Role of the propagule bank in reestablishing submerged macrophytes after removal of free-floating plants for recovery of a shallow lake in Southern Brazil

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Abstract. At eutrophic shallow subtropical lakes, free-floating macrophytes can occupy the entire water surface. The removal of this vegetation favors the recolonization of submerged macrophytes from the propagule bank. Our study presents the response of the propagule bank of a shallow subtropical lake after management to reduce its hypertrophy. We sampled lake sediment in March 2016 at 15 points along three transects to investigate the richness and density of the propagule bank by emergence in the laboratory. We monitored water trophic conditions and restoration of vegetation in the field for 7 months. In the laboratory, 1382 seedlings of eight species emerged. *Stuckenia pectinata* and *Chara zeylanica* dominated the propagule bank. We identified the species *S. pectinata*, *C. zeylanica* and *Ludwigia peploides* in the field. The propagule bank was homogeneous, without difference (*P*>0.05) between lake regions and transects. Sørensen's similarity was 36% between the field and laboratory. When the submerged macrophytes grew in the field, there was a reduction of chlorophyll-a, the water remained clear, and the trophic state index was reduced from hypereutrophic to eutrophic. We concluded that the bank of propagules in shallow lakes is essential for the rapid reestablishment of submerged macrophytes after recovery strategies. These organisms help improve water quality.

[Keywords: seed bank, emergence of seedlings, subtropical]

Resumen. El papel del banco de propágulos en el restablecimiento de macrófitos después de la gestión para la recuperación de un lago somero en el sur de Brasil. En los lagos someros subtropicales eutróficos, los macrófitos que flotan libremente pueden ocupar toda la superficie del agua. Eliminar esta vegetación favorece la recolonización de macrófitos sumergidos del banco de propágulos. Nuestro estudio presenta la respuesta del banco de propágulos de un lago somero subtropical después del manejo para reducir su hipertrofia. En marzo de 2016 tomamos muestras del sedimento del lago en 15 puntos a lo largo de tres transectas para investigar la riqueza y la densidad del banco de propágulos por emergencia en el laboratorio. Además, durante siete meses monitoreamos las condiciones de agua trófica y la restauración de la vegetación en el campo. En el laboratorio emergieron 1382 plántulas de ocho especies. *Stuckenia pectinata* y *Chara zeylanica* dominaron el banco de propágulos. En el campo identificamos las especies *S. pectinata*, *C. zeylanica* y *Ludwigia peploides*. El banco de propágulos fue homogéneo, sin diferencia (*P*>0.05) entre las regiones del lago y las transectas. La similitud de Sørensen fue del 54% entre el campo y el laboratorio. Cuando los macrófitos sumergidos crecieron en el campo, se redujo la clorofila-a, el agua permaneció clara y el índice de estado trófico se redujo de hipereutrófico a eutrófico. Concluimos que el banco de propágulos en lagos someros es esencial para el rápido restablecimiento de macrófitos sumergidos después de las estrategias de recuperación, ayudando a mejorar la calidad del agua.

[Palabras clave: macrófitos acuáticos sumergidos, banco de semillas, emergencia de plántulas, lagos someros subtropicales]

INTRODUCTION

Aquatic macrophytes play an important role in the functioning and maintenance of aquatic ecosystems (Chambers et al. 2008; Hilt et al. 2017). Particularly, in shallow lakes, ecosystem structure and water quality vary at different nutrient concentrations and water turbidity conditions (Scheffer et al. 1993). The development and dominance of submerged macrophytes in these ecosystems promotes clear waters, helps maintain mesotrophic and oligotrophic conditions, and causes the ecosystem to often reach a state of equilibrium (van Nes et al. 2003) typically described for temperate climates (Blindow et al. 1993; Scheffer et al. 2003, 2007). On the other hand, increase in nutrient loading causes changes in primary producers and alters the state of clear water, with submerged vegetation, to a turbid one, with intense growth of phytoplankton (Blindow et al. 2016). Phytoplankton algae proliferation promotes turbid water. It creates unfavorable conditions for the establishment of submerged macrophytes and inhibits their growth (Van den Berg et al. 1998). Many kinds of disturbance (e.g., eutrophication and drought) in aquatic ecosystems affect aquatic vegetation, often suppressing submerged vegetation and leading to phytoplankton development (McFarland and Schafer 2011). For tropical and subtropical regions, a further alternative state may occur, represented by the excessive proliferation of free-floating aquatic macrophytes that are favored by high nutrient concentrations and water stability (Meerhoff and Jeppesen 2009).

Shallow lakes are the most abundant and impacted freshwater ecosystems worldwide, primarily by eutrophication (Verpoorter et al. 2014). In recent decades, considerable efforts and financial resources have been devoted to the restoration of shallow lakes in many countries (Moss et al. 1997; Jeppesen et al. 2005). The success of long-term lake restoration critically depends on submerged macrophyte recovery (Hilt et al. 2006, 2018), a fact that highlights the importance of seed/propagule banks as a possible source of vegetation recovery (McFarland and Schafer 2011). These plants increase the transparency of the water, contribute to the maintenance of an oligotrophic state, and control the excessive growth of phytoplanktonic algae (Hilt et al. 2010). This action occurs by the reduction of particle resuspension (Barko and James 1998), by serving as a refuge for zooplankton-graz-

ing phytoplankton (Jeppesen et al. 1997), the production of allelopathic substances that inhibit algae growth (Gross et al. 2007), and the reduction of the amount of nutrients dissolved in the water (primarily phosphorus) through assimilation (Albertoni et al. 2014). According to Moss et al. (1996), the re-established of diverse plant communities promote a higher diversity of invertebrates, fishes and birds. Among the principles of the different methods of lake restoration it is to restore the maximum biological diversity, increasing the biological structure inside the lake (Moss et al. 1996). Several methods of lacustrine environment restoration have been developed. Among them is the removal of aquatic vegetation, including the free-floating macrophytes, and the control of phytoplankton biomass (Menon and Holland 2014).

Aquatic macrophytes can recolonize a given ecosystem through seeds and oospores, and some species can regenerate from vegetative fragments such as tubers, rhizomes, and turions (Xie et al. 2010). Genetic studies have shown that the method of recolonization, through vegetative fragments (tubers or turions), seeds, or oospores, is species-specific (Nilsson et al. 2010; Bornette and Puijalon 2011). The propagules present in the sediment of aquatic ecosystems can aid in lacustrine and riverine recovery processes after environmental perturbations, and knowledge about their composition can contribute to the development of suitable methods for the management and preservation of these environments (Nielsen et al. 2018).

Different methods are used to evaluate the composition of the sediment seed bank, including direct examination of either seed abundance (Grillas et al. 1993) or the emergence of seedlings from the germination process (Ozimek 2006; Aponte et al. 2010). Difficulties in developing these studies is due to the lack of taxonomic guides for identifying the seeds and seedlings of these environments, as well as a paucity of methods for aquatic ecosystems (Bakker et al. 2013). In this context, this research analyzed the response of the propagule bank of a shallow subtropical lake after management by the removal of free-floating macrophytes to reduce its hypertrophy, accompanying limnological variables of water quality and established species in field. During the follow-up of field restoration, we monitored the germination in the laboratory from the propagule bank.

Materials and Methods

Study area

This study was performed in a shallow subtropical lake (Lake Biguás), located at coastal plain of southern Brazil (central coordinates: 32°01′40′′ S - 52°01′40′′ W) (Figure 1). The climate is humid subtropical according to the classification of Köppen (Maluf 2000). The lake has an area of approximately 1.5 ha, and its depth does not exceed 2 m (Figure 1). It is polymictic, with no physical or chemical stratification of the water column due to wind action and the shallow depth (Trindade et al. 2009). In periods of extreme summers, the lack of rain leaves larges areas of the sediment exposed; these areas often flood with the return of the rainy season. Research related to aquatic macrophytes in this lake has involved primary productivity (Palma-Silva et al. 2008), associated macroinvertebrate fauna (Albertoni et al. 2007), macrophyte decomposition (Carvalho et al. 2015; Albertoni et al. 2018), and a survey of aquatic macrophytes (Pereira et al. 2012a).

Albertoni et al. (2014) observed periods of severe eutrophication in this ecosystem, with alternating development of phytoplankton and of the floating macrophytes *Pistia stratiotes* L. and *Salvinia herzogii* de la Sota, over a period of 13 years. Natural alterations in increased nutrients via excreta of birds sheltered in the central islands and anthropic alterations with buildings at their margin caused an increase in nutrient concentrations. This phenomenon leads to alternation in the dominant primary producers in the ecosystem. In periods of floating macrophyte dominance, there was suppression of submerged plants and phytoplankton (Albertoni et al. 2014).

As of 2012, degradation of the environment favored the growth of the floating species *S. herzogii*, which covered the whole lake during 2013 and the following 2 years and suppressed the submerged macrophytes. In July 2015, removal of the floating macrophytes (Figure 2a and 2b) was performed. This action allowed a return to the clear water state (Figure 2c and 2d) and favorable conditions for the reestablishment of the submerged vegetation. Before the removal, total phosphorus (TP) in the water column was 0.058 mg/L, and the chlorophyll-a concentration was 20.6 µg/L (mean values between January and June 2015). After removal (between July 2015 and February 2016), the mean values were 0.09 mg/L (TP) and 24.46 µg/L (chlorophyll-a concentration). During the first year of growth, the *S. herzogii* biomass reached 147.44 (±42.79) g DW/m^2, with a minimum of 97.94 and maximum value of 228.98 g DW/m^2 (Albertoni et al. 2014). This free-floating plant species has phosphorus values in tissue that ranges from 1.6 to 3.6 g/kg, and total N (TN) from 24.0 to 41.0 g/kg (Albertoni, unpublished data). According to these nutrient contents (and considering the total coverage of lake surface and the total removal of plants), we calculated that 2211.6 kg of *S. herzogii* were removed from the lake. According to the plant tissue P content, 5.75 kg of P and 30.2 kg of N were eliminated from the lake in this removal process.
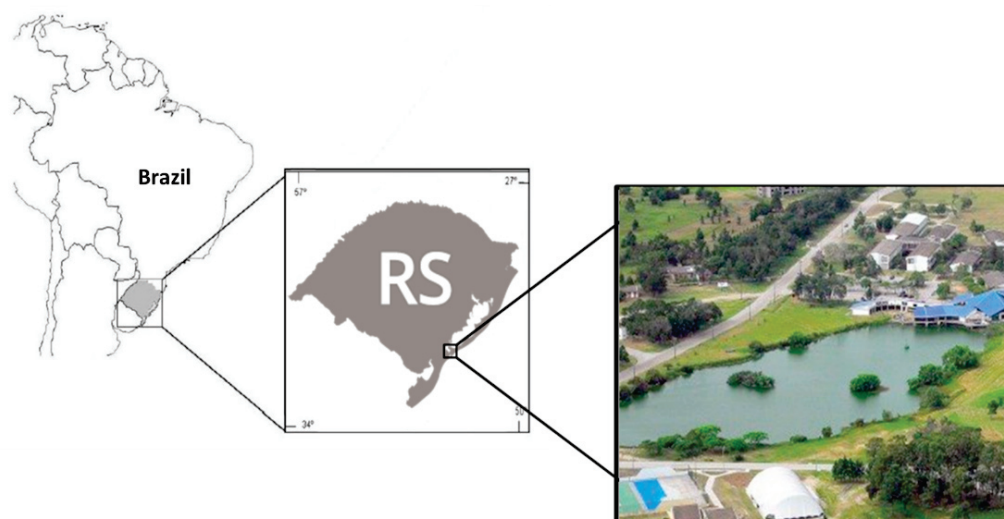

Figure 1. Location and image of the Lake Biguás in Southern Brazil.
Figura 1. Ubicación e imagen del Lago Biguás en el sur de Brasil.

Figure 2. Lake Biguás cleaning procedure, with the removal of the floating aquatic macrophyte *Salvinia herzogii* in the year 2015 (a and b) and after its removal in 2015 (c). Islands in the center of the lake with the presence of *Nannopterum brasilianus* ("Biguá": brazilian cormorant) in 2017 (d).

Figura 2. Procedimiento de limpieza del Lago Biguás, con la eliminación del macrófito acuático flotante *Salvinia herzogii* en el año 2015 (a y b) y después de su eliminación en 2015 (c). Islas en el centro del lago con la presencia de *Nannopterum brasilianus* ("Biguá": cormorán brasileño) en 2017 (d).

Sediment collection

We collected lake sediment in March 2016, at the end of the summer, approximately 8 months after the removal of floating macrophytes in 2015. Following the methods used by Grillas et al. (1993), Brock et al. (1994) and Aponte et al. (2010), we sampled 15 units of sediment in three linear transects from one shore of the lake to another. Along each transect, we distributed five points, which were signaled by a float and monitored monthly to assess the reestablishment of submerged vegetation. At each point, we collected approximately 1.6 kg of sediment with the Van Veen dredge (682 cm² area) and stored them in the dark and at the environmental temperature until they were used in laboratory germination experiments (Brock et al. 1994).

Water quality characterization

In the field, we assessed the abiotic characterization at the moment of the sediment sampling. Subsequently, we evaluated the following variables monthly: dissolved oxygen (DO, mg/L), water temperature (°C), pH, electric conductivity (EC, µS/cm) and turbidity (NTU), all obtained with Horiba®

multisensor. Additionally, we collected one water sample to determine TN (Kjedhal), TP (digestion and mass spectrometry), and chlorophyll-a in the laboratory, all of them according to the APHA (2012).

We used the chlorophyll-a and TP data to determine the trophic state index (TSI), proposed by Carlson (1977) for temperate lakes and modified by Cunha et al. (2013), adapted to tropical and subtropical values. In this work, we used the simple average of the chlorophyll-a values and TP in each sampling period. The TSI was determined using Equations 1-3 below:

$$TSI=[(TSI (TP)+ TSI (Chla)]/2 \qquad (1)$$

where TSI(TP) is the TSI based on TP content, calculated as:

$$TSI (TP)= 10[6- ((-0.27637 \ln TP + 1.329766)/\ln 2)] \qquad (2)$$

TSI(Chla) is the TSI based on the chlorophyll-a concentration.

$$TSI (Chla)= 10[6- ((-0.2512 \ln Chla + 0.842257)/ \ln 2)] \qquad (3)$$

We classified the trophic state according to categories: ultraoligotrophic (≤ 51.1), oligotrophic (between 51.2 and 53.1), mesotrophic (between 53.2 and 55.7), eutrophic (between 55.8 and 58.1), supereutrophic (between 58.2 and 59.0) and hypertrophic (≥ 59.1).

Emergence of seedlings in the laboratory

We quantified seedling emergence from the propagule bank by the seedling emergence method, according to Boedeltje et al. (2002) and adapted from Aponte et al. (2010). Prominent margins of this shallow lake eventually dry, and thus the sediment samples were air dried in the dark for 2 weeks. We placed sediment in plastic trays (20 cm × 30 cm × 6 cm), totaling 2.5 cm of sediment height per tray, distributed randomly in the incubation laboratory at room temperature (24-27 °C) with a 12-h light/12-h dark photoperiod, and maintained with lake water.

We monitored the emergence weekly for 7 months (between March and September 2016). We identified seedlings after germination or transferred them to larger plastic containers until identification. For the identification we used specialists help, and keys such as Forno (1983), and Gil and Bove (2007). We calculated the richness, abundance, frequency, and density (organisms/m^2) of the emerged seedlings.

Monitoring of macrophyte recovery in the field

We followed the vegetation growth in the field once a month, at the same points where we collected the sediment, between March and September of 2016. From a boat, we visually identified the species present in a 1 m^2 area around the sampled point. This proceeding was qualitative, and we aimed to compare the composition of species with those obtained in the laboratory experiment.

Data analysis

We calculated the relative abundance of species in the seed bank as the number of seedlings of a species divided by the total number of emerged seedlings (Aponte et al. 2010). This frequency represents the number of samples in which the species occurred. To compare the species composition between those that emerged from the laboratory and the vegetation reestablished in the field, we used the Sørensen similarity coefficient: $SO=2c/(a+b)$, where a is the number of species in the laboratory seedling, b is the

species in field monitoring, and c the number of species common to both (Combroux and Bornette 2004). We grouped the points in the margins, shallow sections with depths less than 0.60 m (sampling points 1, 5, 6, 10, 11, and 15) and the center, with depths greater than 0.60 m (sampling points 2, 3, 4, 7, 8, 9, 12, 13, and 14), and compared emergent plant densities from these points with an unpaired t-test. In addition, we compared the density of propagules at each point in the different transects of the lake with analysis of variance (ANOVA; data $\log(x+1)$ transformed).

RESULTS

The TSI ranged from 60.37 to 53.98. The major value in March classified Lake Biguás as hypereutrophic, and during the study period the lake showed mesotrophic (April to June) and eutrophic (July to September) water conditions. These values reflected the TP and chlorophyll-a concentration during the monitoring period, where the increased TP was not followed by an increase in phytoplankton (Figure 3). All measured abiotic variables, including nutrients, showed typical values of eutrophic ecosystems (Table 1).

Laboratory follow-up studies on propagule emergence resulted in 1382 seedlings, with a mean density of 1350.9 (±1065.3) seedlings/m^2. The number of emergences per sample ranged from 3 to 249. The total richness was eight species of aquatic macrophytes, belonging to seven genera, and distributed in six families (Table 2). Near the shore of the lake, P1 presented the greatest richness, with six species. On the other hand, the greatest abundance, 249 individuals, was in the central area (P7).

Two submerged macrophytes, *Stuckenia pectinata* (L.) Börner and *Chara zeylanica*, Klein ex Willd. dominated Lake Biguás seed bank, corresponding to 94% and 3% of the total germinated seedlings and reaching maximum densities of 3636 seeds/m^2 and 263 oospores/m^2, respectively. *Stuckenia pectinata* was the main constituent of the lake's propagule bank, being the most abundant in 14 of the 15 sampled points, totaling 1305 emerged seedlings. There was no significant difference in propagule density between the margin and the center points (t-test; df=13, *P*=0.08). There was no difference in seed density among transects (ANOVA; F=0.62, df=2, *P*=0.83).

In the field, we identified three macrophyte species: two submerged, *S. pectinata* and *C. zey-*

Table 1. Trophic state index (TSI) and mean values (±SD) (n=5) of the limnological variables in the Lake Biguás water column from March/2016 to September/2016. T: Temperature (°C); EC: Electric conductivity (µS/cm); Tu: Turbidity (NTU); DO: Dissolved oxygen (mg/L); TS: Total solids (g/L); Chl: Chlorophyll-a (µg/L); TN: Total nitrogen (mg/L); TP: Total phosphorus (µg/L).

Tabla 1. Índice de estado trófico (TSI) y valores medios (±DE) (n=5) de las variables limnológicas en la columna de agua del Lago Biguás de marzo/2016 a septiembre/2016. T: Temperatura (°C); EC: Conductividad eléctrica (µS/cm); Tu: Turbidez (NTU); DO: Oxígeno disuelto (mg/L); TS: Sólidos totales (g/L); Chl: Clorofila-a (µg/L); TN: Nitrógeno total (mg/L); TP: Fósforo total (µg/L).

|	March	April	May	June	July	August	September
Temp	25.3 (±0.5)	20.4 (±1.7)	17.5 (±0.06)	12.9 (±0.4)	19.9 (±0.27)	15.1 (±0.4)	17.3 (±0.5)
pH	8.06 (±0.32)	8.26 (±0.08)	8.51 (±0.36)	7.92 (±0.21)	7.05 (±0.55)	9.04 (±0.45)	9.07 (±0.56)
EC	0.25 (±0.02)	0.14 (±0.001)	0.15 (±0.007)	0.14 (±0.003)	0.06 (±0.002)	1.10 (±0.47)	0.28 (±0.11)
Tu	52.38 (±15.7)	28.70 (±3.62)	11.32 (±4.78)	17.08 (±7.24)	104.38 (±25.2)	31.03 (±3.39)	20.65 (±±4.07)
DO	11.34 (±0.71)	9.80 (±0.28)	9.41 (±0.23)	9.28 (±0.79)	6.12 (±0.78)	12.32 (±0.95)	9.26 (±0.67)
TS	0.16 (±0.016)	0.09 (±0.001)	0.09 (±0.006)	0.09 (±0.002)	0.03 (±0.002)	0.08 (±0.002)	0.03 (±0.01)
Chl	47.70 (±2.34)	13.60 (±0.71)	10.10 (±1.22)	3.80 (±0.59)	9.20 (±0.76)	13.60 (±1.91)	7.30 (±0.38)
TN	5.20 (±1.01)	2.97 (±0.26)	3.62 (±0.13)	3.45 (±1.08)	2.45 (±0.72)	2.70 (±0.45)	3.30 (±1.14)
TP	93 (±0.2)	93 (±0.001)	18 (±0.1)	32 (±0.3)	38 (±0.2)	52 (±0.7)	85 (±0.4)
TSI	60.37 (±2.87)	54.80 (±1.44)	55.41 (±0.97)	53.98 (±1.04)	56.21 (±0.79)	57.21 (±1.02)	56.78 (±0.89)
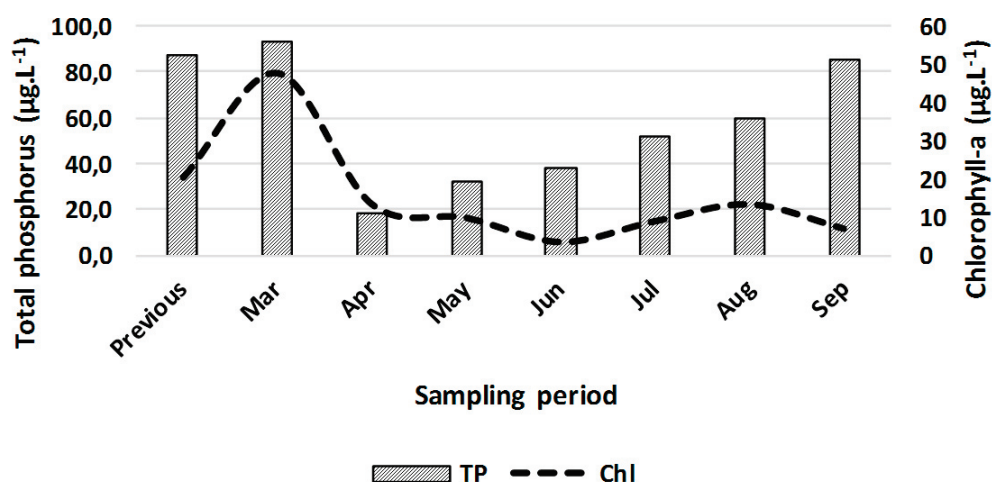
Figure 3. Variation of total phosphorus (TP) and chlorophyll-a (Chl) concentrations during the study period (March to September 2016) at Lake Biguás, Southern Brazil. Previous: Six months prior to field monitoring.

Figura 3. Variación de las concentraciones totales de fósforo (TP) y clorofila-a (Chl) durante el período de estudio (marzo a septiembre de 2016) en el Lago Biguás, en el sur de Brasil. Previous (=Anterior): Seis meses antes del monitoreo a campo.

Table 2. List of species and ecological groups of aquatic macrophytes found in the propagule bank of Lake Biguás. The frequency (%) represents the number of samples in which the species was present.

Tabla 2. Lista de especies y grupos ecológicos de macrófitos acuáticos encontrados en el banco de propágulos del Lago Biguás. La frecuencia (%) representa el número de muestras en las que estuvo presente la especie.

Family/Species	Ecological Group	Frequency (%)
Characeae - Charophyta		
Chara zeylanica Klein ex Willd.	Submerged	3.32
Menyanthaceae		
Nymphoides humboldtiana (L.) Kuntze	Rooted with floating leaves	0.21
Plantaginaceae		
Bacopa monnieri (L.) Pennel	Emerging/Amphibian	0.36
Mecardonia procumbens (Mill.) Small.	Amphibian	0.21
Polygonaceae		
Polygonum ferrugineum Weed.	Emerging/Amphibian	1.15
Potamogetonaceae		
Stuckenia pectinata (L.) Böerner	Submerged rooted	94.4
Cyperaceae		
Eleocharis viridans Kük. Ex Osten	Rooted emergent	0.07
Eleocharis obtusetrigona (Lindl. and Ness)	Rooted emergent	0.21

lanica, and an emergent/amphibious species, *Ludwigia peploides*. We found the submerged macrophyte *S. pectinata* in 14 of the 15 sampled points, except for P15. At P15, the macrophyte *C. zeylanica* was the only species recorded during all the field follow-ups. Both *C. zeylanica* and *L. peploides* were present in five sites, and the macroalgae had a larger register near the northwest of the lake (P6 and P11 to P15).

SO was 0.36, estimated as a result between the field survey over time and the plants that emerged in the laboratory. The propagule bank presented greater richness compared to the vegetation reestablished in the field, with eight and three species, respectively. *Stuckenia pectinata* and *C. zeylanica* occurred in both. The emergent/amphibian *L. peploides* occurred only in the field monitoring, while we observed the macrophytes *Bacopa monnieri* (L.) Pennell, *Nymphoides humboldtiana* (L.) Kuntze, *Eleocharis viridans* Kük. ex Osten, *Eleocharis obtusetrigona* (Lindl. and Ness) Steud., *Polygonum ferrugineum* Wedd. and *Mecardonia procumbens* (Mill.) Small only in the laboratory.

Discussion

Our results showed that even with the increase of the phosphorus values, the reestablishment of the submerged macrophytes kept the phytoplankton biomass at low levels and thus favored the maintenance of the clear water state in this small subtropical lake. Albertoni et al. (2007), Trindade et al. (2009), Pereira et al. (2012b) and Albertoni et al. (2014)

previously observed elevated nutrient levels for this lake. High phosphorus concentrations are one of the main factors responsible for the eutrophication of aquatic ecosystems (Bennett et al. 2001; Menon and Holland 2014), and the values found for this lake in previous studies have likely favored the growth of phytoplankton and aquatic macrophytes. Lu et al. (2018) observed the efficiency of nitrogen and phosphorus uptake by three aquatic macrophytes for mitigating different water quality conditions. In eutrophic environments, the effectiveness of excess nutrient removal by rooted submerged plants has been demonstrated (Verhofstad et al. 2017). The water quality history of the studied lake in the last years has shown an alternation among different states according to their dominant primary producer (Albertoni et al. 2014). Both the phytoplankton and free-floating macrophyte growth reduced water transparency (Meerhoff and Jeppesen 2009) and, consequently, prevented the growth of submerged macrophytes.

The removal of excessive floating vegetation is one strategy suggested for the recovery of submerged vegetation in tropical lakes (von Sperling 1997), although some authors state that the removal of free-floating macrophytes may not be effective for the restoration of submerged ones (van Zuidam et al. 2012). These authors stated that sediments from free-floating dominated ditches, in the Netherlands, had lower potential to recover diverse plant communities, probably from a positive feedback mechanism to maintain the predominance of free-floating vegetation. In 2015, this process

occurred in the studied lake to promote the reestablishment of submerged macrophytes, and our field monitoring showed that this management was effective.

In laboratory experiments, our results showed a low number of seedlings species when compared with another aquatic ecosystems, like temporary wetlands (e.g., Grillas et al. 1993), floodplains (e.g., Abernethy and Willby 1999), Chinese marshes (Liu et al. 2006), or ditches for navigation (e.g., Boedeltje 2003). For shallow lakes, our results were similar to reports from other ones (e.g., Ozimek 2006; Arthaud et al. 2012; Blindow 2016).

The emergence method is largely used for assessing the seed bank (McFarland and Schafer 2011) and much employed in works with restoration and monitoring of many aquatic systems (Boedeltje et al. 2003; Ozimek 2006; Arthaud et al. 2012; Ma et al. 2017). In aquatic ecosystems with periods of drought or with fluctuations in their water regime, the reestablishment of macrophyte communities depends on their emergence from a propagule bank to ensure their maintenance. Factors such as eutrophication and/or climate may influence the potential capability of propagule banks for recovery from the sediments in shallow lakes (Blindow et al. 2016). It can guarantee the survival of populations during periods in which conditions are unfavorable for their presence (Pedro et al. 2006; Bakker et al. 2013). In addition, restoration of eutrophic subtropical lakes through the removal of floating macrophytes and the reestablishment of submerged ones is an efficient method for combatting eutrophication symptoms, improving water quality, and balancing the ecosystem (Zeng et al. 2017).

Among the species that emerged in the laboratory, only one (*P. ferrugineum*) was mentioned in a previous survey of macrophytes conducted for this same lake (Pereira et al. 2012a). Other species, such as *N. humboldtiana (cited as Nymphoides indica)*, occurred in the early 2000s (Palma-Silva et al. 2008), and *S. pectinata* (synonym *Potamogeton pectinatus*) and *C. zeylanica* were cited in the years 2010 to 2012 by Carvalho et al. (2015) and Albertoni et al. (2018). This fluctuation in the register of the presence of different macrophytes is a reflection of the changes in relation to the predominance of different primary producers. These distinctions characterize their alternative states with periods of clear water (submerged plants), dominance of free-float-

ing macrophytes, and dominance of phytoplankton (Albertoni et al. 2014). The absence of differences among the regions of the lake suggests a homogeneous distribution of the propagule bank in the lake sediment. These results indicate that the distribution of the propagule bank is random and occurs evenly among the points of the lake, with no differences in either the depth or the region of the environment. The factors that may contribute to this homogeneous distribution are the small size (1.5 ha) and shallow depth (~2 m) of Lake Biguás, together with the intense wind performance that causes a polymictic circulation regime in this ecosystem (Trindade et al. 2009).

The results of field monitoring reflected the homogeneity found in the germination experiment in the laboratory, although with a lower number of species. The dominant species was *S. pectinata*. The genus *Potamogeton* has a wide distribution, and can be found in several environments with waters of different trophic states (Van Wijk 1988). It maintains its development and establishment in the ecosystem through vegetative propagules and seeds (Van Wijk 1988). *Stuckenia pectinata (*synonym *P. pectinatus*) is among the aquatic plant species that are the most frequently observed in the recolonization of shallow temperate lakes with reduced external nutritional load, and often dominate during the intermediate state of recovery (Hilt et al. 2018). This species is tolerant to high levels of salinity, alkalinity, and eutrophication (Bakker et al. 2013; Costa et al. 2018). These factors may explain its dominance in the propagule bank and its wide distribution in the field.

Charophytes are also excellent colonizers among aquatic macrophytes and are very important for the recolonization of different habitats (Van den Berg et al. 2001; Kalin and Smith 2007). Due to the high production of oospores by charophytes, these structures are very abundant in lake sediments (Grillas et al. 1993; Bonis and Grillas 2002), and this was probably the factor responsible for finding the species *C. zeylanica* to be the second most abundant in our samples. At shallow lakes in The Netherlands, Meijer et al. (1999) evaluated biomanipulation results and reported that submerged macrophytes alternated in dominance between *Chara* sp. and *Potamogeton* sp. These authors cited these two genera as the very rapid colonizers. According to Hilt et al. (2018), after management of restauration in shallow lakes, there were only one or two dominant species.

We observed in the field that the *C. zeylanica* stand was located in a specific region of the lake. We also observed in the laboratory that there was reduced *S. pectinata* germination when it germinated with *C. zeylanica*. These results could suggest some evidence of competition between these two species as has been also found by a study with several species of these genera in shallow lakes (Blindow 1992; Coops and Doef 1996; Van den Berg et al. 1998, 2001, 2002). These authors observed that these species compete for resources, including light, dissolved organic carbon, bicarbonate, phosphorus, and nitrogen, among others. The availability of these resources may influence the growth and development of a species. Hidding et al. (2010) observed that short-term competition for bicarbonate between *Chara* and *Stuckenia* limited the growth of *Stuckenia*. Van den Berg et al. (1998) studied the competition between *Chara aspera* and *P. pectinatus* (currently *S. pectinata*) and concluded that the submerged macrophyte *Potamogeton* was favored when there was a greater incidence of light.

As soon as the lake recovered the conditions of lighting of the water column, demonstrated by the low phytoplankton biomass, the propagules of the submerged macrophytes found favorable conditions suitable for growth. This condition favored the maintenance of clear water, the main condition required for macrophytes to germinate and grow (Bakker et al. 2013). As nutrients remain in high concentrations (meso to eutrophic), species more adapted to these conditions might be more successful (Hilt et al. 2006), such as *P. pectinatus* (Costa et al. 2018) and probably *L. peploides* (emergent). The Sørensen similarity (36%) between laboratory and field species confirmed the importance of propagule bank to recovery of macrophytes in shallow lakes, but it also showed that the success of each species depends on many biotic and abiotic factors. Even at degraded lakes, the seed banks are capable of a response after restoration measures, but the response depends on previous colonizers and may last for different periods (years or decades) for emerging seedlings (Verhofstad et al. 2017). The composition of the diaspore reservoir may be substantially different from the actual vegetation. (Blindow et al. 2016), and many factors might underlie this difference, like herbivory by birds and fishes (Moss et al. 1997), plant competition for nutrient and light (Hidding et al. 2010; Bakker et al. 2013),

light incidence, temperature (Bonis and Grillas 2002), and sediment redox conditions (Kalin and Smith 2007).

Light intensity acts as a trigger for propagule germination (Ozimek 2006). The management procedure of removing the floating macrophytes in Lake Biguás promoted the reestablishment of the submerged macrophytes. The presence of *S. pectinata* and *C. zeylanica* in the field demonstrated the potential of the propagules in the lake sediment to restore clear waters even with high nutrient values in the water column. The development of the emergence experiment in the laboratory and simultaneous monitoring in the field (even for a short period of time) allowed the visualization of the importance of the seed bank and the potentiality for restoration of clear waters in shallow lakes.

Most methods for restoring shallow lakes have been developed for temperate lakes. However, differences in processes between these and tropical and subtropical lakes underscore the importance of biological interactions and long growing seasons as factors for rethinking restoration strategies. (Jeppesen et al. 2007). Future research should seek details on the composition and viability of the seed bank. These findings could contribute to the management and restoration of subtropical shallow lakes. The utilized recovery procedures were effective for favoring the recolonization of the submerged macrophytes from the seed bank present in the sediment, because the lighting conditions in the water column allowed the germination and growth of the submerged plants. However, restoration strategies are only effective with the interruption or significant decrease of phosphorus input to the ecosystem. In the case of the studied lake, the period of clear water and development of submerged macrophytes lasted for 2 years, until middle 2017. Until July 2017, chlorophyll-a values were 0.54 µg/L, and phosphorous values increased up to 370 µg/L. Due to the increase in bird nests in the central islands, and the continuity of nutrient input, a new turbid water state occurred, with extensive growth of phytoplankton. Data from routine monitoring of Lake Biguás reported values of 530 µg/L and 184 µg/L during 2018, and, in August 2019, 944.9 and 456.8 µg/L TP and chlorophyll-a, respectively (Albertoni et al, unpublished data). These values characterize ecosystem hypertrophy.

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