Dense macrophytes influence the horizontal distribution of fish in floodplain lakes

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Abstract Fish species distribution is commonly influenced by aquatic macrophytes. Despite of the usage of these plants as habitats for refuge, feeding and reproduction by fish, too dense macrophyte stands make microhabitats unsuitable for certain fish species. Moreover, the distance from the open water within macrophyte stands may also affect fish species distribution because of increasingly harsh conditions. In order to test differences in species distribution of small-sized fish within macrophyte stands we sampled stands of *Eichhornia* spp presenting low and high levels of macrophyte density and at several distances from the open water (0, 3, 6, 9, 12 and 15 m). We measured depth, temperature, dissolved oxygen, conductivity and pH of the water column and attributes of the fish assemblages. We captured 1,167 individuals of fish belonging to 24 species. Oxygen was significantly higher in lower levels of macrophyte density and similar patterns were found for fish abundance and species richness. These results indicate that, in general, small sized-fish prefer less dense macrophyte stands. In addition, both depth and oxygen were significantly higher at the closest distance from open water, where the composition of fish species was also distinct from those found in other distances. In accordance with changes in species composition, different fish species showed divergent distribution along distances from the open water. Together these results demonstrate that oxygen content influences fish species composition, and indicate that fish species are able to use less suitable microhabitats most likely because of morphological, physiological and behavioral adaptations.

Keywords *Eichhornia* · Ichthyofauna · Littoral zone · Respiratory adaptation · Niche partitioning

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Introduction

Small-sized fish species are diverse and abundant in neotropical aquatic ecosystems, where they commonly inhabit macrophyte stands. These fish usually seek macrophytes for refuge (Persson and Eklov 1995; Sánchez-Botero et al. 2007; Meerhoff et al. 2007b) because the physical structure provided by these plants reduce the chance of being visualized by active predators (Kovalenko et al. 2012), and consequently, they become less likely to be predated (Rozas and Odum 1988). In addition, small-sized fish may also be attracted toward macrophytes because of food availability (Werner et al. 1983a; Werner et al. 1983b). The structure provided by these plants commonly harbor a great density and diversity of periphytic algae (Rodrigues et al. 2003; Schneck et al. 2011) and associated invertebrates

(Tanigushi et al. 2003; Warfe and Barmuta 2006; Thomaz et al. 2008), which are, in turn, the most common feeding items consumed by small-sized fish species (Agostinho et al. 2003; Sánchez-Botero et al. 2007). Considering such conditions of safety and food availability, these fish species may grow and re-produce successfully in macrophyte stands (Conrow et al. 1990; Sánchez-Botero and Araújo-Lima 2001; Sánchez-Botero et al. 2007), explaining the common use of these plants as habitats.

Despite of commonly using structured habitats in contrast to open areas, small-sized fish may select more dense or sparse vegetation depending on how they interact with the habitat. For example, small-sized fish may avoid too dense vegetation stands because of conditions of hypoxia or because macrophyte steams, leaves and roots work as a physical barrier, hampering the movement and obstructing the vision (Harrel and Dibble 2001). Alternatively, some fish species may particularly use habitats provided by dense vegetation due to specific biological adaptations (e.g., tolerance to low levels of oxygen) and particular strategies of life (e.g., ambushers).

In addition to being affected by differences in vege-tation density, the spatial distribution of small-sized fish may differ within macrophyte stands (e.g., Agostinho et al. 2007). The patch formed by these plants commonly provide a mosaic of physical and chemical conditions (Miranda et al. 2000), which is most likely driven by differences in the morphology of lakes and decreasing influence of limnetic zone as the distance from the open water increases (e.g., Agostinho et al. 2007). Conse-quently, the distribution of small-sized fish is a result of tradeoffs between fish avoidance and selectivity re-garding environmental aspects.

Studies describing the distribution of small-sized fish in macrophyte stands commonly focused in testing dif-ferences between vegetated and non-vegetated environ-ments (Agostinho et al. 2003; Pelicice et al. 2005; Gomes et al. 2012), between stands of macrophytes composed by different macrophyte species (Fernandez et al. 1998; Meschiatti et al. 2000; Suarez et al. 2001; Vono and Barbosa 2001; Sánchez-Botero et al. 2003; Meerhoff et al. 2003, 2007a; Prado et al. 2010; Dibble and Pelicice 2010), between macrophytes providing different habitat complexities (Dibble and Pelicice 2010) and between stands of macrophytes of the same species that vary

across spatial scales (Delariva et al. 1994; Pacheco and Da-Silva 2009; Teixeira de Mello et al. 2009; Milani et al. 2010). Despite of this, as far as we know, no investiga-tions concerned to describe concomitantly the distribu-tion of small-sized fish species along a refined gradient of macrophyte patches and vegetation density. This may provide basis for a better understanding of the distribution of small-sized fish within macrophyte stands.

Regarding these aspects, we hypothesized that abun-dance, species richness, evenness and composition of small-sized fish using habitats of different levels of vegetation density and position along macrophyte stands differ. In addition, we hypothesized that the dis-tribution of different species along the horizontal gradi-ent differ because of particular biological aspects and adaptations of fish species. The rationale behind these hypotheses relies on the differences concerning habitat use. In addition, in this study we aimed to describe the variation in the spatial use of habitat by small-sized fish in different vegetation density and in different location of horizontal gradients within macrophyte stands. In order to achieve this objective we sampled large stands of *Echhornia azurea* (~300 m^2), a rooted floating leaved macrophyte, which are broadly distributed in neotropi-cal aquatic ecosystems and provide habitat for small-sized fish.

Materials and methods

Study area

We surveyed three different lakes (Maria Luiza, Careca and Onça) connected to Baia River, a tribu-tary of the upper Paraná River floodplain (Fig. 1). The lakes are shallow (3 m on average) and have extensive stands of aquatic macrophytes along their shores, colonizing the littoral zone for more than 15 m towards open water. Most common macrophyte species dominating the waterscape is *Eichhornia azurea* (Sw.) Kunth (rooted floating leaves), but some *Eichhornia crassipes* (Mart.) Solms, a free floating species which is quite similar regarding morphology, also occur. Taking into ac-count the typical configuration of the stands of aquat-ic macrophytes, we considered for sampling those stands which were at least 300 m^2 (20–40 m along
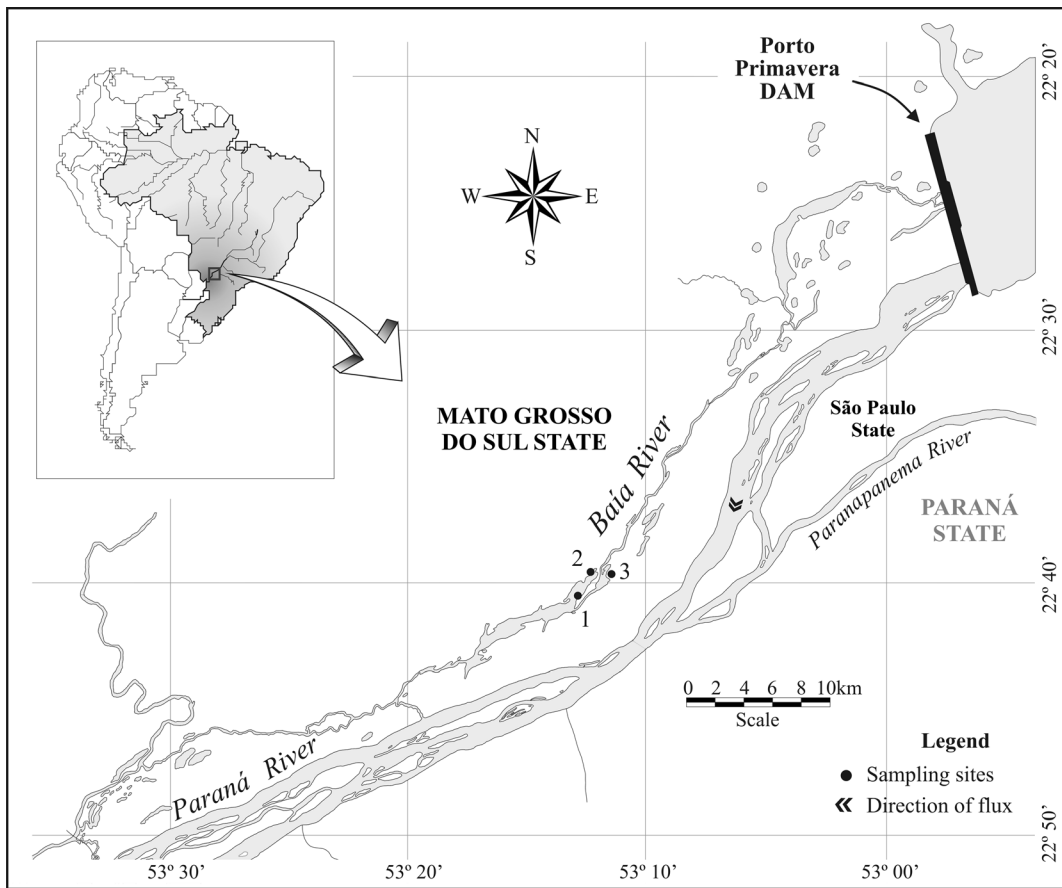
Fig. 1 Map of the study area with the three sampled lakes located in the Baia River, Upper Paraná River floodplain - Brazil. 1 – Maria Luiza Lake, 2 – Careca Lake and 3 – Onça Lake

the margins and 15–25 m towards open water), ensuring large availability of habitat for fish and reduced effect of borders.

Sampling

In December 2011, two macrophyte stands were haphazardly selected in each lake, with at least 100 m of distance between each other. As a rule-of-thumb, one of the stands presented a visually expressive higher macrophyte density (termed hereafter vegetation density) than the other. This characterizes two levels of vegetation density as habitat for fish, for which statistical differences were formalized after the fact (see methods and results). In each stand, we determined six different distances from the threshold between the pelagic zone and macrophyte

patch toward the shore (0, 3, 6, 9, 12 and 15 m), characterizing habitat for fish regarding six different levels of separation from open water. Distances were considered from the threshold between the pelagic zone toward the shore due to three main reasons. First, this area commonly harbor great density of fish; second, some stands may extend further than 15 m towards open water; and third, the morphology of floodplain lakes produce tenuous shorelines, usually presenting harsh conditions for fish.

In each combination of vegetation density and distance from the open water we characterized physical and chemical aspects of water column, measured plant biomass and sampled fish. Physical and chemical characteristics of the water column were described by depth (cm), temperature (°C), dissolved oxygen (mg.L^{-1}),

conductivity ($\mu S.cm^{-1}$) and pH. Measurements were taken twice, early in the morning and in the evening, and mean values were used for analyses. The plant biomass were measured by removing all the submerged structures of macrophytes (including roots and stems) inside a 0.5 × 0.5 m square and drying (60 °C) to constant weight. Values were expressed as $gDW.m^{-3}$.

Fish were sampled using plexigas-type minnow traps (described elsewhere in Dibble and Pelicice 2010 and Cunha et al. 2011) (Fig. 6 in Appendix), which were set early in the morning and checked for fish each 12 h to a total sampling effort of 24 h. This type of gear captures small-sized fish (size range: 0.6–4.7 cm; mean size: 2.4 cm) (Dibble and Pelicice 2010), which are the most common inhabiting macrophyte stands, and provide an representative overview of the assemblage by capturing fish in an effective way and requiring no changes in habitat structure to set up the device (Ribeiro and Zuanon 2006). Fish captured along the 24 h were counted and identified to species according to Graça and Pavanelli (2007) and Mirande (2010), and expressed in terms of abundance index (individuals per trap per 24 h), species richness and evenness.

Data analysis

We used two-way ANOVA to test differences in depth, temperature, dissolved oxygen, conductivity, pH, plant biomass, fish abundance, species richness and evenness between vegetation densities and distances from the open water. Tukey tests were used as *a posteriori* comparisons in order to assess differences between treatments. These analyses were run using the Statistica™ software (Statsoft 2007).

To summarize the structure of the fish assemblage we used a non-metric multidimensional scaling (NMDS) on the Bray-Curtis resemblance matrix obtained from square root transformation of relative abundance of species (Legendre and Gallagher 2001). Differences between vegetation density, distances from the open water and their interaction for species composition were assessed using a permutational analysis of variance (PERMANOVA *main test*) applied to the Bray-Curtis resemblance matrix (Anderson et al. 2008). When the PERMANOVA was significant, we conducted a pairwise test to assess differences between treatments. Monte Carlo permutations (n=9999) were used to test for

statistical significance ($p<0.05$). These analyses were run using the PRIMER 6 with the *add on* Permanova™ software (Clarke and Gorley 2006; Anderson et al. 2008).

The relationships of the environmental variables, other than vegetation density and distance from the open water, with the fish assemblage were evaluated using BioEnv (Clarke and Ainsworth 1993). The purpose of BioEnv is to find the best match between the multivariate among-sample patterns of an assemblage and the environmental variables. BioEnv creates models using all possible combinations of environmental variables. The extent to which the two patterns expressed as dissimilarity matrices match reflects the degree to which the chosen abiotic data are related with the biotic patterns (Clarke and Gorley 2006). For this analysis the abundance matrix was square-root-transformed to obtain Bray-Curtis dissimilarity matrix and environmental variables were normalized before obtaining the environmental matrices based on Euclidean distance. The Spearman correlation coefficient (ρ) was used to measure the association between dissimilarity matrices. This analysis were run using the PRIMER 6 software with the *add on* Permanova™ (Clarke and Gorley 2006; Anderson et al. 2008).

Additionally, to investigate the preference of most abundant species in regard to habitat use along horizontal gradients we tested differences in optimum abundance of fish along transects between fish species and vegetation densities. The optimum abundance indicates at which point of a gradient a given species presents the highest abundance. To estimate the optimum abundance we used the weighted averaging approach, which consists in average the distances where the species occur weighted by its abundance (Šmilauer and Lepš 2014). For calculation, we summed 1 to the values of distance from the open water in order to avoid weighting for 0 and before statistical analysis and graphical representation this constant were subtracted. We used two-way ANOVA to test differences in optimum abundance along transects between vegetation densities, most abundant fish species, and their interactions. Tukey tests were used as a posteriori comparisons in order to assess differences between treatments. These analyses were run using the Statistica™ software (Statsoft 2007).

Results

As the distance within the macrophyte stands increased from the pelagic towards the littoral zone, the depth decreased for both levels of vegetation density (stands with high and low densities) (Fig. 2a). Depth varied significantly with distances from the open water (two-way ANOVA; $F = 3.76$; $p = 0.01$), but not with vegetation density or interaction (two-way ANOVA; $F < 0.13$; $p > 0.50$). The depth at the distance of 0 m differed from the depth at distances of 12 m (Tukey test; $p = 0.04$) and 15 m ($p = 0.03$) (Fig. 2a). Water temperature did not differ according to any factor (two-way ANOVA; $F < 0.06$; $p > 0.98$) (Fig. 2b).

The concentration of oxygen was, in general, greater in the stands with less vegetation density. In general, the highest concentration of oxygen was registered near the pelagic zone (at distance 0 m), and it decreased with increasing distance from the open water (Fig. 2c). This variable differed significantly between levels of vegetation density (two-way ANOVA; $F = 8.28$; $p < 0.01$) and distance from the open water (two-way ANOVA; $F = 15.60$; $p < 0.01$),

but the interaction was not significant (two-way ANOVA; $F = 2.22$; $p = 0.08$). Considering pair-wise comparisons, only the concentration of oxygen registered at the distance of 0 m from open water differed from the oxygen concentrations registered in other distances (Tukey test; $p < 0.01$) (Fig. 2c).

Regarding mean conductivity, this variable generally presented higher values in stands with higher vegetation density, resulting in statistical significant differences (two-way ANOVA; $F = 9.66$; $p < 0.01$). Despite of decreasing values of this variable in response to distance from the open water in the stands with low density, no statistical differences were detected for this factor or for the interaction term (two-way ANOVA; $F < 2$; $p > 0.10$) (Fig. 2d). Finally, pH did not differ according to any factor (two-way ANOVA; $F < 0.80$; $p > 0.58$; check Table 2 in Appendix for more detailed information about variables) (Fig. 2e).

Plant biomass was significantly different between the stands with low and high levels of vegetation density (two-way ANOVA, $F = 9.14$, $p = 0.006$), thus confirming the previous visual determination of
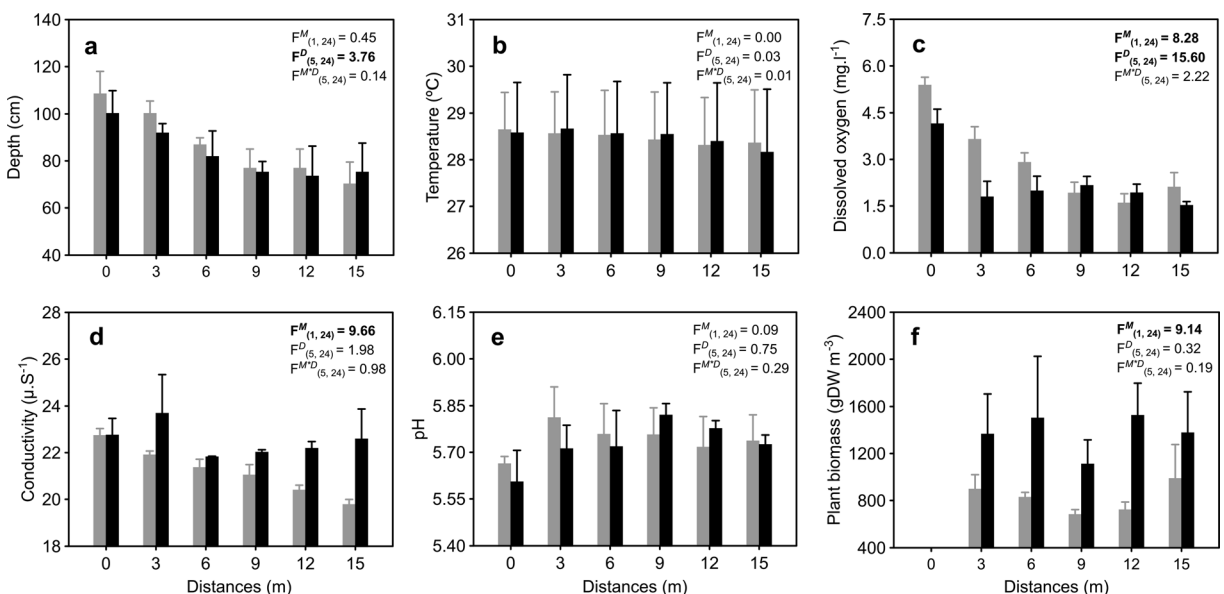
Fig. 2 Mean and standard error of depth (cm) (**a**), temperature (°C) (**b**), dissolved oxygen (mg.L^{-1}) (**c**), conductivity (μS.cm^{-1}) (**d**), pH (**e**) and plant biomass (gDW m^{-3}) (**f**) in macrophyte stands with low (grey) and high (black) vegetation densities (^{M}) and at distances (^{D}) of 0, 3, 6, 9, 12 and 15 meters from open water toward shoreline. Values in bold correspond to $p < 0.05$ in a two-way ANOVA

vegetation density treatments (Fig. 2f). Despite of the difference between low and high vegetation densities, no differences were detected for distance from the open water or for the interaction term (F<0.35; p>0.50) (Fig. 2f).

Regarding fish assemblage, a total of 1,167 individuals were collected in the stands. They belonged to two orders (Characiformes and Perciformes), seven families, 18 genera and 24 species of fish. The most abundant species were in general characids, represented by *Hyphessobrycon eques* (Steindachner, 1882) (n= 249), *Moenkhausia bonita* (Benine, Castro & Sabino, 2004) (n=248), *Serrapinnus heterodon* (Eigenmann, 1915) (n=179), *Aphyocharax anisitsi* (Eigenmann & Kennedy, 1903) (n=147), *Moenkhausia* aff. *sanctaefilomenae* (Steindachner, 1907) (n=90) and *Psellogrammus kennedyi* (Eigenmann, 1903) (n=77) (Table 3 in Appendix).

Considering the abundance of fish, this variable significantly differed between vegetation densities (two-way ANOVA; F = 10.2; p < 0.01); this response variable was higher in stands with low vegetation density (Fig. 3a). With regards to species richness, this variable differed significantly only between levels of vegetation density (two-way ANOVA; F=7.06; p= 0.01). Despite the low richness near to the pelagic zone (0 m from the open water), when compared to richness at other distances from the open water, neither the distance from the open water nor the interaction term was significant (two-way ANOVA; F<2.1; p>0.10) (Fig. 3b). Evenness was also higher in stands with less density, but the factors and their interaction

had no significant effects (two-way ANOVA; F<2.2; p>0.15) (Fig. 3c).

The two-dimensional configuration of the NMDS presented a good representation of the data (stress=0.17 after 9999 interactions). In general, composition of fish species overlapped in different levels of vegetation density, indicating that fish assemblages did not differ (PERMANOVA; Pseudo-F=2.6; p=0.30; Fig. 4a). Despite of the high variability found among distances from the open water, this variable significantly affected fish species composition (Fig. 4b; PERMANOVA; Pseudo-F=2.2; p<0.01). This difference was evidenced by the fish assemblage sampled at the distance of 0 m, which was the only level of distance from the open water differing from other levels (Pair-wise comparisons; p< 0.05 for comparisons between 0 m and all other distances). Considering the interaction between vegetation density and distance from the open water, no significant difference was detected (PERMANOVA; Pseudo-F=1.1; p=0.37).

The BioEnv analysis showed all possible combinations of physical and chemical variables related to abundance of fish species. The ten models with the highest Spearman correlations (ρ) were selected to demonstrate the most important variables (Table 1). Dissolved oxygen was present in all of the best models (10), followed by pH (7) and depth (6). Therefore, among the considered variables, dissolved oxygen was the most important in explaining assemblage structure (ρ=0.44, p<0.01 (Table 1)).
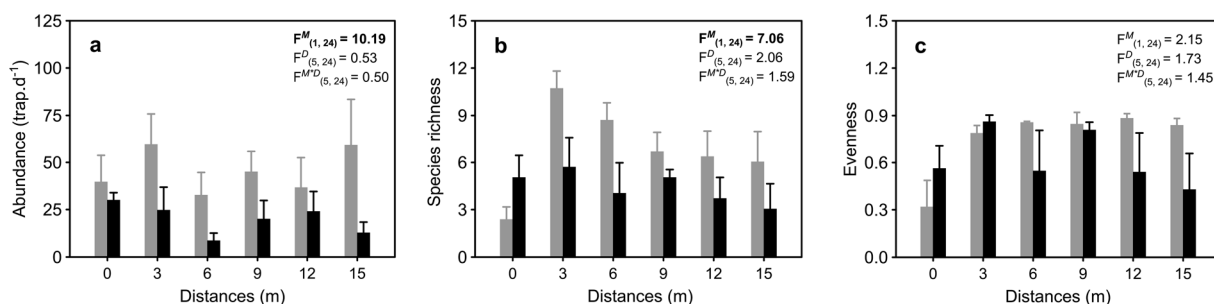
Fig. 3 Mean and standard error of the fish assemblage attributes: abundance (**a**), species richness (**b**) and evenness (**c**) in macrophyte stands with low (grey) and high (black) levels of vegetation density (^{M}) at distances from the open water (^{D}) varying from 0 to 15 meters. Values in *bold* correspond to p<0.05 of a two-way ANOVA
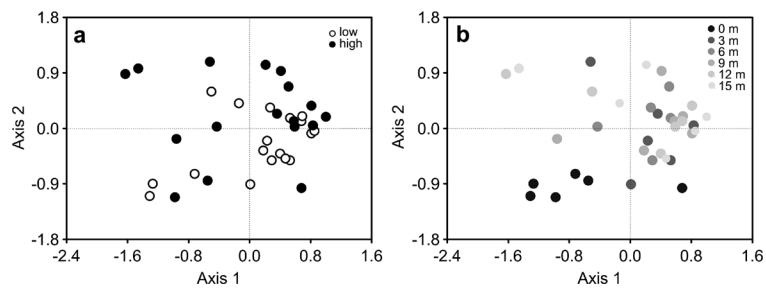
Fig. 4 Ordination results obtained by the non-metric multidimensional scaling (NMDS), which summarized fish assemblages according to the factors vegetation density (macrophytes stands with low and high levels of vegetation density) (**a**) and distance from the open water (0, 3, 6, 9, 12 and 15 m) (**b**)

The optimum abundance of small-sized fish along horizontal gradients differed between fish species (two-way ANOVA; F=4.18; $p<0.05$), but no differences were found between levels of vegetation density (two-way ANOVA; F=3.5; $p=0.07$) or interaction term (two-way ANOVA; F=1.28; $p=0.29$; Fig. 5). In general, *M. bonita* presented its optimum abundance in regions close the open water, and differed from *H. eques*, *S. heterodon* and *P. kennedyi* in terms of habitat use (Tukey test; $p<0.05$). Both *H. eques* and *S. heterodon* presented greatest abundances from the middle of the transect to the farthest distances from the open water, differing significantly from *S. notomelas*. *Psellogrammus kennedyi* had its distributions restricted to the regions farthest from the open water, but was only significant different from *S. notomelas* (Tukey test; $p<0.05$). The species *H. eques*, *M.* aff. *sanctaefilomena* and *S. heterodon* was found in all of the distances from the open water and vegetation density of stands (Table 3 in Appendix).

Discussion

The mean number of fish species and abundance were lower in macrophyte stands with high vegetation density than stands with low vegetation density, indicating that in general small sized-fish prefer less dense macrophyte stands. These patterns may be a result of interaction with different aspects of the environment. For example, species richness decreased with gradually distances from the open water toward shoreline only in stands with low vegetation density. These trends in habitat use by different species were probably related to the reduction of dissolved oxygen, given that oxygen content followed the same patterns. The variability in oxygen concentration is commonly associated with the shallow waters of the littoral region and the horizontal variation in vegetation density (through the width of the stand) and can be explained by different but not excluding mechanisms.

The morphology of floodplain lakes is generally marked by greater depths in the center than near the margins due to depositional processes. This morphology was evident in this study among distances closer to the open water that did not significantly differ in depth. Thus, a greater distance from the limnetic region (i.e., further inside the stand and closer to the shoreline) indicates a shallower depth and a greater influence of the heterotrophic process in the sediment, which in turn lead to low pH because of oxygen consumption caused by decomposition (Miranda and Hodges 2000; Esteves and Gonçalves 2011). The difference between the vegetation density of the stands and the horizontal variation in plant biomass (distances from the open water) can be caused by differences in the densities of roots and leaves, the degree of maturity of the macrophytes, the stage of colonization of epiphyton and the species composition (Miranda et al. 2000). In addition, the stands of macrophytes in this study were composed predominantly of the *E. azurea*, a species with an emergent photosynthetic portion and root structures disposed in the water column. The

Table 1 Best BioEnv models for fish abundance in macrophyte stands with low and high vegetation densities at distances of 0, 3, 6, 9, 12 and 15 m from the open water, in response to physical and chemical variables

Models	Selected variables	Rho (ρ)
1	Dissolved oxygen	0.44
2	Depth+Dissolved oxygen+pH	0.42
3	Depth+Dissolved oxygen+Conductivity+pH	0.42
4	Dissolved oxygen+pH	0.41
5	Depth+Dissolved oxygen	0.40
6	Depth+Temperature+Dissolved oxygen+pH	0.40
7	Depth+Temperature+Dissolved oxygen+ Conductivity+pH	0.40
8	Temperature+Dissolved oxygen+pH	0.39
9	Depth+Dissolved oxygen+Conductivity	0.39
10	Dissolved oxygen+Conductivity+pH	0.39

emergent structures resist the wind action on the water surface, which hampers the diffusion of atmospheric oxygen (Sand-Jensen 1989). These kinds of macrophytes also release most part of the oxygen produced by photosynthesis directly to the
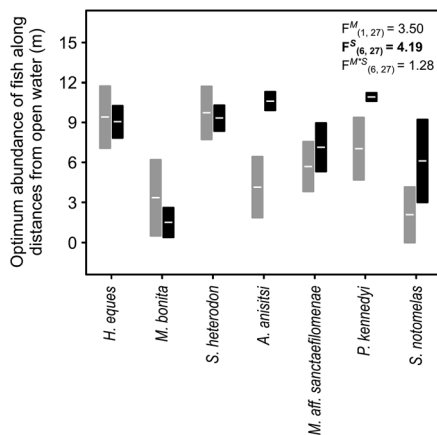
Fig. 5 Optimum abundance of small-sized fish along distances from the open water in macrophyte stands with low (grey) and high (black) levels of vegetation density (M) and different species of fish (S). Horizontal markers and rectangles respectively indicate mean and standard error of the distances from the open water where individuals of fish species most commonly occurred

atmosphere (Pokorný and Rejmánková 1984; Goodwin et al. 2008). Moreover, macrophyte roots retains organic matter (Poi de Neiff et al. 1994), thereby raising oxygen consumption. All of these factors contribute to the low oxygen concentrations in regions close to the shoreline (distances higher than 15 m from the open water), where vegetation tends to be denser, presenting harsh conditions to fish species.

Plant biomass may also lead to abiotic constraints that affect the distribution of small-sized fish. When the entire stand was considered, the ones with higher vegetation density had fewer fishes probably due to the physical restrictions. Regarding the position within the stands, the difference in the fish assemblages of the limnetic region (0 m from open water) compared with those inside the macrophytes stands was previously expected, given that it has been demonstrated in other studies conducted in the same area (Agostinho et al. 2007; Gomes et al. 2012). Though the oxygen content was adequate in the limnetic region, the fish species richness was higher in stands with lower density and at the distance of 3 m from open water toward shoreline for both levels of vegetation density, which is in accordance with the results obtained by Agostinho et al. (2007). They find the highest fish richness near the edge of the macrophyte stands. In the limnetic region (at distance 0 m), we also found lower values for species richness and evenness due to the dominance of *M. bonita*. The preference of small-bodied fishes for the edges of the stands is related to specific levels of vegetation density offered by these environments, which can reduce predation (Sánchez-Botero et al. 2003; Pelicice et al. 2005), and to the widespread availability of food resources due to the adequate concentrations of oxygen.

Despite the changes with increasing distance from the open water, we did not find significant differences in the assemblage structure in relation to this environmental variable. One reason for this was that the range of plant biomass was not a continuum, i.e., vegetation densities varying proportionally with the distance from the edge, and so, detectable changes in assemblage structure are

restricted to closest distance from the open water. Other explanation consider the fact that in some stands the vegetation density decreased at distances of 12 and 15 m, forming oxygenated patches. This may occasionally favor more species of small-sized fish increasing the variation in assemblage structure.

Notwithstanding, we found that the most abundant species seems to select a preferred habitat within macrophyte stands. *Moenkhausia bonita*, for instance, most commonly used the borders of the macrophyte stand (lower distances within the stands) and this might probably mirrors adaptive strategies of exploiting high quality resources, while successfully protecting themselves through schooling behavior. This species are commonly found foraging in groups from 10 to 30 individuals (Benine et al. 2004). In contrast, a congeneric species, *M.* aff. *sanctaefilomenae*, does not share the microhabitat with *M. bonita*, which may indicate displacement caused by lower competitive capabilities. Despite of these, the adaptive plasticity of *M.* aff. *sanctaefilomenae* may allow these species to coexist in broader scale (stand scale), which is also suggested by its feeding plasticity (Crippa et al. 2009). Similar to *M.* aff. *sanctaefilomenae*, *A. anisitsi* and *S. notomelas* coexist because of the food segregation (Hahn and Crippa 2006).

Otherwise, *H. eques* and *P. kennedyi* were quietly restricted to farthest distances from the open water. The distribution of these species remarkably mirrors adaptations to low oxygen conditions, which is also a reasonable explanation to the distribution of other species which were found in many levels of vegetation density and distances from the open water, even at oxygen concentrations below 1.5 mg.L^{-1}. Previous studies show that species of the genera *Hyphessobrycon*, *Aphyocharax*, *Astyanax* and *Acestrorhynchus* may develop dermal lip protuberance, an adaptation for breathing in the water-air layer, in conditions of hypoxia (Scarabotti et al. 2011). Species sampled in our study such as *H. eques*, *A. anisitsi*, *Astyanax altiparanae* (Garutti & Britski, 2000) and *Acestrorhynchus lacustris* (Lütken, 1875) should

also have the same adaptation, considering phylogenetic conservatism (Winemiller 1989; Scarabotti et al. 2011). Other abundant species found in macrophyte stands such as *M.* aff. *sanctaefilomenae*, *S. heterodon* and *P. kennedyi* are considered opportunistic species, which are commonly adapted to survive in extreme conditions (Winemiller 1992; Lourenço et al. 2008; Gonçalves et al. 2011). Other examples of tolerance to low oxygen conditions include less common species, for example, *Hoplerythrinus unitaeniatus* (Agassiz, 1829) and *Erythrinus erythrinus* (Bloch & Schneider, 1801). These species are facultative air breathers (Oyakawa 2003), and have the ability to diffuse atmospheric oxygen into their bloodstream through the swim bladder, capturing gas through frequent ascents to the water surface (Lima-Filho et al. 2012).

In summary, our findings suggest that fish may use different levels of vegetation density and position within stand of *E. azurea*, which is the most widespread macrophyte structuring habitat for fish in neotropical ecosystems. Despite of some restrictive conditions, the horizontal gradient may mediate segregation between different species in terms of distribution. Thus, these results indicate that environmental factors may be determinant to habitat specialization within large stands of macrophytes. This is probably favored by morphological respiratory (air breathing and superficial air breathing), physiological and behavioral adaptations.

Appendix

Table 2 Mean (standard deviation) values for physical and chemical variables in macrophyte stands with low and high densities, at distances from 0 to 15 meters in the Maria Luiza, Careca and Onça lakes

Lakes (Distance)		Depth (cm)		Temperature (°C)		Dissolved oxygen (mg.L^{-1})		Conductivity (µS.cm^{-1})		pH	
		Low	High	Low	High	Low	High	Low	High	Low	High
Maria Luiza	0	110.00 (0.00)	120 (0.00)	30.05 (1.91)	30.50 (2.69)	5.92 (0.98)	4.88 (2.59)	22.10 (0.57)	21.70 (0.99)	5.62 (0.01)	5.50 (0.08)
	3	100.00 (0.00)	100.00 (0.00)	30.00 (2.26)	30.95 (2.76)	3.36 (0.01)	2.60 (0.87)	22.00 (0.42)	21.55 (0.35)	5.85 (0.03)	5.66 (0.12)
	6	90.00 (0.00)	100.00 (0.00)	30.10 (2.55)	30.75 (2.47)	2.23 (2.02)	2.46 (1.75)	21.55 (1.63)	21.85 (0.78)	5.79 (0.10)	5.76 (0.21)
	9	60.00 (0.00)	80.00 (0.00)	30.15 (2.76)	30.80 (2.40)	2.59 (1.79)	2.79 (1.90)	20.59 (2.70)	22.05 (0.64)	5.81 (0.13)	5.83 (0.18)
	12	60.00 (0.00)	100.00 (0.00)	30.05 (2.62)	30.90 (2.40)	2.00 (1.87)	1.47 (1.12)	19.90 (3.12)	22.30 (1.84)	5.81 (0.21)	5.74 (0.15)
	15	50.00 (0.00)	100.00 (0.00)	30.15 (3.18)	30.75 (2.05)	2.50 (2.57)	1.36 (1.20)	20.18 (2.16)	24.70 (5.80)	5.79 (0.26)	5.66 (0.08)
	Mean	78.33 (23.68)	100.00 (11.55)	30.08 (1.09)	30.78 (1.16)	3.10 (1.90)	2.59 (1.66)	21.05 (1.76)	22.36 (2.10)	5.78 (0.14)	5.69 (0.14)
Careca	0	90.00 (0.00)	85.00 (0.00)	27.10 (0.28)	26.55 (1.06)	4.97 (1.19)	4.36 (0.72)	23.25 (1.63)	24.25 (4.31)	5.71 (0.31)	5.82 (0.17)
	3	90.00 (0.00)	85.00 (0.00)	26.75 (0.64)	26.75 (0.78)	3.04 (0.84)	2.00 (0.53)	22.15 (0.07)	22.30 (0.71)	5.61 (0.33)	5.87 (0.33)
	6	80.00 (0.00)	60.00 (0.00)	26.60 (0.57)	26.7 (0.71)	3.11 (0.64)	2.52 (0.18)	21.90 (0.14)	21.85 (0.78)	5.56 (0.34)	5.91 (0.18)
	9	90.00 (0.00)	65.00 (0.00)	26.40 (0.71)	26.9 (1.41)	1.26 (0.20)	1.89 (0.01)	22.00 (0.28)	21.75 (0.64)	5.58 (0.16)	5.89 (0.13)
	12	90.00 (0.00)	65.00 (0.00)	26.30 (0.57)	26.4 (0.28)	0.93 (0.02)	2.51 (1.61)	20.70 (2.97)	21.55 (0.92)	5.51 (0.19)	5.83 (0.13)
	15	80.00 (0.00)	55.00 (0.00)	26.05 (0.64)	25.8 (0.57)	1.09 (0.67)	1.36 (0.01)	19.30 (1.41)	20.00 (0.85)	5.56 (0.06)	5.76 (0.08)
	Mean	88.33 (3.89)	69.17 (12.22)	26.53 (0.55)	26.52 (0.75)	2.40 (1.61)	2.44 (1.13)	21.55 (1.71)	21.95 (1.92)	5.59 (0.20)	5.85 (0.15)
Onça	0	125.00 (0.00)	95.00 (0.00)	28.75 (0.92)	28.65 (1.20)	5.21 (0.04)	3.16 (1.66)	22.80 (1.56)	22.25 (0.78)	5.66 (0.06)	5.50 (0.05)
	3	110.00 (0.00)	90.00 (0.00)	28.90 (1.41)	28.25 (2.33)	4.50 (0.35)	0.74 (0.34)	21.50 (1.13)	27.15 (2.19)	5.97 (0.16)	5.61 (0.09)
	6	90.00 (0.00)	85.00 (0.00)	28.85 (2.05)	28.20 (2.40)	3.34 (1.44)	0.94 (0.06)	20.58 (3.15)	21.70 (4.81)	5.92 (0.18)	5.49 (0.16)
	9	80.00 (0.00)	80.00 (0.00)	28.70 (2.55)	27.90 (2.12)	1.86 (1.07)	1.76 (0.13)	20.48 (3.43)	22.20 (2.55)	5.89 (0.12)	5.75 (0.04)
	12	80.00 (0.00)	55.00 (0.00)	28.55 (2.62)	27.85 (2.05)	1.82 (1.54)	1.74 (0.20)	20.53 (2.36)	22.65 (1.63)	5.84 (0.13)	5.76 (0.04)
	15	80.00 (0.00)	70.00 (0.00)	28.85 (2.90)	27.90 (1.98)	2.70 (2.72)	1.80 (0.25)	19.79 (2.70)	23.00 (1.41)	5.86 (0.10)	5.76 (0.08)
	Mean	94.17 (18.20)	79.17 (13.95)	28.77 (1.62)	28.13 (1.64)	3.24 (1.72)	1.69 (0.97)	20.95 (2.12)	23.16 (2.69)	5.85 (0.14)	5.64 (0.14)
Overall mean		87.50 (18.07)	82.78 (17.99)	28.46 (2.07)	28.47 (2.27)	2.91 (1.74)	2.24 (1.34)	21.18 (1.74)	22.49 (2.28)	5.74 (0.19)	5.72 (0.17)

Table 3 Checklist and abundance (trap.d^{-1}) of fish species associated with macrophyte stands with low and high densities, at distances from 0 to 15 meters in the Maria Luiza, Careca and Onça lakes

Taxa	Low						High					
	0	3	6	9	12	15	0	3	6	9	12	15
OSTEICHTHYES												
CHARACIFORMES												
ANOSTOMIDAE												
Leporinus lacustris Campos, 1945	0	1	0	0	0	0	0	0	0	0	0	0
CRENUCHIDAE												
Characidium sp.	0	4	2	5	0	4	0	0	0	0	0	0
CHARACIDAE												
Astyanax altiparanae Garutti & Britski, 2000	0	2	1	0	0	0	0	0	1	0	2	1
Hyphessobrycon eques (Steindachner, 1882)	1	18	24	47	19	59	0	21	11	9	23	17
Moenkhausia bonita Benine, Castro & Sabino, 2004	112	44	12	7	8	8	50	0	2	5	0	0
Moenkhausia aff. *sanctaefilomenae* (Steindachner, 1907)	0	12	5	17	14	8	10	9	1	3	10	1
Psellogrammus kennedyi (Eigenmann, 1903)	0	2	4	22	6	16	2	11	0	3	4	7
SERRASALMINAE												
Serrasalmus marginatus Valenciennes, 1837	1	2	3	2	4	1	2	1	1	0	0	0
APHYOCHARACINAE												
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	1	24	9	15	25	30	17	4	4	6	12	0
CHARACINAE												
Roeboides descalvadensis Fowler 1932	3	5	5	0	0	0	1	0	0	0	0	0
CHEIRODONTINAE												
Serrapinnus notomelas (Eigenmann, 1915)	0	18	7	0	9	24	5	4	0	0	0	2
Serrapinnus heterodon (Eigenmann, 1915)	0	39	17	15	18	26	0	12	1	26	18	7
Serrapinnus sp 2	0	0	0	0	0	0	1	0	0	0	0	0
ACESTRORHYNCHIDAE												
Acestrorhynchus lacustris (Lütken, 1875)	0	0	0	0	1	0	0	0	0	0	0	0
ERYTHRINIDAE												
Erythrinus erythrinus (Bloch & Schneider, 1801)	0	0	0	0	0	0	0	0	0	0	1	0
Hoplerythrinus unitaeniatus (Agassiz, 1829)	0	0	0	0	0	0	0	0	0	1	0	0
Hoplias aff. *malabaricus* (Bloch, 1794)	0	1	1	0	0	0	1	1	0	1	0	0
LEBIASINIDAE												
Pyrrhulina australis Eigenmann & Kennedy, 1903	0	0	1	1	2	0	0	0	1	0	0	0
PERCIFORMES												
CICHLIDAE												
Apistogramma commbrae (Regan 1906)	0	4	6	3	3	1	0	9	2	4	1	1
Cichla kelberi Kullander & Ferreira, 2006	0	1	0	0	0	0	0	0	0	0	0	1
Cichlasoma paranaense Kullander, 1983	0	0	0	1	0	0	0	0	0	0	0	0
Crenicichla britskii Kullander, 1982	0	1	0	0	0	0	0	1	0	0	0	0
Satanoperca pappaterra (Heckel, 1840)	0	0	0	0	0	0	0	0	1	0	0	0
Laetacara sp.	0	0	0	0	0	0	0	0	0	1	0	0
Abundace (distances)	118	178	97	134	109	177	89	73	25	59	71	37
Total Abundance	813						354					

Table 4 All possible models with one, two, three, four and five variables, shown by BioEnv analysis for fish abundances in the macrophyte stands with low and high densities, at distances from 0 to 15 meters and the associated environmental variables

Number of variables	Models	Selected variables	Rho (ρ)
1	1	Dissolved oxygen	0.44
	2	Depth	0.21
	3	pH	0.13
	4	Temperature	0.05
	5	Conductivity	0.03
Number of variables	Models	Variables selected	Rho (ρ)
2	1	Dissolved oxygen+pH	0.41
	2	Depth+Dissolved oxygen	0.40
	3	Dissolved oxygen+Conductivity	0.38
	4	Temperature+Dissolved oxygen	0.37
	5	Depth+pH	0.24
	6	Depth+Conductivity	0.21
	7	Temperature+pH	0.16
	8	Depth+Temperature	0.16
	9	Conductivity+pH	0.15
	10	Temperature+Conductivity	0.07
Number of variables	Models	Variables selected	Rho (ρ)
3	1	Depth+Dissolved oxygen+pH	0.42
	2	Temperature+Dissolved oxygen+pH	0.39
	3	Depth+Dissolved oxygen+Conductivity	0.39
	4	Dissolved oxygen+Conductivity+pH	0.39
	5	Depth+Temperature+Dissolved oxygen	0.36
	6	Temperature+Dissolved oxygen+Conductivity	0.34
	7	Depth+Conductivity+pH	0.26
	8	Depth+Temperature+pH	0.23
	9	Depth+Temperature+Conductivity	0.18
	10	Temperature+Conductivity+pH	0.16
Number of variables	Models	Variables selected	Rho (ρ)
4	1	Depth+Dissolved oxygen+Conductivity+pH	0.42
	2	Depth+Temperature+Dissolved oxygen+pH	0.40
	3	Temperature+Dissolved oxygen+Conductivity+pH	0.37
	4	Depth+Temperature+Dissolved oxygen+Conductivity	0.35
	5	Depth+Temperature+Conductivity+pH	0.25
Number of variables	Models	Variables selected	Rho (ρ)
5	1	Depth+Temperature+Dissolved oxygen+Conductivity+pH	0.40
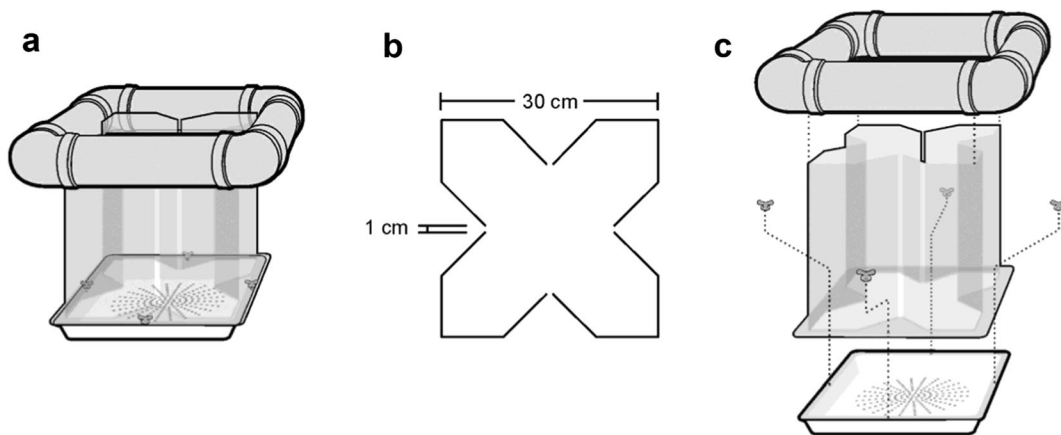
Fig. 6 Schematic illustration of the minnow trap used to collect fish in the stands of macrophytes (available in Cunha et al. 2011 - Supplementary Material). The letter a represents a whole overview of the trap, letter b indicates the dimensions of the trap and letter c demonstrates the parts which constitutes the trap

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