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Helminth endoparasites of endemic fish *Pygocentrus piraya* (Characiformes, Serrasalmidae) from Três Marias reservoir, Minas Gerais, Brazil

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Abstract: Ten endoparasite species found in *Pygocentrus piraya*, which is a piranha species native to São Francisco river, were collected from 108 fish caught in Três Marias reservoir in 2004 and 2005, namely: Digenea - *Austrodiplostomum* sp. (metacercariae); Eucestoda – Proteocephalidae gen. sp. (plerocercoids); and Nematoda - *Procamallanus* (*Spirocamallanus*) *inopinatus*, *Cystidicoloides fischeri* and *Capillostrongyloides sentinosa* (adults); *Spinitectus rodolphiheringi* (juvenile); *Hysterothylacium* sp., *Contracaecum* sp. $_{\text{Type 1}}$, *Spiroxys* sp. and *Goezia* sp. (larvae). In helminth fauna, *P. (S.) inopinatus* has shown higher prevalence and dominance. Fish sex has influenced the prevalence of *Hysterothylacium* sp., which was higher in female specimens. Longer total length of fish has positively influenced the abundance of *C. sentinosa* and *Hysterothylacium* sp.. The rainy season has favored parasitic indices, mainly *P. (S.) inopinatus* abundance, as well *C. sentinosa* and *Hysterothylacium* sp. prevalence and abundance. There were co-occurrences between adult and some larval nematodes. Endemic piranhas, as well as final hosts, are important intermediate and/or paratenic hosts, given the relevant number of larvae (proteocephalideans and nematodes) of heteroxene cycle found in them. Proteocephalidae gen. sp., *C. sentinosa*, *Hysterothylacium* sp., *Contracaecum* sp. $_{\text{Type 1}}$, *Goezia* sp. and *S. rodolphiheringi* are new records parasitizing *P. piraya* in São Francisco basin.

Key words: carnivorous host, freshwater fish helminths, parasites of endemic fish, upper São Francisco river.

INTRODUCTION

São Francisco river basin covers an area of approximately 645,067 km^2; it is the largest basin fully inserted in the Brazilian territory and the third largest basin in Brazil. This basin is of paramount importance to water supply in the semiarid region, as well as to electric power production (Kohler 2003). Três Marias reservoir is located in the upper portion of São Francisco basin, the upper São Francisco, and it was built to regulate the flow of São Francisco river (Cachapuz 2006).

Serrasalmidae comprises 98 fish species and 16 current genera. *Pygocentrus* encompasses four valid species, namely: *Pygocentrus cariba* (Humboldt, 1821); *Pygocentrus nattereri* Kner, 1858; *Pygocentrus palometa* Valenciennes, 1850; and *Pygocentrus piraya* (Cuvier, 1819) (Froese & Pauly 2019). The distribution of this family is limited to the Neotropical region. The incidence of individuals belonging to this family in other places results from their introduction in these

environments. *Pygocentrus* spp. has the ability to adapt to new environments, mainly to lakes and reservoirs (Agostinho et al. 2007). *Pygocentrus piraya*, commonly known as piranha, is endemic to São Francisco river basin (Fink 1993, Reis et al. 2003) and abundant in Três Marias reservoir; it is carnivorous and prefers to feed on other fish (Britski et al. 1988).

Piranhas are neotropical fish capable of attacking bigger animals (Agostinho et al. 1997); their mutilating and opportunistic habit enables them to attack several fish species living in captivity or in natural environments (Sazima & Machado 1990), as well as fish caught in fishing nets (Agostinho & Marques 2001). The fact that *P. piraya* is a predatory species at the top of the food web reveals the key role played by this species in controlling populations of other fish species in the ecosystem. However, it is described as a species capable of causing harm to local fishermen, because it damages their fishing nets (Trindade & Jucá-Chagas 2008).

Although congeneric species *P. nattereri* is native to the Amazon and Paraná river basins, it can be found in several South American countries (Froese & Pauly 2019). Its endoparasite fauna was investigated by Rego & Eiras (1989), Rego & Pavanelli (1990), Moravec (1998), Pavanelli et al. (2004), Thatcher (2006), Barros et al. (2006, 2010), Vieira et al. (2010, 2011), Morais et al. (2011, 2019), Benigno et al. (2012), Cárdenas et al. (2012), Vicentin et al. (2013) and Brito-Junior & Tavares-Dias (2018). The current study has investigated the endoparasite fauna of fish species *P. piraya* because the few studies carried out on this topic (Travassos et al. 1928, Moreira et al. 1994, Brasil-Sato 2003, Moravec et al. 2008, Santos et al. 2009, Monteiro et al. 2016) have indicated that this piranha species is a potential host for peculiar endoparasite fauna in Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

The aim of the present study was to identify species composing the endoparasite community found in piranha *P. piraya* in Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

MATERIALS AND METHODS

For investigation of metazoan endoparasites, 108 specimens of *P. piraya* were caught in the Três Marias reservoir (18º 12' 59" S, 45º 17' 34" W), upper São Francisco river, Três Marias municipality, state of Minas Gerais, in the period between July and August, 2004 (dry period) and January, 2004, December, 2004 and January, 2005 (rainy period). The fish were collected by artisanal fishermen of the Centro Integrado de Recursos Pesqueiros e Aquicultura de Três Marias (1ª CIT) of the Companhia de Desenvolvimento dos Vales do São Francisco e do Parnaíba (CODEVASF), agreed to Companhia Energética de Minas Gerais (CEMIG-GT). Some specimens were necropsied in the Laboratório de Ictiologia da Estação de Hidrobiologia e Piscicultura from CODEVASF, while others were individually fixed in bottles filled with 3% formalin and transported to the Laboratório de Biologia e Ecologia de Parasitos, from the Instituto de Ciências Biológicas e da Saúde, from Universidade Federal Rural do Rio de Janeiro (LABEPAR/ICBS/UFRRJ), where they were subsequently necropsied. During fish necropsies, their total length, weight and sex were recorded on forms. The procedure for fixing and preparing temporary or permanent slides of specimens parasites followed a standardized methodology (Amato et al. 1991).

Digenea metacercariae was identified and classified according to Niewiadomska (2002). The classification of Eucestoda plerocercoids followed Chervy (2002) and Chambrier et al. (2017). Specimens of Nematoda were identified

and classified according to Moravec (1998) and through specialized scientific articles.

Voucher specimens of *P. piraya* were deposited in the Museu de Zoologia of the Universidade de São Paulo (MZUSP), São Paulo, Nº 95149. Voucher specimens of parasites of *P. piraya* were deposited in the Coleção Helmintológica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro and/or in the Academia de Ciências da República Tcheca (ASCR), according to the numbering presented in the results section.

Statistical tests were applied to analyze parasitic infrapopulations and infracommunities in accordance of Bush et al. (1990, 1997). The parasite species were classified within the community according to their importance value (IV) (Bush & Holmes 1986). Species dominance in communities was tested using Simpson's index (*C*) (Stone & Pence 1978). The frequency of dominance, the shared frequency of dominance and the mean relative dominance of each parasite species were calculated according to Rohde et al. (1995). The ratio between the mean parasite variance and abundance (dispersion index - DI) was calculated for each parasite species in order to determinate their distribution pattern. Their significance was tested using the statistical *d*-test (d>1.96) (Ludwig & Reynolds 1988).

Student's *t* test was used to check for possible differences between the weights and sizes of hosts in relation to their sex. The chi-square test (X^2) was used to determine the influence of sex and the period of collection on the prevalence of parasites. Spearman's correlation coefficient by ranks (r_s) was used to evaluate possible correlations between the host's total length and intensity, abundance, richness and parasite diversity. Pearson's correlation coefficient (r) was used to assess the correlation between parasite prevalence in relation to the hosts' size classes, as estimated by Sturges's formula (Sturges 1926). The Mann Whitney test (U) was used to assess the possible differences between intensity, abundance, richness and parasite diversity in relation to sex and period of collection of hosts.

The community descriptors of parasitism that were calculated included the following: mean parasite abundance, mean parasite richness, Shannon-Wiener's parasite diversity (H') and Hill's equivalence modified (E). The DivEs software was used to calculate these indexes (Rodrigues 2019). Berger-Parker's numerical dominance (Dbp), as based on parasite infracommunities, was calculated from the respective abundances (Magurran 1988). The level of significance for all tests was p<0.05 (Zar 1996).

RESULTS

The total number of 108 *P. piraya* specimens were collected in Três Marias reservoir: 56 of them were male and recorded mean total length 18.1±4.4 cm (11.1 to 30.5 cm) and mean weight 169.8±180.1 g (21.0 to 835.0 g), whereas 52 were female and recorded mean total length 21.4±6.0 cm (13.0 to 34.0 cm) and mean weight 323.4±308.4 g (40.0 to 1225.0 g). In the dry season, 53 piranha specimens were collected: 31 were male and recorded mean total length 16.8±5.1 cm (11.1 to 30.5 cm) and mean weight 160.8±224.5 g (21.0 to 835.0 g); whereas 22 were female and recorded mean total length 18.8±6.2 cm (13.2 to 32.0 cm) and mean weight 244.2±320.0 g (48.9 to 967.0 g). In the rainy season, 55 piranha specimens were collected: 25 of them were male and recorded mean total length 19.5±3.0 cm (14.5 to 23.6 cm) and mean weight 181±105.3 g (46 to 390 g), whereas 30 were female and recorded mean total length 23.2±5.2 cm (13.0 to 34.0 cm) and mean weight 381.5±291.3 cm (40.0 to 1225.0g).

Female specimens were larger and heavier than males both in the integral collection (t= 3.25, p= 0.001; t= 3.19, p= 0.002, respectively) and in the rainy season (t= 3.09, p= 0.003; t= 3.26, p= 0.002, respectively), whereas the dry season did not present difference between the size and weight of male and female hosts (t=1.27, p= 0.20; t= 1.11, p= 0.27, respectively).

Component endoparasite community

Not all fish in the analyzed sample were parasitized (n= 6). Ten metazoan helminth species were found; which totaled 737 specimens and 6.8 parasites per fish, on average.

Of the 737 endoparasite specimens collected in the current study, 378 (51.3%) were adult, 358 (48.6%) were larvae and one (0.1%) was juvenile.

Three Nematoda species were found among adult endoparasites, namely: *Procamallanus* (*Spirocamallanus*) *inopinatus* Travassos, Artigas & Pereira, 1928, *Cystidicoloides fischeri* Travassos, Artigas & Pereira, 1928 and *Capillostrongyloides sentinosa* (Travassos, 1927). Seven larval or juvenile endoparasite species were also found: one species of Digenea - *Austrodiplostomum* sp. (metacercariae); one of Eucestoda - Proteocephalidae gen. sp. (plerocercoids) and five species of Nematoda - *Hysterothylacium* sp., *Contracaecum* sp. $_{\text{Type 1}}$, *Spiroxys* sp., *Goezia* sp. and *Spinitectus rodolphiheringi* Vaz & Pereira, 1934 (juvenile specimen) (Table I).

Nematoda was the most representative taxon, since it presented 94.4% parasitism rate (707 specimens) and 6.93 parasites per fish, on average. They presenting the largest number of parasite specimens in the two collection periods analyzed in separate, as well as in the whole collection period. Eucestoda and Digenea specimens were the least representative groups in the endoparasitic community found in *P. piraya* fish living in upper São Francisco river – their parasitism rate was lower than 10% (Table I).

Regarding the endoparasitic community of *P. piraya*, *P. (S.) inopinatus* was the most prevalent (83.3%); it was followed by *Hysterothylacium* sp. (39.8%) and *C. sentinosa* (27.8%). *Austrodiplostomum* sp. and *S. rodolphiheringi* recorded the lowest prevalence and abundance values (0.9% and 0.009, respectively, for both species), as shown in Table I.

The endoparasite community found in *P. piraya* revealed one central species (*P. (S.) inopinatus*), one secondary species (*Hysterothylacium* sp.) and eight satellite species, based on their importance values (Table I).

Simpson's dominance index (C) indicated that was dominance in the endoparasitic community of *P. piraya* (C= 0.27), with *P. (S.) inopinatus* presenting higher frequency dominance value (Table II).

Components of the parasite community found in *P. piraya* have shown typical aggregated or superdispersed distribution pattern, even in *C. fischeri*, whose aggregation was not statistically significant (Table III). The parasite community found in *P. piraya* presented H'= 0.63, Dbp= 0.38 and E= 3.21; it recorded mean richness and mean abundance of 1.89±1.21 and 6.82±8.32, respectively.

Parasite infracommunities

The total number of 737 endoparasite specimens were collected in *P. piraya*; mean number of parasites per infracommunity was 6.82±8.32 and its amplitude reached 1-38 parasites per host.

The richness and diversity of parasite infracommunities were correlated to the total length of hosts (r_s= 0.38, p<0.0001; r_s= 0.43, p<0.001, respectively), but not to their sex (U= 1050.5, p= 0.09; U=1276.0, p= 0.27, respectively). Parasite infracommunities found in *P. piraya*

Table I. Prevalence (P), intensity range (IR), mean intensity (MI) and mean abundance (MA) and their respective standard deviation (SD); importance of values (IV) and site of infection of the metazoan endoparasites of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	P (%)	IR	MI ± SD	MA ± SD	IV	Site of infection
Digenea						
Austrodiplostomum sp. (metacercariae) CHIOC 38499	0.9	1	1.0	0.009±0.09	S_A	E
Eucestoda						
Plerocercoids of Proteocephalidae	2.8	1-26	9.67±14.1	0.27±2.51	S_A	C, AI, MI, S
Nematoda						
Procamallanus (*S.*) *inopinatus* (adults and larvae) CHIOC 36950	83.3	1-23	3.11±2.92	2.59±2.91	C_E	C, IC, AI, MI, PI, S
Cystidicoloides fischeri (adults) CHIOC 35529a-b, ASCR 883	10.2	1-3	2.36±0.81	0.24±0.76	S_A	C, MI, S
Capillostrongyloides sentinosa (adults) CHIOC 35544	27.8	1-9	2.37±2.19	0.67±1.59	S_A	C, IC, AI, MI, S
Hysterothylacium sp. (larvae) CHIOC 36951	39.8	1-30	6.56±8.05	2.61± 5.99	S_E	C, AI, MI, S
Contracaecum sp. $_{\text{Type 1}}$ (larvae) CHIOC 36952	6.4	1-3	1.86±1.07	0.12±0.52	S_A	C
Spiroxys sp. (larvae) CHIOC 36953	12.9	1-6	1.93±1.49	0.25±0.83	S_A	C, IC, AI, G
Goezia sp. (larvae) CHIOC 36954	4.6	1-2	1.2±0.45	0.05±0.27	S_A	C, S
Spinitectus rodolphiheringi (juvenile) CHIOC 36955	0.9	1	1.0	0.009±0.09	S_A	S

C_E = central species; S_A = satellite species; S_E = secondary species; C = coelom; IC = intestinal cecum; AI = anterior intestine; MI = middle intestine; PI = posterior intestine; E=eyes; G = gallbladder; S = stomach.

Table II. Frequency of dominance, shared frequency of dominance, and mean relative dominance of the metazoan endoparasites of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Frequency of dominance	Shared frequency of dominance	Mean relative dominance ± Standard deviation
Procamallanus (*S.*) *inopinatus*	59	9	0.583±0.401
Cystidicoloides fischeri	4	0	0.042±0.162
Capillostrongyloides sentinosa	5	4	0.083±0.186
Hysterothylacium sp.	21	7	0.195±0.290
Spiroxys sp.	2	3	0.040±0.134

have shown mean diversity 0.19±0.19 and Berger-Parker mean dominance 0.78±0.23. The infracommunity recording the highest parasite diversity (*H'*= 0.66) presented five parasite species. Forty-five infracommunities have shown minimal diversity (*H'*= 0). There were four associations in the parasite community in *P. piraya*; one pair of adults and one pair of larval endoparasites have shown correlation between their prevalence and parasitic abundance or only between their abundances (Table IV).

The analyzed sample comprised 52 female and 56 male *P. piraya*, whose prevalence, mean intensity and mean abundance of parasites are shown in Table V. Female specimens recorded mean diversity 0.23±0.20 (0.14–0.66) and richness 2.04±1.30 (1–5 species), whereas male specimens have shown mean diversity 0.16±0.18 (0.06–0.49) and richness 1.77±1.13 (1–6). There was not statistically significant difference between parasite diversity and richness values based on hosts' sex (*U*= 1079.0, *p*= 0.07; *U*= 1050.5, *p*= 0.09, respectively).

Female *P. piraya* were significantly more parasitized by *Hysterothylacium* sp. larvae than males. Parasitic indices recorded for other parasite species analyzed in the current study were not influenced by host's sex (Tables V and VI).

Parasitic indices recorded for *C. sentinosa* (abundance) and *Hysterothylacium* sp. (intensity and abundance) were higher in larger fish (positive correlation). *Spiroxys* sp., despite not show significant values, they presented negative correlation, which indicated higher incidence in smaller fish (Table VII). Both the diversity and richness of infracommunities were greater in larger fish (r_s= 0.35, *p*= 0.0002, r_s= 0.38, *p*<0.0001, respectively).

The total number of 53 piranha fish were collected during the dry season, whereas 55 were collected during the rainy season - their parasite indices are shown in Table VIII. Fish collected during the dry season have shown mean parasite diversity 0.11±0.16 (0–0.66) and mean parasite richness 1.28±0.88 (0-5 species). Fish collected during the rainy season have shown mean parasite diversity 0.28±0.19 (0–0.66) and mean parasite richness 2.49±1.20 (0-6 species). Both diversity and parasitic richness were significantly higher in the rainy season (*U*= 688.0, *p*<0.0001; *U*= 598.5, *p*<0.0001).

Procamallanus (S.) inopinatus intensity and abundance, as well as *C. sentinosa* and *Hysterotyhlacium* sp. prevalence and abundance, were positively correlated to the rainy season (Table IX). During this period, *P. (S.) inopinatus* abundance was significantly higher in female fish. In the dry period, *P. (S.)*

Table III. Values of the dispersion index and the statistical *d*-test of the metazoan endoparasites of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Dispersion index	*d*
Procamallanus (*S.*) *inopinatus*	1.648	4.186*
Cystidicoloides fischeri	1.209	1.494
Capillostrongyloides sentinosa	1.910	5.623*
Hysterothylacium sp.	6.928	23.909*
Spiroxys sp.	1.401	2.719*

***significant values: *d*>1.96.**

Table IV. Analysis of the parasitic descriptors of co-occurring species in *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Pairs of species	Prevalence		Abundance	
	X^2	*p*	r_s	*p*
Adult endoparasites				
Procamallanus (*S.*) *inopinatus* – *Cystidicoloides fischeri*	0.32	0.57	-0.04	0.66
Procamallanus (*S.*) *inopinatus* – *Capillostrongyloides sentinosa*	0.75	0.39	-0.10	0.30
Cystidicoloides fischeri – *Capillostrongyloides sentinosa*	5.99	0.01*	0.24	0.01*
Larval endoparasites				
Hysterothylacium sp. – *Spiroxys* sp.	0.01	0.91	0.25	0.009*

***significant values: $p<0.05$; X^2: Chi-square test with Yates's correction; r_s: Spearman's.coefficient correlation.**

Table V. Prevalence, intensity and mean abundance of metazoan endoparasites of *Pygocentrus piraya* examined by sex from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Prevalence (%)		Mean intensity		Mean abundance	
	Males	Females	Males	Females	Males	Females
Digenea						
Austrodiplostomum sp.	-	0.9%	-	1.0	-	0.02±0.1
Eucestoda						
Plerocercoids of Proteocephalidae	1.8	3.8	26.0	1.5±0.7	0.5±3.5	0.05±0.3
Nematoda						
Procamallanus (*S.*) *inopinatus*	85.7	80.8	2.7±1.8	3.6±3.8	2.3±1.9	2.9±3.7
Cystidicoloides fischeri	10.7	9.6	2.2±1.0	2.6±0.5	0.2±0.7	0.25±0.8
Capillostrongyloides sentinosa	26.8	28.9	2.9±2.8	1.9±1.5	0.8±1.9	0.5±1.2
Hysterothylacium sp.	28.6	51.9	8.4±9.2	5.4±7.2	2.4±6.1	2.8±5.8
Contracaecum sp. $_{\text{Type 1}}$	7.1	5.3	2.3±1.1	1.5±1.0	0.13±0.6	0.1±0.5
Spiroxys sp.	12.5	13.5	1.8±1.8	2.2±1.3	0.25±0.9	0.25±0.8
Goezia sp.	1.8	7.7	1.0	1.25±0.5	0.02±0.1	0.09±0.3
Spinitectus rodolphiheringi	1.8	-	1.0	-	0.02±0.1	-

- Impossible to calculate because no male fish was parasited by *Austrodiplostomum* sp. and no female fish was parasited by *Spinitectus rodolphiheringi*.

Table VI. Analysis of parasite indexes under possible influence of the sex of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Prevalence		Intensity		Abundance	
	X^2	*p*	*U*	*p*	*U*	*p*
Procamallanus (*S.*) *inopinatus*	0.19	0.67	889.00	0.19	1378.50	0.63
Cystidicoloides fischeri	0.03	0.85	11.50	0.58	1443.50	0.94
Capillostrongyloides sentinosa	0.0005	0.98	98.50	0.57	1440.00	0.92
Hysterothylacium sp.	5.20	0.02*	186.50	0.46	1145.50	0.05
Spiroxys sp.	0.02	0.89	15.00	0.27	1425.00	0.84

***significant values: *p*<0.05; X^2: Chi-square test with Yates's correction; *U*: Mann Whitney test.**

Table VII. Analysis of parasite indexes under possible influence of the total length of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Prevalence		Intensity		Abundance	
	r	*p*	r_s	*p*	r_s	*p*
Procamallanus (*S.*) *inopinatus*	0.43	0.28	0.10	0.33	0.10	0.29
Cystidicoloides fischeri	0.06	0.88	0.24	0.46	0.10	0.26
Capillostrongyloides sentinosa	0.60	0.11	0.07	0.70	0.37	<0.0001*
Hysterothylacium sp.	0.68	0.06	0.50	0.0005*	0.38	<0.0001*
Spiroxys sp.	-0.14	0.74	-0.009	0.97	0.001	0.99

***significant values: *p*<0.05; *r*: Pearson's correlation coefficient; r_s: Spearman's.coefficient correlation.**

Table VIII. Prevalence, mean intensity, and mean abundance of the metazoan endoparasites of *Pygocentrus piraya* in the respective collection period (dry and rainy seasons), from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Prevalence (%)		Mean intensity		Mean abundance	
	Dry	Rainy	Dry	Rainy	Dry	Rainy
Digenea						
Austrodiplostomum sp.	-	1.8	-	1.0	-	0.02±0.1
Eucestoda						
Plerocercoids of Proteocephalidae	1.9	3.6	1.0	14.0±16.9	0.02±0.1	0.5±3.5
Nematoda						
Procamallanus (*S.*) *inopinatus*	81.1	85.4	2.4±1.8	3.7±3.6	2.0±1.9	3.2±3.6
Cystidicoloides fischeri	5.7	14.5	2.2±0.9	2.4±0.8	0.2±0.6	0.3±0.8
Capillostrongyloides sentinosa	7.5	47.3	1.0±0.0	2.6±2.3	0.07±0.3	1.2±12.1
Hysterothylacium sp.	17.0	61.8	6.8±10.7	6.5±7.2	1.3±5.2	3.9±6.4
Contracaecum sp. $_{\text{Type 1}}$	1.9	10.9	1.0	2.0±1.1	0.02±0.1	0.2±0.7
Goezia sp.	-	9.1	-	1.2±0.4	-	0.1±0.4
Spinitectus rodolphiheringi	-	1.8	-	1.0	-	0.02±0.1

- Impossible to calculate because no fish parasited by *Austrodiplostomum* sp., by Goezia sp. and by *S. rodolphiheringi* was collected in the dry season.

Table IX. Analysis of parasite indexes under the possible influence of the collection period (dry and rainy seasons) of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Prevalence		Intensity		Abundance	
	X^2	*p*	*U*	*p*	*U*	*p*
Procamallanus (*S.*) *inopinatus*	0.006	0.93	715.00	0.02*	1099.00	0.03*
Cystidicoloides fischeri	0.32	0.56	12.50	0.85	1352.00	0.60
Capillostrongyloides sentinosa	19.29	<0.0001*	-	-	852.50	0.0002*
Hysterothylacium sp.	21.54	<0.0001*	146.00	0.59	839.00	0.0001*
Spiroxys sp.	0.62	0.43	11.00	0.24	1318.00	0.37

***significant values; *p*<0.05; X^2: Chi-square test with Yates's correction; *U*: Mann Whitney test. - Impossible to calculate because all the fish collected in dry period presented only one specimen.**

Table X. Parasitic descriptors during collect periods (dry and rainy seasons, respectively) under possible influence of sex of *Pygocentrus piraya* from Três Marias reservoir, upper São Francisco river, state of Minas Gerais, Brazil.

Parasite species	Dry				Rainy			
	Prevalence		Abundance		Prevalence		Abundance	
	X^2	*p*	*U*	*p*	X^2	*p*	*U*	*p*
Procamallanus (*S.*) *inopinatus*	3.8	0.04*	204.00	0.02*	0.80	0.37	242.50	0.03*
Cystidicoloides fischeri	0.27	0.59	316.50	0.80	0.22	0.63	340.00	0.62
Capillostrongyloides sentinosa	0.27	0.59	317.00	0.81	0.79	0.37	305.00	0.27
Hysterothylacium sp.	3.89	0.04*	243.00	0.10	0.02	0.86	364.50	0.96
Spiroxys sp.	0.14	0.70	308.50	0.69	0.03	0.86	352.50	0.95

***significant values: *p*<0.05; X^2: Chi-square test with Yates's correction; *U*: Mann Whitney test.**

inopinatus prevalence and abundance, as well as *Hysterothylacium* sp. prevalence, were higher in female fish (Table X).

DISCUSSION

The endoparasitic fauna found in *P. piraya* fish collected in Três Marias reservoir, upper São Francisco river, comprised ten endoparasite species. Studies conducted with the endoparasitic community of congeneric species *P. nattereri* in different Brazilian regions have shown that it is richer and more diverse than the endoparasitic fauna found in *P. piraya* fish living in São Francisco river which recorded approximately 21 species, namely: representatives of Digenea - metacercariae of *Austrodiplostomum compactum* (Lutz, 1928) and *Clinostomum marginatum* (Braun, 1899); representatives of Eucestoda - adult *Proteocephalus serrasalmus* Rego & Pavanelli, 1990 and Cestoda gen. sp.; representatives of Nematoda – larvae of *Eustrongylides* sp., *Eustrongylides ignotus* Jäegerskiold, 1909, *Anisakis* sp., *Brevimulticaecum* sp., *Contracaecum* sp. and *Pseudoproleptus* sp.; and adults of *Procamallanus* sp., *P. (S.) inopinatus*, *Philometra nattereri* Cárdenas, Moravec, Fernandes & Morais, 2012, Philometridae gen. sp. and Capillaridae gen. sp.; representatives of Acanthocephala - *Echinorhynchus paranensis* Machado Filho, 1959 and Acanthocephala gen. sp.; and representatives of Pentastomida - *Leiperia gracile* Diesing, 1835, *Sebekia oxycephala* Diesing, 1835, *Subtriquetra* sp. 1 and *Subtriquetra* sp. 2 (Pinto & Noronha 1976, Rego & Eiras 1989, Rego & Pavanelli 1990,

Moravec 1998, Pavanelli et al. 2004, Thatcher 2006, Barros et al. 2006, 2010, Vieira et al. 2010, Morais et al. 2011, 2019, Vital et al. 2011, Benigno et al. 2012, Cárdenas et al. 2012, Vicentin et al. 2013, Brito-Junior & Tavares-Dias 2018).

Austrodiplostomum sp., *P. (S.) inopinatus* and *Contracaecum* sp. were the common species shared by both endoparasitic fauna; they are generalist species that often parasitize several fish species belonging to different orders in different regions (São-Sabas & Brasil-Sato 2014, Santos-Clapp & Brasil-Sato 2014, Duarte et al. 2016, Monteiro et al. 2016, Ribeiro et al. 2016, Almeida-Berto et al. 2018, Fujimoto et al. 2018, Fernandes et al. 2019). Representatives of Acanthocephala and Pentastomida were not found in the endoparasitic fauna observed in *P. piraya* fish living in upper São Francisco river.

The elevated position of *P. piraya* fish in the trophic web features this species as the final host of adult endoparasites found in the current study, such as *P. (S.) inopinatus*, *C. fischeri* and *C. sentinosa*. Specimens belonging to forage fish species *Tetragonopterus chalceus* Spix & Agassiz 1829 and *Triportheus guentheri* (Garman, 1890) living in Três Marias reservoir were considered intermediate hosts of *C. fischeri* by presents these larvae in their endoparasitic community (Albuquerque et al. 2016). The prey-predator relationship established between these forage fish and *P. piraya*, which is predatory and top carnivore, helps maintaining the life cycle of these nematodes in Três Marias reservoir.

Although fish species *P. piraya* is considered a top web predator, the five larval nematodes observed in the endoparasitic community found in this species have indicated that piranha fish can be intermediate or even paratenic hosts. According to Eiras (1994), nematodes use oligochaetes, crustaceans, insect larvae, mainly ephemeropterans, and fish as intermediate hosts. Trindade & Jucá-Chagas (2008) have stated that although *P. piraya* fish are primarily piscivore, terrestrial insects can be found in their stomach content. This finding explains the presence of larval and adult nematodes in the endoparasitic community found in *P. piraya*. Likely final hosts of some of these nematodes, such as alligators, were seen feeding on *P. nattereri* in the Brazilian Pantanal region (Sazima & Machado 1990).

Female *P. piraya* fish were significantly more parasitized by *Hysterothylacium* sp. larvae than male individuals, likely when they were preparing for the reproduction season. According to Pavanelli et al. (1997), the stress experienced by fish during the reproduction season can make them susceptible to infections.

Descriptors such as parasitic richness and diversity are often associated with fish size and collection period (Guégan & Hugueny 1994, Tavares-Dias et al. 2014). Endoparasite diversity, richness and mean total abundance rates in the current study have significantly increased as the fish grew. The abundance of *C. sentinosa* was higher in larger hosts, as well as the intensity and abundance of *Hysterothylacium* sp. larvae. This outcome be explained by the cumulative effect of these parasites on their hosts. According to Neves et al. (2016), larvae who are not eliminated by hosts' immune system can remain viable for a long period-of-time until they reach their final hosts. Larger fish can eat greater amounts and diversity of food items; by doing so, they acquire intermediate and/or paratenic hosts of several parasite species and increase the likelihood of developing infections (Poulin 1995).

The transmission of the most prevalent endoparasite species was favored in the rainy season, since their ecological parasitic descriptors were higher at this time. According to Moravec (1998), the most important biotic factors in Nematoda's life cycle lie on the presence and density of intermediate hosts, as well as on the trophic relationship between them

and their definitive hosts. According to López & Sampaio (2003), rainfall regime and temperature are the factors affecting the composition and abundance of zooplankton communities. In addition, the abundance of Copepoda, among other aquatic invertebrates, is often higher in the rainy season. A mix of these factors seems to influence the greater incidence of these endoparasites during the rainy season.

Proteocephalidae gen. sp., *Contracaecum* sp. and *Hysterothylacium* sp. - larval parasites found in *P. piraya* - are generalist because they parasitize several taxonomically unrelated fish species. Besides *P. piraya*, several fish species living in upper São Francisco river were infected by these larvae (Brasil-Sato 2003, São-Sabas & Brasil-Sato 2014, Santos-Clapp & Brasil-Sato 2014, Albuquerque et al. 2016, Duarte et al. 2016, Vieira-Menezes et al. 2017, Almeida-Berto et al. 2018); thus, they acted as intermediate and/or paratenic hosts for these cestodes and nematodes, who would become adults when these infected fish were ingested by piscivorous birds or other final hosts.

Significant positive associations observed in pairs of adult endoparasites species *C. fischeri* – *C. sentinosa*, and in pairs of larval endoparasite species *Hysterothylacium* sp. – *Spiroxys* sp., may indicate that these associated species have the same ecological requirements and that there are probably frequent and common intermediate hosts for the associated species, as the carnivore host *P. piraya*, revealed in this study.

Some studies have reported some of these helminths parasitizing *P. piraya* living in upper São Francisco river. Brasil-Sato (2003) have mentioned *P. (S.) inopinatus* parasitism in this host. Moravec et al. (2008) have described *C. fischeri* in *P. piraya* and *Serrasalmus brandtii* Lutken, 1875. Santos et al. (2009) observed *Spiroxys* sp. larvae in *P. piraya*, *S. brandtii* and *Cichla kelberi* (Kullander & Ferreira, 2006); whereas Monteiro et al. (2016) recorded *Austrodiplostomum* sp. metacercariae in *P. piraya* and in other fish species living in São Francisco river. Proteocephalidae gen. sp., *C. sentinosa*, *Contracaecum* $_{\text{Type 1}}$, *Hysterothylacium* sp., *Goezia* sp. and *S. rodolphiheringi* were recorded in this serrasalmid fish for the first time; thus, they expanded the list of hosts living in Três Marias reservoir, upper São Francisco river, Brazil.

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