

IMPACTS OF ZEBRA MUSSELS ON AQUATIC COMMUNITIES AND THEIR ROLE AS ECOSYSTEM ENGINEERS

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Abstract

Zebra mussels (*Dreissena polymorpha*) are not only an extremely aggressive invasive species, often dominating water bodies they invade, they are also very effective ecosystem engineers, altering the environments they invade. They are effective engineers, altering both ecosystem structure and function. They change existing and provide new habitat for other organisms, affect trophic interactions and the availability of foods for both pelagic species and other benthic species, and they affect the rates of other ecosystem processes including mineralization of nutrients, oxygen availability and sedimentation rates. These physical impacts on the environment feedback directly to other species that interact with or are impacted by zebra mussels, or indirectly through food chains, disturbance, succession, or other longer-term community and ecosystem processes.

1 Introduction

To date, *Dreissena polymorpha* has been the most aggressive freshwater invader worldwide. Dreissenids are the only freshwater bivalves that attach to hard substrates in high densities and have a planktonic larval stage. This life history facilitates their abilities as invaders, and allows them to become enormously abundant when introduced into a new water body. Once introduced their populations can grow rapidly, and the total biomass of a population can exceed 10 times that of all other native benthic invertebrates (Sokolova et al. 1980a; Karatayev et al. 1994a; Sinitsyna & Protasov 1994). The zebra mussel is frequently competitively dominant over native benthic fauna, and can impact all components of the freshwater ecosystem, especially benthic animals (Sokolova et al. 1980b; Karatayev et al. 1994a; Karatayev & Burlakova 1995a; Karatayev et al. 1997, and others). Most of the impacts of zebra mussels in freshwater systems are a direct result of their functioning as ecosystem engineers.

1.1 WHAT IS AN ECOSYSTEM ENGINEER?

The definition, role and consequences of species as ecosystem engineers were formalized in two papers by Jones et al. (1994, 1997). They defined ecosystem engineers as species that "directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials" (Jones et al. 1994, 1997). Engineering organisms can cause physical modification of the environment, and influence the maintenance or creation of habitats. Their ecological effects on other species can occur because of physical state changes caused, either directly or indirectly, by the engineer, and because engineers affect the control and use of resources by other species.

Many different species have been identified as ecosystem engineers in all types of habitats, and their impacts on systems can vary tremendously. There are many examples of ecosystem engineers from aquatic habitats. These include (but are not limited to) fishes in rivers (Flecker 1996), insects in streams and pools (Wotton et al. 1998), crayfish in riffles and pools (Statzner et al. 2000), angiosperms in marshes (Bruno 2000), and especially bivalves (Dame 1993, 1996).

1.2 BIVALVES AS ECOSYSTEM ENGINEERS

The role of bivalves in and impacts on aquatic ecosystems has long been recognized, however, most of this work has focused on marine bivalves (reviewed in Dame 1993, 1996). In part this is because the ecosystem effects of species are most obvious when they are dense or extremely abundant, as is often seen with marine bivalves that form dense beds or reefs. Dame (1996) identified four main ecosystem level roles of bivalves: trophic, nutrient cycling, structural, and monitors and indicators. Suspension feeding by bivalves will have large impacts on the plankton as well as suspended sediments. The reduction of filtering and suspension feeding bivalves will greatly alter many aspects of the planktonic community and affect benthic-pelagic coupling. Bivalves affect nutrient cycling by consuming particulate and dissolved organic matter and excreting inorganic nutrients. Because of their relatively large body sizes and rapid processing rates, they can have large impacts on nutrient cycling. Structurally, bivalves impact both the physical and biological environment. Physically, bivalves create structure with their shells and can move or stabilize sediments. Biologically they affect community structure (both in the water column and on the benthos) and can influence community stability, diversity and interspecies links. Marine bivalves have also been important indicators of environmental stress and their shells provide important records of environmental changes over both the short and long term.

Most of the research on the role of bivalves as ecosystem engineers has focused on native species, in environments where they are abundant and clearly play important roles. Attention to the natural role of bivalves in these communities has been particularly focused on areas where native species are over harvested or are lost due to disease or human disturbance, resulting in dramatic changes in ecosystems as a result of the loss of these important engineering species. The alternative situation that has recently gained attention is when an invasive bivalve causes dramatic changes in an environment, such as has been seen when the mat forming bivalve, *Musculista senhousia*, invaded near-shore habitats in North America (Crooks & Khim 1999).

2 Zebra mussels as ecosystem engineers

Zebra mussels have all of the properties of marine ecosystem engineers. Just by their presence, they change the characteristics of biotic and abiotic environments in aquatic systems. Other changes are caused by the activities of zebra mussels, especially their feeding and filtering. The changes caused by the presence or activities of zebra mussels can be systems wide, or have just local impacts. Zebra mussels and their activities will impact multiple levels in aquatic systems, affecting species composition, species interactions, community structure, and ecosystem properties. These changes or impacts may be direct or indirect in action (Fig. 1).

2.1 CHANGES TO THE ENVIRONMENT CAUSED BY ZEBRA MUSSEL STRUCTURES

Zebra mussels are macroinvertebrates with hard, calcium carbonate shells. This hard shell surface increases the substratum available for other species that live attached to or associated with hard substrata, including other zebra mussels.

Zebra mussels attach to hard substrata and each other with byssal proteinaceous threads, creating complex three-dimensional structures. This complex creates habitat and refuge for a variety of species, which would otherwise not be common or present as epifauna in a soft bottom habitat.

Their shells do not decompose or dissolve readily in lakes that can support zebra mussel populations. Therefore the shells and shell fragments of dead animals can accumulate on the bottom, creating reef-like structures. These reefs provide additional hard substrata for animals and create a hard-substratum habitat in an otherwise soft sediment environment.

2.2 CHANGES TO THE ENVIRONMENT CAUSED BY ZEBRA MUSSEL FUNCTIONING

Zebra mussels not only cause changes to the environment due to their physical presence, they also have large impacts as a direct result of their biological activity.

2.2.1 *Water clarity*

Zebra mussels constantly filter the water for both feeding and respiration. Water currents are created by the beating of cilia on their ctenidia (gills), and water is almost constantly circulated through their siphons, and across their gills. As water is moved across their gills, particulates are constantly removed. Zebra mussels are extremely efficient at removing particulates from water, and seem to remove all particles larger than 0.4 μm in an unselective manner (Roditi et al. 1996). However, they are very selective in which of these particles they consume (Baker et al. 2000). Filtered particles are either consumed or bound in mucus, preventing immediate resuspension. This efficient filtering by large numbers of zebra mussels will greatly increase water clarity because both inorganic particulates and plankton will be removed.

Increasing water clarity has several impacts on aquatic ecosystems. Depth of the photic zone is extended, total lake volume available for photosynthesis by phytoplankton is greatly enlarged, and macrophytes, whose depth distribution is frequently limited by light, can live at greater depths and cover more of the bottom area. In addition, more light will reach more areas of the bottom of a water body, enhancing primary productivity over greater areas of the bottom.

2.2.2 *Deposition on the bottom*

When zebra mussels are in a water body, they build a direct connection between the planktonic portion of the water body and the benthos (benthic-pelagic coupling) and greatly enhance the rates of deposition of both organic and inorganic material on the bottom. Filtered particles (Section 2.2.1) are sorted, and either consumed, or rejected. Rejected particles are bound in mucus and expelled as pseudofeces, deposited onto the

bottom. In general, this will result in greatly increased organic content of sediments, and provides an enhanced food subsidy for benthic deposit feeders. In addition, sedimentation rates can increase several orders of magnitude.

Ecosystem Engineering Impacts of *Dreissena polymorpha*

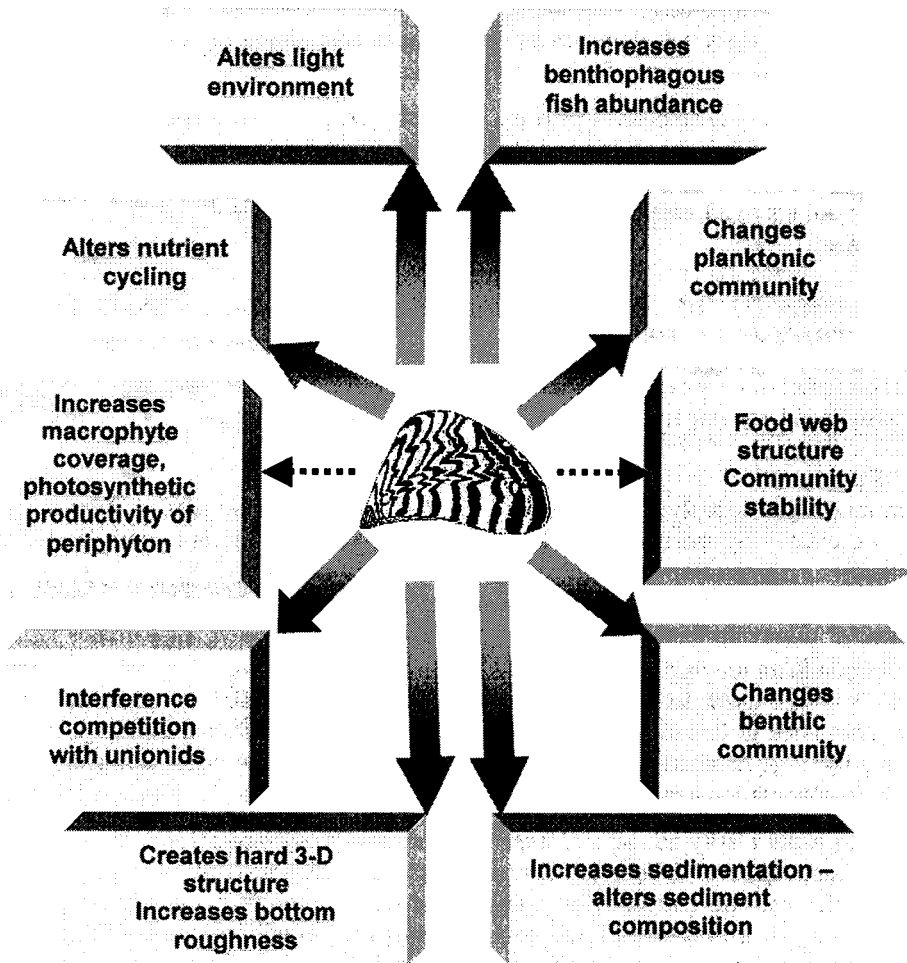


Figure 1. Direct (solid arrows) and indirect (dashed arrows) impacts of *Dreissena* on invaded aquatic ecosystems.

2.2.3 Mineralization and chemical cycles

Zebra mussel physiological activities can have a large impact on cycling of elements in the ecosystem. Through respiration they can have a large impact on oxygen levels, particularly in systems where photosynthesis may be limited by light (Effler & Siegfried

1994; Caraco et al. 2000). Because zebra mussels can be enormously abundant, their high rates of consumption and excretion can affect phosphorus and nitrogen cycles. In addition, zebra mussels secrete hard calcium carbonate shells. These shells are very stable, and will remain long after the animal has died.

2.2.4 Biotic community changes

Zebra mussels can cause a variety of changes in biotic communities as well. Selective feeding and removal of phytoplankton can directly cause changes in the composition of the plankton. Zebra mussels are limited in the size of particles they effectively remove from the plankton, and these limitations appear to be size based rather than quality based, and result from mechanical or functional limitations. Zebra mussels filter particles from 0.4 - 750 μm (Ten Winkel & Davids 1982; Mikheev et al. 1994; Roditi et al. 1996) with some reports to 1200 μm (Horgan & Mills 1997). Changes in substrata availability and the presence of refuges caused by zebra mussel structures (Section 2.1) create habitat for species that would otherwise be infrequent or absent in the environment. Increases in the organic composition of sediments creates a food base for benthic feeding species, again increasing their abundance relative to environments without zebra mussels (Karatayev et al. 1983, 1994a; Karatayev & Burlakova 1992, 1995a; Botts et al. 1996; Stewart et al. 1998).

In addition to these direct impacts on biotic communities, the activities of zebra mussels can have indirect impacts on systems. By increasing light, species composition and community structure can change. Selective removal or selective impact on different species can alter competitive interactions among species in the plankton. Changes in nutrient abundance and cycling can affect community diversity and stability. And, changes in community composition and dynamics can alter food webs and species not directly impacted by zebra mussels.

3 Species and system responses to changes in the environment caused by zebra mussels

The long history of zebra mussel invasion of freshwaters across eastern and western Europe has provided biologists with many systems where the direct and indirect impacts of zebra mussel ecosystem engineering can be measured. Much of the work has been done in regions that are part of the former Soviet Union, Eastern and Western Europe (refs. in Limanova 1964, 1978; Stanczykowska 1977, 1997; Schloesser et al. 1994; Karatayev et al. 1997, 1998). Complimentary work has been done in North America where zebra mussels have invaded lakes and rivers since the mid-1980s. In general, the North American research supports the findings in Europe.

3.1 SPECIES COMPOSITIONAL CHANGES

Dreissena provides food and shelter for many benthic invertebrates, and they increase density and biomass in zebra mussel beds, while others (mainly filter feeders) may decrease or disappear from the community (Sebestyen 1937; Sokolova et al. 1980b; Karatayev et al. 1983; Karatayev & Lyakhovich 1990; Karatayev & Burlakova 1992; Stewart et al. 1998, 1999).

After *Dreissena* invade water body, they dominate the benthos, forming dense populations of very effective filter feeders. This causes a radical shift in the benthic trophic structure (Lvova-Kachanova & Izvekova 1978; Sokolova et al. 1980a,b; Karatayev & Burlakova 1992; Karatayev et al. 1994a, 1997). Native filter feeders are out-competed by *D. polymorpha*, and decrease in abundance. Simultaneously, animals that are deposit feeders greatly increase in abundance (Karatayev & Burlakova 1992; Karatayev et al. 1994a).

Historically, prior to the *D. polymorpha* invasion, the benthic community of Lukomskoe Lake (Belarus) was dominated by species considered to be detritus gatherers (45% of total benthic biomass) and detritus filterers (41%) (Karatayev & Burlakova 1992; Karatayev et al. 1997). After *D. polymorpha* invaded in late 1960s the relative abundance of detritus gatherers increased to 70% of the total biomass (excluding zebra mussel biomass), due to the increased food supply provided by zebra mussel pseudofeces and feces. The relative abundance of predators and omnivores in the community also increased, and the proportion of native detritus filterers decreased 8-fold. Excluding *D. polymorpha*, the benthic community was dominated by animals using food from sediments (Karatayev & Burlakova 1992; Karatayev et al. 1994a). The same patterns have been observed in 4 other water bodies studied in different regions across the former Soviet Union (Karatayev et al. 1994a).

Shelters created by zebra mussel shells have a positive impact on species abundance, providing refuges from predation and other disturbances. Shell habitats created by zebra mussels have been shown to be the primary mechanism for increased abundances of snails and gammarid amphipods (Botts et al. 1996; Stewart et al. 1998). Stewart et al. (1999) suggested that elevated invertebrate densities in natural *Dreissena* beds are caused by reduced predation rates on these organisms, as well as invertebrates immigrating to *Dreissena* beds from other habitats to avoid predators. They found an 8-fold increase in snail survivorship in the presence of *Dreissena* shells.

Dreissena have also been shown to have positive effect on isopods (*Asellus aquaticus*, Wolnomiejski 1970; Karatayev & Lyakhnovich 1990), larval chironomids (*Microtendipes* gr. *chloris* and *Limnochironomus* gr. *nervosus*, Wolnomiejski 1970), leeches (*Helobdella stagnalis*, Wolnomiejski 1970), snails (*Lymnaea lagotis*, Karatayev et al. 1983; *Amnicola*, reviewed in Strayer 1999), amphipods (*Gammarus lacustris*, Karatayev et al. 1983; Karatayev & Lyakhnovich 1990), and oligochaetes (*Aulodrilus limnobius*, *Psammoryctides albicola*, *Limnodrilus hoffmeisteri*, Afanasiev 1987). Botts et al. (1996) found that in Lake Erie the densities of amphipods, chironomids, oligochaetes, turbellarians, and hydrozoans were significantly higher in sand with zebra mussel druses than in bare sand. However, not all species are positively affected by the presence of zebra mussels. Negative effects of zebra mussels were found for native suspension feeders: chironomid larvae, *Glyptotendipes paripes* (Sokolova et al. 1980a,b), *Stictochironomus psammophilus* (Karatayev et al. 1983) and sphaeriid bivalves (Strayer et al. 1998).

Impacts of zebra mussels on unionid bivalves are of special concern because they are presently endangered or threatened in many environments where they were previously in high abundance. High densities of zebra mussels seem to have only negative effects on unionids (reviewed by Karatayev et al. 1997; Burlakova et al. 2000). By attaching to

unionids, zebra mussels can make it more difficult for them to burrow and move through sediment. They can weight down their host unionid, resulting in burial in very soft sediments, can increase drag and the likelihood of dislodgement by water motion for species living near shore, prevent opening unionid valves for respiration, feeding and reproduction, or preventing the closing of the valves. *D. polymorpha* may directly compete with unionid bivalves for food, available space, and cause unionids physiological stress and symptoms of starvation, including declines in glycogen content, declines in organic matter contents in guts, and increased shell deformities.

The impact of zebra mussels on unionids host depends on: (i) *D. polymorpha* density (Lewandowski 1976; Ricciardi et al. 1995; Burlakova et al. 2000); (ii) time since invasion by *D. polymorpha* (Sebestyen 1937; Karatayev et al. 1997; Burlakova et al. 2000); (iii) characteristics of bottom substrata (Karatayev 1983; Burlakova et al. 2000); (iv) unionid species (Lewandowski 1976; Arter 1989; Haag et al. 1993); and (v) unionid sex (Haag et al. 1993).

Mass mortalities of unionids caused by *D. polymorpha* overgrowth are most common during the initial stages of colonization by zebra mussels a new water body, when mussel populations are growing rapidly. This type of mass mortality is well documented both in European (Sebestyen 1937; Karatayev & Burlakova 1995b, Burlakova et al. 2000) and North American water bodies (Haag et al. 1993). However, *D. polymorpha* invasion did not result in complete elimination of unionid bivalves in any European water bodies. Moreover, after initial peaks in zebra mussel abundance, *D. polymorpha* coexist with unionid bivalves (Lewandowski 1976; Karatayev 1983; Miroshnichenko et al. 1984; Miroshnichenko 1987; Ponyi 1992; Nichols & Amberg 1999; Burlakova et al. 2000). Soft sediments provide refuges for unionids. By burrowing in silt, unionids can clean incrustated mussels from their shells (Arter 1989; Nichols & Amberg 1999; Burlakova et al. 2000). Water-level fluctuations and waves may also help to remove attached zebra mussels from unionid shells (Schloesser et al. 1997).

3.2 COMMUNITY CHANGES

As a rule, when *D. polymorpha* invade new freshwaters, they become the dominant benthic species in terms of biomass, with 10-50 times the total mass of all other benthic invertebrates combined (Sokolova et al. 1980a; Lyakhnovich et al. 1988; Protasov & Afanasiev 1990; Karatayev 1992; Karatayev et al. 1994a; Karatayev & Burlakova 1995a). In addition, *Dreissena* aggregations or druses have a dramatic direct effect on benthic communities, and a totally different community forms in their presence (Karatayev et al. 1997). The presence of individual *D. polymorpha* on the bottom, however, does not change the qualitative or quantitative composition of the benthic community (Karatayev 1988; Karatayev et al. 1994a).

After *D. polymorpha* invaded Lukomskoe Lake (Belarus), only 26 of the previous 49 taxa of littoral benthic animals were part of both the sandy littoral community and the community found in zebra mussel druses (Karatayev 1983; Karatayev et al. 1983). After invasion, the sandy littoral community was very similar to pre-invasion, dominated by chironomids and oligochaetes, most of which were small and live within the sediment. The druse community was composed of larger animals such as snails, amphipods, iso-

pod, trichopteran, and leeches. The dominant species in the sand habitat was the chironomid *Stictochironomus psammophilus*, however, only a single individual of this species was found in druses. The snail *Lymnaea lagotis*, and the amphipod *Gammarus lacustris* were dominant in zebra mussel druses, but only a single *L. lagotis*, and no *G. lacustris* were found in sandy areas. Similar patterns were found for subdominant taxa in these two habitat types (Karatayev 1988; Karatayev et al. 1983, 1994a). Invertebrate biomass (excluding zebra mussels) was 8 times greater in druses even though densities were 1.5 times lower than in sandy sediments, thus the community was dominated by larger species. Therefore, druses are responsible for the creation of a new community of bottom invertebrates, not generally found in sandy sediments. Large changes in species composition and density/biomass of benthic invertebrates have been found in all systems where zebra mussels have invaded (Wiktor 1969; Kharchenko & Protasov 1981; Stewart et al. 1998).

Indirect effects, such as increasing light penetration, also have large effects on community composition once zebra mussels invade a water body. Increased light penetration positively affects macrophytes and benthic algae beds (Lyakhnovich et al. 1988; Reeders & bij de Vaate 1990; Skubinna et al. 1995; Lowe & Pillsbury 1995). Vascular macrophytes beds positively affect abundance and diversity of benthic invertebrates, providing them additional food and substrate. In contrast, thick beds of filamentous algae could decrease abundance of macroinvertebrates (Haynes et al. 1999).

3.3 CHANGES IN INTERSPECIES INTERACTIONS

When zebra mussels are added to freshwater communities, they consume phytoplankton and therefore will compete with zooplankton for microalgal foods. Decreases in phytoplankton and concomitant decreases in zooplankton abundance have been seen in a variety of water bodies (Lyakhnovich et al. 1983, 1988; Mitrakhovich et al. 1983; Reeders et al. 1993; Karatayev et al. 1994a; Karatayev & Burlakova 1995a; Pace et al. 1998, and others). Also, as indicated above, zebra mussels compete for planktonic food with benthic suspension feeders, especially unionid bivalves.

In addition to competition for food, zebra mussels can compete for space on hard substrata, and convert sandy substrata to hard substrata, displacing the typical sandy community (Wiktor 1969; Kharchenko & Protasov 1981; Karatayev et al. 1983, 1994a, 1997; Stewart et al. 1998). There is also a suggestion that zebra mussels may compete for benthic space with fish by covering areas used by fish for nests and rearing their young (Marsden 1997).

In addition to these direct effects on species interactions, zebra mussels have indirect effects on species interactions through their effects on nutrient availability and turnover. Inedible algae may increase in abundance through competitive release of nutrients due to the grazing by zebra mussels reducing other algal populations, or by increased availability of limited nutrients through zebra mussel excretion (Arnott & Vanni 1996).

The abundance of benthic feeding fishes is usually enhanced by the presence of zebra mussels because of the increase in density and mean body size of benthic invertebrates (Lyakhnovich et al. 1988; Karatayev 1992; Karatayev & Burlakova 1995a). Planktivorous fish, however, may be negatively impacted if the presence of zebra mussels is

associated with decreased zooplankton abundance, or if increased water clarity increases predation rates on larval fishes (Francis et al. 1996). Piscivorous fish may be positively affected because of an increase in benthic feeding fish.

3.4 CHANGES IN FOODWEBS AND ENERGY FLOW

To our knowledge the only studies on the impact of *D. polymorpha* on food webs and the energy flow through trophic levels have been conducted in Lukomskoe Lake, Belarus (Karatayev 1992; Karatayev & Burlakova 1995a). Before the invasion of zebra mussels, the total primary production in this lake was 2,596 kcal m⁻² (phytoplankton 98%, macrophytes 2%). The secondary production (nonpredatory zooplankton + nonpredatory zoobenthos) was 3.7% of total primary production. Fish production was 0.15% of the total primary production (Karatayev & Burlakova 1995a) (Table 1).

Table 1. Biomass (B, kcal m⁻²) and production (P, kcal m⁻² year⁻¹) of Lukomskoe Lake prior to and following the invasion of zebra mussels (modified from Karatayev & Burlakova 1995a).

Trophic level	Pre-invasion		10 years after invasion		20 years after invasion	
	B	P	B	P	B	P
Phytoplankton	50.9	2,544.5	12.5	624.5	16.1	805.0
Macrophytes	40.9	51.1	132.8	166.0	81.3	101.6
Total primary production	91.8	2,595.6	145.3	790.5	97.5	906.6
Nonpredatory zooplankton	6.40	93.8	0.80	14.8	3.91	68.1
Nonpredatory zoobenthos	0.38	1.4	3.22	12.2	6.44	24.5
Zebra mussels	0.00	0.0	27.80	16.7	40.00	24.0
Nonpredatory zooplankton + nonpredatory zoobenthos	6.78	95.2	31.82	43.7	50.35	116.6
Predatory zooplankton	1.24	13.2	0.23	5.4	0.99	17.2
Predatory zoobenthos	0.02	0.1	0.28	1.0	0.56	2.0
Predatory zooplankton + predatory zoobenthos	1.26	13.3	0.51	6.4	1.55	19.2
Benthivorous+planktivorous fish	8.75	3.5	17.00	6.8	21.25	8.5
Piscivorous fish	1.25	0.5	3.00	1.2	1.25	0.5

Ten years after the zebra mussel invasion in Lukomskoe Lake, macrophyte production had increased 3.3 times, and phytoplankton production decreased more than 4 times (Table 1). Total primary production decreased more than 3 times. Although secondary production declined from 95 to 44 kcal m⁻², the relative role of benthic invertebrates dramatically increased from 3 to 77% of the total production (nonpredatory zooplankton + zoobenthos). Fish production more than doubled. The conversion of primary production to higher trophic levels increased for nonpredatory invertebrates from 3.7% (before zebra mussels invasion) to 5.5% (after invasion), and for fish from 0.15% (before invasion) to 1% (after invasion) of the total primary production. This high rate of fish production is typical of commercial fish ponds, but is much higher than most natural lake communities (Bullion & Winberg 1981).

Twenty years after the initial invasion of the Lukomskoe Lake, the zebra mussel population density declined and, in terms of biomass, became relatively stable. Total primary production had increased 13%, and the contribution of macrophytes to the total decreased from 20% to 11% (Table 1). The production of nonpredatory zooplankton and

zoobenthos more than doubled. Fish production also increased slightly, and remained approximately at 1% of primary production (Karatayev 1992; Karatayev & Burlakova 1995a). Therefore, *Dreissena* became the major consumer of primary productivity, and the most important conduit of energy fixed through photosynthesis by phytoplankton to higher trophic levels in the ecosystem (Table 1).

3.5 SYSTEMWIDE EFFECTS

In most freshwater ecosystems, the benthic community and the pelagic community are considered functionally separate. Dynamics in planktonic systems are often studied completely without consideration of the benthos. In most freshwaters, this distinction is probably not a bad approximation, because in the water column primary productivity is driven by external nutrient inputs, and zooplankton feed primarily on phytoplankton. Larger nekton are often planktivorous, although in Europe, there are many benthic feeding fishes. The major link between the benthos and the pelagic system in water bodies without *D. polymorpha* has been through predation by nektonic feeders, fishes, on benthic invertebrate production. Benthic production is driven by the slow rain of suspended organic material to the bottom and to a small extent by the filtering activity of suspension feeders such as unionids. In the benthos, most species are considered to feed on detritus or other benthic organisms. Thus, the typical benthic freshwater system is considered to be detritus dominated, rather than relying on large amounts of primary productivity or direct links to planktonic processes. And, in general, the benthos are not capable of controlling processes or dynamics in the planktonic system.

However, zebra mussels are functionally different than most benthic invertebrates in freshwater. Although they have large impacts on the structure and function of the benthos (Section 3.1, 3.2), they also have a large direct impact on the planktonic community. They filter large volumes of water and transport this material removed from the water column to the benthos (Lvova 1979; Lvova et al. 1980; Wiktor 1969; Shevtsova and Kharchenko 1981; Protasov et al. 1983; Stanczykowska 1977; Reeders et al. 1989; Karatayev & Burlakova 1995a,b; Karatayev et al. 1997). Therefore, they provide a direct link between processes in the plankton and those in the benthos and by their deposition of pseudofeces and feces, provide a direct conduit for primary productivity in the water column to the benthos to a much larger extent than any other process. In addition, they are capable of controlling pelagic processes by removal of particulate matter and increasing water transparency and the volume of the photic zone. They impact phytoplankton standing stock, and thus can influence planktonic trophic interactions (Lyakhovich et al. 1983, 1988; Mitrakhovich et al. 1983; Shevtsova et al. 1986; Karatayev 1992; Reeders et al. 1993; Karatayev et al. 1994a; Karatayev & Burlakova 1995a). In addition, phytoplankton productivity will influence zebra mussel growth and reproduction, producing the possibility of direct feedback between the benthos and the pelagic system that were not present prior to their invasion.

D. polymorpha shift materials from the pelagic to the benthos by transporting suspended matter including detritus, phytoplankton, bacterioplankton, and small zooplankton from the water column to the benthic community (Lvova 1980; Karatayev 1988, 1992; Lyakhovich et al. 1983, 1988; Kharchenko & Lyashenko 1985; Karatayev & Burlakova 1992, 1995a; Reeders et al. 1993). A small portion of filtered material is metabo-

lised and used for *D. polymorpha* growth and the rest is available to other benthic organisms.

The movement of large amounts of seston from the plankton to the benthos induced changes in all aspects of freshwater ecosystems after the invasion of *D. polymorpha* (Lyakhnovich et al. 1983, 1988; Mitrakhovich et al. 1983, Reeders & Bij de Vaate 1990; Karatayev & Burlakova 1992, 1995a; Reeders et al. 1993; Karatayev et al. 1997). For example, in Lukomskoe Lake shortly after *D. polymorpha* invasion (late 1960s) water transparency in summer increased from 1.8 to 4 m, and seston concentrations decreased 3-fold (Lyakhnovich et al. 1983; Karatayev & Burlakova 1995a). The amount of dissolved organic matter in the water column after *D. polymorpha* invasion also decreased. Increased water transparency resulted in an expansion of macrophyte cover (from 6 to 30% of total lake area) mainly due to an increase in the depth at which macrophytes can grow (from 2.5 to 5 m). After the invasion of zebra mussels, the biomass of phytoplankton and zooplankton declined more than 10 times. In contrast, the biomass of benthic invertebrates increased more than 10 times. Fish productivity doubled, and the composition of the commercial catch in the Lukomskoe Lake is now characterized by benthophagous fishes which feed mainly on zebra mussels including roach, rudd, white bream and bream (Karatayev 1983, 1988, 1992; Lyakhnovich et al. 1983; Mitrakhovich et al. 1983; Lyakhnovich et al. 1988; Karatayev et al. 1994b; Karatayev & Burlakova 1995a).

By the mid-1980s, when *D. polymorpha* abundance in Lukomskoe Lake declined after its initial invasion (late 1960s), summer transparency decreased to 3 m, but remained above pre-invasion levels (1.8-2.0 m). Similar patterns were found for both phytoplankton and zooplankton; their biomass decreased when zebra mussels initially reached very high population density, but increased after *D. polymorpha* densities declined. Again, they did not return to their pre-invasion abundance. The extent of macrophytes also decreased from 30% to 20% of the lake surface area, but still remains higher than pre-invasion levels (6%) (Karatayev 1992; Karatayev & Burlakova 1995a).

D. polymorpha was associated with similar changes in the Naro-chanskies lake system (mesotrophic Naro-ch Lake, eutrophic Myastro Lake and highly eutrophic Batorino Lake). *D. polymorpha* invaded in the mid-1980s, after approximately 40 years of research on these lakes (Ostapenya et al. 1993, 1994a,b). Shortly after the invasion, water transparency increased 1.3-2.4 times, seston was reduced 2.3-6.9 times, and chlorophyll concentration decreased 2.7-6.9 times. Organic carbon content, BOD₅, primary production, respiration and biomass of phytoplankton also decreased (Ostapenya et al. 1993, 1994a,b). After zebra mussels invaded, highly eutrophic Lake Batorino became eutrophic (Ostapenya et al. 1994b), and eutrophic Lake Myastro became slightly eutrophic (Ostapenya et al. 1994a). Thus, *D. polymorpha* can be used to control the negative affects of anthropogenic eutrophication including increased phytoplankton abundance and decreased water clarity (Karatayev 1983, 1992). Some west-European scientists also have proposed using *D. polymorpha* as biofilters to decrease the effects of anthropogenic eutrophication in lakes (Reeders et al. 1989, 1993; Reeders & bij de Vaate 1990; Noordhuis et al. 1992).

Similar changes subsequent to the recent appearance of *Dreissena* have reported in the North American lakes. Following *D. polymorpha* invasion, water transparency (Leach 1993; Fahnenstiel et al. 1995a; Caraco et al. 1997), benthic algal abundance (Lowe & Pillsbury 1995), and macrophyte beds (Skubinna et al. 1995) have increased. At the same time, turbidity has decreased (Skubinna et al. 1995), as has chlorophyll, and phytoplankton abundance and production (Leach 1993; Fahnenstiel et al. 1995a,b; Caraco et al. 1997). The density of native benthic animals increased and was accompanied with changes in benthic community structure (Stewart & Haynes 1994; Wisenden & Bailey 1995; Botts et al. 1996). In all cases, patterns of the effects of *D. polymorpha* are similar to those found in European freshwaters.

Based on data from long-term studies in Europe and recent data from North America, we suggest the following generalizations of aquatic ecosystem response to *D. polymorpha* invasion.

- (i) Water transparency increases 1.5-2 or more times (Stanczykowska 1968, 1977; Lvova 1979; Karatayev 1983, 1992; Fahnenstiel et al. 1995a).
- (ii) The amount of seston in the water column decreases 1.5-10 times (Lvova et al. 1980; Kharchenko & Lyashenko 1985; Leach 1993; Reeders et al. 1993; Ostapenya et al. 1994a,b; Karatayev & Burlakova 1995a).
- (iii) The amount of organic matter in the water column decreases (Kharchenko & Lyashenko 1985; Ostapenya et al. 1994a,b; Karatayev & Burlakova 1995a).
- (iv) The rate of biogeochemical conversion from organic to inorganic matter increases (Kharchenko & Lyashenko 1985; Shevtsova 1989).
- (v) Biochemical oxygen demand in the water column (BOD_5) decreases up to 1.5 times (Kharchenko & Lyashenko 1985; Ostapenya et al. 1994a,b).
- (vi) The total density and biomass of phytoplankton decreases 1.5-4 times, and total chlorophyll decreases (Lyakhnovich et al. 1988; Karatayev 1992; Reeders et al. 1993; Ostapenya et al. 1994a,b; Karatayev & Burlakova 1995a; Caraco et al. 1997). However, the clearance rates and pseudofeces production of *Dreissena* differs for different algal species consumed (Mikheev et al. 1994, Berg et al. 1996; Ten Winkel & Davids 1982), therefore, the net effect will depend on algal community structure as well.
- (vii) There are considerably less data on the effects of zebra mussels on bacterioplankton. Effects may depend on the trophic status of the water body and the bacterioplankton community structure. Zebra mussels can effectively reduce large ($>0.9 \mu\text{m}$) bacteria, while smaller size bacteria could escape predation. Simultaneously, high rates of mussel nutrient excretion may facilitate growth of the small bacteria under low nutrient conditions (Cotner et al. 1995). Small bacteria can also benefit from *Dreissena* grazing on flagellated protozoans, their major predators (Findlay et al. 1998). Ostapenya et al. (1994a,b) found somewhat increased abundance of bacterioplankton after the introduction of zebra mussels.
- (viii) With increased transparency, the photic zone for macrophytes greatly increases. This results in a much greater portion of the lake bottom covered with macrophytes and greater total macrophyte production (Lyakhnovich et al. 1988; Reeders & bij de Vaate 1990; Skubinna et al. 1995).

- (ix) With increased light reaching the bottom, periphyton and benthic algae increase in both standing stock and primary productivity as has been seen in North America (Lowe & Pillsbury 1995).
- (x) Zooplankton abundance decreases (Lyakhnovich et al. 1983; Mitrakhovich et al. 1983; Mitrakhovich 1984; Shevtsova et al. 1986; Karatayev et al. 1994a; Pace et al. 1998). Microzooplankton (rotifers, protozoans, copepod nauplii) may be affected more than larger crustaceans (MacIsaac et al. 1995; Pace et al. 1998). Macrophyte beds associated with clearer water may provide increased spatial refuge for large cladocerans (Mayer et al. 2000). After zebra mussels established in Lukomskoe Lake, the structure of zooplankton community changed - the former dominant complex of species typical for eutrophic lakes shifted to that typical for mesotrophic lakes (Mitrakhovich et al. 1983; Mitrakhovich 1984).
- (xi) Zoobenthos change in abundance and in taxonomic and trophic structure as discussed above (Wiktor 1969; Kharchenko & Protasov 1981; Karatayev 1983, 1992; Karatayev et al. 1983; Karatayev & Burlakova 1992, 1995a; Botts et al. 1996; Stewart et al. 1998).
- (xii) The effect on fish may be direct or indirect. The direction and intensity of these effects are dependent on the feeding method of the majority of the fish in a water body. However, the complexity of food web interactions, and because different life stages of fishes (and zebra mussels) can have different trophic roles, precise predictions are impossible to make. *Dreissena* planktonic larvae can compose up to 70% of zooplankton density in summer months and are readily consumed by many species of fish (Karatayev et al. 1994b, Molloy et al. 1997). In general, we may expect an enhancement of all benthic feeding fishes, even those that do not feed on *Dreissena*, as *Dreissena* increases the biomass of other benthic invertebrates (Kharchenko & Protasov 1981; Karatayev 1983, 1992; Lyakhnovich et al. 1983, 1988; Karatayev & Burlakova 1992, 1995a; Stewart & Haynes 1994, and others). Direct or indirect negative effects could be expected on planktivorous fish through competition with larvae for zooplankton, by increasing fish predation on larvae via increased water clarity (Francis et al. 1996). However, to date, no negative changes in the abundance of planktivorous fish have been found (Trometer & Busch 1999; Mayer et al. 2000).

4 Heterogeneity of impacts of zebra mussels

Although many generalizations can be made about the impacts of zebra mussels and their functioning on freshwater species and ecosystems, it is important to recognize that impacts will not be uniform across a given water body, and impacts and their consequences are likely to change over time.

4.1 LOCAL VERSUS SYSTEM WIDE EFFECTS/IMPACTS

The impacts of zebra mussels, or any other biological agent, are likely to be most intense close to the animals, depend on local and total abundance and densities, and the size of the water body being affected. Zebra mussels are benthic, and will be restricted to a more or less two-dimensional surface. However, the water column above the benthos is a three-dimensional habitat, and the amount of three-dimensional habitat affected

by zebra mussels will depend on the size and bathymetry of the water body. Therefore, we should expect heterogeneity of impacts due to local effects and conditions, and this hinders our ability to predict system or lake-wide long-term impacts at the present time.

Zebra mussels will have a local impact by creating structure, and providing food and shelter for benthic species. However, this effect will not necessarily be important at distances away from druses. Similarly depending on water mixing rates, lake morphology, and turnover rates, the effects of zebra mussels clearing and filtering water will have very different effects (Reed-Andersen et al. 2000) and may be very local in deep water lakes (Ackerman et al. 2001).

Because species composition, food web links, and biotic interactions as well as physical characteristic including nutrient loading can vary tremendously among water bodies, it is presently difficult to predict more than general patterns expected impacts of zebra mussel invasion.

4.2 SHORT-TERM VERSUS LONG-TERM EFFECTS

It is well known that immediately after invasion, populations of *D. polymorpha* grow to very high densities, but due to density-dependent processes total sustainable biomass declines as the system changes. Ultimately densities well below the maximum achieved persist (Sebestyen 1937; Zhadin 1946; Lvova 1980; Karatayev 1983; Karatayev & Burlakova 1995a). However, all populations of zebra mussels do not stabilize and can vary widely over time (Ramcharan et al. 1992; Stanczykowska & Lewandowski 1993).

Shortly after initial invasion, when population levels are climbing and high, *D. polymorpha* will have their largest and most obvious effects on communities, and most of the impacts will be direct effects (Section 3; Karatayev et al. 1997). The effects of *D. polymorpha* on the aquatic communities after the initial stages of invasion are much less predictable, and much more likely to be caused by indirect effects through changes in the ecosystem. These changes may be much more influenced by local conditions than short term direct effects.

At present, we need much more work on whole system impacts of zebra mussel invasion, and especially the mechanistic basis of proposed impacts. Like all areas of science, there is a persistent danger in finding correlations and assuming a causal relationship. Natural systems vary tremendously, and spurious correlations are not uncommon. Therefore, before a given change in a system is attributed to zebra mussel invasion, we need to know the natural variability among systems, and the mechanisms by which zebra mussels cause such impacts. We also need to determine the likelihood that zebra mussel impacts are not strictly linear, but may be very non-linear, for example responding in a threshold fashion, resulting in alternate states in communities and systems rather than simple changes as a function of zebra mussel density. These same problems are faced by all scientists who study environmental impacts, especially those potentially linked to human activity. Use of scientific and statistical methodology developed to test for environmental impacts may prove to be especially useful for assessing and determining the impacts of zebra mussels and other aquatic invaders.