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ORIGINAL PAPER

Helminth fauna of *Megaleporinus obtusidens* (Characiformes: Anostomidae) from Lake Guaíba: analysis of the parasite community

E. W. Wendt[1] · C. M. Monteiro[2] · S. B. Amato[3]

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Abtract
Structure of the helminth community of *Megaleporinus obtusidens* collected in Lake Guaíba was evaluated, and the results indicated that the diversity of helminth species was probably determined by fish behavior and eating habits. The influence of sex, weight, and standard length of hosts for parasitic indices was also analyzed. Sixteen helminth species were found parasitizing *M. obtusidens*, including the following: platyhelminths, with the highest richness, represented by one species of Aspidobothrea; four species of Digenea; and eight species of Monogenea; the latter, presented the highest prevalence. *Rhinoxenus arietinus*, found in nasal cavities, had the greater abundance, and was the only species classified as core. The prevalence of *Urocleidoides paradoxus* was significantly influenced by the sex of the host; females had the highest values. Abundance was weakly influenced by fish weight and the body length of the hosts. *Urocleidoides* sp. had its abundance weakly influenced by the host weight. The other helminths were not influenced by biometric characteristics of the hosts. The total species richness was similar between male and female fish, and both had 14 helminth species of parasites.

Keywords Host–parasite relationship · Fish biology · Lake environment · Southern Brazil

Introduction

Leporinus obtusidens, known as "piava," was recently included in the genus *Megaleporinus* proposed by Ramirez et al. (2017) after phylogenetic study of Anostomidae. *Megaleporinus obtusidens* Ramirez, Birindelli and Galetti, 2017 is the only species of *Megaleporinus* occurring in the State of Rio Grande do Sul, southern Brazil (Reis et al. 2003).

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✉ E. W. Wendt
wendtemi@gmail.com

[1] Laboratory of Ichthyology, Institute of Biosciences, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

[2] Laboratory of Ecology and Parasite Biology, Institute of Biology, Universidade Federal Rural do Rio de Janeiro, Seropédica 23897-000, Brazil

[3] Laboratory of Helminthology, Institute of Biosciences, Universidade Federal do Rio Grande do Sul, Porto Alegre 91501-970, Brazil

It is found from north to south in Brazil, as well as in Argentina, Uruguay, and Paraguay (Britski et al. 2012). Three genetically distinct populations can be separated: (a) basin of the Paraná, Uruguay, and Jacui rivers; (b) São Francisco River; and (c) Paraguay River (Ramirez et al. 2016, 2017). Zaniboni-Filho and Schultz (2003) observed a reduction in the *M. obtusidens* population and related it to agriculture and industrial practices. Thus, species survey studies in this area become crucial in evaluating threats to diversity.

Megaleporinus obtusidens was intensely studied in the 1980s, and aspects of its morphology (Sidlauskas and Vari 2008; Britski et al. 2012), biology (Mello et al. 1999; Hartz et al. 2000; Penchaszadeh et al. 2000; Santos 2000; Piana et al. 2003; Moraes et al. 2009), and ecology (Oldani et al. 1992; Araya 1999; Araya et al. 2005) have been elucidated.

Studies dealing with the helminth fauna of this species, however, are scarce and are concentrated mainly in the States of Paraná and Minas Gerais (Feltran et al. 2004; Takemoto et al. 2009; Kohn et al. 2011). Knowledge about the parasitic community can contribute to better understanding host habits and behaviors and whether they may influence the population dynamics of its host. It is known that some factors can influence the community composition of parasites, such as dietary habits, sex, and host size. Barber and Poulin (2002) stated that males and females have physiological, morphological, and behavioral differences, and these factors may influence parasitism. Studies have shown that the opposite also occurs, that is, parasites can mediate sexual selection (Barber and Poulin 2002). The influence of sex, standard length, and host weight on the helminth community has been poorly studied in *Leporinus* species and especially in the genus *Megaleporinus*.

Scarce information addressing the parasitic fauna of *M. obtusidens* in the State of Rio Grande do Sul, as well as the few studies about community component, motivated the present study, which is composed of description and analysis of the helminth community structure.

Material and methods

Sixty specimens of *M. obtusidens* (20 males and 40 females) were captured by professional fishermen from Lake Guaíba (30°01′S, 51°16′W), State of Rio Grande do Sul, southern Brazil, from August to October 2013 (Fig. 1). The fish were bought directly from the fishermen as they were being taken to the local market immediately after the catch. The study was approved by the Universidade Federal do Rio Grande do Sul (UFRGS) Ethics Committee (Process Number 27531).

The fish were weighed, measured (total and standard length), and necropsied following Amato et al. (1991). The helminths were collected and placed in 0.65% saline solution, fixed, and further stained and/or clarified according to Amato and Amato (2010). Ecological descriptors used—prevalence, mean intensity of infestation or infection, abundance, range, and site of infection—followed Bush et al. (1997). Species with prevalence greater than or equal to 10% were used in the analysis of helminth component community following Bush et al. (1990) recommendations.

Mann–Whitney's "*U*" test was calculated to evaluate if the sex of the host had influence on the parasite abundance and intensity. Fisher's exact test was used to evaluate if the sex of the host had influence on the parasite prevalence. To analyze if the weight and length of the hosts had influenced abundance and intensity of parasites, the Spearman's correlation test "*rs*" was used, and to analyze the influence of this parameter over the prevalence of the parasite species, the Pearson's correlation test "*r*" was used in pre-determined classes of fish size and weight (Zar 1996). The weight and length classes were determined according to the Sturges' rule, using mean values between standard deviations. Hosts were classified in classes according to the ranges presented.

Generalized linear models (GLM) were used for the analysis. First, a model with first-order interactions was fitted: $G(abund) = \text{sex} + \text{Weight} + \text{parasite species} + \text{interation}$; where G is a link function and *abund* represents abundance of species. Abundance was chosen as a dependent variable because it was the index that showed the greatest variability among parasite species; so, we want to explain which other variables influence this first. Weight was considered as covariate and sex and parasite species as factor. General linear models (McCullagh 1984) followed by analysis of variance (ANOVA; F test) was performed to verify which factors influence the abundance of the parasite species (Gaussian model). The significance of the model was tested from the null model test, "rdiagnostic" and observing the values Residual deviance/degree of freedom. Further information on test values and significance is found in the supplemental material.

The co-occurrence of parasite species was evaluated by the Spearman correlation "*rs*" (Zar 1996) and was plotted on a graph using the Corrplot (package in R program). All statistical tests followed the significance level of 0.05 and were calculated with R® program, Version 3.4.1. The relationship between species was also tested using the index of affinity proposed by Fager (1957). The index of affinity between pair of parasite species occurring in the same breeding site was calculated, and we determined if the affinity index obtained was statistically significant using the t test (with $p \leq 0.05$). *Rhinoxenus arietinus* was not included in this analysis because it did not share an occurrence site with any other species. The results of the Fager index and the t test are found in Table I of the Supplementary Material.

The helminth species were classified according to their frequency in the component community as follows: core (prevalence ≥ 66.6%), secondary (prevalence between 33.3% and 66.6%), or satellite (prevalence ≤ 33.3%), following Bush and Holmes (1986). The diversity indices followed Magurran (2004) and Nehring and Von Zuben (2010) to describe the component community with respect to its heterogeneity. The species richness (*S*), Brillouin Diversity (*HD*), Equitability Shannon-Winner (*J*), modified Hill Equitability (*E*), and Dominance Simpson (*D*) were estimated with the aid of DIVES version 3.0 program (Rodrigues 2015). Helminth representative specimens were deposited in the "Coleção Helmintológica do Laboratório de Helmintologia" (CHDZ) of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil. Voucher specimens of *Tereancistrum paranaensis* Karling, Lopes, Takemoto and Pavanelli, 2014 (CHIOC 38085; CHIOC 38086) and *Tereancistrum parvus* Kritsky, Thatcher and Kayton, 1980 (CHIOC 38087; CHIOC 38088) were deposited at the "Coleção Helmintológica do Instituto Oswaldo Cruz" (CHIOC), Rio de Janeiro, RJ, Brazil.

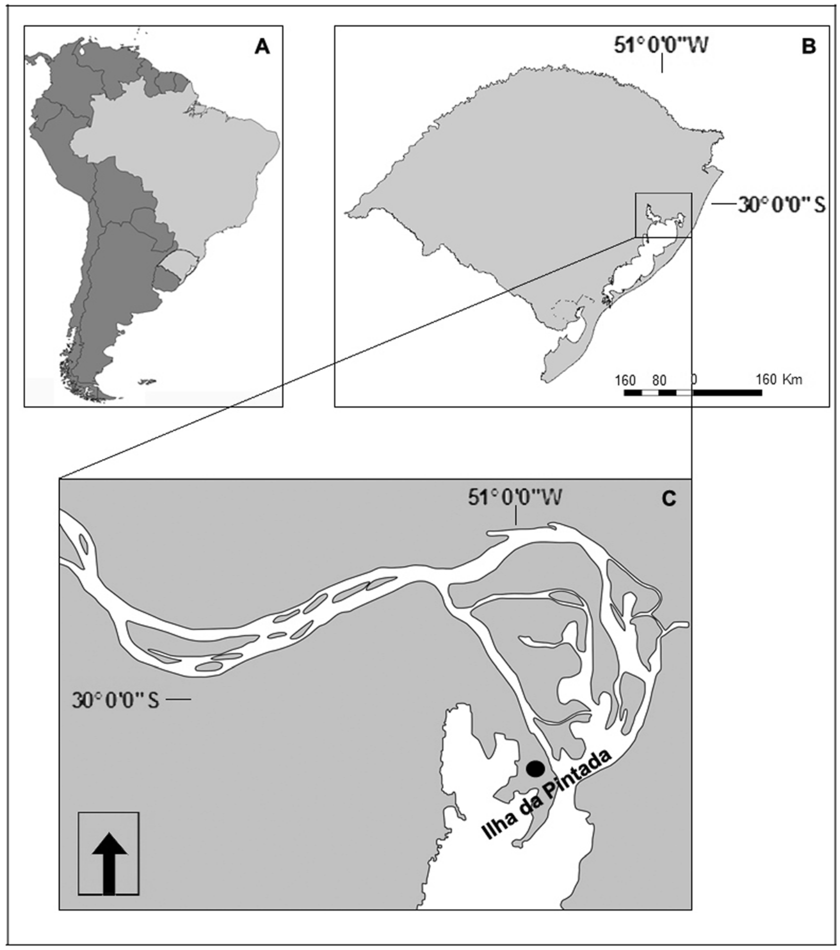


Fig. 1 Collection site; (**a**) South America, Brazil in light gray; (**b**) Rio Grande do Sul; (**c**) Delta do Jacuí, highlighted the Ilha da Pintada

Results

Component community structure

Fifty nine of 60 (98.33%) *M. obtusidens* were parasitized by at least one species of helminth. A total of 2376 helminths were collected; of these, 1720 were classified as endoparasites and the remaining 656 as ectoparasites. The mean abundance and mean intensity of infection were 39.6 and 40.27 specimens/host, respectively. The ecological indices, prevalence, mean intensity, mean abundance, range of infection/infestation, and site infection/infestation are presented in Table 1. Sixteen species of helminths were found, 13 belonging to the phylum Platyhelminthes; one species of Aspidobothrea (Aspidogastridae), four species of Digenea, and eight species of Monogenea. The digeneans were represented by *Saccocoelioides godoyi* Kohn and Fróes, 1986 (31.66%), *Creptotrema lynchi* Brooks, 1976 (21.66%), *Saccocoelioides nanii* Szidat, 1954 (15%), and *Genarchella genarchella* Travassos, Artigas and Pereira, 1928 (3.3%). The most representative group was Monogenea, with eight species, among these, *Kritsky eirasi* Guidelli, Takemoto, and Pavanelli, 2003, the only endoparasite of the group, was found in the ureters of 58.33% of the analyzed hosts. Other monogeneans were ectoparasites, *Rhinoxenus arietinus* Kritsky, Boeger, and Thatcher, 1988, *Urocleidoides paradoxus* Kritsky, Thatcher, and Boeger, 1986, *Urocleidoides* sp., *Tereancistrum parvus* Kritsky, Thatcher, and Kayton, 1980, *Tereancistrum paranaensis* Karling, Lopes, Takemoto, and Pavanelli, 2014, *Jainus piava* Karling, Bellay, Takemoto, and Pavanelli, 2011, and an undetermined species of Dactylogyridae were found. The other species are represented by Acanthocephala, with one species, *Echinorhynchus* sp., while Nematoda was represented by two species, *Cucullanus* sp., (larvae and adults) and *Contracaecum* sp. (larvae), where all these species presenting low ecological indices.

Of all species found in this study, seven were registered for the first time in *M. obtusidens* (Aspidogastridae gen. sp., *S. nanii*, *J. piava*, *T. paranaensis*, *K. eirasi, Urocleidoides* sp., and *Echinorhynchus* sp.). Additionally, eight other species, *G. genarchella*, *C. lynchi*, Dactylogyridae gen. sp., *R. arietinus*, *T. parvus*, *U. paradoxus*, *Contracaecum* sp., and *Cucullanus* sp., were recorded for the first time in Lake Guaíba.

Regarding the contribution of these species to the composition of the parasite community, it was observed that of the 16 species found, nine were endoparasites (Aspidogastridae gen.

Table 1 Helminth parasites of *Megaleporinus obtusidens* ($n = 60$) of Lake Guaíba, Rio Grande do Sul, Brazil

	P (%)	Intensity	Mean intensity X ± SD	Abundance X ± SD	Site of infection /infestation	Importance value
Aspidobothrea						
Aspidogastridae gen. sp.	1.66	1	1.00	0.01	PI	StS
Digenea						
Creptotrema lynchi	21.66	10–60	27.00 ± 32.62	5.85 ± 0.54	IC, S, AI, PI	StS
Genarchella genarchella	3.33	1–2	1.50 ± 0.70	0.05 ± 0.01	S	StS
Saccocoelioides godoyi	31.66	2–300	31.10 ± 66.71	9.88 ± 0.25	IC, S, AI, MI, PI	StS
Saccocoelioides nanii	15.00	2–272	58.33 ± 88.99	8.75 ± 1.48	IC, S, AI, MI, PI	StS
Monogenea						
Dactylogyridae gen. sp.	3.33	1	1.00	0.03	GF	StS
Jainus piava	25.00	1–4	1.80 ± 0.99	0.46 ± 0.01	GF	StS
Kritskyia eirasi	58.33	1–34	5.85 ± 6.07	3.41 ± 0.10	UB, U	SS
Rhinoxenus arietinus	86.66	1–23	5.01 ± 4.79	4.48 ± 0.07	NC	CS
Tereancistrum paranaensis	26.66	1–5	1.43 ± 1.34	0.46 ± 0.02	GF	StS
Tereancistrum parvus	40.00	1–12	2.58 ± 2.44	1.03 ± 0.04	GF	SS
Urocleidoides paradoxus	60.00	1–19	6.04 ± 4.56	2.41 ± 0.07	GF	SS
Urocleidoides sp.	48.33	1–19	4.20 ± 4.48	2.03 ± 0.07	GF	SS
Acanthocephala						
Echinorhynchus sp.	8.33	1–8	3.60 ± 2.70	0.30 ± 0.04	AI, MI	StS
Nematoda						
Contracaecum sp.	3.33	1	1.00	0.03	S	StS
Cucullanus sp.	18.33	1–4	2.00 ± 1.34	0.36 ± 0.02	S, AI, MI, PI	StS

AI (anterior intestine), CS (core species), GF (gills' filament), I (intensity), IC (intestinal caecum), SD (standard deviation), S (stomach), MI (medium intestine), NC (nasal cavity), P (prevalence), PI (posterior intestine), StS (satellite species), SS (secondary species), U (ureters), UB (urinary bladder), X (average)

sp., *G. genarchella*, *S. godoyi*, *S. nanii*, *C. lynchi*, *K. eirasi*, *Echinorhynchus* sp., *Contracaecum* sp., and *Cucullanus* sp.) and seven were ectoparasites (Dactylogyridae gen. sp., *J. piava*, *R. arietinus*, *T. paranaensis*, *T. parvus*, *U. paradoxus*, and *Urocleidoides* sp.). Digenean trematodes with 1472 specimens represented the clear majority of the helminths found (61.95% of specimens), followed by monogeneans with 861 specimens (36.23%), nematodes with 24 specimens (01.01%), Acanthocephala with 18 specimens (0.75%), and Aspidogastrid represented by a single specimen (0.04%). With respect to species richness, Monogenea was the most representative group, with eight species, thus contributing to half of parasitic richness estimated to this host species for this geographical location. Digenea was the second most representative group with four species (25%), followed by Nematoda with two species (12.5%), Acanthocephala and Aspidobothrea each represented by a single species (6.25%).

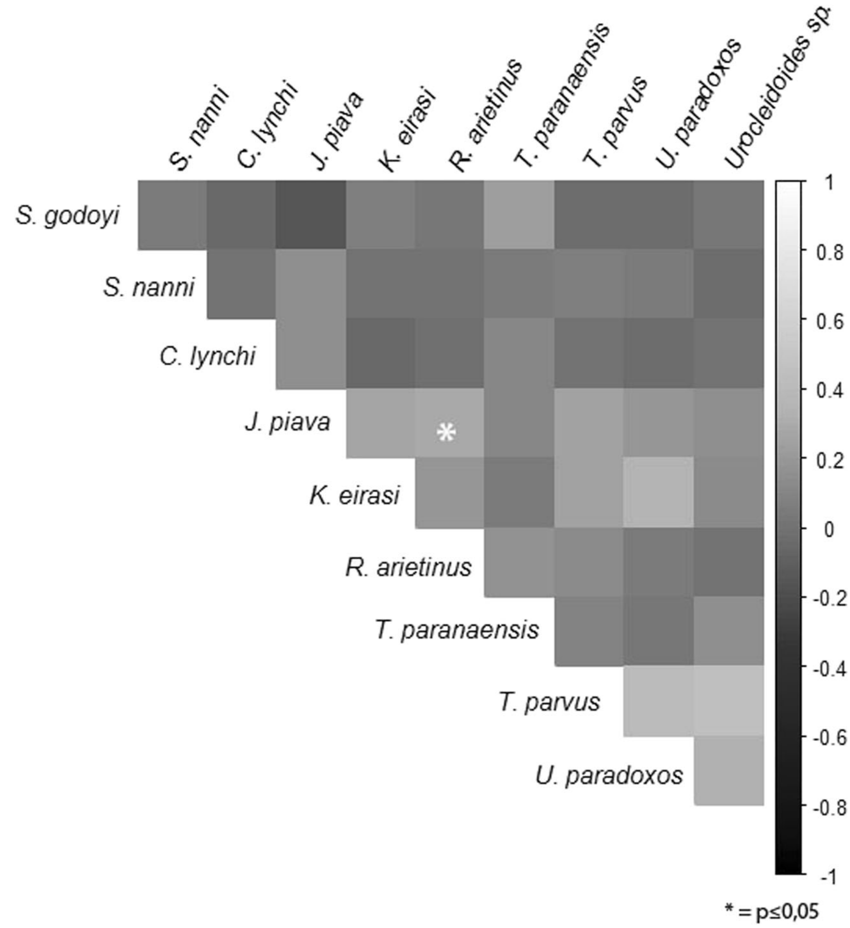
The species classification, following the value of importance, is indicated in Table 1. Only one species, *R. arietinus*, was considered core; *K. eirasi*, *T. parvus*, *U. paradoxus*, and *Urocleidoides* sp. were classified as secondary and the others were classified as satellite.

The analysis of co-occurrences of helminth species, using the Spearman correlation test (Fig. 2), showed that 20 pairs of species were formed, five formed by endoparasites, and 15 by ectoparasites. Just a pair of species (*J. piava*–*R. arietinus*) showed a significant negative correlation, when *J. piava* was found in fish gills, *R. arietinus* was absent in the nose. However, although this result is significant, the value of this correlation is low. On the other hand, the affinity test was performed with 28 pairs of species of the gastrointestinal tract and 15 pairs of species parasitizing host gills. Only three pairs of affinities obtained significance ($p \leq 0.05$), all occurring in the gills. The relationships between *T. parvus* with *U. paradoxus* ($I_{AB} = 0.677$; $t = 2.596$), *T. parvus* with *Urocleidoides* sp. ($I_{AB} = 0.750$; $t = 3.498$), and *U. paradoxus* with *Urocleidoides* sp. ($I_{AB} = 0.666$; $t = 2.397$) presented high affinity values.

The influence of sex, standard length, and weight of the host on the ecological index of the component helminth population

Sixty fish were analyzed, 20 (40%) were males and 40 (60%) were females, and the biometric data are indicated in Table 2.

Fig. 2 Co-occurrence of the helminth species of *Megaleporinus obtusidens* of Lake Guaíba, Rio Grande do Sul, Brazil



Females were larger ($t = -3.458$, $p = 0.001$) and heavier ($t = -4.941$, $p < 0.001$) than males. The prevalence of *U. paradoxus* ($rr = 0.444$, $p = 0.048$) was significantly higher in females than in males, basing on Fisher's exact test (Table 3). Regarding the mean intensity, only one species (*K. eirasi*) presented a significant difference between this index and the size of the host ($r_s = 0.35$, $p = 0.03$). Other helminths showed no significant influence of host sex on ecological values, and no correlation between the intensity of infection/infestation of any helminth with the weight and/or standard length of the hosts, based on correlation analyses (Tables 3 and 4).

However, abundance had correlation analyses significant in some cases. There was correlation between the abundance and weight of the hosts for *U. paradoxus* ($rs = 0.312$, $p = 0.015$) and *Urocleidoides* sp. ($rs = 0.262$, $p = 0.044$) (Table 4). We also observed correlation between the standard length of the fish and the abundance of *U. paradoxus* ($rs = 0.315$, $p = 0.014$); however, this correlation value was low (< 0.5) (Table 4).

Significant correlation between body weight of the host and the prevalence of four species of helminths was found (Table 5). *Creptotrema lynchi* was the only species which presented a significant negative correlation ($r = -0.827$, $p = 0.042$). *Urocleidoides paradoxus* ($r = 0.947$, $p = 0.004$) and *Urocleidoides* sp. ($r = 0.841$, $p = 0.036$) presented a positive significant correlation between body of the host and prevalence of helminths as well as the nematode *Cucullanus* sp. ($r = 0.818$, $p = 0.047$). According to the correlation analyses, the standard length of hosts and prevalence of helminths were not significant (Table 5).

The GLM analysis showed a significant difference between the abundance and the parasite species ($F = 3.1769$; $p < 0.001$), where two species had higher infection rates, being *C. lynchi* and *R. arietinus* (Table 6). In addition, there was a significant influence on the abundance of *S. godoyi* when the sex and species factors were analyzed ($F = 2.3609$; $p < 0.01$), as well as when the weight, sex, and species factors were analyzed ($F = 3.7428$; $p < 0.001$) (Table 6).

Diversity index component community

The richness of parasite communities in males and females was similar for the 14 species of helminths (Table 7). *Genarchella genarchella* and *Echinorhynchus* sp. were recorded only in females. Aspidogastridae gen. sp. and Dactylogyridae gen. sp. were recorded only in male hosts.

Table 2 Biometric data of *Megaleporinus obtusidens* ($n = 60$) of Lake Guaíba, Rio Grande do Sul, Brasil and size intervals in weight (g) and standard length (mm) obtained using Sturges' rule, followed by number of specimens (*N*) corresponding to each class

Parameters	Male ($n = 20$)	Female ($n = 40$)	Geral ($n = 60$)	
	$X \pm$ SD (A)	$X \pm$ SD (A)	$X \pm$ SP (A)	
Weight (g)	750.25 ± 213.08 (410–1100)	1038 ± 340.38 (560–2500)	942.53 ± 331.67 (410–2500)	
Standard length (cm)	31.45 ± 2.35 (26.5–35.1)	34.97 ± 2.72 (30.1–41.5)	33.80 ± 3.08 (26.5–41.5)	
Sturges' rules				
	Weight		Standard length	
Class	Interval	*n*	Interval	*n*
A	410.00–758.33	17	26.50–28.67	3
B	758.34–1.060.93	24	28.68–30.85	9
C	1.060.94–1.363.53	15	30.86–33.03	14
D	1.363.54–1.666.13	2	33.04–35.21	14
E	1.666.14–1.968.73	1	35.22–37.39	11
F	1.968.74–2.271.33	1	37.40–39.57	7
G	–	–	39.58–41.75	2

n, number of hosts; *X*, average; SD, standard deviation; A, amplitude

When the same analysis was performed, but separately for endo- and ectoparasites, seven species of endoparasites were observed in males, while in females, eight species were found (Table 7). Regarding ectoparasites in male hosts, seven species were found, while in female hosts six species were found (Table 7); this difference was not significant.

The helminth component community was analyzed with the aid of the diversity index, dominance, and evenness (Table 7). Differences between the ecological indices were small and were not significant for most of them. For the total parasites in male and female, the Brillouin diversity index showed a significant difference, where females of *M. obtusidens* showed a greater diversity ($t = -2.379$, $p = 0.021$) than males (Table 7).

When ectoparasites of hosts of different sexes were analyzed, there was a significant difference in the Equitability Index Shannon–Wiener ($t = -2.535$, $p = 0.014$), which was higher for female hosts. Likewise, the modified Hill's evenness index showed differences between males and females ($t = -2.224$, $p = 0.029$), in which males had the higher evenness. For the other indices compared, there were no significant differences.

Table 3 Comparison of the prevalence, intensity and abundance of helminth parasites of different sexes of *Megaleporinus obtusidens* ($n = 60$) of Lake Guaíba, Rio Grande do Sul, Brazil

Helminth	Prevalence		Intensity		Abundance	
	rr	*P*	*U*	*P*	*U*	*p*
Creptotrema lynchi	0.638	0.512	13.00	0.735	358.00	0.361
Saccocoelioides godoyi	0.924	1.000	34.00	0.659	395.00	0.924
Saccocoelioides nanni	1.417	0.464	8.00	0.624	368.00	0.419
Jainus piava	1.000	1.000	19.50	0.471	394.50	0.910
Kritskyia eirasi	1.071	1.000	117.00	0.462	389.00	0.858
Rhinoxenus arietinus	0.615	0.421	231.50	0.258	303.50	0.127
Tereancistrum paranaensis	0.485	0.218	18.50	0.876	331.00	0.163
Tereancistrum parvus	0.807	0.780	46.00	0.369	383.50	0.769
Urocleidoides paradoxus	0.444	0.048*	89.00	0.366	257.00	0.200
Urocleidoides sp.	0.712	0.419	75.00	0.648	341.00	0.317
Cucullanus sp.	1.143	1.000	13.50	0.917	389.50	0.807

rr, Fisher's exact test; *U*, Mann–Whitney test; *p*, level of significance; *, significant values $p \leq 0.05$

Table 4 Influence of the weight and standard length of *Megaleporinus obtusidens* ($n = 60$) of Lago Guaíba, Rio Grande do Sul, Brazil, over intensity and abundance of helminths

Helminths	Intensity				Abundance			
	Weight (g)		Standard length (cm)		Weight (g)		Standard length (cm)	
	r_s	p	r_s	P	r_s	p	r_s	p
Creptotrema lynchi	0.800	0.795	− 0.861	0.780	− 0.132	0.315	− 0.133	0.311
Cucullanus sp.	0.134	0.306	0.158	0.228	− 0.463	0.151	− 0.325	0.330
Saccocoelioides godoyi	0.275	0.254	0.151	0.538	0.179	0.171	0.199	0.127
Saccocoelioides nanni	0.183	0.637	0.133	0.732	0.087	0.511	0.120	0.360
Jainus piava	0.257	0.357	0.248	0.372	0.030	0.819	0.140	0.286
Kritskyia eirasi	0.262	0.130	0.353	0.038*	0.090	0.493	0.160	0.221
Rhinoxenus arietinus	0.079	0.576	0.173	0.221	− 0.016	0.905	0.064	0.628
Tereancistrum paranaensis	0.204	0.450	− 0.159	0.556	0.024	0.858	0.039	0.769
Tereancistrum parvus	0.074	0.732	− 0.069	0.747	− 0.104	0.429	− 0.071	0.588
Urocleidoides paradoxus	0.008	0.963	0.131	0.447	0.312	0.015*	0.315	0.014*
Urocleidoides sp.	0.007	0.973	− 0.109	0.573	0.262	0.044*	0.249	0.055

r_s, Spearman's correlation; p, significance level; *, significant values $p \leq 0.05$; g, in grams; cm, in centimetres

Discussion

Component community structure

A narrow 3-month time window was used in this study on parasite diversity in *M. obtusides*, and continuation of the work should involve more time and all the seasons of the year. Despite this, our data show an important preliminary view of the component community of the parasites in *M. obtusidens*.

Table 5 Influence of the weight and standard length of *Megaleporinus obtusidens* of Lake Guaíba, Rio Grande do Sul, Brazil, on the prevalence of helminths

Helminths	Prevalence			
	Weight (g)		Standard length (cm)	
	R	p	R	p
Creptotrema lynchi	− 0.827	0.042*	− 0.584	0.301
Cucullanus sp.	0.818	0.047*	0.377	0.531
Saccocoelioides godoyi	0.400	0.432	0.765	0.131
Saccocoelioides nanni	0.341	0.508	0.255	0.679
Jainus piava	0.477	0.339	0.445	0.453
Kritskyia eirasi	0.125	0.813	0.453	0.443
Rhinoxenus arietinus	− 0.257	0.622	− 0.107	0.864
Tereancistrum paranaensis	0.025	0.963	0.670	0.216
Tereancistrum parvus	0.203	0.700	0.368	0.542
Urocleidoides paradoxus	0.947	0.004*	0.872	0.054
Urocleidoides sp.	0.841	0.036*	0.814	0.094

r, Pearson's correlation; p, significance level; *, significant values $p \leq 0.05$; (g) in grams; (cm) in centimetres

The large number of helminth species recorded for the first time for Lake Guaíba is probably due to the scarcity of studies carried out with *M. obtusidens* in this region, and most previous work was focused on gastrointestinal parasites, leaving out the monogeneans, which in the present study contributed with most of the richness.

The structure of helminth populations showed that the ectoparasites, especially monogeneans, were more prevalent than the endoparasites, especially digeneans. This is directly associated with the food habit of "piava," because this fish feeds mainly on plant material (Hartz et al. 2000), decreasing contamination with endoparasites, which are usually associated with intermediate hosts. However, as previously seen, infection rates were always higher in endoparasites. Shaw and Dobson (1995) justify this result stating that parasitism tends to be a supra-dispersal phenomenon, in which few hosts will have most of the parasite species. The factors that lead to aggregation distribution are not well understood but it is believed that the intrinsic characteristics of each individual, such as agility in predation, age, length, and host weight, are the most likely variables (Anderson and Gordon 1982; Shaw and Dobson 1995; Bandilla et al. 2005; Poulin 2013). In addition, heterogeneity in parasite exposure and susceptibility to them has divided opinions on the causes of aggregation (Poulin 2013). Additionally, the life cycle of the digenean trematodes where there is larval multiplication within the mollusk host explains the high intensity of some species of Digenea (Gibson et al. 2002; Guidelli et al. 2011).

According to Yamaguti (1975), redia and cercariae of *G. genarchella* develop in snails *Littorina australis* Gray, 1826, which are ingested by fish where the cercariae will develop to the adult stage. But, Yamaguti also mentioned that fish of the

Table 6 GLM analysis demonstration the influence of sex, weight, and species of parasite on the abundance parasite in *Megaleporinus obtusidens* from Lake Guaíba, Rio Grande do Sul, Brazil

Variable or factor	Degree of freedom	Deviance residual	Degree of freedom	Resid. dev	Model *F*	*p*
Null			959	219,893		
Weight	1	165.8	958	219,728	0.7898	> 0.05
Sex	1	436.4	957	219,291	2.0790	> 0.05
Species	15	10,002.8	942	209,288	3.1769	< 0.001*
Weight + Sex	1	469.2	941	208,819	2.2354	> 0.05
Weight + Species	15	1524.3	926	207,295	0.4841	> 0.05
Sex + Species	15	7433.6	911	199,861	2.3609	< 0.01*
Weight + Sex + Species	15	11,784.7	896	188,077	3.7428	< 0.001*

*=Significant values

genus *Leporinus* were incapable of hosting *Genarchella*, being only an erratic host for this digenean trematode. So, this observation could explain the low prevalence found in the present study, as well as the immaturity of two out of three specimens collected. Other authors mention mollusks and Cypriniform fish as intermediate hosts for this species of parasite (Martorelli 1989; Scholtz et al. 1995; Lefebvre and Poulin 2005), being these, food items little or never consumed by *M. obtusidens*.

Digeneans of the genus *Saccocoelioides* have gastropods as intermediate hosts; the metacercariae encyst on aquatic vegetation, and the adults are found in freshwater fish (Díaz and González 1990).

The low prevalence of *Echinorhynchus* sp. is probably related to its life cycle, to be found by the intermediate host where it will develop to cystacanth to infect the definitive, or the paratenic host (Schmidt and Nickol 1985). Yamaguti (1963) mentioned that species of *Echinorhynchus* have

Table 7 Diversity, dominance, and evenness index of helminth parasites component community of *Megaleporinus obtusidens* (*n* = 60) of Lago Guaíba

Parameters	Males	Female	*t*	*p*
Hosts collected	20	40	–	–
Parasitized hosts	19	40	–	–
Prevalence of parasitism	95%	100%	–	–
Total helminths	X ± SD	X ± SD		
Richness	4 ± 2.655	4.85 ± 1.942	− 1.410	0.169
Brillouin Diversity Index	0.268 ± 0.225	0.394 ± 0.175	− 2.379	0.021*
Simpson's Dominance Index	0.408 ± 0.325	0.372 ± 0.203	0.519	0.606
Shannon–Wiener Index	0.641 ± 0.380	0.732 ± 0.221	− 1.169	0.247
Modified Hill's Index	1.952 ± 4.876	13.276 ± 63.557	− 0.792	0.431
Ectohelminths				
Richness	2.45 ± 1.877	3.125 ± 1.343	− 1.602	0.115
Brillouin Diversity Index	0.193 ± 0.203	0.276 ± 0.145	− 1.808	0.076
Simpson's Dominance Index	0.448 ± 0.393	0.419 ± 0.231	0.351	0.727
Shannon-Wiener Index	0.486 ± 0.455	0.733 ± 0.293	− 2.535	0.014*
Modified Hill's Index	0.449 ± 0.643	2.056 ± 3.157	− 2.224	0.029*
Endohelminths				
Richness	1.55 ± 1.099	1.65 ± 0.892	− 0.378	0.707
Brillouin Diversity Index	0.071 ± 0.122	0.114 ± 0.128	− 1.247	0.217
Simpson's Dominance Index	0.604 ± 0.420	0.638 ± 0.340	− 0.333	0.740
Shannon-Wiener Index	0.486 ± 0.455	0.415 ± 0.406	0.615	0.541
Modified Hill's Index	3.621 ± 8.020	6.433 ± 11.914	− 0.823	0.414

SD, standard deviation; *t,* Student's "*t*" test; *p*, significance level; *, significant values $p \leq 0.05$

Ampithoe rubricate Montagu, 1818, *Calliopius rathkei* (Zaddach, 1844), *Pontoporeia jemorata* and *Cyphocaris challengeri* Thorsteinson, 1941 as intermediate hosts while Marcogliese (1995) and Measure and Bossé (1993) found the amphipods *Aeginina longicornis* (Krøyer, 1843) and *Gammarus lawrencianus* Bousfield, 1956 infected with *Echinorhynchus*. The low prevalence observed in our sample may mean that microcrustaceans and/or paratenic hosts of *Echinorhynchus* sp. are rare in the environment or in the diet of the studied host.

Species of *Contracaecum* also have microcrustaceans as intermediate hosts, which might explain the low prevalence of this nematode in *M. obtusidens*. Anderson (2000) reported several intermediate hosts for species of *Contracaecum*; namely, cnidarians, gastropods, polychaetes, copepods (microcrustaceans), amphipods, decapods, and echinoderms, but copepods are probably the most important hosts for this helminth. Low levels of *Contracaecum* sp. indicate that the above-mentioned food items are uncommon in the diet of "piava" of Lake Guaíba. These results corroborate those reported by Hartz et al. (2000) when they analyzed the diet of "piava" of Lake Guaíba and reported plants and sediment as the most consumed items, followed by mollusks (*Corbicula* spp., *Ampullaria* spp., and *Heleobia* spp.) and lastly microcrustaceans.

The low prevalence of endohelminths was also observed in previous studies. Guidelli et al. (2011) reported that most digeneans present in *M. obtusidens* showed no prevalence above 10%, but the intensity range of 1–150 specimens/hosts probably reflects the presence of larvae grouped in intermediate and/or paratenic hosts. The acanthocephalans are among the least reported helminth species in *Leporinus*, a genus similar to *Megaleporinus*, when present always showed low prevalence (Guidelli et al. 2011). *Octospiniferoides incognita* Schmidt and Hugghins, 1973 and *Quadrigyrus torquatus* Van Cleave, 1920 were recorded in *Leporinus lacustris* Amaral Campos, 1945 in upper Rio Paraná, with prevalences of 0.66 and 1.33%, respectively.

On the other hand, the ectoparasitic monogeneans showed high prevalence (above 25%) in this study, as in previous studies with species of *Leporinus* (Guidelli et al. 2006, 2011; Takemoto et al. 2009). These helminths, unlike digeneans, acanthocephalans and nematodes, do not rely on diet or intermediate hosts to complete their life cycle (Thatcher 2006); thus, the parasitic rates are usually higher, because they depend on their active search for the appropriate host. Contact or proximity among the fish facilitates the transference between hosts which corroborates to high indices of infestation. During or near to the reproductive periods, fish are more aggregate, thus facilitating new infestations.

Therefore, the data presented in this study demonstrated that the helminth fauna of *Leporinus* and *Megaleporinus* tend to be similar for the most part. This can be explained by the phenotypic plasticity of the parasite species, which may parasitize more than one host species, either because they are hosts with similar characteristics or simply because of the ability to use another resource (Agosta et al. 2010). This has already been explained by Agosta (2006), Agosta et al. (2010), and other authors when they mention the ecological fitting of the parasites, which have the capacity to switch between generalists and specialists throughout their evolution.

The influence of sex, standard length, and weight of the host on the ecological index of the component helminth population

The influence of sex, standard length, and weight of the host on the helminths was tested in a few studies with species *Leporinus* and *Megaleporinus*. For *L. lacustris* and *L. friderici*, Guidelli et al. (2006) tested these factors and found no significant influence of the parasitic indexes. Feltran et al. (2004) analyzed fish from the Ponte Nova Dam in the State of Minas Gerais, and found no significant correlation between the total intensity of infection of nematodes and the length of *L. friderici*. However, the same authors found a positive correlation between the length of *M. obtusidens* with the intensity of nematode infection. In this sense, the present work is configured as one of the few to examine the influence of sex, weight and standard length of hosts on the ecological indices for *M. obtusidens*. However, there are several other studies that have addressed the relationship of these factors to the parasitic load, where most showed a significant correlation of at least one of the factors on the ecological indices (Takemoto and Pavanelli 2000; Guidelli et al. 2003; Monteiro et al. 2011; Karling et al. 2013).

The significant correlation of *U. paradoxus* in female hosts could be linked to hormonal factors, or different sexual behavior between male and female hosts. The correlation between abundance of *U. paradoxus* and the size of the host (weight and length) is related to the quantity of energy resources where bigger fish can support larger parasite infrapopulations. Moreover, variation in body size probably reflects variation in susceptibility, leading to different ecological indices (Poulin 2013). The same seems to happen to larger infrapopulations of *Urocleidoides* sp. in heavier fish.

The significant relationship between the parasite load and the type of species, demonstrated in the GLM analysis, showed that it is the species itself that defines infection rates and may be linked mostly with the life cycle of the species or with their capacity in infecting the host. As discussed previously, some species have a supra-dispersed distribution as proposed by Shaw and Dobson (1995), where some hosts have a larger parasitic infection, such as *C. lynchi*. Moreover, the significance of infection rate with host sex and weight is justified by the fact that there is a significant difference in biometric characteristics between males and females.

Diversity index component community

The species richness of Monogenea found in this study for *M. obtusidens* was similar to that found in other studies using species of *Leporinus*, resembling them relative to ecological indices and species diversity, possibly due to the phylogenetic proximity between both genera. Previous studies on helminth fauna in *Leporinus* spp., found species of *Tereancistrum*, *Urocleidoides*, *Jainus*, *Kritskyia*, and *Rhinoxenus*, all are monogeneans (Pavanelli et al. 1997; 2008; Takemoto et al. 2009; Guidelli et al. 2011). Species of these genera also are included in the helminth component community of piava from Lake Guaíba. Such genera probably are more adapted to species of *Leporinus* and *Megaleporinus* and so are often found in these hosts, both in the basin of Guaíba as Paraná, corroborating several studies that affirm the existence of specific inter host–parasite relationships in Monogenea (Boeger and Kritsky 1997; Desdevises et al. 2002a, 2002b; Braga et al. 2014).

The number of digenean species reported in the present study was similar to other studies (Pavanelli et al. 1997; 2008; Takemoto et al. 2009; Guidelli et al. 2011). However, regarding the parasite diversity, surveys of *M. obtusidens* from the Paraná River showed the presence of different species, such as *Herpetodiplostomum* sp., *Megacoelium* sp., *Neodiplostomum* sp., and *Paralecithobotrys brasiliensis* Freitas, 1947, which were not found in Lake Guaíba. Nematodes in other studies had greater richness than in the present study, with seven species reported in *M. obtusidens* from the upper Paraná River (Takemoto et al. 2009; Guidelli et al. 2011). In this sense, the latitudinal gradient is probably one factor that could be interfering with the results found, such as differences in temperature and/or other abiotic conditions. Fish diet is another important factor that can account for the differences found related to the parasitic infrapopulations (Poulin 2001). In addition, the sampling effort becomes one factor of extreme importance to compose the species richness of a region, collections with a seasonal monitoring or repeated during several years can include rare helminth species and/or seasonal differences in helminths population densities.

Still, it is noteworthy that Aspidogastrea, *Echinorhynchus* sp., and *Cucullanus* sp. were reported in *M. obtusidens* and Lake Guaíba for the first time. The helminth fauna including both ecto- and endo species, found in *M. obtusidens* in the present study had the third largest richness (Feltran et al. 2004; Takemoto et al. 2009; Chemes and Takemoto 2011; Guidelli et al. 2011). Guidelli et al. (2011) found 28 helminth species in *Leporinus friderici* Bloch, 1794, followed by 27 species in *L. lacustris*, 21 in *M. obtusidens* and 21 in *Leporinus elongatus* (synonyms for *Megaleporinus elongatus*) Valenciennes, 1850. Takemoto et al. (2009) found 20 species of helminths in *M. obtusidens* in the Paraná river.

The present study showed a clear difference between the population organization of endo- and ectoparasites. Endoparasites showed lower prevalence than the ectoparasites, which may be associated with the eating habits of this fish host which feed mainly on vegetation. It was also observed that some species of helminths had their indexes influenced by biotic host factors (weight, standard length, and/or sex).

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