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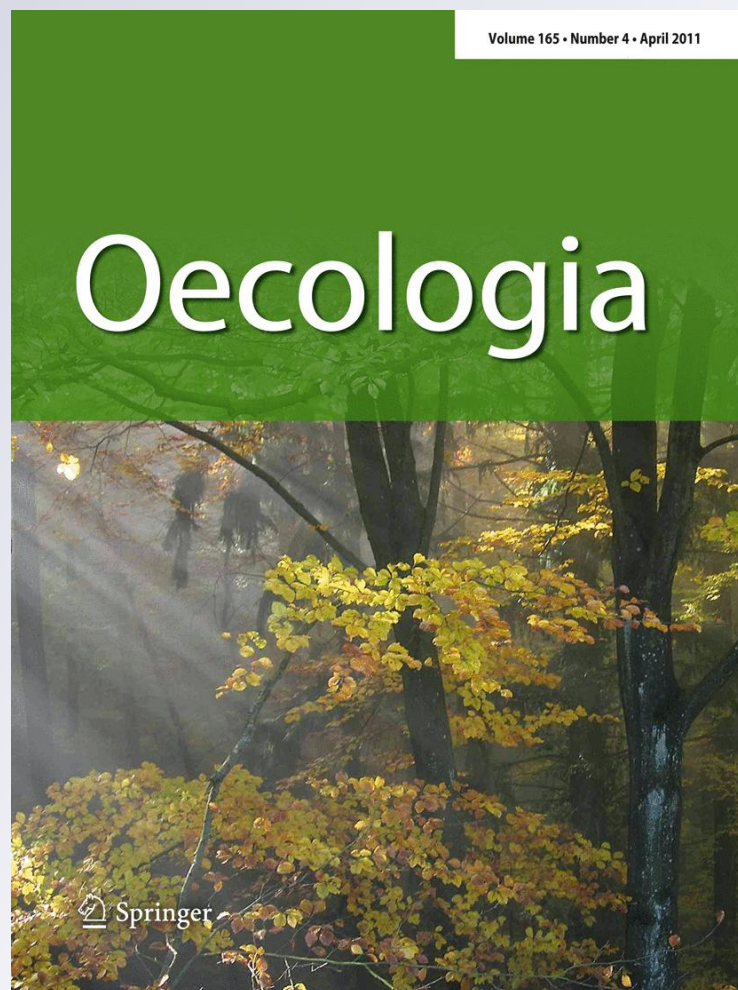
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Long-term changes in a population of an invasive bivalve and its effects

David L. Strayer · Nuria Cid · Heather M. Malcom

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Abstract Although the ecological and economic effects of non-native species probably often change through time, few studies have documented such effects. The zebra mussel (*Dreissena polymorpha*) is an important invader that has had large ecological and economic effects on the ecosystems it has invaded in North America and western Europe. Our 20-year study of the Hudson River, New York, showed that the characteristics of a zebra mussel population and its effects on other benthic animals both changed substantially through time. Over the period of study, annual survivorship of adult zebra mussels fell >100-fold, which caused the aggregate filtration rate of the population to fall by 82%. Population size and body size of zebra mussels may also have fallen. In the early years of the invasion, densities of nearly all benthic animals in deepwater sites fell steeply (by 80–99%). After about 8 years of decline, these populations began to recover, and are approaching pre-invasion densities. The littoral zoobenthos showed neither the initial decline nor the subsequent recovery. Although the mechanisms behind these changes are not fully clear, our study shows that the effects of an invader may change considerably over time.

Keywords Invasive species · Alien species · Estuary · Resilience · Ecosystem recovery

Introduction

Non-native species change ecosystems, endanger native species, and damage economies around the world (e.g., Lockwood et al. 2007; Davis 2009). Although a great deal is now known about invasion ecology, several important questions are still unanswered. One of the most important of these is: how do the impacts of a non-native species change through time? Although several common ecological and evolutionary mechanisms ought to change the impacts of non-native species over time, actual observations of such long-term changes are rare (Strayer et al. 2006; Hawkes 2007). Knowing whether the impacts of a non-native species are likely to remain stable, moderate, or intensify through time should help in devising effective management plans for invaded ecosystems. Here, we describe long-term changes in a population of an important invader, the zebra mussel, and some of its ecological effects in the Hudson River, New York.

The zebra mussel (*Dreissena polymorpha*) is a Ponto-Caspian species that has been widely introduced throughout western Europe and North America, where it has caused profound ecological change and economic damage (e.g., Connelly et al. 2007; Strayer 2009). Although claims have often been made about the long-term trajectory of zebra mussel populations and their effects, only a few researchers have actually tested whether zebra mussel populations and their effects change through time. Neither Strayer and Malcom (2006) nor Burlakova et al. (2006) reported any directional long-term change in zebra mussel populations, although these papers were based on relatively short runs of

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D. L. Strayer (✉) · N. Cid · H. M. Malcom
Cary Institute of Ecosystem Studies,
P.O. Box AB, Millbrook, NY 12545, USA
e-mail: strayerd@caryinstitute.org

Present Address:

N. Cid
Departament d'Ecologia, Facultat de Biologia,
Universitat de Barcelona, Diagonal 645,
08028 Barcelona, Catalonia, Spain

data (13 and 7 years, respectively). In an extensive meta-analysis, Ward and Ricciardi (2007) were unable to detect any change over time in the effects of zebra mussels on benthic animals. In contrast, the effects of zebra mussels on the Hudson River ecosystem appear to be moderating over time, at least for native bivalves (Strayer and Malcom 2007) and zooplankton (Pace et al. 2010).

Here, we show that the demography and characteristics of the Hudson River zebra mussel population have been changing over time, and that one of its most important effects—declines in benthic animal populations—has moderated after an initial period of severe impacts. This paper extends several earlier papers that used shorter runs of data to report on the Hudson River zebra mussel population (Strayer et al. 1996; Strayer and Malcom 2006) and its effects on native bivalves (Strayer and Malcom 2007) and other benthic animals (Strayer et al. 1998; Strayer and Smith 2001). This more extended analysis shows new dynamics in both the invader and the invaded community that were not detected by these earlier papers using shorter runs of data.

Materials and methods

The study area

The study area is the freshwater part of the Hudson River estuary, extending from a dam at Troy (RKM 248 = river kilometers north of the mouth of the Hudson at Battery Park in New York City) to Newburgh (RKM 99), where sea salt is often detectable by late summer. The water in the Hudson is warm, turbid, alkaline, and nutrient-rich (phytoplankton production is not nutrient-limited; Cole and Caraco 2006). Except below RKM 120, where salinity sometimes reaches 1–2 psu during times of low freshwater flow, the water in the study area is fresh. Twice-daily tides of 0.8–1.6 m amplitude occur throughout the entire study area. Net movement of water downriver is dwarfed by tidal flows, which keep the water column well mixed vertically. Although parts of the Hudson were badly polluted by industrial and municipal waste, and significant contamination remains in places, overall water quality in the study area is good, and the freshwater tidal Hudson is used for recreation and drinking water. Pollution does not appear to be an important determinant of benthic community structure in the study area (Simpson et al. 1986; Llanso et al. 2003).

The mean depth of water in the study reach is 8.3 m, but ~15% of the study area is <3 m deep at low tide and supports rooted vegetation (chiefly *Vallisneria americana* and *Trapa natans*) (Nieder et al. 2004). About 7% of the river bottom is stony, with the remainder being composed of var-

ious combinations of sand, silt, and clay with a high organic content (Strayer et al. 1996; Strayer and Smith 2001).

Macrozoobenthos

Methods for sampling zoobenthos were described in detail by Strayer et al. (1998) and Strayer and Smith (2001). We sampled zoobenthos at two stations at each of four sites (Castleton = RKM 216, Kingston = RKM 146, Poughkeepsie = RKM 122, Newburgh = RKM 100) in 1990–1999, 2001–2002, and 2005–2006. At each site except Poughkeepsie, where a littoral zone is almost absent, we sampled one littoral station and one deepwater station. All the littoral stations (<1 m deep at low tide) were heavily vegetated (chiefly with *Vallisneria americana*), while none of the deepwater sites (>5 m deep at low tide) supported rooted vegetation. The sampling stations were deliberately selected before zebra mussels arrived to cover a wide range of geographic locations and environmental conditions throughout the estuary. Samples were taken in September–October. Until the late 1990s, sampling stations were relocated by using loran, which has a precision of ~35 m; since then, we have used GPS to relocate stations. We used a petite PONAR grab (15 × 15 cm) to take five replicate samples at each station. We lowered the PONAR slowly (<1 m/s) to the sediment surface to avoid creating a pressure wave. We sieved samples in the field through a 0.5-mm-mesh sieve and preserved them in 10% buffered formalin.

In the laboratory, samples were stained overnight with rose bengal, then sorted under ×6 magnification. Animals were counted, removed from the samples, and placed into 10% formalin, 70% ethanol, or Koenike's fluid for long-term storage. At least 20% of the samples were picked twice to allow us to calculate sorting efficiency using the removal method (Zippin 1958) and to correct the data for actual sorting efficiencies. To account for fragmentation of oligochaetes, we counted only specimens that had a head. Only four of the five replicates/station were sorted for 2006.

Because high spatial variation obscured temporal patterns in macroinvertebrate densities, we normalized all densities to the long-term mean density at each station, as follows. After \log_{10} -transforming the data, we calculated the density in a given year at a station as the residual from the long-term mean density at that station. We show the long-term trends in these residuals averaged separately over all deepwater stations and all littoral stations. This procedure removes the large spatial variation in macroinvertebrate densities and allows us to examine temporal changes.

We did not conduct any formal statistical tests of temporal trends in these residuals because we did not have any a priori hypotheses about what trends to expect, beyond an expectation that zebra mussels would reduce densities of other benthic animals at deepwater sites but not at littoral

sites. Our previous studies showed that the initial post-invasion decline in zoobenthic densities in deepwater stations indeed were statistically significant (Strayer et al. 1998; Strayer and Smith 2001). Specifically, we did not have an a priori hypothesis that benthic animal populations would recover at some time after the initial outbreak of zebra mussels, nor when such a recovery might occur. Simply fitting a post hoc model to the observed data would overestimate the significance of such a recovery. Instead, we merely present the temporal pattern of macroinvertebrate densities, and indicate whether they are statistically different ($p < 0.1$, two-tailed t test) from pre-invasion densities.

We summarized variation in community structure of benthic macroinvertebrates with nonmetric multidimensional scaling (NMS) ordinations in PC-ORD version 5. We ran all ordinations on $\log_{10}(X + 1)$ -transformed densities of each taxon. Because of high spatial variation in macroinvertebrate communities, ordinations based on data from all stations and years considered together showed very little interpretable pattern, so we ran ordinations separately for each station. We ran all these ordinations as two-dimensional NMS, after excluding zebra mussels and rare taxa (those present in fewer than three samples). To test whether taxonomic composition varied significantly among three time-periods suggested by the time-trends in animal densities (pre-invasion = 1990–1992, early invasion = 1993–2002, late invasion = 2005–2006), we used Multi-response Permutation Procedures in PC-ORD version 5 (we used Sørensen distances as our distance measure for consistency with the NMS ordinations).

Zebra mussels

The program specifically targeted to sample zebra mussels and native unionid mussels was described in detail by Strayer et al. (1996) and Strayer and Malcom (2006, 2007). We took samples of soft sediments (sand and mud) using a standard (23 × 23 cm) PONAR grab, then sieved samples in the field through a 2.8-mm-mesh screen. The residue remaining on the sieve was placed on ice and returned to the laboratory, where it was frozen, then later thawed and sorted to recover all unionids and zebra mussels (including those attached to the shells of unionid mussels). These PONAR samples were taken in late June–July 1993–2009 at 44 sites arrayed in a stratified random design covering the entire freshwater tidal Hudson, as well as at fewer sites in 1991–1992 (Strayer and Smith 1996; Strayer et al. 1996).

Rocky sediments too hard or coarse to collect with a PONAR grab were sampled for zebra mussels in 1993–2009 using a diver, who collected ten rocks (15–40 cm in maximum dimension) from each sampling point. These rocks were placed into a cooler and returned to the labora-

tory, where all zebra mussels >2 mm long were removed and counted. The projected area of each rock was estimated by tracing its outline and weighing the tracing. We measured shell length and dry tissue mass on large subsamples of zebra mussels from each sample. We usually took these diver samples at six or seven sites throughout the estuary in August, and often took samples in June as well.

Demographic analyzes of zebra mussels were restricted to samples taken from rocky sediments at three sites in the middle part of the estuary (RKM 151–213), a habitat that contains >75% of the zebra mussels in the estuary. These were the only samples that consistently contained the large numbers of mussels needed for cohort analyses. We placed zebra mussels into 1-mm-wide classes by shell length, and used finite mixture analysis (using the software package Rmix—Du 2002, <http://www.math.mcmaster.ca/peter/mix/mix.html>) to estimate the mean shell length and percentage composition of each age-class (see Strayer and Malcom 2006 for details). We used these estimates of cohort size to calculate mortality rates for each large cohort. Aggregate filtration rate of the zebra mussel population was estimated by combining data on density and shell length of animals collected from the Hudson with the regressions of Kryger and Riisgard (1988). Previous work (Roditi et al. 1997) showed that such estimates agree well with filtration rates estimated in situ.

Although zebra mussels were first detected in the Hudson in 1991 (Strayer et al. 1996), we treat 1990–1992 as “pre-invasion” years. Biomass and filtration capacity of the zebra mussel population were very low until September 1992, just a few weeks before we took the zoobenthos samples that year. It therefore seems more reasonable to treat 1991–1992 as pre-invasion years than post-invasion years.

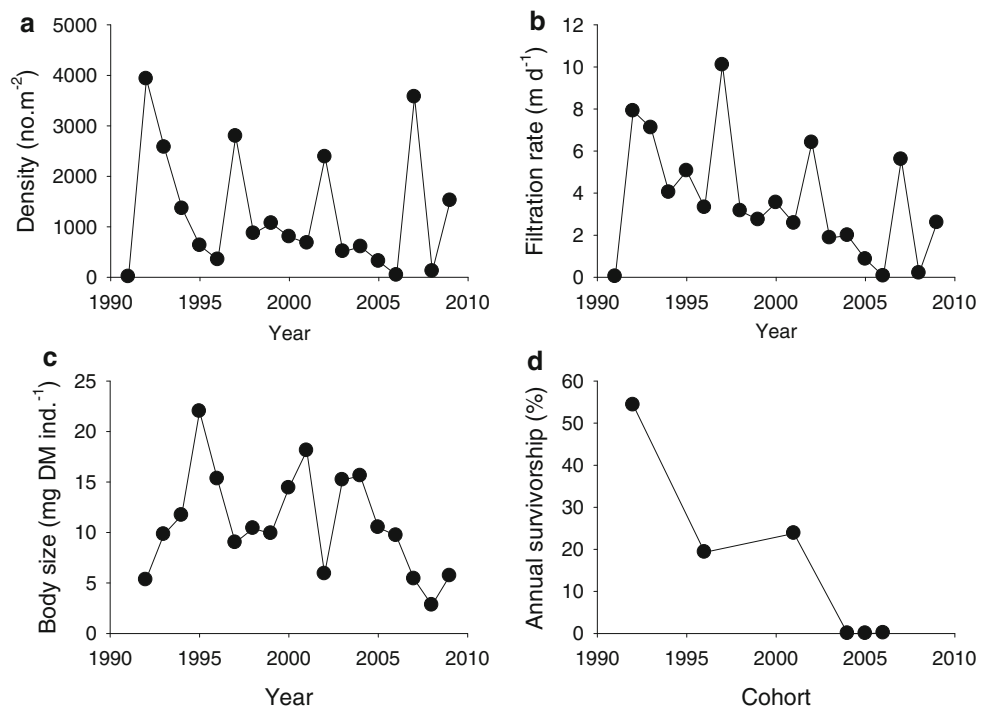
Results

The zebra mussel population

The Hudson's zebra mussel population continues to go through pronounced cycles of population density and body size (Fig. 1a, b), as was discussed in detail by Strayer and Malcom (2006). Overlaid onto this cycling are long-term trends toward declines in both population density and body size. Neither of these trends is statistically significant because of the high variance resulting from the population cycles (If a 5-year cycle is filtered out of the data series by simply subtracting from the value for the year Y the mean of the years $Y - 10$, $Y - 5$, Y , $Y + 5$, $Y + 10$, etc., both long-term declines are, however, significant at $p < 0.05$).

The long-term trends in declining population and body size combine to produce a large and highly significant decline in aggregate filtration rate of the zebra mussel

Fig. 1 Long-term dynamics of the zebra mussel (*Dreissena polymorpha*) population in the Hudson River, New York, USA. **a** Riverwide mean population density ($r^2 = 0.10$, $p = 0.20$); **b** aggregate filtration rate of the population, estimated by combining data on density and shell length of animals collected from the Hudson with the regressions of Kryger and Riisgard (1988) ($r^2 = 0.38$, $p = 0.007$); **c** mean body size of animals collected from hard substrata ($r^2 = 0.10$, $p = 0.19$); **d** annual survivorship of cohorts from age 1 to age 2 years ($r^2 = 0.85$, $p = 0.009$); cohorts were identified from size-frequency distributions of shell length (see text for details). All regression statistics refer to linear regressions against time for 1992–2009



population (Fig. 1c). According to the fitted regression, aggregate filtration rates fell 82% between 1992 and 2009.

The cause of these changes in density, body size, and filtration rate is the very large and highly significant decline in annual survivorship of adult zebra mussels between 1993 and 2007 (Fig. 1d). In the past few years, annual survival rates of adult zebra mussels have been 1% or less of those in the early years of the invasion.

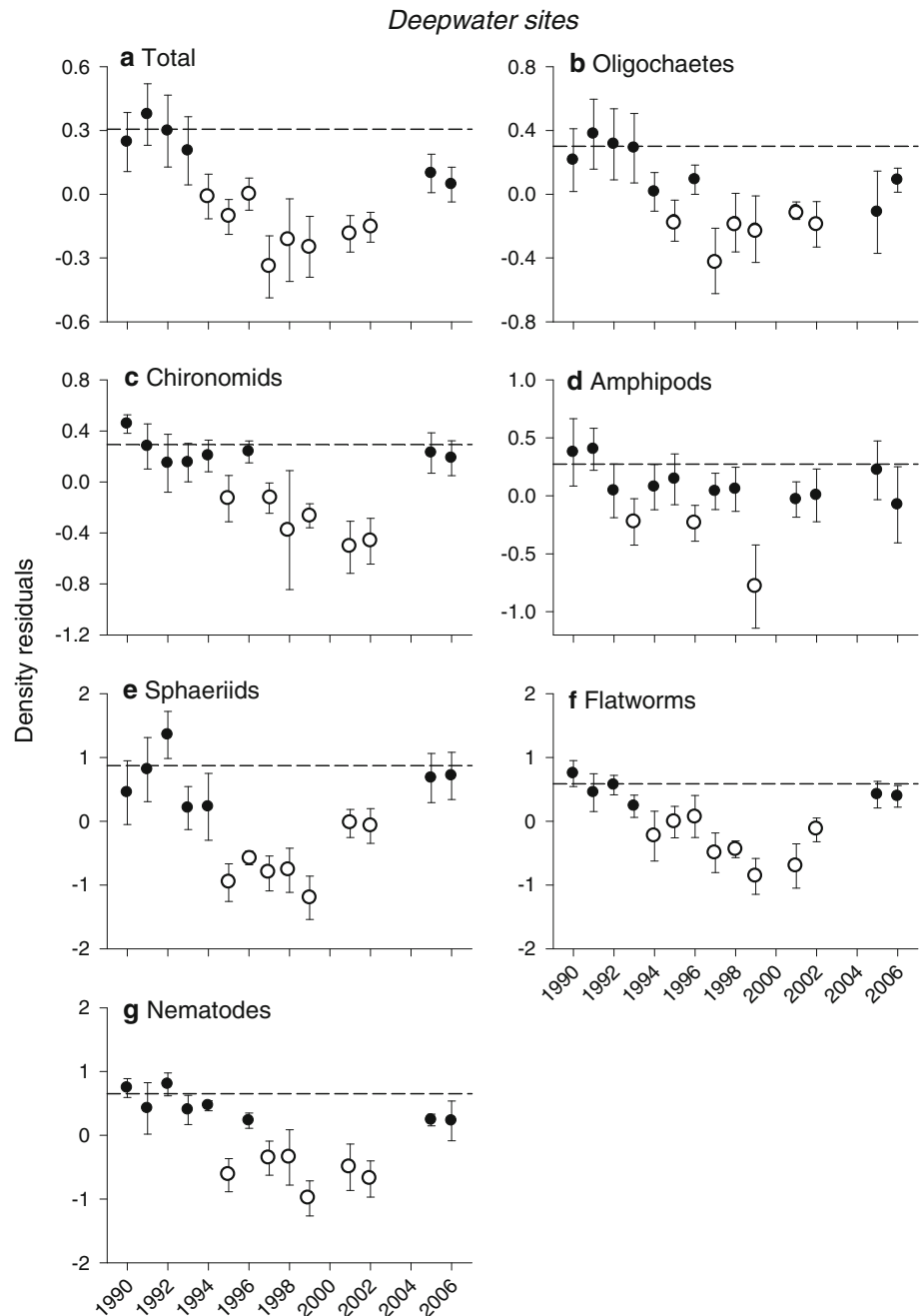
Responses of benthic animals

The Hudson’s zoobenthos is diverse, and is dominated by oligochaetes, chironomids, and amphipods (Table 1). The pattern of temporal change following the zebra mussel invasion differed between deepwater and littoral stations (Figs. 2, 3). In the deepwater stations, population densities of most benthic animals fell after the zebra mussels arrived

Table 1 Mean densities (no. m⁻²) of major taxonomic groups of macrozoobenthos in deepwater and littoral sampling sites, averaged over all sites for each of three time-periods (pre-invasion = 1990–1992; early invasion = 1993–2002; late invasion = 2005–2006)

Taxon	Deep water			Littoral		
	Pre-invasion	Early invasion	Late invasion	Pre-invasion	Early invasion	Late invasion
Oligochaeta	6,178	3,528	4,810	4,530	3,243	3,086
Chironomidae	713	456	515	2,492	2,796	2,039
Amphipoda	2,497	801	672	582	704	385
Sphaeriidae	959	97	909	826	421	373
Nematoda	158	23	44	934	756	876
Gastropoda	70	82	73	398	561	556
Turbellaria	216	68	155	307	474	375
<i>Dreissena</i>	0	53	11	0	346	474
Isopoda	105	100	25	3	3	15
Trichoptera	57	7	19	42	108	90
Acari	5	5	42	60	112	107
Ceratopogonidae	25	6	2	216	46	77
Others	136	24	217	31	113	300

Fig. 2 Long-term trends in populations of benthic animals at deepwater sites ($n = 5$) in the Hudson River. **a** Total, **b** oligochaetes, **c** chironomids, **d** amphipods, **e** sphaeriids, **f** flatworms, **g** nematodes. Densities are expressed as residuals from the mean density at each station (± 1 SE) after $\log_{10}(X + 1)$ transformation (see “Materials and methods” for details); thus, a difference of 0.3 indicates a twofold change and a difference of one indicates a tenfold change in population density. The dashed horizontal line shows the pre-invasion mean, and open circles indicate values that are significantly different ($p < 0.1$, two-tailed t test) from the pre-invasion means

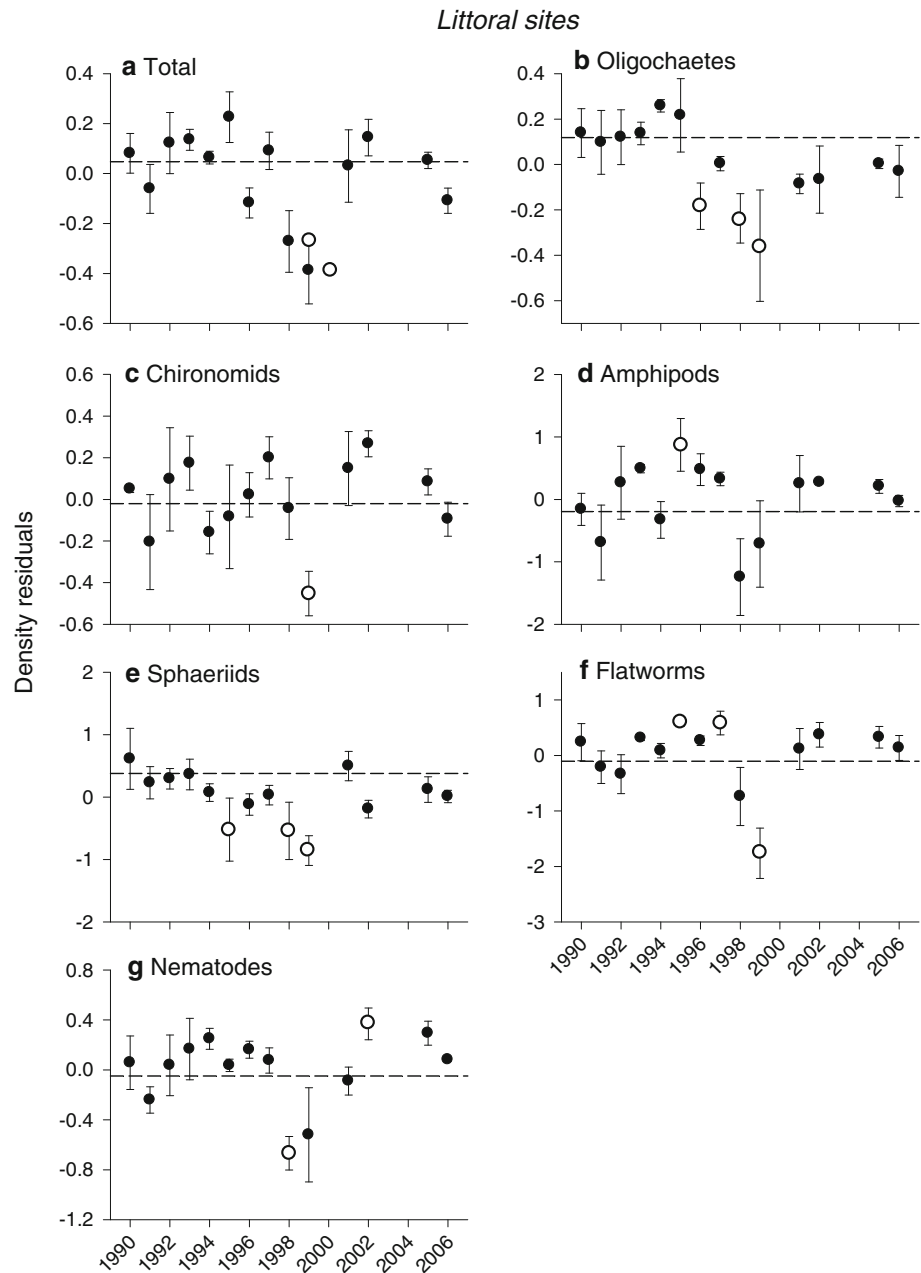


until about the year 2000, then recovered to near pre-invasion levels (Fig. 2). This initial decline was statistically significant (Strayer et al. 1998; Strayer and Smith 2001). Densities at the low point around the year 2000 were $\sim 22\%$ of pre-invasion densities for total zoobenthos, and ranged from a low of $\sim 1\%$ for sphaeriids to a high of 15–20% for oligochaetes and chironomids. The only taxon that did not follow this pattern was the Amphipoda, which did not show such a clear temporal pattern of decline or recovery. Neither the mean density of total macrobenthos nor the change in benthic densities between succeeding years was significantly

correlated ($p = 0.05$) with aggregate filtration rates of the zebra mussel population.

A very different dynamic occurred in littoral stations. Total zoobenthos and most individual taxa did not show any clear pattern of decline or recovery (Fig. 3). Only the oligochaetes and sphaeriids showed a pattern similar to what occurred in deep water. Even for these taxa, the decline was not as deep in littoral stations as in deepwater stations (the low points were ~ 33 and 6% of pre-invasion densities for oligochaetes and sphaeriids, respectively, in littoral stations).

Fig. 3 Long-term trends in populations of benthic animals at littoral sites ($n = 3$) in the Hudson River. **a** Total, **b** oligochaetes, **c** chironomids, **d** amphipods, **e** sphaeriids, **f** flatworms, **g** nematodes. Densities are expressed as residuals from the mean density at each station (± 1 SE) after $\log_{10}(X + 1)$ transformation (see “Materials and methods” for details); thus a difference of 0.3 indicates a twofold change and a difference of one indicates a tenfold change in population density. The dashed horizontal line shows the pre-invasion mean, and open circles indicate values that are significantly different ($p < 0.1$, two-tailed t test) from the pre-invasion means



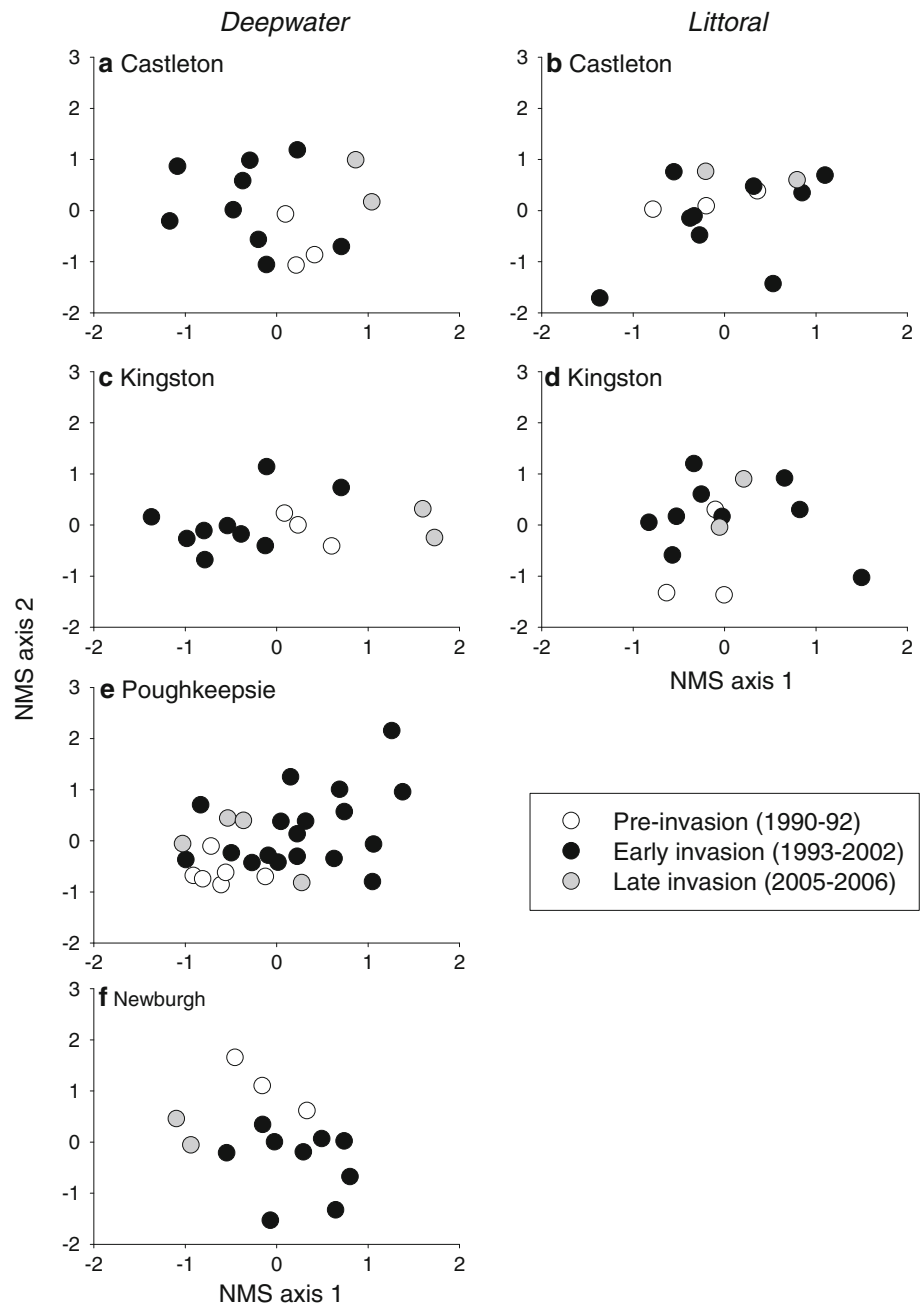
Ordinations confirmed the pattern of change and recovery in deepwater stations but not littoral stations (Fig. 4, Table 2). There were significant differences in taxonomic composition among time-periods at all four deepwater stations (Table 2). Generally, at deepwater stations (lefthand panels in Fig. 4) communities shifted away from pre-invasion (1990–1992) composition in the early years of the invasion (1993–2002), then tended to shift back toward pre-invasion composition in 2005–2006 (i.e., the gray circles cluster near the white circles in Fig. 4). This shift was significant at two of the deepwater stations (Kingston and Poughkeepsie). No such clear pattern of shift and recovery

occurred at littoral stations (righthand panels of Fig. 4; Table 2).

Discussion

The characteristics of the Hudson River zebra mussel population and its effects changed through time. The zebra mussel population itself showed both short-term cycling and longer-term declines in survivorship. The cycling appears to be a result of strong interactions between adults and juveniles, and may be a persistent characteristic of

Fig. 4 Results of NMS ordinations of zoobenthic community structure at deepwater sites (*left*) and littoral sites (*right*) in the Hudson River. Each *circle* shows an individual year, with pre-invasion years (1990–92) in *white*, post-invasion years (1993–2002) in *black*, and late invasion years (2005–2006) in *gray*. Sites are shown in order from upriver (*top*) to downriver (*bottom*). Because both of the sampling stations at Poughkeepsie are in deep water, they are combined in this figure. Ordination of the data from the littoral site at Newburgh did not produce interpretable results



food-limited zebra mussel populations (Strayer and Malcom 2006). The >100-fold decline in survivorship of adult zebra mussels led to declines in aggregate population filtration rate, and perhaps population density and body size; the latter are, however, partially obscured by the population cycling. The decline in aggregate filtration rate of the population (already down by 82%) is especially important, because filtration is the strongest functional link between zebra mussel populations and the ecosystems they invade (Strayer 2009). If this decline continues, we expect that many parts of the Hudson River ecosystem will recover toward pre-invasion levels.

Although these long-term changes themselves are relatively clear, the reasons behind them are not. Blue crabs currently appear to be important predators of zebra mussels in Hudson (Carlsson et al. 2010). Current mortality rates from blue crabs and from all causes other than crab predation are each much higher than total mortality rates on zebra mussels early in the invasion (Carlsson et al. 2010), but we have no evidence that populations of crabs or other predators in the Hudson have increased. It seems likely that at least some part of the increased mortality on zebra mussels results from increases in per capita predation rates of native predators (Carlsson and Strayer 2009; Carlsson et al.

Table 2 Statistical analyses of the ordinations shown in Fig. 4. The chance-corrected within-group agreement measures the effect size of differences among the three time-periods (1990–1992, 1993–2002, 2005–2006), and ranges from zero if within-group heterogeneity equals what would be expected by chance to one if the species composition was identical within each group (McCune and Grace 2002). The p (recovery) was tested with a one-tailed t test of whether the ordination scores (as shown in Fig. 4) from the late invasion period (2005–2006) were significantly closer to the pre-invasion (1990–1992) scores than to the early invasion (1993–2002) scores

Station	Chance-corrected within-group agreement (p)	p (recovery)
C3 (deep)	0.137 (0.005)	0.29
K6 (deep)	0.239 (0.0007)	0.00004
P1 + P6 (deep)	0.108 (0.00009)	0.02
N7 (deep)	0.182 (0.002)	0.30
C1 (littoral)	0.039 (0.16)	0.09
K8 (littoral)	0.092 (0.03)	0.86
N1 (littoral)	No interpretable ordination	

2009, 2010). Finally, it is possible that some poorly monitored disease or parasite of zebra mussels has increased in the Hudson. Because we do not understand the reasons for the increased mortality rates, we cannot be sure that they will continue into the future.

At deep, unvegetated sites, populations of most benthic animals declined sharply after the zebra mussel invasion, then recovered. This parallels a similar pattern of steep loss and delayed recovery of zooplankton (Pace et al. 2010) and native bivalves (Strayer and Malcom 2007) in the Hudson. We saw a very different pattern in littoral sites, where most benthic animals showed no clear temporal dynamic following the zebra mussel invasion. It seems likely that losses of planktonic food were buffered by increases in production by macrophytes and attached algae in the littoral zone (Caraco et al. 2000; Strayer and Smith 2001; Strayer et al. 2004), damping any response of littoral food webs to the zebra mussel invasion.

We do not know the precise mechanisms (if any) that link the changes in the Hudson's zebra mussel population to the recovery of the deepwater zoobenthos. The density of benthic animals was not simply correlated with the aggregate filtration rate of the zebra mussel population. The declines in zebra mussel filtration have not resulted in increased phytoplankton biomass (Pace et al. 2010), although it is possible that the composition or seasonal dynamics of the phytoplankton have changed in a way that benefits the zoobenthos. For instance, it is possible that centric diatoms, which sink quickly and support benthic animal growth in lakes (Johnson and Wiederholm 1992; Goedkoop and Johnson 1996) and are not captured very effectively by zebra mussels (Bastviken et al. 1998), now form a greater

proportion of the Hudson's phytoplankton than in past years. Unfortunately, coarsely resolved data on phytoplankton composition do not support this idea (Fernald et al. 2007), and we do not have any detailed data on phytoplankton composition with which to test this idea.

Although it is possible that some external factor is driving zoobenthic dynamics in the Hudson, this seems unlikely to us. None of the obvious candidates for external drivers is a promising explanation. The pattern of decline and recovery in the zoobenthos does not correspond to patterns of variation in freshwater flow and water temperature, and at least deepwater zoobenthos appears to be relatively insensitive to variation in flow (cf. Strayer et al. 2008). Recent changes in nutrient loadings to the Hudson are thought to be modest, and primary production in the study area is not nutrient-limited (Cole and Caraco 2006).

Whatever its causes, the recovery of benthic animals and zooplankton probably is important for the Hudson's fish populations. These animals provide the forage base for fish in the Hudson. By the late 1990s, the zebra mussel invasion had caused the biomass of fish forage in the Hudson to fall by 50% (Strayer and Smith 2001). Forage in the open-water of the river fell by 56%, while actually rising in the littoral zone. This shift in fish forage was associated with declines in population sizes and growth rates of open-water fish species, and increases in population sizes and growth rates of littoral fishes (Strayer et al. 2004). After zebra mussels invaded, populations of open-water fishes tended to be centered further downriver (away from the zebra mussel population), while populations of littoral fishes tended to be centered further upriver (where zebra mussels were abundant). Zooplankton biomass in the Hudson has already reached pre-invasion levels (Pace et al. 2010), and now that benthic invertebrates are recovering, we predict that fish abundance, growth, and distribution will likewise recover toward pre-invasion values.

It is unclear whether the changes that have occurred in the Hudson have also occurred in other ecosystems that zebra mussels have invaded. Although it is often said that zebra mussels decline after an initial outbreak phase, very few satisfactory long-term datasets on zebra mussels have been published with which to test this idea.

Several papers have described increases in benthic animal populations within zebra mussel beds (Haynes et al. 2005; Ward and Ricciardi 2007, and papers cited therein), or declines in benthic animal populations in entire ecosystems that have been invaded by zebra mussels (Strayer and Smith 2001; Nalepa et al. 2003, 2007, 2009). However, there is scant evidence that these effects diminish with time. Nalepa et al. (2003) and Haynes et al. (2005) reported that initially severe effects of *Dreissena* moderated a few years after invasion, perhaps responding to temporal declines in

Dreissena abundance or biomass. Because neither of these studies was continuous over the long term, it is unclear whether these changes were long-term trends or short-term variation. In contrast, Ward and Ricciardi (2007) found that time since invasion was not a useful predictor of zebra mussel impacts on zoobenthos, and Nalepa et al. (2009) reported that impacts of *Dreissena* on benthic invertebrates in Lake Michigan were increasing with time.

These discrepancies across studies may have several explanations. First, some studies focus largely on benthic animals that live in and among zebra mussel beds, rather than on entire ecosystems, which may lead to differences in conclusions among studies (cf. Strayer 2009). Alternatively, it may be that the large differences among the sites in Ward and Ricciardi's meta-analysis obscured any temporal changes, or that the studies included in the meta-analysis did not span a long enough period of time for temporal changes to be detectable. On the other hand, the pattern of decline and recovery that we observed in the Hudson may actually occur only at some subset of invaded sites. We are not aware of any special characteristics of the Hudson that would make it differ from other ecosystems in this respect, but it is difficult to say more without seeing the results of long-term studies in more ecosystems.

More generally, our study shows that the effects of a non-native species may vary considerably over time. Knowing whether the severe effects of an invader that are observed early in an invasion are likely to be permanent or just a transient effect could be very helpful in guiding management responses. Unfortunately, at this point, we know very little about how the ecological effects of non-native species change through time (Strayer et al. 2006). It will be difficult to make progress on this problem without more long-term studies of the ecological effects of invaders.

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