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Macrophyte assemblages in relation to environmental, temporal and spatial variations in lakes of a subtropical floodplain-river system, Argentina



Z.Y Marchetti ^{a,*}, P.A. Scarabotti ^b

- a CONICET-Universidad Nacional del Litoral, Facultad de Ingeniería y Ciencias Hídricas, Santa Fe, C.C. 217 (3000), Argentina
- ^b Instituto Nacional de Limnología, (UNL-CONICET), Ruta 168, Paraje El Pozo (3000) Santa Fe, Argentina

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ABSTRACT

This work analyses the variation in the structure of macrophyte assemblages in relation to environmental (lake morphometry and water physico-chemistry), temporal and spatial variables, in seven floodplain lakes placed in the surrounding of the Salado and the Paraná Rivers confluence in the Paraná floodplain-river system. We recorded the variations in cover of thirteen of the most important macrophyte species among rooted and free-floating life forms. A discriminant analysis of the main coordinates showed significant differences among floodplain lakes (spatial variation), as well as among the 13 months studied (temporal variation). Redundancy analysis indicated that electrical conductivity, maximum depth, shoreline development index, lake area and water temperature had significant influence on macrophyte assemblages. In a partial RDA, environmental and temporal variables accounted for a similar percentage of total explained variation (\sim 50%), whereas spatial variables, including distance to main channel, accounted for 30.6%. Results show that the environmental variables of lakes, temporal descriptors, and the spatial position of lakes along the floodplain can explain a significant fraction of variation of macrophyte assemblages. These results allow us to understand the dynamic of macrophyte assemblages along temporal and spatial scales and their association with flooding regime, considering local (physico-chemical and morphometric) and landscape (spatial) characteristics of the floodplain environments.

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1. Introduction

Subtropical floodplain-river systems are among the most biodiverse and productive ecosystems in the world (Lewis et al., 2000; Hamilton et al., 2007). The natural dynamic of these systems is largely driven by the seasonal water level variation that interacts with floodplain geomorphology and determines different degrees of connectivity of floodplain lakes.

The spatio-temporal heterogeneity of floodplain-river systems provides habitats for a wide variety of macrophyte species, which usually appear in multispecific assemblages. Macrophytes are responsible for the high primary productivity, modify nutrient cycling, and affect other organisms like invertebrates and fishes, acting as key elements in the structure and functioning of the entire floodplain-river system (Petr, 2000; Thomaz and Ribeiro da Cunha, 2010; Scarabotti et al., 2011).

Floods have been referred as the most important factor affecting the dynamic of macrophyte assemblages in floodplain-river systems (Junk et al., 1989; Neiff et al., 2014; Morandeira and Kandus, 2015). Flood pulses replenish the nutrient stocks in the floodplain (Junk et al., 1989) and tend to increase environmental similarity among aquatic ecosystems (Thomaz et al., 2007). Additionally, flooding can act as a recurrent disturbance factor that resets the successional process of plant communities and maintains the system in an immature but highly productive and diverse stage (Puckridge et al., 1998; Marchese et al., 2002).

During periods of low water level, lakes become isolated and differentiate in their physico-chemical internal conditions that affect aquatic communities. Perimeter, area and depth have been pointed to affect the macrophyte distribution (Santos and Thomaz, 2007), as well as nutrient availability and conductivity (Neiff and Poi de Neiff, 2003; Schneider et al., 2015). Small changes in the degree of connectivity between water courses and fluvial lakes can strongly affect lake morphometry, physico-chemical variables, and macrophyte assemblage composition (Thomaz et al., 2008).

^{*} Corresponding author.

E-mail address: zuleicayael@hotmail.com (Z.Y Marchetti).

Although earlier studies on macrophyte assemblages of the Paraná River included successional changes in the relationship between macrophyte and physico-chemical variables (Neiff, 1975, 1979; Franceschi and Lewis, 1979; Neiff and Neiff, 2003; Sabattini and Lallana, 2007), these relationships have not been studied in combination with hydrological connectivity. A recent contribution shows an association between macrophyte species richness and composition and the degree of connectivity, lake morphometry and abiotic factors (Schneider et al., 2015). However, none of these studies evaluated how the environmental variables and macrophyte assemblages were modified during different periods of connectivity.

This work was conducted to analyze the temporal and spatial variation of macrophyte assemblages in relation to morphometric and physico-chemical changes of floodplain lakes associated with different degree of connectivity of a subtropical floodplain-river system. We separately considered the relationships between macrophyte assemblages and three different dimensions: environmental (including morphometry and physico-chemical), temporal (months during a year) and spatial (location of lakes). This was carried out in order to assess the relative importance of these terms in determining macrophyte assemblage structure.

2. Materials and methods

2.1. Study area

The study area is located in the final reach of the Salado River, three kilometers upstream of the mouth into the Paraná River. The Salado River belongs to the La Plata River basin and it is an affluent of the Middle Paraná River (Fig. 1A-B), with a high conductivity (mean 3000 μ Scm $^{-1}$; range 460–7000; Devercelli, 2008) compared to the low conductivity of Middle Paraná River (range between 30 and 120 μ Scm $^{-1}$; Depetris and Pasquini, 2007). It originates in northwestern Argentine and flows through 1500 km up to its mouth. In its final reach, it has a meandering channel of about 100 m in width and 7 in depth, which runs in a floodplain being approximately 2.5 km wide with islands, swamps, paleo-channels and oxbow lakes (INCyTH, 1986; FICH, 2006).

The hydrometric regime of the Salado River (Fig. 2) is characterized by high water periods that generally occur in summer and autumn (between December and April) and low water periods at the beginning of spring (between September and October). In the lower reach of the Salado River, the average variation in the water level between both periods is about two meters and it is strongly influenced by the water level of the Paraná River. During high water periods, floodplain lakes become connected with one another and with the Salado River through temporary channels.

The region receives an annual rainfall of 1000 mm, concentrated between December and March, and the monthly mean temperature varies from 11 $^{\circ}$ C in July to 24 $^{\circ}$ C in January.

2.2. Sampling

Seven floodplain lakes located in two different locations of the Salado River floodplain were selected for the present study (Fig. 1C). Los Sapos Island (S 31° 39′ 09′′, W 60° 45′ 16′′) is a 200-ha land area situated at the east of the Salado River main channel. The island includes 20 oxbow lakes at their northern end from which five lakes differing in surface area (from 0.52 to 1.76 ha) and distance to the main channel were selected for this study. Santo Tomé swamp (S 31° 39′ 46′′, W 60° 45′ 06′′) is a lowland extension placed on the western bank of the river that communicates with the neighbouring highlands and presents two floodplain lakes (0.76 and 1.61 each), which were also selected as sampling sites (Fig. 1C).

The sampling period spanned 13 months in which the hydrometric levels of the Salado River remained in the average variations. Samples were taken in all lakes within a one-week period every month from August 2004 to August 2005, but they did not start simultaneously in all the lakes: Lakes 1, 2 and 3 were sampled during the whole period; Lakes 4, 5 y 7 in September. Sampling in Lake 6 was initiated in November because it was dry at the beginning of the study. We did not register dry out events in any of the remaining lakes.

We performed monthly sampling transects covering the entire lake perimeter and registered the contour of lakes by means of line drawings on printed and scaled aerial photographs used as reference (1:5000 taken in March 2004 in the low water period). These drawings were then digitalized and georeferenced to measure the surface area, maximum length (fetch), maximum width (breadth) and perimeter for each lake using the software Global Mapper. In order to describe the shape of the lake, we calculated the shoreline development index, i.e. the relation between perimeter (P) and surface area (A), as follows, $P/(4\pi A)^{0.5}$. Additionally, we considered as a measure of spatial connectivity the shortest distance in water from the floodplain lakes. The Salado River hydrometic level was measured in Santo Tomé city and it was provided by the Instituto Nacional de Limnología (INALI). Lakes were weekly visited while hydrometric levels rose, then the overflow level of each lake was determined by recording the date in which they became connected with the river, and observing the hydrometric level of these date. Once overflow level for each lake was obtained, the number of days in which lakes were connected and isolated from the Salado River were calculated by using software PULSO (Neiff and Neiff, 2003). The fluvial connectivity index (FCQ) was also obtained from the ratio between number of the connected days and number of the disconnected days (Neiff and Neiff, 2003). Finally, physico-chemical variables such as water depth, transparency, temperature, electrical conductivity, pH, and dissolved oxygen were measured at the deepest point of each lake and between 9:00 and 13:00 hs, to avoid variation associated to daily cycles of these variables.

Additionally, during the monthly sampling surveys, we registered the contour of all patches of emergent and floating macrophytes. For each patch, we visually estimated the proportion of cover of each species. As described for lake measurements, we used Global Mapper software to measure the surface area of each macrophyte patch. The coverage of each species within each patch was calculated multiplying the surface area of the patch by the visually estimated proportion of coverage of each species. Finally, we calculated the area covered by each species in all the lake summing up their coverage across all patches.

2.3. Quantitative analyses

Macrophyte species occurring in less than 5 samples (<6% occurrence) were not included in the quantitative analyses to avoid biases generated by rare species. These species rarely surpassed 1% of the whole vegetation cover in the samples. For multivariate analysis, species data were transformed by Hellinger-standardization because it offers a better compromise between linearity and resolution for linear ordination methods (Legendre and Gallagher, 2001).

We applied a Canonical Analysis of Principal coordinates (CAP; Anderson and Willis, 2003) based on a linear discriminant analysis, in order to detect differences in floristic composition among floodplain lakes and among months. To use the same ecological distance as in the following linear ordination methods, we used the Euclidean distance together with 1000 random permutations without restrictions (Manly, 1997). Once significant differences in species composition were checked for floodplain lakes and months (p<0.05 obtained from CAP), contrasts between all pairs of lakes and months were evaluated by the Multi-Response Permutation

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