Universidade Estadual Paulista – UNESP
Instituto de Biociências de Botucatu
Programa de Pós Graduação em Ciências Biológicas – Zoologia

Resistência e Resiliência de assembleias zooplanctônicas (Copepoda, Cladocera e Rotifera) frente a perturbações físicas e químicas: flutuações espaciais e temporais na utilização do habitat

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Universidade Estadual Paulista “Júlio de Mesquita Filho”
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Tese apresentada ao Instituto de Biociências da Universidade Estadual Paulista – Campus de Botucatu, como parte dos requisitos para a obtenção do título de Doutor em Ciências Biológicas, Área de concentração: Zoologia.

Orientador: Prof. Dr. Marcos Gomes Nogueira

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Palavras-chave: Drawdown artificial; Ovos de resistência; Planície de inundação; Reservatórios tropicais; Zooplâncton.

Dedico esse trabalho para todas as pessoas que apreciam
um por do sol, uma vista do alto da montanha, ou a beira de um rio
em qualquer momento do dia…

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Sumário

Apresentação

No **capítulo 1** deste trabalho, pretende-se mostrar a importância da pesquisa básica como suporte para formas gerenciamento de reservatórios tropicais. Mais especificamente o controle e manejo de macrófitas aquáticas através de um deplecionamento artificial (artificial drawdown) no reservatório de Salto Grande, rio Paranapanema. Dessa maneira, analisamos os efeitos do processo de depleção sobre os atributos ecológicos das assembleias zooplanctônicas em duas lagoas marginais (Lagoa Pedra Branca e Guaritá) ao reservatório de Salto Grande.

Além dessa proposta, foi realizado um experimento de eclosão dos ovos de resistência de zooplâncton a partir do sedimento coletado durante o processo de deplecionamento nessas duas lagoas marginais. O objetivo dessa proposta foi verificar qual a importância dos ovos de resistência na resiliência dessas comunidades, sobre tal distúrbio. O delineamento experimental foi executado, porém sem resultados satisfatórios.

A partir dessa ideia de trabalho, eu tive a oportunidade de realizar um estágio na linha de pesquisa com ovos de resistência no instituto de pesquisa “Murray Darling Freshwater Research Centre”, na Austrália, com a equipe do professor Daryl Nielsen (Doutorado período sanduíche CAPES processo PDSE BEX 12951/12-9).

O estudo foi realizado em uma planície de inundação no rio Murray, sudeste da Austrália. Apresentado no **capítulo 2**, o objetivo desse trabalho foi examinar a distribuição espacial e características dos bancos de ovos de resistência de zooplâncton e sementes de plantas na planície de inundação Barmah Forest. A parceria com a equipe de zooplâcton do professor Daryl Nielsen ainda se mantém. O próximo passo será a realização de um pós-doutorado, incluindo novas parcerias brasileiras, como a professora Dra. Claudia Bonecker. A presente proposta é também uma oportunidade para o candidato dar continuidade à linha de pesquisa com ovos de resistência de zooplâncton em regiões tropicais.

Managing aquatic macrophytes by artificial drawdown in a tropical reservoir: impacts on zooplankton communities

JORGE LAÇO PORTINHO & MARCOS GOMES NOGUEIRA

Chapter 1

Chapter 1. Managing aquatic macrophytes by artificial drawdown in a tropical reservoir: impacts on zooplankton communities

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Abstract

Enhanced growth of aquatic macrophytes have been recorded from some Brazilians rivers regulated for hydropower generation, and has challenged environmental managers for the development of new and novel ways of management. One partial remedy that has been proposed involves using of artificial drawdown whilst maintaining ecological diversity and function. This study assessed the suitability of such a strategy by examining the impact of artificial drawdown on zooplankton communities from Salto Grande Reservoir, Paranapanema River, Brazil. Our study focused on the analyses of two lateral lakes along a planned artificial drawdown, which lasted about 15 days. Despite same differential responses between both lakes due to the distinct connectivity, the artificial drawdown led to increases in zooplankton density and changed the community structure associated with a temporarily variation in water nutrients. Furthermore, favored the increases in taxon richness, and community composition whilst still maintaining all zooplankton taxa present before the artificial drawdown in the both lakes. This suggests that artificial drawdown could potentially be used as an alternative method of aquatic macrophytes control without affecting the aquatic biota. Our study also demonstrates that knowledge on ecology and biology of *Egeria najas* and *Egeria densa* is fundamental for prediction of further spatial reorganization, in order to avoid undesirable post event growth and optimize this management strategy.

Keywords Biodiversity; Microcrustaceans; Rotifers; Regulated Rivers, Remedial measures; Submerged Plants

Introduction

A large number of reservoirs have been constructed in the last decade in Brazil, manly in order to supply the increasing energetic demands. Rivers regulation strongly affects many aquatics environments with associated declines in biodiversity (Tundisi *et al*., 2014). The excessive growth of the submerged macrophyte, for instance, can restrict the multiple uses of tropical reservoirs (Bini & Thomaz, 2005). The *Egeria densa* Planch. and *Egeria najas* Planch. are two Hydrocharitaceae native to South America (Cook & Urmi-Köning, 1984). Frequently, these species are associated to clogging of turbines and impracticability of navigation and recreational activities in tropical reservoirs (Bini & Thomaz, 2005; Thomaz *et al*., 2006; Boschilia *et al*., 2012).

The difficulties associated with management of aquatic plants in tropical reservoir systems, have increased the need for the development and implementation of novel and specific solution (Thomaz, 2002). Use of herbicides to control aquatic macrophytes and mechanical methods of harvesting and cutting have been carried out in Jupiá Reservoir (Paraná River, State of São Paulo, Brazil) (Marcondes *et al*., 2003; Velini *et al*., 2005). One potential way of dealing with these challenges is through artificial drawdown, and thereby maintaining ecological values with minimal impact on biodiversity of the aquatic ecosystems (Thomaz, 2002). This would involve the maintenance of a decreased water level during winter season, period of natural plant senescence, in order to expose shore macrophytes to dehydration with the aim of decreasing their biomass; the dead plants are partially removed before restoration of the normal water level. This is a hydrological manipulation which could be analogous to winter drawdown in temperate regions (Pieterse & Murphy, 1990; Rørslett & Johansen, 1996).

Induced depletion of the reservoir levels by artificial drawdown (short-term) occur more rapidly than water level fluctuations in reservoirs by operational procedures for hydropower production and seasonality. Studies have showed that the changes in reservoir water level fluctuation constitute a primary factor influencing limnological conditions (e.g. nutrients dynamics) (Brandimarte *et al*., 2008; Naliato *et al*., 2009; Valdespino-Castillo *et al*., 2014), the structure and dynamic of fauna, as well as all trophic levels of the entire basin (Nogueira, 2001; Nadai & Henry, 2009; Shimabukuro & Henry, 2011; Santos *et al*., 2013; Valeriano-Riveros *et al*., 2014; Zerlin & Henry, 2014). In contrast, knowledge about the effects of artificial short-term drawdown in physical, chemical and biological conditions in tropical reservoirs is limited.

In this study we use a zooplankton dataset coupled with an artificial drawdown, to elucidate the microcrustaceans and rotifers responses to sudden major shifts in the water level of two lateral lakes adjacent to Salto Grande Reservoir. The regional hydroelectric company deliberately decrease the reservoir water level just prior to the natural drought period (winter season), as an alternative method for aquatic macrophytes control along the reservoir margins (shoreline area).

There are no comparable studies about the effects of artificial drawdown (short-term) on zooplankton communities of tropical reservoirs. However, we suspect that the artificial drawdown is likely to cause significant changes in zooplankton dynamics due to interplay of environment processes, distinct biological responses of zooplankters and interference in the complex gradient of connectivity between the river channel and lateral lakes. It was hypothesized that i) artificial drawdown would cause a reduction in density and richness of zooplankton, ii) altering the composition of communities in the lateral lakes.

Materials and Methods

Study sites

The study lakes, Pedra Branca and Guaritá, are highly connected to Salto Grande Reservoir (22°57' S–49°57'W), a run-of-river system of the Paranapanema River, southeast Brazil (Figure 1). The reservoir basin has an area of 12 km^2, a volume of 44.2 hm^3, a mean water retention time of only 1.5 days and a mean water discharge of 395 km^3 s^{-1} (Nogueira *et al.*, 2012). In Salto Grande Reservoir watershed, the land is intensively used for agricultural activities (corn, sugar, cane, and soy bean) and livestock grazing. As consequence, the tributaries of this reservoir exhibit a high turbidity and transport considerable nutrient loads (detailed limnological description can be found in Nogueira *et al.*, 2006). Aquatic plants are easily found along the reservoir margins and arms and also in the two mentioned lakes (Pedra Branca and Guaritá) adjacent to the reservoir middle channel (Figure 1).

The Lake Pedra Branca (area 0.44 km^2) is located on the right margin of the Paranapanema River, and Lake Guaritá (area 0.23 km^2) on the left margin (Figure 1). Both lakes are shallow, with a maximum depth of approximately 3 m, and are densely colonized by submerged aquatic macrophytes, especially *Egeria densa* and *Egeria najas*, though Pedra Branca has a higher density of these plants. The lakes have a permanent hydrological connection with Salto Grande Reservoir. The water bodies adjacent to reservoirs of the Paranapanema River (e.g. lakes, lagoon) are strategically important for the maintenance of the regional river system vertebrate and invertebrate diversity (Nadai & Henry, 2009; Ferrareze & Nogueira, 2011). They are usually shallow and colonized by aquatic macrophytes, which are important components influencing ecological process and attributes of aquatic fauna (Thomaz & Cunha, 2010; Shimabukuro & Henry, 2011; Ferrareze & Nogueira, 2011). Thus, the lateral lakes Pedra Branca and Guaritá provided an opportunity to study the effect of short duration drawdown on the zooplankton community organization based on the analysis of the following periods: before (pre phase), during (drought phase) and after (post phase) reconnection to the Salto Grande Reservoir, in the Paranapanema River.

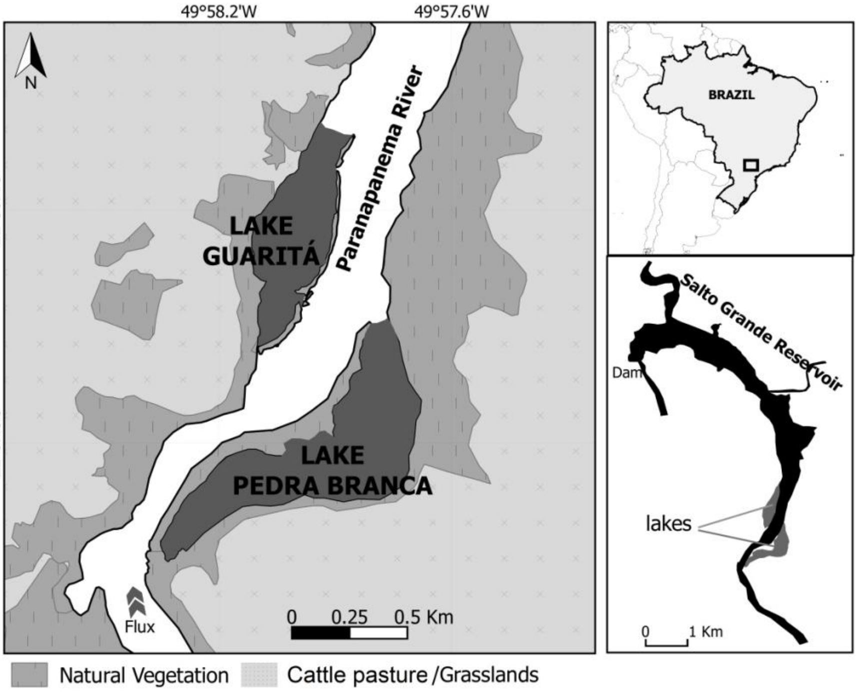

Figure 1. Geographic location of study area showing the position of the Lakes Lakes Pedra Branca and Guaritá

Artificial drawdown

In Salto Grande Reservoir, upstream of the power plant, on a low flow reach of the Paranapanema River, *E. najas* and *E. densa* developed large stand along the shoreline areas. There are many conflicts with local residents and tourists, as these plants make it difficult the access to the open water area of the reservoir. Macrophytes can also, interferes negatively with hydropower production due to obstruction of water intake to the turbines. Within this socio-economic and environmental scenario, reservoir management is conducted. The artificial drawdown is part of a permitted water manipulation undertaken by the energy company, which consists in the reservoir water level depletion of *ca.* 2 m for 15 consecutive days (Figure 2). The depth and volume of both lateral lakes are strongly diminished as well (see appendix I and II).

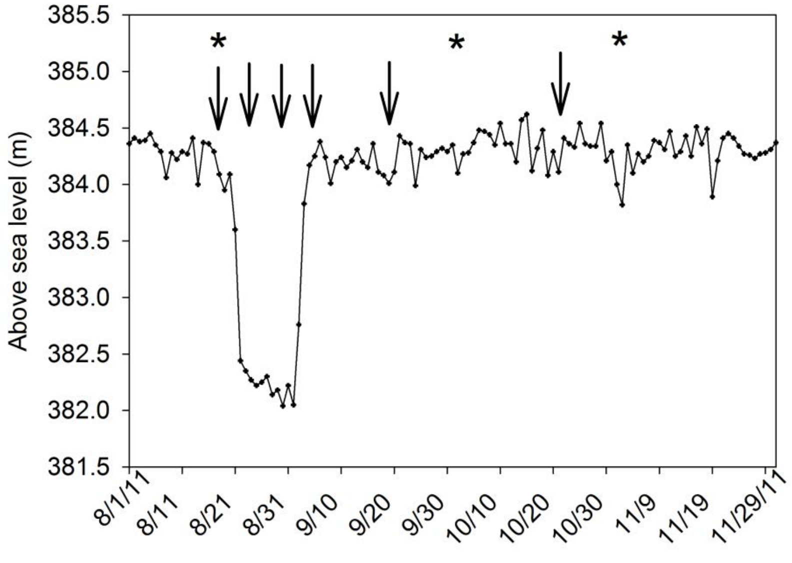

Figure 2. Water level fluctuation in Salto Grande Reservoir during the artificial drawdown. The reservoir water level rapidly decreased after the operational procedure reaching 2 m below it is an average water level (which is at 384 m above sea level: a.s.l.), from days 20th August to 2nd September, after which it recovered again. The arrows represent the six zooplankton sampling dates, and asterisk three sampling dates for aquatic macrophytes

Sampling methods

The field work was carried out in the lateral lakes on days 19th, 24th, 30th August, 2nd, 19th September and 22th October, 2011 to characterize the system both before and after the artificial drawdown, and also during the operational water level decrease. Samplings were performed in three points of the central zone, next to the mouth, middle and end of each lake.

Aquatic macrophytes

E. najas and *E. densa* biomass was measured on the following dates: 20th August 2011: before the artificial drawdown; and 01st October and 01st November: 43 days and 74 days (respectively) after the water level recovered. Samples of biomass were taken from 49 sites[1]; 24 of them distributed along the lentic zone (shoreline areas) and in one arm of the reservoir (Novo

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[1] FUNDIBIO (UNESP) - Duke Energy Geração Paranapanema contract (0100015003).

River) and 25 sites in the reservoir upstream zone (7 in shoreline areas, 9 in Pedra Branca and 9 in Guaritá lakes). Samples were collected using a rake (area of $0.1134 m^2$), washed and dried in the laboratory at 105°C to constant weight.

Zooplankton sampling and identification

Zooplankton was sampled in the lateral lakes on days 19th, 24th, 30th August, 2nd, 19th September and 22th October, 2011 to characterize the community both before and after the artificial drawdown, and also during the operational water level decrease. For quantitative analysis, nine samples (100 L each) were collected with a bucket in the center of each lake on every sampling date, filtered through a 55 µm mesh size zooplankton net and preserved in the field using 4% formalin. Rotifers were counted in a 1-mL Sedwick-Rafter counting cell under optical microscope (Zeiss, standard 25): subsamples were taken with a Hensel-Stempel pipette. Microcrustaceans (adult copepods and cladocerans) were examined under a stereomicroscope (Zeiss Stemi SV6). A minimum of 200 individuals were counted, or, in cases of low abundance, the whole sample was analyzed. Data for juvenile zooplankton unidentifiable to species (copepodids and nauplii), generally in high abundance, were excluded from this study. The zooplankton taxa were identified to level of genus or species using specialized literature (e.g. Koste, 1978a, Koste, 1978b; Reid, 1985; Elmoor-Loureiro, 1997). Numerous studies across wide range of biota have indicated that taxonomic resolution at this level is sufficient to detect significant ecological changes (Clarke & Warwick, 2001).

During the field word activities sediment samples for resting eggs experiments and zooplankton samples in distinct reservoir compartments were also sampled for additional studies, presently under development (Post-Doctoral project).

Environmental conditions

Simultaneously to the zooplankton sampling, the depth of the water column was determined with Speedtech sonar. The water temperature, pH, conductivity, dissolved oxygen were measured in situ, in the center of each lake, from surface to the bottom, using the water analyzer Multiprobe Horiba (Model U22). Water transparency was determined with a Secchi disk. Water samples were obtained from surface (Van Dorn bottle) for determination of chlorophyll *a*, (Talling & Driver, 1963), total nitrogen (Mackreth *et al.*, 1978), total phosphorus (Strickland & Parsons, 1960), and total suspended matter (mineral and organic) (Cole, 1979).

Data analysis

For statistical analysis PRIMER v6.0 (Clarke & Gorley, 2006) was used. The zooplankton count data were converted to densities (animals m^{-3}) prior to undertaken any analyses. One-way Permanova, with ‘phases dataset’ (pre *vs* drought *vs* post) as a fixed factor, was undertaken to examine the phase’s variation in density, taxon richness, and Shannon-Wiener diversity in the Lakes Pedra Branca and Guaritá. The ‘pre phase dataset’ was represented by 9 samples corresponding to the 19th August (before artificial drawdown); the ‘drought phase dataset’ was represented by 18 samples corresponding to the 24th and 30th August (during artificial drawdown), and the ‘post phase dataset’ was represented by 27 samples corresponding to the 2nd and 19th September and 22th October, 2011 (post artificial drawdown). In this design, we considered the sampling date as replicates of the respective phases dataset in the Lakes Pedra Branca and Guaritá. This could be done because Permanova results are not affected by unbalanced (e.g. differences in the number of replicates) datasets (Anderson *et al*., 2008). All analyses were derived from Euclidian distance matrices, and performed square-root transformed data to reduce the influence of outliers (Anderson *et al*., 2008). Where significant main effects were detected, pairwise comparisons were undertaken to determine which treatment group differed.

Among phases, differences in zooplankton community structure and composition (presence-absence transformed data) were also examined using Non-Metric Multidimensional Scaling (nMDS) in Primer v6.0 (Clarke & Warwick, 2001) in conjunction with the same one-way Permanova design used for the univariate analysis. All multivariate analyses were derived from Bray-Curtis similarity matrices, and performed on square-root transformed density data. A One-way analysis of similarity (ANOSIM) was used to test the null hypothesis of no difference in zooplankton community structure and composition (presence-absence transformed data) among phases (Clarke and Warwick, 2001). Similarity percentages analyses (SIMPER) were used to identify those taxa contributing most to similarities within phases of the artificial drawdown.

Among phases variation in environmental conditions (water temperature, suspended matter, pH, conductivity, dissolved oxygen, chlorophyll *a*, total nitrogen and total phosphorus) was examined using Principle Components Analysis (PCA), and one-way Permanova derived from Euclidian distance matrices (Permanova + from Primer (Anderson *et al*., 2008). We used the same one-way Permanova design ‘phases-dataset’ (pre *vs* drought *vs* post) as a fixed factor, as mentioned above for zooplankton dataset. Prior to undertaking any PCA and Permanova analyses, environmental variables were $\log_{10}(x+1)$ transformed (except pH) and normalized.

Pearson's correlation coefficients were calculated to elucidate which environmental variables (Table 1) were more strongly related to zooplankton communities in the Lakes Pedra Branca and Guaritá ($\alpha = 0.05$), using Statistica 6.0 package (Statsoft, 2001). For this analysis are present the results obtained with the dataset 'phase-dataset' for drought and post phases. No consistent correlation was observed for pre phase data. The Permanova test, nMDS plots, SIMPER and Person's correlation were performed with all taxa density (total zooplankton), and also separately with densities of microcrustacean and rotifers taxa.

Results

Egeria densa and *Egeria najas* biomass response

The response of *E. densa* and *E. najas* biomass (dry weight) to artificial drawdown was significant, with different effects on the biomass at Salto Grande Reservoir areas sampled (Figure 3). In the reservoir (shoreline areas), after a minor decrease, there was a remarkable increase in biomass as seen in day +74 (post phase). Nevertheless, the plant biomass in the reservoir upstream compartment, as well as in Lakes Pedra Branca and Guaritá, dropped after the water level reduction and did no recovery was observed even 74 days after recovery to the normal operational al level (Figure 3).

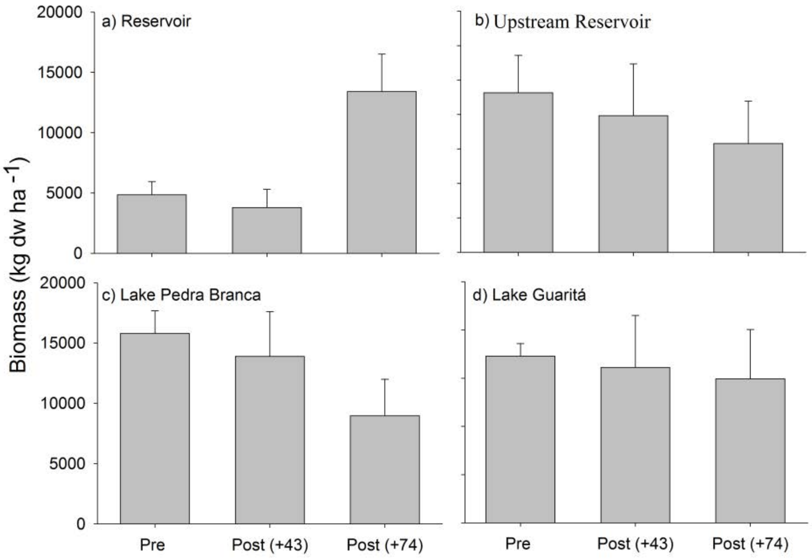

Figure 3. Biomass of *Egeria densa* and *Egeria najas* in the different compartments of Salto Grande Reservoir (**a-d**) before the artificial drawdown (pre phase), and after (+43 and +74) restoration to the normal operational water level (post phase)

Environmental conditions

The artificial drawdown of the reservoir, including lakes Pedra Branca and Guaritá, began at 22th August (pre phase), reducing water depths by approximately 2.0 m, with all sampling days showing Secchi transparency of 100% of total depth. Water temperature at Lake Pedra Branca ranged from 22°C in the pre phase and still maintaining during drought; then decreased to 19°C at the beginning of post phase (2nd September) and raised to 24°C in the last day sampled on day 10th September. In Lake Guaritá water temperature ranged from 20°C in the pre phase, 25°C during drought phase, declined to 20°C at the beginning of post phase (2nd September) and reached 22°C in the last day of sampling, September 22th. Water temperature differed significantly among phases (pre-drought-post) in Lake Guaritá, but not in the Lake Pedra Branca. The other environmental variables varied significantly according to the time (pre-drought-post phases), but with differential responses when compared Lake Pedra Branca *vs* Lake Guaritá (Table 1). These results and environmental conditions occurring in each lake related to the artificial drawdown are reported in the appendix I and II. The drought phase was significantly different in the Lake Pedra Branca, in terms of nitrogen concentration, and pH for the Lake Guartiá (Table 1). The tendencies along the process are clearly seen in the plots of the PCA analysis, as described below.

Table 1. Pseudo-*F* ratios, significance and *post hoc* pairwise comparisons for Permanova comparisons among phases (pre-drought-post) of the environmental variables response for each lake. * P < 0.05, ** P< 0.01, ***P < 0.001, ns, non-significant

	Lake Pedra Branca		Lake Guaritá	
df 2 Environmental variables	Pseudo *F*-ratios	Pairwise test phases	Pseudo *F*-ratios	Pairwise test phases
Water temperature (°C)	ns		2.85*	pre,drought< post
Suspended matter (mg L^{-1})	8.79**	drought, post > pre	ns	
pH	12.28***	drought,post > pre	9.95***	pre,post < drought
Conductivity (µS cm^{-1})	3.37*	drought,post > pre	ns	
Dissolved oxygen (mg L^{-1})	6.81**	pre,drought > post	10.03***	pre,drought > post
Chlorophyll *a* (µg L^{-1})	ns		4.88*	pre,drought < post
Total nitrogen (µg L^{-1})	2.69**	pre,post < drought	ns	
Total phosphorus (µg L^{-1})	4.98**	drought,post > pre	6.65**	drought,post > pre

For the Lake Pedra Branca, PCA indicated that the three phases of the artificial drawdown experience were separated (Figure 4a). Pre phase and day 24th August, when began the drought phase, was distinguished by high dissolved oxygen and pH. In comparison, during drought phase (on days 24th and 30th August) and soon after artificial drawdown on day 2nd, were characterized by high conductivity, nitrogen and phosphorus concentrations, and relatively high of total suspended matter and chlorophyll *a*. The post phase was characterized by high depth and warm water temperatures (Figure 4a).

For the lake Guaritá, pre phase separated from the other phases because it was distinguished by relatively high depth (Figure 4b). The drought phase was separated from pre and post phase because of the relatively high water temperature, total solids, pH, conductivity, dissolved oxygen, nitrogen and phosphorus concentrations. Post phase was characterized by high chlorophyll *a* (Figure 4b).

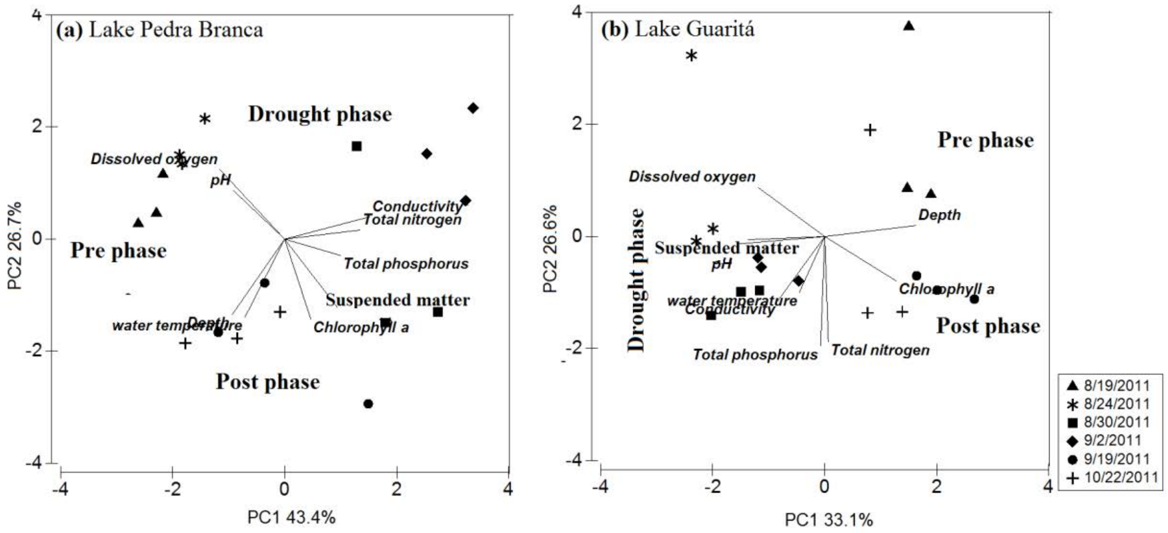

Figure 4. PCA ordination biplot showing the relative position of the phases (pre-drought-post) in Lakes Pedra Branca (a) and Guaritá (b) with respect to 9 measured limnological conditions (n = 18). Pre phase day 19th August, drought phase 24th and 30th August, and post phase 2nd, 19th September and 22th October, 2011

Zooplankton density, taxon richness and diversity index

PERMANOVA indicated significant difference among phases (pre-drought-post) in the Lake Pedra Branca for the density and taxon richness of total zooplankton, microcrustacean and rotifer (Table 2, Figure 5). They varied significantly among phases and were all higher during drought and post phase when compared with pre phase (all comparisons $P < 0.05$). Similarly, diversity index (Shannon-wiener) varied according to the time and overall zooplankton diversity was higher during drought (Table 2, Figure 5).

In the Lake Guaritá, total zooplankton density, taxa richness and diversity did not vary significantly over time, however values were generally higher during drought and post phase (Table 2, Figure 6). Microcrustacean density, taxa richness and diversity varied significantly among-phases (Table 2). Although microcrustacean density, richness and diversity were generally higher during drought phase, they were markedly reduced after artificial drawdown, when the water level returned to normal (Figure 6). By contrast, rotifers varied significantly in density with greater values in post phase, but did not vary significantly in richness and diversity among phases (pre-drought-post); (Table 2, Figure 6).

Table 2. Pseudo-*F* ratios and significance levels for Permanova comparisons among phases (pre-drought-post) for zooplankton community responses in each lake. * P < 0.05, ** P< 0.01, ***P < 0.001, ns, non-significant

				Pseudo-*F* ratio	
Analysis subject	Variable type	Response variable	df	Lake Pedra Branca	Lake Guaritá
Zooplankton	Univariate	Density	2	13.36***	ns
	Univariate	Richness	2	3.58**	ns
	Univariate	Diversity index	2	3.25**	ns
Microcrustacean	Univariate	Density	2	21.18***	3.00*
	Univariate	Richness	2	3.46**	14.38***
	Univariate	Diversity index	2	4.28**	11.90***
Rotifera	Univariate	Density	2	2.53*	3.18*
	Univariate	Richness	2	2.70*	ns
	Univariate	Diversity index	2	3.16**	ns

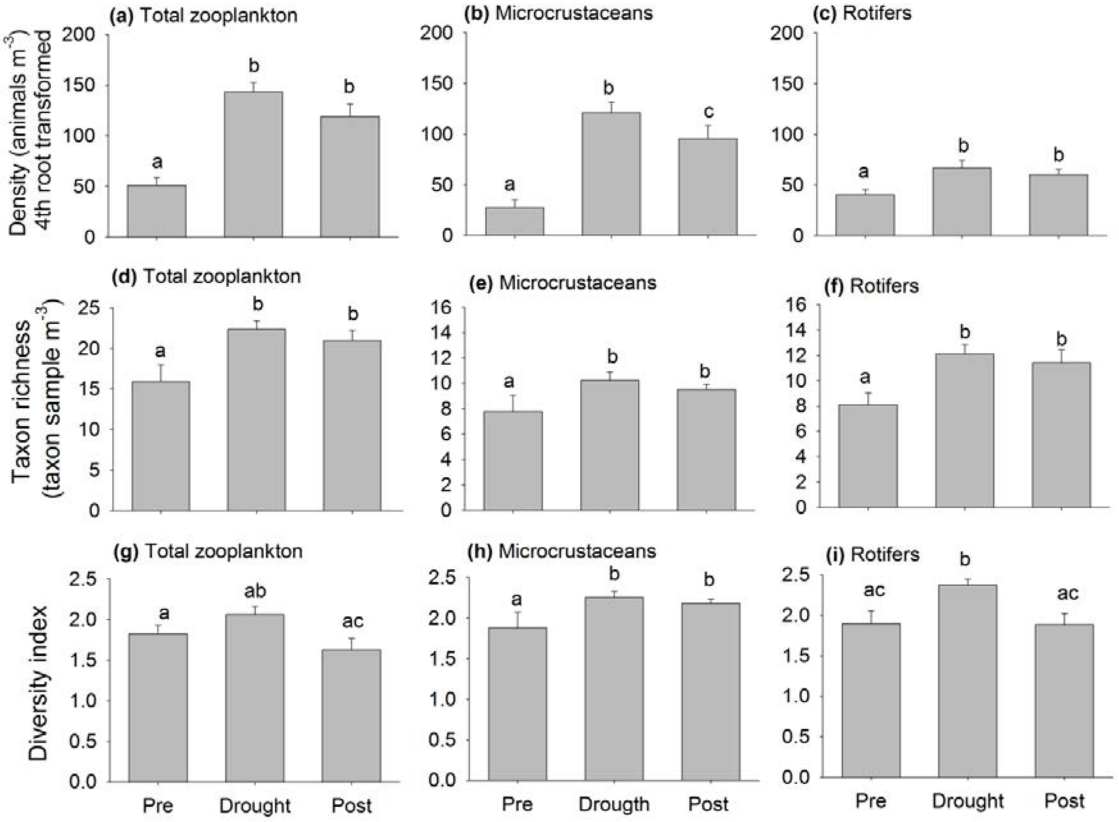

Figure 5. Mean and standard error of density (**a-c**), taxon richness (**d-e**), and diversity index (**g-i**) of total zooplankton, microcrustaceans and rotifers during the phase's pre-drought-post artificial drawdown in Lake Pedra Branca. There was no significant difference (P > 0.05) amongst phases sharing the same *letter*

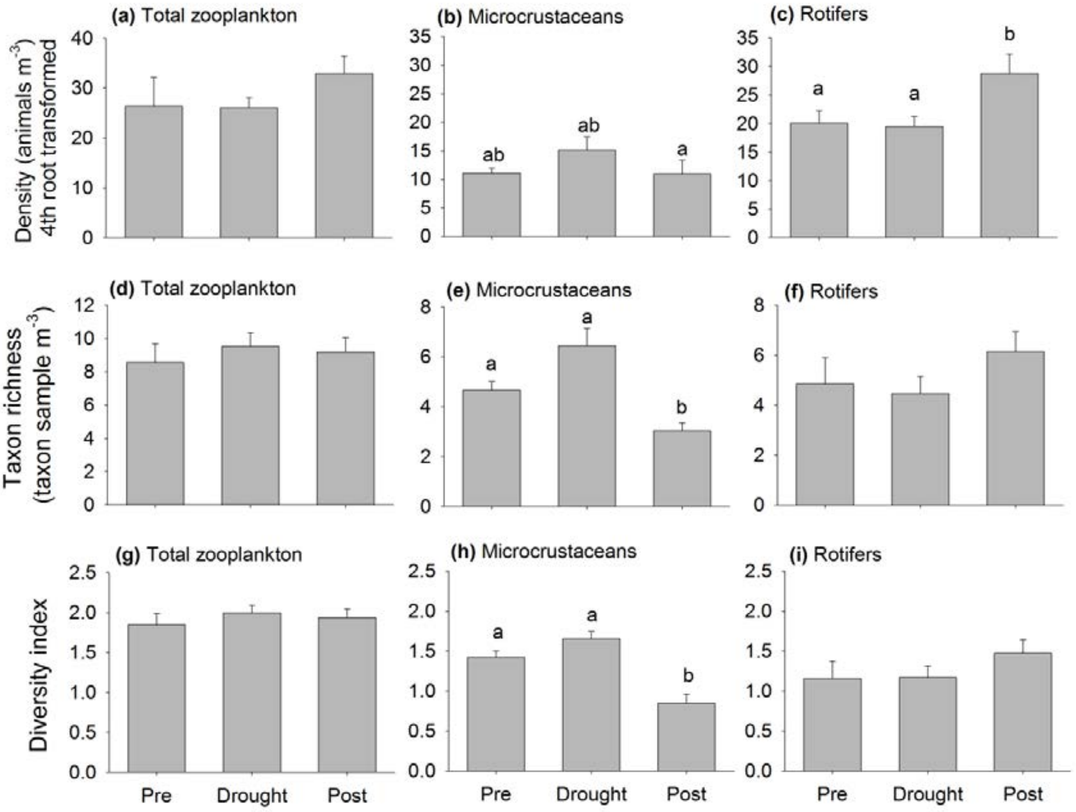

Figure 6. Mean and standard error of density (**a-c**), taxon richness (**d-e**), and diversity index (**g-i**) of total zooplankton, microcrustaceans and rotifers during the phase's pre-drought-post artificial drawdown in Lake Guaritá. There was no significant difference ($P > 0.05$) amongst phases sharing the same *letter*

Correlations between zooplankton and environmental conditions

For the Lake Pedra Branca, during the drought phase Pearson's correlations were significant and positive between suspended matter and rotifer density, and between conductivity and microcrustacean richness and diversity (Table 3). In the post phase, Pearson's correlations were significant and negative between water temperature and total zooplankton density and microcrustacean density while positive with total zooplankton diversity (Table 3). Suspended matter had a significant positive correlation with rotifer density, richness and diversity. The pH was negatively correlated with microcrustacean richness and diversity. Conductivity was positively correlated with total zooplankton and microcrustacean density and negatively with total zooplankton diversity (all Pearson's correlations $P < 0.05$) (Table 3).

In the Lake Guaritá, Pearson's correlations analysis showed that during the drought phase water temperature had a significant positive correlation with microcrustacean density, richness and diversity. The suspended matter was negatively correlated with total zooplankton diversity. Chlorophyll *a* showed a negative correlation with total zooplankton richness and diversity while phosphorus concentrations showed a positive correlation with same community attributes (Table 3). In the post phase, Pearson's correlation analysis showed that water temperature had a significant positive correlation with microcrustacean richness and diversity. Chlorophyll *a* was negatively correlated with microcrutacean diversity (all Pearson's correlations $P < 0.05$) (Table 3).

Table 3. Summary of Pearson's correlation coefficients between environmental variables and total zooplankton, microcrustaceans and rotifers (density, richness and diversity) in drought and post phase in each lake. * $P < 0.05$, ** $P < 0.01$, ***$P < 0.001$

		Water temperature	Suspended matter	pH	Conductivity	Dissolved oxygen	Chlorophyll *a*	Total nitrogen	Total phosphorus
Lake Pedra Branca									
Drought phase									
Microcrustaceans	Richness				0.83*				
	Diversity				0.84*				
Rotifers	Density		0.85*						
Post phase									
Total Zooplankton	Density	-0.92***			0.93***				
	Diversity	0.81**			-0.85**				
Microcrustaceans	Density	-0.93***			0.92***				
	Richness			-0.74*					
	Diversity			-0.74*					
Rotifers	Density		0.76**						
	Richness		0.71*						
	Diversity		0.72*						
Lake Guaritá									
Drought phase									
Total Zooplankton	Richness						-0.85*		0.84*
	Diversity		-0.82*				-0.90*		0.90*
Microcrustaceans	Density	0.91*							
	Richness	0.95**							
	Diversity	0.93**							
Post phase									
Microcrustaceans	Richness	0.85**							
	Diversity	0.79*					-0.80**		

Zooplankton community structure and composition

We found significant differences among phases in Lake Pedra Branca for the total zooplankton community structure and composition (Table 4). Similar significant values were also obtained considering microcrustacean and rotifer separately (Table 4). Post hoc ANOSIM comparisons revealed that total zooplankton, microcrustacean and rotifer structure and composition are statistically distinguishable among phases pre, drought and post (Table 4). Results from the NMDS corroborate the structural differences among phases, and also show that the phase before artificial drawdown (pre) was the most dissimilar when compared to the drought and post phase (Figure 7). The table 5 shows the main zooplankton taxa detected by SIMPER analysis as responsible for differences related to the phases in Lake Pedra Branca.

In Lake Guaritá, post hoc ANOSIM test and NMDS showed that the total zooplankton structure and composition differed significantly among phases (pre-drought-post) (Table 4, Figure 7). In addition to the post hoc ANOSIM test singled out rotifers composition of the post phase differed significantly from pre and drought phase. Nevertheless, the microcrustacean community structure and composition was similar among phases before, during and after the artificial drawdown and not varied significantly (Table 4). This was also clear in the NMDS plot, where for microcrustacean, the pre-drought-post phases are more spread on the plots and they partially overlap (Figure 7). The analysis SIMPER indicated the main zooplankton taxa as responsible of the differences related to the phases in Lake Guaritá (Table 5).

Table 4. Global *R* and significance levels results from ANOSIM for variation in total zooplankton, microcrustaceans and rotifers structure (square-root transformed data) and composition (presence-absence transformed data) among phases (pre-drought-post) in each lake. * P < 0.05, ** P< 0.01, ***P < 0.001, ns, non-significant

Lake Pedra Branca							
Community structure				Community composition			
Global *R* values	Zooplankton	Microcrustaceans	Rotifers	Global *R* values	Zooplankton	Microcrustaceans	Rotifers
	0.29***	0.30***	0.22***		0.34***	0.32***	0.27***
Pairwise Tests				Pairwise Tests			
Groups	Zooplankton	Microcrustaceans	Rotifers	Groups	Zooplankton	Microcrustaceans	Rotifers
pre, drought	0.83***	0.77***	0.63***	pre, drought	0.65***	0.41***	0.66***
pre, post	0.27**	0.35**	0.21**	pre, post	0.37***	0.42***	0.25**
drought, post	0.14**	0.13**	0.19**	drought, post	0.24***	0.26***	0.17**
Lake Guaritá							
Community structure				Community composition			
Global *R* values	Zooplankton	Microcrustaceans	Rotifers	Global *R* values	Zooplankton	Microcrustaceans	Rotifers
	0.20***	0.03 (ns)	-0.05 (ns)		0.20***	0.06 (ns)	0.148**
Pairwise Tests				Pairwise Tests			
Groups	Zooplankton	Microcrustaceans	Rotifers	Groups	Zooplankton	Microcrustaceans	Rotifers
pre, drought	0.24**	0.02 (ns)	0.02 (ns)	pre, drought	0.41***	(ns)	0.08 (ns)
pre, post	0.27**	0.06 (ns)	-0.15 (ns)	pre, post	0.27*	(ns)	0.21*
drought, post	0.18***	0.01 (ns)	-0.02 (ns)	drought, post	0.16**	(ns)	0.13**

Table 5. SIMPER analysis (square-root density data) showing the main common taxa contributing to within-phases similarity in zooplankton communities for each lake. In bold the three main taxa, cut-off 90%. den=density data, cont%= percentage of contribution

	Lake Pedra Branca						Lake Guaritá					
	Pre		Drought		Post		Pre		Drought		Post	
	Ave. simi 41.11		Ave. simi. 48.97		Ave. simi. 34.93		Ave. simi. 30.23		Ave. simi. 27.98		Ave. simi. 22.62	
Taxa	den.	cont%	den	cont%	den	cont%	den	cont%	den	cont%	den	cont%
Cladocera												
Alona guttata							1.49	2.73				
Alona sp.			16.9	3.57								
Bosmina freyi	**21.78**	**6.57**	**71.26**	**19.38**	**69.13**	**23.65**			3.35	7.54	5.34	3.16
Ceriodaphnia silvestrii	5.74	5.51	**41.37**	**9.69**	**27.12**	**4.62**			3.48	6.79		
Chydorus pubescens							**9.69**	**49.18**	**9.61**	**26.23**	2.52	3.61
Daphnia gessneri	5.96	4.21			15.9	5.05						
Diaphanosoma spinulosum			9.63	1.65								
Macrothrix sp			13.59	2.06	8.33	1.96	1.97	4.17	2.68	4.69		
Moina minuta					16.92	2.09						
Copepoda												
Microcyclops sp.					9.81	1.96						
Notodiaptomus henseni	5.65	3.8	38.07	7.82	15.4	3.7			**5.47**	**8.66**	3.56	12.36
Thermocyclops decipiens			**49.1**	**13.15**								
Thermocyclops sp.					**20.71**	**6.64**			1.75	3.05		
Rotifera												
Bdelloidea					7.44	1.28					**7.37**	**14.58**
Brachionus sp.									6	8.93	5.74	6.23
Cephalodella sp.									4.64	7.78	5.37	6.28
Collotheca sp.	**18.25**	**8.88**	10.12	1.75								
Conochilus unicornis	10.71	5.73							3.85	4.03	3.66	3.02
Euchlanis sp.	**11.28**	**6.79**	30.66	6.04	15.63	2.85	**8.53**	**17.43**			4.27	2.18
Keratella lenzi			12.19	2.96	8.88	1.71						
Lecane cf. *leontina*			20.59	4.86								
Lecane sp.	9	4.56										
Lecane arcula			13.25	2.12	6.73	1.37						
Lecane bulla											**8.54**	**12.46**
Lecane decipiens			10.97	2.51	13.61	2.36						
Lecane cf. *elsa*			13.63	1.86	11.75	2.33						
Lecane lunaris											3.06	2.01
Lecane signifera			12.03	1.7								
Lepadella sp.	5.46	4.75			10.42	2.14	4.67	2.63	3.06	2.78	4.08	3.54
Macrochaetus sp.			12.66	2.85	6.83	1.19						
Trichocerca sp.	6.08	2.96			9.93	1.85			3.7	3.57		
Trichotria tetractis	5.74	2.62	14	2.8			**13.89**	**15.59**	**4.66**	**4.48**	**9.84**	**10.72**
Platyias quadricornis					9.1	1.06						

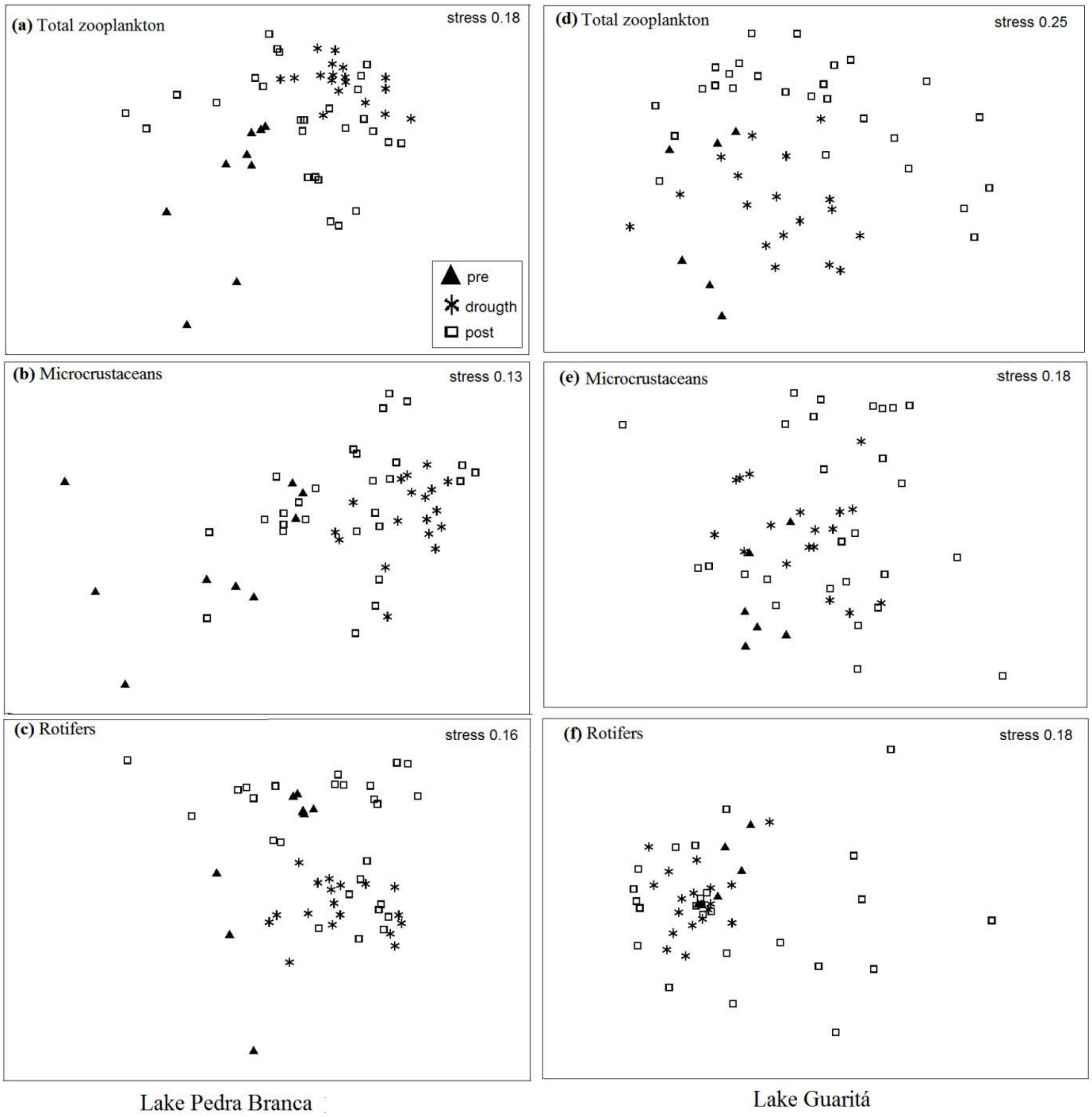

Figure 7. Non-metric multidimensional scaling of total zooplankton, microcrustaceans and rotifers structure among phases (pre-drought-post) related to the artificial drawdown in each lake

Discussion

The response of Egeria densa and Egeria najas biomass to artificial drawdown

The artificial drawdown caused a decrease in the biomass of *Egeria densa and Egeria najas* in the upstream compartment of the reservoir and in the Lakes Pedra Branca and Guaritá, but the plant was not eliminated from the system. In the more lacustrine compartment, named Reservoir in our results, the expected macrophytes reduction was not achieved. After a minor decrease registered in the first monitoring posterior to the water level recovery (43th day), there was a huge growth of *Egeria* spp in terms of biomass, reaching more than double compared to the pre drawdown values (74th day). This indicates that this species has a strong ability to regenerate from the stress caused by short-term drought. Similar tendency was observed for a large subtropical reservoir (Itaipu) following natural drawdowns (Thomaz *et al.*, 2006; Boschilia *et al.*, 2012).

There is a possible explanation for this spatial reorganization of the plants. During the artificial drought, a considerable amount of the submersed macrophytes were exposure to aerial conditions and they suffered from desiccation and died. In the upstream compartment of the reservoir, mainly in the lakes Pedra Branca and Guaritá, even during the drawdown phase, it was observed several remaining pools and a high humidity in the exposed sediments. These conditions favored a quick regeneration of the plants from the seed banks and propagules which may remain viable during depletion, representing a potential source of propagules for re-invasion (Cook and Urmi-König, 1984). When the water level recovered, the vast masses of seed bank and propagules material flushed out from lateral lakes and colonized the downstream reservoir shore areas. This could be considered an undesirable side effect of the operational water level diminution. Therefore, the efficiency of water level drawdown to control aquatic macrophytes, especially *Egeria*, is controversial, showing that some remedial measures should be tested in field-scale trials. A combined effort using different measures is often more practical and effective (Rørslett & Johansen, 1996).

Zooplankton dynamics in response to the artificial drawdown

The zooplankton communities present in the Lakes Pedra Branca and Guaritá at the beginning of the study were similar to those reported in other studies carried out in Salto Grande Reservoir and other reservoirs of Paranapanema River (Perbiche-Neves *et al.*, *in press*; Panarelli *et al.*, 2010; Ferrareze & Nogueira, 2011; Perbiche-Neves & Nogueira, 2013).

This study document a macro scale experiment on zooplankton communities in two lateral lakes, in response to active lowering of reservoir water level in order to manage nuisance growth of *E. densa* and *E. najas.* The artificial drawdown contributed for the increase of total zooplankton, microcrustacean and rotifer densities in Lakes Pedra Branca and Guaritá and in a temporary change in the community structure. Furthermore, it favored increases in taxa richness or community composition. This suggests that the artificial drawdown could potentially be used to control the excessive growth of *E. densa* and *E. najas* in the Salto Grande Reservoir without affecting negatively the density and diversity of the zooplankton communities.

Density and community structure changes

In contrast to the predicted by the first hypothesis, artificial drawdown resulted in an immediate increase in density of total zooplankton, microcrustacean and rotifer and associated alteration in the community structure for both lakes. Despite the similar patterns of variations, the Lake Pedra Branca showed more pronounced changes in environmental conditions and zooplankton community structure during the artificial drawdown. The most likely explanation is related to the morphology of this lateral lake, which becomes completely disconnected from the main axis of the reservoir during the drawdown event, whereas Lake Guaritá still maintain water exchange with the main channel of the Salto Grande Reservoir. Thus, in the Lake Guaritá, microcrustacean and rotifer communities structure was similar among phases and was largely influenced by the resident populations of the main axis of the Salto Grande Reservoir (Portinho *et al*., *in preparation*).

The zooplankton community structure in the Lake Pedra Branca differed among phases related to the artificial drawdown, largely due to the increase in density of the common taxa in the drought and post phase when compared with pre phase. In this way, the communities responded to two structuring processes: during the drought phase, an apparent concentration effect (reduction in colonization area and volume of lakes) was seen and can be attributed to the dominance of smaller cladocerans, clyclopoids and rotifers associated with the water nutrients (phosphorus and nitrogen). By contrast, in post phase a dilution effect occurred in the Lake Pedra Branca when the water level returned to normal, allowing subsequent decline in density, but with values still higher when compared to the pre phase. The multivariate analysis of variance here performed support the existence of three distinct phases and highlight the high dissimilarity between pre phase from those phases during and after the artificial drawdown.

The artificial drawdown altered the abiotic attributes of the Lake Pedra Branca in such way that contributed to the density peaks in the microcrustacean and rotifer populations during the artificial drawdown. Regionally, the zooplankton community dynamics are strongly influenced by the abiotic changes associated with the hydrological regime (Nogueira, 2001; Nadai & Henry, 2009). During the drought, the Lake Pedra Branca was characterized by high chlorophyll *a*, and nitrogen and phosphorus concentrations. However, despite the fact that total suspended matter was significant and positively correlated only with rotifer density, and conductivity positively only with microcrustacean density, we can assume that related alterations (e.g. nutrient concentrations) affect all zooplankton density. That is because the dominance of some taxa recorded during drawdown, was usually associated with an increase in water nutrients. Increasing trophic conditions associated to dominant taxa was already observed (Dodson *et al.*, 2000; Bonecker *et al.*, 2007).

The SIMPER analysis of the community allowed a deeper examination of the zooplankton community responses and the main taxa contribution in each phase. For drought, among the Cladocera, Bosminidae was the dominant family mainly represented by *Bosmina freyi* De Melo & Herbert 1965. The high density of this specie in tropical aquatic environments (Bonecker *et al.*, 2007; Lansac-Tôha *et al.*, 2009), as well as the cyclopoid *Thermocyclops decipiens* Kiefer, 1929, can be an indicative of higher thophic conditions, as previously mentioned. Higher values of total zooplankton density are related the numerical contribution of microcrustacean in the Lake Pedra Branca. However, rotifer also contributed to the density peaks during drought and post phase, probably due to opportunistic features of this group, such as wide range of consumed food items and high turnover rate to disturbance events (Allan, 1976; Matsumura-Tundisi *et al.*, 1990; Paranarelli *et al.*, 2003; Casanova *et al.*, 2009).

Taxon richness and community composition

In the present study, the artificial drawdown appeared to have minor impact on zooplankton taxa richness, diversity and community composition (the presence or absence of taxa). The overall suite of taxa present (pre phase) was unaltered, indicating that a drawdown effect in both lakes is unlikely to result in a net loss of taxa. This finding adds support to the idea that the artificial drawdown could potentially be used to manage nuisance growth of *E. densa* and *E. najas* in the Salto Grande Reservoir whilst still maintaining ecological values of zooplankton communities in the lateral lakes Pedra Branca e Guaritá.

Despite the apparent resistance of zooplankton composition in both lakes, when compared pre phase with droughts and post phase, an increase in zooplankton richness and consequently change in zooplankton communities composition was evident. The increase in richness and change of composition during drought phase was related to the relative increase in area covered by aquatic macrophytes, enhancing the number of available habitats. For the post phase, it was related to: i) the contribution of species coming from emergence of diapausing eggs deposited in sediment; and ii) contribution by lateral influx of river reservoir system.

During the drought phase, both lakes reduced the water depths by approximately 2.0 m and the exchange between the persistent rooted emergent macrophyte and open water zone was seen. Thus, the increase of richness and consequently change in composition could probably be due to dispersion of the living fauna linked to aquatic macrophytes. The role of macrophytes as physical structure that increases habitat complexity or heterogeneity in aquatic systems is widely recognized (Maia-Barbosa & Guimarães, 2007; Thomaz & Cunha, 2010), for instance, through providing a refuge for zooplankton (Jeppensen *et al*., 1997; Iglesias *et al*., 2007). Hence, the number of zooplankton taxa identified increase from 11 (pre phase) to 17 (drought phase) in Lake Pedra Branca and from 6 (pre phase) to 12 (drought phase) in Lake Guaritá; and all taxa recorded are commonly linked to aquatic macrophytes in tropical lakes, for instance, species of families Chydoridae, Lecanidae and Trichocercidae (Lansac-Tôha *et al*., 2009; Nadai & Henry, 2009; Maia-Barbosa & Guimarães, 2007); see more details about exchange of zooplankton communities in Table 5.

In the post phase, the rise in the water level coming from river reservoir system causes more extensive connections between environments and wash-out from aquatics macrophytes. The lateral water influx introduces species by water drift from the Paranapanema River and favored the exchange of fauna among the environments previously dried, as well as between pelagic and littoral zones within each lake. Furthermore, the abiotic factors associated with water level changes may have provided a cue for the hatching of zooplankton resting eggs from sediments and sheltered in macrophytes stands (Crispim & Watanabe, 2001; Maia-Barbosa *et al*., 2003; Battauz *et al*., 2014), could be also potential source of organisms and responsible for the increase in zooplankton richness and community composition (the presence or the absence of taxa) in both lakes studied (Gyllström & Hansson, 2004; Pallazo *et al*., 2008; Panarelli *et al*., 2008).

Experiments on hatching of resting eggs from sediment of these two lakes were performed during my PhD. Some of the species found in this study were record; nevertheless we do not have absolute hatching success in the experimental design (low hatching rate). So in this case, we decided not include data on zooplankton emergence, for considering them preliminary. A new sample processing with improved experimental design is presently on course. See more details in appendix III.

Our findings evidence that the artificial drawdown in the run-of-river Reservoir of Salto Grande could potentially be used for management of nuisance growth of *E. densa* and *E. najas* and does not compromise some components of biotic community – zooplankton communities (Copepoda, Cladocera and Rotifera) in lateral lakes. However, further research is required to understand the impacts of managing reservoir in this manner, taking into account biodiversity restoration, human economic interest and mainly due to undesired side effects, as mentioned above. The challenges faced by freshwater managers of tropical reservoir systems in recent years have resulted in a rethink about how we deal with the often conflicting demands of various human waters uses associated with alternative remedial measures that maintain the biodiversity. Whilst the impact of reservoir management on individual elements of the biotic community may not appear to be significant, effects may be amplified when community interactions are considered.

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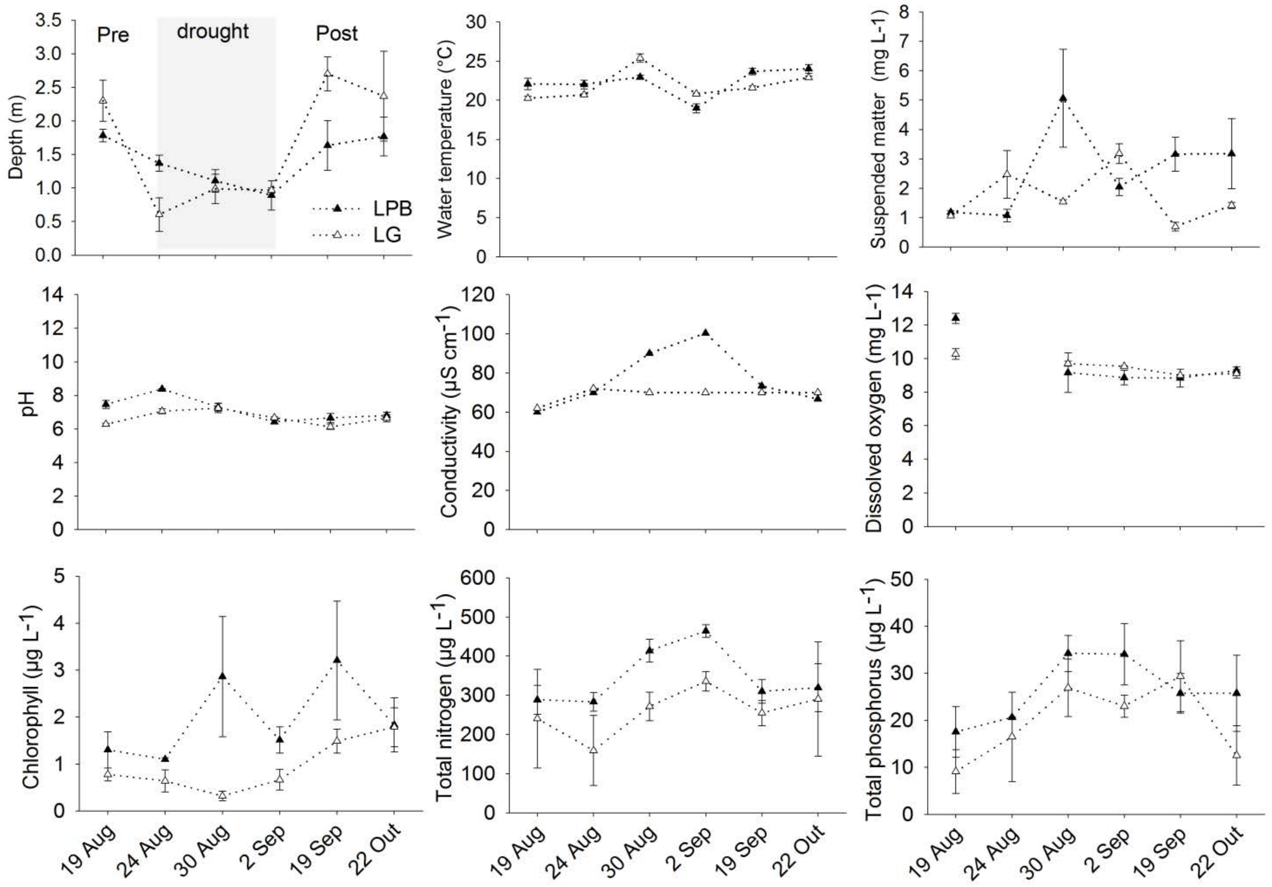
Supplementary information

Appendix I. Mean values and standard deviation of limnological variables measured at Lakes Pedra Branca and Guaritá along the study period. Pre phase day 19th August, drought phase 24th and 30th August, and post phase 2nd, 19th September and 22th October, 2011

Lake Pedra Branca						
Days	8/19	8/24	8/30	9/2	9/19	10/22
Phase	Pre phase	Droguth phase		Post phase		
Environmental variables						
Depht (m)	1.8±0.1	1.4±0.1	1.1±0.2	0.9±0.2	1.6±0.4	1.8±0.3
Water temperature (°C)	22±0.7	22±0.6	22.9±0.2	19±0.6	23.6±0.4	24±0.6
Suspended matter (mg L^{-1})	1.2±0.1	1.1±0.2	5.1±1.7	2.0±0.3	3.2±0.6	3.2±1.2
pH	7.5±0.2	8.4±0.1	7.3±0.2	6.4±0.1	6.6±0.3	6.8±0.2
Conductivity (µS cm^{-1})	60	70	90	100±6.1	73.3±3.3	66.7±3.3
Dissolved oxygen (mg L^{-1})	12.4±0.3	–	9.2±1.2	8.9±0.4	8.8±0.5	9.3±0.2
Chlorophyll *a* (µg L^{-1})	1.3±0.4	1.1±0.1	2.9±1.3	1.5±0.3	3.2±1.3	1.8±0.6
Total nitrogen (µg L^{-1})	288±36.7	283±23.7	413.8±29	464±15.7	309.9±29.8	319.4±61.6
Total phosphorus (µg L^{-1})	17.5±5.4	20.6±0.1	34.2±3.8	34.1±6.5	25.7±4.3	25.8±8.1

Lake Guaritá						
Days	8/19	8/24	8/30	9/2	9/19	10/22
Phase	Pre phase	Droguth phase		Post phase		
Environmental variables						
Depht (m)	2.3±0.3	0.6±0.2	1.0±0.2	1.0±0.1	2.7±0.3	2.4±0.7
Water temperature (°C)	20.2±0.3	20.7±0.1	25.4±0.5	20.8±0.1	21.6±0.2	22.9±0.2
Suspended matter (mg L^{-1})	1.0±0.1	2.5±0.8	1.5±0.1	3.2±0.3	0.7±0.1	1.4±0.1
pH	6.3±0.1	7.1±0.1	7.2±0.3	6.7±0.1	6.1±0.2	6.6±0.2
Conductivity (µS cm^{-1})	60	70	70	70	70	70
Dissolved oxygen (mg L^{-1})	10.3±0.3	–	9.7±0.2	9.5±0.1	9.0±0.1	9.1±0.3
Chlorophyll *a* (µg L^{-1})	0.8±0.1	0.6±0.2	0.3±0.1	0.7±0.2	1.5±0.3	1.8±0.4
Total nitrogen (µg L^{-1})	240.4±125.9	158.9±89.2	271.4±36.8	335.6±24.4	254.6±32.2	290.3±146.1
Total phosphorus (µg L^{-1})	9.1±4.7	16.5±9.6	26.9±6.1	23±6.1	29.4±7.6	12.5±6.3

Appendix II. Mean values and standard deviation of limnological variables measured at Lakes Pedra Branca and Guaritá along the study period. Pre phase day 19th August, drought phase 24th and 30th August, and post phase 2nd, 19th September and 22th October, 2011. Code: LPB= Lake Pedra Branca and LG= Lake Guaritá



Appendix III. Images of Lakes Pedra Branca and Guaritá during the different phases related to artificial drawdown in Salto Grande Reservoir. (a) Lake Pedra Branca pre phase, (b) drought phase and (c) post phase. (d) Lake Guaritá pre phase, (e) drought phase, (f) post phase. (g-j) Sediment collection for assessing propagule bank communities, and (l-m) experimental design

Spatial distribution and characteristics of river-floodplain zooplankton and aquatic plant propagule bank communities

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Chapter 2

Chapter 2: Spatial distribution and characteristics of river-floodplain zooplankton and aquatic plant propagule bank communities

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Summary

1. Zooplankton and aquatic plant propagule banks are central components of river-floodplain ecosystems. However, very little is known about their spatial distribution on the floodplain or the factors related to their distribution.
2. This study investigated the distribution of zooplankton and aquatic plant propagule bank communities on the floodplain of a temperate Australian river system in relation to hydrological conditions, surrounding vegetation, and sediment composition.
3. This was achieved by assessing zooplankton emergence and aquatic plant germination from the propagule banks in sediments collected at 10 randomly selected sites within a 25 km^2 area of the floodplain in conjunction with hydrological conditions (as estimated by elevation, CTF, flood history), EVC, and sediment composition.
4. Results from the study indicated that zooplankton and aquatic plant propagule bank communities varied greatly among sites in terms of community structure and composition. These findings support the view that propagule banks are heterogeneously distributed on the floodplain, and suggest that hydrological conditions and physical factors play an important role in directly or indirectly supporting this heterogeneity.
5. They also imply that the characteristics of emerging zooplankton and germinating aquatic plant communities are not overwhelmingly determined by the local factors affecting their emergence/germination, and instead, that factors affecting the distribution of the propagules they originated from are also likely to play a strong role.

Keywords: Egg bank, floodplain, hydrology, seed bank

Introduction

Understanding hydrological connectivity is a key aspect of community dynamics of large floodplain systems. These systems experience temporal changes in environmental conditions that are associated with changes in the water level in the main channel (Junk, Bayley & Sparks, 1989). Floodplains represent an intermittently flood zone with high flood frequency water bodies close to main channel, others connect to the main channel only during the high flows and isolated water-bodies that are only inundated under the most extreme floods (Tockner, Malard & Ward, 2000; Amoros & Bornette, 2002). A mosaic of habitats is shaped by this gradient of connectivity and as consequence may lead to changes in population viability and community composition (Baranyi *et al*., 2002; Stanford, Lorang & Hauer, 2005).

The gradients of connectivity and disturbance regimes (e.g. flow and flooding) are fundamental in ecology and are related to biotic diversity of a floodplain (Ward, Tockner & Schiemer, 1999). Many studies have highlighted the importance of flow and flood pulse as the main determinants of zooplankton and plants communities in composition and abundance in floodplains (Reckendorfer *et al*., 1999; Casanova & Brock., 2000; Campbell, Johns & Nielsen, 2014). In addition, a number of studies have suggested that plants and microfauna communities respond to changes in hydrological connectivity in a predictable pattern (Blom & Voesenek, 1996; Casanova & Brock, 2000; Nielsen, Watson, & Petrie, 2005; Górski *et al*., 2013). The ecology of zooplankton and plants communities to inundation is well documented (Brock & Casanova, 1997; Shiel, Green & Tan, 2001; Nielsen *et al*., 2013, and others). However, knowledge concerning the dynamics for the dormant aquatic seeds of floodplain plants and eggs of zooplankton in response to hydrological connectivity (frequency and duration of flooding) across large spatial and temporal scale is poor.

Dormancy in zooplankton eggs-banks is analogous to that in seed-banks (De Stasio, 1989), and consequently, many studies have simultaneously considered both forms of biota (Brock *et al*., 2003; Nielsen *et al*., 2000, 2003; Ning, Nielsen & Baldwin, 2011b). Studies examining the influence of hydrology on these communities indicate their abundance and richness was related to water residence time and zonation within wetlands (Casanova & Brock, 2000; Nielsen *et al.*, 2013). Moreover, both propagules banks are produced at different temporal scales and determine the dynamics of active populations (Hairston, 1996) and dispersal of species (Cáceres & Soluk, 2002), reflecting the evolutionary history and environmental conditions of a given system (Gyllström & Hansson, 2004).

This study was undertaken within the Barmah-Millewa Forest (BMF), a floodplain forest located in the mid-section of the Murray River near Echuca, southeastern Australia (Fig. 1). Most of this area is dominated by stands of river red gum (*Eucalyptus camaldulensis*), and the entire asset is listed as a Ramsar wetland (Australian Nature Conservation Agency, 1996). Important gradients in the BMF are the spatial and temporal distribution of flood waters, providing the primary source of moisture in this region (MDBA, 2012). Furthermore, the hydrological gradients in BMF are a function of local geomorphology and connectivity, thus we predict that the production of dormant seeds and eggs across the floodplain will respond to changes in hydrological connectivity. We compared the patterns of emergence of zooplankton from eggs and germination of aquatic plants from seeds from floodplain sediment to assess differences in the propagule banks communities structure and composition in response to differences in the frequency of inundation. We wished to test the hypothesis that a greater abundance and richness will occur in areas of the floodplain that are subjected to a low or intermediate frequency of flooding compared to floodplain areas that are more frequently inundated.

Methods

Study area

The study was undertaken on the Barmah Millewa Forest (BMF) floodplain in the mid-section of the Murray River in southeastern Australia. The Barmah–Millewa Forest supports the largest River Red Gum (*Eucalyptus camaldulensis*) forest in Australia and covers an area of 660 km^2 (Figure 1). Flooding is highly regulated via the use of regulators and levees that prevent water flowing onto the floodplain, allowing the water level in the main river channel to be maintained at capacity without loss of water. Once inflows exceed 11,000 ML day^{-1} upstream of the forest at Tocumwal, regulators are opened and flooding occurs (Ecological Associates & SKM 2011).

The region in which the BMF is located was influenced by persistent drought from 2000 through to 2010 (MDBA, 2012). During this period the entire area in which the sites were located had remained dry (K. Ward pers. comm.). Widespread flooding from mid 2010 through to late in 2012 inundated and connected all sites (Figure 2).

Site selection

A 25 km^2 sampling area was randomly selected (Figure 1) within BMF, and divided into 1 km^2 grids to form a total of 625 sites (each one 1 km^2). Ten of these sites were selected using a random number generator. Each site was then divided in one hundred 0.1 km^2 quadrants from which five were randomly chosen to collect sediment from (Figure 1). Thus, a total of the 50 samples (i.e. 10 sites x 5 quadrants/site) were collected across all sites. At the time of sampling, all sites were dry.

Sediment collection for assessing propagule bank communities

Sediment samples were collected from each site between 19 March and 16 May 2013. Within each site, samples were randomly collected in the five quadrants by shoveling the top 2 – 3 cm of sediment until approximately 10kg of sediment containing eggs and seeds had been collected and placed in a plastic bag following the methods of Nielsen *et al.* (2003, 2007) and Brock, Nielsen & Crosslé (2005). Published reports of seed and egg bank sampling have shown that only the top three centimeters of the soil is required for representing different communities present in wetlands (Cáceres & Hairston, 1998). The sediment was taken back to the Murray-Darling Freshwater Research Centre (MDFRC) facility in Wodonga (Victoria), where it was sieved, lightly crushed and air dried. This ensured that only dormant propagules remained and that they were uniformly mixed prior to sub-sampling for use in the emergence/germination trails (Nielsen *et al.*, 2008).

Experimental design

Trays (17.2 x 12 x 5.8 cm) were filled with 250g (dry weight) of wetland sediment. For both zooplankton and aquatic plants three replicate subsamples were taken from each of the 50 samples, resulting in an experimental design using 300 subsamples (150 for zooplankton and 150 for aquatic plants). All samples were incubated in a constant temperature room set at 25°C and 12:12 light/dark cycle (Vandekerkhove *et al.*, 2005).

Zooplankton emergence and sample processing

Zooplankton emergence trays were inundated with aged tap water and oxygenated using aquarium bubblers. Each tray was sampled twice weekly for a period of 28 days by gently pouring the water from each 2-L container through a 50-µm sieve, with minimum disturbance to the sediment (Nielsen *et al.*, 2007). Twenty-eight days has been shown to be sufficient for overall hatching success as a prerequisite in zooplankton richness and diversity studies (Boulton & Lloyd, 1992; Vandekerkhove *et al.*, 2005; Ning & Nielsen, 2011a), and twice weekly sampling minimizes the potential for reproduction by any individuals that emerge (Nielsen *et al.*, 2007, 2008). On each occasion, the collected sample was put into a 200-ml storage jar and preserved in 70% ethanol, while the sediment remaining in each incubation container was re-inundated with aged tap water. At the end of the 28 day period, zooplankton samples were sub-sampled prior to processing. One millitre aliquots were successively placed into a Sedgewick-Rafter counting chamber, and identified and counted using dark field microscopy until either a minimum of 300 individuals or 20% of the sample had been analyzed. All zooplankters were identified to the level of Family or Genus. Identification to either of these taxonomic levels has been shown to be suitable for detecting changes in zooplankton communities in response to environmental change (Nielsen, Shiel, & Smith, 1998). Taxa were identified using relevant keys in Shiel (1995).

Aquatic plant germination and sample processing

Plant germination trays were inundated with aged tap water to a depth of 2 cm and maintained at this depth for a period of 12 weeks. At the end of the 12 week period all emergent plant seedlings were identified and taxon richness and abundance recorded for each tray. Identification and nomenclature of angiosperms and ferns followed Harden (1990-1993) and Cunningham *et al.* (1992). Liverwort identification followed Sainty & Jacobs (2003). Plants were assigned to the broad functional groups of Brock & Casanova (1997) so that they could be assessed according to their responses to water regime rather than their taxonomic group. Individuals are categorized based on their mechanism of germination, growth and reproductive response (Brock & Casanova 1997).

Environmental conditions

Hydrological conditions were characterized at each site by assessing their elevation on the floodplain and their commence-to-flow (CTF) threshold. CTF thresholds at each quadrant were measured as the magnitude of flow within the Murray River channel upstream at Tocumwal required to inundate each site. Both CTF thresholds and floodplain elevations were derived from a Barmah Forest digital elevation model (DEM) with ArcGIS 9 (ESRI) software (Table 1 and Figure 2).

The Ecological Vegetation Class (EVC) (Woodgate *et al*., 1996) at each site was characterized in accordance with EVC units. These vegetation classes consist of one or a number of floristic communities that appear to be associated with a recognizable environmental niche, and which can be characterized by a number of their adaptive responses to ecological processes that operate at the landscape scale (Frood & Ward, 2001).

Sediment composition was also characterized at each site by measuring the percentage of moisture, solids, silt+clay and clay. The samples of the sediment were assessed by taking five samples at each site. The analyses of the percentage of silt, and clay in the organic fraction were determined through Hydrometer Method and Soil Moisture using standard methods described in Grimshaw, H. M. (1989) and reported as percentages (Table 1).

Table 1. Characteristics of the 10 sites examined in our study. EVC=Ecological Vegetation Class; DEM= Digital elevation model

						Sediment composition			
Sites	Latitude	Longitude	EVC	DEM	Flow average Ml day^{-1}	% Moisture	%Solids	Silt+Clay	%Clay
S1	5.55 °E	45.16 °S	VC 816	95.07	39,000	15.58	84.42	47.80	30.00
S2	5.54 °E	45.09 °S	VC 812	95.79	62,000	15.17	84.83	54.56	37.64
S3	5.54 °E	145.3 °S	VC 812	96.44	52,333	21.37	78.63	32.00	20.56
S4	5.55 °E	145.2 °S	VC 816	96.03	48,000	14.92	85.08	39.04	22.00
S4	5.54 °E	145.3 °S	VC 816	95.61	42,800	21.47	78.53	43.52	29.60
S6	5.52 °E	145.2 °S	VC 816	95.01	25,800	15.40	84.60	47.96	30.40
S7	5.52 °E	145.1 °S	VC 812	94.71	20,000	15.11	84.89	48.64	28.52
S8	5.53 °E	145.2 °S	VC 816	95.66	33,000	18.70	81.30	47.88	31.92
S9	5.52 °E	145.3 °S	VC 816	96.12	44,000	15.95	84.05	54.32	34.40
S10	5.55 °E	145.3 °S	VC 812	95.50	24,250	24.69	75.31	36.36	22.80

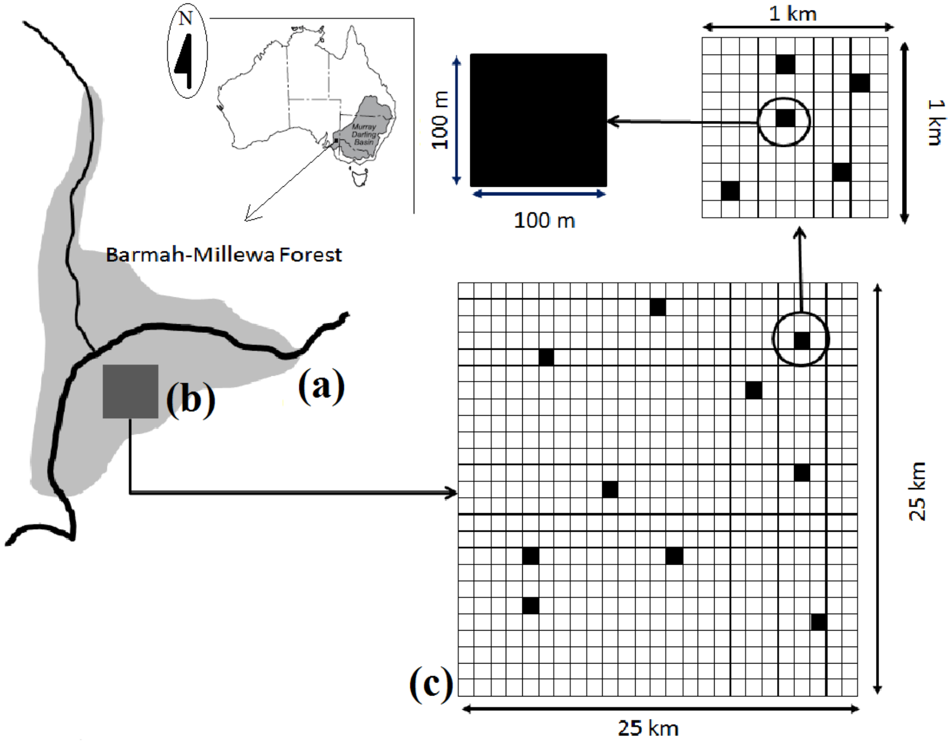


Figure 1. A schematic representation of the experimental design showing the location of the BMF in Australia within the MDB (a), the location of the 25 km^2 study area within the BMF (b), and the spatial arrangement of the 10 sites within the 25 km^2 study area (c) (see geographic coordinates in Table 1)

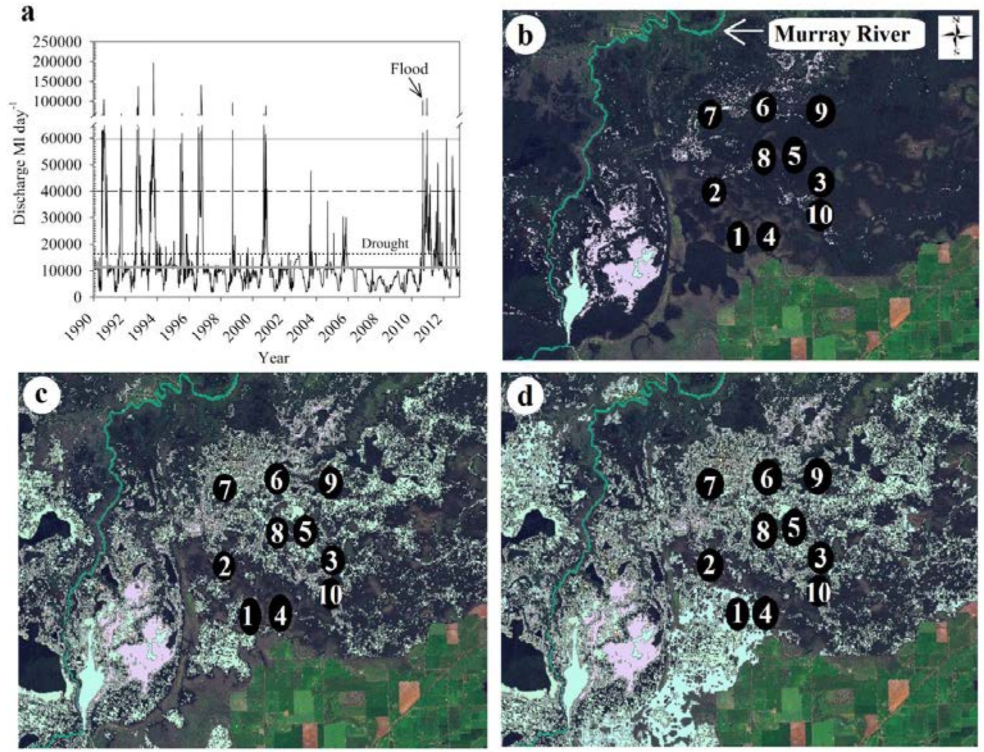


Figure 2. BMF digital elevation model and map detail showing the location of the all sites. (a) Discharge patterns at BMF. *Grey* line & (b) indicate flooding commences in the BMF at 11,000 Ml day^{-1}; *Dotted line* & (b) indicate areas inundated at 15,000 Ml day^{-1}; *Medium dash* line & (c) indicate areas inundated at 40,000 Ml day^{-1} and *Black solid line* & (d) indicate areas inundated once flooding exceeds 60,000 Ml day^{-1}

Data analysis

Zooplankton and aquatic plant counts were expressed per tray and the replicates from each site (*n*=15) were averaged to give a mean number of plants and microfauna.

Univariate analyses were undertaken, using PERMANOVA, on taxon richness, abundance, Pielou's species evenness and Shannon-Wiener diversity. Data was log(x+1) transformed prior to converting to a Euclidian distance matrix to reduce the influence of outliers (Anderson, Gorley & Clarke, 2008).

Multivariate analyses were used to examine the distribution of zooplankton and plants across sites. Prior to analysis all data was square-root transformed. Non-metric multidimensional scaling (nMDS) derived from a Bray-Curtis similarity matrix was used to display patterns of community similarity between sites (Clarke & Warwick, 2001). A One-way analysis of similarity (ANOSIM) was used to test the null hypothesis of no difference in zooplankton and plant communities composition between sites (Clarke and Warwick, 2001). The taxa discriminating the sites were calculated by a SIMPER-analysis (Similarity Percentages) which takes into account both the contribution to average similarity within a site and average dissimilarity between sites groups (Clarke & Warwick, 2001). Finally, distance-based linear models procedure DISTLM (Anderson, Gorley & Clarke, 2008) was used to evaluate the percentage of variability in the zooplankton and plants community explained by the environmental variables listed in table 1. The communities DISTLM were constructed using the step-wise selection procedure and the adjusted R^2 as selection criterion to enable the fitting of the best explanatory environmental variables in the model (Anderson, Gorley & Clarke, 2008). Euclidian distance was used as resemblance measure in all DISTLM procedures.

All multivariate analyses and diversity analyses were undertaken using PERMANOVA+ for PRIMER (PRIMER software, v.6 Primer-E Ltd, Plymouth).

Results

Communities

Forty nine zooplankton taxa and twenty six plant taxa hatching/germinated from the sediments. The 49 zooplankton taxa consisted of 39 rotifers genera and 8 microcrustacean including Cladocera, Ostracoda, Harpacticoida and Copepoda groups. The twenty-six plant taxa were comprised of submerged, amphibious and terrestrial plant groups.

The nMDS analysis showed that the zooplankton and plants communities have a spatial separation which define a gradient of decrease in density and differences in the community structure and composition among sites from south to north in Barmah forest (BMF) (Figures 4 a, b and 5 a, b). Differences between communities in the sites were supported by ANOSIM and SIMPER analysis ($P < 0.001$). In general, the both pairwise test comparison revealed that most dissimilarity were among sites S1 from S7 (ANOSIM test R= 0.996, $P = 0.008$, and SIMPER average dissimilarity 56.64%) for zooplankton (Table 2), and site S1 showed the greatest distinction from S7 and S10 in their plant community (ANOSIM test R= 0.988 and 0.984, $P < 0.001$, and SIMPER average dissimilarity 67.45% and 61.45%, respectively) (Table 6). For all comparisons, the communities tended to be dissimilar, especially among two main groups of sites that comprised sites S1 – S5 and S10 from sites S6 –S9 for zooplankton and sites S1 – S5 from sites S6 –S 10 for plants (Table 2 and 6).

Zooplankton

Zooplankton communities were less density and richness in the most frequently flooded sites S6, S7, S8 and S9 in the BMF, but in general these sites had high diversity (H') and evenness (J') compared to the other sites (Figure 3 a, b, and c; see discharge patterns Figure 2). The Communities from these sites were characterized by microcrustaceans (cladocerans and copepods nauplii) (Figure 4). In contrast, the sites group S1 –5 and S10 had the greatest proportion in density by rotifers (e.g. *Cephalodella* and Bdelloidea) (Figure 4). PERMANOVA indicated there were significant differences in zooplankton community structure in terms of all measured attributes among sites, except for evenness attribute ($P < 0.05$) (Table 3).

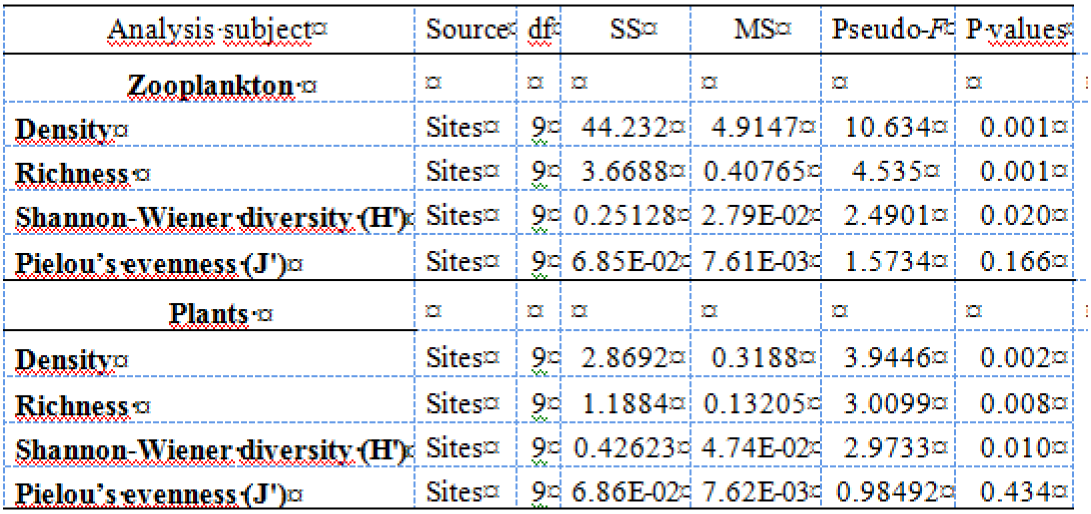
Taxon richness data from all sites were pooled and the number of sites in which individual taxa occurred was calculated (Figure 3d). Only two sites had more than 15% of the taxa emerging. This suggests that spatial isolation and specific environmental conditions (e.g. elevation and flow) to promote local distribution in wetlands groups formed.

Subsequent SIMPER analysis found that the rotifers, *Cephalodella*, and Bdelloidea, and the microcrustacean, Ostracoda, contributed the great proportion of similarity within sites group S1 –5 and 10 from sites S6 –9 (Table 4). DistLM analysis indicated that zooplankton community structure was best related to northing (r^2 = 0.13; $P < 0.001$); although the best overall explanatory model was produced by the combination of northing, flow and elevation (r^2= 0.21) (Table 5).

Table 2: Results from the analysis of similarity ANOSIM (in white) illustrating the results from pairwise comparisons of zooplankton communities among sites and the SIMPER test (in dark grey) showing the average dissimilarity % among sites

		SIMPER Average dissimilarity (%)									
	ites	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
ANOSIM R values		–	1.49	7.34	4.39	4.28	8.71	6.64	51.52	0.93	9.19
		.796	–	1.52	2.32	3.34	3.05	3.57	41.59	3.57	8.53
		.664	.336	–	9.59	3.23	1.42	8.35	44.20	3.98	3.15
		.500	.104	.164	–	2.84	3.84	9.74	46.56	7.45	8.96
		.580	.544	.208	.424	–	8.23	5.49	40.35	9.89	5.84
		.828	.260	.408	.280	.360	–	1.88	37.04	1.08	6.02
		.996	.312	.728	.604	.816	.400	–	37.58	4.09	7.18
		.924	.208	.588	.452	.524	.056	.200	–	0.05	3.23
		.644	.040	.252	.232	.156	.020	.144	-0.024	–	6.59
		.660	.592	.564	.556	.344	.648	.728	0.580	.364	–

Table 3. Results of PERMANOVA test performed on the zooplankton and aquatic plant density, taxon richness, Shannon-Wiener diversity taxa and Pielou's species evenness (Log +1 transformed data and Euclidean distance) emerging from 10 sites at BMF



Analysis subject	Source	df	SS	MS	Pseudo-*F*	P values
Zooplankton						
Density	Sites	9	44.232	4.9147	10.634	0.001
Richness	Sites	9	3.6688	0.40765	4.535	0.001
Shannon-Wiener diversity (H')	Sites	9	0.25128	2.79E-02	2.4901	0.020
Pielou's evenness (J')	Sites	9	6.85E-02	7.61E-03	1.5734	0.166
Plants						
Density	Sites	9	2.8692	0.3188	3.9446	0.002
Richness	Sites	9	1.1884	0.13205	3.0099	0.008
Shannon-Wiener diversity (H')	Sites	9	0.42623	4.74E-02	2.9733	0.010
Pielou's evenness (J')	Sites	9	6.86E-02	7.62E-03	0.98492	0.434

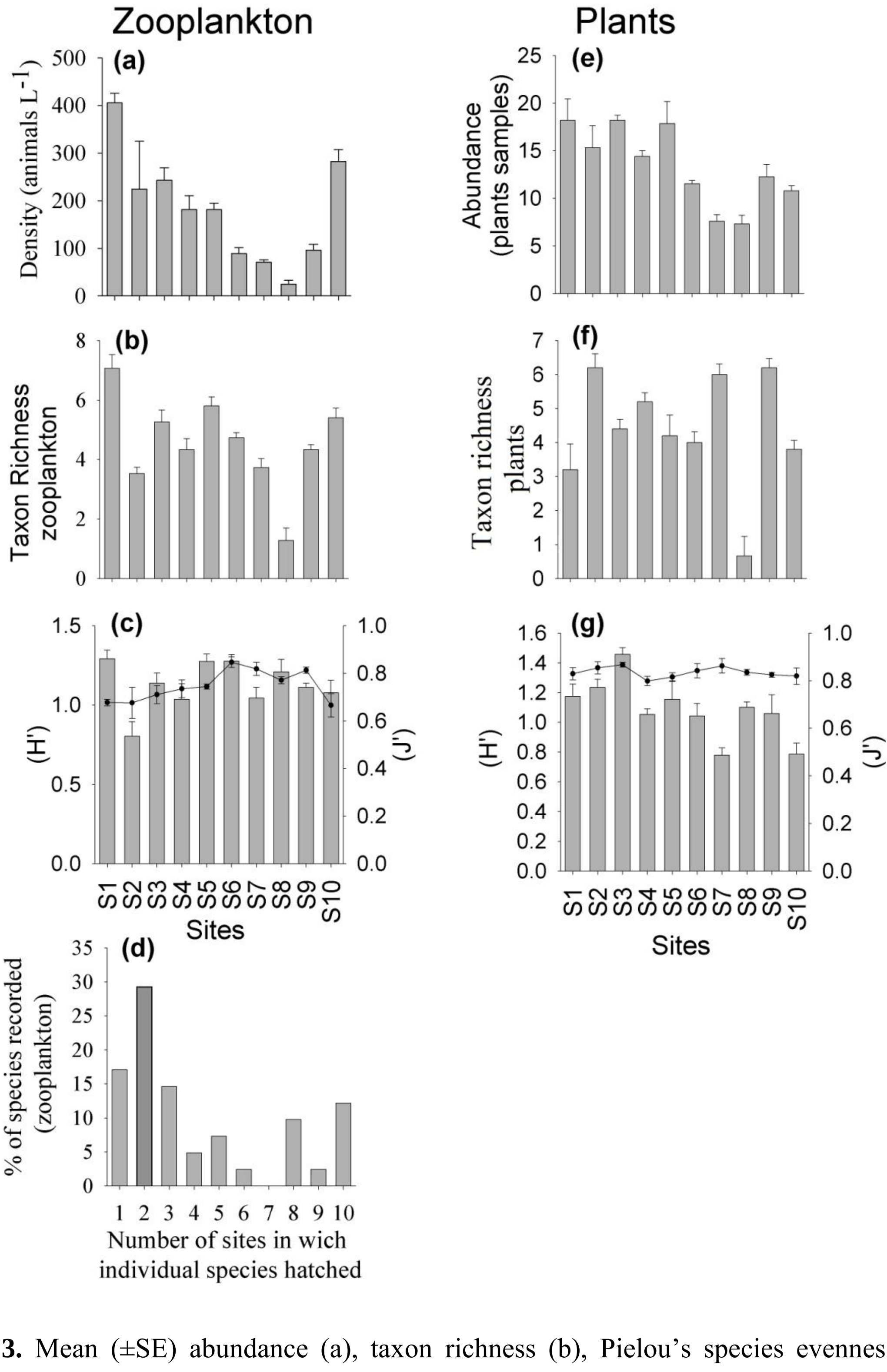


Figure 3. Mean (±SE) abundance (a), taxon richness (b), Pielou's species evenness and Shannon-Wiener diversity (c) of the zooplankton communities emerging from the 10 study sites. Figure 4d uniqueness of zooplankton communities as measured by the number of sites from which a given zooplankton taxa hatched

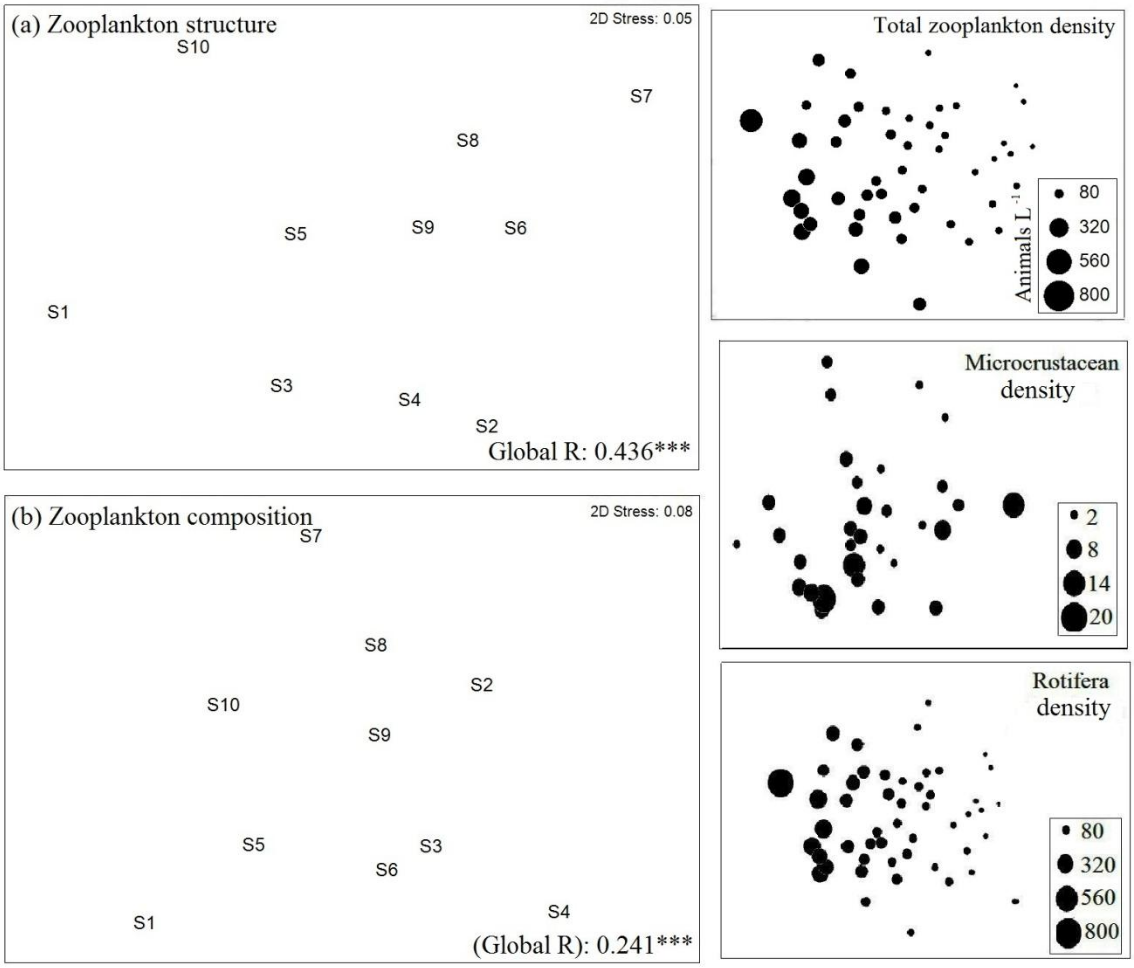
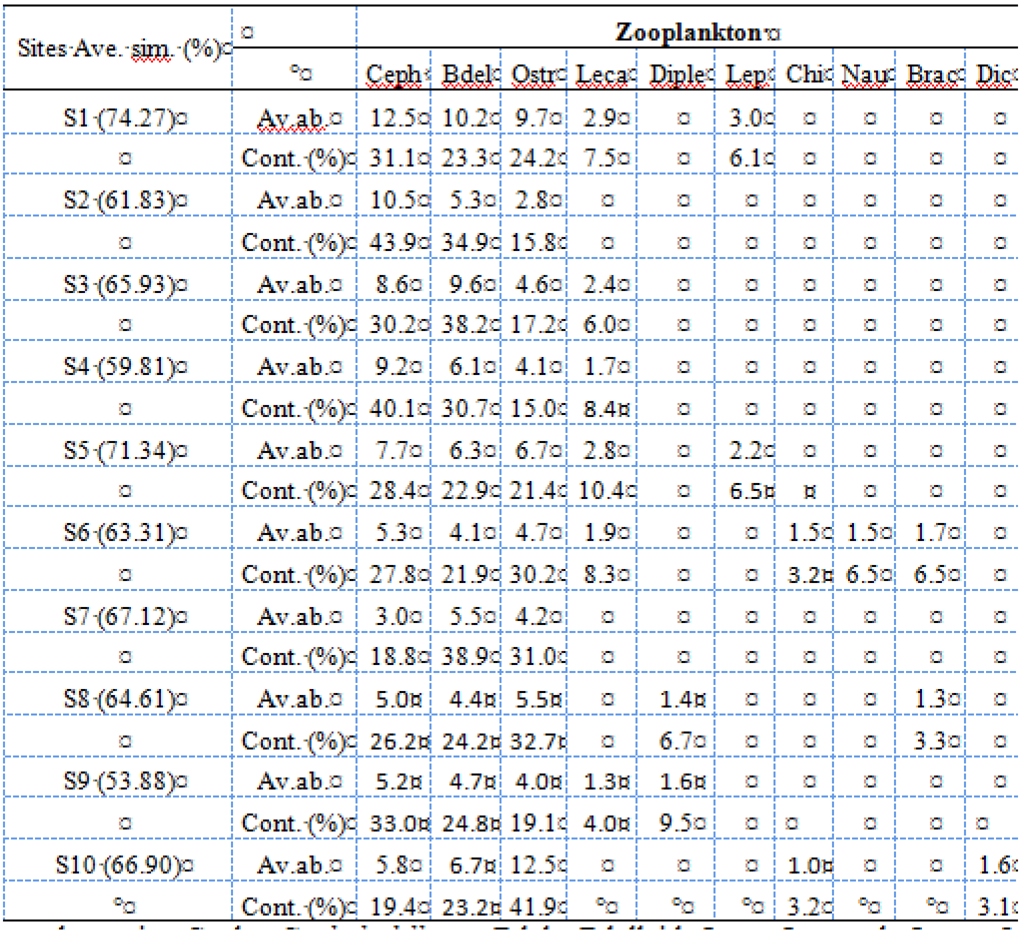


Figure 4. Multidimensional plots of zooplankton communities hatched from sediments from BMF. Bubbles are scaled to reflect the mean abundance of each plot's total zooplankton, microcrustacean and rotifer communities in sites at BMF

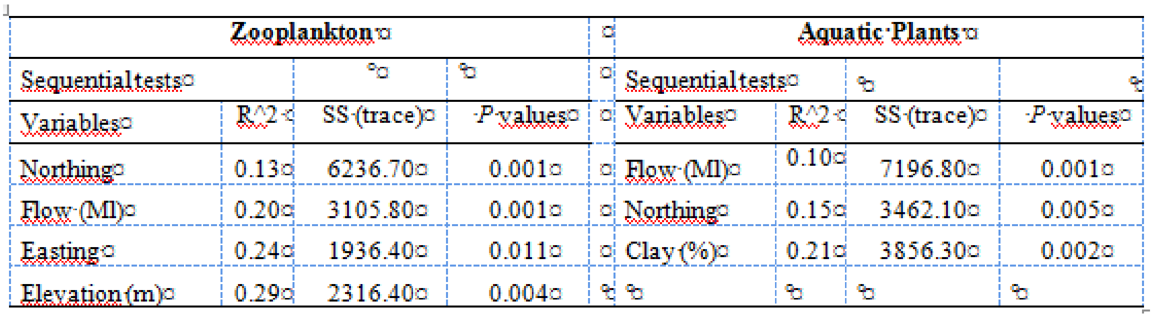
Table 4. SIMPER values (square-root transformed density data) showing the main zooplankton taxa contributing to within-site group similarity. Ave. sim.= Average similarity; Av. Ab.= Average abundance; Cont(%)= percentage of contribution



Sites Ave. sim. (%)		Zooplankton									
		Ceph	Bdel	Ostr	Leca	Diple	Lep	Chi	Nau	Brac	Dic
S1 (74.27)	Av.ab.	12.5	10.2	9.7	2.9		3.0				
	Cont. (%)	31.1	23.3	24.2	7.5		6.1				
S2 (61.83)	Av.ab.	10.5	5.3	2.8							
	Cont. (%)	43.9	34.9	15.8							
S3 (65.93)	Av.ab.	8.6	9.6	4.6	2.4						
	Cont. (%)	30.2	38.2	17.2	6.0						
S4 (59.81)	Av.ab.	9.2	6.1	4.1	1.7						
	Cont. (%)	40.1	30.7	15.0	8.4						
S5 (71.34)	Av.ab.	7.7	6.3	6.7	2.8		2.2				
	Cont. (%)	28.4	22.9	21.4	10.4		6.5				
S6 (63.31)	Av.ab.	5.3	4.1	4.7	1.9			1.5	1.5	1.7	
	Cont. (%)	27.8	21.9	30.2	8.3			3.2	6.5	6.5	
S7 (67.12)	Av.ab.	3.0	5.5	4.2							
	Cont. (%)	18.8	38.9	31.0							
S8 (64.61)	Av.ab.	5.0	4.4	5.5		1.4				1.3	
	Cont. (%)	26.2	24.2	32.7		6.7				3.3	
S9 (53.88)	Av.ab.	5.2	4.7	4.0	1.3	1.6					
	Cont. (%)	33.0	24.8	19.1	4.0	9.5					
S10 (66.90)	Av.ab.	5.8	6.7	12.5				1.0			1.6
	Cont. (%)	19.4	23.2	41.9				3.2			3.1

**Note* code species: Ceph = *Cephalodella* sp.; Bdel = Bdelloid; Ostr = Ostracods; Leca = *Lecane* sp.; Diple = *Dipleuchlanis* sp.; Lep = *Lepadella* sp.; Chi= Chydoridae; Nau=Nauplii; Brac=*Brachionus* sp.; Dic=*Dicranophorus* sp.

Table 5. Results of the DISTLM test on the BMF dataset. Results of the sequential tests show the affect of environmental parameters on zooplankton and plants communities in the combined model (stepwise selection with R^2 criterion)



Zooplankton					Aquatic Plants			
Sequentialtests					Sequentialtests			
Variables	R^2	SS (trace)	P values		Variables	R^2	SS (trace)	P values
Northing	0.13	6236.70	0.001		Flow (Ml)	0.10	7196.80	0.001
Flow (Ml)	0.20	3105.80	0.001		Northing	0.15	3462.10	0.005
Easting	0.24	1936.40	0.011		Clay (%)	0.21	3856.30	0.002
Elevation (m)	0.29	2316.40	0.004					

Aquatic plants taxa

Abundance values were significantly lower at sites group S6 –10 than at sites group S1 –5. The highest taxon richness values were found at site S2 and S9. Shannon-Weiner index of species richness ranged from 0.77 to 1.45, with the highest values recorded at site S3 and the lowest at site S7 (Figure 3a, b and c). PERMANOVA indicated there were significant differences in the abundance and richness of plants and the diversity of plants but there was no significant difference in Evenness (P < 0.05) (Table 2).

The nMDS analysis revealed that the relative density and community composition varied among sites (Figure 5). For example, for the 3 most abundant taxa *Elatine* spp. alone or in combination with *Callitriche* spp., was the most frequently occurring dominant plant community in sites group S1 –5; *Centipeda* spp. was the most dominant species in sites group S6 –10. Some species were restricted to specific sites, for example: *Triglochin* spp. sites S3 and S4; *Joyweed* spp., *Isotoma* spp. and *Potamogeten* spp. only site S5; *Glossotigma* spp. only germinated in site S6 and *Polown grass* site S9. In general, the sites had different combinations of species with different dominants and co-dominants, and endemic plants. A similar pattern was found also for zooplankton communities, which it can be seen that the 10 sites form wetland mosaics at BMF with differences occurring along a gradient form north to south.

From the analysis of the average dissimilarity performed through SIMPER between sites based on individual plant species abundance procedure ranged between minimum of

36.41% for sites S7 and S10 and maximum of 67.42% for sites S1 and S7 (Table 6). The table 7 showed the results of the SIMPER analysis with the main taxa were responsible for this dissimilarity, as such of sites groups S1 –5 from S6 –10 sites. The DistLM analysis indicated that plant community structure was best related to flow (r^2 = 0.10; $P < 0.001$); although the best overall explanatory model was produced by the combination of flow, northing, clay, elevation and easting ($r^2 = 0.26$) (Table 5).

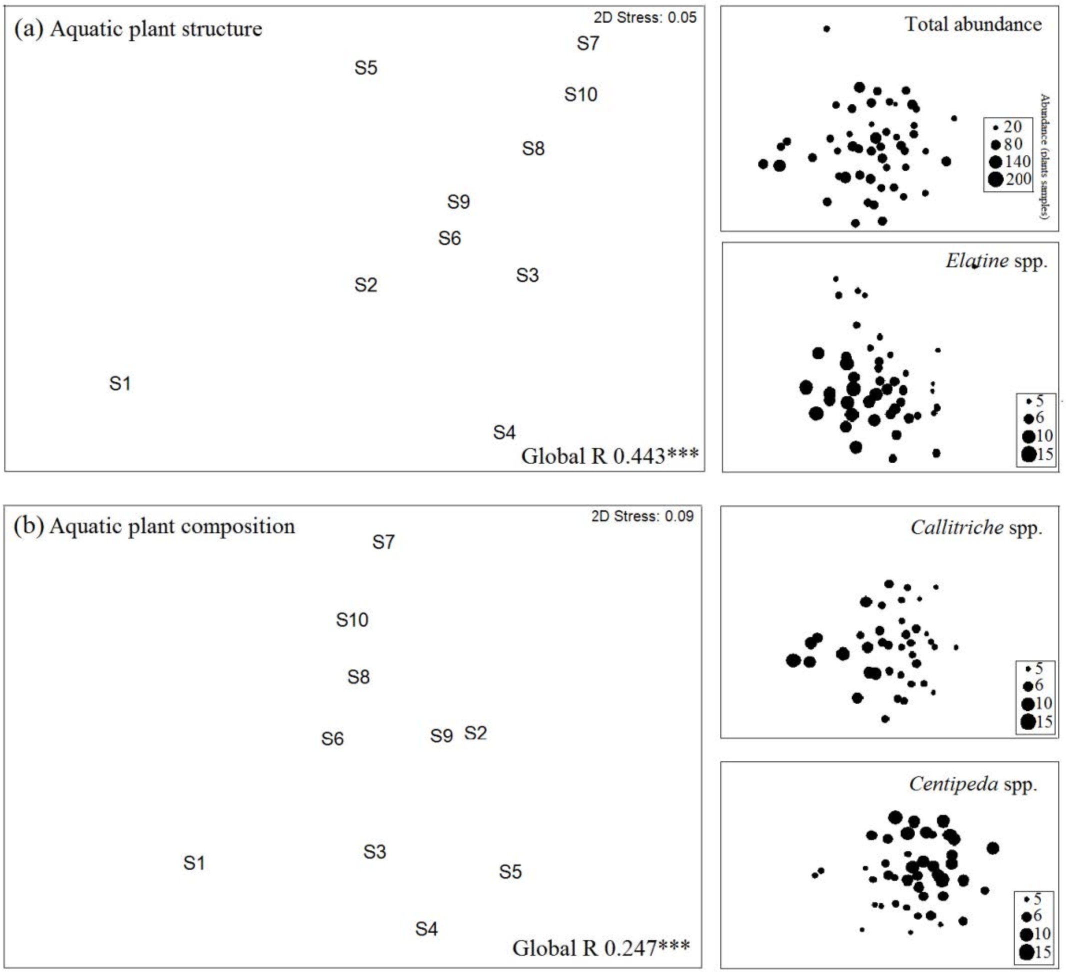
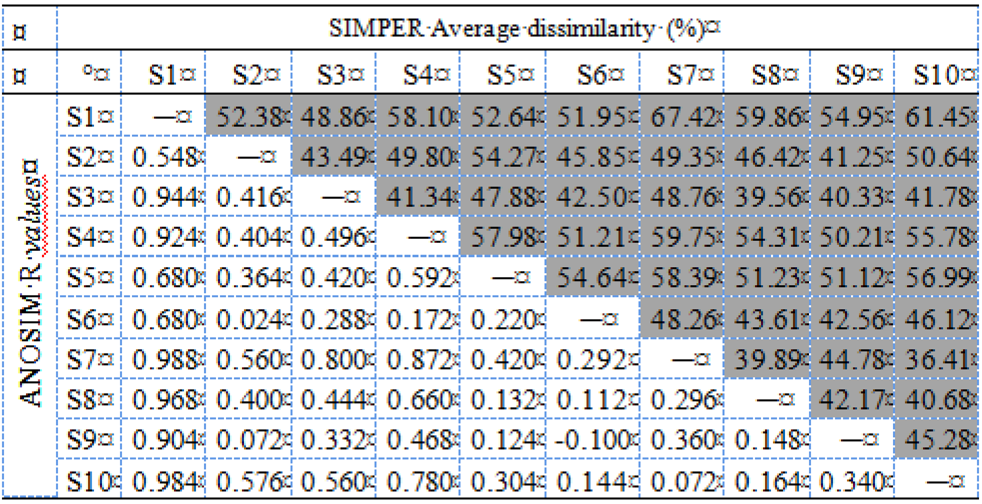


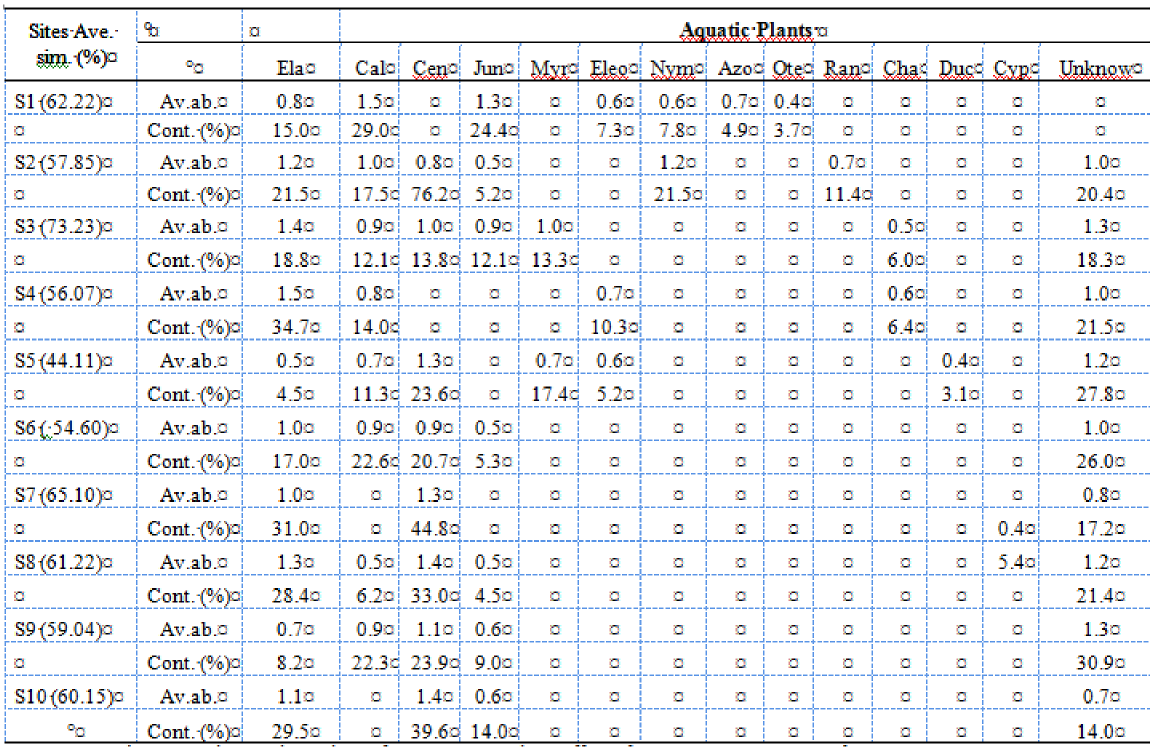
Figure 5. Multidimensional plots of aquatic plant communities that germinated from sediments at BMF. Bubbles are scaled to reflect the mean abundance of each plot’s total aquatic plant abundance, and the three main taxa contributing to the variation in seeds among sites at BMF

Table 6: Results from the analysis of similarity ANOSIM (in white) illustrating the results from pairwise comparisons of plants communities among sites and the SIMPER test (in dark grey) showing the average dissimilarity % among sites



		SIMPER Average dissimilarity (%)									
	°	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10
ANOSIM R values	S1	—	52.38	48.86	58.10	52.64	51.95	67.42	59.86	54.95	61.45
	S2	0.548	—	43.49	49.80	54.27	45.85	49.35	46.42	41.25	50.64
	S3	0.944	0.416	—	41.34	47.88	42.50	48.76	39.56	40.33	41.78
	S4	0.924	0.404	0.496	—	57.98	51.21	59.75	54.31	50.21	55.78
	S5	0.680	0.364	0.420	0.592	—	54.64	58.39	51.23	51.12	56.99
	S6	0.680	0.024	0.288	0.172	0.220	—	48.26	43.61	42.56	46.12
	S7	0.988	0.560	0.800	0.872	0.420	0.292	—	39.89	44.78	36.41
	S8	0.968	0.400	0.444	0.660	0.132	0.112	0.296	—	42.17	40.68
	S9	0.904	0.072	0.332	0.468	0.124	-0.100	0.360	0.148	—	45.28
	S10	0.984	0.576	0.560	0.780	0.304	0.144	0.072	0.164	0.340	—

Table 7. SIMPER values (square-root transformed abundance raw data) showing the main taxa contributing to similarity in plants communities to within-site group similarity. Ave. sim. = Average similarity; AV. Ab.= Average abundance; Cont(%)= Contribution



Sites Ave. sim. (%)			Aquatic Plants												
		Ela	Cal	Cen	Jun	Myr	Eleo	Nym	Azo	Ote	Ran	Cha	Duc	Cyp	Unknow
S1 (62.22)	Av.ab.	0.8	1.5		1.3		0.6	0.6	0.7	0.4					
	Cont. (%)	15.0	29.0		24.4		7.3	7.8	4.9	3.7					
S2 (57.85)	Av.ab.	1.2	1.0	0.8	0.5			1.2			0.7				1.0
	Cont. (%)	21.5	17.5	76.2	5.2			21.5			11.4				20.4
S3 (73.23)	Av.ab.	1.4	0.9	1.0	0.9	1.0						0.5			1.3
	Cont. (%)	18.8	12.1	13.8	12.1	13.3						6.0			18.3
S4 (56.07)	Av.ab.	1.5	0.8				0.7					0.6			1.0
	Cont. (%)	34.7	14.0				10.3					6.4			21.5
S5 (44.11)	Av.ab.	0.5	0.7	1.3		0.7	0.6						0.4		1.2
	Cont. (%)	4.5	11.3	23.6		17.4	5.2						3.1		27.8
S6 (;54.60)	Av.ab.	1.0	0.9	0.9	0.5										1.0
	Cont. (%)	17.0	22.6	20.7	5.3										26.0
S7 (65.10)	Av.ab.	1.0		1.3											0.8
	Cont. (%)	31.0		44.8										0.4	17.2
S8 (61.22)	Av.ab.	1.3	0.5	1.4	0.5									5.4	1.2
	Cont. (%)	28.4	6.2	33.0	4.5										21.4
S9 (59.04)	Av.ab.	0.7	0.9	1.1	0.6										1.3
	Cont. (%)	8.2	22.3	23.9	9.0										30.9
S10 (60.15)	Av.ab.	1.1		1.4	0.6										0.7
	Cont. (%)	29.5		39.6	14.0										14.0

**Note* code species: Ela= *Elatine* spp.; Cal= *Callitriche* spp.; Cen= *Centipedia* spp.; Jun= *Juncus* spp.; Myr= *Myriophyllum* spp.; Eleo= *Eleocharis* spp.; Nym= *Nymphoides* spp.; Azo= *Azolla* spp.; Ote= *Otella* spp.; Ran= *Ranunculus* spp.; Cha= *Charophyte* spp.; Duc= *Duckweed* spp.; Cyp= *Cyperus* spp.

Discussion

We examined the role of the hydrological connectivity on the distribution of dormant seeds and eggs within the floodplain sediment of Barmah Forest (BMF). The data indicates that there are differences in community composition along a south to north gradient with more abundant and diverse communities occurring in the southern regions compared to the northern regions.

In cases where habitat patches suffer frequent disturbances, both aquatic plants and microfauna have persistent egg and seed banks like as potential by diversity reservoir in wetlands and rapidly emerge when are rewetted (Brock, 1998; Nielsen *et al*., 2000). Floodplain wetlands are usually influenced by the effects of flooding (Ward, Tockner & Schiemer, 1999; Thomaz, Bini & Bozelli, 2007). Flood characteristics such as the magnitude, duration and recurrence intervals of flows (Whited *et al*., 2007) can all influence changes in the mosaic of floodplain habitats through space and time.

Historically, BMF experienced large floods, such as the flood of 2010, which resulted in widespread inundation across the floodplain. Indeed, all of the sites sampled in this study would have been inundated at some stage in the past, some more frequently than others. The variation in flood characteristics among sites would have created a mosaic of patches on the floodplain, which would promote different patterns in the communities present across both small and large spatial scales (Shiel, Green & Tan, 2001; Campbell, Johns & Nielsen , 2014).

The spatial distribution of communities amongst sites in BMF may have been strongly influenced by their location in association with the main river channel, flood-runners and secondary channels. The magnitude of the flow in the main river channel and the elevation of a wetland on the floodplain interact to determine when the wetland will receive water, as well as the duration and frequency of flooding that it will experience (Junk, Bayley & Sparks, 1989). The Murray River has a mean discharge of 18,330ML/day. Flows greater than 60,000 ML/day exceed the capacity of the River Murray through the BMF and result in flooding of the forest’s wide range of floodplain swamps, marshes, billabongs, rushlands, grasslands and lakes (MDBA, 2012). The Murray River’s flow regime directly influences the hydrological connectivity regime at the BMF by affecting the regularity, extent, duration, seasonality and hydrology of flooding of the floodplain forest, and indirectly influences structural connectivity by affecting sedimentation and erosion processes (MDBA, 2012). The sites located in the northern part of the BMF (S6 – S9) are likely to have greater hydrological connectivity and be more frequently inundated for longer periods of time due to their lower elevation on the floodplain compared to the other sites. These areas are likely to be more permanently inundated under natural flow regimes. In contrast, the more southern sites (S1 – S5 & S10) are higher on the floodplain and consequently less likely to receive frequent inundation and when inundation does occur it is likely to be of short duration.

More microcrustaceans (copepods and cladocerans) were recorded as emerging from the potentially more permanently flooded lower sites. Higher hydrological connectivity and increased duration of flooding plays an important role in production of large-bodied cladocerans and copepods (Lair, 2006; Paggi & Paggi, 2008). In contrast more rotifers emerged from higher and potentially more temporarily flooded sites and there was a higher incidence of rarer species. Water that is retained in a floodplain wetland for a relatively short time favor species with quick development rates (Reynolds, 2000; Baranyi *et al*., 2002). The rotifer *Cephalodella* sp., Bdelloid and the Ostracoda were the only taxa that were more numerous in all sites. Our results suggest that difference in flood pulse and consequent hydrological connectivity contribute to spatial heterogeneity of floodplain, which results in differences in the structure and composition of eggs banks wetlands, providing evidence for a metacommunity structure.

We also observed significantly lower densities and diversity of plants in the lower more permanent wetlands at BMF. The water residence time in floodplain was the mechanism that selects which species develop (Van Der Valk & Welling, 1989). For example, *Centipeda* spp. was more abundant in the more permanent wetlands compared to the higher and more temporary wetlands. Broadly those species defined as amphibious (Casanova & Brock, 200) (e.g. *Elatine* spp., *Callitriche* spp.) were those that are more abundant in temporary wetlands. Indeed, the variation in species composition in our study was comparable to that reported previously in other Australian wetlands (Casanova & Brock, 2000; Brock *et al*., 2003; Raulings *et al*., 2010; Barrett, Nielsen & Croome, 2010; Nielsen *et al*., 2013; Campbell, Johns & Nielsen, 2014), and was probably again reflective of species adaption to the hydrological gradient across the BMF floodplain. It is broadly recognized that flood pulse is disturbance that can alter local environmental and can affect species richness (Connell, 1978) which create hydrological conditions and provide the basic control of wetlands structure (Junk, Bayley & Sparks, 1989).

Our findings are evidence for the density and diversity of propagule banks dependence of the distribution of sites at floodplain, and are consistent with the proposal that different plant and zooplankton communities are found in wetlands that have been exposed to different water regimes (Shiel, Green & Nielsen, 1998; Brock *et al*., 2003; Barrett, Nielsen & Croome, 2010). The apparent variation in seed and egg banks across sites at BMF is not only influenced by the degree of connectivity due to the frequency and magnitude of flooding, but also by other abiotic and biotic factors such as dispersal capacity, colonization rate and establishment (Brendock & De Meester, 2003; Cohen & Shurin, 2003; Louette & De Mester, 2005). However, hydrological connectivity important in that it creates a mosaic of wetland patches within the landscape that act over a long time scale and drivers of changes as a determinant taxonomic composition of the microfauna and plants communities in floodplain.

This study suggests that historic flood pulse, flow dynamics and hydrological connectivity together with floodplain wetlands types concertedly influence the ecological structure and function of banks of zooplankton egg- and aquatic plant seed-banks at BMF. Finally, our work also points out to a critical issue in conservation wetlands in large scale. More attention should be to investigating the climatic changes trends (see Nielsen & Brock., 2009), as well as to develop hypothesis about the water regime modification. The provision and maintenance of a variety of hydrological patterns across the landscape will be essential to preserving the natural function and diversity of floodplain egg and seed-banks.

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