Effects of Limnological and Morphometric Factors Upon $Z_{\text{min}}$, $Z_{\text{max}}$ and Width of Egeria spp Stands in a Tropical Reservoir

Sandra Andréa Pierini and Sidinei Magela Thomaz*

1Faculdade Integrada de Campo Mourão; Rodovia BR 158; km 207; 87300-970; Campo Mourão - PR - Brasil.
2Universidade Estadual de Maringá; Av. Colombo, 5790; 87020-90; Maringá - PR - Brasil

ABSTRACT

In this work, regression analyses were used to test the effects of fetch, littoral slope and Secchi disk depth upon the stand width ($W_i$) and maximum ($Z_{\text{max}}$) and minimum ($Z_{\text{min}}$) colonization depths of Egeria spp in a large tropical reservoir (Rosana Reservoir). Littoral slope was the only variable correlated with $W_i$, which was larger in locations with lower slopes. The higher $W_i$ values (up to 260m) were found in locations where slopes were lower than 0.05 m.m$^{-1}$. $Z_{\text{min}}$ and $Z_{\text{max}}$ were correlated positively with fetch. Nevertheless, different relationships were found at lower and higher fetch values observed in the arms and in the main body of the reservoir, respectively. At lower values, Secchi disk depth was the main variable explaining Egeria $Z_{\text{max}}$. On the other hand, in locations where fetch was longer (i.e. in the main axis of the reservoir), it was the only variable that explained $Z_{\text{max}}$ significantly. Despite the great variability, the results indicated that the measured limnological (Secchi disk) and morphometric (fetch and slope) variables were important determinants of Egeria spp colonization in the Rosana Reservoir.

Key words: Egeria, fetch, littoral slope, Secchi disk

INTRODUCTION

The ecological role of aquatic macrophytes as habitats for macro-invertebrates (Bailey, 1988) and fish (Agostinho et al., 2003; Pelicice et al., 2005), in shore stabilization (Sand-Jensen, 1998), nutrient cycling (Esteves and Camargo, 1986) and in affecting water chemistry (Taniguchi et al., 2004) has been greatly emphasized. The importance of macrophytes in processes and patterns of other aquatic communities depends, however, on their degree of colonization (Bini, 2001). Aquatic ecosystems are not homogeneously colonized by macrophytes, which are usually found in mono or multi-species patches varying in distribution and area (Sand-Jensen, 1998). Although there is no consensus about the factors that affect the aquatic macrophyte populations and community attributes on different scales (Duarte and Kalff, 1986; 1988; 1990; Chambers and Kalff, 1985; Hudon et al., 2000; Riss and Hawes, 2003), littoral slope, fetch and Secchi disk depth have been frequently used in studies that aimed to predict their occurrence and degree of colonization. However, models proposed for north temperate regions have not yet been tested in warm South American environments (Neiff and Poi de Neiff, 2003).

* Author for correspondence: smthomaz@nupelia.uem.br
The minimum depth of colonization (\(Z_{\text{min}}\)) has been frequently related with the degree of wave exposure caused by fetch, wind velocity and wind duration (Spence, 1982; Chambers, 1987; Canfield and Hoyer, 1988; Riss and Hawes, 2003). On the other hand, the maximum depth of colonization (\(Z_{\text{max}}\)) is usually related with Secchi disk depth (Spence, 1982; Chambers and Kalff, 1985; Scheffer et al., 1992; Middelboe and Markager, 1997; Hudon et al., 2000; Bini, 2001). Both \(Z_{\text{min}}\) and \(Z_{\text{max}}\) are attributes that express the degree of colonization of submerged plants (Chambers and Kalff, 1985; Chambers, 1987; Riss and Hawes, 2003). Their values are helpful in assessing the areas that are potentially most affected by plant growth, as well as in predicting the areas of potential colonization by submerged macrophytes. Few studies have been carried out to measure the degree of colonization and to understand the main factors affecting the aquatic macrophytes in tropical and sub-tropical reservoirs (Neiff et al. 2000; Marcondes et al., 2003; Martins et al., 2008). Nevertheless, some large reservoirs in South America (especially Brazil) have been greatly affected by excessive growth of submerged vegetation. Among the main species that are considered nuisances and damaging to water use, especially energy production, are the submerged macrophytes \textit{Egeria densa} and \textit{E. najas} (Thomaz and Bini, 1998; Cavenaghi et al., 2003; Marcondes et al., 2003; Martins et al., 2008). In this investigation, the effects of three widely used morphometric and limnological parameters (fetch, littoral slope and Secchi disk depth) was tested upon \(Z_{\text{min}}, Z_{\text{max}}\) and width (\(W_i\)) of \textit{Egeria} spp stands. In spite of being exploratory, the results allow the assessment of the importance of each factor in the colonization of this genus and the building of the first predictive models of plant colonization in a large tropical reservoir.

\section*{STUDY AREA}

This investigation was carried out in the Rosana Reservoir, Brazil (Fig. 1). It was built in 1986 and dammed the Paranaapanema River, one of the main tributaries of the Paraná River. The reservoir has an area of ca. 27,600 ha and a mean residence time of 18.6 days (CESP, 1998). Rosana is the last reservoir of a cascade in the Paranaapanema River and it is shallow (depths < 5.0m, in general), which allows extensive areas propitious for macrophyte colonization. Based on samplings carried out every three months in 2002, the Secchi disk depths varied from 0.3m to 2.7m (mean = 1.7; SD = 0.8) and the alkalinity fluctuated from 191\(\mu\text{M/L}\) to 513\(\mu\text{M/L}\) (mean = 392; SD = 109). Low concentrations of total nitrogen (294-552\(\mu\text{g/L}\); mean = 370; SD = 79) and total phosphorus (9-18\(\mu\text{g/L}\); mean = 11; SD = 3), suggest that this reservoir is oligotrophic.

In intensive surveys carried out previously in the Rosana Reservoir, 37 species of aquatic macrophytes were recorded. In these surveys, \textit{Egeria najas} and \textit{E densa} were the most frequent submerged species. These species occur either individually or together, forming large stands both in the arms and in the main axis of the reservoir.
MATERIALS AND METHODS

The samplings were carried out in August 2003 and February 2004 in the main axis and in the five principal arms of the reservoir (Fig. 1). A total of 176 sampling stations were selected in an attempt to encompass sites with different environmental characteristics. Nevertheless, only 82 and 87 transects were colonized by *Egeria* in August and February, respectively. In the main axis of the reservoir, transects were distributed at intervals varying from 1 to 1.5 km, covering the distance from the upper (fluvial) to the lower (lacustrine) region of the reservoir. Given that *E. najas* and *E. densa* were found together in several stands, and since their identification in the field was difficult due to the similarity of vegetative structure of the two species, both the species were considered together and attributed the results to the genus *Egeria*.

In each transect, *Egeria* $Z_{\text{min}}$ and $Z_{\text{max}}$ were recorded and their positions assessed using a GPS. The distances between both the points corresponded to the $Wi$ values. The limits of colonization ($Z_{\text{min}}$ and $Z_{\text{max}}$) were found after intensively surveying the sediments with a rake attached to a 4.5m aluminum pipe. Surveys started always close to the shore and finished at 5-6 meters depths. When necessary (i.e., in depths greater than 4.0m), additional surveys were carried out using a hook hold on a 10m line.

The values of $Z_{\text{min}}$ and $Z_{\text{max}}$ and the distance between them were used to estimate the littoral slope at each sampling site. Its values were expressed as the slope of a regression between $Z_{\text{min}}$ and $Z_{\text{max}}$ (Bini, 2001). Secchi disk depth was used to represent light availability. The degree of exposure to waves (fetch) was estimated as

$$F = \left( \frac{\sum x_i \cos y_i}{\sum \cos y_i} \right) s',$$

where $x_i$ was the distance between point $i$ and the nearest shore (or island) and $y_i$ the angle used to measure this distance (distances were measured every 10° ending at 180°). $s'$ was the map scale to transform $F$ into km. The distances ($x_i$) were measured using maps with a scale of 1:20,000. Note that the fetch values were not corrected for wind and thus their meaning could only be related with the “potential” effect of waves upon the shores surveyed. Despite this shortcoming, other investigations found reasonable predictions of aquatic plant community attributes using similar measurements of fetch as an independent factor (Thomaz et al., 2003).

Stepwise multiple regressions, using the standard procedure, were applied to assess which independent variable (or combination of variables - littoral slope, fetch and Secchi disk) could best explain the dependent variables ($Wi$, $Z_{\text{max}}$, and $Z_{\text{min}}$). The assumptions of the analyses were verified using residual analyses and Shapiro-Wilk test was used to assess the residuals distribution. When necessary, the data were log (natural logarithm) or square root transformed. Since the independent variables had values <1.0, all analyses (including the figures) were done by adding 1.0 to each value before log transformation. The variable was considered significant when $P<0.05$. Multiple regressions were applied using Statistica 5.5.

The scatterplot between littoral slope and $Wi$ was not linear. The points in the biplot figure were concentrated inside triangles (or envelopes). The probability of having such a concentration of points inside the triangle at random was assessed using the routine “Macroecology” from ECOSIM 7.22 (Gotelli and Entsminger, 2001). A Monte Carlo randomization, with 10,000 permutations, was applied to obtain the probabilities.

RESULTS

In general, a wide range of values was recorded for all the variables (Table 1). For example, $Wi$ values varied from 1 to 261m, $Z_{\text{min}}$ between 0.20 and 4.00m and $Z_{\text{max}}$ between 1.40 and 6.00m. The multiple regression model explained 51% of $Wi$ variability ($N = 87; F_{1,80} = 27.77; P < 0.001$). According to this multiple regression, only littoral slope explained a significant proportion of the variability, but fetch and Secchi disk depth were not significant (Table 2; Fig. 2). The distribution of the studentized residuals was normal ($W = 0.98; P = 0.337$) and 95% of their values remained between −1 and +1. Two outliers (>2) were observed in the distribution. Nevertheless, graphic inspections showed that the dispersion of the observed versus predicted values did not present any specific tendency. Analysis of the scatterplot formed by $Wi$ and littoral slope suggested that points were accumulated inside a triangle (or envelope) (Fig. 2a).
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### Table 1 - Descriptive statistics of the variables measured in the Rosana Reservoir (SD = standard deviation).

| Variables          | N  | Mean  | Minimum | Maximum | SD   |
|--------------------|----|-------|---------|---------|------|
| $W_i$ (m)          | 157| 32.66 | 1.00    | 261.30  | 39.94|
| $Z_{\text{min}}$ (m) | 129| 1.52  | 0.20    | 4.00    | 0.74 |
| $Z_{\text{max}}$ (m) | 104| 3.31  | 1.40    | 6.00    | 0.78 |
| Littoral slope (m.m$^{-1}$) | 87 | 0.09  | 0.01    | 0.52    | 0.09 |
| Fetch (km)         | 169| 3.58  | 0.36    | 5.98    | 1.71 |
| Secchi disk (m)    | 163| 2.26  | 0.65    | 3.45    | 0.64 |

Figura 2 - Relationship between *Egeria* $W_i$ and littoral slope (a), fetch (b) and Secchi disk depth (c). Only the littoral slope was significant, according to the multiple regression analysis. The triangle indicates the envelope (a) that was tested using Monte Carlo randomization procedures.

The variability of $W_i$ was usually higher where the slopes were lower. At slope values greater than 0.15 m.m$^{-1}$, $W_i$ values were always lower than 3m. Thus, in addition to using the multiple regression analysis to quantify the relationship, a Monte Carlo randomization procedure was applied to test the probability of finding such a concentration of points by chance alone. According to this analysis, the probability was 0.042. This meant that the triangular relationship between $W_i$ and littoral slope was statistically significant using this method.

Considering *Egeria* $Z_{\text{min}}$, the multiple regression results showed that 51% of the variability of its values was accounted for by the model ($N = 86; F_{3.73} = 25.41; P < 0.001$). Nevertheless, fetch was the only variable significantly related to $Z_{\text{min}}$ and Secchi disk and littoral slope were not significant (Table 2; Fig. 3). The distribution of residuals was normal ($W = 0.99; P = 0.887$). Despite the observation of five outliers (>2), the residual analysis indicated that the model was suitable to describe *Egeria* $Z_{\text{min}}$ in the Rosana Reservoir. Applying the multiple regression to $Z_{\text{max}}$ showed that littoral slope and Secchi disk depth did not contribute to explain this variable which was significantly explained only by fetch ($N = 86; F_{3.82} = 6.29; P < 0.001$) (Table 2; Fig. 4). Nevertheless, the coefficient of determination was very low (19%). In addition, the distribution of residuals was not normal ($W = 0.96; P = 0.011$).
Table 2 - Results of the multiple regression analysis assessing the effect of fetch, littoral slope and Secchi disk depth on *Egeria* stand width (Wi), Z\text{\textsubscript{min}} and Z\text{\textsubscript{max}}. Beta = standardized coefficients; SE = coefficient standard errors; t = test t to assess the coefficient significances.

|        | Beta | Coefficients | SE  | t     | P     |
|--------|------|--------------|-----|-------|-------|
| Wi     | Interception | 3.37          | 0.47 | 7.21  | <0.001|
| Log slope | -0.72 | -7.92         | 0.87 | -9.08 | <0.001|
| Log fetch | -0.05 | -0.10         | 0.16 | -0.56 | 0.577 |
| Log Secchi | 0.13  | 0.63          | 0.39 | 1.61  | 0.112 |
| Z\text{\textsubscript{min}} | Interception | 0.71          | 0.17 | 4.10  | <0.001|
| Log fetch | 0.73  | 0.52          | 0.06 | 8.66  | <0.001|
| Log slope | -0.14 | -0.50         | 0.29 | -1.71 | 0.092 |
| Log Secchi | -0.16 | -0.26         | 0.14 | -1.90 | 0.061 |
| Z\text{\textsubscript{max}} | Interception | 1.30          | 0.16 | 8.03  | <0.001|
| Log fetch | 0.33  | 0.18          | 0.06 | 3.22  | 0.002 |
| Log slope | 0.18  | 0.52          | 0.29 | 1.77  | 0.080 |
| Log Secchi | 0.12  | 0.15          | 0.13 | 1.12  | 0.266 |

Figure 3 - Relationship between *Egeria* Z\text{\textsubscript{min}} and littoral slope (a), fetch (b) and Secchi disk depth (c).

A more detailed analysis of the dispersion diagram between the predicted and studentized residuals obtained from regressing only Z\text{\textsubscript{max}} on fetch showed that, in general, discrepant values (both positive and negative) were found where fetch was lower than 2km. Such sampling sites were located in the arms of the reservoir. This indicated that the relationship between Z\text{\textsubscript{max}} and the independent variables could be different if only the sampling sites less exposed to wind effect were considered. Then, an additional multiple regression was carried out separately for the sampling sites of the main axis (N = 69) and arms (N = 17). When both datasets were analyzed separately, a considerable difference was found by multiple regressions. Despite the great dispersion ($R^2 = 21.8\%$), fetch explained a significant portion of Z\text{\textsubscript{max}} in the main axis of the reservoir (N = 69; $F_{3,65} = 6.024; P = 0.001$). On the other hand, Secchi disk depth explained a significant proportion of Z\text{\textsubscript{max}} in the arms of the reservoir (N = 17; $F_{1,15} = 20.09; P < 0.001$). This regression was described by the model: $Z_{\text{\textsubscript{max}}}^{0.5} = 1.38\times$log Secchi. For this regression, the determination coefficient was very high ($R^2 = 62\%$) and the distribution of the residuals was normal ($W = 0.951; P = 0.576$). Nevertheless, the intercept was not significantly different from zero (Table 3).
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Figure 4 - Relationship between $Egeria$ $Z_{\text{max}}$ (square root transformed) and littoral slope (a), fetch (b) and Secchi disk depth (c).

Table 3 - Results of the multiple regression analysis assessing the effect of fetch, littoral slope and Secchi disk depth on $Egeria$ ($Z_{\text{max}}$)$. Beta = standardized coefficients; SE = coefficient standard errors; $t$ = test $t$ to assess the coefficient significances. The analyses were carried separately for values recorded in the reservoir main axis and in its arms.

|                | Main axis |            |            |        |        |
|----------------|-----------|------------|------------|--------|--------|
|                | Beta      | Coefficients | SE         | $t$    | $P$    |
| Intercept      | 0.44      | 1.19       | 0.20       | 6.05   | <0.001 |
| Log fetch      | 0.17      | 0.35       | 0.09       | 3.96   | <0.001 |
| Log slope      | 0.006     | 0.006      | 0.11       | 0.05   | 0.960  |
| Log Secchi     |           |            |            |        |        |
| Arms           | -0.16     | -0.34      | 0.45       | 0.76   | 0.466  |
|                | -0.11     | -0.30      | 0.37       | -0.81  | 0.435  |
|                | 0.77      | 1.38       | 0.37       | 3.71   | 0.004  |

DISCUSSION

These results showed that $Egeria$ colonized mainly areas with lower littoral slopes. This morphometric variable has been considered among the main factors affecting the limits of occurrence of submerged plants within aquatic ecosystems of temperate regions (Duarte and Kalff, 1986; 1990). Present analyses showing $Egeria$ $W_i$ significantly related to littoral slope indicated that this independent variable was a useful predictor of the degree of submerged plant colonization in the Rosana Reservoir.

The influence of littoral slope on aquatic macrophytes can be associated with the physical and chemical characteristics of sediment. For example, littoral slope affects the chemical composition, thickness, grain size and stability of sediments, as well as the way in which wave energy is dissipated (Duarte and Kalff, 1986; 1988; 1990; Cyr, 1998). According to Cyr (1998), areas with steeper slopes are less stable since they have a higher probability of sediment slumping and sliding. As a result, sites with greater slopes have, in general, lower rates of small particle deposition (that are richer in nutrients). Littoral
slopes also influence the horizontal extent of the weedbed, possibly because the plants growing on steep slopes reach the depth of light compensation much closer to shore than would be the case with gentle slopes (Duarte and Kalff, 1988). Despite the significant relationship between Wi and slope, the biplot graphic display of both variables suggested that the use of a traditional regression model, which assumed a continual and gradual process (Duarte and Kalff, 1990), was not totally suitable to describe such a relationship. According to Bini (2001), who investigated *E. najas* distribution in a large subtropical reservoir (Itai, Brazil/Paraguay), the relationships in the shape of “envelopes” have lower predictive capacity; however, such relationships allow, within certain limits, the determination of the limits of occurrence of *Egeria* stands. For example, in regions where slopes are lower than 0.05 m.m⁻¹, *Egeria* Wi may reach up to 260m. Thus, this prediction indicates that prioritizing monitoring in areas with such low slopes would increase the efficiency of plant management in the Rosana Reservoir. Present results also corroborated the ones recorded by Duarte and Kalff (1986; 1990) and Scheffer et al. (1992), who showed that sites with lower slopes were usually more colonized by submerged macrophytes. *Egeria* $Z_{min}$ was positively affected by fetch. This kind of relationship is usually explained by direct and indirect mechanisms acting upon the aquatic vegetation. An example of an indirect mechanism is the deposition of fine particles, richer in nutrients. The great energy derived from waves resuspends mainly the fine particles and thus, in sites having longer fetches, the finer (and richer) particles are deposited in deeper sediments (Keddy, 1982; Chambers, 1987; Cyr, 1998; Riis and Hawes, 2003). As a result, sediments retained close to the shore (shallow areas) tend to have lower nutrient concentrations, reducing the capacity for plants to colonize and grow in these places. This inference was confirmed in the field experiments that showed that wave energy at shallow sites diverted small, richer particles to deeper sites, reducing submerged plant growth (Duarte and Kalff, 1988).

Waves also affect $Z_{min}$ directly by causing physical damage to aquatic plant tissues. Due to this damage, fetch is considered in several studies a measure associated with the disturbance (direct physical damage to plant tissues) (Spence, 1982; Keddy, 1983; Wilson and Keddy, 1986; Chambers, 1987; Riis and Hawes, 2003), in addition to be also a measure of stress (i.e. indirect effects caused by turbidity and nutrient availability). Physical damage to *Egeria* tissues may be severe because this genus usually grows close to the water surface, forming well-developed canopies. This is an advantageous strategy since the plants concentrate their photosynthetic tissues in well-illuminated areas, escaping the adverse effects of high turbidity (Scheffer et al., 1992; Bini, 2001). Nevertheless, as a result of such a strategy, canopy-forming plants such as *Egeria* (known as “eloideids”) are also more susceptible to wave damage (that may be considered a disturbance) than plants with linear, ribbonlike leaves and/or rosettelike forms growing close to the bottom. In fact, the natural distribution of plants in relation to wave energy provides correlational evidence of wave impacts (Doyle, 2001). Wind effect upon plant biomass was not suggested only from data obtained in the field. Experiments carried out in the laboratory clearly showed that several morphological attributes of *Vallisneria americana*, a submerged species, were affected by wave effect, even at moderate wave intensities (Doyle, 2001). In addition, waves may also affect the colonization by preventing the propagules from settling and by increasing their detachment from sediments (Rea et al., 1998; Hudon et al., 2000; Riis and Hawes, 2003).

Although the present investigation did not allow distinguishing between any direct (e.g. disturbance) or indirect (e.g. nutrient limitation) mechanism, it could be inferred that the potential degree of wave exposure (our fetch measurements) was the main factor controlling *Egeria* $Z_{min}$ in the Rosana Reservoir. Nevertheless, specific experiments manipulating plant growth in more versus less-exposed sites are still necessary to assess this inference. Differently from $Z_{min}$, the responses of $Z_{max}$ to the independent variables measured seem to be more complex. The relationships between *Egeria* $Z_{max}$ and the explanatory variables in the Rosana Reservoir were different if one considered the more-exposed versus the more-protected sites. In the main axis of the reservoir, $Z_{max}$ was affected mainly by fetch. The positive correlation between $Z_{max}$ and fetch indicated that *Egeria* colonized more deeply at the more-exposed sites. This could be considered a response to escape from the physical effects caused by wave disturbance (Duarte and Kalff, 1988; Hudon et al., 2000).
deepest areas colonized by *Egeria* varied, in general, from 3.6 to 4.0m, although depths down to 6.0m were also found. These depths were higher than those found in other Brazilian reservoirs, where turbidity was higher. In Itaipu Reservoir, for example, *Egeria Z* \(_{\text{max}}\) is, on average, 1.5m (Bini, 2001). In fact, the non-significant correlation between Secchi disk depth and *Z* \(_{\text{max}}\) in the main axis of the reservoir suggests that underwater radiation (or turbidity) has a secondary effect upon *Egeria* growth in this compartment.

The coefficient of determination of the multiple regression performed for *Z* \(_{\text{max}}\) in the main axis was very low (\(R^2 = 19\%\)), indicating that other factors not accounted for in this study interact to determine *Z* \(_{\text{max}}\). Other morphometric features, chemical characteristics of the water and sediment, and flow velocity, among other factors, could be important in this respect (Canfield and Hoyer, 1988; Chambers *et al*., 1991; Hudon *et al*., 2000; Pezzato and Camargo, 2004).

On the other hand, results obtained in the reservoir arms showed that Secchi disk depth significantly explained *Z* \(_{\text{max}}\) variability. In several investigations, Secchi disk depth has been successfully used to predict submerged plant *Z* \(_{\text{max}}\) (Chambers and Kallf, 1985; Scheffer *et al*., 1992; Bini, 2001). In general, the regressions in these studies found positive intercepts significantly different from zero (Scheffer *et al*., 1992; Bini, 2001), which meant that stem elongation occurred even under low underwater radiation. This could be explained by the plant physiology, since species with this strategy could store carbohydrates in underground organs or in the stems (Scheffer *et al*., 1992; Middelboe and Markager, 1997; Bini, 2001). According to Bini (2001), it is possible that *Egeria* stores carbohydrates in its stem, although no experiments to verify this hypothesis have been performed. Thus, growth up to the surface could only occur, independent of underwater radiation availability, if during a previous time period radiation was available to the plant (i.e. if underwater radiation reached the sediment where the plant was starting to grow). Differently from the studies considered previously, the intercept of the relationship between *Z* \(_{\text{max}}\) and Secchi disk depth (using only data collected in the reservoir arms) was not significantly different from zero (see Table 3). This indicates that *Egeria* did not colonize successfully sites with low Secchi disk depth values (<1.0m) in sheltered places in the Rosana Reservoir. However, this result was unexpected because the plants with canopy (such as *Egeria*) use sub-surface light and, thus, they are more independent from underwater radiation than the plants that do not form canopy. This way, canopy forming plants generally grew even at low levels of radiation which could cause the intercept between Secchi versus *Z* \(_{\text{max}}\) to be positive and significant.

A possible explanation for an intercept not different from zero could be that in more-protected areas (lower fetch values), the waves may not have enough energy to remove part of the periphyton attached to the plant surface. Although it was not measured, substantial periphyton accumulation upon *Egeria* was observed at the more-protected sites in this study. The presence of periphyton may reduce light availability to submerged macrophytes. In addition, at sites protected from wave exposure, phytoplankton and/or free-floating macrophytes may accumulate, negatively affecting sub-surface and underwater radiation (Scheffer *et al*., 1992; Weisner *et al*., 1997). Thus, it could be inferred that *Egeria Z* \(_{\text{max}}\) was at least partially controlled by competition for light with other autotrophic aquatic organisms at sheltered sites.

Using the regression between *Z* \(_{\text{max}}\) and Secchi depths and the values of irradiance obtained by Pierini (2005) in the Rosana Reservoir, it was estimated that the light intensity at *Z* \(_{\text{max}}\) in the reservoir arms was 6.9% (on average) of the surface PAR. This value was lower than the one estimated by Chambers and Kallf (1985) for several angiosperms (21%) and also for *E. najas* colonizing Itaipu Reservoir (12% - Bini, 2001). The radiation reaching *Z* \(_{\text{max}}\) might change according to water level fluctuation; nevertheless, such alterations were usually small in the Rosana Reservoir (where water level fluctuation < 1.0m year\(^{-1}\) has been recorded). According to Sculthorpe (1967), the underwater radiation at the compensation point of several submerged species varies from 1 to 4%. Thus, the present values are close to the higher limit presented by Sculthorpe (1967) for several angiosperms.

In summary, the results indicated that the extension of *Egeria* stands in the Rosana Reservoir might be generally described using some simple morphometric and limnological variables. Littoral slope, for example, was useful in predicting the width of *Egeria* stands (\(W_i\)). Higher \(W_i\) values were usually found where the slopes were smaller and it could be attributed to instability of the steeper areas. The minimum depth of colonization...
(Z_{\text{min}}) could be predicted by potential wave exposure (fetch). In addition, fetch also apparently interacted with other factors to determine Egeria Z_{\text{max}}. For example, at sites protected from wind exposure (arms) Secchi disk depth was an important variable for Z_{\text{max}} prediction, while at more-exposed sites (main axis) fetch was important in determining Z_{\text{max}}. Thus, Egeria tends to colonize deeper places at more exposed sites. Despite the general predictions outlined in this work, a great variability of data was not explained by the independent variables. Future studies in tropical reservoirs should consider other important factors such as sediment and water characteristics, which will certainly increase the predictive capacity of the models.

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