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PRIMARY RESEARCH PAPER

Ecological interactions between invasive and native fouling species in the reservoir of a hydroelectric plant

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Abstract In this study, we investigate the main ecological interactions between fouling aquatic organisms (both invasive and native) present in the reservoir of the Governador José Richa hydroelectric plant, located in southern Brazil, and to identify the most suitable period for the interruption of machinery operation for cleaning and maintenance of the hydraulic systems of this plant. A total of 32 experimental plates were fixed to a metallic structure positioned close to the plant's water intake. Three species of invasive fouling were identified in our samples (*Limnoperna fortunei* [Mollusca], *Cordylophora* sp., and *Hydra* sp. [Cnidaria]) and six native taxa belonging to the phyla Protozoa, Ciliophora, Amoebozoa, and Arthropoda. Spring and summer were the seasons with the highest fouling rates, as well as densities of fouling organisms. The highest levels of diversity were recorded during the colder seasons. Several interactions between the organisms were identified, such as mutualism, commensalism, competition, epibiosis, cannibalism, and predation. The data obtained suggest that, from the biological point of view, the most suitable period for machine shutdown destined for the removal of biological fouling in the

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hydraulic systems of the studied plant is between the end of spring and the beginning of summer.

Keywords Ecological succession · Facilitation · Freshwater environment · Biofouling · Seasonality

Introduction

Fouling invasive aquatic organisms have caused severe economic impacts around the world (Morton, 1977; Callow, 1993; Simberloff & Von Holle, 1999; Pimentel et al., 2001; Ricciardi & MacIsaac, 2008; Nakano & Strayer, 2014; Simberloff & Vitule, 2014). There have been records of clogging of pipes in water collection and treatment stations (Melo & Bott, 1997; Pu et al., 2009; Rajagopal & van der Velde, 2012). Industries such as pulp and paper mills are also frequently impacted by fouling organisms, as these sectors depend directly on the capture of water from natural bodies to carry out their production processes (Coetser & Cloete, 2005; Rajagopal & van der Velde, 2012). In these cases, the damage caused by fouling organisms is associated with both increased corrosion rates and clogging of hydraulic structures (Characklis, 1981; Melo & Bott, 1997; Pu et al., 2009; Martin et al., 2016; Farhat et al., 2019; Singh et al., 2020). However, the most widely affected sector has been hydroelectric power generation (Armour et al., 1993; MacIsaac, 1996; Cataldo, 2001; Boltovskoy et al., 2006; Portella et al., 2009; Boltovskoy & Correa, 2015; Mansur et al., 2016; Boltovskoy, 2017; Jernelöv, 2017).

In hydroelectric projects affected by fouling, the frequency of interventions aimed at cleaning and maintaining hydraulic structures increases due to the accumulation of biological fouling (e.g., molluscs, cnidarians, protozoans), with a consequent increase in operating costs (Flemming & Grohmann, 2008b; Cloete 2010; Flemming, 2011; Booy et al., 2017; Nelson, 2019). Each machine stoppage requires skilled labor to carry out cleaning activities, in addition to the interruption of energy production during the entire cleaning period. Frota et al. (2014), based on the value of the energy priced in the Brazilian spot market, concluded that the lost profits for the energy not generated in a single day of maintenance of a 44 MW Francis turbine would be US$ 180,000. The associated economic impact is even greater when considering that machine shutdown for maintenance and cleaning are always greater than 24 h (Flemming, 2002; Grohmann, 2008a; Pucherelli et al., 2018). Therefore, identifying the most suitable periods for machine shutdowns for maintenance and cleaning would allow the optimization of efforts and costs in the mid- and long-term, given that it would allow for maintenance efforts to be more effective and concentrated in time, which in turn would minimize control efforts in the intervening months (Grohmann, 2008c; Venkatesan & Murthy, 2008; Oreska & Aldridge, 2011; Frota et al., 2014; Boltovskoy et al., 2015b; Latombe et al., 2017).

In South America, three fouling invasive aquatic species have been reported to cause significant operational and economic losses to companies in the hydroelectric sector: the Asian clam, *Corbicula fluminea* (OF Müller, 1774), the cnidarian *Cordylophora caspia* (Pallas, 1771), and the golden mussel *Limnoperna fortunei* (Dunker, 1857). *Corbicula fluminea* obstructs heat exchangers of plants due to the accumulation of their shells (Karatayev et al., 2005; Ludwig et al., 2014; Mansur et al., 2016). *Cordylophora caspia* affects hydraulic pipes, filters, and protective grids (Danrigran & De Drago, 2000; Portella et al., 2009; Sylvester et al., 2011; Nakano & Strayer, 2014). Finally, *L. fortunei* causes damage to the protection grids (Darrigran, 2002), filters, generators, floodgates (Boltovskoy et al., 2006), pipes, and heat exchangers (Cataldo et al., 2003; Darrigran & Damborenea, 2011; Uliano-Silva et al., 2013).

In addition to the economic impacts, fouling aquatic organisms have generated several negative impacts on the ecosystem in freshwater environments, interfering on the food webs of native species (David et al., 2017; Emery-Butcher et al., 2020). There are relatively well-documented cases of competition between these organisms and incumbent species for food and/or space, as well as shifts of nutrient cycling, among other environmental disturbances (Ricciardi & MacIsaac, 2011; David et al., 2017). Invasive species often interact with each other and often act as "facilitators" (a term that refers to those species that have direct positive effects on other species) (Hacker & Gaines, 1997). This interaction can favor the increase in density or biomass of at least one of the involved species, which can facilitate the bioinvasion process (Ricciardi & MacIsaac, 2000; Rodriguez, 2006; Velde & Rajagopal, 2006; Silknetter et al., 2019). Thus, this type of interaction would contribute to the increase in the number of establishment or spread of species in aquatic environments into aquatic environments (Simberloff & Von Holle, 1999). The impacts of facilitating species are more frequent when they favor or provide a limiting resource, increasing the complexity of the habitat, functionally replacing a native species or competing for resources and ecological niche (Ricciardi et al., 1996; Simberloff & Von Holle, 1999; Ricciardi, 2001; Simberloff, 2006; Kéfi et al., 2016). The present study aimed to investigate the main ecological interactions between the invasive fouling aquatic species and the native species present in the reservoir of a hydroelectric plant located in the southern region of Brazil and to evaluate the most suitable period for machine shutdown for cleaning and maintenance of the hydraulic systems of this plant.

Methods

Study design

The experiment was carried out between September 2018 and December 2019, at the HPP Governador José Richa reservoir (25° 32′ 34.99″ S, 53° 29′ 45.82″ W), located in the Lower Iguaçu River section, in the border between the municipalities of Capitão Leônidas Marques and Nova Prata do Iguaçu, state of Paraná, Brazil. Samples were obtained using polystyrene experimental settlement plates (15 × 15 cm), fixed with nylon clamps to a metallic structure of 0.58 m^2. This structure was positioned one meter below the surface and was fixed by ropes to the log boom located near the dam of the HPP. For five seasons (Spring/2018: October, November, and December; Summer/2019: January, February, and March; Autumn/2019: April, May, and June; Winter/2019: July, August, and September; Spring /2019: October, November, and December), a total of 32 experimental plates were sequentially installed, six plates (two replicas/month) in each season, and two more test plates that were installed in the first month (September 2018) and removed only in the last month (December 2019). Each month, two experimental plates were removed, so that at the end of the season, all six seasonal plates had been removed (two plates/month). At the beginning of the next season, the procedure was repeated (Fig. 1).

The experimental settlement plates removed from the floating structures were packed in plastic bags. The biological material was fixed in 6% formaldehyde and preserved in 70% ethanol. Automated hourly measurement of the reservoir water temperature during the 15 months of the study was carried out and the data made available by Companhia Paranaense de Energia.

Analysis of experimental plates

In the laboratory, all experimental settlement plates were photographed, both with a digital camera (Nikon, Coolpix B500 Brindes, Japan) and in a stereoscopic microscope (Zeiss, Stereo Discovery.V8 Crisp, Germany), in order to organize an image database for visual analysis of the fouling process. The images were analyzed using the ImageJ software (version 1.52a) (Schneider et al., 2012) to identify the recruitment pattern and the degree of occupation of the experimental plates. The calculation of the coverage area in each experimental plate was performed using the Watershed plugin, a tool that calculates based on the intensity or gray level of the pixels present (Papadopulos et al., 2007). The values were then transformed into the percentage of the fouled area in relation to the total area of the plate. After measuring the area occupied by fouling organisms, macroscopic individuals (> 1 cm) were removed from the experimental plates, with the aid of surgical instruments, fixed in 4% formaldehyde buffer, preserved in 70% alcohol, identified to the lowest possible taxonomic level, and quantified. The mollusks were also weighed to obtain the wet total weight (tissue and shell), on a scale (Bell Engineering, S2202h—2200 g, Italy), making it possible to calculate the relative biomass (g/cm^2).

For the identification and quantification of microscopic organisms (< 1 cm), two methodological procedures were established. When the incrusted area was greater than 30% of the total area of the experimental settlement plate (as observed in Fig. 2a), subsampling was performed to quantify the organisms. For this purpose, a standardized grid was used, containing 225 squares (1 × 1 cm), of which 20 (8.8% of the total area) were analyzed. The selection of the squares was carried out randomly over the entire plate, including non-fouled surfaces (Fig. 2b), following the methodology proposed by Borges (2013). After this procedure, the biological material embedded in these

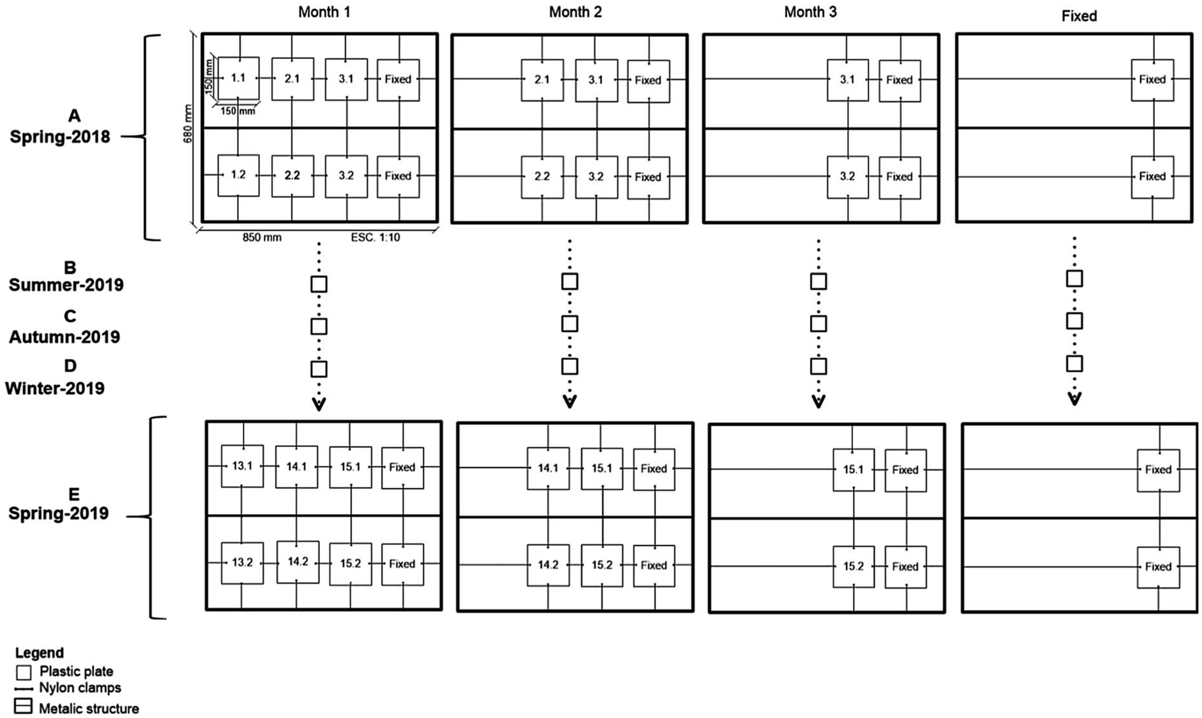


Fig. 1 Schematic representation of the supporting structure of the experimental settlement plates and the methodological procedures adopted: at the beginning of each season, the structure had eight experimental plates; at the end of each month, two of them were removed for analysis of incrustations and two remaining plates ("fixed") were removed after 15 months of monitoring; **A** Spring-2018, **B** Summer-2019, **C** Autumn-2019, **D** Winter-2019, and **E** Springer-2019

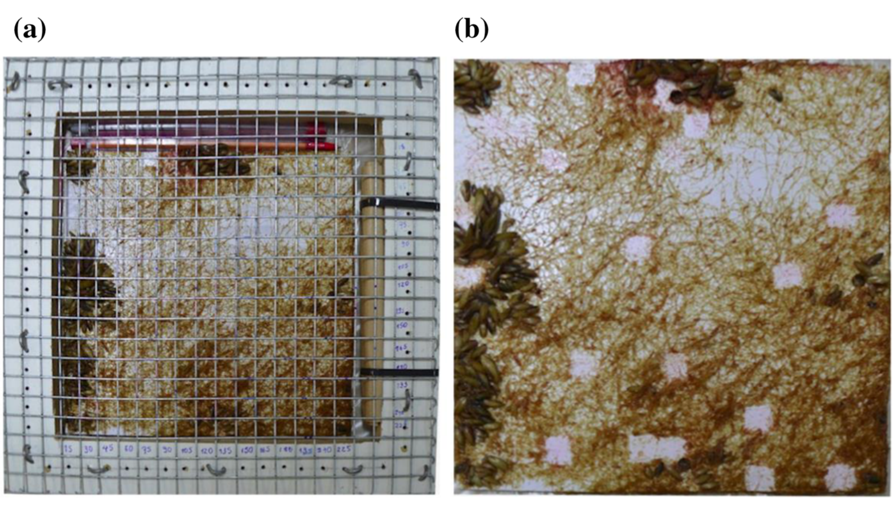


Fig. 2 Auxiliary structure for analyzing recruitment patterns of fouling and native invasive aquatic groups. **a** Grid with 225 squares (1 × 1 cm) showing the pattern of visualization of the incrustation on the experimental settlement plate, below the grid; **b** experimental settlement plate after taking samples in the 20 random squares

selected cells was removed with the aid of a scalpel, stained with cane rose, and identified using a stereoscopic microscope (Pinto-Coelho, 2004). Alternatively, if the fouling area covered 30% or less of the experimental settlement plates, they were scrapped, the material stained with a cane rose and analyzed in a stereomicroscope. The relative density of each taxon on each plate was directly calculated for Amoebidae, Daphniidae, Calocalanidae, Chironomidae, Vaginicolidae, Centropyxidae, and Mytilidae. However, obtaining reliable counts for Cnidaria is made dificult by the frequent presence of fragmented individuals in the samples, mainly in the case of Cordylophoridae. Therefore, the analysis of Cordylophoridae and Hydridae was done qualitatively, considering the number of hydrorrhizae (filaments) or hydrae present in each sample. The recruitment patterns, as well as interactions between the groups found, were based on direct observations under a stereoscopic microscope. The observational data were supplemented with bibliographic information about the reproductive biology, behavior, and ecological relationships between individuals invading limnic environments, as well as between invasive and native species.

Data analysis

We used the Shannon–Wiener diversity index to characterize the diversity of organisms by sampling period (Pielou, 1966). Normality and homogeneity of the variances of density, biomass, diversity, and temperature data were analyzed by the Levene and Cochran tests; the homoscedasticity was analyzed using the residuals of variance. The Kruskal–Wallis analysis was used to determine the significant differences between the variables tested, always at the 95% confidence level. Spearman's correlation coefficient was applied to assess the degree of association between dependent variables (coverage area, density, biomass, diversity) and water temperature (independent variable). The analyses were performed using the software Statistica 10.0 (StatSoft®).

Results

Environmental conditions

The highest average water temperatures in the reservoir were recorded in January 2019 and the lowest in August 2019. When temperatures are compared across seasons, they were similar ($P > 0.05$) in spring (2018

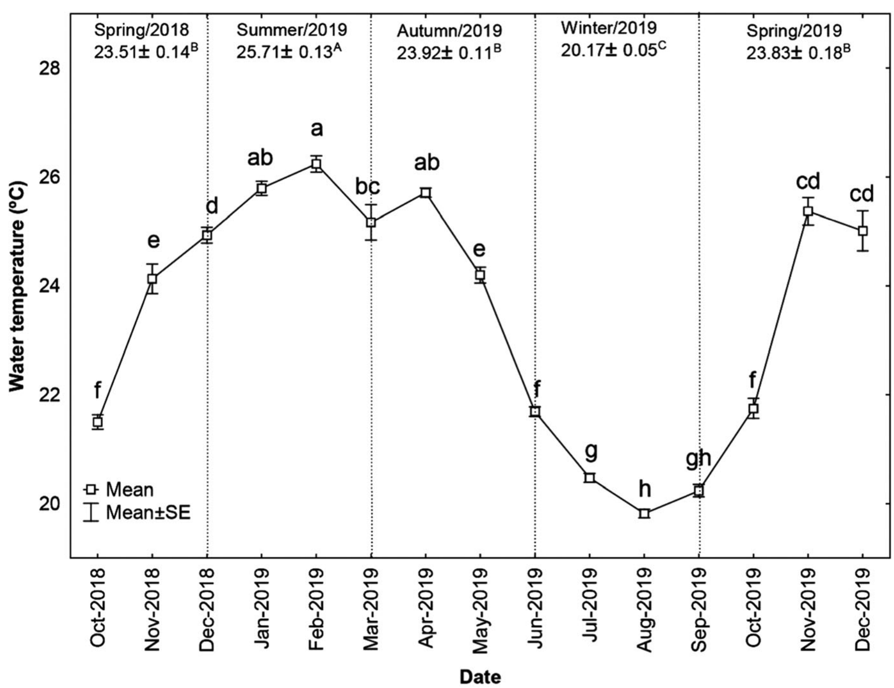


Fig. 3 Temporal variation (average values and standard error) of the water temperature in the reservoir of the HPP José Richa, from October 2018 to December 2019. Similar capital letters indicate statistical significance between the seasons and the lower letters between the months of the year

and 2019) and in autumn (2019), but higher in summer and lower in winter (Fig. 3).

Identification of the recorded taxa

Macro and microinvertebrate organisms present in the analyzed samples were identified, and three of them (*Limnoperna fortunei*, *Cordylophora* sp. and *Hydra* sp.) are considered fouling invasive species belonging to the phyla Mollusca and Cnidaria (Table 1).

Recruitment pattern of identified taxa

The plates kept submerged for 15 consecutive months had, on average, 79.3% of their area occupied by colonizing organisms. The highest colonization rate was recorded in the spring of 2018 (56.0%) of the occupied area by colonizing organisms. In relation to the seasons, the highest occupations involved plates obtained during the spring of 2018, which showed 56.0% of their occupied area at the end of three months. The values quantified in these periods were significantly higher than those observed in other seasons (Fig. 4a). The average density of organisms present in the test experimental settlement plates was higher in the spring 2018 and the summer 2019 (Fig. 4b). The highest rates of seasonal diversity were recorded in the winter and autumn of 2019, with lower diversities observed on the test experimental settlement plates kept submerged for 15 months and in the spring of 2019 (Fig. 4c). The period considered most critical regarding the presence of fouling invasive organisms took place between late spring and early summer. In the following seasons, the relative density of these organisms was significantly reduced. Particularly in the case of specimens (plates) kept submerged for 15 months, the density was close to the values found in early summer, with the difference that in this case, there were practically only one encrusted species (*L. fortunei*) (Fig. 4d).

The average density of organisms was 10.4 individuals/cm^2 during the spring 2018, 6.3 in the summer 2019, 0.3 in the spring 2019, 0.2 in the autumn 2019, and 0.1 in the winter 2019. *Limnoperna fortunei* was the predominant invasive organism throughout the analyzed period. The average density of *L. fortunei* was higher in the spring 2018 and the summer 2019. This species also completely dominated the experimental settlement plates kept submerged for 15 consecutive months (Fig. 5). The largest biomass of *L. fortunei* was recorded in the experimental settlement plates kept submerged for 15 months in the reservoir. The highest seasonal biomasses were recorded in winter (Table 2). There was a significant ($P < 0.05$) but low correlation ($r = -0.39$) between the biomass of *L. fortunei* and water temperature.

Ecological interactions between the families of the identified organisms

The ecological interactions between the main groups identified in the experimental settlement plates were classified as positive and direct (mutualism), positive and indirect (commensalism), negative and direct (competition), negative and indirect (epibiosis, cannibalism, and predation) (Fig. 6). Mutualism was

Table 1 Taxonomic classification of families identified in the experimental settlement plates in the reservoir of the HPP Gov. José Richa

Phylum	Class	Order	Family	Species	Category
Protozoa	Lobosa	Amoebida	Amoebidae	NI*	Native
Arthropoda	Branchiopoda	Cladocera	Daphniidae	NI	Native
Arthropoda	Maxillopoda	Calanoida	Calocalanidae	NI	Native
Arthropoda	Insecta	Diptera	Chironomidae	NI	Native
Ciliophora	Oligohymenophorea	Sessilida	Vaginicolidae	NI	Native
Amoebozoa	Tubulinea	Tubulunida	Centropyxidae	NI	Native
Mollusca	Bivalvia	Mytilida	Mytilidae	*Limnoperna fortunei*	Invasive
Cnidaria	Hydrozoa	Anthoathecata	Cordylophoridae	*Cordylophora* sp.	Invasive
Cnidaria	Hydrozoa	Anthoathecata	Hydridae	*Hydra* sp.	Invasive

*NI - Taxa that could not be identified at the species level

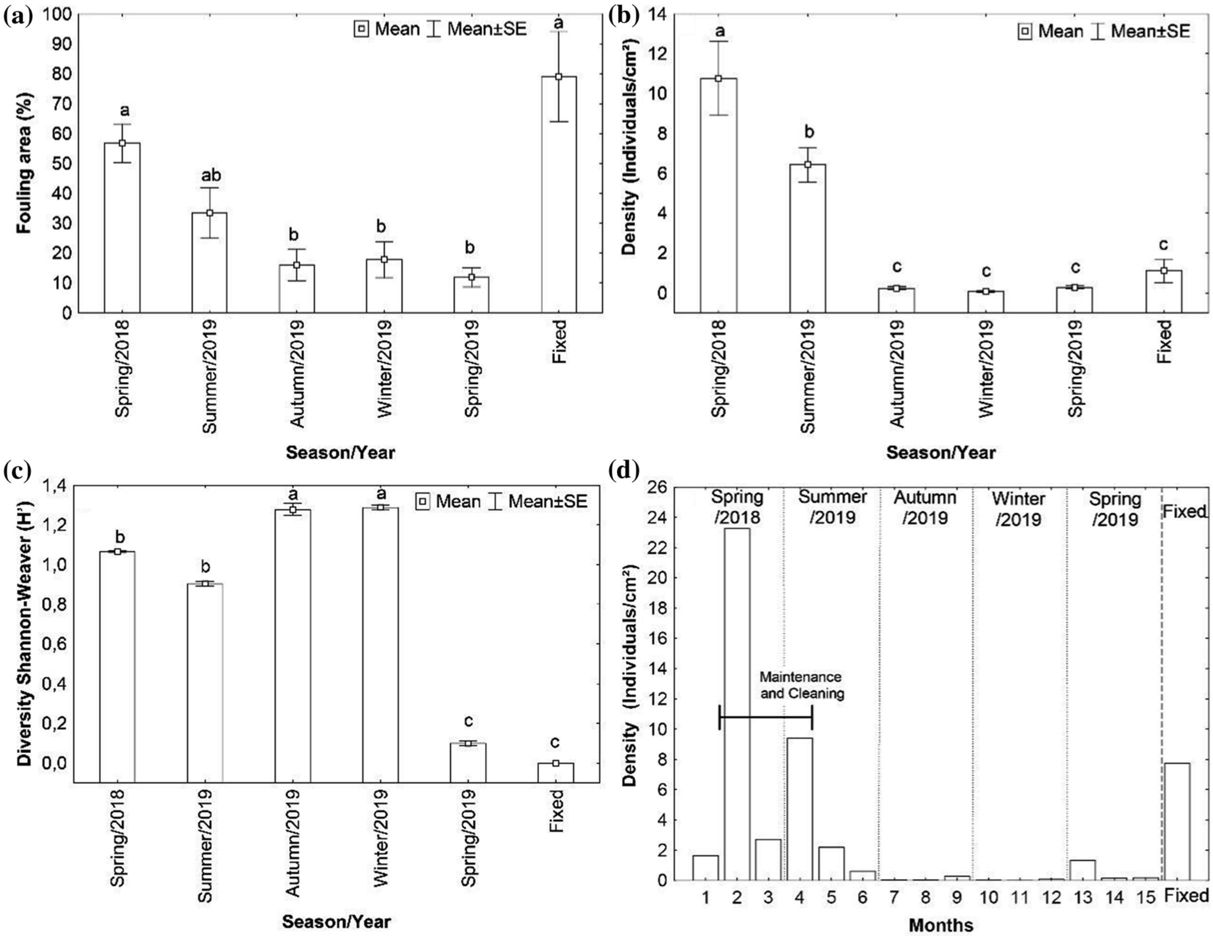


Fig. 4 **a** The area occupied by invasive and native organisms. **b** Seasonal variation in the total density of identified organisms. **c** Seasonal variation of the Shannon–Wiener diversity index. **d** Monthly density and the recommended period for the maintenance and cleaning of the hydraulic installations (Month: 2- November; 3-December; and 4- January) of the Governador José Richa hydroelectric power plant

observed between adult and juvenile individuals of the family Mytilidae, as well as between individuals of the families Cordylophoridae and Mytilidae. Commensalism occurred between Mytilidae and insect larvae of the Chironomidae family. Competition for food and space was observed among fouling invaders (Cordylophoridae, Mytilidae, and Hydridae), especially when the space available for fouling on the substrate was more limited. Competition was observed between invasive and native organisms (Daphniidae, Calocalanidae, Chironomidae, Vaginicolidae, and Centropyxidae). Cannibalism was identified only in adult individuals of Mytilidae, which can feed on larvae of the same species. Epibiosis was characterized by the use of organisms from certain groups, such as basibionts. For example, individuals from Hydridae were used as substrate by Cordylophoridae, Mytilidae, and Centropyxidae. Cordylophoridae, on the other hand, were recorded hosting Hydridae, Centropyxidae, and Mytilidae. Among the organisms involved in epibiosis, the relationship between Cordylophoridae and Mytilidae was the most evident and recorded on several occasions. Predation was observed, with Hydridae preying on Chironomidae, Daphniidae, and Calocalanidae. Cordylophoridae can feed on larvae of Mytilidae, as observed in the study by Molina et al. (2015), as well as individuals from the family Daphniidae and Calocalanidae in the juvenile and adult phases. Mytilidae can prey on protozoa including Vaginicolidae and Centropyxidae, and microcrustaceans in the juvenile stage like Daphniidae and Calocalanidae.

Discussion

In subtropical aquatic environments, higher temperatures tend to have positive effects on the rates of fouling and colonization of aquatic communities (Rodrigues et al., 2015; Lansac-Tôha et al., 2019), especially on the density of micro- and macroinvertebrates (Belz et al., 2010; Borges, 2014; Borges et al., 2017). Temperature interferes with reproductive cycles, the supply of recruits, and the trophic conditions of aquatic environments (McPherson et al., 1984; Patil & Anil, 2005; Cifuentes et al., 2010; Chen et al., 2019; Mieczan & Rudyk-Leuska, 2019). In the present study, water temperature did not positively influence the composition or abundance of most identified communities. Temperature correlated only with the biomass of *L. fortunei*, with a weak, negative correlation ($r = -0.39$). On the other hand, the highest rates of fouling and density of organisms in the experimental settlement plates were recorded during spring and summer. The density of organisms present on the plates installed during spring 2018 and spring 2019 did not follow the same pattern of fouling or maximum achieved densities. This seasonal and interannual variation underscores the high degree of complexity of fouling processes by invasive aquatic organisms, which has also been reported in other studies (Underwood & Anderson, 1994; Berntsson & Jonsson, 2003; Dehmordi et al., 2011; Fortunato et al., 2017). It is possible, therefore, to postulate that other environmental factors may have contributed to the results, even those that were not individually monitored here, but were observed in other studies. Among these factors, we can highlight the availability of nutrients and food, precipitation patterns, incidence of sunlight (Melo & Bott, 1997; Pamplin et al., 2006; Fernandez & Navarrete, 2015; Masi et al., 2016; Navarrete et al., 2019), or related to the physical characteristics of the reservoir, such as hydrodynamics or its depth (Albano & Obenat, 2019), which might have contributed to the results obtained.

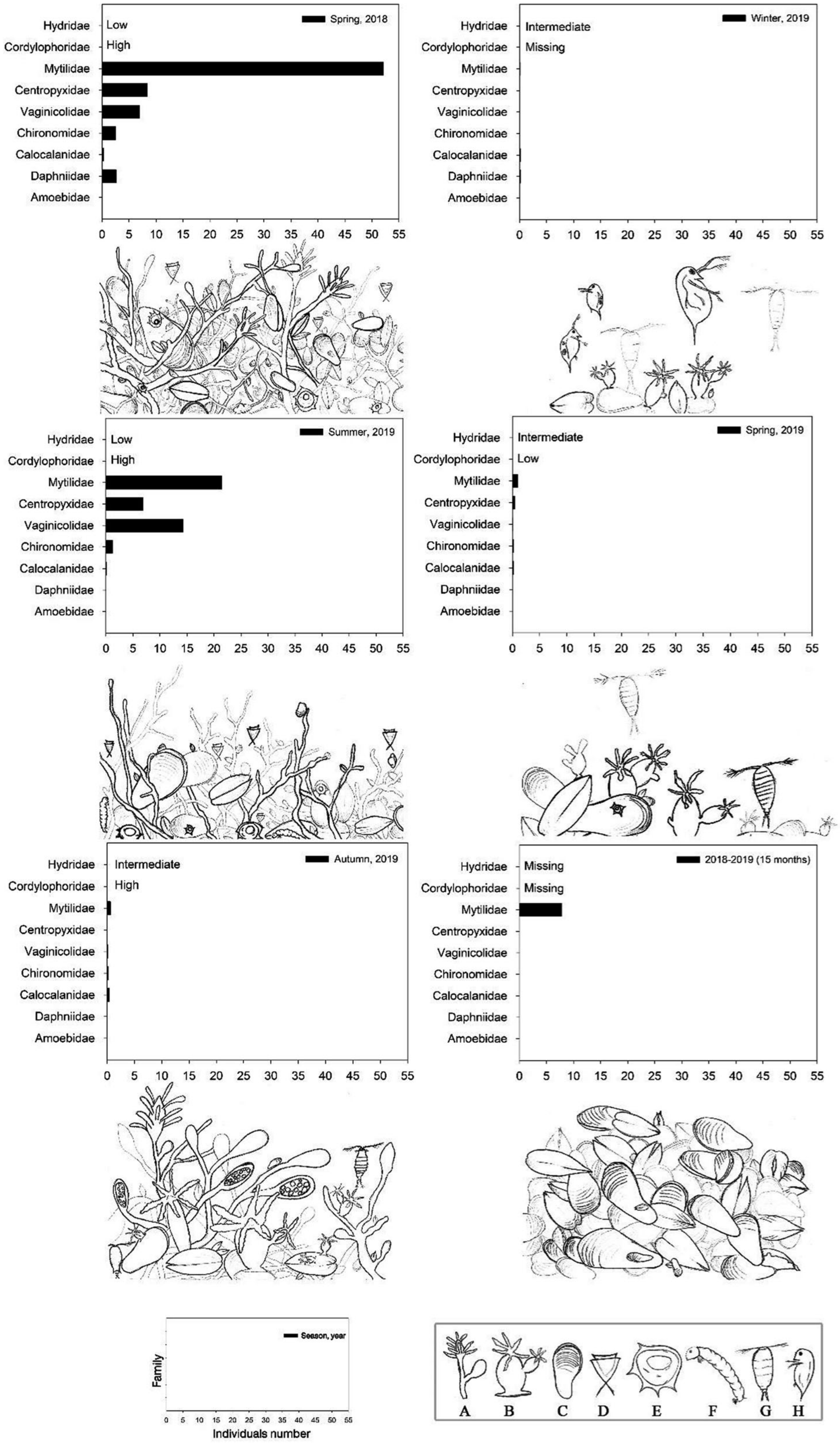
Both the density and the area occupied in the experimental plates by invading organisms were to those related to native organisms. It is known that the behavior of invasive species is associated with their

Fig. 5 Schematic representation of the ecological succession ▶ observed in the experimental settlement plates in the reservoir of the Governador José Richa HPP, indicating the groups of dominant organisms throughout the seasons: Spring 2018; Summer 2019; Autumn 2019; Winter 2019; Spring 2019. The experimental settlement plates kept submerged for 15 months ("Fixed" treatments are those that will remain for the entire 15 months). The values presented graphically represent the average density of the organisms. **a** Cordylophoridae, **b** Hydridae, **c** Mytilidae, **d** Vaginicolidae, **e** Centropyxidae, **f** Chironomidae, **g** Calocalanidae, and **h** Daphniidae

biological characteristics (such as high growth rates, the existence of successful reproduction strategies, and ease of dispersal) and, mainly, reproductive (early sexual maturity and high fertility), which facilitate the bioinvasion process. Such characteristics are present in *Cordylophota* sp. (Folino-Rorem, 2000; Folino-Rorem et al., 2006; Nakano & Strayer, 2014), *Hydra* sp. (Hobmayer et al., 2012; Rodrigues et al., 2016; Deserti et al., 2017), and *L. fortunei* (Darrigran, 2002; Boltovskoy, 2015a, b; Boltovskoy & Correa, 2015; Boltovskoy et al., 2015a).

The settlement periods of the studied groups were well defined, mainly for *L. fortunei*, in all monitored seasons. This observation coincides with Damborenea & Penchaszadeh (2006), which concluded that *L. fortunei* could produce sperm and oocytes continuously throughout the year. Boltovskoy & Correa (2015) showed that in about 80% of the time series studied in South American reservoirs, researchers had identified a density of at least 10 larvae/m^3 of golden mussel in the analyzed samples. In the present study, the highest occurrence of *L. fortunei* settlement occurred in spring 2018 and summer 2019 coinciding with the reproduction peaks already reported in several other studies (Magara et al., 2001; Canzi et al., 2005; Darrigran & Damborenea, 2006; Boltovskoy et al., 2009).

The biomass of *L. fortunei* was higher in those experimental settlement plates maintained throughout the study period. On these plates, the individuals present were predominantly adults. In adulthood, *L. fortunei* generally shows greater adaptation to ecological ranges and to stressful environmental factors (Liu et al., 2020). The smallest golden mussel biomass was observed in autumn 2019. This period was characterized by intermediate temperatures, which tend to limit the growth rates of individuals and interfere with the quality and availability of food (Boltovskoy et al.,



Spring, 2018
Hydridae Low
Cordylophoridae High
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
Winter, 2019
Hydridae Intermediate
Cordylophoridae Missing
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
Summer, 2019
Hydridae Low
Cordylophoridae High
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
Spring, 2019
Hydridae Intermediate
Cordylophoridae Low
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
Autumn, 2019
Hydridae Intermediate
Cordylophoridae High
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
2018-2019 (15 months)
Hydridae Missing
Cordylophoridae Missing
Mytilidae
Centropyxidae
Vaginicolidae
Chironomidae
Calocalanidae
Daphniidae
Amoebidae
0 5 10 15 20 25 30 35 40 45 50 55
Season, year
Family
0 5 10 15 20 25 30 35 40 45 50 55
Individuals number
A B C D E F G H

Table 2 Variation of the mean biomass of *Limnoperna fortunei* in the experimental settlement plates kept in the reservoir of Governador José Richa HPP. Different letters indicate statistical significance ($p < 0.05$) among seasons

Season/Year	The average number of specimens	Biomass (mg/cm^2) of *Limnoperna fortunei* Mean	SE
Spring, 2018	30	0.9[abc]	0.13
Summer, 2019	78	0.5[c]	0.04
Autumn, 2019	46	0.5[c]	0.07
Winter, 2019	40	1.1[a]	0.12
Spring, 2019	40	0.9[abc]	0.14
2018–2019 (15 months)	175	293.8[a]	87.50

2009; Nakano et al., 2011; Boltovskoy & Correa, 2015; Oliveira et al., 2015).

Over the course of ecological succession, the supporting organisms are the first to establish themselves (microorganisms, filamentous algae, diatoms, protozoa, and others) (Martín-Rodríguez et al., 2015; Silknetter et al., 2019), followed by macroinvertebrates (mollusks, insects, and cnidarians) (Abarzua & Jakubowski, 1995). *Cordylophora* sp. and *L. fortunei* were predominant in this process. The cnidarian has hydrorrhizae, a filamentous structure responsible for adhesion and incrustation on different substrates. These filaments end up serving as the preferred substrate for the settlement of *L. fortunei* larvae, which use them to adhere, protect themselves from local hydrodynamics, and develop during the first stages of life. Similar behavior has also been reported between *Cordylophora caspia* and *Dreissena polymorpha* (Pallas, 1771) in North America (Ackerman et al., 1994; Folino-Rorem et al., 2006; Pucherelli et al., 2016).

The trophic position and the capacity that each group has to occupy the substrate changes in the structuring of these communities over time. Some individuals end up dominating the substrates and making them more homogeneous (Ricciardi & MacIsaac, 2011; Simberloff & Ricciardi, 2020). In the present case, the highest levels of diversity occurred in a period of lower rates of incrustation of the experimental plates. As *L. fortunei* was the dominant species in almost all seasons, when it was less abundant, there was a greater opportunity for the colonization of the experimental plates by other organisms, which increased the diversity indexes. Spaccesi & Rodrigues (2012) also recorded lower rates of diversity in substrates dominated by *L. fortunei* in the La Plata River. The authors also report that diversity was also lower in periods of low temperatures (autumn and winter).

Experimental studies carried out in South American reservoirs that assess ecological interactions, including fouling and native invasive groups, are still relatively limited (Nakano et al., 2011; Boltovskoy & Correa, 2015). In the present case, it was possible to identify interactions with positive effects (mutualism and commensalism) and indirect negative effects (competition, cannibalism, epibiosis, and predation). The substrate used for the settlement can be a limiting resource in certain environments and, when mutualistic interactions occurred, in the present case, they involved the sharing of substrates by *L. fortunei* and *Cordylophora* sp. Portella et al. (2009) evaluated biological fouling in the same reservoir of HPP José Richa and reported the presence of these two invaders in coexistence, that contribute to operational and economic impacts to the plant. According to Simberloff & Von Holle (1999) and Gallardo & Aldridge (2018), mutualistic relationships between freshwater invaders are poorly studied in the literature. However, understanding the role of each group involved in mutualism is of great importance, given that the effects of both species individually, in addition to their ecological interactions, often lead to severe negative economic impacts (Green et al., 2011; Rolla et al., 2019; Wegner et al., 2019). This mutualistic relationship can also contribute to establishing and magnify the spread of secondary invaders at different levels of the ecosystem (Ricciardi & Reiswig, 1994; Ricciardi, 2001, 2015; Green et al., 2011).

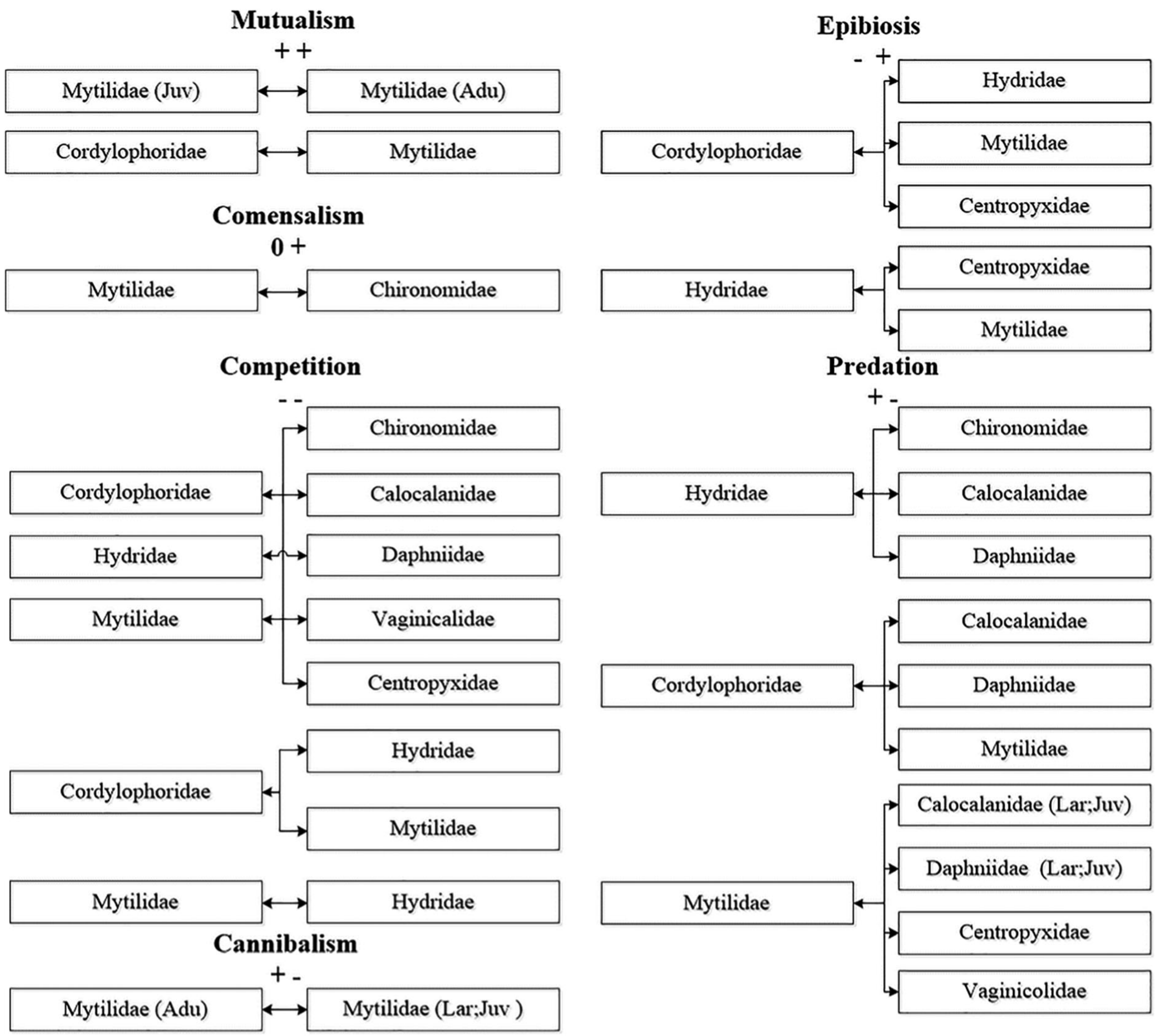


Fig. 6 Schematic representation of the ecological interactions recorded between the families of the fouling and native invader groups present in the experimental settlement plates positioned in the reservoir of the Governador José Richa HPP

Invaders also modify the habitats of native species and contribute to making these environments more homogeneous (Ricciardi & MacIsaac, 2011; Simberloff & Ricciardi, 2020). For example, *L. fortunei* may favor an increase in the number of macroinvertebrates in the Chironomidae family. This happens due to the accumulation of shells of the golden mussel clusters, which end up increasing the physical complexity of the substrate (Gutiérrez et al., 2003; Burlakova et al., 2012), as well as enriching these environments with the increase of stool bio-deposits and pseudofeces (Darrigran et al., 1998; Sardiña et al., 2008). This enrichment causes changes in the density of benthic fauna, as well as leading to the biological imbalance of these environments (Karatayev et al., 2007; Darrigran & Damborenea, 2011). Burlakova et al. (2012) evaluated the composition of communities in locations with the presence and absence of two ecosystem engineers: *L. fortunei* and *D. polymorpha*. Where the species were present, the authors observed an increase in the richness and density of native macroinvertebrates (Burlakova et al., 2012). However, over time, native communities tend to become more homogeneous (Stewart et al., 1998; Ricciardi, 2001;

Ricciardi & MacIsaac, 2011; Simberloff & Ricciardi, 2020).

Among the potential interactions, competition was the most prevalent, as in other (Jackson; Kuebbing & Nuñez, 2015). This relationship can happen for several reasons, including competition for territories, substrates, and food (Jones et al., 2012). *Limnoperna fortunei* and *Cordylophora* sp. compete for substrate, especially when they are scarce. These organisms are fixed in common structures (both species can be found in the same type of substrate), which makes them close at different times or stages of life during the bioinvasion process. Competition for substrates is also reported between *C. caspia* and *D. polymorpha* (Folino-Rorem et al., 2006; Pucherelli et al., 2016).

Cannibalism was recorded among adults and larvae of *L. fortunei*. Adult mollusks can feed on particles ranging in size from 4 to 1000 µm in length, which includes their own larvae (Molina et al., 2015). In studies with *D. polymorpha*, cannibalism was responsible for mortality rates of up to 70% (Maclsaac et al., 1991). In epibiosis, *Cordylophora* sp. and *Hydra* sp. can serve as a substrate for other groups, such as *L. fortunei* and individuals of the family Centropyxidae. The relationship between *Cordylophora* sp. and *L. fortunei* is the most evident and involves several stages during the fouling process. However, it is more noticeable when *L. fortunei* is in its settlement phase, when they prefer to settle in places protected from turbulent currents (Cataldo & Boltovskoy, 1999; Sylvester et al., 2007).

Simultaneously with epibiosis, the facilitation relationship can occur between these same invaders (*L. fortunei* and *Cordylophora* sp.). The colonies of *Cordylophora* sp. have a three-dimensional structure, which initially favors the settlement of *L. fortunei*. After settling on Cordylophora sp. colonies, the mussels develop a preference for harder substrates and to continue their development they start to colonize these hard substrates originally occupied by *Cordylophora* sp., compromising the survival of the organisms of this species. Epibiosis between zebra mussels and other different groups of fouling invaders is well studied, especially the sponges *Ephydatia fluviatilis* (Linnaeus, 1759) (Ricciardi et al., 1996; Gaino, 2005; Ricciardi, 2005), *Eunapius fragilis* (Leidy, 1851) (Molloy et al., 1997; Ricciardi, 2005); the bryozoans *Pectinatella magnifica* (Leidy, 1851), *Plumatella fungosa* (Pallas, 1768) (Ricciardi & Reiswig, 1994), *Lophopodella carteri* Hyatt, 1866 (Lauer et al., 1999; Cummings & Graf, 2010); and also with the cnidarian *Cordylophora caspia* (Pucherelli et al., 2016).

Predation has also been described for several groups in this study, for example, between *Cordylophora* sp. and larvae of *L. fortunei*. This cnidarian can also use juvenile and adult golden mussel shells as substrate (Olenin & Leppäkoski, 1999; Folino-Rorem et al., 2006). *Limnoperna fortunei* can prey on juvenile micro crustaceans, such as Daphniidae and Calocalanidae, as well as protozoa Vaginicolidae and Centropyxidae. Micro-crustaceans are among the favorite foods of the golden mussel, as they have a larger size and even greater biomass compared to phytoplankton (Molina et al., 2015).

It is recommended that maintenance and cleaning of hydraulic structures to remove biofouling should be carried out preferentially in late spring or early summer. This recommendation is based on abundance values, recruitment patterns, ecological succession, and the interactions observed between dominant groups in the José Richa HPP. This is the most critical period in terms of recruitment of young forms of fouling organisms and, in particular, *L. fortunei*, which is the species that most causes problems with the clogging of filters, grids, and pipes. In autumn and winter, biological fouling rates naturally fall by up to 80%, reducing the operational and economic risks of the machine shutdowns and cleaning. This conclusion is also supported by other studies, which reported decreased fouling levels and speed during colder seasons, which would be related to the heterothermia of invertebrates and their consequent dependence on temperature for regulating metabolic processes (Pörtner, 2002; Poloczanska et al., 2010); (Underwood & Anderson, 1994; Berntsson & Jonsson, 2003; Dehmordi et al., 2011; Fortunato et al., 2017). Therefore, by promoting the shutdown of machines and cleaning of hydraulic systems in the most critical period of this process, there would be less time for the establishment of colonies during the peak of spring and clean structures during the beginning of peak summer colonization, ensuring operating conditions.

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Data availability Raw data used in our analyses are available from the authors upon request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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