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HABITAT COMPLEXITY

The role of submerged trees in structuring fish assemblages in reservoirs: two case studies in South America

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Abstract The importance of subaquatic structures in determining fish assemblages is well documented in the literature, but few studies have examined the influence of submerged vegetation resulting from river impoundments in which arboreal vegetation was not removed. The purpose of this study was to evaluate the role of submerged trunks determining abundance and composition of fish assemblages by comparing habitats with and without them in two reservoirs of different ages. The results of this study demonstrated the importance of structured areas (with submerged vegetation) to the abundance of fish in both reservoirs. However, the role of these structures in maintaining species richness and diversity was significant only during the initial years after the impoundment. The occupation of these habitats by small invertivorous fish indicates that the non-removal of arboreal vegetation in these reservoirs contributes to the increase of their biogenic capacity. In addition, vegetation provides shelter against predation. Considering the conservation of fishery resources, we conclude that the pre-removal of arboreal vegetation in new reservoirs should be allowed only to the extent necessary to maintain acceptable water quality, even considering transitory and localized hypoxic processes.

Keywords Habitat complexity · Submerged vegetation · Habitat heterogeneity · Community attributes · Ichthyofauna

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Introduction

Although the importance of subaquatic structures in determining fish assemblages has long been the subject of discussion (Noble, 1980; Crowder & Cooper, 1982; Ploskey, 1985, Carpenter & Lodge, 1986), most of the studies on this topic have been restricted to examining the role of macrophytes (Dibble et al., 1996; Miranda & Hodges, 2000; Slade et al., 2005; Agostinho et al., 2007a, Pelicice et al., 2008; Padial et al., 2009) and artificial structures

(Freitas & Petrere, 2001; Santos et al., 2008, 2011a, b). However, some studies have evaluated the role of fallen trunks and the impact of their removal on the biota of a given area and have also highlighted the role of submerged trunks in creating structure within habitats (Sass et al., 2006; Roth et al., 2007, Helmus & Sass, 2008; Ahrenstorff et al., 2009). An extensive study by Miranda et al. (2010), conducted in almost 500 North American reservoirs, revealed that the scarcity or the absence of macrophytes and submerged trunks is the main factor to be considered for the restoration of fish habitat in these environments.

In the species-rich neotropical reservoirs, there is a lack of studies evaluating the effects of flooding arboreal areas to create reservoirs (e.g., flooded forest) on the ichthyofauna, even considering some perception about the relevance of subaquatic structures to the aquatic biota (see Agostinho & Gomes, 1997). The preservation of this vegetation causes conflicts among resource users and is, consequently, a recurring source of discussion each time a new reservoir is built. Thus, the removal of terrestrial vegetation, a poorly studied theme, leads to contradictory views regarding what, how, when, how much, and where the vegetation should be preserved, and can lead to erroneous decisions.

The previous removal of vegetation has been required to reduce problems with water quality (hypoxia). However, the removal of vegetation has been limited to the trunks, whereas labile materials, such as litter, branches, and leaves, which are largely responsible for acute problems of oxygen depletion in the recently built reservoirs, are left intact (Agostinho et al., 2007b). In addition, removing vegetation completely from large reservoirs typically takes a long time. This allows vegetation to sprout again and large-scale herbaceous colonization is more likely to cause problems associated with acute hypoxia, which can kill fish (Ploskey, 1985). On the other hand, submerged vegetation can have positive effects on the biota and aquatic biodiversity of a given region. Some studies have shown that the structural complexity of habitats produced by trunks, branches, macrophytes, and other submerged structures provides a higher variety of micro-habitats. This allows for the existence of a more diverse assemblage (Weaver et al., 1997; Smokorowski & Pratt, 2007), which directly or indirectly supports aquatic food webs (Petr, 2000; Roth et al., 2007; Helmus & Sass, 2008; Carey et al., 2010). In general, maintaining flooded arboreal vegetation should provide several benefits for fish, such as (i) creating substrates for the periphyton and benthos; (ii) preventing overfishing; (iii) creating areas for reproduction and refuge; (iv) increasing biological productivity in coastal areas by providing organic matter, nutrients and structural diversity; and (v) attenuating the impacts of marginal erosion caused by waves and variation in water levels (Agostinho et al., 2007b).

Various mathematical models based on biomass and water turnover are available for accurate estimation of the variation in oxygen concentration in space and time. This contrasts with the lack of knowledge of the role that submerged trees play in structuring fish fauna in reservoirs. This knowledge is needed to determine the spatial and temporal dimensions required to suppress the vegetation. In this context, this study evaluates the influence of the structural complexity provided by the presence of physical structures, such as submerged trunks and branches, on the abundance, diversity, and evenness of the fish assemblages in two reservoirs of different sizes and ages in the Paraná River basin. It is expected that structured environments allow for a greater abundance and diversity of fishes than do areas from which vegetation was removed.

Materials and methods

Study areas

The biological material used in this study was sampled in the Itaipu and Mourão reservoirs. The Itaipu Reservoir is located in the Paraná River, alongside the Brazil–Paraguay border (24°05′–25°33′S, 54°00′–54°37′W). This reservoir extends to approximately 150 km (170 km at the maximum quota) and has an area of 1.350 km^2 and an average depth of 22 m, which can be as high as 170 m near the dam. The average residence time is 40 days, and there are three different zones within the reservoir (fluvial, transition, and lacustrine), which are defined based on longitudinal gradients in sedimentation rate, limnological characteristics, and ichthyofauna (Okada et al., 2005). In Itaipu, sampling was conducted at two stations (Santa Helena and Foz do Iguaçu), both of which are located in the lacustrine area of the reservoir. The Santa Helena station is located around the island where the Santa Helena Biologic Refuge is sited, near the mouth of the São Francisco Falso River, which is a large tributary on the left (eastern) side of the reservoir. The Foz do Iguaçu station is located near the dam in the Bela Vista Biological Refuge. For both stations, sampling was conducted in areas with and without the presence of submerged trees, at least 1,000 m apart.

The Mourão Reservoir is located in the Mourão River, a tributary on the left (southern) bank of the Ivaí River in the Paraná River basin (52°20′W and 24°04′S). The dam was closed in 1964; currently, it has an area of 11.3 km^2 and an average residence time of 70 days (Júlio et al., 2005). Before the formation of this reservoir, the arboreal vegetation in some areas was removed. After more than 40 years, regions that had not previously been cleaned still show partially submerged trunks, which dominate the landscape.

Sampling and data analysis

In the Itaipu Reservoir, sampling was performed monthly from January 1984 to December 1987, which represents the period from the 2nd to the 5th year after the reservoir was formed. Gill nets of different mesh sizes (3–16 cm between opposite knots) were used at two sampling stations (Santa Helena and Foz do Iguaçu), both of which included habitat with and without submerged trees (Fig. 1a, b). Exploratory analyses (Detrended Correspondence Analysis: DCA; Gauch, 1986; results not presented) of the samples obtained in the reservoir demonstrated a larger degree of overlap in the structure of the fauna between the Santa Helena and Foz do Iguaçu stations, which therefore allowed the sites to be grouped.

Sampling in the Mourão Reservoir was performed quarterly from September 1995 to February 1999, representing the period from the 31st to the 35th year after the formation of this reservoir. Considering that the variation between communities in vegetated and unvegetated areas is much more perceptible in recent reservoirs (Agostinho et al., 1999), data collected in Mourão was not analyzed considering the years. Gill nets of different mesh sizes (3–16 cm between opposite knots) were used for sampling both reservoirs in areas with or without submerged trees (Fig. 1c, d).

The analyses were performed based on the catch per unit effort (CPUE; individual or kg/1,000 m^2 net/24 h) for both reservoirs. The Indicator Value (INDVAL; Dufrêne & Legendre, 1997) was used for identifying the representative species in each habitat and was calculated by the expression IND-VAL (%) $= A_{ij} \times B_{ij} \times 100$, where i denotes the species; j the habitats, A_{ij} the specificity estimate, and B_{ij} the fidelity of the species in relation to the habitats being considered. When randomization of the original matrix (Monte Carlo; 1,000 times) identified significant INDVALs, the indicator species were analyzed in relation to the variation patterns in environments with and without submerged trees.

The fish diversity in both habitats were analyzed considering three community attributes: species richness (S), the Shannon Diversity Index [$H' = -$S (pi*ln (pi)), where pi is the ratio of the total number of individuals occurring in species i], and evenness of individuals' distribution among the species ($E = H'/\ln S$) (Magurran, 1988). Analysis of variance (ANOVA) was employed to test differences in the mean values of these attributes between habitats (with and without vegetation). When needed, the data were transformed to meet the assumptions of ANOVA. As the data in Itaipu were collected shortly after the impoundment, the temporal variations in these attributes were examined.

The software Pc-Ord (McCune & Mefford, 1999) was utilized to conduct DCA, INDVAL, and to calculate the community attributes, whereas the software statistics (StatSoft Inc., 2005) was utilized to calculate ANOVA.

Results

Itaipu Reservoir

The fish abundance, which was estimated using CPUE, was significantly different between locations ($F = 13.27$; $P < 0.001$) and years ($F = 4.20$; $P < 0.01$), and the interaction between these factors was also significant ($F = 3.86$; $P = 0.011$). Therefore, the abundance of fish between habitats with submerged trees varied according to the year considered, with higher values in areas with submerged trees after the second year of the study. Yet, the greater difference

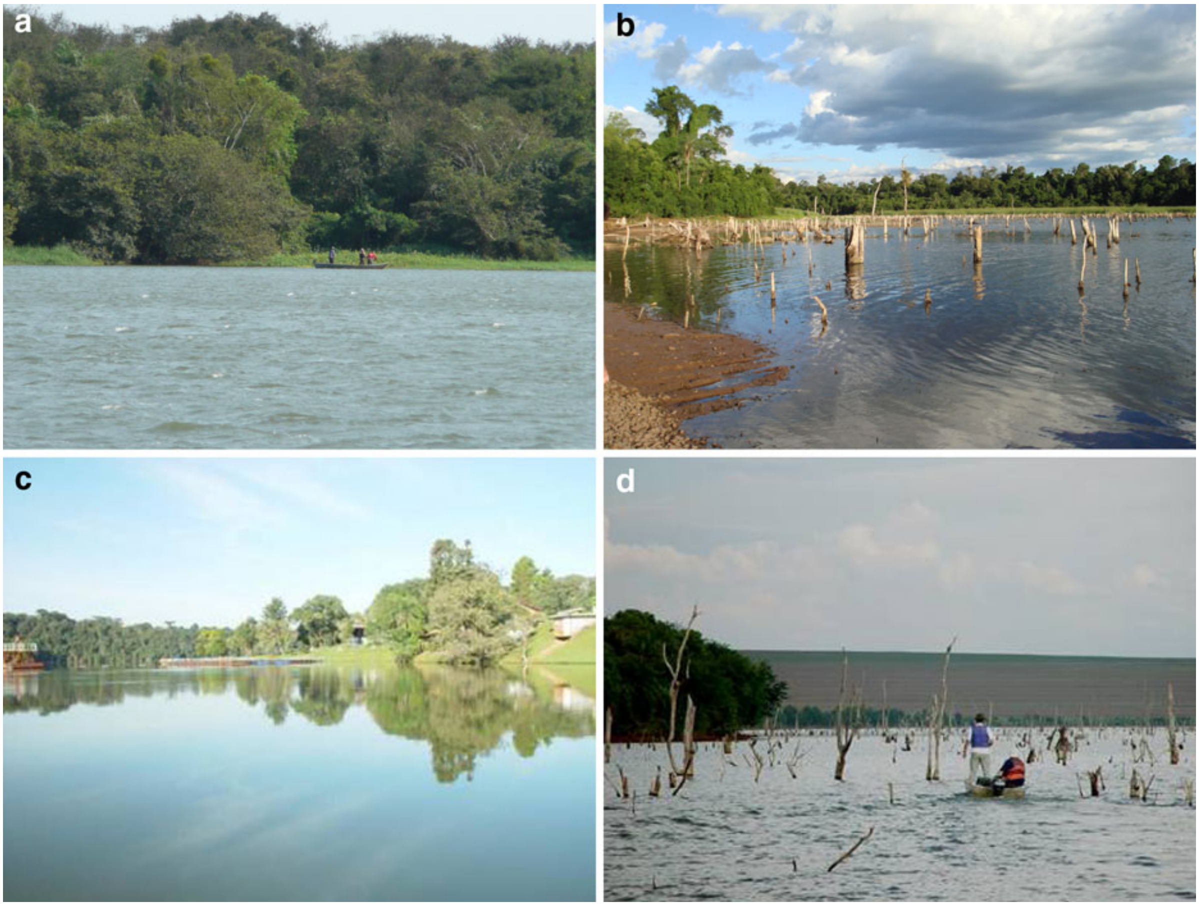


Fig. 1 Itaipu Reservoir (**a**, **b**) and Mourão Reservoir (**c**, **d**) showing areas with no submerged trees (**a**, **c**) and with submerged trees (**b**, **d**)

between areas with and without submerged vegetation was observed in the last year of the study (Fig. 2).

Out of the 70 species of fish captured, 12 were identified as indicator species (17%), of which the following 10 occurred within habitats with submerged trees: *Acestrorhynchus lacustris*, *Auchenipterus osteomystax*, *Staindachnerina insculpta*, *Satanoperca pappaterra*, *Hoplias malabaricus*, *Loricariichthys* sp., *Pimelodus maculatus*, *Plagioscion squamosissimus*, *Roeboides paranensis*, and *Serrasalmus marginatus.* For the habitat without submerged trees, the species that presented significant INDVALs were *Galeocharax knerii* and *Pinirampus pirinampu* (Table 1).

The mean values of the abundance of indicator species (CPUE) in the habitats with and without submerged trees in the Itaipu Reservoir are shown in

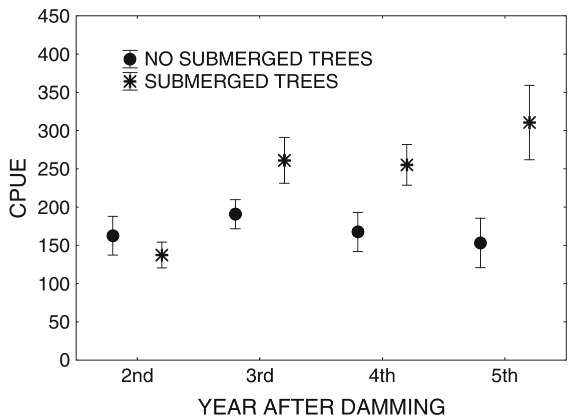


Fig. 2 Means (±SE) of catch per unit effort (CPUE: individuals/1,000 m^2 net/24 h) in the Itaipu Reservoir during the initial years after the impoundment in the two types of habitats sampled (with and without submerged trees)

Table 1 Indicator value (INDVAL) of species associated with habitats with and without submerged trees in the Itaipu and Mourão reservoirs

Species	Submerged trees		*P* value
	No	Yes	
Itaipu Reservoir			
A. lacustris	14	40	0.008
A. nuchalis	25	50	0.036
S. insculpta	3	31	0.000
S. pappaterra	1	23	0.002
H. malabaricus	3	30	0.000
Loricariichthys sp.	1	27	0.000
P. maculatus	15	42	0.009
P. squamosissimus	31	58	0.015
R. paranensis	7	31	0.017
S. marginatus	32	57	0.002
G. knerii	24	4	0.023
P. pirinampu	36	12	0.006
Mourão Reservoir			
H. malabaricus	14	40	0.0004
O. paranensis	3	94	0.0084

Only the species with significant values are presented (Monte Carlo test)

Fig. 3 using grouped annual data. In agreement with the analysis presented above, the species associated with submerged trees showed a high mean catch in this habitat. The species *G. knerii* and *P. pirinampu* presented the opposite pattern, with a higher CPUE value observed in the habitat without submerged trees.

Among the assemblage attributes considered, species richness (*S*) and the Shannon Diversity Index (H') showed significant differences between locations ($F = 28.88$; $P < 0.001$ and $F = 11.40$; $P < 0.001$, respectively) and years ($F = 8.30$; $P < 0.001$ and $F = 11.95$; $P < 0.001$), and the interaction between these two factors was also significant ($F = 22.16$; $P < 0.001$ and $F = 19.55$; $P < 0,001$). Habitats with submerged trees showed lesser variability in the mean values of these attributes during the initial years following the formation of the reservoir, whereas non-structured habitats showed a decrease in the mean value for the previous year (Fig. 4a, c). The evenness in the distribution of individuals among the species, with a higher variability, did not show significant differences between locations and years ($P > 0.05$).

Mourão Reservoir

The mean abundance presented significant differences between habitat types ($F = 6.12$; $P = 0.02$); the catches in the habitat with submerged trees were almost two times those in non-structured environments (Fig. 5a). However, the biomass captured in these two habitats did not show significant differences ($F = 1.49$; $P = 0.24$) (Fig. 5b).

Only two of the 19 species caught in the Mourão Reservoir were considered to be indicator species (10% presented significant INDVALs). Both of these species, *Hoplias* cf. *malabaricus* and *Oligosarcus paranensis* (Table 1), showed a preference for habitats with submerged trees.

The mean values for the numeric abundance and biomass (weight) of the indicator species in the habitats with and without submerged trees in the Mourão Reservoir are presented in Fig. 6, considering the annual grouped data. *Oligosarcus paranensis* and *H. malabaricus* presented higher values of abundance and biomass in the habitat with submerged trees, demonstrating the importance of structured habitat for these species.

Mean values of fish species richness, evenness, and Shannon Diversity Index in Mourão Reservoir were lower than those for Itaipu Reservoir. However, contasting with from Itaipu, in Mourão there were no significant differences between habitats ($P > 0.40$) (Fig. 7).

Discussion

The results of this study confirm the important role that submerged trees play in structuring the ichthyofauna, maintaining and increasing species abundance, not only in recently built reservoirs but also in older reservoirs. Therefore, the structuring effect was observed in both studied reservoirs, corroborating the results observed at other latitudes (Sass et al., 2006; Roth et al., 2007) and in studies conducted in South America that examined submerged macrophytes (Pelicice et al., 2008) and artificial substrates (Santos et al., 2008, 2011b). The noticeable increase in the fish preference for submerged trees after the second year, especially in the fifth year, probably originated from the expected instability in new environments and from the time that pre-existing species requires to

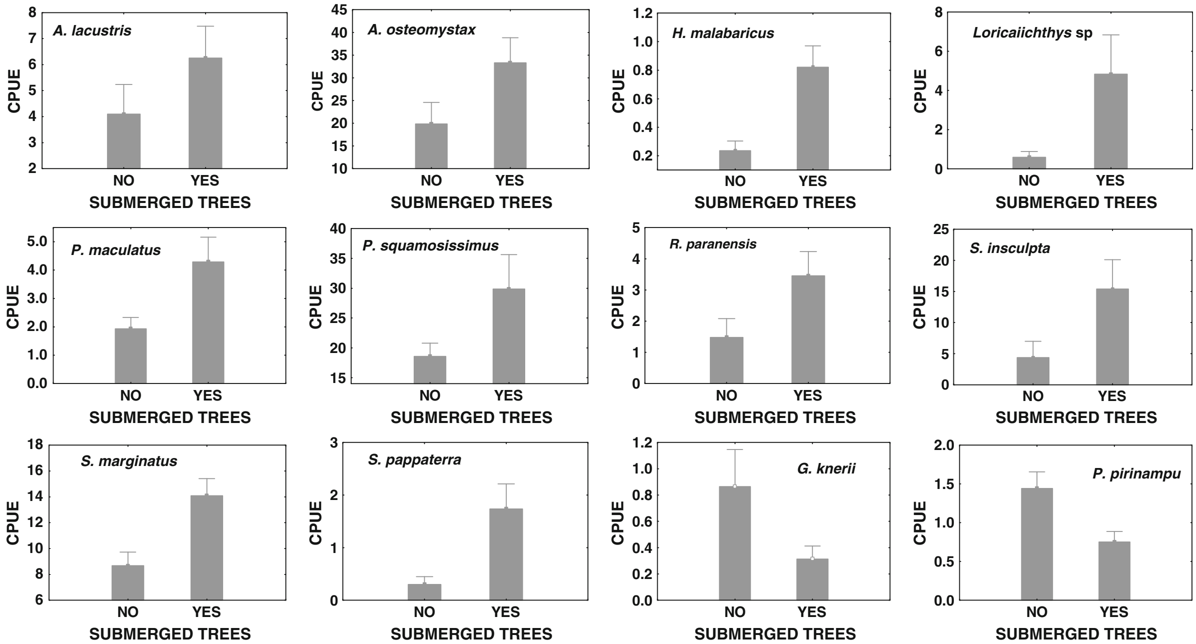


Fig. 3 Means (±SE) of catch per unit effort (CPUE: individuals/1,000 m^2 net/24 h) of indicator species in habitats with and without submerged trees in the Itaipu Reservoir during the initial years after its formation (different scales)

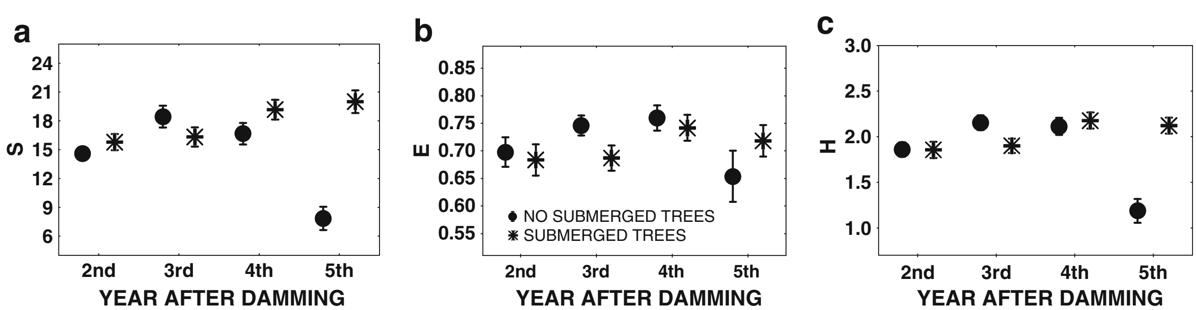
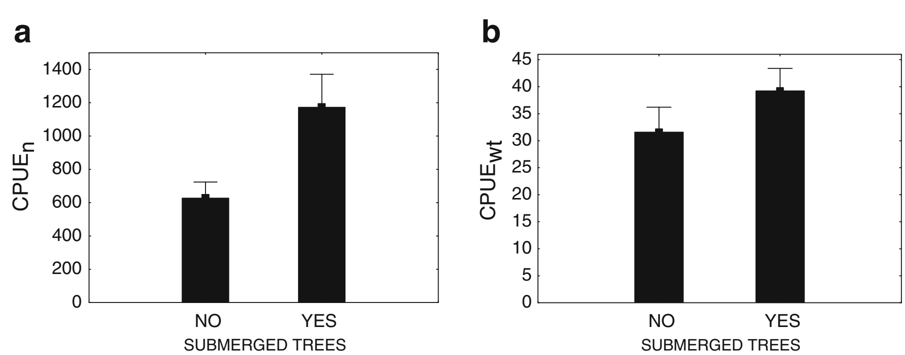


Fig. 4 Mean (±SE) of species richness (**a**; S), evenness (**b**; E), and Shannon Diversity Index (**c**; H) evaluated over the years in the two types of habitats (with and without submerged trees) sampled in the Itaipu Reservoir

Fig. 5 Mean (±SE) numbers (**a**) and weights (**b**) of fish caught in areas with and without submerged trees in the Mourão Reservoir, from the 31st to 35th year after impoundment



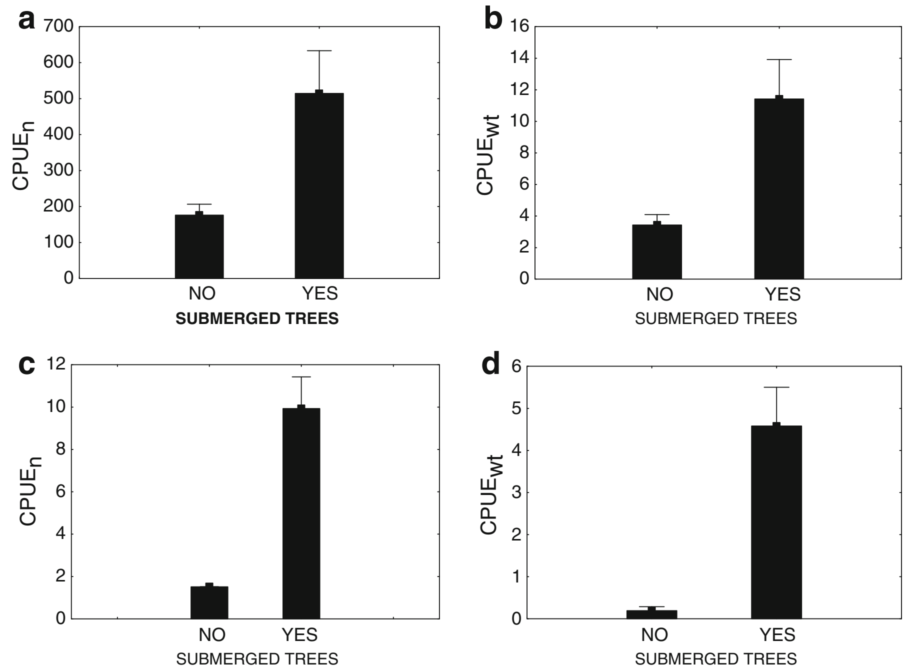


Fig. 6 Mean (±SE) abundance and biomass per sample of indicator species in habitats with and without submerged trees in the Mourão Reservoir (**a**, **b** *Oligosarcus paranensis*; **c**, **d** *Hoplias* cf *malabaricus*)

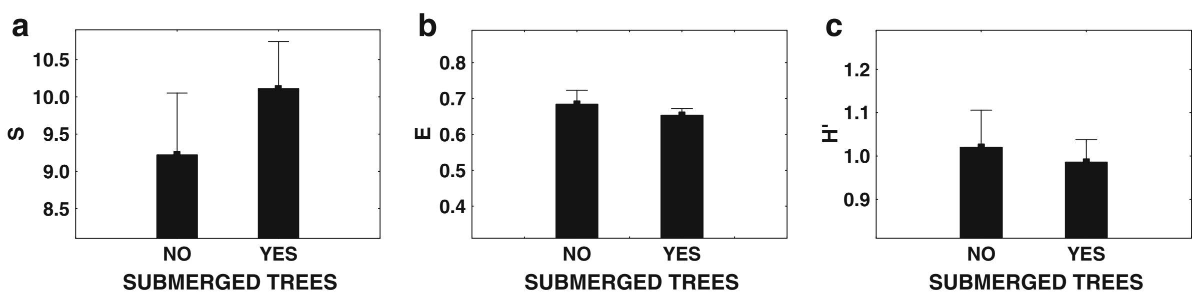


Fig. 7 Mean (±SE) of species richness (**a**; S), evenness (**b**; E), and Shannon Diversity Index (**c**; H') for habitats with and without submerged trees in the Mourão Reservoir

adjust to the distinct habitats created in the inundated area (Agostinho et al., 1999, 2008). The observation that non-structured environments did not show relevant variations in the CPUE in the first years after the impoundment (unlike in the structured areas) suggests that the high productivity that characterizes the initial years of reservoir formation (heterotrophic or upsurge period; Kimmel & Groeger, 1986, Petrere, 1996, Agostinho et al., 2007b) should be supported by spatially complex habitats. In addition, the high number of catches registered in areas containing submerged trees in both reservoirs (five first years, the Itaipu Reservoir; more than 30 years old, the Mourão Reservoir) indicates that the use of these habitats by the ichthyofauna is consistent and occurs throughout the reservoir aging.

In effect, higher densities in structured areas have been described in the literature, not only for fish (Warfe & Barmuta, 2004) but also for invertebrates (Carlisle & Hawkins, 1998; Diehl & Kornijow, 1998). For example, when comparing the fish biomass in basins with and without flooded arboreal vegetation in the seven reservoirs of different ages in Kansas (USA), Willis & Jones (1986) found that biomass values were significantly higher in areas with submerged vegetation. It is important to highlight the fact that the formation of large reservoirs leads to the loss of complex fluvial habitats and/or its replacement by habitats essentially pelagic, which are substantially more homogeneous (Agostinho et al., 2008). The existence of spatially complex environments, such as regions containing submerged trees, can create spots of high diversity and increased biogenic capacity inside the impounded area.

High values for species richness and diversity (assessed using the Shannon index) are also characteristic of regions containing submerged trees. In the case of the Itaipu Reservoir, it was possible to verify the decrease in the fish richness and diversity in habitats without submerged trees during the first years, a pattern that, as recorded for the CPUE, suggests, as mentioned, a period of the fauna adjustment in the new environment. An experiment conducted by Santos et al. (2011b) in which artificial substrates were installed in one of the regions sampled during the present study (in the Itaipu Reservoir), was in agreement with the patterns observed here. These authors observed that, in the structured regions, the richness, in addition to the abundance and biomass, were higher than those in the non-structured regions, demonstrating the importance of spatial heterogeneity to biodiversity in aquatic environments. The experiments by Santos et al. (2011b) were performed in the 23rd year after the Itaipu Reservoir was formed. However, Mourão Reservoir did not present significant differences between habitats in terms of species richness, evenness, or diversity. Although this can be partially explained by the higher variability between the samples, especially in habitats without submerged structures, the fact that the Mourão Reservoir is older appeared to be important. It is possible that significant decomposition of branches and thinner trunks occurred within the Mourão Reservoir, reducing the structural complexity of the habitat during the 30 years since this reservoir was established. This phenomenon can diminish the quality of the available microhabitats, restricting the permanence of some species. It is important to highlight the fact that, even with similar richness levels between habitats, the fish catch in this reservoir was much higher inside the flooded forest. This indicates that the flooded forest still maintains an elevated abundance and biomass of fish decades after the formation of the Mourão Reservoir.

The predominance of indicator species in regions with submerged trees suggests that these species prefer spatially complex and structured habitats, and this is true for both benthic species (*P. squamosissimus*, *S. pappaterra*, and *P. maculatus*) and pelagic species (*O. osteomystax*). The presence of submerged structures should benefit such species, even for those that live in particular stratum of the water column. In effect, *P. squamosissimus* and *A. osteomystax* represented the largest proportion of the catches in regions with submerged trees. The trahira *Hoplias malabaricus* (among the indicator species for both reservoirs) is characterized as a typical piscivorous ambusher (Súarez et al., 2001) and, therefore, has advantages in structured environments (Luz-Agostinho et al., 2008; Petry et al., 2010). The same is true for the other indicator species in the Mourão Reservoir (*O. paranensis*), which is also classified as a piscivorous ambusher (Casatti et al., 2001). Invertivorous species, which were generally small and mid-sized species (*A. osteomystax*, *R. paranensis*, and *S. pappaterra*), were particularly abundant in structured environments and likely benefited from the availability of refuges where they were protected from predation and where their food is abundant, as reported for similar habitat in the literature (Petr, 2000; Roth et al., 2007). Although a larger number of indicator species present in the structured area have a piscivorous diet (*S. marginatus*, *P. squamosissimus*, and *A. lacustris*, in addition to *H. malabaricus* and *O. paranensis*), most of these species also include invertebrates in their diet (Hahn et al., 1997, 1998). The presence of dentritivores species, such as *S. insculpta* and *Loricarichthys* sp., in areas where the vegetation was not removed is also expected, especially in the first years after the reservoir is established, when more labile vegetation is decomposing (Ploskey, 1985). *Pimelodus maculatus*, which is considered to be an omnivorous species (Lobón-Cerviá & Bennemann, 2000), primarily ingested invertebrates in the first years after the formation of the Itaipu Reservoir (Hahn et al., 1998). The only two species in the Itaipu Reservoir with a clear preference for non-structured habitats were *P. pirinampu* and *G. knerii*. Although there is no additional information available on the habitat use of *G. knerii*, *P. pirinampu* is the largest of the indicator species identified (standard length up to 95 cm) and is a pelagic species, unlike the other species of the Pimelodidae family observed in the basin (Agostinho et al., 1999, 2003a, b).

Smaller fish are more vulnerable to predation and search for protection in structured environments. This was evident from our results in the Mourão Reservoir. Although the fish biomass did not differ between the structured and the non-structured areas in this reservoir, fish abundance was significantly higher in the former, demonstrating high abundance of small fish. The benefits of submerged structures for the fish assemblages are associated with a balance between predator foraging efficiency and prey refuge requirements (Heck & Thoman, 1981; Dionne & Folt, 1991; Miranda & Hodges, 2000).

Conclusion

The present study clearly indicates that the maintenance of arboreal vegetation in the bermed areas contributes to an increase in fish abundance in the more structured areas and to the maintenance of species assemblages in the system. Moreover, the results of this study indicate that submerged trees have an immediate effect in the first years after a reservoir is formed as they enable the installation of a more rich and abundant fish assemblage. Therefore, the presence of submerged trees increases the biogenic capacity of reservoirs, leading to higher productivity and providing protection to fries and smaller species. In terms of preserving fishery resources, the decision process on vegetation removal should not consider the complete suppression of arboreal vegetation. Only what is necessary to maintain an acceptable level of water quality should be removed, even when transitory and localized hypoxia processes occur because of the presence of submerged vegetation.

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