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Limnoperna fortunei as an invasive biofouling bivalve species in freshwater: a review of its occurrence, biological traits, risks, and control strategies

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ABSTRACT

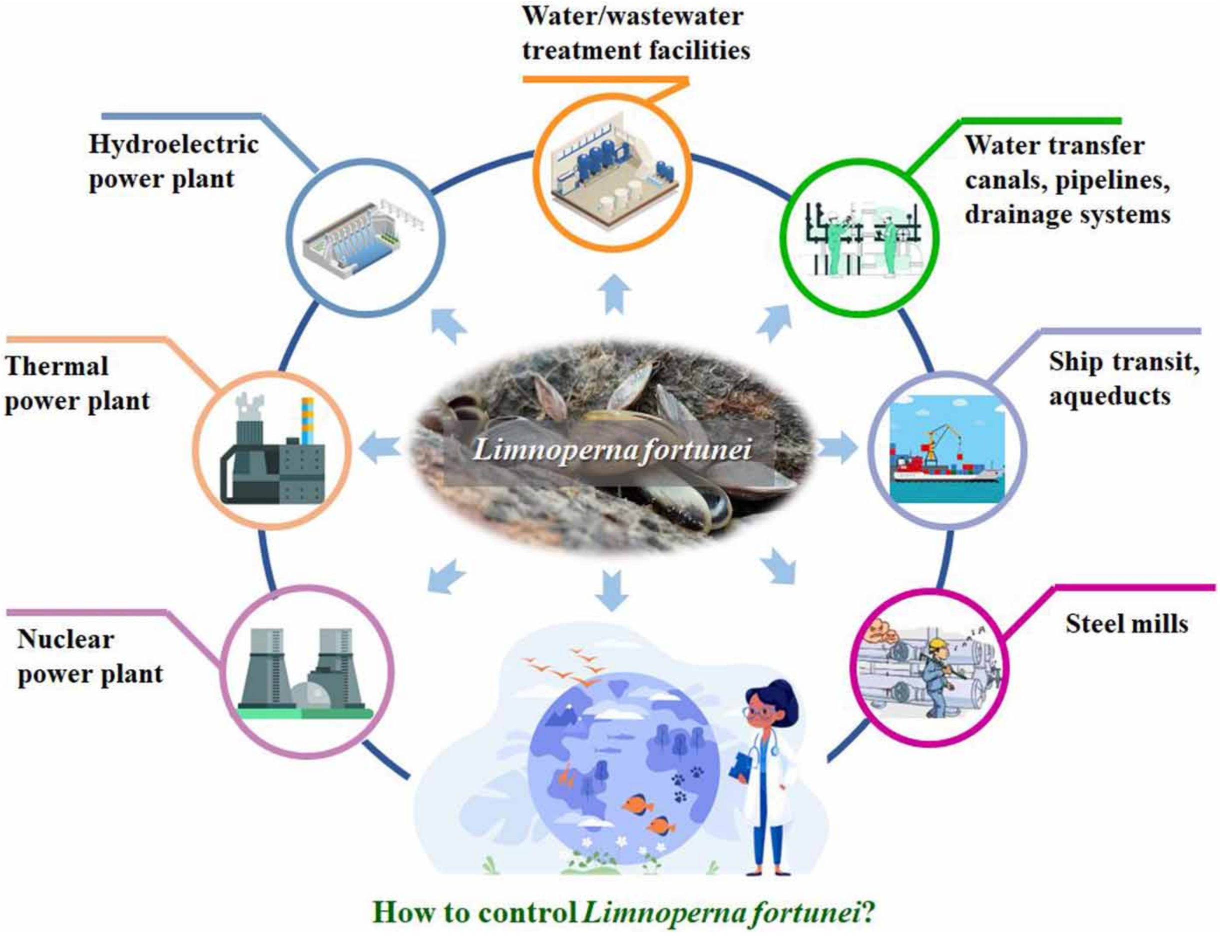
Concerns have been raised about the significant biofouling and environmental problems caused by the large numbers of *Limnoperna fortunei* clinging to water intake facilities. This review first provides a summary of the occurrence of *L. fortunei* in typical regions including China, South America, and Japan. Furthermore, this article provides a comprehensive overview of the biological traits, risks, and control of *L. fortunei*. Importantly, the planktonic larval stage is a critical period for the expansion of *L. fortunei*. Its biofouling process mainly relies on the adhesion of byssus to substrates. Various physical and chemical methods have been proposed and used to control *L. fortunei*. Among these methods, sodium hypochlorite has been shown to be effective in preventing the adhesion of *L. fortunei* by dissolving its byssus at much lower concentrations. Overall, effective and environmental-friendly antifouling strategies are still rare, particularly in drinking water treatment systems, and are encouraged to develop in future studies. This review not only provides a comprehensive understanding of *L. fortunei* but also helps to guide the prevention and control of *L. fortunei*.

Key words: biofouling, control, freshwater, *Limnoperna fortunei*, occurrence

HIGHLIGHTS

- The occurrence of *Limnoperna fortunei* in typical regions is reviewed.
- The impacts of *L. fortunei* on the environment are summarized.
- A comprehensive overview of the control strategies on *L. fortunei* is provided.
- Sodium hypochlorite can dissolve the byssus of *L. fortunei* at even low concentrations.

GRAPHICAL ABSTRACT



1. INTRODUCTION

Biological invasions are global issues arising from progressively interconnected world and increasing human activity (Pyšek *et al.* 2020). The golden mussel *Limnoperna fortunei*, which is native to China and Southeast Asia, has become a significant freshwater bioinvader in East Asia and South America (Boltovskoy & Correa 2015; Morton 2015; Xu *et al.* 2015b; do Amaral *et al.* 2019). In the 1960s, *L. fortunei* was introduced into the potable freshwater supply system of Hong Kong in China, and firstly attracted scientific attention. Specifically, *L. fortunei* was firstly recorded as an invasive species in 1965 in Hong Kong, China (Morton 1977). The first record of biological invasions caused by *L. fortunei* in South America dates from 1991 in Argentina (Oliveira *et al.* 2015). In 1992, *L. fortunei* was found in Japan (Magara *et al.* 2001). At present, *L. fortunei* is well-known as a biofouler that adheres to water intake facilities, leading to major biofouling and environmental problems (Nakano & Strayer 2014; Sousa *et al.* 2014; Pyšek *et al.* 2020).

The invasion of *L. fortunei* is mainly due to its high environmental adaptability, which allows it to survive in a very wide range of aquatic habits (Darrigran *et al.* 2012; Zhao *et al.* 2019). It is worth noting that the spread of *L. fortunei* is mainly accomplished by its juveniles, due to the fact that its adults cannot travel a long distance (Goto 2002). The adults of *L. fortunei* grow on the walls of pipes or other water-passing buildings, such as water intake pump station, water transmission pipeline, power station condensation system, water plant collecting well, sedimentation tank, and other water areas, resulting in the blockage of water passage, the changes of its surface characteristics, and difficulties in normal maintenance and repair work (Ricciardi 1998; Li *et al.* 2018). Their droppings can cause secondary pollution in the surrounding water. At the same time, the growth of *L. fortunei*, especially for its adults, will consume the dissolved oxygen in the water, deteriorate the water quality and cause biofouling (Wei *et al.* 2016). Severe biofouling of *L. fortunei* has caused substantial economic losses and ecological damage in numerous countries such as China, Japan, and Argentina (Zhan *et al.* 2012; Boltovskoy *et al.* 2015b; Correa *et al.* 2015; Xia *et al.* 2018). Moreover, this biological invasion accelerates biodiversity loss, and compromises the supporting, provisioning, regulating, and cultural services (Vila & Hulme 2017; Gattás *et al.* 2018; Xia *et al.* 2020).

Various physical and chemical measures have been performed to eliminate the negative effects caused by *L. fortunei* (Perepelizin & Boltovskoy 2015; Wei *et al.* 2016; Li *et al.* 2019; Li *et al.* 2021). The biofouling mussels can be temporarily dislodged through physical methods such as oxygen deprivation (Perepelizin & Boltovskoy 2015) and thermal treatment (Perepelizin & Boltovskoy 2011). Nevertheless, physical methods are usually inefficient and harmful to facility surfaces. Although chemical reagents such as hydrogen peroxide and sodium hypochlorite are effective, their residues in water pose potential risks to aquatic ecosystems (Claudi & de Oliveira 2015). The water quality prediction model may be used to determine the density of *L. fortunei* (Imani *et al.* 2021; Park *et al.* 2022; Sheikh Khozani *et al.* 2022; Wu & Wang 2022). Then, to determine the corresponding dosage of chemical reagents. Besides, it is well-known that advanced oxidation processes can be used to reduce organic water pollution (Salvestrini *et al.* 2020; Gallo-Cordova *et al.* 2021; Januário *et al.* 2021). For example, Liu *et al.* (2019) reported that ozone-based advanced oxidation process (AOP) and in particular combination of UV with ozone and H_2O_2 is efficient to degrade micropollutants. Also, increasing the concentration of ozone and H_2O_2 can enhance the degradation efficiency of micropollutants. Therefore, advanced oxidation technology may also be one of the methods to get rid of *L. fortunei*. Temporally, there is still a lack of environmental-friendly antifouling strategies to prevent the spread of *L. fortunei* in water supply systems, particularly in drinking water treatment systems.

Despite the research progress on the occurrence and control of *L. fortunei* over the past 50 years, the full understanding of the biological traits and environmental-friendly antifouling strategies of this freshwater bioinvader is still lacking. Therefore, the first objective of this review is to provide a comprehensive understanding of the occurrence of *L. fortunei* in typical regions, including China, South America, and Japan. The second objective of this review is to summarize the biological traits about *L. fortunei* and its impacts on the human and natural environment. More particularly, the impacts of *L. fortunei* on the human environment, such as man-made structures and facilities, will be discussed. Finally, this review aims to provide a comprehensive overview of the control strategies on *L. fortunei*, and provide guidance for developing effective control strategies to prevent undesirable invasions.

2. OCCURRENCE OF *LIMNOPERNA FORTUNEI* IN TYPICAL REGIONS

2.1. Occurrence of *L. fortunei* in China

L. fortunei was first described by Dunker (1856) from specimens collected from China (Huang & Jiang 2008). Xu (2015) reported that *L. fortunei* originate from the Pearl River basin, from where it was transferred by ships to the estuaries of rivers in Fujian and Zhejiang, and then entered the Yangtze, Yellow, Huaihe, and Haihe River basins. It further spread downstream to Hong Kong in around 1965 (Morton 1975) and to Taiwan probably in 1986 (Huang & Jiang 2008) or 1990 (Ricciardi 1998). Xu (2015) recorded that *L. fortunei* gathered in the middle to downstream areas of the Yangtze River and the central and eastern regions of China before the year 1980. Coincidentally, *L. fortunei* also occurred at the river basins in Fujian and Zhejiang simultaneously with the Yangtze River from the year 1960 to 1980, this presumably facilitated by the temperature rise after the 1950s (Shen 2003). According to Xu (2015), *L. fortunei* was found in 1980 in Tianjin, a city near the Bohai Sea in northern China, probably introduced by coastal shipping activities. The invasion of *L. fortunei* in the Yellow, Huaihe, and Haihe River basins occurred after the year 1980, 20 years later than that in river basins of Fujian and Zhejiang and Yangtze River. This is estimated to be explained by the colder climate in northern China before 1980. In recent years, *L. fortunei* has appeared in the middle reaches of the Yellow River basin in Zhengzhou, and even further north in the Shisanling reservoir in the northern suburbs of Beijing (Ye *et al.* 2011; Xu 2015; Li *et al.* 2019). To date, the available studies about *L. fortunei* are still within the Pearl River basin (Liu *et al.* 2020; Zhou *et al.* 2021).

Table 1 demonstrates the available records of *L. fortunei* after 2000 in China. It can be found that, *L. fortunei* is mainly distributed in the Pearl and Yangtze River basins in China. Northwards, it is occasionally found in the Yellow and Haihe River basins. North-western China could not be invaded by *L. fortunei* due to the fact that many river basins in north-western China are endogenous and have no connection with waterbodies with biofouling mussels. However, the inter-basin water transfer projects have brought opportunities for the invasion of *L. fortunei*, and the massive introduction of the larvae and adults of *L. fortunei* promotes the rapid dispersion in the inland region of northern China.

Table 1 | Occurrence and distribution of *Limnoperna fortunei* in China, South America, and Japan after 2000

Region	River basin	Area	Year recorded	Reference	Main finding
China	Pearl River basin	Lower Hongshuihe River	2007	Xu (2015)	*Limnoperna fortunei* is mainly distributed in the Pearl and Yangtze River basins. The dispersal of *Limnoperna fortunei* in inland region of northern China was facilitated by the massive introduction of larvae and adults through water transfer projects.
	Pearl River basin	Middle Xi River	2009	Pan *et al.* (2011)	
	Pearl River basin	Xijiang River	2018	Zhou *et al.* (2021)	
	Pearl River basin	Xizhijiang River	2019	Liu *et al.* (2020)	
	Yangtze River basin	Wujiang River	2006	Chen *et al.* (2010)	
	Yangtze River basin	Fujiang River	2007	Xu (2015)	
	Yellow River basin	Middle Yellow River	2009	Xu (2015)	
	Haihe River basin	Tributary of the middle Haihe River	2009	Ye *et al.* (2011)	
	Northern suburbs of Beijing	Shisanling reservoir	2017	Li *et al.* (2019)	
South America	Río de la Plata Basin	Port of Nueva Palmira, Uruguay	2001	Brugnoli *et al.* (2005)	The main basins colonized by *Limnoperna fortunei* in South America are Río de la Plata basin, Guaíba basin, Patos-Mirim basin, Tramandaí basin, and Mar Chiquita basin currently.
	Río de la Plata Basin	Coast of the Río de la Plata estuary	2002	Brugnoli *et al.* (2005)	
	Río de la Plata Basin	Itaipu Dam in Brazil	2001	Oliveira *et al.* (2015)	
	Río de la Plata Basin	Paraná River	2002–2004	Ruckert *et al.* (2004)	
	Río de la Plata Basin	Paranaíba River	2004	Campos *et al.* (2012)	
	Río de la Plata Basin	Tietê River	2004–2006	Avelar *et al.* (2004); Pareschi *et al.* (2008)	
	Río de la Plata Basin	Iguaçu River	2003	Oliveira *et al.* (2015)	
	Río de la Plata Basin	Palmar Dam, Negro River	1999–2002	Oliveira *et al.* (2015)	
	Río de la Plata Basin	Yí River	1999–2002	Oliveira *et al.* (2015)	
	Río de la Plata Basin	Baygorria Dam, Negro River	2002	Brugnoli *et al.* (2005)	
	Río de la Plata Basin	Uruguay River	2002	Brugnoli *et al.* (2005)	
	Río de la Plata Basin	The upper Paraná River floodplain	/	de Amo *et al.* (2021)	
	Guaíba and Patos-Mirim Basins	Arroio Pelotas River	2002	Burns *et al.* (2007)	
	Guaíba and Patos-Mirim Basins	Mirim Lake	2005	Burns *et al.* (2007)	
	Guaíba and Patos-Mirim Basins	Jacuí River	2009	Oliveira *et al.* (2015)	
	Guaíba and Patos-Mirim Basins	Guaíba Lake	2009	Darrigran *et al.* (2009)	
	Tramandaí River Basin	Quadros Lake	2008	Oliveira *et al.* (2015)	
	Tramandaí River Basin	Tramandaí River	2009	Oliveira *et al.* (2015)	
	Tramandaí River Basin	Peixoto, Quadros, and Itapeva lakes	2013	Oliveira *et al.* (2015)	
	Mar Chiquita Basin	Primero River	2006	Darrigran *et al.* (2009)	
	Mar Chiquita Basin	Segundo River	2006	Darrigran *et al.* (2009)	
	Río Grande do Sul State	Lake Guaiba, Viamão District	2000–2001	Giglio *et al.* (2016)	
	Upper Paraná River floodplain	Paraná River; Ipoitã channel; Ivinhema River; Baía River; Curutuba channel	2011–2012	Ernandes-Silva *et al.* (2016)	

(*Continued.*)

Table 1 | Continued

Region	River basin	Area	Year recorded	Reference	Main finding
	Paranaíba river basin	River Paranaíba, downstream of the confluence with the Barreiro river	/	Andrade *et al.* (2015)	
	Upper Uruguay River basin	Campos Novos, Barra Grande, Machadinho, Itá, and Foz do Chapecó reservoirs	2018	Hermes-Silva *et al.* (2021)	
	Southeast and southern regions of Brazil	Chavantes Reservoir, Paranapanema River, Brazil	2018–2019	de Rezende Ayroza *et al.* (2021)	
Asia and South America	All hydrographic basins except for the Amazon basin	Paraná River, Southeast Atlantic, Uruguay River, and Sao Francisco river basins	/	Ludwig *et al.* (2021)	*Limnoperna fortunei* is still rapidly expanding in Brazil at present.
Japan	/	Lake Biwa-Yodogawa River System		Data in Invasive Species of Japan from Environmental Risk Research Center	In Japan, the distribution and density of *Limnoperna fortunei* are increasing.
	/	Kisogawa River System			
	/	Lake Oshio			
	/	Tonegawa River System,			
	/	Tenryu River,			
	/	Uregawa River			

2.2. Occurrence of *L. fortunei* in South America

According to Oliveira *et al.* (2015), the golden mussel *L. fortunei* probably reached South America in the ballast water of transoceanic ships from Asia in around 1990. It spread into the inland waters following the navigation routes, most likely attached to the hull of ships and barges. The first record of *L. fortunei* in South Americas was in 1991 at Bagliardi Beach, in the Argentinian littoral zone of Río de La Plata (Pastorino *et al.* 1993). The occurrence of registration was reported to be 80,000 mussels/m^2 in Bagliardi beach, Argentina (Darrigran & Pastorino 1995). Then, the number of individuals increased dramatically, and the densities of *L. fortunei* was up to 100,000 mussels/m^2 within a short period (Cataldo *et al.* 2002). The explosive growth of *L. fortunei* is probably due to the discharge of thousands of tons of ballast water with a high concentration of bivalve larvae (Oliveira *et al.* 2015). Since then, *L. fortunei* has become the third invading freshwater bivalve species in South America from southeastern Asia via the Río de La Plata. Later, *L. fortunei* occurred in 1995 at several sites along Paraná River in Argentina (Boltovskoy *et al.* 2006). In 1996, *L. fortunei* was recorded in the Santa Lucía River (Uruguay) (Brugnoli *et al.* 2005).

In 1998, the mussel was found in both the Salado River in Paraguay and the Paraguay river in Brazil (Darrigran *et al.* 2000). Paraguay River is a major tributary of the Paraná, which is one of the largest wetlands in the world and is considered an area of great ecological importance. *L. fortunei* extended its range with 1,200 km upstream in the Paraguay river within about 7 years, most probably as adult mussels encrusted on vessels of the many ports along the Paraná and Río de la Plata estuary (Oliveira *et al.* 2011). In 2001, it was registered in high Paraná River, Itaipu Reservoir, and Uruguay River (Oliveira *et al.* 2015), probably transported overland by fouled fishing or leisure boats from an infested downstream location. It is noteworthy that *L. fortunei* expanded to the north reaching the Paranaíba River in 2004. However, it was not present in the tributaries of the Paranaíba River as of 2008 (Oliveira *et al.* 2015). Water levels and flow rates in Paranaíba River are controlled by hydroelectric plants, with the narrower, faster, and more turbulent reaches, and therefore the larval densities are significantly decreased or absent, which may hinder the permanence of self-sustaining mussel populations.

Along the coast of the southern Brazilian and Uruguayan, there is a complex system of lakes including the Guaíba, Patos, Mirim, and Mangueira lakes, and the rivers and lakes in this complex system are interconnected. The first record of *L. fortunei* in Guaíba Lake was in 1998 (Burns *et al.* 2007). At present, *L. fortunei* extends to most of the Jacuí River, Guaíba and

Patos lakes in Brazil, and the northeast section of Mirim Lake in Uruguay. *L. fortunei* was found in Mirim Lake in 2005, probably due to the secondary seeding of ship ballast water from freshwater ports in Argentina and/or Uruguay (Darrigran *et al.* 2009). The first discovery of *L. fortunei* in the Tramandaí River basin was at Quadros Lake in 2008, and then was found in Tramandaí River in 2009. In addition, *L. fortunei* was recorded in the Mar Chiquita Basin at Primero River and Segundo River dams in 2006 (Darrigran *et al.* 2009), most likely transferred overland attached to a fishing or leisure boat from the nearby reservoir Embalse de Río Tercero or the river Río Tercero, which have been colonized by the mussel since 1998.

Recently, Ludwig *et al.* (2021) collected *L. fortunei* specimens in Asia and all hydrographic basins in South America except for the Amazon basin, and the results revealed that China is the main genetic source of propagules and the high connectivity and migration potentiate the invasion of *L. fortunei* in South America. In addition, *L. fortunei* is still rapidly expanding in Brazil at present, and the Amazon hydrographic basin is facing an alarming threat of invasion (Ludwig *et al.* 2021).

L. fortunei has aggressively invaded South American freshwaters, having travelled more than 5,000 km upstream across five countries. As is shown in Table 1, the main basins colonized by *L. fortunei* in South America are Río de la Plata basin, Guaíba basin, Patos-Mirim basin, Tramandaí basin, and Mar Chiquita basin currently. The countries colonized by *L. fortunei* in South America are Argentina, Brazil, Paraguay, Uruguay, and Bolivia. It is time to take some measures in advance to prevent it from invading the Amazon hydrographic basin.

2.3. Occurrence of *L. fortunei* in Japan

In Japan, *L. fortunei* was first found in Lake Biwa in 1992 (Matsuda & Uenishi 1992; Goto 2002; Ito 2015). *L. fortunei* has been expanding relentlessly since its first record in the 1990s. The golden mussel expanded its distribution from 46% to 83% of the shoreline of Lake Kasumigaura from 2006 to 2012, and the density in 2012 was on average 3.8 times higher than that in 2006 (Ito 2015). *L. fortunei* was recorded to be introduced into various rivers and lakes in Japan by inadvertent mixing in edible clams imported from China, then they were deliberately released into rivers and lakes, resulting in its invasion and spread (Ito 2015).

According to the data in Invasive Species of Japan from Environmental Risk Research Center (https://www.nies.go.jp/biodiversity/invasive/DB/detail/70200e.html), *L. fortunei* has been reported in 10 of 47 prefectures as of 2017 (Matsui *et al.* 2019). As is shown in Table 1, the spread range of *L. fortunei* in Japan mainly including Lake Biwa-Yodogawa River System, Kisogawa River System, Lake Oshio, Tonegawa River System, Tenryu River, and Uregawa River. Before the early 2000s, *L. fortunei* was found in only two river systems (the Kiso-Nagara-Ibi River system and the Lake Biwa-Yodo River system) in western Japan (Ito 2015; Nakano *et al.* 2015). It was then found in eastern Japan, including the Tokai and Kanto regions and the Yahagi River system in the 2000s and 2004, respectively (Ito 2015). One year later, the invasion of *L. fortunei* was reported in the Kabura-Gawa irrigation canal leading from the Ohshio Reservoir, and in Lake Kasumigaura (Sunoh 2006; Ito 2007, 2015; Ito & Shibaike 2021). In 2007, *L. fortunei* was found in the Tone River up to about 120 km from the estuary (Ito 2012). In recent years, it has been found in Minamishiio Reservior, Kasumigaura Pumping Station and Nagara River (Ito *et al.* 2018), Ibaraki Prefecture (Osawa & Ito 2015), river systems in Honshu Island (Nakano *et al.* 2015), and an urban tidal river inside the management area of the Osaka Public Works Bureau (Matsui *et al.* 2019). With the increase in its density and distribution, *L. fortunei* have caused increasing damage to the infrastructure used in human activities in Japan, such as water purification plants, hydraulic power plants, and irrigation facilities (Magara *et al.* 2001; Nakano & Strayer 2014).

3. BIOLOGICAL TRAITS OF *LIMNOPERNA FORTUNEI*

L. fortunei is called golden mussel because of its yellow-brown shells, which looks golden in water (Morton 1973; Ricciardi 1998; Darrigran 2002). It has a benthic lifestyle that adheres to a variety of hard substrates, both natural substrates, such as trunks, aquatic plants, and compact siltsand, as well as artificial substrates like docks, tubes, walls. The larvae settle on small pebbles where hard substrates are rare, and new mussels grow on older specimens of bivalve species. By this means, they produce a hard substrate composed of shells (Darrigran 2002). Figure 1 clearly shows *L. fortunei* attached to the rocks and chains. Most of the *L. fortunei* above the water surface are dead and probably grew when the water level was high. When *L. fortunei* are removed, it can be seen the byssus connected with the substrate.

Figure 1 | *Limnoperna fortunei* attached to the rocks and chains in a riverside (Nanjing, China).

3.1. Development

As summarized in Table 2, the development of *L. fortunei* can be divided into two main stages. The first stage of growth is nonshelled development from fertilization until the formation of the trochophore larva (Morton 2015). The second stage is characterized by shelled forms from veliger to plantigrade larvae, at which point it is capable of binding to the substrate (Morton 2015). It is worth noting that a key biological trait of *L. fortunei* is the planktonic larval stage in their lifecycle (Xu *et al.* 2015a; Nakano *et al.* 2017). Due to the high dispersal ability of the larvae, the planktonic period is an important factor in the expanding distribution of this species (Nakano *et al.* 2012).

Shell: The shell of *L. fortunei* has four stages: prodissoconch I, prodissoconch II (the veliger), nepioconch, and dissoconch, respectively (Morton 2015). The first two stages are both free-swimming larval stages, reaching a length of about 115 and 320 μm, respectively (Daniel *et al.* 2005; Morton & Dinesen 2010). The third stage is also called the plantigrade stage due to its long, thin, crawling foot, reaching a shell length of approximately 1,300 μm. The final shell stage is formed by the juvenile individual and becomes the permanent shell of the adult. The shell length of adult *L. fortunei* can reach about 45 mm, but

Table 2 | Biological traits of *Limnoperna fortunei*

Biological traits			**Main findings**
Development	Main stages	Nonshelled: from fertilization until the formation of the trochophore larva Shelled forms: from veliger to plantigrade larvae	Planktonic larval stage is key biological trait of *Limnoperna fortunei* in their lifecycle.
	Shell	Prodissoconch I: Free-swimming larval stage, reaching a length of about 115 μm Prodissoconch II (the veliger): Free-swimming larval stage, reaching a length of about 320 μm Nepioconch: Plantigrade stage, reaching a shell length of approximately 1,300 μm Dissoconch: Final shell stage, formed by the juvenile individual and becomes the permanent shell of the adult. The usual size ranges from 20 to 30 mm, some can reach about 45 mm	
	Longevity	Variable: 2–5 years, even over 10 years	
Diets	Phytoplankton	Cyanobacteria, Chlorophyceae, Xanthophyta, Bacillariophyceae, Euglenophyta, and Dinophyta	*Limnoperna fortunei* showed a positive food selectivity for organisms with limited escape ability and low to moderate size.
	Zooplankton	Rotifera, Cladocera, Copepoda, Protista, Ostracoda, and Nematoda, *Limnoperna fortunei* larvae	
Behaviour	Great invasive potential; High reproductive rates; Strong viability		It is most effective and economical to manage *Limnoperna fortunei* at early stages of invasion.

the more usual size ranges from 20 to 30 mm (Morton 2015). The outer shell is brown, yellowish-green, or dark brown. The inner surface of the shell is rose-violet from the top of the shell to the end of the ventral margin, and the other parts are light blue and shiny.

Growth: L. fortunei was recently reported to have the highest density in November and March and the lowest density from June to August on net cages in a subtropical reservoir (de Rezende Ayroza *et al.* 2021). Moreover, Xu *et al.* (2015b) conducted experiments to monitor the growth, reproduction, and attachment of *L. fortunei* in water diversion projects. They observed the mussel's reproduction and attachment characteristics. In general, the mussels completed three generations in a year, and reproduced three times from March to November. At the same time, they found that the growth of mussel's shell length is strongly related to environmental parameters, such as water temperature, total nitrogen concentration, and total phosphorus concentration. Moreover, the precipitation of silt and clay hampers the filter feeding, respiration, and attachment to the habitat of mussels, which greatly affected the attachment density of mussels. This provides an idea for the restraining attachment of mussels, preventing the veligers from entering the tunnel is one of the effective strategies for controlling mussel invasion.

Longevity: L. fortunei was found in some facilities of Hanshin Water Supply Authority in Japan in 1994, its occurrence caused various problems such as sampling pipes clogging (Goto 2002). Therefore, they conducted 6-year investigations of *L. fortunei* in water supply facilities and found that *L. fortunei* spawned in summer, growing up to approximately 20 mm in shell size in a year, then it began to die out and became detached immediately in most cases (Goto 2002). However, Maroñas *et al.* (2003) concluded that the longevity of *L. fortunei* is variable and its life span was 3.2 years in the natural environment of Bagliardi Beach, Argentina. In comparison, Iwasaki & Uryu (1998) suggested longevity of 2 years in the Uji River, Japan; 4–5 years in Korea; and over 10 years in Central China.

3.2. Diets

According to Molina *et al.* (2010), the feeding of *L. fortunei* is mainly centred on the phytoplankton (98.6% of the total diet) with zooplankton also making up a fraction of their diet. They reported a total of 156 taxa in the stomach contents of *L. fortunei*, with a wide size ranging from 2 to 1,178 μm, and representing a great variety of organisms. Among them, algae were characterized by 81 taxa including Cyanobacteria, Chlorophyceae, Xanthophyta, Bacillariophyceae, Euglenophyta, and Dinophyta, while animals were represented by 46 species of Rotifera, 17 of Cladocera, 4 of Copepoda, several kinds of Protista, Ostracoda, and Nematoda, as well as *L. fortunei* larvae. The results also pointed out that *L. fortunei* showed a positive food selectivity for organisms with limited escape ability and low to moderate size.

3.3. Behaviour

L. fortunei has a great invasive potential due to its reproductive and opportunist characteristics, and rapidly reaches its sexual maturity and high reproductive rates, as well as having the capacity of establishing colonies in varied environmental conditions and high physiological tolerance (Darrigran & Damborenea 2015). They can even adapt to the extremely harsh environment characterized by low dissolved oxygen, high flow velocity, and severe pollution (Xu *et al.* 2015b). Studies on the behaviour of *L. fortunei* suggest that they preferentially attach to the shaded underside of boulders, the upper side of tunnels, and into cracks, angles, and crevices of hard substrata, usually selecting sites already colonized by conspecifics (Iwasaki 2015). These biological traits of *L. fortunei* can help better understand the mechanisms of its invasion and provide a basis for better control.

4. RISKS OF *L. FORTUNEI* ON THE ENVIRONMENT

4.1. Risks of *L. fortunei* on the human environment

It is reported that a large number of man-made structures and facilities have serious fouling problems caused by *L. fortunei*, including water and wastewater processing plants, municipal and industrial water supply systems, water intake structures of drinking water treatment plants, water transfer canals and aqueducts, agricultural irrigation systems, balancing reservoirs and balancing tanks, watercraft, fish culture facilities, steel mills, refineries, aquaculture, ship transit, nuclear power plants, hydroelectric power plants, and thermal power plants (Boltovskoy *et al.* 2015b; Uliano-Silva *et al.* 2017; de Medeiros Fortunato & Andrade Figueira 2022). Figure 2 shows the fouling problems of water pipes caused by *L. fortunei*, which seriously affects the normal operation of the water system and leads to huge maintenances costs and secondary fouling pollution when maintaining and cleaning the facilities.

Table 3 summarises the facilities and fouling problems affected by *L. fortunei*. As early as the 1970s, fouling brought by *L. fortunei* appeared in cooling water pipes at one of the largest steel mills, the Wuhan Iron and Steel Corporation, in Hubei, central China (Boltovskoy *et al.* 2015b; Xu *et al.* 2015b). Mussels clogged the pipes of water supply systems and caused expensive clean-up costs or plants shutdowns. In the 1980s, fouling problems became prevalent, which generally affected the industrial and water transfer facilities. Some water treatment plants, such as the water treatment plants in Suzhou, were even temporarily closed due to pipe clogging caused by *L. fortunei* (Luo *et al.* 2006; Boltovskoy *et al.* 2015b). Similarly, several water treatment plants have also been affected by *L. fortunei* biofouling problems, including mass attachment of mussels on water screening structures, blocks in strainers and pipes for water quality monitoring, accumulation of dead mussels in settling and flocculation chambers, and blockage of cooling system pipes for intake pumps, in the

Figure 2 | The fouling problems of water pipes caused by *Limnoperna fortunei*.

Table 3 | The facilities and fouling problems affected by *Limnoperna fortunei* (adapted from Boltovskoy *et al.* (2015b) and Ricciardi (1998))

Facilities	Fouling problems	Area/Location
Water and wastewater treatment facilities	• Mass attachment of mussels on raw water screening structures • Obstruction in strainers and pipes for water quality monitoring • Accumulation of dead mussels in settling and flocculation chambers • Blockage of cooling system pipes for intake pumps • Heavy clogging of water intake grates	• Jyr-Tan pumping station, Taiwan, China • Suzhou, China • Hanshin Water Supply Authority, Japan • Lake Biwa-Yodo River system, Japan • Osaka Prefectural Water Works Department, Japan • AySA La Plata, Argentina
Municipal and industrial water supply systems	• Colonize crevices, seams and joints in pipelines and conduits • Reduce flow through narrow pipelines	/
Water transfer canals, pipelines, drainage systems, ship transit, and aqueducts	/	• Shenzhen Dongjiang, China • Xizhijiang River, China • East River, China • others
Steel mills	/	• Wuhan Iron and Steel Corporation, China • Acindar, Argentina
Nuclear power plants	• Mussel growth on intake screens and headrace channels • Obstruction of bulwark pipes • Causing gauge malfunctions and failures • Blockage of electric generator cooling water pipes	• Central Nuclear Embalse, Argentina • Central Nuclear Atucha I, Argentina
Hydroelectric power plants	• Clogging concrete underwater structures, valves, trash racks, gates, etc • Increasing resistance to water flow • Enhancing corrosion • Clogging pipes • Jamming mobile components • Pose serious safety risks for the plant's personnel	• Shisanling, Beijing, China • Langyashan, Anhui, China • Tianhuangping, Zhejiang, China • Guangxu, Shenzhen, China • Yahagi River, Japan • Itaipu, Brazil/Paraguay • Yacyretá, Argentina/Paraguay • Salto Grande, Argentina/Uruguay • Fitz Simon, Cassafousth, Reolín, Piedras Moras, San Roque, La Calera, Argentina • Constitución, Uruguay • Over 30 plants on the upper Paraná River, Paranaíba/Aporé/Claro/etc./Brazil
Thermal power plants	/	• Central Puerto, Argentina
Refineries	/	• Shell CAPSA (Dock Sud), ESSO (Campana), Argentina
Food processing plants	/	• Tres Cruces, Argentina
Fish culture facilities	• Clogging of net cages for pacu	• Longtan Reservoir, Guangxi, China • Itaipu Reservoir, Brazil/Paraguay

(*Continued.*)

Table 3 | Continued

Facilities	Fouling problems	Area/Location
	• Clogging of fish farming components for sturgeon	• Esturiones del Río Negro, Uruguay
Navigation dams	/	• Brazil
Watercraft	/	• Widespread in Argentina, Brazil, Paraguay, • Uruguay
Agricultural irrigation systems	• Mass attachment on intake screens, irrigation channels, balancing reservoirs, and balancing tanks • Obstruction of strainers and pipeworks	• Widespread in China and Japan
Stream level gauging components	/	• Widespread in Japan
Fish diversion components	/	• Widespread in Japan
Common raw water components	• Clogging (living *Limnoperna fortunei* and/or dead, dislodged shell clusters), pressure loss, overheating • Corrosion, erosion, abrasion • Deterioration of metal, concrete and other materials • Wear, like pump and turbine shaft seals, pumps and turbine wear rings, slurry pump seals • Jamming mobile components • Poor tightness, like stopping logs, valves, boat underwater rudder and propulsion components • Sediment accumulation • Accumulation of dead specimens • Pollution, decomposition of dead mussels and mussel waste leads to the deterioration of water quality	• Heat exchangers and condensers • Pipes • Strainers, filters, trash racks, grates, screens • Penstocks • Holding ponds, storage tanks, pump suction chambers, pump wells • Water intake tunnels • Sand filtration systems • Pumps, nozzles, sprinklers • Vent lines, air release valves • Grit chambers, flocculators • Submerged monitoring instrumentation, level gauges • Pump and turbine shafts, seals, wear rings • Boat engines (like cooling water ducts, filters pumps), submerged rudder, propulsion components

Yodo River system in Japan (Boltovskoy *et al.* 2015b). In addition, Oliveira *et al.* (2015) illustrated that hydropower and nuclear facilities associated with these dams had been experiencing fouling problems due to the mussel since around 2000.

Moreover, the structures and facilities of numerous inter-basin water diversion projects are invaded by *L. fortunei*. In particular, the huge 'South-to-North Water Transfer Project' in China, aimed at connecting the water-rich areas of the middle and lower Yangtze River with water-poor Beijing, is also suffering from further worsening biofouling problems by *L. fortunei* (Wang *et al.* 2022). In addition, all the related reservoirs, lakes, and water transfer systems have already been colonized by *L. fortunei*, thus requiring maintenance and cleaning tasks which incur huge costs per year (Xu 2013). The yearly costs were estimated to be U$700 000 for the maintenance of a main hydroelectric power plant on the São Francisco River (in Paulo Afonso) due to clogging of pipelines and corrosion caused by the mussel (Uliano-Silva *et al.* 2017).

4.2. Risks of *L. fortunei* on the natural environment

The rapid expansion and great densities of *L. fortunei*, besides the caused fouling problems to various man-made structures and facilities, can greatly impact the native biota and ecosystems (Boltovskoy *et al.* 2015a; Rong *et al.* 2021). In particular, it poses a threat to the aquatic ecological environment, such as affecting the circulation of nutrients and the growth of aquatic organisms (phytoplankton, zooplankton, benthic animals, and fishes). Besides, *L. fortunei* affects benthic invertebrates (Duchini *et al.* 2018). Moreover, Darrigran *et al.* (2012) demonstrated that *L. fortunei* has caused a severe impact on the natural environment, altered the native biodiversity, ecosystem structure and function, and even caused serious economic losses during its invasion in South America.

Cataldo *et al.* (2012a) carried out the laboratory and field experiments, and the results indicated that the presence of *L. fortunei* in the freshwater environments decreased concentrations of organic matter and increases those of ammonia, nitrate, especially phosphate. Besides, data resulting from experimental laboratory and field tests show that *L. fortunei* has a strong impact on the growth of phytoplankton and aquatic plant, nutrient recycling, and water transparency (Sylvester *et al.* 2005; Boltovskoy *et al.* 2015a). It is noteworthy that the long-term series of field data confirm these results to some extent. In addition, the results of Cataldo *et al.* (2012b) strongly suggest that *L. fortunei* promote cyanobacteria growth, regardless of the tolerance of *L. fortunei* to microcystin. Another research also illustrates that the presence of *L. fortunei* may help foster cyanobacteria blooms (Silva & Giani 2018). Overall, *L. fortunei* is a harmful aquatic pest and should be carefully monitored.

5. CONTROL OF *LIMNOPERNA FORTUNEI*

5.1. Physical methods

5.1.1. Antifouling materials and coatings

Matsui *et al.* (2002) tested various antifouling substrata about their effectiveness in inhibiting the *L. fortunei* attachment. The field experiments revealed that surface properties affected the antifouling capabilities of nontoxic substrata. They observed that there were three silicone resin-based coatings with smooth surface and low surface free energy of hydrogen bonding force component possessing antifouling capabilities. This indicates that antifouling materials and coatings can be effective in preventing the invasion of *L. fortunei*, and can be used in special locations of important facilities.

5.1.2. Oxygen deprivation

Perepelizin & Boltovskoy (2015) reported that they have carried out an experiment assessment on the tolerance of *L. fortunei* to oxygen deprivation. The results indicate that total mortality is achieved after 10–12 days (27 °C) to 21–29 days (20 °C) with dissolved oxygen levels lower than 0.16 mg/L. In addition, the results also found that small (7 mm) mussels are significantly less tolerant than large individuals (20 mm) at 20 °C. It is suggested that oxygen deprivation may be a feasible alternative to control mussel biofouling in industrial installations.

5.1.3. Thermal treatment

Heat treatment has been gaining importance as a comparatively economical, nonchemical, and environmentally innocuous antifouling method. Perepelizin & Boltovskoy (2011) assessed the tolerance of *L. fortunei* to upper lethal temperatures in industrial installations. The results showed that juvenile (7 ± 2 mm) and adult (21 ± 2 mm) mussels were alive under laboratory conditions at 12–28 °C. At 34–36 °C, the total time of mortality was 25.0–644.3 h, and mussels acclimated at 12 °C die extremely faster than those acclimated at 28 °C. Moreover, from 38 to 43 °C, all mussels die after 0.7–17.5 h. These results indicate that heat treatment is a practical alternative for efficient control in fouled systems compared with conditions used in the industry.

5.1.4. Desiccation

Montalto & Ezcurra de Drago (2003) had conducted laboratory and outdoor experiments to analyse the tolerance of *L. fortunei* to desiccation. They found that *L. fortunei* is tolerant to desiccation, and the tolerance increases with mussel size. In the laboratory tests, small (up to 6 mm) mussels died after 72 h of exposure to desiccation conditions, medium-sized (6–15 mm) ones for 192 h, and maximum-sized (15–27) adults for 276 h. In the outdoor experiments, small, medium-sized, and maximum-sized mussels died at 72, 96, and 108 h, respectively. This provides a new indicator for controlling the spread of *L. fortunei* by desiccation.

5.1.5. Ultrasound

Recently, Zhou *et al.* (2021) proposed that ultrasound can be used to effectively control the invasive golden mussel *L. fortunei*. They reported minimum exposure times to kill juveniles and adults at ultrasound powers ranging 300–600 W from a fixed distance of 8.5 cm. Legg *et al.* (2015) also reported better control of macrofouling of lower ultrasonic frequencies. The results indicate that the biomass of *L. fortunei* could be effectively reduced by ultrasound, especially for the early stages of life history without or only immature shells.

5.1.6. Low water temperature

L. fortunei exhibit extensive tolerance to many environmental factors. However, the low water temperature can affect reproduction, filtration rate, growth rate, and overwintering survival rate, which is expected to limit the distribution of mussels at high latitudes (Ricciardi 1998; Tagliarolo *et al.* 2016; Zhao *et al.* 2019). Oliveira *et al.* (2010) found that *L. fortunei* reached 100% mortality after 38 days at 5–7 °C, and suggested that 5 °C was a critical lower threshold for extended survival in winter. However, Xia *et al.* (2021) recently claimed that golden mussels from both sites lived for more than 108 days in water <5 °C, and some individuals survived near-freezing conditions *in situ*, indicating greater cold tolerance. Their findings suggest enhanced cold tolerance of *L. fortunei* and wider potential distribution than currently exists.

As shown in Table 4, in addition to the above methods, the most common methods for controlling *L. fortunei* are manual and mechanical cleaning, filtration, and manipulations of water flow (Nagaya *et al.* 2001). Among them, manual and mechanical cleaning is one of the most direct and effective methods in a short time. Although both larvae and adults can be temporarily removed by these physical methods, some methods are not particularly time-sensitive and some can damage facility surfaces. Appropriate and effective measures should be taken based on the actual situation.

5.2. Chemical methods

5.2.1. Oxidizing chemicals

Chemical oxidants have been proposed to potentially control fouling mussels by affecting the oxidation of 3,4-dihydroxyphenylalanine, which is associated with byssus adhesion (Li *et al.* 2019). At present, numerous high-concentrated chemical oxidants, such as chlorine, sodium hypochlorite, hydrogen peroxide, potassium permanganate, chloramine T, calcium hypochlorite, and sodium dichloroisocyanurate appear to be efficient in killing mussels without harming facilities (Cataldo *et al.* 2003; Claudi & de Oliveira 2015; Li *et al.* 2019).

Chemical reagents. Chlorine as chlorine gas or sodium hypochlorite has been usually used for water disinfection and prevention of biofouling. For example, adult *L. fortunei* completely died at >5 mg/L sodium hypochlorite after 14 days of exposure (Cataldo *et al.* 2003). Recently, Li *et al.* (2019) conducted an experiment, in which *L. fortunei* adults were exposed to four oxidants, namely sodium hypochlorite, potassium permanganate, hydrogen peroxide, and chloramine at concentrations of 0.5–5 mg/L for one week. The results showed that sodium hypochlorite and hydrogen peroxide significantly inhibited byssus production and increased byssus shedding rate. Moreover, the results indicated that only sodium hypochlorite can dissolve byssus at even low concentrations. This suggests that sodium hypochlorite can be used as an environmental-friendly alternative chemical agent to control biofouling from *L. fortunei* through weakening byssus adhesion.

Nanoparticles. Girardello *et al.* (2021) found that ZnO nanoparticles alter the redox metabolism of *L. fortunei*. Moreover, another recent study investigated the effects of recoverable magnetic ferroferric oxide nanoparticles on byssus adhesion mediated biofouling golden mussel *L. fortunei* (Li *et al.* 2021). The results confirmed the effectiveness and underlying mechanisms of magnetic ferroferric oxide nanoparticles on mitigating *L. fortunei* biofouling, which provides a reference for developing efficient and environmental-friendly antifouling strategies against fouling mussels.

5.2.2. Nonoxidizing chemicals

According to Montresor *et al.* (2013), the concentrations of NaOH used in the test varied from 40 to 800 mg/L and resulted in a pH range of 11–13. The results showed that 88.51 mg/L (pH = 11.5) of NaOH for 96 h could kill 50% of the exposed individuals. In addition, some hydroelectric power plants in Brazil have used NaOH for a long time to control *L. fortunei* and

Table 4 | Summary of methods available for controlling *Limnoperna fortunei*

Type	Method	Advantage	Disadvantage	Reference	Main findings
Physical method	• Antifouling materials and coatings • Manual/mechanical cleaning • Filtration • Oxygen deprivation • Thermal treatment • Desiccation • Ultraviolet treatment • Ultrasound • Low water temperature • Manipulations of water flow	• Quick and effective in a short time • No chemical pollution	• Timeliness is short • It needs to be repeated • The economic effect is poor • Increase the roughness of the materials	Matsui *et al.* (2002); Montalto & Ezcurra de Drago (2003); Ohkawa & Nomura (2015); Perepelizin & Boltovskoy (2011, 2015); Zhao *et al.* (2019); Zhou *et al.* (2021)	Ultrasound could effectively reduce the early stages of *Limnoperna fortunei*. Sodium hypochlorite can dissolve byssus at even low concentrations. Preventing them from entering the tunnels is the most efficient method to avoid biofouling by *Limnoperna fortunei*.
Chemical method	• Chlorine • Chlorine dioxide • Chloramine • Ozone • Hydrogen peroxide • Sodium dichloroisocyanurate • Potassium permanganate • Ferrate • pH adjustment • Copper sulphate • Salinity • MXD-100 • Ammonia • Ammonium chloride • Nanoparticles • TiO_2	• Simple and efficient • Dissolving byssus • Long-term inhibition of its growth	• The dosage is not easy to control • Waste of resources • Cause secondary risk	Claudi & de Oliveira (2015); Girardello *et al.* (2021); Li *et al.* (2019); Li *et al.* (2021); Montresor *et al.* (2013); Nunes *et al.* (2020)	
Biological method	• Ecological pool • Fish	Environmental-friendly	Low efficiency	Godoy *et al.* (2018); Xu *et al.* (2015a)	
Combined control	• Combination of multiple strategies	High efficiency	High costs	Darrigran & Damborenea (2015); Liu *et al.* (2020)	

achieved positive results (Montresor *et al.* 2013). However, it is noteworthy that it is important to test pH adjustment in the raw water before the consideration of adjusting pH as a mitigation strategy.

Although these oxidants can be effective, their excessive residual reagents and prolonged exposure will pose a potential threat to the environment. In practical application, it is a good choice to try to use low-dose chemical reagents as far as possible to achieve effective control without affecting the normal operation of the ecological environment.

5.3. Biological methods

Xu *et al.* (2015a) conducted an experimental study on the ecological pool for preventing the golden mussel invasion in the scale model tunnels. The main technology of the ecological pool was to prevent mussels from entering the tunnel by attracting the veligers to attach to the geotextile, further attracting mussels to attach to bamboo, and using high-frequency turbulence to kill mussels. The results found that the golden mussel veligers can be killed by high-frequency turbulence. Thus, the ecological method is found effective in controlling *L. fortunei* biofouling.

In aquatic ecosystems, pollution by contaminants and invasive species is the main anthropogenic factor (Miranda *et al.* 2021). The presence of contaminants alters the dissolved oxygen dynamics in water, and it is unclear whether this will affect the survival of invasive mussels. Miranda *et al.* (2021) recently investigated the influencing mechanisms of glyphosate, 2,4-D, which is a broad-spectrum, nonselective, and post-emergence herbicide commonly used worldwide, and its mixture on the survival of *L. fortunei*. The results showed that *L. fortunei* mortality increases when glyphosate is present alone or mixed with 2,4-D. They also demonstrated that the pure herbicides (glyphosate and 2,4-D) have negative effects on the survival of the golden mussel *L. fortunei*, providing new insights into the harmful impact of herbicides on non-target organisms. This study contributes to understanding the mechanisms of *L. fortunei* invasion in freshwater systems under the influence of agrochemicals.

Furthermore, it may also be possible to control *L. fortunei* by releasing certain fishes that feed on them. For example, Godoy *et al.* (2018) evaluate the presence of *L. fortunei* in the digestive tract of three native species of fish cultivated in cages in the Itaipu reservoir. It concludes that there are two kinds of fish able to consume and control the *L. fortunei* (Godoy *et al.* 2018).

5.4. Combined control

It has been a worldwide challenge for decades to control the invasion and spread of *L. fortunei* (Darrigran *et al.* 2012). As mentioned above, a number of antifouling strategies have been proposed to solve the biofouling of *L. fortunei*, but many of them have restrictions. For instance, manual or mechanical cleaning causes damage to tunnel walls and other facilities and costs a lot; chemical regent residue causes secondary risk, sodium hypochlorite can react with various organic matters to form harmful disinfection by-products (Zhang *et al.* 2021); the biological method has limited efficacy and may influence other organisms. Therefore, based on the previous experience, effective prevention and control measures should be combined with the biological traits of *L. fortunei* and the actual environmental situations of the biofouling (Darrigran & Damborenea 2015). Different physical, chemical, and biological methods can also be combined to achieve effective control of biofouling.

In order to select the effective control strategies, Liu *et al.* (2020) set five levels for the environmental factors (water temperature, dissolved oxygen concentration, pH, and ammonium ion concentration and four levels for light intensity). They proposed a combination of multiple strategies to control the biofouling of *L. fortunei* according to their ecological amplitudes and the practical situation. To be specific, the mussels can be effectively killed by maintaining a high water temperature (>35°C), a low dissolved oxygen concentration (<1.4 mg/L) or a high pH value (>9.7) and strong (>55,000 light intensity) and continuous light illumination can expel the mussels (Liu *et al.* 2020). The results demonstrate that the adjustment of environmental conditions with high water temperatures, low dissolved oxygen, high pH values, or strong and continuous light illumination is suggested as a potentially effective control strategy of the biofouling caused by *L. fortunei*.

Finally, once *L. fortunei* spread into the water transfer works, they are extremely difficult to eliminate because they exhibit very high environmental adaptability. Therefore, preventing them from entering the tunnels is considered to be the most efficient method to avoid biofouling by *L. fortunei*.

5.5. Other methods

According to Darrigran *et al.* (2011), natural environmental factors can restrict the invasion process of *L. fortunei* in the Neotropical region. Although *L. fortunei* had been widely existing throughout the lower Paraguay river before 2005, it disappeared in the Salado del Norte River, which flowed into the middle Paraná (Oliveira *et al.* 2015). It is speculated that three factors (high concentrations of suspended sediments, high salinities, and intermittent flow) probably restrict the colonization of this river (Drago *et al.* 2008; Darrigran *et al.* 2011). Additionally, de Amo *et al.* (2021) reported that hydrological connectivity drives the propagule pressure of *L. fortunei* in a tropical river floodplain system.

L. fortunei has invaded both the human environment and the natural environment, and therefore it is crucial to prevent new invasions and control the spread of existing mussels with the following suggestions. First, all facilities that use raw water from water bodies in the invaded area must take measures to prevent and control the biofouling of *L. fortunei*. Second, specific control methods are encouraged to develop and adopt for specific sites, such as valves clogged with *L. fortunei*, which can be removed by ultrasound, considering the corrosion of chemicals. When a large number of pipes are blocked, chemicals such as sodium hypochlorite can be used to eliminate them. Third, it is recommended to disinfect the ballast water from foreign ships, and adopt effective control of ballast water discharge in ports to prevent the invasion of other organisms. Fourth, in terms of management, countries can strengthen their biosecurity regulations and implement more effective intrusion-related management strategies. Finally, the long-term studies addressing *L. fortunei* and the effective control strategies are still rare and are encouraged to conduct in future studies.

6. CONCLUSIONS AND SUGGESTIONS

6.1. Conclusions

The golden mussel *L. fortunei* has become one of the most aggressive freshwater invaders and spread in Asia and South America. It has a benthic lifestyle that adheres to a variety of hard substrates though byssus. Mussel biofouling has caused severe negative consequences in aquatic ecosystems and resulted in significant ecological impact and huge economic loss globally. In general, the ecological impacts of *L. fortunei* include: (1) affecting the normal operation of the water pipe system, (2) changing the ecological systems of lakes or rivers, (3) odour and dead shells caused by rotten corpses filling up water pipes, and (4) the increase in economic costs. Although various physical, chemical, and biological methods have been employed to eliminate *L. fortunei*, effective and environmental-friendly antifouling strategies still need to be explored.

6.2. Suggestions

Further exploration about the biological traits of *L. fortunei* can help better understand the mechanisms of its invasion and spread, and the development and diets of *L. fortunei* are suggested to be further studied. Furthermore, invasion bivalve *L. fortunei* may be used as models to study biological invasion.

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DATA AVAILABILITY STATEMENT

All relevant data are included in the paper or its Supplementary Information.

CONFLICT OF INTEREST

The authors declare there is no conflict.

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