

Recovery of native zooplankton associated with increased mortality of an invasive mussel

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Abstract. Impacts of alien species may change with time but there are few long-term studies of invasions. Here, we present an example of a substantial change in the impact of an alien species that appeared more than a decade after initial invasion. We studied an invasion of zebra mussels (*Dreissena polymorpha*) into the Hudson River (New York, USA) over a 22 year period (1987–2008) including five years of pre-invasion observations. Zebra mussels caused a substantial and sustained decline in phytoplankton, and until recently, zooplankton. However from 2005–2008, the abundance of copepods, copepod nauplii, and rotifers recovered while tintinnid ciliates partially recovered. These changes are consistent with an increased mortality of larger (> 20 mm) zebra mussels that has altered the filter-feeding impact of the population. Large mussels had a threshold relationship with the abundance of nauplii, rotifers, and zebra mussel veligers suppressing these microzooplankton when filtration by large mussels was > 0.5 m³ m⁻² d⁻¹. Zooplankton biomass declined approximately 50% after the zebra mussel invasion but has recovered to pre-invasion levels. Overall, while zebra mussels are still present and abundant in the Hudson River, their impact on zooplankton has significantly diminished.

Key words: alien species; *Dreissena polymorpha*; Hudson River; invasion; long-term studies; population size structure; zebra mussels; zooplankton.

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INTRODUCTION

Biological invasions are widely recognized as one of the major factors altering the structure and function of modern ecosystems (Lockwood et al. 2007, Davis 2009). Alien species are found in all types of ecosystems, and they can affect populations of native species, biogeochemical cycling, physical habitat structure, ecosystem services, and economic values (Lockwood et al. 2007, Keller et al. 2008). While many impacts of invasive species are known, remarkably few studies consider how invaders and their effects change over time. Most studies are limited to a few years and are typically done either immedi-

ately after the invader appears or decades to centuries after the invasion (Strayer et al. 2006). Consequently, there are few examples of how invader impacts change despite the evidence that temporal changes can be large (Strayer et al. 2006, Hawkes 2007).

Several mechanisms can lead to long-term changes in the effects of invaders. These include evolution of the invader and/or species within the invaded community, shifts in functional attributes of species including the invaders as a consequence of phenotypic plasticity, shifts in species composition within invaded communities, changes in biogeochemical cycles and/or physical structure within the invaded ecosystem,

and interactions with other variables (such as climate) that change over time (Strayer et al. 2008). All of these mechanisms probably are common, operate over a wide range of time-scales, and can lead to large changes in the effects of the invader (Strayer et al. 2006). Although some hypotheses suggest that the effects of invaders should moderate over the long term because enemies accumulate (e.g., Hawkes 2007), other mechanisms could cause the effects of the invader to intensify. Thus, currently there are few generalizations about how much the effects of an invader will change through time, the time over which changes will occur, and even whether the effects are likely to increase or decrease.

Freshwater ecosystems are typically susceptible to invasion by alien species, and these invasions represent an important force of ecological change (Strayer 2010). Here, we present an example of a substantial change in the impact of an alien species for a freshwater tidal ecosystem that appeared more than a decade after initial invasion. We have studied an invasion of zebra mussels (*Dreissena polymorpha*) into the Hudson River (New York, USA) over a 22 year period including five years of pre-invasion observations. Zebra mussels have sustained high abundance since they invaded and caused changes in the abundance, distribution, biomass and productivity of many groups of organisms (Strayer 2009). For example, an 80–90% decline in the biomass of phytoplankton occurred soon after the invasion (Caraco et al. 2006). Similar declines occurred in some zooplankton groups (Pace et al. 1998, Strayer et al. 2008). Zebra mussels can collectively filter a large size-spectrum of particles ranging in size from bacteria ($< 1 \mu\text{m}$) to small zooplankton (MacIsaac et al. 1995, Wong et al. 2003). However, individual feeding ability varies with size. Larger mussels ($> 20 \text{ mm}$) feed more effectively on zooplankton (MacIsaac et al. 1995). In this study, we document a recent recovery of zooplankton toward their pre-invasion abundance and biomass. This change is consistent with an increased mortality of larger zebra mussels that has altered the filter-feeding impact of the population.

METHODS

Our analysis is based on regular sampling of

the freshwater Hudson River estuary since 1987. We have previously described the study site and the methods in detail (Pace et al. 1992, Strayer et al. 2008) and provide only a brief summary here.

Study site

The Hudson River estuary extends 250 km from Manhattan Island in the south to Troy, New York in the north where further tidal flow is stopped by a dam. Most of the estuary is freshwater rather than saline. The average depth of the freshwater estuary is 8.3 m, and because of the relatively shallow depth along with winds and tides, the freshwater estuary is nearly always completely mixed vertically. The Hudson is turbid due to high concentrations of suspended particles. The water has high ionic content, is well buffered, and rich in nutrients.

Zebra mussels

Beginning in 1992 within approximately a year of their initial appearance, zebra mussel abundance was quantified using two methods. On soft sediments mussels were sampled using a 23 cm \times 23 cm PONAR grab. These samples were sieved through 2.8 mm mesh screen. The material retained on the screen was frozen. Subsequently, the samples were thawed, and zebra mussels were enumerated and measured (shell length). Rocky sediments were sampled by a diver who collected rocks from each sampling site. Mussels $> 2 \text{ mm}$ on these rocks were counted and removed. The area of the rock was estimated in order to convert abundances to areal units. Subsamples of the mussels removed from the rocks were measured to generate size distributions. The relative area of rocky versus soft sediments was estimated using PONAR grab samples at numerous sites based on samples that failed to return sediment. Abundances of mussels for the entire system were estimated based on a stratified random sampling of 48 PONAR sites in June and July and diver samples of 6 to 7 sites in August (every year) and June (for 11 of the 17 years).

Plankton

We visited a temporal sampling station located at river kilometer 152 near Kingston, New York every two weeks during the ice-free season (April to December) throughout the study (1987–2008).

Triplicate samples for macrozooplankton (post-naupliar copepods and cladocerans) were made with an open diaphragm bilge pump. Approximately 100 liters was pumped through an 80 μm mesh net. For microzooplankton (nauplii, rotifers, tintinnids), triplicate samples of two liters were collected with a peristaltic pump and filtered through a 35 μm mesh net. Samples were preserved in a formalin solution. Each replicate macrozooplankton and microzooplankton sample was counted with a stereomicroscope and inverted microscope, respectively to determine abundance.

The macrozooplankton at the long-term sampling station are dominated by two species of cyclopoid copepods and a cladoceran (*Bosmina* sp.) (Pace et al. 1992). For the purposes of this analysis we calculated the mean annual abundance of copepods and cladocerans. The microzooplankton are dominated by unidentified copepod nauplii, numerous rotifer species, and a tintinnid ciliate. For the purposes of this analysis, we calculated the mean annual abundance of nauplii, rotifers, and tintinnids. When there were missing values within a year, we estimated the value by averaging the values immediately before and after the missing abundance. Missing values were few except in 1988 where we only measured the abundance of microzooplankton at every other visit.

Zebra mussels have a pre-settlement planktonic life history stage known as a veliger. When zebra mussels appeared in the river, we begin collecting samples to determine veliger abundance. Initially (1992–1995), we enumerated veligers from live samples. Subsequently, we counted veligers in preserved samples, because of time constraints in our continuous sampling program. These two methods might give different estimates of abundance and so we do not make statistical tests on these data.

Whole water (unfiltered) samples were also collected at each visit to the Kingston station. Particles in these samples were concentrated onto GF/F filters under low vacuum. Chlorophyll was extracted from the filters and measured with a fluorometer.

Analysis

Zebra mussel filtration rates for the total population and for three size classes (small,

<10 mm; medium 10–20 mm; and large > 20 mm shell length) were estimated using an empirical model that relates body size to filtration (Strayer et al. 2008). We calculated the mean annual concentration of chlorophyll *a* (as a measure of phytoplankton biomass) and mean annual abundances of tintinnid ciliates, rotifers, copepod nauplii, cladocerans, and post-naupliar copepods from the temporal samples. Below we compare the abundances of zooplankton with mussel filtration rates for three time periods: “pre-invasion” (years 1987–1992), “post-invasion” (years 1993–2004), and “recovery” (years 2005–2008). The “recovery” period is justified below based on the abundance and size structure of the zebra mussel population.

To test for differences among periods we used a one-way analysis of variance grouping years into the three categories above. Data were transformed to equalize variance among groups. If the ANOVA was significant, a post-hoc means test (Tukey’s Honest Significant Difference) was used to distinguish among the three means. The interesting test in the current analysis concerned how abundances during the “recovery” years were similar to or different from the pre- and post- zebra mussel periods.

RESULTS

Zebra mussels have varied but sustained high abundance in the Hudson since their invasion (Fig. 1). The abundance of mussel size classes has also varied with a decline in the largest size class (> 20 mm) particularly in the most recent years (Fig. 1). Based on this decline in large individuals, we identified the years 2005–2008 for analysis of potential recovery of plankton. Experimental studies that have followed groups of mussels at specific sites found declines in abundance during mid to late summer with greater rates of decline observed in mussels outside of cages (Carlsson et al., unpublished data). These experimental studies indicate significant predator mortality while the population and size structure data presented here indicate the population has become increasingly variable with greater dominance by individuals in the small and medium size classes.

Zebra mussel filtration has declined since an initial large population was established in 1993 shortly after the invasion (Appendix). Filtration,

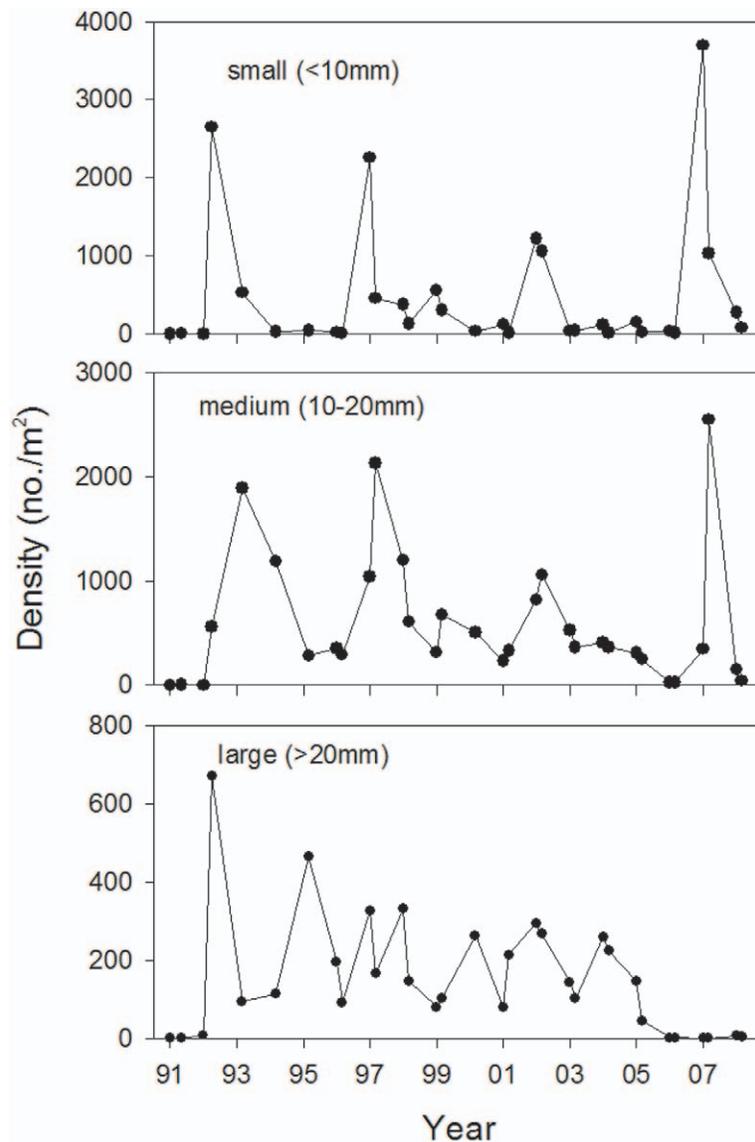


Fig. 1. Zebra mussel population dynamics for small 0–10 mm, medium 10–20 mm, and large 20–30 mm size classes. Data are for the freshwater Hudson River estuary.

however, has not declined monotonically but has varied with fluctuations in the population from $< 1 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ to $> 10 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$. Even in recent years relatively high mussel filtration rates occurred, as for example in 2007, when rates were in the range of $3\text{--}6 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ due to a large population of small and medium mussels (Fig. 1). Beginning in late summer of 2005, large mussel abundance and consequently filtration rates of this group declined to very low levels. Specifically, in June 2005 large mussel filtration

rates were $1.06 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ while in August 2005 rates were $0.26 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$. Subsequently, large mussel grazing rates were $< 0.03 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ for all estimates in 2006–2008.

Zebra mussel grazing has regulated the biomass and production of phytoplankton since the mussel population established in late 1992 (Caraco et al. 2006). Throughout the post-invasion period including the “recovery” period of 2005–2008, average annual chlorophyll concentrations were $< 10 \mu\text{g liter}^{-1}$ excepting one

year (2001). These values contrast sharply with means $> 15 \mu\text{g liter}^{-1}$ observed prior to the invasion (Appendix). Despite recent changes in the mussel population, phytoplankton biomass has remained low suggesting grazing is still regulating the community (Appendix). This interpretation is supported by ANOVA. While there was a significant difference among time periods, the comparison of means test indicated post-invasion and recovery means were not distinguishable (Table 1).

Macrozooplankton changes in response to the zebra mussel invasion and during the “recovery” period were less obvious than phytoplankton (Appendix). For copepods, ANOVA indicated significant differences among time periods with the pre-invasion and recovery periods grouping together (Table 1). Hence, copepods declined following the invasion and abundances in 2005–2008 returned to pre-invasion levels. Annual average cladoceran abundances were highly variable – with high (> 20 animals liter^{-1}) and low (< 10 animals liter^{-1}) values observed both before and after the invasion (Appendix). These dynamics partly reflect the negative impacts of both zebra mussels and high river discharge (Strayer et al. 2008). There was not an increase in the cladoceran population during the recovery period (Table 1).

Abundances of copepod nauplii and rotifers increased during the 2005–2008 “recovery” period approaching levels observed prior to the mussel invasion (Appendix), and these changes were highly significant (Table 1). Tintinnid ciliates were slightly more abundant during the recovery period, but abundances did not approach pre-invasion levels (Table 1). Zebra mussel veligers obtained high abundances dur-

ing the initial years of population establishment. After about 1993, average veliger abundance was low until increases similar to those observed in rotifers and nauplii occurred from 2005 onward (Appendix).

Why did nauplii, rotifers, and veligers increase significantly during 2005–2008 while phytoplankton did not? The change is consistent with the size-dependent feeding impacts of mussels where large mussel filtration rates have a threshold-like relationship with the abundance of naupli and rotifers (Fig. 2a, b). Prior to the invasion, filtration by large mussels was zero and nauplii were abundant (open circles in Fig. 2). When filtration by large mussels exceeded $0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ (years 1993–2004), nauplii and rotifer abundances tended to average < 30 and < 100 animals liter^{-1} , respectively (Fig. 2a, b). During the recovery period (2005–2008) when average annual large mussel filtration was $< 0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$, nauplii abundance varied from 30 to near 80 animals per liter, while rotifer densities varied from near 200 to greater than 800 animals per liter (red circles in Fig. 2a, b). The increases in copepod nauplii during recovery likely explain the increases in post-naupliar copepods as the latter forms are not effectively consumed by zebra mussels (MacIsaac et al. 1995). Further evidence of a threshold-like relationship between large zebra mussels and zooplankton is indicated by the lack of substantial increases in abundance rotifers or nauplii during years when large mussels were at lower abundance prior to the recovery period (e.g., 1999, 2001, 2003, see Fig. 1). During these years minimum densities were always > 79 large mussels m^{-2} and filtration was apparently sufficient (i.e., $> 0.5 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$) to sustain the suppression of rotifers and nauplii.

Table 1. Results of one-way ANOVAs where annual means were grouped into three periods: “Pre” invasion (1988–1991), “Post” invasion (1992–2004), and “Recovery” (2005–2008).

Group	F ratio	P	Means
Chlorophyll	31.3	< 0.0001	Pre ^A Recovery ^B Post ^B
Copepods	6.3	0.0076	Pre ^A Recovery ^A Post ^B
Cladocerans	3.4	0.0551	Pre ^A Post ^A Recovery ^A
Rotifers	36.2	< 0.0001	Pre ^A Recovery ^A Post ^B
Nauplii	16.7	< 0.0001	Recovery ^A Pre ^A Post ^B
Tintinnid Ciliates	37.4	< 0.0001	Pre ^A Recover ^B Post ^C

Notes: Columns are respectively groups, F-ratio for ANOVA, P-value for ANOVA, results of means tests where means are ranked (highest to lowest) and similar means are grouped by a common superscript letter (e.g., means with an ‘A’ are distinct from means with a ‘B’). All ANOVAs had 2 and 19 degrees of freedom. Chlorophyll, rotifer, and tintinnid ciliate data were log-10 transformed to equalize variances. Nauplii data did not require transformation.

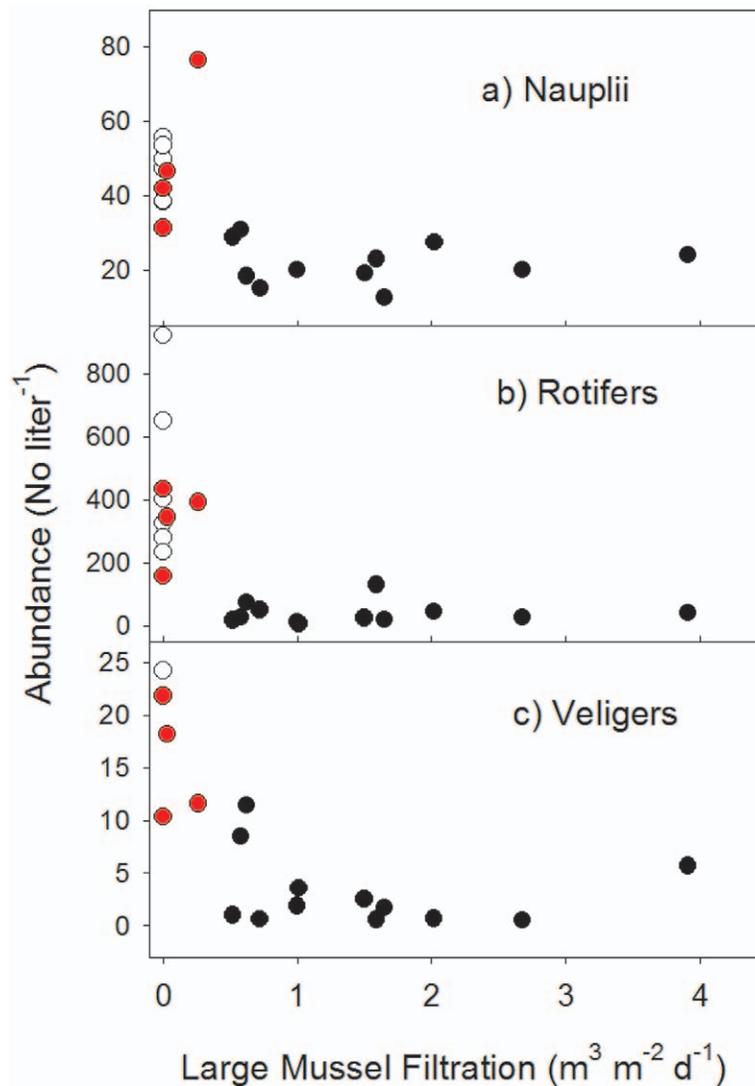


Fig. 2. Filtration by large zebra mussels (> 20 mm) and the mean annual abundance of a) copepod nauplii, b) rotifers, and c) zebra mussel veligers. Open circles are pre-invasion (1988–1992), closed circles are post-invasion (1993–2004), and red circles are “recovery” (2005–2008). The year 1992 was a transitional year where a large zebra mussel population built up late in the year but zooplankton abundances were mainly at pre-invasion levels until late in the year. The lower 95% confidence intervals for pre-invasion annual means of rotifers and nauplii respectively are 238 and 40.5 animals per liter. Note that all the post-invasion values fall below these intervals.

Similar to nauplii and rotifers, veligers were more abundant when large mussel filtration was low (Fig. 2c). The impact of large mussel filtration does not have the same sharp threshold observed for the other two groups of microzooplankton since large mussels both produce and consume veligers. In the 1993 and 1994 when the zebra mussel population was first estab-

lished, relatively high mean veliger abundance ($\sim 13\text{--}14\text{ liter}^{-1}$) occurred even when large mussel filtration was near the $0.5\text{ m}^3\text{ m}^{-2}\text{ d}^{-1}$ threshold (closed circles in Fig. 2c). Veligers were also more abundant on average in the year of highest filtration rates (1995) than in other post-invasion years when filtration was in the range of $0.5\text{ to }2.7\text{ m}^3\text{ m}^{-2}\text{ d}^{-1}$ (Fig. 2c). Overall, large

mussels had a negative but more variable impact on veligers, but as with the other microzooplankton, there was an apparent increase in veligers during the recovery period.

DISCUSSION

Zebra mussel impacts are changing mainly as a result of changes in the traits (size structure, filtration rate, and diet spectrum) of the population rather than simply changes in population size. During the recovery years mussel densities were typically above densities that had previously suppressed microzooplankton except in 2006 when mussel densities were < 100 animals m^{-2} . For example, in 2007 mussel densities were > 3000 animals m^{-2} on both survey dates and similar to other years of peak mussel abundance (e.g., 1993, 1997, 2002, Fig. 1). Similarly, while the filtration rate of the mussel population has declined over time, the population filtration was $> 3 m^3 m^{-2} d^{-1}$ in 2007—a rate normally sufficient to suppress microzooplankton. However, filtration by the largest size class was essentially nil during 2007. Hence, the recovery of rotifers and nauplii is consistent with differential feeding by larger mussels. These results illustrate how the impacts of an invader can change independently of abundance, requiring an assessment of population traits and their temporal variability (Parker et al. 1999).

Zebra mussel size structure is changing because of increased mortality. At the outset of the invasion, survival from age 1 to age 2 was about 50% (Strayer and Malcom 2006). Recent estimates indicate survival from age 1 to 2 is $< 1\%$ (Strayer et al., *unpublished manuscript*). Predators including blue crabs (*Callinectes sapidus*) are partly responsible for the mortality of zebra mussels (Molloy et al. 1997). In addition, other predators, disease and poor physiological condition resulting from limited or poor quality food may also be important in the increased mortality of zebra mussels (Molloy et al. 1997, Vanderploeg et al. 2009). We do not know if predation is size selective which might help explain the shifts in the population. Recent studies do indicate differences in feeding rates on zebra mussels between experienced and naive predators indicating potential adaptation of predators (Carlson and Strayer 2009). While we cannot exactly

specify the causes for the changing mortality rates, the consequences for plankton are significant.

Changes in planktivory might have contributed to the recovery of zooplankton. Earlier studies documented shifts in fish populations and declines in plantivores (Strayer et al. 2004). However, diet studies of planktivorous larvae of *Morone* spp. indicate that post-naupliar copepods and cladocerans, not microzooplankton, are the main prey (Limburg et al. 1997). Further, it seems unlikely that planktivory would have declined during the recovery period when zooplankton increased. Hence, we doubt that changes in planktivory explain the changes; however, population data of fishes and planktivorous invertebrates are not available to assess this hypothesis. In the special case of zebra mussel veligers, compensatory changes could occur with high adult mussel mortality promoting increased veliger survival through reduced predation by adult mussels and possibly higher food concentrations (e.g., future increases in phytoplankton). The cyclical dynamics of zebra mussels (Strayer and Malcom 2006) provide support for this idea.

Assessment of invader impacts is difficult and often does not extend beyond qualitative or quantitative measures for specific populations (Parker et al. 1999). In this study, we can assess the overall impacts of zebra mussels on the Hudson zooplankton community by estimating shifts in biomass. For this estimate we used previously determined average masses of individuals in the four main groups (rotifers, nauplii, post-naupliar copepods, and cladocerans, Pace et al. 1992) and our annual abundance values. Average biomass in the post-invasion years of 1992–2004 was $18 \mu g C L^{-1}$ compared to $35 \mu g C L^{-1}$ prior to the invasion. Thus, zooplankton biomass after the invasion was on average about 50% of the pre-invasion level (Fig. 3). The impact of the invasion on zooplankton productivity was likely even greater since the smallest forms were differentially impacted, dominated pre-invasion biomass, and typically have the fastest growth rates. For the years 2005–2008 average zooplankton biomass was $39 \mu g C L^{-1}$, similar to pre-invasion levels (Fig. 3). While zebra mussels are still present and abundant in the Hudson, their impact on zooplankton biomass has disappeared.

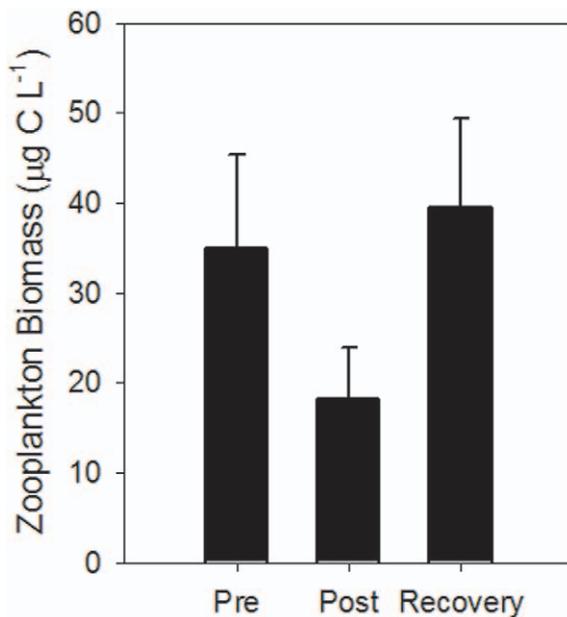


Fig. 3. Averages of annual zooplankton biomass for the pre-invasion, post-invasion, and recovery time periods. Error bars are 1 SD of the mean.

This study provides an example of the changing impacts of an alien species over time. The change appears to be driven by mortality that shifts size structure and the consequent impacts of the alien population through its feeding. While the impact of zebra mussels on zooplankton has diminished substantially, the mussels still have strong system-wide effects as evidenced by the sustained low phytoplankton biomass. Nevertheless if zebra mussel mortality rates remain high then the chronic (meaning longer-term, ongoing) impacts of the zebra mussel on the Hudson system might further relax. Alternatively, lower mussel mortality in the future should reduce zooplankton, especially microzooplankton. Because there are few long-term studies of alien species, we cannot conclude that alien impacts like those described in this paper typically lessen with time but this possibility represents an interesting hypothesis.

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APPENDIX

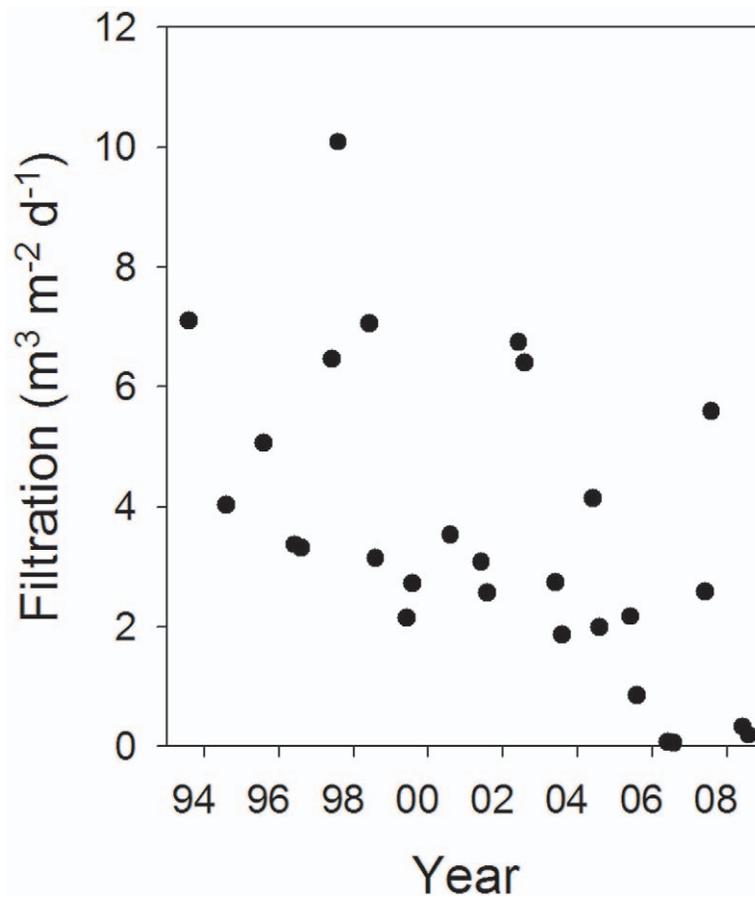


Fig. A1. Zebra mussel filtration rates 1987–2008, averaged for the entire freshwater tidal Hudson River. Rates are in cubic meters filtered per square meter of river per day.

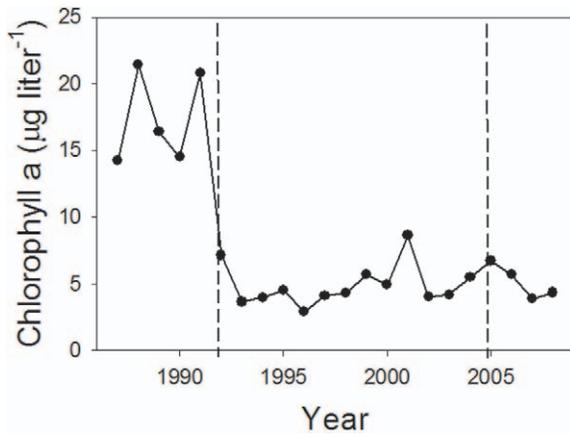


Fig. A2. Mean annual chlorophyll *a* concentrations in the Hudson River at Kingston from 1987–2008.

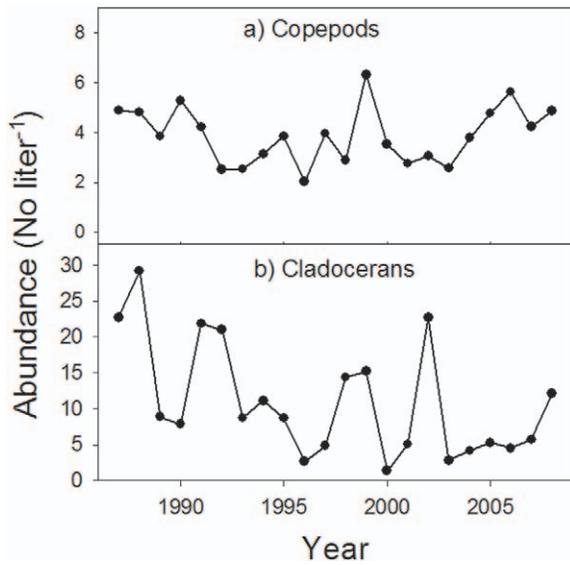


Fig. A3. Mean annual abundance of a) post-naupliar copepods b) cladocerans at Kingston from 1987–2008.

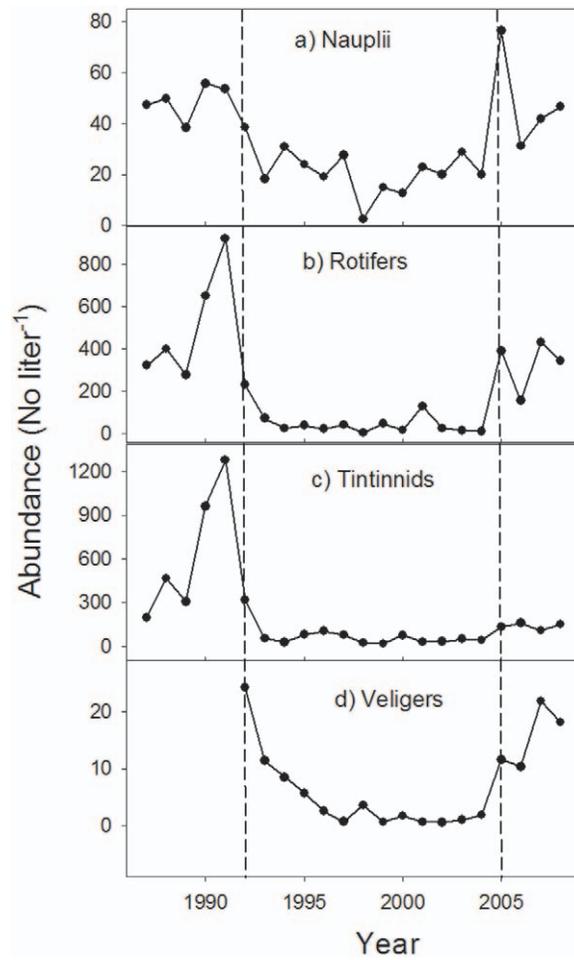


Fig. A4. Mean annual abundance of a) copepod nauplii, b) rotifers, c) tintinnids, and d) zebra mussel veligers at Kingston from 1987–2008.