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Is the community of fish gill parasites structured in a Neotropical floodplain?

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Abstract

Sixty-one specimens of the piranha *Serrasalmus marginatus* Valenciennes, 1837 were analyzed, aiming at assessing the community structure of their gill parasites. The samples were collected in lagoons of the Paraná, Ivinheima and Baia Subsystems within the Upper Paraná River Floodplain (Brazil). Host size and sex had little or no influence on the abundance and prevalence of parasites. The organization of the gill parasite infracommunities of *S. marginatus* was significantly non-random according to null models and ordination analyses. In general, parasite infrapopulations were not affected by interspecific associations or host characteristics (e.g. size, sex), what highlights the importance of local habitat characteristics to community organization of gill parasites of *S. marginatus* in the Upper Paraná River Floodplain.

Keywords

Freshwater fish, *Serrasalmus marginatus*, metazoan parasites, monogeneans, diversity, co-occurrence, null models

Introduction

Host-parasite systems are good models for understanding community structuring (Šimková *et al*. 2001, Gotelli and Rohde 2002). Co-occurrence, nestedness and intra/interspecific spatial aggregation of parasites have pointed out to great variability in community structure, showing a gradient from non-random to random communities (Guégan and Hugueny 1994; Poulin 1996; Morand *et al*. 1999; Poulin and Guégan 2000; Gotelli and Rohde 2002; González and Poulin 2005; Krasnov *et al*. 2006, 2010; Bellay *et al*. 2011). Besides, positive interactions (e.g. facilitation) can generate richer parasite infracommunities than expected by chance, as they allow coexistence with energy profit (Poulin 1996), whereas negative interactions (e.g. competition) tend to promote high niche segregation, allowing the development of more diverse infracommunities (Scott-Holland *et al*. 2006).

During fish development, several factors might affect the structure of the parasitic fauna. During maturation, for example, hormones can trigger behavioral and physiological differentiations between male and female hosts, and form distinct patterns of parasite infestation or infection. During host growth, complexity increases, and the fish offers higher number of habitats, and consequently it may shelter more parasites. Environmental variables, as well as host size and sex, affect the structure of parasite communities (Esch *et al*. 1988; Guégan and Hugueny 1994; Takemoto *et al*. 2005). However, there are few studies comparing species co-occurrence patterns among communities from different habitats (Krasnov *et al*. 2010).

Physical and chemical fluctuations in the characteristics of aquatic environments may cause alterations in fish parasite infrapopulations of the Upper Paraná River Floodplain (Pavanelli *et al*. 2004). The aquatic habitats observed in the Upper Paraná River Floodplain have particular limnological characteristics and can be differentiated according to the rivers which they are connected to (Thomaz *et al*. 2004). According to Thomaz *et al*. (2004), the lagoons connected to the Paraná River have high concentration of total ions, high water transparency, and low values of phosphorus, as observed also in the lagoons connected to the Ivinheima River. These authors state that in aquatic habitats connected to the Baia River, low values of dissolved oxygen and pH can be observed. The structural variability and limnological characteristics of these rivers in the floodplain enable studies at subsystem level (Paraná, Baia and Ivinheima).

After the construction of the Itaipu Dam in 1983, located 150 km downstream at Sete Quedas waterfall, several fish species from Middle Paraná colonized the Upper Paraná River Floodplain, including the piranha *Serrasalmus marginatus* Valenciennes, 1837. This species is well adapted to local condi-

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tions, and became one of the most abundant species in the floodplain (Agostinho *et al*. 2004).

In this study, we analyzed the community structure (infrapopulations, component populations, infracommunities and component communities, following Bush *et al*. 1997) of gill parasites of *S. marginatus*, collected in the Upper Paraná River Floodplain. Hosts were grouped according to subsystem, in order to test for possible influences of limnological characteristics on the parasite fauna. Gill parasite community structure was evaluated using co-occurrence null models and multivariate analyses. The community structure was expected to have a non-random co-occurrence pattern at different levels in the studied floodplain (local and regional), as a response to biotic interactions, biological development stages, and local habitat preferences.

Materials and methods

Sampling and preparation of parasites

Sixty-one specimens of *S. marginatus* were collected in February 2008 in the Upper Paraná River Floodplain (22°50´–22°70´S; 53°15´–53°40´W), using gill nets with different mesh sizes (2–16 cm). Sampling was carried out in five lagoons of the three subsystems: (i) Paraná-Garças Lagoon (22°43´27.2″S; 53°13´4.6″W; n = 20); (ii) Ivinheima-Patos Lagoon (22°49´33.6″S; 53°33´9.9″W; n = 11) and Ventura Lagoon (22°51´23.7″S; 53°36´1.0″W; n = 9); and (iii) Baia-Guaraná Lagoon (22°43´16.7″S; 53°18´9.3″W; n = 17) and Fechada Lagoon (22°42´37.9″S; 53°16´33.1″W; n = 4). Data were recorded for each fish captured: date, sampling site, standard length (cm), sex and gonadal maturity stage (young when immature and adult thereafter). Gills were removed from fish and fixated in 5% formol, and then examined for parasites under a stereomicroscope. Parasites were identified through morphological characteristics, and then prepared and mounted following Eiras *et al*. (2006). Sampling was carried within the Long-Term Ecological Research Program (LTER/CNPq/UEM/NUPELIA – site 6) developed by Universidade Estadual de Maringá in the Upper Paraná River Floodplain.

Data analysis. Host characteristics

The Kruskal Wallis test (H) was used to test for differences in standard length of hosts from the three subsystems. A Student's *t* test was used to test for differences in standard length between male and female fishes, for each subsystem separately.

Parameters of infrapopulations and component populations of parasites

Parasite prevalence (P%), mean intensity (MI) and mean abundance (MA) were calculated following Bush *et al*. (1997). Pearson correlation coefficient (r) was calculated to test for the relationship between the prevalence of each gill parasite species and host standard length; angular transformation of prevalence data and division of host samples into length classes were carried out before the analysis (Zar 2009). Spearman rank correlation coefficient (rs) was used to test for a correlation between the abundance of each gill parasite species and host standard length (Zar 2009). To test for the effect of host sex on prevalence and abundance of each parasite species, G (log-likelihood) and Mann-Whitney tests were used, respectively (Zar 2009). These tests were calculated for each subsystem separately and only for parasite species with prevalence over 10% (Bush *et al*. 1990).

Parameters of the infracommunities and component communities of parasites

The infracommunity structure of gill parasites was analyzed using the co-occurrence index C-Score (*Checkerboard score*) (Stone and Roberts 1990), a null model based on a presence-absence matrix. Cells in the presence-absence matrix had value 1 when the species was found in a given host, and value 0 when not.

The C-Score calculates the mean number of pairs of parasite species that do not co-occur considering all possible pairs in each infracommunity. The number of pairs of parasite species that do not co-occur (UC) is calculated with the formula: UC = $(r_i\text{-}S)(r_j\text{-}S)$, in which S is the number of shared hosts (hosts containing both species), and r_i and r_j are the number of hosts in which the parasite species *i* and *j* occur, respectively. The C-Score index is calculated with the formula:

$$\text{C-Score} = \frac{\sum UC}{R\left(\frac{R-1}{2}\right)}$$

where *R* is the total number of parasite species in the matrix.

In this study the algorithm SIM9 was used (Gotelli 2000), in which columns represent hosts and rows parasites. SIM9 fixed marginal totals for rows and columns, thus the prevalence of each parasite species and the species richness for each infracommunity were maintained. For each randomized matrix the C-Score was recalculated, originating a mean value of this index for all random matrices. The significance of the C-Score was estimated by comparing the value measured for the empirical matrix (observed value) with the average value of the randomized matrices (value expected at random). When the observed C-Score value is higher than expected by chance, it indicates species segregation, and when it is lower than expected, it indicates species aggregation. The C-Score index has already been successfully used in null model analyses testing hypotheses related to parasite communities (Mouillot *et al*. 2003; Krasnov *et al*. 2006, 2010; Tello *et al*. 2008).

Analyses were performed using matrices with data from all parasite infracommunities, as well as for each community separately, regarding sex, development phase (young or adult) or host environment. For each matrix analyzed 20,000 randomizations were made in the software EcoSim 7 (Gotelli and Entsminger 2001).

The chi-square test (X^2; Ludwig and Reynolds 1988) was used for testing interspecific interactions in the infracommunities of gill parasites with prevalence over 10% (Bush *et al*. 1990). The Kruskal Wallis test was used for comparing parasite abundance among infracommunities of the three subsystems. A Detrented Correspondence Analysis (DCA; Jongman *et al*. 1995) was performed, aiming at detecting similarities in parasite species composition in terms of abundance among infracommunities of the three subsystems, as well as between male and female hosts, and among host habitats (lagoons). An ANOVA was performed on the scores of the first or second axis of the DCA to test for differences among subsystems, sexes and lagoons. Differences were considered significant when $P \leq 0.05$. The DCA was performed in PC-Ord v.3.15 (McCune and Mefford 1997), and other statistical tests were carried out in STATISTICA 7.1 (StatSoft Inc. 2005).

Results

Host characteristics

The mean standard length (with standard deviation) of hosts was 12.6 ± 3.01 cm. Fish did not differ in standard length among subsystems (H = 1.12; P = 0.57). Only two specimens were not sexed and 31 males and 28 females were analyzed. Thirty young (Paraná: 1 male, 7 females; Ivinheima: 6 males, 4 females; Baia: 6 males, 6 females) and 29 adults (Paraná: 5 males, 6 females; Ivinheima: 6 males, 4 females; Baia: 7 males, 1 female) were collected. No significant difference in standard length between male and female hosts was observed (Paraná: t = –0.67, P = 0.51; Ivinheima: t = –0.54, P = 0.60; Baia: t = –0.20, P = 0.84).

Gill parasites of S. marginatus

In the present study 6,784 parasites were collected from the gills of *S. marginatus*. Morphological characteristics of para-

Table I. Parasites and infestation levels on the gills of *S. marginatus* in subsystems of the Upper Paraná River Floodplain

Parasites	NI	NP	P%	MI	MA
Paraná Subsystem					
Anacanthorus sp. 1	20	530	100	26.50	26.50
Anacanthorus sp. 2	20	227	100	11.35	11.35
Anacanthorus sp. 3	3	3	15	1.00	0.13
Amphithecium sp.	20	300	100	15.00	15.00
Notozothecium sp.	1	1	5	1.00	0.05
Notothecium sp.	20	228	100	11.40	11.40
Ascocotyle sp.	18	112	90	6.22	5.60
Acarina	1	3	5	3.00	0.15
Ivinheima Subsystem					
Anacanthorus sp. 1	20	645	100	32.25	32.25
Anacanthorus sp. 2	19	315	95	16.57	15.75
Anacanthorus sp. 3	3	43	15	14.33	2.15
Amphithecium sp.	18	263	90	14.61	13.15
Notothecium sp.	19	435	95	22.89	21.75
Ancyrocephalinae gen. sp. 1	3	4	15	1.33	0.20
Ancyrocephalinae gen. sp. 2	4	6	20	1.50	0.30
Ancyrocephalinae gen. sp. 3	4	15	20	3.75	0.75
Ascocotyle sp.	6	12	30	2.00	0.60
Acarina	1	1	5	1.00	0.05
Baia Subsystem					
Anacanthorus sp. 1	21	978	100	46.57	46.57
Anacanthorus sp. 2	20	164	95.23	8.20	7.80
Anacanthorus sp. 4	1	1	4.76	1.00	0.04
Anacanthorus sp. 5	1	1	4.76	1.00	0.04
Amphithecium sp.	21	565	100	26.90	26.90
Demidospermus sp.	1	2	4.76	2.00	0.09
Notothecium sp.	21	1,718	100	81.80	81.80
Ancyrocephalinae gen. sp. 1	9	157	42.86	17.44	7.47
Ancyrocephalinae gen. sp. 2	6	41	28.60	6.83	1.95
Ancyrocephalinae gen. sp. 3	4	7	19.05	1.75	0.33
Ancyrocephalinae gen. sp. 4	1	1	4.76	1.00	0.04
Ascocotyle sp.	4	5	19.04	1.25	0.23
Acarina	1	1	4.76	1.00	0.04

NI, no. of infested/infected fish; NP, no. of parasites collected; P%, prevalence; MI, mean intensity; MA, mean abundance.

sites revealed 15 taxonomic entities distributed in three metazoan groups: Monogenea, Digenea and Acarina (Table I). Parasitism levels of the infrapopulations for each subsystem are presented in Table I. Monogeneans represented approximately 98% of the analyzed parasites and were the group with the highest species richness in all subsystems. In addition, the

Table II. Observed and average randomized values of the C-Score calculated for infracommunities of gill parasites of *Serrasalmus marginatus* collected in February 2008 in the Upper Paraná River Floodplain

Level	**N**	**S**	**C-SCORE**			
			Obs	**Exp**	**SD**	**P**
Floodplain	61	15	12.30	11.05	0.37	<0.01*
Subsystem						
Paraná	20	8	0.25	0.25	0.00	1.00
Ivinheima	20	10	2.48	2.43	0.09	0.31
Baia	21	13	1.88	1.91	0.08	0.62
Paraná × Ivinheima	40	11	6.58	6.11	0.39	0.13
Paraná × Baia	41	15	6.00	5.03	0.24	<0.01*
Ivinheima × Baia	41	14	6.20	6.14	0.15	0.32
Sex						
Female						
Total	28	13	3.12	2.94	0.21	0.19
Paraná × Ivinheima	21	11	1.34	1.53	0.20	0.03* (Obs ≤ Exp)
Paraná × Baia	20	12	1.74	1.40	0.13	0.02*
Ivinheima × Baia	15	12	1.47	1.48	0.07	0.55
Male						
Total	31	11	6.01	5.58	0.15	0.01*
Paraná × Ivinheima	18	9	2.25	2.00	0.12	0.07
Paraná × Baia	19	11	2.85	2.61	0.10	0.03*
Ivinheima × Baia	25	11	3.07	3.08	0.10	0.55
Development stage						
Young						
Total	32	13	4.87	4.47	0.15	<0.01*
Male	13	10	1.09	1.10	0.07	0.58
Female	17	12	1.54	1.34	0.10	0.05*
Subsystem						
Paraná × Ivinheima	19	9	1.75	1.65	0.13	0.30
Paraná × Baia	22	13	2.82	2.48	0.11	<0.01*
Male	7	9	0.67	0.71	0.05	0.90
Female	13	11	1.02	0.78	0.09	0.02*
Ivinheima × Baia	23	13	2.59	2.58	0.08	0.45
Adult						
Total	29	12	3.83	3.35	0.23	0.04*
Male	18	10	2.15	1.71	0.13	<0.01*
Female	11	10	0.55	0.63	0.10	0.95
Subsystem						
Paraná × Ivinheima	21	11	2.25	2.11	0.21	0.23
Paraná × Baia	19	12	1.35	1.02	0.12	0.03*
Male	12	10	0.84	0.54	0.07	0.01*
Female	7	8	0.28	0.32	0.06	1.00
Ivinheima × Baia	18	11	1.54	1.45	0.08	0.15
Connected lagoons						
Total	48	15	10.13	8.83	0.32	<0.01*
Garças × Patos	31	11	3.74	3.07	0.29	0.04*
Male	11	8	1.10	0.76	0.07	<0.01*
Female	19	11	0.98	1.10	0.17	0.93
Garças × Guaraná	37	15	6.00	5.04	0.23	<0.01*
Male	18	11	2.85	2.62	0.11	0.04*
Female	18	12	1.74	1.40	0.13	0.02*
Patos × Guaraná	28	14	4.71	4.72	0.10	0.50
Disconnected lagoons						
Ventura × Fechada	13	7	0.57	0.59	0.02	1.00

N, number of hosts analyzed; S, richness; Obs, observed value; Exp, expected value; SD, standard deviation; P, probability that the observed number of pairs of species that do not co-occur is equal or larger than the simulated number of pairs of species that do not co-occur, assuming the null hypothesis of a random structure of the infracommunities; *significant data.

species *Anacanthorus* sp. 1, *Anacanthorus* sp. 2, *Amphithecium* sp. and *Notothecium* sp. represented together 93.84% of the collected parasites.

Parameters of the infrapopulations and component populations of parasites

For the species presented in Table I with prevalence over 10%, only *Anacanthorus* sp. 3 exhibited a significant negative correlation between prevalence and host standard length (Ivinheima Subsystem; r = –0.94; P = 0.01). In Paraná Subsystem there was a significant correlation between parasite abundance and host standard length for the species *Anacanthorus* sp. 1 (rs = 0.44; P = 0.04), *Anacanthorus* sp. 2 (rs = 0.54; P = 0.01) and *Ascocotyle* sp. (rs = 0.56; P < 0.01). Relationships between the sex of the host and parasite abundance or prevalence were not observed.

Infracommunity structure

The random organization of the gill parasite infracommunities of *S. marginatus* in all subsystems was rejected by the co-occurrence index C-Score, which pointed out a species segregation pattern (Table II). The overall co-occurrence pattern was directly affected by the infracommunities of the Paraná and Baia Subsystems, the only ones that exhibited differences in parasites diversity (see Table I), as observed in the null model analysis.

The analysis of the effect of sex on infracommunity structure, considering the three subsystems, indicated a random pat-

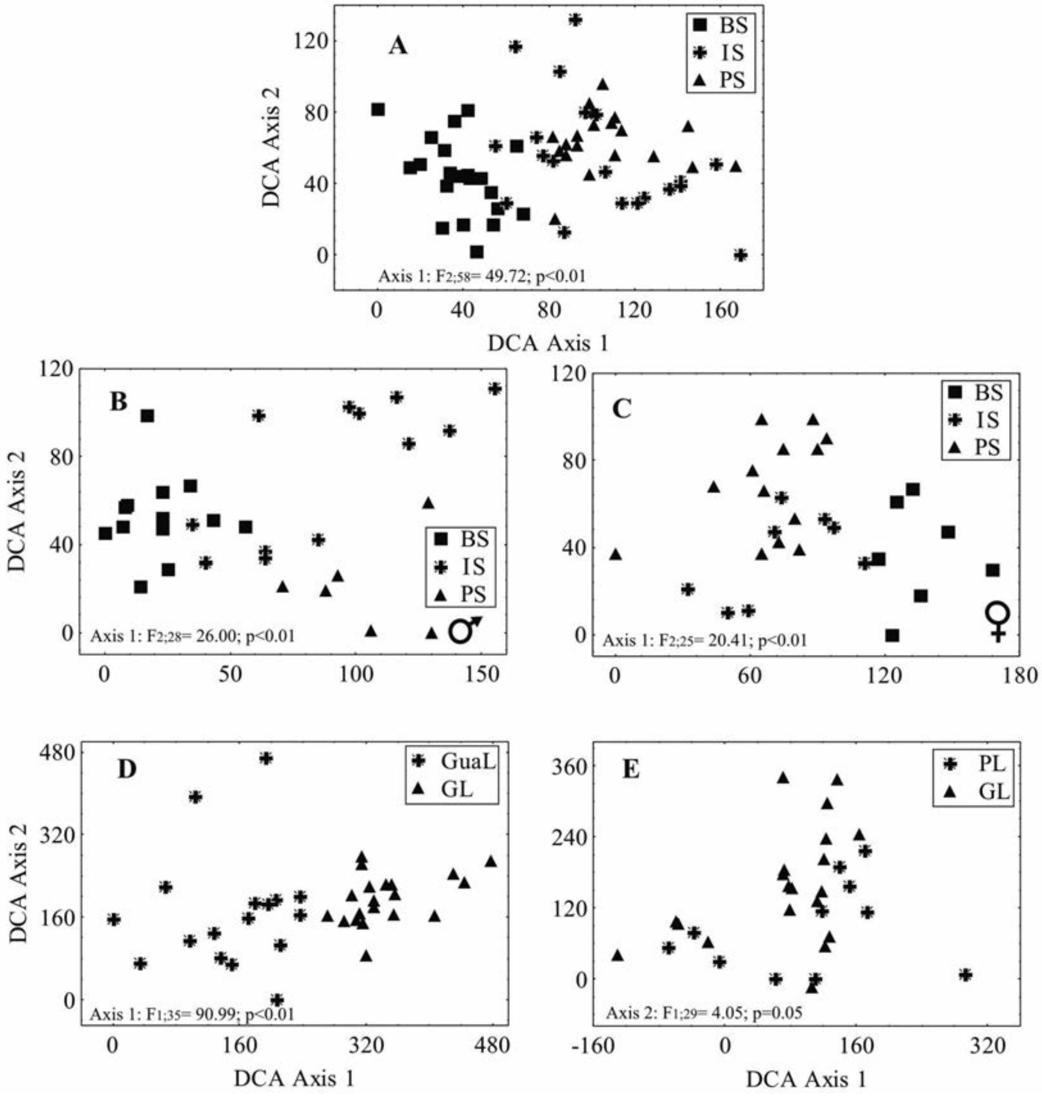

Fig. 1. DCA ordination for abundance data of infracommunities of gill parasites of *S. marginatus*. **A.** Ordination of the infracommunities by subsystem. **B.** Ordination of infracommunities of male hosts. **C.** Ordination of the infracommunities of female hosts. **D.** Ordination of infracommunities of hosts from Garças and Guaraná lagoons. **E.** Ordination of infracommunities of hosts from Garças and Patos lagoons. BS, Baia Subsystem; IS, Ivinheima Subsystem; PS, Paraná Subsystem; GuaL, Guaraná lagoon; GL, Garças lagoon; PL, Patos lagoon

tern of the parasite community structure in female hosts, in contrast to male hosts. However, when only female hosts were considered, co-occurrence patterns were observed, indicating segregation between parasite species of the Paraná and Baia Subsystems, and aggregation between parasite species of the Ivinheima and Baia Subsystems. The non-random co-occurrence pattern observed between the Paraná and Baia Subsystems (Table II) might be explained by the presence of exclusive parasite species in both subsystems (see Table I): *Notozothecium* sp., *Demidospermus* sp. and Ancyrocephalinae gen. sp. 4 occurred only in females and the other species in males. Species aggregation pattern in female hosts detected in the Paraná and Ivinheima Subsystems occurred due to the high species similarity observed between these hosts.

Co-occurrence analyses considering host development stage (young or adult) separately showed species segregation patterns. These patterns were determined by the infracommunities of gill parasites of the Paraná and Baia Subsystems, mainly for young females and adult males. In Paraná Subsystem, *Anacanthorus* sp. 3 and *Notozothecium* sp. occurred mainly in adults, whereas the seven species that were present in Baia Subsystem did not occur in young hosts of Paraná Subsystem. Most parasite species that were not shared by the hosts of these subsystems occurred in young hosts of Baia Subsystem.

Considering only the connected lagoons, host infracommunities from the lagoons Patos (Ivinheima Subsystem) and Guaraná (Baia Subsystem), when analyzed together, presented random parasite infracommunity structure. In contrast, the parasite infracommunities of Garças Lagoon (Paraná Subsystem) show evidence of species segregation, when analyzed together with the parasite infracommunities of Guaraná Lagoon (evidence in male and female hosts; the same patterns were observed between hosts of the Paraná and Baia Subsystems) or Patos Lagoon (evidence in male hosts). The parasite infracommunities of the lagoons Garças and Patos did not share only two species (Ancyrocephalinae gen. sp. 1 and Ancyrocephalinae gen. sp. 3), these species were present only on the hosts of Patos Lagoon and, that did not co-occur with *Ascocotyle* sp. in male hosts. Analyses considering connected and disconnected lagoons were not carried out because of the limited number of individuals collected in the latter, especially in Fechada Lagoon.

Interspecific associations of gill parasites of *S. marginatus* were not recorded in the studied subsystems. The exception was the pair of species *Notothecium* sp. and *Anacanthorus* sp. 2, which exhibited a negative association in hosts of Ivinheima Subsystem ($X^2 = 4.49$; $P < 0.05$); in two infracommunities these species did not co-occur.

The abundance of gill parasites in infracommunities exhibited significant differences among subsystems ($H = 14.07$; $P < 0.01$), especially for the high abundance values observed in Baia Subsystem; the abundance ordination gradients of parasites in the infracommunities corroborated the structure patterns detected by the co-occurrence null model (Fig. 1). There was a separation between parasite infracommunities, mainly from the Paraná and Baia Subsystems, regarding the first axis of the DCA (Fig. 1A; eigenvalues – axis 1: 0.208; axis 2: 0.096). This pattern was observed also for the ordinations carried out separately with the infracommunities of male hosts (Fig. 1B; eigenvalues – axis 1: 0.193; axis 2: 0.085) and female hosts (Fig. 1C; eigenvalues – axis 1: 0.230; axis 2: 0.058). A separation between parasite infracommunities was also observed when DCA ordinations were carried out only with hosts from Garças and Guaraná lagoons (Fig. 1D; eigenvalues – axis 1: 0.22; axis 2: 0.07) and Garças and Patos lagoons (Fig. 1E; eigenvalues – axis 1: 0.16; axis 2: 0.05).

Discussion

The high variability in richness and organization observed in parasite infracommunities is more evident when the infracommunities belong to different component communities, and are directly exposed to different environmental variations (Kennedy 1978, Marcogliese and Cone 1991, Poulin 1996, Hamilton and Poulin 2001, Valtonen *et al*. 2001). Many host traits, such as size, ontogeny and sex, can also affect the parasite fauna. Larger hosts may offer more space and shelter, and broader range of spatial niches for parasitic exploitation, enabling the co-occurrence of more parasite species (Poulin 1995).

In the present study specimens of *S. marginatus* did not differ in standard length among the three subsystems analyzed, though higher abundance of three parasite species was observed in larger fish of Paraná Subsystem. On the other hand, the negative correlation between the prevalence of *Anacanthorus* sp. 3 and the standard length of hosts of Ivinheima Subsystem might be related to the emergence period of parasite larvae (see Eiras 1994), so that the larvae (oncomiracids) may be found at higher abundance in the rest period in young hosts; this period is different in adults (Sazima and Machado 1990, Almeida *et al*. 1998), what reflects distinct exposures to parasitism. Oliveira (in preparation) did not observe morphological differences between males and females of *S. marginatus* in the Upper Paraná River Floodplain; this might explain the lack of effect of the sex of the host on parasitism levels in this study.

The lack of association between parasite species in this study might be a consequence of non-saturated ecological niches (Mouillot *et al*. 2003, Poulin 2004, Bagge *et al*. 2005); the absence of infracommunity structure patterns indicated by the null model analysis when the subsystems were considered separately corroborates these ideas. The main factors structuring the parasite communities of the Upper Paraná River Floodplain are acting more intensely among subsystems, at regional level, than inside each subsystem. In a study on metazoan ectoparasites of marine fish little evidence of non-randomized interactions of their component communities was found (Gotelli and Rohde 2002); this pattern was also observed in endoparasites of marine fish by Bellay *et al*. (2011). The segregation between parasite infracommunities of the

Paraná and Baia Subsystems, of both host sexes, was directly affected by the local habitat of the host and its development stage, which reflects also possible ecological differences between young and adult *S. marginatus*.

Low values of dissolved oxygen and pH, as in the lagoons of Baia River, tend to decrease fish mobility, and potentially contribute for the increase of stress, facilitating infestation by ectoparasites (Pavanelli *et al*. 2008). These characteristics can explain the high parasite species richness and high abundance observed in the infracommunities of Baia Subsystem. When considering the abundance ordination gradients of parasites in the infracommunities, the Ivinheima Subsystem was placed intermediate to the other subsystems, though closer to the pattern presented by Paraná Subsystem, feature that confirms parasite co-occurrence patterns (species aggregation tendency for female hosts). Parasite infracommunities patterns observed among the subsystems of the Upper Paraná River Floodplain corroborate limnological patterns of this environment (see Thomaz *et al*. 2004).

Our results reinforce that physical (habitat structure), chemical (variability in water chemical parameters) and biological (individual development stages) factors associated with the three main rivers of this system affect the spatial organization of the gill parasite fauna of *S. marginatus*, segregating species among lagoons of different subsystems, mainly between the Paraná and Baia Subsystems. Future studies should be carried out considering seasonal variations in the whole system, in order to test for a possible maintenance of the patterns observed in the present study between different hydrological periods.

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