

Transformation of Freshwater Ecosystems by Bivalves

A case study of zebra mussels in the Hudson River

David L. Strayer, Nina F. Caraco, Jonathan J. Cole, Stuart Findlay, and Michael L. Pace

Bivalves (clams and mussels) are among the most familiar of aquatic organisms. Many have been used by humans for centuries as important sources of food and ornament, and some species are economically important pests, fouling water intakes and other structures. It is only recently, however, that ecologists have begun to understand that bivalves also play many important roles in ecosystems (e.g., Dame 1996). The functional importance of bivalves, especially in fresh water, is still not fully appreciated. For example, recent fresh water ecology textbooks (Wetzel 1983, Horne and Goldman 1994, Allan 1995, Petts and Calow 1996) scarcely mention the ecological roles of bivalves (the words "bivalve," "clam," and "mussel" do not even appear in the index of any of these books). By contrast,

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Human activities often radically alter the density and composition of bivalve communities, inadvertently transforming ecosystem structure and function

pelagic grazers, such as *Daphnia*, are widely recognized as having strong effects on ecosystems (e.g., Leibold 1989, Carpenter and Kitchell 1993, Jiirgens 1994, Pace et al. 1998b).

In this article, we show that bivalves are in fact dominant filter-feeders in many shallow-water ecosystems. Moreover, human activities often radically alter the density and composition of bivalve communities, in so doing inadvertently transforming ecosystem structure and function. We illustrate these points with a detailed case study of the effects of the zebra mussel (*Dreissena polymorpha*) invasion on the Hudson River ecosystem.

Bivalves as dominant filter-feeders

Bivalves constitute the majority of zoobenthic biomass in many rivers, streams, lakes, estuaries, and shallow coastal waters (Table 1; Dame 1996). The filtration rates of bivalve populations may be substantial,

amounting to 10–100% of the water column per day. These rates often equal or exceed those of other filter-feeders in the ecosystem, including pelagic grazers.

The ecological impact of bivalve filter-feeding depends on the magnitude and nature of other processes that supply or remove edible particles (e.g., phytoplankton primary production, loading of organic material from the catchment, sedimentation, consumption by other filter-feeders, and downstream advection). Because downstream advection is a large loss term for edible particles in many flowing waters and estuaries, Dame (1996) suggested that bivalve grazing rates must exceed advective losses if bivalves are to exert control over the concentration or composition of suspended particles. In many shallow-water ecosystems (rivers, estuaries, and coastal marine waters), bivalve grazing rates are greater than advective losses (Figure 1; see also Dame 1996), implying that bivalves may affect the structure and function of these ecosystems.

Human influences on bivalve populations

Human activities have frequently caused sudden, large increases or decreases in bivalve populations. Species used for food or ornament have been harvested intensively, causing severe declines or local extinctions of formerly dense populations. Harvests as high as 6 15 million kilograms per year in Maryland waters alone helped to reduce the Ches-

Table 1. Typical biomasses and community filtration rates of some ecologically important freshwater bivalves.^a

Family	Biomass (shell-free dry mass; g/m ³)	Filtration rate (m ³ ·m ⁻² ·d ⁻¹)	Habitats
Unionidae	1-10	0.01-0.3	Rivers, littoral zone of lakes
Sphaeriidae	0.02-2	0.002-0.2	Lakes, ponds, streams, rivers
Corbiculidae ^b	1-30	0.3-10	Streams, rivers, littoral zone of lakes and reservoirs
Dreissenidae ^b	0.5-20	0.1-5	Lakes, rivers

^aThe figures pertain to the entire ecosystem, not just to areas of suitable habitat, which may support biomasses and filtration rates more than 10-fold higher than shown. The data were compiled from a large number of published studies.

^bThese invasive bivalves typically have high standing stocks and activity.

peake Bay oyster (*Crassostrea virginica*) population to 1% of its former size (Rothschild et al. 1994, Dame 1996). Likewise, in the heyday of the American pearl button industry, over 13 million kg of shells from living unionids were harvested from Illinois rivers in one year (1913; Claassen 1994). Similarly large harvests of the mussel *Margaritifera margaritifera* for freshwater pearls are a primary cause of the loss of 90% of the global population of this species (Ziuganov et al. 1994). Pollution and habitat

alterations have also destroyed or depleted bivalve populations in many shallow waters (Neves 1993). Communities of native bivalves, many of them both dense and species rich, were completely eliminated from thousands of kilometers of streams and rivers in the United States by impoundments, channelization, toxic and organic pollution, and other human impacts (Ortmann 1909, van der Schalie 1958, Isom 1969, Stansbery 1970, Starrett 1971, Strayer 1980).

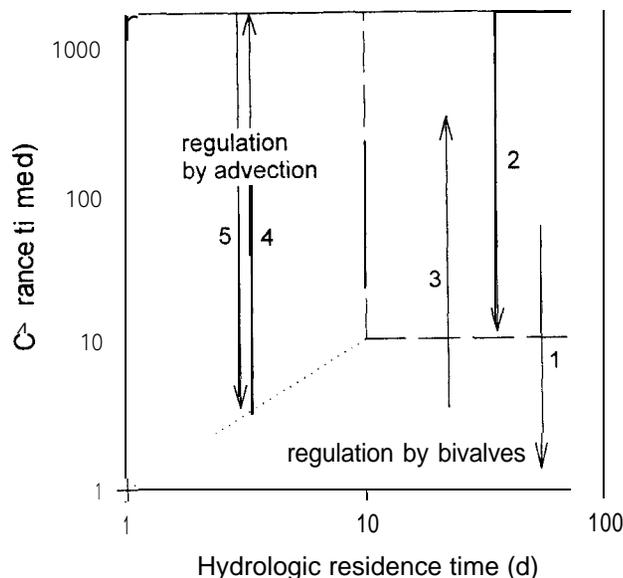
At the same time that native popu-

lations were being destroyed by human activities, massive populations of invasive bivalves developed throughout the world as a result of human introductions, both deliberate and accidental. Species such as *Dreissena* spp., *Corbicula* spp., *Limnoperna fortunei*, *Potamocorbula amurensis*, and *Rangia cuneata* are now well established outside their native ranges and continue to spread (e.g., Carlton 1992, Morton 1997). These invasive species often develop dense populations with high filtration rates (Table 1).

Human-induced changes in bivalve populations may have produced large changes in many ecosystems. Figure 1 shows the estimated filtration rate of several bivalve populations or communities before and after human intervention. In these ecosystems, aggregate bivalve filtration rates have changed 100-1000-fold. Significantly, these large changes have moved ecosystems into and out of the domain of potential control by bivalves.

Although ecologists have focused on changes in phytoplankton and in consumers that depend on phytoplankton as the primary consequences of bivalve invasions (and losses), the bivalve-ecosystem linkage is complex and might affect ecosystems in several important ways (Figure 2). Bivalves could selectively remove edible particles (especially phytoplankton) from the water column (pathway 1), reduce populations of consumers that depend on phytoplankton (pathway 2), increase populations able to use bivalves or their waste products (pathway 3), free up resources such as nutrients formerly used by phytoplankton and other edible particles (pathway 4), and increase populations that are able to use these freed-up resources (pathway 5). Indeed, our analysis of the response of the Hudson River ecosystem to the zebra mussel invasion shows that all five pathways may be important. Further details about the Hudson's response, including statistical analyses of zebra mussel effects, can be found in Strayer and Smith (1996), Strayer et al. (1996b, 1998), Caraco et al. (1997), Bastviken et al. (1998), Findlay et al. (1998), Pace et al. (1998a), and Smith et al. (1998).

Figure 1. Control of phytoplankton and human-induced changes in bivalve populations in some aquatic ecosystems. Extending the model of Dame (1996), we recognize three domains of control of phytoplankton: a region of control by bivalves, if grazing rates are large compared to advective losses and phytoplankton growth rates; a region of advective control, if advective losses of phytoplankton are large compared to bivalve grazing rates and phytoplankton growth rates; and (above and to the right of the dashed lines) a region in which neither grazing nor advective losses are large compared to phytoplankton net growth. (In nature, the boundaries between domains of control are not sharp and may differ greatly from those shown, depending on net phytoplankton growth rates.) Arrows show how bivalve clearance rates changed in (1) the Hudson River after the arrival of zebra mussels (*Dreissena polymorpha*; Abood et al. 1992, Strayer et al. 1996b, Caraco et al. 1997); (2) Suisun Bay, California, after the arrival of an Asian bivalve, *Potamocorbula amurensis* (Walters et al. 1985, Kimmerer et al. 1994); (3) the Chesapeake Bay after the decline of oysters from overharvesting, pollution, and disease (Dame 1996); (4) a 10 km



reach of a typical stream in eastern North America after pollution and habitat degradation destroyed unionid clams (Kryger and Riisgard 1988, Strayer et al. 1996a); and (5) the midsection of the freshwater tidal Potomac River after the invasion of the Asiatic clam, *Corbicula fluminea* (Cohen et al. 1984). Data for the Hudson include all species of bivalves; in other ecosystems, only the indicated species is included.

Zebra mussels in the Hudson River ecosystem

Zebra mussels were first seen in the Hudson River in May 1991. The population spread and grew rapidly, reaching suitable habitats throughout the freshwater part of the estuary by the end of 1992. By this time (17 months after initial detection), the biomass of zebra mussels exceeded that of all other heterotrophs in the freshwater tidal Hudson (details of the invasion are given by Strayer et al. 1996b). The filtration rate of the zebra mussel population, perhaps the best measure of its impact on the ecosystem, also grew rapidly from 1991 to 1993 and has remained high ever since (Figure 3). These filtration rates correspond to theoretical turnover times of 1.2–3.6 days for the entire freshwater estuary. The freshwater tidal Hudson is well mixed by strong tidal flows, so vertical profiles of temperature and water chemistry are nearly flat under most conditions (Findlay et al. 1991, Cole et al. 1992, Raymond et al. 1997). Thus, zebra mussels have access to the entire water column.

Like many bivalves, zebra mussels are able to remove a wide range of particle types and sizes from the water, including phytoplankton, some bacteria and zooplankton, detritus, and silt (e.g., Sprung and Rose 1988, Lei et al. 1996, Silverman et al. 1996, Horgan and Mills 1997). Much of this material is passed out undigested in feces or pseudofeces and may be resuspended in the water column. Laboratory studies have shown that zebra mussels remove both phytoplankton and silt from Hudson River water with nearly equal efficiency (Roditi et al. 1996) and that small cyanobacteria and large cryptomonads are removed more efficiently than diatoms (Bastviken et al. 1998). Thus, perhaps the most obvious expected impact of the zebra mussel invasion is a selective decline in the density of edible particles in the water (pathway 1 in Figure 2). Phytoplankton and small zooplankton (rotifers, tintinnids, and copepod nauphi) declined precipitously with the zebra mussel invasion of the Hudson, dropping to 10–20% of their pre-invasion levels (Figure 4; Caraco et al. 1997, Pace et al. 1998a). Although

Figure 2. Ecological changes induced by increasing bivalve populations. Bold boxes and lines show components that tend to increase with the bivalve population, and thin boxes and dotted lines show components that tend to decrease. See text for details.

all phytoplankton populations declined, cyanobacteria declined much more sharply than diatoms, consistent with the results of laboratory feeding trials (Bastviken et al. 1998, Smith et al. 1998).

A second change to be expected from the zebra mussel invasion is a loss of consumers that depend on phytoplankton and other edible particles (pathway 2 in Figure 2). Although zooplankton are the best-known consumers of phytoplankton, the clearest changes in consumer populations in the Hudson were seen not in the zooplankton but in

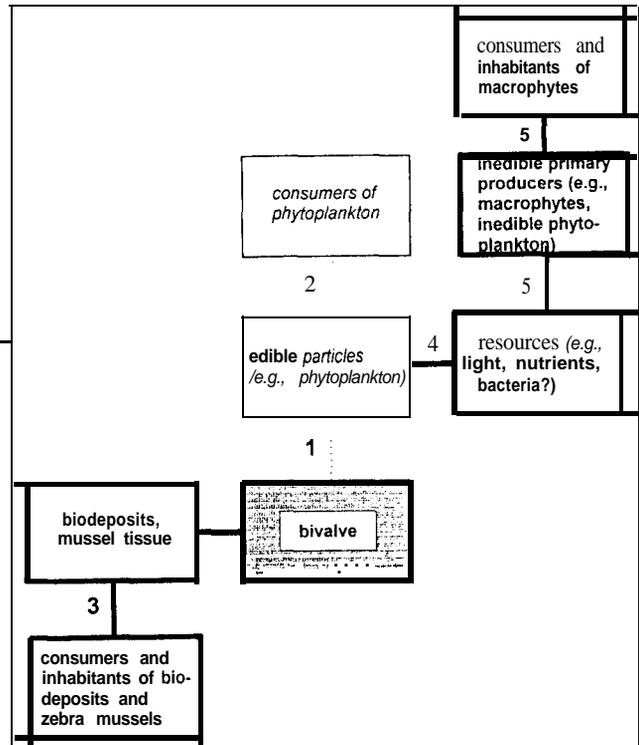


Figure 3. Key variables driving the Hudson River ecosystem, 1987–1996. (a) Freshwater discharge at Kingston, NY. (b) Water temperature at Kingston, NY. (c) Estimated filtration rate of zebra mussels (hatched bars) and all other filter-feeders (open bars), averaged over the entire freshwater tidal Hudson River. Zebra mussel filtration rates were estimated by applying Kryger and Riisgard's (1988) regression to observed size densities and distributions of Hudson River zebra mussels. The dashed lines show the point at which zebra mussels became abundant. Data are annual means for June–August.

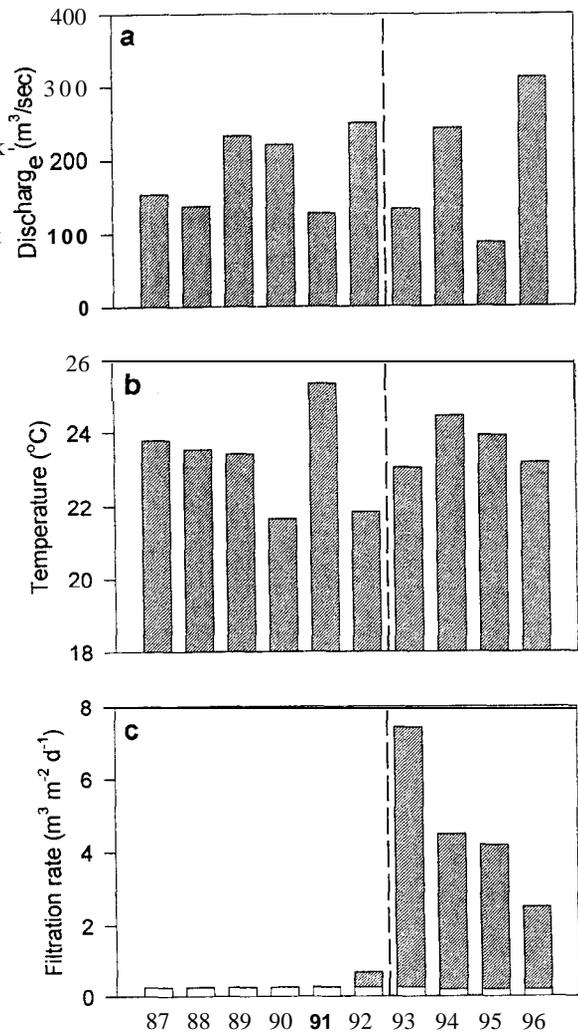
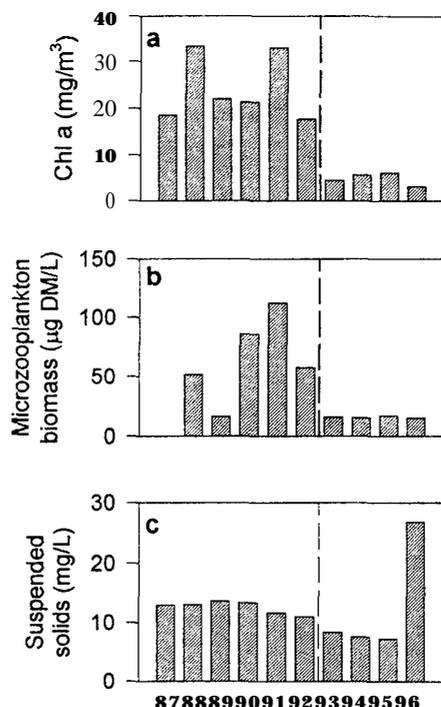


Figure 4. Changes in concentrations of edible and inedible particles (pathway 1 in Figure 2) in response to the arrival of zebra mussels in the Hudson River. (a) Phytoplankton biomass, as measured by chlorophyll *a*. (b) Microzooplankton (tintinnids, rotifers, and copepod nauplii) biomass. DM, dry mass. (c) Suspended solids. The dashed lines show the point at which zebra mussels became abundant. Data are annual means from Kingston, NY, during June-August; zooplankton data are geometric means. Unusually heavy summer rains are responsible for the high suspended solids in 1996.



the benthos. The effect of reduced phytoplankton biomass on small zooplankton is confounded by direct consumption of these animals by zebra mussels, which probably accounts for most of the decline in small zooplankton (Pace et al. 1998a). The larger crustacean zooplankton, consisting of copepods and the cladoceran *Bosmina* in the Hudson, probably are not eaten in large numbers by zebra mussels (e.g., MacIsaac et al. 1991, 1995), but they might be expected to decline because of the loss of their phytoplankton food. Nevertheless, copepod populations did not change with

the arrival of the zebra mussel (Pace et al. 1998a). *Bosmina*, on the other hand, declined by well over 50%, but because of large interannual variability this decline is only marginally significant statistically. Overall, therefore, large zooplankton may have declined in numbers in the Hudson (Figure 5), but this decline is not statistically significant. Furthermore, the continued presence of copepods, a preferred prey of young fish (Limburg et al. 1997), may have insulated higher trophic levels in the Hudson from the negative effects of the zebra mussel population.

In the Hudson, the important issue of interactions between zebra mussels and large zooplankton, which are strongly connected to populations of young anadromous fish (e.g., Limburg et al. 1997), therefore remains unresolved. Perhaps a

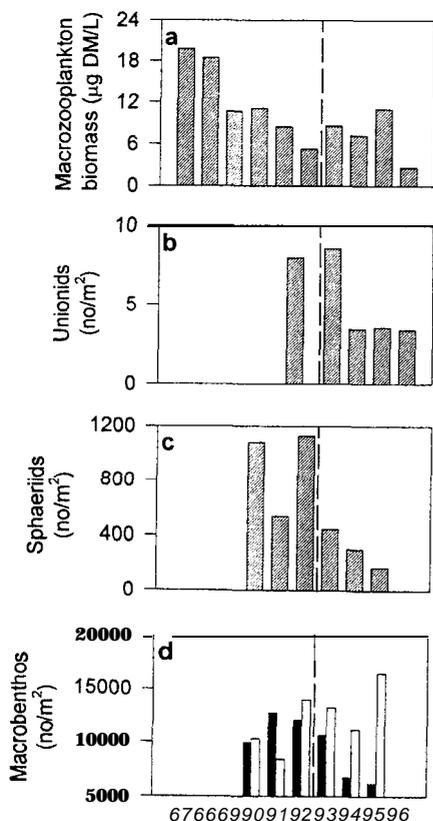


Figure 5. Changes in populations of consumers that are thought to depend on phytoplankton (pathway 2 in Figure 2) in response to the arrival of zebra mussels in the Hudson River. (a) Macrozooplankton (chiefly copepods and *Bosmina*) biomass. DM, dry mass. (b) Unionid clams. (c) Sphaeriid clams. (d) Macrobenthos in deep-water sites (solid bars) and shallow-water sites (open bars). The dashed lines shows the point at which zebra mussels became abundant. Data in (a) are geometric means for June-August at Kingston, NY; others are riverwide means from a single annual measurement.

longer record will allow us to demonstrate an effect of zebra mussels on large zooplankton in the Hudson. On the other hand, if large zooplankton did not in fact respond to the zebra mussel invasion, then food must not limit populations of large zooplankton, and factors such as predation or advection must be more important controls (Pace et al. 1998a).

In contrast to large zooplankton, populations of benthic consumers clearly declined in the Hudson (Figure 5), probably because of reduced availability of edible particles. Populations of both families of native bivalves (Sphaeriidae and Unionidae) dropped sharply and significantly after the zebra mussel arrived. Furthermore, among the large unionid clams, body condition (i.e., body mass at a given shell length) declined by approximately 40%, and young-of-year recruitment fell by 90% (Strayer and Smith 1996). Two of the three species of formerly abundant unionids appear to be headed for imminent local extinction. Because few of the unionid clams and none of the sphaeriid clams were fouled by zebra mussels, which has been identified as the predominant way that zebra mussels kill clams in other ecosystems (e.g., Ricciardi et al. 1995, Schloesser et al. 1996), we believe that native clams are suffering from inadequate phytoplankton food. Other sediment-dwelling animals (chiefly oligochaetes and amphipods) declined as well, but only at deep-water sites (solid bars in Figure 5d), again suggesting that zebra mussels may have reduced the flux of edible suspended particles to the sediments (Strayer et al. 1998).

Much of the material removed from the water column by zebra mussels and other bivalves is not lost from the ecosystem as bivalve respiration or burial; instead, as pathway 3 of Figure 2 shows, it is diverted to the surface sediments in the form of bivalve tissue and biodeposits (i.e., feces and pseudofeces). For example, during the peak in the zebra mussel population in the Hudson in 1993–1994, gross carbon biodeposition was 3 g·m⁻²·d⁻¹, carbon production was 0.1–0.2 g·m⁻²·d⁻¹, and carbon respiration was approximately 0.5 g·m⁻²·d⁻¹ (Strayer et al. 1996b, Roditi et al. 1997). Thus, even though most

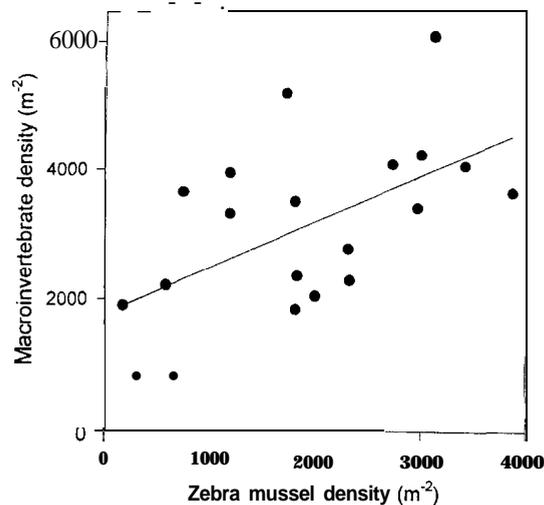
of the biodeposits may be resuspended before being used by benthic consumers, the increase in benthic resources in and around zebra mussel beds may be substantial. Consequently, consumer populations may increase markedly around zebra mussel beds (Figure 6; Stewart and Haynes 1994). Local increases in macroinvertebrate populations are due not only to increased deposition of organic matter but also to the shelter and surface area provided by the zebra mussel shells (Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998). Although the microbial communities associated with zebra mussel beds have not been well studied (but see Roditi et al. 1997), we expect that zebra mussels also cause local increases in microheterotroph biomass and production.

Resources formerly used by the particles eaten by zebra mussels (i.e., phytoplankton and small zooplankton) may increase following invasion (pathway 4 in Figure 2). Because phytoplankton control resources such as light and nutrients in many ecosystems, these resources might be expected to increase after zebra mussels invade. In the Hudson River, soluble reactive phosphorus almost doubled, and light penetration increased by almost 50%, during the summer growing season, except in 1996, when heavy rains resulted in low light penetration through much of the summer (Figure 7; Caraco et al. 1997). Nitrate increased slightly but not significantly (Figure 7).

Similar increases in light and soluble nutrients have been reported in other ecosystems invaded by zebra mussels (Holland 1993, Fahnenstiel et al. 1995, Holland et al. 1995, Johengen et al. 1995, Effler et al. 1997). The size of such increases varies widely, depending on the size of the zebra mussel population, the extent to which edible particles (as opposed to inedible particles such as silt) controlled light penetration, and whether phytoplankton and bacterioplankton were nutrient limited.

Another possible example of pathway 4 is the release of planktonic bacteria from microzooplankton grazers. Like phytoplankton, small zooplankton nearly disappeared from the Hudson after the zebra mussel arrived (Figure 4). Before ze-

Figure 6. Density of macroinvertebrates other than zebra mussels as a function of zebra mussel density. Each point represents a rock taken near the low tide mark at Cruger Island in the Hudson River, August-November, 1992; the slope of the regression is significantly different from zero ($r^2 = 0.33$, $P < 0.01$). David L. Strayer and Lane C. Smith, unpublished data.



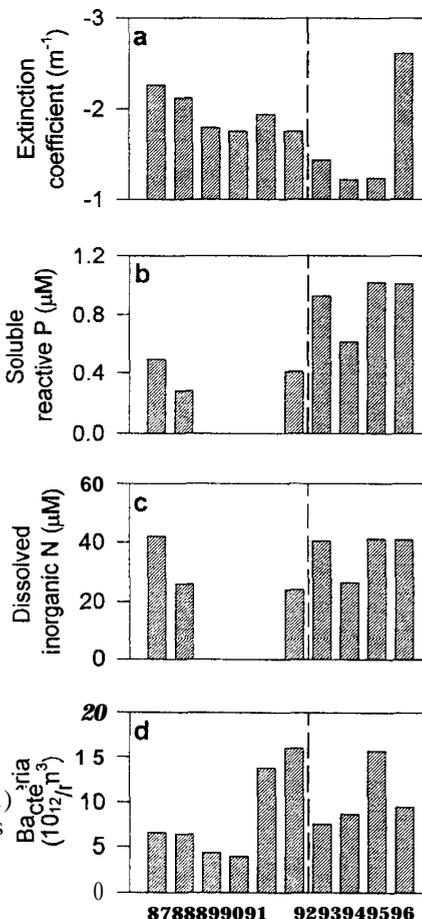
bra mussels arrived, these small zooplankton were sometimes important predators of bacteria in the Hudson (Vaqué et al. 1992). Although zebra mussels can eat some bacteria, they do not graze effectively on most planktonic bacteria in the Hudson (Findlay et al. 1998). Consequently, the net effect of the zebra mussel invasion may be to increase densities of bacterioplankton, as has occurred in experimental microcosms and perhaps in the Hudson (Figure 7; Findlay et al. 1998).

Primary producers that are not eaten by zebra mussels (i.e., inedible phytoplankton, submersed macrophytes, and attached algae) may respond to the increased availability of light and nutrients with increased production or biomass (pathway 5 in Figure 2). In some large lakes (but not in the Hudson), blooms of large colonial cyanobacteria (especially *Microcystis*) followed the zebra mussel invasion (MacIsaac 1996). All phytoplankton taxa in the Hudson declined, although centric diatoms declined much less than cyanobacteria (Smith et al. 1998), in part because zebra mussels consume centric diatoms less efficiently than they consume small cyanobacteria (Bastviken et al. 1998).

The lack of blooms of inedible large, colonial cyanobacteria in the Hudson may be related to the frequent strong mixing of the Hudson by tidal currents, which eliminates

spatial refuges in which colonies of cyanobacteria could grow too large to be eaten by zebra mussels (Bastviken et al. 1998, Smith et al. 1998). Neither macrophytes nor attached algae were monitored closely in the Hudson before zebra mussels arrived, but anecdotal reports (Lake 1996) and ongoing analysis of aerial photographs and models based on photosynthesis irradiance curves (Harley and Findlay 1994) suggest that both

Figure 7. Changes in resources formerly used by phytoplankton and microzooplankton (pathway 4 in Figure 2) in response to the arrival of zebra mussels in the Hudson River. (a) Light extinction. (b) Soluble reactive phosphorus. (c) Nitrate. (d) Bacterioplankton. Data are annual means at Kingston, NY, during June-August. The aberrant extinction coefficient in 1996 is due to unusually heavy summer rains.



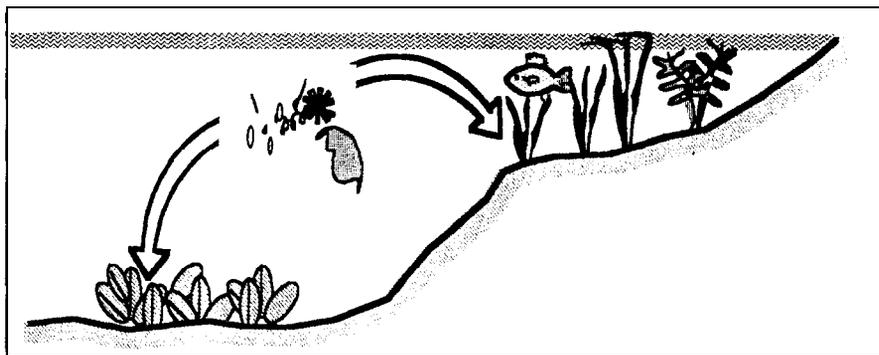


Figure 8. Diversion of resources by zebra mussels from the open water and deep-water sediments to vegetated shallows and zebra mussel beds.

the spatial extent and productivity of submersed macrophytes in the Hudson have increased substantially since zebra mussels arrived (Stuart Findlay; Elizabeth Blair and William Nieder, Hudson River National Estuarine Research Reserve; Eugenia Barnaba and Susan Hoskins, Cornell University, unpublished data).

Consumers that eat or inhabit macrophytes, periphyton, or phytoplankton not eaten by zebra mussels may consequently also increase following the arrival of zebra mussels. The only example of such an increase in the Hudson is the increase in shallow-water macrobenthos, which contrasts sharply with the concurrent decline in deep-water macrobenthos (Figure 5). We believe that increased macrophytes and attached algae in the shallows of the Hudson following the zebra mussel invasion provided increased food and shelter to benthic animals, more than offsetting the loss of sedimenting edible particles from the water column (Strayer et al. 1998).

The overall effect of the zebra mussel invasion on the Hudson ecosystem was to divert resources from the pelagic zone and deep-water sediments to the vegetated shallows and zebra mussel beds (Figure 8). The effects of the zebra mussel invasion ramified throughout the ecosystem in both the open water and on the sediments, and in fundamental biological, chemical, and physical properties of the ecosystem. The broad spread of effects stemmed from the multiple pathways of interaction that radiate from the central bivalve-phytoplankton axis (Figure 2). Furthermore, the effects of zebra mussels on the Hudson's ecosystem were not only widespread, but

large: Values of many ecological variables shifted by more than 50% (Figures 4-7). Because long-term studies of zebra mussel populations are rare, it is difficult to project the long-term trajectory of the zebra mussel population in the Hudson or to predict the permanence of its ecological impacts. It seems likely that zebra mussels will be a dominant part of the Hudson's ecosystem for years to come. Few other human-caused events in the history of the river have had such large, widespread, and potentially long-lasting effects on the Hudson ecosystem.

Even though the broad outlines of the ecosystem response to the zebra mussel invasion of the Hudson are clear, several important issues remain unresolved. Bacterial numbers appear to have risen substantially in the Hudson, but the data are noisy (Figure 7). A rise in bacterial biomass could partly compensate for the loss of phytoplankton (Findlay et al. 1998) by providing an alternative food source for some planktonic consumers. Unfortunately, large temporal variability in zooplankton populations obscures the actual effect of zebra mussels on these animals, and the large changes we observed are only marginally significant (Pace et al. 1998a). Finally, analysis of changes in the ecologically and economically important anadromous fish populations in the Hudson is complicated by uncertain population estimates, high interannual variability, and independent changes in community structure and commercial harvest.

Ecosystem responses to bivalves

The general sequence of events that we observed in the Hudson has been

seen in other systems invaded by zebra mussels and other bivalves. Lakes and rivers colonized by zebra mussels often experience 50-75% declines in the biomass of phytoplankton and small zooplankton and a corresponding rise in water clarity of 50-100% (MacIsaac 1996, Karatayev et al. 1997). Populations of filter-feeding zooplankton and native bivalves drop by more than 50% in ecosystems invaded by zebra mussels. Macrophyte beds often thicken and spread, and populations of benthic animals associated with beds of plants or zebra mussels proliferate. According to Karatayev et al. (1997), in European lakes the biomass and production of fish approximately doubled after zebra mussel colonization as a result of an increase in benthic prey and a shortening of food chains. Thus, although some of the changes that we saw in the Hudson did not occur or have not been well studied elsewhere, it is clear that zebra mussels often have large, wide-reaching effects on freshwater ecosystems.

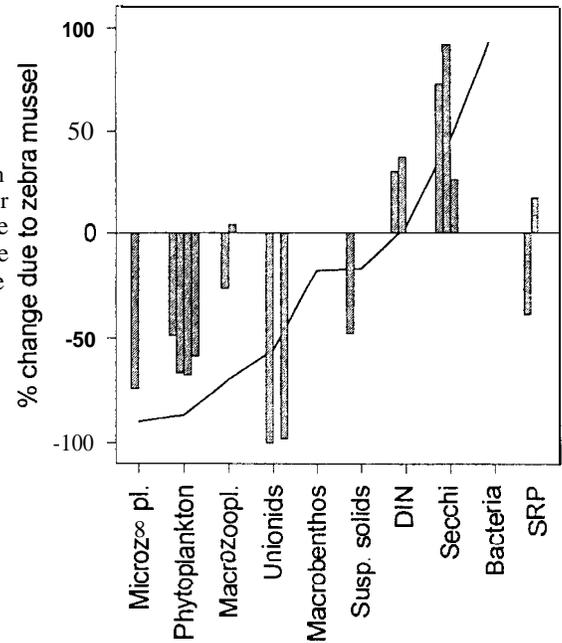
Such effects also have been seen with other invasive freshwater bivalves. In the Potomac River, the invasion of *Corbicula fluminea* caused phytoplankton biomass to drop by approximately 50%, which led to increases in water clarity and in populations of fish and birds associated with expanding beds of macrophytes (Cohen et al. 1984, Phelps 1994). An Asian bivalve, *Potamocorbula amurensis*, invaded oligohaline sections of San Francisco Bay and caused phytoplankton and copepod zooplankton to decline by approximately 80% (Nichols et al. 1990, Alpine and Cloern 1992, Kimmerer et al. 1994). It seems unlikely that such strong effects are restricted to introduced bivalves. Although it is technically more difficult to demonstrate the ecological effects of a native species than an invader, mesocosms and model calculations suggest that native bivalves have strong effects on marine ecosystems (e.g., Sullivan et al. 1991, Ulanowicz and Tuttle 1992, Dame 1996). We suggest that abundant native bivalves may likewise exert strong control over some freshwater ecosystems (Figure 1; see also Welker and Walz 1998).

Nevertheless, examination of the

interactions diagrammed in Figure 2 suggests that ecosystems will differ in their responses to bivalves because the various interaction pathways will differ in strength across ecosystems. For example, the loss of edible particles per unit of bivalve grazing (pathway 1) depends on such properties as the vertical and horizontal heterogeneity of the water column, the size structure of the bivalve and plankton populations, and the growth rate and controls of plankton populations (Caraco et al. 1997). The consequent loss of consumers (pathway 2) depends on the diet breadth of the consumers, the availability of alternative foods (e.g., allochthonous organic matter), and the nature of limits on consumer populations (including whether the populations are food limited at all). Depending on whether biodeposits are retained on the bottom and what sorts of benthic animals live in the ecosystem, the increase in benthic consumers of zebra mussel products (pathway 3) may be large or small. The increase in resources (pathway 4) depends on the nature of those resources, the extent to which they are controlled by edible particles rather than by other factors (e.g., advective losses of nutrients or light absorption by inedible substances), and the ability of diminished populations of edible particles to use these resources (e.g., luxury uptake of phosphorus by phytoplankton). Obviously, the strength of pathway 5 depends not only on the strength of pathways 1 and 4, but also on the local species pool of inedible primary producers (and the consumers that use them) and the morphology of the ecosystem, which determines the amount of potential habitat for benthic plants and algae.

Thus, there is much scope for variation in the response of ecosystems to changing bivalve communities. In support of this view, the responses of North American ecosystems to the zebra mussel invasion are variable, although they conform qualitatively to a general pattern (Figure 9). The characteristics of the bivalve, the characteristics of the ecosystem, and the interaction between bivalve and ecosystem all help to determine the response of an ecosystem to changing bivalve populations.

Figure 9. Variation in the response of North American freshwater ecosystems to the zebra mussel invasion. All ecosystems have estimated zebra mussel filtration rates of 70-125% of the water column per day during the summer growing season. The black line shows the response of the Hudson River, and the hatched bars show responses for a subset or all of the following ecosystems: Lake Erie, Lake St. Clair, Saginaw Bay, and Oneida Lake (Holland 1993, Fahnenstiel et al. 1995, Fanslow et al. 1995, Holland et al. 1995, Johengen et al. 1995, MacIsaac et al. 1995, Mellina et al. 1995, and Horgan 1996). Response variables, from left to right, are microzooplankton, phytoplankton, macrozooplankton, unionid clams, macrobenthos, suspended solids, dissolved inorganic nitrogen (DIN), secchi disk transparency, planktonic bacteria, and soluble reactive phosphorus (SRP).



Conclusions

As we have shown for the Hudson River, human-caused changes in bivalve populations may drive large changes in ecosystem structure and function. These changes derive from the high filtration activity of bivalve populations, which are often dense (Table 1), and from the strong axis of interaction between bivalves and suspended edible particles, especially phytoplankton, which often interact strongly with many other parts of the ecosystem (Figure 2). The role played by bivalves in shallow-water ecosystems is in some ways analogous to that of the planktonic grazer *Daphnia* in lake ecosystems, which by virtue of its abundance and filtration activity has come to be recognized as a key controller of lake ecosystems (e.g., Leibold 1989, Carpenter and Kitchell 1993, Jürgens 1994, Pace et al. 1998b) and whose effects are also expressed largely through the grazer-phytoplankton axis.

However, *Daphnia* and bivalves differ in several important ways. *Daphnia* overlaps spatially with its planktonic food, exhibits a higher degree of particle selection and consequently processes smaller volumes of inedible particles, and has a rapid life cycle, which allows it to track phytoplankton blooms by increas-

ing its population. In contrast, bivalves are able to suppress phytoplankton for long periods during which bivalve growth is negative. Also, *Daphnia* is subject to predatory control (by fish) to a greater degree than are most bivalves. Thus, these two classes of important grazers have different functional characteristics.

Because bivalves are often key players in shallow-water ecosystems and are often affected by harvesting, pollution, habitat degradation, or species introductions, these human activities may have strong unintended effects that ramify throughout aquatic ecosystems. Furthermore, because human-induced changes in bivalve populations may be irreversible (global extinctions or species introductions) or have decades- to centuries-long time constants (local extinctions or severe overharvesting), the bivalve-mediated effects of human activities on ecosystems may be extremely long lasting or permanent.

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