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Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: the beginning of the end or the end of the beginning?

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Abstract. The long-term effects of an alien species may differ from transient effects that occur shortly after its invasion of a new ecosystem. Conservationists fear that the invasion of North America by the zebra mussel since 1985 may lead to the extinction of many populations and species of native bivalves. The appearance of zebra mussels in the Hudson River estuary in 1991 was followed by steep declines (65–100%) in population size of all species of native bivalves between 1992 and 1999. The body condition of all unionids and growth and recruitment of young unionids also declined significantly. Initial declines in population size and body condition were correlated primarily with the filtration rate of the zebra mussel population but not with fouling of native bivalves by zebra mussels. However, samples taken since 2000 have shown that populations of all 4 common native bivalves have stabilized or even recovered, although the zebra mussel population has not declined. The mechanisms underlying this apparent reversal of fortune are not clear. Recruitment and growth of young mussels have shown limited recovery, but the body condition of adults has not. We found no evidence that spatial refuges contributed to this reversal of population declines. Simple statistical models project now that native bivalves may persist at population densities about an order of magnitude below their preinvasion densities. These results offer a slender hope that zebra mussels may coexist with unionids and sphaeriids in North America, as they do in Europe.

Key words: invasive species, alien species, nonindigenous species, biodiversity, long-term, estuary, river, extinction, transient dynamics.

Alien species can cause large changes to the biodiversity, biogeochemistry, and economy of areas that they invade (e.g., Cox 1999, Mack et al. 2000, Mooney et al. 2005) and are now one of the most important ways by which humans affect the Earth's ecosystems. These changes often are assumed to be permanent, irreversible, or at least long-lasting, although several common ecological and evolutionary processes should modulate the effects of alien species across time (Strayer et al. 2006). Distinguishing between long-lasting and transient effects of alien species and describing the dynamics of transient effects is necessary to understand and manage the consequences of invasions by alien species.

One of the most dramatic and dismaying effects of the zebra mussel (*Dreissena polymorpha*) invasion of North America has been the fouling and destruction of native bivalve populations. Photographs of unionid mussels covered by zebra mussels have appeared in both the popular and scientific press, and many publications (e.g., Schloesser and Nalepa 1994, Nalepa et al. 1996, Ricciardi et al. 1996) documented the decline and disappearance of unionid populations in the first few years after the zebra mussel invasion. Indeed, one model (Ricciardi et al. 1998) suggested that the zebra mussel invasion would drive ~60 native North American species of unionids into extinction. Although much less well studied, populations of sphaeriid clams also have declined since the zebra mussel invasion (Lauer and McComish 2001, Lozano et al. 2001, Strayer and Smith 2001). Most American scientists have identified fouling (overgrowth) as the key mechanism by which zebra mussels kill native bivalves, but sphaeriids are small and usually are not heavily overgrown by zebra mussels. Exploitative competition for food has been suggested as an important interaction between zebra mussels and unionids (Strayer and Smith 1996).

In contrast, unionids, sphaeriids, and zebra mussels coexist at European sites where zebra mussels have occurred for decades to millennia (e.g., Lewandowski 1976, Ponyi 1992, Burlakova et al. 2000). This coexistence sometimes follows mass die-offs of unionids early in the zebra mussel invasion (e.g., Lake

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Balaton; Sebestyen 1938, Ponyi 1992). The long-term survival of European unionids might be possible because these animals have a long shared evolutionary history with *Dreissena* (which occurred throughout Europe in interglacial times) and have developed some resistance to its effects. However, North American unionids co-occur with zebra mussels in refuge sites where they are protected against the effects of fouling and competition (Nichols and Wilcox 1997, Zanatta et al. 2002, Bowers and de Szalay 2004). Coexisting European populations simply may have continued to occupy such refuge sites after unionids were eliminated from nonrefuge sites. Also, there may be other mechanisms of long-term accommodation between zebra mussels and other bivalves that are not yet understood that account for differences between North America and Europe.

We have been measuring the population density, size structure, and body condition of native bivalves in the Hudson River since 1990–1991, just before zebra mussels appeared in the river. Early postinvasion data showed severe and statistically significant declines in population density, recruitment, and body condition of native bivalves (Strayer and Smith 1996, 2001). However, since 2000, we have seen an apparent recovery of native bivalve populations. The goals of our article are to describe the long-term dynamics of native bivalve populations in the Hudson River after the zebra mussel invasion and to evaluate evidence that native bivalve populations might be recovering after an initial period of decline.

Methods

Study area

The study area is the freshwater tidal Hudson River in eastern New York. The freshwater tidal Hudson River extends from the dam at Troy at river kilometer ([RKM] distance from the Battery in New York City) 248 to RKM 99, where traces of sea salt commonly occur in late summer. Mean water depth is 8 m, mean channel width is 0.9 km, and the study area covers 140 km^2. About 15% of the study area is shallow (<3-m deep at mean low tide) and supports extensive beds of submersed vegetation (Findlay et al. 2006). The entire study area is tidal, with a tidal range of 0.8 to 1.6 m. Tidally driven currents run in both directions and reach peak velocities of 40 to 80 cm/s, ~10× as great as typical net downriver currents (Geyer and Chant 2006). The water is moderately hard (pH = 7.6, Ca = 27 mg/L) and fertile (NO_3-N = 0.5 mg/L, PO_4-P = 11 μg/L; Caraco et al. 1997). Most of the river bottom is sand or mud (Simpson et al. 1986, Strayer and Smith 2001). The organic C budget is dominated by allochthonous inputs (Cole and Caraco 2006), but phytoplankton production and macrophyte production both appear to be important in supporting the food web (Strayer and Smith 2001).

Survey methods

Our methods were described in detail by Strayer et al. (1994) and Strayer and Smith (1996, 2001). We collected unionids and sphaeriids by different sampling programs. We sampled unionids annually from 1991 to 2005 between mid-June and August along 11 transects, each of which contained 4 randomly located stations. The same stations were sampled each year and were relocated using loran or global position system (GPS). We sampled unionids with a standard (23 × 23 cm) PONAR grab. We took 5 grabs at each station and sieved them in the field through a 2.8-mm-mesh screen. We placed individual unionids in separate bags, and if the sieve residue was voluminous, we saved it for later examination in the laboratory. We placed mussels and residue in a cooler and froze them on return to the laboratory. After thawing the samples, we picked out remaining unionids from the samples. We counted and measured the shell lengths of zebra mussels on each unionid, and measured the shell length, width, and height of unionids with calipers. We removed their soft body parts and weighed them after drying overnight at 60°C.

We sampled sphaeriids annually between 1990 and 2002 in September to October from 8 stations along the course of the river using a petite (15 × 15 cm) PONAR grab. We sieved 5 replicate samples from each station through a 0.5-mm-mesh screen in the field and preserved the contents of the sieve in buffered formalin. We washed the sieved samples in tap water and sorted them under 6× magnification in the laboratory. We picked sphaeriids and other macrobenthos from the samples and preserved them in 70% ethanol. We picked a subset of samples twice to enable us to correct for sorting efficiency. We did not take samples in 2000.

As an index of recruitment in unionid populations, we calculated the proportion of small animals in each species. The size structure of unionid populations in the Hudson River is strongly bimodal (Strayer et al. 1994); we defined as small animals included in the left-hand peak of the bimodal distribution. These animals probably are immature and <5-y old. Specifically, we defined as "small" animals with shell lengths <20 mm (*Elliptio complanata*), 40 mm (*Anodonta implicata*), or 30 mm (*Leptodea ochracea*).

Rings in unionid shells are commonly interpreted as winter growth stops and are used for studies of unionid growth (e.g., Neves and Moyer 1988, Haag and Staton 2003), although some studies have shown that these rings are not always annual (Kesler and Downing 1997, Anthony et al. 2001). The shells of adult unionids taken from the Hudson River do not have interpretable rings (Strayer et al. 1994), but small animals do have clear rings that may represent winter growth stops. We tentatively interpret these rings as annual, although we have not verified this assumption. We used only the first 2 rings of young *E. complanata* (young animals of other unionid species were too rare to support such an analysis) for an analysis of shell growth in different time periods. We compared growth in 3 time periods: preinvasion (1988–1991 year classes for 1st-y growth, 1988–1990 year classes for 2nd-y growth), early postinvasion (1993–1998 year classes for 1st-y growth, 1993–1997 year classes for 2nd-y growth), and later postinvasion (2000–2004 year classes for 1st-y growth, 2000–2003 year classes for 2nd-y growth).

We defined body condition as dry body mass (g) of an animal of a given shell size. We analyzed condition by running a series of regressions that included shell length (mm), width (mm), and height (mm), as well as measures of zebra mussel impact and time. We used 2 measures of zebra mussel impacts: 1) filtration rate of the zebra mussel population (taken from Strayer and Malcom 2006), indicating the strength of exploitative competition (cf. Strayer and Smith 1996), and 2) number of zebra mussels attached to each unionid (indicating the strength of local interactions, including both mechanical interference and local exploitative competition). These 2 measures are only loosely correlated (Fig. 1). Time was defined as a dummy variable having a value of 0 in 1991 to 1999 and 1 in 2000 to 2005. Thus, a significant positive value of the dummy variable would show that body condition improved from 1991–1999 to 2000–2005, given the same values of zebra mussel filtration and fouling. We ran multiple regressions using all possible combinations of zebra mussel filtration, zebra mussel fouling, and time as independent variables, and we present 2 estimates of the importance of each independent variable in predicting body condition. First, we present the sum of Akaike weights, which is the likelihood that the most appropriate model to describe the data includes that variable (Burnham and Anderson 2002), for all models containing a given variable. High Akaike weights show that an independent variable is an important predictor. Second, we present model-averaged estimates of the slopes for each variable, averaged across all possible models, including those in which the variable does not appear.

It has been suggested that some habitats, particularly shallow waters, serve as refuges for unionids against the effects of zebra mussels (Nichols and Wilcox 1997, Zanatta et al. 2002, Bowers and de Szalay 2004). We tested whether decline or recovery of unionid populations differed among regions or habitats in the Hudson River. We calculated mean densities of *E. complanata* in shallow (<3-m deep, $n = 4$) and deep (>3-m deep, $n = 12$) sites in the upper river (RKM 213–248). We used analysis of covariance (ANCOVA) to compare decline rates in 1992–1999 in these 2 habitats, then used a *t*-test to determine whether the residuals of data from 2000–2005 from this regression differed between the 2 habitats. We used similar methods to compare decline and recovery rates of *E. complanata* between the upper estuary (RKM 213–248) and the lower estuary (RKM 99–151). Densities were too low to compare decline and recovery rates for other species or other parts of the Hudson River.

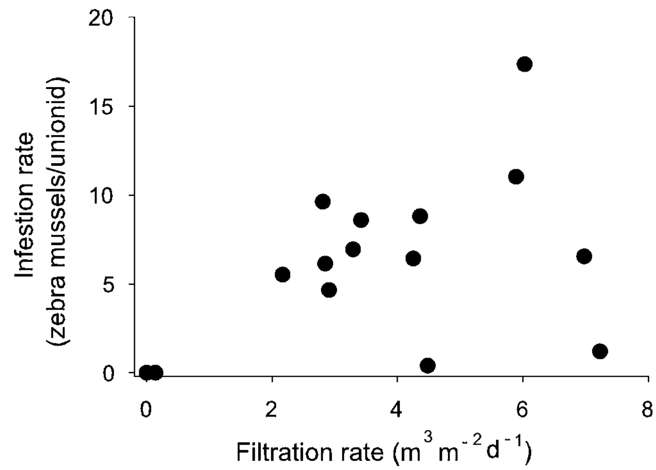

FIG. 1. Correlation between 2 measures of zebra mussel impact (filtration and fouling rates) on native bivalve populations in the Hudson River ($r^2 = 0.18$, 1-tailed $p = 0.06$).

We also compiled data on unionid and sphaeriid densities from North American waters before the arrival of zebra mussels and in the first few years after the outbreak of zebra mussel populations and from European lakes and rivers well after the zebra mussel invasion. We restricted these data sets to include only data from spatially extensive (e.g., lakewide) surveys rather than local estimates of bivalve densities.

Results

Filtration and fouling rates of zebra mussels

Zebra mussels were first detected in the Hudson River in 1991 (Strayer et al. 1996). Their population has fluctuated about an order of magnitude from year to year (Fig. 2A), but the aggregate filtration rate of the

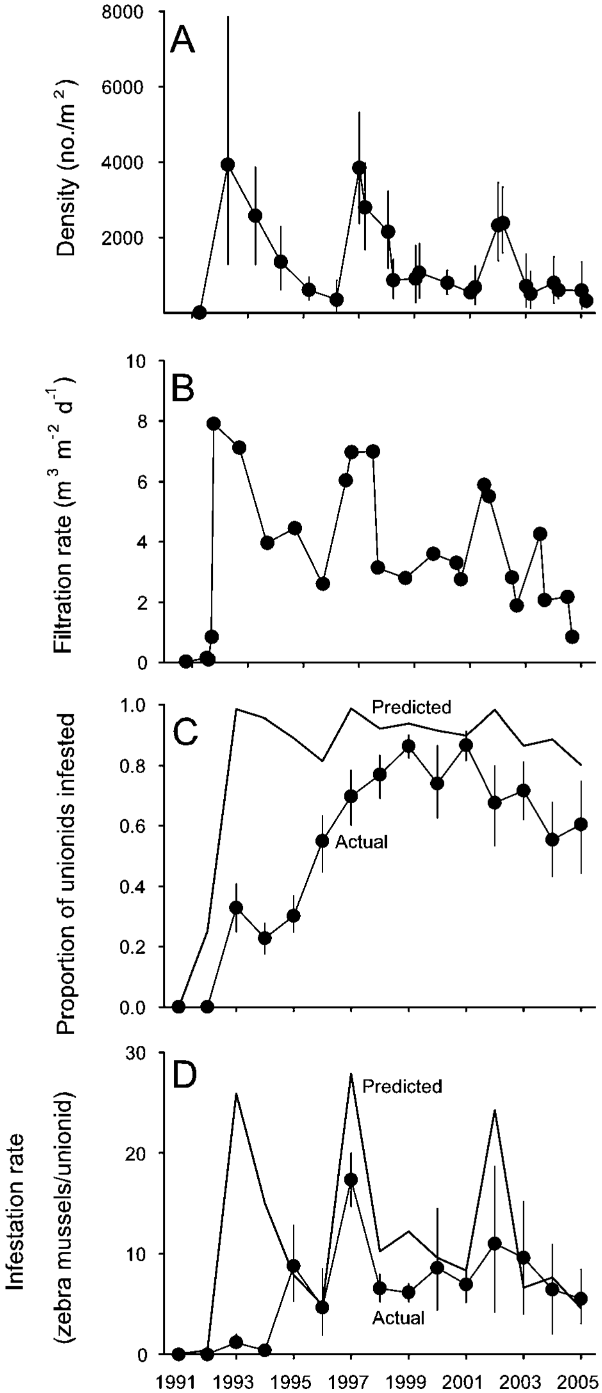

FIG. 2. Mean area-weighted riverwide population density (A), estimated filtration rate of the zebra mussel population (B), proportion (± 90% confidence limits) of the unionid population infested by ≥1 zebra mussel (C), and the mean number (± 90% confidence limits) of zebra mussels attached to each unionid (D). Predicted values in (C) and (D) are based on equations 13 and 14 of Ricciardi et al. (1995). Confidence limits around estimates of zebra mussel population size and infestation rates were calculated by resampling (version 5.0.2, Resampling Stats, Arlington, Virginia). Panels (A) and (B) are updated from Strayer and Malcom (2006).

population has been high since September 1992 (Strayer and Malcom 2006; Fig. 2B), and phytoplankton populations have been severely depleted at most times and places in the Hudson River since then (Caraco et al. 2006).

In contrast, fouling rates on unionids were low for the first few years of the zebra mussel invasion (Fig. 2C, D). Fouling rates rose in the mid-1990s and have been near levels in other North American rivers and lakes since then, based on the density of the zebra mussel population in the Hudson River (Fig. 2A). We do not routinely calculate fouling loads (Ricciardi et al. 1996), but the median length (n = 4932) of zebra mussels fouling unionids in the Hudson River was 15.9 mm, so we have no reason to suspect that fouling loads in the Hudson River were unusually low. We have never seen a zebra mussel attached to *Pisidium* in the Hudson River. Neither filtration rates nor fouling rates declined appreciably after 1999 (Fig. 2B, C).

Population dynamics of native bivalves

Seven taxa of native bivalves were known from the Hudson River at the time of the zebra mussel invasion (Strayer and Smith 2001). Four of these (*E. complanata*, *A. implicata*, and *L. ochracea* in the Unionidae, and *Pisidium* sp. in the Sphaeriidae) were abundant enough to appear regularly in our samples. All 4 of these taxa declined steeply after the zebra mussel invasion (Fig. 3), with annual decline rates of 19 to 57%/y in 1993–1999. By 1999, population densities of these 4 native species had fallen by 65 to 100% from their preinvasion values; neither *A. implicata* nor *L. ochracea* was collected at all in 1998 or 1999. Our data are not sufficient to support a formal statistical analysis of variation in rates of interannual population decline, but we note that decline rates of unionid populations were not markedly lower during the early years of the zebra mussel invasion when fouling rates were low (Fig. 2D), suggesting that fouling was not the primary mechanism of mortality.

Populations of all 4 native bivalves stabilized or recovered in 2000–2005, deviating strongly from the trajectories predicted by the 1990–1999 data (Fig. 3). Simple exponential decay models based on the entire 1990–2005 data set suggest that populations of these 4 species will stabilize at 4 to 22% of their preinvasion densities (Fig. 4).

Population size structure

The size structure of unionid populations differed significantly among the 3 periods (χ^2 test, $p < 0.001$): 1) preinvasion (1991–1992), 2) early postinvasion (1993–1999), and 3) late postinvasion (2000–2005). The

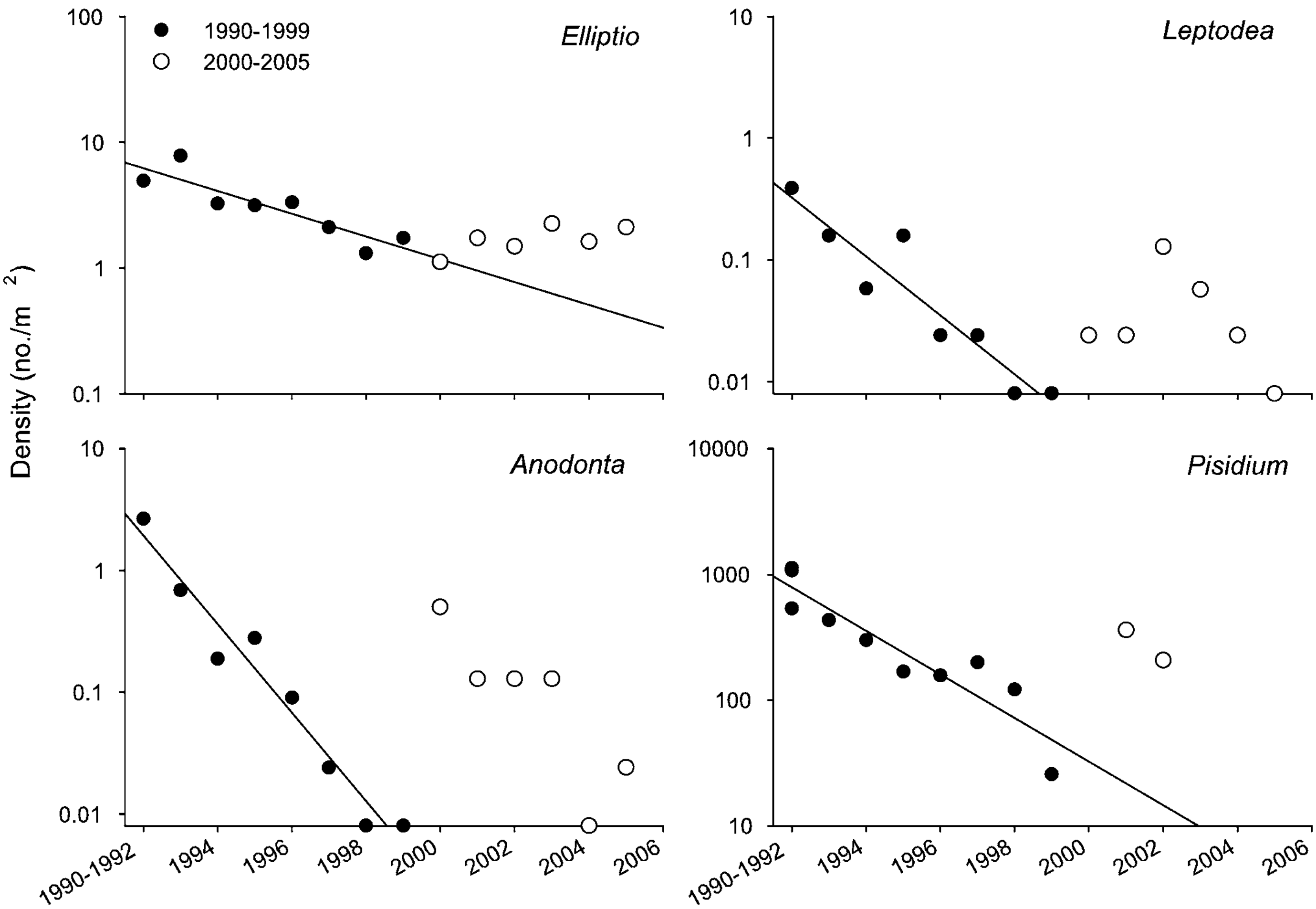

FIG. 3. Population trajectories of 4 species of native bivalves in the Hudson River estuary plotted on a semilogarithmic scale. Regression lines are based on data from 1990–1999 and have the following slopes: *Elliptio* (–19%/y), *Anodonta* (–57%/y), *Leptodea* (–43%/y), and *Pisidium* (–33%/y) (all $p < 0.003$).

proportion of animals that were small fell from 9.2 ± 0.90% (SE) in 1990–1992 to 5.9 ± 0.75% in 1993–1999, then rose to 14.1 ± 1.61% in 2000–2005. However, the absolute density of small animals was much lower in 2000–2005 than in 1991–1992 (0.30/m^2 vs. 2.83/m^2 for all species combined) because overall population density was much lower in 2000–2005 than in 1991–1992.

Growth and condition of unionids

If we accept the rings on small unionids as winter rings, then growth rates of *E. complanata* in their 1st growing season fell from 3.95 ± 0.24 (SE) mm in 1991–1992 to 2.84 ± 0.18 mm in 1993–1999, then rose to 4.78 ± 0.20 mm in 2000–2005. There was only a subtle indication that growth in the 2nd growing season recovered in 2000–2005 (6.00 in 2000–2005 vs 5.55 mm in 1993–1999; *t*-test, 1-tailed $p = 0.19$), but animals were larger at the end of their 2nd winter in 2000–2005 (10.64 ± 0.41 mm) than in 1993–1999 (8.24 ± 0.42 mm) because of the growth advantage in their 1st growing season, although they had not recovered to preinvasion values (13.67 ± 0.55 mm). Differences in shell length among time periods were significant for both 1- and 2-y-old animals (ANOVA, $p < 0.0001$).

The body condition of the unionids fell sharply after the zebra mussel invasion. Mean body mass at a given shell length fell by 25, 31, and 34% between 1991–1992 and 1993–2005 for *E. complanata*, *A. implicata*, and *L. ochracea*, respectively. Condition was strongly and negatively correlated with the filtration rate of the zebra mussel population (Table 1). Summed Akaike weights equaled 1 for all 3 unionid species, showing that the best models must include zebra mussel filtration as an independent variable. Models estimated that body mass for a given shell size fell by 26, 35, and 54% between the years of the highest and lowest zebra mussel filtration rates for *E. complanata*, *A.*

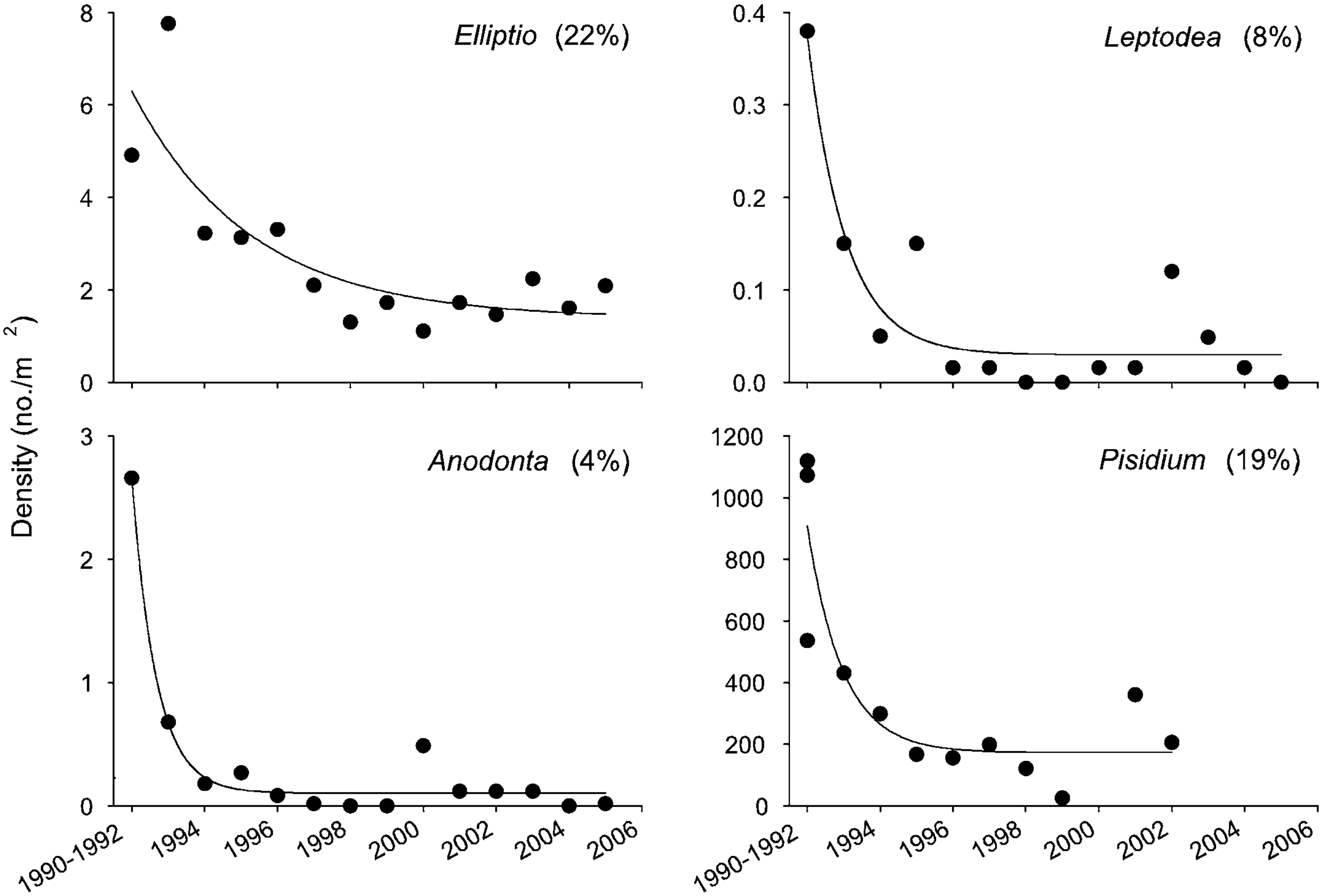

Fig. 4. Population trajectories of 4 species of native bivalves in the Hudson River estuary. The fitted line is an exponential decay curve of the form $Y = Y_0 + ae^{-bx}$, where Y_0 is the asymptote. The numbers in parentheses after the genus names are the estimated asymptotes as a percentage of the initial population size. The estimated asymptotes (SE, 1-tailed p) are: *Elliptio* $= 1.39/\text{m}^2$ (0.68, $p = 0.03$), *Anodonta* $= 0.10/\text{m}^2$ (0.043, $p = 0.03$), *Leptodea* $= 0.030/\text{m}^2$ (0.015, $p = 0.04$), and *Pisidium* $= 174/\text{m}^2$ (72, $p = 0.02$).

implicata, and *L. ochracea*, respectively. Condition was only weakly correlated with fouling rates with summed Akaike weights of 0.31 to 0.62. Body mass for a given shell size fell by only 2.4, 0.02, and 8.3% between unionids fouled at the 2.5^{th} percentile (no zebra mussels/unionid) and those fouled at the 97.5^{th} percentile (27 zebra mussels/unionid) for *E. complanata*, *A. implicata*, and *L. ochracea*, respectively. Last, body condition did not show a consistent recovery (i.e., a positive regression coefficient) in 2000–2005.

Spatial refuges

We found no evidence that decline or recovery rates of *E. complanata* differed across habitats or sections of the river. Neither slopes of decline (ANCOVA, $p = 0.90$) nor degree of recovery (t-test, $p = 0.98$) differed between shallow (<3-m deep) and deep (>3-m deep) sites in the upper river (Fig. 5A). Likewise, slopes of decline (ANCOVA, $p = 0.79$) and degree of recovery ($p = 0.95$, t-test) were similar between the upper river (RKM 213–248) and the lower river (RKM 99–151) (Fig. 5B).

Table 1. Summed Akaike weights and model-averaged slope (in parentheses) for each variable in statistical models that tested for the effects of 2 measures of the zebra mussel population (filtration rate and fouling rate) and time (1991–1999 vs 2000–2005) on body condition of unionids (i.e., variation in shell-free body mass not accounted for by shell length, height, and width).

Independent variable	*Elliptio complanata*	*Anodonta implicata*	*Leptodea ochracea*
Zebra mussel filtration rate (m/d)	1.00 (−0.016)	1.00 (−0.023)	1.00 (−0.033)
Zebra mussel fouling rate (no./unionid)	0.62 (−0.00039)	0.31 (−0.000004)	0.53 (−0.0014)
Time	1.00 (−0.057)	0.68 (−0.0056)	0.35 (0.023)

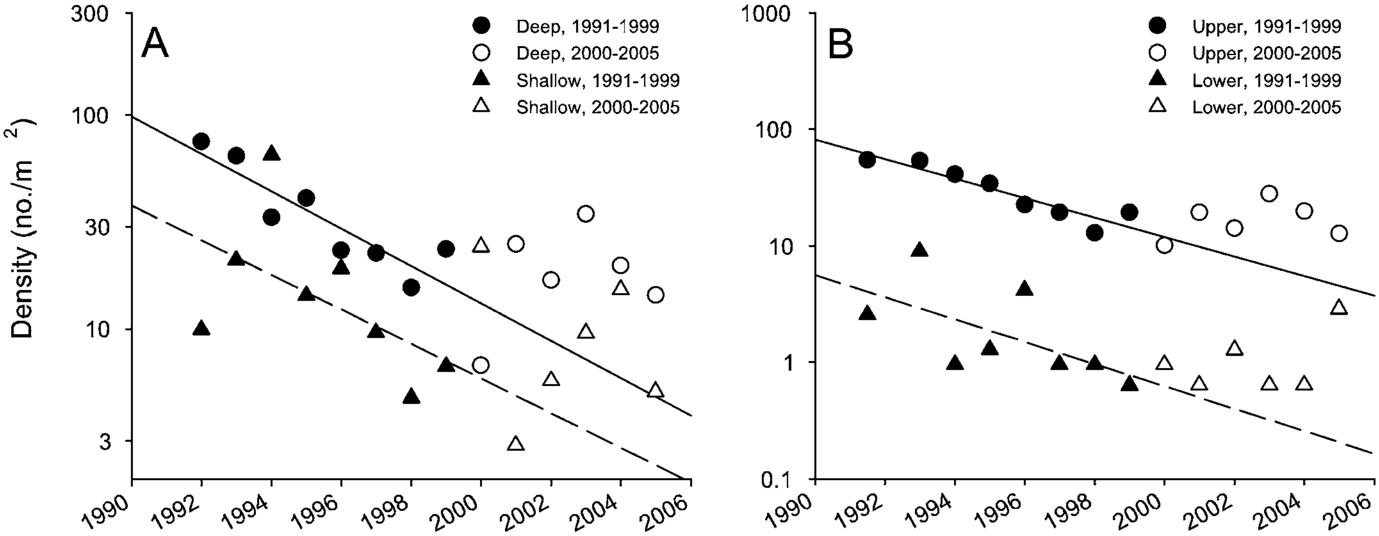

FIG. 5. Decline and recovery of populations of *Elliptio complanata* in shallow (<3-m deep) and deep (>3-m deep) sites in the upper estuary (A) and in the upper (RKM = 213–248) and lower (RKM 99–151) estuary (B). Regression lines are fitted for 1991–1999.

Declines in unionids and sphaeriids at other sites invaded by zebra mussels

Both unionid and sphaeriid populations declined precipitously in the first 1 to 6 y after the outbreak of zebra mussel populations in North America, often falling below the detection limit of the sampling programs (Fig. 6A, B). The few data available for North American sites other than the Hudson River that record abundances of native populations >6-y postoutbreak do not show any signs of recovery.

Densities of unionids and sphaeriids in European waters invaded by zebra mussels are similar to those that occurred in North America before zebra mussels arrived (Fig. 7A, B). It is difficult to make any rigorous comparisons between North American and European data because the data shown in Fig. 7 arose, not from a representative sampling program, but from a haphazard selection of sampling sites, many of which presumably were chosen because of their dense bivalve populations. Nevertheless, the European data at least show that dense populations of unionids and sphaeriids can coexist with zebra mussels.

Discussion

The response of native bivalve populations to the zebra mussel invasion of the Hudson River is clearly separated into 2 time periods. The early postinvasion period began in September 1992, when the zebra mussel population grew rapidly and removed most of the plankton (Caraco et al. 1997, Pace et al. 1998). All native bivalves responded in a similar dramatic fashion. Their populations declined along nearly perfect semilogarithmic lines (implying constant interannual rates of decline), with slopes of −19% to −57%/y. Recruitment, growth, and body condition of all unionid species also fell sharply during this early postinvasion period. By the end of the 1st period in 1999, populations of all native bivalve species in the Hudson River had fallen by 65% to below the detection limits of our sampling program and appeared to be headed for extirpation.

Dramatic declines similar to these early-postinvasion-period dynamics have been reported for unionid populations in many North American waters (Fig. 6A). Likewise, the few long-term observations on North American sphaeriid populations after the zebra mussel invasion have found sharp declines in these populations (Fig. 6B). These grim findings led to predictions of widespread loss of populations and species of native bivalves across North America (e.g., Ricciardi et al. 1998, Strayer 1999).

However, instead of disappearing from the Hudson River, populations of native bivalves in the Hudson River entered a distinctly different late postinvasion period in 2000–2005. Populations of all species stabilized or rose, and recruitment and growth of young unionids recovered to preinvasion levels. Nevertheless, not all indicators of population status rebounded; the body condition of unionids in 2000–2005 was no better than in 1993–1999. Simple statistical extrapolations of population densities now predict that native bivalves will persist, albeit at much reduced densities, rather than disappearing from the Hudson River. We are not aware of data from any other North American body of water that show such recovery of native bivalve populations after an extended period of

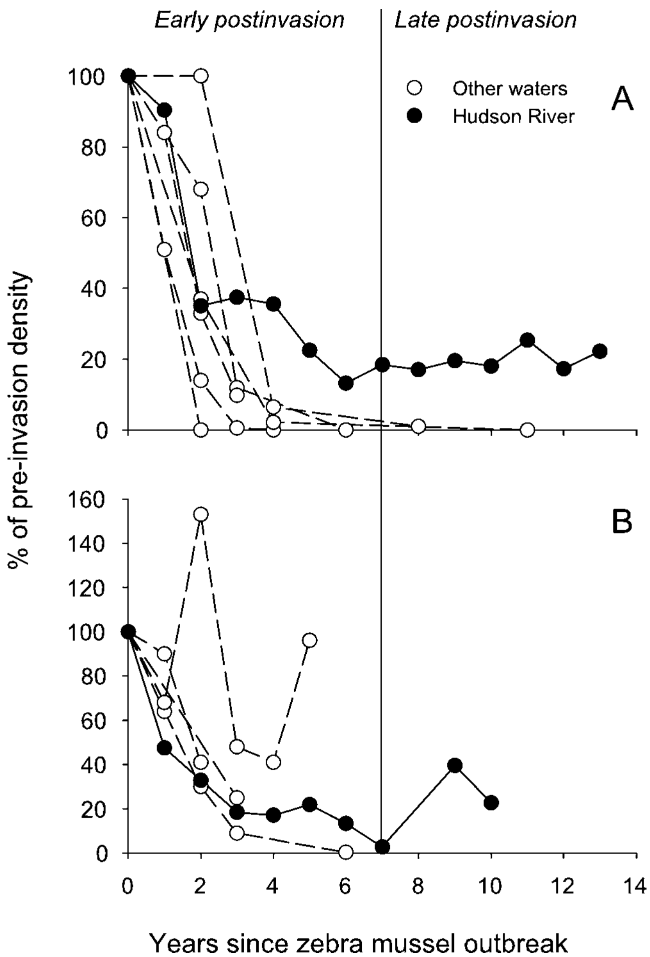

Fig. 6. Declines of native unionid (A) and sphaeriid (B) bivalves in North America in the early postinvasion period after the outbreak of zebra mussel populations in the Hudson River and other bodies of water in North America. Data compiled from Schloesser and Nalepa (1994), Nalepa et al. (1996, 1998, 2001, 2003), Ricciardi et al. (1996), Dermott and Kerec (1997), Schloesser et al. (1998, 2006), Schloesser and Masteller (1999), Lauer and McComish (2001), Martel et al. (2001), and Hunter and Simons (2004). The outlier for sphaeriids is from Saginaw Bay in Lake Huron.

postinvasion decline. Populations of unionids in the Detroit River (Schloesser et al. 2006) and the open waters of Lake St. Clair (Hunter and Simons 2004) were near zero 8 to 11 y after the outbreak of zebra mussel populations, although shallow areas near the inflow to Lake St. Clair still supported substantial unionid populations about a decade after the zebra mussel outbreak (Zanatta et al. 2002). Nevertheless, the apparent recovery of Hudson River bivalves is consistent with observations of coexistence of unionids, sphaeriids, and zebra mussels in European waters that were invaded by zebra mussels decades to centuries ago (Fig. 7A, B).

The mechanisms behind the dynamics of native bivalve populations in the Hudson River are not entirely clear. The declines of the early postinvasion period appear to be a result of exploitative competition for food. The declines in body condition as well as population density, somatic growth, and recruitment all are consistent with this mechanism. Furthermore, statistical analysis showed that declines in body condition were closely associated with zebra mussel filtration (Table 1). Evidence for the effects of fouling is much weaker. Declines in unionid populations were just as steep in 1993–1995, when fouling rates were very low, as in later years when fouling increased. Fouling had only weak effects on the body condition of unionids (Table 1). Furthermore, populations of the sphaeriid *Pisidium* fell sharply even though we have never seen a zebra mussel attached to this tiny bivalve.

We do not understand the causes for the changes of the late postinvasion period, nor do we know if they are transient or permanent. Neither zebra mussel filtration nor fouling fell appreciably in 2000–2005. Phytoplankton biomass did not recover (Caraco et al. 2006), nor were there obvious changes in phytoplankton composition in 2000–2003 (Hazzard et al. 2006) that would be easy to link to the recovery in bivalve populations. Our analysis uncovered no evidence for spatial refuges in the Hudson River where populations of native bivalves might survive and grow, nor have we ever observed dense populations of unionids in the shallows of the Hudson River in the course of other studies of the littoral zone (Strayer et al. 2003, Strayer and Malcom, in press). Zebra mussel filtration and fouling rates varied from year to year, so it is possible to imagine that there might be brief periods of time during which zebra mussel impacts are low and native bivalves could recruit. However, the young unionids that we collected in 2000–2005 belonged to several year classes (data not shown), so they were not produced during a single favorable year. It is possible that evolution resulting from very strong selection (annual loss rates of 19–57%) could favor genotypes leading to phenotypes with physiological or behavioral characteristics resistant to zebra mussel effects. We have no evidence with which to evaluate this possibility. However, the rapid response and synchrony in recovery among 4 species with different life histories, breeding systems, and population sizes seem inconsistent with a simple evolutionary explanation.

The mechanisms (whether the same or different from those in the Hudson River) that have allowed the coexistence of unionids, sphaeriids, and zebra mussels in Europe also have not been identified. Possible mechanisms can be divided into 2 broad classes: fast processes that occurred in the few decades to centuries

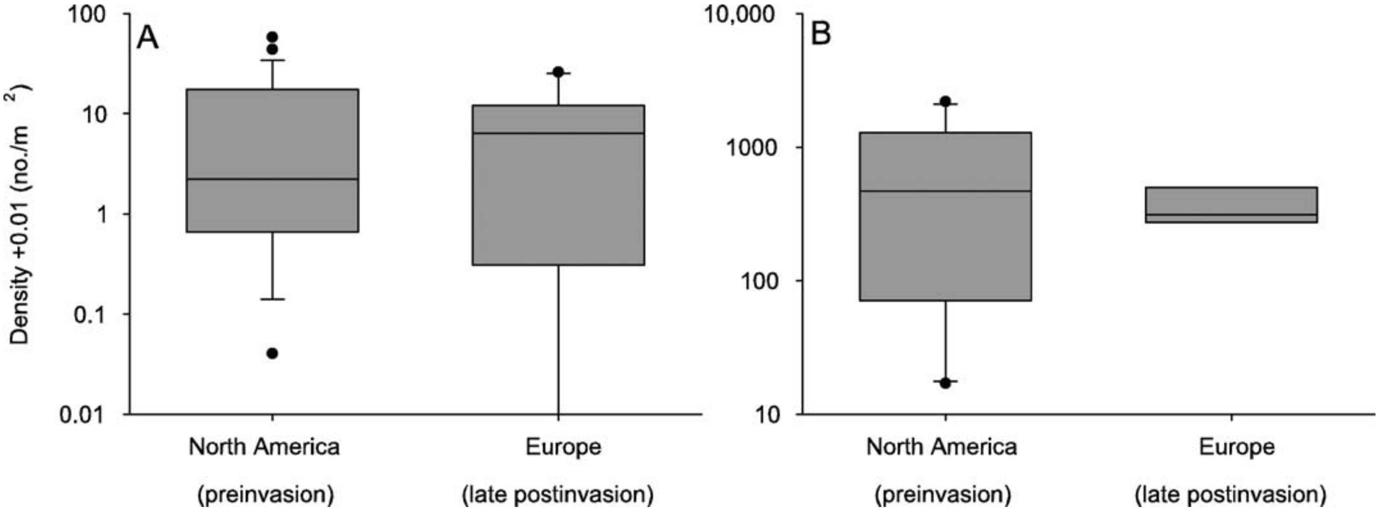

FIG. 7. Box-and-whisker plots of densities of unionid (A) and sphaeriid (B) bivalves in North American lakes and rivers before the zebra mussel invasion and in European lakes and rivers long (typically >50 y) after the zebra mussel invasion. In each plot, the horizontal line is the median, the box encompasses the 25th and 75th percentiles, whiskers are the 10th and 90th percentiles, and dots are outliers. Data are only approximately comparable because of differences in methods and sampling designs. Data compiled from Lundbeck (1926), Cole and Underhill (1965), Negus (1966), Magnin and Stanczykowska (1971), Tudorancea (1972), Lewandowski and Stanczykowska (1975), Fisher and Tevesz (1976), Tudorancea et al. (1979), Bloomfield (1978), Strayer et al. (1981, 1994, 1996), Walter (1985), Hanson et al. (1988), Holland-Bartels (1990), Huebner et al. (1990), Ponyi (1992), Kesler and Bailey (1993), Schloesser and Nalepa (1994), Balfour and Smock (1995), Nalepa et al. (1996, 1998, 2001, 2003), Ricciardi et al. (1996), Dermott and Kerec (1997), Johnson and Brown (1998), Schloesser et al. (1998), Welker and Walz (1998), Schloesser and Masteller (1999), Lauer and McComish (2001), Martel et al. (2001), and Jonasson (2004).

since zebra mussels reinvaded central and western Europe, and slow processes that occurred across the long interglacial period during which zebra mussels lived in much of Europe and presumably coexisted with other European bivalves. Identifying the nature and speed of processes that led to coexistence in Europe may help to clarify prospects for North American native bivalves. If key processes are slow, requiring millennia, then many members of the native fauna may be unable to adapt and will disappear as predicted by Ricciardi et al. (1998). On the other hand, if the processes are fast, as the Hudson data may suggest, then species that survive the short, critical period of transient losses may be able to coexist with zebra mussels in the long term.

Thus, the data from the Hudson River and from Europe offer, at least, a slender hope that native North American bivalves may be able to persist over the long term in waters invaded by zebra mussels, although the Hudson data may simply show a temporary, idiosyncratic respite of no long-term significance. At least, the European data show that the short-term effects of the zebra mussel invasion (disastrous losses of native bivalves) are not the same as the long-term chronic effects of zebra mussels (long-term coexistence) and highlight the challenge for ecologists to separate the transient short-term effects of species invasions from their long-term, chronic effects. We encourage others to look for evidence of changing dynamics in native bivalve populations after the zebra mussel invasion and to explore mechanisms that might promote the long-term coexistence of zebra mussels and other freshwater mussels in North America and Europe.

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