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Feeding ecology of fishes associated with *Egeria* spp. patches in a tropical reservoir, Brazil

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Abstract – This research characterised feeding ecology of fishes associated with patches of *Egeria najas* and *Egeria densa*, two submerged macrophytes, in Rosana Reservoir, Upper Paraná River basin, Brazil. Fishes were sampled using a 1 m^2 throw trap in patches of different macrophyte biomass and in three diel periods during a wet season. Fish diet (10 species) was primarily composed of autochthonous items (zooplankton, algae and aquatic insect larvae). Almost all intra-specific diet patterns had moderate to low levels of diet similarity, indicating a high variability in diet. Some species showed no diel patterns in feeding activity, whereas others were primarily diurnal or nocturnal. No differences in feeding activity were observed among habitats of medium and high macrophyte biomasses, and species tended to feed on the same items among these habitats. The most abundant fish species demonstrated low inter-specific diet overlap and appear not to compete for food resources. We suggest that *Egeria* patches are feeding grounds and shelter for small-sized fish species.

Key words: submerged macrophytes; fish assemblages; feeding patterns; feeding activity; diet variability; inter-specific overlap

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Aquatic macrophytes are important habitats for many groups of organisms (Carpenter & Lodge 1986; Lalonde & Downing 1992; Dibble et al. 1996; Agostinho et al. 2003). Many fish species are found in these habitats, benefiting from a diversity of food items as well as refuge from predation. Some empirical patterns are known for temperate environments, where the structure of fish assemblages has been related to the presence, abundance, composition and architecture of aquatic plants (reviewed by Dibble et al. 1996; Petr 2000; Agostinho et al. 2003).

Some of these trends have been recently documented in tropical regions, and macrophytes seem to play a similar role in structuring fish assemblages, especially for small-sized species and juveniles (Meschiatti et al. 2000; Vono & Barbosa 2001; Agostinho et al. 2002; Petry et al. 2003; Pelicice et al. 2005). Although most studies are essentially descriptive, some hypotheses are being addressed, concerning empirical relationships and mechanisms involved (Agostinho et al. 2002; Petry et al. 2003; Pelicice et al. 2005).

In some large basins in South America, reservoir proliferation has led to the massive development of submerged macrophytes, especially in basins with cascades of dams. In particular, two native species of rooted-submerged macrophytes, *Egeria najas* Planch. and *Egeria densa* Planch., are becoming widespread in shallow areas of many reservoirs in the Upper Paraná River basin, south/southeast Brazil. These beds constitute an important habitat for algae, invertebrates and small-sized fishes (Casatti et al. 2003; Mazzeo et al. 2003), forming a complex structure of dense underwater foliage and ramified stems (Dutartre et al. 1999). In a previous work, Pelicice et al. (2005) demonstrated that biomasses of these macrophytes positively influence fish assemblage attributes such as fish density and diversity.

In spite of the positive aspects of biodiversity maintenance, *Egeria* beds show high nuisance potential and the authorities are concerned about future

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water quality and hydroelectric functioning (Thomaz & Bini 1999). Therefore, understanding the role macrophytes play in structuring fish assemblages is fundamental when the aim is habitat management and biodiversity conservation (van Nes et al. 2002; Agostinho et al. 2003). In this sense, the present work is an observational field research that contributes with much needed information regarding feeding ecology of fishes associated with *Egeria* patches in a neotropical reservoir during a wet season. Explicitly, the patterns examined were (i) food items consumed, (ii) intra-specific diet variability, (iii) diel feeding activity, (iv) diet and feeding activity in patches of different biomasses, and (iv) inter-specific food partitioning. Additionally, we discuss that resource availability may be one of the mechanisms aggregating fishes in these patches.

Material and methods

Study area

Rosana is the last reservoir of a cascade in the lower Paranapanema River (22°36′S, 52°52′W), a major tributary of the Brazilian segment of the Paraná River system (the second longest river in South America). The reservoir has a surface area of 276 km^2, is shallow (depth <10 m), has high water transparency (Secchi depth varying from 1.0 to 3.5 m) and is oligotrophic. Rosana Reservoir is characterised by high macrophyte diversity (37 taxa; Thomaz et al. 2005), but recently large stands of *Egeria* have become ubiquitous in Rosana and many others reservoirs of this system. These beds form patches of different areas and biomasses ($\sim$1–530 g m^{-2} of dry weight, DW; Pelicice et al. 2005) in shallow areas (maximum depth usually <3.0 m). A map of this reservoir, the description of fish assemblage structure, as well as effects of plant density and diel period upon the ichtyofauna can be found in Pelicice et al. (2005).

Data collection

Fishes were sampled at six sites in the reservoir during the wet season (January 15–21, 2003). Three sites were located in Euclides da Cunha Paulista district ($n = 28$ samples), 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). At each site, a 1 m^2 throw trap (1.5 m height) was used to sample fish in patches of *E. densa* and *E. najas* of different biomasses in littoral areas (depths <1.4 m). Here, each throw trap procedure was considered as an independent 'sample' (an enclosed area of 1 m^2), including fish and macrophytes trapped inside. A total of 59 samples were collected, distributed in three diel periods: morning (06:00 h; $n = 20$), midday (13:00 h; $n = 21$) and dusk (18:30 h; $n = 18$).

An explicit description of methodology used for fish and macrophyte sampling can be found in Pelicice et al. (2005). Briefly, macrophyte dry weight biomass (g m^{-2}) was calculated for each sample. All samples were characterised as having low ($\sim$1–70 g m^{-2}; $n = 19$), medium (71–200 g m^{-2}; $n = 25$) or high (200–530 g m^{-2}; $n = 15$) macrophyte biomass. It was not possible to evaluate DW biomass in dusk samples, so macrophyte biomass was visually categorised as low, medium or high. All fish captured were preserved in 10% formaldehyde, taken to the laboratory and subsequently identified, counted and measured (standard length, cm). A general description of the sampling design is shown in Table 1.

After fish evisceration, stomach fullness was assessed by visual inspection and categorised as 0 (empty), 1 (1–25% of stomach volume occupied by food), 2 (25–75%) and 3 (75–100%). Only stomachs with fullness 2 and 3 were kept for content analysis. Contents were identified under stereoscopic microscopy to the lowest taxonomic level. For each food item, volume (ml) was measured using graduated cylinders and millimetre-scale plates.

Diet characterisation

Analyses were performed only for (i) patches of medium and high macrophyte biomasses, because in low biomass habitats few individuals were caught (see Pelicice et al. 2005) and most had empty stomachs, and (ii) for species with more than five individuals. The feeding index IA$_i$ was calculated to characterise fish species diets (Kawakami & Vazzoler 1980), which combines total volume (%) and frequency of occurrence (%) of each item (lowest taxonomic level).

$$\mathrm{IA}_i = \frac{F_i * V_i}{\sum_{i=1}^{L} F_i * V_i}$$

where F_i is the frequency of occurrence of item i (%), V_i is the relative volume of item i (% of total) and L is the number of items.

For remaining analyses some items were pooled, forming broader categories: algae (ALG), fungi

Table 1. The number of samples collected in each category of macrophyte biomass and diel period. Each throw trap procedure was considered an independent sample, totalling 59 samples.

	Diel period			
Macrophyte biomass	Morning	Midday	Dusk	Total
Low	6	7	6	19
Medium	10	11	4	25
High	4	3	8	15
Total	20	21	18	

(FUN), bryophyte (BRT), higher plants (VEG), invertebrates (INV), Ostracoda (OST), Cladocera (CLA), Copepoda (COP), Decapoda (SHP), aquatic insects (AQUI), terrestrial insects (TEI), unidentified arthropods (ART), fish fins (FIN), fish scales (SCA), sediment (SED) and detritus (DET). Because Ostracoda, Cladocera and Copepoda were the main items consumed by almost all species, they were not pooled.

Intra-specific diet variability

IA_i calculations are useful in providing a general description of species diet. However, these values have a great potential to give misleading conclusions, as they do not measure any variability existent in the diet among individuals (to characterise diet, volumes from all individuals are pooled by food item). For this reason, an overlap index was used as a measure of intra-specific diet variability. Using the software ECOSIM v7.2 (Gotelli & Entsminger 2001), Pianka's overlap index (Pianka 1973) was calculated between all individuals of the same species using the matrix of volume in percentage:

$$O_{12} = \frac{\sum_{i=1}^{L} P_{i2} * P_{i1}}{\sqrt{\sum_{i=1}^{L} (P_{i2}^2) * (P_{i1}^2)}}$$

where p_{i2} is the % volume of item i in the diet of individual 2 and p_{i1} is the % volume of item i in the diet of individual 1. A mean intra-specific general overlap was obtained from all overlap combinations (hereafter 'between' samples mean overlap), which permits evaluation of intra-specific diet variability, e.g., the degree of diet similarity among individuals. This index ranges between 0 (no diet overlap, high variability) and 1 (complete overlap, no variability).

To explore (indirectly) the influence of local environmental conditions on intra-specific diet variability, Pianka's index was calculated among individuals of a same species by sample (patch), providing a mean overlap 'within' samples (considering only species present in more than three samples, with more than two individuals in each). Mean overlap 'within' samples was then compared to the mean overlap 'between' samples. In addition, the coefficient of variation (CV = standard deviation/mean) was calculated for both groups to compare the variability among overlap values observed in 'within' and 'between' samples.

Feeding activity

To determine diel and habitat feeding activity, the mean stomach fullness (M_f) was calculated for representative species ($N > 25$ individuals; species abundance is detailed in Pelicice et al. 2005) for each diel period and macrophyte biomass category:

$$M_f = \frac{(N_0 * 0) + (N_1 * 1) + (N_2 * 2) + (N_3 * 3)}{N}$$

where N_0 is the number of individuals with stomach fullness of 0, N_1 is the number of individuals with stomach fullness of 1, N_2 is the number of individuals with stomach fullness of 2 and N_3 is the number of individuals with stomach fullness of 3; N is the total number of individuals analysed.

One-way ANOVAs were used to test for significant differences in M_f values between diel periods and macrophyte biomass categories. Two-way designs were not used because of unbalanced data distributions among levels of factors. Bonferroni probability correction ($\alpha = 0.05$/number of tests) was considered to avoid type I error. Parametric assumptions were checked prior to analysis. Means were compared using Tukey's *post hoc* test. All analyses were performed using STATISTICA v5.5 (StatSoft 2000).

Effect of macrophyte biomass on diet

To compare overall dietary patterns between patches with medium and high macrophyte biomasses, diet similarity between habitats was measured using Pianka's overlap index. Volumes of each item were pooled from all individuals collected in each category of macrophyte biomass. The resulting matrix of relative volumes (%, by food items) was used to calculate diet overlap between habitats and to explore differences in species diet between patches with medium and high macrophyte biomasses. Only species with a sufficient number of individuals ($N > 5$) in both categories of macrophyte biomasses were analysed.

Overlap among species

To evaluate diet overlap among species, Pianka's overlap index was calculated for species pairs in each sample independently. Volumes of each item were pooled from all individuals collected within each single patch, by species. The resulting matrix of relative volumes (%) was used to calculate diet overlaps among species, considering all species pairs within each sample (patch). Therefore, an overall mean overlap and its standard error, for each species combination, were obtained. This procedure gives more realistic results, as overlap is measured among potential competitors (i.e., individuals collected in the same patch). Additionally, to explore co-occurrence patterns, the occurrence (%) of species pairs in the 40 samples (medium/high biomass) and the occurrence (%) of species pairs feeding in a same patch, were calculated. Only the most abundant species were analysed ($N > 15$ stomachs).

Results

Diet characterisation

From a total of 559 fishes caught in 59 samples (20 species; Pelicice et al. 2005), only 202 (10 species) had stomach fullness of 2 or 3 (Table 2). These species consumed autochthonous items almost exclusively. Out of 32 items identified, 22 were autochthonous, six allochthonous and four of unknown origin. According to IA_i values, the main food items consumed were (in decreasing order of importance) zooplankton (Ostracoda, Cladocera and Copepoda), filamentous algae and aquatic larval insects. Few individuals fed on higher plants, sediment or detritus.

Of the 10 species examined (Table 2), five fed almost exclusively on zooplankton (i.e., *Hyphessobrycon eques* (Steindachner), *Hemigrammus marginatus* Ellis, *Roeboides paranensis* Pignalberi, *Metynis maculatus* Kner and *Oligossarcus pintoi* Campos). Items of minor importance consumed by these species included algae and bryophytes (*H. eques* and *M. maculatus*), aquatic insect larvae (*H. marginatus*, *O. pintoi*, *M. maculatus* and *R. paranensis*) and adult terrestrial insects (*H. marginatus* and *O. pintoi*). *Eigenmannia trilineata* López & Castello consumed mostly insect larvae but also fed heavily on zooplankton. *Serrassalmus marginatus* Valenciennes and *Satanoperca pappaterra* (Heckel) had unique diets. The diet of *S. marginatus* was dominated by fish fins and scales (approximately 60%), although larvae of aquatic insects were also important (30%). *S. pappaterra* was the only species to incorporate higher plants and detritus more consistently in the diet. *Hyphessobrycon* sp. and *Serrapinus notomelas* (Eigenmann) were the only herbivores, feeding almost exclusively on algae and bryophytes.

Intra-specific diet similarity

Practically all species showed low values of intra-specific diet similarity (Pianka's index), indicating high diet variability among individuals (Table 3;

Table 2. Diet of fishes associated with patches of *Egeria*. Item values are the feeding index (IA_i), which combines frequency of occurrence (%) and volume (%) of each item.

	H.equ	H.mar	Hyphe	S.not	R.par	S.mar	M.mac	O.pin	E.tri	S.pap
N	51	21	7	16	34	37	6	13	10	7
Samples ($n = 37$)	16	8	4	9	13	17	5	11	3	5
SL (cm)	2.0–3.2	1.7–3.4	2.6–2.9	2.0–3.4	1.8–5.0	1.4–3.6	2.0–2.6	2.9–4.3	4.6–24.0	2.7–4.6
Autochthonous										
Algae	4.54	0.01	56.59	95.52	0.03	0.15	14.24	2.79	2.17	5.00
Bryophyte	9.56		34.37	1.89	<0.01	0.02	0.86	0.03		1.83
Ostracoda	9.89	38.43	4.51		9.22	2.33	22.87	4.58	25.69	3.07
Cladocera	1.60	33.92	0.79	1.59	5.64	1.29	34.75	5.70	10.96	26.76
Copepoda	70.05	10.91	1.34	0.03	66.75	0.7	5.04	42.17	1.53	
Ephemeroptera	0.29				1.01	25.98		14.23	19.79	
Trichoptera		1.99	0.08		5.38	0.68	5.47	0.33	7.99	
Odonata					0.26	1.69				
Chironomidae	2.55	0.41	1.74		6.93	6.65	5.15	0.92	27.05	
Diptera (others)	0.06				0.01	0.15		1.12	0.04	
Hemiptera								8.37		
Fish fins						51.36				
Fish scales	<0.01	0.06			1.68	8.70	4.72	0.05	<0.01	34.41
Others†	0.22	0.17			2.96	0.06	6.16		4.76	3.46
Total	98.76	85.91	99.42	99.03	99.87	99.76	99.26	80.29	99.98	74.53
Allochthonous										
Hymenoptera		4.82						16.75		
Others‡	0.03	8.15				0.12	0.09	2.75	0.01	
Total	0.03	12.97	0.00	0.00	0.00	0.12	0.09	19.50	0.01	0.00
Unidentified										
Higher plants	0.15	1.10	0.09	0.64	0.08	0.07				14.95
Detritus	0.96			0.21		<0.01				9.86
Others§	0.11	0.02	0.49	0.12	0.05	0.05	0.66	0.22	0.01	0.67
Total	1.22	1.12	0.58	0.97	0.13	0.12	0.66	0.22	0.01	25.48

Codes: *N* = number of stomachs analysed; Samples = number of patches from which all stomachs came; SL = range of standard length.

Names: H.equ = *Hyphessobrycon eques*; H.mar = *Hemigrammus marginatus*; Hyphe = *Hyphessobrycon* sp.; S.not = *Serrapinus notomelas*; R.par = *Roeboides paranensis*; S.mar = *Serrassalmus marginatus*; M.mac = *Metynnis maculatus*; O.pin = *Oligossarcus pintoi*; E.tri = *Eigenmannia trilineata*; S.pap = *Satanoperca pappaterra*.

†Others: Rotifera, Protozoa (Difflugiidae), Nematoda, Oligachaeta, Gastropoda, Conchostraca, Decapoda, Homoptera, Hydracarina.

‡Others: Diptera, Thysanoptera, Coleoptera, Arachnida, unidentified Arthropoda.

§Others: Fungi and sediment.

Table 3. Intra-specific diet variability 'between' and 'within' samples, expressed as mean values of Pianka's overlap index (O_{12}) and its coefficient of variation (CV). Overlaps were calculated from all individuals' pair combinations (% total volume; overlap between samples) and from pair combinations within each sample (overlap within samples).

	Overlap between samples			Overlap within samples			
Species	N	O_{12}	CV	n	N	O_{12}	CV
H. eques	51	0.31	1.02	10	45	0.56	0.47
H. marginatus	21	0.25	1.49	06	19	0.35	0.65
Hyphessobrycon sp.	07	0.46	0.89				
S. notomelas	16	0.83	0.36	05	12	0.76	0.53
R. paranensis	34	0.49	0.75	04	25	0.76	0.22
S. marginatus	37	0.50	0.76	08	28	0.59	0.52
M. maculates	06	0.31	0.72				
O. pintoi	13	0.25	1.46				
E. trilineata	10	0.77	0.19				
S. pappaterra	07	0.25	1.13				

N NN = number of individuals; n = number of samples.

between samples). For all species, the mean general overlap observed remained below 0.50, except for *S. notomelas* and *E. trilineata*, which presented the most conservative diets (least variable), although the latter may be biased (eight out 10 individuals were caught in a unique sample).

Diet similarity 'within samples' was evaluated for five species: *H. eques*, *H. marginatus*, *S. notomelas*, *R. paranensis* and *S. marginatus*. Except *S. notomelas*, an individual's diet similarity 'within' samples was always higher than similarity 'between' samples (Table 3), suggesting that these species have a diet that is more site dependent.

In addition, 'between' samples showed higher variation in overlap measures (CV) for all species, except *S. notomelas*. In some instances, 'between' samples had CV values twice higher than 'within' samples, such as *H. eques*, *H. marginatus* and *R. paranensis*. This result indicates that, in addition to higher mean overlaps, 'within samples' also had lower variation among overlap measures.

Feeding activity

This analysis was based on seven species: *H. eques*, *H. marginatus*, *O. pintoi*, *R. paranensis*, *S. marginatus*, *S. notomelas* and *S. pappaterra*. Some species restricted feeding activity to diurnal periods, such as *H. eques*, *S. marginatus* and *S. notomelas* (Fig. 1). *R. paranensis* was the only species that presented nocturnal feeding (Fig. 1). Others showed no diel pattern in feeding activity (one-way ANOVA; $P > 0.0071$; Bonferroni correction for seven tests). *H. marginatus* and *O. pintoi* probably feed continuously during day/night periods (Fig. 1). Although test significance correction excluded statistical diel differences for *S. pappaterra*, this species tended to feed more at dusk (Fig. 1), and an analysis with more individuals may provide evidence for such a pattern.

No species showed different feeding activity between sites with medium and high macrophyte biomasses (one-way ANOVA; $P > 0.0071$; Bonferroni correction for seven tests).

Effect of macrophyte biomass

Because of sample sizes, this analysis was based only on four species: *H. eques* ($N_{\text{high}} = 40$; $N_{\text{medium}} = 11$), *S. notomelas* ($N_{\text{high}} = 05$; $N_{\text{medium}} = 11$), *R. paranensis* ($N_{\text{high}} = 10$; $N_{\text{medium}} = 24$) and *S. marginatus* ($N_{\text{high}} = 27$; $N_{\text{medium}} = 10$). In general, diet composition was very similar between patches of medium and high macrophyte biomasses. Individuals of *H. eques*, *S. notomelas* and *S. marginatus* fed on the same items in both areas, with overlap values (Pianka's index) of 0.95, 0.99 and 0.98, respectively. Only *R. paranensis* tended to change its diet ($O_{12} = 0.36$), consuming more zooplankton in areas with medium macrophyte biomass and aquatic insect larvae in higher macrophyte biomass.

Overlap among species

This analysis compared inter-specific dietary overlap among five species: *H. eques*, *H. marginatus*, *R. paranensis*, *S. marginatus* and *S. notomelas*. In general, these species exhibited low dietary overlap (Table 4). The highest mean overlap (Pianka's index) was observed between *H. eques* and *R. paranensis* ($O_{12} = 0.58$); both species consumed mainly zooplankton. These species co-occurred in 40% of the patches, but were feeding together in only 25% of these patches. The second highest mean overlap occurred between *S. marginatus* and *R. paranensis* ($O_{12} = 0.43$), because of the shared resource of aquatic insect larvae. These species co-occurred in 45% of the patches, but were feeding together in only 33% of these patches.

Intermediate levels of dietary overlap occurred between *H. eques* and *S. notomelas* ($O_{12} = 0.37$), because of consumption of algae and bryophyte, and between *H. eques* and *H. marginatus* ($O_{12} = 0.32$), owing to some overlap in Ostracoda and Copepoda consumption. However, with intermediate levels of dietary overlap these species pairs were seen feeding together more frequently (>50%; Table 4).

In general, *S. notomelas* had the lowest values of inter-specific diet overlap, because of its unique diet based on algae. Similarly, *S. marginatus* had low dietary overlaps, but it is interesting to note that this species frequently co-occurred feeding together with other species (Table 4).

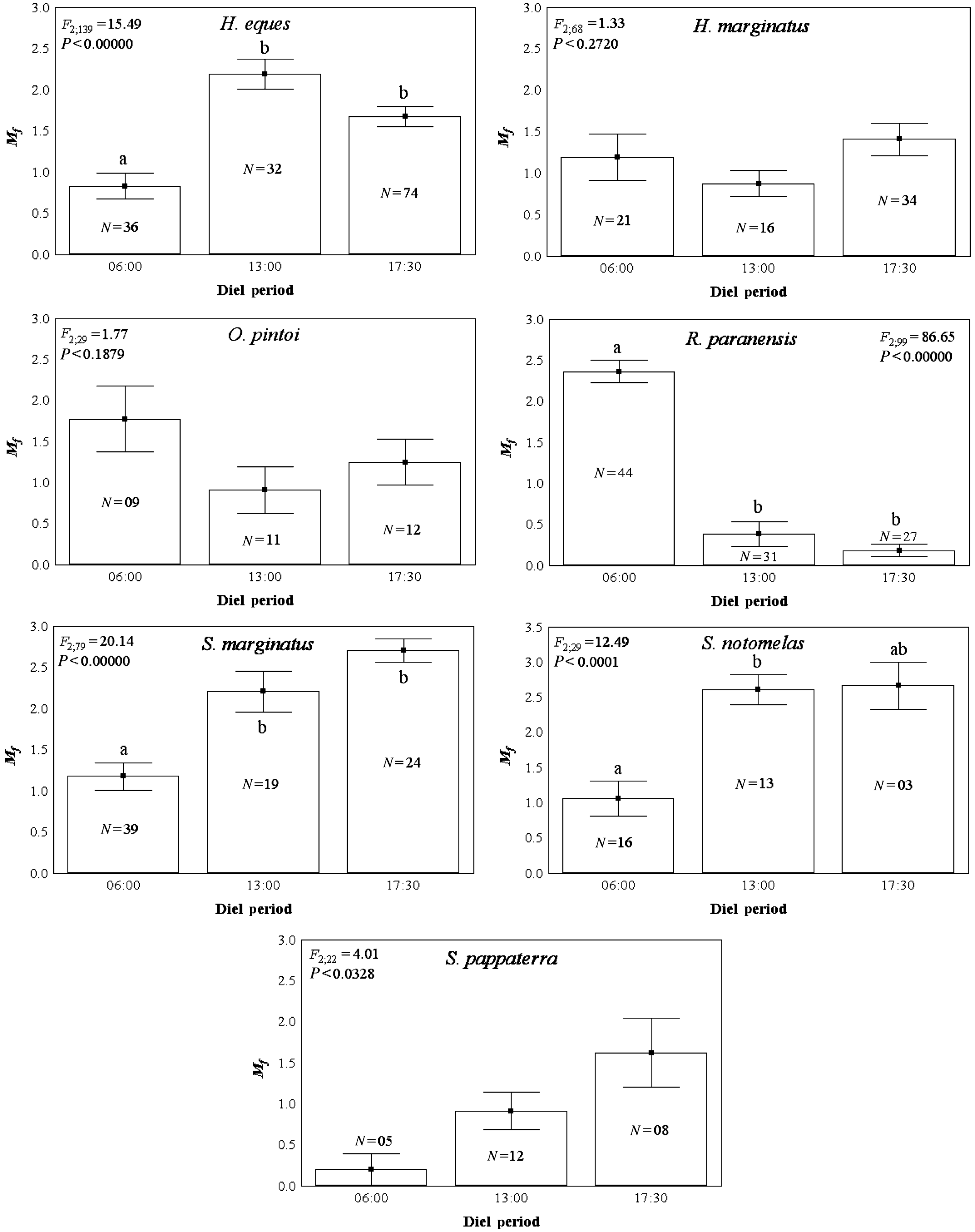

Fig. 1. Diel feeding activity of fishes associated with *Egeria* patches. M_f is the mean stomach fullness. One-way ANOVAs were used to test for differences in M_f values, considering Bonferroni probability correction (seven tests; $\alpha < 0.0071$). Error bars represent standard errors and letters indicate statistically different means (Tukey's *post hoc* test; $\alpha < 0.05$).

Table 4. Diet overlap (% total volume) among fish species associated with *Egeria*. Pianka's overlap index was calculated for each species pair within samples in which species co-occurred, generating a mean overlap and its standard error (SE). Pair occurrence illustrates the percentage of patches in which each species pair co-occurred (total) and the percentage of those patches in which both species were feeding (feed). Values shown in parentheses following species names are the species occurrence (%) in the 40 patches (medium and high biomasses).

	Mean overlap (SE)				
	H. eques	*H. marginatus*	*S. notomelas*	*R. paranensis*	*S. marginatus*
Pair occurrence (total/feed)					
H. eques (65)		0.32 (0.13)	0.37 (0.16)	0.58 (0.18)	0.11 (0.05)
H. marginatus (43)	35/50		0.05 (0.05)	0.20 (0.20)	0.09 (0.04)
S. notomelas (38)	30/67	20/25		0.01 (0.01)	0.07 (0.07)
R. paranensis (63)	40/25	28/27	25/20		0.43 (0.16)
S. marginatus (65)	50/50	25/40	30/67	45/33	

Discussion

A greater food supply is a current hypothesis explaining fish aggregation in macrophyte beds (Araújo-Lima et al. 1986; Rozas & Odum 1988; Casatti et al. 2003; Mazzeo et al. 2003). Because invertebrate distribution in *Egeria* beds was unknown and fish diets in other habitats were not evaluated, our results cannot test explicitly the hypothesis that 'mono-specific' *Egeria* patches are fish feeding grounds. However, in Rosana Reservoir, fishes associated with *Egeria* consumed almost exclusively autochthonous resources (more than 90% of items consumed), mainly zooplankton, epiphytic algae and aquatic insects. Many studies have shown that small invertebrates and algae are commonly found associated with macrophytes, utilising plants as substrate, refuge, feeding ground and direct nutrient source (Stansfield et al. 1997; Cheruvelil et al. 2000; Burks et al. 2001; Marklund et al. 2001; Lima et al. 2003). If *Egeria* patches constitute a suitable habitat for these organisms, as observed by Mazzeo et al. (2003), fish might be benefiting from many food resources. Although it is clear that appropriate experimental designs are needed to test the fish feeding ground hypothesis, the considerable consumption of autochthonous invertebrates and epiphytic algae suggest that *Egeria* patches might be playing this role during the wet season.

Although most species tended to feed preferentially on some food items, fish species in *Egeria* patches had moderate to low intra-specific diet similarity, revealing also a broad niche breadth. This high variability in diet highlights a well-known fish behaviour: individuals generally feed on resources available in a particular moment (Larkin 1956; Abelha et al. 2001; Jepsen & Winemiller 2002), a pattern that is strongly space/time dependent. Accordingly, to calculate the general intra-specific diet similarity we compared individuals collected in different places ('between' samples, which included more than 10 patches for some species), where environmental conditions and food availability may differ in quality and quantity. This procedure may account for a great amount of variation observed in diet.

Local environmental conditions, therefore, must influence considerably diet composition. Indeed, when intra-specific diet overlap was calculated separately for each patch ('within' samples), results supported the site-dependency of fish diet: diet similarity 'within' samples tended to be considerably higher than 'between' samples, e.g., individuals inhabiting a single patch presented a diet more alike. In addition, another important result was the lower variability in overlap values for 'within' samples, indicating that the level of diet overlap is more similar among patches than among all individuals. All these results indicate (indirectly) that individual's diet may be correlated with local environmental conditions and suggest that individuals are feeding in an opportunistic way among macrophyte patches, probably in response to the most abundant resource(s). Such a pattern reveals a clear individualistic behaviour, in which the 'feeding phenomena' depends completely on the phenomena of the individual fish (sensu Gleason 1917), that is, each fish of a particular species responding distinctly to environmental stimulus (intra-specific variability). Adequate measures of the range of this intra-specific variability are necessary to understand and predict fish feeding behaviours. Although the use of some indices (such as IA$_i$) and graphical methods (such as the method of Costello 1990) can be useful tools expressing the overall diet or general patterns in fish feeding ecology, the high degree of variability inherent to fish feeding behaviour can seriously mislead 'fixed' characterisations.

The lack of differences in fish diet between patches of medium and high macrophyte biomasses indicates that fish species feed on the same resources in both habitats. However, it is important to emphasise that the present analysis evaluated the overall diet, as calculations did not consider intra-specific variability within habitats (volumes from all individuals are summed by food item for each habitat type). For example, low values of intra-specific diet similarity were observed within each biomass category (data not showed), and these values approached the 'between' samples intraspecific mean overlap. Therefore, we may conclude that for some fish species the overall diet is similar between *Egeria* patches of medium and high macrophyte biomasses, but small differences in food consumption occur. The only exception was *R. paranensis*, which showed marked changes in diet between macrophyte habitats. Because this species showed nocturnal activity, it would be interesting to test if some invertebrates have diel movements among patches with medium and high macrophyte biomasses.

To evaluate fish feeding ecology, Casatti et al. (2003) sampled multispecific macrophyte stands in Rosana Reservoir, formed by *Egeria*, *Sagittaria*, *Salvinia* and *Eichhornia*. Compared to our results, differences can be noticed in the overall diet of common fish species. For example, they observed a high consumption of insect larvae by *H. marginatus*, *H. eques* and *R. paranensis*. Differently, in *Egeria* patches insect larvae comprised less than 10% of the diet of these species. Because neither overall fish diet nor feeding activity changed remarkably between *Egeria* patches of medium and high biomasses (which constitute distinct habitats), it is likely that plant architecture (macrophytes with different morphologies) play a major role in determining invertebrate assemblages and, thus, resource availability for fishes. As discussed, local environmental conditions influence fish diet among *Egeria* patches, but it is likely that substantial modifications in habitat qualities are needed to modify profoundly the overall diet, such as aquatic plants with prominent differences in morphology or life-strategies (Dionne & Folt 1991; Chick & McIvor 1997; Dibble & Harrel 1997).

Many freshwater fish species show well-marked patterns of diel activity (Reebs 2002; Hohausová et al. 2003), as a feeding behaviour or as a mechanism to avoid predation. In the present study, we observed marked diel feeding patterns for almost all species, the majority with diurnal activity and only one strictly nocturnal (*R. paranensis*). Pelicice et al. (2005) observed that these same fish species are all resident and do not leave the macrophyte patches during day/night periods. Therefore, these observations permit the conclusion that *Egeria* patches represent more than feeding areas for these small-sized fishes, as they remain associated with *Egeria* patches even when not feeding. Hence, we suggest that in habitats containing *Egeria* patches (i) the situation of open water profitability (Dewey et al. 1997) do not exist, because fish resources are more abundant in littoral areas and fish assemblages associated with *Egeria* are essentially formed by small-sized individuals (Casatti et al. 2003; Mazzeo et al. 2003; Pelicice et al. 2005), and (ii) some other mechanism influences fish aggregation inside *Egeria* beds, such as predation pressure (Chick & McIvor 1997). Large piscivores are found in this reservoir (for instance *Hoplias malabaricus*, adult *S. marginatus* and *Acestrorhynchus lacustris*), and the diet of these piscivores includes some of the small-sized species collected in the present study (Almeida et al. 1997). In addition, the fin-clipping behaviour of juvenile piranhas (*S. marginatus*) is a constant and less macrophyte-dependent impact. It is likely that predator–prey dynamics are very complex in these habitats, where predation pressure is diversified. Trade-offs between foraging and sheltering may not be clear, because fish remain constantly associated with vegetation.

Food partitioning is a common feature of fish assemblages (Ross 1986) and, accordingly, we observed low food overlap among species. It is interesting to note that, in addition to noticeably low diet overlaps, all species analysed, except *R. paranensis*, showed overlapping feeding periods (diurnal). Consequently, these results indicate that even feeding at the same period – and frequently in the same patches (see *S. marginatus*) – this fish assemblage shows a high degree of resource partitioning, based primarily on food choice and patch segregation. For example, although *H. eques* and *H. marginatus* consumed mostly zooplankton, *H. eques* preferred Copepoda whereas *H. marginatus* consumed mainly Ostracoda and Cladocera. In addition, when diet overlap was higher (the highest diet overlaps was observed with *R. paranensis*), we observed an interesting diel pattern of resource sharing. In this case, *R. paranensis* shared resources with other species but restricted its activity to another period (nocturnal). So, differences in food choice, low frequency of co-occurrence among potential competitors and differences in temporal resources use, as detected in this study, can prevent strong trophic competition. May (1986) reports that even when species demonstrate intense niche overlap, other factors can promote species coexistence, such as spatial heterogeneity and habitat complexity, allied with environmental, temporal, population and behavioural stochasticities.

In conclusion, fish species inhabiting *Egeria* patches in Rosana Reservoir presented a well-defined feeding structure, consuming basically autochthonous resources. It is likely that the use of microhabitats within macrophyte patches, together with particularities in resources use and activity, prevent trophic competition and permit the coexistence of several fish species (approximately five species) in habitat patches smaller than 1 m^2 of area (Pelicice et al. 2005).

Resumen

1. Esta investigación caracterizó la ecología trófica de las especies de peces asociadas a manchas de *Egeria najas* e

E. densa, dos macrofitas sub-aquaticas, en la represa de Rosana (alto Río Paraná, Brasil). Los peces fueron colectados con un *throw trap* de 1 m^2 en manchas con distintas biomasas de macrófitas y en tres períodos del día, durante la estación lluviosa.

2. La dieta de 10 especies estuvo compuesta principalmente de componentes autóctonos (zooplancton, algas y larva de insectos acuáticos). Casi todas las especies presentaron patrones de dieta intra-específica con similitudes moderadas o bajas (elevada variabilidad). Algunas especies no mostraron ningún patrón de actividad alimenticia durante el día mientras que otras fueron principalmente diurnas o nocturnas. No se observó ninguna diferencia de actividad alimenticia entre los habitats de media y alta biomasa de macrófitas, y las especies tendieron a alimentarse de los mismos componentes entre estos habitats.

3. Las especies de peces más abundantes mostraron un solapamiento alimenticio bajo y parecen no competir por recursos alimenticios. Sugerimos que las manchas de *Egeria* funcionan como lugar de alimentación y abrigo para los peces de pequeño tamaño.

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