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Niche differentiation between a native and an invasive species of submersed macrophyte in a subtropical reservoir

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ABSTRACT

Submersed macrophytes have important ecological roles but non-native invasive species may affect biodiversity and water uses. We investigated the native macrophyte *Egeria najas* and the invasive *Hydrilla verticillata* and measured their maximum colonization depth and its relationship with Secchi disk depth, their biomass along the depth gradient and their preferred depths of occurrence. The Itaipu Reservoir was monitored for seven years, during which maximum colonization depth and Secchi disk depth were measured. During a separate sampling, plants were collected to determine biomass along the depth gradient. Ancova showed that the maximum colonization depth of both species increased with increasing Secchi disk depth, but the maximum colonization depth of *H. verticillata* increased faster with increasing water transparency than did that of *E. najas*. Quadratic regression revealed that the biomass of each species peaks at intermediate depths. *Hydrilla verticillata* colonizes deeper regions than does *E. najas*. The patterns found in the present study can be explained by underwater light and, probably, wave disturbances. The preference of *H. verticillata* for deeper sites indicates that the ecological niches of the two macrophytes differ, and that *H. verticillata* has great potential to spread and accumulate biomass in reservoirs.

Keywords: colonization depth, depth occurrence, Hydrocaritaceae, invasive species, submerged macrophyte

Introduction

Invasive species are a cause of concern for ecologists and managers because new invasions are still increasing at accelerated rates (Seebens *et al*. 2017). These species may gradually replace the native ones, causing their extinction and homogenization of ecosystems, and altering nutrient cycles and energy fluxes (Mack & Simberloff 2000; Agostinho *et al*. 2005; Espínola & Junior 2007; Powell *et al*. 2011; Padial *et al*. 2020). Aquatic macrophytes have important roles in aquatic ecosystems (Gomes *et al*. 2012; Santos *et al*. 2020; Mabidi *et al*. 2020; Turunen *et al*. 2020). However, excessive growth of macrophytes can result in ecological and economic impacts (Marcondes 2003), which can be worse for invasive species since, in general, these species have traits that enhance their competitive ability and facilitate their growth and expansion (Gurovitch 2011; Rejmánek 2011; Sousa 2011; Silveira *et al*. 2018; Huang *et al*. 2019).

Aquatic macrophytes may colonize extensive areas in natural and artificial ecosystems (*e.g.*, reservoirs). The extension of the colonization of rooted submersed aquatic macrophytes can be measured by their depth of occurrence (Chambers & Kalff 1985; Thomaz & Esteves 2011). Depth of occurrence may be influenced by several environmental factors, like underwater light, slope and organic matter

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sediment, among others (Spence 1982; Duarte & Kalff 1986; Thomaz 2002). However, underwater light is by far the most important determinant of the distribution and biomass of submersed macrophytes (Spence 1982; Sarvala *et al*. 2020). Its effect is more intense in deeper regions of lakes because in this situation, light intensity may not be sufficient for photosynthesis. The maximum colonization depth of macrophytes (Z_{max}), for example, can be accurately predicted by underwater light intensity, which can be measured by Secchi disk transparency (Chambers & Kalff 1985).

In contrast, minimum colonization depth (Z_{min}, *i.e.*, the shallowest place a plant can colonize) is usually inversely proportional to wave action, because this factor represents a disturbance to organisms inhabiting the littoral zone (Spence 1982; Chambers & Kalff 1987; Doyle 2001). Direct effects of waves on plants mainly include damage and uprooting of established individuals and the consequent reduction in plant survival (Doyle 2001). Because light limits Z_{max} and wave disturbance limits Z_{min}, the colonization of submerged macrophytes can be favored in intermediate depths, compared to shallower and deeper zones (Spence 1982).

The most frequent rooted submersed macrophytes species in the Itaipu Reservoir of the Paraná River (Brazil/Paraguay) are the native *Egeria najas* and the invasive *Hydrilla verticillata*, both Hydrocharitaceae (Mormul *et al*. 2010). *Hydrilla verticillata* is a highly invasive species that has reached all continents except Antarctica (Langeland 1996). In less than two years from its first record in the Paraná River, this species became the most frequent submersed macrophyte species in several habitats of the Upper Paraná River basin, including the arms of the Itaipu Reservoir (Thomaz *et al*. 2009; Souza *et al*. 2017). In high densities, *H. verticillata* can cause economic and ecological damages (Langeland 1996; Sousa 2011), especially because of some physiological distinctions (*e.g.*, broad tolerances for environmental factors, which might include underwater light) (Sousa *et al*. 2009; Sousa 2011). For example, this invasive plant negatively affects the biomass of the native *E. najas* (Sousa 2011; Silveira *et al*. 2018). *In situ* monitoring of these two species becomes essential for predicting their distributions and high-density occurrences in reservoirs, for predicting future impacts of the invasive species over the native biota and to offer information for future management and conservation plans.

In this study we investigated the light and depth preferences of *E. najas* and *H. verticillata*. We tested the following hypotheses: (i) the Z_{max} of *E. najas* and *H. verticillata* is positively related to Secchi disk depth, but the responses of these species to this factor differ; (ii) both species have higher biomass in intermediate depths, and biomass decreases towards the shore (shallower zones) and the pelagic zone (deeper zones); and (iii) *H. verticillata* occurs in deeper zones than *E. najas*.

Materials and methods

Study area

The study was carried out in the Itaipu Reservoir of the Paraná River (24°15' S and 54°00' W). The reservoir was flooded in 1982, has an area of 1,350 Km^2 and a residence time of approximately 40 days. Its eastern (Brazilian) shore (where our samplings were conducted) has eight main arms formed by tributaries, where we conducted the samplings to estimate Z_{max} (Fig. 1). Owing to its great area, Itaipu has long fetches, which affects macrophyte colonization (Thomaz *et al*. 2009).

The most frequent submersed macrophyte species in these arms are *Egeria densa* Planch., *E. najas* Planch., *H. verticillata* (L. f.) Royle and *Nitella* spp. (Mormul *et al*. 2010). These arms are characterized as meso- to eutrophic; other details about water physical and chemical features can be found in Thomaz *et al*. (2009).

Relationship between Secchi disk depth and submersed macrophytes Z_{max}

We used data from a long-term survey to test the relationship between Secchi disk depth and Z_{max} [(hypothesis (i)]. Sampling occurred twice a year from 2008 to 2010, and from 2014 to 2017, for a total of 14 samples. Each sampling involved inspecting 230 to 235 georeferenced sampling stations on the Brazilian (eastern) side of the reservoir. Frequencies of *E. najas* and *H. verticillata* varied temporally and they occurred in less than 40 % of the sites. On each sampling occasion, we determined Z_{max} at some sites where stands were well developed, indicating that the plants were established and subjected to local conditions for a relatively long period of time. We had a total of 110 Z_{max} values for *E. najas* and 86 for *H. verticillata*.

To measure Z_{max}, we inspected sediment with a rake attached to a 4-m long aluminum pipe, in a transect perpendicular to the shore in search for the deepest occurrence of each species. Z_{max} occurs where there is the presence of small individuals (<10 cm), which marks the deepest limit of colonization. When macrophytes occurred in sites deeper than 4.0 m, we searched the Z_{max} with a multiple hook attached to a rope. These two methods gave consistent results compared to measurements made with echo sound sonar (data not shown), making us confident in the results obtained with the rake and hook. The Secchi disk depth was also measured in the same places.

The data of Z_{max} obtained by the above method, along with the survey conducted in September 2018 (see below), were also used to test hypothesis (iii).

Biomass of Egeria najas and Hydrilla verticillata along depth gradients

The hypotheses (ii) and (iii) were tested with an additional sampling conducted in September 2018, when

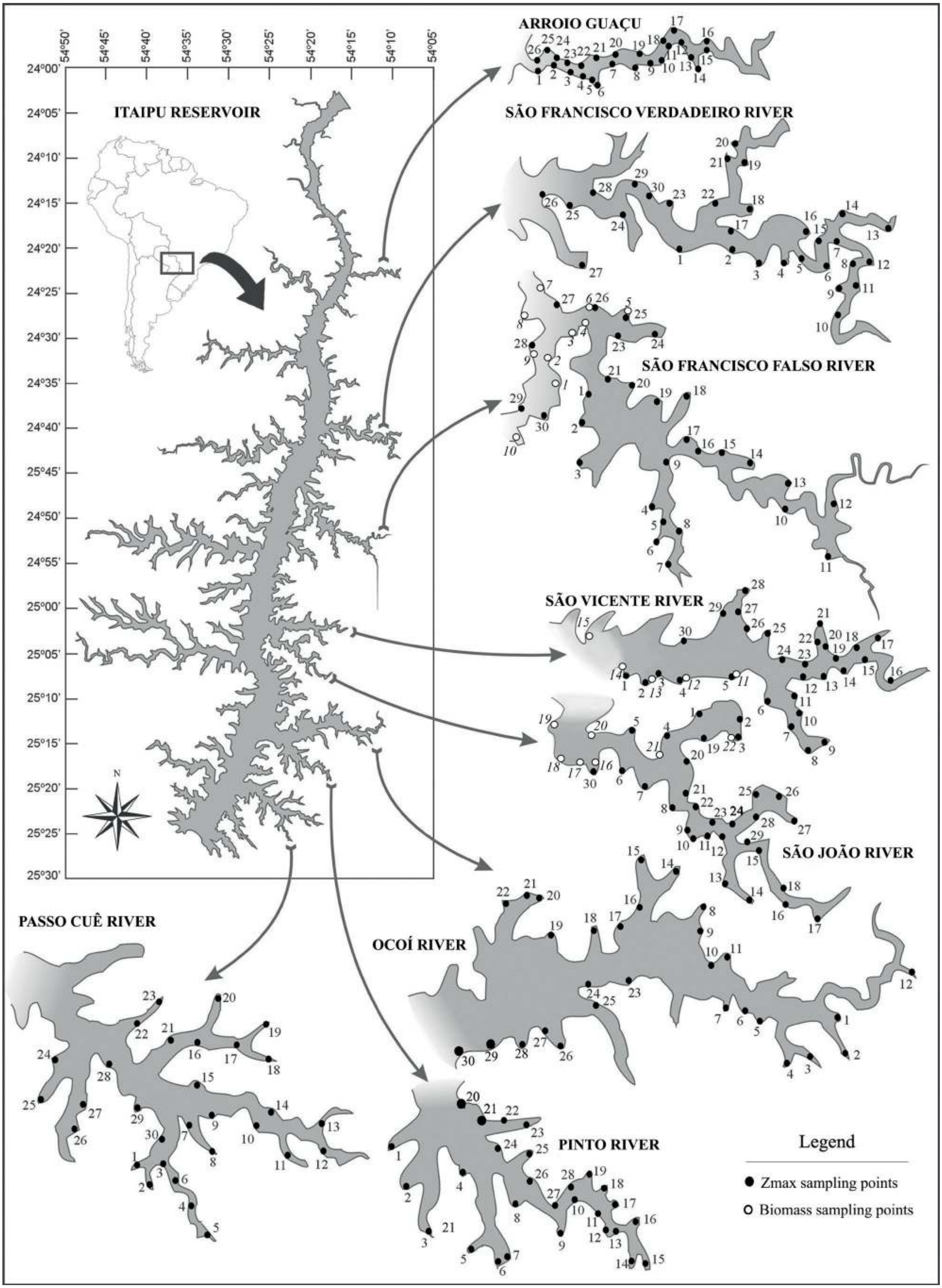

Figure 1. Map of the Itaipu Reservoir and its principal arms and sampling points of the long-term survey.

we evaluated the biomass of both species at different depths. We sampled 22 sites during this sampling, 10 in the arm of the São Francisco Falso River, five in the arm of the São Vicente River and seven in the arm of the São João River (Fig. 1). We chose sites which fulfilled three conditions: (i) they should have stands with at least one of the mentioned species; (ii) the stands had to be well developed so as to allow sampling of different plant densities at different depths; and (iii) the stands should be dominated by one of the species under study. The second condition is important because sampling small stands (*i.e.*, at the early stages of colonization) would not allow us to find a gradient of biomass along different depths, a condition necessary to test hypotheses (ii) and (iii). The third condition frees us from the following concerns: stands with several species could influence the biomass of the presented species because of possible competition among them, and a diverse community could affect the biomass sampled by each rake.

One transect of approximately 50 m (perpendicular to the shore) was established in each macrophyte stand and its position recorded using a GPS. Sampling was performed at five to seven points in each transect to measure macrophyte biomass, with depth also being measured at each of the points. We used a rake attached to a 4-m long aluminum pipe to sample biomass by positioning it in contact with the sediment, turning it 720º and pulling it up. This method allows branches to get attached to the rake and, when pulled up, both below and aboveground biomass are harvested. The biomass collected at each point was washed in the field, stored in an individual plastic bag and then dried at 70 ºC until constant weight (dry weight; DW). Because we used the same protocol at all points, we expressed biomass values in g DW per rake.

During this sampling, mean water temperature was 23.3 ºC (SD = 0.87), mean pH was 7.58 (SD = 0.26), mean conductivity was 0.05 $S.cm^{-1}$ (SD = 0.0008) mean dissolved oxygen was 9.03 $mg.L^{-1}$ (SD = 0.60), mean turbidity was 2.73 UNT (SD = 2.08) and mean Secchi disk depth was 2.35 m (SD = 0.71). These water variables, with the exception of Secchi disk depth, were measured with a multi-parameter HORIBA sensor.

Statistical analysis

Hypothesis (i) was tested by Ancova, which was applied to log transformed data obtained from the sampling of 2008-2010 and 2014-2017 (N = 186). This analysis allowed assessing if Z_{max} is related to Secchi disk depth and if this relationship differs between species (*E. najas* and *H. verticillata*). The test was carried out with R software (R Development Core Team 2019), using the "tidyverse" (Wickham *et al.* 2019), "stats" (R Development Core Team 2019) and "car" (Fox & Weisberg 2019) packages.

To test the relationship between the biomass of *E. najas* and *H. verticillata* and depth [hypothesis (ii)], we used log(x+1) transformed biomass data sampled in 2018. A Polynomial Regression was used to test the relationship between the depth of each point (continuous predictor variable) and macrophyte DW (response variable). The polynomial model was chosen because we verified a quadratic trend in our data during a visual inspection of the biomass values along the depth gradient with a scatterplot. We used the following equation:

$$Z = \text{constant} + b(\text{depth}) + c(\text{depth}^2)$$

where *Z* is the DW of *E. najas* or *H. verticillata*, *b* is the partial coefficient of the linear relationship between DW and depth and *c* is the partial coefficient of the quadratic relationship between DW with depth. The analysis was performed in R software (R Development Core Team), using the "dplyr" package (Wickham *et al.* 2020).

We tested hypothesis (iii) using two strategies: first we compared Z_{max} obtained in the long-term sampling; and second, we compared the depths of occurrence obtained in the 2018 survey. Both normality and homoscedasticity were met for Z_{max}, so we used Anova to generate isolated models for each species. The Shapiro-Wilk test found that normality was not met by the depths of occurrence data measured in 2018, so we used the non-parametric Kruskal-Wallis test. Anova and the Kruskal-Wallis test were performed with Statistica™ 7.1 (StatSoft 2005).

Results

Ancova revealed that the relationship between Z_{max} and Secchi disk depth depends significantly on the species (Secchi disk depth*Species: *F* = 8.15; *P* = 0.004). The intercept of the fitted model of *E. najas* ($\alpha_1 = 0.84$) is higher than the intercept for the model of *H. verticillata* ($\alpha_2 = 0.46$), but the slope of the relationship between Z_{max} and Secchi disk depth for the latter ($\beta_2 = 0.49$) is higher than that for the former ($\beta_1 = 0.24$). This shows that while depth colonized by *E. najas* and *H. verticillata* increases with increasing water transparency, this response occurs at a greater extent for *H. verticillata* than for *E. najas* (see also trend lines crossing in Fig. 2).

From the biomass sampling conducted in 2018, the minimum depth reached by *E. najas* was 0.4 m, the maximum depth was 3.0 m and the mean depth was 1.69 m. The maximum biomass reached by *E. najas* was 144 g DW per rake, obtained at 1.20 m depth. For *H. verticillata*, the minimum depth was 1.00 m, the maximum depth was 3.50 m and the mean depth was 2.43 m. The maximum biomass reached for *H. verticillata* was 68 g DW per rake, obtained at a 1.50 m depth.

The quadratic model using depth as the predictor variable explained 28 % of the variation in biomass for *E. najas* (*N* = 39; $F_2 = 8.35$; *P* = 0.001) and 26 % for *H. verticillata* (*N* = 26; $F_2 = 5.46$; *P* = 0.01) (Tab. 1). This relationship indicates that, for both species, an increase in biomass occurs with increasing depth, to a certain depth limit where biomass peaks, after which biomass values decrease significantly with increasing depth (Fig. 3). This result indicates that both species show a maximum biomass accumulation at intermediate depths. Comparison of the graphs for *E. najas* and *H. verticillata* reveals that the biomass curve for latter species is shifted to the right relative to the former. That is, *H. verticillata* reaches greater depths on average than *E. najas*, and its optimum point of growth, where the highest values of biomass are found, also tends to occur at greater depths.

The value of Z_{max} differed significantly between the species (Anova; $F = 4.905$, $P = 0.028$), evidencing that the invasive species is able to colonize deeper sites (mean = 4.11 m ± 1.34) than the native species (mean = 3.65 m ± 1.03). The data from biomass sampling conducted in 2018 reveals that depth of occurrence also differed between the species (Kruskal-Wallis test; $X^2 = 3.895$, $P = 0.04$), being higher for *H. verticillata* (mean = 2.43 ± 0.82) than *E. najas* (mean = 1.81 m ± 0.92).

Discussion

Based on the results, our three hypotheses were corroborated. In fact, Z_{max} of both macrophyte species increased with increasing underwater light, and the responses of Z_{max} to Secchi depth differed between the two (Fig. 2). In addition, the abundance of both species peaks at intermediate depths (Fig. 3) and *H. verticillata* occurred in deeper zones than *E. najas* (Figs. 2 and 3). In general, these results support the importance of underwater light and, indirectly, the potential role of wave disturbances in determining the biomass gradients of the two investigated species, and that the native and invasive species differ in their responses to underwater light and water depth. Thus, our findings indicate that their niches related to use of light and depth colonization differ.

The results of the Ancova demonstrated that increased light availability increases Z_{max} of both species, while the comparison of the two species shows that at the same Secchi disk depth (for values > 1.5m), *H. verticillata* is able

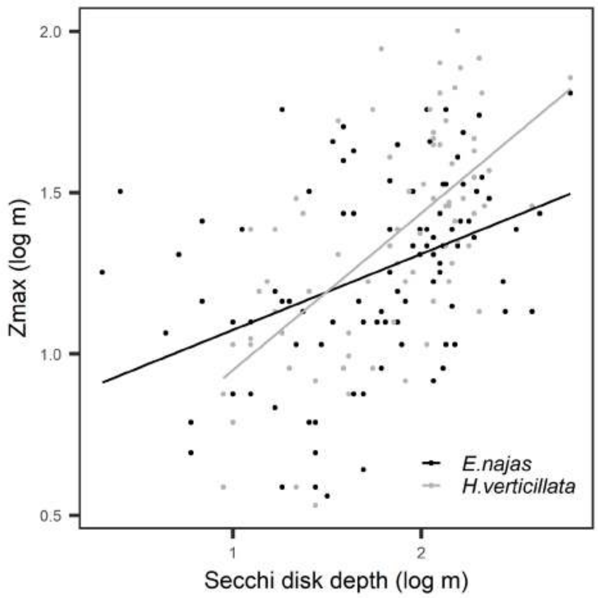

Figure 2. Relationship between the maximum colonization depth (Z_{max}) of *E. najas* and *H. verticillata* and Secchi disk depth in the Itaipu Reservoir.

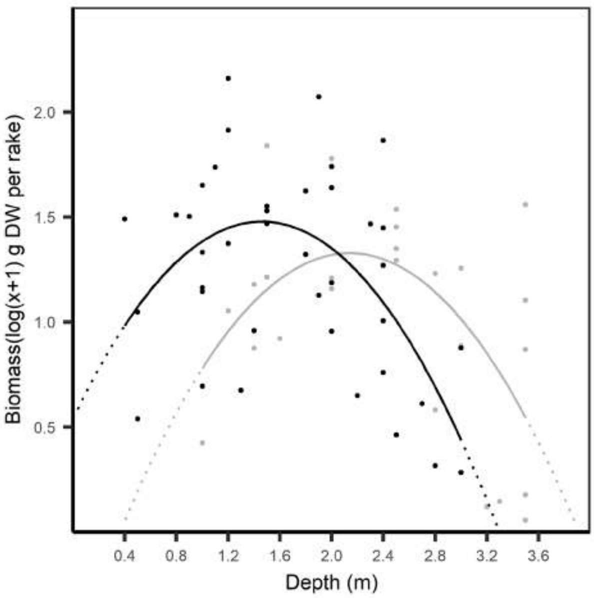

Figure 3. Relationship between a depth gradient and log(x+1) transformed dry biomass of *E. najas* (black line) and *H. verticillata* (grey line), using data collected in the Itaipu Reservoir in September 2018.

Table 1. Results of the Polynomial Regression Analysis assessing the effect of depth on *Egeria najas* and *Hydrilla verticillata* biomass (SE = coefficient standard error; t = t-test to assess coefficient significance).

	Coefficients	SE	t	P
Egeria najas				
Intercept	0.54	0.35	1.50	0.14
Depth	1.28	0.45	2.80	0.008
Depth^2	-0.43	0.13	-3.34	0.001
Hydrilla verticillata				
Intercept	-0.60	0.83	-0.72	0.47
Depth	1.80	0.75	2.39	0.02
Depth^2	-0.42	0.15	-2.68	0.01

to colonize deeper sites (higher Z_{max}) than *E. najas* (Fig. 2). The biomass samplings agree with these results, since it was evident that the biomass of the invasive species peaks in greater depths than the biomass of the native species (Fig. 3). Z_{max} is influenced mostly by suspended inorganic matter and phytoplankton, which negatively affect underwater light (Spence 1982; Chambers & Kalff 1987). These factors together help explain the reduction of Z_{max} with reduced water transparency. In regard to differences between species, recent studies have shown that *H. verticillata* is able to regenerate from tubers and allocate resources for stem elongation rather than branch development under complete darkness (Huang *et al.* 2019), which helps explaining why *H. verticillata* is found at greater depths than *E. najas*.

At first glance, these findings contradict those recorded in the Upper Paraná floodplain and in experiments, which indicate that *H. verticillata* prefers sites with higher water transparency and less turbidity than *E. najas* (Sousa *et al.* 2009; Sousa 2011; Silveira 2015). In view of these previous data, *H. verticillata* would be expected to be found in shallower sites (where light intensity is higher) than *E. najas*. Thus, we infer that other factors may act in combination with transparency to explain the depth gradient of these two species in the Itaipu Reservoir. For example, organic matter sediment has been another important determinant of the success of these two species, with the invasive preferring less organic sediments (Sousa *et al*. 2009; Sousa 2011; Silveira & Thomaz 2015). Shallow areas of the Itaipu Reservoir are highly colonized by macrophytes (Thomaz *et al*. 2009) and it is possible that organic matter accumulation in shallow areas prevents *H. verticillata* colonization in these areas. In addition, the set of variables that might act on the degree of colonization of deeper areas is much more complex, including the water flow velocity and differences in the chemical composition of the sediment (including nutrients and granulometry) between shallow and deep zones, for example (Duarte & Kalff 1990; Chambers *et al.* 1991). Finally, other features peculiar to each species might also help to explain differences. For example, *H. verticillata* has faster root growth compared to other species of Hydrocaritaceae, which provide a very efficient anchoring system (Silveira *et al*. 2009). However, these possible explanations need further experimental exploration before any firm conclusions can be made in this regard.

The polynomial regression analysis showed that the growth of both species (indicated by biomass) is related with depth. Peak biomass for both species occurred at intermediate depths with biomass decreasing towards shore (shallower areas) and the pelagic zone (deeper areas). Decreased macrophyte biomass with increasing depth is explained by the same factors used to discuss Z_{max}: underwater light and, alternatively, sediment composition.

In contrast, factors other than light influence the decrease in biomass toward shallower areas. Although we did not directly measure wave disturbance, we infer that this is the main factor explaining decreased biomass toward shallower areas. Wave disturbance (wind generated) is one of the most important factors that prevents macrophyte colonization of shallow areas (Spence 1982; Chambers 1987), including in the Itaipu Reservoir (Thomaz *et al*. 2003; 2009). Wave disturbance reduces plant colonization and damages macrophyte tissues (Neiff *et al*. 2000; Doyle 2001; Cunha-Santino *et al*. 2016). This damage reduces the colonization and plant biomass in places with greater wave impact, that is, in shallower places (Keddy 1982). Wave disturbance is directly related to fetch (distance at which the wind acts on the surface of a water body without obstruction), which in turn also affects macrophyte minimum colonization depth, since the higher the fetch, the greater the erosive potential of waves and, by extension, the greater the potential for macrophyte disturbance (Spence 1982). Despite suspecting that wave disturbance is the main factor responsible for decreased macrophyte biomass in shallower areas, we cannot discard other factors. For example, high light intensity may limit submersed plants in shallow sites (Jin *et al*. 2020). In addition, water level fluctuations and the presence of floating and emergent vegetation (common in Itaipu; Thomaz *et al*. 2009) may also have a role in decreased biomass toward the shores of the reservoir.

Our findings can be useful from a plant management perspective. Reservoirs usually have low water flow, high sedimentation and high water transparency (Barbosa *et al*. 1999), which favor the presence and proliferation of submerged vegetation, as we found in Itaipu. Manipulation of the water level is a tool that may be used in some reservoirs to control submerged plants (Thomaz 2002). Water level depletions could prevent infestations of submerged macrophytes, especially invasive species that are favored by the high-water transparency caused by impoundments. According to our results that evidence that *H. verticillata* prefers deeper sites, the control of infestations of this plant would need the use of greater water level depletions than would the control of native species, like *E. najas*. As the reservoirs are built to retain water, control of *H. verticillata* using water level manipulation becomes a challenge.

In summary, using long term data about Z_{max} and one sampling of macrophyte biomass, we show that the invasive *H. verticillata* and the native *E. najas* differ in depth preferences, with the former preferring deeper sites. We also found that the biomass of both species peaks at intermediate depths and that the biomass of *H. veriticillata* peaks at greater depths than the biomass of *E. najas*. Thus, our field data suggest the niches of these two species (in terms of light use and depth colonization), differ. The patterns we found are related to limitations of underwater light toward deeper areas and probably wave disturbance in shallower areas, although other factors like light saturation and presence of macrophytes along the shores may also play a role in the depth gradients we found. Finally, the success of *H. verticillata* in deeper areas indicates that this species is able to escape from wave disturbances (which occur mainly in shallow areas) and may succeed and cause damage in large reservoirs. Experimental studies about the colonization and growth phases of these species at different depths, and subjected to a gradient of disturbances caused by waves, would bring important contributions to explain the mechanisms involved in the patterns we detected *in situ*.

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