

Original article

Fish assemblages associated with *Egeria* in a tropical reservoir: investigating the effects of plant biomass and diel period

Fernando Mayer Pelicice ^{a,*}, Angelo Antonio Agostinho ^b, Sidinei Magela Thomaz ^b

^a Postgraduate Course in Ecology of Inland Aquatic Ecosystems, Maringá State University, Maringá, Paraná, Brazil

^b Department of Biology/NUPELIA, Maringá State University, Paraná, Brazil

Received 15 March 2004; accepted 23 August 2004

Available online 13 October 2004

Abstract

Studies investigating fish/macrophyte associations in the neotropics are rare. Aquatic vegetation enhances structural complexity of the environment, potentially influencing predator–prey relationships. The present work characterizes fish assemblages associated with beds of *Egeria*, a submerged rooted macrophyte, in Rosana Reservoir, Brazil. The main subject of this study was to investigate effects of plant biomass and diel period on fish assemblage attributes (density, total weight, taxa richness and diversity), testing the hypothesis that macrophyte density and diel period greatly influences fish assemblage structure. Fishes were sampled with a 1-m² throw trap at morning, midday and dusk, at six sites. The assemblages were primarily composed of small-sized species (e.g. Characiformes) and juveniles, with few large species (Gymnotiformes and Cichlidae). Around 95% of the individuals were captured in habitats with medium and high vegetation biomass. Fish assemblage attributes differed significantly with respect to macrophyte biomass. Highest values of these attributes were observed in maximum plant biomass, in contrast with trends observed in previous works, where higher values (mainly of fish density) were found in intermediate plant coverage. Oxygen, temperature and pH were within normal ranges, therefore, variation in assemblage attributes is assumed to be explained primarily by plant density. No pattern of diel variation was observed, perhaps reflecting sedentary characteristics of these taxa. Results from this study illustrate that procedures to reduce macrophyte density in reservoirs of the Paraná-Tietê-Parapanema systems, may cause strong alterations in the fish assemblages, resulting in lower fish density, biomass and species richness of taxa utilizing *Egeria* beds.

© 2004 Elsevier SAS. All rights reserved.

Keywords: Fish assemblage; Macrophyte stands; Habitat structure; Reservoir management

1. Introduction

Aquatic macrophytes play a fundamental role structuring aquatic environments and increasing spatial complexity (Benson and Magnuson, 1992; Weaver et al., 1996; Weaver et al., 1997; Grenouillet and Pont, 2001). Aquatic habitats with higher structural complexity can maintain more fish species and individuals due to the presence of suitable spawning substrates, abundant food resources and refuges against predators (Rossi and Parma de Croux, 1992; Dibble et al., 1996; Duffy and Baltz, 1998; Agostinho et al., 2003).

To understand structuring processes in relation to aquatic macrophytes, studies generally follow one of the three

approaches: (i) macrophyte presence, (ii) vegetation density, (iii) and plant morphologic characteristics (Killgore et al., 1989; Dionne and Folt, 1991; Chick and McIvor, 1997; Dibble and Harrel, 1997; Meschiatti et al., 2000; Agostinho et al., 2002). These differences in approach reflect different spatial scales, ranging from habitat to micro-habitat.

Studies concerning fish/macrophyte associations in tropical environments are rare, with the majority focusing only on the macrophyte presence, which limits small-scale inferences (Cordivola de Yuan et al., 1984; Araujo-Lima et al., 1986; Delariva et al., 1994; Hendersen and Hamilton, 1995; Meschiatti et al., 2000). The Paraná River Basin supports a diverse ichthyofauna and aquatic flora, as much in species composition as in functional groups (Agostinho et al., 1995; Thomaz et al., 2003), however little is known about the ecological aspects of this interaction. Great dispersal abilities (Santamaría, 2002), allied with widespread impoundment of

* Corresponding author. Present address. Bloco H90, 5790, Avenida Colombo, 87020900 Maringá, Paraná, Brazil.

E-mail address: fmpelicice@ig.com.br (F.M. Pelicice).

rivers in this basin, favors the development of large stands of certain macrophyte groups. Recently, proliferation of submerged plants has been noticed in several reservoirs of Paraná-Tietê-Parapanema Basins, especially the species *Egeria najas* and *Egeria densa* which form large beds in littoral areas (Thomaz and Bini, 1999; Marcondes et al., 2003). This phenomenon has an enormous potential in compromising water multiple uses (Bianchini-Júnior, 2003).

The present work characterizes the structure of fish assemblages associated with *Egeria densa* and *E. najas* beds in Rosana Reservoir, Parapanema River, and related differences in assemblage structure to macrophyte biomass, diel periodicity and abiotic variables. We tested the hypotheses that: (i) presence and biomass of aquatic macrophytes are determinant factors on the composition and structure of fish assemblages in this reservoir, resulting in habitats with higher values of fish density, total weight, species richness and diversity; and (ii) diel period influences fish activity, resulting in changes in assemblage structure during a day period inside macrophyte beds.

2. Material and methods

2.1. Study area

The Parapanema River is a major tributary of the Upper Paraná River Basin and forms the division between Paraná and São Paulo states (22°36'S, 52°52'W). Samples were collected in Rosana Reservoir (Fig. 1), the last reservoir in a cascade along the Parapanema River. Rosana dam was completed in 1986, flooding a shallow (depths usually lower than 10 m) area of 276 km². Total drainage area of the reservoir is 99,000 km², with a water residence time of approximately 18.6 days (CESP, 1998). The reservoir is characterized by large beds of *E. densa* and *E. najas*, species

native to this basin (Cook and Urmi-Konig, 1984), that form patches of different densities in depths <2 m. One of the main limiting factors to submerged macrophyte growth is underwater radiation (Thomaz and Bini, 1999). In Rosana Reservoir, colonization by submerged macrophytes is facilitated by low turbidity and lower phytoplanktonic primary production than in other southeastern systems (CESP, 1998).

2.2. Data collection

A total of 59 samples were collected between January 15 and 21, 2003 in beds of *E. densa* and *E. najas* at six sites (Fig. 1). Three sites were located in Euclides da Cunha Paulista district ($n = 28$), São Paulo State (22°34'07"S, 52°33'34"W), and three in Diamante do Norte district ($n = 31$), Paraná State (22°38'29"S, 52°47'16"W) closer to the dam. Sampling sites were selected to incorporate the full range of densities of *Egeria* and maximum depth <1.4 m, due to equipment restriction. Samples were collected in three diel periods: morning (6:00 h; $n = 20$), midday (13:00 h; $n = 21$) and dusk (18:30 h; $n = 18$).

A 1-m² throw trap was used to sample fish and macrophytes. The trap was constructed with a 1.5-m height aluminum frame with small mesh (0.5 cm) covering all laterals. At each site a boat was silently positioned above the *Egeria* bed and used as a platform for trap deployment. Immediately following boat positioning, the trap was quickly thrown into the water and pressed to the bottom. A suite of physicochemical variables was measured following trap deployment: oxygen (mg/l and % of saturation), temperature (°C), pH, conductivity (µS/cm) and depth (m). Transparency (Secchi, m) was measured in deeper sites close to sampling stations. Next, macrophytes were removed from the trap, washed and weighed (wet weight). A subsample was kept for drying (60 °C for 7 days) to obtain macrophyte biomass in dry weight (DW g m⁻²). Dry weight biomass was determined for 41 samples (morning and midday periods) and classified as low (0–70 g m⁻²), medium (71 and 200 g m⁻²) or high macrophyte densities (200–530 g m⁻²). In the 18 remaining samples (dusk period), macrophyte biomass was visually classified into low, medium and high categories.

After vegetation removal, fish were collected with an aluminum dip-net (49 × 49 cm frame and 0.5 cm net mesh size). Hauls were made inside the trap area, until 10 successive hauls resulted in no additional individuals captured. To evaluate dip net capture efficiency, 5 l of sodium hypochlorine were poured into the area following the dip-netting protocol of two collections. The water was mixed vigorously and the dip-net procedure repeated to capture any remaining individuals. All fish captured were preserved in 10% formalin, taken to the laboratory and subsequently identified, counted, measured (standard length) and weighed.

2.3. Statistical analysis

To evaluate completeness of fish taxa sampling, a taxa accumulation curve was constructed using all 59 samples.

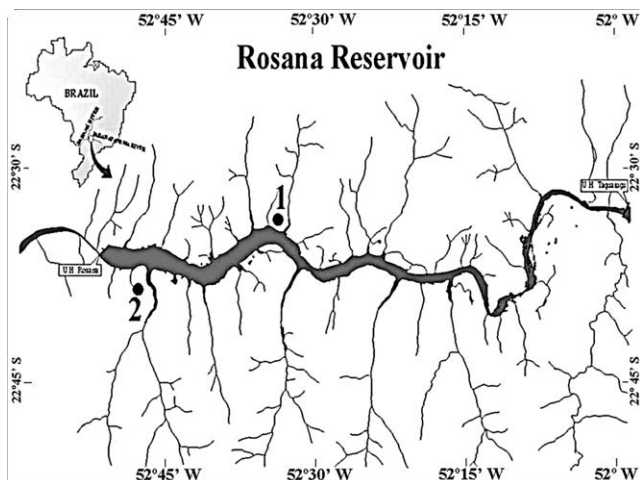


Fig. 1. Rosana Reservoir, the last reservoir of Parapanema River before its confluence with the Paraná River. Sampling sites: (1) region of Euclides da Cunha Paulista district, São Paulo State; (2) region of Diamante do Norte district, Paraná State.

The software EstiMateS (Colwell, 1997) was used to calculate a rarefaction curve after 50 randomizations (expected accumulation curve; Gotelli and Colwell, 2001). Rarefaction curves were also constructed with samples collected in each category of macrophyte biomass (low, medium and high).

Using macrophyte biomass and diel period as factors, we examined if abiotic variables and fish assemblage attributes (density, total weight, taxa richness and Shannon-Wiener diversity index: $H = -\sum p_i \cdot \ln p_i$; Magurran, 1988) showed significant variation among different macrophyte biomass categories (low, medium and high) and among the three sampling periods (06:00, 13:00 and 18:30). We used two-way ANOVAs to test for statistical differences and Tukey's test to compare means. Some variables were transformed ($\log + 1$) to normalize distribution and correct data dispersion (heterocedasticity), but data presented in tables and figures are not transformed. We considered differences to be significant at the $\alpha = 0.05$ level, using the software STATISTICA version 5.5 (StaSoft, 2000) for these analysis.

3. Results

3.1. Abiotic conditions

Abiotic variables showed little variation among sampling stations. Site depth ranged from 50 to 138 cm, water transparency was high (mean value for Secchi = 175 cm ± 5.57 S.E.), with a mean conductivity of 41.4 $\mu\text{S cm}^{-1}$ (S.E. = 0.61). Additionally, dissolved oxygen (7.26 mg $\text{l}^{-1} \pm 0.24$ S.E.), pH (7.42 ± 0.12) and temperature (30.53 $^{\circ}\text{C} \pm 0.23$), important factors influencing fish distributions (Jackson et al., 2001), did not differ among classes of macrophyte biomass (two-way ANOVA; Table 1). Although significant difference for oxygen was observed among biomass classes ($\log + 1$; $p < 0.0451$), Tukey's test evidenced no significant difference among means ($p > 0.05$). Significant variations in abiotic variables were observed only in relation to diel periodicity (two-way ANOVA; Table 1), with lowest values occurring in the morning, as expected for these parameters (Esteves, 1998). Not one of the abiotic variables measured exhibited extreme values that would be expected to restrict fish distributions.

Table 1

Mean values (\pm standard error) of oxygen (mg), pH and temperature ($^{\circ}\text{C}$) observed in *Egeria* beds, in different macrophyte biomass and diel period. Statistical differences were observed only between hours of day (two-way ANOVA) and letters indicate means statistically different (Tukey's test). Interactions among factors were not statistically significant for all variables ($P > 0.05$). Oxygen was log-transformed ($\log + 1$) to perform analysis

Variables	Macrophyte biomass			Hours of day (h)		
	Low (n = 19)	Medium (n = 25)	High (n = 15)	06:00 (n = 20)	13:00 (n = 21)	18:30 (n = 18)
Oxygen	6.95 \pm 0.43	7.49 \pm 0.39	7.26 \pm 0.46	5.13 \pm 0.22a	8.40 \pm 0.16b	8.28 \pm 0.33b
		$F_{2,50} = 3.30$; $P < 0.0451$			$F_{2,50} = 58.54$; $P < 0.000001$	
PH	7.33 \pm 0.19	7.62 \pm 0.20	7.22 \pm 0.21	6.81 \pm 0.10 ^a	7.74 \pm 0.22 ^b	7.72 \pm 0.20 ^b
		$F_{2,50} = 2.73$; $P < 0.0751$			$F_{2,50} = 7.71$; $P < 0.0012$	
Temperature	30.43 \pm 0.37	30.82 \pm 0.37	30.19 \pm 0.46	29.12 \pm 0.25 ^a	31.47 \pm 0.34 ^b	31.02 \pm 0.37 ^b
		$F_{2,50} = 1.54$; $P < 0.2239$			$F_{2,50} = 12.44$; $P < 0.00004$	

^{a,b} Statistically different means (Tukey's test).

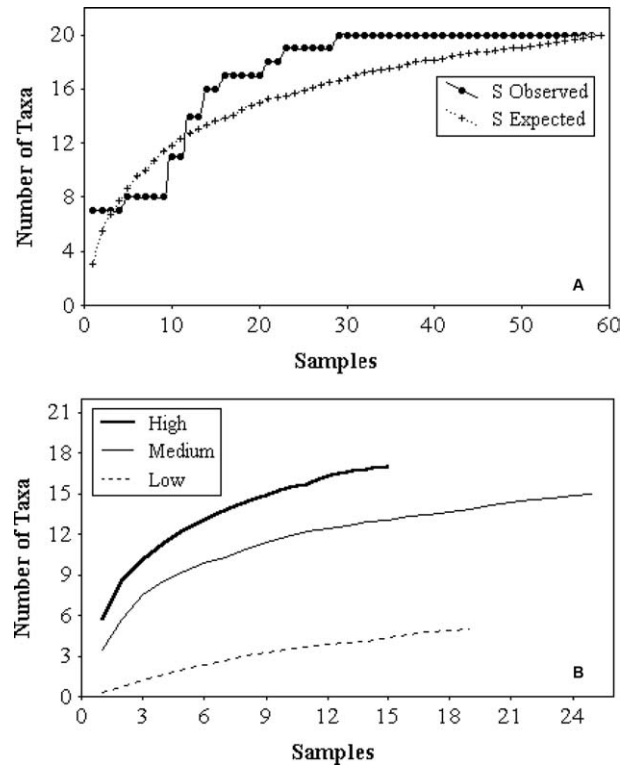


Fig. 2. Fish taxa accumulation curve (Observed S) and rarefaction curve (Expected S) calculated from 59 samples collected in *Egeria* beds (A); fish taxa rarefaction curves calculated for each category of macrophyte biomass (B).

3.2. Fish assemblage

No taxon was added to the taxa accumulation curve (Fig. 2A) after the 29th sample. Although an asymptote was not reached in the rarefaction curve, the number of additional taxa decreased considerably after the 40th sample. It is therefore, likely that most of the taxa present in this habitat were captured. In addition, evaluation of fish capture efficiency using sodium hypo-chlorine showed that only 7.2% of individuals remained within the trap and, more important, no additional taxon was captured after the dip netting procedure.

Twenty fish taxon were collected during the sampling period, belonging to four orders: Characiformes (12), Siluriformes (1), Gymnotiformes (4) and Perciformes (3). A total of 589 individuals were captured, with a total weight of

714.28 g (Table 2). The seven most common species comprised 89% of captures: *Hyphessobrycon eques* (25.3%), *Roeboides paranensis* (18.2%), *Hemigramus marginatus* (15.1%), *Serrassalmus marginatus* (14.9%), *Serrapinus notomelas* (5.4%), *Oligossarcus pintoii* (5.4%) and *Satanoperca pappaterra* (4.6%). About 96% of all individuals were caught in medium and high macrophyte densities (MED/HI). In these habitats, the most abundant species were also the most frequently present and 95% of samples in these habitats contained fish. Considering only abundant taxa (>2.5% of total captures), *S. notomelas*, *O. pintoii*, *Hyphessobrycon* sp. and *Eigenmannia trilineata* were caught exclusively in MED/HI samples. In contrast, no taxon was exclusive to samples with low macrophyte biomass (LOW), and *H. eques*, *H. marginatus* and *S. marginatus* were the most abundant, although with sporadic occurrence (<20% of samples). In LOW habitats 79% of samples contained no fish.

Small sized taxa dominated these assemblages, with a mean standard length of 3.2 cm in MED/HI areas and 2.6 cm in LOW areas. However, mean lengths are not significantly different among habitats (one-way ANOVA; $F_{1,587} = 1.01$; $P < 0.3148$). Smaller sized taxa belonged mainly to subfam-

ily Tetragonopterinae (small characids), and the largest taxa belonged to order Gymnotiformes (Table 2). In MED/HI areas, 40.9% of all individuals collected were immature, and reproductive individuals accounted for 43.3% of the total abundance (e.g. *H. eques*, *H. marginatus* and *S. notomelas*). Some taxa showed high percentage of immature individuals (>40%) as *S. marginatus*, *S. pappaterra*, *R. paranensis* and *O. pintoii* (Table 2).

3.3. Macrophyte biomass and diel periodicity

Macrophyte biomass in 41 samples ranged from 1.2 to 301.57 DW g m⁻², with one outlier (529.1 DW g m⁻²). All fish assemblage attributes differed statistically among macrophyte biomass classes, but no significant diel variation was observed, considering only data obtained in MED/HI areas (two-way ANOVA; Table 3). No interaction (biomass × period) was statistically significant (Table 3). Higher mean values of fish density (Tukey's test; 22.13 ind m⁻²; Fig. 3A) and total weight (34.26 g m⁻²; Fig. 3B) were found in beds with high macrophyte biomass. Lower values were observed at sites with low vegetation biomass (1.32 ind m⁻² and

Table 2

Fish assemblage associated with *Egeria* spp. in Rosana Reservoir (N = number of individuals; TW = total weight (g); SL = mean standard length (cm ± standard error) ME/HI (%) = percentage of individuals captured in areas with medium and high macrophyte biomass; PI (%) = percentage of sexually immature individuals; PRPD (%) = percentage of reproductive individuals)

Taxa	N	TW	SL	ME/HI (%)	PI (%)	PRPD (%)
CHARACIFORMES						
CHARACIDAE						
<i>Hemigramus marginatus</i>	89	37.18	2.49 ± 0.45	84.27	13.04	68.12
<i>Hyphessobrycon eques</i>	149	95.75	2.72 ± 0.26	95.97	5.71	89.29
<i>Hyphessobrycon</i> sp.	20	10.97	2.67 ± 0.07	100	0	21.05
<i>Serrapinus notomelas</i>	32	20.79	2.69 ± 0.08	100	0	76.67
<i>Roeboides paranensis</i>	107	60.33	2.89 ± 0.09	99.01	55.88	22.55
<i>Acestrorhynchus lacustris</i>	1	6.58	8.20	100	100	0
<i>Oligossarcus pintoii</i>	32	36.25	3.53 ± 0.10	100	41.94	3.23
<i>Metynnis maculatus</i>	7	3.57	2.19 ± 0.10	100	100	0
<i>Serrassalmus marginatus</i>	88	44.20	2.22 ± 0.08	96.59	100	0
ANOSTOMIDAE						
<i>Leporinus</i> sp.	2	2.15	3.35 ± 0.35	100	100	0
<i>Schizodon borellii</i>	1	1.59	4.10	100	100	0
<i>Schizodon nasutus</i>	4	18.17	5.38 ± 1.33	100	66.67	33.33
GYMNOTIFORMES						
RHAMPHICHTHYIDAE						
<i>Rhamphichthys hahni</i>	2	2.56	7.35 ± 2.35	100	100	0
GYMNOTIDAE						
<i>Gymnotus carapo</i>	1	16.55	23.50	100	0	0
STERNOPYGIDAE						
<i>Eigenmannia trilineata</i>	15	135.59	13.03 ± 1.59	100	26.67	73.33
<i>Sternopygus macrurus</i>	2	120.85	27.25 ± 7.75	100	0	50
SILURIFORMES						
LORICARIIDAE						
<i>Loricariichthys platymetopon</i>	1	0.08	2.70	100	100	0
PERCIFORMES						
CICHLIDAE						
<i>Cichlasoma paranaense</i>	5	4.83	2.48 ± 0.39	100	100	0
<i>Crenicichla britskii</i>	4	3.08	3.25 ± 0.27	100	100	0
<i>Satanoperca pappaterra</i>	27	93.21	4.00 ± 0.31	96.27	88.46	0
Total	589	714.28	3.17 ± 0.11	95.76	40.92	43.30

Table 3

Two-way ANOVAs to test for differences in fish assemblage structure among different macrophyte biomass classes (low, medium and high) and periods of the day (morning, midday and dusk). Fish abundance and total weight were transformed ($\log + 1$) to perform analysis

Variables	DF	F	P<
Abundance ($\log + 1$)			
Biomass	2	40.32	0.000001
Period	2	0.46	0.6338
Biomass \times period	4	0.83	0.5087
Total weight ($\log + 1$)			
Biomass	2	46.98	0.000001
Period	2	0.50	0.6084
Biomass \times period	4	1.16	0.3411
Species richness			
Biomass	2	34.03	0.000001
Period	2	0.32	0.7295
Biomass \times period	4	0.77	0.5517
Diversity H'			
Biomass	2	31.66	0.000001
Period	2	0.32	0.7257
Biomass \times period	4	0.31	0.8727

0.805 g m⁻²). High variability of fish total weight among samples in dense *Egeria* beds was due to the presence or absence of Gymnotiformes, which were caught predominantly in these habitats. Similarly, higher mean values of fish taxa richness ($S = 5.6$ taxa m⁻²; Fig. 3C) and Shannon diversity ($H' = 1.37$; Fig. 3D) were found in high biomass *Egeria* stands. Sites with low vegetation biomass had both low mean richness ($S = 0.47$ m⁻²) and diversity ($H' = 0.10$). A similar trend was observed when we used rarefaction curves to analyze fish species richness. After 15 samples, habitats with high macrophyte biomass were richer in fish species

than areas with medium and low macrophyte biomass (Fig. 2B).

4. Discussion

The present work suggests that beds of *Egeria* are important for the maintenance of a particular fish fauna composed of small sized individuals. When frequencies of individuals are compared between MED/HI and LOW areas, it becomes clear that these individuals are dependent on vegetation density: they are only frequent adjacent areas (with sparse vegetation) sporadically, maybe searching for some specific resource or when moving among beds. Similar to patterns observed in stands of other macrophyte species, fishes with standard lengths <5 cm predominated, especially species of the order Characiformes (Delariva et al., 1994; Meschiatti et al., 2000; Agostinho et al., 2002). In high density stands, Gymnotiformes were also an important component of the fish assemblage. The sedentary behavior and the vulnerability of gymnotids and small characids to predation are characteristics that could partially explain their association with macrophytes. On the other hand, the relatively low abundance of Siluriformes (a dominant order in neotropical freshwaters) may be related to the benthic behavior of the majority of these species, a pattern also observed in other studies (Delariva et al., 1994; Agostinho et al., 2002).

Considering that the ichthyofauna was composed predominantly of sedentary small-sized species and juveniles, the spatial structure provided by *Egeria* may be an appropriate substratum for food provision as well as a refuge from predation (Mazzeo et al., 2003). Perhaps, these fishes move only

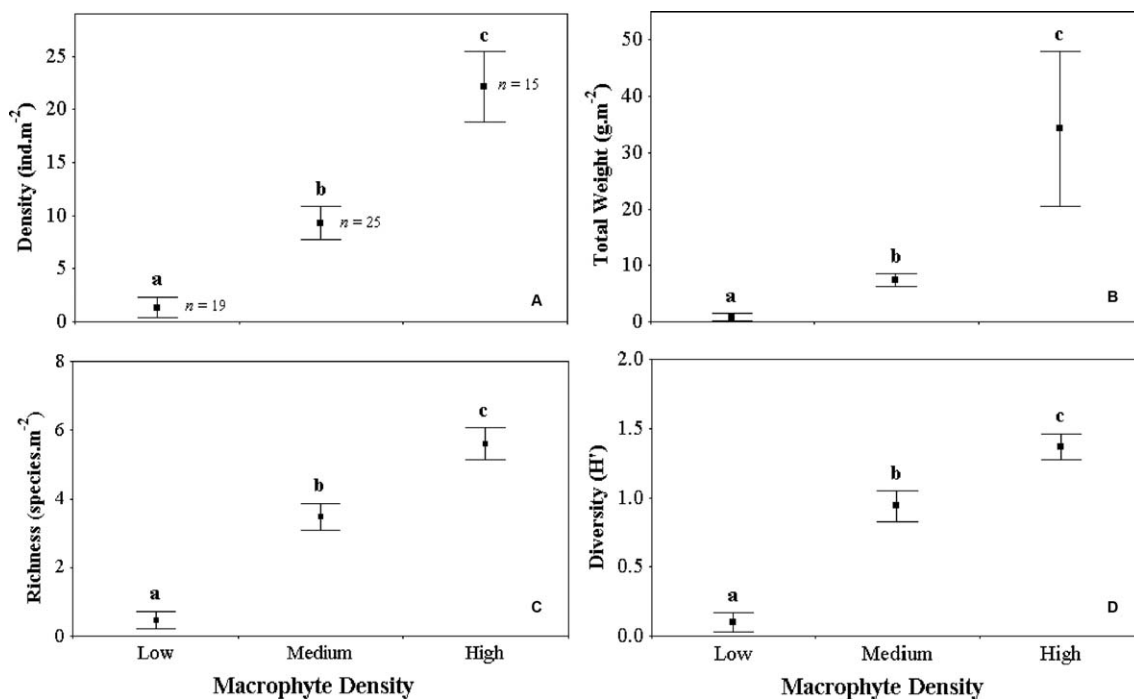


Fig. 3. Mean values (\pm standard error) of fish density (A), total weight (B), taxa richness (C) and Shannon diversity (D) in habitats with different macrophyte biomass. Different letters indicate means that differed statistically (Tukey's test). Two-way ANOVAs results are shown in Table 3.

short distances, to reach another stand or different structures (submerged trunks and rocks). Some studies highlight the importance of diel periodicity on fish activity (Jacobsen and Perrow, 1998; Gaudreau and Boisclair, 1998; Agostinho et al., 2002), where fish movements can promote changes in fish assemblage composition in the stands as well as an increase of predation pressure at dawn and dusk. However, we did not observe any significant effects in relation to diel periodicity.

Current hypotheses to explain fish/macrophyte associations include high food supply, substrate for spawning, and refuge from predation. Although aquatic macrophytes can be used directly in feeding (Gerking, 1994; Agostinho et al., 2003), the main contribution to fish trophic chains is detritus production (Araújo-Lima et al., 1986; Benedito-Cecilio et al., 2000) and as substratum for periphyton and invertebrates (Cyr and Downing, 1988; Mazzeo et al., 2003; Takeda et al., 2003). A recent study in Rosana Reservoir found an important contribution of autochthonous material in the diet, mainly invertebrates and algae (Casatti et al., 2003). Assessing the available food items associated with *Egeria* stems for comparison with fish stomach contents may be an easy way to test this hypothesis.

The role of macrophytes as substrate for spawning and development of young has been investigated in several works (Hendersen and Hamilton, 1995; Grenouillet and Pont, 2001; Ferrer-Montanó and Dibble, 2002). In the present study, a high proportion of juveniles (immature gonads) and reproductive fish comprised the assemblage. For some species, individuals in different development stages were captured, indicating that these species use this habitat throughout their life cycle (Cordivola de Yuan et al., 1984). Medium size species seem to use the environment temporarily as a spawning site and/or nursery habitat (e.g. *Metynnis maculatus*, *S. marginatus* and some anostomids). Other authors noted many medium sized species associated with macrophytes as juveniles (Sánchez-Botero and Araújo-Lima, 2001; Meschiatti and Arcifa, 2002).

The effects of predation on fish/macrophyte associations receive considerable attention, because of the potential influence on the two factors discussed above (i.e. influencing fish feeding activity and restricting juvenile distribution). The role of macrophytes as mediator in predator–prey interactions has been well studied (Jacobsen and Perrow, 1998). For example, using artificial vegetation, Priyadarshana et al. (2001) demonstrated that high macrophyte density can decrease predator efficiency by reducing visual contact with prey and hindering movement (Priyadarshana et al., 2001). With the exception of one *Acestorhinchus lacustris*, large piscivores were not caught in the present study. However, three species that feed on scales, fins or small individuals (*R. paranensis*, *O. pintoii* and juvenile *S. marginatus*) (Hahn et al., 1997), occurred in high abundance. These small-sized predators may produce strong predation pressure on other small sized species, because they are able to get access into densely vegetated areas. In this case, refuges may be essen-

tial for survival and maintenance of populations of small sized individuals (Rozas and Odum, 1988; Chick and McIvor, 1997), but dynamics involved may be more complex than predator–prey relationships observed in temperate regions.

The importance of macrophytes in structuring fish assemblages has been demonstrated by several studies in temperate regions (Chick and McIvor, 1994; Dibble et al., 1996; Weaver et al., 1996; Weaver et al., 1997; Grenouillet and Pont, 2001). In Neotropical areas, however, studies of fish/macrophyte associations are rare, and the role of macrophytes in structuring fish assemblages and their effects on ecosystem dynamics and productivity in wetlands have only recently been recognized (Esteves, 1998; Thomaz and Bini, 2003). According to Rossi and Parma de Croux (1992), the lack of attention given to relationships between vegetation and fish distributions, especially in the Paraná River basin, is in contrast with its ecological importance.

Meschiatti et al. (2000) attributed the scarcity of fish/macrophyte association studies to a lack of appropriate sampling methodologies. However, a variety of gears have been developed and tested for sampling biota of macrophyte stands (Kushlan, 1981; Jacobsen and Kushlan, 1987; Serafy et al., 1988; Agostinho et al., 2002). Studies evaluating the performance of a 1-m² throw trap demonstrated that it was effective within dense vegetation, sub-sampling only rare and large species (Kushlan, 1981; Jacobsen and Kushlan, 1987; Jordan et al., 1997). This restriction may be due to the small trap area and difficulties in the throw procedure and fish recapture. The development of a correction factor, based on an evaluation of the performance of throw traps in tropical regions, may be used to produce more precise density estimates (as already discussed by Kushlan, 1981). Although overall capture efficiency of our throw trap was not assessed, our procedure may be considered efficient, given that only 7% of fishes remained inside the trap after dip-net hauling.

Highest values for all fish assemblage attributes were observed in sites with high macrophyte densities. Vono and Barbosa (2001) also observed higher fish density and diversity in locations with higher macrophyte coverage. However, several studies have demonstrated that highest values, mainly of fish density and species richness, are detected in areas of intermediate macrophyte density (Killgore et al., 1989; Dibble et al., 1997; Miranda and Hodges, 2000) or in the open-water/macrophyte interface (Agostinho et al. 2002). This trend may be related to adverse conditions at high plant biomass, such as a decrease in water quality or difficulties in fish movement and foraging (Killgore et al., 1989; Miranda and Hodges, 2000). In the present work, it is likely that critical values of oxygen, temperature and pH could be found in the inner-most areas of extensive beds, due to limited water exchange and reduced atmospheric contact, or in situations when stands are senescing. As neither extensive nor senescing beds were sampled, no abiotic variables showed extremes that might restrict fish distribution. According to Thomaz (personal communication), based on 5 years of

research in Itaipu Reservoir, it is unlikely that beds of *E. najas* attain higher biomass than the values observed in the present study (maximum of approximately 250 g m⁻²). However, further research is required to ascertain the biomass range of *E. densa* in reservoirs of southern Brazil.

4.1. Management implications

About 30% of the approximately 70 listed species in Rosana Reservoir (CESP, 1998; project PRONEX/CNPq, H.I. Suzuki, personal communication) reside in *Egeria* beds. Because the fish inventory on this reservoir is incomplete, additional species will be found. In fact, in the present work the four taxon collected were never caught before in this reservoir (*Hyphessobrycon* sp., *O. pintoi*, *G. carapo* and *S. macrurus*). Brown (2003) contested the value of *E. densa* beds as a suitable habitat for native fish populations in estuaries, because many fish species associated to these beds were alien. Differently, all fish species associated with *Egeria* in Rosana Reservoir were native to this basin, and fish/macrophyte interactions may be very old.

Fish/macrophyte associations are largely dependent on macrophyte species present in the reservoir, but the lack of vegetation in places previously vegetated drastically alters fish assemblages (Duffy and Baltz, 1998; Agostinho et al., 2003). Even by restricting the reduction of macrophyte biomass, this action, although considered necessary to facilitate multiple water uses (Olson et al., 1998; Agostinho et al., 2003), may be deleterious to the suite of fishes dependent on high macrophyte density such as Gymnotiformes. Habitat loss has been implicated in recent declines in fish diversity (Maitland, 1995). Our approach—to study fish assemblages at a local, habitat scale—and our results suggest that conservation of macrophyte beds is essential to the maintenance of fish assemblages. We predict a reduction in littoral fish density, biomass and species richness in response to the control and removal of macrophytes in Rosana Reservoir, activities already begun in other reservoirs of the same basin (Marcondes et al., 2003).

Acknowledgements

We thank Universidade Estadual de Maringá, PEA and NUPELIA for creating ideal conditions for the research. Pitágoras Piana, Raul Ribeiro and Sandra Pierini helped with data sampling. David Hoeinghaus provided helpful comments and corrected the English. CAPES/CNPq provided a scholarship for the first author.

References

Agostinho, A.A., Gomes, L.C., Julio Jr., H.F., 2003. Relações entre macrófitas e fauna de peixes. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e Manejo de Macrófitas Aquáticas*. EDUEM, Maringá, pp. 261–279.

- Agostinho, A.A., Thomaz, S.M., Baltar, S.L.S.M.A., Gomes, L.C., 2002. Influence of aquatic macrophytes on fish assemblage structure of the Upper Paraná River floodplain (Brazil). In: *Proceedings of the 11th EWRS International Symposium on Aquatic Weeds, Moliets et Maà, France*. pp. 69–72.
- Agostinho, A.A., Vazzoler, A.E.A.M., Thomaz, S.M., 1995. The high River Paraná basin: limnological and ichthyological aspects. In: Tundisi, J.G., Bicudo, C.E.M., Tundisi, T.M. (Eds.), *Limnology in Brazil*. Brazilian Academy of Sciences, Brazilian Limnological Society, São Paulo, pp. 59–103.
- Araújo-Lima, C.A.R.M., Portugal, L.P.S., Ferreira, E.G., 1986. Fish–macrophyte relationship in the Anavilhanas archipelago, a black water system in the Central Amazon. *J. Fish Biol.* 29, 1–11.
- Benedito-Cecílio, E., Araujo-Lima, C.A.R.M., Forsberg, B.R., Bittencourt, M.M., Martinelli, L.C., 2000. Carbon sources of Amazonian fisheries. *Fish. Manag. Ecol.* 7, 305–315.
- Benson, B.J., Magnuson, J.J., 1992. Spatial heterogeneity of littoral fish assemblages: relation to species diversity and habitat structure. *Can. J. Fish. Aquat. Sci.* 49, 1493–1500.
- Bianchini-Junior, I., 2003. Modelos de crescimento e decomposição de macrófitas aquáticas. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e Manejo de Macrófitas Aquáticas*. EDUEM, Maringá, pp. 85–126.
- Brown, L.R., 2003. Will tidal wetland restoration enhance populations of native fishes? In: Brown, L.R. (Ed.), *Issues in San Francisco Estuary Tidal Wetlands Restoration, San Francisco Estuary and Watershed Science*, Volume, Issue 1, Article 2. Available: <http://repositories.cdlib.org/jmie/sfews/vol1/iss1/art2>.
- Casatti, L., Mendes, H.F., Ferreira, K.M., 2003. Aquatic macrophytes as feeding site for small fishes in the Rosana reservoir, Paranapanema river, southeastern Brazil. *Braz. J. Biol.* 63 (2), 213–222.
- CESP, 1998. *Conservação e manejo nos reservatórios: limnologia, ictiologia e pesca. Série Divulgação e Informação 220*, São Paulo, 166 p.
- Chick, J.H., McIvor, C.C., 1994. Patterns in the abundance and composition of fishes among beds of different macrophytes: viewing a littoral zone as a landscape. *Can. J. Fish. Aquat. Sci.* 51, 2873–2882.
- Chick, J.H., McIvor, C.C., 1997. Habitat selection by three littoral zone fishes: effects of predation pressure, plant density and macrophyte type. *Ecol. Fresh. Fish* 6, 27–35.
- Colwell, R.K., 1997. *EstiMateS: statistical estimation of species richness and shared species from samples (Software and User's Guide)*, Version 5 Available: <http://viceroy.eed.unconn.edu/estimates>.
- Cook, C.D.K., Urmi-Konig, K., 1984. A revision of the genus *Egeria* (Hydrocharitaceae). *Aquat. Bot.* 19, 73–96.
- Cordiviola de Yuan, E., Oldani, N., Oliveros, O., Pignalberi De Hassan, C., 1984. Aspectos limnológicos de ambientes próximos a la ciudad de Santa Fé (Paraná Médio): poblaciones de peces ligadas a la vegetación. *Neotropica* 30, 127–139.
- Cyr, H., Downing, J.A., 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. *Fresh. Biol.* 20, 365–374.
- Delariva, R.L., Agostinho, A.A., Nakatani, K., Baumgartner, G., 1994. Ichthyofauna associated to aquatic macrophytes in the upper Parana river floodplain. *Revista Unimar* 16 (3), 41–60.
- Dibble, E.D., Harrel, S.L., 1997. Largemouth bass diets in two aquatic plant communities. *J. Aquat. Plant Manage.* 35, 74–78.
- Dibble, E.D., Killgore, K.J., Harrel, S.L., 1996. Assesment of fish–plant interactions. In: Miranda, L.E., Devries, D.R. (Eds.), *Multidimensional approaches to reservoir fisheries management*. American Fisheries Society Symposium 16, Bethesda, MD. pp. 357–372.
- Dionne, M., Folt, C.L., 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. *Can. J. Fish. Aquat. Sci.* 48, 123–131.
- Duffy, K.C., Baltz, D.M., 1998. Comparison of fish assemblages associated with native and exotic submerged macrophytes in the lake Pontchartrain estuary, USA. *J. Exp. Mar. Biol. Ecol.* 223, 199–221.
- Esteves, F.A., 1998. *Fundamentos de limnologia*, 2nd ed. Interciência, Rio de Janeiro pp. 575.

- Ferrer-Mantano, O.J., Dibble, E.D., 2002. Aquatic plants densities and larval fish abundance in vegetated habitats on the Tenesse-Tombigbee waterway system. *J. Fresh. Ecol.* 17 (3), 455–460.
- Gaudreau, N., Boisclair, D., 1998. The influence of spatial heterogeneity on the study of fish horizontal daily migration. *Fish. Res.* 35, 65–73.
- Gerking, S.D., 1994. *Feeding Ecology of Fish*. Academic Press, San Diego pp. 416.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Grenouillet, G., Pont, D., 2001. Juvenile fishes in macrophyte beds: influence of food resources, habitat structure and body size. *J. Fish. Biol.* 59, 939–959.
- Hahn, N.S., Andrian, I.F., Fugì, R., Almeida, V.L.L., 1997. Ecologia trófica. In: Vazzoler, A.E.A.M., Agostinho, A.A., Hahn, N.S. (Eds.), *A Planície de Inundação do alto rio Paraná, Aspectos físicos, biológicos e socio-econômicos*. EDUEM, Maringá, pp. 209–228.
- Hendersen, P.A., Hamilton, H.F., 1995. Standing crop and distribution of fish in drifting and attached floating meadow within an Upper Amazonian varzea lake. *J. Fish. Biol.* 47, 266–276.
- Jackson, D.A., Peres-Neto, P.R., Olden, J.D., 2001. What controls who is where in freshwater fish communities—the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* 58, 157–170.
- Jacobsen, T., Kushlan, J.A., 1987. Sources of sampling bias in enclosure fish trapping: effects on estimates of density and diversity. *Fish. Res.* 5, 401–412.
- Jacobsen, L., Perrow, M.R., 1998. Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. *Ecol. Fresh Fish* 7, 78–86.
- Jordan, F., Coyne, S., Trexler, J.C., 1997. Sampling fishes in vegetated habitats: effects of habitat structure on sampling characteristics of the 1-m² Throw Trap. *Trans. Am. Fish. Soc.* 126, 1012–1020.
- Killgore, K.J., Morgan II, R.P., Rybicki, N.B., 1989. Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac river. *N. Am. J. Fish Manage.* 9, 101–111.
- Kushlan, J.A., 1981. Sampling characteristics of enclosure fish traps. *Trans. Am. Fish Soc.* 110, 557–562.
- Maitland, P.S., 1995. The conservation of freshwater fish: past and present experience. *Biol. Cons.* 72, 259–270.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurements*. Croom Helm, London pp. 179.
- Marcondes, D.A.S., Mustafá, A.L., Tanaka, R.H., 2003. Estudos para manejo integrado de plantas aquáticas no reservatório de Jupia. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e manejo de macrófitas aquáticas*. EDUEM, Maringá, pp. 299–317.
- Mazzeo, N., Rodríguez-Galego, L., Kruk, C., Meerhoff, M., Gorga, J., Lacerot, G., Quintans, F., Loureiro, M., Larrea, D., Garcia-Rodríguez, F., 2003. Effects of *Egeria densa* Planch beds on a shallow lake without piscivores fish. *Hydrobiologia* 506, 591–602.
- Meschiatti, J., Arcifa, M.S., 2002. Early life stages of fish and the relationships with zooplankton in a tropical Brazilian reservoir: lake Monte Alegre Braz. *J. Biol* 62, 41–50.
- Meschiatti, J., Arcifa, M.S., Fenerich-Verani, N., 2000. Fish communities associated with macrophytes in Brazilian floodplain lakes. *Env. Biol. Fish.* 58, 133–143.
- Miranda, L.E., Hodges, K.B., 2000. Role of aquatic vegetation coverage on hypoxia and sunfish abundance in bays of a eutrophic reservoir. *Hydrobiologia* 427, 51–57.
- Olson, M.H., Carpenter, S.R., Cunningham, P., Gafny, S., Herwig, B.R., Nibbelink, N.P., et al., 1998. Managing macrophytes to improve fish growth: a multi-lake experiment. *Fish. Manag.* 23 (2), 6–12.
- Priyadarshana, T., Asaeda, T., Manatunge, J., 2001. Foraging behaviour of planktivorous fish in artificial vegetation: the effects on swimming and feeding. *Hydrobiologia* 442, 231–239.
- Rossi, L.M., Parma de Croux, M.J., 1992. Influencia de la vegetación acuática en la distribución de peces del rio Paraná, Argentina. *Ambiente Subtropica* 2, 65–75.
- Rozas, L.P., Odum, W.E., 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* 77, 101–106.
- Sánchez-Botero, J.I., Araujo-Lima, C.A.R.M., 2001. As macrófitas aquáticas como berçário para a ictiofauna da várzea do rio Amazonas. *Acta Amazônica* 31 (3), 437–447.
- Santamaría, L., 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. *Acta Oecol.* 23, 137–154.
- Serafy, J.E., Harrel, R.M., Stevenson, J.C., 1988. Quantitative sampling of small fishes in dense vegetation: design and field testing of portable “pop-nets”. *J. Appl. Ichthyol.* 4, 149–157.
- StaSoft, Inc., 2000. *STATISTICA for Windows (Computer Program Manual)*. Version 5.5.
- Takeda, A.M., Souza-Franco, G.M., Melo, S.M., Monkolski, A., 2003. Invertebrados associados às macrófitas aquáticas da planície de inundação do alto rio Paraná. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e Manejo de Macrófitas Aquáticas*. EDUEM, Maringá, pp. 243–260.
- Thomaz, S.M., Bini, L.M., 1999. A expansão das macrófitas aquáticas e implicações para o manejo de reservatórios: um estudo na represa de Itaipu. In: Henry, R. (Ed.), *Ecologia de Reservatórios: Estrutura, Função e Aspectos Sociais*. FAPESP/FUNDIBIO, Botucatu, pp. 599–626.
- Thomaz, S.M., Bini, L.M., 2003. Análise crítica dos estudos sobre macrófitas aquáticas desenvolvidos no Brasil. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e Manejo de Macrófitas Aquáticas*. EDUEM, Maringá, pp. 19–38.
- Thomaz, S.M., Bini, L.M., Pagioro, T.A., 2003. Macrófitas aquáticas em itaipú: ecologia e perspectivas para o manejo. In: Thomaz, S.M., Bini, L.M. (Eds.), *Ecologia e Manejo de Macrófitas Aquáticas*. EDUEM, Maringá, pp. 319–341.
- Vono, V., Barbosa, F.A.R., 2001. Habitats and littoral zone fish community structure of two natural lakes in southeast Brazil. *Env. Biol. Fish.* 61, 371–379.
- Weaver, M.J., Magnuson, J.J., Clayton, M.K., 1996. Habitat heterogeneity and fish community structure: inferences from North Temperate Lakes. In: Miranda, L.E., Devries, D.R. (Eds.), *Multidimensional Approaches to Reservoir Fisheries Management*. American Fisheries Society Symposium 16, Bethesda, MD. pp. 335–346.
- Weaver, M.J., Magnuson, J.J., Clayton, M.K., 1997. Distribution of littoral fishes in structurally complex macrophytes. *Can. J. Fish. Aquat. Sci.* 54, 2277–2289.