'La Niña' phenomenon and the relationship between decapod populations and fishes in temporarily isolated shallow lakes

María Victoria Torres[A,D], *Federico Giri*[A,B] *and Pablo Agustín Collins*[A,B,C]

[A]Instituto Nacional de Limnología (CONICET-UNL), Ciudad Universitaria Paraje El pozo s/n, CP 3000, Santa Fe, Argentina.

[B]Facultad de Humanidades y Ciencias, (UNL), Ciudad Universitaria Paraje El pozo s/n, CP 3000, Santa Fe, Argentina.

[C]Facultad de Bioquímica y Ciencias Biológicas (UNL), Ciudad Universitaria Paraje El pozo s/n, CP 3000, Santa Fe, Argentina.

[D]Corresponding author. Email: mavictoriatorres@gmail.com

Abstract. The 'La Niña' phenomenon causes temporary isolation of shallow lakes in rivers with floodplain. Furthermore, as abiotic conditions become more extreme, and intra–interspecific relationships intensify, the risk of local species extinction increases. The Paraná River in South America is a river with an extensive floodplain with many shallow lakes. In these environments, freshwater prawns and many fish species coexist. The aim of the work was to study the interaction between two species of prawns (*Palaemonetes argen*tinus and *Macrobrachium borellii*) and fishes during 'La Niña' phenomenon. Density variations of prawns and fishes were examined in three shallow lakes at Paraná River. The samples were collected monthly at several points of each aquatic environment with a trawl net. Abiotic and biotic factors were measured. Density and population structure varied in both prawns, and fishes, and the changes have not been simultaneous. These variations might be associated with predation, aggressive behaviour of the prawns and internal micro-migrations. The effect of La Niña creates additional stress on prawn populations when water inflow is delayed. This fact could promote the decrease or the complete disappearance of one or both prawn species in the environments, and modify the trophic web in the next phase of the shallow lakes.

Additional keywords: connection phases, floodplain, freshwater decapods, isolation phases, predatory fishes.

Introduction

The seasonal hydrology of some rivers comprises high and low water levels that drive ecological processes (Poff *et al.* 1997; Winemiller 2004). In rivers with floodplains, hydrological fluctuations connect the main channel and the floodplains in a dynamic unit, enabling the lateral exchanges of materials and organisms between both, and facilitating the ecosystem structure and function (Junk *et al.* 1989; Neiff 1990; Poff and Allan 1995; Benke *et al.* 2000; Tockner *et al.* 2000; Winemiller 2004). Floodplain systems provide different sizes, temporality of shallow lakes, and conditions that change with the flood stage of the adjacent river (Drago 1989; Doss 1993). Depending on river flow, these aquatic environments are interconnected or isolated from the main river. Moreover, some aquatic habitats in a floodplain are isolated from each other, and subjected to local driving forces during low-water periods (Thomaz *et al.* 1997; Lewis *et al.* 2000; Carvalho *et al.* 2001). In this sense, hydrological fluctuations constitute a macrofactor that affects physiochemical variables, and influences the richness, distribution and abundance of organisms that live in these systems (Neiff *et al.* 2001; Aoyagui and Bonecker 2004; Winemiller 2004; Arrington *et al.* 2006; Balcombe and Arthington 2009; Mayora *et al.* 2013). These effects could be intensified by the 'La Niña–El Niño' phenomena when the duration of high and low water levels increase (Depetris *et al.* 1996). These phenomena are part of a global natural cycle of climate known as El Niño–Southern Oscillation (ENSO). This global cycle has two phases, namely, a warm phase known as 'El Niño' and a cold phase known as 'La Niña'. The phenomenon of 'La Niña' causes extreme weather effects in different macro-regions of the planet, such as periods of drought in South America (as the phenomenon discussed in this work) and heavy rainfall associated with floods in eastern Australia (Vicario *et al.* 2015).

Populations of freshwater decapods that live in floodplain ecosystems move continuously according to the dynamics of each environment. These movements can be induced by biotic and abiotic factors in a dynamic system, and they occur over different spatial and temporal scales (Williner *et al.* 2010).

Additionally, hydrological fluctuations in a floodplain system modulate the dispersion and the presence or absence of decapods in a particular habitat (Ranta *et al.* 1998; Fernandez and Collins 2002; Ruetz *et al.* 2005; Collins *et al.* 2007). The regular movements of decapods that live in a floodplain can be characterised by the displacements within lakes, ponds or rivers that can occur in either a passive or active manner (Williner *et al.* 2010).

Also, the hydrological dynamics of a system within a floodplain can influence species interactions. For example, when the water level decreases, shelters are lost and populations of species are concentrated, increasing the contact among individuals (Fernandez and Collins 2002). Freshwater decapod populations can also be affected by potential predators in a floodplain system. The importance of decapods in the trophic webs lies in their high densities, and in the nutritional quality that is transferred energetically towards different trophic levels and environments (aquatic, semi terrestrial and terrestrial (Collins *et al.* 2006*a*). Several authors have found that freshwater prawns are the principal prey of many fishes and birds species in floodplain ecosystems, taking part in the matter–energy exchange between aquatic and terrestrial systems (Oliveros and Del Barco 1991; Oliveros and Rossi 1991; Beltzer and Muñoz 2001). Besides, fishes are well known to structure invertebrate communities in littoral areas of permanent ponds and lakes (Pierce and Hinrichs 1997; Balcombe *et al.* 2005; Rossi *et al.* 2007). In many river systems, fish community structure and production are directly related to the quality and quantity of connections between the main river and off-channel flood habitats (De Graaf 2003; Balcombe and Arthington 2009; Górski *et al.* 2012).

In these ecosystems, the crustacean populations show a spatial distribution ruled by physical and biological factors that mark some heterogeneity within the ecosystems (Walker 1994; Carter *et al.* 1996), where the elimination of decapods in an area occurs frequently or rarely, for prolonged or short periods of time, owing to the intensity of the disturbance (e.g. flooding, drought, thermal extremes, loss of refuge; Collins 2000). Also, the presence of prawns in an environment depends on the habitat–vegetation (e.g. species and plant age)–sediment (e.g. type of sediment and size) relationship, physicochemical properties, food abundance and presence of prey, among others (Poi de Neiff and Carignan 1997; Pothoven *et al.* 2004; Collins *et al.* 2006*a*).

The Paraná River, the second largest river of South America, is 4000 km long and its alluvial valley is progressively expanding (Drago 2007). The watercourse divides into several channels, enclosing complex formations of low islands. The shallow lakes of the floodplain are strongly influenced by the seasonal fluctuations of the Paraná and tributary rivers and they are interconnected with or isolated from the main course (Drago 1989, 2007). These freshwater systems with floodplains shelter two sympatric prawn species, *Palaemonetes argentinus* (Nobili, 1901) and *Macrobrachium borellii* (Nobili, 1896). These have similar geographical distributions (southern Brazil, Paraguay, Uruguay and Argentina), but temporal and evolutionary distances in the adaptation to freshwater environments (Boschi 1981). These species of prawns show great similarity in their ecological requirements (Collins and Paggi 1997; Collins 1999).

Considering that populations and their biological interactions could be influenced by the fluctuations of a hydrological system, which modulates the environmental variables, the aim of this work was to analyse the effect of La Niña event on the relationship between decapod crustacean populations and the potential predatory fishes at different phases of isolation–connection of shallow lakes.

Materials and methods

Sampling area

The current study was undertaken during the period 1995–1996 of the La Niña phenomenon (considered as mild period of drought) in three shallow lakes located on the floodplain of the Paraná River, 'Don Felipe', 'Number 1' and 'Alejandra' (Fig. 1). The water level of the Paraná River declines from summer to winter, and flooding occurs each spring. The river has an average annual discharge of $18\,000\,\text{m}^3\,\text{s}^{-1}$ (Bonetto and Wais 1995). Don Felipe (31°39′S, 60°41′W) is a shallow lake located in the floodplain of the Paraná River near the Colastiné River, a connected secondary branch of the main channel (Fig. 1). The volume of this oxbow lake changes depending on the input of freshwater from the Colastiné River. In isolation, its maximum and mean depths are 2 and 0.66 m respectively (Collins and Paggi 1997). The Number 1 lake (31°40′S, 60°30′W) is a meander scroll lake located near the Salado River (i.e. a river with a high dissolved salt concentration; Fig. 1). The lake volume changes depending on inflows from the Salado and Santa Fe rivers and its average depth is ~0.55 m during the isolated phase. Alejandra Lake is an overflow lake with a direct connection to the Coronda River (Fig. 1). It is 0.8 km long, with a surface of ~75 000 m^2 during isolation.

Field and laboratory procedures

Palaemonid and fish populations were sampled in three points in each shallow lake (considered as pseudo-replicates). Specimens were collected with a trawl bottom net (8-m length and 1-mm mesh) along 10 m^2 approximately in each point, and were immediately anesthetised with ice and fixed in 96% alcohol. These samples were taken monthly (August to November) during pre-isolation, Isolation 1, Isolation 2 (first and second month of isolation) and post-isolation phases. These phases were defined according to connectivity or isolation of the shallows lakes with the main channel. So, pre-isolation phase was when water level of the principal channel tended towards low, but the main channel was still connected with the shallow lakes; isolation phases were when water of the main channel declined, and the main channel was isolated from the shallow lakes; and post-isolation phase was when water of the main channel rose and re-entered the shallow lakes, reconnecting the main channel with the shallow lakes. Data on the daily hydrometric level of each site was obtained from Facultad de Ingeniería Hídrica (Universidad Nacional del Litoral, Santa Fe Province, Argentina).

Environmental variables were measured at each sample site as indicators of environmental quality. Temperature, conductivity and pH were determined using a digital sensor (HANNA Instruments, HI198130, Mauritius). Transparency was measured with a Secchi disc. Depth was measured in the middle
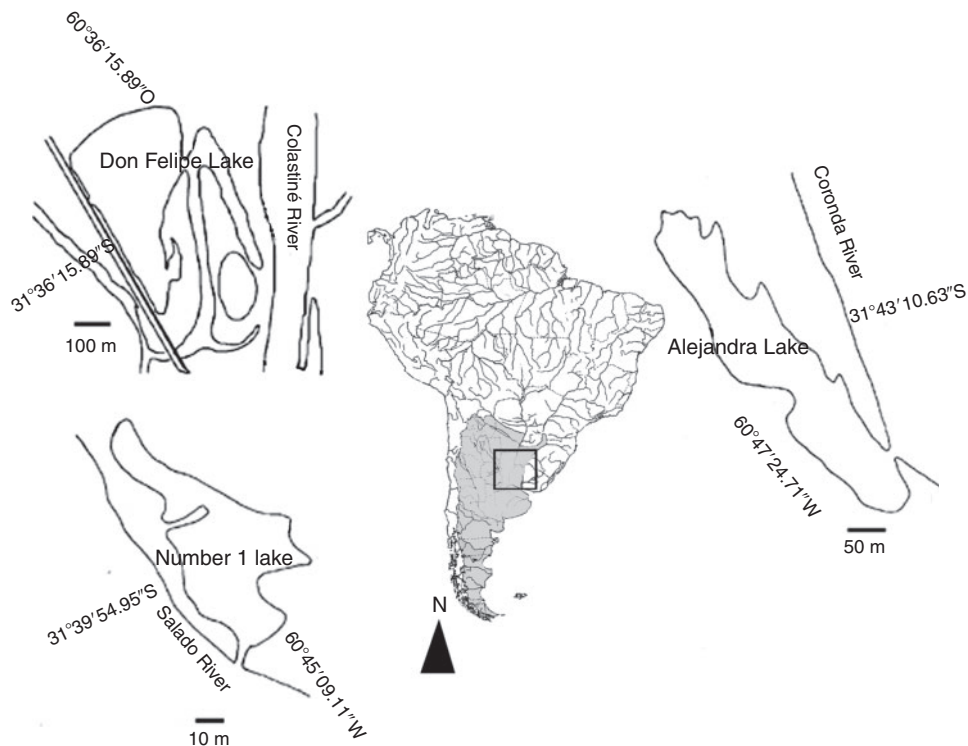
Fig. 1. Location of the study area. Shallow lakes sampled (Don Felipe, Number 1 and Alejandra), located on the floodplain of the Paraná River.

of each lake (fixed point) using a metric stick. The surface of each shallow lake was measured with topographic methods using GPS tracking.

In the laboratory, freshwater prawn species were identified following Boschi (1981) and counted. Then, their population density was determined (prawns m^{-2}). Cephalothorax length (CL) was measured from the tip of the rostrum to the posterior margin in the midline, using a calliper under a stereoscopic microscope. Fish specimens were identified according to Almirón *et al.* (2008), measured according to standard length, and their population density was determined (fish m^{-2}). Fish stomachs were removed, and the contents were extracted and examined under a stereoscopic microscope. Prawn remains found in the guts were measured and counted, and mean prawn occurrence in fish stomachs (%) was determined.

Data analysis

The relationship between environmental and biotic variables was explored through principal component analysis (PCA) based on correlation matrix. This analysis included chemical variables (i.e. temperature, conductivity and pH), physical variables (hydrometric level, water transparency, water depth and surface) and prawn population parameters (i.e. population density of prawns, prawn size), considering each phase of isolation–connection. This analysis was undertaken to explore the relationships among environmental variables, phases of isolation/connection and shallow lakes. Normality and homoscedasticity of each variable were tested.

Descriptive analyses were performed to understand the relationships among shallow lakes and among isolation–connection phases. The differences in chemical and physical variables among shallow lakes and phases were evaluated with a Kruskal–Wallis test. Comparisons of density of each prawn and the prawn's CL among shallow lakes and phases of isolation–connection were analysed by ANOVA.

So as to characterise population variation, prawn density (dependent variable) was studied with respect to different independent variables with a Markov chain Monte Carlo sampler for multivariate generalised linear mixed models (MCMCglmm), which has special emphasis on correlated random effects (Hadfield 2010). In this model, we included physical and chemical variables, shallow lakes, phases of isolation–connection, species of prawns and prawn size as independent variables of a fixed effect. Species of prawns were taken into account because the density of prawns is characteristic to a species. The phases of isolation–connection and shallow lake variables were considered as a random effect because of the possible temporal and spatial dependence between the two variables. The quantitative variables were standardised ($\log_{10}$ transformation) to run the mixed model. Also, Gaussian distribution was used and confidence envelopes were estimated as 95% confidence intervals of 1000 random samples from the posterior distribution. Before running this model, co-linearity among physical and chemical variables (to elucidate the relations among variables) was calculated by non-parametric Spearman correlation coefficient. Regarding the pair of variables that presented co-linearities ($r > 0.70$), only one variable of each
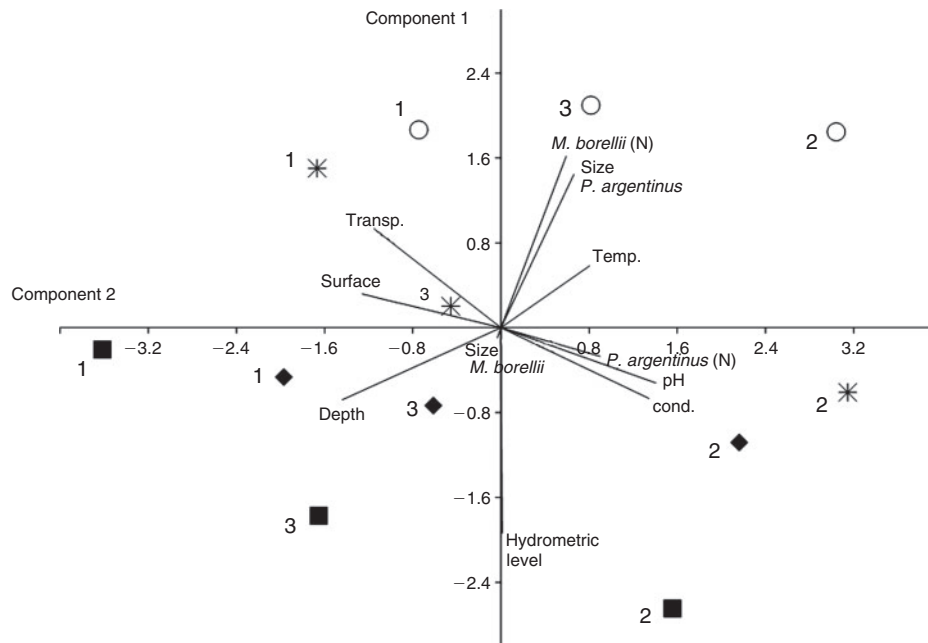
Fig. 2. Principal component analysis with the variables measured during phases of connection. Environmental variables: cond., conductivity; temp., temperature; pH; hydrometric level, depth and surface; population parameters: population density and size of cephalothorax of each species of prawn (*M. borellii* and *P. agentinus*). Arrangement by phases of isolation–connection: pre-isolation, closed square; isolation 1, asterisk; isolation 2, open circle; post-isolation, closed diamond. Arrangement by shallow lakes: 1, Don Felipe; 2, Number 1; 3, Alejandra.

pair were selected. Then, the inter-relationships of population density and the significant variables (of the MCMCglmm running at first) were tested with ANOVA interaction model, using the interaction with the random variable that most contributed to the variation in population density (which had a greater value of posterior mean in the MCMCglmm).

The differences in occurrence of prawns in fish stomachs (%) among phases of isolation–connection and between the families of fishes were analysed with a Kruskal–Wallis test. The relationship between prawn and fish (with prawns in their stomachs) densities was calculated by parametric Pearson correlation coefficient throughout the phases of the shallow lakes, so as to analyse the interspecific relation (according to densities) with their predatory fishes. All analyses were conducted with R software (R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org).

Results

The first two components of PCA explained the 41.41 and 21.55%, showing the variations among shallow lakes and phases of isolation–connection during La Niña phenomenon (Fig. 2). Environmental variables, such as pH, conductivity, transparency and surface characterised the shallow-lake variation. The pH and conductivity increased in Number 1 lake (lake near to Salado River), whereas transparency and surface decreased in this lake, and increased in Don Felipe lake (Fig. 2, Table 1). The differentiation among the phases of isolation–connection was identified by depth, hydrometric level, temperature, density of *M. borellii* and prawn size (Fig. 2). Temperature, density of

Table 1.   Correlation values of environmental and biological variables on the first and second principal components
PCA, principal-component analysis

Variable	Correlations of PCA	
	Component 1	Component 2
Hydrometric level	0.03699	−0.8485
Temperature	0.5052	0.2942
pH	0.9055	−0.2759
Conductivity	0.8701	−0.3316
Transparency	−0.7611	0.3623
Depth	−0.9242	−0.3646
Surface	−0.8129	0.1229
Population density of *Macrobrachium borelii* (*n*)	0.2035	0.7673
Population density of *Palaemonetes argentinus* (*n*)	0.6396	0.004127
Size of *Macrobrachium borellii*	−0.03859	−0.08055
Size of *Palaemonetes argentinus*	0.4197	0.7099

M. borellii and the CL of *P. argentinus* increased during the Isolation 1 and Isolation 2 phases. Moreover, the CL of *M. borellii* was larger during pre-isolation and post-isolation phases (Fig. 2, Table 1).

The hydrometric level of each lake during the isolation phases was between 2 and 4 m (Fig. 3, Appendices 1, 2). Water-level dynamics were similar among lakes but were
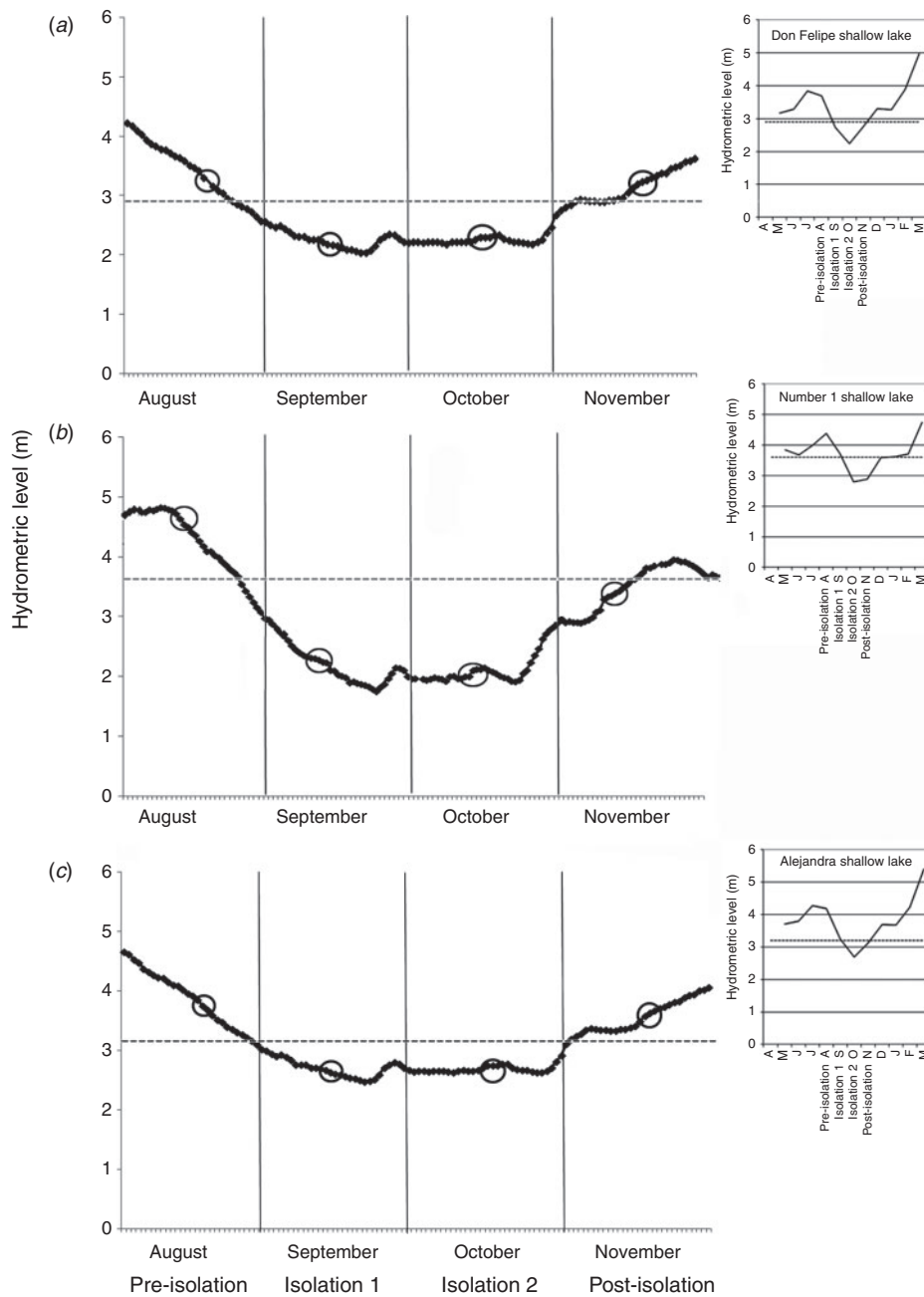
Fig. 3. (*a–c*) Daily hydrometric level during the months of isolation–connection phases (shallow lakes). Circles indicate the sampling times (days) in each shallow lake. Figures of the right show the general variation of hydrometric level by month (phases) of each shallow lake. Dotted lines indicate the waterline during isolation in each shallow lake.

statistically different among the phases (Table 2). However, this variable was similar between Isolation-1 and Isolation-2 phases (first and second month of isolation; $H = 8.987$, $P = 0.8248$) when water level was lower and between pre-isolation and post-isolation phases ($H = 8.987$; $P = 0.184$) when water level was higher. The pre-isolation phase was in August, Isolation phases (1 and 2) were in September and October, and post-isolation phase was in November (Fig. 3). The shallow lakes lost aquatic

vegetation during the isolation phases. Temperature was not different among the shallow lakes, but it was different among phases, increasing throughout of the duration of the study (months; Appendix 2, Table 2). The Number 1 lake (shallow lake near to Salado River) presented higher values of conductivity and pH was different among the lakes (Appendix 1, Table 2). Transparency presented differences among the lakes, showing lower values for Number 1 lake (shallow lake),

Table 2.   Values of the Kruskal–Wallis test between physico-chemical variables of shallow lakes and phases of isolation–connection
Statistically significant differences: *, $P < 0.05$

| Physico-chemical variable	Shallow lakes		Phases of isolation/connection	
	H	P	H	P
Hydrometric level	1.0800	0.5825	8.9870	0.0294*
Water temperature	1.2210	0.5430	8.4230	0.0380*
pH	9.8460	0.0072*	0.3710	0.9460
Conductivity	9.8460	0.0072*	0.3710	0.9460
Transparency	6.9620	0.0307*	1.5640	0.6676
Depth	5.3460	0.0690	5.3590	0.1473
Lake surface	9.8460	0.0072*	1.0510	0.7888
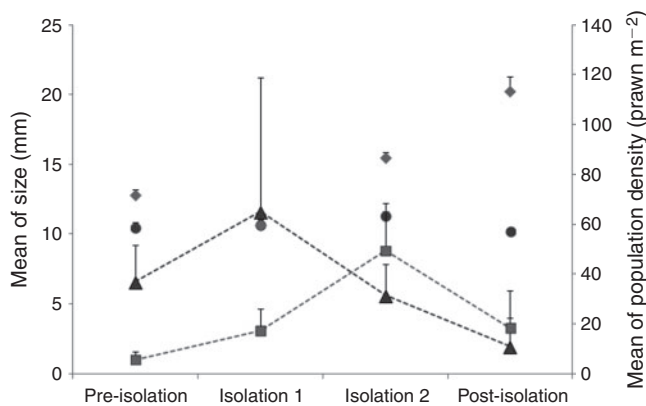
Fig. 4. Variability of population density (mean population density) and mean cephalothorax size of the two freshwater prawn species during phases of isolation–connection: pre-isolation, Isolation 1, Isolation 2, post-isolation. Population density: *P. argentinus*, dark grey triangle; *M. borellii*, light grey square. Cephalothorax length: *P. argentinus*, dark grey circle; *M. borellii*, light grey rhomboid.

whereas depth did not present differences among the lakes (Appendix 1, Table 2). Surface was greater in Don Felipe, presenting a difference among the lakes (Table 2). These last variables (conductivity, pH, transparency, depth and surface) did not show high variations among the phases of isolation–connection (Appendix 2, Table 2).

In total, 14 100 individuals of *P. argentinus* and *M. borellii* were collected and measured during the study. Population density of both prawns was similar among the shallow lakes (d.f. = 2, $F = 3.1440$, $P = 0.0922$) and among phases in *P. argentinus* (d.f. = 3, $F = 1.6223$, $P = 0.2595$). However, population density of *M. borellii* presented a significant difference between pre-isolation and Isolation 2 (d.f. = 3, $F = 7.4121$, $P = 0.0073$), being greater during Isolation 2 (Fig. 4).

Palaemonetes argentinus had less variation in CL among the phases of isolation–connection (Fig. 5). However, cephalothorax size was significantly different between Isolation 2 and pre-isolation, and Isolation 2 and post-isolation (d.f. = 3, $F = 8.7033$, $P < 0.05$). The CL of *M. borellii* was significantly different in each phase (d.f. = 3, $F = 138.4500$, $P < 0.05$), and increased as the study progressed (Fig. 5).
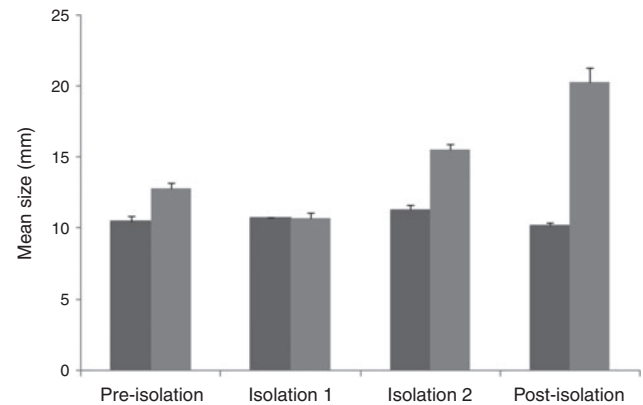
Fig. 5. Mean sizes of prawn (mm) during phases of isolation–connection. *Palaemonetes argentinus*, dark grey bar; *Macrobrachium borellii*, light grey bar.

Table 3.   Results of predictor variables of population density from the Markov chain Monte Carlo sampler for multivariate generalized linear mixed models (MCMCglmm)
Deviance information criterion (DIC): 29.4627. The variables of fixed effect that presented statistically significant differences were included. Statistically significant differences: *, $P < 0.05$; **, $P < 0.005$

Variable	Posterior mean	P-value
Prawn species	0.71580	0.0040**
Prawn size	3.6950	0.010*

Table 4.   Results of ANOVA interaction model using the significant variables of MCMCglmm and the interaction with isolation–connection phases
Statistically significant differences: *, $P < 0.05$

Interaction model	d.f.	F-value	P-value
$\log_{10}$(abundance) ~species × phase	3	4.8064	0.0163*
$\log_{10}$(abundance) ~$\log_{10}$(size) × phase of connection	3	3.6118	0.0364*

The pH and conductivity were excluded of GLM model analysis because they presented co-linearity with others variables. Thus, the population variation with regard to prawn density in the MCMCglmm was represented by phases of isolation–connection, shallow lakes, hydrometric level, transparency, depth, temperature, surface, species of prawn and prawn size. The random effects that contributed to population variation were the phases, with a greater value of posterior mean (284 308 707) than for shallow lakes (87 322). The fixed effects that presented statistically significant differences in the population density were the species and size of prawn (Table 3).

In relation to linear models of interaction and the significant fixed variables, the densities of *P. argentinus* and *M. borellii* differed among the isolation–connection phases. Prawn population density showed a statistically significant interaction of prawn species and phases (Table 4). Also, the prawn density

Table 5. Fishes sampled during the Isolation-1, Isolation-2 and post-isolation phases in shallow lakes

n, mean of fish numbers; Oc, mean prawn occurrence in fish stomachs (%)

Family and species	Isolation 1		Isolation 2		Post-isolation	
	n	Oc	*n*	Oc	*n*	Oc
Family Characidae						
Charax gibbosus	5 ± 1.18	0	3 ± 1.00	0	5 ± 2.17	0
Astyanax aff. fasciatus	9 ± 2.12	83 ± 16.01	47 ± 6.35	60 ± 14.1	24 ± 10.44	20 ± 8.74
Astyanax bimaculatus	8 ± 1.88	20 ± 7.49	8 ± 1.08	29 ± 6 89	14 ± 6.09	33 ± 14.35
Astyanax sp.	4 ± 1.00	15 ± 6.34	0	0	75 ± 22.65	18 ± 8.98
Family Anostomidae						
Leporinus sp.	1 ± 1.00	0	0	0	1 ± 1.00	0
Family Curimatidae						
Prochilodus lineatus	0	0	0	0	2 ± 1.00	0
Curimata sp.	91 ± 21.34	0	8 ± 1.45	0	94 ± 20.89	0
Family Pimelodidae						
Hypophthalmus sp.	1 ± 1.00	0	0	0	0	0
Iheringichthys sp.	1 ± 1.00	0	0	0	0	0
Parapimelodus valenciennesi	13 ± 3.60	0	0	0	4 ± 1.71	25 ± 10.88
Pimelodella sp.	0	0	5 ± 1.00	0	1 ± 1.00	0
Pimelodus albicans	6 ± 1.41	50 ± 11.75	6 ± 1.00	50 ± 13.02	28 ± 12.18	22 ± 14.22
Pimelodus maculatus	2 ± 1.00	50 ± 5.17	3 ± 1.00	66 ± 15.51	1 ± 1.00	0
Rhamdia quelen	0	0	0	0	24 ± 12.45	0
Family Callichthyidae						
Corydoras paleatus	8 ± 1.88	0	0	0	50 ± 21.75	0
Hoplosternum sp.	0	0	0	0	1 ± 1.00	0
Family Loricariidae						
Loricaria sp. A	1 ± 1.00	0	0	0	5 ± 2.17	0
Loricaria sp. B	17 ± 3.99	0	2 ± 1.00	0	13 ± 5.66	0
Family Hypopomidae						
Brachyhypopomus brevirostris	0	0	0	0	3 ± 1.00	0
Family Sciaenidae						
Plagioscion macdonaghi	1 ± 1.00	0	0	0	0	0
Pachyurus sp. A	0	0	0	0	1 ± 1.00	0
Pachyurus sp. B	0	0	0	0	3 ± 1.00	0
Family Cichlidae						
Gymnogeophagus sp.	1 ± 1.00	0	0	0	1 ± 1.00	0

within each size category was different in each phase (e.g. pre-isolation, Isolation 1, Isolation 2 and post-isolation; Table 4). The population pattern along the phases differed between the two prawn species; *P. argentinus* was more abundant during pre-isolation and Isolation-1 phases, whereas *M. borellii* was more abundant during Isolation-2 and post-isolation phases (Fig. 4). This showed a divergent population density pattern along the phases between the two prawn species. Following an increase in density during the first and second months of isolation, prawn density decreased when the water re-entered the lakes (pre-isolation and post-isolation). During Isolation 2, *P. argentinus* individuals were at their largest physical size and had a decreased population density. Also *M. borellii* increased in size when the population density decreased. In post-isolation phase, the prawns were at their largest size but with a low density (Fig. 4).

Twenty-three fish species ranged in size between 6 and 490 mm and were collected during first and second month of isolation and post-isolation phases. These fishes were generally small and several had prawns in their guts (Table 5). The majority of prawns identified in fish stomachs were

P. argentinus (95% prawns in fish guts). Descriptively, the consumption of prawn (occurrence in fish stomachs) was greatest during Isolation-1 and Isolation-2 phases (Table 5). However, statistically there were no significant differences among the phases ($H = 0.0612$, $P = 0.9699$). This absence of significance could be due to the low numbers of occurrence of some fishes and a lot of zero occurrences (no occurrence) obtained in this analysis. Prey size (prawn) varied from 2- to 7-mm CL, and most prey was consumed by the families Characidae (*Astyanax* genera) and Pimelodidae (*Pimelodus* genera) during the Isolation 1 and Isolation 2 (Table 5), with the differences of occurrence in fish stomachs between families being statistically significant ($H = 21.58$, $P = 0.0029$). The fishes of the Characidae family had a higher percentage of occurrence of prawns in their stomachs than did those of the Pimelodidae family (Table 5). The Pearson correlation coefficient showed that density of fishes with prawns in their stomachs was negatively correlated, although not statically significantly, with *P. argentinus* density ($r = -0.30$, $P = 0.6953$) and positively correlated, although not statically significantly, with *M. borellii* density ($r = 0.56$, $P = 0.4339$; Fig. 6).
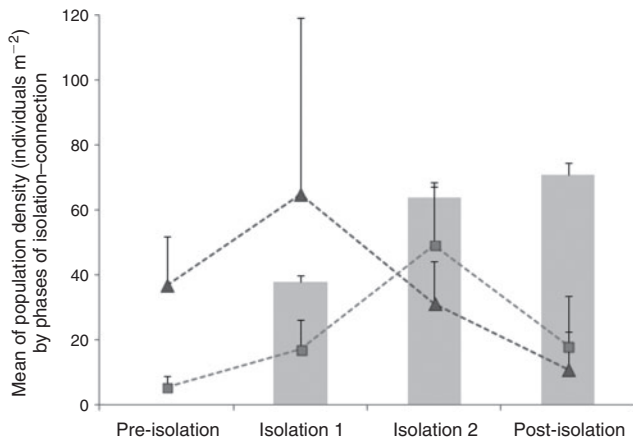
Fig. 6.   Mean of population density (individuals m^{-2}) and standard deviation bars of the two prawns and fishes with prawns in their stomachs during phases of isolation–connection: pre-isolation, Isolation 1, Isolation 2, post-isolation. *P. argentinus*, dark grey triangle; *M. borelii*, light grey square. Grey bars show density of fishes with prawns in their stomachs.

Discussion

The population dynamics of *P. argentinus* and *M. borellii* in shallow floodplain lakes in a period of La Niña were affected by the hydrological regime and the time elapsed since the phenomenon, which determines the connectivity or isolation of an environment. Although different environmental variables characterised each shallow lake, river fluctuations and the level of connection–disconnection were the most important factors influencing the population dynamics considered in the present study.

In the last decades, La Niña phenomenon has frequently caused isolation of ponds from rivers, for a long period each time. This produces stress within the populations of decapods and fishes; if they do not escape from the ponds, this would result in mortality of the whole population, such as occurred in the freshwater crab *Dilocarcinus pagei* (Fernandez and Collins 2002). For the species of prawns in the present study, the survival strategies were decisive to persist in the aquatic environment during the isolation phase. It would indicate that the intraspecific and interspecific relationships become stronger with the decrease in the area of the lakes, shelters and food, among others (Delong *et al.* 2001). Although the shallow lakes were characterised by the environmental variables, the river fluctuations, which determine the connectivity or isolation of the shallow lakes, together with different biological interactions, were important factors influencing the population dynamics considered in the study.

The hydrological regime in rivers with floodplain systems is considered a macrofactor that drives environmental variables and ecological functioning (richness, distribution and abundance; Junk *et al.* 1989; Neiff 1990; Winemiller 2004; Mayora *et al.* 2013). The ecological strategies of many organisms change in relation to hydrological fluctuations (Delong *et al.* 2001; Winemiller 2004; Arrington *et al.* 2006; Montoya *et al.* 2006; Rossi *et al.* 2007). Accordingly, four different stages of palaemonid and trichodactilid density have been recognised in the Middle Paraná River that coincide with events in the

hydrological cycle and are associated with the movement of animals (Collins *et al.* 2006*b*, 2007; Williner *et al.* 2010). In a similar study, *M. amazonicum* (Heller, 1862) populations in the Amazon River were associated with prawn migrations during floods (Walker and Ferreira 1985). Further evidence of this effect has been demonstrated by the impact of an extreme drought on crustacean populations in a tropical river in Puerto Rico (Covich *et al.* 2003).

The present study showed that the greatest prawn population density occurred during isolation phases of the lakes, when the water level was low. The fluctuations in water level determine the level of connectivity between lentic and lotic environments, as well as the duration of water residence, which in turn determines the rates of exchange between nutrients and organisms (Benke *et al.* 2000; Tockner *et al.* 2000; José de Paggi and Paggi 2007). The overflow of the lentic bodies in the alluvial valley dilutes biotic densities; however, the biological abundance is recovered rapidly during the isolation or low-water period (Bonetto and Wais 1995; Baranyi *et al.* 2002). In the summer, there is a decrease in the density of freshwater decapods and an increase in the hydrological level in the lake and surrounding area (Collins *et al.* 2007). This occurs through a process of dilution, combined with a migratory event towards new flooded areas and other channels (Collins *et al.* 2007). 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). Also, the effects of floods reduce spatial variability, increasing the homogenisation and the connectivity between water bodies and, with this, the dispersion of organisms (Thomaz *et al.* 2007). For example, fish larvae show passive dispersion towards the floodplain water bodies during flood pulses (Nakatani *et al.* 2004; Thomaz *et al.* 2007). Also, a decline in the low water level can induce movements of the crayfish *Procambarus fallax* from high to low elevation, increasing the abundance concentration of individuals (Cook *et al.* 2014). In addition, seasonal shrimp migration from the main-channel habitats to flooded areas seems to explain the low abundance of shrimp in the river during floods (Walker and Ferreira 1985; Collins *et al.* 2007). In this way, the floodplain system strongly influences the population dynamics of freshwater prawns. In rivers with seasonal regime, the movement of palaemonid prawns among aquatic habitats may be important in the persistence of the population (Odinetz-Collard and Magalhães 1994; Montoya *et al.* 2014).

Also, prawns were the largest (according to cephalothorax size) and their population density was lowest during the post-isolation phase. Although there is no literature reporting this, we suggest that this size–density relationship is due to the 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; Freire and González-Gurriarán 1998). Additionally, crustaceans have generally differentiated movements over time and space, moving the females and juveniles on one side and males on the other (Miquel *et al.* 1985). In the prawn *M. jelskii*, the use of different areas by individuals of different sizes was observed, and that this could be due to differential swimming ability of adults and juveniles,

possibly indicating some kind of age gap in relation to trophic activities (Williner and Collins 2002). Also, significant spatial and temporal differences among biotypes in the composition and structure of the fish larvae assemblages were observed by Gogola *et al.* (2013).

A divergent population density pattern was observed regarding the two prawn species. The prawn *P. argentinus* was more abundant than was *M. borelllii* during pre-isolation and during the first month of isolation. Then, during the second month of isolation and post-isolation phases, *M. borellii* was more abundant than was *P. argentinus*. Both palaemonids are sympatric and have similar trophic niches (Collins and Paggi 1997; Collins 1999). When species utilise similar resources, they tend to differ in spatial and temporal use of the shared resource (Volterra 1927; Gause 1934; Veen *et al.* 2010). These prawn species seem to co-exist because of small displacements in several dimensions of their niches. For example, these species differ in their daily feeding activity; *M. borellii* feeds during night and the foraging activity of *P. argentinus* occurs during the day (Collins 2005). In aquatic environments where *M. borellii* is present at high densities, *P. argentinus* is founded at low densities (P. A. Collins, pers. obs.), and this is probably due to hierarchical and aggressive behaviour of *M. borellii* (e.g. larger size) and micromigratory movements (Williner and Collins 2000; Williner *et al.* 2010).

Additionally, hydrologic fluctuations modulate these interactions by affecting population dynamics and the presence and dispersion of decapods in a particular habitat (Fernandez and Collins 2002; Collins *et al.* 2006*b*, 2007; Williner *et al.* 2010). During isolation, lakes, linked to the dynamics of the river, act as refuge areas for species (Zalocar de Domitrovic *et al.* 2007), and this may influence biotic interactions between species-associated gaps. For example, when the water level decreases, especially during the La Niña phenomenon, the shelters are lost and the populations of each species are concentrated, increasing contact between individuals in the lakes (Fernandez and Collins 2002). In this sense, biological interactions (such as competition and predation) may also be adjusted to the water regime (Corti *et al.* 1997; Azevedo and Verdade 2012). In this manner, Dorn and Trexler (2007) observed that hydrological variation and competition affected the population dynamics of two species of crayfish, namely *P. alleni* (Faxon, 1884) and *P. fallax* (Hagen, 1870), which co-exist in a subtropical flowing slough in southern Florida.

Also the strength and relative importance of biotic interactions (e.g. competition versus predation), consumer response and food resources are influenced by the hydrologic cycle (Corti *et al.* 1997; Delong *et al.* 2001). Fishes in this work, for example, consumed (descriptively) more prawns during the isolation phase. The effects of vertebrate predation on the structure of invertebrate communities in floodplain are mediated by pond permanence (Corti *et al.* 1997). In more permanent ponds, predators could maintain prey densities at levels that preclude strong competitive interactions among prey (Wilbur 1987). So, when water levels are low, the biological communities in each floodplain habitat follow distinct temporal trajectories because of the effects of local driving forces (e.g. an efficient predator trapped in some lagoons or lakes and not in others; Thomaz *et al.* 2007). Prawn consumption by fishes was highest when prawns were most abundant. Prey selection could be based on the actual abundance and availability of prey within the environment (Gill 2003; Hinz *et al.* 2005).

Moreover, fishes consumed more individuals of *P. argentinus* than of *M. borellii*, and fish density was negatively correlated with *P. argentinus* density and positively correlated with *M. borellii* density. According to Hutchinson (1961), if one of two species is either less limited by the same predator or limited by a different predator, the co-existence of the two species is possible. Although two species in direct competition rarely form a stable ecosystem, they often co-exist under the dominance of a common predator (Cheon and Ohta 2004). Traditional ecological theory suggests that abundance of predators is limited by the availability of prey (Solomon 1949; Hairston *et al.* 1960; Menge and Sutherland 1987). Predator abundance can also be affected by behavioural responses of both predators and prey (Begon *et al.* 1986). Furthermore, the organisation of fish assemblages is related to hydrological variability, given that when floodwaters recede, fish are forced off the floodplain into the main river channel (Poff and Allan 1995; Balcombe and Arthington 2009; Layman *et al.* 2010). It is known that some species of Pimelodidae family prefer open and turbid waters, whereas some species of Characidae family prefer clear waters; this can be related to the sensory adaptations to underwater visibility (Rodríguez and Lewis 1994; Pouilly and Rodríguez 2004; Scarabotti *et al.* 2011). In the present work, despite the low transparency because of the sediment load and algae biomass, Characidae family presented a higher percentage of occurrence of prawns in their stomachs. However, the shallow lakes lacked aquatic vegetation, reducing shelter; thus, we suggest that this would promote direct contact between predators and preys, causing an increase in prawn vulnerability. Also the sensory adaptations to visibility can explain the negative correlations between the density of fishes and the density of the prawn *P. argentinus*, and the positive correlation with *M. borellii*, as well as the higher predation on *P. argentinus.* As already discussed in previous paragraphs, the foraging activity of *P. argentinus* occurs during the day (Collins 2005); therefore, this species may be more susceptible to predation during the day by predators such as characiforms that usually are diurnal and rely on vision (Rodríguez and Lewis 1994; Pouilly and Rodríguez 2004).

Conclusions

We have here presented evidence about the changes in populations of two freshwater prawns along different phases of isolation–connection of shallow lakes in a period of La Niña. This work has documented the importance of the biological interactions (between species of prawns and predatory fish species) during the La Niña phenomenon in a floodplain context. Biological interactions become stronger and acquire relevant importance in lakes with prolonged periods of isolation (La Niña phenomenon). The population of organisms implied in these interactions should adjust to the dynamics of the river, which determines the connectivity or isolation of the lakes that the organisms inhabit. Hydrological fluctuations constitute a macrofactor that regulates the dispersion of freshwater fauna and the population and biotic interactions (e.g. competition and

predation) of prawns. In rivers with seasonal flow regimes, movement and biological interactions throughout aquatic habitats may be important for persistence of freshwater prawn population.

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Appendix 1.   Values of physical and chemical variables measured in the shallow lakes in each phase of isolation–connection

HL, hydrometric level; Temp., water temperature; C, conductivity; T, transparency; D, depth

Phase of isolation–connection	Shallow lakes	HL (m)	Temp. (°C)	pH	C (μS cm^{-1})	T (cm)	D (m)	Surface (m^2)
Pre-isolation	Don Felipe	3.26	11.50	6.20	95	50	2.00	472 656.30
	Number 1	4.52	15.00	8.20	3000	5	1.00	16 664.70
	Alejandra	3.80	15.40	7.10	130	30	1.80	93 364.20
First month of isolation	Don Felipe	2.22	20.00	7.00	100	45	1.45	390 625.00
	Number 1	2.94	26.00	8.00	3100	7	0.35	9686.10
	Alejandra	2.69	19.40	7.20	170	24	1.15	75 000.00
Second month of isolation	Don Felipe	2.26	22.20	6.50	85	31	0.90	219 726.60
	Number 1	2.65	23.00	8.20	3100	15	0.30	8287.50
	Alejandra	2.69	22.80	7.30	230	28	0.54	43 402.80
Post-isolation	Don Felipe	3.23	26.00	6.30	90	12	1.60	516 601.60
	Number 1	3.14	26.50	8.40	3400	10	0.55	15 763.40
	Alejandra	3.55	23.90	7.10	590	18	1.44	102 044.80

Appendix 2.   Mean and standard deviation values of physical and chemical variables in each phase of isolation–connection

HL, hydrometric level; Temp., water temperature; C, conductivity; T, transparency; D, depth

Phase of connection	HL (m)	Temp (°C)	pH	C (μS cm^{-1})	T (cm)	D (m)	Surface (m^2)
Pre-isolation	3.85 ± 0.63	13.96 ± 2.14	7.16 ± 1.00	1075.00 ± 1667.19	28.33 ± 22.54	1.60 ± 0.52	194 228.40 ± 199 352.7
Isolation 1	2.61 ± 0.36	21.80 ± 3.64	7.40 ± 0.52	1123.33 ± 1712.20	25.33 ± 19.03	0.98 ± 0.56	158 437.03 ± 166 332.83
Isolation 2	2.53 ± 0.23	22.66 ± 0.41	7.33 ± 0.85	1138.33 ± 1700.93	24.66 ± 8.50	0.58 ± 0.30	90 472.30 ± 92 514.05
Post-isolation	3.30 ± 0.21	25.46 ± 1.37	7.26 ± 1.05	1360.00 ± 1784.29	13.33 ± 4.16	1.19 ± 0.56	211 469.93 ± 218 617.04