

# Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the Upper Paraná River floodplain (Brazil)

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**Abstract** The architecture of aquatic macrophytes adds structural complexity to the littoral region. This increased habitat heterogeneity prompts greater diversity and stability of biotic communities. However, there are few studies that explore the ecological role of macrophytes in the Neotropical region. Then, the aim of this study was to determine spatial and diel influence of near-shore *Eichhornia azurea* stands on fish assemblage attributes and structure, in the Upper Paraná River floodplain, considering a meso-habitat scale. To achieve this objective, fish were trapped in four stands of macrophytes, in three positions (middle and border of the stand and open area) with samplings taken at different times of the day (6 h, 12 h and 18 h). A total of 537 fish of 16 species were caught. Dissolved oxygen varied significantly among positions. Fish assemblage attributes (species richness, evenness and Shannon Diversity Index) also varied among positions. Fish assemblage structure (summarized by a detrended correspondence analysis) and size structure were strongly influenced by times of the day and positions. The patterns observed can be explained by factors such as oxygen concentration, food resource availability and predation, all influenced by macrophytes. We suggest that any

strategy to manage fish diversity and fish stocks has to consider aquatic macrophytes.

**Keywords** Conservation · Diversity · Fish · Fish–macrophytes relationships · Neotropical region

## Introduction

Aquatic macrophytes play an important role in structuring fish assemblages (Carpenter and Lodge 1986; Dibble et al. 1996; Agostinho et al. 2003; Slade et al. 2005). They provide higher carrying capacity for food resources due to the availability of substrates for prey and higher productivity. Also, macrophytes affect the balance of the forage efficiency of predators with refuge needs for prey (Miranda and Hodges 2000; Harrel and Dibble 2001). Thus, the increased habitat heterogeneity resulted from the presence of macrophytes, prompts greater diversity and stability (Schramm et al. 1987). However, high densities of these plants can lead to physical and chemical restrictions for fish, especially hypoxia at night during the hot season (Miranda et al. 2000). It is expected that these positive and negative effects on fish can explain their horizontal distribution and diel movements in lentic habitats near stands of macrophytes. The degree of response to these conditions is variable depending on fish assemblage composition, dominant life strategies and ontogenetic stage.

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However, fish densities are generally higher in stands with intermediate plant coverage (Dibble et al. 1996).

The role of macrophytes in the ecology of neotropical ichthyofauna is still not understood. There are some studies evaluating the effect of macrophytes coverage on fish assemblage structure in South America (Delariva et al. 1994; Fernandez et al. 1998; Meschiatti et al. 2000; Suarez et al. 2001; Vono and Barbosa 2001). For example, in shallow lakes, free-floating and submerged plants can be differently used by fish, depending on species, size classes and feeding habits (Meerhoff et al. 2003). Previous studies on shallow neotropical freshwater environments also showed that, in general, fish associated with macrophytes are typically small-sized species or juveniles of large species (Meschiatti et al. 2000; Delariva et al. 1994). Yet, when compared to open areas (macrophyte-free habitat), the littoral regions of neotropical systems have greater fish densities and species richness (Agostinho et al. 2003; Pelicice et al. 2005).

Meso-scale studies (comparisons between littoral and open areas) are scarce for the neotropical region, probably because sampling fish in vegetated habitats is difficult. In addition, most of the studies carried out in this region that tried to determine the importance of macrophytes on fish assemblages, sampled fish inside stands composed of different plant species, and/or inside stands with varying plant biomass, all lacking simultaneous catches in open areas. Similarly, previous studies on lagoons of the Upper Paraná River just inferred about the importance of macrophytes to fish. These studies did not consider simultaneous measurements of fish assemblage attributes in different habitats (pelagic vs. littoral regions) and they also did not apply experimental approaches that allow comparisons between these areas (e.g., Delariva et al. 1994). Therefore, in this study we used automatic pop nets to simultaneously sample inside and outside stands of macrophytes to test the hypotheses that fish assemblage richness and composition, as well as their diel fluctuation, are affected by the presence of plants.

#### Sampling area

Samplings were carried out in September 2001, in the Baía River, a semi-lentic tributary (water velocity  $< 0.05 \text{ m s}^{-1}$ ) of the Upper Paraná River

floodplain (located between  $22^{\circ}40' - 22^{\circ}50'$  S and  $53^{\circ}10' - 53^{\circ}24'$  W). Depth in the pelagic region is around five meters during high water but macrophytes colonize areas shallower than two meters. Bottom ranges from muddy to sand-muddy. Grasses dominate the bank and the landscape is used for ranching.

Four stands dominated by *Eichhornia azurea* were sampled. This plant is rooted in the sediment and its long floating stems (up to 8 m) develop within a few centimeters below the water surface, forming dense stands which can reach more than 50 m wide. It also has well developed roots attached to its nodes, remaining in contact with the water medium. Therefore, *E. azurea* stems and roots give additional structural complexity to the littoral regions.

#### Methods

A square floating enclosure trap type pop net (similar to the one described by Larson et al. 1986), with  $1.0 \times 1.0 \text{ m}$  and 2.0 m height, was used to capture fish. This gear has a net (5 mm mesh size) attached to a floating frame, which is maintained close to the bottom by a heavy metallic structure. An electronic mechanism activated by remote control releases the floating frame, which rapidly reaches the surface, enclosing plants and fishes inside it. Three pop nets were used simultaneously in each habitat (two underneath macrophytes and one in the pelagic region). Samplings were repeated in four consecutive days in different stands.

Before sampling, the trap remained at least 6 h onsite to minimize the effects of installation disturbance on fishes. To test the effect of time, samplings were carried out at 6 h, 12 h and 18 h, named here “time of the day” (4 replicates at each time of day). To test the spatial effect (meso-habitat) of aquatic vegetation, the trap was positioned in the pelagic region (open area) and in two places underneath macrophyte stands: in the middle of the stand and in its border (close to the pelagic zone), named here “positions” (4 replicates at each position). In all 36 samples, fish and aquatic macrophytes from inside the trap were collected. Aquatic plants were identified and fishes were counted, identified and measured (as standard length). To better understand the effect of the macrophyte stands on fish, selected abiotic factors

(water temperature and dissolved oxygen—YSI meter, and pH—Digimed meter) were measured with field equipments immediately after each sample at the sub-surface. To avoid obtaining biased readings due to water disturbances, measurements were done not inside but next to each pop net and boat approximations were made at very low speed. In addition, the pop net functioning mechanism (which goes from the bottom to the surface) minimizes water disturbances.

A two-way ANOVA was used to determine differences in abiotic factors according to time of the day and position (factors in ANOVA terminology). In relation to fish assemblages, the attributes species richness, evenness and Shannon Diversity Index were calculated. Differences in these attributes according to the factors considered were also tested through two-way ANOVA. As three tests were performed from the results of the same data matrix, we applied a multivariate analysis of variance (MANOVA) to assess if the differences on the assemblage attributes are not simply at random (Johnson 1998). This approach is also called protected ANOVA and the purpose is to reduce the probability of Type I error (Scheiner 1993). If the MANOVA is significant, it indicates the appropriateness of using the two-way ANOVAs for each attribute separately.

A detrended correspondence analysis (DCA, downweighting rare species to minimize their effect on the ordination) was performed to summarize fish assemblage structure (composition and abundance). Then, sample scores of the ordination were generated and analyzed through two-way ANOVA (time of the day and position as factors). We assumed that samples apart on the ordination presented distinct fish assemblage structure. Also, two-way ANOVA was used to determine differences in mean standard length of the fish assemblage, according to the same factors. An a posteriori Tukey test was applied whenever significant differences were found by ANOVA, to identify significant differences between individual pair of means.

## Results

Stands of *Eichhornia azurea* (the dominant species) were mixed with species such as *E. crassipes*, *Hydrocotyle ranunculoides*, *Salvinia auriculata*,

*S. minima*, *Oxycarium cubense*, *Limnobium laevigatum*, *Paspalum repens* and *Polygonum* spp.

Considering all times of the day (6 h, 12 h and 18 h) and positions (border, middle and open water) sampled, water temperatures were generally high. Averages ranged from 27.3°C (SE = 1.4) at 6 h in the middle of the stand to 29.4°C (SE = 2.5) at 12 h in the same position. Values of pH were slightly acid, average ranged from 6.5 (SE = 0.3) in the middle at 6 h to 6.9 (SE = 0.2) in the border at 18 h. For both variables, no significant differences among times of the day and positions were found (ANOVA;  $P > 0.05$ ).

Dissolved oxygen concentrations were usually greater than 6.0 mg l<sup>-1</sup>. Low concentrations (3.4–4.4 mg l<sup>-1</sup>) were recorded in only one sampling time, at 18 h, in all positions (inside and outside the stand). Mean oxygen concentration differed significantly only among positions (two-way ANOVA;  $F = 3.51$ ;  $P = 0.04$ ). The open area exhibited higher oxygen concentration (8.31 mg l<sup>-1</sup>) than middle (6.53 mg l<sup>-1</sup>) and border (7.68 mg l<sup>-1</sup>) of the stand (Tukey test a posteriori;  $P < 0.02$ ).

A total of 537 individuals belonging to 16 species were collected, most of them Characiformes (11 species) and Gymnotiformes (3 species). Captured fish were juveniles or small-sized species (size ranging from 1.1 to 26.2 cm; standard length—SL), with 87% smaller than 10.0 cm SL (Table 1). Abundant species were three characids (*Roeboides paranensis*, 41.6%; *Moenkhausia sanctaefilomenae*, 20.8%; *Hyphessobrycon* sp., 8.4%) and one gymnotid (*Eigenmannia virescens*, 7.3%). Only one species of Siluriformes was caught (*Hypostomus* sp., 1.9%).

The MANOVA applied to species richness, evenness and Shannon's diversity index was significant for time of the day (Wilks lambda = 0.61;  $P < 0.05$ ) and position (Wilks lambda = 0.49;  $P < 0.05$ ). Interaction was not significant (Wilks lambda = 0.48,  $P = 0.07$ ). These results indicate the appropriateness of applying separate ANOVAs for each attribute. Then, for all attributes, only the position factor showed significant differences (two-way ANOVAs, Table 2) and species richness, evenness and the Shannon diversity index were greater at the border (Tukey test a posteriori;  $P < 0.05$ ) (Fig. 1). All 16 species were recorded at the border. Six species were restricted to the border microhabitat (*Hypostomus* sp., *Aphyocharax anisitsi*, *Crenicichla britskii*,

**Table 1** Variation of abundance (fish. 4 m<sup>-2</sup>) and mean standard length (SL, cm; se = standard error) of fish species, considering sample position and time of the day

Species	Middle of the stand				Border of the stand				Open area						
	6 h	12 h	18 h	Total	SL ± se	6 h	12 h	18 h	Total	SL ± se	6 h	12 h	18 h	Total	SL ± se
	<i>Asyanax fasciatus</i>						6	2		<b>8</b>	3.0 ± 0.1		1		<b>1</b>
<i>Schizodon borellii</i>						1		4	<b>5</b>	7.2 ± 2.1					
<i>Aphyocharax anisitsi</i>								3	<b>3</b>	3.4 ± 0.2					
<i>Serrapinnus</i> sp.						8			<b>8</b>	3.1 ± 0.1					
<i>Serrapinnus notomelas</i>								1	<b>1</b>	3.4					
<i>Eigenmannia</i> sp.	3	1	1	<b>4</b>	8.8 ± 2.1	4		17	<b>21</b>	9.6 ± 0.9	5			<b>5</b>	10.3 ± 1.7
<i>Eigenmannia trilineata</i>	6	9		<b>15</b>	11.5 ± 0.3	13			<b>13</b>	7.7 ± 1.5		1		<b>1</b>	24.1
<i>Eigenmannia virescens</i>	6	4	4	<b>10</b>	8.9 ± 1.3	15		1	<b>16</b>	4.0 ± 0.6		13		<b>13</b>	12.6 ± 0.2
<i>Hyphessobrycon</i> sp.	1			<b>1</b>	3.0	31	6		<b>37</b>	2.9 ± 0.1		7		<b>7</b>	3.2 ± 0.2
<i>Moenkhausia intermedia</i>		8		<b>8</b>	2.9 ± 0.1	6			<b>6</b>	3.0 ± 0.2					
<i>Moenkhausia sanctaefilomenae</i>		10	22	<b>32</b>	3.7 ± 0.1	49	4	23	<b>76</b>	3.7 ± 0.1		4		<b>4</b>	3.7 ± 0.3
<i>Roeboides paramensis</i>	17	22	19	<b>58</b>	4.6 ± 0.2	80	39	36	<b>155</b>	4.8 ± 0.1	10			<b>10</b>	5.2 ± 0.3
<i>Hypostomus</i> sp.							9	1	<b>10</b>	3.4 ± 0.4					
<i>Crenicichla britskii</i>								1	<b>1</b>	14.2					
<i>Hoplias malabaricus</i>						1			<b>1</b>	16.2	2			<b>2</b>	24.1 ± 2.1
<i>Serrasalminus marginatus</i>							1		<b>1</b>	8.5			4	<b>4</b>	6.1 ± 0.2
Total	<b>33</b>	<b>40</b>	<b>55</b>	<b>128</b>		<b>214</b>	<b>61</b>	<b>87</b>	<b>362</b>		<b>17</b>	<b>26</b>	<b>4</b>	<b>47</b>	

Numbers in bold represent totals

**Table 2** Results of the analysis of variance (ANOVA) applied to assemblage attributes

Variables	Factors	DF (effect; error)	F	P
Species richness	Times (1)	2;27	0.90	0.42
	Positions (2)	2;27	<b>10.62</b>	<b>&lt;0.001</b>
	1*2	2;27	2.17	0.10
Evenness	Times (1)	2;27	0.29	0.75
	Positions (2)	2;27	<b>7.18</b>	<b>&lt;0.01</b>
	1*2	2;27	2.17	0.52
Shannon index	Times (1)	2;27	0.27	0.76
	Positions (2)	2;27	<b>10.69</b>	<b>&lt;0.001</b>
	1*2	2;27	1.03	0.41

Numbers in bold represent significant effects

*Serrapinnus* sp., *S. notomelas* and *Schizodon borelli*), whereas other six were recorded in all positions, but with different abundances (*Eigenmannia* sp., *E. trilineata*, *E. virescens*, *Hyphessobrycon* sp., *M. sanctaefilomenae* and *R. paranensis*). No species was restricted to the middle and open areas (Table 1).

Fish assemblage structure (summarized by a DCA) showed significant differences (interaction times of the day \* position;  $F = 3.71$ ;  $P = 0.02$ ) only for the first DCA axis (eigenvalues = 0.84). Species that contributed most to the formation of this axis are shown in Fig. 2a. Species distribution patterns among positions (middle, border and open area) were strongly influenced by time of the day (6 h, 12 h and 18 h) (Fig. 2b), suggesting an intense fish movement in the area.

The percentage of fish caught was greater in the border (67.3%) and lower in the open area (8.7%). This trend was verified throughout all time of the day, but differences in abundance increased in the morning. In the open area, maximum abundance of fish occurred at noon, whereas in the middle area at dusk.

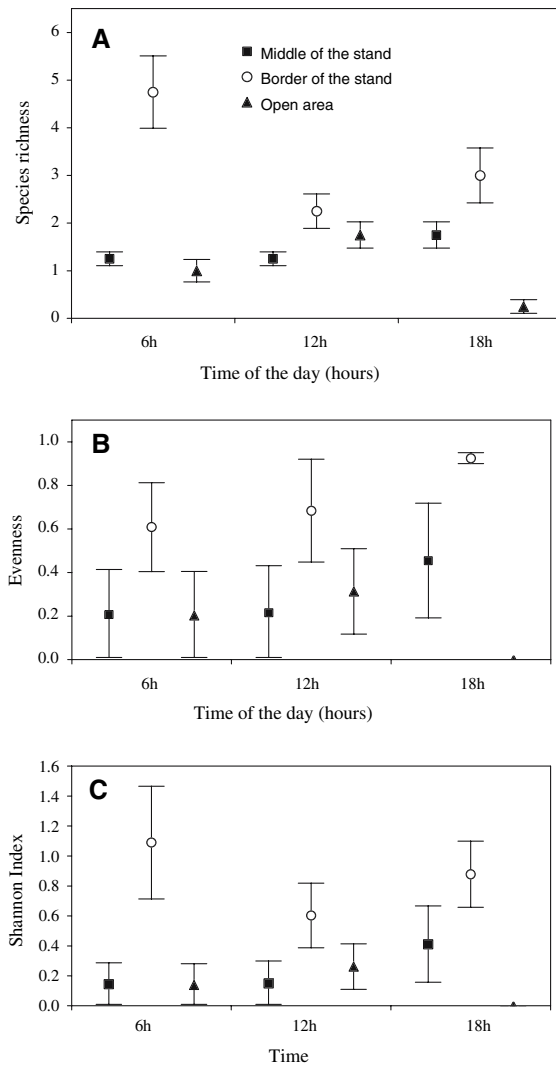
Mean standard length of fishes also showed spatial and temporal differences. The interaction among time of the day and position was significant (two-way ANOVA;  $F = 3.71$ ;  $P < 0.02$ ), indicating that fishes of different sizes moved in distinct ways in the area. Larger fishes were recorded in the morning in the open area (*Hoplias malabaricus*; *Eigenmannia trilineata*). A similar trend occurred at noon, but the main species was *Eigenmannia virescens*, smaller than *E. trilineata*. At dusk, mean standard lengths were more homogeneous among positions. Intra-specific variations on the standard length among

positions were conspicuous for the six species with broader distribution. In general, the largest individuals were caught in the open area, and the smallest in the middle of the stands (Table 1).

## Discussion

*Eichhornia azurea* colonizes channels, lagoons and backwaters of the Upper Paraná River floodplain where it may reach biomasses of up to 900 gDW m<sup>-2</sup> (Bini 1996). It is usually the dominant species of macrophyte and its relative abundance (biomass) in the lagoons fluctuates from 40% to 91% (average = 69%; SD = 22%; Thomaz, unpublished data). The presence of other species inside stands dominated by *E. azurea*, together with its architecture provides a complex structure to the littoral region. This is probably the main reason why fish assemblage attributes measured in our study were significantly affected by the “positions” of samplings (inside the stand × open area).

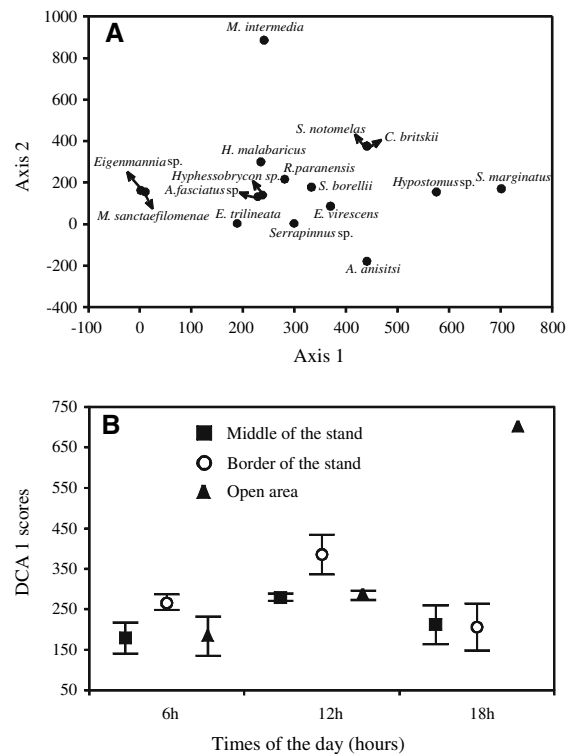
Aquatic macrophytes and their attached microorganisms usually have strong effects on water quality inside the stands (Carpenter and Lodge 1986; Esteves 1998). Dissolved oxygen, temperature and pH are among the most affected factors. Dissolved oxygen is an important abiotic variable determining fish distribution and it experiences wide diel fluctuations in littoral regions (Miranda et al. 2000). In fact oxygen concentrations were significantly lower in the middle of the stands. However, values were not restrictive to fish and the extent to which it can be related to the absence of some species



**Fig. 1** Species richness (A), evenness variations (B) and Shannon's Index (C), according to the time of the day and sampling position (vertical bars = standard error). Legend is the same for all figures

(lower richness) and to lower abundance inside stands deserves further investigation. Although we did not detect restrictive oxygen conditions, daily variations in floodplain lagoons are tremendous, and oxygen concentrations can be close to zero under floating macrophytes right before sunset (Jedike et al. 1989). If a similar situation occurred in our samples, it could explain the differences we observed between positions.

Values of water temperature were as expected for the September period, and pH was slightly acidic as



**Fig. 2** Results of the detrended correspondence analysis (DCA). Ordination of the species (A) and mean values of the sample scores for axis 1, according to time of the day and position (B) (vertical bars = standard error)

usual in lagoons of the Upper Paraná (Thomaz et al. 1997) and most of the inland waters of Brazil (Esteves 1998). Dominance of floating and emergent vegetation, along with massive decomposition of detritus in the littoral are the causes for such pH values. However, they were not restrictive to fish. Dominance of *E. azurea* provides a different habitat than submerged plants. The latter may lead to pH values close to 10 during periods of intense photosynthesis (Jones et al. 1996; Pierini and Thomaz 2004), which is restrictive for several fish species (Matthews 1998).

The dominance of small characids in vegetated water areas has also been described for other neotropical environments (Araújo Lima et al. 1986; Delariva et al. 1994; Meschiatti et al. 2000), but with different fish composition. This trend is common in lentic and semi-lentic habitats in the Paraná River floodplain where oxygen concentrations are low close to the bottom. This dominance can be explained by the ability of characins to uptake oxygen from the

surface layers of the water, which tend to contain more oxygen. In fact, Siluriformes, a group better associated with the bottom, were rare both in number of species and abundance (only one species was caught; *Hypostomus* sp.), in opposite to the regional pattern of the fish fauna (68 species of siluriformes out of 170; Agostinho and Julio 1999).

The significant effect of macrophytes on fish richness we observed is supported by other studies in the neotropical region (Vono and Barbosa 2001; Agostinho et al. 2003; Pelicice et al. 2005). The greater species richness and total catch registered in the border of the stand reflect the intermediate conditions of biotic and abiotic pressures (Agostinho et al. 2003). Restrictions on the efficacy of foraging for large (Matthews 1998; Priyadarshana et al. 2001) and small (Harrel and Dibble 2001) predators and low oxygen concentrations in the middle of the stands (Miranda et al. 2000) are not expected at the border. The decline on foraging efficacy is attributed to the effect of structure on swimming performance and reduction of the visual field volume (Manatunge et al. 2000). A solid cover of floating plants also prevents photosynthesis by shading, reduces the contact area between water and atmosphere and presents itself a partial decay, leading to low oxygen concentrations (Riemer 1984).

Predation might explain the absence of species restricted to the open area and differences in size composition, according to time of the day and position. In fact, smaller individuals (more vulnerable to predation) were caught in the middle of the stands, where protection against predation is expected to be higher. Experiments carried out in other freshwater ecosystems have shown that fish can detect predators by chemical and visual cues that lead them to spend more time in the vegetation (Lehtiniemi 2005).

Size variability, greater in the open area, also indicates movement among the positions considered. Size reductions were observed at dusk in the open area, for all six most abundant prey species. As light level declines, at dusk, a decrease in predation from visual hunters is expected (Wootton 1990). Then, smaller fish can occupy the open area, making spatial differences in size composition not conspicuous. The feeding activity of the two main predators (*Hoplias malabaricus* and *Serrasalmus marginatus*) is higher in the morning and middle of the day (Loureiro and Hahn 1996; Agostinho et al. 1997). Birds, which are

mainly active during the day, are also abundant in the Upper Paraná River floodplain (Gimenes and Anjos 2004; Mendonça et al. 2004), and they are another potential source of predation upon small fish. It has been shown, for example, that the function of *Phragmites* (an emergent macrophyte) as a refuge against bird predation was the probable cause of a strong daytime preference for macrophytes exhibited by several fish groups (Okun and Mehner 2005).

Fish assemblage structure and its daytime variations, described in this study, could be explained by factors such as food resource availability, predation (presence of piscivores) and probably oxygen restrictions, all recognized as important for fish distribution specially when macrophytes are present (Mittlebach 1981; Savino and Stain 1982; Miranda et al. 2000). In spite of the limitation imposed by our dataset (low sampling effort through time), it appears that the presence of *E. azurea* is a key factor in the conservation of the high fish diversity in the floodplain of the Upper Paraná River. Apparently the role of this plant has become more important in recent years, since the abundance of the introduced piscivorous peacock-bass *Cichla kelberi* is increasing in floodplain lagoons, and consequently, intensifying predation pressure. As *E. azurea*, along with several other species of macrophytes, is common in other freshwater ecosystems in South America (e.g., Nogueira and Esteves 1990; Cavenaghi et al. 2003; Henry and Costa 2003), strategies to manage fish diversity and fish stocks have to seriously consider the role-played by aquatic macrophytes in these ecosystems.

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