable are combining processes with different time scales in different systems, and they will, therefore, be relatively insensitive in detecting temporal changes in invasions.

Management implications

The long-term response of fish populations and other parts of the ecosystem to changes in bivalve populations is particularly challenging to understand and manage because (i) many bivalve populations in lakes, rivers, estuaries, and coastal waters are changing dramatically in response to pollution, habitat change, overharvest, restoration, and species invasions (Carlton 1999; Karatayev et al. 2007; Beck et al. 2011; Haag 2012; Sousa et al. 2013; Strayer and Malcom 2014); (ii) many bivalves are long-lived, so the dynamics of changes in bivalve populations may take several years to many decades to fully resolve (Strayer and Malcom 2014); and (iii) as shown here and in other studies of biological invasions (Strayer et al. 2006; cf. Hamilton 2012), the ecosystem itself may take years to decades to respond to the initial invasion or changes in the dynamics of the invader. The joint effects of these lags and slow dynamics mean that the full responses to changes in bivalve populations (whether losses, gains, or species substitutions) may not be observed for decades after the initial event (e.g., pollution, species invasion, change in harvest regulation) that affected the bivalve population.

Invasions may be difficult to manage because their effects are unpredictable; if these effects change over the long term, they may be even more difficult to manage. Three attributes of this long-term change may pose special challenges for environmental managers. First, the ecosystem may continue to change for decades after the initial invasion, requiring active monitoring and management for many years. In addition, because many aquatic ecosystems are heavily invaded (Mills et al. 1996; Ruiz et al. 1999; Ricciardi 2006; Jackson and Grey 2013), the manager will be dealing with the shifting effects on the ecosystem to multiple invaders, which may interact with one another. Second, the asynchronous response of different ecosystem components means that it will not be sufficient for a manager to monitor and manage one part of the ecosystem as an indicator of how other parts of the ecosystem are doing. Third, the long-term responses of an ecosystem to an invader often are strongly context dependent. In the case of bivalve effects on fish, we have argued (Strayer et al. 2004) that strong context dependence would cause different

Fig. 9. Growth curves for juveniles of selected fish species (closed symbols, openwater species; open symbols, littoral species) in the Hudson River during the early invasion (1993–2004, circles) and late invasion (2005–2010, triangles) periods. DECBSS, New York State Department of Environmental Conservation beach seine survey data; UBSS, utilities’ beach seine survey data. Error bars show 1 SE.

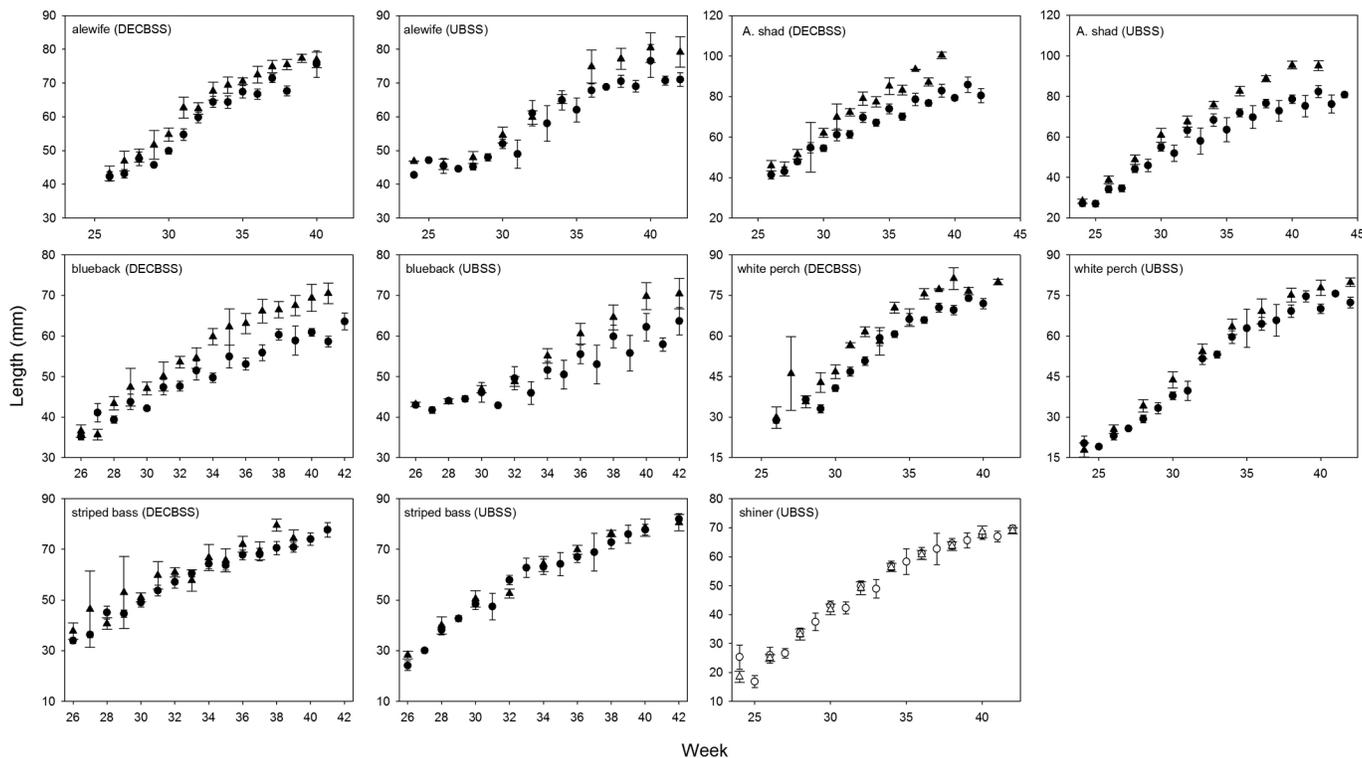


Table 3. Statistical models to predict apparent growth rates of fish in the Hudson River.

Species	Body length	Flow ($\times 10^{-5}$, $m^3 \cdot s^{-1}$)	Temperature ($^{\circ}C$)	Invasion period
Post-yolk-sac larvae				
American shad	—	0.263	0.999	0.267
	-0.012 (0.0020)	0.3 (1.1)	0.0125 (0.0031)	-0.0017 (0.0052)
White perch	—	0.535	0.824	0.279
	-0.022 (0.0059)	-0.9 (1.7)	0.011 (0.0033)	0.0014 (0.0040)
Striped bass	—	0.255	1.00	0.247
	-0.018 (0.0036)	-0.2 (1.0)	0.022 (0.0028)	0.0003 (0.0030)
0+ juveniles				
Alewife (UBSS)	—	0.273	0.860	0.252
	-0.00084 (0.00034)	-0.3 (0.9)	0.0036 (0.0021)	0.0003 (0.0019)
Alewife (DECBSS)	—	0.847	0.298	0.723
	-0.0018 (0.00027)	-4.9 (3.0)	-0.0002 (0.0007)	0.0093 (0.0079)
American shad (UBSS)	—	0.382	0.259	0.684
	-0.0025 (0.00018)	-0.6 (1.0)	0.00002 (0.00035)	0.0105 (0.0097)
American shad (DECBSS)	—	0.325	0.932	0.994
	-0.0013 (0.00013)	-0.4 (0.9)	0.0017 (0.0007)	0.014 (0.0041)
Blueback herring (UBSS)	—	0.390	0.295	0.506
	-0.0014 (0.00065)	-1.0 (1.7)	-0.0004 (0.0009)	0.0068 (0.0090)
Blueback herring (DECBSS)	—	0.299	0.272	0.953
	-0.0014 (0.00019)	-2.5 (3.7)	-0.00004 (0.0027)	0.011 (0.0045)
White perch (UBSS)	—	0.395	0.361	0.634
	-0.0034 (0.00024)	-2.4 (3.6)	0.0006 (0.0011)	0.0094 (0.0097)
White perch (DECBSS)	—	0.274	0.925	0.750
	-0.0023 (0.00024)	-0.03 (0.9)	0.0028 (0.0013)	0.0097 (0.0077)
Striped bass (UBSS)	—	0.983	0.756	0.353
	-0.0039 (0.00029)	-14 (4.7)	-0.0042	0.0043 (0.0078)
Striped bass (DECBSS)	—	0.293	0.397	0.326
	-0.0036 (0.00031)	0.7 (1.9)	-0.0008 (0.0014)	-0.0023 (0.0049)
Spottail shiner (UBSS)	—	0.873	0.697	0.279
	-0.0038 (0.00018)	-3.5 (4.1)	-0.0014 (0.0012)	-0.0007 (0.0021)

Note: Table shows the summed Akaike weight for each variable (upper number) along with the model-averaged slope and standard error (lower numbers) for each variable. UBSS, utilities beach seine survey of 0+ juveniles; DECBSS, Department of Environmental Conservation beach seine survey of 0+ juveniles.

Fig. 10. Model-averaged estimates of change in apparent growth rates of fish in the Hudson River between 1993–2004 and 2005–2010 (closed circles, openwater species; open circles, littoral species). We give 80% confidence limits (one-tailed for openwater species, two-tailed for littoral species) as thick lines and 95% confidence limits as thin lines. For one-tailed tests, significant results are indicated if the confidence limit is above the horizontal line. For reference, apparent growth rates typically are ~ 0.04 week⁻¹. In cases where two estimates are shown, the left-hand results are based on data from the New York State Department of Environmental Conservation and the right-hand results are based on data from the utilities' beach seine survey.

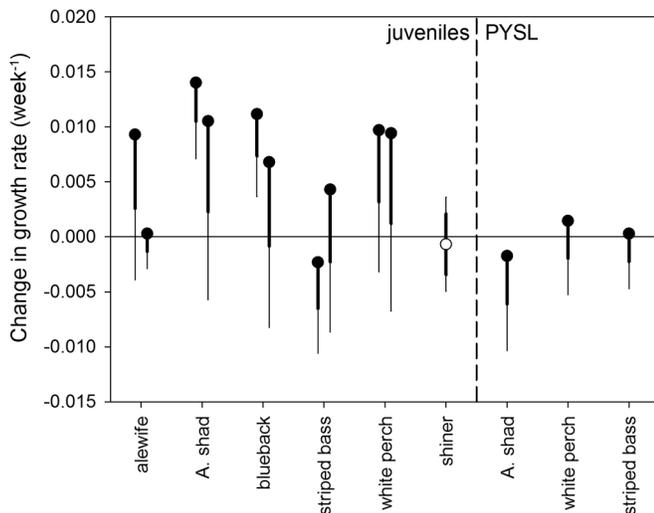


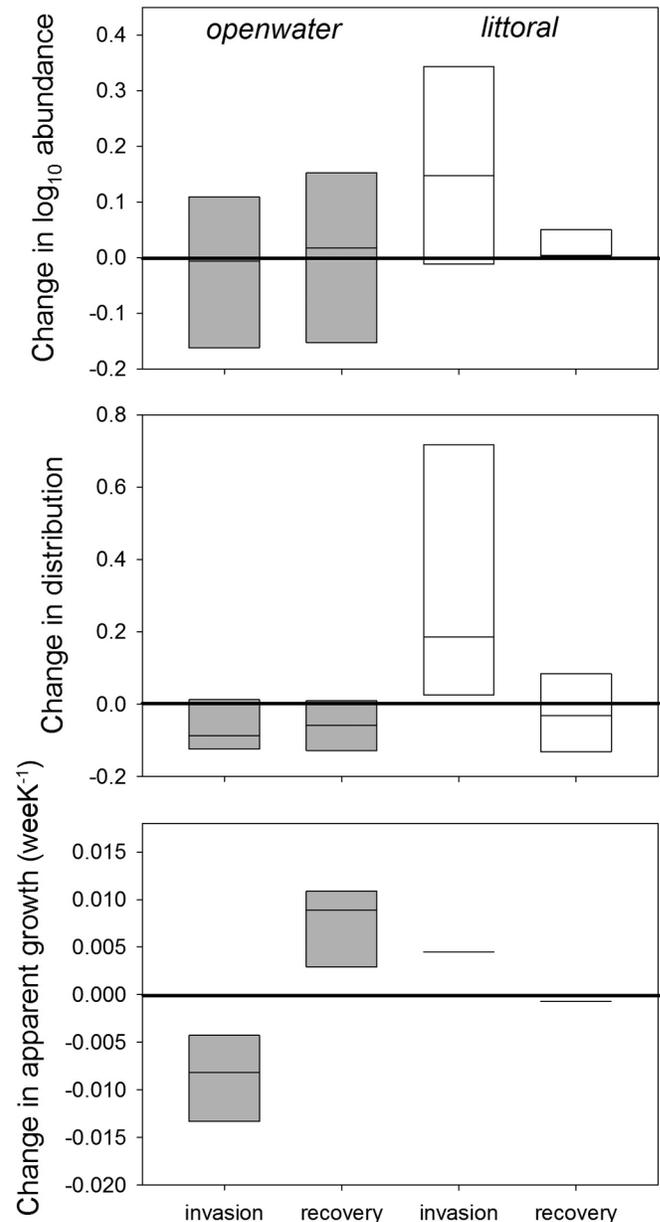
Table 4. Week-by-week comparison of mean length of fishes in the early invasion period (1993–2004) and the late invasion period (2005–2011), based on data from New York State Department of Environmental Conservation.

Species	Larger during early invasion	Larger during late invasion
Openwater species total	21	92
Alewife	4	15
American shad	0	18
Atlantic menhaden	6	7
Blueback herring	2	18
Gizzard shad	1	3
Striped bass	7	13
White perch	1	18
Littoral species total	19	27
Brown bullhead	2	5
Largemouth bass	8	8
Smallmouth bass	4	7
Yellow perch	5	7

Note: The table shows the number of weeks in which mean length was larger in each time period for weeks in which at least five individual fish were measured in both the early invasion and late invasion periods. There was a significant difference between time periods for the openwater species ($p < 0.0001$) but not for the littoral species ($p = 0.30$); in addition, there was a significant difference in proportions between the openwater species and the littoral species ($p = 0.003$).

ecosystems to respond very differently to the same bivalve invasion. We expect that this context dependence also would apply to any recovery of fish populations from bivalve invasions over the long term, even though we do not have sufficient data from different ecosystems to explore any context dependence.

Fig. 11. Summary of changes in attributes of juvenile Hudson River fishes resulting from the initial invasion of the zebra mussel (comparison of 1974–1991 vs. 1993–1999, modified from Strayer et al. 2004) and the recent hypothesized recovery (comparison of 1993–2004 vs. 2005–2011). Horizontal lines show the median change estimated by model-averaging (over all models), and boxes show the 25th and 75th percentiles for all species and data sets analyzed. Shaded box, openwater species; open box, littoral species.



Acknowledgements

We thank the Hudson River Foundation for funding this analysis; Bill Dey, Nancy Decker, and John Young of ASA Analysis and Communication for their kind help in providing the utilities' data sets; everyone who collected and measured all those fish over the years; and two reviewers for helpful comments.

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