





Environmental predictors of charophytes in a subtropical reservoir

Preditores ambientais de carófitas em um reservatório subtropical

Thamis Meurer¹ , Roger Paulo Mormul¹  and Norma Catarina Bueno^{2*} 

¹Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá – UEM, Av. Colombo 5790, Bloco H-90, CEP 87020-900, Maringá, PR, Brasil

²Programa de Pós-graduação em Conservação e Manejo de Recursos Naturais, Universidade Estadual do Oeste do Paraná – UNIOESTE, Rua Universitária, 2019, Jardim Universitário, CEP 85819-110, Cascavel, PR, Brasil

*e-mail: normacatarina@hotmail.com

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Abstract: Aim: In this study we check whether three simple environmental factors are good predictors of charophytes occurrence. **Methods:** The Characeae material was sampled two times a year during the years of 2001, 2002 and 2003, over 235 sites distributed along eight rivers located in Itaipu, a large subtropical reservoir. While sampling the biological material, the measurement of environmental descriptors pointed out as the most important variables predicting the occurrence of submerged macrophytes were simultaneously taken. At each sampling site, using a four meter long pipe rake, the presence and absence of Charophytes were recorded, the biological material was sampled and fixed to posterior identification in laboratory following specialized literature, and measurements of the electrical conductivity, Secchi depth and the effective fetch were taken. **Results:** A total of 13 species, belonging to the genus *Chara* and *Nitella*, were identified. An increase of the charophytes frequency towards the dam was found, which may reflect the gradient of sedimentation and reduction of the inputs of solids and nutrients, leading to a higher underwater transparency, a suitable condition to the development of submerged macrophytes. The genus *Nitella* occurred in all rivers and was more frequent than the genus *Chara*. Regarding the effect of electrical conductivity over the charophytes, the frequency of the genus *Chara* was found to be affected by this variable, while the effective fetch, variable that indicates wave disturbance, affected genus *Nitella*. **Conclusions:** The water transparency, related with Secchi depth, was the best predictor for the charophytes occurrence, agreeing with the distribution pattern of other submerged macrophytes of this large subtropical Reservoir.

Keywords: aquatic macrophyte; Brazil; *Chara*; Itaipu reservoir; *Nitella*.

Resumo: Objetivo: Neste estudo, verificamos se três simples fatores ambientais são bons preditores de ocorrência de carófitas. **Métodos:** O material de Characeae foi amostrado duas vezes ao ano, durante os anos de 2001, 2002 e 2003, em 235 locais distribuídos ao longo de oito rios localizados em Itaipu, um grande reservatório subtropical. Simultaneamente à coleta do material biológico, medidas de descritores ambientais apontados como os preditores mais importantes para a ocorrência de macrófitas submersas foram aferidos. Em cada local de amostragem, usando um garfo coletor de 4 metros de comprimento, a presença e ausência dos carófitos foi registrada. O material biológico coletado foi fixado para posterior identificação em laboratório seguindo literatura especializada, e medidas da condutividade elétrica, profundidade de Secchi e fetch efetivo foram tomadas. **Resultados:** Um total de 13 espécies, pertencentes aos gêneros *Chara* e *Nitella*, foram identificadas. Um aumento na frequência dos carófitos foi encontrado em relação à distância da barragem, o que pode refletir o gradiente de sedimentação e redução da entrada de sólidos e nutrientes, levando a uma maior



transparência subaquática, uma condição apropriada para o desenvolvimento de espécies submersas. O gênero *Nitella* ocorreu em todos os rios e foi mais frequente que o gênero *Chara*. Com respeito ao efeito da condutividade elétrica sobre os carófitos, a frequência do gênero *Chara* foi mais afetada por esta variável, enquanto o fetch efetivo, variável relacionada ao distúrbio das ondas, afetou o gênero *Nitella*. **Conclusões:** A transparência da água, relacionada à profundidade do Secchi, foi o melhor preditor da ocorrência dos carófitos, concordando com a distribuição de outras macrófitas submersas deste grande reservatório subtropical.

Palavras-chave: macrófita aquática; Brazil; *Chara*; reservatório artificial; *Nitella*.

1. Introduction

The aquatic macrophytes of the family Characeae (known as stoneworts), found on every continent (except Antarctica), constitute a group of algae that colonize fresh and brackish water ecosystems and are considered the closest living relatives of the lineage that originated land plants (Karol et al., 2001; Soulié-Märsche, 2008). Charophytes are rapid colonizers that have the potential of strongly compete with angiosperms in clear water, what can be related with the formation of dense macrophyte beds (Van den Berg et al., 1999) and with its ability of acting as nutrient sink, such as bicarbonate and phosphorus (Kufel & Ozimek, 1994; Kufel & Kufel, 2002; Hidding et al., 2010). These attributes make the charophytes an important component to keep the environment in clear water state, affecting environmental variables and limiting also phytoplankton growth (Van den Berg et al., 1998).

On the other hand, the importance of environmental factors on the distribution and composition of particular species of aquatic macrophyte assemblages has been suggested in several studies (e.g. Van den Berg et al., 1999; Thomaz et al., 2003; Sousa et al., 2009). For example, exposure to wave disturbances caused by wind has been considered an important factor regulating macrophytes in tropical and subtropical environments, constraining their colonization and expansion (Doyle, 2001; Azza et al., 2007; Thomaz et al., 2012). More specifically, several studies show the importance of nutrient availability in the water column to charophytes success and suggest that charophytes decline may be related to eutrophication (Kłosowski et al., 2006; Cirujano et al., 2007; Lambert & Davy, 2011). Such environmental condition could affect direct and indirectly this assemblage due to changes in water characteristics other than nutrients, such as water transparency, which is one of the most important conditions for the establishment of submersed plants (Blindow, 1992; Van den Berg et al.,

1998; Steinman et al., 2002). The establishment of charophytes are also affected by connectivity between environments (Bornette & Arens, 2002), fluctuations in water level (Casanova, 1994; Havens et al., 2004), substrate type and depth (Torn et al., 2004).

Considering physical and chemical environmental characteristics, the former is suggested to be more important to determine species richness and diversity of charophytes, but it could not affect species composition (Makkay et al., 2008). In subtropical lentic environments, radiation seems to be a strong regulator of the charophytes community, increasing its effects during periods of low water level (Steinman et al., 1997, 2002). Under these conditions the region near the substrate becomes more adequate for their growth with a rapid germination response in relation to other submerged plants (Harwell & Havens, 2003), specially in regions less exposed to wind (Havens et al., 2004).

Identifying environmental factors that could potentially be used as predictors of the composition of aquatic macrophyte assemblage may be important in determining the suitable conditions for different species (Scheffer et al., 1992; Barendregt & Bio, 2003; Van den Berg et al., 2003). However, despite the general importance of macrophytes in maintenance of clear water state (Blindow et al., 2002) and its effects on the interaction between fish and invertebrates (Perrow et al., 1999), nearly all of the published research about the charophytes is based on investigations from temperate regions (Steinman et al., 2002), what may bias the main conclusions regarding the ecology of this specific group in tropical and subtropical regions. Thus, in this study we used data from a large subtropical reservoir obtained during a three years sampling to address a single question: could simple environmental data predict the occurrence of charophytes of the genera *Chara* and *Nitella*?

2. Material and Methods

2.1. Study area

The study was carried out on the Brazilian side of the Itaipu Reservoir, formed on the Paraná River (24°05'S – 25°33'S; 54°00'W – 54°37'W) in 1982, close to the border of Brazil and Paraguay. It has an area of 1350 km² in the normal operation water level (ca. 219.9 m above sea level) and length of about 130 km. The water has an estimated residence time of ca 40 days, and according to nutrient concentrations, the central body of the reservoir is mesotrophic, while the tributaries along the eastern shore may be oligo to eutrophic (Bini et al., 1999).

2.2. Data sampling

Charophyte material was sampled twice a year during 2001, 2002 and 2003. We sampled 235 georeferenced sites distributed over the eight main tributaries in the Brazilian side of the Itaipu Reservoir (approximately 30 sites per tributary): Arroio Guaçu River (AG), São Francisco Verdadeiro River (SFV), São Francisco Falso River (SFF), São Vicente River (SV), São João River (SJ), Ocoí River (OC), Pinto River (RP) and Passo Cuê River (PC) (Figure 1). In each sampling site we stopped the boat and scrapped the sediment using a rake in a 4 m long pipe to record presence/absence of charophytes,

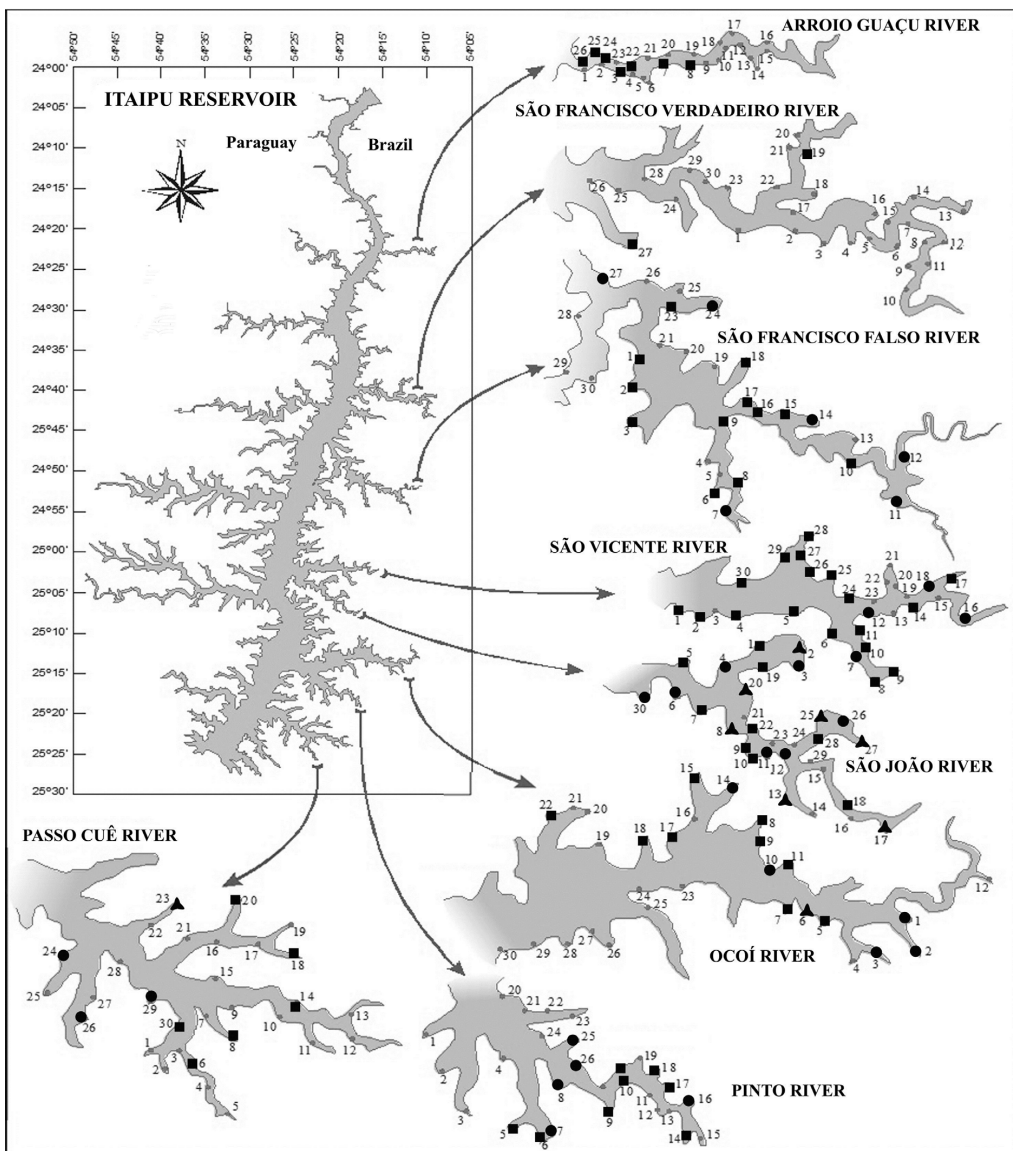


Figure 1. Map of the Itaipu reservoir indicating the sampling points and presence of *Chara* sp., *Nitella* sp. or both. Where: ■ *Nitella*; ▲ *Chara*; ● “Co-occurrence”. Numbers in the tributaries indicate the sampling sites. Modified from Thomaz et al. (2009).

which were preserved for later identification in laboratory following the classification of Krause (1997). Itaipú Reservoir sustain a high diversity of charophytes, with 13 species of *Chara* and *Nitella* (Meurer & Bueno, 2012). However, the occurrence of each particular species in Itaipu reservoir is relatively rare, and the analyses of the genera was proved to be more appropriate. Then, the frequency of occurrence of each genus was considered as the relative frequency to the total samples obtained per tributary. In addition, during the survey, electrical conductivity (e.g. Sousa et al., 2009), Secchi depth and fetch (e.g. Mormul et al., 2010), were measured at each site and considered as potential predictors of submerged aquatic vegetation. Fetch is considered here as the potential to wave disturbance. The greater the fetch the greater can be the wind energy exerted on the water surface to create waves, which in turn, can reaches the shoreline of the reservoir and affect macrophyte distribution along the littoral area. Also, we assessed fetch using the effective fetch (not corrected for wind speed; see details on effective fetch in Bini & Thomaz, 2005).

2.3. Data analyses

Environmental variables were considered as the response variables to verify spatial patterns among reservoir tributaries using Kruskal-Wallis test and Multiple Comparison Z-value test as post-hoc test. In addition, we applied logistic regression taking conductivity, Secchi depth and fetch as predictors of probability of occurrences of *Chara* and *Nitella*. To the logistic regression data reached the analysis assumptions. Data analyses were performed using the software STATISTICA 7.0 and SAM v4.0 considering values of $p < 0.05$ as significant results.

3. Results

The mean values of electrical conductivity ranged from 44.8 to 56.1 $\mu\text{S}\cdot\text{cm}^{-1}$ (Figure 2A). The tributaries differed in relation to conductivity (Kruskal-Wallis: $H_{(7; 235)}=131.4$; $p < 0.001$), and Passo Cuê River was statistically different from all other tributaries, except from São João River. The mean values of Secchi depth ranged from 0.92 m to 2.11 m (Figure 2B), and tributaries differed

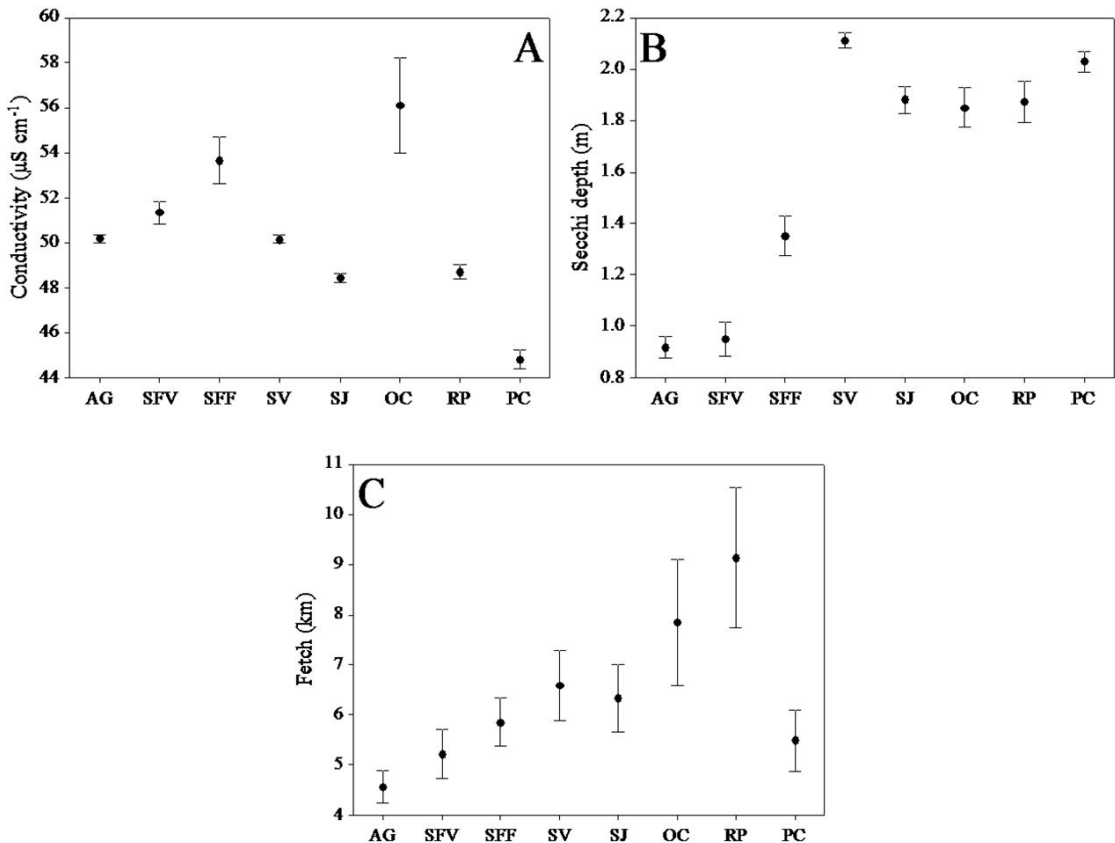


Figure 2. Mean and standard error for conductivity (A), Secchi depth (B) and fetch (C) in each reservoir tributaries. AG = Arroio Guaçu; SFV = São Francisco Verdadeiro; SFF = São Francisco Falso; SV = São Vicente; SJ = São João; OC = Ocoí; RP = Rio Pinto; PC = Passo Cuê.

significantly for this variable (Kruskal-Wallis: $H_{(7; 235)}=141.8$; $p < 0.001$); Arroio Guaçu River, São Francisco Verdadeiro River and São Francisco Falso River had the lowest values for Secchi and were statistically similar to each other, but different from all others. Fetch values ranged from 4.56 (at Arroio Guaçu River) to 8.94 km (at Pinto River) and were not significantly different among tributaries (Figure 2C; Kruskal-Wallis: $H_{(7; 235)}=9.7$; $p=0.2$).

The genus *Nitella* occurred in all tributaries and was the most frequent genus (Figure 3, mean frequencies of 45% for *Nitella* and 19% for *Chara*). *Nitella* showed the lowest frequency of occurrence at São Francisco Verdadeiro River (< 10%), and the highest at São Vicente River (> 70%). *Chara* was absent at Arroio Guaçu River and São Francisco Verdadeiro River, and its frequency of occurrence

varied approximately from 13% at Passo Cuê River to 50% at São João River (Figure 3). At the São João, Ocoí and Passo Cuê River, *Chara* occurred in sampling stations where *Nitella* was not recorded, whereas at São Francisco Falso, São Vicente and Pinto River, *Chara* co-occurred with *Nitella* in all sampling stations (Figure 3).

Logistic regression showed that the probability of occurrence of both genera was not affected by conductivity values (Figure 4A; Table 1). Light availability positively affected the probability of occurrence of *Chara* and *Nitella*, but more strongly the latter one (Figure 4B; Table 1). Finally, the probability of occurrence of *Chara* was not affected by fetch values, while the occurrence of *Nitella* was negatively influenced by this predictor variable related to wind effect (Figure 4C; Table 1).

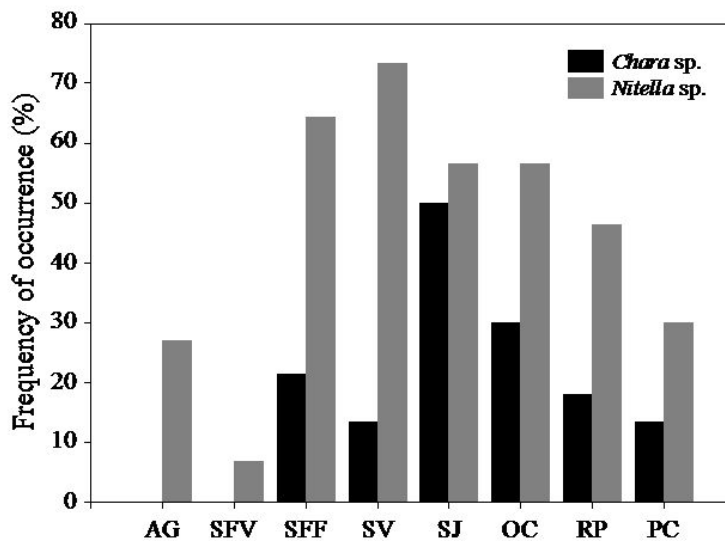


Figure 3. Frequency of occurrence of *Chara* sp. and *Nitella* sp. in each tributary of the Itaipu reservoir. AG = Arroio Guaçu; SFV = São Francisco Verdadeiro; SFF = São Francisco Falso; SV = São Vicente; SJ = São João; OC = Ocoí; RP = Rio Pinto; PC = Passo Cuê.

Table 1. Results of the logistic regression using the presence of *Chara* sp. and *Nitella* sp. as dependent variables and conductivity, Secchi disk and fetch (km) as predictors.

	Estimate	χ^2	p	Odds ratio	McFadden's ρ^2
Conductivity					
<i>Chara</i> sp.	-3.752	3.07	0.07	1.04	0.013
<i>Nitella</i> sp.	-1.847	1.97	0.15	1.03	0.006
Secchi depth					
<i>Chara</i> sp.	-2.585	4.039	0.04*	1.91	0.018
<i>Nitella</i> sp.	-1.742	14.103	<0.01*	2.55	0.044
Fetch					
<i>Chara</i> sp.	-1.171	1.522	0.21	0.95	0.007
<i>Nitella</i> sp.	0.319	6.712	<0.01*	0.92	0.021

*Significant results McFadden's ρ^2 estimates the proportion of variation explained by a logistic regression model. The odds ratio tests the odds of genera occurrence according to conductivity, Secchi and fetch. χ^2 is the comparison between the observed distribution to a theoretical one. p = the probability of obtaining test results at least as extreme as the results actually observed.

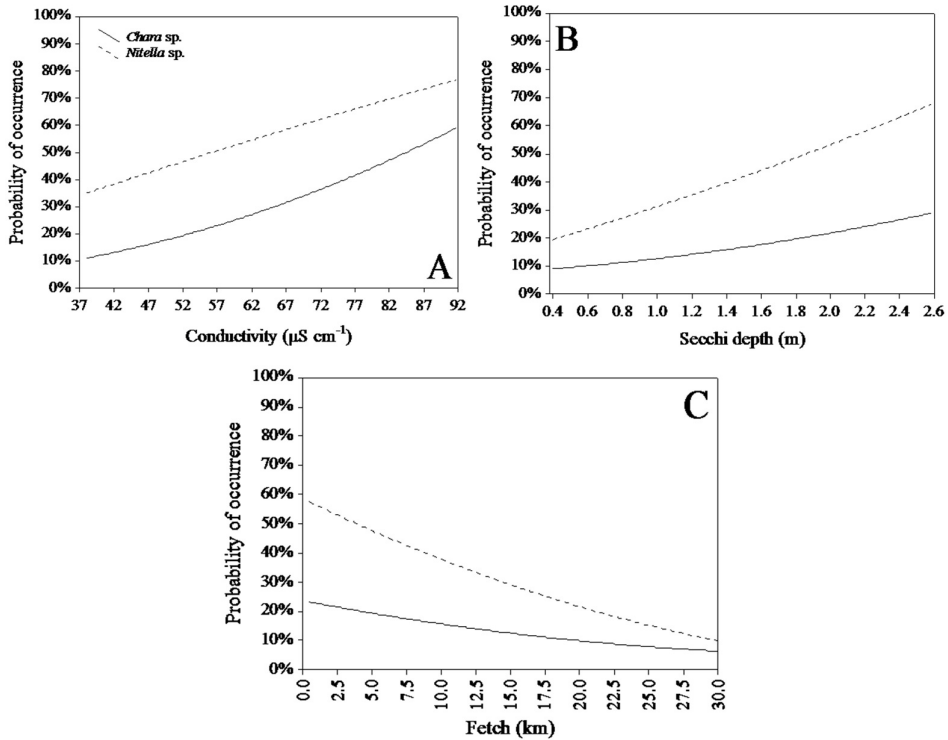


Figure 4. Probability of occurrence of *Chara* sp. and *Nitella* sp. by conductivity (A), Secchi depth (B) and fetch (C) considering the whole reservoir.

4. Discussion

Itaipu reservoir presents differences in the species composition of aquatic macrophytes among the main tributaries along the main axis of the reservoir with dominance of free floating species closer to the riverine zone and submerged species from the middle portion down to the dam (Mormul et al., 2010). These differences in vegetation observed in the tributaries may reveal a pattern of organization that reflects the gradient of reduction of sedimentation and inputs of solids and nutrients toward to the dam in the main axis of the reservoir (Pagioro & Thomaz, 2002). Similarly, we found an increase of frequency of charophytes towards to the dam, in tributaries with better environmental conditions to development of submerged species, such as higher underwater transparency. Conductivity, light attenuation coefficient and fetch have been pointed out as the most important variables predicting the occurrence of the angiosperm *Egeria najas* in Itaipu reservoir (Bini & Thomaz, 2005). Although marginally, our findings also suggest that conductivity affect the frequency of occurrence of *Chara* more than *Nitella*. The potential explanation for this pattern is that conductivity may indicate the amount of nutrients and inorganic carbon that

is used in photosynthetic processes of charophytes, which has distinct preferences in the use of different carbon sources (Vieira Junior & Necchi Junior, 2003, 2006). In addition, the increased availability of inorganic carbon could contribute to charophytes to outcompete submerged angiosperms (Van den Berg et al., 2002). Also, *Chara* is effective in use HCO_3^- , usually forming CaCO_3 encrustations on the thalli (Pełechaty et al., 2013), and both compounds are available under high conductivity. It is worth noting that the relationship between *Nitella* and conductivity is similar to *Chara*, and perhaps was not significant due to a slight data variation. Secchi depth was positively correlated to the presence of *Chara* and *Nitella*, suggesting that charophytes tend to be more frequent in clearer waters. In fact, light availability is a limiting factor for charophytes (Rip et al., 2006), which are negatively related with turbidity (Van den Berg et al., 2002). Moreover, increased light availability provides a favorable habitat for oospores germination, establishment and maintenance of charophytes (Winton et al., 2004). In addition, we also observed that although the highest frequency of both genera were recorded in clearer water tributaries, only *Nitella* occurred in all rivers, including those with predominance of floating macrophytes,

eutrophic conditions, frequent algal blooms, and therefore reduced underwater light. Charophytes present a range of light compensation point for photosynthesis from 1 to 7 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Van et al., 1976; Andrews et al., 1984; Schwarz et al., 1996; Vieira Junior & Necchi Junior, 2003) and ability to cope with low light levels (Chambers & Kaiff, 1985), what can enable species to growth in habitats such as Arroio Guaçu and São Francisco Verdadeiro tributaries, which had predominance of floating macrophytes and reduced underwater light. Finally, these findings may suggest that *Nitella* could be more tolerant to low light availability than *Chara*, which was better predicted by secchi depth than *Nitella*. As a potential surrogate of the wave action created by wind, fetch affected negatively only the occurrence of *Nitella* in our study, while affected also submerged angiosperms in other studies in the same place (e.g. Thomaz et al., 2003; Bini & Thomaz, 2005). This negative relationship may be related mainly to light availability, but the mechanism may occur in opposite ways. First, after colonization of charophytes, sediment resuspension may be reduced and sediment rates increased by charophytes growth (Van den Berg et al., 1998) maintaining water clearer. Or second, fetch may prevent the colonization of charophytes due to the reduction of light availability by increase turbidity with sediment resuspension (Istvánovics et al., 2008). In addition, wave action may prevent charophytes colonization by producing hydraulic forces that uproot propagules (Schutten et al., 2005). More specifically, the negative relationship between fetch and frequency only for *Nitella*, could be due to the fact that *Chara* has a potentially stronger anchoring system, even without strengthening tissue (Schutten et al., 2005), leading to more tolerance to wind exposure and no relationship with fetch.

5. Conclusions

Overall our study showed that the distribution of the charophytes are similar to the distribution pattern of other submerged macrophyte in Itaipu Reservoir (Thomaz et al., 2009; Mormul et al., 2010), and simple environmental factors can be used as predictors of charophytes occurrence. Water transparency was the variable that most affected the occurrence of the study group, confirming previous investigations that demonstrated it as one of the factors that contribute greatly to the establishment of these community (Van den Berg et al., 2003). In a nutshell, considering our results obtained in an artificial freshwater environment, we suggest that our simple environmental predictors should be

applied as a main key of prediction of occurrence of these genera in reservoir monitoring programs. In addition, we suggest that studies of other factors that potentially influence the establishment, maintenance and germination of charophytes, as well as biotic interactions, should be measured and used together with our predictors to better understand the dynamics of these macroalgae in reservoirs.

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References

- ANDREWS, M., MCINROY, S. and RAVEN, J.A. Culture of *Chara hispida*. *British Phycological Journal*, 1984, 19(3), 277-280. <http://dx.doi.org/10.1080/00071618400650291>.
- AZZA, N., VAN DE KOPPEL, J., DENNY, P. and KANSIIME, F. Shoreline vegetation distribution in relation to wave exposure and bay characteristics in a tropical great lake, Lake Victoria. *Journal of Tropical Ecology*, 2007, 23(3), 353-360. <http://dx.doi.org/10.1017/S0266467407004117>.
- BARENDREGT, A. and BIO, A.M.F. Relevant variables to predict macrophyte communities in running waters. *Ecological Modelling*, 2003, 160(3), 205-217. [http://dx.doi.org/10.1016/S0304-3800\(02\)00254-5](http://dx.doi.org/10.1016/S0304-3800(02)00254-5).
- BINI, L.M. and THOMAZ, S.M. Prediction of *Egeria najas* and *Egeria densa* occurrence in a large subtropical reservoir (Itaipu Reservoir, Brazil-Paraguay). *Aquatic Botany*, 2005, 83(3), 227-238. <http://dx.doi.org/10.1016/j.aquabot.2005.06.010>.
- BINI, L.M., THOMAZ, S.M., MURPHY, K.J. and CAMARGO, A.F.M. Aquatic macrophyte distribution in relation to water and sediment conditions in the Itaipu Reservoir, Brazil. *Hydrobiologia*, 1999, 415, 147-154. <http://dx.doi.org/10.1023/A:1003856629837>.
- BLINDOW, I. Decline of charophytes during eutrophication: comparison with angiosperms. *Freshwater Biology*, 1992, 28(1), 9-14. <http://dx.doi.org/10.1111/j.1365-2427.1992.tb00557.x>.
- BLINDOW, I., HARGEBY, A. and ANDERSSON, G. HARGEBY, A. and ANDERSSON, G. Seasonal changes of mechanisms maintaining clear water in a shallow lake with abundant *Chara* vegetation. *Aquatic Botany*, 2002, 72(3-4), 315-334. [http://dx.doi.org/10.1016/S0304-3770\(01\)00208-X](http://dx.doi.org/10.1016/S0304-3770(01)00208-X).
- BORNETTE, G. and ARENS, M.F. Charophyte communities in cut-off river channels: The role of connectivity. *Aquatic Botany*, 2002, 73(2), 149-162. [http://dx.doi.org/10.1016/S0304-3770\(02\)00017-7](http://dx.doi.org/10.1016/S0304-3770(02)00017-7).

- CASANOVA, M. Vegetative and Reproductive Responses of Charophytes to Water-level Fluctuations in Permanent and Temporary Wetlands in Australia. *Australian Journal of Marine and Freshwater Research*, 1994, 45(8), 1409-1419. <http://dx.doi.org/10.1071/MF9941409>.
- CHAMBERS, P.A. and KAIFF, J. Depth distribution and biomass of submersed aquatic plant communities in relation to Secchi depth. *Canadian Journal of Fisheries and Aquatic Sciences*, 1985, 42(4), 701-709. <http://dx.doi.org/10.1139/f85-090>.
- CIRUJANO, S., CAMBRA, J., SÁNCHEZ CASTILLO, P.M., MECO, A. and FLOR ARNAU, N. *Flora ibérica: algas continentales: carófitos (Characeae)*. Madrid: Real Jardín Botánico, 2007.
- DOYLE, R.D. Effects of waves on the early growth of *Vallisneria americana*. *Freshwater Biology*, 2001, 46(3), 389-397. <http://dx.doi.org/10.1046/j.1365-2427.2001.00668.x>.
- HARWELL, M.C. and HAVENS, K.E. Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. *Aquatic Botany*, 2003, 77(2), 135-151. [http://dx.doi.org/10.1016/S0304-3770\(03\)00101-3](http://dx.doi.org/10.1016/S0304-3770(03)00101-3).
- HAVENS, K.E., SHARFSTEIN, B., BRADY, M.A., EAST, T.L., HARWELL, M.C., MAKI, R.P. and RODUSKY, A.J. Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. *Aquatic Botany*, 2004, 78(1), 67-82. <http://dx.doi.org/10.1016/j.aquabot.2003.09.005>.
- HIDDING, B., BREDERVELD, R.J. and NOLET, B.A. How a bottom-dweller beats the canopy: inhibition of an aquatic weed (*Potamogeton pectinatus*) by macroalgae (*Chara* spp.). *Freshwater Biology*, 2010, 55, 1758-1768. <http://dx.doi.org/10.1111/j.1365-2427.2010.02409.x>.
- ISTVÁNOVICS, V., HONTI, M., KOVÁCS, A. and OSZTOICS, A. Distribution of submerged macrophytes along environmental gradients in large, shallow Lake Balaton (Hungary). *Aquatic Botany*, 2008, 88(4), 317-330. <http://dx.doi.org/10.1016/j.aquabot.2007.12.008>.
- KAROL, K.G., MCCOURT, R.M., CIMINO, M.T. and DELWICHE, C.F. The closest living relatives of land plants. *Science*, 2001, 294(5550), 2351-2353. <http://dx.doi.org/10.1126/science.1065156>. PMID:11743201.
- KŁOSOWSKI, S., TOMASZEWICZ, G.H. and TOMASZEWICZ, H. The expansion and decline of charophyte communities in lakes within the Sejny Lake District (north-eastern Poland) and changes in water chemistry. *Limnologica*, 2006, 36(4), 234-240. <http://dx.doi.org/10.1016/j.limno.2006.07.001>.
- KRAUSE, W. *Charales (Charophyceae): süßwasserflora von Mitteleuropa*. Stuttgart: Gustav Fischer Verlag, 1997. vol. 18.
- KUFEL, L. and KUFEL, I. *Chara* beds acting as nutrient sinks in shallow lakes: a review. *Aquatic Botany*, 2002, 72(3-4), 249-260. [http://dx.doi.org/10.1016/S0304-3770\(01\)00204-2](http://dx.doi.org/10.1016/S0304-3770(01)00204-2).
- KUFEL, L. and OZIMEK, T. Can *Chara* control phosphorus cycling in Lake Luknajno (Poland)? *Hydrobiologia*, 1994, 275/276(1), 277-283. <http://dx.doi.org/10.1007/BF00026718>.
- LAMBERT, S.J. and DAVY, A.J. Water quality as a threat to aquatic plants: discriminating between the effects of nitrate, phosphate, boron and heavy metals on charophytes. *The New Phytologist*, 2011, 189(4), 1051-1059. <http://dx.doi.org/10.1111/j.1469-8137.2010.03543.x>. PMID:21087261.
- MAKKAY, K., PICK, F.R. and GILLESPIE, L. Predicting diversity versus community composition of aquatic plants at the river scale. *Aquatic Botany*, 2008, 88(4), 338-346. <http://dx.doi.org/10.1016/j.aquabot.2007.12.011>.
- MEURER, T. and BUENO, N.C. The genera *Chara* and *Nitella* (Chlorophyta, Characeae) in the subtropical Itaipu Reservoir, Brazil. *Brazilian Journal of Botany*, 2012, 35(2), 219-232. <http://dx.doi.org/10.1590/S1806-99592012000200009>.
- MORMUL, R.P., FERREIRA, F.A., MICHELAN, T.S., CARVALHO, P., SILVEIRA, M.J. and THOMAZ, S.M. Aquatic macrophytes in the large, sub-tropical Itaipu Reservoir, Brazil. *Revista de Biologia Tropical*, 2010, 58(4), 1437-1451. PMID:21246998.
- PAGIORO, T.A. and THOMAZ, S.M. Longitudinal patterns of sedimentation in a deep, monomictic subtropical reservoir (Itaipu, Brazil-Paraguay). *Archiv für Hydrobiologie*, 2002, 154(3), 515-528. <http://dx.doi.org/10.1127/archiv-hydrobiol/154/2002/515>.
- PEŁĘCHATY, M., PUKACZ, A., APOLINARSKA, K., PEŁĘCHATA, A. and SIEPAK, M. The significance of *Chara* vegetation in the precipitation of lacustrine calcium carbonate. *Sedimentology*, 2013, 40(4), 1017-1035. <http://dx.doi.org/10.1111/sed.12020>.
- PERROW, M.R., JOWITT, A.J.D., STANSFIELD, J.H. and PHILLIPS, G.L. The practical importance of the interactions between fish, zooplankton and macrophytes in shallow lake restoration. *Hydrobiologia*, 1999, 395/396, 199-210. <http://dx.doi.org/10.1023/A:1017005803941>.
- RIP, W.J., RAWEE, N. and DE JONG, A. Alternation between clear, high-vegetation and turbid, low-vegetation states in shallow lake: the role of birds. *Aquatic Botany*, 2006, 85(3), 184-190. <http://dx.doi.org/10.1016/j.aquabot.2006.03.003>.
- SCHEFFER, M., REDELIJKHEID, M.R. and NOPPERT, F. Distribution and dynamics of

- submerged vegetation in a chain of shallow eutrophic lakes. *Aquatic Botany*, 1992, 42(3), 199-216. [http://dx.doi.org/10.1016/0304-3770\(92\)90022-B](http://dx.doi.org/10.1016/0304-3770(92)90022-B).
- SCHUTTEN, J., DAINY, J. and DAVY, A.J. Root anchorage and its significance for submerged plants in shallow lakes. *Journal of Ecology*, 2005, 93(3), 556-571. <http://dx.doi.org/10.1111/j.1365-2745.2005.00980.x>.
- SCHWARZ, A.M., HAWES, I. and HOWARD-WILLIAMS, C. The role of photosynthesis/light relationships in determining lower depths limits of Characeae in South Island, New Zealand lakes. *Freshwater Biology*, 1996, 35, 69-80. <http://dx.doi.org/10.1046/j.1365-2427.1996.00481.x>.
- SOULIÉ-MÄRSCHÉ, I. Charophytes, indicators for low salinity phases in North African sebkhet. *Journal of African Earth Sciences*, 2008, 51(2), 69-76. <http://dx.doi.org/10.1016/j.jafrearsci.2007.12.002>.
- SOUSA, W.T.Z., THOMAZ, S.M., MURPHY, K.J., SILVEIRA, M.J. and MORMUL, R.P. Environmental predictors of the occurrence of exotic *Hydrilla verticillata* (L.f.) Royle and native *Egeria najas* Planch. in a sub-tropical river floodplain: the Upper River Paraná, Brazil. *Hydrobiologia*, 2009, 632(1), 65-78. <http://dx.doi.org/10.1007/s10750-009-9828-3>.
- STEINMAN, A.D., HAVENS, K.E., RODUSKY, A.J., SHARFSTEIN, B., JAMES, R.T. and HARWELL, M.C. The influence of environmental variables and a managed water recession on the growth of charophytes in a large, subtropical lake. *Aquatic Botany*, 2002, 72(3-4), 297-313. [http://dx.doi.org/10.1016/S0304-3770\(01\)00207-8](http://dx.doi.org/10.1016/S0304-3770(01)00207-8).
- STEINMAN, A.D., MEEKER, R.H., RODUSKY, A.J., DAVIS, W.P. and HWANG, S.J. Ecological Properties of Charophytes in a Large Subtropical Lake. *Journal of the North American Benthological Society*, 1997, 16(4), 781-793. <http://dx.doi.org/10.2307/1468171>.
- THOMAZ, S.M., CARVALHO, P., MORMUL, R.P., FERREIRA, F.A., SILVEIRA, M.J. and MICHELAN, T.S. Temporal trends and effects of diversity on occurrence of exotic macrophytes in a large reservoir. *Acta Oecologica*, 2009, 35(5), 614-620. <http://dx.doi.org/10.1016/j.actao.2009.05.008>.
- THOMAZ, S.M., SILVEIRA, M.J. and MICHELAN, T.S. The colonization success of an exotic Poaceae is related to native macrophyte richness, wind disturbance and riparian vegetation. *Aquatic Sciences*, 2012, 74(4), 809-815. <http://dx.doi.org/10.1007/s00027-012-0264-5>.
- THOMAZ, S.M., SOUZA, D.C. and BINI, L.M. Species richness and beta diversity of aquatic macrophytes in a large sub-tropical reservoir (Itaipu Reservoir, Brazil): the influence of limnology and morphometry. *Hydrobiologia*, 2003, 505(1-3), 119-128. <http://dx.doi.org/10.1023/B:HYDR.0000007300.78143.e1>.
- TORN, K., MARTIN, G., KUKK, H. and TREI, T. Distribution of charophyte species in Estonian coastal water (NE Baltic Sea). *Scientia Marina*, 2004, 68(1), 129-136. <http://dx.doi.org/10.3989/scimar.2004.68s1129>.
- VAN DEN BERG, M.S., COOPS, H., SIMONS, J. and PILON, J. A comparative study of the use of inorganic carbon resources by *Chara aspera* and *Potamogeton pectinatus*. *Aquatic Botany*, 2002, 72(3-4), 219-233. [http://dx.doi.org/10.1016/S0304-3770\(01\)00202-9](http://dx.doi.org/10.1016/S0304-3770(01)00202-9).
- VAN DEN BERG, M.S., JOOSSE, W. and COOPS, H. A statistical model predicting the occurrence and dynamics of submerged macrophytes in shallow lakes in the Netherlands. *Hydrobiologia*, 2003, 506-509(1-3), 611-623. <http://dx.doi.org/10.1023/B:HYDR.0000008610.97044.39>.
- VAN DEN BERG, M.S., SCHEFFER, M., COOPS, H. and SIMONS, J. The role of Characean algae in the management of eutrophic shallow lakes. *Journal of Phycology*, 1998, 34(5), 750-756. <http://dx.doi.org/10.1046/j.1529-8817.1998.340750.x>.
- VAN DEN BERG, M.S., SCHEFFER, M., VAN NES, E. and COOPS, H. Dynamics and stability of *Chara* sp and *Potamogeton pectinatus* in a shallow lake changing in eutrophication level. *Hydrobiologia*, 1999, 408/409, 335-342. <http://dx.doi.org/10.1023/A:1017074211970>.
- VAN, T.K., HALLER, W.T. and BOWES, G. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiology*, 1976, 58(6), 761-768. <http://dx.doi.org/10.1104/pp.58.6.761>. PMID:16659762.
- VIEIRA JUNIOR, J. and NECCHI JUNIOR, O. Photosynthetic characteristic of charophytes from tropical lotic ecosystems. *Phycological Research*, 2003, 51(1), 51-60. <http://dx.doi.org/10.1111/j.1440-1835.2003.tb00170.x>.
- VIEIRA JUNIOR, J. and NECCHI JUNIOR, O. Photosynthetic characteristics of a tropical population of *Nitella cernua* (Characeae, Chlorophyta). *Brazilian Journal of Plant Physiology*, 2006, 18(3), 379-388. <http://dx.doi.org/10.1590/S1677-04202006000300004>.
- WINTON, M.D., CASANOVA, M.T. and CLAYTON, J.S. Charophyte germination and establishment under low irradiance. *Aquatic Botany*, 2004., 79(2), 175-187. <http://dx.doi.org/10.1016/j.aquabot.2004.01.013>.

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