APPLIED ISSUES

Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River

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SUMMARY

1. We monitored the density, recruitment and condition (body mass at a given shell length) of unionid clams in the freshwater tidal Hudson River before and during the early years of the zebra mussel (*Dreissena polymorpha*) invasion of the river. Zebra mussels were first seen in the river in 1991 and were dominant by the end of 1992.
2. Despite high densities of zebra mussels in the Hudson, only 30% of the unionids were infested with zebra mussels, far fewer than predicted by published models of zebra mussel–unionid interactions. We do not know why so few unionids were colonized.
3. After the arrival of the zebra mussel, densities of unionid clams fell by 56%, recruitment of young-of-the-year unionids fell by 90%, and condition of unionids fell by 20–50%. These changes occurred in all three of the common unionid species in the river.
4. *Elliptio complanata* appears to have been less severely affected by the zebra mussel than were *Anodonta implicata* and *Leptodea ochracea*, judging by declines in density, recruitment and condition.
5. Our results suggest that unionids may be affected by zebra mussels by competition for food as well as by fouling.

Introduction

Zebra mussels (*Dreissena polymorpha* (Pallas)) have caused profound ecological changes in the freshwater ecosystems of North America since their arrival in the mid-1980s, including losses of phytoplankton and microzooplankton (Nicholls & Hopkins, 1993; Fahnenstiel *et al.*, 1995; MacIsaac, 1996; Caraco *et al.*, 1996), local alterations of zoobenthos in and around zebra mussel beds (Stewart & Haynes, 1994; Dermott & Kerec, 1995), and changes in migration patterns of waterfowl (Wormington & Leach, 1992). One effect of special concern is the widespread mortality of unionid clams caused by the zebra mussel invasion (see reviews by Ricciardi, Whoriskey & Rasmussen, 1995; Schloesser, Nalepa & Mackie, 1996). North America has a rich, endemic fauna of unionids which already is in danger from habitat alterations and pollution (Neves, 1993; Williams *et al.*, 1993), so the zebra mussel invasion has been seen as a serious threat to this troubled fauna.

Previous studies of the effects of zebra mussels on unionids (summarized by Ricciardi *et al.*, 1995; Schloesser *et al.*, 1996) have focused on fouling (overgrowth) of unionids by zebra mussels as the primary cause of unionid death. Typically, North American

workers have reported that unionids are heavily colonized by zebra mussels (100–10 000 zebra mussels/unionid) soon after the arrival of zebra mussels. This fouling interferes with normal valve movements (opening and closing of the shell) needed for feeding and respiration, and presumably increases the costs of locomotion, burial, etc. for the host unionid, as well as sometimes deforming the unionid's shell. The energy reserves of the fouled unionids decline (Hebert *et al.*, 1991; Haag *et al.*, 1993), after which there is mass mortality of unionids. Zebra mussels cause such high mortality rates that the entire unionid community of an infested waterbody may disappear within 5 years of the arrival of zebra mussels.

Here, we describe a case study that differs from this typical pattern in two important ways: (i) unionids were not heavily colonized, despite dense populations of zebra mussels in nearby habitats; and (ii) unionids nevertheless suffered serious impacts, suggesting that competition for food, as well as the better known impacts from fouling, may be a strong interaction between zebra mussels and unionids. This study is a continuation of the work done in the Hudson River by Strayer *et al.* (1994) before the arrival of the zebra mussel, and is part of a comprehensive assessment of the ecological effects of the zebra mussel invasion on the Hudson River ecosystem (Strayer *et al.*, 1996; Caraco *et al.*, 1996).

Materials and methods

Study area

The study area is the entire freshwater, tidal part of the Hudson River, extending from RKM 99 (RKM = river kilometre; i.e. 99 km upriver from The Battery near the mouth of the Hudson River in New York City) near Newburgh to RKM 248 at Troy (Fig. 1). This reach covers 140 km^2 and has a mean depth of 8.3 m and a daily tidal range of 0.8–1.6 m. Mean annual freshwater discharge is 384–533 m^3 s^{-1}, depending on location within the study area, but net downriver discharge is dwarfed by tidal exchanges, which keep the water column well mixed. The water in the Hudson is hard (calcium 25–30 mg l^{-1}), nutrient rich (nitrate-N 0.4 mg l^{-1}; soluble reactive phosphorus *c.* 20 µg l^{-1}), and moderately turbid (Secchi disk transparency 1–2 m; suspended solids *c.* 20 mg l^{-1}). Although the Hudson is contaminated with PCBs (Limburg, Moran
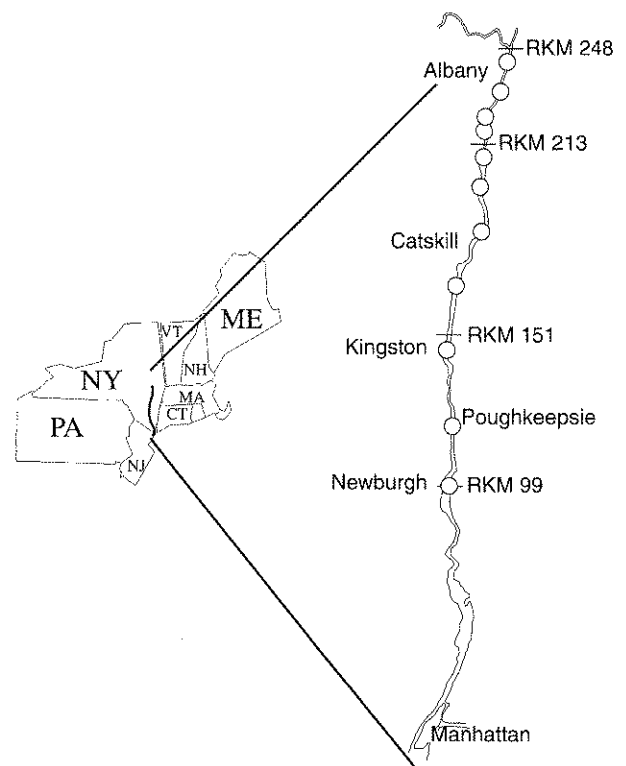

Fig. 1 Map of the study area showing location of sampling transects (open circles). RKM = river kilometre (i.e. kilometres upriver of The Battery in Manhattan).

& McDowell, 1986), water quality in the study area usually is considered to be good, and several municipalities draw drinking water from the river. This summary was taken from Strayer *et al.* (1994) and Caraco *et al.* (1996), and compiled from various sources.

Zebra mussels were first detected in the Hudson in 1991, and spread rapidly through the study area (Strayer *et al.*, 1996). Because of the timing and location of sampling, collections from 1991–92 represent pre-zebra mussel conditions (Strayer *et al.*, 1994), and those from 1993–95 represent post-invasion conditions.

Methods

Methods for 1991–92 were described in detail by Strayer *et al.* (1994). During June–August we took unionids at eighty-nine stations, sampling in a two-stage, stratified random design. At each station we took five replicate grabs from a boat with a standard (23 cm × 23 cm) PONAR grab, and sieved the samples through a 2.8-mm mesh sieve in the field. We identified all unionids collected, and measured the length, height
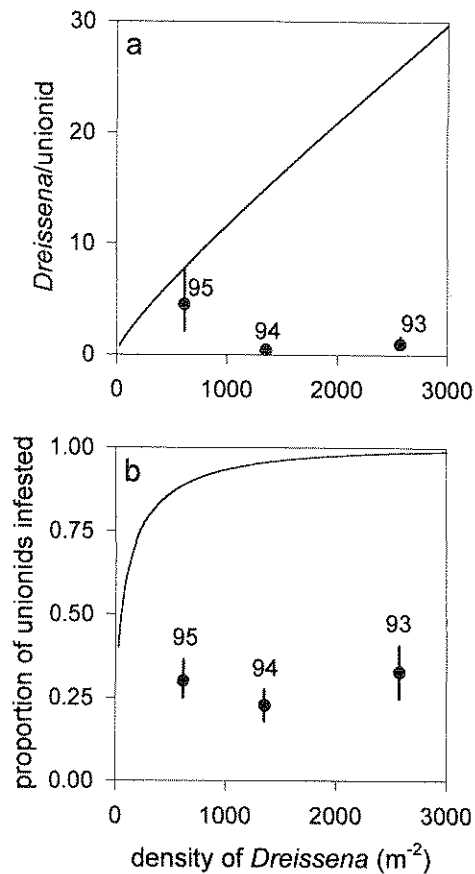
Fig. 2 Infestation of unionids by zebra mussels in the Hudson River, 1993–95: (a) mean number of zebra mussels per unionid; (b) proportion of the unionid population infested by zebra mussels. Vertical bars show 90% confidence limits of means. Numbers of unionids examined were 301 (1993), 189 (1994) and 162 (1995). Solid lines show predictions from eqns 13 and 14 of Ricciardi *et al.* (1995), which were based on data from various rivers and lakes in North America. Data for the Hudson are weighted means for the study area.
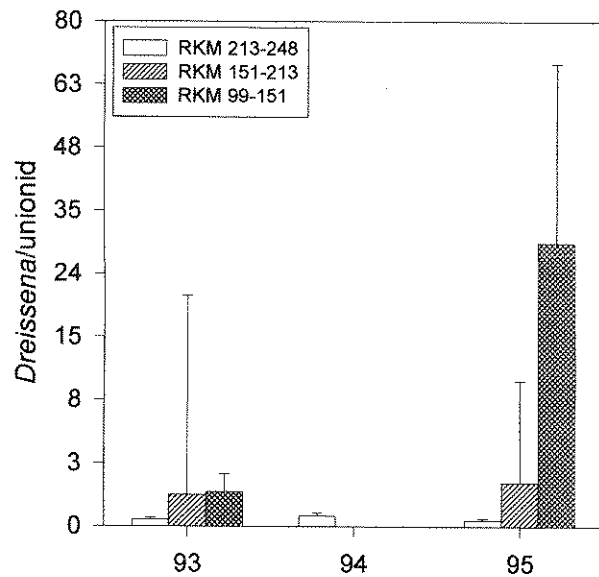

Fig. 3 Infestation of unionids by zebra mussels in various sections of the study area, 1993–95. Vertical bars show 90% confidence limits of means. The ordinate is square-root scaled.

and width of their shells as well as the shell-free dry mass of their bodies.

In 1993–95 we sampled unionids along eleven transects (Fig. 1), which were grouped into three strata (RKM 99–151, RKM 151–213 and RKM 213–248), based on the results of our 1991–92 survey. Each transect contained four stations, randomly located across the river. Ten of the transects and forty of the stations were included in the 1991–92 survey. As in 1991–92, we took five grabs with a standard PONAR grab at each station, and sieved the samples in the field through a 2.8-mm mesh sieve. Samples were taken in July and August of each year.

Each individual unionid was placed in a separate bag, then placed on ice until returned to the laboratory, where it was frozen. We counted and measured the shell lengths of the zebra mussels on each unionid. We measured the length, width and height of unionid shells to the nearest 0.1 mm using vernier calipers. We removed the soft parts, dried them overnight at 60 °C, and weighed them.

Although we were not able to determine the age of unionids from shell structure (Strayer *et al.*, 1994), we could recognize young-of-year animals by their small size. An animal was assumed to be young-of-year if its shell length was less than 18 mm (*Elliptio complanata* (Lightfoot)), 31 mm (*Anodonta implicata* Say), or 20 mm (*Leptodea ochracea* (Say)) (cf. Fig 4 of Strayer *et al.*, 1994).

Data on spent shells were collected only in 1992 (pre-zebra mussel) and 1995 (post-zebra mussel), and only in the upper section of the study area (RKM 213–248), where unionids are most abundant (Strayer *et al.*, 1994). Along each of nine transects in 1992 and four transects in 1995, we visited four randomly selected stations, collecting five grabs with a standard PONAR grab at each station. Spent shells collected on a 2.8-mm mesh sieve were identified and counted; any shell fragment representing more than half a valve was counted as a valve, and unpaired valves were counted as half shells.

Unless otherwise noted, data are presented as weighted means for the entire study area. Confidence
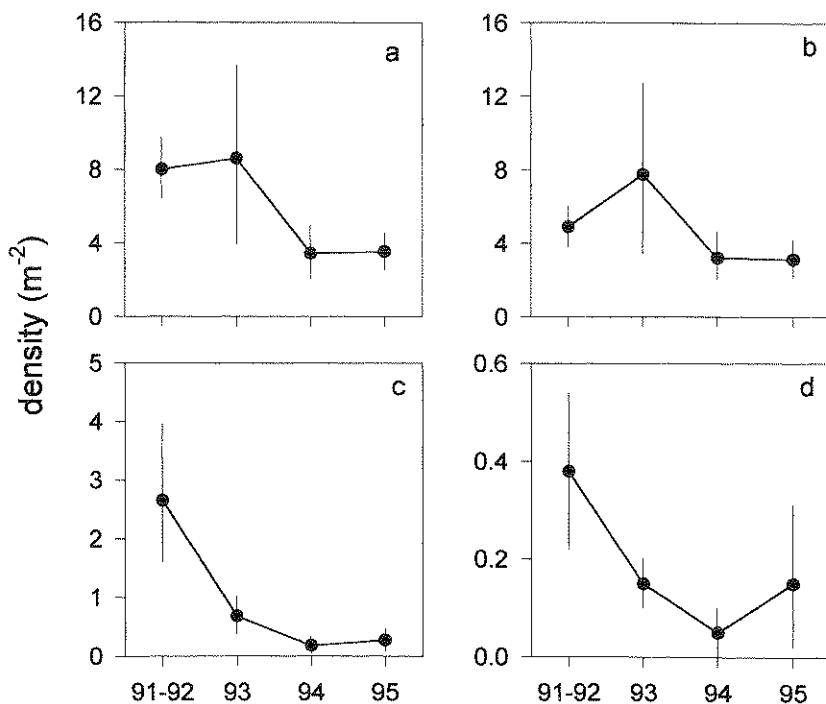
Fig. 4 River-wide mean densities of: (a) all unionids; (b) *Elliptio complanata*; (c) *Anodonta implicata*; (d) *Leptodea ochracea*. Vertical bars show 90% confidence limits of the means. The significance of differences between 1991–92 and 1995 are < 0.001 for all unionids and for *Anodonta implicata*, 0.03 for *Elliptio complanata*, and 0.08 for *Leptodea ochracea*.

intervals around estimates of densities (i.e. Figs 4 and 6) were calculated by bootstrapping using 1000 runs with Resampling Stats® (Bruce, 1993). Differences between 1991–92 and 1995 in unionid densities and spent shell densities (i.e. Figs 4 and 5) were likewise tested by resampling, using 1000 runs.

To identify the factors related to the intensity of infestation (i.e. the number of zebra mussels/unionid), we ran an ANCOVA using year, section of river (RKM 99–151, RKM 151–213, RKM 213–248), species of unionid and shell length as independent variables. The dependent variable was the square root of the (number of zebra mussels + 1).

Results

Zebra mussels were first seen in the Hudson River in May 1991, and quickly became abundant: river-wide mean densities between September 1992 and August 1995 were 600–3900 ind. m^{-2}, and local densities on hard substrata often exceeded 10 000 ind. m^{-2} (Strayer *et al.*, 1996, and unpublished). Nevertheless, infestation of unionids by zebra mussels has been small and far below that seen in other lakes and rivers in North America (Fig. 2). The average shell length of zebra

mussels found on unionids in the Hudson in 1993–95 was 13.9 mm ($n = 410$).

Infestation intensity was significantly related ($P < 0.005$) to year, section of river (Fig. 3) and shell length, but not to the species of unionid (i.e. all three species were infested equally). Nevertheless, the overall fit of this ANCOVA was low ($r^2 = 0.18$).

During this time of low infestation, densities of all three unionid species in the Hudson River declined sharply (Fig. 4). The severity of the decline differed among the species: 90% for *Anodonta implicata*, 61% for *Leptodea ochracea* and 36% for *Elliptio complanata*. Combined density of all unionids fell by 56% between 1991–92 and 1995.

Confirming this substantial mortality of unionids, the densities of spent shells of all three common unionid species rose sharply between 1992 and 1995 in the upper part of the study area (RKM 213–247, the only area for which we have data; Fig. 5). The observed increase in spent shell density in this area closely balanced the observed decline in density of live unionids for each of the three species.

The increase in mortality of unionids between 1991–92 and 1995 was paralleled by a drop in recruitment of young-of-year of all three species of unionids (Fig. 6). Again, the severity of this drop differed among the
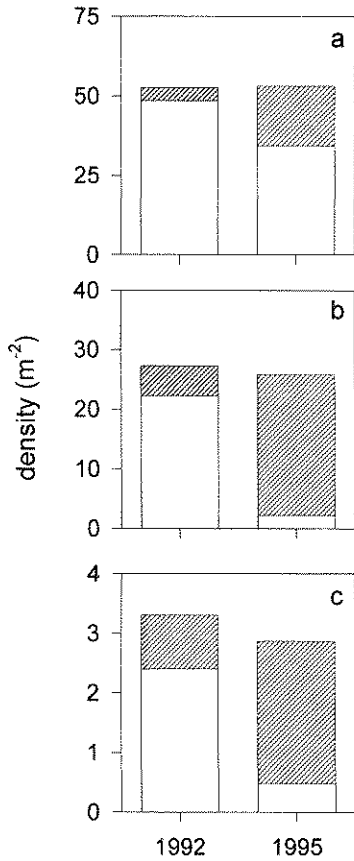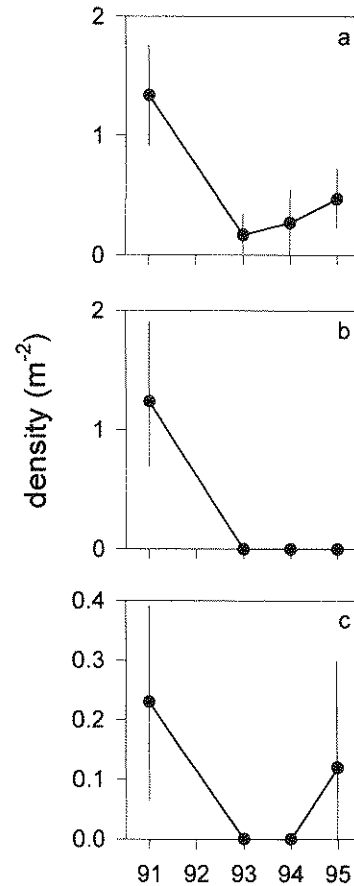
Fig. 5 Densities of live animals (white) and spent shells (hatched) in the upper section of the Hudson estuary (RKM 213–247) in 1992 and 1995: (a) *Elliptio complanata*; (b) *Anodonta implicata*; (c) *Leptodea ochracea*. Differences in spent shell densities are significant at $P = 0.003$ (*Anodonta implicata*) and $P < 0.001$ (other species).

Fig. 6 River-wide mean density of young-of-year of: (a) *Elliptio complanata*; (b) *Anodonta implicata*; (c) *Leptodea ochracea*. Vertical bars show 90% confidence limits of the means.

unionid species: 77% in *Elliptio complanata* and 83% in *Leptodea ochracea*. Young-of-year *Anodonta implicata*, which were abundant in 1991, were entirely absent from our samples in 1993–95.

The condition (body mass at a given shell length) of all three species of unionids fell between 1991–92 and 1993–95 (Fig. 7). The number of zebra mussels on a unionid was not a significant ($P > 0.05$) covariate in the ANCOVA model for any species. The declines in condition look small in Fig. 7 but were substantial: the body mass of a 60-mm-long specimen fell by 25% in *Elliptio complanata*, 37% in *Anodonta implicata* and 45% in *Leptodea ochracea*.

Discussion

By several important measures, the unionid community in the Hudson declined sharply following the

arrival of the zebra mussel. Density dropped by more than 50% in just 3 years, and densities of spent shells rose correspondingly. Recruitment of young-of-year unionids fell by 90%. Finally, the body condition of the remaining living unionids declined substantially. It is clear that 1993–95 were bad years for the unionids of the Hudson River.

During the time that these striking declines occurred, most of the unionids in the Hudson were not infested by zebra mussels, and even the infested animals suffered from light loads by comparison with those observed elsewhere in North America (Ricciardi *et al.*, 1995, 1996; Schloesser *et al.*, 1996). Schloesser *et al.* (1996) suggested that unionids die if they are infested with more than 100–200 zebra mussels, and Ricciardi *et al.* (1996), whose work described 'the lowest mean infestation at which an impact has been documented', suggested that mortality may occur at mean infestations as low as ten zebra mussels/clam if
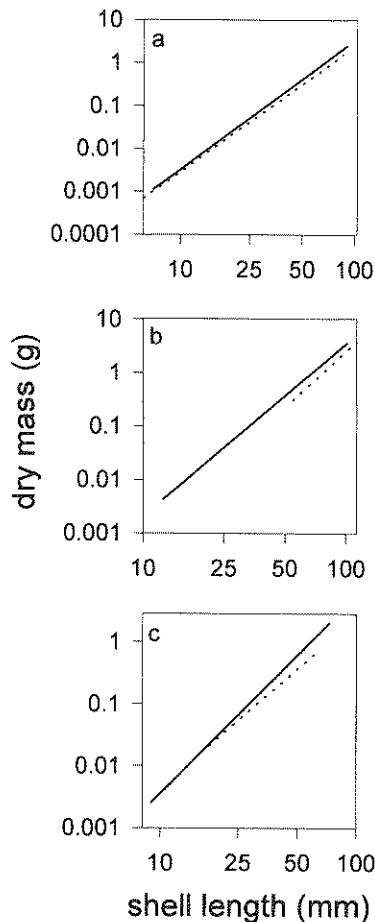
Fig. 7 Regression between shell length and dry body mass for: (a) *Elliptio complanata*; (b) *Anodonta implicata*; (c) *Leptodea ochracea*. Solid lines show results from 1991–92 (pre-zebra mussel) and dashed lines show data from 1993–95 (post-zebra mussel). In each case, the regression lines from the two time periods are significantly different at $P < 0.0001$ (ANCOVA). See Table 1 for details of regressions.

the zebra mussels are large. Specifically, they suggested that mass mortality will occur if the mean infestation 'load' (the ratio of the wet mass of zebra mussels to the wet mass of the unionid on which they live) approaches 1. Only eight of the 652 clams we collected in the Hudson in 1993–95 bore more than ten zebra mussels, and none carried more than 100 zebra mussels. Furthermore, although we did not estimate the infestation load of unionids in the Hudson, the zebra mussels in the Hudson were not very large ($<$ 15 mm long, on average), so the infestation load must have been small (on the order of 1%). Thus, by criteria developed elsewhere in North America (which focused on fouling as the chief mechanism of impact), the

unionids in the Hudson should not have suffered severe impacts from zebra mussels.

We see three obvious possible interpretations of our data on unionid decline in the Hudson. Possibly this decline had nothing to do with zebra mussels, but was part of the normal dynamics of a unionid community. Long-term demographic and physiological data on large-river unionid populations are rare, but it is reasonable to guess that survival, condition and, especially, recruitment of young-of-year (cf. Miller & Payne, 1988, 1993; Payne & Miller, 1989) vary from year to year. Thus, our study might have documented a normal downswing in the unionid community. Arguing against this interpretation are the magnitude of the decline, the temporal coincidence of unionid decline with the growth of the zebra mussel population, the involvement of all three unionid species (at least two of which breed at different seasons and use different host fish: Watters, 1994), and the pervasive nature of the decline, which involved several attributes of the unionids (survival of adults, recruitment of young-of-year and body condition), both demographic and physiological. Although we cannot definitively refute the hypothesis that the decline we observed was part of the normal dynamics of a large-river unionid community, this is unlikely.

A second possible interpretation is that the threshold infestation intensity at which unionids are affected is much lower than previously thought, and that even one or two zebra mussels attached to a unionid can kill the host. While light fouling may have contributed to the death or decline in condition of some unionids in the Hudson, the number of unionids that died exceeded the number of unionids that were infested, especially in the case of *Anodonta implicata* (cf. Figs 2 and 5). Many of the spent shells collected in 1994–95 showed no evidence of ever having been fouled by zebra mussels (zebra mussels or tufts of byssal threads). Furthermore, unionid condition was not correlated with infestation intensity. Therefore, we do not believe that light fouling was a primary cause of the unionid decline in the Hudson.

The third explanation for the decline of unionids in the Hudson is that zebra mussels outcompeted them for food. As a result of the zebra mussel invasion, the biomass of phytoplankton in the Hudson dropped sharply beginning in September 1992. During the growing seasons of 1993–95, phytoplankton biomass was only 10–20% of pre-invasion (i.e. 1986–91) levels

Table 1 Parameters of regressions between $\log_{10}$ of shell-free dry mass (g) and $\log_{10}$ of shell length (mm) for freshwater clams in the Hudson River before (1991–92) and after (1993–95) the zebra mussel invasion. Standard errors of parameter estimates are given in parentheses

Species	Time period	Intercept	Slope	n	r^2	P
Elliptio complanata	1991–92	–5.49 (0.04)	3.01 (0.02)	684	0.96	<0.0001
Elliptio complanata	1993–95	–5.46 (0.06)	2.92 (0.03)	579	0.94	<0.0001
Anodonta implicata	1991–92	–5.89 (0.07)	3.22 (0.04)	325	0.95	<0.0001
Anodonta implicata	1993–95	–6.56 (0.41)	3.48 (0.22)	56	0.83	<0.0001
Leptodea ochracea	1991–92	–5.65 (0.11)	3.20 (0.07)	35	0.99	<0.0001
Leptodea ochracea	1993–95	–5.10 (0.43)	2.75 (0.26)	16	0.90	<0.0001

(Caraco *et al.*, 1996). Such a severe drop in food resources could explain the community-wide decline in condition of unionids. Others have reported that mass die-offs of unionids follow a severe decline in body condition (Haag *et al.*, 1993; Ricciardi, Whoriskey & Rasmussen, 1996; Schloesser *et al.*, 1996). We suggest that zebra mussels in the Hudson reduced food resources to a level below that needed to meet the physiological needs of adult and young-of-year unionids, so that body condition declined and death ensued.

Unionids can be strongly affected by zebra mussels through heavy fouling, as pointed out by Ricciardi *et al.* (1995, 1996) and Schloesser *et al.* (1996). Our work suggests that unionids may also be strongly affected by zebra mussels in the near absence of fouling. A probable mechanism for this is competition for food. Of course, in many ecosystems both fouling and competition for food could combine to affect unionids.

A few other aspects of our results deserve comment. It is puzzling why infestation rates were so low in the Hudson. Our data fall well below the predictions of the empirical model of Ricciardi *et al.* (1995), which was based on data from various rivers and lakes in North America. We have no explanation for these low rates, except to note that Ricciardi *et al.* (1995) suggested that infestation intensities might be lower in rivers than in lakes. The Hudson might be an extreme example of this phenomenon, whatever its cause. Furthermore, we do not know whether low infestation rates will be a permanent feature of zebra mussel–unionid relations in the Hudson, or whether these low rates are just a transient feature of the early invasion period.

It appears from our results that the unionid species might be differentially affected by the zebra mussel invasion of the Hudson. Although the density, recruitment and condition of *Elliptio complanata* were signi-

ficantly reduced, this species was much less seriously affected than *Anodonta implicata* and *Leptodea ochracea*. *Anodonta implicata* appears to have been especially strongly affected, with a large decline in density (–90%), recruitment (–100%) and body condition (*c.* –40%). These differential effects occurred even though infestation intensity did not differ among the three species of unionids. We do not know what mechanisms underlie these differential impacts, but our findings serve to underscore the ecological robustness of *Elliptio complanata*, which is the most common and widespread unionid in north-eastern North America (cf. Strayer, 1993).

We are pessimistic about the long-term prospects for unionids in the freshwater tidal Hudson River. Based on our data and the experience of others in North America (Ricciardi *et al.*, 1995, 1996; Schloesser *et al.*, 1996), we think there is a strong possibility that *Anodonta implicata* and *Leptodea ochracea* will disappear entirely from the Hudson in the next decade, and even *Elliptio complanata* may become scarce. The first two species are restricted to coastal rivers (many of which probably will be infested by zebra mussels) and ponds (Johnson, 1946, 1947; Strayer, 1993), and were rare enough before the zebra mussel invaded their ranges to merit a conservation status of 'special concern' (Williams *et al.*, 1993). As the zebra mussel spreads into their ranges, these two species may become regionally or globally imperilled.

Finally, our results have important implications for developing strategies for the conservation of North American unionids. Preliminary strategies for mitigating impacts of zebra mussels have relied on measures of infestation intensity to identify unionid populations that are at risk, and have proposed physical removal of zebra mussels from unionids as a way to reduce zebra mussel impacts to an acceptable level (Ricciardi *et al.*, 1995, 1996; Schloesser *et al.*, 1996). Our findings

suggest that it is necessary to consider both the degree of fouling and the degree of loss of food resources when assessing the prognosis for infested unionid populations or the suitability of proposed refugia for unionid populations. Unionids will persist only where they are neither fouled nor starved by zebra mussels.

Acknowledgments

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