

Biotic resistance on the increase: native predators structure invasive zebra mussel populations

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SUMMARY

1. Abundant native predators, parasites and pathogens that switch to consuming a hyper-successful exotic species may be able to control the invasive population. Native predators may, however, need time to adapt to feed effectively on an exotic resource. In this case, mortality on an exotic population from native predators could increase over time even without a numerical increase in the predator population.
2. We measured mortality of zebra mussels (*Dreissena polymorpha*) in the Hudson River both in controls open to predation and in enclosures that excluded large predators to estimate mortality of zebra mussels from large predators and other causes.
3. We found that predation by the blue crab (*Callinectes sapidus*), and perhaps other predators, causes high mortality on zebra mussels in the Hudson River estuary. This predation apparently led to increased mortality and altered population structure in the invader over time.
4. Long-term data from the Hudson River suggest that components of the invaded ecosystem, like rotifers, are recovering through predator-caused release from zebra mussel grazing. Increased mortality on hyper-successful exotic populations over time may be a common phenomenon with both ecological and management implications.

Keywords: adaptation, biotic resistance, ecosystem recovery, hyper-successful exotic species, native predators

Introduction

Hyper-successful exotic species have profound effects on native species, ecosystem functioning and human economies (Carlsson, Brönmark & Hansson, 2004; Lockwood, Hoopes & Marchetti, 2007). The mechanisms behind these effects are diverse, but often include a substantial transfer of materials and energy from the invaded ecosystem into the exotic population. The exotic population may therefore become a

large resource for any native species that can access it (King, Ray & Stanford, 2006; Watzin *et al.*, 2008; Carlsson, Sarnelle & Strayer, 2009a).

Abundant native predators that switch to eat a hyper-successful exotic species may start to resist its invasion or control its population (Carlsson *et al.*, 2009a). Such partial biotic resistance, in which the ecosystem is invaded by an exotic species, but native predators determine the exotic species' spread, abundance and effects (Carlsson & Strayer, 2009; Carlsson *et al.*, 2009a), could have important consequences for the invaded ecosystem. In many cases, the native predators need time to build up their own populations or adapt to feed efficiently on exotic prey (Carlsson

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et al., 2009a), so their potential to provide biotic resistance against exotic species may increase over time.

Here, we provide an example in which a native predator (the blue crab *Callinectes sapidus*), alone or in concert with other predators, causes high mortality on a problematic invader (the zebra mussel *Dreissena polymorpha*) in the Hudson River estuary. The zebra mussel (*Dreissena polymorpha*) is a hyper-successful invader in both Europe and North America with well-documented negative economic and ecological effects in invaded habitats (Strayer, 2009). Zebra mussels started to spread in the Hudson river in 1991, where they rapidly colonized available, hard substrata (Strayer *et al.*, 1996). As in other habitats invaded by zebra mussels, these filter-feeders attained great densities and shunted organic matter from the pelagic to the benthos in the Hudson River. In the early years of the invasion, zebra mussel biomass was *c.* 3 000 000 kg (dry mass, excluding shells), more than half of all heterotrophic biomass in the ecosystem (Strayer *et al.*, 1996).

It was therefore expected that native predators, like the omnivorous blue crabs (*Callinectes sapidus*) that migrate into the freshwater portion of estuaries during the summer, would start to feed on the zebra mussels in the Hudson River. Early experiments confirmed that blue crabs ate zebra mussels in aquaria (Molloy, Powell & Ambrose, 1994) and that blue crabs introduced into field enclosures could cause drastic reductions in zebra mussel numbers (Boles & Lipcius, 1997). The importance of predation by freely migratory blue crabs, with access to alternative food sources, on zebra mussels over larger spatial scales in the Hudson River estuary, however, was not known.

Here, we report the results of a field experiment to measure predation rates on zebra mussels by blue crabs and other mortality agents *in situ* in the Hudson River estuary, a site in which the dynamics of zebra mussels and their effects are well known (Strayer *et al.*, 1999; Caraco, Cole & Strayer, 2006; Strayer & Malcom, 2006; Strayer, Cid & Malcom, 2011).

Methods

Experiments

To investigate mortality on zebra mussels from predators, we conducted enclosure experiments at two sites along the freshwater tidal Hudson River. We

collected 100 fist-sized rocks containing zebra mussels from the tidal portion of the Hudson River (river kilometre 163) using SCUBA and placed them into plastic containers filled with river water. Ten of these rocks (mean projected surface area $72 \pm 19 \text{ cm}^2$) were randomly selected and brought back to the laboratory for analysis of zebra mussel number per rock, size-structure and dry weight/shell length relationship. In the laboratory, all mussels from each rock were counted and measured to the nearest 0.01 mm with electronic callipers.

Remaining rocks were randomly chosen and glued, mussel-side-up, to the centre of a concrete block, using Z-SPAR[®] (Carboline Company, St. Louis, MO, USA) underwater epoxy (Fig. 1). Experimental controls and enclosures were constructed by placing concrete blocks ($0.3 \times 0.3 \times 0.05 \text{ m}$) into tight-fitting

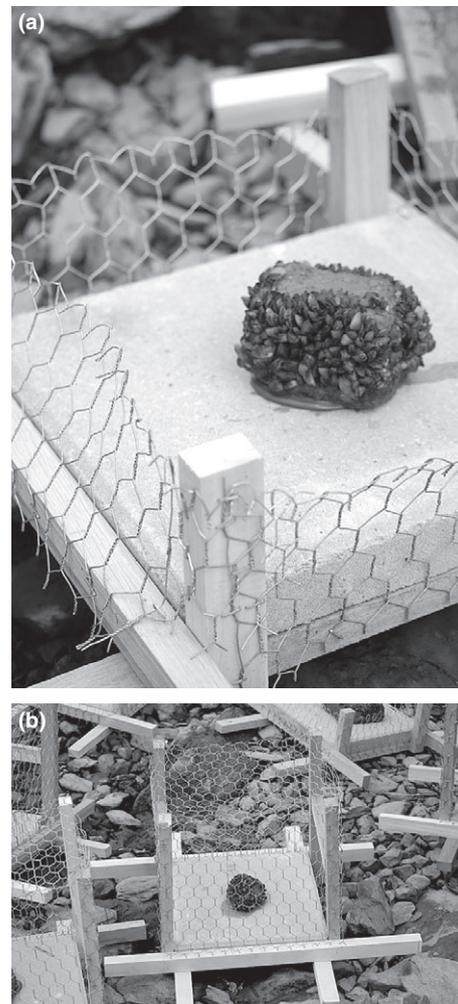


Fig. 1 (a–b) Controls and enclosures used in the experiment.

horizontal wooden frames that extended 0.2 m from each corner. This design resisted flipping in the strong tidal current. Controls mimicked the surroundings and were open to predation, but chicken wire (25 mm mesh), stapled to an additional 0.35-m-high vertical wooden frame created a box ($0.3 \times 0.3 \times 0.3$ m) that excluded larger predators from enclosures. This design did not exclude smaller potential predators such as leeches, crayfish or small fish.

All experimental units were deployed on the river bottom by scuba diving and attached with cable ties to one of two 20-m-long wire cables, which had been placed out in advance and anchored at each end by a concrete block. Controls were alternated with enclosures to smooth out spatial differences.

On 24 June 2008, we placed 34 experimental units (17 controls and 17 enclosures) at the 'southern site' (river kilometre 134) at a water depth of 5–7 m. On 27 June, we placed 36 experimental units (18 controls and 18 enclosures) at the 'northern site' (river kilometre 163) at a depth of 8–10 m. Depth was determined at slack-tide during high water with a diving computer.

The experiment ran for 92 days. Four controls and four enclosures were selected randomly and brought up at each site every 23 days after the start of the experiment in four consecutive, destructive samplings. The zebra mussels from each rock were scraped off with a knife, placed in a plastic bag and brought back to the laboratory in coolers. All mussels were counted, and the first 100 were measured to the nearest 0.01 mm with electronic callipers. On the last sampling date, the number of juvenile mussels that had settled on both the rocks and the concrete blocks was counted. One enclosure was not found at the time of sampling on the last sampling date at the northern site; this enclosure was found 7 days later and included in the analysis. Differences between treatments were tested using *t*-tests of \log_{10} -transformed numbers of zebra mussels per rock.

Four commercial-style crab traps (0.61 m wide and deep and 0.53 m high) baited with chicken were placed at each experimental site. Crab traps were checked and rebaited weekly. Crabs caught were sexed, and their carapace width was measured to the nearest 5 mm.

Long-term field studies

Pace *et al.* (2010) found that densities of planktonic rotifers in the Hudson declined substantially after

zebra mussels arrived and persisted at very low densities for the first 12 years following the invasion. After this time period, rotifer densities recovered, almost to pre-invasion densities. Pace *et al.* (2010) attributed this recovery to the disappearance of large zebra mussels from the Hudson River, since only large mussels are able to effectively ingest rotifers (MacIsaac, Lonnee & Leach, 1995). Because we found that the intense mortality from crabs, and perhaps other predators, was highly seasonal (see Results), we hypothesised that rotifer recovery would also be seasonal. Specifically we hypothesised that rotifer abundances would be higher during late summer and early fall after heavy zebra mussel mortality occurred. We tested this hypothesis using data on microzooplankton taken every other week during the ice-free season near Kingston (RKM 152) in the Hudson from 1987 to 2008. Samples were collected by pumping 2 L of water through a 35- μ m mesh net. The formalin-preserved samples were later counted under an inverted microscope (see Pace *et al.*, 2010 for details).

Results

Experiments

A total of 35 blue crabs were caught at the southern (20) and northern (15) sites. Mean carapace width was 150–155 mm. The first blue crab was caught at the southern site the 5th of August and at the northern site the 28th of August (Fig. 2).

The number of zebra mussels declined in both controls and enclosures during the 92-day experiment (Fig. 2). There was no difference in zebra mussel numbers between controls and enclosures at either site at the first two sampling times, before crabs appeared (Table 1). At the third and fourth sampling times, after crabs appeared, the number of surviving zebra mussels was significantly lower in controls where predation could occur than in enclosures from which large predators were excluded. At the last sampling time, mean zebra mussel numbers in controls were only 15.3% (southern site) and 6.8% (northern site) of those in enclosures.

Mean shell length of zebra mussels increased from 9.81 ± 1.91 to 13.30 ± 1.71 mm (mean of all enclosures \pm SD at start and last sampling). This corresponds to a mean dry weight increase from 3.8 to 8.6 mg or 126% during the course of the experiment. At the end of the

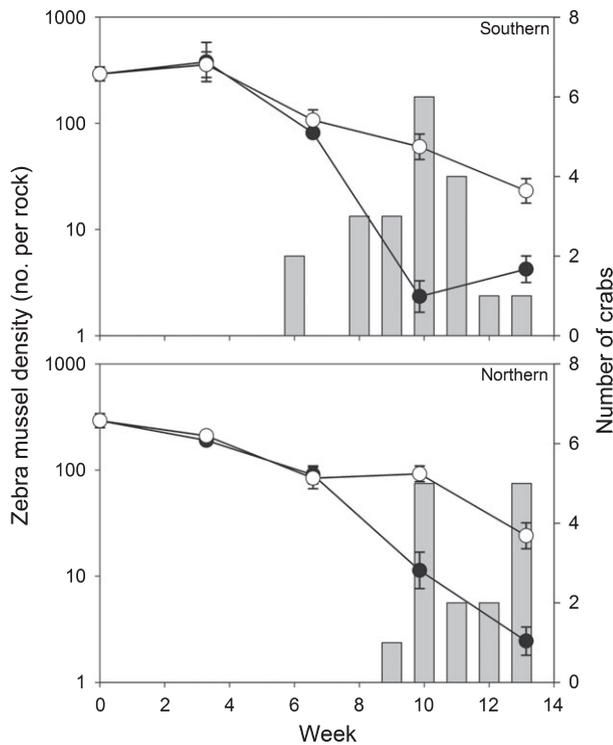


Fig. 2 Zebra mussel numbers in predator exclusions (white) and control blocks (black) at two study sites in the Hudson River, along with crab numbers (number of crabs per week, grey bars). Error bars are standard errors. Please note the log scale on the y-axis.

Table 1 Results of statistical analyses of effects of predator exclusion on densities of zebra mussels at the two study sites

Time	Norrie	Tivoli
Day 23	0.12 (0.91)	-0.67 (0.53)
Day 46	-1.18 (0.28)	0.24 (0.82)
Day 69	-7.41* (0.00031)	-4.85* (0.0028)
Day 92	-4.34* (0.0049)	-5.50* (0.0015)

Table shows the *t*-values of differences between the two treatments, with *P*-values in parentheses, for $\log(X + 1)$ -transformed data of 4 replicates per treatment at each site (i.e. 6 d.f.). The Bonferroni-corrected *P*-value to give an experiment-wide *P*-value of 0.05 is 0.00625; values that are significant at this value are marked with an asterisk.

experiment, there were marked differences in body sizes of zebra mussels in controls and exclusions (Fig. 3), with many fewer large zebra mussels in the controls than in the exclusions. We also found more settling zebra mussels on the concrete blocks and rocks in exclusions than on the control rocks and concrete blocks at both sites (Fig. 4).

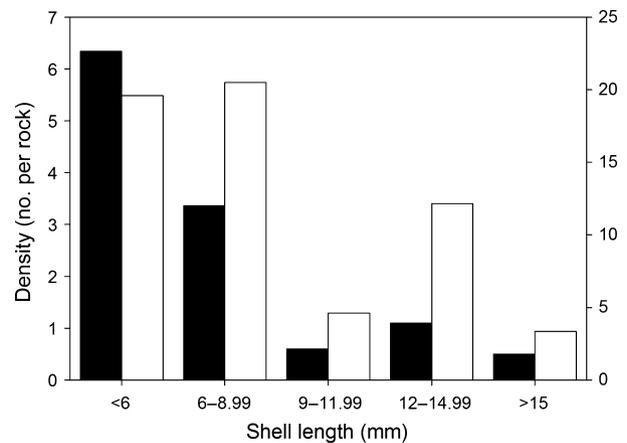


Fig. 3 Body sizes of zebra mussels on the final sampling date in the controls (black bars and left-hand y-axis) and exclusions (white bars and right-hand y-axis). The two size distributions are significantly different ($\chi^2 = 19.88$, d.f. = 4, $P = 0.0005$). Data for the two study sites are combined to increase sample size because of small numbers of mussels in some size classes at the northern sampling site.

Long-term field studies

Planktonic species like rotifers that are too large for small zebra mussels to filter efficiently (i.e. MacIsaac *et al.*, 1995) are recovering with seasonal dynamics that correspond to the time period of high mussel mortality observed in our experiments. For example, prior to the invasion, rotifer abundances were on the order of 1000 animals per litre from June to September (Fig. 5). Following the invasion, rotifer abundance was severely reduced (typically < 100 per litre) and summer maxima rarely exceeded 200 animals per litre (Fig. 5). During recent years (2005–08), following the reduction in large mussels in late summer/early fall maxima of >1000 animals were observed as were brief periods of high rotifer abundance in spring (Fig. 5).

Discussion

Before blue crabs arrived in late summer, there was no difference in adult zebra mussel mortality between controls open to predation and predator exclusions. When blue crabs arrived, however, numbers of adult zebra mussels dropped sharply in controls open to predation at two geographically separated experimental sites. This shows that large predators caused the high rates of mortality in adult zebra mussels that we recorded in the Hudson River. We find it likely

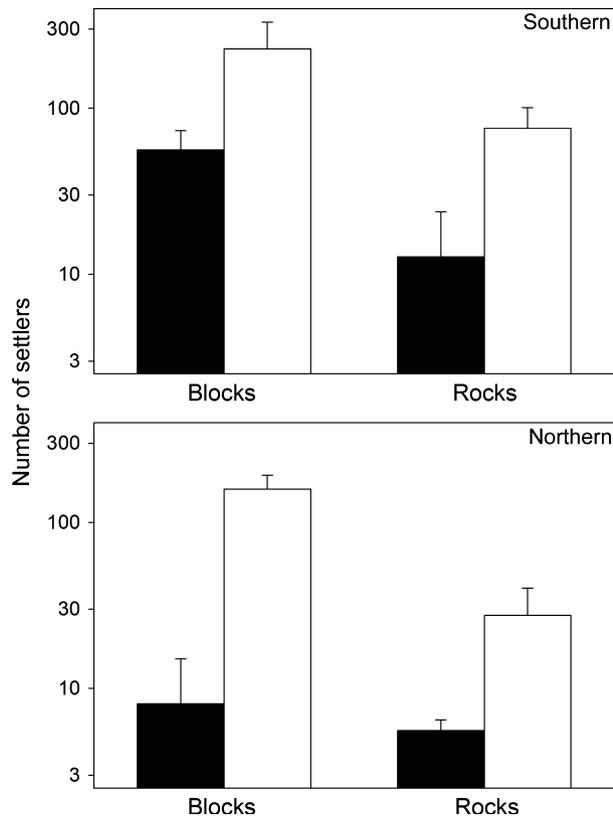


Fig. 4 Number of newly settled zebra mussels (+1 SE) on concrete blocks and rocks at the two study sites on the final sampling date. All differences between exclosures (white bars) and controls (black bars) were significant (southern site blocks, $P = 0.02$; southern site rocks, $P = 0.04$; northern site blocks, $P = 0.004$, northern site rocks, $P = 0.008$).

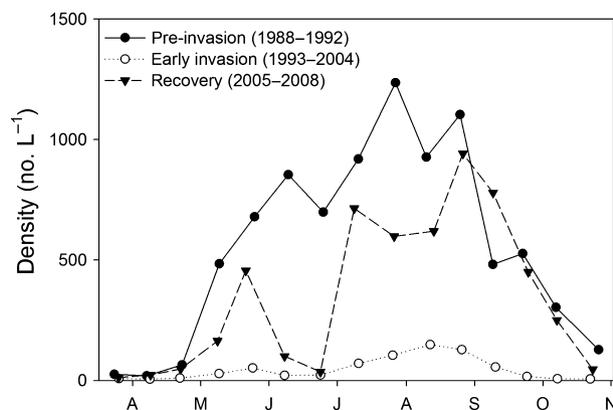


Fig. 5 Mean rotifer dynamics in pre-invasion (1987–92), post-invasion (1993–2004) and recovery years (2005–08).

that migratory blue crabs were responsible for the majority of the zebra mussel mortality during this time period but we cannot exclude the possibility that other large-bodied predators, for example predatory

fish, appeared at the same time as blue crabs at both our experimental sites and contributed to the predation recorded.

Although many native predators consume exotic zebra mussels (e.g. Petrie & Knapton, 1999; Bulté & Blouin-Demers, 2008; Pothoven & Madenjian, 2008), predation of this magnitude on adult, exotic zebra mussels has rarely been described. At the end of the experiment, we recorded marked differences in body sizes of zebra mussels in controls and exclosures, with many fewer large zebra mussels in the controls than in the exclosures. Migratory blue crabs, and perhaps other predators, in the Hudson River may thus have the potential to structure the zebra mussels by reducing the population to a single cohort of the smallest (and youngest) adult year class.

The mechanism behind the structuring of the zebra mussel population is therefore not size-selective predation, but rather a removal of almost all adult mussels. The remaining population consists of only minute, newly settled mussels.

In addition to blue crabs, there are other important sources of mortality for zebra mussels in the Hudson River. Zebra mussel numbers started to decline even before the arrival of blue crabs and in late July, we noted large numbers of dead mussels still attached to the substratum in both controls, exclosures and on surrounding rocks. Some of these zebra mussels still had flesh in them. This mortality did not differ between controls and exclosures. We therefore attribute this decline in zebra mussel numbers to factors other than direct predation, such as spawning fatigue, infection, parasites and high water temperatures alone or in combination, or to other, yet unknown factors.

Most interestingly, long-term data on the zebra mussel population in the Hudson River show that survival rates have declined steeply over time since the zebra mussels appeared in 1991. Total mortality of zebra mussels in 1993 (46% per year; Strayer *et al.*, 2011) was much lower than either the non-large-bodied predator-induced mortality (92% per 13 weeks, estimated from losses in the exclosures) in 2008 or the additional large-bodied predator mortality (85–93% per 13 weeks, estimated from the difference between exclosures and controls). We do not know the mechanisms behind this large change but discuss some plausible scenarios below. Whatever the cause, however, there are reasons to expect that these higher mortality rates may allow parts of the invaded

ecosystem to recover. For example, the shift in population size structure to dominance by smaller mussels led to lower overall filtration rates in the Hudson (Strayer *et al.*, 2011). Smaller mussels are also less effective at filtering larger particles (MacIsaac *et al.*, 1995), and this has allowed some larger planktonic species to recover (Pace *et al.*, 2010).

The seasonal pattern of zooplankton recovery also suggests the importance of predator control of zebra mussels. Rotifer abundances are high in spring but decline in early summer when the zebra mussels become large enough to filter them. Rotifer populations then recover later in the summer when intense predation and other mortality remove adult zebra mussels. While we cannot conclude that there is a causal relation between crab predation, mussel mortality and rotifer increases, the association of these dynamics is consistent with our hypothesis.

Declines in zebra mussel survival cannot be simply attributed to increasing blue crab numbers. Limited population data collected in the Hudson River by the New York State Department of Environmental Conservation did not indicate an increase in blue crab numbers for the relevant time period (Kenney, 2006 and Gregg H. Kenney, New York State Department of Environmental Conservation, pers. comm.). Therefore, per capita consumption rates of zebra mussels by crabs may have increased. Annual variation in crab numbers is high, and surprisingly, blue crab numbers were low and quite similar in the Hudson River in 1993 and 2008. On top of this, mortality in zebra mussels from causes other than blue crabs has increased.

Long-term data on invaders are rare (Strayer *et al.*, 2006), but increased mortality and lower population sizes (or even crashes) in previously hyper-successful exotic species may be common in nature (Simberloff & Gibbons, 2004). Increased predation by native predators can contribute to such declines because predators start to target the abundant invaders and because predators switch to the invader out of necessity if their original prey has been reduced. These shifts could result from increasing numbers of native predators or increased per capita consumption rates of the exotic by the predator. Native predators may become more efficient in consuming exotic prey through several mechanisms, including learning, social transmission, ontological changes in morphology and evolutionary adaptations (Carlsson *et al.*, 2009a). For instance, native predatory fish with pre-

vious long-term exposure to zebra mussels eat many more zebra mussels than fish of the same species that have shorter or no previous exposure to zebra mussels (Carlsson & Strayer, 2009). A plausible explanation for the declining zebra mussel survival rates in the Hudson River is that blue crabs (and perhaps other native predators) have adapted to feed more efficiently on zebra mussels, although we have no data with which to test this hypothesis. The increase in non-crab mortality in the Hudson River could likewise be an effect of parasites and diseases adapting to use zebra mussels more efficiently. Similarly, Bartsch, Bartsch & Gutreuter (2005) found that zebra mussel disappearance in cages open to fish predation in the Mississippi River increased over time even though numbers of native predatory fish did not. A promising approach to unravel the generality and mechanisms behind such findings would be to compare consumption rates of exotic prey between different populations of the same native predatory species with varying exposure times to the exotic prey.

Native predators may contribute to biotic resistance against exotic invaders, and this resistance may increase over time, allowing some ecosystem recovery. However, overharvest (e.g. Pauly *et al.*, 1998) or habitat loss may drive down predator populations, facilitating invasions and making their effects more severe and longer term. For example, blue crab populations are reduced by intense harvest along the North American East Coast (Silliman & Bertness, 2002). Because blue crabs resist the exotic European green crab (*Carcinus maenas*) (deRivera *et al.*, 2005) and exotic Rhaps whelks (*Rapana venosa*) (Harding, 2003) as well as the zebra mussel, these declines in a native, omnivorous key predator may have encouraged invasions in this heavily invaded region (Fofonoff *et al.*, 2009). Such interactions between overharvest of native predators and invasion intensity are probably to be common in many areas of the world where predatory fish communities are depleted rapidly (Myers & Worm, 2003), but reductions in predatory birds (Gruner, 2005) or mammals (Carlsson *et al.*, 2009b) also enhance invaders. Even if exotic invaders are initially released from natural enemies, native predators could be important in regulating their long-term dynamics and thus, effects. Conservation or sustainable harvest of native predators may promote both ecosystem stability (Daskalov *et al.*, 2007) and the management of harmful invaders.

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