CHAPTER 38

Impacts of *Dreissena* on Benthic Macroinvertebrate Communities

Predictable Patterns Revealed by Invasion History

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ABSTRACT

Invasive dreissenid mussels (zebra mussel *Dreissena polymorpha* and quagga mussel *Dreissena rostriformis bugensis*) are transforming benthic macroinvertebrate communities in lakes and rivers throughout Europe and North America. Significant changes to these communities are documented typically within a few years to a decade following dreissenid invasion. These changes almost invariably include increased abundance and richness, and reduced evenness, of mussel-associated macroinvertebrate communities. Nearshore communities (excluding *Dreissena*) typically increase by 2–3 times in density and biomass because of increased interstitial habitat from mussel aggregations and nourishment from mussel biodeposits. In contrast, deepwater communities decline by a similar magnitude, likely as a consequence of particulate organic matter being shunted to nearshore areas at the expense of offshore areas by filtration activities of dreissenid populations. Impacts of *Dreissena* on nearshore communities differ among taxa, with disproportionately strong positive effects on mayflies (Ephemeroptera), leeches (Hirudinea), flatworms (Turbellaria), gastropods, and gammarid amphipods. In habitats supporting dense dreissenid populations (>10^3 mussels/m^2), severe declines in native bivalves (Unionidae and Sphaeriidae) commonly occur. The magnitude of these effects varies across space and time with dreissenid population structure and habitat conditions.

INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) continue to invade and ecologically transform lakes and rivers throughout Europe and North America (Brown and Stepien 2010, Zhulidov et al. 2010). Their impacts on benthic macroinvertebrate communities, in particular, have been the focus of a growing number of studies in recent decades. Collectively, these studies enable quantitative comparisons to determine whether dreissenid impacts are consistent across different ecosystems or, if not, whether their variation follows predictable patterns. A predictive understanding of such impacts is of practical importance to environmental management, given that benthic macroinvertebrates are: (1) valuable indicators of water quality (Washington 1984, Gabriels et al. 2005); (2) functionally important in freshwater ecosystems as mediators of nutrient cycling and energy flow (Covich et al. 1999); and (3) an essential food resource for higher consumers (Vander Zanden and Vadaboncoeur 2002, Schummer et al. 2008). Indeed, changes in the composition and abundance of benthic macroinvertebrates can alter the diet and condition of fish (Owens and Dittman 2003, McNickle et al. 2006). Moreover, accurate models to predict impacts are needed to ensure that observed changes caused by *Dreissena* are not mistakenly attributed to watershed management schemes (e.g., phosphorus abatement) and other environmental stressors, such as contaminants and climate change (MacNeil and Briffa 2009, Atalah et al. 2010).

MECHANISMS OF IMPACTS: FILTRATION AND SUBSTRATE ALTERATION

Dreissena can alter benthic macroinvertebrate communities in lakes and rivers through a variety of mechanisms, but most directly through physical alteration of substrates (Figure 38.1). Like their marine relatives (Suchanek 1986, Lohse 1993), zebra and quagga mussels form dense aggregations (clumped shells of live and dead individuals) by attaching to substrates and to each other's shells with byssal threads; these aggregations provide colonizable surfaces for algae and structurally complex habitat for macroinvertebrates (Ricciardi et al. 1997, Stewart et al. 1998a). Interstitial spaces between mussel shells passively trap sediments and are used by smaller invertebrates as refugia from predation and environmental stressors such as wave action (Gutiérrez et al. 2003, Beekey et al. 2004, Reed et al. 2004). Although common in coastal marine systems where byssally attached molluscs abound (Suchanek 1986), this type of habitat engineering was nonexistent in European and North American freshwater habitats prior to colonization by *Dreissena*.

Dreissenid mussels link offshore planktonic and nearshore benthic communities by filtering suspended particles from the water column and depositing the material as mucus-bound feces and undigested pseudofeces (Karatayev et al. 1997, Gergs et al. 2009). This link has been referred to as the pelagic-to-benthic shunt because it reduces available planktonic resources and increases the organic content of sediments surrounding dreissenid mussel beds (Karatayev et al. 1997, Stewart et al. 1998a, Hecky et al. 2004). Mussel

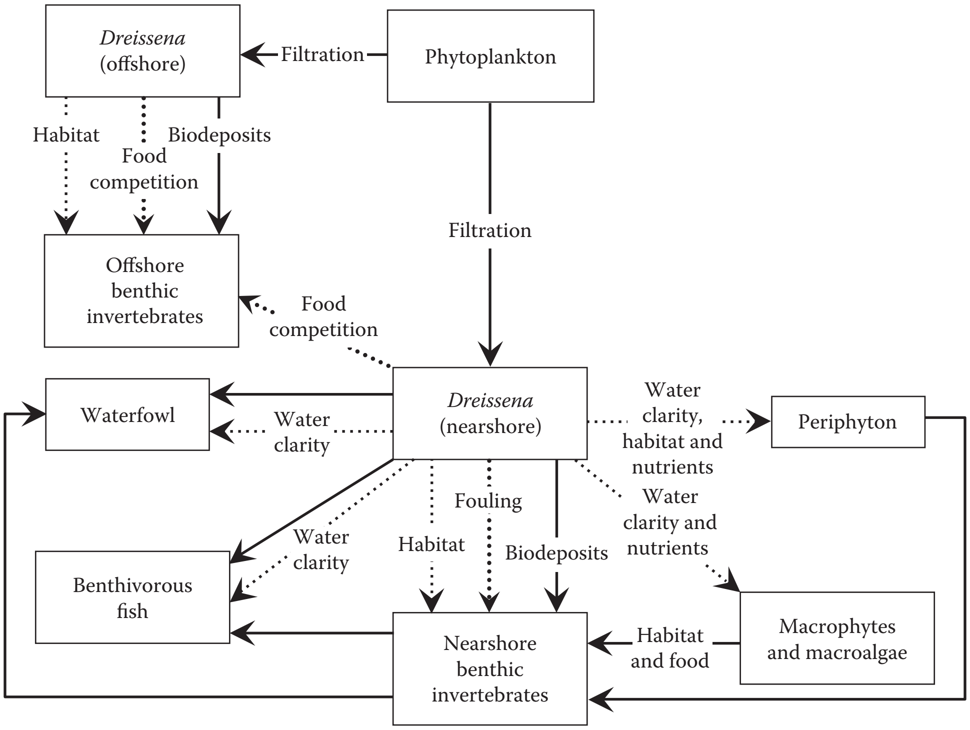

Figure 38.1 Mechanisms of interactions between *Dreissena* and benthic invertebrates through direct food web connections (solid lines), habitat engineering (thick dashed lines), and fouling (thin dashed lines). "Habitat" can be defined as a change in physical conditions (e.g., created by mussel shells or altered sediment composition and chemistry created by mussel biodeposits: feces and pseudofeces). Water clarity potentially improves efficiency of predation by waterfowl and fish on benthic invertebrates. Fouling (dense colonization) of sedentary invertebrates with shells or exoskeletons (e.g., native bivalves and odonate nymphs) impairs metabolism and imposes energetic costs that may reduce survivorship. Offshore invertebrates are affected by competition for seston (from both local and nearshore dreissenid populations) as well as by habitat and biodeposits generated locally.

feces and pseudofeces contain both live and dead phytoplankton, organic detritus, and inorganic particles (Roditi et al. 1997), which can be a source of nourishment to detritivores (Izvekova and Lvova-Katchanova 1972, Stewart et al. 1998a). Growth in gammarid amphipods and chironomid larvae, for example, readily occurs when dreissenid biodeposits are the food source (Izvekova and Lvova-Katchanova 1972, González and Burkart 2004), and both these taxa increase prolifically with dreissenid colonization (Ricciardi et al. 1997, Ward and Ricciardi 2007).

Through their filtration activity, dreissenids increase the depth to which light penetrates in lakes and large rivers, thereby stimulating benthic production even at distances remote from mussel beds (Vanderploeg et al. 2002, Cecala et al. 2008). The resultant enhanced growth of benthic algae and macrophytes can provide food or physical habitat to macroinvertebrates, particularly grazers, causing an expansion of littoral populations (Mayer et al. 2002). Also, at various sites in the lower Great Lakes and St. Lawrence River, there have been observations of increased abundance of freshwater sponges (Early et al. 1996, Ricciardi et al. 1997), whose algal symbionts allow them to grow luxuriantly in enhanced light conditions. On the other hand, blooms of filamentous macroalgae have also been linked to dreissenid filtration activity (Auer et al. 2010) and these blooms have mixed effects on benthic macroinvertebrates (reviewed by Ward and Ricciardi 2010).

Dreissenid colonization has strong negative effects on some benthic taxa (Ward and Ricciardi 2007). High filtration capacity and biomass (Karatayev et al. 1997, Vanderploeg et al. 2002) of dreissenid populations allow them to outcompete native filter feeders for food. Some evidence suggests mussels displace large net-spinning caddisfly larvae (Trichoptera) by fouling their preferred attachment sites on rocky substrates (Ricciardi et al. 1997). Similarly, abundances of large snails (i.e., individuals of comparable or greater size than dreissenids) may be reduced on dreissenid-covered substrates, perhaps because of foraging inefficiency (Wisenden and Bailey 1995, Ricciardi et al. 1997, Ward and Ricciardi 2007). In addition, *Dreissena* attaches to exoskeletons and shells of other macroinvertebrates that have no evolutionary experience with fouling organisms. High densities of attached dreissenids can impair normal activities of snails (Van Appledorn et al. 2007, Van Appledorn and Bach 2007) and, especially, of other bivalves (Baker and Hornbach 1997, 2000; see Impacts On Native Bivalves). Attachment of dreissenids on dragonfly larvae has caused reductions in emergence rates, larval mobility, foraging efficiency, and survivorship (Fincke et al. 2009, Fincke and Tylczak 2011)—the latter possibly resulting from energy loss and increased exposure to predators (Fincke et al. 2009). Attachment to crayfish has also been observed and is believed to impose an energetic cost to individuals (Brazner and Jensen 2000, Ďuriš et al. 2007), but consequences to crayfish fitness have not been studied.

IMPACTS ON MACROINVERTEBRATE ABUNDANCE, DIVERSITY, AND COMPOSITION

Generalizations can be made regarding the impacts of dreissenids on the abundance, diversity, and composition of benthic macroinvertebrate communities. In a meta-analysis of published data (Ward and Ricciardi 2007), we quantified the relative effects of *Dreissena* by dividing the value of a response variable (e.g., macroinvertebrate abundance) after *Dreissena* colonization (X_{+D}) by its value before *Dreissena* colonization (X_{-D}) and then normalized this metric by natural logarithmic (ln) transformation. Typically, dreissenid invasions are associated with increases in the local abundance and taxonomic richness of benthic macroinvertebrates (excluding unionids and dreissenids), whereas community evenness (i.e., Simpson's indices) generally declines following dreissenid invasion (Figure 38.2). Collectively,

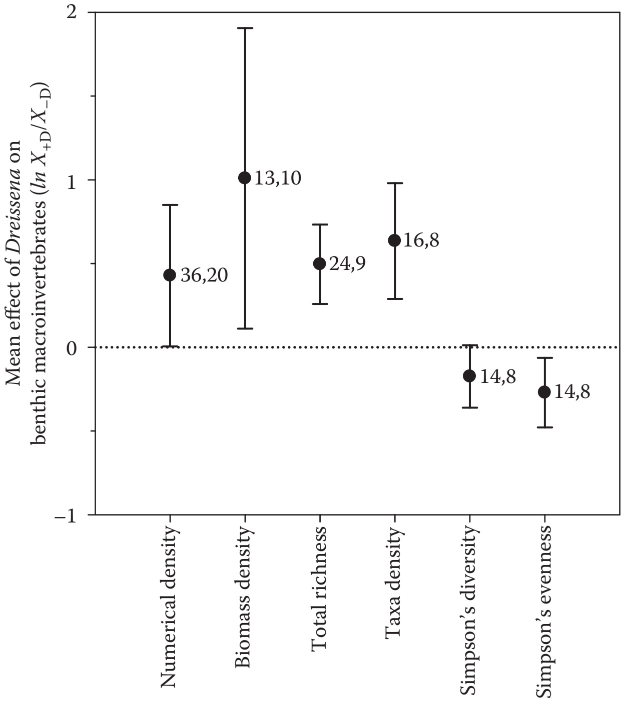

Figure 38.2 Mean impacts of *Dreissena* on benthic macroinvertebrate density (no./m^2), biomass density (g/m^2), total richness (number of taxa), taxa density (no./m^2), and Simpson's diversity and evenness. All calculations exclude Unionidae and *Dreissena*. Relative effects were calculated by dividing the value of a response variable after *Dreissena* colonization (X_{+D}) by its value before *Dreissena* colonization (X_{-D}), followed by ln-transformation (Ward and Ricciardi 2007). Numbers (a,b) shown beside data points are (a) the number of study sites used to calculate each average and (b) the number of studies that served as data sources. Only sites with dreissenid densities >100/m^2 were used as post-colonization data. Positive effects indicate an increase and negative effects indicate a decrease following *Dreissena* invasion. Error bars are 95% confidence intervals. Effect sizes are statistically significant when they do not overlap zero.

these impacts show that dreissenid invasions tend to positively influence benthic macroinvertebrates, but some taxa benefit disproportionately. Experiments and field surveys have demonstrated that communities associated with dense *Dreissena* colonies are dominated by a few abundant taxa such as snails, flatworms, chironomid larvae, and amphipods; these patterns are robust across studies (e.g., Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a,c, Mörtl and Rothhaupt 2003, Karatayev et al. 2010).

The direction and magnitude of dreissenid effects vary across different substrate types (Figure 38.3). Dreissenid colonization of rocky substrates is almost always accompanied by a contemporaneous increase in densities of other macroinvertebrates. The increase in density may be an order of magnitude higher than the density before dreissenid colonization; this strong positive effect can be attributed to increased interstitial habitat provided by mussel aggregations and, to a lesser extent, by mussel filtration and biodeposition activities (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998a, Horvath et al. 1999, Mörtl and Rothhaupt 2003). Dreissenid colonization of mixed substrates (including fine sediments) also generally enhances densities of associated macroinvertebrates, but results are much more varied. These patterns reflect differential responses by various functional groups of macroinvertebrates. In general, after dreissenid colonization there is an increase in densities of epifaunal taxa (i.e., those that normally occupy solid surfaces) and a decline in densities of infaunal or burrowing taxa. The latter response reflects the transformation of preferred habitat by dense mussel colonies extending onto soft sediments (Ward and Ricciardi 2007). The inhibition of burrowing macroinvertebrates by byssally attached mussels has also been reported in marine systems where sediments underlying dense mussel beds may become inhospitable for infauna through smothering and anoxia (Creese et al. 1997, Robinson and Griffiths 2002). Similarly, severe oxygen depletion may occur in sediments covered by dreissenid mussels, which can reduce the richness of invertebrates occupying these sediments (Beekey et al. 2004). Despite these negative effects, dreissenid colonization of sandy and silty substrates usually produces an overall increase in richness of local macroinvertebrate communities (Figure 38.3) by offering surfaces for colonization by invertebrates adapted to rocky substrates (Ward and Ricciardi 2007).

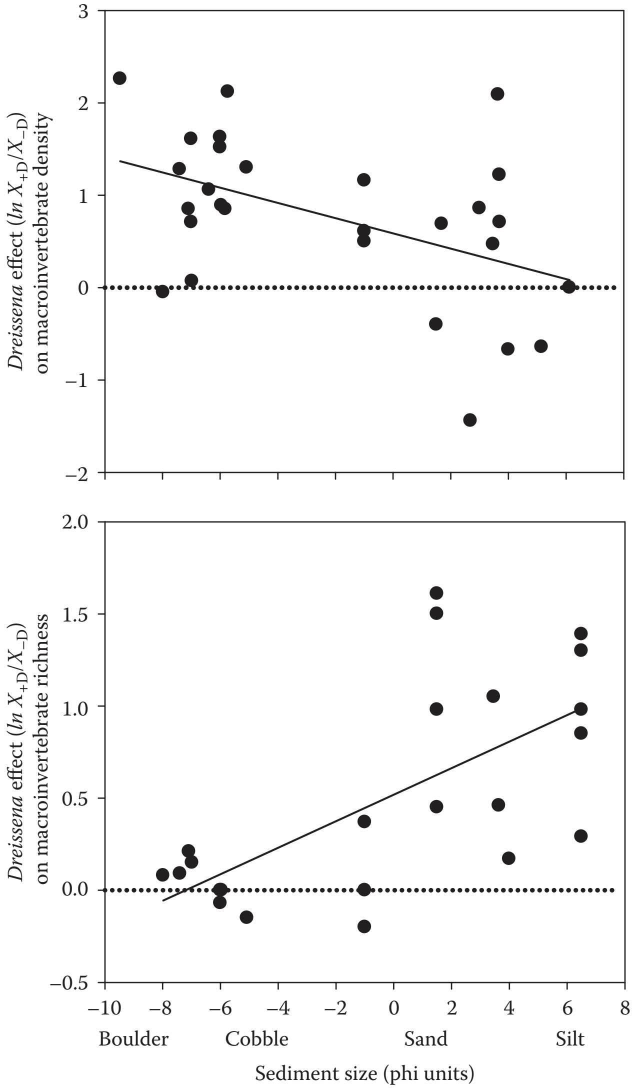

Figure 38.3 Community-level impacts of *Dreissena* as a function of mean size of surrounding substrate (phi units = $-\log_2$ diameter in mm). Effects were calculated as in Figure 38.2. As substrate particle size becomes smaller (increasing phi), the effect of *Dreissena* on density becomes more variable and less positive (a: $r = -0.47$, $P = 0.01$), whereas the effect on total taxonomic richness becomes stronger and more positive (b: $r = 0.66$, $P = 0.0006$). Lines generated by least-squares regression. (After Ward, J.M. and Ricciardi, A., *Divers. Distrib.*, 13, 155, 2007.)

After dreissenid invasions of lakes, conspicuous reductions in some nondreissenid benthic macroinvertebrates can occur in the littoral zone (Haynes et al. 1999, Ratti and Barton 2003), but reductions are more pronounced in sublittoral and deepwater regions (Figure 38.4). In the Great Lakes, precipitous declines of the native deposit-feeding amphipod *Diporeia* spp. coincided with the introduction and spread of dreissenids (Nalepa et al. 1998, 2003, Dermott 2001). Prior to its collapse, *Diporeia* was the most abundant benthic macroinvertebrate at deepwater sites, often found at densities of 2000–8000/m^2 (Owens and Dittman 2003). Declines of *Diporeia* and other macroinvertebrates at offshore sites are thought to be a response to the reduced influx of food particles caused by the enormous filtration capacity of nearshore dreissenid populations (Dermott and Kerec 1997, Nalepa et al. 1998, Dermott 2001, Lozano et al. 2001, Soster et al. 2011).

Effects of *Dreissena* on macroinvertebrate densities are more predictable for some taxonomic groups than for others (Figure 38.5). Dreissenid colonization is frequently associated with increased local densities of leeches (Hirudinea), flatworms (Turbellaria), snails (Gastropoda), and mayfly nymphs (Ephemeroptera). Small snails and other herbivorous taxa (such as heptageniid mayflies) that scrape substrates for food likely

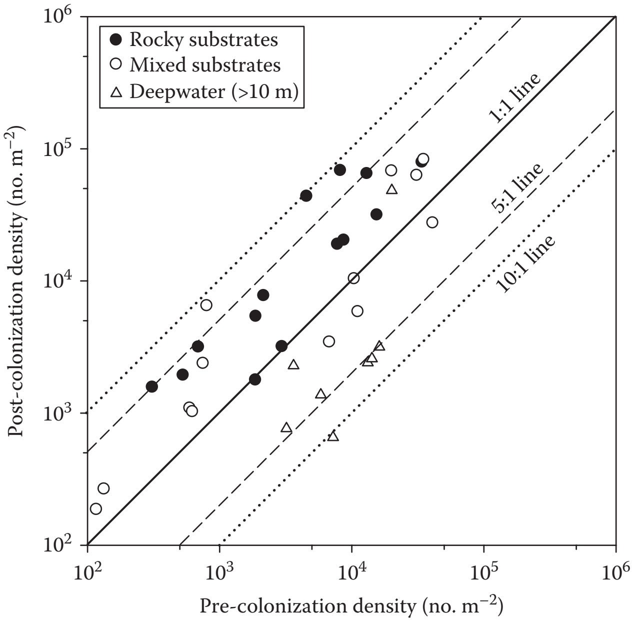

Figure 38.4 Density (no./m^2) of benthic macroinvertebrates (excluding *Dreissena* and Unionidae) reported on littoral rocky substrates, littoral mixed substrates, and substrates of deepwater environments in pre- and post-*Dreissena* periods. Each point represents a study site (n = 33 sites in 13 water bodies). Points above the 1:1 line indicate increased density of benthic macroinvertebrates. Data sources: Dusoge (1966), Dermott et al. (1993), Griffiths (1993), Stewart and Haynes (1994), Karatayev and Burlakova (1995), Botts et al. (1996), Dermott and Kerec (1997), Ricciardi et al. (1997), Stewart et al. (1998c), Horvath et al. (1999), Kuhns and Berg (1999), Bially and MacIsaac (2000), Lozano et al. (2001), Strayer and Smith (2001), Mayer et al. (2002), Nalepa et al. (2002), Mörtl and Rauthhaupt (2003), Owens and Dittman (2003), and Beekey et al. (2004).

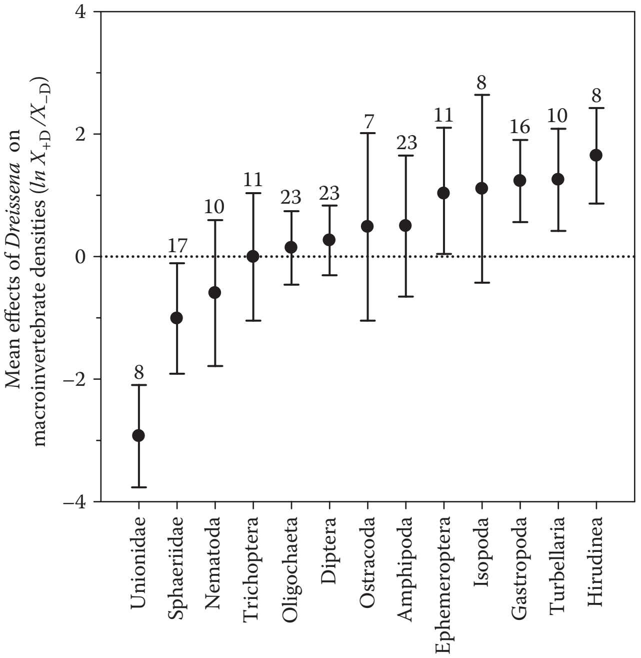

Figure 38.5 Mean effects of *Dreissena* on densities (no./m^2) of major taxonomic groups of benthic macroinvertebrates. Effects were calculated as in Figure 38.2. The number of study sites used to calculate each average is given above each data point. Positive values indicate increased density and negative values indicate decreased density in response to *Dreissena*. Error bars are 95% confidence intervals, and effect sizes are statistically significant when they do not overlap zero. Data sources for Unionidae: Ponyi (1992), Nalepa (1994), Ricciardi et al. (1995), Schloesser and Masteller (1999), Martel et al. (2001), Schloesser et al. (2006), Strayer and Malcom (2007), and Maguire et al. (2003). Data sources (20 published studies) for other taxonomic groups are provided in Ward and Ricciardi (2007). (Derived and modified from Ward, J.M. and Ricciardi, A., *Divers. Distrib*., 13, 155, 2007.)

benefit from increased grazing area and spatial refugia provided by dreissenid shells, although large-bodied snail taxa (e.g., Pleuroceridae) tend to be reduced or displaced (Wisenden et al. 1995, Ricciardi et al. 1997, Ward and Ricciardi 2007). Increased densities of leeches, flatworms, and other predatory species associated with dreissenids likely reflect responses of these taxa to refugia from benthivorous fish and to increased availability of positively affected prey (Ricciardi et al. 1997, Stewart et al. 1998a, Ward and Ricciardi 2007, Gergs and Rothhaupt 2008).

Several broad taxonomic groups are characterized by a mixture of positive and negative responses to dreissenids (Figure 38.5), which reflects variation among species within the group. For instance, families within the group Trichoptera (larval caddisflies) have distinct feeding strategies (Wiggins 1996) and thus may be influenced by dreissenids in diverse ways. Larvae in the Helicopsychidae family, like other small grazers, are positively affected by dreissenid shells (Ricciardi et al. 1997, Horvath et al. 1999). Small filter-feeding caddisflies, such as *Brachycentrus* (Brachycentridae), appear to exploit filtration currents generated by dreissenids, whereas large net-spinning caddisflies in the family Polycentropodidae avoid currents generated by dreissenid filtration or become excluded when dense colonies of *Dreissena* interfere with the construction and placement of their nets (Ricciardi et al. 1997). Similarly, although meta-analysis indicates a nonsignificant, highly variable effect of dreissenids on the density of Amphipoda as a group, more consistent patterns occur at a finer taxonomic resolution (Ward and Ricciardi 2007). Large increases in densities of epibenthic gammarid amphipods (e.g., *Gammarus fasciatus* and *Echinogammarus ischnus*) are correlated with *Dreissena* colonization (Ricciardi 2003), whereas densities of deepwater amphipods (*Diporeia*, as described earlier) typically decline.

IMPACTS ON NATIVE BIVALVES

Dreissena has consistent negative effects on densities of native bivalves (Figure 38.5). Declines in sphaeriid clams (Sphaeriidae) have frequently occurred at local and habitat-wide scales following *Dreissena* invasion and are attributed primarily to effects of competition with *Dreissena* for food (Nalepa et al. 1998, Lauer and McComish 2001, Lozano et al. 2001, Strayer and Smith 2001). Impacts on unionid mussels (Unionidae) are more conspicuous and have received more attention. Unionids had already suffered declines throughout North America in response to habitat degradation during the previous century, but their rate of population loss increased 10-fold, on average, in habitats where dense *Dreissena* populations (>3000/m^2) became established (Ricciardi et al. 1998). Rapid declines of unionid populations were observed following *Dreissena* colonization in the Great Lakes (Nalepa 1994, Schloesser and Nalepa 1994, Schloesser and Masteller 1999, Schloesser et al. 2006), St. Lawrence River (Ricciardi et al. 1996), Hudson River (Strayer and Malcom 2007), Ohio River (Ricciardi et al. 1998, Watters and Flaute 2010), and various smaller water bodies (Harman 2000, Martel et al. 2001). These events have been attributed to both the effects of fouling (overgrowth of unionid shells by attached dreissenids) and, to a lesser extent, competition for food (Parker et al. 1998, Baker and Levinton 2003). Indeed, there is a strong correlation between fouling intensity by dreissenids and mortality of unionids (Figure 38.6). This correlation is supported by experimental studies that show attachment by dreissenids interferes with normal metabolic activities of unionids and weakens their physiological condition (Haag et al. 1993, Baker and Hornbach 1997, 2000, Sousa et al. 2011), whereas the removal of attached dreissenids enhances unionid survival (Hallac and Marsden 2001). Empirical models predict that unionid populations will undergo severe (>90%) declines when individual unionids carry, on average, more than their own weight in attached dreissenids—a condition that generally occurs at mean fouling intensities of >100 dreissenids per unionid and dreissenid population densities on the order of 10^3/m^2 (Ricciardi et al. 1995, 1998). North American water bodies that support such dreissenid densities may experience near total extirpation of unionid populations within 4–8 years following *Dreissena* invasion (Ricciardi et al. 1998). However, unionids may persist at low densities in the presence of *Dreissena* (Strayer and Malcom 2007) or in refugia with locally reduced dreissenid densities within systems invaded by *Dreissena* (Zanatta et al. 2002, Crail et al. 2011).

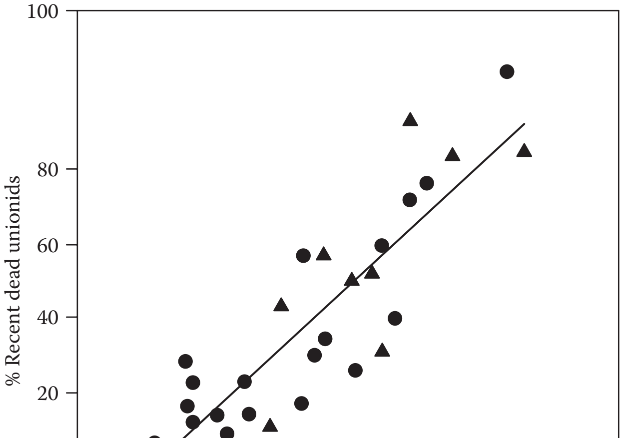

Figure 38.6 Percentage of recent-dead unionids as a function of dreissenid fouling intensity on unionid populations in North America. Fouling intensity defined as the mass of attached dreissenids divided by the mass of unionid host. Data are from the upper St. Lawrence River (20 sites), Detroit River (1 site), western Lake Erie (1 site), Lake St. Clair (1 site), Lake Wawasee (1 site), Richelieu River (4 sites), and Lake Champlain (1 site), referenced in Ricciardi (2003). Line fitted by least-squares linear regression: $\sin^{-1}(y^{0.5}) = 0.48 \log x + 1.0$ ($R^2 = 0.75$, $P < 0.0001$).

The European experience has not provided a useful reference for predicting impacts of *Dreissena* on native bivalves in North America. Mass mortalities of unionids have rarely been reported for European water bodies invaded by *Dreissena* (reviewed by Karateyev et al. 1997, Ricciardi et al. 1998), possibly because impacts that might have occurred early in the *Dreissena* invasion (e.g., up to two centuries ago) were undocumented. In addition, *Dreissena* had already expanded into central Europe prior to the last glaciation before subsequently retreating to the Ponto-Caspian basins (Stańczykowska 1977). Thus, unionids in Europe might have already experienced evolutionary pressures to adapt to dominant macrofouling organisms such as *Dreissena* and not have the same ecological sensitivity to fouling as unionids in North America (Ricciardi et al. 1998). Evidence to support this hypothesis may be found in the recent invasion of Irish lakes by *Dreissena*. Unlike continental European assemblages, the fauna of these lakes have no evolutionary experience with *Dreissena*, and their unionids have suffered strong negative impacts resembling those in North America (Maguire et al. 2003).

PREDICTORS OF *DREISSENA* IMPACT

Impacts of an introduced species are expected to be a function of its abundance (Parker et al. 1999). Relationships between impact and abundance have been demonstrated experimentally and statistically for *Dreissena* density and impacts on phytoplankton (Bastviken et al. 1998), nutrient cycling (Mellina et al. 1995), unionid mortality (Ricciardi et al. 1995), and macroinvertebrate abundance on rocky substrates (Ricciardi 2003). Hence, impacts of *Dreissena* are moderated by environmental variables that limit its abundance (e.g., Ramcharan et al. 1992, Mellina and Rasmussen

1994, Jones and Ricciardi 2005), which implies that the magnitude of impact may be predictable from habitat conditions. In fact, variation in fouling intensity on unionids across sites can be partly explained by differences in water chemistry—specifically, local calcium concentrations (Jokela and Ricciardi 2008). Other important moderators of *Dreissena* impacts on macroinvertebrates include the mean particle size of ambient substrates (Figure 38.3) (Ward and Ricciardi 2007, Jokela and Ricciardi 2008) and the local abundance of molluscivores (Kuhns and Berg 1999). Hydrological variables may also play an important role; there is empirical evidence that the level of fouling on unionids associated with a given *Dreissena* population density is higher in lakes than in rivers (Figure 38.7).

In addition to dreissenid abundances, the extent of dreissenid impacts also depends on the composition of the benthic community prior to invasion. In particular, feeding mode, body size, and substrate preference of individual macroinvertebrate taxa may prove useful to forecast responses to *Dreissena* colonization (Ward and Ricciardi 2007). Impacts are also altered by the presence of other introduced macroinvertebrates (van Overdijk et al. 2003), other habitat engineers (Ward and Ricciardi 2010), and native and exotic predators (Stewart et al. 1998b, Kuhns and Berg 1999, Mörtl et al. 2010). Predation by molluscivorous waterfowl in Lake Constance during winter 1999–2000 and 2001–2002 reduced dreissenid densities by 80% at depths down to 7 m; the resultant loss of *Dreissena*-generated physical habitat and biodeposits was accompanied by reductions in chironomid larvae, mayfly nymphs, and oligochaetes (Mörtl et al. 2010).

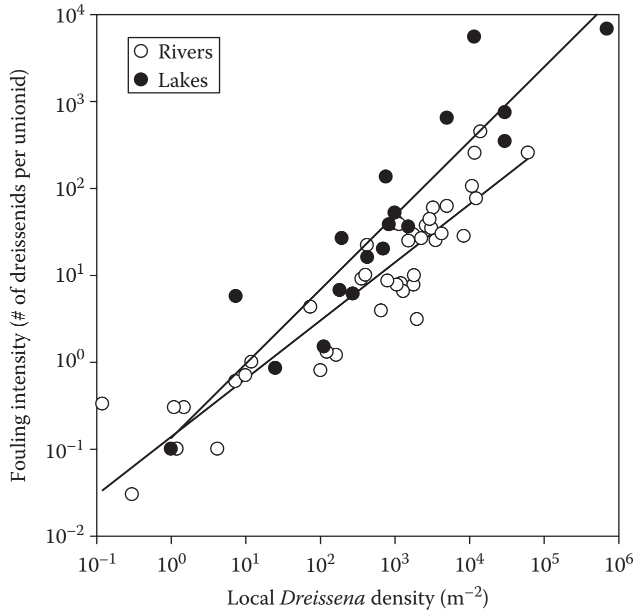

Figure 38.7 Relationship between fouling intensity (the mean number of attached dreissenids per unionid) and local *Dreissena* density at multiple invaded sites in North America and Europe. Lines are fitted by least-squares linear regression. Regression lines for lakes (log $Y = -0.87 + 0.85\ X$, $R^2 = 0.85$, $P < 0.0001$) and rivers (log $Y = -0.85 + 0.67\ X$, $R^2 = 0.86$, $P < 0.0001$) are significantly different (ANCOVA, $P < 0.0001$). (Data are from Ricciardi, A., *Freshwat. Biol.*, 48, 972, 2003.)

TEMPORAL VARIABILITY OF IMPACT

It is increasingly evident that long-term variability in environmental conditions and dreissenid populations (abundance and age structure) can cause dreissenid impacts to change over time (Haynes et al. 1999, Strayer and Malcom 2007, Strayer et al. 2011). In Lake Michigan, the magnitude and spatial extent of impacts on *Diporeia* increased over a decade as dreissenid biomass also increased (Nalepa et al. 2009). In the Hudson River, densities of benthic macroinvertebrates at deepwater sites declined by >80% in the early years of *Dreissena* colonization but began to recover several years later following a long-term decline in adult dreissenid survivorship and aggregate filtration rate (Strayer et al. 2011). Conversely, in southwestern Lake Ontario, increased abundance and diversity of nondreissenid macroinvertebrates observed a few years after *Dreissena* colonization were followed by declines to levels similar to or lower than pre-invasion levels; the development of thick beds of filamentous algae several years after invasion may have been a contributing factor to these declines, particularly for snails that prefer to graze on diatoms (Haynes et al. 1999). Given these disparate outcomes, it is perhaps no surprise that "time since invasion" is not a significant predictor of *Dreissena* impacts on benthic communities (Ward and Ricciardi 2007).

CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

The invasion history of *Dreissena* in Europe and North America has revealed broad patterns of impacts on benthic communities. Benthic macroinvertebrates in the littoral areas of lakes and rivers typically increase (often doubling) in abundance and taxonomic richness following dreissenid colonization. These increases are accompanied by a decline in community evenness because of disproportionate effects on particular taxonomic and functional groups. For example, *Dreissena* has consistent and strong positive effects on densities of gammarid amphipods, leeches, flatworms, and certain insects, but has strong negative effects on native bivalves. Furthermore, although densities of gastropods generally increase following *Dreissena* colonization, large-bodied snails tend to be displaced from dreissenid-covered substrate; thus, the alteration of hard substrates by *Dreissena* can reduce the mean size of resident gastropods, as has been observed for marine mussels (Griffiths et al. 1992).

The impact of these gastropod shifts on periphyton communities has not been examined. At system-wide scales, macroinvertebrate richness tends to decrease in the presence of *Dreissena*. In littoral regions, the most severe reduction in diversity is the catastrophic decline in populations of native unionid mussels. In deepwater regions, declines in macroinvertebrate abundance and richness (particularly of oligochaete worms, sphaeriid clams, and burrowing amphipods) are hypothesized to be a response to reduced influx of food particles from littoral sites dominated by filter-feeding dreissenids. These and other impacts are typically observed within a few years to a decade of dreissenid colonization.

This review of dreissenid–macroinvertebrate interactions has revealed several research gaps in our understanding of the impacts of *Dreissena* invasions. The most challenging of these from a predictive standpoint is how impacts are altered by habitat conditions. Some impacts are strongly mediated by water chemistry (Jokela and Ricciardi 2008), turbidity (Osterling et al. 2007), or substrate quality (Ward and Ricciardi 2007) and frequently involve complex interactions between dreissenids and other invasive or habitat-engineering species. For example, the round goby (a benthic fish predator) and *Cladophora* (a benthic macroalga) both modify the effects of dreissenids on benthic invertebrate communities (Kuhns and Berg 1999, Lederer et al. 2006, Ward and Ricciardi 2010) and have become common drivers of community-level change in the Great Lakes basin. Such interactions produce synergies that complicate efforts to predict impacts of *Dreissena*, but are rarely studied. There is also a need to investigate how impacts of nearshore dreissenid populations on deepwater benthic communities are moderated by limnological characteristics of lakes (e.g., phytoplankton growth rate, water residence time, water flow patterns). A greater understanding of these interactions could be obtained through the development of models guided by marine studies of the context-dependent ecosystem effects of bivalves (Dame 1996, Prins et al. 1997).

The mechanisms by which byssally attached mussels moderate benthic diversity remain a research focus (e.g., Borthagaray and Carranza 2007, Buschbaum et al. 2009, Ward and Ricciardi 2010). In marine systems, the patch dynamics of mussels affects benthic diversity at multiple spatial and temporal scales (Tsuchiya and Nishihira 1985, Tanaka and Magalhães 2002, Cole 2010). This relationship has hardly been explored for *Dreissena*, although studies have shown that species richness of the macroinvertebrate community occupying dreissenid patches increases with patch area (Bially and MacIsaac 2000), and the topography of dreissenid patches is an important driver of variation in macroinvertebrate richness and evenness over small (<1 m^2) spatial scales (Ward and Ricciardi 2010).

Another research question is whether benthic communities associated with zebra mussels differ in composition and abundance from communities associated with quagga mussels. Recognizing such differences, if they exist, would help predict the community-wide consequences of dreissenid species replacements occurring in North America and Europe (Ricciardi and Whoriskey 2004; Wilson et al. 2006, Zhulidov et al. 2010). Recent independent invasions of the southwestern United States by zebra and quagga mussels (Wittmann et al. 2010) provide opportunities for researchers to compare the effects of these two species in isolation. It would be useful to determine whether byssally attached mussels in general (such as *Dreissena* spp., the golden mussel *Limnoperna fortunei*, and the dark false mussel *Mytilopsis leucophaeata*) have similar impacts on benthic communities; this appears to be the case for *D. polymorpha* and *L. fortunei* (Karatayev et al. 2010). If such effects are concordant, it would suggest universality in the interactions between invasive mussels and benthic macroinvertebrates in freshwater and marine systems.

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