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Temporal and spatial patterns of freshwater decapods associated with aquatic vegetation from floodplain rivers

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Abstract The presence of freshwater decapods may be considered dependent on the habitat and vegetation characteristics in floodplain rivers. Water level can influence the availability of macrophytes and the associated species composition of freshwater decapods. Changes in the sex ratios, abundances and body sizes of *Macrobrachium borellii*, *Palaemon argentinus* and *Trichodactylus borellianus* were investigated focusing on the type (floating, emergent) and the presence/absence of macrophytes in the Middle Paraná River floodplains. Organisms were sampled and analysed from river sites with floating, emergent vegetation and vegetation-free waters during different hydrological periods. The presence of macrophytes and some environmental variables during different hydrological and seasonal periods affected the variations in the species composition of decapods. *M. borellii* and *T. borellianus* tended to increase with the increase in floating vegetation in high waters, while *P. argentinus* was abundant in emergent vegetation and vegetation-free waters in low waters. Macrophytes provide food and shelter for freshwater decapods, influencing the species abundance according to the ecological response of each species. Variations in macrophytes composition due to water-level fluctuations modify the abundance of freshwater decapods, altering the species composition of decapod assemblages. Floodplain rivers are complex systems that act as macrofactors that regulate other factors that impact species composition.

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Introduction

Freshwater decapods are an important component of community biomasses in tropical and subtropical rivers (Odinetz-Collard, 1987; Nessimian et al., 1998; Richardson & Cook, 2006; Collins et al., 2007; Montoya et al., 2014). They play major roles within river food webs; their nutritional quality and energy values are energetically transferred to different

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trophic levels (Covich et al., 1999; Dudgeon, 1999; Collins et al., 2007).

Floodplain rivers, together with their hydrological connectivity, support and maintain high biological diversity and abundant populations within dynamic and heterogeneous contexts (Junk et al., 1989; Amoros & Bornette, 2002; Winemiller, 2004; Mayora et al., 2013). The main factor that is used to model the dynamics of rivers and their floodplains is the hydro-sedimentological cycle, which is constituted of high and low water cycles (Junk et al., 1989; Neiff, 1990). The distinctive characteristic of this cycle is that it acts as a macrofactor that regulates other factors (conductivity, transparency, flow velocity) that affect the richness, distribution and abundance of organisms that live in these systems (Junk et al., 1989; Neiff, 1990; Aoyagui & Bonecker, 2004; Winemiller, 2004; Arrington et al., 2006; Mayora et al., 2013).

Hydrological fluctuations of floodplain systems modulate the dispersion and the presence or absence of decapods, influencing the availability of shelter (e.g. submerged or floating aquatic vegetation) that generates changes in populations and communities associated with vegetation (Collins, et al., 2006, 2007; Williner et al., 2010; Montoya et al., 2014). On the other hand, in the study of the changes in species composition of decapods in dynamic rivers with floodplains, physical and chemical factors are important (Williner et al., 2010; Montoya et al., 2014). For example, the water temperature usually coincides with the seasonal cycle in temperate regions, which makes it difficult to determine the factor that is more important (Williner et al., 2010). These cycles could be associated with the biological cycles of decapods, such as the timing and duration of their reproductive cycle (Collins et al., 2007; Williner et al., 2010). In this manner, the heterogeneity of a floodplain system also has an impact on the sex ratio, body size distribution and reproductive cycle of decapods (Williner et al., 2010).

In aquatic systems, macrophytes play a relevant role in habitat structuring regarding the establishment and/or mobility of organisms and influencing species abundance and diversity (Taniguchi et al., 2003; Warfe et al., 2008; Lucena-Moya & Duggan, 2011; St Pierre & Kovalenko, 2014). Macrophytes provide food, shelter and foraging locations for several communities (Thomaz & Cunha, 2010; Lucena-Moya & Duggan, 2011). Additionally, their influence on the compositions of different species depends on the type of macrophyte (e.g. submerged, emergent, free-floating) (Meerhoff et al., 2003; Cazzanelli et al., 2008). On the other hand, the presence of aquatic vegetation can be affected by water-level fluctuations of floodplain systems and climatic seasonality (Neiff et al., 2001; Sabattini & Lallana, 2007; Cremona et al., 2008). In this sense, changes in macrophyte species composition due to water-level fluctuations of floodplain systems might indirectly modify the richness, abundance and biomass of macroinvertebrates, altering the biotic relationships among species (Sabattini & Lallana, 2007; Cremona et al., 2008).

Knowledge of the variations in the species composition of freshwater decapods associated with macrophytes in floodplain contexts is relevant because decapods are significant components of the trophic spectrum of aquatic and terrestrial fauna (fishes, amphibians, mammals), as decapods transfer matter and energy within the aquatic system, as well as to the semiterrestrial and terrestrial systems (Covich et al. 1999; Dudgeon, 1999; Collins et al., 2007). Furthermore, understanding the patterns of species composition changes is critical to explaining the ecological dynamics of systems (Chiarucci et al., 2011). Temporal and spatial environmental changes are known to influence the distribution of life history strategies in local assemblages, the population stability, the food network structure and ecosystem productivity, and therefore, can also affect community assembly dynamics (Fitzgerald et al., 2017). In the Paraná floodplain, the freshwater prawns *Macrobrachium borellii* (Nobili 1896) and *Palaemon argentinus* (Nobili 1901), and the crab *Trichodactylus borellianus* (Nobili 1896) are active participants in aquatic food webs, as they are prey as well as predators (Collins et al., 2007). These species are associated with aquatic vegetation and show similar ecological requirements such as habitats and nutrition (Collins, 2005; Williner et al., 2010). They scatter passively through floating vegetation, and prawn species also move actively through micro-migratory movements (Williner et al., 2010). Furthermore, species of prawns are sympatric and can co-exist because of small displacements in several dimensions of their niches (Collins, 2005).

The presence of freshwater decapods in aquatic macrophytes in floodplain environments such as the Middle Paraná River was registered by several authors (Poi de Neiff & Neiff, 1980, 1997, 2006; Collins, 2005; Collins et al., 2006; Williner et al., 2010). However, quantitative studies have not been published on the changes in the sex ratio, abundance and body sizes of these organisms living together in macrophytes in a hydrodynamic system. On the other hand, studies on the changes in species composition have been conducted on submerged vegetation and free-floating plants in river systems (Nicolet et al., 2004; Poi de Neiff & Neiff, 2006; Meerhoff et al., 2007; Cremona et al., 2008; Thomaz et al., 2008; Warfe et al., 2008; Van Onsem et al., 2010; Kornijów et al., 2016); however, few studies have included emergent vegetation (Wessell et al., 2001; Nicolet et al., 2004; Tessier et al., 2007; Cazzanelli et al., 2008; Choi et al., 2014) because invertebrate abundance is usually higher on submerged than on floating/emergent macrophytes (Tessier et al., 2007; Cazzanelli et al., 2008; Cremona et al., 2008). Additionally, few studies have analysed in detail the changes in the abundance of a smaller number of species that are associated with vegetation in dynamic contexts of floodplain (Nicolet et al., 2004; Montoya et al., 2014).

In the present study, the temporal and spatial variations of the species composition of decapods were investigated, considering the different types of aquatic vegetation in the dynamic system of the Paraná River floodplains. We documented the changes in the sex ratio, abundance and body size of the freshwater prawns *M. borellii* and *P. argentinus* and the crab *T. borellianus*, focusing on the type and the presence/absence of macrophytes (including emergent vegetation) in a dynamic context (temporal and spatial) in floodplain rivers. We predicted that changes in species composition (abundance and body size) of decapods would be associated with the presence and type of macrophytes during different hydrological periods. Macrophytes would influence the availability of resources and habitat suitability as a refuge from predation and reproduction. Moreover, crab and prawn species abundance would respond in different ways according to type and the presence/absence of macrophytes during different hydrological periods due to the ecological characteristics of each species.

Materials and methods

Sampling sites

Populations of prawns and crabs were sampled from different sites located on the shores of the littoral zones of the Paraná, Saladillo, Salado and Coronda rivers (Fig. 1a). The Paraná, Salado and Coronda rivers are classified as large rivers. The Saladillo and Paraná rivers connect and later join with the Salado River, which ends in the Coronda River (Fig. 1a). The floodplain of the Middle Paraná River is approximately 20,000 km^2 and extends 1,000 km along the river valley (Bonetto & Wais, 1995). The floodplain is a complex mosaic of geomorphic units that vary in their connectivity with the main channel, topographic level, slope, floodwater residence time and type of vegetation (Iriondo, 2004; Marchetti et al., 2013). Within this fluvial hydrosystem, the Middle Paraná segment encompasses the area 700 km upstream from Paraguay. The main factor used to model the dynamics of the river and its floodplain is the hydro-sedimentological cycle (Neiff, 1990). The waters begin to rise typically during spring, presenting the maximum height in summer and fall in autumn with the lowest heights in winter (Neiff, 1990). However, for the past 10 years, the hydrological regimes have exhibited relatively low seasonal predictability due to the extraordinary flows mainly associated with *El Niño* southern oscillation events (Robertson & Mechoso, 1998; Depetris & Pasquini, 2007). Furthermore, the construction of dams in the Upper Paraná River Basin has also affected the hydrological levels of the system. In this sense, the Paraná River presents non-linear properties of hydrological systems; thus, according to the hydrometric level, the systems present a chaotic-deterministic dynamic (Giri & Devercelli, unpublished data). The Salado River sources arise in the eastern foothills of the Andes and join the Paraná River in its middle course (Iriondo & Paira, 2007). The southeastern corner of the distal region of the Salado River is composed of a series of large, stable paleochannels. The rest of the distal region is formed by clayey silt of swampy origin. The area is flooded for several months in humid years (Iriondo & Paira, 2007). The Salado River is a small tributary of the Paraná River that falls into the Santa Fe Province. The basin of the Saladillo River includes two major river systems: Saladillo Dulce (600 km) and Saladillo
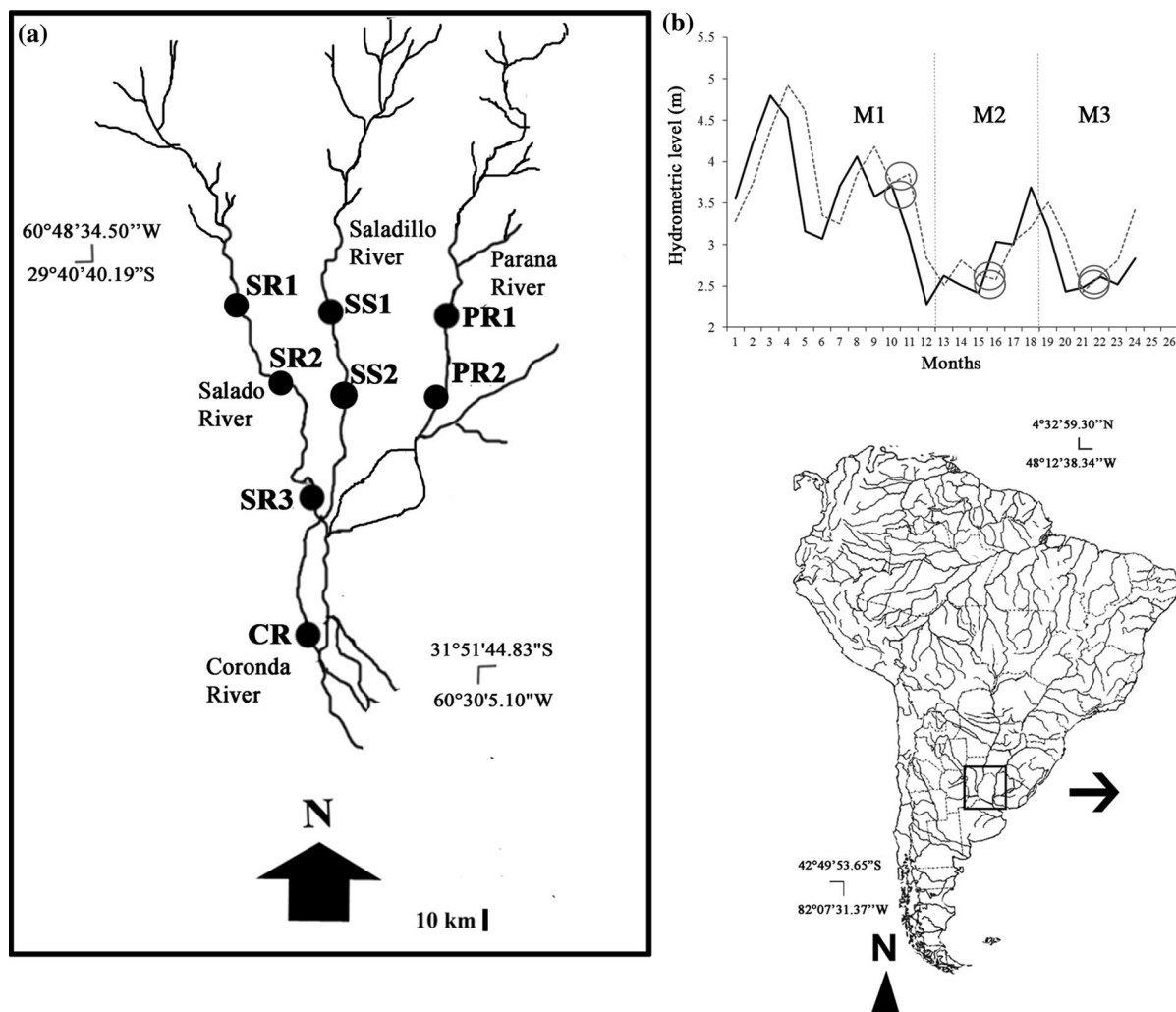
Fig. 1 a Sampling sites: *PR1* Paraná River 1, *PR2* Paraná River 2 (Paraná River); *SS1* Saladillo Stream 1, *SS2* Saladillo Stream 2 (Saladillo River); *SR1* Salado River 1, *SR2* Salado River 2, *SR3* Salado River 3 (Salado River); *CR* Coronda River (Coronda River). **b** Sampling times in relation to hydrological periods of the Paraná River (black line) and the Salado River (grey dashed line). The circles indicate the exact sampling time. M1: high waters (end of high waters, when waters begin to decrease); M2: low waters (end of low waters, before waters begin to rise) and M3: low waters

Amargo (490 km); both flow into the Saladillo River (Drago & Paira, 1985). In this sub-basin, there are several small temporary and permanent aquatic environments (José de Paggi & Koste, 1988).

The sample sites for this study were the Paraná River 1 (PR1), Paraná River 2 (PR2); Saladillo Stream 1 (SS1), Saladillo Stream 2 (SS2); Salado River 1 (SR1), Salado River 2 (SR2), Salado River 3 (SR3); Coronda River (CR) (Fig. 1a). Samples from these sites were collected at different times of the hydrological periods of the Paraná and Salado rivers (Fig. 1b). These sampling times were established in

relation to water fluctuations that were called "microfluctuations" in this study because they occurred within ordinary periods of high and low waters. These fluctuations are noted as M1: high waters (end of high waters, when the waters begin to decrease); M2: low waters (end of low waters, before the waters begin to rise) and M3: low waters.

Sampling and study of organisms

Prawns and crabs were sampled using a hand net with a handle (1260 cm^2 opening area and 47 l volume,

1 mm mesh) from waters with floating and emergent vegetation and waters that were free of vegetation along the shores of the channels, depending on the characteristics of the environments regarding the presence or absence of floating vegetation. The sampling depth of each site was between 0.5 and 1.0 m. The hand net was moved from the bottom-up sweeping along the water column when sampling waters with floating and emergent vegetation and waters that were free of vegetation. After the hand net was submerged in the water, it was extracted to remove the individuals, and these were preserved in 96% ethanol. Additionally, the hand net was moved to extract the floating vegetation from the water to capture the individuals from the roots. The unit of sampling efforts was established by time (half an hour per sampling point), which corresponded to ten samples (the number of times that the net was submerged and extracted). Physical and chemical variables, such as conductivity, pH and temperature, were obtained from each site with a digital sensor (HANNA 198130). Data on the hydrometric level were obtained from local ports and the *Facultad de Ingeniería y Ciencias Hídricas* (*Universidad Nacional del Litoral*).

In the laboratory, the population structure (sex ratio and body size) and abundance (number of individuals) of each sampled species were determined. Species of prawns and crabs were determined following the identification keys by Boschi (1981) and Magalhães & Türkay (1996), respectively. In addition, the sex of each individual was determined from the presence of a masculine appendix in the first and second pleopods in prawns and male pleopods in crabs. The cephalothorax length (CL) in prawns and cephalothorax width (CW) in crabs were measured from images obtained from the left side in prawns and the dorsal cephalothorax in crabs using the tpsDig2 2.16 program (Rohlf, 2010). The CL was measured from the distal tip of the rostrum to the posterior border of the cephalothorax. The CW corresponded to the distance between postorbital spines.

The type and presence/absence of vegetation were grouped into three categories: vegetation-free waters (absence) (FW), emergent vegetation (EV) and floating vegetation (FV). Species of aquatic plants were recorded at each site and hydrological period and were identified following Pott & Pott (2000). The categories of vegetation were established according to the type of shelter for decapods and not necessarily to the life form of the vegetation species. For example, rooted aquatic plants with floating stems that extended over the water surface were classified as floating vegetation due to the shelter provided. Emergent macrophytes were defined as plants that were rooted in the bottom of the water or in soils that were periodically inundated (Neiff et al., 2014). These plants were rooted emergent plants that did not have floating stems that extended over the water surface.

Additionally, this categorisation was determined by the predominant type of plant recorded at each site (floating or emergent). The percentage of vegetation coverage was determined by photographs only when there were floating plants.

Data analysis

The frequency of sites that presented different types of vegetation (vegetation-free waters, emergent and floating vegetation) at each hydrological period and in each river are shown descriptively with a histogram.

Physical and chemical variables were tested with ANOVA with interaction between types of vegetation and sampling times because there could be an interaction effect between these variables. Additionally, physical and chemical variables were tested between rivers with one-way ANOVA (according to the model normality).

The sex ratio (male/female) of decapods was calculated in the samples for each type of vegetation, hydrological period and river. Then, a χ^2 test for given probabilities was performed to test whether the sex ratio differed from the expected proportion of 1:1 (Zar, 2010). Changes in abundance and sizes of the individuals were analysed to evaluate the variables that best explained these variations. Generalised linear mixed-effects models (GLMM), applied using the *glmer* function of the lme4 package (Bates et al., 2015), were used to analyse the abundance of each species with a Poisson distribution. Linear mixed models (LMM) using the *lmer* function from the package lmerTest 2.0-6 (Kuznetsova et al., 2014) were used to examine the size of each species with a Gaussian distribution. These models were chosen based on Akaike information criterion (AIC), starting with all fixed factors: physical and chemical variables (conductivity, pH, temperature and hydrometric level), the interaction between type of vegetation and

hydrological periods, and rivers; and with random effects: hydrological periods, rivers and sites due to the possible temporal and spatial dependence of these. The models included the interaction of hydrological period and type of vegetation as a fixed effect because there could be an interaction effect between these variables. This interaction term was not considered for explaining the abundance and size of the crab species because it was found in only one type of vegetation. In this case, hydrological periods and vegetation type were considered separately without interaction. Models with the lowest AICc values were considered to include the best variables to explain the abundance and size of each species. Candidate models were then run to test the significance of the variables. The quantitative data were standardised (with standard score) to run the mixed models. Before running the models, collinearity among variables (to elucidate the relations among them) was calculated by the non-parametric Spearman correlation coefficient. Regarding the pair of variables that presented co-linearities ($r > 0.70$), only one variable of each pair was selected.

The link between the combined abundance of species and the environmental, spatial and temporal conditions was studied through a canonical correspondence analysis (CCA) using the "vegan package" (Oksanen et al., 2007). In this study, the abundance matrix of each species was included as a dependent variable, and physical and chemical variables (conductivity, pH, temperature and hydrometric level), type of vegetation, hydrological periods and rivers were included as independent variables. After running the CCA, the variance inflation factors (VIF) were used to test for multicollinearity in the CCA model that related the two matrices (abundance and variables). Then, ANOVA with 1,000 permutations was applied to the CCA model to obtain the p-values between variables.

All analyses were conducted with R software version 3.3.1 (R Foundation for Statistical Computing, Vienna, Austria, see: http://www.R-project.org) (R Development Core Team, 2016).

Results

In relation to physical and chemical variables (Table 1), the hydrometric level (HL) differed among hydrological periods (F: 12.8070, df = 2, $P = 0.0006$) and rivers (F: 21.3746, df = 3, $P < 0.0001$). In M1,

the HL was higher, decreasing in M2 and M3. Saladillo Stream (SS) presented low HL values, and Salado River (SR) presented high HL values (Table 2). The conductivity differed significantly among rivers (F: 3.4321, df = 3, $P = 0.0465$), and the SR showed the highest values. The pH was similar among hydrological periods, rivers and types of vegetation. Temperature varied significantly among hydrological periods (F: 10.5781, df = 2, $P = 0.0015$), decreasing in M3. Lastly, none of these physical or chemical variables showed significant differences in the interaction term among hydrological periods and types of vegetation.

Eichhornia crassipes (Mart.) Solms was recorded on the Paraná and Salado rivers during all hydrological periods, while in the Coronda River, it showed up in only M1 and M2 (Table 2). In the SS, some species (floating and emergent macrophytes) were recorded, mainly from the Poaceae family and *Paspalum repens* P. J. Bergius, but not *E. crassipes*. The SR had similar species depending on the site and hydrological period (*E. crassipes*, *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & R. Keller and the Poaceae family) (Table 2). According to the type of vegetation, floating vegetation (FV) was principally represented by *E. crassipes*, and emergent vegetation was represented by the Poaceae family (Table 2). The percentage of floating vegetation coverage tended to decrease with the approach of the dry season, and it was lower in M3 (low waters) than in M1 and M2 (M1: 62 ± 22.80, M2: 52.5 ± 25 and M3: $15 \pm .7.07$) (Table 2). In this sense, M3 was better represented by vegetation-free waters (FW), and M1 was better represented by floating vegetation (FV). The last period presented more sites with emergent vegetation (EV) than M3. No sites showed EV in M2 (Table 2). The Paraná River (PR) presented more sites with FV than the SS and SR. These last rivers presented EV, and the SR was better represented by FW (Table 2).

Organisms sampled and temporal and spatial variations in sex ratio, abundance and body size

In total, 255 prawns of *M. borellii*, 800 prawns of *P. argentinus* and 161 crabs of *T. borellianus* were sampled. Females prawns were more abundant than male prawns. However, of the crab *T. borellianus*, males were more abundant than females (Table 3). Statistically significant variations in the sex

Table 1 Values of physical and chemical variables measured in each hydrological period, river and type of vegetation

	Cond. (μS cm^{-1})	pH	Temp.	HL
Hydrological periods				
M1	1278.75 ± 1529.46	8.17 ± 0.29	24.73 ± 3.53	3.35 ± 1.04
M2	1102.50 ± 1680.31	8.06 ± 0.16	22.37 ± 2.10	2.66 ± 1.21
M3	1418.37 ± 1589.28	8.36 ± 0.42	18.21 ± 2.94	2.35 ± 1.04
Rivers				
PR	127.66 ± 21.96	8.13 ± 0.28	20.28 ± 4.90	2.85 ± 0.66
SS	1150.66 ± 1324.25	8.09 ± 0.16	21.30 ± 3.83	1.36 ± 0.25
SR	2415.44 ± 1697.67	8.36 ± 0.42	22.63 ± 3.81	3.68 ± 0.83
CR	329.33 ± 88.32	8.07 ± 0.13	23.13 ± 2.89	2.85 ± 1.02
Type of vegetation				
FV	907.54 ± 1354.58	8.15 ± 0.29	23.55 ± 2.44	2.76 ± 0.95
EV	1997 ± 1910.18	8.23 ± 0.37	23.22 ± 5.25	2.74 ± 1.52
FW	1380.66 ± 1630.03	8.24 ± 0.37	18.95 ± 3.46	2.85 ± 1.30

Cond. conductivity, *Temp.* temperature, *HL* hydrometric level, *M1* high waters (end of high waters, when the waters begin to decrease), *M2* low waters (end of low waters, before the waters begin to rise), *M3* low waters, *PR* Paraná River, *SS* Saladillo stream, *SR* Salado River, *CR* Coronda River, *FV* floating vegetation, *EV* emergent vegetation, *FW* vegetation-free waters

composition were observed at M1 in *M. borellii*, at M3 in the prawn *P. argentinus* and at M2 in *T. borellianus* (Table 3). In the SR, the three species showed statistically significant differences in their sex compositions. In the PR, both prawn species presented differences, while in the SS, only *P. argentinus* showed significant differences in its sex composition (Table 3). The three species differed in sex composition when they were sampled from FV, although *P. argentinus* was also different in FW (Table 3).

The model selected by the AIC that explained the most variation of *M. borellii* with the lowest AICc value (175.45) included the interaction among hydrological periods and vegetation type, conductivity and pH. The same model was selected by the AIC in *P. argentinus* to explain the abundance of *P. argentinus*, but this also included the temperature (AICc = 302.98). The selected abundance model in *T. borellianus* included hydrological period, type of vegetation, conductivity and pH (AICc = 121.04). According to the size variation, the best models selected by the AIC in *M. borellii* (AICc = 648.0) and *P. argentinus* (AICc = 1858.5) included all fixed variables of the initial model (interaction among hydrological periods and type of vegetation, conductivity, pH, temperature, hydrometric level and rivers). On the other hand, for the crab *T. borellianus*, only the

hydrological period and type of vegetation were the selected variables that best explained its size variation (AICc = 411.4).

The abundances of the prawns *M. borellii* and *P. argentinus* and the crab *T. borellianus* varied significantly among hydrological periods (Table 4), with higher abundances of *M. borellii* in M1 and M3, *P. argentinus* in M3 and *T. borellianus* in M1 (Fig. 2a–c). The abundances of these species also varied with the type of vegetation (Table 4). The occurrence of FV dominated by *E. crassipes* favoured the abundance of *M. borellii* and *T. borellianus* (which was not found in vegetation-free waters or emergent vegetation) (Fig. 2d, f). *P. argentinus* presented greater abundance in EV and FW (Fig. 2e). Furthermore, *M. borellii* and *P. argentinus* also presented differences among hydrological periods in relation to the type of vegetation (interaction term) (Table 4). *Macrobrachium borellii* presented greater abundance in FV in M1, while *P. argentinus* was more abundant in FW in M2 and M3 (Fig. 3a, b). Prawns and crab species showed statistically significant differences between abundance and conductivity and pH (Table 4). The higher abundances of *M. borellii* and *T. borellianus* occurred when the conductivity was lower (negative coefficient in the regression of the glmer function), while *P. argentinus* became more abundant with the increase in

Table 2 Species of aquatic plants recorded and coverage percentage (only to floating and emergent vegetation) on sampling sites and hydrological periods

Hydrological periods	Sites	Rivers	Species	Type	Coverage (%)
M1	PR1	Parana River	*Eichhornia crassipes*	FV	40
	PR2		*Eichhornia crassipes*	FV	60
	SS1	Saladillo Stream	*Salvinia auriculata* Aubl.—*Nymphoides indica* (L.) O. Kuntze—*Paspalum repens*- *Panicum elephantipes* Nees ex Trin.—*Limnobium laevigatum* Humb. & Bonpl. ex Willd.	FV	90
	SS2		Poaceae	EV	–
	SR1		*Schoenoplectus americanus*	EV	–
	SR2	Salado River	Poaceae	EV	–
	SR3		*Eichhornia crassipes*	FV	80
	CR	Coronda River	*Eichhornia crassipes*	FV	40
M2	PR1	Parana River	*Eichhornia crassipes*	FV	40
	PR2		–	FW	–
	SS1	Saladillo Stream	Poaceae—*Paspalum repens*	FV	90
	SS2		–	FW	–
	SR1	Salado River	–	FW	–
	SR2		–	FW	–
	SR3		*Eichhornia crassipes*	FV	40
	CR	Coronda River	*Eichhornia crassipes*	FV	40
M3	PR1	Parana River	*Eichhornia crassipes*	FV	10
	PR2		–	FW	–
	SS1	Saladillo Stream	Poaceae	EV	–
	SS2		–	FW	–
	SR1	Salado River	–	FW	–
	SR2		–	FW	–
	SR3		*Eichhornia crassipes*	FV	20
	CR	Coronda River	–	FW	–

The percentage of floating vegetation coverage is shown in each

PR1 Paraná River 1, *PR2* Paraná River, *SS1* Saladillo Stream 1, *SS2* Saladillo Stream 2, *SR1* Salado River 1, *SR2* Salado River 2, *SR3* Salado River 3, *CR* Coronda River, *M1* high waters (end of high waters, when waters begin to decrease), *M2* low waters (end of low waters, before waters begin to rise), *M3* low waters, *FV* floating vegetation, *EV* emergent vegetation, *FW* vegetation-free waters

conductivity (positive coefficient). The abundance of the three species decreased with the pH (negative coefficient). The prawn *P. argentinus* also presented statistically significant differences between abundance and temperature (Table 4), increasing with this variable (positive coefficient).

The sizes of *M. borellii* were significantly different among the types of vegetation, rivers and hydrometric levels (Table 4). The largest sizes were found in EV and FW (with the smallest in FV), in the SR and SS and at high hydrometric levels (positive coefficient) (Fig. 4a, b). The sizes of *P. argentinus* differed among hydrological period, type of vegetation, conductivity, pH, temperature and hydrometric level and among hydrological periods in relation to the vegetation (interaction term) (Table 4). The largest sizes occurred at M1 and M3 in FV and EV (with the smallest in FW) and in the PR, with the presence of

Table 3 Sex ratio (F:M), χ^2 test values (χ^2) and probability of significance (P) of sampled specimens

Species	F:M	χ^2	P value
Macrobrachium borellii			
Hydrological periods			
M1	1: 0.60	6.6881	0.0097*
M2	1:0.74	1.1852	0.2763
M3	1:0.69	3.2472	0.0715
Rivers			
PR	1:0.81	6.7222	0.0095*
SS	1:0.76	0.9245	0.3363
SR	1:0.56	4.4138	0.0356*
CR	1:0.81	0.7101	0.3994
Type of vegetation			
FV	1:0.62	10.776	0.0010**
EV	1:0.91	0.0434	0.8348
FW	1:0.51	0.6666	0.4142
Palaemon argentinus			
Hydrological periods			
M1	1:0.81	1.5306	0.216
M2	1:0.84	2.3195	0.1278
M3	1:0.58	19.9170	< 0.0001***
Rivers			
PR	1:0.56	7.0225	0.0080*
SS	1:0.79	4.8729	0.0272*
SR	1:0.66	11.5210	0.0006***
CR	1:1.46	1.1250	0.2888
Type of vegetation			
FV	1:0.53	19.4700	< 0.0001***
EV	1:0.85	0.5505	0.4581
FW	1:0.81	4.7100	0.0299*
Trichodactylus borellianus			
Hydrological periods			
M1	1:1.35	2.0851	0.1487
M2	1:2.66	9.0909	0.0025**
M3	1:3.00	1.0000	0.3173
Rivers			
PR	1:1.25	0.4444	0.5050
SS	1:1.33	0.2857	0.5930
SR	1:2.12	6.4800	0.0109**
CR	1:1.80	3.4286	0.0640

Table 3 continued

Species	F:M	χ^2	P value
Type of vegetation			
FV	1:1.67	9.1268	0.0025**
EV	–	–	–
FW	–	–	–

M1 high waters (end of high waters, when waters begin to decrease), *M2* low waters (end of low waters, before waters begin to rise), *M3* low waters, *PR* Paraná River, *SS* Saladillo Stream, *SR* Salado River, *CR* Coronda River, *FV* floating vegetation, *EV* emergent vegetation, *FW* vegetation-free waters

(–) indicated χ^2 test cannot run because 0 values

Statistically significant differences, *P < 0.05, **P < 0.005, ***P < 0.001

some large individuals in the SS (Fig. 4c–e). Prawns were large in M1 and M3 in FV and EV and in M3 in FW (Fig. 5). The size of this species decreased with the increases in conductivity and pH (negative coefficients) and increased with the increases in temperature and hydrometric level (positive coefficients). The crab *T. borellianus* presented differences in the sizes among hydrological periods (Table 4), and it was larger in M1 and M3 than in M2 (Fig. 4f).

The hydrological periods and the presence or absence of aquatic plants (floating or emergent) were the principal variables that influenced the abundance of each species, in addition to environmental variables (such as conductivity and pH). These variables also affected the size variations of the species but with some differences according to species. Hydrological periods (for *P. argentinus* and *T. borellianus*), type of vegetation and rivers (for *M. borellii* and *P. argentinus*) and hydrological periods in relation to the vegetation (for *P. argentinus*) affected the size variations jointly with physical and chemical variables in *M. borellii* (hydrometric level) and *P. argentinus* (conductivity, pH, temperature and hydrometric level). Finally, an opposite pattern was observed between sizes and abundance in relation to vegetation in the two species of prawns. *Macrobrachium borellii* was more abundant but smaller in size in floating vegetation than in the other vegetation types (largest sizes occurred in FW); on the contrary, *P. argentinus* was more abundant but smaller in size in FW than in the other vegetation types.

Table 4 Significant variables of models selected by AIC

Abundance	z value	P value
Macrobrachium borellii		
HP*V + Cond. + pH		
HP	5.165	< 0.001***
V	6.406	< 0.001***
Cond.	− 4.346	< 0.001***
pH	− 5.297	< 0.001***
HP*V	− 2.266	0.0234*

Body size	t value	P value
Macrobrachium borellii		
HP*V + Cond. + pH + Temp.+ HL + Rivers		
V	3.155	0.0018**
HL	2.699	0.0074*
Rivers	4.388	< 0.001***

Abundance	z value	P value
Palaemon argentinus		
HP*V + Cond. + pH + Temp		
HP	6.497	< 0.001***
V	4.876	< 0.001***
Cond.	3.938	< 0.001***
pH	− 12.619	< 0.001***
Temp.	11.574	< 0.001***
HP*V	5.784	< 0.001***

Body size	t value	P value
Palaemon argentinus		
HP*V + Cond. + pH + Temp.+ HL+ Rivers		
HP	− 6.374	< 0.001***
V	− 3.113	0.0019**
Cond.	− 2.543	0.0111*
pH	− 2.088	0.0370*
Temp.	2.978	0.0029**
HL	2.313	0.0209*
Rivers	5.402	< 0.001***
HP*V	4.670	< 0.001***

Abundance	z value	P value
Trichodactylus borellianus		
HP + V + Cond. + pH		
HP	− 3.496	< 0.001***
V	8.055	< 0.001***
Cond.	3.068	0.0021**
pH	− 3.385	< 0.001***

Table 4 continued

Body size	t value	P value
Trichodactylus borellianus		
HP + V		
HP	− 4.068	< 0.001***

Generalised linear mixed-effect models (GLMM) using *glmer* function to test abundance, and Linear Mixed Models (LMM) using *lmer* function to test body size. Random effects: hydrological periods, rivers and sites. Hydrological periods (HP), type of vegetation (V), conductivity (cond.), temperature (temp.), hydrometric level (HL)

Statistically significant differences, *P < 0.05, **P < 0.005, ***P < 0.001

Temporal and spatial variations of the relationship between species abundance and environmental variables

The hydrological periods and types of vegetation explained the abundance among species through axis 1 (CCA1), with a high percentage of explanation (69.97%) (Fig. 6). The other variables were formulated through the two axes (CCA1 and CCA2). The abundances of *M. borellii* and *T. borellianus* increased at M1, and the abundance of *P. argentinus* increased at M2 and M3 (Fig. 6). The abundance of *M. borellii* and *T. borellianus* increased with the presence of floating vegetation (FV), while *P. argentinus* increased in emergent vegetation and vegetation-free waters (Fig. 6). According to the ANOVA test with permutation, the relationship among species abundance (analysed jointly) showed significant differences between periods (*F*: 5.9782; df = 2; *P* = 0.0380) and between types of vegetation (*F*: 6.0258; df = 2; *P* = 0.0280). In FV, the prawn *M. borellii* was slightly more abundant than *P. argentinus*, and both were more abundant than the crab *T. borellianus* (Fig. 7a). *Palaemon argentinus* was more abundant than *M. borellii* in EV. Additionally, *M. borellii* decreased in EV and even more in FW with the drastic increase in *P. argentinus* (Fig. 7a). The crab *T. borellianus* was absent in EV and FW (Fig. 7a). In M1, the abundances of the three species were similar (Fig. 7b). Then, in M2 and M3, *P. argentinus* was more abundant than *M. borellii* and *T. borellianus*, increasing drastically in M3 (Fig. 7b).
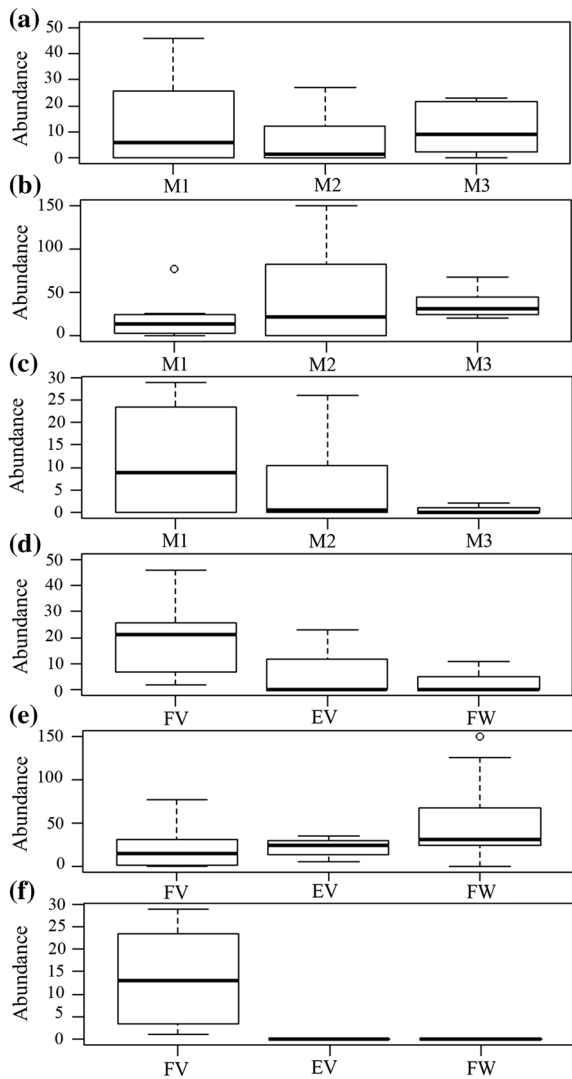
Fig. 2 Abundance of *Macrobrachium borellii* (**a**, **d**), *Palaemon argentinus* (**b**, **e**) and *Trichodactylus borellianus* (**c**, **f**) according to hydrological periods: M1, high waters (end of high waters, when waters begin to decrease); M2, low waters (end of low waters, before waters begin to rise); M3, low waters and type of vegetation: floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW). The lower and upper limits of each box represent the quartile 1 (25% of data) and the quartile 3 (75% of data), respectively. The line inside the boxes represents the median (quartile 2, 50% of data). The whiskers of the boxes represent the maximum and minimum values, and the unfilled circles the outlying data points

Discussion

The presence of macrophytes (floating or emergent) and different hydrological periods influenced the abundance of freshwater decapods. Aquatic plants
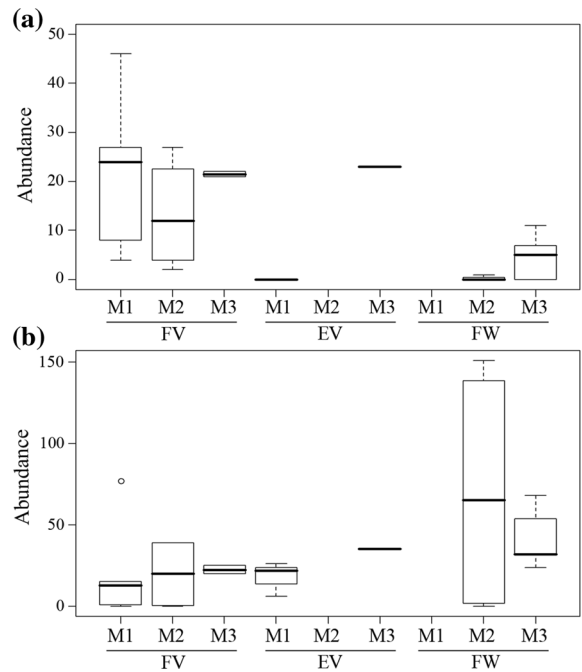
Fig. 3 Abundance of *Macrobrachium borellii* (**a**) and *Palaemon argentinus* (**b**) according to hydrological periods in relation to type of vegetation: M1, high waters (end of high waters, when waters begin to decrease); M2, low waters (end of low waters, before waters begin to rise); M3, low waters. Floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW). The lower and upper limits of each box represent the quartile 1 (25% of data) and the quartile 3 (75% of data), respectively. The line inside the boxes represents the median (quartile 2, 50% of data). The whiskers of the boxes represent the maximum and minimum values, and the unfilled circles the outlying data points

usually increase the richness, biomass and density of macroinvertebrates in freshwater systems (Thomaz & Cunha, 2010; Fontanarrosa et al., 2013). Changes in macrophyte species composition due to water-level fluctuations of floodplain systems could then indirectly modify the composition and biomass of macroinvertebrates, altering the biotic relationships among species (Sabattini & Lallana, 2007; Cremona et al., 2008). Additionally, the hydrometric level promotes the displacement or death of aquatic plants at the margins, inducing changes in the presence or absence of vegetation jointly with changes in the associated macroinvertebrates in different places of the riverbanks (Sabattini & Lallana, 2007).

Populations of *M. borellii* and *T. borellianus* tended to increase with the presence of floating vegetation. In contrast, the prawn *P. argentinus* was more abundant
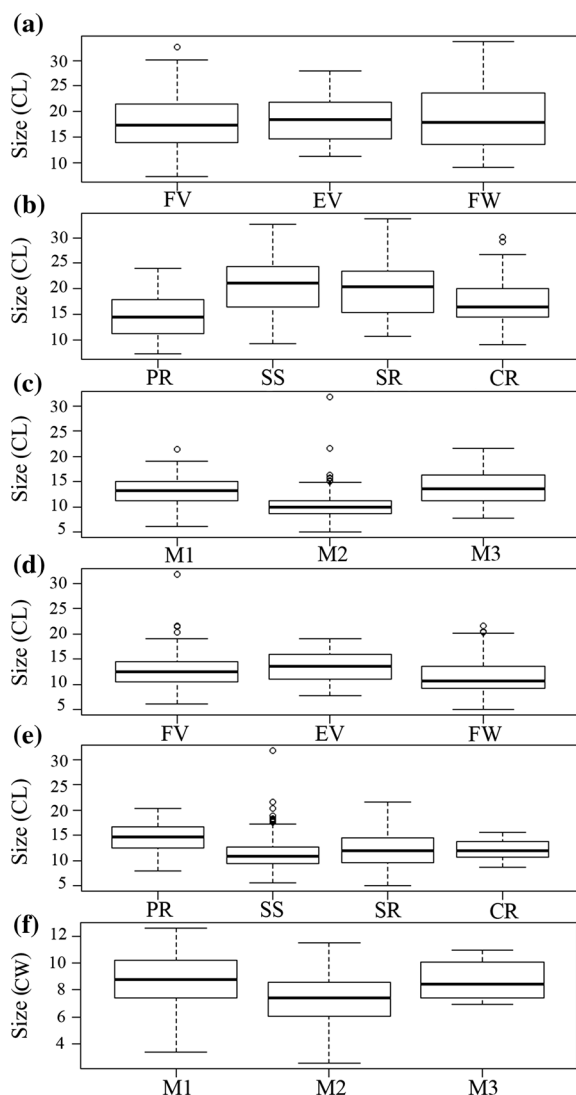
(a)

(b)

(c)

(d)

(e)

(f)

Fig. 4 Sizes (*CL* cephalothorax length, *CW* cephalothorax width) of *Macrobrachium borellii* (**a**, **b**), *Palaemon argentinus* (**c–e**) and *Trichodactylus borellianus* (**f**) according to hydrological periods (*P. argentinus* and *T. borellianus*): M1: high waters (end of high waters, when waters begin to decrease); M2: low waters (end of low waters, before waters begin to rise) and M3: low waters; type of vegetation (*M. borellii* and *P. argentinus*): floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW) (only for *P. argentinus*); rivers (*M. borellii* and *P. argentinus*): Paraná River (PR); Saladillo Stream (SS); Salado River (SR); Coronda River (CR). The lower and upper limits of each box represent the quartile 1 (25% of data) and the quartile 3 (75% of data), respectively. The line inside the boxes represents the median (quartile 2, 50% of data). The whiskers of the boxes represent the maximum and minimum values, and the unfilled circles the outlying data points
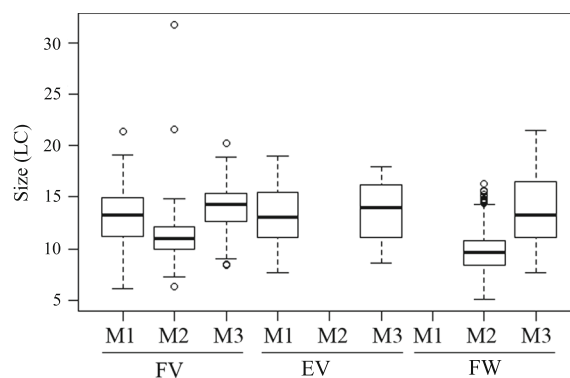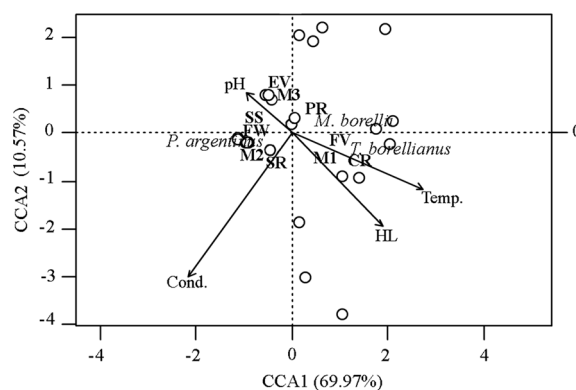

Fig. 5 Sizes (*CL* cephalothorax length) of *Palaemon argentinus* according to hydrological periods in relation to type of vegetation: M1, high waters (end of high waters, when waters begin to decrease); M2, low waters (end of low waters, before waters begin to rise); M3, low waters. Floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW). The lower and upper limits of each box represent the quartile 1 (25% of data) and the quartile 3 (75% of data), respectively. The line inside the boxes represents the median (quartile 2, 50% of data). The whiskers of the boxes represent the maximum and minimum values, and the unfilled circles the outlying data points

Fig. 6 Relationship between abundance of *Macrobrachium borellii, Palaemon argentinus* and *Trichodactylus borellianus* through Canonical Correspondence Analysis (CCA) according to hydrological periods: M1: high waters (end of high waters, when waters begin to decrease); M2: low waters (end of low waters, before waters begin to rise) and M3: low waters; rivers: Paraná River (PR); Saladillo Stream (SS); Salado River (SR); Coronda River (CR); type of vegetation: Floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW) and physical and chemical variables: pH, Cond. (conductivity), Temp. (temperature), HL (hydrometric level)

in emergent vegetation and vegetation-free zones. It is known that the crab *T. borellianus* is an important member of littoral communities that colonise floating plant (Poi de Neiff & Neiff, 1980, 2006, Poi de Neiff & Carignan, 1997; Collins et al., 2006). Additionally, the
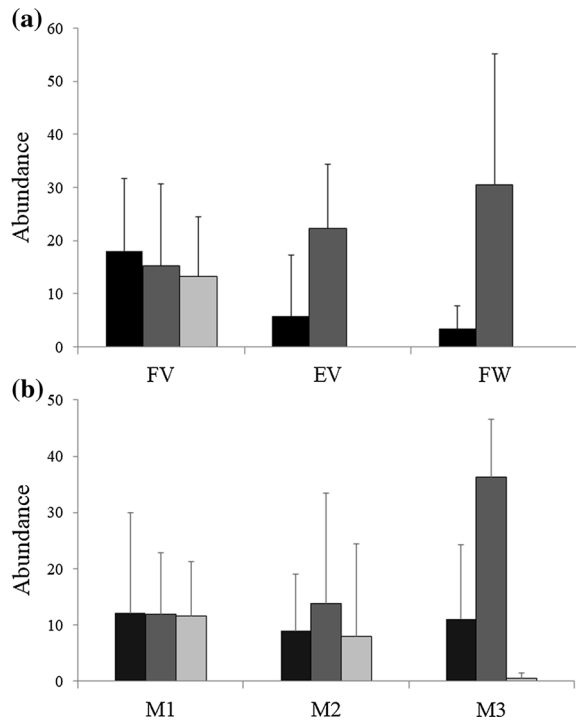
Fig. 7 Mean abundance and standard deviations of *Macrobrachium borellii* (black bars)*, Palaemon argentinus* (dark grey) and *Trichodactylus borellianus* (light grey) in relation to **a**) Type of vegetation: floating vegetation (FV), emergent vegetation (EV) and vegetation-free waters (FW) and **b**) Hydrological periods: M1: high waters (end of high waters, when waters begin to decrease); M2: low waters (end of low waters, before waters begin to rise) and M3: low waters

prawn *M. borellii* has been found to be associated with floating aquatic plants such as *E. crassipes* in the Paraná River (Collins, 2005; Poi de Neiff & Neiff, 2006; Williner et al., 2010). The close association of prawns of the genus *Macrobrachium* with *E. crassipes* was also examined by Montoya (2003), indicating that the transport of hyacinth mats during high water periods probably contributes to the distribution patterns of shrimps in the Orinoco Delta. In addition, the presence of *P. argentinus* in vegetation-free waters, as well as in floating and emergent plants, was recorded (Collins, 1999, 2005). Although the crab *T. borellianus* was not found in emergent plants or vegetation-free waters, *M. borellii* and *P. argentinus* appeared in these environments. This result could be due to the differences in the morphotypes of the studied decapods. Prawns have deployed abdomens that allow for greater dispersion and mobility, in contrast to other decapods such as crabs (Ruppert & Barnes, 1994).

Crabs would have less capacity to escape in vegetation-free zones or emergent plants with low complexity and, therefore, would be more vulnerable to predation. In this sense, floating vegetation such as *E. crassipes* appeared to be the best shelter for *T. borellianus,* suggesting an antipredator behaviour for this crab species (Collins et al., 2006).

High densities of macroinvertebrates on floating plants (as with the abundance of *M. borellii* and *T. borellianus*) are associated with different factors, including the availability of refuge related to the shape of the plant, development of periphyton depending on light penetration and retention capacity for particulate matter of roots (Poi de Neiff & Neiff, 2006). The submerged parts of the floating vegetation form a complex intertwined root and rhizome system, making a special biotope that can harbour diverse aquatic organisms (from phytoplankton and zooplankton to micro and macroinvertebrates) (Ohtaka et al., 2011). Moreover, floating macrophytes can supply oxygen to the water around the roots and change the habitats to habitat that are more preferable to animals due to their capacity to transport atmospheric oxygen or oxygen produced by photosynthesis to the roots through the aerenchyma tissues (Jedicke et al., 1989; Colmer, 2003; Hirota & Tsuchiya, 2003). Furthermore, floating vegetation was principally represented by *E. crassipes*, which is a free-floating plant with well-developed adventitious roots, lateral roots and epidermal hairs (Ohtaka et al., 2011). Meerhoff et al. (2007) found higher densities of plant-associated macroinvertebrates in free-floating plants than in submerged rooted ones. The stems, leaves and stolons of *E. crassipes* build a complex structure that offers suitable habitats or shelter for numerous organisms (Ohtaka et al., 2011). For example, the selection of habitat by zooplankton could be influenced by the higher structural complexity and therefore higher shelter offered by floating plant beds than those offered by emergent plants (Cazzanelli et al., 2008).

However, plants with complex architectures did not necessarily host greater biomasses than those hosted by simpler plants, which is inconsistent with the generally accepted hypothesis that complex plant assemblages constitute more favourable conditions for macroinvertebrates (Cremona et al., 2008). In this sense, higher densities in submerged plants than those in free-floating plants have usually been reported (Tessier et al., 2007; Cazzanelli et al., 2008; Cremona

et al., 2008). Some authors justify this finding because the long and narrow tape-shaped leaves of the studied submerged plants allow more light penetration and nutrient exchange than allowed by beds of denser plants (Cremona et al., 2008). Nevertheless, in this study, it has been reported that not only a significant relation between abundance and vegetation but also a significant relation between vegetation and hydrological periods influence the abundance of prawn species (*M. borellii* and *P. argentinus*). In this manner, the greatest abundance of the prawn *M. borellii* in floating vegetation in high waters (M1) coincided with the higher frequency of sites with floating vegetation and the higher frequency of sites with higher cover percentages in this particular hydrological period. This phenomenon also occurred with the crab *T. borellianus* because the high abundance in M1 was related to the presence of this species in only floating vegetation, and this type of vegetation was more frequent in M1 than in the other waters. The density of macroinvertebrates in *E. crassipes* in high waters increased as a result of the increased water flow through the roots (Poi de Neiff & Carignan, 1997). Additionally, Neiff et al. (2001) observed that periods of flooding (high waters) favoured the growth of *E. crassipes* in different ponds; in contrast, an increase in the biomass of dead vegetation was observed during low waters periods due to nitrogen limitations.

On the other hand, the abundance of the prawn *M. borellii* increased independently during particular hydrological periods; it was higher in high waters (M1) and low waters (M3). This finding could be due to the micro-migratory movements of this species of prawn in rivers with floodplains (Williner et al., 2010). These micro-movements could be caused by the exhaustive use of patches and the search for new patches (Williner et al., 2010). With changes in water level, organisms are forced to leave habitat patches that become unsuitable and colonise new ones (Arrington et al., 2005; Layman et al., 2010; Montoya et al., 2014). Accordingly, four different stages of palaemonid and trichodactilid density have been recognised in the Middle Paraná River that coincide with events in hydric and thermal cycles and are associated with the movements of animals (Collins et al., 2007; Williner et al., 2010). Additionally, the higher abundance coincided with the spring season (M1 and M3), in which increases in the populations occurred due to the input of new cohorts and the migration of specimens from other subpopulations. At this stage, reproductive aggregations, a decrease in predation, an increase in available refuges in the vegetation and trophic diversity and the presence of alternative preys in the littoral community are observed (Collins, 2000; Collins et al., 2007).

As in the present study, the presence of *P. argentinus* in vegetation-free zones, as well as in floating and emergent plants, was also recorded by Collins (1999, 2005). In addition, a species of the *Palaemonetes* genus was found in emergent aquatic plants in the floodplain systems of a Florida river (Wessell et al., 2001). This species was always abundant in semiaquatic *Panicum* (Poaceae family, emergent plant) during high waters, and it was less abundant in *E. crassipes* (Beck & Cowell, 1976). On the other hand, the abundance of *P. argentinus* increased in vegetation-free zones and low waters (M3) and with the relation between these variables (interaction term between hydrological periods and type of vegetation). This result coincided with the decrease in the floating vegetation in M3 and with the high frequency of sites that presented vegetation-free waters in M3. When floating vegetation was absent, this species would move to the vegetation-free zones. Additionally, this could be a result of the spatial microdisposition presented by the two species of prawns studied in this work. *Macrobrachium borellii* has a greater preference to use vegetated environments, and this would displace *P. argentinus* towards the bottom or unvegetated zones (Williner & Collins, 2000). These prawn species seem to co-exist because of small displacements in the differential use of the spatial and temporal dimensions of their niches (Collins, 2005). When species use similar resources, they tend to differ in the spatial and temporal uses of their shared resources (Veen et al., 2010). In aquatic environments where *M. borellii* is present at high densities, *P. argentinus* is found at low densities (Torres et al., 2016), and this is probably due to the hierarchical and aggressive behaviours of *M. borellii* and micro-migratory movements (Williner & Collins, 2000; Williner et al., 2010). In this sense, the colonisation of macrophytes by macroinvertebrates may be influenced or limited by the biology of organisms as well as by the architecture of plant structures such as leaves and stems (Laurindo da Silva et al., 2011).

According to the environmental variables, there was a negative relation between the abundance of the analysed species and pH. This relation coincided with the presence of some species of macrophytes (floating in *M. borellii* and *T. borellianus* and emergent in *P. argentinus*) that are favoured by environmental conditions that include low pH values (Pagano & Titus, 2004; Szabo et al., 2005). Aquatic vegetation is responsible for determining the physical and chemical properties of water (Poi de Neiff & Neiff, 2006; Kaller et al., 2015). Moreover, vegetation can sometimes provide refuge for zooplankton because physical and chemical conditions such as pH, oxygen and temperature may limit the efficiency of fish predation (Burks et al., 2002). On the other hand, there was a negative relation between abundance and conductivity in *M. borellii* and *T. borellianus* and a positive relation in *P. argentinus.* This result could be related to the decreased conductivity in high water periods due to the dilution of salt dilution and an increase in low water periods due to the concentration of salt (Mayora et al., 2013; Musin et al., 2015). This pattern coincides with the increases in *M. borellii* and *T. borellianus* in M1 (high waters) and *P. argentinus* in M3 (low waters). Furthermore, the increases in *M. borellii* and *T. borellianus* that occurred when the conductivity decreased could be related to the high abundance of these species in FV; floating vegetation such as *E. crassipes* absorbs nutrients (along with many ions) through the roots, which leads to a salinity reduction (Sooknah & Wilkie, 2004). Finally, the positive relationship between the abundance of *P. argentinus* and conductivity could be due to the physiological characteristics of this species that indicate its recent ingression from marine to freshwater environments; this species presented a high tolerance to increases in salinity, which were possibly explained by the enzyme activities that allow it to survive and reproduce in environments with wide salinity ranges (Ituarte et al., 2008).

Coincidently with this study, a greater abundance of females in floating vegetation was also indicated by Lima et al. (2014) regarding *M. amazonicum* Heller 1862. These authors suggest that these high abundances were driven by the differences in the occurrence of macrophytes and opportunities for refuge from predation. Females and juveniles of *M. amazonicum* spend more time than males in submerged vegetation to obtain shelter and food, while males tend

to be found at the bottom (Mantelatto & Barbosa, 2005). On the other hand, macrophytes not only provide shelter but also generate better habitat conditions by providing attachment and oviposition sites (Dube et al., 2017). Some authors have suggested that reproductive strategies could be employed by females that seek protected habitats (Copatti et al., 2016; Williams et al., 2016). The variation in the male:female ratio in *T. borellianus* is negatively correlated with river height; however, there is no relation with other parameters (e.g. temperature and aquatic vegetation) (Collins et al., 2006). In this case, males of *T. borellianus* show a higher numeric variability, indicating reproductive movements (Collins et al., 2006).

The larger sizes of *P. argentinus* and *T. borellianus* in high waters (M1) and low waters (M3) coincided with the spring season when the populations increase due to the migrating specimens and reproductive aggregations (Collins, 2000; Collins et al., 2006, 2007). Although the ovigerous females were not differentiated from the rest of the specimens in this study, the larger sizes could be due to the presence of large breeding females during the spring season. Additionally, females of these species are larger than males (Torres, 2016). The sizes of *M. borellii* were larger in EV and FW than in FV, and the sizes of *P. argentinus* were larger in FV and EV than in FW. In a study on the prawn *M. amazonicum*, smaller sizes were observed beneath floating macrophytes, suggesting that these meadows serve as nursery habitats (Collart & Moreira, 1993). Furthermore, macrophyte complexity has been found to influence body size distributions, leading to an increase in the abundance of small individuals and a simultaneous decrease in the number of large individuals (MacAbendroth et al., 2005; Ferreiro et al., 2010). Floating vegetation was mostly composed of *E. crassipes,* which build complex structures that offer suitable habitat or shelter for numerous organisms (Ohtaka et al., 2011). In contrast, the sizes of *P. argentinus* were small in FW. This result indicated that macrophytes could provide refuges and oviposition sites for large breeding females (Dube et al., 2017) and not for small prawns (juveniles) of this species. Moreover, the presence of the smallest *P. argentinus* individuals in vegetation-free waters could be due to the negative effect of predation on macroinvertebrate sizes (Crowder & Cooper, 1982; Diehl, 1992). An increase in predation would lead to size spectra with lower numbers of

individuals with large body sizes. In addition, unvegetated areas would promote direct contact between predators and preys, causing an increase in prawn vulnerability (Gribben & Wright, 2014; Torres et al., 2016). Lastly, exposure to predation risk cues during embryonic development of *P. argentinus* resulted in a smaller size and a shorter rostrum of the juvenile stage (Ituarte et al., 2014).

A pattern that prawns were the largest and their population abundance was the lowest was observed. Torres et al. (2016) suggested that the size–density relationships of these species are due to differences in habitat use and movement patterns of juveniles and adults, which show ontogenetic habitat shifts related to differences in selective pressure (e.g. predation risk, growth and reproduction optimisation). The different periods of the water fluctuations also explained the abundance relationship of the decapod species.

The variations in the body sizes of *P. argentinus* according to rivers were related to the environmental characteristics of the rivers. Large sizes were found in water with low conductivity, which coincided with the large prawns in the Paraná River (low conductivity values). In contrast, *M. borellii* presented large sizes in the Salado River and Saladillo Stream (high conductivity). This finding indicates that the responses of the sizes and distribution in these species of prawns differ. It is known that species traits often vary substantially across geographical gradients (Gaston et al., 2008); among them, body size is of central relevance because it is directly related to several ecological and physiological processes (Blueweiss et al., 1978). Geographical body size clines are evident across multiple faunal taxa and have been observed in aquatic environments (Blanck & Lamouroux, 2007).

In addition, the sizes of prawns (*M. borellii* and *P. argentinus*) increased with the hydrometric level and temperature (for only *P. argentinus*). In systems with floodplains, the body sizes of individuals can change according to river dynamics, with variations during isolation and flood periods (José de Paggi & Paggi, 2007). Hydrological fluctuations constitute a macrofactor that affects physical and chemical variables and influences the richness, distribution and abundance of organisms that live in these systems (Aoyagui & Bonecker, 2004; Winemiller, 2004; Arrington et al., 2006; Mayora et al., 2013). Additionally, in the Middle Paraná River, higher food consumption occurs at the beginning of spring until autumn, when macrofactors (hydric and thermal cycle) exhibit their maximum values. In this period, growth, development and reproduction are active events that require the accompaniment of a successful trophic activity (Collins et al., 2007). Physical and chemical variables influenced the size variations of the prawn *P. argentinus*. In aquatic environments, temperature and body size are the primary factors that influence the ecological and physiological processes of organisms (Hildrew et al., 2007). In decapods, the moulting frequency is affected by extrinsic factors such as temperature, salinity, light intensity and pH (Renzulli & Collins, 2000; Pervaiz et al., 2015) For example, the size of the crab *T. borellianus* was found to increase with the increase in temperature under controlled laboratory conditions (Renzulli & Collins, 2000). On the other hand, in the shrimp *P. varians*, there was a reduction of the intermoult period when the temperature increased (Jefferies, 1964). In relation to pH, a delay in the growth of the freshwater prawn *M. rosenbergii* was also registered with an increase in pH (Chen & Chen, 2003). According to conductivity, the negative relation between size and conductivity coincided with the pattern that was registered in *Palaemonetes pugio* Holthuis 1949, in which higher fecundity and larger size at maturity were observed in a population living in a less-saline habitat (Alon & Stancyk, 1982). Despite the inferences regarding the body size variations and physical and chemical variables, it is possible that there are other variables that affect these variations more strongly but were not considered in this study; for example, biological interactions such as predation that could influence body size variations (Emmerson et al., 2006).

Similar to what was expressed in previous paragraphs, the type of vegetation and hydrological periods were significant factors that regulated the abundance of species when these were analysed together. Different responses to these variables were observed in each species and coincided with the previous analysis of individual abundance; the abundances of *M. borellii* and *T. borellianus* were high with the presence of floating vegetation (FV) and in high waters, while the abundance of *P. argentinus* was high in emergent vegetation and vegetation-free waters in low waters. These findings were similar to those registered by Fontanarrosa et al. (2013), who indicated that the structure of macroinvertebrate assemblages (species analysed jointly) was affected by both

hydrological fluctuations and changes in the taxonomic composition and relative abundances of macrophytes. In this sense, it is relevant to understand how the presence of macrophytes (submerged, emergent or floating vegetation) and hydroperiods affect the aquatic invertebrate community structure in floodplain systems (Dube et al., 2017). Finally, changes in macrophyte species composition due to water fluctuations could indirectly modify the composition and biomass of the macroinvertebrate community, altering the biotic relationships among species (Neiff et al., 2001; Paillisson & Marion, 2006; Beklioglu et al., 2007; Sabattini & Lallana, 2007; Cremona et al., 2008). Hydrological fluctuations constitute a macrofactor that affects physiochemical variables and influences the richness, distribution and abundance of organisms that live in these systems (Aoyagui & Bonecker, 2004; Winemiller, 2004; Arrington et al., 2006; Mayora et al., 2013). Thus, even though changes in macrophyte species composition and abundance may reflect the functional organisation of macroinvertebrate assemblages, the influence of the hydroperiod is paramount in floodplain systems (Fontanarrosa et al., 2013).

Conclusion

In the present study, it was asserted that the presence of macrophytes (floating and emergent vegetation) during different hydrological and seasonal periods in a floodplain system affected the species composition (abundance, sex ratio and body sizes) of freshwater decapod species. Additionally, environmental variables such as conductivity and pH affected the species composition, which could be related to the presence of vegetation, the different hydrological periods and the physiological processes of organisms. Moreover, the abundance of each species had different responses according to type and presence/absence of vegetation during different hydrological periods due to the ecological characteristics of each species. *Macrobrachium borellii* and *T. borellianus* tended to increase with the increase in floating vegetation in high waters, while *P. argentinus* was abundant in emergent vegetation and vegetation-free waters in low waters. On the other hand, the type of vegetation and hydrological periods structured the abundance of decapods when these factors were considered

together. Macrophytes provide shelter and foraging locations for freshwater decapods, influencing the species abundance. In addition, changes in macrophyte species composition due to water-level fluctuations of floodplain systems modify the abundance of freshwater decapods, altering the species composition of decapod assemblages. In studies carried out in dynamic systems of floodplains, it becomes necessary to consider the greatest number of variables that influence the species compositions and relationships of aquatic organisms. Floodplain rivers are complex systems that act as a macrofactor that regulates other factors (e.g. physical and chemical variables) that indirectly affect the richness, distribution and abundance of freshwater decapods through aquatic vegetation and play a relevant role in structuring communities in aquatic ecosystems.

Compliance with ethical standards

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

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