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Environmental variables driving the larval distribution of *Limnoperna fortunei* in the upper Paraná River floodplain, Brazil

Variáveis ambientais que direcionam a distribuição larval de *Limnoperna fortunei* na planície de inundação do alto rio Paraná, Brasil

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Abstract: Aim: To verify the temporal dynamics of *Limnoperna fortunei* larval stages and to identify the main environmental variables driving the larval density patterns in an area highly impacted by reservoirs. **Methods:** Samplings were performed quarterly, from February to December 2014, in 10 transects along to the Paraná River main channel. For each sample site, 100 L of water were filtered. The filtrated was fixed in alcohol 80%, and the larval stages were counted and classified under the optical microscope. Concomitant to biological collections we took some of the main water variables. We performed a Redundancy Analysis (RDA) in order to summarize the variations in densities of larval stages in relation to the main physical and chemical water variables. **Results:** We found a total of 200,590 *L. fortunei* larvae, in which 83.6% were identified as the initial stages. The most abundant months in *L. fortunei* larvae were December and February. The first two axes of RDA sum up 96% of the total data variation, and the most significant environmental variables explaining variations in larval densities were: water temperature, total nitrogen, electrical conductivity, phosphate, dissolved oxygen, depth and ammoniac ion. The warmer months were influenced by the major values of water temperature and depth, besides the higher densities of all larval stages. **Conclusions:** Our results indicate that *L. fortunei* reproduction follows a general pattern throughout the upper Paraná River floodplain, what seems to occur mainly between February and December. Thus, we suggest that measures for the *L. fortunei* control should be done during low-density periods (i.e., April to August), when the water level is low, and consequently, the dispersion of this species might be limited.

Keywords: area of environmental preservation; propagule pressure; golden mussel; reproduction.

Resumo: Objetivo: Verificar a dinâmica temporal dos estágios larvais de *Limnoperna fortunei*, e identificar as variáveis ambientais direcionadoras desses padrões, em uma área altamente impactada pela construção de reservatórios. **Métodos:** As amostragens foram realizadas trimestralmente, de

fevereiro a dezembro de 2014, em 10 transectos ao longo do canal principal do rio Paraná. Para cada local de amostragem, foram filtrados 100 L de água. O filtrado foi fixado em álcool 80%, e os estágios larvais foram contados e identificados sob microscópio óptico. Concomitantemente às coletas biológicas, avaliamos as principais variáveis limnológicas nos pontos de amostragem. Realizamos uma ordenação pela Análise de Redundância (RDA), para sumarizar a variação das densidades dos estágios larvais em relação as principais variáveis físicas e químicas da água. **Resultados:** Encontramos um total de 200.590 larvas de *L. fortunei*, do qual 83,6% foram identificados como estágios iniciais. As densidades mais elevadas de larvas de *L. fotunei* foram os meses de dezembro e fevereiro. Os dois primeiros eixos da RDA sumarizaram 96% da variação total dos dados, e as variáveis ambientais significativas para explicar as variações nas densidades larvais foram: temperatura da água, nitrogênio total, condutividade elétrica, fosfato, oxigênio dissolvido, profundidade, e íon amônio. Os meses quentes foram influenciados pela temperatura e profundidade, juntamente com as maiores densidades dos estágios larvais. **Conclusões:** Nossos resultados indicam que a reprodução segue um padrão geral ao longo de toda a planície, acontecendo principalmente nos meses de fevereiro e dezembro. Assim, sugerimos que medidas de controle de *L. fortunei* devem ser tomadas nos períodos de baixas densidades (junho e agosto), quando o nível da água está baixo, e consequentemente, sua dispersão está limitada.

Palavras-chave: área de preservação ambiental; pressão de propágulo; mexilhão dourado; reprodução.

1. Introduction

Limnoperna fortunei (Dunker, 1857) is an invasive bivalve in South America (Darrigran & Ezcurra de Drago, 2000), which was reported by the first time in 1991 at the Rio de la Plata, Argentina (Pastorino et al., 1993). The species was quickly dispersed between 1995 and 1996, and it was recorded in the lower basin of the Paraná River (Darrigran & Ezcurra de Drago, 2000), by which it spreads at a speed rate of 240 km per year (Darrigran, 2002). The first *L. fortunei* occurrence in Brazil dates of 1999 (Mansur et al., 1999). In this country, the bivalve has already been established in several States, such as Rio Grande do Sul (Mansur et al., 2003), Paraná (Takeda et al., 2003), São Paulo (Avelar et al., 2004), Mato Grosso do Sul and Mato Grosso (Oliveira et al., 2006).

This freshwater bivalve presents a planktonic larval stage (Darrigran & Ezcurra de Drago, 2000), which is its main way of propagule pressure (e.g., Simberloff, 2009; Ernandes-Silva et al., 2016b), while the adult form is normally related with fouling of individuals on the substrate (Darrigran & Damborenea, 2009). Thus, the wide distribution of *L. fortunei* in flooding areas might be related to high water periods (see Ernandes-Silva et al., 2016b), when connectivity increases among environments (Junk et al., 1989) and facilitates the displacement of both larvae by passive dispersion in the water and adults fouling at vessels traffic (Darrigran & Damborenea, 2009).

Since its first record, *L. fortunei* has been reproducing exponentially and reached densities of 150,000 ind.m^{-2} at some Argentina water bodies (Darrigran & Ezcurra de Drago, 2000). Cataldo & Boltovskoy (2000) have also registered high larval densities in this country near to the mouth of the Paraná River, with reaching 20,000 ind.m^{-3}. In this way, it is supposed that the high densities displayed by *L. fortunei*, promote its dominance over the resource uses (Baskin, 1994), and the consequent impact on the resident biota (e.g., Ricciardi & MacIsaac, 2000).

The upper Paraná River floodplain is one of the ecosystems that have been colonized by *L. fortunei.* The presence of *L. fortunei* in this area is worrisome, mainly because this floodplain is considered as an area of great biodiversity, which encompasses three major conservation areas (Brasil, 2002). Despite the native biota in the upper Paraná River floodplain is adapted to the marked temporal dynamic in physical and chemical water variables (Thomaz et al., 2007), it seems that *L. fortunei* achieve great success in its establishment in this area, and has been found throughout its total extension (Pestana et al., 2008, 2010; Ernandes-Silva et al., 2016a).

Once established, an invasive species such as *L. fortunei*, can hardly be eradicated (Oliveira et al., 2006). However, measures seeking to control their negative impacts can be taken by understanding the species biology, and the factors driving their density and distribution (Barbosa & Melo, 2009). Despite the fact that such kind of studies have been conducted with *L. fortunei* at the upper Paraná River floodplain (Pestana et al., 2008, 2010; Pinha et al., 2013; Ernandes-Silva et al., 2016a, b), these investigations were restricted only to a portion of the floodplain, showing patterns that might be local.

Considering the species invasion as a major threat to biodiversity, we analyzed the *L. fortunei* distribution across 230 km of extension of the

upper Paraná River floodplain in a portion located between Porto Primavera and Itaipu reservoirs. Our main objectives are i) to verify the temporal dynamics in the larval stages of this species, and ii) to identify the environmental variables driving the larval density patterns in an area highly impacted by dam constructions, a common environmental scenario in Brazil.

2. Material and Methods

2.1. Study area

The study area comprises a non-dammed portion of about 230 km at the upper Paraná River floodplain (Figure 1). This floodplain encompasses a high biodiversity, which has been recognized since 2002 as an area of extreme biological diversity by

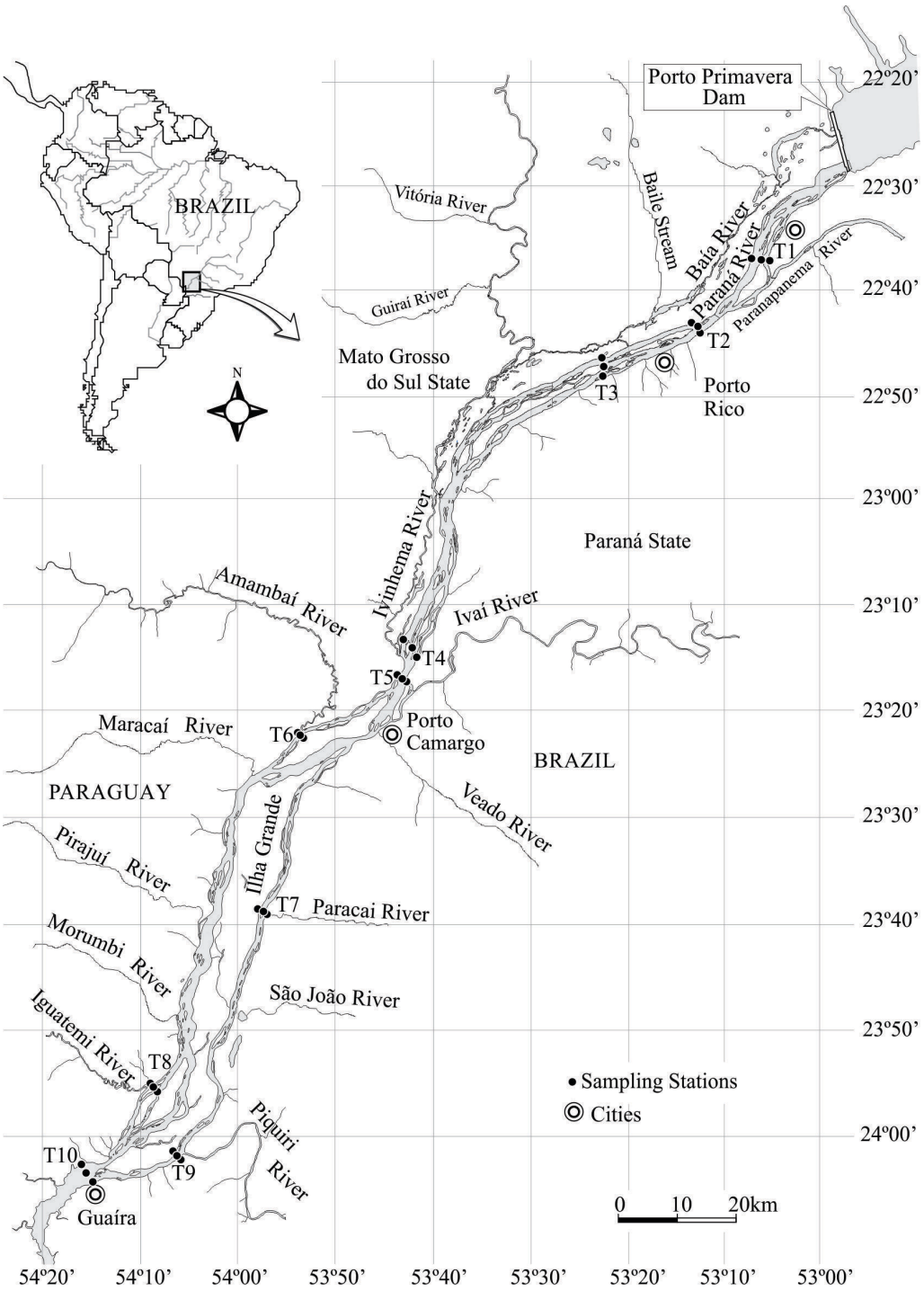

Figure 1. Sampling area at the upper Paraná River floodplain free of dams. T1 to T10 = sampled transects in the Paraná River main channel.

the Brazilian Government, resulting in the creation of three new conservation areas, the Ilha Grande National Park, the wetlands of Ivinhema River State Park and the Environmental Protection Area of the islands and floodplains of the Paraná River.

2.2. Data sampling

The samplings were performed quarterly, from February to December 2014, in 10 transects (margins and center) at the Paraná River main channel. Transects were sampled before and after the main tributaries of the Paraná River. They were: Paranapanema, Ivaí and Piquiri Rivers, located in the left bank of Paraná River, and the Baía, Ivinhema, Amambai e Iguatemi Rivers, located in the right bank.

Three water samples of 100 L each were filtered in each transect (left margin, right margin and the center region), with motorized pump (Still Model) and plankton net (63 µm mesh size) for determination of *L. fortunei* larvae densities. The filtrated was fixed in alcohol 80%. In laboratory, samples for determination of *L. fortunei* larval densities were counted in total under the optical microscope in Sedgwick-Rafter chambers. *L. fortunei* larvae were measured for length and width of their valves and classified according to methods adopted by Santos et al. (2005) into five larval stages: D-Shaped larvae (90-130 µm), Straight Hinged veliger (140-180 µm), Umbonated veliger (190-220 µm), Pediveliger (230-270 µm) and Plantigrades (280-490 µm).

Concomitant to larval samplings we took some of the main water variables related to development and spread of *L. fortunei*: water temperature (°C, thermometer coupled to the oximeter, respectively), dissolved oxygen ($mg.L^{-1}$, portable oximeter), conductivity (μScm^{-1}, portable potentiometer), pH (portable potentiometer), turbidity (NTU, portable turbidimeter), depth (m), alkalinity ($\mu Eq.L^{-1}$, Carmouze, 1994), total nitrogen, ammoniac and nitrate ions ($\mu g.L^{-1}$, Mackereth et al., 1978) and total phosphorus and phosphate ($\mu g.L^{-1}$, Golterman et al., 1978).

2.3. Data analysis

Densities of *L. fortunei* were achieved by multiplying the abundance matrix with the total volume of filtered water (i.e., resulting in $ind.m^{-3}$). Temporal variations of age structure of larvae were evaluated with bar graphs using the mean values of each larval size as age classes. This evaluation was conducted in Statistica 7.0 software (Statsoft, 2005).

We performed a Redundancy Analysis (RDA; Rao, 1964) in order to summarize the variations in larval stages densities in relation to the main physical and chemical water variables. We conducted a multicollinearity test for the relationship among the environmental variables according to variance inflation factors using the *packfor* package (Dray et al., 2009) in the R software. Variables with variance inflation factors values above 10 were removed. By multicollinearity test, the variable "dam distance" was removed from the analysis. Correlations among the log of biological data with the environmental variables were performed by Redundancy Analysis – RDA, as a way to get the most important environmental variables related to variations in temporal age classes of *L. fortunei*. Subsequently, we selected a subset of environmental variables according to Blanchet et al. (2008) method. The selection procedure involves two stages to control the probability of Type I error and the overestimation of the explained variance. The first one evaluate the assumption of linearity between data, i.e., there is at least a model which explain the biological variations, while the second, based on the forward selection, shows us the significance levels of each variable over biological data. We carried out the Blanchet's selection and the RDA analyses using *vegan* (Oksanen et al., 2015) and *packfor* (Dray et al., 2009) package of the R program (R Core Team, 2012).

3. Results

We found a total of 200,590 *L. fortunei* larvae, in which 83.6% (i.e., 167,685 individuals) were identified as the first two larval stages: D-Shaped larvae (59,920 individuals; 29.9%) and Straight Hinged (107,765 individuals; 53.7%). In general, the averages of larval densities were spatially high among the sampled sites, varying from 587 to 5,192.50 $ind.m^{-3}$. *L. fortunei* larvae were most abundant in December and February (Table 1, Figure 2), both among sampled sites (Figure 2) and periods (Table 1, Figure 2).

By variations in densities for each larval stage, we observed remarkable temporal differences as the decreasing in values from February to December, when a possible new cycle seems to restart, and the densities increase again. Exceptions are done to final stages, Pediveliger and Plantigrades, which were reducing their densities along the study (Table 1). We observed a similar pattern for the spatial approach (Figure 2), where the densities also decreased from February (maximum density = 16,000 $ind.m^{-3}$) to

Table 1. Mean and standard deviation of stages larval densities of *L. fortunei* during the year of 2014.

	D-Shaped		Straight Hinged		Umbonated		Pediveliger		Plantigrades	
	M	SD	M	SD	M	SD	M	SD	M	SD
Feb	1,433.7	3,175.9	1,805	1,294.6	671.33	496.5	85.3	55.6	10.7	8.13
Apr	63.7	108.2	160.9	142.7	75.1	111.12	20.9	34.5	1.6	1.7
Aug	3.3	4.15	17.3	15.9	10.7	11.6	5	5.03	0.66	1.4
Dec	495	865.3	1,413.7	2,308.1	26.3	24.2	3	3.99	0.33	1.05

M=Mean; SD=Standard Deviation; Feb=February; Apr=April; Aug=August; Dec=December.

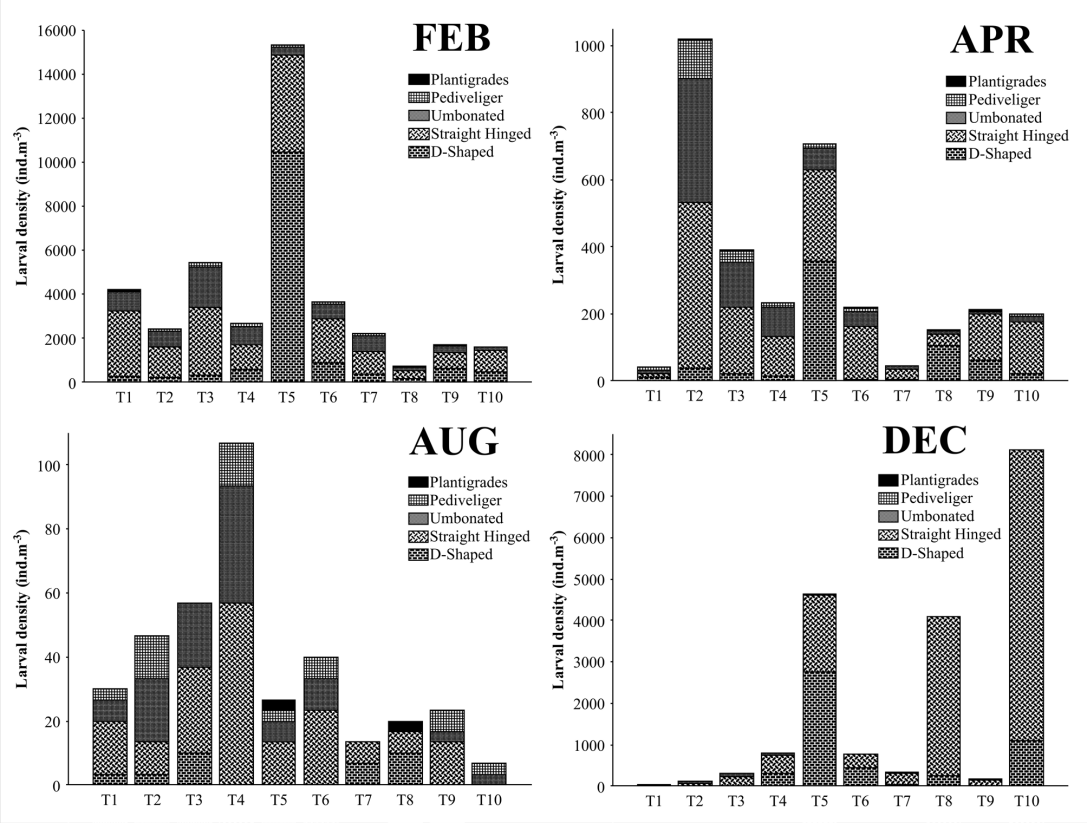

Figure 2. Densities of *L. fortunei* larval stages along the sampled sites and periods. Feb = February; Apr = April; Aug = August; Dec = December.

August (maximum density = 100 ind.m^{-3}), and it turning back to increase in December (maximum density = 8,000 ind.m^{-3}).

The transect T5 were dominated by D-Shaped larvae in almost all sampled months. Straight Hinged larvae were the most abundant larval stage in February, except in T5, where D-Shaped larvae were the dominant larval stage. In February we also observed high larval densities in all sampled sites, with the lowest density registered in T8 (the average density = 1,000 ind.m^{-3}). In April, by contrast, the highest densities were correspondent with the lowest of February (i.e., 1,000 ind.m^{-3} in T2), mainly by contribution of Straight Hinged veliger. In addition, densities of Umbonated larvae in April were proportionally higher than in February. In August we found the lowest total densities (maximum of 100 m^{-3}, approximately, in T4), and the proportion of Pediveliger increased in relation to the other months. In December, as aforementioned, the larval densities turned back to increase, especially due to the increase of initial larval stages (D-Shaped larvae and Straight Hinged) in the downstream sites.

February was the warmest month of the all sample period, followed by December. August was the coldest and oxygenated month, followed by April, and both also had the highest values of alkalinity. April was the richest month in relation to PT and PO4 concentrations, while nitrogen compounds (NT and NO3) were more abundant in December (Table 2).

The first two axes of RDA sum up 96% ($R^2_{adj.}$ = 0.77) of the total data variation

Table 2. Mean and standard deviation of limnological variable for each month of the sample period.

	WT	DO	EC	pH	Turb	Depth	Alk	TN	NO3	NH4	TP	PO4
Feb	30.5 ± 0.5	7 ± 0.3	56.2 ± 4.7	6.9 ± 0.5	4.5 ± 5.2	4.2 ± 2.3	501 ± 175	581.3 ± 119.3	202.1 ± 57.7	4.4 ± 4.1	13.3 ± 7.2	4.8 ± 2.5
Apr	24.1 ± 0.8	7.5 ± 0.5	54.6 ± 9.1	7.1 ± 0.3	8.1 ± 6.4	3.5 ± 2.7	751 ± 126.9	672.3 ± 83.4	264.5 ± 100.9	11.6 ± 8.7	26.6 ± 15.5	17.4 ± 4.2
Aug	21.5 ± 0.4	8.3 ± 0.4	59.9 ± 11.9	7.4 ± 0.3	9 ± 5.6	3.2 ± 2.3	691 ± 132.8	868.6 ± 150.8	256.4 ± 150.8	5.1 ± 5.4	19 ± 6	11.2 ± 4.1
Dec	27.5 ± 0.5	7.45 ± 0.5	59.3 ± 8.3	7.1 ± 0.7	8.7 ± 9.6	3.9 ± 1.9	415.5 ± 58.8	1301 ± 184.3	267.6 ± 111.4	8.1 ± 7.2	19.8 ± 8.25	11.6 ± 7.1

Feb=February; Apr=April; Aug=August; Dec=December; WT = Water Temperature; DO = Dissolved Oxygen; EC = Electrical Conductivity; Turb = Turbidity; Alk = Alkalinity; TN = Total Nitrogen; TP = Total Phosphorus.

(axis 1: eigenvalue = 26.48 and 74.42% of explanation; axis 2: eigenvalue = 7.75 and 21.77% of explanation). Variations in both axes were statistically significant (axis 1: $F_{(1,34)}$ = 140.46; p<0.05 and axis 2: $F_{(1,34)}$ = 41.08; p<0.05). According to Blanchet's selection, the most significant environmental variables explaining variations of *L. fortunei* larval densities were: water temperature, total nitrogen, electrical conductivity, phosphate, dissolved oxygen, depth and ammoniac ion (Table 3).

From the dispersion graph of the RDA scores, we observed a temporal grouping of the data (Figure 3). April and August (colder months) were grouped at the positive values of axis 1 and were influenced by the higher values of alkalinity, dissolved oxygen, NO_3, PO_4, TP, TN and by the lower densities of *L. fortunei*. On the other hand, February and December (warmer months) were grouped at the negative values of axis 1. These points were influenced by the major values of water temperature and depth besides the higher densities of all larval stages.

Table 3. Significance and proportion of explanation of the most influent variables for variations of *L. fortunei* densities.

Variables	R^2	Cum. R^2	Cum. R^2_{Adj}	$F_{(13,26)}$	*P*
WT	0.479	0.479	0.465	34.898	<0.05
TN	0.130	0.609	0.588	12.291	<0.05
EC	0.092	0.701	0.676	11.124	<0.05
PO_4	0.040	0.741	0.711	5.368	<0.05
DO	0.023	0.763	0.729	3.246	<0.05
Depth	0.020	0.783	0.744	2.984	<0.05
NO_3	0.021	0.804	0.761	3.432	<0.05

Cum. = Cumulative; Adj = Adjusted; WT = Water Temperature; TN = Total Nitrogen; EC = Electrical Conductivity; DO = Dissolved Oxygen.

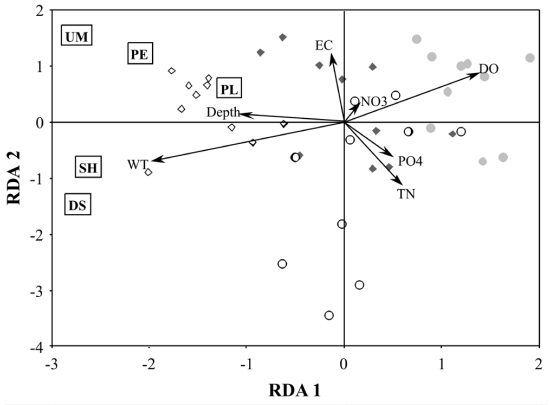

Figure 3. Dispersion graph from the Redundancy Analysis performed between larval density stages and limnological variables in relation to the sampled period. DS= D-Shaped larvae; SH= Straight Hinged larvae; UM= Umbonated; PE= Pediveliger; PL= Plantigrades; EC= Electric Conductivity; TN= Total Nitrogen; WT= Water Temperature; DO= Dissolved Oxygen; ◇= February; ◆= April; ●= August; •= December.

4. Discussion

The highest densities of *L. fortunei* larvae between February and December along all sampled transects, suggest this period as the main reproductive season for the species at the upper Paraná River floodplain. December represents the beginning of summer season in the South hemisphere, which is characterized by high values in both air temperatures and amount of rain. High temperatures seems to affect *L. fortunei* reproduction (Boltovskoy et al., 2009), but also accelerate *L. fortunei* development. Experimental studies have shown that the time between spawning and the second last larval stage (pediveliger) can be reduced from 480 hours to 265 hours with an increase of 8 °C in the water temperature (Cataldo et al., 2005). Additionally, seasonal changes have a major influence in flooding areas such as the upper Paraná River floodplain (Agostinho et al., 2004), where major temporal variations in physical, chemical and biological conditions can be attributed to the flood pulse effects (Thomaz et al., 2007), a fundamental phenomenon to keep the integrity of these ecosystems (Junk et al., 1989; Neiff, 1990). Temperature and depth positively affected all larval stages in our study. Considering that *L. fortunei* is an invasive species, it is a matter of concern, because the period with higher density and intense development of larvae, coincides with the periods of high environmental connectivity provided by the flood pulse.

Other studies have reported higher densities of *L. fortunei* larvae in plankton with peaks of spawns in high temperature periods (e.g. Boltovskoy & Cataldo, 1999; Cataldo & Boltovskoy, 2000; Magara et al., 2001). Cataldo & Boltovskoy (2000) have found a similar temporal pattern in the reproduction peaks (e.g., in Argentina it occurs mainly between October to February) and the authors suggested that *L. fortunei* might reproduce continuously during these months.

Synchronicity in the *L. fortunei* reproduction during flood periods had already been suggest before by Ernandes-Silva et al. (2016b), and the results of the present study corroborates this idea. It is also

important to highlight the fact that this temporal variation in reproduction promotes a higher *L. fortunei* propagule pressure which increases both the establishment probability at new areas and the size of previously established populations, given that the greater the amount of individuals arriving in a new region, the greater could be the success of population establishment (Lockwood et al., 2005). In this way, the annual arrival of propagules during flood periods together with daily ship transportation of adults fixed in its hull (Karatayev et al., 2007), increase the invasion probability at new areas of the upper Paraná River floodplain, which have not yet colonized by *L. fortunei*.

In some floodplain areas, such as the Paraguay River, the flood period is characterized by sudden decreases in dissolved oxygen concentration in water, which act as a controlling factor on the density of *L. fortunei* (Oliveira et al., 2010). Although the dimensionality of dissolved oxygen and larval stages of *L. fortunei* were located in opposite quadrants in the RDA, the mean values of oxygen were considerably high, with a minimum of 7 $mg.l^{-1}$ in February. Despite Eilers et al. (2011) observed a decrease in the larval density of *L. fortunei* during periods of lower dissolved oxygen concentration, our results did not present such pattern, since the month with the lowest values of dissolved oxygen (February) had higher peaks of larval density (16,000 $ind.m^{-3}$). February was the most populous month of our whole sample period.

In contrast to majority studies conducted about *L. fortunei* reproduction, which did not evaluate the differences in the larval types, our study demonstrated variations in densities of larval stages according to both months and sites. The dominance of smaller larval stages at plankton (D-Shaped larvae and Straight Hinged) compared to larger ones, suggest that the last stages (Umbonated, Plantigrade and Pediveliger) have already tried some settlements on the substrates or they were naturally lost. Eilers et al. (2011) when studying larval densities of *L. fortunei* in the Miranda and Paraguay Rivers also found higher densities of the initial stage (D-Shaped larvae), with a great population decrease together with the larvae maturing, with a reduction of ~80% of D-shaped larvae and ~10% of Umbonated.

We observed a strong relationship between larval densities of *L. fortunei* and limnology conditions. The variations in the densities of larval stages of *L. fortunei* throughout the year and in all sampled sites were not related only to higher temperature values, cited as the main factor limiting larval development of the species (Kimura & Sekiguchi, 1996; Cataldo et al., 2005; Darrigran et al., 2007). Our results agree with Oliveira et al. (2011) and Spaccesi (2013), and suggest that the temperature per se is not able to explain the population dynamic of *L. fortunei* neither the periods of spawns. By contrast, we have showed that dissolved oxygen, P and N concentrations, electrical conductivity and depth are also important variables to explain both temporal and spatial variations of *L. fortunei* larvae, mainly when the different larval stages of the species is considered.

Our results indicate that *L. fortunei* reproduction follows a general pattern throughout the upper Paraná River floodplain, and it seems to occur mainly between February and December. Temporal variations observed in larval densities across sampled sites and periods have great importance to procedures to avoid this invasive species to achieve new areas or even to control those already established populations. Thus, we suggest that actions to control *L. fortunei* populations should be done from April to August, period in which, according to our study, *L. fortunei* is recorded in low density in the upper Paraná River floodplain, and the river water level is low, limiting the dispersion of this species.

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