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Thermal tolerance of *Limnoperna fortunei* to gradual temperature increase and its applications for biofouling control in industrial and power plants

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The acute upper lethal temperature (AULT) at different rates of increase was evaluated as a tool for the design of cheaper and environmentally friendlier control strategies for the invasive bivalve *Limnoperna fortunei*. Survivorship of 6 ± 2 mm and 20 ± 2 mm mussels acclimated to 12, 23 and 28°C and subjected to different heating rates (1°C per 5, 15 and 30 min) was estimated in the laboratory. The temperatures required to kill 50% (LT_{50}) and 100% (SM_{100}) of the mussels, and the mean death temperature (MDT) varied between 42.2 and 51°C over 54 experiments. Heating rates significantly ($p < 0.001$) affected LT_{50}, SM_{100}, and MDT. AULT was not affected by mussel size and acclimation temperatures. *Limnoperna* appears to be more resistant to high temperatures than *Dreissena polymorpha*, a mussel invasive in the USA and Europe. Lethal temperatures of *L. fortunei* are within the current thermal operational industrial capacities, suggesting that heat treatment is a viable alternative for controlling its fouling in utility systems.

Keywords: golden mussel; *Limnoperna fortunei*; upper lethal temperature; heat treatment

Introduction

Limnoperna fortunei Dunker (1857), the golden mussel, a bivalve mollusc native to the freshwaters of mainland China, was unintentionally introduced in Hong Kong, Taiwan, Japan, and South America between 1965 and 1990 (Morton 1979; Ricciardi 1998). In Argentina, it was first detected along the coasts of the Río de la Plata estuary (*ca* 35°S) in 1991 (Pastorino et al. 1993), from where it subsequently spread northwards and westwards at up to 240 km $year^{-1}$ (Boltovskoy et al. 2006). By 2006 it was present as far north as the Pantanal (*ca* 19°S) and the States of São Paulo and Minas Gerais, in Brazil (Darrigran 2002; Boltovskoy et al. 2006; Oliveira et al. 2006). At present, *L. fortunei* is one of the most common macroinvertebrate species and a major fouling pest in the Paraná-Uruguay basin, with reported population densities over 200,000 mussels m^{-2} (Boltovskoy et al. 2006). *L. fortunei* attaches to any hard surface as well as to some less firm substrata such as plant roots and soft sediments covered by a hardened crust.

The growth of *Limnoperna* beds in raw cooling water conduits has become a problem for many industrial and power plants. Clogging of, for example, water intake sieves and filters, pipes, heat exchangers and condensers has become a major nuisance for plants that use raw river or lake water, chiefly for cooling purposes (Goto 2002; Cataldo et al. 2003). Fouling by the mussel reduces the effective bore of pipes and increases internal surface roughness thus retarding flow. Fouling is facilitated by the planktonic larvae of the mussel which attach to the inner surface of metal pipes and other components. Many nuclear and hydroelectric power plants, distilleries, and refineries in countries in Asia and South America have experienced clogging and pressure loss due to fouling by *L. fortunei* (McNeill 2001; Nagaya et al. 2001; Matsui et al. 2002; Goto 2002; Cataldo et al. 2003) Nuclear power plants in Argentina had temporary shutoffs due to this problem.

A variety of methods has been proposed to control the adverse effects of freshwater fouling molluscs on the operation of industrial plants. Most of these are based on the experience gained in Europe and North America from two invasive pests, the Asian clam *Corbicula fluminea* (Muller 1774) and the zebra mussel *Dreissena polymorpha* (Pallas 1771). Because the spread of *Limnoperna* beyond its native range is a recent phenomenon, research on control methods is still restricted to few topics, such as attachment strength and antifouling materials and coatings (Ohkawa et al. 1999; Matsui et al. 2001, 2002; Nagaya

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et al. 2001), tolerance to desiccation (Montalto and Ezcurra de Drago 2003) and anoxia (Perepelizin and Boltovskoy 2011), and the use of toxicants (Morton et al. 1976; Cataldo et al. 2003). The use of oxidizing chemicals, in particular chlorine, is widespread in industry. However, adults of *L. fortunei* are highly resistant to low doses of chlorine (Cataldo et al. 2003). In addition, most oxidizing chemicals are highly corrosive and chlorination of raw water produces carcinogenic trihalomethanes and adsorbable organic halides (Daling and Johnson 1985). Thus, alternative economically viable and environmentally innocuous methods are sought.

Successful examples of heat treatment programs to control zebra mussels and other fouling molluscs have been implemented for many years in North America (Graham et al. 1975; Stock and Strachan 1977; Claudi and Mackie 1994), and in Europe (Jenner 1982; Rajagopal et al. 1997). In order to determine the upper thermal limits of biofouling organisms with the aim of using this information for their control, the experimental approach should mimic the actual operating conditions of industrial and power plants. Heat treatment involves an increase in the water temperature through thermal backwash, recirculation of thermal discharge, or steam/hot water injection (Miller et al. 1992; McMahon and Ussery 1995). In this type of operation, the rate at which water temperature can be increased is a strong limiting factor, which underscores the importance of defining the mortality of *Limnoperna* at different rates of temperature increase.

The temperature at which experimental organisms die after having been exposed to specific rates of temperature increase is known as Acute Upper Lethal Temperature (AULT). Usually, results of AULT are presented as lethal temperatures, including the temperature required to kill 50% of the animals (LT_{50}), or the entire sample (100% sample mortality or SM_{100}), or the mean death temperature (MDT), at a specific heat rate increase and starting (acclimation) temperature (Stirling 1982; McMahon and Ussery 1995). Despite the many advantages of thermal treatments for biofouling control, no data on the AULT of *Limnoperna* have been produced so far.

The aim of this study was to determine the upper lethal temperature of small and large adults of *L. fortunei* subjected to different rates of temperature increase. This information will prove useful for the design of cheaper and more environmentally friendly control strategies.

Materials and methods

Experiments on AULT consisted of exposing approximately 20 small (6 ± 2 mm in length) and large (20 ± 2 mm) mussels to different temperature increase rates (1°C per 5, 15 or 30 min), starting from three different initial temperatures (12, 23 and 28°C), until 100% mortality in all replicates was reached. All experiments were conducted in triplicate (54 experiments in total, involving 1112 mussels) plus one control for each starting temperature and mussel size (6 controls in total, involving 123 mussels; a single control was used for different experiments starting simultaneously). Controls were set up under identical experimental conditions (but without increasing the starting temperature), and monitored simultaneously with the experiments.

Experimental specimens were collected manually from natural populations along the coast of the Río de la Plata estuary in the city of Buenos Aires (34°36′S, 58°20′W) on five occasions in spring (1 September and 5 November 2008), summer (1 and 20 January 2009), and winter (18 June 2009). Mussels were immediately transported to the laboratory, where they were rinsed and transferred to 20 l aquaria with aerated dechlorinated (by active air bubbling for 24 h) tap water at the *in situ* collection temperature. All mussels were utilized in the experiments within 40 days of collection.

Acclimation from river temperature (13.5 to 28.0°C) to starting experimental temperature (12, 23, and 28°C) was performed at a rate of 1°C day^{-1}. Mussels were fed daily with commercial fish food ('Vitafish baby', 44% proteins, 13% lipids, 14.5% minerals, 5.4% calcium, 2% phosphorus) at a concentration of 0.02 g l^{-1}. The water in the acclimation aquaria was renewed every 3 days for mussels acclimated to 23 and 28°C, and every 7 days for those acclimated to 12°C. These renewal periods minimized mussel disturbance-related stress, while controlling excessive proliferation of algae and, especially, bacteria, which grow faster at higher temperatures. Experiments at different starting temperatures were scheduled so that the range between the starting temperature and *in situ* collection temperature was minimized. Thus, tests starting at 23 and 28°C were conducted in the spring–summer using mussels collected in water around 19.0–28.0°C, whereas those starting at 12°C were carried out during the winter on animals retrieved from water at 13.5–15.5°C. These starting temperatures were chosen because they are representative of summer (28°C), spring (23°C), and winter (12°C) temperatures in the lower delta of the Paraná River.

Once acclimation was completed, groups of 20–23 individuals per size class were isolated, placed in 9 cm Petri dishes covered with a 1 mm mesh nylon cloth to prevent escape, and returned to the aquarium for further work. After 24 h, Petri dishes were examined, loose mussels (ie not firmly attached to each other or to the bottom of the dish) were eliminated, and the nylon

mesh was removed to start the experiments. Only mussels attached by their byssi were used because loose, unattached organisms can have a reduced tolerance to stress (McMahon et al. 1992; Rajagopal et al. 2005).

One Petri dish was placed in each experimental vessel, consisting of a plastic container filled with 3 l of dechlorinated tap water. Plastic containers were immersed in an 8 l controlled temperature (± 0.1°C) water bath and covered with a perforated plastic lid. Water in the bath and the containers was actively mixed by bubbling air to ensure a homogeneous temperature distribution. After acclimation of the organisms to the experimental conditions (*ca* 30 min), the bath was set to operate at selected temperature increase rates, viz. 1°C per 5, 15 or 30 min. These rates were chosen because they are operationally feasible in many industrial raw water cooling systems (McMahon and Ussery 1995).

During the course of the experiments (which lasted between 1.7 and 15.5 h, see 'Total experimental time' in Table 1), mussels were not fed. The water temperature and dissolved oxygen were permanently monitored with a Hach sensION156 pH-conductivity-dissolved oxygen meter (nominal accuracy, dissolved oxygen: ±1%, temperature: ±0.3°C). From the moment animals began to die (1 to 6 h after start of experiment), dead mussels were identified and removed at regular intervals (5–15 min). The temperature continued to be increased at the corresponding rate until all test animals were dead. Mussels were considered alive when they were seen actively filtering water (valves slightly open, mantle edge protruding and siphons extended), or when they closed their valves under a gentle stimulus with a dissection needle between the valves in the region of the siphons (Payne et al. 1998), or they resisted forcible valve opening (Iwasaki 1997). At the end of each run, experimental mussels were allowed to cool to room temperature and rechecked for viability after 12 h.

In addition to mortality, the temperature at which maximum filtration activity, as indicated by completely extended siphons, was noted; this temperature is known as the Preferred Filtration Temperature (PFT). The highest temperature at which filtration was observed was also assessed (Maximum Filtration Temperature, or MFT). For this purpose, all experimental mussels were visually examined at regular intervals (5–30 min).

A 3-way analysis of variance (ANOVA) model was used to analyze the effects of starting temperature, heating rate, and mussel size (as categorical independent variables) on each AULT outcome (LT_{50}, MDT, or SM_{100} as simple dependent variables). LT_{50} values were obtained after fitting the Probit Model (BenchMark Dose Software, version 1.4.1c). PFT contrasts were calculated by analysis of covariance (ANCOVA), with the proportion of the mussels' activity (as

Table 1. Acute upper lethal temperature limit for small (6 ± 2 mm) and large (20 ± 2 mm) *L. fortunei* acclimated at 12, 23 and 28°C and exposed to different rates of temperature increase (mean ± 1 SD).

Starting temperature (°C)	Rate of temperature increase (1°C/min)	Mussel size (mm)	*N*	LT_{50} (°C)	MDT (°C)	SM_{100} (°C)	Total experimental time (h)
12	5	6	60	46.0 ± 0.1	47.9 ± 0.7	50.0 ± 1.0	3.2 ± 0.2
		20	60	47.3 ± 0.8	48.8 ± 0.5	50.3 ± 0.6	3.2 ± 0.1
	15	6	60	43.7 ± 0.3	44.6 ± 0.2	45.3 ± 0.6	8.1 ± 0.1
		20	62	43.7 ± 0.2	44.5 ± 0.4	45.2 ± 0.8	8.0 ± 0.2
	30	6	60	42.4 ± 0.1	42.9 ± 0.1	43.5 ± 0.0	15.3 ± 0.0
		20	63	42.6 ± 0.1	43.1 ± 0.1	43.7 ± 0.3	15.3 ± 0.1
23	5	6	60	45.7 ± 0.4	47.1 ± 0.9	48.3 ± 1.2	2.1 ± 0.1
		20	62	45.7 ± 0.3	47.4 ± 0.3	49.0 ± 1.0	2.2 ± 0.1
	15	6	61	44.1 ± 0.1	44.8 ± 0.3	45.5 ± 0.5	5.6 ± 0.1
		20	60	43.8 ± 0.2	44.5 ± 0.1	45.2 ± 0.3	5.5 ± 0.1
	30	6	63	43.2 ± 0.1	43.8 ± 0.2	44.3 ± 0.3	10.7 ± 0.1
		20	62	42.8 ± 0.1	43.3 ± 0.1	43.8 ± 0.3	10.4 ± 0.1
28	5	6	65	45.6 ± 0.4	46.8 ± 0.4	48.3 ± 0.6	1.8 ± 0.1
		20	63	45.4 ± 0.7	47.1 ± 0.2	49.3 ± 0.6	1.8 ± 0.1
	15	6	63	44.3 ± 0.1	45.1 ± 0.2	45.8 ± 0.3	4.5 ± 0.1
		20	63	43.6 ± 0.1	44.3 ± 0.1	45.0 ± 0.0	4.3 ± 0.0
	30	6	63	43.1 ± 0.1	43.8 ± 0.2	44.3 ± 0.3	8.2 ± 0.1
		20	62	42.6 ± 0.3	43.1 ± 0.3	43.8 ± 0.3	7.9 ± 0.1

Note: LT_{50} = temperature required to kill 50% of the animals; MDT = mean death temperature; SM_{100} = temperature required to kill 100% of the animals. Total experimental time is the mean time for the three replicates to complete the experiment. LT_{50}, MDT and SM_{100} were significantly different ($p < 0.001$, ANOVA) for different heating rates, whereas differences between acclimation temperatures and mussel sizes were non-significant. All values are based on three replicates with ≥20 mussels each.

indicated by completely extended siphons) as covariate. Starting temperature, heating rate, and mussel size were established as categorical independent variables, and each AULT outcome (LT_{50}, MDT, or SM_{100}) as simple dependent variables. MFT values were assessed by ANOVA followed by Tukey's *post hoc* tests for each acclimation and heating rate. Data were not transformed and controls were not included in the statistical analyses.

Results

LT_{50}, MDT and SM_{100} varied between 42.2 and 51°C (Table 1). The time to achieve 100% mortality increased with both the decreasing starting temperature and the decreasing rate of temperature increase. Slower heating rates were clearly and significantly associated with lower lethal temperatures (ANOVA $p < 0.001$ for LT_{50}, MDT, and SM_{100}). Decreasing the heating rate from 1°C per 5 min to 1°C per 30 min led to a 3°C drop in LT_{50}, 4°C drop in MDT, and 5°C drop in SM_{100} (Table 1 and Figure 1). In contrast, neither mussel size nor starting temperature had a significant impact on the outcome of the experiments (ANOVA, $p > 0.444$ and $p > 0.129$, respectively). Post-assay recovery of unresponsive mussels was very rare and was always <5% (1 mussel) of the total of each experimental group. Mortality was always 0% in all control groups.

Exponential regressions indicated that all AULT curves (LT_{50}, MDT, and SM_{100}) had a similar behavior. In general terms, the temperatures needed to kill the mussels were higher and the change more rapid when heating was faster. As heating rates declined, lethal temperatures (ie LT_{50}, MDT, and SM_{100}) tended to become increasingly similar. Since differences between size classes and starting temperatures were not significant, curves were based on pooled data for all acclimation temperatures and both size classes (Figure 1).

For all experimental groups, the highest filtering activity (PFT) was recorded at 31 ± 3.6°C. Differences between size classes, starting temperatures, and heating rates were not significant (ANCOVA, $p > 0.054$). Also, the proportions of actively filtering mussels were not associated with PFT values (ANCOVA, $p > 0.536$). The maximum filtration temperature (MFT) varied between 32 and 40°C, increasing with starting temperature ($p < 0.001$, ANOVA; since differences between size classes were not significant, data for small and large mussels were pooled, Figure 2).

Discussion

Total mortalities of *L. fortunei* (SM_{100}) exposed to gradually increasing temperatures occurred at 43.5–51.0°C. These values were not associated with acclimation temperature or mussel size. Rather, SM_{100} values were significantly coupled with water heating rates, with slow rates (1°C/30 min) yielding total mortalities at temperatures >5°C lower than faster ones (1°C/15 or 5 min). The reason for this relationship, also noticed in other bivalves under similar experimental conditions (eg the zebra mussel, *D. polymorpha*, invasive in USA and Europe; McMahon and Ussery 1995), is most probably a delay in the biological response of the animals to the deleterious thermal conditions. In practice, this implies that in biofouling control, operational constraints that limit the temperature increase rate can be compensated by increasing the treatment time.

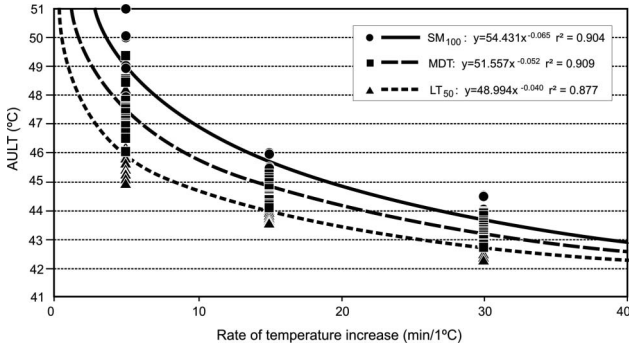

Figure 1. Exponential regressions of acute upper lethal temperatures (AULT) *vs* rate of temperature increase (minutes per°C) to achieve effective control of *L. fortunei*. Note: SM_{100} = temperature required to kill 100% of the animals in each experimental treatment; MDT = mean death temperature; LT_{50} = temperature required to kill 50% of the animals.

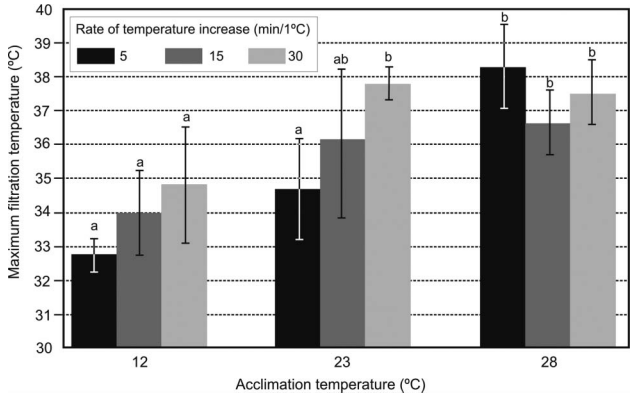

Figure 2. Highest temperatures at which filtration activity was observed ('maximum filtration temperature' – MFT) for different starting temperatures and temperature increase rates (mean ± 1 SD). Note: a, ab, b: significant differences ($p < 0.040$, ANOVA, Tukey's *post hoc* test).

At temperatures >40°C, *L. fortunei* stopped all feeding activities (Figure 2) and closed their valves until death. This behavior has been documented for mussels subjected to sudden temperature changes. Receptors located in the mantle cavity trigger the closing of the valves (Trueman and Lowe 1971), forcing the animals to use stored food reserves and anaerobic respiration until energy resources are depleted or metabolic wastes reach a toxic level (Bayne et al. 1976). The physiological responses to elevated temperatures also include degeneration of the gill filaments and histological changes in the stomach and intestine (Head 1962; Gonzalez and Yevich 1976).

The results indicate that *L. fortunei* is more resistant to heat stress than the other widespread invasive freshwater fouling bivalve, the zebra mussel *D. polymorpha*. 100% mortality of *D. polymorpha* occurs at 39°C at a heating rate of 1°C/30 min, 40°C at a heating rate of 1°C/15 min, and 41°C at a heating rate of 1°C/5 min (McMahon and Ussery 1995). Under similar experimental conditions, 100% mortality of *L. fortunei* occurs at temperatures 5–8°C higher (44, 45, and 49°C, respectively). Interestingly, as opposed to previous results with *D. polymorpha* (Griffiths 1992; Claudi and Mackie 1994; McMahon and Ussery 1995; Rajagopal et al. 1997), the upper lethal temperatures for *L. fortunei* did not vary with acclimation temperature. This may be the result of the fact that *Limnoperna* is an eurythermic organism, capable of adapting to swift temperature changes.

The fact that *Limnoperna* is considerably more tolerant to heat stress than *Dreissena* can be related to the prevailing thermal regimes of their areas of origin and of their current geographic ranges. Although *Dreissena* has been shown to tolerate water temperatures up to 30°C (reviewed in Karatayev et al. 1998, 2006), it is native to the Ponto-Caspian basin, where the climate is arid, sharply continental, with freezing winter temperatures. Its invasive area (most of Europe and eastern North America) is climatically heterogeneous, but mostly cold to temperate, where winter water temperatures around 0°C are common. The indigenous range of *Limnoperna*, on the other hand, is tropical and subtropical Southeast Asia, where water temperatures vary between *ca* 14°C in winter and >30°C in summer (Mizuno and Mori 1970). In its invasive area in South America, the temperature of lakes and rivers is quite similar (~14 to 33°C, Darrigran 2002). In tropical waters of Brazil, *Limnoperna* has been documented surviving in water temperatures of ~30°C for about 7 months of the year, and undergoing larval development in temperatures up to 33°C (Oliveira et al. 2010). However, despite its clear affinity for warmer waters (in the present study the highest filtering activity of the species was recorded at 31°C), *Limnoperna* has been observed to thrive at temperatures as low as 5–8°C (Magara et al. 2001; Goto 2002), and even around 0°C (Choi and Shin 1985). Thus, as opposed to some predictions (eg Oliveira et al. 2010), it is probable that cold water temperatures will have a limited effect on the expansion of *Limnoperna* into higher latitude areas. This ample thermal span may not only define a wider tolerance, but also confer *Limnoperna* with the ability to adapt rapidly to swift temperature changes, a trait that seems to be reflected in the lack of association between the upper lethal temperatures and acclimation temperatures (Table 1).

Interestingly, while the upper thermal limits of these two invaders are very similar (~33–35°C; Karatayev et al. 2006, 2007), their resistance to heat stress is quite different (see above). This suggests that, as opposed to environmental conditions in the indigenous geographic area, the upper thermal limits are not an adequate indicator of resistance to thermal treatment in these species.

Of the three indicators of heat treatment efficiency assessed in this work, SM_{100} is obviously the most relevant for industry. However, LT_{50} and MDT may also be useful when operational constraints impose limitations on maximum temperatures and heating rates because they provide guidelines for implementing more gradual biofouling control protocols allowing the reduction (rather than elimination) of the mussel populations. Such strategies may also be necessary to avoid massive detachment of mussel colonies in heavily fouled installations and subsequent clogging of system components by these clumps. Additionally, LT_{50} and MDT are useful for physiological assessments of mussel behavior.

Thermal treatment is economical and environmentally safer than most other control methods, especially chemical treatments (Claudi and Mackie 1994). Heat treatment is usually conducted by recirculating (rather than discharging) water heated in the condensers back to the pre-condenser sections of a cooling system. This process is repeated until the water has reached an appropriate temperature to kill the mussels. Different protocols at temperatures of 35–43°C have been developed, including 1–10 h treatments, with frequencies of once every 3–6 weeks to 3–4 treatments per year (Chadwick et al. 1950; Fox and Coheran 1957; Stock and Strachan 1977; Whitehouse et al. 1985; Jenner et al. 1998). Temperature differences between intake and outfall water (ΔT) can be as high as 20°C (Stock and Strachan 1977; Jenner 1982). In the lower Río de la Plata basin, the water temperature is ~28°C during the summer. Therefore, the ΔT required to kill *Limnoperna* in the cooling system is ~16–19°C. This may involve final treatment temperatures ~44–47°C at heating rates

about 1°C/10–30 min, roughly the rate achievable at most power plants (Jenner 1982; Whitehouse et al. 1985). Operational treatment times for this range would be between 3 and 8 h. Plants capable of applying a longer treatment (heating rates of more than 1°C/30 min) would need a lower ΔT than those that need to return to normal operational conditions faster (Figure 1). Application of acute thermal treatments during the rest of the year (eg spring, winter) will require a longer duration of lethal temperature. Thus, at heating rates of 1°C/10–30 min about 4–15 h may be necessary. In readily accessible installations, hot water spraying (Morse 2009; Comeau et al. 2011) or steam injection (Miller et al. 1992) can be used to complement the effects of thermal treatment.

Intervals between heat treatments must be defined based on the reproductive activity and growth rates of the organisms to be treated. Optimum cost-to-benefit ratios are achieved when the treatment is aimed at limiting the maximum size of the mussels inside the installations. In comparison with small (5–10 mm) individuals, large ones (>15 mm) generate rougher internal coatings on the pipes interfering with the flow, are more firmly attached, have harder shells, and can clog the narrow (usually *ca* 20 mm) heat exchanger tubes. Furthermore, dead mussels detach in large numbers from the colonized surfaces a few days or weeks after the treatment. Clumps of large animals with hard shells can clog pipes, sieves, filters and other components, whereas small ones are often not retained, or are easily destroyed and eliminated. In Paraná-Río de la Plata waters *L. fortunei* reproduces continuously for 9–10 months of the year (Boltovskoy et al. 2009), and grows to *ca* 20 mm during the first year (Boltovskoy and Cataldo 1999); thus, 3–5 thermal treatments per year would limit the maximum size of the fouling animals to about 5 mm, which is a relatively harmless size.

Although thermal manipulation is currently used as a successful mussel biofouling control method, its application has some restrictions. Industrial installations must anticipate alternatives to allow reverse and alternative water flows. These provisions for the cooling water system are generally required at an early stage of plant design. *A posteriori* adaptations are often expensive or technically difficult (Jenner and Janssen-Mommen 1993). In addition, the method is limited to industries where excess heat is available. Furthermore, some components may not be amenable to heat treatment because of their remoteness (eg service water systems), where heat loss could make the method ineffective. Complications associated with thermal expansion of equipment and piping, as well as environmental regulations on maximum effluent temperature (Rajagopal et al. 1997), may also limit the usefulness of this approach.

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