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GLOBAL RANGE EXPANSION OF THE ASIAN MUSSEL *LIMNOPERNA FORTUNEI* (MYTILIDAE): ANOTHER FOULING THREAT TO FRESHWATER SYSTEMS

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The Asian freshwater mussel *Limnoperna fortunei* was first documented as a major fouling pest when it colonized Hong Kong's water supply system in the late 1960s. It has since fouled municipal waterworks and power plant cooling systems in Korea, Japan, Taiwan, and most recently, in South America. Dense accumulations of byssally-attached mussels obstruct flow in water conduits, causing impacts similar to those of the Eurasian zebra mussel (*Dreissena polymorpha*). *Limnoperna* has demonstrated potential for global range expansion through the oceanic transport of its planktonic larvae in ship ballast tanks. Therefore, unless effective controls are imposed upon ballast-water transport, the mussel will continue to invade and impact aquatic systems on other continents. Given that shipping traffic from both Asia and South America has already resulted in recent introductions of exotic bivalves to the USA, a future North American invasion by *L. fortunei* is highly probable.

Keywords: freshwater fouling; *Limnoperna*; *Dreissena*; zebra mussel; exotic species

INTRODUCTION

Problems posed by freshwater fouling organisms have grown in tandem with the development of water supply systems worldwide (Morton, 1979; Callow, 1993). Fouling bivalves, in particular, have become serious threats to the normal functioning of both aquatic ecosystems and water intake systems, as demonstrated by the recent invasion histories of the Eurasian zebra mussel

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Dreissena polymorpha and the Asiatic clam *Corbicula fluminea*; both of these species have caused profound ecological and technological impacts in North America (McMahon, 1983; MacIsaac, 1996). The introduction of these and other fouling pests can be traced to human activity (Morton, 1979), and increased international trade will likely accelerate their global spread (Carlton & Geller, 1993; Jenkins, 1996).

Advance information on harmful invasive species would provide valuable criteria for developing control measures and allocating resources to maximize detection (Willan, 1987; Jenkins, 1996). Among the species that should be carefully monitored is the Asian freshwater mytilid mussel *Limnoperna fortunei* (Dunker), which has become a significant fouling pest on two continents in recent decades. This paper reviews the biology and invasion history of *L. fortunei*, and evaluates its potential range expansion into North America.

SYSTEMATICS AND BIOLOGY

Limnoperna fortunei has been reported under a variety of synonyms, including *L. siamensis* and *L. lacustris* (Morton, 1973); other probable synonyms include the riverine mussels *L. depressa* (Brandt & Temcharoen, 1971) and *L. supoti* (Brandt, 1974). An Australian mussel, *Xenostrabus securis*, which invaded Japanese estuaries in the 1970s, was initially misidentified as a new subspecies, *L. fortunei kikuchii* (B Morton, personal communication). This plethora of species synonyms reflects the high phenotypic variation that allows *Limnoperna* to thrive in a broad range of aquatic environments.

L. fortunei is strikingly similar to the Eurasian zebra mussel in terms of its heteromyarian shell morphology, byssal attachment to solid substrata, gregariousness, rapid growth, short life span, and possession of a planktonic (veliger) larval stage (Morton, 1973). Adult *L. fortunei* are dioecious, with two-thirds of the population being female, and reproduce at least once or twice per year. In northern China, *L. fortunei* spawns from September to November when water temperatures are 16–21°C; in southern China, spawning occurs during June–July at 27–28°C and again during January–February at 16–17°C (Morton, 1977, 1982). Gametes are discharged into the water column for external fertilization. Veliger larvae are produced during extended spawning periods of up to 9 months (Morton, 1977). The mean duration of the larval stage probably falls within the range of other mytilids, *i.e.* 30–70 d (Ackerman *et al.*, 1994). The mussels reach sexual maturity in the first year of a 2–3 yr lifespan, attain a maximum shell length of 30–40 mm (Morton, 1977, 1982), and form dense aggregations (*c.* 10,000–80,000 mussels m^{-2}) on any firm substrate (Morton, 1975; Huang *et al.*, 1981; Darrigran & Pastorino, 1995). In reservoirs, they are abundant at depths ranging from a few centimeters to several meters, and preferentially colonize cryptic and shaded surfaces in byssal-bound aggregations (Morton, 1977; Uryu *et al.*, 1996).

CURRENT DISTRIBUTION AND INVASION HISTORY

Unlike other mytilid mussels, which occur primarily in marine and estuarine environments, *L. fortunei* is widely distributed in freshwater lakes and rivers throughout southeast Asia. Owing to its broad salinity tolerance (0–12‰; Deaton *et al.*, 1989), *L. fortunei* is also common in the brackish waters of estuaries (Huang *et al.*, 1980, 1981; Darrigran & Pastorino, 1995). It occurs naturally in China (Miller & McClure, 1931; Tchang *et al.*, 1955; Morton, 1973; Huang *et al.*, 1980, 1981), Thailand (Mizuno & Mori, 1970; Brandt, 1974; Temcharoen, 1992), Korea (Uryu *et al.*, 1996), Laos, Cambodia, Vietnam, and Indonesia (Brandt & Temcharoen, 1971; Brandt, 1974). Within the last 30 years, it has been unintentionally introduced to Hong Kong (Morton, 1975), Japan (Nakai, 1995), Taiwan (Morton, personal communication), and South America (Darrigran & Pastorino, 1995).

In the late 1960s, *L. fortunei* invaded the Hong Kong potable water supply system as a result of the intake of planktonic larvae in raw water diverted from a tributary of the Pearl River. Within 2–3 years, it achieved a population density of 11,000 mussels m^{-2} in tunnels and pumping stations of the China pipeline, and established a permanent breeding population in the Plover Cove reservoir (Morton, 1975).

In the early 1990s, *L. fortunei* was discovered in Lake Biwa and the Ibi and Nagara rivers in Japan (Nakai, 1995; Uryu *et al.*, 1996). The mussel also occupies the upper section of the Yodo River, where it fouls hydroelectric installations (Morton, personal communication). In 1991, *L. fortunei* became established in the Rio de la Plata estuary in Argentina, by the transport of larvae in ballast water released by Asian cargo ships (Darrigran & Pastorino, 1995). Within 2 years, dense colonies of up to 82,150 mussels m^{-2} were found at littoral sites along a ~ 100 km coastline of the estuary (Darrigran & Pastorino, 1995). More recently, *L. fortunei* colonized the Uruguay and Paraná rivers, where it occurs at maximum densities of $>50{,}000$ mussels m^{-2} (Boltovskoy, personal communication). Peak larval concentrations of 21,000 m^{-3} were recorded in the upper Rio de la Plata estuary in December 1997 (Boltovskoy, personal communication). *Limnoperna* became a serious fouling problem in the municipal water treatment facility at La Plata in 1994 (Darrigran, 1997) and, subsequently, in several power plants that draw water from the Paraná River and the Rio de la Plata estuary (Boltovskoy, personal communication).

PROJECTED FUTURE INVASIONS

L. fortunei possesses many of the characteristics attributed to successful invaders (Ehrlich, 1989), *i.e.* a short generation time, phenotypic plasticity, gregariousness, abundance in its native habitat, wide environmental tolerance, and commensal association with human activity (Brandt, 1974; Morton, 1973, 1977, 1982; Deaton *et al.*, 1989; Uryu *et al.*, 1996). Previous invasion success suggests that, if given the opportunity, *Limnoperna* will colonize North American waters. The likely mode of invasion will be ballast water release of larvae from Asian freighters visiting Pacific American ports, resulting in the establishment of pioneer populations in the lower reaches of rivers. Every year, Pacific ports receive hundreds of cargo ships carrying thousands of tons of ballast water with high concentrations of bivalve larvae (Carlton & Geller, 1993). The net tonnage of ballasted ships from Asian ports has increased over the last three decades (Cordell *et al.*, 1992), coinciding with the introduction of a variety of aquatic fauna, including several Asian molluscs (Carlton, 1992; Crooks, 1996). Because mytilid larvae remain planktonic for over a month (Ackerman *et al.*, 1994), *L. fortunei* veligers should survive an average two-week voyage between Asian and North American ports (Carlton & Geller, 1993). Indeed, bivalve larvae from the ballast water of ships travelling between North America and Asia have been observed to settle readily in laboratory culture tanks (Chu *et al.*, 1997). The entry of *L. fortunei* into the USA could also result from repeated visits by South American freighters at ports along the Gulf of Mexico, a dispersal pathway that has apparently already facilitated the introduction of a mytilid (*Perna perna*) from the Atlantic coast of South America to Texas (Hicks & Tunnell, 1993). The likelihood of unintentional introductions of *L. fortunei* and other aquatic species may be reduced by recent regulations requiring ships to exchange ballast water in the open ocean, but such measures are compromised by non-compliance and frequent incomplete ballast-water exchange (Locke *et al.*, 1993). Because *L. fortunei* tolerates high salinities (Deaton *et al.*, 1989), its larvae may remain in residual water after partial, or even complete exchange.

Once established in North America, downstream dispersal of planktonic larvae and overland dispersal of byssally-attached juveniles and adults (*e.g.* on trailered recreational boats) may facilitate the rapid spread of *L. fortunei*, as has been the case for *D. polymorpha* (Johnson & Carlton, 1996). Mussels may also be transported long distances upriver by attaching externally to commercial vessels (Keevin *et al.*, 1992). Based on its thermal tolerances (Table I), *L. fortunei* appears capable of colonizing a broad range extending from the lower North American Great Lakes into Central and South America. In its native range, *L. fortunei* occurs in water bodies whose surface temperatures regularly exceed 30°C for prolonged periods (Mizuno & Mori, 1970). Low water temperatures and short summer seasons would limit the distribution and size of mussel populations at high temperate latitudes, unless *L. fortunei* develops a tolerance for cold temperatures (like the Asian clam *Corbicula fluminea*; Janech & Hunter, 1995). The potential North American range of *L. fortunei* would thus overlap with *D. polymorpha* and *C. fluminea* in the southern USA, adding to the impacts of these macrofouling pests and complicating control strategies.

Moreover, *L. fortunei* is a threat to habitats that are inhospitable to *D. polymorpha* (Table I). While *D. polymorpha* occurs primarily in calcium-rich, mesotrophic waters (McMahon, 1996), *L. fortunei* can colonize soft-water habitats, heated waters, and organically-enriched waters subject to periodic hypoxia (Morton, 1977; Deaton *et al.*, 1989; Darrigran & Pastorino, 1995). For example, dense colonies of *L. fortunei* have been

TABLE I A comparison of environmental tolerance limits for *L. fortunei* and *D. polymorpha* populations[†]

	L. fortunei	*D. polymorpha*
Salinity, ‰	0–12	0–5
Calcium, $mg\,l^{-1}$	≥3	≥12
pH	≥6.4	≥7.4
Temperature, °C		
Adult survival	8–35[‡]	2–30
Larval development	16–28	12–24
Oxygen, $mg\,l^{-1}$	≥1.0	≥1.8

[†] Data sources for *L. fortunei*: Mizuno & Mori, 1970; Morton, 1975, 1977, 1982; Deaton *et al.*, 1989; Darrigran & Pastorino, 1995; Boltovskoy, personal communication. Data sources for *D. polymorpha*: Spidle *et al.*, 1995; McMahon, 1996.

[‡] This range is based on confirmed occurrences; the true tolerance limits are probably wider.

found in highly-polluted waters near raw sewage outlets along the Rio de la Plata (Boltovskoy, personal communication).

POTENTIAL IMPACTS

Fouling of Water Supply Systems

The entrainment of planktonic larvae in intake currents allows *L. fortunei* to invade municipal and industrial water supply systems rapidly. In pipelines and conduits, *L. fortunei* initially colonizes crevices, seams and joints, and then spreads from these foci to cover adjacent surfaces with clusters of byssally-attached mussels (Morton, 1973, 1975; Uryu *et al.*, 1996). Mussel growth within intake systems is likely to be rapid because they provide a continuous supply of food and oxygen and a stable environment free of predators (Jenner & Janssen-Mommen, 1993). The attachment and dense accumulation of shells reduces flow through narrow pipelines and may cause expensive clean-up costs or plant shut-downs. Reservoirs, navigation locks, dams, and other artificial structures can also become intensely fouled (Morton, 1979; Huang *et al.*, 1981; Temcharoen, 1992; Uryu *et al.*, 1996). High larval densities and rapid colonization magnify these fouling problems; in the Plover Cove reservoir, densities of newly settled mussels increased by 1000-fold between 1972 and 1974 to form a breeding population that reinfects Hong Kong's water supply system annually (Morton, 1977).

Control methods are not well-documented. Application of $1.0\,\mathrm{mg\,l^{-1}}$ chlorine over a period of several days at 2–3 month intervals is effective in keeping conduits clear, although dense fouling may require an initial high dose, *e.g.* $200\,\mathrm{mg\,l^{-1}}$ (Morton *et al.*, 1976). Chemical applications should be planned after a spawning period to prevent newly settled mussels from recolonizing the system. Ecologically-sensitive alternatives to chlorine are currently being tested in South America; ongoing studies have found that some non-oxidizing molluscicides known to be effective for *Dreissena polymorpha* will induce dislodgement or death of *L. fortunei*, but at significantly higher doses and/or exposure times (Boltovskoy, personal communication). Heat treatment is a method that has proven effective in controlling mussel fouling (Jenner & Janssen-Mommen, 1993; Rajagopal *et al.*, 1995) and may be useful in reducing *L. fortunei* infestations in power plants, provided that such treatment is compatible with plant design. However, the most effective treatment program would likely integrate a combination of physical and chemical applications (Jenner & Janssen-Mommen, 1993).

Ecological Impacts

Most freshwater ecosystems around the world have evolved in the absence of fouling bivalves and are sensitive to their impacts, as demonstrated by the North American *D. polymorpha* invasion (MacIsaac, 1996). The high filtration rates of mytilids (200–3000 ml min^{-1}; Bayne *et al.*, 1976) suggest that suspension feeding by dense *L. fortunei* populations will affect phytoplankton standing stocks and nutrient cycling. *L. fortunei* is well-adapted for efficiently removing seston from flowing waters (Morton, 1973), and thus may alter the normal functioning of riverine ecosystems (*cf.* Phelps, 1994; Caraco *et al.*, 1997) and outcompete native suspension feeders (*cf.* Strayer & Smith, 1996). Documented impacts of other introduced bivalves suggest that the filtration activity of a dense *L. fortunei* population would reduce phytoplankton biomass and turbidity levels (promoting prolific macrophyte growth), suppress zooplankton populations (limiting food availability to larval and planktivorous fish), increase sedimentation rates, and alter contaminant cycling in lentic habitats and large rivers (Phelps, 1994; Kimmerer *et al.*, 1994; MacIsaac, 1996; Caraco *et al.*, 1997). Additionally, the respiration of a dense mussel bed may cause a severe reduction in dissolved oxygen in flowing waters (Effler & Siegfried, 1994).

As a thin-shelled mollusc, *L. fortunei* may provide a food source for a variety of molluscivorous fishes and waterfowl, and alter the diets and distributions of these predators (*cf.* Wormington & Leach, 1992; Morrison *et al.*, 1997). Furthermore, because mussels rapidly bioaccumulate contaminants, *L. fortunei* may transfer metals and organochlorines to higher trophic levels (*cf.* de Kock & Bowmer, 1993; MacIsaac, 1996). In the Plover Cove reservoir, carps (*Cyprinus* spp.) feed on *L. fortunei*, but not exclusively (Morton, 1975). Owing to the mussel's high recruitment rate (Morton, 1977), predation is unlikely to control its abundance.

Dense colonization of hard substrata by *L. fortunei* would increase benthic macroinvertebrate abundance by providing habitat structure and biodeposits (*cf.* Ricciardi *et al.*, 1997). Conversely, because *L. fortunei* readily attaches to other molluscs (Brandt, 1974), it may reduce native mussel populations by intense fouling similar to that caused by *D. polymorpha* (Ricciardi *et al.*, 1995, 1996). For example, in the Paraná River (Argentina), *L. fortunei* uses the introduced Asiatic clam *C. fluminea* as substrate; in some cases, the byssal threads of *L. fortunei* seal the clam's valves shut, effectively smothering it to death (Boltovskoy, personal communication). With 12% of *c.* 300 described species presumed extinct and an additional 60% endangered, unionid clams are the most imperiled faunal group in

North America (Ambramovitz, 1996; Ricciardi *et al.*, 1998). The introduction of *L. fortunei* could thus have adverse consequences for North American molluscan biodiversity, particularly if it invades softwater habitats that serve as refugia for threatened clam populations against *D. polymorpha* infestation.

CONCLUSIONS

The recent invasion history of *L. fortunei*, coupled with a life cycle that is strikingly similar to that of *D. polymorpha*, identifies this mollusc as a harmful aquatic pest that should be carefully monitored. The potential global spread of *L. fortunei* has been demonstrated by its trans-oceanic dispersal from Asia to South America. Increased shipping traffic resulting from enhanced trade with Pacific Rim and South American nations makes a North American invasion by this opportunistic species probable within the next decade, and emphasizes the need for effective controls on ballast-water discharge in ports. European and North American experiences with *D. polymorpha* may prove useful in guiding efforts to control *L. fortunei* fouling.

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