Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*

Alexander Y. Karatayev, Demetrio Boltovskoy, Lyubov E. Burlakova and Dianna K. Padilla

Abstract *Limnoperna fortunei* (the golden mussel), *Dreissena polymorpha* (the zebra mussel), and *Dreissena rostriformis bugensis* (the quagga mussel) are considered among the most aggressive freshwater invaders. All three species share several biological traits, such as their sessile mode of life attached to hard substrata by a byssus (although quagga mussels can also dwell on muddy bottoms), similar sizes, similar longevity, and similar time to sexual maturity. The spawning period, however, is usually longer for *L. fortunei*. Ecologically, they also share similarities (e.g., suspension feeding mode), but the dreissenids thrive and reproduce in colder waters (especially *D. r. bugensis*), and are significantly less tolerant to low pH and calcium concentrations, hypoxic conditions, and pollution. Rates of intrabasin spread of *L. fortunei* in South America are roughly similar to those of *D. polymorpha* in North America, but interbasin spread is generally faster for the zebra mussel, probably partly due to cultural and economic differences between their respective invasive ranges. Geographic spread of quagga mussels has been much slower than that of

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A. Y. Karatayev (✉)
Great Lakes Center, SUNY Buffalo State, 1300 Elmwood Avenue, Buffalo, NY 14222, USA
e-mail: karataay@buffalostate.edu

D. Boltovskoy
Facultad de Ciencias Exactas y Naturales, Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEBA), Universidad de Buenos Aires-CONICET, Ciudad Universitaria, 1428 Buenos Aires, Argentina
e-mail: demetrio@ege.fcen.uba.ar

Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’-CONICET,
Buenos Aires, Argentina

L. E. Burlakova
The Research Foundation of The State University of New York, SUNY Buffalo State,
Buffalo, NY 14222, USA
e-mail: burlakle@buffalostate.edu

D. K. Padilla
Department of Ecology and Evolution, Stony Brook University,
Stony Brook, NY 11794-5245, USA
e-mail: padilla@life.bio.sunysb.edu

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zebra mussels, but once the former colonize waterbodies already populated by zebra mussels, they usually become dominant, both spatially and numerically. Judging from their respective environmental tolerance limits, in particular calcium concentrations, it is expected that both species of *Dreissena* may eventually colonize much of Europe, Asia, and North America, but colonization of South America, Africa, and Australia is less likely. In contrast, *L. fortunei,* which tolerates much lower calcium concentrations, could spread to areas presently occupied by the dreissenids as well as Africa and Australia. Should the three species overlap, it seems likely that *L. fortunei* will outcompete the dreissenids in warmer, more polluted, less oxygenated, and more acidic waters as well as in waters with lower calcium concentrations. However, the outcome of their competitive interactions when conditions are suitable for all three species is unclear. *L. fortunei* and both species of *Dreissena* are functionally similar, and as a consequence, many of their impacts on the systems they invade are also similar, yet the magnitude of these effects, and in some cases even their sign, can differ widely depending on the invasive species and environmental constraints. Future research on the golden mussel should focus on shedding light on the many unknown aspects of its biology and ecology, which are particularly critical for a comprehensive assessment of its interactions with local biota.

Keywords *Limnoperna fortunei* · *Dreissena polymorpha* · *Dreissena rostriformis bugensis* · Ecological impact · Distribution · Environmental tolerance · Geographic spread

Introduction

Although *Limnoperna fortunei* (the golden mussel) is taxonomically unrelated to *Dreissena polymorpha* (the zebra mussel) and *Dreissena rostriformis bugensis* (the quagga mussel), they have similar life histories, share many ecological traits, and are functionally similar. Therefore, their ecological and economic impacts on waterbodies they invade are often similar as well. Due to their high rates of spread, large numbers of colonized waterbodies, and the extent of their ecological and economic impacts, both species of *Dreissena* and *L. fortunei* are considered among the most aggressive freshwater invaders (Karatayev et al. 2007a, 2010a). All three are spreading at virtually all spatial scales and are expected to continue doing so (Karatayev et al. 2007a, 2007b, 2011, 2015; Pollux et al. 2010; Benson 2014; Boltovskoy and Correa 2015).

The overall impact of an invader depends on many factors, including, among others, the number of waterbodies colonized, its total population density in a given waterbody, its population dynamics, and distribution within a waterbody (Karatayev et al. 2010b, 2011). The number of waterbodies colonized will depend on the invader's ability to use different transport vectors, propagule pressure, environmental limits, and its life history and biological parameters (e.g., fecundity, growth, and survival), which ultimately determine total population size, population dynamics, and distribution within an invaded waterbody. Therefore, to accurately predict the potential spread and ecological impacts of invaders, it is essential to know their environmental limits and their biology. Although *D. polymorpha* is among the best studied freshwater invertebrates, less data are available for *D. r. bugensis* and *L. fortunei* (Karatayev et al. 2007a, 2007b, 2015, 2014a; Nalepa 2010; Boltovskoy and Correa 2015).

The aims of this chapter are to review similarities and differences among *L. fortunei* and both species of *Dreissena* in their biological traits, environmental limits, rates of spread, population dynamics, and ecological impacts, and to identify the essential information needed to better understand their geographic spread and their effects on ecosystems.

Life History

L. fortunei belongs to the largely marine bivalve family Mytilidae, while zebra and quagga mussels belong to the Dreissenidae, which is of brackish water origin. *L. fortunei* and *Dreissena* spp. represent an unusual ecological type in freshwaters and have traits typical of marine mussels, including free-swimming larvae and a sessile, attached adult stage.

Extensive research has been conducted on the biology, reproduction, growth and other life history traits of *D. polymorpha,* but relatively fewer studies have focused on *D. r. bugensis* and *L. fortunei* (Karatayev et al. 2007a, 2007b, 2014a, 2015; Nalepa 2010). We know that all three species mature at approximately the same age, and have a similar body size (Table 1).

In *L. fortunei* and *D. polymorpha* gonads are fully developed by the spring, and spawning typically occurs in spring–summer (Lvova and Makarova 1994; Boltovskoy et al. 2009b; see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume). In cold deep waters, gonads of *D. polymorpha* and *D. r. bugensis* may be ripe for a longer period of time during the year and spawning extends over more months, producing smaller recruitment events over a longer period (Bacchetta et al. 2010; Nalepa 2010). The duration of the reproductive period depends on the temperature regime and is longer in warmer regions. In the northern part of its range, spawning of *Dreissena* spp. lasts for about 3–5 months (Lvova and Makarova 1994). In Lake Mead (Arizona-Nevada, USA), however, quagga mussel veligers are present in the plankton year round, suggesting a much longer spawning season (Wong et al. 2012), similar to the spawning season of golden mussels in the tropics and subtropics (up to 10 months, Boltovskoy et al. 2009b). In contrast, in temperate and cold-temperate areas (Japan, Korea) *L. fortunei* produces larvae for only 1 month or less each year (Choi and Shin 1985; Nakano et al. 2010a) (see Figs. 2 and 3 in Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*", this volume).

For *L. fortunei,* most studies from Asia and South America concur that reproduction starts when water temperatures reach around 15–18 °C (Morton 1977; Choi

Table 1 Size and life history parameters for *Limnoperna fortunei, Dreissena polymorpha,* and *Dreissena rostriformis bugensis*

Parameter	*L. fortunei*	*D. polymorpha*	*D. r. bugensis*
Typical [maximum] length (mm)	20–30 (Boltovskoy et al. 2009a), [50.5] (Karatayev et al. 2010a)	20–30 (Karatayev et al. 2007a), [49] (Son 2007)	20–30 (Karatayev et al. 2014c)
Longevity (years)	2–3 (Boltovskoy and Cataldo 1999)	4–5 (Lvova et al. 1994b, Karatayev et al. 2006)	4–5 (Mills et al. 1996; Orlova et al. 2004)
Time to sexual maturity (months)	3–4 (Boltovskoy and Cataldo 1999; Darrigran et al. 1999)	3–11 (Lvova and Makarova 1994); 8–10 (McMahon and Bogan 2001)	No data
Typical spawning period (months/year)	<1 (temperate areas) to 10 (tropical and subtropical areas) (Choi and Shin 1985; Boltovskoy et al. 2009b; Nakano et al. 2010a)	3–5 (Lvova and Makarova 1994)	3–10 (Nalepa et al. 2010; Wong et al. 2012)
Fecundity (eggs per reproductive season)	No data	275,000–300,000 (Lvova 1977); up to 1,000,000 (Sprung 1991)	No data

and Shin 1985; Cataldo and Boltovskoy 2000; Nakano et al. 2010a; Brugnoli et al. 2011). So far, the golden mussel has not been reported from waterbodies where year round temperatures are below 15–18 °C, although there are many records from areas where water temperature is always above 15–18 °C (Mata 2011; Oliveira et al. 2011). Interestingly, in these tropical waterbodies the reproductive cycle is less regular, and slows noticeably in the winter (July–August in the southern hemisphere). Even when water temperatures are well above the threshold for reproduction (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume), larval production typically decreases or even ceases in the winter. Zebra mussels usually initiate spawning when water temperatures reach 12–15 °C, typically in the late spring (May to June in the northern hemisphere), and continue to spawn until the end of summer (August or September) (Table 1; Sprung 1987; Borcherding 1991; Lvova et al. 1994a; Karatayev et al. 1998, 2010b; Pollux et al. 2010). Quagga mussels, which usually live deeper, can spawn at water temperatures as low as 4.5–6.0 °C (Nalepa 2010). However, in areas where they co-occur with zebra mussels, both dreissenid species may initiate spawning at the same time (e.g., 18–20°C; Claxton and Mackie 1998).

Thus, the golden mussel requires higher temperatures for reproduction (15–18 °C), followed by the zebra mussel (12–15 °C), and the quagga mussel can reproduce in much colder waters (variable, but occasionally as low as 5–6 °C).

Fecundity data are only available for *D. polymorpha* (Table 1). 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). In the absence of similar data for quagga mussels, their fecundity is often assumed to be the same as for zebra mussels (e.g., Keller et al. 2007). However, this may be not the case. Zebra and quagga mussels have very different population dynamics in the waterbodies they invade. The time lag between when a species is first detected in a waterbody and when it reaches its maximum population size being much shorter for zebra mussels (2.5 ± 0.2 years) than for quagga mussels (12.2 ± 1.5 years) (Karatayev et al. 2011). The shorter lag time for zebra mussels may reflect their higher reproductive potential. Information for *L. fortunei* is still too scant and fragmentary for comparison, but the few data at hand seem to indicate that the lag time is closer to that of the quagga than the zebra mussel (see Chapter "*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics" in this volume). This, however, does not necessarily imply comparatively lower fecundity because carrying capacity depends on many intrinsic (e.g., fecundity), and extrinsic traits (e.g., predation pressure, competition, etc.).

Longevity of zebra mussels (up to 4–5 years, reviewed in Lvova et al. 1994b; Mills et al. 1996; Orlova et al. 2004; Karatayev et al. 2007b), seems somewhat greater than that of *L. fortunei* (around 2–3 years; Morton 1977; Boltovskoy and Cataldo 1999) (Table 1).

Environmental Limits

Temperature

The lower temperature limit for both species of *Dreissena* is close to 0 °C. The upper temperature limit for *D. polymorpha,* determined from field observations in both Europe and North America, is around 32–33 °C (Aldridge et al. 1995; Karatayev et al. 1998; Allen et al. 1999; Table 2). Field observations indicate that quagga mussels are likely somewhat less tolerant of high temperatures than zebra mussels (reviewed in Mills et al. 1996; Karatayev et al. 1998; Garton et al. 2014). Data from the Zaporozhskoe Reservoir (Ukraine) show that quagga mussels survive in waters ≤ 30.5 °C, while zebra mussels tolerate waters ≤ 33 °C (Dyga and Zolotareva 1976).

For *L. fortunei,* the upper thermal limit is around 35 °C, which is somewhat higher than that of both dreissenids (Table 2). In South America, minimum winter temperatures of the waterbodies colonized by *L. fortunei* are around 10 °C, but in Japan golden mussels survive at water temperatures of 5–6 °C (Magara et al. 2001), and in Korea *L. fortunei* populations have been reported from the Paldang Reservoir, which freezes for 1–2 months every winter (Choi and Kim 1985; Choi and Shin 1985; Park et al. 2013; Hae-Kyung Park, pers. comm.).

While on the basis of these data, it is tempting to speculate that low winter temperatures are unlikely to be a deterrent for the spread of *L. fortunei* into cooler waterbodies, minimum survival temperature may not be a good indicator of the

Table 2 Environmental limits for *Limnoperna fortunei, Dreissena polymorpha,* and *Dreissena rostriformis bugensis*. Values given are those that allow for survival of adult individuals, but not necessarily reproduction or survival of larvae (unless otherwise noted)

Factors	*L. fortunei*	*D. polymorpha*	*D. r. bugensis*
Upper salinity limit (‰)	Continuous: 2 (Angonesi et al. 2008; Sylvester et al. 2013); discontinuous, punctuated by periods of fresh water: up to 23 (Sylvester et al. 2013)	6 (reviewed in Karatayev et al. 1998)	3.5 (reviewed in Lyakhnovich et al. 1994)
Lower temperature limit for adult survival (°C)	0 (Choi and Kim 1985; Choi and Shin 1985)	0 (Luferov 1965)[a]	0 (Orlova 1987)
Upper temperature limit (°C)	35 (Oliveira et al. 2011)	32–33 (reviewed in Karatayev et al. 1998, 2006, 2007b; Allen et al. 1999)	31 (reviewed in Karatayev et al. 1998, 2007b)
Lower temperature limit for reproduction (°C)	15–17 (Morton 1977; Cataldo and Boltovskoy 2000; Nakano et al. 2010a; Brugnoli et al. 2011)	12–15 (Sprung 1987; Borcherding 1991; Lvova et al. 1994a; Karatayev et al. 1998; Pollux et al. 2010; Garton et al. 2014)	5–7 (Roe and MacIsaac 1997; Nalepa 2010)
Lower pH limit	<6.0 (Oliveira et al. 2011)	7.3–7.5 (Sprung 1987; Ramcharan et al. 1992; Burlakova 1998; Hallstan et al. 2010)	No data
Lower calcium limit (mg/L)	1 (Oliveira et al. 2011)	23–28 (Ramcharan et al. 1992; Burlakova 1998)	No data
Lower oxygen limit at 20 °C (mg/L)	0.5 (Boltovskoy et al. 2006)[b]	1.8–2.4 (Spiridonov 1972; Shkorbatov et al. 1994)	1.5 (Shkorbatov et al. 1994)
Tolerance to pollution	High (Villar et al. 1999; Belaich et al. 2006; Boltovskoy et al. 2006; Bonel et al. 2013; Young et al. 2014)	Medium (bij de Vaate et al. 1992; Jantz and Neumann 1992; Burlakova 1998)	No data
Distribution within a waterbody	Littoral, sublittoral (Boltovskoy et al. 2009a; Karatayev et al. 2010a)[d]	Littoral, sublittoral (Karatayev et al. 1998, 2014c; Burlakova et al. 2006)	Littoral, sublittoral, and profundal (Patterson et al. 2005; Watkins et al. 2007; Nalepa et al. 2009a; Nalepa 2010; Karatayev et al. 2014b, 2015)

Table 2 (continued)

Factors	*L. fortunei*	*D. polymorpha*	*D. r. bugensis*
Substrate type	Natural or artificial hard substrata, aquatic macrophytes, avoids soft silt (Boltovskoy et al. 2006, 2009a; Rojas Molina 2010)[e]	Natural or artificial hard substrata, avoids soft silt (Karatayev et al. 1998, 2014c; Burlakova et al. 2006)	Natural or artificial hard substrata and soft silt (Nalepa 2010; Karatayev et al. 2015, 2014c)

[a] Based on records in the upper River Volga, which freezes in winter

[b] In experimental conditions, at 20 °C large (20 mm) mussels survive up to 29 days at 0.16 mg/L (Perepelizin and Boltovskoy 2011)

[c] In experimental conditions, at 17.5 °C mussels survive anoxia for up to 18 days (Matthews and McMahon 1994)

[d] Highest densities are normally recorded along the coastal fringe, where hard substrata are normally much more abundant than at depth. However, results with artificial substrata indicate higher densities of recruits in the deeper layers (5–18 m) than closer to the surface (Morton 1977, Nakano et al. 2010b, Brugnoli et al. 2011)

[e] See Chapter "*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics" in this volume

mussel's ability to maintain self-sustaining populations. Reproductive cycles (as evidenced by the presence of larvae in the water column) clearly show that temperature is the dominant factor for spawning (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume). The shorter the periods of high temperature, the shorter is the spawning season. Thus, while in the Upper Paraná River, where water temperatures range around 18 to >30 °C, larvae are produced for 9–10 months each year, in Japan, at ~7–25 °C, larval output is restricted to 1–2 months, and in Korea, at 0–30 °C, reproduction is restricted to around 20 days (Choi and Shin 1985; Nakano et al. 2010a; Hamada 2011; Mata 2011; see Fig. 2, 3 and 10 in Chapter "Reproductive output and Seasonality of *Limnoperna fortunei*" in this volume). Interestingly, in all of these waterbodies, summer water temperatures are high. Even Paldang Reservoir, which freezes in the winter, reaches ~30 °C in the summer (Choi and Shin 1985). This suggests that the magnitude and duration of warm summer temperatures determine whether self-sustaining populations are possible, rather than minimum winter values. Data at hand indicate that the lowest temperatures at which *L. fortunei* spawns are around 15–18 °C (see Chapter "Reproductive Output and Seasonality of *Limnoperna fortunei*" in this volume), which suggests that waterbodies whose temperature is always below these values are unlikely to be colonized by this mussel. Therefore, Andean Patagonian lakes located south of ~38 °S, most of which do not freeze but never reach temperatures above 13–15 °C (Baigun and Marinone 1995; Díaz et al. 2000) are most probably not at risk of colonization by *L. fortunei*. In contrast, the North American Great Lakes, which may freeze in the winter, but usually have 3–4 month periods when water temperatures are above 16 °C (except Lake Superior; National Oceanic and Atmospheric Administration, NOAA 2014), are probably suitable for colonization by *L. fortunei*.

Salinity

In Europe and North America, *D. polymorpha* can form stable populations at salinities below 6 ‰, which is only slightly higher than the limit for quagga mussels (Table 2). For *L. fortunei,* constant salinities around 2 ‰ are the upper limit for extended survival (Huang et al. 1981; Angonesi et al. 2008; Barbosa and Melo 2009; Sylvester et al. 2013). However, at intermittent saltwater-freshwater conditions, such as those normally present in tidal estuaries, golden mussels can tolerate short periods (hours) of salinities up to 23 ‰ without significant mortality (Sylvester et al. 2013; see Chapter "Chemical Strategies for the Control of the Golden Mussel (*Limnoperna fortunei*) in Industrial Facilities" in this volume). This suggests that tests at constant salinity underestimate the tolerance of this species, and probably other freshwater molluscs, to saltwater exposure. Because estuarine ports represent ~70 % of nonmarine ports globally, they constitute major donor and recipient hotspots for the spread of nonnative species into continental aquatic ecosystems via shipping. It is probable that the tolerance of *L. fortunei* to estuarine conditions contributes to this species' success as an invader (Sylvester et al. 2013).

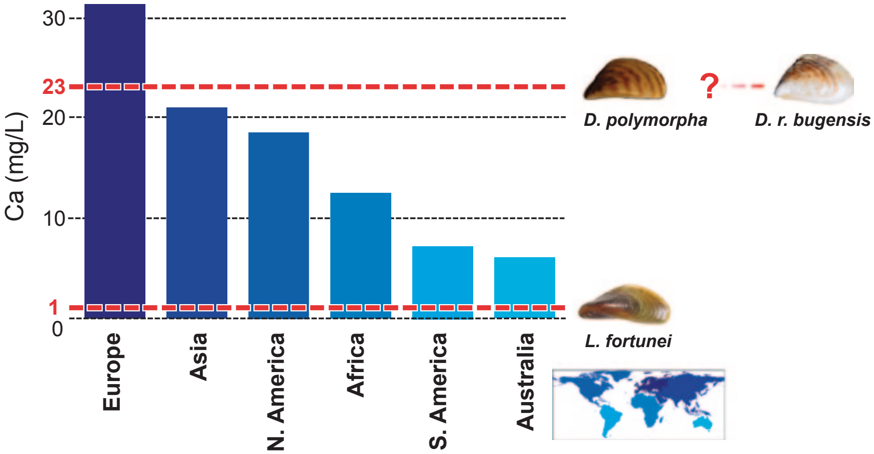

Fig. 1 Mean calcium concentrations in rivers on different continents (Wetzel 1975) and minimum calcium requirements for *Dreissena polymorpha* and *Limnoperna fortunei*

pH and Calcium

Zebra mussels are restricted to waters with neutral or alkaline pH (>7.3–7.5; Table 2). To our knowledge, there are no published data on pH limits for quagga mussels. Both in Europe and in North America, zebra mussels have colonized many more waterbodies than have quagga mussels. With few exceptions, almost all lakes had already been colonized by zebra mussels when quagga mussels invaded, suggesting that the pH limits for both species of *Dreissena* largely overlap. The threshold for calcium needed to support sustainable populations of zebra mussels is >23 mg/L (Fig. 1, Table 2), although values as low as 8–15 mg/L have been reported (Mellina and Rasmussen 1994; Jones and Ricciardi 2005). However, these lower values may reflect limits for the survival of adult mussels, rather than the establishment of locally sustainable populations (Sprung 1987).

The calcium limits for both species of *Dreissena* are substantially higher than those for *L. fortunei* (Fig. 1). Calcium is generally scarce in South American floodplain rivers colonized by the golden mussel (3-9 mg/L; Maglianesi 1973, Bonetto et al. 1998), and values as low as 1 mg/L of Ca and pH<6 have been reported from some areas successfully colonized by *L. fortunei*, such as the Upper Paraguay River (Oliveira et al. 2011).

Dissolved Oxygen

D. polymorpha is intolerant of even moderate hypoxia. Although it may colonize the deep oxygenated areas of some lakes, it usually is restricted to littoral and sublittoral zones (reviewed in Karatayev et al. 1998, 2015) (Table 2). In contrast, *D. r. bugensis* survives at lower oxygen concentrations than the zebra mussel (Shkorbatov et al.

1994), which may be related to its lower respiration rate (Stoeckmann 2003), and at least partially explains the ability of quagga mussels to colonize the profundal zone of deep lakes. However, both species of *Dreissena* are absent from hypoxic areas (e.g., central basin of Lake Erie; Karatayev et al. 2014c).

In contrast, *L. fortunei* survives in areas with very low oxygen concentrations, high organic loads, and industrial pollution (Villar et al. 1999; Belaich et al. 2006; Boltovskoy et al. 2006; Perepelizin and Boltovskoy 2011; Bonel et al. 2013; Young et al. 2014). In the delta of the Lower Paraná River, dense *L. fortunei* beds are present in the vicinity of urbanized and industrialized areas which discharge untreated domestic and industrial wastes. These waters and sediments contain pollutants at levels several times above those considered hazardous for aquatic life (e.g., Zn, Cr, Cu, Benzo[a] pyrene, polychlorinated biphenyls (PCBs), etc.), where other organisms (e.g., the Asian clam, *Corbicula fluminea*) do not survive (Cataldo et al. 2001a, 2001b).

Substrata

Within a waterbody, one of the main factors that affect the distribution of both *L. fortunei* and *Dreissena* spp. is the availability of suitable substrata. These mussels usually require hard substrate for attachment, and therefore their distribution is extremely patchy, with harder and coarser substrata yielding the highest densities and biomass of mussels. The most favorable substrata for these species are rocks, gravel, shells, and consolidated sediments (Karatayev et al. 1998, 2010a; Boltovskoy et al. 2006, 2009a; Burlakova et al. 2006).

In South American rivers, where hard substrata are scarce, plants may constitute important sites for attachment. Roots, rhizomes, and stolons of the water hyacinth (*Eichhornia crassipes, Eichhornia azurea*) seem to be particularly important substrata. Although densities of *L. fortunei* on these plants are comparatively low (see Chapter "*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics" in this volume), the abundance and widespread distribution of species of *Eichhornia* make them key elements of seeding sites (Callil et al. 2006; Marçal and Callil 2008, 2012; Rojas Molina 2010; Rojas Molina et al. 2010; Ohtaka et al. 2011; see Fig. 3e in Chapter "*Limnoperna fortunei* colonies: structure, distribution and dynamics" in this volume).

D. polymorpha and *L. fortunei* usually avoid pure mud, where they only occur on isolated hard objects, such as wood fragments, shells, stones, or artificial substrata (e.g., discarded debris). Mussels can use the hard fragments for initial attachment and subsequently attach to each other forming druses (Karatayev et al. 1998, 2010a, 2015).

Although the pattern of distribution of *L. fortunei* across substrate types is similar to *D. polymorpha,* the golden mussel appears to reach higher densities and especially higher biomass per unit area (Karatayev et al. 2010a). Both zebra and golden mussels are largely limited to the littoral zone and usually avoid soft sediments of the cold profundal zone (Karatayev et al. 1998, 2010a, 2015; Burlakova et al. 2006; Boltovskoy et al. 2009a). It is not clear, however, if golden mussels favor the shallow, coastal fringe because that is where hard substrata are most often found

(Boltovskoy et al. 2009a), or because they prefer shallower sites, regardless of substrate type. Colonization of artificial substrata suggests that recruits prefer settling at depth (6–18 m), rather than closer to the surface (Morton 1977; Nakano et al. 2010b; Brugnoli et al. 2011), but this pattern may also reflect differences in predation pressure. Comparison of samples scraped from the concrete wall of a penstock of the hydroelectric Yacyretá power plant (Upper Paraná River) yielded higher densities at 10 m (248,200 ind./m^2), than at the surface (170,400 ind./m^2), and at 40 m (54,400 ind./m^2) (Darrigran et al. 2007). While differences in densities at these three depths may reflect differences in hydrodynamics specific to this particular water intake structure, they still show that when offered adequate substrate, within these limits depth does not curtail the survival of *L. fortunei*.

In addition to the littoral zone, quagga mussels can colonize silty sediments, especially those found in the profundal zones of deep large lakes (Patterson et al. 2005; Watkins et al. 2007; Nalepa et al. 2009a; Nalepa 2010; Karatayev et al. 2015, 2014c). In these soft sediments, *D. r. bugensis* usually has a more even distribution across the bottom, and rarely forms large druses. Instead, single mussels or small aggregations almost float on the surface of the silty bottom (Nalepa 2010; Karatayev et al. 2014c). Therefore, in deep lakes with large profundal zones, quagga mussels may be found at higher overall numbers across the whole lake than either zebra or golden mussels.

Rate of Spread

Of the three species considered in this Chapter, *D. polymorpha* has by far the longest and the best-documented history of invasion. This species began to spread from its native range in Europe in the early 1800s (Karatayev et al. 2007b, 2011, 2015; Pollux et al. 2010; van der Velde et al. 2010; bij de Vaate et al. 2014).

At the global scale, three major phases in the spread of the zebra mussel can be recognized: (1) An initial exponential phase in the nineteenth century in Europe, where it spread at a rate of ~3.9 geographic regions (countries, or geographic provinces within large countries) per decade; (2) A period of extremely slow spread for almost a century during the industrial revolution and increased water pollution; and (3) A second period of exponential spread that started in the 1960s, and included expansion in both Europe and North America (where zebra mussels were introduced in the 1980s, Carlton 2008), when it spread at an average rate ~6.6 regions/decade (Karatayev et al. 2011).

Although there was extensive ship traffic between areas inhabited by *D. r. bugensis* (the Dnieper-Bug Liman and the lower reaches of the Southern Bug River in Ukraine) and other regions of eastern and western Europe through the middle of the twentieth century, quagga mussels remained restricted to their native range until the 1940s (Zhulidov et al. 2004; Karatayev et al. 2007b, 2011; Son 2007; van der Velde et al. 2010; Zhulidov et al. 2010). Starting in the mid-1980s, quagga mussels spread in Europe and North America (where this species was first discovered in 1989, Mills et al. 1993) at a rate of 7.4 regions/decade, which is significantly faster than the initial spread of zebra mussels in Europe, but similar to the current rate of spread of zebra mussels at a global scale (Karatayev et al. 2011, 2014a). The delay in the spread of *D. r. bugensis* was likely due to its inability to use mechanisms and vectors responsible for the spread as efficiently as *D. polymorpha*. Quagga mussels appear to be less resistant to dislodgment than zebra mussels (Mackie 1991; Dermott and Munawar 1993; Peyer et al. 2009, 2010). As a result, zebra mussels may be more likely to remain attached to boat hulls than quagga mussels, facilitating their transport to new habitats.

In Europe, most waterbodies had already been colonized by zebra mussels long before quagga mussels began to spread, making it difficult to compare their rates of spread. However, North America was colonized by both species at approximately the same time (1980s), in the same area (Lake Erie), making their rates of spread in North America directly comparable. By 2008, zebra mussels had colonized twice as many US states as quagga mussels, almost eight times more counties, and over 15 times more waterbodies (Karatayev et al. 2011). By 2010, 25 years after their introduction into North America, *D. polymorpha* had colonized 17 times more waterbodies than *D. r. bugensis* (Benson 2014). These differences clearly show that zebra mussels are far more efficient at colonizing new waterbodies than quagga mussels.

It has been shown that estimates of the rates of spread of exotic bivalves depend upon the spatial resolution of the scale of spread, and may be accelerated or slowed by various human activities (reviewed in Karatayev et al. 2007b; see Chapter "Distribution and Colonization of *Limnoperna fortunei:* Special Traits of an Odd Mussel" in this volume). In general, the rate of spread is slower at finer spatial scales. For example, aquatic exotic species may quickly spread along connected waterways within a recently invaded continent, and soon reach their maximum range across the continental scale. However, it takes much longer to colonize all regions within an invaded continent, and much longer again to spread to every isolated lake and river (waterbody scale) within a region. This difference in the rate of colonization across different spatial scales may be several orders of magnitude. For example, in the nineteenth century it took less than 40 years for *D. polymorpha* to spread across Europe, chiefly through canal systems, to present day Belarus, Poland, the Baltic states, Great Britain, the Netherlands, Germany, Belgium, and France (reviewed in Karatayev et al. 2007b). On the other hand, at the regional scale it took over 150 years for *D. polymorpha* to spread across geographical barriers to Alpine regions (Kinzelbach 1992), and almost 200 years to colonize Ireland (Minchin 2000) and Spain (bij de Vaate et al. 2002).

The spread of *L. fortunei* outside of its purported native range in China, south of the Yangtze River, into tropical Indochina (Cambodia, Laos, Thailand, Vietnam), likely occurred centuries ago (Morton and Dinesen 2010), but the first documented record of expansion was in 1965, when this species colonized Hong Kong (Morton 1975). In the late 1980s, it was recorded in Japan (Matsuda and Uenishi 1992). In the early 1990s, it spread to South America (Pastorino et al. 1993), and is presently found in Argentina, Uruguay, Paraguay, Bolivia, and Brazil (see Chapter "Colonization and Spread of *Limnoperna fortunei* in South America" in this volume). A rough comparison of the rates of spread shows that *D. polymorpha* spread ~2800 km

(Minneapolis to New Orleans in 7 years (1986–1993), whereas *L. fortunei* spread 3400 km (Río de la Plata estuary to the Pantanal wetland) in 8–9 years (1990–1998). Thus, the rates of expansion in these areas have been generally similar, but the major pathways used for expansion likely differed. Once *D. polymorpha* colonized the uppermost reaches of the Mississippi River system (in 1991; Benson 2014), it swiftly expanded southwards by means of its downstream drifting larvae (Stoeckel et al. 2004). In contrast, *L. fortunei* first invaded the outlet of the Río de la Plata watershed (the Río de la Plata estuary), and spread northwards and upstream. Upstream expansion was obviously facilitated by attachment of adult individuals to the hulls of commercial boats that operate along the Paraná-Paraguay waterway, thus fitting the "jump dispersal" mode (MacIsaac et al. 2001). For *L. fortunei,* the importance of boat traffic as a dispersal vector is reinforced by the fact that in the Uruguay River, much of which is not navigable, the upstream expansion has been much slower than in the Paraná-Paraguay system (Boltovskoy et al. 2006).

Rates of spread across river basins, on the other hand, have apparently been faster for *D. polymorpha,* especially in the USA, than for *L. fortunei*. In Japan, the golden mussel is still restricted to a rather limited part of the country (see Chapter "Colonization and Spread of *Limnoperna fortunei* in Japan" in this volume), whereas in South America in more than 20 years only one major basin has been colonized (the Río de la Plata basin), and a few minor ones (Mar Chiquita, Patos-Mirim, Guaíba, Tramandaí; see Chapter "Colonization and Spread of *Limnoperna fortunei* in South America" in this volume).

The main mechanisms for interbasin dispersal of freshwater mussels are man-made canals and aqueducts, and overland transport. Canals and aqueducts are partly responsible for the spread of *L. fortunei* in China (see Chapter "Distribution and Spread of *Limnoperna fortunei* in China" in this volume), and in Japan (see Chapter "Colonization and Spread of *Limnoperna fortunei* in Japan" in this volume), but, for different reasons, their impact has been limited. In China, many of the major hydraulic projects are very recent, suggesting that the effects of invasion are still underway. In Japan, there are 400,000 km of man-made canals, many of which connect watersheds (Ministry of Agriculture, Forestry and Fisheries 2003); however, because of the country's topography, watersheds are numerous and very small (Japan Commission on Large Dams 2009). Despite a millennium of efforts by man to reshape the drainage network (according to the International Commission on Large Dams, of the 20 oldest dams in the world, 15 are located in Japan), many are still isolated. This may explain why the overall spread of *L. fortunei* in Japan has been comparatively slow (see Chapter "Colonization and Spread of *Limnoperna fortunei* in Japan" in this volume). In contrast, there are many large, navigable rivers in the USA, and almost 20,000 man-made canals, including several major interbasin transfer aqueducts, some of which are known to have been instrumental for the rapid dispersal of dreissenids (Benson 2014). In comparison, natural basins in South America have suffered little modification (with the exception of dams, especially in the Río de la Plata watershed, see Chapter "Colonization and Spread of *Limnoperna fortunei* in South America" in this volume), and there are no man-made interbasin

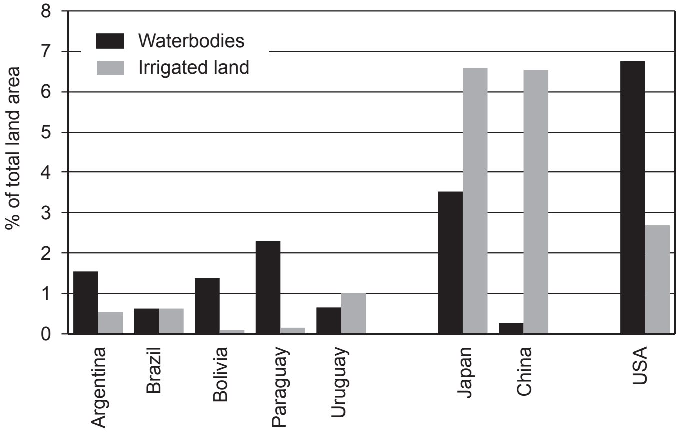

Fig. 2 Percentage of total land area occupied by waterbodies and artificially irrigated in countries invaded by *Limnoperna fortunei* or *Dreissena* spp.

connections (although plans to interconnect all major navigable waterways have been under consideration for years).

For freshwater byssate mussels, overland interbasin transfer is chiefly accomplished through fouling of recreational boats (Balcom 1994; Padilla et al. 1996; Buch and McMahon 2001; Johnson et al. 2001). Thus, invasion pressure on unconnected waterbodies is highly dependent on the number of boats (chiefly trailered), which in turn is associated with income and living standard levels. By all indices, the USA has higher economic development than China and the five South American countries where *L. fortunei* is invasive, and most probably has a significantly higher number of recreational, trailerable watercraft.

Another potentially important factor is the number and density of waterbodies. Areas where lakes and rivers are more numerous would be more susceptible to the dispersal of aquatic species than those where such features are scarcer. In the USA, the surface of lakes and rivers accounts for 6.8% of the total land area, which is 3–10 times higher than in any of the South American countries invaded by *L. fortunei,* and 2 and 24 times higher than in Japan and China, respectively (Fig. 2).

Potential for Future Spread

Dispersal of exotic species can be considered at different spatial scales, including the global, regional, local, and waterbody scales, each characterized by particular environmental constraints (Karatayev et al. 2007b). Because different exotic bivalves have different environmental limits (Table 2), their current and potential ranges are also different. Based on thermal tolerance alone, all three species have the potential to invade all continents except Antarctica, but none has fully reached

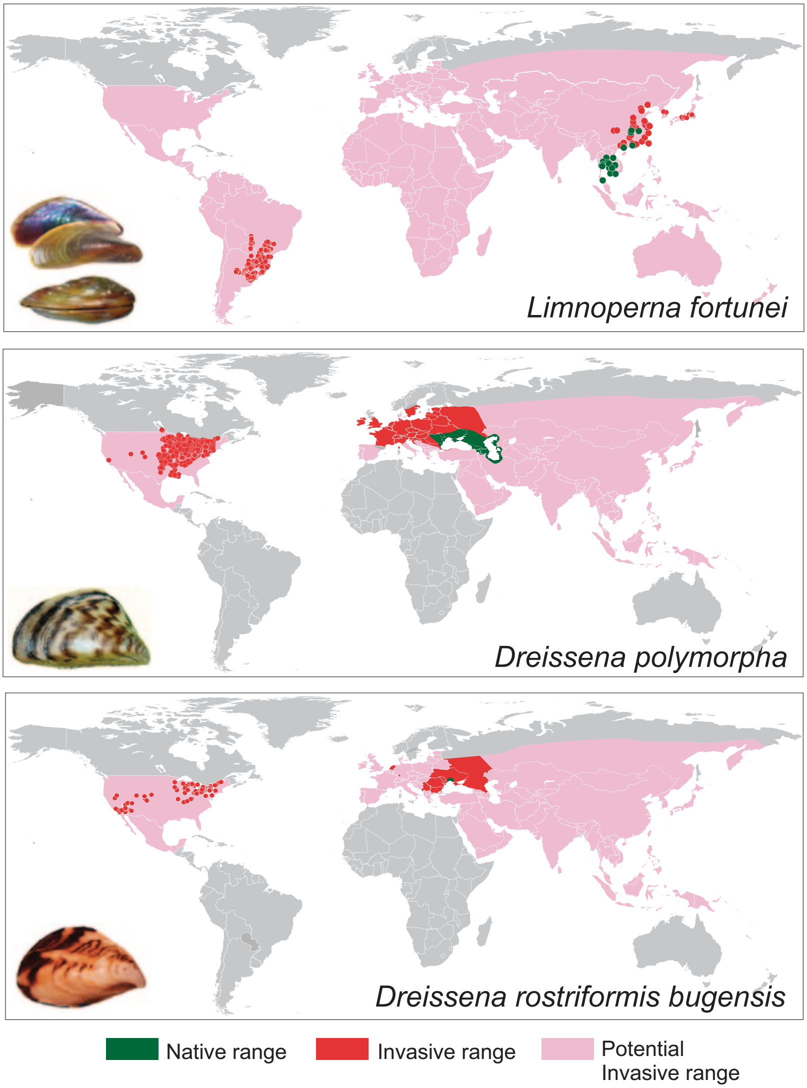

Fig. 3 Current and potential worldwide distribution of *Limnoperna fortunei, Dreissena polymorpha,* and *Dreissena rostriformis bugensis*. For *L. fortunei,* records in Indochina (denoted as native) are probably areas invaded before the twentieth century. (Distribution of *D. polymorpha* and *D. r. bugensis* in North America, courtesy of the United States Geological Service, Nonindigenous Aquatic Species)

this potential (Karatayev et al. 2007b). Both species of *Dreissena* are expanding their range in eastern and western Europe and have invaded North America. Neither has yet invaded Asia, Africa, South America, or Australia (Fig. 3). *L. fortunei* is spreading in Asia and has invaded South America (Fig. 3). Colonization of Asia and

Africa by *D. polymorpha* and *D. r. bugensis* has been anticipated (e.g., Starobogatov and Andreeva 1994), but high calcium requirements (Ramcharan et al. 1992; Burlakova 1998; Karatayev et al. 2007b) may curtail their spread into these continents. Most Australian and South American fresh waters have low concentrations of calcium, averaging 4 and 7 mg/L, respectively, while many North American and most European freshwaters have calcium concentrations that normally exceed 20–30 mg/L (Wetzel 1975; Payne 1986; Fig. 1). In South American Patagonia (Argentina and Chile), the temperature of many lakes located along the Andes cordillera south of ~38°S seems adequate for colonization by zebra and quagga mussels (2–3 to ~16 °C), but, again, the levels of dissolved calcium are most likely too low for these mussels. Of 21 lakes analyzed by Díaz et al. (2000), only two have Ca levels above 7 mg/L.

In contrast, it seems likely that *L. fortunei* may colonize many of the areas presently occupied by species of *Dreissena,* as well as those where *Dreissena* cannot live, including North America, Europe, Africa, and Australia (Karatayev et al. 2007b). Temperature may represent a deterrent in some regions, but the fact that the golden mussel thrives in Paldang Reservoir (Korea) suggests that as long as peak summer temperatures are high (>18 °C) it might establish viable populations and survive winter temperatures as low as 0 °C. Colonization of other major South American watersheds, especially those that drain into the Atlantic Ocean (Tocantins, São Francisco, Amazonas, Orinoco, Magdalena), is probably inevitable (Boltovskoy et al. 2006; Oliveira et al. 2010), but so far no records of invasion by *L. fortunei* have been reported from these basins.

The spread of these three species is still far from complete. For example, in 2008, after more than 200 years of invasion in Belarus, only 33 % of all colonizable lakes were invaded by the zebra mussel (Karatayev et al. 2010a). Similarly, less than 10 years after the initial invasion of North America, zebra mussels had spread throughout most of the major connected river systems east of the continental divide; however, this spread has been much slower at the regional scale, and even slower at the waterbody scale (Padilla 2005). After more than 20 years of invasion, only 120 of more than 15,000 inland lakes in Wisconsin (<1 %) were invaded by 2013 (reviewed in Karatayev et al. 2014a). To date, quagga mussels have not invaded any of the inland lakes in Belarus or in Wisconsin. Similarly, in Argentina, the golden mussel is present in a small fraction of the potentially colonizable waterbodies (Fig. 4). In Buenos Aires Province alone, <10 % of the ~530 permanent lentic waterbodies (Toresani et al. 1994) are currently invaded by *L. fortunei*. This mussel has not yet expanded its range beyond the large Río de la Plata watershed, a few minor basins in Uruguay and southern Brazil, and a small endorheic basin (Mar Chiquita) located in central Argentina (see Chapter “Colonization and Spread of *Limnoperna fortunei* in South America” in this volume).

It should be noted that monitoring of South American waterbodies for the presence of golden mussels is nowhere as systematic and thorough as that for dreissenids in the northern hemisphere. None of the countries invaded has a comprehensive program aimed at the early detection of *L. fortunei,* and efforts at tracking its expansion are isolated and uncoordinated. Furthermore, while so far the golden mussel has

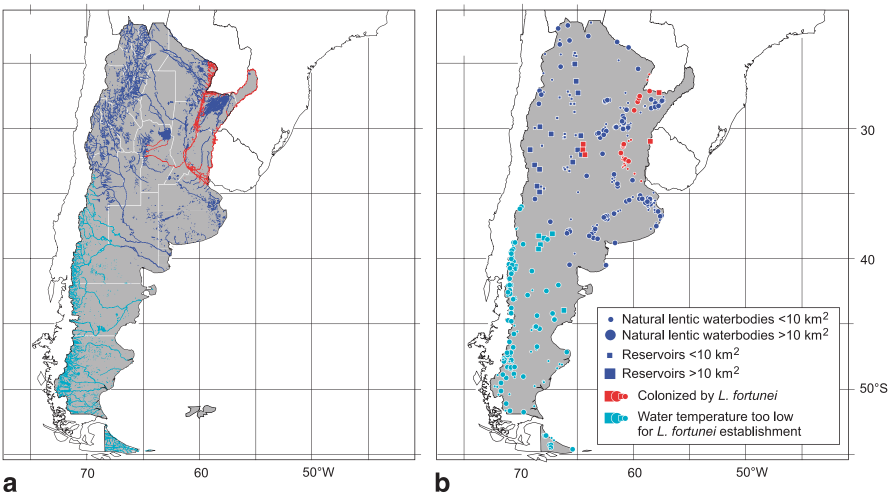

Fig. 4 Waterbodies (**a:** lakes and rivers, **b:** major lakes and reservoirs) colonized by the golden mussel in Argentina (*red*). *Light blue* denotes waterbodies where water temperatures are probably too low for the establishment of *Limnoperna fortunei*

been spreading in populated and industrialized areas of the Río de la Plata watershed, where the presence of this invader seldom went unnoticed, the next major watershed, the Amazon, is largely a very sparsely populated dense rainforest where most of the population lives in a few larger cities. Thus, the presence of the golden mussel is less likely to be noticed swiftly, and it is even less likely to be reported in the literature. On the other hand, because rivers are the main paths of transportation for people and produce, once colonization of the Amazon basin starts, the spread of golden mussels will likely be very fast.

Competition

The distributional ranges of zebra and quagga mussels overlap in Europe and in North America, and both species have the potential to overlap with *L. fortunei* in the future (Fig. 3). When co-occurring, species with similar habitat use will be expected to compete. Zebra and quagga mussels coexist in their native range in the Dnieper River delta and Dnieper-Bug Liman, Ukraine (reviewed in Zhulidov et al. 2010; Karatayev et al. 2011, 2014a). However, where the invasive ranges of both species overlap (Fig. 3), quagga mussels seem to outcompete zebra mussels over time (Nalepa 2010; Zhulidov et al. 2010; Karatayev et al. 2011, 2014a). This is especially typical for deep waterbodies and is likely due to the greater energetic efficiency of *D. r. bugensis* (Mills et al. 1999; Diggins 2001; Baldwin et al. 2002; Stoeckmann 2003; Karatayev et al. 2010c; Nalepa 2010). In addition, *D. r. bugensis* can colonize silty habitats, is more tolerant of low oxygen levels, has higher growth rates and lower mortality, and reproduces at lower temperatures than *D. polymorpha* (Mills et al. 1996; Claxton and Mackie 1998; Karatayev et al. 1998, 2010c, 2014c; Nalepa 2010). These demographic and physiological traits of quagga mussels allow them to colonize the large, cold profundal zone of deep lakes, which is unsuitable for zebra mussels. Thus, they can colonize the entire lake achieving much higher total population sizes, and outcompete zebra mussels by depleting food resources to levels that are too low for zebra mussels, but sufficient to support quagga mussels (Nalepa 2010; Karatayev et al. 2011, 2014a, 2015). In contrast, due to their tolerance of some abiotic factors (Table 2), greater rate of byssal thread production, and higher attachment strength (Peyer et al. 2009, 2010), zebra mussels are likely to be better adapted to the unstable, high-energy environment of the upper littoral zone, where fluctuations in temperature, currents, and wave action are prominent (reviewed in Karatayev et al. 2011, 2014a, 2015). Zebra mussels can still have an advantage in shallow lakes and rivers and coexist with quagga mussels (Zhulidov et al. 2004, 2010; Grigorovich et al. 2008; Peyer et al. 2009; Karatayev et al. 2011, 2015). Even in Lake Erie, where ≥ 95 % of the mussels in the central and eastern basins are quagga mussels, *D. polymorpha* still composes 30 % of the mussels in the shallow western basin after more than 20 years of coexistence (Karatayev et al. 2014c).

Because at present *L. fortunei* does not co-occur with either species of *Dreissena,* it is difficult to predict if they will compete, and if they do, under what conditions which species will prevail. Data at hand suggest that such co-occurrence is most likely to happen in Europe, Asia, and/or North America (Fig. 3). *D. polymorpha* has recently been found on barges imported to Argentina from the USA for grain transport along the Paraná-Paraguay rivers (Pablo Almada, personal observation), indicating that ballast water is not the only pathway for intercontinental transport of invaders. However, no live mussels were found in the few samples examined, and even if they had zebra mussels would probably not survive in the Río de la Plata watershed (see above). From their corresponding environmental tolerance ranges (Table 2), it seems likely that *L. fortunei* will outcompete the dreissenids in warmer, more polluted, less oxygenated and more acidic waters, as well as in waters with lower Ca concentrations. However, the outcome of their competitive interaction when conditions are suitable for all three species is unclear. The niche of *L. fortunei* within a waterbody appears to be more similar to that of zebra mussels than quagga mussels, suggesting that the competition may be stronger between the former two species (Table 2). However, similarities between zebra mussels and golden mussels also suggest that the impact of *D. r. bugensis* on *L. fortunei* may be similar to the one observed on *D. polymorpha*.

Impacts of Invasion

L. fortunei and both species of *Dreissena* are functionally similar, and as a consequence, many of their impacts on the systems they invade are also similar (Table 3). All three species are ecosystem engineers, sessile suspension feeders that attach to substrate with byssal threads. All three form druses, increasing habitat complexity for other benthic invertebrates, and affect planktonic communities, trophic relationships, and nutrient cycling via their feeding and filtering activities (Karatayev et al. 1997, 2002, 2007a, 2007b, 2015; Darrigran 2002; Beekey et al. 2004; Boltovskoy et al. 2006, 2009a; Burlakova et al. 2012; Boltovskoy and Correa 2015). However, the magnitude of these effects, and in some cases even their sign, depends on the invasive species, the other species present in the native community, and waterbody type.

Effects on Benthic Invertebrates

By creating reef-like three-dimensional structure, both species of *Dreissena* and *L. fortunei* change the physical habitat and provide refuge from predation and from physical stressors (waves, currents, desiccation) for benthic organisms that would otherwise be scarce or absent. In addition to increased habitat complexity, the impact of these byssate bivalves is compounded by their role as suspension feeders. All three species increase the rates of deposition of both inorganic and especially organic material on the bottom, providing an enhanced food subsidy for benthic deposit feeders. Many studies have shown that both *D. polymorpha* and *L. fortunei* have positive effects on most native invertebrates, which take advantage of both the structural complexity and food resources provided by zebra and golden mussels (Botts et al. 1996, Karatayev et al. 1997, 2002, 2007a, 2007b, 2010a; Darrigran et al. 1998; Stewart et al. 1998; Gutierrez et al. 2003; Beekey et al. 2004; Sardiña et al. 2008, 2011; Burlakova et al. 2012; Boltovskoy and Correa 2015; see Chapter “Relationships of *Limnoperna fortunei* with Benthic Animals” in this volume). At the same time, a few species of invertebrates have occasionally been found to be less abundant in mussel beds than in nearby bare sediments. Sardiña et al. (2011) reported that some snails, ostracods, nematodes, and chironomids may be less abundant in *L. fortunei* beds than in nearby bare sediments. However, the overall diversity, density, and biomass of native invertebrates is always higher in druses and mussel beds compared to nearby bare sediments (Table 3).

While in the littoral zone the effects of *D. r. bugensis* are probably similar to those of zebra and golden mussels (Bially and MacIsaac 2000; Yakovleva and Yakovlev 2011), in the cold profundal zone of deep lakes (where, unlike zebra and golden mussels, quagga mussels can be very abundant; Patterson et al. 2005; Watkins et al. 2007; Nalepa 2010; Karatayev et al. 2015, 2014c), their effects are quite different. Quagga mussels usually do not create large druses, but rather live individually or form small aggregates that float on the surface of soft silt (rather than sink), separated by the length of their siphons (Dermott and Kerec 1997, Karatayev and Burlakova, personal observations). Thus, they provide fewer refugia for benthic taxa and can compete with native invertebrates for space and food decreasing their overall diversity, density, and biomass (Dermott and Kerec 1997; Lozano et al. 2001;

Table 3 Effects of freshwater, byssate invasive mussels or mussel-related processes on invaded freshwater systems

Parameter	*L. fortunei*	*D. polymorpha*	*D. r. bugensis*
Water transparency	Increase (Boltovskoy et al. 2009a; Kawase 2011; Cataldo et al. 2012a; Boltovskoy and Correa 2015)[a]	Increase (Karatayev et al. 1997, 2002, 2007a, 2007b; Vanderploeg et al. 2002; Higgins and Vander Zanden 2010; Kelly et al. 2010)	Increase (Barbiero and Tuchman 2004; Nalepa 2010; Pothoven and Fahnenstiel 2014)
Seston concentration	Decrease (Boltovskoy et al. 2009a; Kawase 2011; Cataldo et al. 2012a, 2012b; Boltovskoy and Correa 2015)[a]	Decrease (Karatayev et al. 1997, 2007a, 2007b; Higgins and Vander Zanden 2010)	Decrease (Shevtsova 1989)
Nutrients	Alter nutrient cycling (Boltovskoy et al. 2009a; Kawase 2011; Cataldo et al. 2012a, 2012b; Boltovskoy and Correa 2015)[a]	Alter nutrient cycling (Karatayev et al. 2002, 2007a, 2007b; Vanderploeg et al. 2002; Higgins and Vander Zanden 2010; Kelly et al. 2010)	Alter nutrient cycling (Nalepa 2010)
Phytoplankton and chlorophyll	Decrease, changes in community composition (Boltovskoy et al. 2009a; Cataldo et al. 2012a; Di Fiori et al. 2012; Boltovskoy and Correa 2015)[a]	Decrease, changes in community composition (Karatayev et al. 2002 2007a, 2007b; Higgins and Vander Zanden 2010; Kelly et al. 2010)	Decrease, changes in community composition (Barbiero and Tuchman 2004; Fahnenstiel et al. 2010; Nalepa 2010; Pothoven and Fahnenstiel 2013)
Macrophytes, periphyton, benthic algae	Increase biomass and extent (Boltovskoy et al. 2009a; Cataldo et al. 2012b; Boltovskoy and Correa 2015)[a]	Increase biomass and extent (Karatayev et al. 1997; Nalepa et al. 1999; Vanderploeg et al. 2002; Hunter and Simons 2004, Karatayev et al. 2007a, Karatayev et al. 2007b; Higgins and Vander Zanden 2010)	Increase biomass and extent (Nalepa 2010)
Zooplankton	Decrease density, change community composition (Rojas Molina et al. 2010; Fachini 2011; Rojas Molina et al. 2011, 2012; Boltovskoy and Correa 2015)[b]	Decrease density, change community composition (Karatayev et al. 1997, 2007a, 2007b; Vanderploeg et al. 2002; Higgins and Vander Zanden 2010; Kelly et al. 2010)	Decrease? (reviewed in Nalepa 2010; Pothoven and Fahnenstiel 2014)

Table 3 (continued)

Littoral zoobenthos	Increase density and diversity; changes in community composition (Darrigran et al. 1998; Sylvester 2006; Sylvester et al. 2007a, 2007b; Sardiña et al. 2008, 2011, Karatayev et al. 2010a; Burlakova et al. 2012)[c]	Increase density; changes in community composition (reviewed in Karatayev et al. 1998, 2007b; Higgins and Vander Zanden 2010; Kelly et al. 2010)	Increase density; changes in community composition (Bially and MacIsaac 2000; Yakovleva and Yakovlev 2011)
Profundal zoobenthos	Normally *L. fortunei* absent or very scarce because of lack of adequate substrata[d]	*D. polymorpha* normally absent	Decrease, changes in community composition (Dermott and Kerec 1997; Nalepa et al. 1998, 2007, 2009a, 2009b; Lozano et al. 2001; Watkins et al. 2007; Nalepa 2010; Soster et al. 2011)
Unionids	Probably negative (Mansur et al. 2003; Scarabino 2004; Karatayev et al. 2010a)[e]	Negative (reviewed in Karatayev et al. 1997, 2007b; Burlakova et al. 2000; Lucy et al. 2014)	Negative (Schloesser and Masteller 1999; Zhulidov et al. 2010; Sherman et al. 2013; Lucy et al. 2014)
Adult and larval fishes	Probably positive from enhanced food resources (Montalto et al. 1999; Penchaszadeh et al. 2000; Boltovskoy et al. 2006; Paolucci et al. 2007; Paolucci et al. 2010a, 2010b; Boltovskoy and Correa 2015)[f]	Increase density of benthivorous fishes, changes in community composition (reviewed in Karatayev et al. 1997, 2002, 2007b; Molloy et al. 1997; Kelly et al. 2010)	Decrease density and changes in community composition in profundal zone (reviewed in Nalepa 2010; Karatayev et al. 2015)

[a] See Chapter “Nutrient Recycling, Phytoplankton Grazing, and Associated Impacts of *Limnoperna fortunei*” in this volume

[b] See Chapter “Impacts of *Limnoperna fortunei* on Zooplankton” in this volume

[c] See Chapter “Relationships of *Limnoperna fortunei* with Benthic Animals” in this volume

[d] See Chapter “*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics” in this volume

[e] *L. fortunei* have been observed to attach to unionid shells, but the potential impact has not been investigated

[f] See Chapters “Trophic relationships of *Limnoperna fortunei* with larval fishes” and “Trophic relationships of *Limnoperna fortunei* with adult fishes” in this volume

Nalepa et al. 2007, 2009a, 2009b; Watkins et al. 2007; Soster et al. 2011; Burlakova et al. 2014; Karatayev et al. 2015, 2014c).

Effects on the Water Column

The effects of *L. fortunei* and dreissenids on the water column are associated with their roles as suspension feeders, and effects can be system-wide, as opposed to effects on benthic invertebrates, which are mostly local. Suspension feeding not only affects nutrients and planktonic communities, it also transfers materials from the water column to the benthos, enhancing the coupling between planktonic and benthic components of the ecosystem, which can trigger a suite of changes that increase the relative importance of the benthic community—a process sometimes referred to as "benthification" (Mayer et al. 2014). The intensity and extent of these effects depend on many factors, including mussel population density and distribution in a waterbody, food resources available for the bivalves, water mixing rates, lake morphology, and plankton turnover rates (Karatayev et al. 1997, 2002; Kelly et al. 2010; Boltovskoy and Correa 2015). Because *D. polymorpha* is usually restricted to the littoral zone, its impacts may be significantly greater in small, shallow lakes than in large, deep ones (Karatayev et al. 2015). The impacts of *L. fortunei* may be similar, but this has not been confirmed by ad hoc studies. In contrast, quagga mussels are found throughout the entire waterbody, and, in deep lakes, they have larger total population sizes. As a consequence, they may have greater system-wide effects than golden or zebra mussels (reviewed in Karatayev et al. 2015).

Although there are more data on the system-wide impacts of zebra mussels than those of quagga and golden mussels, because of their functional similarity, their impacts on waterbodies are likely to be similar (Table 3), although the final outcome may differ depending on waterbody characteristics. The feeding activity of these invasive bivalves boosts nutrient concentrations and alters their proportions, in particular increasing the phosphorus to nitrogen (P:N) ratio (Conroy and Culver 2005; Cataldo et al. 2012b). Consumption of organic particles, including phyto- and zooplankton, and the rejection of organic and inorganic suspended matter as feces and pseudofeces decreases plankton densities and turbidity, which in turn favors light penetration and growth of macrophytes and periphyton. These effects have been described repeatedly in European, Asian, and North and South American waterbodies colonized by dreissenids or *L. fortunei* (see references in Table 3; see Chapter "Nutrient Recycling, Phytoplankton Grazing, and Associated Impacts of *Limnoperna fortunei*" in this volume). However, their net impacts on the systems investigated are not necessarily identical, especially when comparing cold-temperate North American lakes with tropical and subtropical South American freshwater habitats. The Paraguay-Paraná-Uruguay floodplain river system invaded by *L. fortunei* is quite different than the colder, clearer, and more oligotrophic North American waterbodies colonized by *Dreissena*. A particularly important contrast are the mean concentrations of particulate organic carbon (POC), which are much higher in South America (about 3.5 mg/L in the Paraná River, 20–40 % of it labile and available for biologic consumption; Depetris 1976; Depetris and Pasquini 2007) than in many of the waterbodies invaded by *Dreissena* (typically around 0.15–1 mg/L in the Great Lakes; Fanslow et al. 1995; Barbiero and Tuchman 2004; Johengen et al. 2008). Filtering organisms are generally scarce and probably not food limited in South America (Sylvester et al. 2005), which suggests that competitive impacts with suspension-feeding native animals, such as those described in North America (Bartsch et al. 2003; Thorp and Casper 2003; Raikow 2004), are less likely in South America. Furthermore, indigenous suspension-feeding organisms in the Río de la Plata watershed are scarce, and the main source of energy for animals is of detrital origin. Most of the suspended organic matter is flushed out into the ocean through the Río de la Plata estuary (~1,000,000–2,000,000 t of POC per year; Depetris and Kempe 1993; Guerrero et al. 1997). *L. fortunei,* the only abundant macrobenthic suspension-feeder, intercepts part of this organic matter and retains it in the system for use by a wide array of animals. The ecosystem-wide effects of this new energetic subsidy to the benthos have not been investigated, but are likely significant (Boltovskoy et al. 2006).

One of the most contentious questions is the impact of exotic bivalves on toxic cyanobacteria, in particular *Microcystis* spp. Several authors have suggested that *Dreissena* spp. promote toxic blooms via selective grazing and rejection of toxic strains of blue-green algae and excretion of soluble waste products at low nitrogen to phosphorus ratios (Conroy and Culver 2005; Bykova et al. 2006; Fishman et al. 2009). Other studies (in both North America and Europe) have found that zebra mussels may actively consume and reduce the density of *Microcystis* spp. (Baker et al. 1998; Strayer et al. 1999; Dionisio Pires et al. 2005, 2010). It was suggested that the positive effect of dreissenids on *Microcystis* spp. is restricted to lakes with low to moderate total phosphorus concentrations (<25 µg total P/L), whereas those with high nutrient loadings are not affected (Vanderploeg et al. 2001; Nicholls et al. 2002; Sarnelle et al. 2005; Knoll et al. 2008). In contrast, *L. fortunei* boosts *Microcystis* spp. growth at very high P concentrations (50–100 µg/L; Cataldo et al. 2012b).

Trophic Interactions with Fishes

In Europe and North and South America, dreissenids and *L. fortunei* provide an abundant food resource for fishes. At least 38 species of fish in Europe and in North America feed on *Dreissena* spp. (Molloy et al. 1997), and almost 50 species of fish consume *L. fortunei* in South America (see Chapter "Trophic Relationships of *Limnoperna fortunei* with Adult Fishes" in this volume). The importance of mussels in fish diets varies depending on the feeding mode and fish age, season of the year, and the morphology of the waterbody (Karatayev et al. 2002, 2007a; Strayer et al. 2004; Boltovskoy and Correa 2015).

In dreissenid-invaded areas, shortly after invasion there has been an increase in benthivorous fishes, especially in the littoral zone. This is true even for those that do not feed on dreissenids because of the increase in biomass of native benthic invertebrates that occurs with invasion (Karatayev et al. 2002, 2007a; Higgins and Vander Zanden 2010; Kelly et al. 2010; Burlakova et al. 2012). In Europe, a shift to dreissenid-based diets has resulted in increased growth, average and maximum sizes, and condition for some species of fish (Lyagina and Spanowskaya 1963; Poddubnyi 1966). In contrast, in the profundal zone of the Great Lakes, the introduction of zebra, and especially quagga mussels has been linked to the decline in the abundance, condition, and growth of several fish species. This effect has been associated with a decrease in their main food, the amphipod *Diporeia* spp., and to the lower energy content of the new food resource (mussels), which replaced the original forage base (Lozano et al. 2001; Hoyle et al. 2008; Nalepa et al. 2009a, 2009b; Rennie et al. 2009). Limited data suggest that dreissenids can have both negative and positive effects on planktivorous fishes. Suspension feeding by mussels can reduce planktonic food resources. Increased water transparency can result in increased predation on larval fish, but may also facilitate prey capture by visual fish predators (Francis et al. 1996; Mayer et al. 2001, 2014; Mills et al. 2003). In the long term, however, the effects of *Dreissena* spp. on fish were found to decrease with time (Strayer et al. 2014).

Following the introduction of the golden mussel in South America, several fish species shifted their diet from plants and detritus to the energetically more profitable *L. fortunei* (Boltovskoy et al. 2006; see Chapter "Trophic Relationships of *Limnoperna fortunei* with Adult Fishes" in this volume). *L. fortunei* is consumed not only by fishes that can detach mussels from a clump and grind their valves, but also by species that swallow whole individuals, and even others that nibble on extended siphons and mantle edges. Many of these midsized fishes are in turn consumed by larger, piscivorous species with high commercial value, suggesting that improved feeding conditions for their prey are likely to have a positive impact on these large species as well.

Consumption of *L. fortunei* veligers by fish larvae is probably even more significant than the consumption of adult mussels. Of 25 larval fish taxa surveyed in the Paraná, Paraguay, and Uruguay rivers, 18 feed on veligers, especially their earliest life stage (protolarvae) (Paolucci et al. 2007; Paolucci 2010; see Chapter "Trophic Relationships of *Limnoperna fortunei* with Larval Fishes" in this volume). Veligers are not only more abundant and easier to capture than crustacean zooplankton, but they also represent an energetically more profitable food resource yielding significantly higher growth rates than crustaceans (Paolucci et al. 2010b).

Concluding Remarks

Limnoperna fortunei was originally described in 1856 (as *Volsella fortunei;* Dunker 1856), and subsequently referred to under various different names including *Modiola lacustris, Limnoperna lacustris, Modiola siamensis, Limnoperna siamensis, Modiola cambodgensis, Modiola (Limnoperna) siamensis* (Morton and Dinesen 2010), in chiefly taxonomic and distributional studies. It was a species of little interest until it invaded Japan and South America around 1990. After that time, the number of publications dedicated to the golden mussel soared from <0.3/year as of

1992, to > 20/year after 1993 (see "Preface" in this volume). The striking similarity between *L. fortunei* and species of *Dreissena* has been noticed since the very first detailed studies of the biology of the golden mussel, when it invaded Hong Kong ~ 1965 (Morton 1975). By then, *D. polymorpha* had been expanding across Europe for centuries, and there was abundant information on its biology, ecology, and impacts. Thus, using *Dreissena* as a model and a recurrent reference in subsequent literature on the golden mussel was an obvious outcome.

The growing body of information on *L. fortunei* clearly shows that, indeed, parallels with the dreissenids, in particular with *D. polymorpha,* are numerous and warranted. However, proven similarities also encouraged ascribing to *L. fortunei* processes, and particularly impacts, reported for zebra mussels in the northern hemisphere. Although many researchers were cautious in their conclusions, stating that such effects were merely a possibility, others were not. These assumptions had a snowball effect whereby subsequent publications indiscriminately extrapolated results on the impacts of zebra mussels in the northern hemisphere to those of *L. fortunei* in South America.

Boltovskoy and Correa (2015) noted that "Complications for interpreting the effects of *L. fortunei* on the ecosystem are even more critical when attempting to label the impacts as negative or positive. A basic precautionary principle and the long list of examples where introduced species have been shown to have devastating effects on the biota (Simberloff 2003) clearly support the need to make all efforts possible to keep biological invasions at bay, or to eradicate them if feasible. However, once a nonnative species has been introduced and its eradication is out of the question (as is the case of *L. fortunei*), analyses of its interactions with the local biota should be based on evidence, rather than on extrapolations from other invasives and geographic areas. Much of the literature on the golden mussel has been oriented at forcibly demonstrating the environmental harm caused by this invader, thus biasing if not the results, the interpretation of the evidence obtained (Bujes et al. 2007; Defeo et al. 2013)".

As shown in this review, impacts of these invasive mussels vary widely among geographic areas and waterbodies, and even in different sectors within the same waterbody. Furthermore, interactions with the local biota change as a function of mussel species, their densities, and with time after initial colonization. Using data on the much more thoroughly researched dreissenids furnished useful guidelines for defining potential interactions and fruitful research topics, but it has also tended to hinder assessment of differences between the golden mussel and *Dreissena* spp., many of which have been shown to be responsible for quite dissimilar environmental impacts (Boltovskoy et al. 2006; Boltovskoy and Correa 2015). We contend that in order to effectively widen our current knowledge, research on *L. fortunei* should center on identifying contrasts and dissimilarities with dreissenids, rather than on confirming parallels.

Future research should aim at shedding light on the many unknown aspects of the biology and ecology of the golden mussel, which are particularly critical for a comprehensive assessment of its interactions with the local biota. So far, only a few effects at local scales have been explored, whereas at the ecosystem scale our understanding of interactions of *L. fortunei* with the environment is still very limited. For example, although mussel densities are a key element for gauging the impacts of the invader on ecosystems, so far only one attempt has been made at assessing this parameter over an entire waterbody (Boltovskoy et al. 2009a). Several potential traits (e.g., fecundity, metabolism) and interactions of utmost importance (e.g., biomagnification and transfer of contaminants, thermal shifts due to changes in water transparency, the homogenization of faunal composition across environments, facilitation of other invasive species, changes in macrophyte growth, modifications in benthic oxygenation, overgrowth of other organisms, trophic relationships with waterfowl and aquatic vertebrates other than fishes, etc.) have practically not been addressed so far.

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