

## THE INVASIVE BIVALVES *DREISSENA POLYMORPHA* AND *LIMNOPERNA FORTUNEI*: PARALLELS, CONTRASTS, POTENTIAL SPREAD AND INVASION IMPACTS

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**ABSTRACT** We contrast ecological and life history traits of the well studied freshwater invader, the zebra mussel (*Dreissena polymorpha*), with the lesser known invasive golden mussel (*Limnoperna fortunei*) to compare salient biological traits and environmental limits, and to predict the potential spread and ecosystem impacts of *L. fortunei* in areas where it is introduced. Both species are sessile, byssate bivalves with a planktonic larval stage and extremely high reproductive capacity. For both species adults attain much higher biomass in waterbodies they invade than all of the native invertebrates combined, and they create substrate complexity otherwise not found in freshwater systems. Both are very active suspension feeders, greatly enhance benthic-pelagic coupling, and act as effective ecosystem engineers. Although taxonomically unrelated, their ecosystem impacts are surprisingly similar and follow from the novel ecological niche they share, rather than being species specific. The golden mussel has broader environmental tolerances and therefore may be a much more successful invader than *D. polymorpha* in regions dominated by acidic, soft and contaminated waters. In the near future *L. fortunei* may colonize the southern and central parts of North America, much farther north than has been previously predicted. Although to date the zebra mussel is considered the most aggressive freshwater invader, soon many waterbodies may receive another, even more aggressive invader.

**KEY WORDS:** zebra mussel, *Dreissena polymorpha*, *Limnoperna fortunei*, environmental limits, aquatic invader, ecosystem impacts, invasive species

### INTRODUCTION

The zebra mussel (*Dreissena polymorpha* [Pallas]) is considered the most aggressive freshwater invader in the northern hemisphere, and has caused serious ecological and economic impacts both in Europe and North America (reviewed in Nalepa & Schloesser 1993, Karatayev et al. 1997, 2002). The golden mussel (*Limnoperna fortunei* Dunker) was unintentionally introduced to fresh and brackish waters in Hong Kong, Taiwan and Japan from Mainland China between 1965 and 1990 (Morton 1975, Nakai 1995), and subsequently invaded South America in 1989–1990 (Pastorino et al. 1993). It has already colonized Argentina, Uruguay, Paraguay, Bolivia, and Brazil and had significant economic (Cataldo & Boltovskoy 2000) as well as substantial ecological impacts (reviewed in Darrigran 2002, Boltovskoy et al. 2006). Although taxonomically unrelated (in different families, *D. polymorpha* is a dreissenid, *L. fortunei* is a mytilid), these two species have surprisingly similar life histories, share many ecological traits, and therefore may have similar ecosystem impacts. Both are sessile, byssate bivalves with a planktonic larval stage, high reproductive capacity, and are suspension feeders. Both attain extremely high densities, physically change the substrate, and because they are such effective suspension feeders they greatly enhance benthic-pelagic coupling. Their reproductive mode and lifestyle are more typical of marine mussels, but are rare in freshwater habitats. As a consequence, they occupy a unique ecological niche, and perform as powerful ecosystem engineers (reviewed in Karatayev et al. 1997, 2002, Darrigran 2002, Boltovskoy et al. 2006).

The history of the invasion by *Dreissena* is well documented (reviewed in Kinzelbach 1992, Starobogatov & Andreeva 1994, bij de Vaate et al. 2002). It first spread beyond its natal habitat in the early 1800s, and has been the focus of intensive international research on its ecological and economic impacts for over 100 y. In contrast, *L. fortunei* is a relatively recent invader, and therefore there is significantly less information available for this species. Ricciardi (1998) published a preliminary paper summarizing what was known about this species, however, at that time research on the spread and impacts of *L. fortunei* was only in its infancy. Chiefly through the efforts of South American and Japanese researchers since 1998, we now know much more about the reproduction, dispersal, ecology, feeding, behavior, and environmental impacts as well as potential means for control of the golden mussel. *Limnoperna fortunei* is currently spreading rapidly throughout South America, and it is very likely to colonize other continents, including North America and Europe, in the very near future. A critical assessment of the potential spread and ecosystem impacts of this new invader is urgently needed.

The goals of this paper are: to contrast ecological and life history traits of the zebra mussel and the golden mussel, to compare their respective environmental limits, and to predict the potential spread and ecosystem impacts of *L. fortunei* relative to those areas vulnerable to invasion by the zebra mussel.

### Life History

*Dreissena polymorpha* and *L. fortunei* have very similar life histories, including planktonic free-swimming larvae and benthic sessile adult stages (Table 1). Both species have similar longevity

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TABLE 1.  
Life history parameters for *Dreissena polymorpha* and *Limnoperna fortunei*.

Parameter	<i>Dreissena polymorpha</i>	<i>Limnoperna fortunei</i>
Eggs and larvae		
Habit	Planktonic	Planktonic
Egg size ( $\mu\text{m}$ )	96–100 (Lvova & Makarova 1994)	85–100 (Cataldo et al. 2005c)
Larval size range ( $\mu\text{m}$ )	50–300 (Lvova et al. 1994a)	85–400 (Cataldo et al. 2005c)
Adults		
Habit	Benthic, sessile	Benthic, sessile
Typical length (mm)	20–30	20–30
Maximum length (mm)	46 (Burlakova 1998)	42 (Karatayev, Burlakova & Boltovskoy, unpublished data)
Feeding type	Suspension feeder	Suspension feeder
Food spectrum	Detritus, phytoplankton, zooplankton, bacterioplankton (Mikheev 1994, Wong et al. 2003)	Detritus and phytoplankton (Sylvester et al. 2005a, Cataldo et al. 2005a)
Filtration rate (mL g total wet weight $\text{h}^{-1}$ )	35–110 (reviewed in Karatayev et al. 1997)	20–102 (Cataldo et al. 2005a)
Typical longevity (years)	3–4 (reviewed in Lvova et al. 1994b)	3 (Boltovskoy & Cataldo 1999)
Time to sexual maturity (months)	3–11 (Lvova & Makarova 1994) 8–10 (McMahon & Bogan 2001)	3–4 (Darrigran & Damborenea 2005, Boltovskoy & Cataldo, 1999)
Sexes	Separate	Separate
Sex ratio	1:1 (Lvova 1980)	1:1 (Darrigran et al. 1998b)
Fertilization	External	External
Duration of reproductive period (months)	3–5 (reviewed in Lvova & Makarova 1994)	8 (Boltovskoy & Cataldo 1999, Cataldo & Boltovskoy 2000)
Fecundity (eggs per reproductive season)	275,000–300,000 (Lvova 1977) up to 1,000,000 (Sprung 1991)	No data

and their patterns of reproduction share several salient features. Both species reproduce seasonally, although the reproductive period for *L. fortunei* is much longer than that of *D. polymorpha*. Female zebra mussels can spawn up to  $10^6$  eggs, and males up to nearly  $10^{10}$  sperm, comprising more than 30% of their body weight prior to spawning (Sprung 1991). For *Limnoperna* data on fecundity are not yet available, but its very high rates of colonization indicate that fecundity must be very high as well. In the laboratory fresh female mussels induced to spawn produce ~11,000 eggs ( $n = 10$ , range 133–29,800 eggs per female, Cataldo & Boltovskoy, unpublished data), which is similar to zebra mussels induced to spawn in the laboratory (Stoeckel et al. 2004). Egg size and larval duration in *Dreissena* and *Limnoperna* are almost identical (Table 1).

Newly settled juvenile *D. polymorpha* are somewhat mobile, crawl with aid of their foot, and eventually attach to the substrate with byssal threads. Depending on the substrate type, food and oxygen conditions, *Dreissena* may form single- or multilayered druses, which in extreme cases may be up to 15 cm thick (Karatayev 1983). Although adult zebra mussels occasionally detach their byssus and crawl, large druses and aggregations are usually quite stable, and adults are unlikely to move far. In *Limnoperna* the ability to move once attached seems to be limited to young individuals. *Limnoperna* kept in well aerated tanks in the laboratory often crawl up the glass to the water-air interface; as the water-level goes down most of mussels do not detach or move, and eventually die of desiccation. Similar to *Dreissena*, *Limnoperna* may form single- or multilayered aggregations on various substrates up to 10–15 cm thick (Boltovskoy, personal observation).

Adult zebra mussels and golden mussels are typically similar in size, and they appear to have similar diets. They both feed on seston in general, including bacterioplankton, phytoplankton, and small zooplankton (Table 1). *Dreissena polymorpha* feeds on particles from 0.4–1.3  $\mu\text{m}$  (Sprung & Rose 1988, Silverman et al. 1995, Roditi et al. 1996) to 750  $\mu\text{m}$  (Ten Winkel & Davids 1982), and even 1200  $\mu\text{m}$  (Horgan & Mills 1997). For *Limnoperna* information is scarce. Cataldo et al. (2005a) found that they could collect particles from 3–4 to ~100  $\mu\text{m}$ , but did not find any selectivity regarding particle quality or phytoplankton species. *Dreissena polymorpha*, on the other hand, has been reported to be highly selective, with strong preferences for certain algal species (Mikheev 1994, Baker et al. 2000).

Laboratory experiments indicate that maximum filtration rates of *L. fortunei* can exceed 590 mL g total wet weight  $\text{h}^{-1}$  (Sylvester et al. 2005a, Cataldo et al. 2005b), which is among the highest rates ever reported for bivalve molluscs. However, average filtering rates are very similar to those reported for the zebra mussel (20–120 mL g total wet weight  $\text{h}^{-1}$ ; Cataldo et al. 2005a).

#### Environmental Limits

*Dreissena polymorpha* and *L. fortunei* colonize similar types of waterbodies, but the golden mussel has a much higher upper salinity limit. In the Río de la Plata estuary, where salinities can vary from 5‰ to 15‰ within a matter of hours (Guerrero et al. 1997), the golden mussel is found at salinities as high as 13.7‰ (D. Giberto, personal communication). Therefore, *Limnoperna*

is expected to have a much wider distribution than the zebra mussel, ranging into estuaries and other brackish waters with salinities as high as 14‰. *Limnoperna fortunei* is also more tolerant of lower pH, lower oxygen and calcium concentrations than *D. polymorpha*, which allows it to flourish in slightly acidic and soft waters, where the zebra mussel cannot survive (Boltovskoy et al. 2006, de Oliveira et al. 2006). As expected from its wider environmental tolerances, *Limnoperna* is also much more resistant to pollution than *Dreissena*. Along the Buenos Aires shores of the Río de la Plata, *Limnoperna* thrives in large numbers in the highly polluted storm water outlets (Boltovskoy et al. 2006). In the lower Paraná Delta *Limnoperna* is abundant in areas with waters and sediments polluted with Zn, Cr, Cu, benzo(a)pyrene, and PCBs (Topalian et al. 1990, Villar et al. 1998, Cataldo et al. 2001). In contrast, zebra mussels have disappeared from several lakes and rivers in Europe because of pollution, and were only able to recolonize some of them after the water quality was significantly improved (bij de Vaate et al. 1992, Jantz & Neumann 1992, Burlakova 1998).

Prior work suggested that *L. fortunei* was restricted to warm water, and had a low temperature limit of about 8°C (reviewed in Ricciardi 1998). However, in Japan the golden mussel survives winter water temperatures of 5°C to 6°C (Magara et al. 2001), and in Korea *L. fortunei* populations have been reported from the Paldang Reservoir, with winter surface water temperatures as low as 0°C (Choi & Kim 1985, Choi & Shin 1985). Thus, the lower thermal limit of *L. fortunei* appears to be quite similar to that of *D. polymorpha*, and low winter temperatures are unlikely to be a deterrent for its northward spread in the northern hemisphere, contrary to predictions by Ricciardi (1998). On the other hand, *Limnoperna* has a comparatively higher high temperature limit (around 35°C), suggesting that it may successfully colonize areas that are too warm for the zebra mussel.

*Dreissena polymorpha* require hard substrates for attachment and are known to form high densities on rocks, stable sand, and macrophytes, but usually avoid silt. *Limnoperna* has generally similar behavior. As with *Dreissena*, they are occasionally observed on silt or mud (Boltovskoy et al. 2006), but these substrates are not preferred. Zebra mussels usually form high densities in littoral and sublittoral zones of lakes and reservoirs, and are particularly well adapted to canals and rivers with regulated water flow, but do not prosper in streams and rivers with unstable sediments and periodic flooding

(reviewed in Karatayev et al. 1998, 2005). *Limnoperna* is very abundant in the Paraná and Uruguay rivers, which are dominated by soft, unstable sediments, and seasonal floods. However in these areas they chiefly thrive on rock outcrops, the roots of reeds, driftwood, large cobble, and consolidated sediments (Boltovskoy et al. 2006).

Based on the environmental limits of *D. polymorpha* and *L. fortunei* we expect that these species are likely to overlap in the near future, mostly because of the spread of the golden mussel to North America and Europe. Because of its ability to reproduce at lower temperatures *D. polymorpha* will probably spread farther north in the northern hemisphere than *L. fortunei* (Table 2). However, the golden mussel can occupy more southern areas where high water temperatures can limit zebra mussels during the summer months. Most waterbodies currently colonized by zebra mussels may also be colonized by the golden mussel. In addition, *L. fortunei* will be able to colonize many waterbodies that are too acidic, too polluted, or have water that is too soft for zebra mussels.

#### Ecological Impacts

Both *D. polymorpha* and *L. fortunei* are very effective ecosystem engineers, altering both ecosystem structure and function (Karatayev et al. 1997, 2002, 2005; Johannsson et al. 2000, Darrigran 2002, Boltovskoy et al. 2006). Thus, their impacts are more likely to follow from the novel ecological niche they share, rather than to be species specific. As effective suspension feeders, they are very likely to have similar effects on the ecosystems they invade. Much more information is available for *D. polymorpha* than for *L. fortunei*, but because their overall forcing on aquatic communities and freshwater ecosystems in general may be similar, the information available for zebra mussels could be used to predict the impacts of the golden mussel. However, although the mechanisms of change imposed by the two mussels may be the same, the final outcome within a community may be quite different depending on system constraints and the rest of the species in the community (Boltovskoy et al. 2006). The effects of invasion can be local, mostly affecting the benthos, especially those areas where mussels settle, or system-wide, where the invasion influences large areas or entire water bodies through both direct and indirect effects of the mussels on physical, chemical, and biological properties of the environment.

TABLE 2.  
Environmental limits for *Dreissena polymorpha* and *Limnoperna fortunei*.

Factors	<i>Dreissena polymorpha</i>	<i>Limnoperna fortunei</i>
Upper salinity limit (‰)	6 (reviewed in Karatayev et al. 1998)	15 (reviewed in Boltovskoy et al. 2006)
Lower temperature limit (°C)	0 (Luferov 1965)	0 (Choi & Shin 1985, Choi & Kim 1985)
Upper temperature limit (°C)	33 (reviewed in Karatayev et al. 1998)	35 (reviewed in Ricciardi 1998)
Minimal temperature for reproduction (°C)	12–15°C (reviewed in Lvova et al. 1994a)	17°C (Morton 1977, Cataldo & Boltovskoy 2000)
Lower pH limit	7.3–7.5 (Ramcharan et al. 1992, Burlakova 1998)	5.5 (Boltovskoy et al. 2006)
Lower calcium limit (mg L <sup>-1</sup> )	25–28 (Ramcharan et al. 1992, Burlakova 1998)	3 (Boltovskoy et al. 2006)
Lower oxygen limit at 20°C (mg L <sup>-1</sup> )	1.8–2.4 (Spiridonov 1972, Shkhorbatov et al. 1994)	0.5 (Boltovskoy et al. 2006)
Resistance to pollution	Medium (bij de Vaate et al. 1992, Jantz & Neumann 1992, Burlakova 1998)	High (Cataldo & Boltovskoy 2000, Boltovskoy et al. 2006)

### Local Effects

Large aggregations of *D. polymorpha* create three-dimensional habitats altering the surface of the substrate and providing shelter and food for other benthic invertebrates (reviewed in Karatayev et al. 1997, 2002, 2005). Both European and North American studies agree that *D. polymorpha* has positive effects on some species (e.g., amphipods, isopods, leeches, turbellarians, hydrozoans, and some oligochaetes and chironomids), and negative impacts on others (Table 3). The overall biomass of native invertebrates is usually higher in *Dreissena* druses (reviewed in Karatayev et al. 1997, 2002, 2005). Impacts of *Dreissena* on unionid bivalves are of special concern. High densities of *Dreissena* have pronounced negative effects on native unionids in both Europe and North America (Schloesser & Nalepa 1994, reviewed in Karatayev et al. 1997, Burlakova et al. 2000). Unionids with zebra mussels attached to

TABLE 3.

**The impact of *Dreissena polymorpha* and *Limnoperna fortunei* on benthic communities.**

Invertebrates	<i>D. polymorpha</i>	<i>L. fortunei</i>
Isopoda	Positive (Wolnomiejski 1970, Karatayev & Lyakhnovich 1990)	Positive (Darrigran et al. 1998a)
Amphipoda	Positive (Karatayev & Lyakhnovich 1990, Botts et al. 1996, Stewart et al. 1998)	Positive (Darrigran et al. 1998a)
Gastropoda	Positive (Karatayev et al. 1983, Botts et al. 1996, Stewart et al. 1998)	Negative (Darrigran et al. 1998a), Positive (Sylvester et al. in preparation)
Chironomidae	Positive (Botts et al. 1996), Negative (Sokolova et al. 1980, Karatayev et al. 1983)	Positive (Darrigran et al. 1998a)
Trichoptera	Positive (Karatayev et al. 1983)	No data
Hirudinea	Positive (Wolnomiejski 1970, Karatayev et al. 1983)	Positive (Darrigran et al. 1998a, Sylvester et al. in preparation)
Oligochaeta	Positive (Sokolova et al. 1980, Afanasiev 1987, Botts et al. 1996) Negative (Afanasiev 1987)	Positive (Darrigran et al. 1998a, Sylvester et al. in preparation)
Turbellaria	Positive (Botts et al. 1996)	Positive (Darrigran et al. 1998a)
Nematoda	No data	Positive (Darrigran et al. 1998a)
Hydrozoa	Positive (Botts et al. 1996)	No data
Tanaidacea	No data	Positive (Darrigran et al. 1998a, Sylvester et al. in preparation)
Unionidae	Negative (Haag et al. 1993, Gillis & Mackie 1994, Schloesser & Nalepa 1994, reviewed in Karatayev et al. 1997, Burlakova et al. 2000)	Negative (Darrigran et al. 1998a, Mansur et al. 2003)

their shells can have difficulty burrowing and moving through sediment, or the extra weight can result in burial in very soft sediments. Attached mussels can prevent unionids from opening their valves for respiration, feeding and reproduction, or can prevent closing valves as well. Attached mussels can also increase drag and the likelihood of dislodgment by water motion for species living near shore. Mass mortalities of native unionids overgrown by zebra mussels have been documented both in Europe (Sebestyen 1937, Burlakova et al. 2000) and North America (Haag et al. 1993, Gillis & Mackie 1994, Schloesser & Nalepa 1994), and are most common when zebra mussel populations are growing rapidly during the initial stages of colonization of a new water body. However, invasion by zebra mussels usually does not result in the extirpation of unionids; after initial peaks in abundance, zebra mussels and unionids coexist (Ponyi 1992; Nichols & Amberg 1999; Burlakova et al. 2000).

Limited data from South America suggests that *L. fortunei* has similar impacts on the benthos. Darrigran et al. (1998a) observed that *Limnoperna* was associated with increases in isopods, amphipods, oligochaetes, chironomids, and turbellarians (Table 3), but some gastropods (*Chilina fluminea* and *Gundlachia concentrica*) were probably negatively impacted. Sylvester, Boltovskoy & Cataldo (in preparation) examined the benthic invertebrates associated with *Limnoperna* aggregations on experimental panels. All animals abundant enough for reliable comparative assessment (rotifers, nematodes, oligochaetes, leeches, copepods, chironomids, gastropods and nauplii) were more abundant in *Limnoperna* beds than open areas, suggesting that *Limnoperna* provides shelter and/or food for these species. *Limnoperna* also colonizes crustacean carapaces and unionid valves, and may negatively impact these species (Darrigran & Ezcurra de Drago 2000, Mansur et al. 2003).

### System-wide Effects

As suspension feeders that attach to hard substrates, *D. polymorpha* and *L. fortunei* are functionally different from most benthic freshwater invertebrates. They both have high filtration rates (Table 1), form large populations, and act as powerful biofilters (reviewed in Karatayev et al. 1997, 2002, 2005, Sylvester et al. 2005a, Cataldo et al. 2005a). By filtering large volumes of water they transfer energy and material from the water column to the benthos, providing a strong direct link between planktonic and benthic components of the ecosystem (benthic-pelagic coupling), and induce major changes in the ecosystems invaded (reviewed in Morton 1997, Karatayev et al. 1997, 2002, 2005, Johannsson et al. 2000, Darrigran 2002, Vanderploeg et al. 2002, Mayer et al. 2002, Mills et al. 2003, Burlakova et al. 2005, Boltovskoy et al. 2006).

### Abiotic Parameters

The filtering activity of *D. polymorpha* and *L. fortunei* has similar effects on the abiotic parameters of the aquatic systems they invade, including increased water transparency and light penetration, decreased concentrations of seston and organic matter, decreased BOD, and increased concentrations of ammonia, nitrates, and phosphates (reviewed in Karatayev et al. 1997, 2005, Mayer et al. 2000, Idrisi et al. 2001, Vanderploeg et al. 2002, Cataldo et al. 2005a). On the other hand, the deposition of large amounts of detritus on the bottom can increase siltation (reviewed in Karatayev et al. 1997,

Zhukova 2001), thus decreasing substrates available for further attachment of new recruits (Lvova 1977). Cataldo et al. (2005a) conducted 12 h mesocosm (400 L) experiments with *Limnoperna* in the Río Tercero reservoir (Córdoba Province, Argentina), and they found similar impacts on water transparency and on the sedimentation of suspended matter, as has been found with zebra mussels.

#### Phytoplankton

Invasion by *D. polymorpha* results in decreased phytoplankton density and chlorophyll concentrations (reviewed in Karatayev et al. 1997, 2002, 2005, Idrisi et al. 2001, Vanderploeg et al. 2002). However, the clearance rates of zebra mussels depend on the composition of phytoplankton (Ten Winkel & Davids 1982, Berg et al. 1996) and the overall grazing effect on planktonic communities may be different in different lakes (Raikow et al. 2004). Impacts can also result from selective grazing and from changes in nutrient concentrations. Unpalatable algae may increase in abundance because of enhanced rejection, and nutrient regeneration and input by *Dreissena* may selectively favor some phytoplankton groups (Arnott & Vanni 1996, Vanderploeg et al. 2001, but see Dionisio Pires et al. 2005). Preliminary experiments with *Limnoperna* in 400 L mesocosms indicate that dense populations (2–3 ind. L<sup>-1</sup>) filter practically all of the phytoplankton (initial concentration: 2000–2500 cells mL<sup>-1</sup>) from the water in about 6 h (Cataldo et al. 2005a).

#### Macrophytes and Periphyton

Increased light penetration caused by the filtering activity by *D. polymorpha* allows macrophytes and periphyton to grow deeper and cover larger portions of the lake bottom (reviewed in Karatayev et al. 1997, 2002, 2005, Mayer et al. 2002, Vanderploeg et al. 2002). This action creates positive feedback because macrophyte beds are an excellent substrate for attachment for zebra mussels. *L. fortunei* attach less extensively to submerged macrophytes, but golden mussels have been found on *Elodea* (Tomás Chalde, personal observation), as well as on the roots of several reeds, such as *Scirpus* (Mansur et al. 2003).

#### Zooplankton

Zooplankton density and biomass usually decrease after *Dreissena* invasion (reviewed in Karatayev et al. 1997, Johannsson et al. 2000, Kryuchkova & Derengovskaya 2000, Wong et al. 2003). This decline may be because of competition for food (phytoplankton and bioeston in general), direct filtering of small crustaceans and rotifers, or to more complex interactions, such as increased predation of zooplankton by fish larvae. In many lakes the introduction of zebra mussels is associated with an increase in benthivorous fishes, whose larvae feed on zooplankton, including *Dreissena* larvae (reviewed in Molloy et al. 1997). Thus far there are no data for *L. fortunei*, but the golden mussel is likely to have a similar effect (see later).

#### Fishes

The impacts of zebra mussels on the fish community may be direct or indirect, and to a large extent depend on the feeding mode of the fishes (Karatayev et al. 2002). *D. polymorpha* may be associated with an increase in all benthic feeding fishes, even

those that do not feed on zebra mussels, because zebra mussel invasion is associated with an increase in the biomass of native benthic invertebrates (reviewed in Karatayev et al. 1997, 2002, Molloy et al. 1997). The larvae of *Dreissena* are readily consumed by many species of fish and can comprise over 70% of the zooplankton density during the summer (reviewed in Molloy et al. 1997).

In South American water bodies recently invaded by *Limnoperna*, like the Salto Grande Reservoir on the Uruguay River, larvae of *Limnoperna* can comprise 30% to 35% of the zooplankton from June to September. In the Río de la Plata estuary, where *Limnoperna* first invaded around 1990, from spring to fall golden mussel larvae are 8–9 times more abundant than the combined densities of copepods and cladocerans. Preadult stages of the dominant fishes seem to adjust well to this new resource: in the Paraná River larvae of 10 out of 15 fish species surveyed between October 2000 and March 2001 feed regularly on golden mussel veligers (Paolucci et al. 2005).

Thirty-eight species of fish have been reported to feed on adult *D. polymorpha* (reviewed in Molloy et al. 1997), and at least 16 species of fish feed on *L. fortunei* (Montalto et al. 1999, Freis et al. 2000, Penchaszadeh et al. 2000, Cataldo et al. 2002, Armengol & Casciotta 1998). In the Paraná and Río de la Plata Rivers some of the commercially most valuable species, like *Pterodoras granulosus* and *Leporinus obtusidens*, have been observed to feed preferentially on *L. fortunei*. Up to 100% of fish collected in the summer have their guts filled predominantly or exclusively with golden mussel remains (Freis et al. 2000, Penchaszadeh et al. 2000, Cataldo et al. 2002). *In situ* experiments with *L. fortunei*-colonized panels with and without screening to protect against fish predation showed that exposed mussels are swiftly eliminated by predators (Cataldo et al. 2002, Sylvester et al. 2005b). The positive effects of golden mussel invasion on fish communities is directly on molluscivores, and indirectly on picivores that feed on mollusc-eating fishes, which include many of the larger and commercially most valuable species (Boltovskoy et al. 2006).

In the Paraná basin over 60% of the fish biomass is represented by a single detritivorous species: the sábalo, *Prochilodus lineatus* (Sverlij et al. 1993, Iwaszkiw 2001). Enrichment of the sediments with organic matter will likely enhance the densities of sábalo in the system (as observed with other fish species in the presence of *D. polymorpha*, e.g., Thayer et al. 1997), which is the primary food of most picivores in the system (Sverlij et al. 1993, Iwaszkiw 2001). Data on freshwater fish yields support the assumption that *L. fortunei* has had a positive effect on fish biomass in the Río de la Plata system. Argentina is the only South American country where catches consistently increased after 1990, and grew according to FAO statistics, from around 10,000 tons per year (1950–1991), to 30,416 tons in 2003 (<http://www.fao.org>), when *Limnoperna* expanded along the Río de la Plata-Paraná waterway, which yields 90% of the country's freshwater fish landings (Boltovskoy et al. 2006).

Increases in benthivorous fishes may pose a strong negative feedback on mussel populations. In Europe fish may consume >80% of zebra mussel production (Lvova 1977, Yablonskaya 1985). Sylvester et al. (2005b) estimated that predators eliminate around 6 kg of *Limnoperna* biomass m<sup>-2</sup> (total wet mass) per year, which represents ~85% of the mussel's production.

However, there is no evidence of long-term decline of mussel populations caused by the effects of predation (reviewed in Molloy et al. 1997, Sylvester et al. 2005b). Karatayev et al. (2002) suggested that piscivorous fish may be positively affected by *Dreissena* because of an increase in benthic feeding fish, but because most fishes change their dietary habits throughout their life, equivocal conclusions can be drawn when only adults are taken into account.

Planktivorous fishes could be negatively affected by the introduction of bivalve suspension feeders because they decrease phytoplankton and zooplankton abundance, or because they increase predation on fish larvae caused by increased water transparency (Lozano et al. 2001). Alternatively, several positive indirect effects have been suggested that could mitigate the negative effect of dreissenids on planktivorous fish. The increase in transparency and light penetration associated with invasion may positively affect visually feeding fish (Mayer et al. 2001, Mills et al. 2003). Expansion of aquatic vegetation into deeper waters caused by the increase in light penetration provides both refuge from piscivores and increased sites for production of invertebrate prey (MacIsaac 1996). There are data suggesting that the decline in the abundance of a whitefish (*Coregonis clupeaformis*) in lakes Ontario and Michigan (USA) is related to a decline of their main food item, *Diporeia hoyi*, in turn associated with the introduction of dreissenids (Hoyle et al. 1999, Pothoven et al. 2001). However, other factors, including disease caused by pathogens and/or pollution may also be responsible for the thinning of *Diporeia hoyi* populations (reviewed in Mills et al. 2003). Thus, to date strong evidence supporting a negative impact of *Dreissena* on planktivorous fish is lacking (Trometer & Busch 1999, Mayer et al. 2000).

#### Parasites and Commensals

At least 34 species and higher taxa of parasites and commensals are known to be associated with *Dreissena*, including ciliates, trematodes, mites, nematodes, leeches, chironomids, oligochaetes, and bacteria (reviewed in Molloy et al. 1997). Among these at least six species of ciliates and three species of trematodes are found exclusively in *Dreissena*, and are only found in European populations. Only nonspecific organisms (e.g., nematodes, chironomids, oligochaetes, mites) are found in North American populations of *Dreissena*. And only one trematode, *Bucephalus polymorphus*, is known to cause parasitic damage to zebra mussels (Molloy et al. 1997). The trematodes that use zebra mussels as an intermediate host usually have waterfowl or fish as definitive hosts (reviewed in Molloy et al. 1997).

In contrast to the wide variety of parasites and commensals found in zebra mussels, almost no information is available in this respect for *Limnoperna*. Ogawa et al. (2004) identified widespread infections by bucephalid trematodes in several cyprinid fishes from the Uji River, suggesting that the infections started with the accidental introduction of infested first intermediate hosts – *L. fortunei*.

#### CONCLUSION

*Dreissena polymorpha* and *L. fortunei* have very similar life histories, including planktonic free swimming larvae and sessile byssate benthic stages, suggesting that very similar vectors are likely to be involved in their spread. *Limnoperna fortunei* reaches densities as high as or higher than *Dreissena*, and their filtering rates are comparable as well. Therefore, we predict that the ecosystem effects of the golden mussel will be at least as great as those of the zebra mussel. Although *D. polymorpha* seems to be more resistant to cold temperatures, *L. fortunei* has higher tolerance to many environmental parameters, including high temperature, low pH and low calcium content, as well as water pollution. Wider ecological tolerances will allow the golden mussel to invade waters unsuitable for zebra mussels. Soon most of the waterbodies that are invaded by *D. polymorpha* may be invaded by another even more aggressive species, *L. fortunei*. We anticipate that *L. fortunei* is capable of colonizing the southern and central parts of North America, much farther north than was predicted by Ricciardi (1998). *L. fortunei* may be particularly successful in regions dominated by slightly acidic, soft and contaminated waters, as well as estuarine waters that are not suitable for *D. polymorpha*. Zebra mussel and the golden mussel are very effective ecosystem engineers that have local and system-wide effects. Although taxonomically unrelated, their ecosystem impacts are more likely to follow from the novel ecological niche they share, rather than being species specific.

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