# Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary

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**Abstract:** Despite predictions that the zebra mussel (*Dreissena polymorpha*) invasion of North America would damage fisheries, analyses of actual effects on fish have been few and equivocal. We analyze 26 years of data on fish populations in the Hudson River to quantify changes associated with the zebra mussel invasion. Based on our measurements of changes in the lower food web, we predicted that populations of open-water fish species (e.g., *Alosa* spp.) would suffer and populations of littoral fish species (e.g., Centrarchidae) would prosper from the zebra mussel invasion. We found that the median decrease in abundance of open-water species was 28%, whereas the median increase in abundance of littoral species was 97%. Populations of open-water species shifted downriver away from the zebra mussel population, whereas those of littoral species shifted upriver. Median apparent growth rates fell by 17% among open-water species and rose by 12% in the single littoral species studied. Many of the observed changes were large and involved species of commercial or recreational importance (e.g., American shad (*Alosa sapidissima*), black basses (*Micropterus* spp.)). The influence of zebra mussels on fish should vary widely across ecosystems as a function of system morphology, factors that limit primary production, and diets of the fish species.

**Résumé :** Malgré les prédictions voulant que l'invasion des moules zébrées (*Dreissena polymorpha*) en Amérique du Nord soit néfaste pour les pêches, les analyses d'effets réels sont rares et équivoques. Nos analysons 26 années de données sur les populations de poissons du fleuve Hudson pour quantifier les changements associés à l'invasion des moules zébrées. D'après notre évaluation des modifications de la partie inférieure du réseau alimentaire, nous avions prédit que les populations de poissons d'eau libre (e.g., *Alosa* spp.) seraient défavorisées et que les populations littorales (e.g., les Centrarchidae) seraient avantagées par l'invasion des moules zébrées. Le déclin médian de l'abondance des espèces d'eau libre est de 28 %, alors que l'accroissement médian de l'abondance des espèces littorales est de 97 %. Les populations d'espèces d'eau libre se sont déplacées vers l'aval loin de la population de moules zébrées, alors que celles des espèces littorales ont remonté vers l'amont. Les taux médians apparents de croissance ont chuté de 17 % chez les espèces d'eau libre et augmenté de 12 % chez la seule espèce littorale étudiée. Plusieurs des changements observés sont considérables et impliquent des espèces d'importance commerciale ou sportive (e.g., l'alose savoureuse (*Alosa sapidissima*), les achigans (*Micropterus* spp.)). Les effets des moules zébrées sur les poissons devraient varier beaucoup dans les écosystèmes en fonction de la morphologie des systèmes, des facteurs limitants de la production primaire et du régime alimentaire des espèces de poissons.

[Traduit par la Rédaction]

## Introduction

Species introductions are now one of the most important of human impacts on the world's ecosystems (e.g., Office of Technology Assessment 1993; Mack et al. 2000). Ecosystems near centers of human activity often contain dozens to hundreds of introduced species, with more arriving each year. These invasions may have large, diverse ecological and economic effects that are difficult to mitigate or reverse. The effects of species invasions can be difficult to quantify, requiring good measurements of the ecosystem before and after the invasion. Indirect effects of an invader that are propagated through the ecosystem can be especially difficult to measure or predict because the initial effect of the invader can be damped, amplified, or even reversed by the ecosystem.

The impact of zebra mussels (*Dreissena polymorpha*) on fish populations is an example of an important indirect effect that has been difficult to measure. When zebra mussels appeared in North America in 1988, experts predicted economic damages of US$ 4 billion in the first 10 years in the Great Lakes alone (Roberts 1990), largely from losses of sport fisheries. However, no evidence of damage to sport fisheries has yet appeared.

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In fact, while zebra mussels have been shown to have strong effects on phytoplankton (e.g., Caraco et al. 1997; Smith et al. 1998), zooplankton (MacIsaac et al. 1995; Pace et al. 1998), vegetation (Skubinna et al. 1995; Stuckey and Moore 1995), water chemistry (Fahnenstiel et al. 1995*b*; Effler et al. 1996), and zoobenthos (Nalepa et al. 1998; Strayer and Smith 2001), the few studies on fish have had inconsistent results. Experimental studies in which fish were exposed to different densities of zebra mussels showed that fish growth can increase (Thayer et al. 1997), decrease (Jennings 1996), or be unaffected (Richardson and Bartsch 1997) by the mussels. In any case, it is difficult to apply the results of these studies to nature because they were conducted on such short scales of time and space that they excluded many potentially important mechanisms.

Detecting zebra mussel impacts from field data requires long runs of high-quality data, preferably including the parts of the food web that link zebra mussels to fish, and is often complicated by changes in other external variables during the invasion period. Consequently, such analyses are few and have given equivocal results. Scientists detected little or no effect of the zebra mussel invasion on abundance or growth of young-of-the-year (YOY) fish in the open waters of Lake Erie (Gopalan et al. 1998; Dermott et al. 1999; Trometer and Busch 1999), but these analyses are complicated by the invasion of an important alien fish species (white perch (*Morone americana*)) and large reductions in nutrient loading in Lake Erie during the period of analysis. Likewise, the zebra mussel invasion did not seem to reduce phytoplankton or zoobenthos biomass in Rice Lake, Ontario, and did not affect the diets or growth rates of two of three fish species studied (Mercer et al. 1999). Growth rates of the third species (pumpkinseed (*Lepomis gibbosus*)) increased. In Oneida Lake, New York, Mayer et al. (2000) found that apparent growth rates of YOY yellow perch (*Perca flavescens*) rose following the zebra mussel invasion but that the abundance of YOY and the abundance and apparent growth rates of adult perch were unchanged. In contrast, Ryan et al. (1999) reported that the catch rates of many species of fish in Long Point Bay (Lake Erie) fell significantly when zebra mussels invaded. In southeastern Lake Michigan, the diet of lake whitefish (*Coregonus clupeaformis*) changed and body condition and growth declined after the zebra mussel invasion caused the abundance of a favored food item (the amphipod *Diporeia*) to decline (Pothoven et al. 2001). Karataev and Burlakova (1995) reported very large increases in the biomass and production of fish in Lukomskoe Lake, Belarus, following the arrival of zebra mussels and linked this increase to increases in zoobenthic prey. Unfortunately, a large powerplant began operations on this lake at almost the same time as the zebra mussel invasion, so it is difficult to separate powerplant effects (e.g., entrainment, temperature) from zebra mussel effects. No clear picture emerges from these analyses of field data, except that zebra mussels might have strong effects in some cases and no effects in others and that analyses have been hampered by inadequate data.

Here, we analyze extensive long-term (up to 26 years) data sets on YOY fish in the Hudson River estuary, New York, to quantify zebra mussel effects on fish. Unlike most other ecosystems that have been studied, we also have access to long-term records of most other parts of the Hudson's food web over the invasion period, and there is no evidence of major confounding changes in external driving variables to the Hudson River ecosystem during the invasion period.

## Materials and methods

### Study area

The study area is the Hudson River estuary, which extends 248 km from New York City to Troy in eastern New York. Over most of its length, the Hudson estuary is 1–4 km wide and 5–20 m deep, although the morphology is varied and there are extensive shallows and areas as deep as 66 m (Cooper et al. 1988). Above about river kilometre (rkm) 100 (kilometres upriver from The Battery in New York City), the river usually is fresh, but below rkm 100, sea salt may be present in various concentrations, depending on freshwater flow and tides. The entire area is subject to tides of ~1 m; tidal flows are much larger than the average freshwater flow of 577 $m^3 \cdot s^{-1}$ (Cooper et al. 1988). The water in the Hudson is alkaline (pH ~ 7–8), warm (annual mean 12 °C), turbid (Secchi transparency ~ 1 m), and nutrient rich ($PO_4$-P > 10 $\mu g \cdot L^{-1}$, $NO_3$-N ~ 0.4 $mg \cdot L^{-1}$) (Limburg et al. 1986; Caraco et al. 1997).

Allochthonous matter dominates organic carbon inputs to the Hudson (69% of total), but primary production by phytoplankton and submersed macrophytes is important (Howarth et al. 1996; Caraco et al. 2000). Primary production by phytoplankton (and presumably submersed macrophytes) is light limited (Cole et al. 1992; Harley and Findlay 1994). The Hudson's zooplankton is dominated by rotifers and the cladoceran *Bosmina freyi* (Pace et al. 1998), and its diverse zoobenthos is dominated by tubificid oligochaetes, amphipods, and chironomid midges (Strayer and Smith 2001). The estuary supports warmwater fishes, including several abundant diadromous species.

Zebra mussels first appeared in the Hudson in 1991 and have been a dominant part of the Hudson's biota since September 1992 (Strayer et al. 1996). Since that time, combined suspension-feeding by all species increased 30-fold, biomass of phytoplankton fell 80%, biomass of microzooplankton fell 76%, biomass of macrozooplankton fell 52%, biomass of deepwater zoobenthos fell 40%, and biomass of shallow-water zoobenthos rose 10% in the freshwater tidal parts of the Hudson (Strayer et al. 1999; Strayer and Smith 2001). The 45% increase in water clarity may have led to increases in the coverage and productivity of submersed macrophytes (Strayer et al. 1999; Caraco et al. 2000), although this process has not been well studied in the Hudson. Zebra mussels are quantitatively important only in freshwater parts of the Hudson, and their effects extend from the head of the estuary (rkm 248) down to approximately rkm 100 (Strayer et al. 1996; Caraco et al. 1997; Pace et al. 1998). Most relevant to the fish, we found that the biomass of forage invertebrates (i.e., zooplankton and macrozoobenthos excluding the large bivalves that are eaten by few species of fish in the Hudson (Schmidt et al. 1995; Strayer 2004)) fell by 70% in the pelagic zone, fell by 40% in the deepwater benthos, and rose by 10% in the shallow-water benthos (Pace et al. 1998;

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Strayer and Smith 2001). We suspect that our estimate of the increase in shallow-water benthos in the Hudson is too low, as it is based on the areal density of macroinvertebrates per square metre of macrophyte bed and excludes any increases that may have occurred in the extent of macrophyte beds. Such increases in macrophyte coverage have been seen in other ecosystems invaded by bivalves (e.g., Phelps 1994; Skubinna et al. 1995) but have not been quantified in the Hudson.

## Hypotheses

We hypothesized that these changes in the food web might have affected the Hudson's fish community. Larvae and juveniles of several abundant fish species in the Hudson (i.e., American shad (*Alosa sapidissima*), blueback herring (*Alosa aestivalis*), alewife (*Alosa pseudoharengus*), gizzard shad (*Dorosoma cepedianum*), white perch, and striped bass (*Morone saxatilis*)) feed heavily on plankton and drifting benthic invertebrates in the water column (summarized by Strayer and Smith 2001) and so might be negatively affected by the zebra mussel invasion. We hypothesized that the abundance or growth rates of these species would decline following the zebra mussel invasion or that their distributions within the river would shift downriver away from the zone of greatest zebra mussel impacts. In contrast, many fish species (common carp (*Cyprinus carpio*), spottail shiner (*Notropis hudsonius*), fourspine stickleback (*Apeltes quadracus*), banded killifish (*Fundulus diaphanus*), redbreast sunfish (*Lepomis auritus*), bluegill (*Lepomis macrochirus*), pumpkinseed, smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), and tessellated darter (*Etheostoma olmstedi*)) are associated with vegetated shallows in the Hudson, where they feed chiefly on benthic invertebrates (summarized by Strayer and Smith 2001). We hypothesized that the abundance or growth rates of these species would increase following the zebra mussel invasion or that their distributions within the river would shift upriver into the zone of greatest zebra mussel impacts.

## Sources of data

Our analysis was based on three data sets: the utilities' long-river ichthyoplankton survey (LRS), the utilities' beach seine survey (UBSS), and the Department of Environmental Conservation's beach seine survey (DECBSS) (the "utilities'" surveys are conducted by contractors of the electric utilities, which are required to monitor fish populations in the river as a condition for withdrawing cooling water from the Hudson). The utility companies collected ichthyoplankton samples annually from 1974 to 1999. This program 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, and 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 m$^2$ and mesh of 505 μm result-

ing in a typical sample volume of ~300 m$^3$. Species and life stages (egg, yolk-sac larva, post-yolk-sac larva, or 0+ juvenile) were identified and enumerated, 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 from this data set. We excluded data from "region 0" (rkm 0–21), which was not sampled before 1988. Post-yolk-sac larvae of blueback herring and alewife were combined into a single taxon called "river herring" for our analysis because the early life stages of these two species cannot be readily distinguished; presumably, most river herring are bluebacks.

The UBSS began in 1974. This survey was riverwide, with the goal of measuring the distribution and abundance of selected species. Samples were 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 from this survey for YOY (i.e., 0+ juveniles) only.

We analyzed data from the DECBSS from 1985 to 1999. The goal of this survey was to estimate relative abundance of juvenile *Alosa* spp., primarily American shad and blueback herring. Samples were taken biweekly (alternating with the UBSS) from late June to 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 from this survey for YOY (i.e., 0+ juveniles) only.

## Statistical analyses

### *Abundance*

We tested for effects of the zebra mussel invasion on the estimated riverwide population of fish ("riverwide standing crop") using two data sets, the LRS of post-yolk-sac larvae and the UBSS of 0+ juveniles. In the LRS, we calculated the mean number of post-yolk-sac larvae in the river over the weeks 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). This time period differed among species as follows: American shad, weeks 19–27; river herrings, weeks 18–27; white perch, weeks 18–27; striped bass, weeks 20–27; common carp, weeks 21–27; tessellated darter, weeks 19–27.

We modeled log-transformed abundance using multiple regression with the following independent variables: year (which allows for temporal trends in the data), mean water temperature and mean freshwater flow during the period of analysis, and the presence or absence of zebra mussel effects (coded as 0 for 1974–1992 and 1 for 1993–1999). If the data set contained zeroes, we substituted a $\log(X + c)$ transformation, where $c$ was the minimum nonzero value observed for that species. Because we could not exclude the single or combined influence of any of these variables, we ran all pos-

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

| Species | Year | Flow (m³·s⁻¹, ×10⁻⁵) | Temperature (°C) | Zebra |
|---|---|---|---|---|
| **Post-yolk-sac larvae** | | | | |
| Blueback herring + alewife | 0.34 | 0.31 | 0.71 | 0.34 |
| | 0.015 (0.022) | 33 (99) | –0.21 (0.12) | –0.24 (0.37) |
| American shad | 0.82 | 0.23 | 0.41 | 0.99 |
| | 0.022 (0.010) | –1.9 (39) | –0.055 (0.044) | –0.58 (0.19) |
| Striped bass | 1.00 | 0.23 | 0.27 | 0.24 |
| | 0.064 (0.008) | –1.9 (41) | 0.031 (0.047) | 0.065 (0.19) |
| White perch | 0.82 | 0.27 | 0.27 | 0.65 |
| | 0.018 (0.010) | –12 (32) | –0.018 (0.046) | –0.25 (0.17) |
| Common carp | 1.00 | 0.29 | 0.27 | 0.27 |
| | 0.16 (0.026) | –125 (60) | 0.096 (0.15) | 0.37 (0.60) |
| Tessellated darter | 0.87 | 0.24 | 0.26 | 0.31 |
| | 0.013 (0.006) | –0.70 (30) | 0.016 (0.035) | 0.014 (0.15) |
| **0+ juveniles** | | | | |
| Alewife | 0.99 | 0.26 | 0.86 | 0.41 |
| | –0.048 (0.015) | –34 (89) | 0.19 (0.076) | 0.30 (0.25) |
| American shad | 0.41 | 0.46 | 0.37 | 0.72 |
| | –0.010 (0.008) | 120 (122) | –0.045 (0.040) | –0.22 (0.097) |
| Blueback herring | 0.68 | 0.24 | 0.50 | 0.29 |
| | –0.027 (0.014) | 8.7 (97) | –0.14 (0.091) | –0.073 (0.31) |
| Gizzard shad | 0.47 | 0.31 | 0.44 | 0.36 |
| | 0.028 (0.023) | 88 (162) | 0.17 (0.15) | 0.29 (0.41) |
| Striped bass | 0.36 | 0.51 | 0.33 | 0.33 |
| | –0.005 (0.009) | –67 (50) | –0.017 (0.057) | 0.028 (0.16) |
| White perch | 0.80 | 0.47 | 0.24 | 0.48 |
| | –0.030 (0.011) | –98 (35) | –0.020 (0.072) | –0.36 (0.23) |
| Spottail shiner | 0.44 | 0.37 | 0.34 | 0.35 |
| | –0.007 (0.008) | –111 (103) | 0.004 (0.054) | –0.032 (0.14) |
| Banded killifish | 0.99 | 0.98 | 0.30 | 0.48 |
| | –0.048 (0.014) | –239 (67) | –0.066 (0.076) | 0.34 (0.24) |
| Fourspine stickleback | 0.91 | 0.30 | 0.49 | 0.56 |
| | –0.073 (0.024) | –149 (106) | –0.15 (0.12) | –0.72 (0.42) |
| Bluegill | 0.56 | 0.33 | 0.48 | 0.49 |
| | –0.021 (0.019) | –44 (88) | 0.095 (0.089) | 0.30 (0.31) |
| Redbreast sunfish | 0.39 | 0.97 | 0.28 | 0.55 |
| | 0.023 (0.020) | –385 (109) | –0.078 (0.12) | 0.48 (0.29) |
| Pumpkinseed | 0.33 | 0.82 | 0.28 | 0.28 |
| | –0.009 (0.015) | –180 (74) | –0.027 (0.089) | 0.038(0.24) |
| Smallmouth bass | 0.44 | 0.25 | 0.51 | 0.73 |
| | 0.021 (0.015) | –26 (76) | 0.10 (0.07) | 0.47 (0.19) |
| Largemouth bass | 0.33 | 0.33 | 0.54 | 0.36 |
| | 0.00 (0.015) | –30 (96) | –0.10 (0.086) | 0.12 (0.24) |
| Tessellated darter | 1.00 | 0.35 | 0.21 | 0.91 |
| | –0.041 (0.012) | –56 (121) | –0.006 (0.055) | 0.44 (0.17) |

**Note:** The 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. Year is number of years since 1974.

sible subsets of regression models and presented 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. Second, we present the model-averaged estimates of the slopes ($\bar{\beta}_i$) for each variable, along with their standard errors. There are two ways in 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) for a discussion of this point). We present the former estimate, which is interpreted as an estimate of the slope given that the variable is assumed to be included in the model. The slope estimates based on all models can be calculated as the product of the Akaike weight and the slope estimates that we present. Inspection of autocorrelation and partial autocorrelation func-

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**Fig. 1.** Abundance of post-yolk-sac larvae of several species of fish in the Hudson River before (solid circles) and after (open circles) the zebra mussel invasion based on data from the utilities' long-river survey. The regression lines are fit to preinvasion data. Open circles falling below the line indicate that a species decreased after the zebra mussel invasion, whereas open circles falling above the line indicate that a species increased after the zebra mussel invasion. Note that the *y* axes are logarithmic.
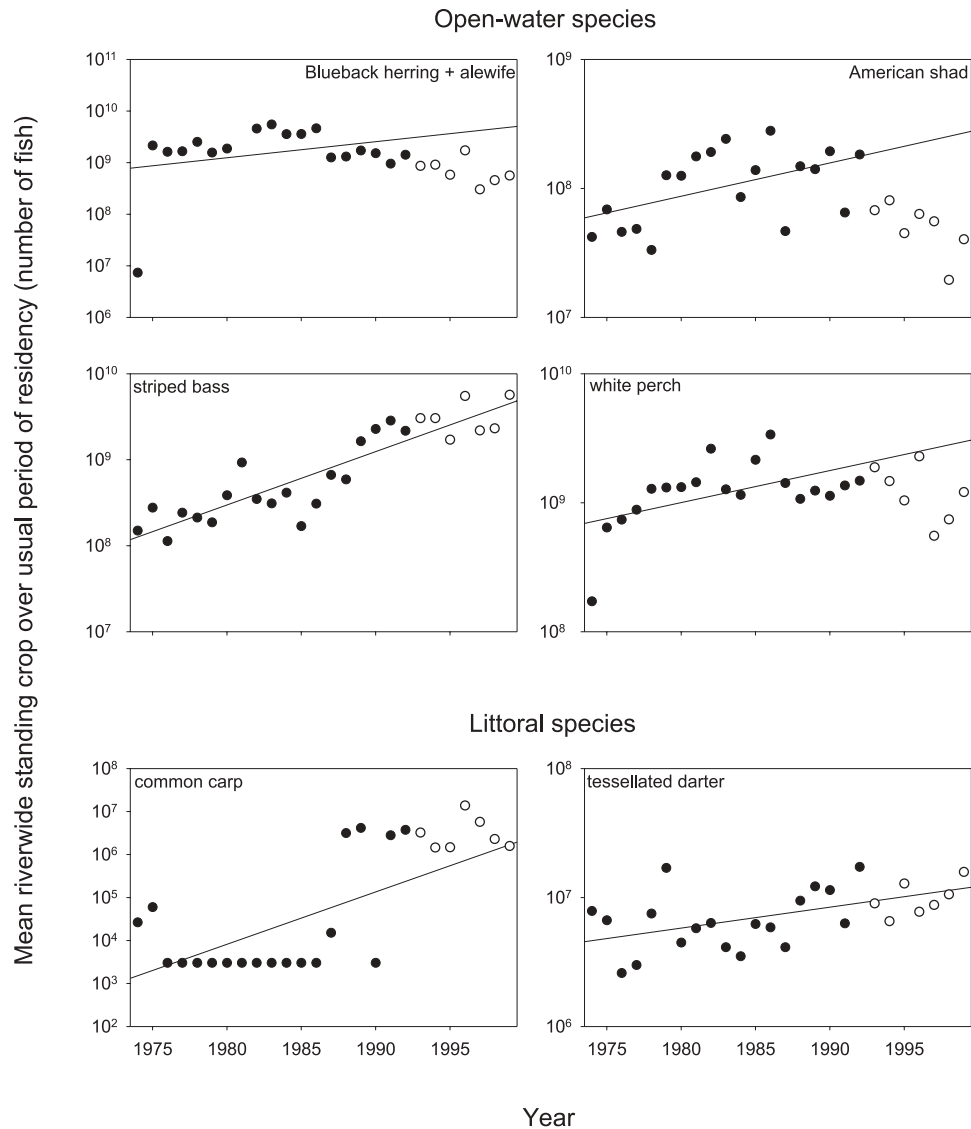


tions of the residuals from a selection of the best models (those with the lowest values of the Akaike information criterion) suggested that the residuals were not significantly temporally autocorrelated.

UBSS data were consistently available only for weeks 32–40 each year, so we restricted our analysis to this period. The dependent variable was the mean riverwide standing crop over weeks 32–40, and the analysis proceeded as for the LRS.

### Distribution

To assess the distribution of fish within the Hudson, we compared the number of fish of each species in the freshwater estuary, which has been heavily affected by the zebra mussel invasion, with that in the brackish estuary, which presumably has been affected little or not at all 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*)

$$D = \log\left(\frac{\text{standing crop above rkm 100}}{\text{standing crop below rkm 100}}\right)$$

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 described for modeling abundance. Inspection of auto-

**Fig. 2.** Abundance of YOY of several species of fish in the Hudson River before (solid circles) and after (open circles) the zebra mussel invasion based on data from the utilities' beach seine survey. The regression lines are fit to preinvasion data. Open circles falling below the line indicate that a species decreased after the zebra mussel invasion, whereas open circles falling above the line indicate that a species increased after the zebra mussel invasion. Note that the *y* axes are logarithmic.
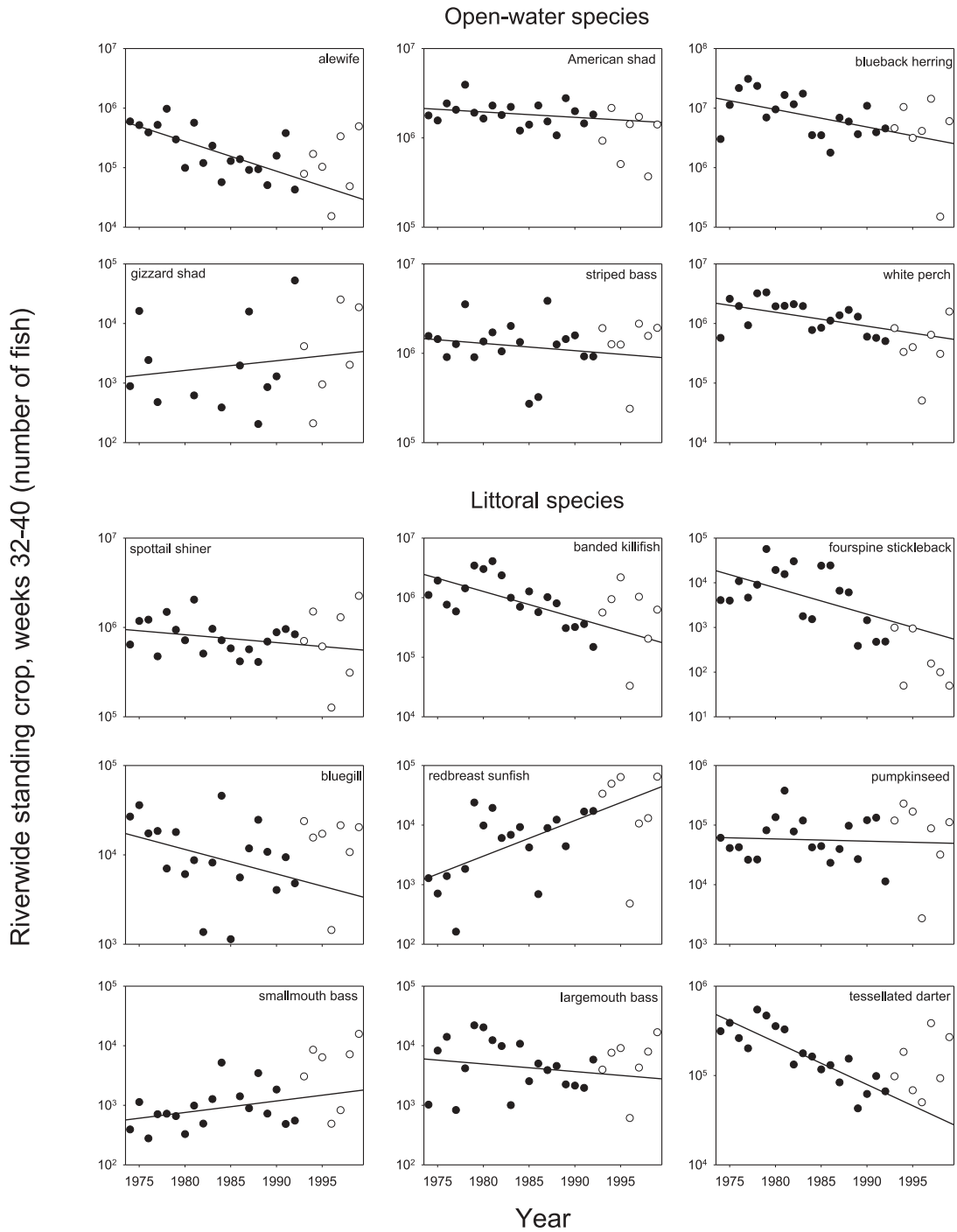


correlation and partial autocorrelation functions of residuals from a selection of the best models showed that temporal autocorrelations were small and insignificant.

### *Apparent growth*

We analyzed trends in apparent growth rates of YOY fish in three data sets: LRS, UBSS, and DECBSS. We define ap-

parent growth rate (*g*) as the rate of change in mean fish size between two successive sampling dates. Thus,

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

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 sepa-

rately (see below). We estimated apparent growth rates only if $n \geq 30$ fish were measured in a given week (we relaxed this standard to $n \geq 10$ fish for alewife in the DECBSS data to allow us to analyze the apparent growth of this less frequently caught species). We modeled growth by multiple regression. Models contained the following independent variables: mean freshwater discharge and water temperature (during the 2 weeks in which growth was estimated), mean body length of fish, and a term to represent zebra mussel effects. This term was 0 in 1974–1992 and below rkm 100 and was 1 only for estimates made above rkm 100 in 1993–1999. Body length was included in all models. Preliminary models showed that population size (i.e., density dependence) was ineffective at predicting growth rates, so this factor was not included in our final models. Growth data from the LRS of post-yolk-sac larvae were not available before 1979 (striped bass) or 1982 (white perch and American shad).

Most of the littoral zone species whose growth rates that we hypothesized would increase were not caught in sufficient numbers to support a complete statistical analysis. We supplemented our formal analysis with a simpler, less formal procedure to try 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 in the upper river (rkm 195–226) for each week (regardless of year) before and after the zebra mussel invasion. That is, we pooled the data for 1985–1992 and for 1993–1999 for each species. We required only five fish to be measured to estimate mean length for a given week over these two time periods. We then simply compared whether mean length was larger for each week before or after the zebra mussel invasion.

For all analyses, we use two levels of statistical significance: the traditional $\alpha = 0.05$ as well as $\alpha = 0.2$. We believe that Type II errors have serious consequences in our study and have followed recent advice to adopt more lenient $\alpha$ values to more nearly balance Type I and Type II errors.

## Results

### Abundance

Many of the fish in the Hudson had temporal trends in abundance prior to or unrelated to the zebra mussel invasion: post-yolk-sac larvae of American shad, common carp, striped bass, white perch, and tessellated darter all have been increasing, whereas 0+ juveniles of alewife, blueback herring, banded killifish, fourspine stickleback, white perch, and tessellated darter all have been decreasing (Table 1; Figs. 1 and 2). Neither temperature nor freshwater flow was significantly correlated with abundance of most fish species in the Hudson (Table 1).

Changes in the estimated riverwide abundance of several species of fish (over what would have been expected given temporal trends, flow, and temperature) coincided with the zebra mussel invasion (Table 1; Figs. 1 and 2). Significant ($p < 0.2$) declines in post-yolk-sac larvae of American shad and white perch and 0+ juveniles of American shad and white perch were associated with the zebra mussel invasion (Fig. 3). In contrast, the zebra mussel invasion was associated with significant increases in 0+ juveniles of banded

**Fig. 3.** Summary of the effects of the zebra mussel invasion on abundance of fish in the Hudson River: (*a*) post-yolk-sac larvae; (*b*) 0+ juveniles. The circle represents the mean effect, and the thick and thin vertical bars represent the 60% and 90% confidence intervals on the mean (i.e., the 20% and 5% significance levels in one-tailed tests). The horizontal lines indicate no change owing to the zebra mussel invasion.
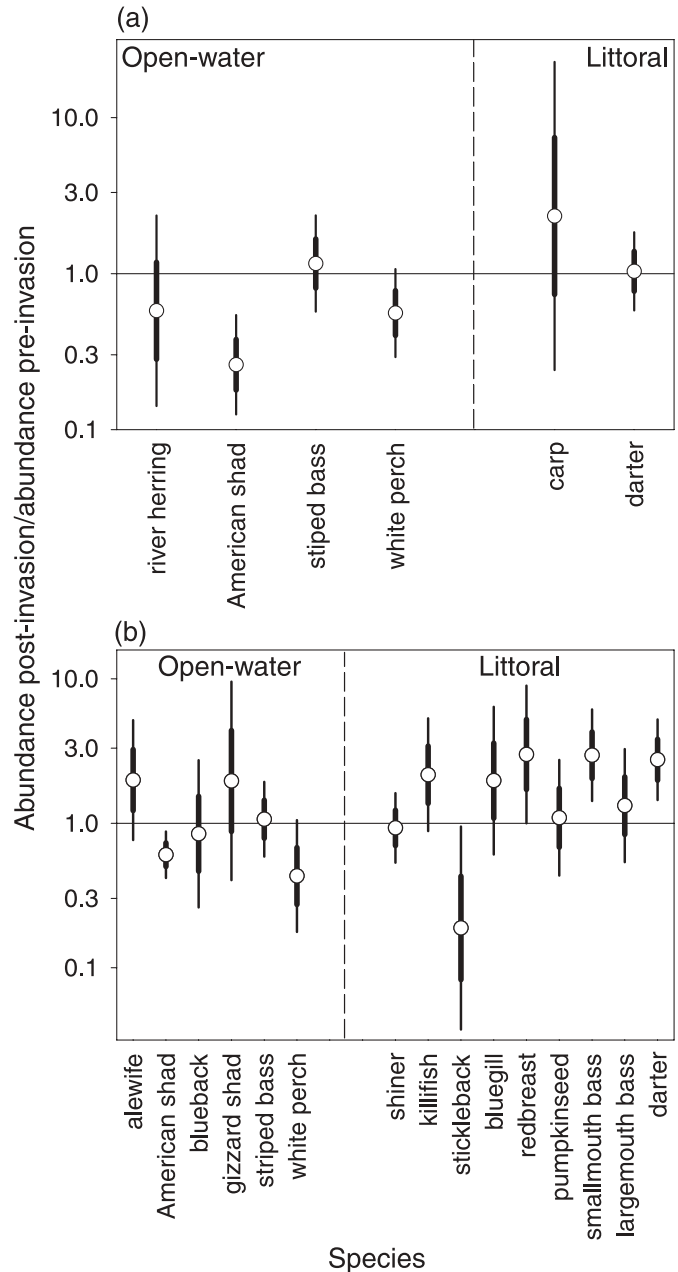


killifish, bluegill, redbreast sunfish, smallmouth bass, and tessellated darter (Fig. 3). Abundance of 0+ juveniles of alewife and fourspine stickleback changed in a direction opposite to our hypotheses. The median change in log-transformed abundance of open-water species was 0.15, corresponding to a decline of 28%, whereas the median log-transformed abundance of littoral species rose by 0.295, corresponding to an

**Table 2.** Statistical models to predict distribution of fish within the Hudson River.

| Species | Year | Flow ($m^3 \cdot s^{-1}$, $\times 10^{-4}$) | Temperature (°C) | Zebra |
|---|---|---|---|---|
| **Post-yolk-sac larvae** | | | | |
| Blueback herring and alewife | 0.26 | 0.86 | 0.29 | 0.31 |
| | 0.004 (0.014) | −15 (5.3) | 0.062 (0.10) | 0.17 (0.22) |
| American shad | 0.56 | 0.93 | 0.27 | 0.35 |
| | 0.026 (0.016) | −22 (7.1) | 0.077 (0.12) | 0.27 (0.30) |
| Striped bass | 0.31 | 0.38 | 0.48 | 0.38 |
| | <0.001 (0.007) | −2.7 (3.6) | 0.045 (0.039) | −0.09 (0.11) |
| White perch | 0.57 | 0.34 | 0.29 | 0.45 |
| | 0.009 (0.006) | 4.0 (3.6) | 0.020 (0.044) | 0.13 (0.11) |
| Common carp | 0.38 | 0.25 | 0.66 | 0.74 |
| | −0.023 (0.084) | 1.5 (12) | 0.21 (0.12) | −0.69 (0.36) |
| Tessellated darter | 0.51 | 0.27 | 0.81 | 0.30 |
| | 0.015 (0.011) | 7.2 (9.6) | 0.15 (0.073) | 0.08 (0.24) |
| **0+ juveniles** | | | | |
| Alewife | 0.58 | 0.51 | 0.29 | 0.38 |
| | 0.033 (0.022) | −19 (16) | 0.055 (0.12) | −0.29 (0.44) |
| American shad | 0.96 | 0.61 | 0.23 | 0.56 |
| | 0.030 (0.012) | −10 (5.4) | 0.023 (0.062) | −0.30 (0.19) |
| Blueback herring | 0.32 | 0.61 | 0.36 | 0.39 |
| | 0.007 (0.019) | −16 (8.7) | 0.16 (0.15) | −0.24 (0.29) |
| Gizzard shad | 0.70 | 0.68 | 0.25 | 0.33 |
| | −0.033 (0.016) | 21 (10) | 0.027 (0.12) | −0.25 (0.34) |
| Striped bass | 0.96 | 0.23 | 0.28 | 0.25 |
| | 0.026 (0.008) | −1.2 (5.8) | 0.041 (0.057) | −0.008 (0.20) |
| White perch | 0.38 | 0.34 | 0.46 | 0.39 |
| | 0.008 (0.009) | −4.8 (6.1) | 0.068 (0.055) | 0.14 (0.15) |
| Spottail shiner | 0.57 | 0.75 | 0.60 | 0.29 |
| | 0.021 (0.013) | −16 (7.2) | 0.13 (0.073) | −0.11 (0.26) |
| Banded killifish | 0.94 | 0.29 | 0.25 | 0.97 |
| | 0.040 (0.014) | −6.0 (2.7) | −0.039 (0.074) | 0.74 (0.25) |
| Fourspine stickleback | 0.60 | 0.31 | 0.45 | 0.74 |
| | −0.047 (0.033) | 11 (15) | −0.18 (0.14) | 0.86 (0.52) |
| Bluegill | 0.30 | 0.89 | 0.25 | 0.76 |
| | 0.012 (0.022) | −26 (9.0) | 0.053 (0.11) | 0.53 (0.24) |
| Redbreast sunfish | 0.89 | 0.84 | 0.26 | 0.31 |
| | 0.073 (0.025) | −39 (14) | −0.086 (0.17) | 0.51 (0.59) |
| Pumpkinseed | 0.99 | 0.47 | 0.28 | 0.27 |
| | 0.051 (0.016) | −13 (7.8) | 0.063 (0.089) | −0.006 (0.38) |
| Smallmouth bass | 0.53 | 0.49 | 0.25 | 0.95 |
| | −0.029 (0.021) | −14 (9.5) | −0.041 (0.10) | 0.76 (0.33) |
| Largemouth bass | 0.68 | 0.66 | 0.25 | 0.43 |
| | 0.025 (0.035) | −14.5 (7.0) | 0.038 (0.082) | 0.29 (0.22) |
| Tessellated darter | 0.76 | 0.40 | 0.26 | 0.31 |
| | 0.018 (0.011) | −7.1 (3.8) | −0.007 (0.065) | 0.08 (0.20) |

**Note:** The dependent variable is the log(number of fish upriver of rkm 100/number of fish downriver of rkm 100); thus, positive values indicate a predominance of fish in the freshwater part of the estuary and negative values indicate a predominance of fish in the brackish part of the estuary. The 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. Year is number of years since 1974.

increase of 97%. Fish abundance changed consistent with our hypotheses; some of these changes were large (>50%).

### Distribution

The distribution of several fish species shifted significantly upriver over time (Table 2; Figs. 4 and 5). In addition, freshwater flow was significantly correlated with distribution of many species in the Hudson. Generally, populations were centered further downriver in years of high flow (Table 2). The gizzard shad showed the opposite pattern, with populations centered further upriver in high-flow years.

The zebra mussel invasion was associated with changes in the distributions of several fish species (Table 2; Fig. 4). Post-yolk-sac larvae of common carp showed a significant distributional change associated with the zebra mussel invasion in a direction opposite to that we postulated (Fig. 4).

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**Fig. 4.** Distribution of post-yolk-sac larvae of several species of fish in the Hudson River before (solid circles) and after (open circles) the zebra mussel invasion based on data from the utilities' long-river survey. The regression lines are fit to preinvasion data. Open circles falling below the line indicate that an increased proportion of the population was found downriver after the zebra mussel invasion, whereas open circles falling above the line indicate that an increased proportion of the population was found upriver after the zebra mussel invasion.
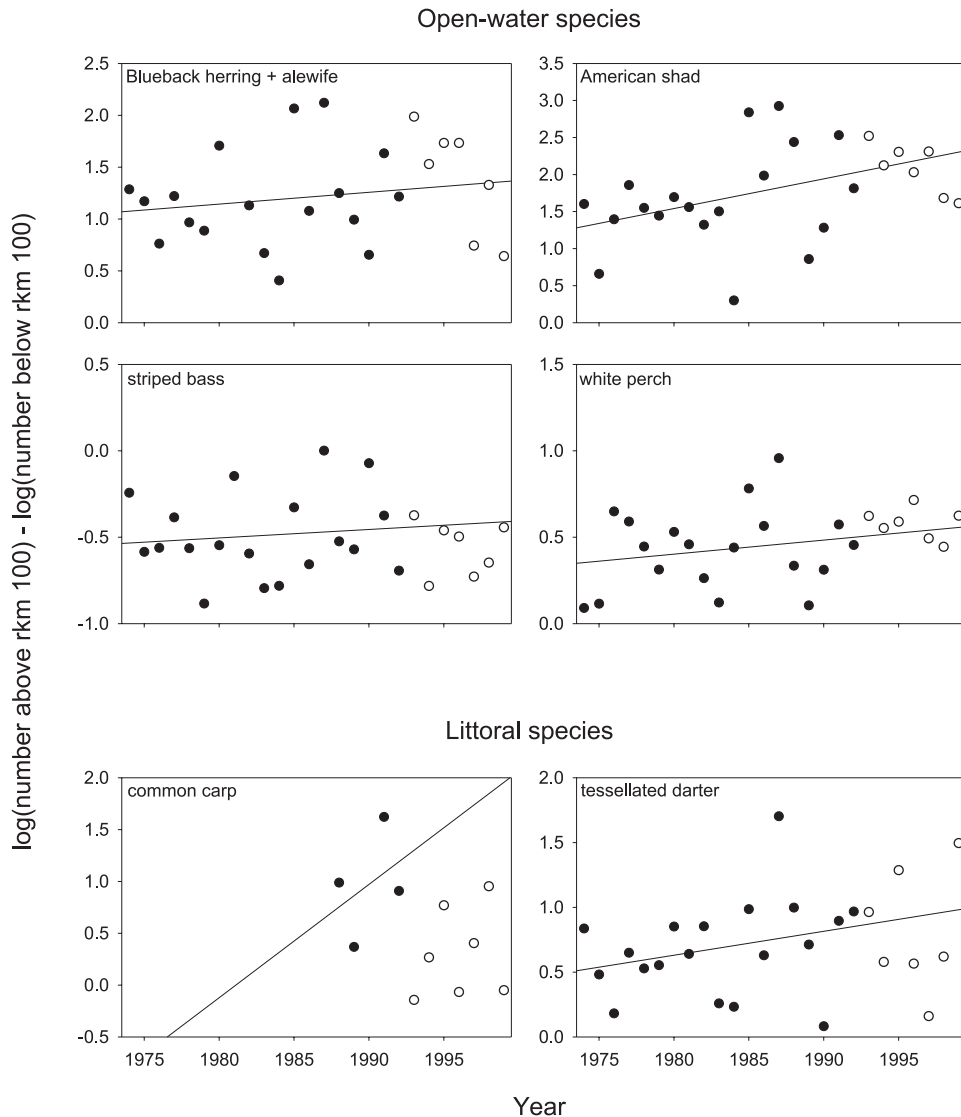


Among 0+ juveniles, populations of almost all littoral species were centered further upriver after the zebra mussel invasion; this change was significant ($p < 0.2$) for banded killifish, fourspine stickleback, bluegill, redbreast sunfish, smallmouth bass, and largemouth bass (Fig. 5). Although populations of post-yolk-sac larvae of clupeids were centered slightly further upriver after the zebra mussel invasion, clupeid 0+ juveniles tended to occur further downriver after the invasion. Both post-yolk-sac larvae and 0+ juveniles of white perch tended to occur further upriver after the zebra mussel invasion, contrary to our hypothesis. While distributional changes among post-yolk-sac larvae were not consistent, the median distributional index for 0+ juveniles of open-water species dropped by 0.24, indicating that the ratio (freshwater population/brackish water population) fell by 43%, while the median distributional index for littoral species rose by 0.51, indicating that the ratio of freshwater population to

brackish water population rose by 224%. Thus, we observed shifts in the distribution of 0+ juveniles within the river that were large and consistent with the hypothesized zebra mussel effect (Fig. 6).

**Apparent growth**

We were able to test for effects of the zebra mussel invasion on apparent growth of fish in 14 cases (Table 3). In nearly all cases, apparent growth changed in the direction that we postulated; the change was significant ($p < 0.2$) in nine of these cases. We observed no significant changes in apparent growth that contradicted our hypotheses (Fig. 7). In many cases, the changes in apparent growth rates were large (Table 4; Fig. 7). Median apparent growth of open-water species, averaged over all life stages and species, fell by 17%, while apparent growth of the single littoral species rose by 12%. Other important determinants of apparent

**Fig. 5.** Distribution of YOY of several species of fish in the Hudson River before (solid circles) and after (open circles) the zebra mussel invasion based on data from the utilites' beach seine survey. The regression lines are fit to preinvasion data. Open circles falling below the line indicate that an increased proportion of the population was found downriver after the zebra mussel invasion, whereas open circles falling above the line indicate that an increased proportion of the population was found upriver after the zebra mussel invasion.
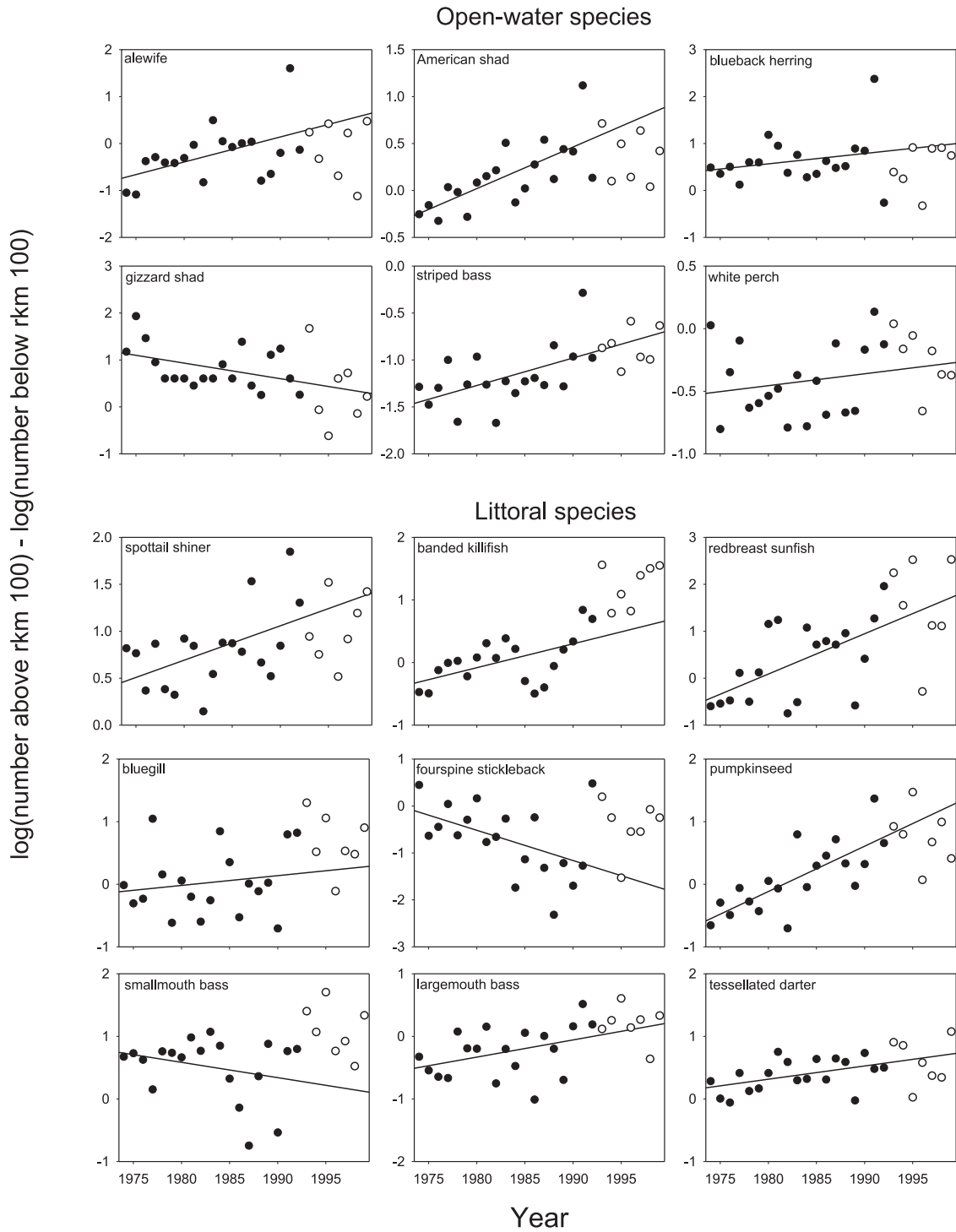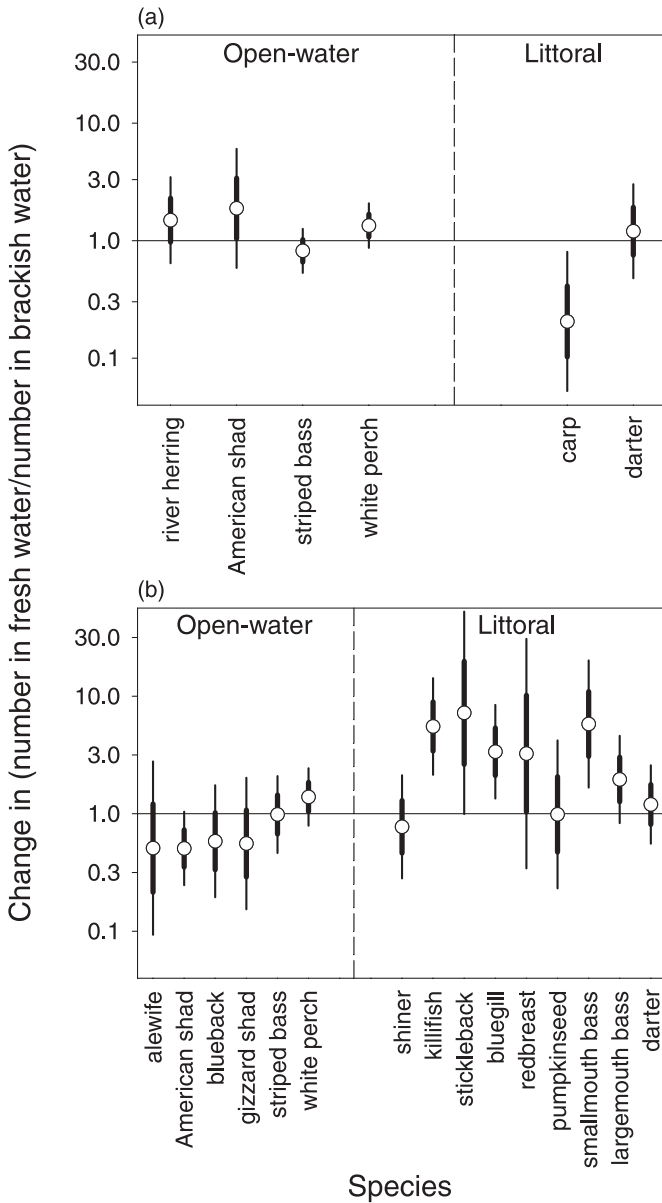


growth rates were fish size (strongly negative) and freshwater flow (negative); temperature and region occasionally were important.

The less formal analysis of changes in fish lengths also supported the hypothesis of differential impacts on apparent growth in different groups of fish species. For *Alosa* spp. (shad and herrings) and *Morone* spp. (white perch and striped bass),

we found that preinvasion lengths were greater than post-invasion lengths in 68 of 86 cases, while for the very few littoral species other than spottail shiner for which we had data (yellow bullhead (*Ameiurus natalis*), largemouth and smallmouth bass, and yellow perch), we found that post-invasion lengths were greater in five of nine cases. A $\chi^2$ analysis of these data gives a value of 11.97 ($p = 0.0005$),

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**Fig. 6.** Summary of the effects of the zebra mussel invasion on distribution of fish in the Hudson River: (*a*) post-yolk-sac larvae; (*b*) 0+ juveniles. The circle represents the mean effect, and the thick and thin vertical bars represent the 60% and 90% confidence intervals on the mean (i.e., the 20% and 5% significance levels in a one-tailed test). The horizontal lines indicate no change owing to the zebra mussel invasion.



water fishes such as *Alosa* spp. and *Morone* spp. declined in abundance, had their populations shift downriver away from the infested part of the Hudson, and suffered declines in apparent growth rates. At the same time, littoral zone species (centrarchids and several others) showed exactly the opposite effects. These changes are highly consistent with our hypotheses about the effects of a changed forage base on the fish community.

To the extent that we can discern differential effects among species, it appears that *Alosa* spp. and centrarchids responded most strongly to the zebra mussel invasion (although in opposite directions), while the response of *Morone* spp. and littoral species other than centrarchids was more muted. Although our estimates of effect sizes are imprecise, many of the changes associated with the zebra mussel invasion were large. Many of the changes in fish abundance and distribution were >50% and many of the changes in growth rates were >20% of preinvasion growth rates. We do not have the information needed to calculate changes in the overall biomass or production of the Hudson River fish community. Because open-water species are much more abundant than the littoral species, overall biomass and production of YOY fish in the Hudson probably fell after the zebra mussel invasion.

Two other changes could have affected fish populations in the Hudson during 1974–1999. Improving environmental quality around Albany (rkm 228) and New York City (~rkm 10) made these areas more suitable for fish. Changes in harvest of two major anadromous species outside the Hudson itself (increased protection of immature striped bass in ocean waters in 1984–1995 (Kahnle and Hattala 2001) and rising offshore catches of American shad starting in the mid-1980s (Hattala and Kahnle 1998)) would be expected to affect populations in the Hudson. While we saw evidence that these changes affected fish populations in the Hudson, it is difficult to see how these changes could have caused the complex pattern of change that we attributed to the zebra mussel invasion. The timing, direction of changes, geographical pattern of changes, multiple variables involved, and differential effects on open-water versus littoral species are highly consistent with a zebra mussel effect but not with these other causes.

### How strong is the connection between suspension-feeding bivalves and fish?

Changes in bivalve populations can cause large changes in phytoplankton in lakes, rivers, estuaries, and shallow coastal waters (e.g., Cohen et al. 1984; Dame 1996; Makarewicz et al. 1999). In some cases, these effects have been shown to reach primary consumers such as zooplankton (e.g., Kimmerer et al. 1994; Pace et al. 1998) and zoobenthos (e.g., Stewart and Haynes 1994; Nalepa et al. 1998), but most studies of the zebra mussel invasion have reported small or no effects on the fish community. The two studies that did find effects on fish were contradictory, with Karataev and Burlakova (1995) reporting increases in fish populations but Ryan et al. (1999) reporting decreases in fish populations.

Why do bivalve effects on fish vary so much among studies? Some of the differences between our findings of large effects and prior studies that reported little or no effect may

supporting our hypothesis that the apparent growth of littoral zone fishes increased after the zebra mussel invasion at the same time that apparent growth of open-water fishes decreased.

## Discussion

### Overview of effects in the Hudson

The zebra mussel invasion was associated with large, pervasive changes in YOY fish in the Hudson River. Open-

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

| Species | Body length | Flow (m$^3$·s$^{-1}$, ×10$^{-5}$) | Temperature (°C) | Region | Zebra |
|---|---|---|---|---|---|
| **Post-yolk-sac larvae** | | | | | |
| American shad | — | 0.41 | 1.00 | 0.38 | 0.28 |
| | –0.025 (0.003) | –4.1 (3.5) | 0.024 (0.005) | –0.018 (0.018) | –0.006 (0.018) |
| Striped bass | — | 0.85 | 1.00 | 0.30 | 0.27 |
| | –0.021 (0.003) | –7.1 (3.1) | 0.023 (0.003) | 0.007 (0.013) | 0.000 (0.017) |
| White perch | — | 0.42 | 1.00 | 0.35 | 0.37 |
| | –0.038 (0.004) | –2.7 (2.4) | 0.026 (0.003) | –0.010 (0.012) | –0.014 (0.015) |
| **0+ juveniles** | | | | | |
| Alewife (UBSS) | — | 0.51 | 0.31 | 0.63 | 0.36 |
| | –0.021 (0.0007) | –12 (8.1) | 0.003 (0.006) | –0.028 (0.017) | –0.011 (0.019) |
| Alewife (DECBSS) | — | 0.81 | 0.33 | 0.32 | 0.62 |
| | –0.001 (0.0005) | –13 (5.9) | –0.0018 (0.0032) | –0.0037 (0.0083) | –0.020 (0.012) |
| American shad (UBSS) | — | 0.32 | 0.80 | 0.30 | 0.60 |
| | –0.0020 (0.0006) | –12 (8.9) | 0.0040 (0.0056) | –0.0028 (0.018) | –0.016 (0.018) |
| American shad (DECBSS) | — | 0.99 | 0.47 | 0.42 | 0.35 |
| | –0.0018 (0.0002) | –6.7 (2.1) | –0.0012 (0.0009) | –0.0028 (0.0025) | –0.0038 (0.0046) |
| Blueback herring (UBSS) | — | 0.70 | 0.28 | 0.33 | 0.84 |
| | –0.0021 (0.0005) | –7.4 (3.9) | 0.00018 (0.0014) | –0.0054 (0.0097) | –0.018 (0.008) |
| Blueback herring (DECBSS) | — | 0.40 | 0.30 | 0.28 | 0.49 |
| | –0.0017 (0.0003) | –3.1 (2.9) | 0.00059 (0.0012) | –0.00028 (0.0038) | –0.0093 (0.0068) |
| Striped bass (UBSS) | — | 0.93 | 0.84 | 0.31 | 0.69 |
| | –0.0033 (0.0002) | –7.7 (2.9) | –0.0027 (0.0011) | 0.0008 (0.008) | –0.014 (0.0077) |
| Striped bass (DECBSS) | — | 0.28 | 0.62 | 0.99 | 0.96 |
| | –0.0034 (0.0003) | –0.9 (4.3) | –0.0028 (0.0016) | 0.015 (0.0043) | –0.025 (0.0086) |
| White perch (UBSS) | — | 0.46 | 0.51 | 0.30 | 0.29 |
| | –0.0033 (0.0002) | –2.9 (2.3) | 0.0012 (0.0009) | 0.0028 (0.0050) | 0.0028 (0.0062) |
| White perch (DECBSS) | — | 0.93 | 0.35 | 0.44 | 0.70 |
| | –0.0027 (0.0002) | –9.8 (3.7) | 0.00098 (0.0012) | 0.0039 (0.0034) | –0.010 (0.0055) |
| Spottail shiner (UBSS) | — | 0.31 | 0.51 | 0.28 | 0.47 |
| | –0.0034 (0.0003) | –2.8 (4.7) | –0.0026 (0.0018) | –0.0016 (0.0095) | 0.0096 (0.0074) |

**Note:** The 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's beach seine survey of 0+ juveniles.

be due to differences in statistical power among the analyses. However, there is every reason to expect that the effects of bivalves truly differ across ecosystems.

The impact of bivalves is propagated through the ecosystem, where it may be damped or amplified. Several pathways link suspension-feeding bivalves to fish, and the strength of each of these pathways varies across ecosystems. Neglecting direct effects, in which bivalves serve as food (e.g., French 1993; French and Bur 1996) or spawning sites (e.g., Chatelain and Chabot 1983; Reynolds et al. 1997) for fish, there are three indirect pathways leading from suspension-feeding bivalves to fish (Fig. 8). For simplicity, we describe the changes expected from an increase in bivalve populations, but the opposite changes may be induced by a decline in bivalve populations (e.g., the decline of oysters in Chesapeake Bay (Newell 1988; Ulanowicz and Tuttle 1992)).

### *Links to fish via phytoplankton and edible consumers*

Bivalve grazing may reduce phytoplankton, leading to losses of edible consumers and then fish (arrows 1, 3, and 6 in Fig. 8). This presumably is the pathway responsible for the large declines in abundance and apparent growth rates of open-water fishes in the Hudson. To affect fish populations

by this pathway, bivalve grazing must be large enough to reduce biomass or production of phytoplankton. Specifically, grazing rates must be large compared with phytoplankton growth and other loss terms (i.e., advection, sinking, grazing by other suspension-feeders (Dame 1996; Strayer et al. 1999)). Further, the bivalve population must coincide in space and time with areas and periods of phytoplankton growth. Finally, if the increase in light and nutrients resulting from bivalve grazing stimulates the growth of remaining phytoplankton or increases the depth of the photic zone (Idrisi et al. 2001), there may be little change in phytoplankton biomass, and phytoplankton production may even increase (Caraco et al. 1997).

All three of these conditions favored large losses of phytoplankton in the Hudson. Zebra mussel grazing is much larger than advective losses or grazing by other suspension-feeders (Strayer et al. 1999), and it is focused precisely on those areas of the river that formerly supported the greatest phytoplankton growth (Caraco et al. 1997). The increases in dissolved nutrients that accompanied the zebra mussel invasion in the Hudson (Caraco et al. 1997) did not stimulate growth of the light-limited phytoplankton (Cole et al. 1992), and light penetration increased only modestly because trans-

**Fig. 7.** Summary of the effects of the zebra mussel invasion on apparent growth of fish in the Hudson River. The circle represents the mean effect, and the wide and thin vertical bars represent the 60% and 90% confidence intervals on the mean (i.e., the 20% and 5% significance levels in a one-tailed test). The horizontal lines indicate no change owing to the zebra mussel invasion. For comparison, mean apparent growth rates before the zebra mussel invasion were 0.11·week$^{-1}$ for post-yolk-sac larvae and 0.06·week$^{-1}$ for 0+ juveniles. LRS, long-river survey; DECBSS, Department of Environmental Conservation's beach seine survey; UBSS, utilities' beach seine survey.
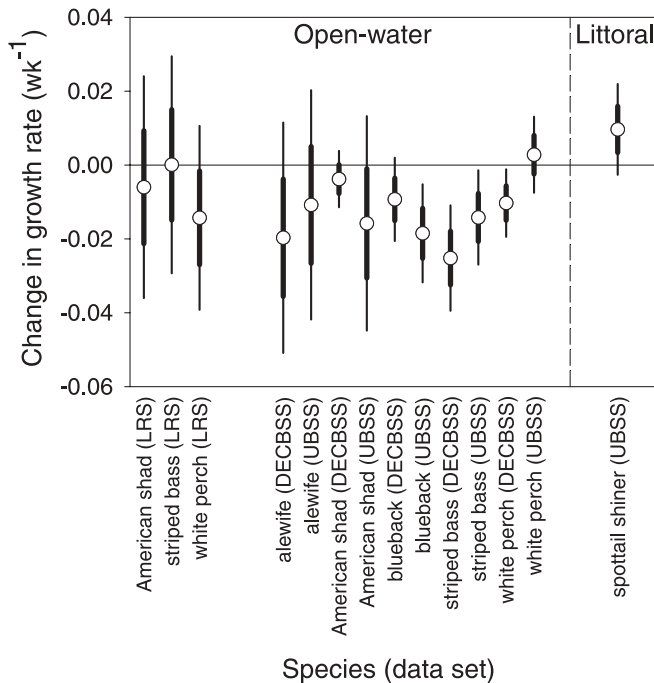


parency of the Hudson is controlled chiefly by inedible silt particles. Consequently, the feedback loop from the grazer to the phytoplankton was weak, and phytoplankton biomass fell steeply (80%) (Caraco et al. 1997).

Conditions in other lakes and rivers invaded by zebra mussels often lead to smaller impacts on phytoplankton (Table 5). Populations of zebra mussels often are too small to control phytoplankton (>50% of European lakes invaded by zebra mussels had lakewide mean densities of <300·m$^{-2}$ and estimated filtration rates of <15% of the mixed zone/day (from Strayer 1991)). In stratified or large lakes, spatial separation between zebra mussels and phytoplankton provides a refuge for phytoplankton. This spatial separation probably is responsible for the modest losses of phytoplankton in the offshore waters of the Great Lakes (Makarewicz et al. 1999). Finally, increased light and nutrients from grazing substantially increase growth rates of remaining phytoplankton or the depth of the photic zone in many lakes (e.g., Fahnenstiel et al. 1995a; Idrisi et al. 2001).

To the extent that bivalve populations reduce phytoplankton, zooplankton and zoobenthos that depend on phytoplankton should decrease. Declines in zooplankton (e.g., Beeton and Hageman 2001) and zoobenthos (e.g., Dermott and Kerec 1997; Nalepa et al. 1998; Strayer and Smith 2001) following the zebra mussel invasion have been attributed to this mech-

anism. Thus, the size and spatial distribution of the zebra mussel population and the nature of factors that limit plankton determine whether bivalves and fish are strongly or weakly linked by this pathway.

### *Links via biodeposits and shelter in zebra mussel beds*

The food (feces and pseudofeces) and shelter provided by zebra mussel beds may lead to large increases in populations of forage invertebrates (e.g., amphipods and chironomid midges) living among those beds (e.g., Ricciardi et al. 1997; Stewart et al. 1998). These increases in forage invertebrates may benefit fish, although the structural complexity provided by bivalve beds may make fish foraging inefficient (Stewart et al. 1999; Mayer et al. 2001), so fish may not receive the full benefit of this increased forage. This pathway (arrows 5 and 6 in Fig. 8) does not require that the bivalve population be large enough to deplete phytoplankton but merely that either biodeposition or shelter provided by the bivalves be large enough locally to benefit invertebrates. Presumably, the larger the area of sediment covered by bivalves, the larger the effect on fish. This pathway should benefit fish that feed on benthic invertebrates. It is not clear if this pathway is important in nature; we know of no examples of changes in fish that can be clearly attributed to this mechanism.

### *Links via enhanced littoral production*

The loss of phytoplankton may clear the water enough to benefit submersed macrophytes and attached algae, the invertebrates that feed on or live among these plants, and ultimately fish (arrows 1, 2, 4, and 6 in Fig. 8). For this pathway to be important, it is first necessary for the bivalve population to significantly reduce phytoplankton (see discussion above). Further, this pathway will be important only if macrophytes and attached algae are light limited and the ecosystem contains substantial areas of sediment lying in the photic zone. This pathway should benefit fish that live among macrophytes and feed on benthic and epiphytic invertebrates and presumably is behind the observed increases in abundance and growth of littoral fishes (e.g., centrarchids) in the Hudson.

The strength of this pathway should vary widely across ecosystems. We expect to see large changes in littoral fish following the zebra mussel invasion in shallow, clear lakes and rivers and much smaller effects in deep lakes and rivers in which light penetration is controlled by inedible particles (e.g., silt). Although the increase in light penetration that accompanied the zebra mussel invasion of the Hudson was modest (~45%; Caraco et al. 1997) and only ~15% of the Hudson is shallow enough to support littoral production (Findlay et al. 2004), littoral primary production may have doubled (Caraco et al. 2000). In lakes or rivers where large areas of the bottom are at or near the limit of the photic zone, the increase in benthic primary production following bivalve invasion may be even larger (e.g., Fahnenstiel et al. 1995a; Skubinna et al. 1995).

### *Net effects of bivalves on fish*

The net effect of suspension-feeding bivalves on fish populations depends on the strength and balance among all of the interaction pathways. In general, planktivorous fish should

**Table 4.** Summary of analyses of effects of the zebra mussel invasion on apparent growth rates of fish in the Hudson River.

| Species | Mean growth rate (week$^{-1}$) before invasion | Change (week$^{-1}$) | Change (%) |
|---|---|---|---|
| **Post-yolk-sac larvae** | | | |
| American shad | 0.105 | –0.006 | –6 |
| Striped bass | 0.119 | 0.00006 | 0 |
| White perch | 0.118 | –0.014 | –12 |
| **0+ juveniles** | | | |
| Alewife (UBSS) | 0.056 | –0.011 | –19 |
| Alewife (DECBSS) | 0.051 | –0.020 | –39 |
| American shad (UBSS) | 0.071 | –0.016 | –22 |
| American shad (DECBSS) | 0.054 | –0.004 | –7 |
| Blueback herring (UBSS) | 0.037 | –0.018 | –50 |
| Blueback herring (DECBSS) | 0.037 | –0.009 | –25 |
| Striped bass (UBSS) | 0.084 | –0.014 | –17 |
| Striped bass (DECBSS) | 0.070 | –0.025 | –36 |
| White perch (UBSS) | 0.086 | 0.003 | +3 |
| White perch (DECBSS) | 0.069 | –0.010 | –15 |
| Spottail shiner (UBSS) | 0.079 | 0.010 | +12 |

**Note:** The mean growth rates are simple unweighted means from the preinvasion period and are given to indicate the size of the changes attributed to the zebra mussel invasion by the regression models. UBSS, utilities' beach seine survey of 0+ juveniles; DECBSS, Department of Environmental Conservation's beach seine survey of 0+ juveniles.

**Fig. 8.** Schematic diagram of indirect interactions that link bivalve populations to fish.
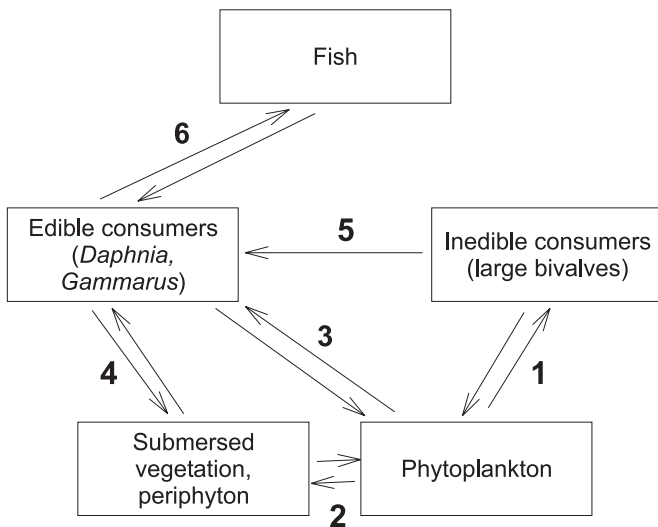


suffer and littoral zone fish should benefit, as was seen in the Hudson, but the size of these changes may vary widely. It will be difficult to predict the responses of fish that feed on open-water benthos (which may rise or fall with rising bivalve populations), fish that are flexible enough to exploit various kinds of food, and the overall production or biomass of all fish species combined. Increasing populations of suspension-feeding bivalves could have net positive or negative effects on fish populations, shift the composition but not biomass of the fish community, or have no effect. Consequently, instead of simply extrapolating from our study to predict the response of fish to changes in suspension-feeders

in other ecosystems, it is necessary to consider the interaction pathways that link suspension-feeding bivalves to fish.

Table 5 suggests that the effects of zebra mussels on fish and zoobenthos are more variable across ecosystems than the effects on phytoplankton. The indirect effects of alien species (or any species) probably are usually more variable and less predictable than their direct effects because of the variable modulation of effects through different ecosystems.

**Analytical issues**

Analyzing the response of fish to the zebra mussel invasion (or any perturbation) in a large ecosystem presents analytical problems. Because of natural variability in fish population size, distribution, and somatic growth and the difficulty in estimating these variables accurately, analyses of temporal or spatial changes in fish populations are plagued with large errors. Consequently, the statistical power to detect zebra mussel effects may be low, and estimates of effect sizes usually are imprecise. In our analyses, changes in abundance of <1.5-fold usually were too small to attain statistical significance even at $p = 0.2$. Likewise, the thresholds for statistical detection of effects (at $p = 0.2$) in fish distribution and apparent growth were ~1.7-fold and ~0.011·week$^{-1}$, respectively. Changes below these thresholds certainly could be of interest, but our analysis was simply not powerful enough to detect them statistically.

Two strategies to improve the detection of impacts on fish communities are to use variables with high signal to noise ratios and to use long runs of data. Apparent growth rates were a more sensitive indicator of zebra mussel impacts than fish distribution or population size (64% of tests of growth rates were significant at $p = 0.2$ compared with 33% and 43% for abundance and distribution, respectively). Growth rates may be a good indicator because average fish size is

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**Table 5.** Effects of the zebra mussel invasion on food webs in several lakes and rivers where fish populations have been studied.

| Site | Phytoplankton biomass | Zooplankton biomass | Zoobenthic biomass | Fish response |
|---|---|---|---|---|
| Rice Lake, Ontario | No change | No data | No change? | Increase in pumpkinseed growth; no changes in growth of bluegill or yellow perch |
| Lake Erie (offshore) | –43% to no change | –20% to no change | +4–82% | Few changes in growth or abundance of any fish species |
| Oneida Lake, New York | –25% | No change | Increase in shallow bays only | Modest changes in growth and diet of yellow perch |
| Long Point Bay, Lake Erie | No data | No data | No data | Declines in abundance of five species |
| Lukomskoe Lake, Belarus | –72% | –60% | +1200% | Very large increase (>200%) in fish biomass; increase in benthic species |
| Hudson River, New York | –80% | –70% | –40% | Widespread decreases in growth and abundance of open-water species; corresponding increases in littoral species; changes in fish distribution |

**Note:** Zoobenthic biomass excludes large bivalves (Unionidae and Dreissenidae); data on Lake Erie zooplankton are based on deviation from expected biomass as predicted from total phosphorus (Johannsson et al. 1999). From Karataev and Burlakova (1995), Caraco et al. (1997), Mayer (1998), Pace et al. (1998), Johannsson et al. (1999, 2000), Makarewicz et al. (1999), Mercer et al. (1999), Idrisi et al. (2001), Strayer and Smith (2001), and Mayer et al. (2002).

easier to estimate precisely than are fish numbers or distribution and because covariates (fish length, freshwater flow, and temperature) can account for some of the variation in apparent growth rates. An alternative explanation, that apparent growth rates were affected more severely than population size or distribution, seems not to be true: the median absolute change in apparent growth rates was 16%, whereas the median absolute change in abundance was 57%.

The second strategy to increase statistical power is to increase the length of the data record. Most published analyses of zebra mussel effects on fish used fewer than 5 years each of pre- and post-invasion data, which reduced statistical power to undesirable levels. Unfortunately, long runs of data are expensive to collect and often do not exist. Further, as the length of the data record increases, so does the possibility that the study system was subject to important changes other than the zebra mussel invasion, which may confound the analysis. Thus, practical problems limit the extent to which statistical power may be increased by lengthening data runs.

### Implications for understanding and managing fish populations in the Hudson

Our analyses shed light on processes other than the zebra mussel invasion that may affect fish populations in the Hudson. Years of high freshwater flow were associated with slow apparent growth and downriver movement of fish populations. Wet years are years of poor development of plankton in the Hudson because of light limitation and high advective losses (Caraco et al. 1997; Pace and Lonsdale 2004). Presumably, this low plankton production, possibly along with lower light levels, translates to poor feeding conditions for young fish in the freshwater part of the river.

In addition to the large distributional shifts associated with the zebra mussel invasion, the distribution of most species of fish shifted upriver before the zebra mussel invasion. This upriver movement of fish populations may have been a response to the improvement of upriver habitats associated with the control of pollution from the Albany metropolitan area in the mid- and late 1970s.

Finally, our results have important implications for the management of fish populations in the Hudson. The changes that we observed in abundance, distribution, and growth of young fishes may well translate into changes in adults, the life stage of interest to the multimillion dollar recreational and commercial fisheries. The changes that we observed may lead to fewer adults of species such as American shad and striped bass and more adults of species such as redbreast sunfish and black basses in the Hudson. The magnitude and persistence of any such changes are unclear at this point.

The zebra mussel invasion has imposed an additional important constraint on fish populations in the Hudson that limits the scope of possible management activities. For instance, the sharply reduced recruitment of American shad limits the range of possible combinations of recreational harvest, commercial harvest, and habitat management that will result in a sustainable fishery for this species. Management of the affected fish species will become more difficult.

Further, changes in the dynamics of fish populations in the Hudson will make it more difficult to predict the impacts of management actions. Management of anadromous fish in the Hudson relies on monitoring abundance or relative abundance of different life stages or ages, monitoring of survival between life stage or age, and modeling the interactions among these parameters. Where possible, information on interactions between fish and characteristics of the environment such as flow or water temperature is added. Such models allow us to identify optimum characteristics of fish populations and harvest and to predict the implications of various harvest options on these characteristics. These population models are based on a long time series of data and assume some sort of average steady state in intra- and inter-specific interactions. When the ability of a system to support young fish changes, the steady state changes. This introduces added uncertainty to fish population models and models become

less able to predict future conditions. This in turn complicates the crafting and evaluation of management measures.

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