CONTRASTING DISTRIBUTION AND IMPACTS OF TWO FRESHWATER EXOTIC SUSPENSION FEEDERS, *DREISSENA POLYMORPHA* AND *CORBICULA FLUMINEA*

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Abstract: *Dreissena polymorpha* and *Corbicula fluminea* are among the most aggressive freshwater invaders world wide, and often dominate water bodies they invade. They occur in similar habitats, however, their tolerance and preference for certain characteristics of freshwaters differ in important ways, and they can have different impacts on the environments they invade. We identify similarities and contrast differences between these species, and highlight important questions yet to be addressed, including: the ability to link short-term laboratory findings to large scale and long-term effects of invasion, the consequences of invasion by both species together rather than considering each in isolation, and identification of local versus system-wide effects when these non-native ecosystem engineers invade.

Keywords: Zebra mussel, Asiatic clam, invasive species, physiological limits, habitats, food selectivity, filtration rate, predators, parasites, ecosystem impacts

INTRODUCTION

The role of marine and estuarine bivalves as ecosystem engineers has long been recognised (reviewed in Dame 1993). However, most of this research has focused on native species, in environments where they are dominant and clearly play important roles. Although historically the role of estuarine and marine bivalves concentrated on pristine and relatively undisturbed habitats, recently, the focus has shifted to areas where they are over harvested or are lost due to disease or human disturbance, and the resultant dramatic changes in ecosystems as due to the loss of these important engineering species. The opposite situation occurs in fresh waters when suspension-feeding bivalves invade and cause dramatic changes in an environment.

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Invasive species are currently one of the greatest environmental threats around the world, and the total estimated annual cost of their impact in the US alone exceeds $125 billion (Pimentel et al. 2000). The zebra mussel (*Dreissena polymorpha*) and the Asiatic clam (*Corbicula fluminea*) are among the most aggressive freshwater invaders worldwide (Morton 1979, Karatayev et al. 2002). These two species are not only extremely aggressive invaders, often dominating water bodies they invade, they are also very effective ecosystem engineers, altering both ecosystem structure and function (Phelps 1994, Karatayev et al. 1997, 2002, McMahon 1999). They change existing and provide new habitats for other organisms, affect trophic interactions and the availability of food for both pelagic species and other benthic species, and affect the rates of ecosystem processes, including mineralization of nutrients, oxygen availability and sedimentation rates (Mattice 1979, Morton 1997, Hakenkamp and Palmer 1999, Karatayev et al. 1997, 2002). As a consequence, direct feedbacks are created with other species that interact with or are impacted by these invaders, as well as indirect feedbacks through food chains, disturbance, succession, and other longer-term community and ecosystem processes.

D. polymorpha is native to the fresh and brackish waters of the Caspian and Black Sea drainage basins (Mordukhai-Boltovskoi 1960, Starobogatov and Andreeva 1994). In the late 1700's - early 1800's, zebra mussels spread through canals built for commerce to connect the Black and Caspian Seas with the Baltic (reviewed in Karatayev et al. 2003b). The range of *D. polymorpha* in Europe is still expanding, in 1993/4 zebra mussels were found in Ireland (Minchin 2000).

Zebra mussels were first discovered in North America in Lake St. Clair in the mid-1980s (Hebert et al. 1989). Since their introduction, zebra mussels have spread throughout the Great Lakes, the Hudson, Ohio, Illinois, Tennessee, Mississippi and Arkansas rivers, as well as other lakes and rivers in 21 states and the provinces of Quebec and Ontario in Canada (McMahon and Bogan 2001).

C. fluminea, native to Southeast Asia, Australia, and Africa, has successfully invaded North American freshwaters over the last 60 years (reviewed in McMahon 1999). First found in 1938 in the Columbia River, Washington, it subsequently spread throughout 36 continental states, Hawaii, and northern and central Mexico. *C. fluminea* was introduced into South America and Europe in the late 1970s (reviewed in McMahon 1999). In Europe, *C. fluminea* is in France, Portugal, Spain, Germany, Belgium, and the Netherlands. In 1998 *C. fluminea* was found in the U.K. for the first time (Howlett and Baker 1999).

Both *C. fluminea* and *D. polymorpha* can create large populations in waterbodies they invade. However, *C. fluminea* are solitary, and burrow in sediments (Britton and Murphy 1977). In contrast, *D. polymorpha* attaches by byssus to hard substrates and each other, often in high densities, and can create new 3-D habitat, providing not only food, but shelter for benthic invertebrates (reviewed in Karatayev et al. 1997, 2002). Moreover, although both species are suspension feeders, *C. fluminea* also feeds directly from the sediment (Reid et al. 1992). Therefore these two species are likely to have different ecosystem effects in waterbodies they invade. Our goal is to compare and contrast potential ecosystem impacts of these two powerful suspension-feeders in Europe and North American waterbodies of various types and draw attention to important questions that are yet to be studied.

PHYSICAL ENVIRONMENT

Dreissena and *Corbicula* occur in similar habitats; however, they differ in some important ways in their tolerance and preference for certain physical characteristics of freshwaters. Although most studies of physical tolerances and preferences are short-term laboratory experiments, the patterns described below are usually confirmed with field-based observations and experiments.

Salinity

Both *D. polymorpha* and *C. fluminea* can colonize brackish and fresh waters, however these two species differ in their upper salinity limit (Table 1). There are several subspecies of *D. polymorpha*, each with a different tolerance to salinity (reviewed in Karatayev et al. 1998). Although as a species *D. polymorpha* has a wide salinity tolerance, from fresh to 18‰, *D. p. polymorpha,* the subspecies that invaded Western Europe and North America, lives in salinities < 6.2 ‰. *D. p. andrusovi* populates areas of the Caspian Sea where salinities range from 2 - 12‰ (Shkorbatov et al. 1994). *D. p. obtusicarinata* and *D. p. aralensis* were the dominant benthic species in the Aral Sea and had an upper salinity limit of 18.4‰ (Lyakhnovich et al. 1994) and 17.6‰ (Khusainova 1958), respectively. By 1980, after an increase in salinity, both subspecies disappeared from the Aral Sea (Starobogatov and Andreeva 1994). In contrast to *D. p. polymorpha, C. fluminea* has a much higher salinity tolerance, up to 17‰ (Table 1).

Temperature

The lower temperature limit is slightly lower for *D. polymorpha* (0°C) than for *C. fluminea* (2°C) (Table 1), which will restrict the northern distribution of *Corbicula*. In regions with winter temperatures lower than 2°C, *C. fluminea* is usually restricted to areas heated by thermal power plants (Graney et al. 1980, French and Schloesser 1996). During warmer times of the year *C. fluminea* populations may expand out of heated water areas, however, when winter water temperatures drop below 2°C most of the clams in unheated areas die (Graney et al. 1980, French and Schloesser 1996). 10 - 11°C is the minimal temperature for growth and development in both *D. polymorpha* and *C. fluminea* (Table 1). The upper temperature limit, however, is substantially higher for *C. fluminea* (37°C) than for *D. polymorpha* (33°C). Therefore, *C. fluminea* may spread much further south than *D. polymorpha,* while zebra mussels may colonize areas that are too cold for the Asiatic clam.

Table 1. Environmental limits for *Dreissena polymorpha* and *Corbicula fluminea*

Factors	*Dreissena polymorpha*	*Corbicula fluminea*	References
Upper salinity limit (‰)	4 - 6.2	10 - 17	Reviewed in Karatayev et al. 1998, Evans et al. 1979
Lower temperature limit (°C)	0	2	Luferov 1965, Mattice 1979, Rodgers et al. 1979
Minimal temperature for growth and development (°C)	10 - 11	10 - 11	Reviewed in Karatayev et al. 1998, Joy 1985, Fritz and Lutz 1986, Boltovskoy et al. 1997
Upper temperature limit (°C)	31.5 - 33	36 - 37	Reviewed in Karatayev et al. 1998, Dreier and Tranquilli 1981, Britton and Morton 1982
Lower pH limit	7.3 - 7.4	5.6	Ramcharan et al. 1992, Burlakova 1998, Kat 1982
Density - rocky substrates (m^{-2})	1580 - 5540	0 - 377	Reviewed in Karatayev et al. 1998, Abbott 1979, Leff et al. 1990
Density - sand, silty sand substrates (m^{-2})	211 - 3930	54 - 1215	Reviewed in Karatayev et al. 1998, Abbott 1979, Belanger et al. 1985, Leff et al. 1990
Density - shelly substrates (m^{-2})	1081	43	Reviewed in Karatayev et al. 1998, Karatayev et al. 2003a
Density - submerged macrophytes (m^{-2})	1246 - 3545	0	Reviewed in Karatayev et al. 1998, Karatayev et al. 2003a
Density - silt (m^{-2})	0 - 64	3.6	Reviewed in Karatayev et al. 1998, Karatayev et al. 2003a
Density in lakes (m^{-2})	6 - 3453	39 - 1278	Stanczykowska and Lewandowski 1993, Burlakova 1998, Beaver et al. 1991
Density in reservoirs (m^{-2})	838 - 3150	30 - 796	Lyakhov and Mikheev 1964, Lvova 1977, Burlakova 1998, Abbott 1979, Dreier and Tranquilli 1981, Karatayev et al. 2003a
Density in rivers (m^{-2})	7 - 138	315 - 3206	Reviewed in Karatayev et al. 1998, Rodgers et al. 1979, Belanger et al. 1985, Boltovskoy et al. 1997
Density in streams (m^{-2})	Usually absent	54 - 974	Lyakhnovich et al. 1994, Leff et al. 1990, Arias, 2004
Density in canals (m^{-2})	40000 - 61000	2255 - 16688	Reviewed in Karatayev et al. 1998, Eng 1979, Marsh 1985

pH

D. polymorpha is limited to waters with neutral or alkaline pH < 7.3 (Ramcharan et al. 1992, Burlakova 1998). There are no published data on the pH limits for *C. fluminea*, however, some studies have found this clam in waters with relatively low pH. Populations of *Corbicula* are found in the Parana River delta, Argentina, where pH averages 6.9 and ranges from 6.5 - 7.2 (Boltovskoy et al. 1997), and the Ogeechee River, Georgia (USA), where pH ranges from 6.6 - 7.2 (Stites et al. 1995). However, in Mosquito Creek, Florida (USA) (pH 5.6), shell dissolution may be a major source of mortality for *Corbicula* over 3 years old (Kat 1982).

Oxygen

Both *D. polymorpha* and *C. fluminea* are intolerant of even moderate hypoxia (reviewed in Karatayev et al. 1998, McMahon 1999), therefore, both species are usually restricted to littoral and sublittoral zones. They can also be found in well-oxygenated profundal areas (Fast 1971, Karatayev et al. 1998, McMahon 1999).

Substrates

One of the main factors that affects the distribution and abundance of *D. polymorpha* (Zhadin 1946, Lyakhnovich et al. 1994, Karatayev et al. 1998) and *C. fluminea* (Leff et al. 1990, Karatayev et al. 2003a) is suitable substrate. In most waterbodies rock and sometimes sand can be the most suitable substrate for zebra mussel attachment (Table 1). However, in shallow parts of large lakes and reservoirs, even on suitable substrates, particularly sands, zebra mussels can be limited by water motion (reviewed in Karatayev et al. 1998). Shelly sediments and silty sand can also be suitable substrates for *D. polymorpha*. In addition, zebra mussels can be extremely abundant on submerged macrophytes. The poorest substrate for zebra mussels is silt.

The best substrate for *C. fluminea* is sand, sometimes mixed with silt or clay (Table 1). Asiatic clams are in much lower densities on rocks and in silt. *C. fluminea* also usually avoids sediments under beds of submerged macrophytes (Karatayev et al. 2003a).

Both species can be very abundant on sand and, silty sand and both avoid pure silt. However *C. fluminea* usually avoids rocks, the best substrate for zebra mussel attachment. In addition, in contrast to *C. fluminea, D. polymorpha* may aggregate in high densities on submerged macrophytes.

HABITAT

Zebra mussels and Asiatic clams can be found in a wide range of types of waterbodies (reviewed in Karatayev et al. 1998, McMahon 1999), however, most work on *D. polymorpha* has been focused on factors affecting its presence and abundance in lakes. In contrast, most of the research on *C. fluminea* has been conducted in rivers. This difference may reflect the fact that in general zebra mussels usually form higher densities and play a much more important role in lakes and reservoirs (Lyakhnovich et al. 1994, Karatayev et al. 1998) and Asiatic clams, in contrast, are much more abundant in rivers and even small streams than in lakes (Britton and Morton 1982, McMahon 1983).

Lakes

Trophic type affects the probability of finding zebra mussels in a lake. Zebra mussels are found most often in mesotrophic lakes, less often in oligotrophic and meso-oligotrophic lakes, least often in eutrophic lakes, and do not inhabit dystrophic lakes (Karatayev et al. 2003b). However, the highest densities of *D. polymorpha* are found in eutrophic lakes (Karatayev and Burlakova 1995b). *C. fluminea* also differ in abundance among lakes of different trophic types. Beaver et al. (1991) found that Asiatic clam abundance in Florida lakes generally increased with trophic state. Clam densities were 39 ± 17 m^{-2} in oligotrophic lakes, 368 ± 328 m^{-2} in mesotrophic lakes, and 1278 ± 1047 m^{-2} in eutrophic lakes. In two hypertrophic lakes the density of clams averaged 198 m^{-2} (Beaver et al. 1991).

Reservoirs

In reservoirs *D. polymorpha* colonizes all suitable substrates, often at high densities (reviewed in Karatayev et al. 1998). Especially high densities of *D. polymorpha* are found in reservoirs created by flooding forested areas, where zebra mussels colonize flooded stumps, trunks and branches of trees and brushwood. For example in Kamskoe Reservoir (Russia), the density of *D. polymorpha* in flooded forest areas was as high as 371,703 m^{-2} with a biomass density (total wet mass) of 11.4 kg m^{-2} (Gubanova 1968). *C. fluminea* may form high densities in certain areas of reservoirs, but their overall average density is usually lower than in lotic waters (Table 1).

Rivers

In rivers, zebra mussels are usually limited by unidirectional water flow, disturbance due to water flow, suspended sediment, and limited suitable attachment substrates (Karatayev et al. 1998, Schneider et al. 2003). Another factor that reduces zebra mussel densities in rivers is disturbance due to periodic flooding (Lyakhnovich et al. 1994). Constant water flow can make it difficult for *Dreissena* local populations in rivers to increase in density, as zebra mussel's planktonic larvae are swept downstream (Schneider et al. 2003). In contrast, *C. fluminea* larvae primarily crawl away rather than float in the plankton, thus they avoid being swept downstream in the river currents. Upon release from the maternal clam, they can slowly crawl along the bottom and, move upstream as easily as downstream (Britton and Morton 1982). In addition, *C. fluminea* may alternate filter and pedal feeding (Reid et al. 1992, Hakenkamp et al. 2001) and thus survive during periods of high concentrations of suspended matter that may inhibit their filtering activities. *C. fluminea* lives on the surface or buries as much as two centimeters below the surface (Britton and Murphy 1977). In contrast to *D. polymorpha*, they do not depend on hard substrates or stable sediment. Therefore, *C. fluminea* usually form higher densities in rivers than in lakes or reservoirs (Table 1). The average density of *C. fluminea* in Nacogdoches Reservoir is 15.6 ± 5.3 m^{-2} (Karatayev et al. 2003a) and in small stream (< 5 m width) flowing from this reservoir is 462 ± 133 m^{-2} (Arias 2004). In contrast, zebra mussels almost never form high densities in upper courses of large rivers and usually do not colonize small rivers and streams.

Canals

Canals are distinct from lakes and reservoirs in that there is a constant, unidirectional water current which delivers nutrients and oxygen, and different from rivers because bottom sediments are much more stable and the concentration of suspended matter is much lower than in rivers, particularly during periodic floods. Both *D. polymorpha* and *C. fluminea* may have extremely high densities in canals (Britton and Morton 1982, McMahon 1983, Karatayev et al. 1998).

BIOLOGY

Food Selectivity - size and quality

Many of the effects of zebra mussels and Asiatic clams on freshwater ecosystems are linked to their filtering. They circulate water for respiration and feeding, and remove particles from the water, which are either consumed, or bound as pseudofeces and expelled to the benthos. However, the size range of particles filtered by *D. polymorpha* is larger than for *C. fluminea*. The smallest particles that zebra mussel can filter are between 0.4 and 1.3 μm (Sprung and Rose 1988, Silverman et al. 1995, Roditi et al. 1996) and the maximum particle size is between 750 μm (Ten Winkel and Davids 1982) and 1200 μm (Horgan and Mills 1997). Although they filter all particles out of the water, they are very selective in which of these particles they consume (Baker et al. 2000). *C. fluminea* has a similar lower size limit (< 1 μm) for filtered particles (McMahon and Bogan 2001), however their upper size limit is much smaller, about 20 μm (Way et al. 1990). Boltovskoy et al. (1995) found that *C. fluminea* consume algae with a spherical diameter up to 50 μm, and with the largest dimension up to 170 μm.

Both species can effectively remove detritus, bacteria and algae (reviewed in Mikheev 1994, McMahon 1999, Boltovskoy et al. 1995). In addition, *D. polymorpha* has been reported to filter small zooplankton (reviewed in Mikheev 1994, MacIsaac et al. 1995, Wong et al. 2003).

Filtration Rate

Although many researchers have investigated the filtering of *D. polymorpha* (reviewed in Karatayev et al. 1997) and *C. fluminea* (Cohen et al. 1984, Lauritsen 1986, Leff et al. 1990, Way et al. 1990, Boltovskoy et al. 1995, Cahoon and Owen 1996, et al.), standardized methodology has not been used, and often experimental setups are not adequately described to permit direct comparisons of results.

To compare estimates of filtration calculated by different authors, Karatayev et al. (1997) converted all available literature data to volume of water filtered (mL) per gram of zebra mussel wet total mass (WTM). These common units were chosen because they provide the best correlation with filtration rates across seasons, independent of the reproductive status of mussels (Karatayev 1983). They found a relatively narrow range of measured filtration rates for *D. polymorpha* (from 35 to 110 mL g WTM^{-1} h^{-1}, avg. = 64 mL g WTM^{-1} h^{-1}), in spite of the fact that these studies were made by different researchers, for different waterbodies, and using different methods. Because very different methods have been used to study *C. fluminea* as well, it is similarly difficult to compare among studies. Prokopovich (1969) measured a filtration rate of 20 mL g WTM^{-1} h^{-1} for *C. fluminea*. Similar rates (24.1 mL g WTM^{-1} h^{-1}) were measured by Cohen et al. (1984). These data suggest that *D. polymorpha* filter at a much higher rate than *C. fluminea*. Silverman et al. (1995) found that on a mussel-dry-weight basis *D. polymorpha* cleared bacteria 30 to 100 times faster than *C. fluminea*. However, on a gill surface area basis, the rate of bacteria clearance by *C. fluminea* was greater than that by *D. polymorpha* (Silverman et al. 1997). Both species cleared bacteria many times faster than any of six unionid species examined.

Role as a Biofilter

Because both zebra mussels and Asiatic clams occur in high densities over large areas, they can filter large volumes of water in short periods of time and deposit vast quantities of pseudofeces on the bottom. *D. polymorpha* populations have been estimated to filter the volume of water equivalent to that of an entire waterbody in 1.3 to 123 days, depending on the mussel density, mussel biomass and size of the waterbody (Table 2). However, some of these estimates may be suspect and are very dependent on the methods used for estimation and assumptions about mussel densities and size structure. Because *C. fluminea* populations tend to dominate smaller waterbodies, such as streams, they may filter the volume of water equivalent to that of the entire waterbody from 16 min to 4 days.

Table 2. Estimated time for *Dreissena polymorpha* and *Corbicula fluminea* to filter the volume of water equivalent to that of the waterbody.

Waterbody	Time (days)	References
D. polymorpha		
Pyalovskoe Reservoir, Russia	20	Mikheev 1967
Uchinskoe Reservoir, Russia	45	Lvova 1980
Chernobyl Nuclear Station Cooling Reservoir, Ukraine	5 - 6	Protasov et al. 1983
Two Dutch lakes	15 - 30	Reeders et al. 1989
Lake Lukomskoe, 1975, Belarus	17	Karatayev and Burlakova 1995a
Lake Lukomskoe, 1990, Belarus	45	Karatayev and Burlakova 1995a
Lake Naroch, Belarus	123	Karatayev and Burlakova 1995b
Lake Myastro, Belarus	17	Karatayev and Burlakova 1995b
Lake Batorino, Belarus	54	Karatayev and Burlakova 1995b
Hudson River, USA	1.2- 3.6	Strayer et al. 1999
Long Point Bay, Lake Erie, USA	17	Petrie and Knapton 1999
C. fluminea		
Potomac River, USA	3 - 4	Cohen et al. 1984
Upper Chowan River, USA	1 - 1.5	Lauritsen 1986
Meyers Branch Stream, USA	1	Leff et al. 1990
Clear Fork of the Trinity River, USA	0.01	McMachon and Bogan 2001

D. polymorpha and *C. fluminea* are extremely efficient at filtering water, and filtered water is almost free of suspended matter. Non-ingested particles are deposited on the bottom as pseudofeces, and post-digested material is deposited as feces. Both provide rich carbon sources for organisms feeding on the benthos. For example, in the Potomac River (USA) *C. fluminea* may reduce phytoplankton abundance 40 - 60% (Cohen et al. 1984). In Lake

Esrom (Denmark), 9 - 18% of the net phytoplankton production is ingested and assimilated by *D. polymorpha* (Hamburger et al. 1990).

Although there are no quantitative data about the deposition rates of seston by *Corbicula* at the scale of whole waterbodies, there have been many studies of *Dreissena* (reviewed in Karatayev et al. 1997). For example, in the Uchinskoe Reservoir (Russia) *D. polymorpha* deposits 1,071 g m^{-2} of seston annually (Lvova 1980). Prior to the invasion of zebra mussels, the annual deposition of sediment was only 470 g m^{-2}. In the Pyalovskoe Reservoir (Russia), zebra mussels deposit more than 36,000 tonnes of seston per year (Mikheev 1967), and in the Volgograd Reservoir (Russia) zebra mussels mineralize about 700,000 tonnes of organic matter in one growing season (Spiridonov 1973). Deposition of large amounts of suspended matter by *D. polymorpha* significantly improves the food base for many benthic animals. In Mikolajskie Lake (Poland) the annual dietary requirement for all of the non-carnivorous animals is met by 16% of the seston deposited each year by bivalves, and *D. polymorpha* alone produce 160 of the 164.5 tonnes of dry seston deposited by all bivalves in this lake (Alimov 1981).

In Lake Lukomskoe, all benthic suspension feeders filtered the volume equivalent of that of the lake in 15 years, and planktonic filterers filtered that same volume in 5 days prior to *D. polymorpha* invasion. After invasion, zooplankton abundance declined, and the time required to filter the equivalent of the volume of the lake increased to 17 days (Karatayev and Burlakova 1992, 1995a). In contrast, due to the presence of *D. polymorpha,* the filtering capacity of benthic invertebrates had increased 320 times by 1975, and the volume equivalent to the lake could be filtered in 17 days.

NATURAL ENEMIES

Predators

176 species of various predators are known to feed on zebra mussels, including fish (15 predators on planktonic larvae and 38 on attached mussels) and birds (36 species). In addition, copepods and cnidarians are known to consume veligers, and leeches, crabs, crayfish and rodents are reported to feed on adult zebra mussels (reviewed in Molloy et al. 1997). Few quantitative studies have been conducted on the impact of predators on *D. polymorpha*. In some cases, fish may consume > 80% of zebra mussel production (Lvova 1977, Yablonskaya 1985) and birds may eat 20 to 70% of annual *D. polymorpha* production (Mikulski et al. 1975, Stempniewicz 1974). However

there is no evidence of any long-term decline of zebra mussel populations due to the effects of predation (Molloy et al. 1997).

Similar animals that feed on zebra mussels are reported to consume *C. fluminea,* including 14 species of fish, 13 species of ducks, racoons, crayfish, and flatworms (reviewed in Sickel 1986). There is some evidence suggesting that fish predation may be a major cause of reduction in *C. fluminea* density (Dreier and Tranquilli 1981, Robinson and Wellborn 1988). In Fairfield Reservoir, Texas, fish predation reduced *C. fluminea* abundance 29 fold (Robinson and Wellborn 1988).

Parasites

34 species of endosymbionts are known to be associated with zebra mussels, including ciliates, trematodes, mites, nematodes, leeches, chironomids, oligochaetes, and bacteria (reviewed in Molloy et al. 1997). At least six species of ciliates (*Conchophthirus acuminatus, C. klimentinus, Hypocomagalma dreissenae, Sphenophrya dreissenae, S. naumiana,* and *Ophryoglena* sp.) are known to be species specific. There is also some evidence that the trematodes *Bucephalus polymorphus, Phyllodistomum folium*, and *P. dogieli,* are quite specific to *Dreissena.* All of these parasites are found exclusively in Europe. Only nonspecific symbionts (e.g., nematodes, chironomids, oligochaetes, mites) are found in North American zebra mussels. Only one parasite, the trematode *B. polymorphus*, has been well documented as being seriously debilitating to zebra mussels (i.e., it destroys gonads) (Molloy et al. 1997).

In contrast to the wide variety of endosymbionts found in zebra mussels, only two species are known to be associated with *C. fluminea*: the oligochaete *Chaetogaster limnaei* (Sickel and Lyles 1981) and a mite (authors unpublished data). The endosymbiotic fauna of *C. fluminea* in their native region may be more diverse. *C. fluminea* could be a second intermediate host of *Echinistoma revolutum* and may be a vector of echinostomiasis in humans (Anazawa 1929). There are no data on the effect of *C. fluminea* parasites on their abundance.

ECOSYSTEM IMPACTS

Local Effects

D. polymorpha attaches by byssus to hard substrates and each other, and can create new 3-D habitat, providing not only food, but shelter for bottom invertebrates. These effects on benthic communities are well documented (reviewed in Karatayev et al. 1997, 2002). Zebra mussels have positive effects on isopods (Wolnomiejski 1970, Karatayev and Lyakhnovich

1990, Kuhns and Berg 1999), larval chironomids (Wolnomiejski 1970, Botts et al. 1996, Stewart et al. 1998, Kuhns and Berg 1999), leeches (Wolnomiejski 1970), snails (Karatayev et al. 1983, Stewart et al. 1998, reviewed in Strayer 1999), amphipods (Karatayev et al. 1983, Karatayev and Lyakhnovich 1990, Botts et al. 1996, Stewart et al. 1998, Kuhns and Berg 1999, Riccardi 2003), oligochaetes (Afanasiev 1987, Botts et al. 1996), turbellarians (Botts et al. 1996), and hydrozoans (Botts et al. 1996, Stewart et al. 1998). Negative effects are documented for native unionids (reviewed in Schloesser et al. 1996, Karatayev et al. 1997, Burlakova et al. 2000, Riccardi 2003), chironomid larvae (Sokolova et al. 1980, Karatayev et al. 1983) and sphaeriid bivalves (Strayer et al. 1998, Lauer and McComish 2001, Mills et al. 2003).

In contrast *C. fluminea* is solitary, burrows in sediments and does not change the surface of the sediments. Therefore its role in benthic communities may be much smaller. To date there is no evidence of effects of *C. fluminea* on benthic macroinvertebrates (Karatayev et al. 2003a) or on meiofauna (Hakenkamp et al. 2001). McMahon (1999) hypothesised that *C. fluminea* detrital feeding could negatively impact other burrowing detritovores. However, in experiments conducted in Lake Nacogdoches, where clams were placed at different densities in trays with sand and the benthic community was allowed to develop for 30 d, there was no difference in species composition or the density of benthic animals with or without live *C. fluminea*, independent of clam density (R. Mood, A. Karatayev and L. Burlakova, unpublished data).

The shells of zebra mussels may accumulate in large quantities and alter the sediments and change benthic community (Karatayev et al. 2002). Similarly, *C. fluminea* dead shells may affect the benthos (Prokopovich 1969). In the experiments described above, amphipod densities were significantly higher in trays of sand with dead *C. fluminea* shells than pure sand without shells (R. Mood et al. unpublished data).

System-wide Effects

Zebra mussels and Asiatic clams are functionally different than most benthic invertebrates in freshwater. They filter large volumes of water and transport material removed from the water column to the benthos, providing a direct link between processes in the plankton and those in the benthos (benthic-pelagic coupling). The shift of suspended matter from the water column to the bottom induces changes in all aspects of freshwater ecosystems they invade (reviewed in Morton 1997, Karatayev et al. 1997, 2002, McMahon 1999, Vanderploeg et al. 2002, Mayer et al. 2002, Mills et al. 2003) (Table 3).

To a large extent the overall impact of *D. polymorpha* and *C. fluminea* as suspension feeders on freshwater ecosystem may be similar, however, information is much more available for zebra mussels than Asiatic clams. The filtering activity of both species causes water transparency to increase and decreases seston concentration, BOD, and phytoplankton density (Table 3). With increased transparency, a greater portion of the lake bottom covered with macrophytes. Increased macrophyte beds may provide additional substrate for the zebra mussel attachment and thus increase *D. polymorpha* populations. In contrast, increased macrophyte beds may cover previously available substrate for *C. fluminea* and negatively affect their overall density in a waterbody.

Table 3. The impact of *Dreissena polymorpha* and *Corbicula fluminea* on freshwater ecosystems.

Parameter	*D. polymorpha*	*C. fluminea*
Water transparency	Increases (reviewed in Karatayev et al. 1997, 2002, Vanderploeg et al. 2002)	Increases (Buttner 1986, Phelps 1994)
Seston concentration	Decreases (reviewed in Karatayev et al. 1997, 2002, Vanderploeg et al. 2002)	Decreases (Buttner 1986, Leff et al. 1990, McMahon 1999)
BOD in the water	Decreases (reviewed in Karatayev et al. 1997, 2002)	Decreases (Buttner 1986)
Nutrients	Alters nutrient cycling (Johengen et al. 1995, Arnott and Vanni 1996, Makarewicz et al. 2000)	Alters nutrient cycling (Beaver et al. 1991, Lauritsen and Mozley 1989)
Phytoplankton	Decreases density and chlorophyll content (reviewed in Karatayev et al. 1997, 2002, Vanderploeg et al. 2002)	Decreases density and chlorophyll content (Cohen et al. 1984, Beaver et al. 1991)
Macrophyte coverage	Increases (reviewed in Karatayev et al. 1997, 2002, Vanderploeg et al. 2002)	Increases (Phelps 1994, McMahon 1999)
Periphyton	Increases (Lowe and Pillsbury 1995).	No data
Zooplankton	Decreases (reviewed in Karatayev et al. 1997, 2002)	No data
Zoobenthos	Increases (reviewed in Karatayev et al. 1997, 2002)	No data
Fish	Increases quantity of benthophages (reviewed in Karatayev et al. 1997, 2002)	Increases (Phelps 1994)

No comparable data are available for the impacts of *C. fluminea* on periphyton, zooplankton, and benthic animal communities. In contrast, the impacts of *D. polymorpha* in these communities is well documented (Table 3). Zebra mussel filtering results in periphyton and benthic algal increases in both standing stock and primary productivity. Total zooplankton density and biomass decreases.

Introduction of both *C. fluminea* and *D. polymorpha* may result in increased fish production (Table 3). Although much more data are available on the impact of zebra mussels on fish, generalizations are far from being clear. Many authors have reported an enhancement of all benthic feeding fishes, even those that do not feed on zebra mussels, because zebra mussel invasion is often associated with an increase in biomass of native benthic invertebrates (e.g., Kharchenko and Protasov 1981, Lyakhnovich et al. 1988, Karatayev and Burlakova 1995a, Stewart and Haynes 1994). In contrast, planktivorous fishes could be negatively affected because of decreased phytoplankton abundance and associated decreases in zooplankton, competition with benthic species, and by increasing fish predation on larvae due to increased water transparency (Francis et al. 1996, Lozano et al. 2001). The decline in abundance and body condition in lake whitefish (*Coregonis clupeaformis*) in lakes Ontario and Michigan (USA) is believed to be related to a decline of *Diporea hoyi*, an important item in fish diets, following the appearance and proliferation of dreissenid mussels (Hoyle et al. 1999, Pothoven et al. 2001).

GENERAL FINDINGS AND FUTURE DIRECTIONS

Although many generalisations can be made about the impacts of Asiatic clams and zebra mussels and their function in freshwater systems, specific predictable impacts are far from clear. The most important aspects of this problem and needed targets for future study are:

Methodological Problems

Because these two species are invaders and can cause environmental and economic damage, many aspects about their biology and ecosystem impacts are simplified or exaggerated to draw attention to the problem of invasive species and their spread. Many of these generalisations and exaggerations are then repeated or assumed proven without scientific rigor. Scientists must be careful, especially when extrapolating from short-term laboratory experiments to large scale and long term effects of invaders. We need more studies that link these two approaches before we can draw accurate predictions or assess real impacts.

The methodology used to determine impacts is also critical because different methods often yield different results. For example, filtering rates for both *Dreissena* and *Corbicula* when feeding on mixed plankton versus single species, as well as filtered versus unfiltered lake water (with seston concentration higher than the incipient threshold seston concentration) may differ, and measures in small volumes of still water are likely to be different than measures made in larger volumes and flowing water. Filtration rates are also reported based on different units. They may be calculated on shell length, wet total mass (WTM, shell plus soft tissue), dry body mass (DBM, soft tissue only), or per ash-free dry mass (AFDM, soft tissue only), and it is not often clear how to convert among these different units. Former Soviet Union scientists generally calculate the filtration rate of *D. polymorpha* based on shell length or WTM (Lvova 1977, Karatayev and Burlakova 1995b), as do many other Europeans (Reeders and Bij de Vaate 1990, Wisniewski 1990), although some Europeans calculate filtering rate per DBM (Kryger and Riisgård 1988). The majority of North American scientists also calculate the filtration rate of zebra mussels per DBM (Aldridge et al. 1995) or per AFDM (Fanslow et al. 1995, Lei et al. 1996).

Common units are essential for cross-study comparisons. We suggest that for zebra mussels the most appropriate units to use are mL of water filtered per g WTM per hour. WTM is very easy to measure, even in the field, and for individuals is much more highly correlated with filtration rate than other measures such AFDM or DBM, which vary greatly with season and reproductive condition (Karatayev 1983). We also recommend that field estimates of filtering rates for *Dreissena* and *Corbicula* be calculated as a function of WTM, not density. Different sized mussels will filter at different rates, and similar densities of mussels with different size frequency distributions will have dramatically different filtering rates and therefore their ecosystem impact may vary widely (Young et al. 1996). In any case, appropriate conversions among measures need to be established.

C. fluminea and *D. polymorpha* Co-effects

To date, there are no data on the co-effects of *D. polymorpha* and *C. fluminea* invasion on aquatic communities. Both of these invaders continue to spread throughout North America and Europe, and increasingly they are both found in the same freshwater bodies. The effects of both *Dreissena* and *C. fluminea* may be additive, or we may see synergistic effects, where their impacts are much more than would be expected by the impacts of either species alone.

C. fluminea vs. D. polymorpha Distribution

Although both of these invaders are frequently lumped together because they are bivalves and invade fresh waters, the ecology of *D. polymorpha* and *C. fluminea* are different, and therefore their ecosystem impacts are likely to be different. *D. polymorpha* are more abundant in lakes and large rivers and do not occur in high densities in streams. In contrast, in addition to lakes and large rivers, *C. fluminea* may be extremely abundant in small streams. Therefore, we may expect to find both similarities and differences in the ecosystem response to the presence of these two invaders. Although they overlap, each has areas where the other is less abundant and they rarely compete for space. The presence of one will not necessarily eliminate the other, and the relative interactions between the two will depend on characteristics of the system, e.g., streams *vs.* lakes *vs.* canals.

C. fluminea vs. D. polymorpha Local Effects

The impacts of Asiatic clams and zebra mussels, or any other biological agent, are likely to be most intense close to individuals. The biology and natural history of the zebra mussel and Asiatic clam are different. *D. polymorpha* can live only on the surface of the sediments where they attach to hard substrates creating structure, and providing food and shelter for benthic species. In contrast *C. fluminea* lives solitary, burrows in sediments and does not alter the surface of sediments. However the accumulation of dead shells of both species may have a similar effect by altering substrate and thereby affecting the benthic community. Moreover, although both species are suspension feeders, *C. fluminea* also collects food particles from the sediment. Therefore *C. fluminea* may compete for food with benthic infauna.

C. fluminea vs. D. polymorpha System-wide Effects

Depending on water mixing rates, lake morphology, and turnover rates, the effects of suspension feeders on aquatic ecosystems will vary greatly (Ackerman et al. 2001) and may be very local in deep water lakes (Reed-Andersen et al. 2000). Although *D. polymorpha* and *C. fluminea* impacts on the environment may be similar, feed backs may be different for different invaders. Invasion of both species may increase macrophyte coverage of waterbodies they invade, however increased macrophyte community will provide additional substrate for zebra mussels attachment and therefore may cause further increase of *D. polymorpha* population size and their impact on ecosystem. In contrast, increased macrophyte coverage may decrease habitat available for *C. fluminea* and therefore may cause a decrease of Asiatic clam population size and their impact on ecosystem.

Freshwater *vs.* Marine Bivalves

Marine and estuarine bivalves have long been recognized as ecosystems engineers (reviewed in Dame 1993). Invasive zebra mussels and

Asiatic clams function similarly in fresh waters. Contrasting the impact of freshwater invasive bivalves on cosystems they recently colonized *vs.* estuarine, and marine bivalves in ecosystems were they were naturaly dominant but are recently lost, may help us to undestand the role of these important suspension feeders as ecosystem engineers in various waterbodies.

Both *Dreissena* and *Corbicula* are important freshwater invaders and, as a consequence, have been the focus of much research. However, we still have to learn a great deal about both their biology as well as their impacts on ecosystems that they invade. It is clear from the direct comparison of these two species there remain many "missing pieces" of the picture. We hope that our review will help to focus future efforts such that we will be able to construct the "whole picture" for these two aggressive invaders and their effects on the freshwater ecosystems. These two invaders will continue to provide important information about the capabilities of suspension feeders as well as the functioning of freshwater ecosystems. In addition, these species may be important models that will help us predict the spread and impacts of future invaders.

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