



Review Paper

What we know and don't know about the invasive golden mussel *Limnoperna fortunei*

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Abstract An overview of the knowledge of the invasive freshwater golden mussel (*Limnoperna fortunei*) is presented, with particular emphasis on the voids of our current understanding of its ecology and its effects on the systems invaded. *L. fortunei* started spreading northwards in China after 1960, and ~1990 it invaded Japan and South America. These invasions fostered a strong increase in the interest in the mussel. However, coverage of its biology, ecology, and impacts has been very uneven. Geographic distribution and spread, seasonal dynamics and methods for controlling its fouling in industrial plants and other human-made facilities have received most of the

attention, while many other important issues (e.g., multiannual density changes, competition with native organisms, predation by invertebrates, reptiles, birds, and mammals) lag far behind. The effects of the golden mussel on environmental traits and resident organisms have been investigated almost exclusively in laboratory or mesocosm settings, but extrapolation of these results to waterbody scales is contentious, mainly because system-wide densities are largely unknown. The information available suggests that most environmental impacts of *L. fortunei* are mixed, context- and stakeholder-dependent, with both positive and negative effects. In contrast, its impacts on human-made facilities and infrastructure are clearly always negative and costly.

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Introduction

In this section, a general overview of the state of knowledge of the invasive bivalve *Limnoperna fortunei* (Dunker) (the golden mussel) is presented. The focus of this article is identifying the issues that have been covered (occasionally in excess), and those on which the information available is still scant or practically nil.

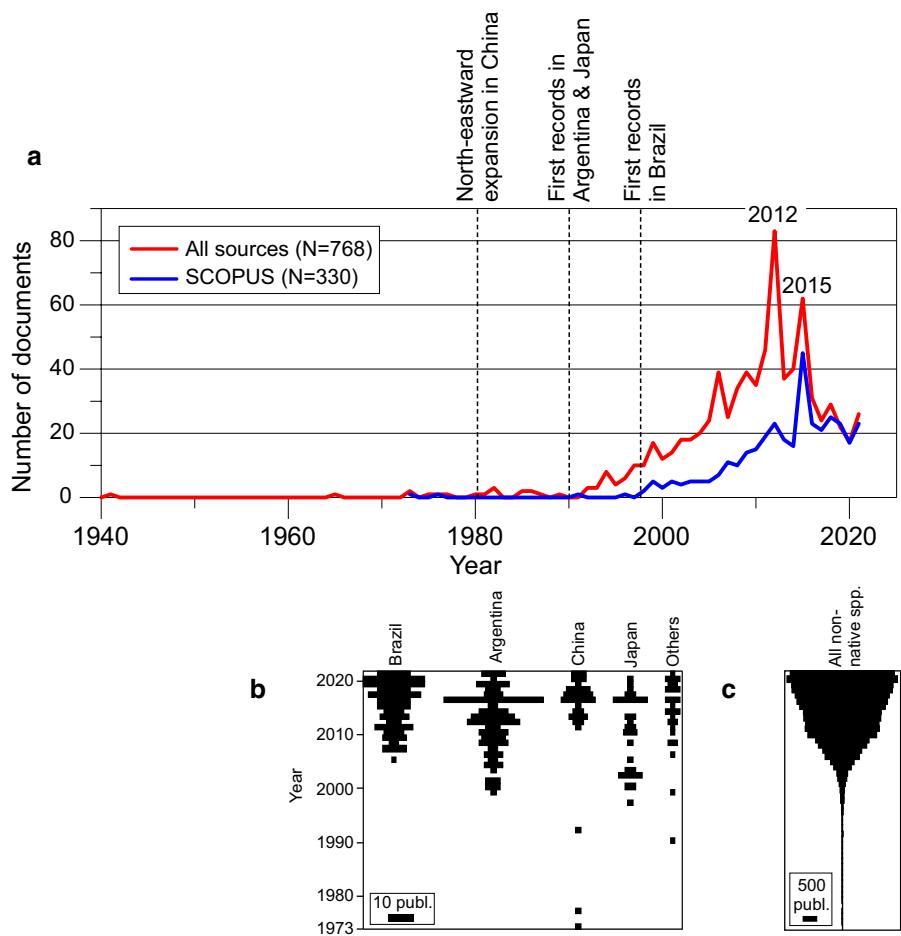
A few multi-authored books covering various aspects of the knowledge of the golden mussel have been published in the last decades (Darrigran & Damborenea, 2006, 2009; Mackie & Claudi, 2010; Mansur et al., 2012b; Boltovskoy, 2015b). In the most recent of these (Boltovskoy, 2015b) much of the

literature encompassing most aspects of the studies on *L. fortunei* was covered by a team of 40 experts from Argentina, Brazil, Canada, China, Italy, Japan, and the USA. The present review is largely based on the information summarized in these publications supplemented with information that appeared after 2014 (~20% of the overall total in 2021), or was not covered in these reviews.

Research efforts, timeline and subjects: an overview of the literature

As of September 2021, the SCOPUS database included 330 documents centered on *L. fortunei*, and a total of 5642 citations (Fig. 1a). However, when all sources are considered (including institutional reports, news articles, theses, patents, web pages, meeting presentations, books and book sections, etc.),

Fig. 1 **a** Number of documents on *L. fortunei* per year since 1973. Data according to our own records (“All sources”), and according to SCOPUS based on (“*Limnoperna fortunei*” or “Golden mussel”) in the title or keywords. “All sources” includes journal (indexed and non-indexed) articles, meeting presentations, book chapters, books, and miscellaneous documents (brochures, reports, news articles, theses, patents, web pages, etc.). **b** Numbers of documents per year produced since 1973 by country of affiliation of the first author (based on SCOPUS). **c** Total numbers of documents per year produced since 1973 on non-native species (based on SCOPUS, using the search string (“invasive species,” or “non-native species” or “nonnative species” or “alien species”), in the title, abstract or keywords. SCOPUS searches performed on 8 September 2021



this number doubles (768; Fig. 1a). The latter figure, however, clearly overestimates the research performed on the mussel because much of the “grey literature” includes preliminary results which are subsequently published in journals (see also Barbosa, 2014, for a review of the literature between 1982 and 2012). As opposed to Argentina, Brazil, and Japan, where the surge in the numbers of publications is clearly associated with the mussel’s introduction (Fig. 1a, b), in its native country (China), interest in this species started later, around 2010 (Fig. 1b). Overall, however, research on *L. fortunei* grew in time, as did research on non-native organisms in general (Fig. 1c).

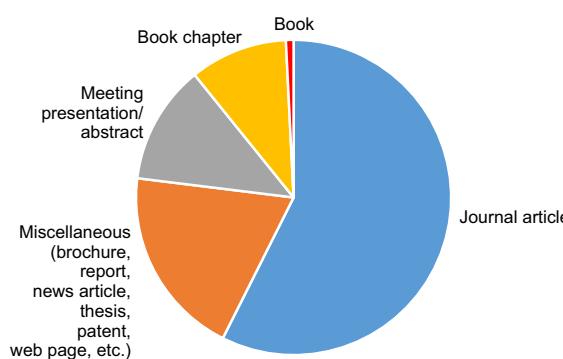
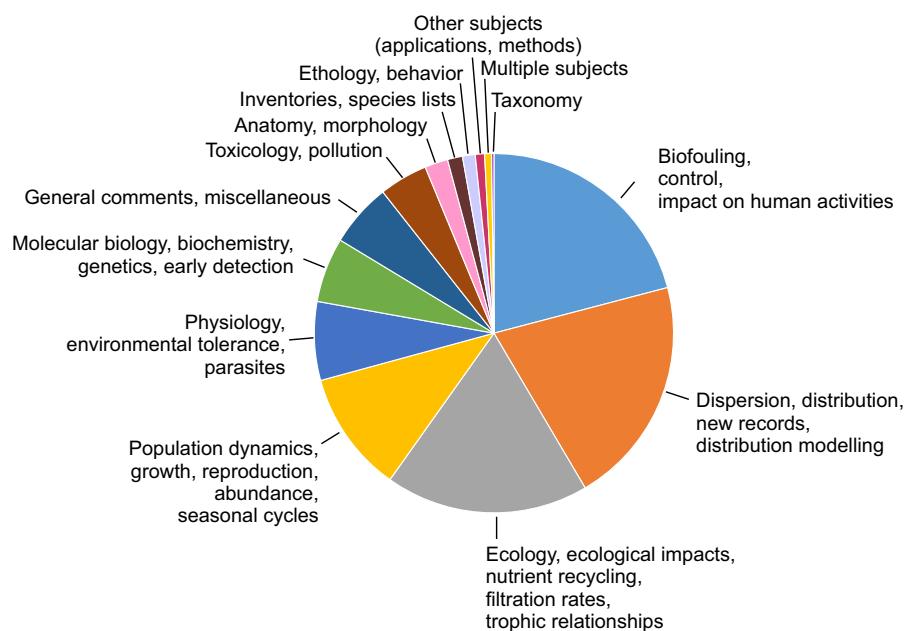


Fig. 2 Proportions of documents on *L. fortunei* according to source type, based on all sources ($N=789$; see Fig. 1)

Fig. 3 Proportions of documents centered on various aspects of the studies on *L. fortunei* based on all sources ($N=789$; see Fig. 1). Documents covering several subjects are included in more than one category



Over half of the publications produced have been journal articles, followed by miscellaneous items, meeting abstracts and book chapters (Fig. 2). The subjects most intensively studied have been biofouling control methods, geographic distribution, ecology (mostly trophic relationships), population dynamics, and physiology (chiefly environmental tolerance to temperature, salinity, suspended solids, etc., often in the context of control methods) (Fig. 3). Judging from the country of affiliation of the first author (which largely represents that of all contributing authors), Brazil and Argentina contributed around 70% of the documents, followed by China (13%), and Japan (10%). The remaining ~8% was contributed by eight other countries (Fig. 4).

Until 1999, the cumulative number of documents was ~7 (SCOPUS), averaging ca. 0.2 documents per year. In the late 1990s the number of reports starts growing swiftly. These trends are obviously related to the introduction of the mussel in Argentina and Japan around 1990 (Matsuda & Uenishi, 1992; Pastorino et al., 1993), and in Uruguay, Paraguay and Brazil a few years later (Oliveira et al., 2015), and particularly to its biofouling impacts on human-made infrastructure (Boltovskoy et al., 2015c; Rebelo et al., 2018). The 2012 peak (Fig. 1a, “All sources”) is due to the inclusion of ~40 chapters of the book edited by Mansur et al. (2012b; which also covers several

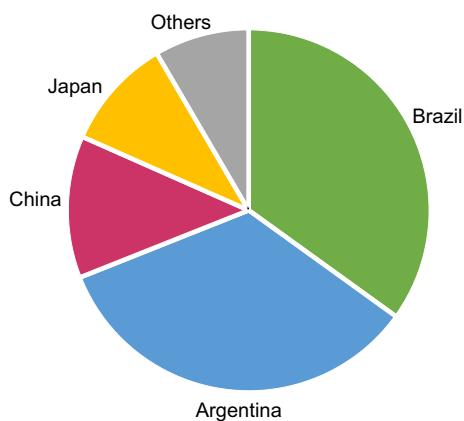


Fig. 4 Proportions of documents on *L. fortunei* based on the affiliation country of the first author. With the exception of the United States of America, for most countries the affiliation of the first author is usually the same as that of the coauthors. Others includes Australia, Canada, Germany, Ireland, Italy, Russia, Uruguay, and the United States of America. Several papers not included in SCOPUS (and in the graph) were produced by first authors from Cambodia, India, Korea, Paraguay, Taiwan, Thailand, United Kingdom, and Vietnam (see Fig. 1)

other freshwater molluscs introduced in Brazil; not included in SCOPUS), while the one in 2015 reflects the 28 chapters of the book edited by Boltovskoy (Boltovskoy, 2015b; restricted to *L. fortunei*), but numbers stabilize again thereafter at ca. 20 documents per year (Fig. 1a).

The stabilization in the number of reports after ~2010 (Fig. 1a) is probably due to a combination of factors. First, the presence of this invasive species has gradually ceased being a novelty, and several key issues of its biology and effects on the ecosystems invaded (in particular its reproduction and population dynamics, its control methods in industrial facilities, and a few others) had already been covered in a number of studies (Table 1, Fig. 3). Second, industry, which is clearly the most negatively impacted sector (see “**Impacts on human-made infrastructure**” below), has been learning how to cope with filter and pipe clogging by mussel colonies, either by adjusting maintenance operations, and/or by implementing control strategies (chiefly chemical; about 20% of the reports produced so far focus on the control of *L. fortunei* in industrial facilities; Fig. 3). Third, the geographic spread of the mussel has proven to be much slower than anticipated (see “**Future spread**” below),

which has also reduced interest of academia and the media in *L. fortunei* (although apocalyptic essays still make headlines, e.g., Moutinho, 2021).

Although *L. fortunei* is native to southern China and has spread to Indochina (Cambodia, Vietnam, Laos, Thailand) in historical times (Morton & Dinesen, 2010), and to Korea probably around 1980 (Xu, 2015), interest in this mussel has been very limited in these invaded Asian countries. In China, the northwards spread of its range due to the construction of large water transfer pipelines (e.g., the South-to-North Water Transfer project), which facilitated the geographic expansion of the mussel (Zhan et al., 2015) has fostered an increase in studies (Fig. 1b). Obviously, these figures have to be interpreted in the context of the growing number of publications on introduced species worldwide (>20% per year between 1973 and 2010, but decreasing to ~4% after 2010; Fig. 1c).

Taxonomy, systematics, and evolution

Asian freshwaters have been colonized by representatives of the Mytiloidea, *L. fortunei* and *Sinomytilus harmandi* (Rochebrune) relatively recently and on two occasions from a common ancestor (Morton, 2015a; see also Kartavtsev et al., 2018; Morton et al., 2020).

Throughout Asia, since the 1800s *L. fortunei* (originally erected as *Volsella fortunei* by Dunker in 1856) (Dunker, 1856) has been redescribed under several names, including *Dreissena siamensis* Morelet, *Limnoperna lacustris* Morelet, *L. depressa* Brandt and Temcharoen, *Limnoperna lemeslei* Rochebrune, *Limnoperna siamensis* Morelet, *Limnoperna supotii* Brandt, *Modiola cambodgensis* Clessin, *Modiola lacustris* Martens, *Modiola siamensis* Morelet, *Mytilus martensi* Neumayer), which are currently considered as junior synonyms (Morton & Dinesen, 2010; Morton, 2015b; Ng et al., 2020). However, on the basis of the sequences of three DNA markers, *L. siamensis* from Thailand (Mun River) was recently concluded to be a valid species, which split from the *L. fortunei* lineage at the Miocene-Pliocene boundary (Sokolova et al., 2021). *Limnoperna coreana* Park and Choi, was described as a new species from the Baengnyong Cave, Korea, in 2008 (Park & Choi, 2008), but was subsequently synonymized

Table 1 Summary of the degree of knowledge of different aspects of the biology, ecology and effects of *L. fortunei* in Asia and in South America. Degree of knowledge, 0: Poor or nil; 1: Marginal; 2: Fair; 3: Good

Subject	Degree of knowledge	Remarks (A: Asia; SA: South America)
Taxonomy, systematics, and evolution	2	Analyzed in a few surveys (A)
Anatomy and morphology	2	Fairly well covered (chiefly A)
<i>Current distribution and future spread</i>		
Current distribution	2.5	Good for SA, Japan, and China, almost no data for the rest of Asia
Potential future distribution, modelling	0.5	Anticipated fast dispersion not occurring, models of spread perform poorly
<i>Population dynamics, reproduction, seasonality, and abundance</i>		
Population dynamics, seasonality	3	Many surveys in most of its range
Larval development	2.5	Good for tropical and subtropical areas; no data for temperatures below 15–20 °C (A & SA)
Fecundity	0	No information
Density (selected sites)	3	Numerous assessments for small selected spots and experimental substrates (A & SA)
Density (system-wide)	0	Almost no system-wide data
Long-term (multiannual) changes	0	Few data for larvae only (SA), practically no data for adult populations
<i>Ecological effects of <i>L. fortunei</i></i>		
<i>Effects on the water-column</i>		
Nutrient recycling (experimental)	2	Data from laboratory and mesocosm studies moderately abundant (SA)
Nutrient recycling (system-wide effects)	0	Almost no system-wide data
Grazing on bacteria	0	No information
Grazing of phytoplankton (experimental)	2	Several data from laboratory and mesocosm studies, field data scarce
Grazing of phytoplankton (system-wide effects)	0	Almost no system-wide data
Enhancement of cyanobacterial blooms	2	Several experimental studies, some field data available (SA)
Grazing of zooplankton (experimental)	1	Few data
Grazing of zooplankton (system-wide effects)	0	Almost no system-wide data
Grazing selectivity (experimental)	2	Several reports
Grazing selectivity (system-wide effects)	0	Almost no system-wide data
Macrophytes and macroalgae	0	Practically no data
<i>Effects on the benthos</i>		
Sediment accumulation rates and properties	0.5	Some laboratory and mesocosm data, no information on system-wide effects
Abundance and diversity of benthic invertebrates	1	Most data from experimental settings, field-based information scarce
Periphytic communities	1	Some data from experimental settings, field-based information nil
Overgrowth of other organisms	0	Several isolated observations, quantifications of damage practically nil
Competition with native organisms	0	No data
<i>Predation by other organisms</i>		
Predation by invertebrates	0	Presumably high, but direct evidences practically nil
Predation by larval fishes	2	Several reports for experimental and field data
Predation by adult fishes	3	Many reports, most with quantitative data
Predation by reptiles, birds and mammals	0	Almost no data
Physiology, environmental tolerance	2	Data available for some major environmental parameters

Table 1 (continued)

Subject	Degree of knowledge	Remarks (A: Asia; SA: South America)
Parasites	1	Some data for Asia, information for SA restricted to one virus. Impacts unknown
Genetics	2	Data on the genome and genetic diversity available (A & SA)
Behavior	3	Several reports including field and experimental data (A & SA)
<i>Impacts on human-made infrastructure</i>		
Impacts on industrial infrastructure facilities	2	Many observations on facilities impacted, very scarce reliable data on economic impacts
Impacts on fish farming	1	Few reports from Brazil only, no data on economic impacts
<i>Management</i>		
Early detection	3	Several publications, mostly on molecular-based methods
Control	3	Many reports on a wide variety of methods
Manual and mechanical cleaning	3	Well covered, most data based on <i>Dreissena</i> spp.
Antifouling materials and coatings	2	Several studies available, chiefly from Japan
Chemical methods	3	Several studies available, chiefly from Argentina & Brazil
Other techniques	2	Several studies available, most nonviable in industrial facilities
<i>Uses of the golden mussel</i>		
Sentinel organisms	2	Several studies available (biaccumulation of toxicants, etc.) (SA)
Other uses	0	Very scarce data (SA)

Values are based on the authors' general appraisal of the literature surveyed, rather than on a quantitative indicator (e.g., number of publications)

with *L. fortunei* (<https://www.molluscabase.org/aphia.php?p=taxdetails&id=868376>). *Limnoperna fortunei kikuchii* Habe, erected by Habe (1981), was found to be a misidentification of *Xenostrobus securis* (Lamarck) (also invasive in Japan) by Kimura et al. (1999).

The external morphology of *L. fortunei* is unique among freshwater bivalves, and, therefore, unlikely to be misidentified. However, its similarity with the brackish mytilid *Mytella charruana* (d'Orbigny) is striking. *M. charruana* is native to the eastern coast of South America from Venezuela to Argentina, and in the Pacific from Mexico to El Salvador, and invasive in southeastern USA, Philippines, Singapore, Thailand, and India (Calazans et al., 2017). However, unlike *L. fortunei*, *M. charruana* does not tolerate freshwaters, and only occasionally co-occurs with the golden mussel in estuarine conditions with frequent and strong salinity changes (Giberto & Sardiña, 2009).

Anatomy and morphology

An exhaustive account of the anatomy and functional morphology of *L. fortunei* was produced by Morton (1973), subsequently expanded in 2015 (Morton, 2015b). Further details on various organs were also reported, in particular the gills (Paolucci et al., 2014b; Paolucci, 2021; Fraga Freitas et al., 2021), the foot and the byssus (Andrade et al., 2015; Li et al., 2018a; b), and the shell (Luo et al., 2006; Montaldo & Rojas Molina, 2014; Nakamura Filho et al., 2014), often aimed at investigating strategies for mitigating the mussel's adhesion in industrial facilities (see Ohkawa & Nomura, 2015, and references therein).

Current distribution and future spread

Current distribution

L. fortunei is native to the Pearl River basin (China), located at the southernmost border of the country's mainland (Figs. 5, 6a). It was recognized as a fouling pest in the municipal water supply system of

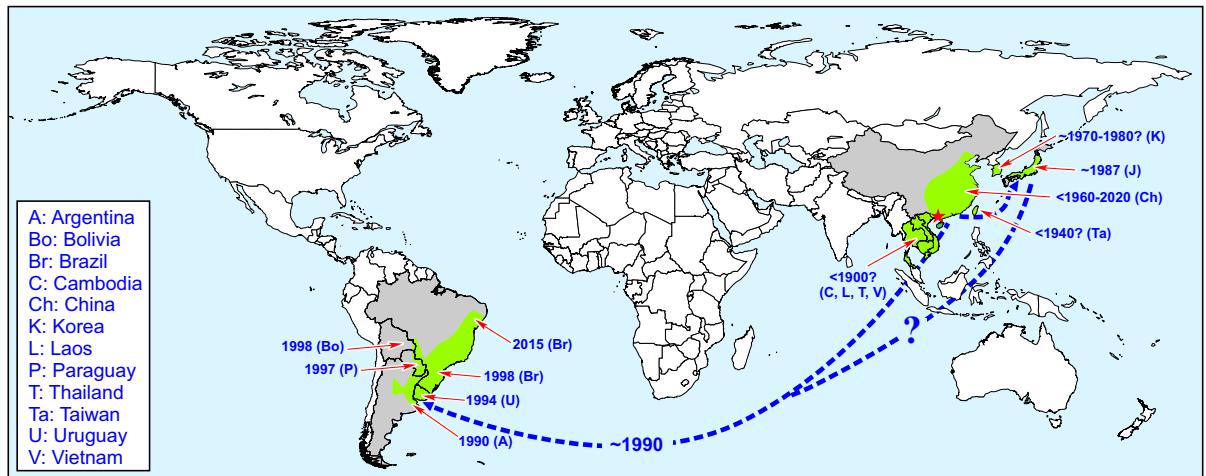


Fig. 5 Worldwide invasive ranges of *L. fortunei*. Red star denotes native area (the Pearl River Basin, China). Gray: countries invaded; light green: areas invaded (in some cases, as in Indochina and Korea, presence of the mussel is restricted

to some basins). Blue arrows denote probable entry routes. Labels denote approximate years of introduction and country/region names. See Figs. 6, 7 and 8 for details

Hong Kong around 1965 (Morton, 1975). *L. fortunei* initially invaded the estuaries of the neighboring Fujian and Zhejiang Regions' River Basins and the northern Yangtze, Huaihe, Yellow, and Haihe River Basins (Fig. 6a) via coastal shipping traffic (Xu, 2015; Fig. 6b). Before 1976, the species was already present in at least five provinces in the Yangtze River Basin (Jiangsu, Anhui, Jiangxi, Hunan, and Hubei; Liu & Wang, 1976). Shortly afterwards (1978–1981), it was found farther upstream in Chongqing in a large number of the sites surveyed (Zeng et al., 1981), and in the Haihe River Basin in 1980 (Tianjin City; Fig. 6b) (Huang, 2008). Adult mussels were found in the lower latitude Huaihe River Basin (Luohu City, Henan province) in May 1985 (Zhao et al., 1986). These records suggest that unwitting invasions of this species within mainland China started rather early. Ghabooli et al. (2013) compared the genetic diversity of *L. fortunei* populations between Asia and South America concluding that the former might have experienced a much higher introduction effort—presumably indicating a longer invasion history—than the latter. Currently, *L. fortunei* has spread considerably upstream in the above-mentioned major river basins. It is present in at least up to the third-order tributaries of the Yangtze River (Xia, unpublished), and Zhengzhou City (Fig. 6b) in the Yellow River Basin (Xu, 2015). Farther upstream dispersal is highly likely

because of increasing anthropogenic activities and climate change effects (see below).

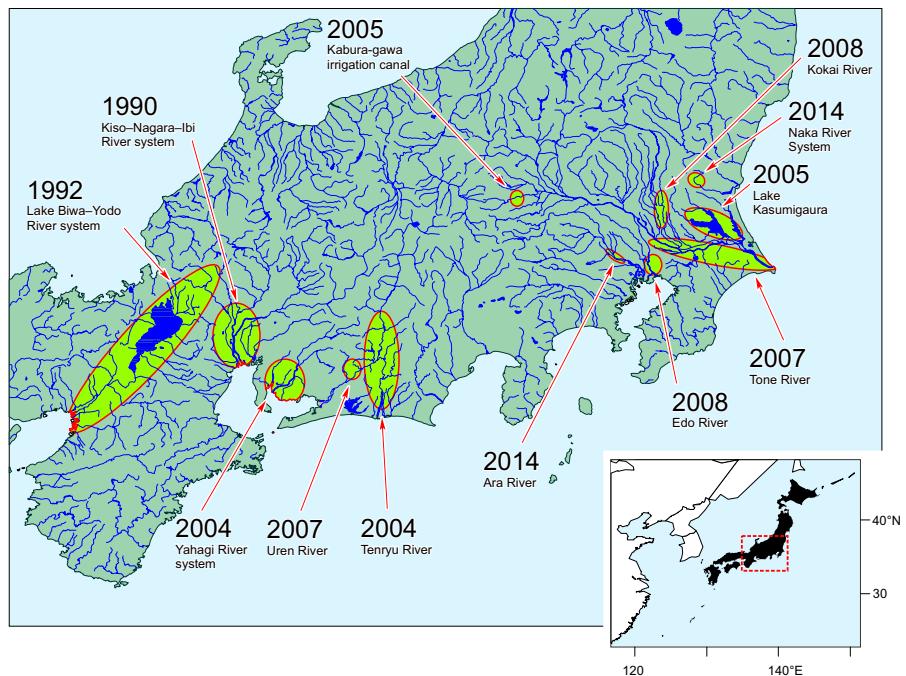
Unlike several Asian countries (i.e., Cambodia, Vietnam, Laos, Thailand), where *L. fortunei* was probably introduced from China before the twentieth century, Taiwan, where it was introduced in 1940 (Kuroda, 1941), and Korea, where it was first noted in ~1970 or 1980 (Yoo, 1969; Morton & Dinesen, 2010; Xu, 2015) (Fig. 5), this species' spread in China (Xu, 2015), Japan (Ito, 2015, 2016), and South America (Oliveira et al., 2015; Barbosa et al., 2016; Hermes-Silva et al., 2021a, b) has been described in detail (Figs. 6, 7, 8). Actually, >20% of the literature on this mussel is centered on new geographic records and its areal spread (Fig. 3). Although many of these publications are of minor significance for defining its distribution limits, as they only mention sightings along waterways at sites between previously known occurrences, or offer general comments on previous knowledge, they can be important for distribution modeling and for understanding how new sites are colonized. The CBEIH (Centro de Bioengenharia de Espécies Invasoras de Hidrelétricas, Brazil) maintains a georeferenced database with most records of the mussel, with emphasis on Brazil (<https://base.cbeih.org/>).

Several investigations also analyzed the potential colonization sources and routes, and the



Fig. 6 **a.** Major river basins in mainland China. **b.** Distribution of *L. fortunei* in China and other southeastern Asian countries. Updated from Xu (2015)

Fig. 7 Distribution of *L. fortunei* in Japan; years indicated are usually those of the first record, actual colonization times may have been earlier. Updated in November 2021 by Dr. Kenji Ito from Ito (2015)



phylogeography of the golden mussel using traditional (Morton & Dinesen, 2010; Morton et al., 2020) and molecular tools (Tominaga et al., 2009; Zhan et al., 2012; Borges, 2014; Paolucci et al., 2014b; Ito, 2015; Nakano et al., 2015a; Borges et al., 2016; Uliano-Silva et al., 2016; Duarte et al., 2018; Furlan-Murari et al., 2019; Ferreira et al., 2020; Morton et al., 2020; Ludwig et al., 2021).

Artificial waterways often act as invasion highways (e.g., Galil et al., 2008; Zhan et al., 2015). The navigable Grand Canal (China), which was constructed in sections since the fifth century B.C., linking Beijing and Hangzhou, has strongly promoted regional economy and communication. However, it might have also have played a critical role in facilitating the inter-basin dispersal of this species. Some sections of the canal are now the east route of the South-to-North Water Diversion Project (Fig. 6b), which has been shown to facilitate fish invasions (Qin et al., 2019).

Increased connectivity in aquatic ecosystems can favor the spread of *L. fortunei* since it fosters propagule pressure (Zhan et al., 2015; de Amo et al., 2021). In recent years, many large artificial water diversion aqueducts were constructed to improve the redistribution of water resources and mitigate water scarcity in northern China. In particular, the middle

route of the South-to-North Water Diversion project (Fig. 6b), which links the Yangtze, Yellow, Huaihe, and Haihe River Basins, has been suggested to facilitate species invasions, including *L. fortunei* (Xu, 2015; Zhan et al., 2015; Zhao et al., 2019; Xia et al., 2021a). The dominantly concrete surface of the canal provides a more suitable habitat for *L. fortunei* than the east route (which mainly utilizes natural waterways for water conveyance), posing a greater threat of *L. fortunei* invasion to recipient waterbodies. Construction of large dams on major rivers, notably the Yangtze, may also facilitate the upstream dispersal of *L. fortunei*, because the resulting lentic waterbodies can provide “stepping-stone” habitats due to reduced water flow and enhanced shipping activity (Johnson et al., 2008). The poleward spread of *L. fortunei* is of critical concern worldwide, and low water temperatures have been expected to restrict its potential distribution (Mackie & Brinsmead, 2017). However, presently, its northern invasion front is beyond 40°N, and the probabilities of colonizing even higher latitude areas are high because it can survive in cold waters (Xia et al., 2021a; see below).

In Japan, *L. fortunei* was recorded in the late 1980s to early 1990s (Nishimura & Habe, 1987; Matsuda & Uenishi, 1992; Kimura, 1994), spreading eastwards since the 2000s (Ito, 2015, 2016; Kanazawa,

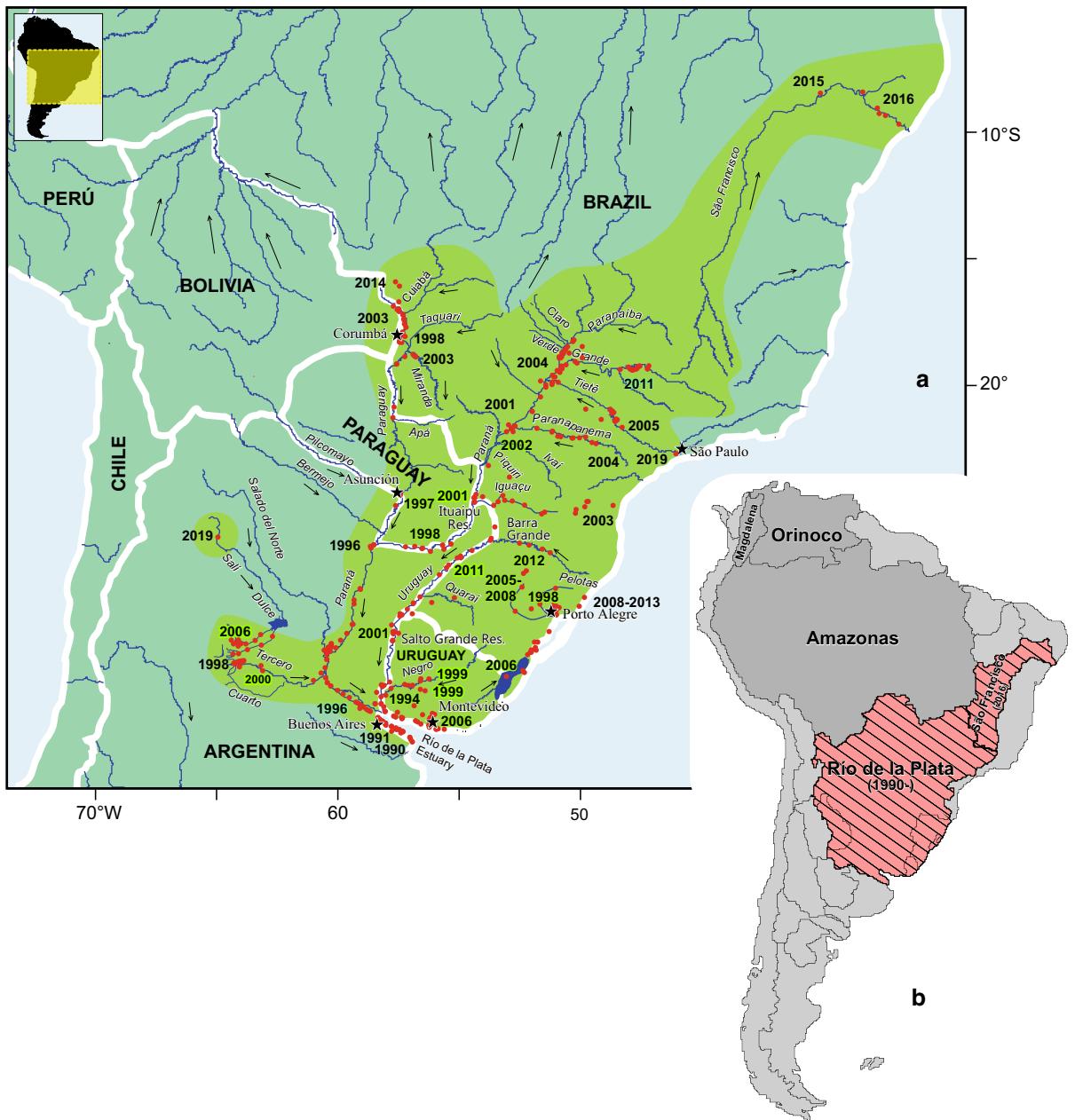


Fig. 8 Distribution of *L. fortunei* in South America. **a** Records (red circles) and selected dates of first sightings throughout the Río de la Plata and São Francisco watersheds, and several small inland and coastal basins. Lighter green denotes colonized area. White lines denote country limits, stars are major cities, river names are in italics, arrows denote direction of water flow. Notice that in several cases earlier records are located farther upstream than later ones; this may be due

2015; Ito & Shibaike, 2021; Nakano et al., 2015a). Its introduction has been attributed to accidental contamination of imports of the freshwater clam *Corbicula*

to random sampling, or to “jump dispersal” events where adult mussels are carried upstream attached to the hulls of commercial ships or barges, detach and produce offspring that subsequently colonize downstream sites (see Boltovskoy et al., 2006). **b** Major South American watersheds. Colonized area is hatched; basins where *L. fortunei* was not recorded are in gray; darker gray denotes basins with presumably highest risk of colonization

fluminea (Müller) from China for human consumption (Nishimura & Habe, 1987; Ito, 2015; Nakano et al., 2015a).

Its introduction in South America (Argentina), through the Río de la Plata Estuary (Pastorino et al., 1993), is thought to have occurred around 1990 via ballast water containing larvae and/or adults being released by oceanic ships that operate in several ports of the lower Paraná River. Zhan et al. (2012) analyzed invasive populations in South America and found that ship-mediated “jump dispersal”, followed by downstream natural dispersal, was the main dispersal pattern of *L. fortunei*. Subsequently it was recorded in Uruguay (1994), Paraguay (1997), and Brazil and Bolivia (1998) (Darrigran & Damborenea, 2006). The spread could have occurred overland (attached to trailered leisure boats), with ballast water of commercial local or international ship traffic, and, in navigable waterways, primarily through the attachment of adults to the hull and other underwater structures of ships and barges allowing upstream dispersal, and subsequent detachment and production of downstream drifting larvae (Boltovskoy et al., 2006; Oliveira et al., 2015) (the “jump-dispersal” mode, MacIsaac et al., 2001) (Fig. 8). Geographic spread associated with sand transport, sports fishing boats and gear, and live fishes (as ingested but not digested individuals, subsequently egested alive elsewhere) was assessed in southern Brazil, but is probably of minor relevance as live mussels in fish guts are almost absent (Belz et al., 2012). Sand transport and sports fishing were assumed to be potentially important vectors, although the numbers of live mussels detected were also generally low (Belz et al., 2012). However, its introduction in the Río Tercero Reservoir (Argentina; Boltovskoy et al., 2006), and some smaller endorheic basins (e.g., the El Cadillal Reservoir, in central Argentina: Anonymous, 2019) has most probably occurred through the attachment to leisure boats trailered overland from other colonized waterbodies.

Genetic studies in Japan and in South America suggest that in both cases there might have been several introduction events (Tominaga et al., 2009; Tominaga & Kimura, 2012; Ghabooli et al., 2013; Ludwig et al., 2021).

The current distribution and invasion history of the golden mussel in China, Japan and South America are fairly well known, but there are few records from Korea, Cambodia, Vietnam, Laos, and Thailand.

Future spread

Projections of the future spread of *L. fortunei* have been frequently mentioned in passing in many surveys (Ricciardi, 1998), and have also been the subject of ad hoc investigations, both locally and globally. These studies used various modeling approaches based on potential donor/recipient ports and shipping networks, and/or interpretations of the mussel’s tolerance limits to environmental factors. Among the latter, usually temperature, Ca concentrations, and dissolved oxygen (see “[Physiology, environmental tolerance](#)” below), and occasionally up to 19 bioclimatic variables (Xia et al., 2021a) (the “environmental match” method; Ito & Takimoto, 2013; Campos et al., 2014; Sieracki et al., 2014; Karatayev et al., 2015; Osawa & Ito, 2015; Campos et al., 2016; Beletsky et al., 2017; Kramer et al., 2017; Mackie & Brinsmead, 2017; Barbosa et al., 2018; Kvistad et al., 2019; Lucy & Tricarico, 2020; Petsch et al., 2021; Xia et al., 2021a) were used. Minimum winter temperatures have often been assumed to limit the poleward expansion of the mussel (Mackie & Brinsmead, 2017; Oliveira et al., 2010d), but Xia et al. (2021a) found that it can survive at least 108 days in water <5 °C, and even near-freezing conditions, which confirms previous records in Japan and Korea at temperatures between 0 and 5 °C (Choi & Shin, 1985; Magara et al., 2001). Moreover, in situ cage experiments at the current north invasion front (the Shisanling Reservoir, China) suggest that the reservoir could be a source of further northwards spread if it is connected with colder waterbodies (Xia et al., 2021a).

Although many global studies have suggested that *L. fortunei* will be present worldwide in the near future (although with low probability in cold and arid areas), and its spread in the Río de la Plata basin and several other minor basins in Argentina, Brazil, and Uruguay has been fast (Boltovskoy et al., 2006; Oliveira et al., 2015), the last new record for a major South American basin was in the São Francisco River, Brazil (Barbosa et al., 2016). More recently (2019), it was reported from two new extreme locations: the Santos-São Vicente and Bertioga Estuary-Bay Complex (Paraná River basin, Brazil; Senske et al., 2019), and in the El Cadillal Reservoir (Argentina), which is part of an endorheic basin draining into the Mar Chiquita hypersaline lake (Anonymous, 2019). Thirty years after its introduction to this

subcontinent, its predicted spread beyond the major Río de la Plata and São Francisco watersheds and several minor ones colonized years ago, in particular into the Amazon and Orinoco basins, has not yet been recorded (although this might also be due to the paucity of research efforts). Neither has it been found in Europe and Central and North America, as predicted by many of the above-mentioned studies up to over 15 years ago.

This suggests that our understanding of the drivers that favor the golden mussel's spread is still poor, and that the variables used in the models predicting its range expansion are equivocal or insufficient. Most studies used the tolerance limits of *L. fortunei* to water physical and chemical trait extremes, in particular water temperature (Mackie & Brinsmead, 2017; Xia et al., 2021a), but other important constraints have rarely been addressed. Among the latter, there are several key factors that deserve closer attention. Suspended sediment loads are a major limiting factor (Darrigran et al., 2011; Tokumon et al., 2015) that has usually been ignored. Propagule pressure, as indicated by the connectivity between waterbodies (de Amo et al., 2021) and the frequency of ocean-going ship-connections between potentially donor and recipient freshwater ports, is another. The length and navigability of the rivers in the recipient area is also a major constraint. Most freshwater ports that service oceanic traffic are located close to the ocean, which means that, unless the mussels can travel farther upstream, their planktonic larvae are bound to be flushed out into the ocean and permanent populations will not succeed in establishing (Boltovskoy, 2015a). Nevertheless, the presence of lotic habitats (wetlands, lakes, reservoirs) along relatively short and fast-flowing rivers may serve as seeding spots that preclude the mussels from being extirpated (Boltovskoy, 2015a; Nakano et al., 2015a). Most of the rivers on the Pacific side of South America, as well as those on the Atlantic side south of Buenos Aires, many of which had been predicted to host future introductions, are relatively short and/or non-navigable, which makes them unlikely to be vulnerable to sea-borne (ballast water) invasion events.

In short, although the current geographic distribution and the invasion history of *L. fortunei* are reasonably well known in parts of Asia and in South America, our capabilities of forecasting its future spread

are limited, and so far the performance of modeling attempts is contentious.

Reproduction, population dynamics, seasonality, and abundance

Fecundity

The fecundity of *L. fortunei* has not been estimated so far. We do not know how many eggs females produce in each reproductive event, how many of these are fertilized, and what proportion reaches the adult stage. Some indirect data are available from experimental studies (Sylvester, 2006), but they are few and imprecise. In the laboratory, D. Cataldo (unpublished) induced spawning of the mussel recording up to ~7500 eggs per female.

Larval development

The first descriptions of *L. fortunei*'s larval development were produced by Choi & Kim (1985) and Choi & Shin (1985) on samples from Korea, and subsequently refined with data from Argentina (Ezcurra de Drago et al., 2006) and Brazil (Santos et al., 2005; Mansur et al., 2012a). However, since all these studies were based of field-collected samples, the timing of each larval stage was undefined. Cataldo et al. (2005) induced spawning of adults in the laboratory and followed the development of the larvae at three water temperatures (20, 25 and 28 °C), which allowed detailed descriptions of morphological changes during metamorphosis, as well as the time it takes the larvae to transition from one stage to the next (egg, trochophore, straight-hinged veliger, umboned veliger, plantigrade), and to reach the settling (plantigrade) stage. The time from fertilized egg to plantigrade varies between ~12 days (at 28 °C), to ~20 days (at 20 °C) (summarized by Cataldo, 2015a). No data on larval development at lower temperatures, which would be useful for assessments of its spread towards higher latitude areas, are available.

Mortality at the larval and earliest juvenile stages is very high, reaching >90% (Sylvester, 2006; Nakano et al., 2017). Nakano et al. (2017) concluded that only 4% of the field-collected larvae reach the plantigrade stage.

Population dynamics and seasonality

The reproductive seasonality and population dynamics (maturation, growth, cohort analysis, longevity) are also among the most intensively studied subjects, with around 40 reports published between 1977 and 2021, covering periods between a few months to >15 years. These investigations used histological methods (gonadal maturation; Boltovskoy et al., 2015b; Xu et al., 2015b; Dei Tos et al., 2016; Giglio et al., 2016), or estimates of temporal changes in larval outputs and/or settling rates of early juveniles, usually on artificial substrates (Boltovskoy et al., 2015b; Duchini et al., 2018; Ernandes-Silva et al., 2017; Nakano et al., 2017; Somma et al., 2020; Ayroza et al., 2021). Gonadal maturation cycles and larval densities show significant differences, but these are most likely due the fact that while the former are indicative of the behavior of isolated mussel clusters, larval densities point at population-wide trends (Boltovskoy et al., 2015b).

The reproduction of the mussel is chiefly driven by temperature. Cataldo and Boltovskoy (2000) concluded that, in areas where winter water temperatures drop below 15 °C, reproduction starts at ~16–17 °C, a threshold that has been generally confirmed in subsequent studies (Boltovskoy et al., 2015b). Larval densities in the water-column show consistent seasonal trends chiefly related to water temperature. Although the larval numbers reported are quite variable, with occasional peaks exceeding 100,000 ind./m³ (Darrigran et al., 2007; Nakano et al., 2010a), in South America monthly means during the periods of highest larval outputs normally range around 3,000–4,000 ind./m³ (Brugnoli et al., 2011; Boltovskoy et al., 2021a; Fabián et al., 2021) and, occasionally, up to >80,000 ind./m³ (Somma et al., 2020). In Japan, where the reproductive period is significantly shorter, peak values are often high also (>80,000 ind./m³; Nakano et al., 2010a). At any rate, instantaneous larval density values are less informative than long-term trends because larval numbers can change in abundance hourly over fivefold in a 24 h period (Boltovskoy et al., 2015b), and change significantly as a function of time elapsed after colonization (Canzi et al., 2005; Pestana et al., 2008; Mata, 2011), as well as other factors, such as cyanobacterial blooms, depth, dissolved oxygen levels, food availability, and

flow speed (Nakano et al., 2010a; Boltovskoy et al., 2013; Pessotto & Nogueira, 2018).

In the Southern Hemisphere (Argentina, Brazil, Uruguay), at water temperatures between 10–28 °C and 20–30 °C, the reproductive period extends for up to 8–9 months, with maxima in the Spring–Summer and early Autumn, and minima in June to September (Boltovskoy et al., 2015b). In waterbodies where temperature is above 20 °C year-round larval density drops can be less marked, yet they also occur during the winter (Canzi et al., 2005; Eilers, 2006; Mata, 2011). In Thailand, at water temperatures between 24.5 °C and 34 °C, recruitment of juveniles on experimental substrates was reported to occur year-round at ~4,500 recruits/m² with generally small oscillations (Lheknim & Leelawathanagoon, 2014).

In Japan, at water temperatures of 5–25 °C, the reproductive period is shorter (2–4 months), but also coincides with the highest temperatures, in June–September, and larval densities are usually higher (Boltovskoy et al., 2015b; Nakano et al., 2015b). Its termination often coincides with temperature drops, but might also be associated with other factors, such as increases in water turbidity (Nakano et al., 2017).

A major departure from the above-described seasonal trend in larval outputs occurs in subtropical lentic waterbodies which are subjected to strong summer cyanobacterial blooms. On the basis of a series of nine years of weekly larval counts and six years of summer-autumn *Microcystis* spp. abundance estimates in Salto Grande Reservoir (Argentina-Uruguay), Boltovskoy et al. (2013) found that, during summers characterized by major toxic cyanobacterial blooms (which in turn are associated with low water discharge rates and enhanced stratification) mussel larvae are practically absent from the water-column. This contrasts sharply with all other South American lentic and lotic waterbodies with larval records for ≥1 year where strong cyanobacterial blooms do not occur. Although *Microcystis* spp. produces a large variety of chemicals that are noxious to many animals (Shirai et al., 1991), the mechanism responsible for these recruitment troughs is probably the toxicity of microcystin-LR to the larvae (which are killed at concentrations of 10–20 µg/L within 48 h), rather than to its effects on the adults (Boltovskoy et al., 2013).

Another seasonally recurring phenomenon that may wipe out *L. fortunei* populations are the extensive anoxic periods lasting several weeks when high

waters returning from the floodplain to the rivers contain little or no dissolved oxygen. These oxygen depletion events, known in Brazil as “dequada”, are typical of the upper Paraguay River, including the Pantanal wetland, and have been reported to strongly reduce or totally eliminate the mussels from these waterbodies (Oliveira et al., 2010b).

In fact, studies of the mussel’s reproductive seasonality, especially in South America, are abundant and, with the exception of some special situations like those described above, additional surveys are unlikely to contribute significantly to the subject.

Growth and longevity have also been examined in multiple studies, mostly based on experimental surveys with artificial substrates (Bonel & Lorda, 2015; Correa et al., 2015; Boltovskoy et al., 2015b; Musin et al., 2015; Nakano et al., 2015b; Xu et al., 2015b; Duchini et al., 2018; Nakano et al., 2017). These reports indicate that *L. fortunei* grows from ~ 10 to > 30 mm (shell length) during its first year, primarily depending on water temperature. Sexual maturation starts at 5–10 mm (Darrigran et al., 1999; Xu et al., 2015b). Adults are usually 20–30 mm in shell length, although specimens up to > 50 mm in size have been reported. The life span is around two years. Water temperature, including the season of each cohort, is the most important factor that determines growth rates. Other constraints such as pH, salinity, dissolved oxygen, suspended solids, chlorophyll a, flood-drought cycles, calcium concentrations, conductivity, pollution, turbidity, cyanobacterial blooms, food availability and intraspecific competition have been suggested to affect growth and reproduction (Morton, 1982; Oliveira et al., 2011; Callil et al., 2012; Lhekrim & Leelawathanagoon, 2014; Ernandes-Silva et al., 2016; Nakano et al., 2017; Ayroza et al., 2019), but, with the exception of pollution (Bonel et al., 2013; Bonel & Lorda, 2015) and blooms of toxic Cyanobacteria (Boltovskoy et al., 2013), the causality of these constraints has rarely been validated (Boltovskoy et al., 2015b).

Density

Densities of adult mussels have been reported in numerous publications with values as high as > 700,000 ind./m² (Spaccesi & Rodrigues Capitulio, 2012), but almost all are restricted to small (< 1 m²) sectors of artificial substrates, or natural sites usually

selected because of their dense colonization by the mussel. Assessments of densities over large areas are greatly complicated by the fact that the areal distribution of the colonies is highly patchy, colonized sites are underwater, and standard benthos samplers (grabs, corers) do not perform well on hard substrates (where mussels dwell). Novel techniques, such as underwater video imaging (Karatayev et al., 2018), are restricted to clear waters, which are uncommon throughout the geographic range of the mussel, especially in tropical-subtropical South America where Secchi disk depths are rarely > 10–20 cm. Thus, we do not know what the actual population densities are in almost all the waterbodies colonized. The only exceptions are probably those of a reservoir in central Argentina which was sampled extensively by SCUBA diving on a single occasion (mean for the entire reservoir: 959 ind./m²; Boltovskoy et al., 2009a), and some floodplain lakes associated with the Middle Paraná River, where mussels attached to the roots of floating aquatic plants were quantified (means for 19 samples from two lakes collected between Nov 2009 and Nov 2010: 982–2766 ind./m²; Musin et al., 2015).

The bottom of most waterbodies colonized by *L. fortunei* are dominated by loose sediments (clay, silt), where the mussel cannot establish. However, living and dead plant substrates (roots, rhizomes stolons, stems, leaves, trunks, branches) can host important colonies as well (Correa et al., 2015), which further complicates estimates of densities over large areas.

This lack of information on waterbody-wide densities strongly limits extrapolation of experimental studies of the mussel’s impacts on nutrient recycling, plankton grazing, trophic relationships with its consumers, and most other system-wide assessments.

Long-term population trends

The long-term (multiannual) dynamics of the mussel have been analyzed on the basis of larval counts for up to 9–15 consecutive years in a large South American reservoir (Boltovskoy et al., 2013; Boltovskoy et al., 2021a), and shorter periods (2–7 years) in a few other waterbodies (Canzi et al., 2005; Mata, 2011; Lhekrim & Leelawathanagoon, 2014; Somma et al., 2020). With the exception of some sharp increases shortly after introduction (Canzi et al., 2005), most of the longer surveys (Mata, 2011; Boltovskoy et al., 2013; Boltovskoy et al., 2021a) did not find clear

increasing or decreasing trends, which might suggest that usually the golden mussel is not subjected to the boom-bust cycles described for other invasive species, in particular *Dreissena polymorpha* (Pallas) (Strayer et al., 2017). It should be noted, however, that larval densities may be uncoupled with those of the adults (Hetherington et al., 2019; Strayer et al., 2019; Strayer, 2020), which casts doubts on larval densities as a reliable indicator of adult populations.

On the other hand, in the Río Tercero Reservoir (Argentina), which was invaded by *L. fortunei* around 1998, adult densities were high in 2006 (~900–1000 ind./m²) (Boltovskoy et al., 2009a) until ~2014, when the mussel started disappearing abruptly and its colonies, which covered densely hard substrates down to ~10 m, vanished almost completely (Mariñelarena et al., 2016). This strong decline was also noted in the much lower biofouling of raw water intake pipes and filters of the Embalse nuclear power plant that uses reservoir water for cooling purposes (R. Manera, pers. comm.). This mortality was tentatively attributed to summer blooms of another invasive species, the dinoflagellate *Ceratium* spp. (*C. furcoides* (Levander) Langhans, *C. hirundinella* (Müller) Schrank) (Mariñelarena et al., 2016), but the timings of *Ceratium* blooms and the decline of *L. fortunei* do not match well. Presently these populations are recovering vigorously (M. Hechem, pers. comm., 2020), but the reasons for this decline and subsequent recovery are unknown.

Mass mortality events have also been observed in Japan (Uchida et al., 2007), but the triggers involved are unclear.

There is practically no information for multiannual changes of adult *L. fortunei* densities, and the few reports available are imprecise and patchy (Darrigran et al., 2003). In the Lower Delta of the Paraná River, visual appreciation of the coverage of coastal revetments suggests that multiannual changes in golden mussel densities do occur, although no quantitative data are available. A comparison of the population densities on artificial substrates deployed in 2002–2004 and in 2013–2014 (~10 and 20 years after introduction, respectively) at the same site in the Lower Delta of the Paraná River indicates that both mussel numbers and the predation pressure on their colonies have increased in the time elapsed (Duchini et al., 2018).

In only one case, mussels first recorded in 2003 in the Piraquara I reservoir of southern Brazil, could not be found during surveys conducted after 2012. This result suggested that the initial *L. fortunei* colonization of this and other nearby waterbodies failed to prosper (Frehse et al., 2018).

Ecological effects of *L. fortunei*

The ecological effects of *L. fortunei* on ambient traits and local organisms attracted much research attention (Fig. 3). The subjects most frequently addressed were the effects of the mussel on nutrient recycling and grazing of phytoplankton, as well as its participation in the degradation of some herbicidal products, such as glyphosate (see “**Sentinel organisms**” below).

Almost all the information available on the ecosystemic effects of the golden mussel are based on laboratory and mesocosm experiments. While useful for further insights into actual ecosystem-wide effects, such extrapolations are subjected to a number of caveats. Among these, mussel densities over large areas, which are a major informational gap (see above), are of key importance. Further, as with most other organisms, the ecological effects of *L. fortunei* are highly context-dependent (Boltovskoy et al., 2021b), which complicates generalizations as effects change in space and time significantly.

A few attempts at forecasting the ecological impacts of the golden mussel within (de Ávila-Simas et al., 2019a) and without (Mackie & Brinsmead, 2017; Zhang et al., 2019) of its present distribution range have been attempted, but their conclusions have not been validated.

Effects on the water-column

Nutrient recycling

Practically all results published until 2014 (summarized in Boltovskoy et al., 2015a), generally confirmed by several subsequent studies, indicate that the presence of *L. fortunei* enhances nutrient recycling increasing the levels of dissolved P and/or N compounds in the water-column (Gattas et al., 2018; Silva & Giani, 2018) and in the sediments (Tokumon et al., 2018). On the other hand, microbial biofilms associated with the mussel’s shell were suggested to

decrease nitrate concentrations in the water (Zhang et al., 2014). All these studies were conducted in experimental settings (laboratory or mesocosms), and, therefore, their extrapolation to natural conditions is uncertain because actual system-wide effects depend on several variables which may differ from those used in the experiments (e.g., mussel densities, lateral advection, water residence times, etc.). The only waterbody for which long-term nutrient dynamics changes in association with the mussel have been surveyed is Río Tercero Reservoir (Argentina). This study (Boltovskoy et al., 2009a) suggested that after the spread of *L. fortunei*, ammonia, phosphates, total phosphorus, and total nitrogen increased in the water-column. Thus, while we do know that the golden mussel has an influence on nutrient concentrations, the significance of this effect on the waterbodies colonized, which is probably quite variable, needs much additional research.

Grazing of bacteria

L. fortunei has been reported to consume bacteria (Zhang et al., 2017b), and its use for the recovery of eutrophicated and biologically contaminated sites has been suggested (see “[Uses of the golden mussel](#)” below).

Grazing of phytoplankton

As with nutrients, practically all the data available are based on laboratory short-term (usually 1 to 24 h), and on mesocosm (up to 35 days) experiments, using either cultured phytoplankton (1–2 species at a time), or mixed plankton. With very few exceptions, actually ingested cells were not differentiated from those rejected in the pseudofeces. The clearance rates reported in ca. 10 studies (Boltovskoy et al., 2015a; Xia et al., 2020) for adult (~14–30 mm) mussels vary widely, from <1 to 29.5 mL/mg of tissue dry weight per h, or 4 to >700 mL/ind. This variability is clearly largely due to differences in the experimental settings used. “Normal” rates at optimum temperatures (~20–28 °C) for adult organisms are probably around 100–300 mL/ind./h, or ca. 7–8 mL/mg of tissue dry weight per h. For the planktotrophic larval stages, 15–32 µL/ind./h were reported (Gazulha, 2010).

Based on stable isotopes and fatty-acid analyses, (Zhang et al., 2017b) estimated that around 20–30%

of the mussel’s diet is based on plankton, ~60% on particulate organic matter, and ~10–20% on resuspended sedimentary organic matter. Among the phytoplankton, *L. fortunei* was found to prefer Chlorophyceae, Cryptophyceae, and Dinophyceae.

Again, the impacts of the mussel’s phytoplankton grazing on whole waterbodies is very poorly known. (Boltovskoy et al., 2009a) compared chlorophyll a and gross primary production for a 12-year period encompassing data obtained before and after the introduction of *L. fortunei* in the Río Tercero Reservoir (Argentina): both parameters declined after the introduction, but the difference was significant for primary production only. Also, some stretches of the Middle Paraná River have been noted to host lower phytoplankton densities after having been colonized by *L. fortunei* (Rojas Molina et al., 2015), but the data available are too sketchy to draw reliable conclusions.

Enhancement of cyanobacterial blooms

Several surveys found that *L. fortunei* consumes Cyanobacteria, including toxic strains of *Microcystis* sp. (Rückert et al., 2004; Gazulha et al., 2012a, b), but in experimental conditions the mussel has been shown to enhance their abundance (Silva & Giani, 2018), both by modifying nutrient availability, and by promoting the formation of colonies which are not consumed by the mussel (Cataldo et al., 2012). Cyanobacterial toxins have strong deleterious effects on human health and on aquatic organisms, including fishes and waterfowl (Paerl et al., 2001), and, paradoxically, they also kill *L. fortunei* larvae (Boltovskoy et al., 2013). Adult mussels have been reported to bioaccumulate cyanotoxins (Minillo et al., 2016; Oliveira et al., 2021), which can be transferred to their consumers and, eventually, to humans.

Grazing of zooplankton

Feeding of *L. fortunei* on zooplankton was reviewed by Rojas Molina et al. (2015) on the basis of samples from the Middle Paraná River, concluding that the mussel consumes >150 different animals which account, on average, for 96% of the ingested biomass (particulate organic carbon was not included in these assessments). Thus, in terms of energy, animals are probably much more important for the mussel than algae. Rotifers, small cladocerans (Chydoridae,

Bosminidae) and nauplii are the preferred food items, whereas copepods are negatively selected (Zhang et al., 2017b). Comparison of zooplankton densities in the Middle Paraná River during two periods previous to the introduction of the mussel (1971–1973 and 1981–1982), with 2004–2005 (after the introduction) suggests significant decreases, especially during the low-water periods, when zooplankton is typically more abundant (Rojas Molina et al., 2015). A significant decrease of zooplankton densities, probably due to grazing by *L. fortunei*, was also observed in mesocosm experiments (Braga et al., 2019).

The long-term series (1982–present) of zooplankton abundance data from Río Tercero Reservoir (Argentina) shows a noticeable drop since 2010 (Ardohain et al., 2014), which might be associated with its grazing by *L. fortunei* and/or the grazing of its food (phytoplankton).

In Salto Grande Reservoir (Argentina-Uruguay), the abundance of *L. fortunei* larvae, adult Cladocera and Copepoda has been monitored using weekly samples from 2004 to the present. Although this survey did not include a pre-invasion period (*L. fortunei* was first recorded in this reservoir in 2001), it likely covered the initial spread of the mussel throughout the reservoir. Between 2004 and 2019 the densities of mussel larvae varied widely, and were chiefly driven by summer troughs associated with strong blooms of Cyanobacteria, which have a major impact on reproduction or larval survival (Boltovskoy et al., 2013), but the overall trend was weakly and non-significantly increasing (Boltovskoy et al., 2021a). In contrast, Cladocera and Copepoda showed consistent decreasing trends, and although these trends were likely chiefly driven by water discharge rates, the effects of mussel grazing cannot be ruled out (Boltovskoy et al., 2021a).

Grazing selectivity

Grazing selectivity was analyzed in a number of experimental surveys but, as with feeding rates, the results differ significantly. Highest impacts are apparently on small (<1 mm) particles (Boltovskoy et al., 2015a; Frau et al., 2016), but significant throughout a wide range of sizes spanning <1 to >50 µm (Xia et al., 2021b). Among the zooplankton, animals <300 µm in size are positively selected (some Cladocera, nauplii, Rotifera), whereas those >300 µm

(mainly Copepoda) show negative selectivity (Fachini et al., 2012).

Macrophytes and macroalgae

Associations between *Dreissena* spp. introductions, clarification of the water-column (through particulate organic matter, including plankton, grazing) and the concomitant enhancement of the growth of benthic algae and macrophytes has been noted in many Northern Hemisphere waterbodies (MacIsaac, 1996; Higgins & Vander Zanden, 2010; Karatayev et al., 2014; Wegner et al., 2019), but for *L. fortunei* such effects have not been reported. This is likely due to the fact that most South American waterbodies investigated are rivers or river-associated floodplain lakes and reservoirs, whose coasts and still-water areas are often densely covered by floating plants (genera *Eichhornia*, *Pistia*, *Ricciocarpus*, *Azolla*, *Hydrocotyle*, *Lemma*, *Wolffia*, *Spirodella*), which have a strong shadowing effect on the water-column. Further, most of these waterbodies have high loads of inorganic suspended particles, which significantly restrict the growth of submerged macrophytes. The only anecdotal observation is that of Boltovskoy et al. (2009a), who reported that, in the relatively clear Río Tercero Reservoir (Argentina), after the invasion of the golden mussel several coastal stretches down to depths of ca. 3–5 m became densely populated by the macrophyte *Elodea* sp., but no quantitative data were provided.

Effects on the benthos

Reported effects of *L. fortunei* on the benthos include changes in sedimentation rates and sediment properties, in the abundance and composition of both sessile communities (periphyton) and mobile epi- and infunal organisms, as well as overgrowth of various macrobenthic animals.

Sediment accumulation rates and properties

Although the fact that filter-feeding organisms in general, and mussels (including native and introduced) in particular, increase sedimentation rates and modify sediment properties is widely known (MacIsaac, 1996; Nalepa & Schloesser, 2014), for *L. fortunei* available data are sparse and restricted to experimental surveys.

Using 20-L flow-through experimental units with and without mussels over a one year period, Tokumon et al. (2018) found that experimental units with mussels yielded almost 2 times more sediments than units without mussels, and the sediments contained significantly higher loads of organic matter and total N, whereas total P did not vary. Sediment accumulation was also observed to be enhanced by the mussels in 1–2 year-long experiments based on artificial substrates deployed in rivers of the Lower Paraná delta (Argentina): substrates protected from predation by meshes (where mussel colonization was highest) yielded significantly higher volumes of accumulated sediments than the unprotected ones, where mussels were scarce (Sylvester, 2006; Duchini et al., 2018).

These results suggest that ecosystem-wide modifications in the living conditions of the benthic epifaunal and infaunal organisms in waterbodies invaded by the mussel are likely significant, although variable locally, regionally, and across taxa (see below). While these effects can increase the rates of sediment accumulation in general, affect reservoir water volumes, and, in the case of freshwater deltas, enhance accretion along their fronts, as well as modify the makeup of the communities that dwell in the sediments (Tokumon, 2021), their significance in nature is debatable.

Abundance and diversity of benthic invertebrates

Surveys of the impacts of the golden mussel on benthic invertebrates have been based on (1) Comparisons between the fauna present within the mussel's colonies with that outside of them, often on artificial experimental substrates, (2) Studies of the benthic invertebrates in sediments influenced vs. non-influenced by nearby mussel colonies, and, more rarely, (3) Analyses of the invertebrates in waterbodies colonized vs. non-colonized by the mussel, or (4) Faunal inventories on natural substrates before and after their colonization by *L. fortunei*.

Sylvester & Sardiña (2015) provided a thorough review of 24 publications prior to 2014 on the reported effects of *L. fortunei* on numerous species of benthic Mollusca, Annelida, Insecta, Crustacea, Rotifera, Turbellaria, Collembola, Bryozoa, Chelicerata, Tardigrada, Nematoda, Hydrozoa, Kamptozoa, and Porifera. Of the 26 Class or Order-level taxa assessed, predominantly positive effects were found on the abundance, biomass and/or species richness

of 22 groups, equal numbers of positive and negative impacts on three, and negative on one (the invasive clam *Corbicula fluminea*). Of the 232 impacts collated, 72% were positive, 23% negative, and 4% neutral. These results were partially confirmed by some subsequent investigations (Leguizamón et al., 2014; Tokumon, 2021), but the magnitude, and sometimes the sign, of the effect differ between taxa and studies.

For example, Silva et al. (2021a) reported that the abundance of gastropods and dipterans is negatively affected by *L. fortunei* (but, on the other hand, the presence of the mussel, which is preyed upon by fishes, decreases the predation pressure on native macroinvertebrates). Sardiña et al. (2011) analyzed the benthic communities influenced by nearby *L. fortunei* colonies at two sites of the lower Paraná River delta with different pollution levels. At both sites, *L. fortunei* had positive effects on epibenthic crustaceans, large scrapers, and deposit-feeding taxa. Some predatory invertebrates, such as isopods and flatworms, were also positively affected by *L. fortunei*, but only at the more pristine site. On the other hand, density and biomass of small scrapers, Chironomidae larvae, nematodes, and ostracods were lower in the vicinity of *L. fortunei*. In their study of 160 sampling sites with and without *L. fortunei* and/or *C. fluminea* (both invasive) collected in four Brazilian reservoirs, Linares et al. (2017) concluded that the two bivalves were associated with a decrease of common soft substrate taxa, such as Chironomidae and Oligochaeta, and an increase in the densities of the invasive gastropod *Melanoides tuberculata* (Müller, 1774). In Japan, Nakano et al. (2015a) found that the density of Trichoptera significantly decreased following *L. fortunei* invasion, but Marçal et al. (2015) studied the association between the abundance of *L. fortunei* and larvae of Trichoptera on the roots of the water hyacinth *Eichhornia crassipes* (Martius) Solms-Laubach in floodplain lakes of the Pantanal (Paraguay River, Brazil), concluding that their densities are not correlated.

The effects on species numbers, diversity and equitability seem even more variable and, in some cases, suggest that *L. fortunei* might decrease diversity and/or promote a higher homogeneity in species compositions (Sardiña et al., 2011; Burlakova et al., 2012; Sylvester & Sardiña, 2015; Linares et al., 2017; Tokumon, 2021), although it enhances the complexity of

benthic communities and provides new energy pathways (Linares et al., 2017).

In short, there is abundant evidence suggesting that *L. fortunei* can enhance the abundance and biomass of many benthic invertebrates, but some taxa or trophic guilds may show declines (Silva et al., 2021b). Species richness, diversity and equitability, on the other hand, have sometimes been found to decrease.

Periphytic communities

As expected from its water clarification, reduction of phytoplankton densities and enhancement of nutrient recycling, *L. fortunei* has strong positive effects on periphytic growth. In an experiment in Salto Grande Reservoir (Argentina-Uruguay), Cataldo et al. (2012) found that, after 35 days, the periphyton in 400 L mesocosms with 300 adult mussels had >600% more ash-free dry weight and 1500% more chlorophyll a than periphyton in mesocosms without mussels. Similar changes were also observed by several subsequent studies centered on the interactions of *L. fortunei* with glyphosate-based herbicides (Pizarro et al., 2015; De Stefano et al., 2018; Gattás et al., 2020).

Overgrowth of other organisms

Although highest mussel densities are almost invariably found on hard substrates such as rocks, submerged tree remains and debris (Boltovskoy et al., 2009a), living organisms may host sizable populations as well. The submerged portions of aquatic plants, including water hyacinth (*Eichhornia* spp.), waterweed (*Egeria* sp.), bahiagrass (*Paspalum* sp.), water thyme (*Hydrilla* sp.), and sedge (*Schoenoplectus* sp.) have been reported to support large densities of juveniles and adults (Marçal & Callil, 2008; Rojas Molina et al., 2010; Ohtaka et al., 2011; Marçal & Callil, 2012; Michelan et al., 2014; Musin et al., 2015). The mussel has been claimed to be responsible for a decline in the coverage of sedge in southern Brazil (Mansur et al., 2003), but the reasons for this decline are debatable and the causality presented is weak.

In South America, attachment to sponges (*Trochospongilla* sp.), bivalves (*Anodontites trapesialis* (Lamarck), *Anodontites trapezeus* (Spix), *Anodontites tenebricosus* (Lea), *Diplodon koseritzii* (Clessin), *Corbicula fluminea*, *Leila blainvilliana*

(Lea)), gastropods (*Pomacea* spp.), and crustaceans (*Aegla platensis* Schmitt, *Trichodactylus borellianus* (Nobili)) has been observed in several reports (Darrigran, 2002; Mansur et al., 2003; Ezcurra de Drago, 2004; Lopes et al., 2009; Karatayev et al., 2010; ojas Molina & Williner, 2013), but the proportions of fouled individuals and the corresponding impacts on their populations have very rarely been estimated. In southern Brazil, 95% of the sites surveyed where both *L. fortunei* and the clam *Corbicula fluminea* (also invasive) were present, hosted some *C. fluminea* overgrown by the mussel (Ragonha et al., 2015). In Poyang Lake (China), Shu & Wu (2005) found that 35% of the bivalves (genera *Arcoonia* and *Larnprotaula*) were overgrown by the golden mussel, with an average of 6.6 mussels per clam. Overgrowth of other bivalves has also been observed in Cambodia (Ng et al., 2020). This suggests that *L. fortunei* may have an impact on resident bivalves.

On the other hand, *L. fortunei* has also been observed to serve as a substrate for some organisms, like freshwater sponges, to a degree that suggests that the sponge may kill its host (Silva et al., 2021a).

Competition with native organisms

Although interactions between *L. fortunei* and native organisms are multiple, aside from the relationships reviewed under other headings (see “[Ecological effects of *L. fortunei*](#)” and “[Predation by other organisms](#)”), direct competition has seldom been explored. Interspecific competition for space is unlikely because the waterbodies invaded by the mussel host few native sessile organisms, some of which (like sessile algae, ciliates, sponges, Hydrozoa, Rotifera) can use bare hard substrates as well as the mussel’s shells (Carvalho Torgan et al., 2009; Silva et al., 2021a). Competition for food is also most probably usually low (although in Japan *L. fortunei* has been suggested to displace native caddisflies by competing for food; Nakano et al., 2015a). The South American lentic and lotic environments invaded are mostly eutrophic, and although in rivers phytoplankton is usually relatively scarce, they host large amounts of particulate organic matter which can be consumed by this and other filter-feeding organisms. Sylvester et al. (2005) estimated that, in the lower Paraná River delta, the supply of particulate organic matter is ten times higher than the mussel’s basal metabolic requirements,

suggesting that it represents its main source of food. This conclusion was subsequently confirmed by Zhang et al. (2017b) in China, who concluded that suspended and resuspended particulate organic matter material account most of the mussel's diet (see “[Grazing of phytoplankton](#)” above). However, the impacts of future invasions and their potentially additive effects (Braga et al., 2019) might change the current situation.

Ecological interactions (mutualism, commensalism, competition, epibiosis, cannibalism, and predation) between fouling aquatic organisms, including *L. fortunei*, and several other introduced and native species, were investigated in Brazil by da Silva Bertão et al. (2021).

Predation by other organisms

Although the waterbodies where *L. fortunei* is present are mostly located in tropical and subtropical regions of very high diversity, and therefore host a wide variety of animals that can prey on the mussel, with the exception of fishes, information on its predators is very scarce and largely anecdotal. Quantitative estimates of the contribution of the mussel to their diets is almost nil. However, data derived from experiments using predator-protected and unprotected artificial substrates suggest that the proportions of the mussel's biomass lost to predation are extremely high, ranging up to 85–97% of its annual production (Sylvester et al., 2007a; Nakano et al., 2010b; Duchini et al., 2018; Silva et al., 2021b).

Predation by invertebrates

Predator inclusion/exclusion experiments carried out in Argentina (Sylvester et al., 2007a; Duchini et al., 2018), and in Japan (Nakano et al., 2010b) show that early juveniles (<1 mm) are the size-class most affected by predation. The predators involved have not been investigated, but they likely comprise leeches, gastropods, copepods, and insect larvae, as suggested for the zebra mussel (Molloy et al., 1997). Only crabs (*Zilchiopsis collastinensis* Pretzmann, and *Trichodactylus borellianus*) have been observed to feed on *L. fortunei* (Torres et al., 2012; Carvalho et al., 2013), but these observations were restricted to experimental settings and did not provide estimates of the importance of this resource for the predators.

Predation by fishes

Information on *L. fortunei* as a trophic resource for fishes is almost entirely based on data from South America. Information for Asia is restricted to some species from China (Wang et al., 2018; Liu et al., 2019), and a few from Japan (Nakano et al., 2015a) and Thailand (Grudpan et al., 2016).

Fishes are probably the most important consumers of *L. fortunei*, and are the only predators for which some system-wide effects can be inferred in South America. This trophic subsidy has been investigated for both larval fishes (which feed on the mussel's planktonic larvae), and for adult fishes (that consume settled mussels). Although the contribution of veligers to the diet of adult planktivorous fish species is likely moderately important, no studies on this trophic pathway have been produced yet, probably due to difficulties associated with the identification and quantification of mussel larvae in adult fish stomachs.

Information on the consumption of veligers of *L. fortunei* by larval fishes in South America has been summarized by Paolucci & Thuesen (2015), concluding that, of the 25 fish taxa studied, 18 consumed veligers of *L. fortunei*, but the contribution of mussel larvae differ between species, developmental stages, and environments. Earliest fish larvae (proto-larvae) are the most active consumers of veligers, which might enhance fish survival because they represent the life stage when mortality rates are the highest. Field data and laboratory experiments suggest that small crustaceans have been largely replaced by *L. fortunei* veligers in the diets of several larval fish species. Laboratory results showed that larvae of the dominant (in terms of biomass) species in the Río de la Plata basin, the sábalo (*Prochilodus lineatus* (Valenciennes)), grow significantly faster when high concentrations of veligers are present in their diet. Subsequent studies (Paolucci et al., 2017), however, suggested that in lentic waterbodies where summer cyanobacterial blooms may suppress *L. fortunei*'s reproduction (see “[Enhancement of cyanobacterial blooms](#)” above), thus uncoupling larval fish trophic demand and veliger availability, the share of *L. fortunei* veligers in larval fish diets may drop substantially.

In South America, feeding of adult fishes on *L. fortunei* juveniles and adults has been addressed in many surveys. A thorough review of the results of 16

reports published between 1998 and 2013 (Cataldo, 2015b) indicated that, in the Río de la Plata basin, 50 fish species feed on *L. fortunei*. Subsequent studies added several tens of species to this inventory. Cataldo (2015b) showed that a number of economically important species, including fishes historically considered as omnivorous, iliophagous, and ichthyophagous, have changed their feeding habits since the mussel's introduction, shifting from plants, detritus and other items to adult mussels. Mussels are consumed by fishes provided with teeth that can crush and grind the shells, as well as by toothless species that swallow whole specimens, usually selecting the smaller size classes (it should be noted, however, that not all fish species that ingest mussels are capable of digesting them; while most fish gut contents show largely crushed shells and obvious signs of tissue digestion, in some, intact, although usually dead, mussels are found: Oliveira et al., 2010a; Belz et al., 2012; de Ávila-Simas et al., 2019b).

Many of these earlier studies (reviewed by Cataldo, 2015b), as well as several other surveys (Vieira & Lopes, 2013; Isaac et al., 2014; Melo de Rosa et al., 2014; Brancolini et al., 2015; Godoy et al., 2018; Melo de Rosa et al., 2018; de Ávila-Simas et al., 2019b; Morato et al., 2019; Melo de Rosa et al., 2021) performed quantitative assessments of the importance of *L. fortunei* for the diet of the fishes, usually calculating the proportions of specimens with mussels in their guts, estimating the fraction of mussel biomass with respect to total gut contents, using stable isotopes, and/or other indices. High mussel consumption rates were reported for ~30 native and non-native freshwater species, as well some marine migrants, like the whitemouth croaker *Micropogonias furnieri* (Desmarest) (López Armengol & Casciotta, 1998).

Recent surveys performed in the Uruguay River concluded that 28 of the 81 fish species recorded feed on *L. fortunei*. Using stable isotope mixing models ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) they concluded that *L. fortunei* is responsible for a significant proportion (~30–66%) of the fish biomass of 8 species (González-Bergonzoni et al., 2020). Similar results, also based on gut contents and isotopic mixing models, were obtained in a reservoir from Sothern Brazil, showing that non-native prey are essential carbon sources for the fish fauna, fueling more than 40% of the biomass in four dominant fish species which account for 80% of the

total fish biomass; in this case, however, the major non-native prey was the prawn *Macrobrachium amazonicum* (Heller), followed by *L. fortunei* (Melo de Rosa et al., 2021).

Predator inclusion/exclusion experiments show that 70% to >90% of the mussel's production is consumed by predators, most of which are presumably fishes (Sylvester et al., 2007a; Nakano et al., 2010b; Duchini et al., 2018; González-Bergonzoni et al., 2020; Silva et al., 2021b). These effects are likely very significant not only for species that consume the mussel, but also for those that benefit from this new food resource indirectly, including large ichthyophagous species feeding on the former, as well as iliophagous fishes that consume the organic matter-enriched sediments by the mussel's feces and pseudofeces.

The availability of *L. fortunei* as a novel food resource in the Río de la Plata basin has probably had a major impact on local fish stocks. The Paraná and Uruguay rivers, where native filter-feeding organisms are scarce, flush between 1,000,000 and 2,000,000 metric tons of particulate organic carbon per year into the sea (Depetris & Kempe, 1993). How much of this drifting organic carbon is now intercepted and retained in the system in a form available to organisms that cannot feed on small suspended particles is unknown, but likely important. The fact that a large fraction of this organic matter is retained in the sediments (Tokumon et al., 2018) was suggested to have boosted landings and exports of the sábalo (*Prochilodus lineatus*) after *L. fortunei*'s spread (Boltovskoy et al., 2006). *P. lineatus* is an intensively exploited and strictly iliophagous species which represents up to >60% of the overall fish catches and biomass in the Río de la Plata basin (Bonetto, 1986), and ~80–90% of Argentine freshwater fish exports (Scarabotti et al., 2021). However, although Argentine sábalo landings did peak noticeably a few years after the mussel's introduction, (Boltovskoy et al., 2006), and the trend remained positive between 1994 and 2019 (Scarabotti et al., 2021), landings and exports are subjected to several variables, including hydrological cycles and habitat connectivity, fishing management and regulations, exploitation pressure, currency exchange and market trends, etc., which complicates disentangling the effects of these factors. Data for other fish species show mixed trends (Scarabotti et al., 2021), which further complicates interpretations of the impacts of the mussel on long-term changes in fish abundance.

Predation by reptiles, birds and mammals

Reptiles, waterfowl, and mammals have been suggested or observed to consume mussels (Bujes et al., 2007; Sylvester et al., 2007a; Boltovskoy et al., 2009a; Cardoso, 2014; Vezzosi et al., 2014), but, with few exceptions, the data are patchy and the contribution of the mussel to the diet of these predators is unknown. Some surveys suggested that this trophic subsidy may be important; for example, the turtles *Phrynops hilarii* (Duméril and Bibron) and *Trachemys dorbigni* (Duméril and Bibron) consumed 40% and 37%, respectively, of the mussels offered, but these values were based on experimental conditions (Cardoso, 2014), which may not reflect actual consumption rates in the wild.

A particularly striking void is the contribution of the mussel to the diet of waterfowl, which, judging from information on *Dreissena* spp. in the Northern Hemisphere (MacIsaac, 1996; Molloy et al., 1997; Werner et al., 2005), are likely to benefit from this trophic resource (but can also serve as an effective conduit for transfer of organic contaminants to higher trophic levels: Mazak et al., 1997).

The delta of the Paraná River hosts around 80 aquatic bird species (Bó et al., 2002), and many more are present farther north, in the Brazilian areas colonized by the mussel (Donatelli et al., 2014). Many of these (cormorants, grebes, gulls, coots, ducks, swans, and others) feed on submerged resources, including detritus, reeds, fish, insect larvae and molluscs, but consumption of *L. fortunei* has not been investigated. The only anecdotal observation is that of diving coots (*Fulica* spp.) in Río Tercero Reservoir (Argentina) emerging with *L. fortunei* in their beaks (M. Hechem, pers. comm.).

Several South American aquatic carnivorous mammals, such as the crab-eating raccoon (*Procyon cancrivorus* Cuvier) the giant otter (*Pteronura brasiliensis* Gmelin) and the river otter (*Lontra longicaudis* (Olfers)) also probably consume golden mussels (see review in Sylvester & Sardiña, 2015), as these species feed chiefly on fish, crustaceans and molluscs (Parera, 2002). In southern Brazil, *L. longicaudis* has been observed to produce feces with remains of *L. fortunei*, but these can derive from *L. fortunei*-eating fish, or from predation on the mollusc itself (Brandt, 2004).

Physiology, environmental tolerance

The tolerance limits of *L. fortunei* have been reported for several major environmental factors, such as temperature (including survival: 0 to 32–35 °C, feeding: 6–35 °C, and reproduction thresholds: 15–17 to >30 °C), pH (~4 to 9), calcium concentrations (1 mg/L), dissolved oxygen (0.5 mg/L), exposure to air (up to >10 days), pollution (high tolerance; see “Sentinel organisms” below), and salinity (<2‰ at constant exposure, up to ~23‰ at intermittent exposure; Sylvester et al., 2013) (see Table 2 in Karataev et al., 2015). Several of these values were derived from the mussel’s geographic distribution, as well as from field and laboratory experiments (Boltovskoy, 2015b; Wei et al., 2016; Cordeiro et al., 2016b; de Andrade et al., 2017; Liu et al., 2020; de Andrade et al., 2021; Xia et al., 2021a), often aimed at exploring methods for mitigating fouling of industrial infrastructure.

The physiology of the golden mussel has had moderate coverage. Several surveys investigated its potential or actual survival, reproduction, filtration rates, growth, and/or physiological responses to temperature and/or starvation (Fang & Xi-hui, 2005; Cordeiro et al., 2016a; de Andrade et al., 2017; Oliveira et al., 2011; Perepelizin & Boltovskoy, 2015b; Paolucci et al., 2019; Xia et al., 2021a); salinity (Kimura et al., 1995; Angonesi et al., 2008; Sylvester et al., 2013); inorganic suspended solid loads (Oliveira et al., 2010c; Tokumon et al., 2015); pH (Montaldo & Marchese, 2003; Oliveira et al., 2010c); air exposure (Montaldo, 2015; Cordeiro et al., 2016b); calcium concentrations (Oliveira et al., 2010c); and dissolved oxygen (Oliveira et al., 2010b; Oliveira et al., 2011; Perepelizin & Boltovskoy, 2015a).

Significant changes in oxygen consumption rates (Fang & Xi-hui, 2005; Paolucci et al., 2019), as well as other biological processes (Cataldo et al., 2005; Fang & Xi-hui, 2005; Boltovskoy et al., 2009b; Nakano et al., 2015b) were recorded at different temperatures, suggesting a plastic metabolic response and the potential ability to colonize a wide range of environments. However, with few exceptions (Xia et al., 2021a) most of these studies were performed within rather narrow temperature ranges, which stresses the need to investigate the mussel’s behavior under a wider range of temperatures.

Other studies analyzed the mussel's foot and byssus, centering on the physiological and biochemical aspects involved in its adhesion to the substrate in the framework of fouling control methods (reviewed by Ohkawa & Nomura, 2015, and subsequent investigations by Li et al., 2018a, b).

Parasites

Bucephalid trematode cercariae were recorded in *L. fortunei* in Thailand, China and Japan (Shimazu, 2014; Wang et al., 2001; see review in Baba & Urabe, 2015), where the mussel acts as the first intermediary host, and various cyprinid and silurid fishes as second intermediary hosts. In Japan, two of these trematodes were introduced with *L. fortunei*, where 13–29 fish species are their second intermediary hosts, and the definitive hosts comprise at least 9 fish species throughout Asia (Baba & Urabe, 2015). In the second intermediary hosts heavy infections of metacercariae cause significant fish health problems, and even death. On the other hand, larval bucephalids castrate *L. fortunei* and may depress their population growth (Baba & Urabe, 2015).

In South America, the only record of a parasite associated with *L. fortunei* is that of the *Golden marseillivirus*, a member of the family of giant viruses Marseilleviridae, capable of infecting amoebas, isolated from golden mussels from Southern Brazil (dos Santos et al., 2016). Recently, Camargo et al. (2022) examined 1000 specimens from the Río Grande (Brazil) watershed, but found no parasites.

Genetics

Several studies were carried out in Japan (Tominaga et al., 2009; Ito, 2015), in South America (Pereira da Silva, 2012; Zhan et al., 2012; Paolucci et al., 2014b; de Souza et al., 2018; Furlan-Murari et al., 2019), comparatively in both areas, including Korea and Taiwan (Ghabooli et al., 2013; Oliveira et al., 2015), and elsewhere (Kartavtsev et al., 2018) on the genetics (usually mitochondrial cytochrome c oxidase subunit I—COI, and nuclear microsatellites) of golden mussel populations aimed at reconstructing its spread history and pathways (see de Paula et al., 2020, for a recent review). These studies revealed interesting

but complex patterns of population genetic structure. For example, different genetic clusters were scattered, rather than continuously distributed, within the same drainages (Zhan et al., 2012). Such patterns imply that human-mediated dispersal is the dominant spread mode, whereas natural dispersal by streams has limited effects on the genetic patterns found. Further, by linking human activities, such as shipping vectors, and population genetic diversity, these studies revealed crucial patterns such as human-mediated introductions and frequent propagule transfers at different geographical scales (continental, regional, and local). However, the observed patchy distributions of genetic clusters cannot totally rule out the contribution of post-establishment environmental selection or local adaptation processes. Owing to the use of a limited number of genetic markers, it was impossible for these studies to conduct further analyses such as genomic scans for outlier loci under selection or the genes/genetic variations responsible for the rapid local adaptations in the process of its range expansions. As local adaptation represents one of the most important mechanisms for invaders to survive and subsequently thrive in alien environments, it is crucial to thoroughly investigate the genetic basis of local adaptation, particularly on identifying the genomic features (e.g., genes and associated networks, genetic variation, etc.), as well as the associated mechanisms involved in the rapid adaptation to local environmental conditions. Such research gaps are expected to be closed by the use of multi-omics-based tools, as well as sound experimental design.

Phenotypic plasticity has been increasingly recognized as an important mechanism for invaders to adapt to novel environments during biological invasions (Smith, 2009; Davidson et al., 2011). Accordingly, plastic responses to changes in local environmental factors along the invasion process allow invaders to rapidly produce multiple layers of phenotypes. Some functional traits, such as relative gill area and shell morphology, differ significantly even among geographically close populations, and, interestingly, such variations are particularly significant in invaded areas, such as the Río de la Plata basin (Paolucci et al., 2014a). Attempts at linking population genetic structure with such morphological differences, however, proved unsuccessful (Paolucci et al., 2014b; Paolucci, 2021). Genetically, the evolution of phenotypic plasticity is complex and can be modeled

in different ways, such as quantitative genetic models and gametic models. Thus, the genetic basis of such morphological plasticity deserves further investigations by using genome-wide data.

Other studies sequenced the genome and the transcriptome for *L. fortunei* in search of genes related to its invasiveness and aiming at identifying potential genetic tools for its control (Uliano-Silva et al., 2014; Uliano-Silva et al., 2015; Uliano-Silva et al., 2016; Uliano-Silva et al., 2018). These studies suggest that HSP70 chaperones and the cytochrome P450 (CYP) gene family might be particularly important for the mussel's invasibility and resilience. Indeed, the genome of *L. fortunei* is far more complex than what we have expected and learned so far. A total of 60,717 coding genes were inferred from a huge genome (1.6 Gb; Uliano-Silva et al., 2018), and approximately 70% unigenes could not be functionally annotated through transcriptome sequencing (Uliano-Silva et al., 2014). Despite the fact that the whole genome has been sequenced and assembled, significant efforts are still needed to successfully dissect the mechanisms associated with its high invasiveness, such as molecular mechanisms for high tolerance to a wide range of environmental variables, and even extreme environments, involved in its range expansions. Further, multi-disciplinary surveys, such as the integration of omics and bioinformatics, should be conducted to investigate which and how genomic arrangements, features and architectures, contribute to the complex interactions between *L. fortunei* and the environment to achieve successful invasions.

Genetic and molecular surveys were also applied for developing early detection protocols (see “[Early detection](#)” below), and for the use of the mussel for assessing environmental stress, in particular pollution (see “[Sentinel organisms](#)” below).

Behavior

The results of early field observations and laboratory studies (Morton, 1975; Morton, 1977; Uryu et al., 1996; Iwasaki, 1997; summarized by Iwasaki, 2015), showed that both young and adult specimens of *L. fortunei* exhibit crawling, climbing, and aggregating activity, with noticeable light-avoidance and negative geotaxis behavior. Small specimens are significantly more active than larger ones. These results

were generally confirmed by subsequent investigations (Duchini et al., 2015; Pereira et al., 2019). As opposed to Iwasaki (2015), who used detached animals whose byssus was cut before placing them in the experimental containers, Duchini et al. (2015) showed that around one third of the 1120 *L. fortunei* attached specimens studied during the five- to eight-day experiments can voluntarily detach from the substratum, crawl and reattach elsewhere. Higher detachment and relocation activity, as well as distances traveled, were observed in dark as opposed to illuminated conditions, and for smaller as opposed to larger animals. No circadian rhythms were detected, and movements did not differ in frequency or distance covered at different temperatures (22 °C and 31 °C), but displacement activity seemed to decrease noticeably after ~5–8 h (Iwasaki, 2015; Pereira et al., 2019).

Several field observations indicated that attachment to the downwards facing surfaces of experimental and natural substrates was significantly higher than on the upwards facing surfaces (Morton, 1975, 1977; Xu et al., 2013; Xu et al., 2015b; Xia et al., 2021a), but Duchini et al. (2015) did not find significant differences in mobility under these two conditions.

Field observations clearly show that initial recruitment is highest in more sheltered environments such as crevices and pits, and, in experiments with artificial substrates, in the angles formed by the intersecting plates (Morton, 1975; Sylvester et al., 2007b; Duchini et al., 2018), as well as sites already colonized by periphyton (Balazote Oliver, 2011), or by older conspecifics (Sardiña et al., 2009). The preference for areas less accessible to predators was also confirmed in laboratory studies (Iwasaki, 2015).

Some studies have noted differences in the density and/or size structure of mussel beds in association with water depth, with higher colonization rates at some distance from the surface than in the uppermost layer (Morton, 1977; Nakano et al., 2010b; Brugnoli et al., 2011). However, these patterns may be due as much to the mussels' behavior in response to various environmental constraints, including light penetration, turbidity, food availability, temperature, dissolved oxygen, as to differences in predation pressure.

Impacts on human-made infrastructure

In contrast to most impacts on the environment and resident species, which, as for many other invasive species, are usually mixed and context-dependent (Boltovskoy et al., 2021b), the impacts of *L. fortunei* on human-made industrial infrastructure are almost invariably deleterious and costly. Fouling by the mussel causes clogging of pipes, sieves and other components, jamming of mobile mechanisms, enhanced flow resistance, sealing failures, corrosion, sediment accumulation, overgrowth of cultivated fish cages, and water pollution (Boltovskoy et al., 2015c).

Impacts on industrial infrastructure facilities

Most industrial facilities, including power and potable water facilities that use river, reservoir or lake water, often for cooling purposes, have been built before the golden mussel started spreading. Although golden mussels are not the only fouling organisms (da Silva Bertão et al., 2021), they are by far the most damaging, and plant design did not anticipate measures aimed at neutralizing the biofouling impacts of these comparatively large, sessile invaders. Among the facilities that have had problems are water processing plants, power plants (nuclear, hydroelectric, thermal), refineries, steel mills, food processing plants, irrigation and water transfer canals, navigation dams, watercraft (commercial and leisure boats, ships), and fish diversion components, among others (see reviews in Nakano & Strayer, 2014; Boltovskoy et al., 2015c). Although clogging and blockage of pipes, heat exchangers, valves, etc., and flow resistance are usually the most serious problems, others such as corrosion, material deterioration, maintenance personnel security, water pollution and abrasion can also be important (Xu et al., 2016; Yao et al., 2017; Castro et al., 2019; Zhao et al., 2019; Wang et al., 2021).

The costs of *L. fortunei* biofouling on industrial facilities, although clearly high, have seldom been estimated. Rebelo et al. (2018) reported that 40% of the Brazilian hydroelectric power plants providing 55% of the country's hydroelectric energy are infested with golden mussels, which might involve maintenance-related costs of ~7–8 million US\$ annually, and losses in energy production shutdowns due to maintenance operations of 45–120 million US\$ per year. These costs, however, might not always be

representative of expenditures effectively due to the mussel alone. In power plants chlorine is often used to control biofouling, such as invasive mussels, even in the absence of the latter (Connelly et al., 2007). Costs have also been noted to decline in time, as managers adopt effective control procedures (Connelly et al., 2007). Further, many plants use closed-circuit refrigeration systems, which strongly diminishes fouling-related problems, whereas in drinking water installations chemicals are added to the raw water immediately after intake (coagulants, flocculants), thus eliminating the mussel's larvae at the start of the process. To the best of our knowledge, not a single plant has ceased operating due to the golden mussel's fouling. Several have had problems and even emergency shutdowns, especially in the 1990s, when problems started appearing, but all managed to cope with them either rescheduling maintenance operations, and/or using alternative control methods (see below).

Impacts on fish farming

Cage fish farming is an important industry in Brazil, Uruguay, and especially in Asia. In China (Longtan Reservoir, Guangxi Province), Uruguay, and Brazil, fish culture facilities have been reported to be affected by the mussel (Boltovskoy et al., 2015c).

Freshwater fish farming is widespread in Brazil (Zaniboni-Filho et al., 2018), where cage nets are deployed in many waterbodies for cultivating Nile tilapia (*Oreochromis niloticus* (Linnaeus)), several carp species, pacu (*Piaractus mesopotamicus* (Holmberg)), tambaqui (*Colossoma macropomum* (Cuvier)), cachara (*Pseudoplatystoma fasciatum* (Linnaeus)), pintado (*Pseudoplatystoma coruscans* (Agassiz)), and several other species. Problems associated with *L. fortunei* are fouling of the nets, which interferes with water flow, causes injury to fishes, increases net maintenance, reduces net durability, and even sinks cages due to the increased weight of adhering mussels (Oliveira et al., 2014). Golden mussel larvae and adults in the vicinity of- and on the net cages are enhanced by the availability of substrate for attachment (the nets), as well as by the enhanced supply of food provided by the higher densities of suspended organic particles (phytoplankton boosted by nutrients, as well as fish food and droppings) (Ayrosa et al., 2019; Vianna et al., 2019; Ayrosa et al., 2021; Portinho et al., 2021). In Brazil, the costs of the

mussel fouling to fish farming of Nile tilapia have been suggested to reach US\$ 0.20 per kg of fish (da Costa et al., 2017). However, some cultivated fish species, such as pacu (in Brazil) and sturgeons (*Acipenser baerii* Brandt, in Uruguay) were found to feed actively on *L. fortunei* (Azcárate et al., 2018; Godoy et al., 2018).

Management

Early detection

Several articles on the early detection of *L. fortunei* have been published since 2006. A few of these were based on modeling approaches (Osawa & Ito, 2015), the presence of larvae in plankton samples (Pestana et al., 2010), and artificial substrates for mussel adhesion (Ito et al., 2018). Most, however, starting with the pioneering work of Pie et al. (2006), used molecular methods (Mahon et al., 2011; Zhan et al., 2013; Zhan et al., 2014; see review in Darrigran & Damborena, 2015; Sun et al., 2015; Pie et al., 2017; Xia et al., 2017; Xia et al., 2018; Oliveira Junior et al., 2018; de Paula et al., 2020; and further information in Capurro Leites, 2021; Ito & Shibaike, 2021; Ribolli et al., 2021).

Early detection of invasive species is widely heralded as a key action for their timely control or eradication, and it has been included in invasive species management plans at the national and international levels (Pitt et al., 2018). While early detection is clearly important for some invasive species, especially terrestrial macro-organisms in geographically restricted areas, and also some aquatic ones where culling initiatives have sometimes proved highly successful (Simberloff, 2020; Perales et al., 2021), for those like *L. fortunei* the chances of eradicating an incipient invasion are much less likely. Even if the mussel is detected in a new watershed shortly after its introduction, the possibilities of eradicating it are close to zero. Its size, mode of life (underwater), densities, dispersion strategies, reproduction potential, and ample environmental tolerance make it a very elusive target. However, in this case, early detection is potentially important for human-made facilities that can undertake actions aimed at anticipating imminent clogging of sensitive components, as well as for tracking the geographic spread of the invader

and reinforcing measures intended for protection of nearby waterbodies.

Control

Along with its geographic spread, the control of *L. fortunei* is one of the most intensively covered subjects in published literature (Fig. 3). Almost all these reports are aimed at its control in human-made facilities. Its control/eradication in the wild is restricted to ancillary observations on measures to avoid further spread, usually in the context of general reviews or analyses of its geographic dispersion, and the impacts of predators on its populations (see above), which usually conclude that although this pressure is high, it is unlikely to significantly affect the mussel's spread or abundance. System-wide eradication has been proposed using genetic engineering tools (CRISPR-Cas9-based gene drive; Rebelo et al., 2018), but the feasibility and safety of this technique are uncertain.

Control methods for fouling bivalves, especially *Dreissena* spp. (Claudi & Mackie, 1994; Mackie & Claudi, 2010), and for *L. fortunei* (Claudi & Oliveira, 2015a, b; Montaldo, 2015; Ohkawa & Nomura, 2015; Perepelizn & Boltovskoy, 2015a, b) have been studied thoroughly. These reviews covered practically all available information published until ~ 2014; thus, in this section citations are largely restricted to publications that appeared after these reviews or were not mentioned in them. Pereira (2019) also summarized control strategies proposed for *L. fortunei* (among other issues), with emphasis on the Brazilian legislation on their use.

In addition to the specific methods outlined below, several publications produced general overviews of the environmental tolerance limits of *L. fortunei* (e.g., water temperature, dissolved oxygen, pH, ammonium ion concentrations, light intensity, etc.) in the context of their manipulation for reducing its fouling impacts (Wei et al., 2016; Zhao et al., 2019; Liu et al., 2020).

From the point of view of the developmental stage targeted, control methods can be aimed at eliminating the planktonic larvae, or killing already settled individuals. While larvae are much more vulnerable to several control methods, a major problem is that they can be present in the water throughout most of the year, which requires permanent management operations, although when successful they can keep the plant totally free of fouling. Targeting large

(1–2 years old) settled individuals, on the other hand, has the advantage of requiring periodic treatments only, but it not only involves coping with already fouled components, but also requires more aggressive methods because adults are more resilient to most antifouling methods. In addition, such shock treatments can result in huge numbers of dislodged mussel clumps fouling downstream components.

The following section presents a succinct overview of the methods proposed for controlling the biofouling of *L. fortunei* in human-made facilities.

Manual and mechanical cleaning

A detailed review of these techniques was published by (Mackie & Claudi, 2010). The methods involved vary widely depending on the components affected, their accessibility, and the diameter of the piping. Mechanical “pigs” or scrubbers can be effective to knock and scrape mussels and other organisms from large-bore pipelines. Underwater cleaning by divers or by remotely operated machinery is often used, especially on the raw water intake protecting screens. High-pressure hydroblasting is routinely performed in the large dewatered structures of hydropower plants (spiral case, intake water wells, etc.) and other facilities. It should be noted that, unless the presence of the mussels effectively represents an operational hazard, their populations within and in the vicinity of the plant involve a low risk of fouling of the sensitive components because the larvae produced by these populations take 10–20 days to reach the settling stage (see “[Larval development](#)” above), and most are therefore flushed out before they are ready to settle. On the other hand, since mussels can voluntarily detach from the substrate (see “[Behavior](#)” above), they still involve some risk of displacing from these innocuous sites and resettling elsewhere.

Most of the manual and mechanical cleaning procedures must be repeated at regular intervals, thus providing a short-term solution. They are labor intensive and costly often requiring partial or total system shutdowns. The potential for damage to the integrity of the surface being cleaned must also be considered. In addition, massive amounts of dead mussels and other debris, which can contain significant toxic substances, must be disposed of with minimal impact to the environment.

Antifouling materials and coatings

Ohkawa & Nomura (2015) produced a detailed review of the biochemical aspects involved in the adhesive traits of the mussel’s byssus (see also Andrade et al., 2015; Li et al., 2018b), as well the ability of a wide range of materials and coatings to inhibit mussel attachment (see also Matsui et al., 2018). Among the materials, silicone and polyethylene showed the lowest detachment forces, whereas among the coatings tested lowest detachment forces were those of silicon-based paints. Among metals, copper (both as a substrate and as a component of antifouling paints) performed best.

Subsequently, several investigations explored the golden mussel antifouling efficiency of various biological products (Siless et al., 2017; Ochi-Agostini et al., 2021), metal alloys (Kobayashi et al., 2017), and antifouling coatings (Fujita et al., 2015; Yao et al., 2015; Xu et al., 2016).

It should be noted that the antifouling properties of different materials, and especially those of paints, decrease significantly over time, in particular due to the development of biofilms. In addition, while useful for the design of new facilities and the retrofitting of older ones, in practice the applicability of these findings for the control of mussel fouling is limited by the technical difficulties involved in rebuilding existing components or applying protective coatings to the internal surfaces of water conduits, sieves, heat exchangers, etc.

Chemical methods

The control of fouling organisms in general, and of *L. fortunei* in particular, by chemical substances added to raw water systems at the intake is one of most widely investigated and used methods, and probably one of the most efficient so far. Claudi & Oliveira (2015b) summarized all published information for the golden mussel until 2014, including the results of 87 assays on the use of 24 oxidizing (ozone, chlorine, chlorine dioxide, sodium dichloroisocyanurate) and non-oxidizing products (pH adjustment, copper sulfate, salinity, several proprietary chemicals) in static and flow-through conditions, both in laboratory and plant settings. Subsequently, Sanson et al. (2020) investigated the effects of niclosamide on the mussel’s proteomic alterations; and Calazans et al. (2013)

and Tang & Aldridge (2019) used various chemicals (potassium chloride, poly-diallyldimethyl ammonium chloride, cationic polymer surfactants, organic anionic salts and others) microencapsulated with an edible coating.

Most oxidizing chlorine-based chemicals, while effective for many soft-bodied organisms, as well as for general sanitation purposes, have limited impacts on adult mussels (but see Li et al., 2018a), which upon contact close their valves allowing survival of long exposure times and high dosages. On the other hand, some proprietary compounds, especially quaternary ammonia, are very efficient at killing the mussels at relatively low concentrations and exposure times. Both daily and seasonal applications have been proposed. Generally around two–three 48–72 h treatments per year (at high water temperatures, when most chemicals are significantly more efficient) some quaternary ammonia molluscicides can successfully avoid the buildup of mussel beds in the system. A disadvantage of chemicals is that they are toxic for all organisms, including humans, and, therefore, detoxification at the outlet is often mandatory, especially in the presence of nearby drinking water intakes.

Other techniques

Filtration. Filtration, aimed at preventing *L. fortunei* larvae and other particles from entering the plant, can be carried out using media filters (e.g., sand filters) or mechanical self-cleaning filter units (Mackie & Claudi, 2010; see review by Claudi & Oliveira, 2015a). However, while adequate for limited volumes of water, most filtration systems cannot handle very large volumes (such as those used by most hydroelectric and, especially, nuclear power plants). In addition, their performance decreases considerably in highly turbid waters, which are characteristic of most waterbodies where *L. fortunei* dwells.

Thermal treatment. Thermal treatments for the control of mussel fouling can be applied either by increasing water temperature gradually until complete die off, or by maintaining a constant (high) temperature for periods long enough to achieve 100% mortality. Temperature increase rates of 1 °C per 5, 15, or 30 min yield 100% mortality after ~2–15 h (at temperatures between 43.6 and 50.2 °C). At 36–34 °C total mortality takes 25–644 h, whereas at 43–38 °C all mussels die after ~1–18 h (Perepelizin

& Boltovskoy, 2015b). Thermal shock has been used successfully both in Europe and in North America for controlling zebra mussel fouling (Mackie & Claudi, 2010).

Thermal treatments have some advantages over other methods of control, especially in subtropical and tropical areas, where ambient water temperatures are closer to the mussel's upper thermal tolerance limit. They can be cost-effective if thermal backwash or recirculation of thermal discharge is used, although this is not always operationally feasible, and it involves plant shutdowns or operation at reduced regimes during the period of treatment. It does not involve the use of toxic substances, but it also is nonselective, killing most of the organisms present, including those that pass through without causing harm. Further, environmental regulations can limit the temperature of discharge water (Perepelizin & Boltovskoy, 2015b).

Anoxia and hypoxia. At 27 °C, dissolved oxygen levels <0.16 mg/L kill 100% of the mussels after 10–12 days, regardless of their size; whereas at 20 °C 21–29 days are required, but small (~7 mm) mussels are significantly less tolerant than large (~20 mm) individuals. Oxygen deprivation may be an economical, non-toxic alternative for the control of mussel fouling in industrial installations by simply sealing off the fouled components and letting oxygen levels to drop, but it may involve rather long shutdown periods, unless alternative backup systems are available. Also, as with most other methods, dead mussels remain in place and detach over time, which may affect downstream components (Perepelizin & Boltovskoy, 2015a).

Desiccation. When exposed to air, *L. fortunei* can survive for 3 to >10 days. Larger individuals are more resilient than smaller ones. Desiccation can constitute an ecologically friendly, cost-effective control strategy, but it requires that fouled components are taken off-line for variable periods of time, which may involve the need for additional backup systems unless operation of the plant is stopped. Further, dead mussels do not detach immediately after death, which after restarting operations may involve variable periods of time with large amounts of drifting mussel clumps and associated debris, including rust, which may clog downstream components (Montaldo, 2015; de Andrade et al., 2021).

Ultraviolet light. Very few trials with UV light for the elimination of golden mussel larvae have been performed (see review in Claudi & Oliveira, 2015a). In clear waters this method has shown good results (in USA and Canada, with *Dreissena* spp. larvae), and was even patented (Yanagawa et al., 2016), but in South America the very high water turbidity (typically around 160 mg of suspended solids per liter), and, therefore, low UV transmissibility (absorbance $\sim 0.25/\text{cm}^2$ for 254 nm UV; Perepelizn & Boltovskoy, 2014) makes UV treatments economically nonviable.

Electric currents. A few studies on the effects of electricity on *L. fortunei* larvae were carried out in Japan (see review in Claudi & Oliveira, 2015a). However, the voltages necessary, the required length of exposure, and the amount of power needed make this technique nonviable for most industrial applications.

Ultrasound. The research performed on the use of sound as a deterrent to mussel settlement, including one study in Brazil with *L. fortunei* larvae (Santos et al., 2012), and a recent report from China (Zhou et al., 2021) is scarce and the results are controversial (see review in Claudi & Oliveira, 2015a).

Manipulations of flow speed and turbulence. The threshold water velocity at which *L. fortunei* larvae can attach to the substrate is $\sim 1.2\text{--}1.5 \text{ m/s}$; above these values larvae are flushed through (see review in Claudi & Oliveira, 2015a, and subsequent information in Zhao et al., 2019). However, very few systems are designed with a view to significantly change flow velocity, which in practice means that assessments of flow rates can help anticipate which components are more vulnerable to fouling, but they can seldom be manipulated to cull bivalve settling, let alone to dislodge attached mussels (Pils de Castro, 2013). Artificially enhanced turbulence in water transfer pipelines was also found to affect larval mortality (Xu et al., 2013; Zhang et al., 2017a), but the practical feasibility of enhancing turbulence for this purpose is likely very variable.

Biological control and bacteria-based compounds. Aside from a few reports highlighting the potential of the effects of predatory fishes for the control of *L. fortunei* in the wild (see “**Predation by fishes**” above), practically no information on this type of approach for industrial facilities is available. Pereira (2019) reviewed a few laboratory studies on the effects of various commercial bacterial products, yet several

proved to be more toxic to other aquatic organisms than to the mussel.

Some bacterial-based compounds were proposed for the control of zebra and quagga mussel adhesion (Asolkar et al., 2010; Rackl et al., 2012; Huang et al., 2014). Recently, the North American company Marrone Bio Innovations started commercializing a *Pseudomonas fluorescens*-based product (patented by Daniel P. Molloy in 2001) under the commercial name of “Zequanox”, advertised as an effective, highly selective, and ecologically innocuous alternative for both industrial plants and infested waterbodies. Independent studies, however, varied in their assessments of the efficacy of this product (Meehan et al., 2014; Lund et al., 2018; Luoma et al., 2019; Whitledge et al., 2015). In any case, all these tests were carried out with *Dreissena* spp., rather than with *L. fortunei*, which is more resilient to adverse settings and, therefore, likely to respond differently to this molluscicide.

Magnetic fields. Standing magnetic fields can allegedly affect mussel settlement, but the evidences are inconclusive (Claudi & Oliveira, 2015a). In southern Brazil, the installation of a commercial magnetic device on a small water intake seemed to have decreased pipe infestation (Ratkiewicz, 2006; Dengo & Carraro, 2013).

Sacrificial substrates. Claudi & Oliveira (2015a) reviewed the use of sacrificial substrates as a means of decreasing downstream settlement of larvae in marine aquaculture in general, as well as for *Dreissena* spp. and *L. fortunei* (on the basis of the work of Xu, 2013). Further studies were published by Liu et al. (2017), Xu et al. (2015a), and Xu et al. (2016), including patents proposing the use of rooted aquatic plants for mussel larvae attachment at the intake (Nakazato, 2004). The technique is based on the installation of easy to remove attractive substrates such as plates, bamboo, fine mesh synthetic or natural (burlap) fiber cloth in front of the areas to be protected, where mussel larvae preferentially settle thus reducing their densities on the outflow side of the device. The efficacy of this method was reported to yield good results (although 100% protection is unlikely), but its dimensions can be a hindrance when large volumes are involved. Further, the work involved in maintaining and replacing the fouled sacrificial surfaces, as well as their disposal, is problematic and highly labor intensive.

Magnetic ferroferric oxide nanoparticles. Recoverable negatively charged polyethylene glycol-coated magnetic ferroferric oxide nanoparticles were reported to reduce byssus production, performance (breaking force and failure location), adhesion rate, and adhesive plaque size (Li et al., 2021).

Uses of the golden mussel

Sentinel organisms

Due to its widespread distribution, size, and its resilience to adverse conditions, *L. fortunei* has often been used to monitor the presence of environmental pollutants (bioaccumulated in the mussel's tissues or shells), and its sensitivity to noxious substances, using chemical and/or genotoxic assessments (Villar et al., 1999; Belaich et al., 2006; Villela et al., 2006; Villela et al., 2007; Pereira et al., 2012; Garcia Marenghi et al., 2013; Young et al., 2014; Matsuzaki et al., 2015; Girardello et al., 2016; Nunes et al., 2018; do Amaral et al., 2019; El Haj et al., 2019; Nunes et al., 2020; Pazos et al., 2020; Balsamo Crespo et al., 2020; Besen & Marengoni, 2021; Girardello et al., 2021; Mendes Sene et al., 2021; Oliveira et al., 2021).

A significant number of studies addressed the biochemical responses of *L. fortunei* to the widely used agricultural herbicide glyphosate in various of its formulations (Iummato et al., 2013; Iummato et al., 2018; El Haj et al., 2019; Miranda et al., 2021), as well as the effects of glyphosate on other freshwater communities in the presence and in absence of the mussel (Di Fiori et al., 2012; Pizarro et al., 2015; Gattas et al., 2016; Iummato et al., 2017; De Stefano et al., 2018; Gattas et al., 2018; Gattas et al., 2020). *L. fortunei* was found to accelerate degradation of glyphosate and enhance nutrient concentrations, and phytoplankton and periphyton growth, probably mediated by the bacterial biofilms on the mussel's shells (Flórez Vargas et al., 2019).

Other uses

Because of its sessile habit and patchy distribution, harvesting *L. fortunei* for human uses is not economically viable. On the other hand, the often large volumes of mussel remains produced as a result of cleaning and maintenance of industrial facilities

and fish farms, which need to be safely disposed of, have been the subject of some investigations of their potential uses. Most of these focused on their use as a complement to farm animal or cultivated fish fodder (Almeida et al., 2006; Canzi, 2011; Bayerle et al., 2017; Wachholz et al., 2017), or for the neutralization of soil acidity and supply of nutrients for plants (Barbosa, 2009; Silva, 2016). While the experimental results were encouraging, the presence of contaminants (Hg, Cd, Pb) was found to involve major challenges.

A few studies analyzed the feasibility of using mussel beds or their shells for the removal of contaminants from water, wastewater, and mussel tissue (Rombaldi et al., 2015; Zhang et al., 2015; Gomes et al., 2018; Cerqueira et al., 2019; Mantovani et al., 2020) but, again, disposal of their contaminated remains was often pointed out as a major hindrance.

Concluding remarks

Table 1 summarizes our general appraisal of the degree of knowledge of the golden mussel, and of its effects on the environments and communities invaded. Clearly, the coverage is very uneven across topics. Further, most of the information on the environmental effects of *L. fortunei* has so far been derived from laboratory or mesocosm experiments, but extrapolation of these data to the real world is contentious because two key pieces of information are almost totally missing: mussel densities over entire waterbodies, and the long-term trends of the biotic and abiotic properties of lentic and lotic environments invaded, especially in relation with ex-ante with ex-post situations.

The lack of long-term studies is a very significant void in our understanding of the process and the outcomes of these invasions. Only larval abundances in the water-column have been followed for several years in a few cases. Although the absence of reliable, long-term pre-invasion information is an insolvable issue, it could be partially mitigated by efforts to monitor present-day properties of waterbodies expected to be colonized in the future. Programs aimed at estimating mussel densities over large areas, on the other hand, would greatly help to interpret the mussel's impacts observed in experimental conditions. In order to achieve measurable changes in reasonably short periods, laboratory and mesocosm experiments often use

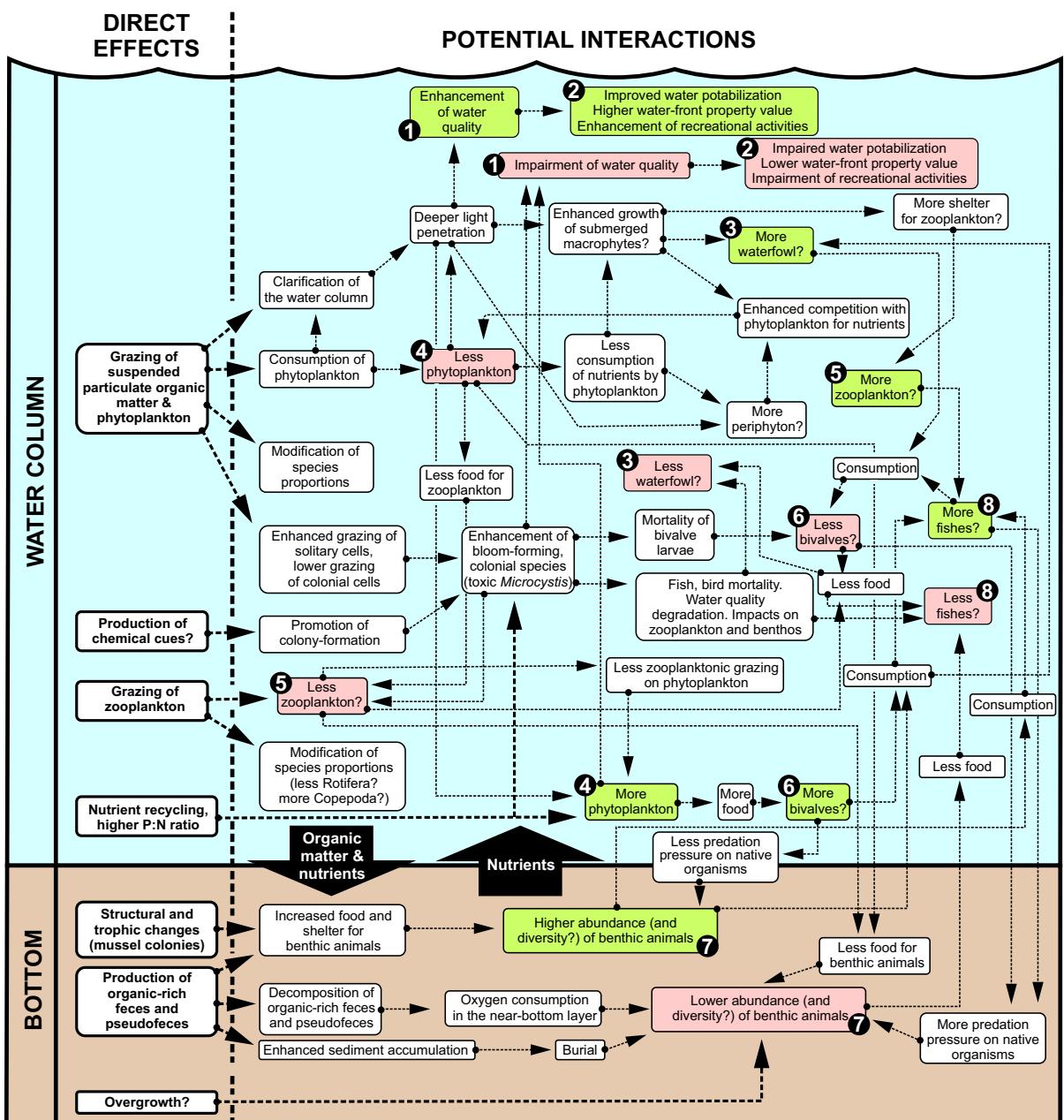


Fig. 9 Schematic diagram of some of the most salient potential and confirmed impacts of *L. fortunei* on freshwater ecosystems. Colored labels denote opposite effects on different communities, ecosystems, or services (green: enhancing; pink: reducing; numbers denote same component or service affected, which can occur simultaneously or at different times and sites). Labels enclosed in dashed lines denote pathways, solid lines

are resulting impacts. Question marks indicate effects assumed or observed in experimental conditions, but not confirmed in system-wide surveys. Large arrows at the water–sediment interface indicate dominant flux of nutrients and organic matter. Notice the complexity of the relationships involved, where the same process can have opposite effects on various physical, chemical and biological compartments

high mussels-to-container volume ratios, which are not always representative of those in the wild. Further, almost all these experiments were performed in

static conditions, which casts doubts on their validity for rivers and reservoirs with short water-retention times.

Several other key aspects of the biology and ecology of *L. fortunei*, crucial for an appraisal of its impacts on the biota, have hardly been touched upon. Among these are its fertility, its metabolism and physiology, its natural enemies (other than fishes), its direct and indirect impacts on other filter-feeding organisms and the benthic microfauna, its synergistic and antagonistic relationships with many other native and introduced species, and the interactions between facilitation/competition and pollution, to mention just a few.

Objective evaluations of its environmental impacts are further complicated by the fact that, with few exceptions (e.g., the promotion of cyanobacterial blooms, which has been observed in some reservoirs, but not in rivers), most are usually mixed, with positive effects for some communities and negative for others. Moreover, the same process can have positive and negative impacts on the same community, which can occur simultaneously in the same or different waterbodies, or shift the overall direction of the impact depending on local conditions, season, or year (Fig. 9). In addition, defining the sign (i.e., positive or negative) of the impact is context-dependent and controversial, since it may be different for different organisms, interests and stakeholders. For example, grazing of phytoplankton reduces phytoplankton densities, which can affect food availability for the zooplankton, but at the same time it enhances water clarity, which can facilitate phytoplankton growth by deepening the photic layer. Clear-water lakes and reservoirs generally facilitate water potabilization, enhance neighboring property value, tourism, and recreational activities, but shores and shallow waters colonized by mussel beds can have the opposite effect on bathers.

As in much of the literature on invasive species, the negative impacts of *L. fortunei* have received much more attention than the neutral or mixed effects, let alone the positive ones. Further, negative impacts on the environment have often been assumed without supporting evidence, or based on data from other regions and species, and occasionally in apocalyptic terms (e.g., the northwards spread of the mussel in Brazil "...would lead to a real ecological catastrophe in a national scale": de Ávila-Simas et al., 2019a; or "...environmental policies could act to prevent a biological catastrophe due to this invasor" (sic.): Morato et al., 2019), especially in popular science and the

social media (Frances, 2014; Ankrom, 2015; Graham, 2015; Moutinho, 2021). Extrapolation of information from the much better studied zebra and quagga mussels is widespread in the literature on *L. fortunei*. Although there are several similarities between the effects of these species (Karatayev et al., 2015), many studies have shown that species-specific and environment-specific differences may result in very different outcomes. While reviews highlighting likely impacts and native organisms potentially at risk that are based on studies of *Dreissena* spp. were important during the early invasional stages of *L. fortunei*, as noted by Sylvester & Sardiña (2015), "The repetition... of untested conclusions can be both misleading and discouraging of research over matters for which we have developed a false perception of understanding".

In contrast to its environmental effects, the impacts of *L. fortunei* on human-made facilities and infrastructure are clearly always negative and costly. However, with the exception of hydroelectric plants (mostly in Brazil; see <https://base.cbeih.org/>), we still do not have an inventory of the industrial facilities affected, let alone the economic impacts involved. The few economic estimates produced are based on a handful of examples and are likely underrated. Unfortunately, this type of information is extremely difficult to gather. Partly because many of the industrial facilities affected do not keep adequate records of the additional operational costs involved, or, when these exist, authorities are reluctant to share them, conceivably because sometimes the control measures used may infringe national or regional regulations, or for other unclear policy or political reasons.

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Declarations

Conflict of interest The authors declare that there is no conflict of interest and no competing interests to declare regarding the publication of this article. The authors have no financial or proprietary interests in any material discussed in this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Ethical approval Not applicable—this study is a review of published data and did not involve animals.

Consent to participate Not applicable—this study did not involve human participants.

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