Distribution and Colonization of *Limnoperna fortunei:* Special Traits of an Odd Mussel

Demetrio Boltovskoy

Abstract The invasional success of *Limnoperna fortunei* was largely determined by the combination of two key components. One of them is rare biological traits of the species, generally unfavorable in freshwater bivalves: the possession of planktonic larvae and a sessile, byssate adult. The other component is man's extensive modification of landscapes, in particular construction of reservoirs, large interbasin connections—canals and aqueducts and freshwater navigation. This combination was instrumental for the fast dispersal and success of a species that would otherwise have remained inconspicuous and restricted geographically. Environmental tolerance, while helpful, was probably of lesser importance. Possession of planktonic larvae results in a significant advantage for adults that manage to travel upstream, but is a major limitation for those that settle too close to the river outlet into the sea because their offspring are doomed due to expatriation into saline waters. Short rivers are therefore less vulnerable to colonization by self-sustaining populations, especially if there are no lakes or reservoirs along their path that can serve as refuge and seeding grounds for reproducing adults. In South America, interbasin spread has not occurred as fast as anticipated, but will most probably continue increasing.

Keywords *Limnoperna fortunei* · Golden mussel · Adaptation · Biological invasion · Geographic spread

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Mussel Traits and Man's Alteration of Earth: A Key Combination for Expansion

The fast dispersal and widespread nuisance effects of freshwater byssate mussels in general, and of *Limnoperna fortunei* in particular, are largely the result of five converging factors. Two of these factors are biological traits of the bivalve: (1) free swimming larvae and (2) a sessile, byssate adult. The other three factors are driven by human activities: (3) increasing interbasin connectivity, (4) construction of reservoirs, and (5) growing navigation in continental waters (Fig. 1).

It is widely acknowledged that the lack of a free-swimming larval stage in the vast majority of freshwater invertebrates is an adaptation to avoid expatriation into hostile marine environments—the sea. In contrast to marine benthic animals, most of which have planktonic larvae (Thorson 1950), the majority of invertebrates that have adapted to freshwaters have lost a planktonic larval stage (Lopez 1988), indicating that in the trade-off between lowering expatriation rates versus maintaining the high dispersal potential of their marine ancestors, evolution favored the former.

Possession of a byssus is also a rarity among freshwater bivalves (it occurs in ~1 % of all North American species: McMahon and Bogan 2001; <1 % of all South American bivalves: Pereira et al. 2014), as most have an infaunal mode of life, burrowing into soft sediment. This, too, probably reflects an adaptation to the scarcity of hard surfaced bottoms in lakes and lowland rivers. When present, hard substrata are normally limited to the shoreline fringe and river bank. Thus, *L. fortunei* is an oddity that has adapted to and survived in freshwaters despite these unfavorable traits.

For millions of years, *L. fortunei* has been constrained to a limited area in continental Southeast Asia, most probably restricted to the south of the Yangtze River (Morton and Dinesen 2010; Ye et al. 2011; see Chapter "Distribution and Spread of *Limnoperna fortunei* in China" in this volume). It somehow succeeded in establishing permanent, seeding populations upstream far enough from the sea for its larvae to complete metamorphosis and settle before being flushed out into saline waters, but it did not expand beyond this region (colonization of Indochina, including Thailand, Laos, Cambodia, and Vietnam, is probably relatively recent and likely associated with the influence of human migrations: Morton and Dinesen 2010). From its present distribution area (Fig. 2a) and the characteristics of the waterbodies where it thrives, it is clear that the range of the golden mussel was limited not because of its narrow ecological requirements, but because it was unable to overcome the geographic barriers involved. Models of its potential worldwide distribution (Kluza and McNyset 2005; Campos 2014; Campos et al. 2014; Fig. 2b) reinforce this assumption. In other words, as shown for other invasives (Kraft et al. 2002; Karatayev et al. 2007b), interbasin transportation was the bottleneck, rather than survival in a different milieu. Indeed, *L. fortunei* is thought to be extremely tolerant of a wide spectrum of environmental conditions (see Chapter "Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*" in this volume; Karatayev et al. 2007a, 2010), which may represent a necessary counterbalance to its primitive, mytiloid,

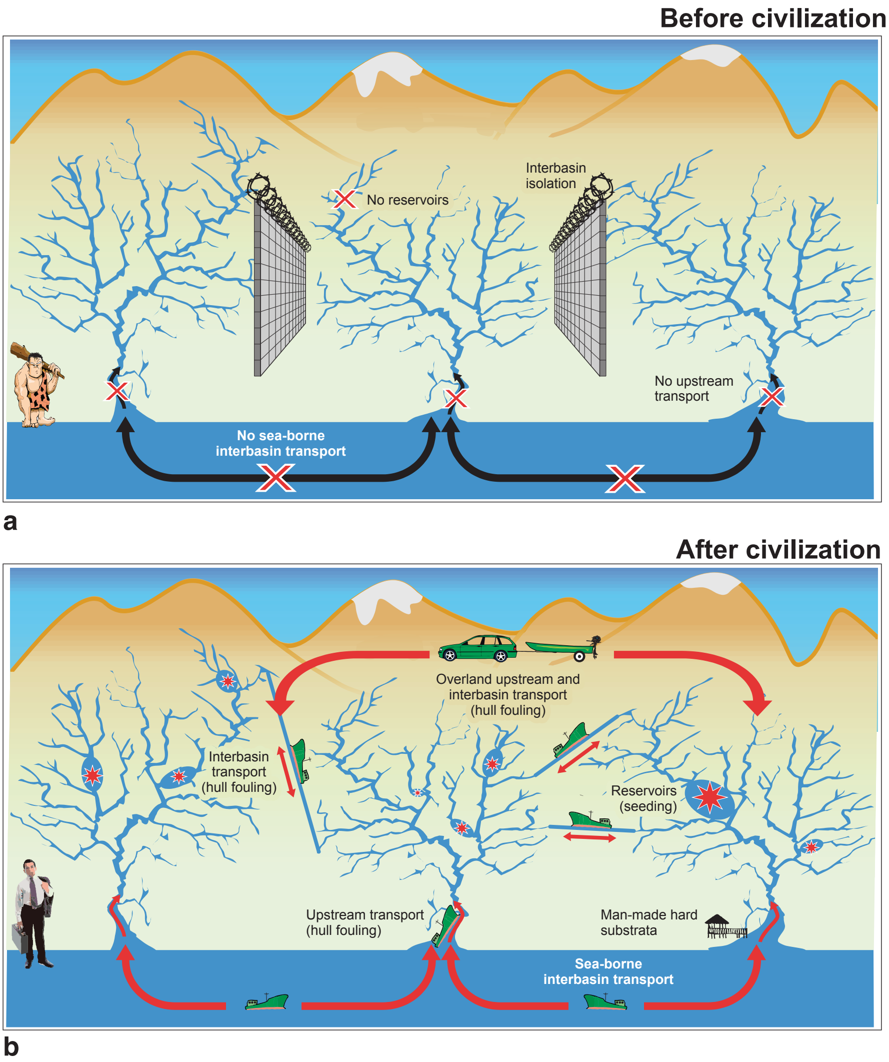

Fig. 1 Expansion vectors and mechanisms instrumental for the geographic spread of *Limnoperna fortunei* before (**a**) and after (**b**) large-scale modifications brought about by man's activities

freshwater-unfavorable traits (planktonic larvae and the requirement of hard substrata), allowing it to survive in a hostile habitat.

It should be stressed that invasional success does not necessarily imply broad environmental tolerance. Objective comparative studies of tolerance to environmental extremes between *L. fortunei* and native mussels have not been performed, but research in other geographic areas suggests that invaders may be less tolerant than native species. McMahon (2002), for example, concluded that *Dreissena polymorpha,* a highly successful invader, is not more resistant to ecological stress than

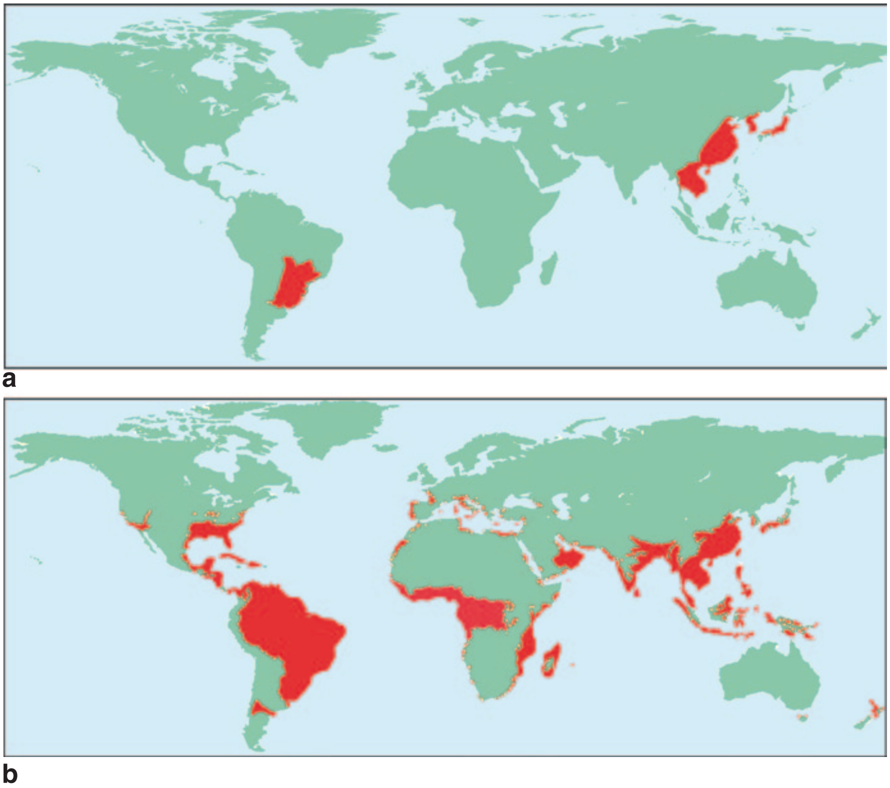

Fig. 2 Current worldwide distribution of *Limnoperna fortunei* (**a**) and potential distribution according to one of many possible modeling results (**b**). (b: modified from Kluza and McNyset 2005)

native unionids, its invasional success being largely explained by the fact that it is a typical r-strategist which recovers swiftly from catastrophic population reductions. *L. fortunei* is also an r-strategist, but unlike the zebra mussel it seems to be more resilient to stress than local mussels. Ancillary observations in various Chinese and Argentine waterbodies indicate that it is regularly present under extreme conditions, particularly in low oxygen and highly polluted waters, where many other organisms fail to survive (Boltovskoy et al. 2006; Contardo-Jara et al. 2009; Young et al. 2014).

The expansion of man is changing drastically the original rules of the game for much of the Earth's biota, but for some species, like *L. fortunei,* the changes are particularly profound and, unlike for many plants and animals, occasionally favorable. Increasing interbasin connectivity due to large hydraulic projects, such as irrigation and shipping canals, and aqueducts, is one significant shift that affects mussels (Minchin and Gollasch 2002; Nehring 2002; Karatayev et al. 2007b). However, large hydraulic projects are not particularly selective for *L. fortunei,* or for other byssate species, as they promote the spread more or less evenly of all freshwater organisms. On the other hand, shipping within continental waters, both natural and new man-made ones, became a key factor for organisms capable of traveling upstream by attaching to watercraft below the waterline (Fig. 1b). In the invasion of the Río de la Plata watershed by *L. fortunei,* the available evidence points at precisely this type of mechanism. After having been introduced in the freshwater estuarine area through the Río de la Plata estuary in ballast water, some adult specimens traveled upstream attached to the hulls of ships and barges that regularly sail on the Paraná-Paraguay rivers as far north as Cáceres (Brazil), over 2500 km upstream from the estuary (Boltovskoy et al. 2006). A similar dispersion vector has been found very important for other freshwater byssate mussels (Minchin et al. 2002; Karatayev et al. 2007b). Once established upstream, seeding the rest of the waterway with downstream drifting larvae was a natural and effortless outcome (see Chapter "Colonization and Spread of *Limnoperna fortunei* in South America" in this volume).

Admittedly, attachment to boat hulls (waterborne or carried upstream overland; Fig. 1b) is not the only vector possible. In Japan, where inland boat traffic is very limited, upstream transportation of *L. fortunei* is probably associated with fish culturing activities (Nomura et al. 2008; see Chapter "Colonization and Spread of *Limnoperna fortunei* in Japan" in this volume). Mussels can also be transported in mud caught in the limbs, wings, feathers, or fur of insects, amphibians, birds, or aquatic mammals (as shown for other freshwater invertebrates: Anastácio et al. 2014), or even in the stomachs of fishes that are known to egest intact animals (Belz et al. 2012), but these mechanisms are likely rare and ineffective for long-distance transport (Johnson and Carlton 1996).

An additional human activity which may have further facilitated geographic expansion of *L. fortunei,* particularly in areas where hard substrata are scarce, is modification of the coastline through the construction of docks, piers, spur dikes, groynes, pilings, breakwaters, revetments, rock armors, gabions, quay walls, etc., as well as deployment of buoys and other waterborne structures. In some areas, these objects are the only hard and stable substrate available for mussels, and although the populations they can harbor are comparatively small, they can be important as seeding areas or stepping stones for further expansion.

The Importance of River Length

Planktonic larvae are clearly advantageous for downstream dispersal. However, in order to benefit from their free-swimming veligers, reproducing adults must have reached safe areas far enough from the river mouth for their larvae to complete development before being flushed into the sea. For populations restricted to the middle or lower river reaches, drifting larvae represent a significant risk. Surface current speeds in major rivers of the Río de la Plata watershed can be around 1–3 m/s. At these speeds larvae, which spend around 10 to more than 20 days in the plankton (Cataldo et al. 2005), can drift downstream over 2000 km before they are ready to settle on a substratum. Thus, large, navigable rivers are more likely to succeed in maintaining reproducing populations of golden mussels than shorter, nonnavigable waterways. Models based on various environmental variables (calcium concentration, temperature, dissolved oxygen, pH, total suspended solids, slope, elevation, flow accumulation, flow direction, precipitation, etc.) simulating prospective spread of this mussel yielded interesting results (Kluza and McNyset 2005; Cohen 2009; Oliveira et al. 2010a, b; Campos 2014; Campos et al. 2014), but constraints associated with limitations imposed by planktonic larvae have not been explicitly addressed. For example, some models (Kluza and McNyset 2005; Campos 2014) indicate that *L. fortunei* could colonize areas along the western coast of South and Central America (Fig. 2b), most of which are characterized by short rivers with high current speeds. However, the above considerations suggest that this is unlikely.

Admittedly, the history of the geographic spread of *L. fortunei* shows that invasions are not restricted to large rivers. The mussel has been successfully colonizing Japan since 1990 (Kimura 1994), where rivers are short and mostly located in areas with steep topographic gradients (Yoshimura et al. 2005; Japan Commission on Large Dams 2009; see Chapter "Colonization and Spread of *Limnoperna fortunei* in Japan" in this volume). Research on expatriation of planktonic organisms by currents, dubbed as the "drift paradox," shows that in order to counterbalance downstream advection thus enhancing the chances of persistence, organisms rely on lateral diffusion, high dispersal rates, and the availability of refugia in hydrodynamically dead zones (Reynolds and Carling 1991; Reckendorfer et al. 1999; Speirs and Gurney 2001; Pachepsky et al. 2005). Local settings, such as embayments, inlets, or backwater areas where water movement is minimal, could significantly improve the ability of *L. fortunei* to survive in short, exorheic rivers, but it is probably the presence of dams that has had the greatest influence on the mussel's chances of establishing self-sustaining populations under these adverse conditions.

The presence of lentic waterbodies in the course of a river is particularly significant, as they serve as refugia for seeding populations (Havel et al. 2005), especially for large species with longer life cycles unable to compensate for downstream transit (Speirs and Gurney 2001; Pollux et al. 2004; Pachepsky et al. 2005; Allan and Castillo 2007). *L. fortunei* has managed to establish self-sustaining populations in these short, fast flowing, and turbulent Japanese rivers because most of them are punctuated by dams and reservoirs. Japan has more than 2600 dams higher than 15 m, and over 60,000 smaller irrigation ponds and dams (Japan Commission on Large Dams 2009). In terms of the number of dams, Japan occupies the fourth place in the world, and is third in number of reservoirs per unit surface (0.71/100 km^2; Yoshimura et al. 2005). Most Japanese rivers have been modified by man, chiefly for flood control and water use for agriculture and other purposes (Japan Commission on Large Dams 2009), thus creating thousands of refugia with significantly higher water residence times where planktonic organisms thrive best (Søballe and Kimmel 1987; Karatayev et al. 2007b).

In addition to dams, canals and pipelines connecting different rivers and watersheds have also greatly facilitated the spread and persistence of *L. fortunei* in Japan. The country is crossed by 400,000 km of man-made canals, chiefly for irrigation purposes, that connect most watersheds (Ministry of Agriculture, Forestry and Fisheries 2003; see Chapter “Colonization and Spread of *Limnoperna fortunei* in Japan” in this volume).

Why Did the Golden Mussel Take So Long to Start Expanding?

Given the fast and apparently effortless colonization of South America, an intriguing question is: “Why didn’t it happen earlier?” While growing trade with Southeast Asia must play an important role (Darrigran and Pastorino 1995; Karatayev et al. 2007b), it is conceivable that the successful ~ 1990 colonization of the Río de la Plata watershed was but one of many previous attempts when mussels were seeded in the area, but whose offspring were entirely swept into the ocean (Boltovskoy et al. 2006). The notion that there might have been several unsuccessful introductions, both in South America and in Japan, before the mussel finally managed to establish local reproductive populations, is supported by biogeographic data (Boltovskoy et al. 2006), and by genetic evidence (Ito 2011; Zhan et al. 2012; Ghabooli et al. 2013) that suggest that there have been multiple successful introductions.

Ballast water-related invasions by overseas freshwater organisms are faced with the problem that most freshwater ports serving ocean-going ships are located in estuarine areas, in the vicinity of and upstream from brackish and saline waters. This may explain why freshwater invasions like those of the golden mussel do not occur more often. Interestingly, the unintentional introduction of *L. fortunei* in South America is exceptional in that practically all other freshwater nonindigenous species recorded in Argentina are the result of deliberate introductions associated with aquarium trade, angling, and aquaculture (Baigún and Quirós 1985; Vigliano and Darrigran 2002).

Future Spread

Since its first records in Hong Kong, and especially after having been found in Japan and South America in the early 1990s, many reports have forecast that *L. fortunei* will rapidly spread northwards to Central and North America, and elsewhere (Morton 1975; Ricciardi 1998; Boltovskoy et al. 2006; Karatayev et al. 2007b; Oliveira et al. 2010b). Comparison of its current geographic range with estimates of its potential worldwide distribution (Fig. 1) suggests that we are only witnessing the beginning of its expansion. However, almost 25 years after it invaded the Río de la Plata watershed, it has not yet been recorded in the next large South American basin—the Amazon, which is considered highly vulnerable and largely suitable for the mussel (Boltovskoy et al. 2006; Oliveira et al. 2010b). In Japan, the geographic expansion of the mussel’s range is relentless but slow (see Chapter “Colonization and Spread of *Limnoperna fortunei* in Japan” in this volume). This may suggest that interbasin transfer is a more important bottleneck than originally anticipated (Karatayev et al. 2007b), but it is very unlikely that watershed limits will deter further colonization indefinitely. In South America, the Cuiabá River, a tributary of the Paraguay River, which has been colonized by *L. fortunei* at least since 2000 (Boltovskoy et al. 2006) is only 150 km from the Teles Pires River in the Tapajós River basin within the Amazon watershed (Calazans et al. 2013). Both this proximity and the fact that the Amazon is navigable to ocean liners of virtually any tonnage, including ships with ballast water from infested ports along the Paraná-Uruguay-Río de la Plata waterways and the Guaiba basin (where compliance with international water ballast regulations in rather loosely enforced; Boltovskoy et al. 2011), suggest that sooner or later *L. fortunei* will invade this basin and, eventually, other freshwater bodies worldwide.

Concluding Remarks

Bivalve traits that evolution allowed reluctantly to persist for millions of years tolerating the existence of such “outlyers” as *L. fortunei,* suddenly became a major asset for expanding a historically small geographic range when man created interbasin dispersion corridors and supplied upstream transportation vectors (Fig. 1).

These conclusions cast a shadow of doubt on the widely accepted assumption that the success of *L. fortunei* stems from the fact that it is particularly well adapted to freshwater habitats. While it obviously does possess many traits which became instrumental for its impressive geographic expansion (e.g., low requirements of calcium, very high fertility, comparatively short life span, early sexual maturation, extended reproductive period, etc.; Morton 1973, 1975), before man’s intervention planktonic larvae and the requirement of hard substrata were most probably major limitations, rather than advantages.

Interestingly, this conclusion conflicts with the notion that the success of invasive species is due to their having the same general suite of traits exhibited by most successful organisms in general, irrespective of their alien or native status (Thompson and Davis 2011). While this has been shown for many invasives (Thompson et al. 1995), alteration of Earth by man is changing the adaptive value of traits acquired in the course of millions of years of evolution in pristine environments.

When contrasted with those of many other species, invasions by golden and zebra mussels indicate that invasive success may be associated with quite dissimilar intrinsic and environmental variables, and that unifying concepts in invasion ecology are far from foolproof. Lumping all invasive species in an attempt to synthesize unique settings that explain success and effects on the ecosystems is probably not only questionable, but may also be counterproductive. As noticed by Gurevitch and Padilla (2004, p. 474), “If we determine that domestic livestock are causing widespread plant extinctions, it is far more informative to focus on the impact of domestic livestock than to say, more generally, that aliens are causing these extinctions.”

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