Long-term responses of native bivalves (Unionidae and Sphaeriidae) to a *Dreissena* invasion

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Abstract: A long-term (28-year) study documented complicated responses of populations of native bivalves (Unionidae and Sphaeriidae) to the dreissenid invasion of the freshwater tidal Hudson River. Early in the invasion (1993–2000), formerly large populations of all native species declined steeply, reaching 0 to 35% of preinvasion densities by the year 2000. These declines in population density were accompanied by large declines in body mass, body condition, and recruitment of natives. Since the year 2000, the population of sphaeriids has recovered to preinvasion densities, and body condition, recruitment, and juvenile growth of unionids have recovered substantially, even though the number of dreissenids in the river has not declined. However, population densities of unionids have not recovered, and 2 of 3 formerly common unionid species (*Anodonta implicata* and *Leptodea ochracea*) have not been collected in several years. The 3rd unionid species (*Elliptio complanata*) also appears to be on the verge of disappearing from the river. Statistical models suggest that the dynamics of native populations were more likely driven by exploitative competition than by fouling. They also suggest that changes in dreissenid body size may have modulated the strength of this exploitative competition over the course of the invasion. The lack of recovery of unionid populations despite substantial recovery of juvenile recruitment and growth, as well as adult body condition, appears to be a result of failure of juveniles to reach adulthood, probably because of high mortality from predators.

Key words: biological invasions, transient dynamics, long-term study, *Dreissena*, Unionidae, Sphaeriidae, Hudson River, recovery, extirpation

INTRODUCTION

The spread of zebra and quagga mussels (*Dreissena polymorpha* and *D. rostriformis*, respectively) throughout North America has led to widespread declines or disappearances of native bivalve populations. Work on these declines has focused primarily on the loss of pearly mussels (Unionidae), although declines of fingernail and pea clams (Sphaeriidae) have been reported from many ecosystems as well (e.g., Strayer and Smith 2001, Ward and Ricciardi 2007, Barrett et al. 2017). The impacts on unionids are especially concerning. Members of this highly diverse family have already suffered from many human activities, to the point that dozens of unionid species are extinct and hundreds more are endangered (e.g., Haag 2012, Lopes-Lima et al. 2017). Scientists have thus warned that the spread of *Dreissena* species may further endanger or extinguish even more of these already imperiled species (e.g., Ricciardi et al. 1998).

The decline of native bivalves follows a common pattern in many ecosystems (see Strayer and Malcom 2007, Burlakova et al. 2014, Lucy et al. 2014, Zanatta et al. 2015, and references cited therein). Typically, dreissenids rapidly develop a large population and settle on unionids in such high numbers that the mass of dreissenids attached to a unionid often exceeds the mass of the unionid itself. The intensity of this fouling is correlated with declining physiological condition of unionids. As a result, many of the unionids die, resulting in steep declines (>95%) or the complete disappearance of unionids within 2 to 7 years. Generally, fouling is accepted as the primary or sole cause for the declines of unionids (Burlakova et al. 2014).
However, there are exceptions to this general pattern. For example, in some water bodies where fouling has caused high mortality, populations have been able to persist in refuges. These refuges are typically shallows or wetlands where fouling is low, usually because of high mortality of dreissenids from high temperature, burial, or predation (see Zanatta et al. 2015, and references cited therein). In addition, unionids can sometimes persist indefinitely in the face of dreissenid fouling (Lucy et al. 2014). These observations and other analyses, chiefly from the Hudson River (Strayer and Smith 1996, Strayer and Malcom 2007, 2014), suggest that mechanisms other than fouling may be responsible for the loss of native bivalves. In particular, dreissenids rarely attach to sphaeriids, so the strong impacts of dreissenids on sphaeriids (Strayer and Smith 2001, Ward and Ricciardi 2007, Barrett et al. 2017) cannot be attributed to fouling. These nonfouling-related impacts usually have been attributed to exploitative competition for food (e.g., Strayer and Malcom 2007), arising from the severe declines in phytoplankton and other edible particles that have been observed in many invaded ecosystems (Higgins and Vander Zanden 2010).

Furthermore, fouling impacts of dreissenids on native bivalves may diminish over time. At sites where some unionids have persisted, fouling rates often declined after ~10 years, either because the dreissenid population declined, or because *D. polymorpha* was replaced by *D. rostriformis*, which is much less likely to settle on unionids (Burlakova et al. 2014, Lucy et al. 2014). If fouling is the primary negative interaction between dreissenids and natives, a reduction in fouling may lead to a relaxation of competitive impacts on natives and possible long-term coexistence (Burlakova et al. 2014). Our most recent analyses of Hudson River populations (Strayer and Malcom 2007, 2014, Strayer et al. 2011) have likewise shown some evidence of recovery of both unionids and sphaeriids at a site where fouling impacts are thought not to be of primary importance, but the mechanisms behind these apparent recoveries are not clear.

Reports of long-term coexistence and reductions in impacts on native species could be important in bivalve conservation. For instance, if severe impacts last for just a few years, then perhaps natives can be protected in natural refuges or held in captivity until the period of severe impacts passes (e.g., Cope and Waller 1995, Newton et al. 2001). However, we do not yet know how native bivalves respond over the long term to dreissenid invasions, what mechanisms underlie those responses, or how responses vary across species and ecosystems. Here, we use data from a long-term, continuous study (1990–2017) in the Hudson River to document responses of native bivalves and further understand how invasive dreissenids affect them. Previous analyses (Strayer and Smith 1996, Strayer and Malcom 2007, 2014) used data collected only up to the year 2010. The additional 7 years included here allowed us to sharpen our analyses of the relative importance of 3 potentially important mechanisms: fouling, exploitative competition, and apparent competition associated with predation.

**METHODS**

**Study area**

The study area is the freshwater tidal portion of the Hudson River in eastern New York (Fig. 1), extending from RKM 99–248 (RKM = river kilometer, measured from The Battery at the southern end of Manhattan in New York City). The average width and depth of the freshwater tidal Hudson are 900 and 8 m, respectively, and mean annual discharge is ~500 m$^3$/s. Extensive shallow areas (<3 m deep at low tide) cover ~15% of the study area and are well colonized by rooted vegetation (chiefly *Vallisneria americana*). The entire study area is tidal. Strong twice-daily tides range between 0.8 to 1.6 m, reverse the direction of water flow except during periods of high freshwater runoff, and prevent stratification of the water column. Nevertheless, sea salt is present in the study area only during extended dry periods, and only in the most downriver reaches (below RKM 120). Even in this lower region, salinity is usually <1 psu (practical salinity unit).

![Figure 1. Map of the study area, from Strayer and Malcom (2014). Dots show the location of transects where unionid samples were taken in 1991–2017. Samples for sphaeriids were taken near Castleton (just south of Albany), Kingston, Poughkeepsie, and Newburgh.](image-url)
The water is turbid (growing-season Secchi depths usually are 1–2 m), hard (calcium = 25–30 mg/L), and nutrient-rich (−0.5 mg/L NO3-N, ~30 μg/L PO4-P) (Caraco et al. 1997). The river bottom is predominately sandy above RKM 150 and muddy below that, but ~7% of the study area is rocky. Further details about the Hudson River are available in Levinton and Waldman (2006) and Strayer (2012).

Native bivalves, belonging to the families Unionidae and Sphaeriidae families, were the dominant suspension feeders in the river (Caraco et al. 1997), and constituted 84% of zoobenthic biomass (Strayer et al. 1994, Strayer and Smith 2001) prior to Dreissena arrival. The unionids are large-bodied and relatively long-lived (life spans of several years to several decades). Adults are suspension feeders and juveniles may pedal feed on sediments. Prior to the Dreissena invasion, 7 species were known from the study area (Strayer et al. 1994), although only 3 were abundant enough to appear regularly in samples. Elliptio complanata, Anodonta implicata (which Williams et al. [2017] assigned to the genus Utterbackiana), and Leptodea ochracea. Among the Sphaeriidae, only Pisidium spp were abundant, although several other species have been reported from the study area (Strayer and Smith 2001). Pisidium is a very small (~3 mm long) burrowing clam that is probably a deposit feeder or interstitial suspension feeder (Lopez and Holopainen 1987).

Zebra mussels (i.e., D. polymorpha) first appeared in the study area in May 1991 and became abundant in the late summer of 1992 (Strayer et al. 1996, Strayer and Malcom 2006, 2014). Their population has been quasi-cyclic, with a period of 2 to 5 years and an amplitude in population size of ~10-fold between years. In addition, very large increases in mortality since the beginning of the invasion (Carlsson et al. 2011) have changed the size structure of the Dreissena population, and large (>20 mm long) animals have been scarce since ~2005, although the population size of dreissenids in the river has not declined. Quagga mussels (D. rostriformis) appeared in the Hudson River in 2008, but have remained uncommon (~10% of the total Dreissena population). Consequently, for the purposes of this paper, we combine the 2 Dreissena species as Dreissena spp. The Dreissena invasion was associated with large, wide-reaching changes in the Hudson River ecosystem (summarized by Strayer et al. 1999, 2014), including an ~80% loss of phytoplankton biomass.

**Study design and sampling methods**

Sampling and processing methods or bivalves were described in detail by Strayer et al. (1994), Strayer and Smith (1996, 2001), and Strayer and Malcom (2007, 2014). Briefly, we used a standard (23 × 23 cm) PONAR grab to sample unionids every year during late June to early August along 11 cross-channel transects deployed in a stratified random design (Fig. 1). Each transect contained 4 stations that were initially chosen randomly, then revisited each year. We used long-range navigation (LORAN) or global positioning system (GPS) to relocate stations. Transects were located from RKM 100 to RKM 235. Five samples were taken at each station and sieved in the field through a 2.8-mm-mesh brass sieve. Unionids large enough to be seen readily in the field (all adults and a few juveniles) were removed from the samples and placed (along with any attached Dreissena) into individual Whirl-Pak™ bags. These specimens and the remaining sieve residue were placed into a cooler, taken to the laboratory, and frozen. These samples were later thawed and the sieve residue was carefully sorted in the laboratory for small unionids. We used calipers to measure shell length (SL), width, and height of all unionids. All dreissenids attached to unionids were counted, identified, and measured (SL with calipers). Soft tissues of unionids were removed, dried at 60°C, and weighed to determine dry mass. The resulting estimates from this sampling program are areally weighted means that apply to the entire 140-km² freshwater tidal river.

We estimated population densities of sphaeriids as part of a long-term program to monitor macrozoobenthos. We sampled 2 stations at each of 4 sites along the study area in late September to early October in 1990 to 1992, 2001 to 2002, 2005 to 2007, and 2012. We used a petite PONAR grab (15 × 15 cm) to take 5 replicate samples at each station. We then sieved samples in the field through a 0.5-mm-mesh sieve and preserved them in buffered formalin. In the laboratory, samples were stained with rose bengal, rinsed, and sorted under a dissecting microscope at 6 to 12× magnification. We double-sorted at least 20% of these replicate samples and used the removal method (Zippin 1958) to estimate sorting efficiencies. We estimated ash-free dry mass (AFDM) of sphaeriids by placing all of the sphaeriids collected in 1 replicate sample from each station into a preweighed aluminum pan, drying them overnight at 60°C, weighing them, combusting them for 2 hours at 500°C, and reweighing them. We then calculated mean AFDM as the difference in mass before and after combustion, divided by the number of specimens in the sample (n = 1–121, mean = 13.5). We collected data on sphaerid body mass only in 1990 to 1999. To test for differences in body mass before (1990–1992) and after (1993–1999) Dreissena became abundant, we calculated the mean AFDM for each sampling station for both 1990 to 1992 and 1993 to 1999 from the annual estimates, then compared the 2 time periods with a 1-tailed paired t-test.

**Body condition of unionids**

We defined body condition of unionids as the residual from a log10–log10 regression of body dry mass (DM) on shell length (SL) that we developed for each species with data from 1991 and 1992 (i.e., before zebra mussel invasion) (cf. the residual index of Jakob et al. 1996). Note that we used a slightly
different procedure than that used in previous papers (Strayer and Smith 1996, Strayer and Malcom 2007, 2014). As calculated here, condition expresses (on a log_{10} scale) how much the body DM of an individual unionid of a given length deviates from the mass expected for that species in pre-zebra mussel years. We used linear regression to model the effects of different zebra mussel attributes on unionid condition. Zebra mussel attributes included total river-wide filtration rate of Dreissena (estimated as described by Strayer et al. 1996 and Strayer and Malcom 2006) subdivided into large (≥20 mm long) and small (<20 mm long) Dreissena, the number of Dreissena fouling each unionid, and the modified fouling ratio (see next paragraph). Our intent was to model both the diffuse, exploitative effects of Dreissena on river-wide food resources and the local effects resulting from fouling on body condition. We separated the effects of filtration by large and small Dreissena because preliminary analyses suggested that large Dreissena have stronger effects than small animals on some zooplankton and bivalves (Pace et al. 2010, Strayer and Malcom 2014). We used the corrected Akaike Information Criterion (AICc) and the summed Akaike weights (w_i) to assess the performance of the different models (Burnham and Anderson 2002).

Several authors have used a ‘fouling ratio’ to quantify the intensity of Dreissena effects on unionids (e.g., Ricciardi et al. 1996). Typically, this measure is simply the ratio of the wet mass of Dreissena attached to a unionid to the wet mass of the unionid itself. We could not calculate a fouling ratio for Hudson River unionids, because we did not measure wet masses of either Dreissena or unionids. However, we calculated a variable that should be similar to the fouling ratio in performance. We routinely measured the SLs of all unionids and all of the Dreissena attached to them. Wet masses should be approximately proportional to the cube of these SLs, so we calculated a modified fouling ratio as the sum of the cubed lengths of all Dreissena attached to a unionid, divided by the cube of the SL of the unionid. The absolute values of this modified fouling ratio are not directly comparable to previously published wet-mass fouling ratios, but it should similarly account for the relative magnitude of fouling by Dreissena on host unionids.

Growth of juvenile unionids

Many unionids lay down annual winter rings (annuli) in their shells (Haag and Commens-Carson 2008). The shells of adult unionids from the Hudson River do not contain interpretable internal annuli (Strayer et al. 1994), but the shells of most small unionids (<20 mm long) do contain clear rings, which we interpreted as winter rings. We measured SL at the first 2 of these presumed winter rings as a measure of growth of young E. complanata. Too few small Anodonta and Leptodea were collected after the Dreissena invasion to track their growth rates.

Food resources

We estimated phytoplankton biomass (expressed as chlorophyll a [Chl a]) as a coarse measure of bivalve food availability from samples taken every 2 weeks during the ice-free season near Kingston (RM 151). Triplicate water samples were taken with a peristaltic pump from 0.5 m below the water’s surface and filtered onto Whatman GF/F filters. Filters were frozen until Chl a was extracted in basic methanol. We used a Turner Designs fluorometer (Caraco et al. 1997) to estimate the amount of Chl a on each filter.

Fate of juvenile unionids

As we will show, large numbers of juveniles of the unionid E. complanata disappeared from the river. To check our estimates of these losses and gain insight into their causes, we recovered all intact empty valves and shell fragments of juvenile unionids (SL < 20 mm) from our samples in 2013. We air-dried and weighed the shell fragments, then estimated how many valves they represented by 2 methods, intended to provide low and high estimates. First, we simply assumed that the crushed shells were the same size as the intact shells that we recovered, which had a mean DM of 0.05 g. However, it appeared that most of the crushed fragments were from shells larger than the intact shells, so to provide an upper bound, we assumed as an alternative that the crushed fragments were from shells that were 15 mm long, which would have had a DM of 0.12 g based on a regression developed from weighing 41 intact shells between 5 and 25 mm long.

Modeling competitive effects of Dreissena

We constructed a simple model to assess the relative effects of ecosystem-wide Dreissena populations and the Dreissena attached directly to unionids (i.e., fouling) on food concentrations reaching a unionid. In particular, we wanted to investigate how local competition with fouling Dreissena compared with competition with the entire population of Dreissena present in the river, and how this relationship changes with degree of water mixing. In poorly mixed waters (e.g., small lakes), a given population of Dreissena should deplete food relatively more severely locally than across the ecosystem as a whole compared with well-mixed waters (e.g., the Hudson). As we will show below, fouling appears to be unimportant in the Hudson, in contrast to its demonstrated importance in other ecosystems. The model is intended to explore one possible reason for this difference. In the initial model, we estimated food concentrations in the water column as a negative exponential function of ecosystem-wide Dreissena population density (cf. Caraco et al. 2006): $C_w = e^{-0.1D_w}$, where $C_w$ is the predicted food concentration in the water column and $D_w$ is the ecosystem-wide Dreissena population density. We then estimated food concentrations reaching an individual unionid by reducing these concen-
trations as a function of the number of Dreissena fouling the unionid and the intensity of water mixing, so that the food reaching the unionid was $C_u = C_w e^{-0.03D_u}$, $C_w e^{-0.1D_u}$, $C_w e^{-0.3D_u}$, for vigorously, moderately, and poorly mixed environments, respectively (where $C_u$ is the food concentration reaching the unionid and $D_u$ is the number of Dreissena fouling the unionid). We further allowed an incomplete mixing regime to affect concentrations of food in the water column (model ‘poorly mixed (2)’ in Fig. 12D) by reducing the effective per capita effect of Dreissena in a poorly mixed water column as $C_w = e^{-0.05D_u}$. These parameters were chosen to illustrate a range of possible model outcomes, and we do not believe that it is feasible at this point to parameterize the model to mimic specific ecosystems. Therefore, the model results should be interpreted as showing a range of possible effects of local (fouling) and river-wide Dreissena populations, rather than predicting actual food concentrations in a particular ecosystem.

RESULTS

Populations of all 4 common species of native bivalves in the Hudson River declined sharply after zebra mussels arrived, reaching 0 to 35% of preinvasion levels by 1999 (Fig. 2A–D). After about 1999, these declines slowed (unionids) or reversed (Pisidium). Two unionids (Anodonta and Leptodea) have not appeared in the last 7 years of sampling (since 2010), and the 3rd (Elliptio) has fallen to 11 to 26% of preinvasion densities in recent years. In contrast, the population of Pisidium rose from a low of 3% of preinvasion densities in 1999 to 71 to 101% of preinvasion densities in our most recent samples (2005–2012).

These changes in population size were accompanied by large changes in the size-structure of the native bivalve populations. The small amount of information available on sphaeriids shows an almost 50% decline in mean body mass of Pisidium between preinvasion and early postinvasion years (Fig. 3). The more extensive data available for unionid populations show more complex size dynamics (Fig. 4A–R).

Figure 2. Time courses of population densities of native bivalves in the freshwater tidal Hudson River: Elliptio (A), Leptodea (B), Anodonta (C), and Pisidium (D). Dreissena first appeared in the study area in 1991, and became abundant at the end of the growing season in 1992 (Strayer and Malcom 2006). Note differences in scale among y-axes.

Figure 3. Mean ash-free dry mass of Pisidium (±1 SE) in 1990–1992 (largely before Dreissena became abundant) and 1993–1999 (after Dreissena became abundant). The difference between the 2 time periods is significant at $p = 0.035$ (1-tailed paired $t$-test).
Before the Dreissena invasion, all 3 unionid species (*Elliptio*, *Anodonta*, *Leptodea*) had bimodal size structures, with distinct peaks presumably representing juveniles and reproductive adults (growth rates of unionids fall steeply at reproductive maturity; Haag 2012). During early postinvasion years (i.e., 1993–2001), the juveniles either disappeared entirely (*Anodonta*) (Fig. 4E, H) or became scarce (*Elliptio, Leptodea*) (Fig. 4D, G, F, I). At this same time, the numbers of adults fell, with the loss rate differing among the 3 species (the declines in adult densities between 1991–1992
Anodonta (Fig. 4K, N, Q) and Leptodea (Fig. 4L, O, R) were too scarce after 2001 to discern further changes in size structure. The number of adult Elliptio continued to decline in 2001 to 2017 (Fig. 4J, M, P), falling to just 6% of preinvasion numbers in 2014 to 2017.

In sharp contrast to these pervasive patterns of decline, the numbers of juvenile Elliptio rose steadily after about the year 2000, whether expressed as absolute densities or as a proportion of the remaining Elliptio population (Fig. 5). During 2005 to 2017, the numbers of juvenile Elliptio were similar to those seen before Dreissena arrived, despite the very low numbers of adult Elliptio.

Unionids in the Hudson River were commonly fouled by Dreissena. Fouling prevalence (the proportion of unionids carrying at least 1 Dreissena) (Fig. 6A, C, E) and intensity (the mean number of Dreissena/unid) (Fig. 6B, D, F) rose with shell length (SL) in unionids, and unionids <40 mm long were rarely fouled. The median SL of all Dreissena attached to unionids was 12.4 mm. Fouling prevalence was very low in unionids was 12.4 mm. Fouling prevalence was very low in unionids were rarely fouled. The median SL of all Dreissena attached to unionids was 12.4 mm. Fouling prevalence was very low in unionids were rarely fouled. The median SL of all Dreissena attached to unionids was 12.4 mm. Fouling prevalence was very low in unionids were rarely fouled. The median SL of all Dreissena attached to unionids was 12.4 mm. Fouling prevalence was very low in unionids were rarely fouled. The median SL of all Dreissena attached to unionids was 12.4 mm. Fouling prevalence was very low in unionids.
able by 2008, and the medium-sized adults (55–69.9 mm) (Fig. 10E) by 2016, leaving only the largest adults (>70 mm long). *Elliptio* will presumably disappear soon in the absence of new recruitment.

Why did this recent pulse of juveniles not reach adulthood? In 2013, the number of empty shells we found was similar to the number of these ‘missing’ juveniles (Fig. 11), confirming that large numbers of juveniles were appearing in the Hudson River and then dying. The majority (77–89%) of the empty juvenile shells we found were crushed, implying mortality was caused by a shell-crushing predator.

Our simple model of the relative strengths of fouling and exploitative competition shows that fouling can be relatively unimportant in vigorously mixed systems (Fig. 12A). Under vigorously mixed conditions, food concentration does not change much along a vertical line of changing fouling intensities, whereas fouling can have strong effects on food concentrations in poorly mixed systems (Fig. 12C, D). Conversely, ecosystem-wide abundances of *Dreissena* can have much stronger effects on the food available to individual unionids in vigorously mixed systems than in poorly mixed systems (i.e., changes in food concentrations along a horizontal
line of changing system-wide Dreissena population densities in Fig. 12A–D).

**DISCUSSION**

Events in the Hudson River deviated in several ways from conventional expectations of how native bivalve populations respond to a Dreissena invasion (rapid decline or disappearance, largely as a result of fouling that leads to severe physiological stress). First, we did not observe steep, monotonic declines in population size or physiological condition. Populations of 2 of the 3 unionid species (Anodonta and Leptodea) did decline immediately and steeply, but small numbers of even these species persisted for at least 18 years after the Dreissena invasion. The other unionid species (Elliptio) still survives more than 25 years after the invasion (although it probably will disappear soon), and population declines did not accelerate in later years, when unionids were fouled at much higher rates (Fig. 2A–C). We did not detect any effect of fouling on unionid body condition, even though our sample sizes were very large (Table 1). Thus, we conclude that the very severe effects of Dreissena in the Hudson River cannot be attributed to fouling, and we found no evidence at all linking fouling by Dreissena with any negative effects on native bivalves in the Hudson River.

Instead, it seems most reasonable to attribute declines in native bivalves to exploitative competition for food arising from the large losses of plankton that were observed in the Hudson River (e.g., Caraco et al. 2006, Pace et al. 2010). This interpretation is supported by observations of declines in body condition or body size of native bivalves (Figs 3, 8A–D) that accompanied the population declines and by the statistical analyses that correlate unionid body condition with dreissenid filtration rates (Table 1), both of which imply food limitation. The fact that Dreissena filtration rates were a better predictor than chlorophyll concentrations of unionid condition implies that estimates of bulk chlorophyll are not good measures of food availability to unionids in the Hudson River. Our results also suggest that the strength of exploitative competition on unionids may depend on the body size of Dreissena, because large dreissenids were more strongly correlated with decreases in body condition than were small dreissenids (Table 1). One explanation for this result is that diet overlap between large Dreissena and unionids may be greater than overlap between small Dreissena and unionids. Recent decreases in Dreissena body size resulting from increased predation (Carlsson et al. 2011) may have, thus, decreased exploitative competition between unionids and dreissenids. Such size-dependent competition could occur widely among bivalves, which have very plastic adult body sizes, and deserves closer investigation.

How can the results from the Hudson River, which contain no evidence that fouling harms unionids, be reconciled with studies from other sites (e.g., Haag et al. 1993, Baker and Hornbach 2000, Hallac and Marsden 2001, Sousa et al. 2011), which unequivocally show that fouling greatly harms union-
ids? Our model (Fig. 12A–D) suggests that the relative strengths of local food depletion resulting from fouling and ecosystem-wide food depletion resulting from system-wide *Dreissena* populations may depend on how well the water column is mixed. If these model results apply in nature, then we may expect fouling to be most important in still waters (e.g., small lakes, quiet streams) and progressively fall in importance in more vigorously mixed waters (e.g., shore zones of large lakes, turbulent rivers, and estuaries). The importance, if any, of this mechanism in nature requires further investigation.

Third, evidence exists that *Dreissena* may exert negative effects on unionids through apparent competition from a shared predator. We know from caging studies (Carlsson et al. 2011) that predation from blue crabs greatly increased mortality rates on *Dreissena* from the early 1990s to 2008, leading to large shifts in the size structure of the population. We do not have any estimates of predation rates on juvenile unionids before the *Dreissena* invasion, but it is apparent from the size structures of all 3 unionid populations that at least some juveniles must have been recruiting successfully into adult size classes. In contrast, by the years 2005 to 2017, few or none of the large numbers of juvenile *Elliptio* appearing in the Hudson River were making it to adulthood. This bottleneck prevented the recovery in recruitment from translating into population recovery. The abundance of crushed shells of juveniles in the Hudson’s sediments sug-

Figure 8. Body condition (±1 SE; see text for definition of condition) of unionids over time: *Elliptio >40 mm* (A), *Anodonta* (B), *Elliptio <40 mm* (C), and *Leptodea* (D). The dashed horizontal line at 0 represents the mean body condition of animals collected in 1991 and 1992, before *Dreissena* became abundant in the Hudson River. All individuals >40 mm long, except for *Elliptio* in panel C.

Table 1. Summary of regression models to predict unionid body condition from characteristics of the *Dreissena* population, 1991–2016. Entries in the table are summed Akaike weights (*w*), model-averaged slopes, and standard errors (SE), averaged over all models. Large = ≥40 mm long, small = <40 mm long. Too few small *Anodonta* or *Leptodea* were collected after the *Dreissena* invasion to permit analysis by size class, so these analyses include only animals >40 mm long. DFR = *Dreissena* filtration rate (m³ m⁻² d⁻¹), subdivided into animals >20 mm long (large, LDFR) and <20 mm long (small, SDFR). Fouling = number of *Dreissena* attached to individual unionids. Ratio = fouling ratio, i.e., the relative mass of *Dreissena* to the mass of the unionid (see Methods for further explanation). Full model results are given in Supplementary Table 1.

| Predictor | Large *Elliptio* (N = 1817) | Small *Elliptio* (N = 637) | *Anodonta* (N = 360) | *Leptodea* (N = 45) |
|-----------|-----------------------------|----------------------------|----------------------|---------------------|
|           | *w* | Slope | SE  | *w* | Slope | SE  | *w* | Slope | SE  | *w* | Slope | SE  |
| LDFR      | 1   | −0.0492 | 0.0025 | 1   | −0.0400 | 0.0073 | 1   | −0.0604 | 0.0091 | 1   | −0.0962 | 0.0244 |
| SDFR      | 1   | −0.0078 | 0.0012 | 0.54 | −0.0033 | 0.0024 | 1   | −0.0181 | 0.0032 | 1   | −0.0253 | 0.0059 |
| Fouling   | 0.27 | 0.00004 | 0.00007 | 0.32 | −0.00288 | 0.00457 | 0.27 | 0.00001 | 0.00050 | 0.43 | −0.00526 | 0.00638 |
| Ratio     | 0.27 | 0.0013 | 0.0058 | 0.31 | −0.0179 | 0.0330 | 0.27 | −0.0106 | 0.0577 | 0.40 | −0.1126 | 0.2179 |
gests that a shell-crushing predator was responsible. The most obvious inference is that the same blue crabs that are killing so many Dreissena (Carlsson et al. 2011), and thereby easing exploitative competition on unionids, are also killing juvenile unionids. However, we do not have any direct evidence to support this inference.

**Conditions for long-term coexistence**

Based on work in the Hudson River and elsewhere, we can identify 3 classes of negative interactions between native bivalves (i.e., unionids and sphaeriids) and Dreissena, all of which must be sufficiently weak to allow for long-term coexistence. First, Dreissena fouls unionids and some other bivalves (e.g., Bódis et al. 2014), although not usually sphaeriids. This fouling can affect the amount of food reaching the native species, and also possibly interfere with locomotion (Van Appledorn and Bach 2007), valve closure, and other behaviors. Fouling intensity could be reduced if the system-wide population density of Dreissena declines, or if D. polymorpha is replaced by D. rostriformis, as often occurs (e.g., Karatayev et al. 2011, Heiler et al. 2013), because the latter species is much less likely to attach to unionids (Bur-lakova et al. 2014). Fouling also could be diminished if predators eat the dreissenids that are attached to unionids (Bowers and de Szalay 2007), or if local conditions are unfavorable to Dreissena (e.g., high temperature in a power plant effluent, Bryan et al. 2014), even if system-wide densities are high. Finally, fouling can be reduced when unionids burrow deeply into the sediment, which apparently kills attached Dreissena (Nichols and Wilcox 1997). Such antifouling behaviors might be increased by environmental conditions that favor unionid burrowing (e.g., high temperature) or possibly by evolution of increased burrowing in response to strong selective pressures from fouling.

Second, native species may suffer from exploitative competition as Dreissena reduces food concentrations in the water column. Such reductions are common and severe (i.e., ~50%, Higgins and Vander Zanden 2010), so exploitative competition probably affects native bivalves in many ecosystems, although it has not been as well studied as fouling. The strength of this competition could diminish if Dreissena populations fall, if the natives adapt to low food concentrations, or if the food niches of native species and Dreissena diverge. Niche differentiation could occur through several mechanisms: developmental plasticity (the feeding structures of bivalves can change in response to the particle mix that they are exposed to, Payne et al. 1995), shifts in body-size structure of the populations (the particles that bivalves capture may depend on their body size, MacIsaac et al. 1995), or long-term evolutionary change. In the Hudson River, it appears that larger Dreissena have much larger negative effects on unionids than small Dreissena (Table 1). The shift to smaller body sizes of Dreissena following increased crab predation (Carlsson et al. 2011), thus, may have eased the pressure of exploitative competition on unionids and allowed the observed recovery of body condition (Fig. 8A–D), juvenile growth (Fig. 9A, B), and recruitment (Figs 5, 10A, B). However, the strength and determinants of exploitative competition for food among freshwater bivalves are still poorly known and require further attention.

The 3rd negative interaction, apparent competition arising from a shared predator, appears not to have received much prior attention. Many predators eat Dreissena (Molloy et al. 1997), and increases in predator population densities, aggregations, or predation rates following Dreissena invasion have been observed for several of these predators (e.g., Daniels et al. 2005, Werner et al. 2005, Carlsson et al. 2011). Most or all of Dreissena’s predators presumably could eat at least small unionids, so it is reasonable to hypothesize that increased predation on small unionids could be a common side-effect

**Figure 9.** Mean shell length (±1 SE) at presumed 1st (A) and 2nd (B) winter rings for Elliptio complanata that were <20 mm long at the time of collection. Horizontal dashed lines show means for animals collected in 1991–1993, whose winter rings would have been formed largely before Dreissena became abundant in the Hudson River.
of Dreissena invasions. Our results suggest that, in the Hudson River, crushing predators eat essentially all of the juvenile unionids before they reach adulthood (Fig. 10A–F). Thus, recovery in body condition (Fig. 8A–D), recruitment (Fig. 5), and juvenile growth (Fig. 9A, B) do not translate into a recovery in unionid numbers. This predation may ultimately doom the Hudson River’s unionids to extirpation. Apart from these results, we know essentially nothing about whether apparent competition via a shared predator is an important mode of interaction between Dreissena and native bivalves (or other macroinvertebrates) or how its strength might vary across ecosystems or through time.

For native bivalves to persist after a Dreissena invasion, the impacts of fouling, exploitative competition, and apparent competition all must be sufficiently weak. These conditions appear to have been met in several circumstances: in refuges along the margins of the Great Lakes (Zanatta et al. 2015), in European waters invaded by Dreissena 100 to 200 years ago (summarized by Strayer and Malcom 2007, Lucy et al. 2014), and now in the Hudson River (for Pisidium).

Figure 10. Dynamics of different size classes (0–9.99 mm [A], 10–24.9 mm [B], 25–44.9 mm [C], 45–54.9 mm [D], 55–69.9 mm [E]; 70–100 mm [F]) of the unionid Elliptio complanata. Dreissena first appeared in the study area in 1991, and became abundant at the end of the growing season in 1992 (Strayer and Malcom 2006). Note different scales on the y-axes.

Figure 11. Comparison of the numbers of ‘missing’ juvenile Elliptio complanata (i.e., the summed number of 5–10-mm long animals collected from 2001–2012, dark gray bar) with 2 estimates of the numbers of empty shells of juvenile Elliptio complanata found in samples from 2013 (light gray and white bars, see Methods for explanation).
To the extent that environmental conditions or the traits of bivalves change over time, these windows of coexistence may open and close. For instance, if Dreissena adapts to higher water temperatures, some of the spatial refuges could be lost. On the other hand, climate warming may expand refuges against Dreissena, which is thermally sensitive (White et al. 2015). Alternatively, natural selection may separate the niches of natives and invaders, promoting coexistence. Non-native bivalves have been recognized as a leading threat to natives for several decades, but we do not yet understand enough about the mechanisms allowing coexistence, or about their changes through time, to know whether natives will continue to decline, or will persist and recover.

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