



Fish parasites from a neotropical tidal river within a biodiversity hotspot

Parasitas de peixes de um rio costeiro neotropical dentro de um hotspot de biodiversidade

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Abstract: Aim: We investigated the ichthyofauna parasite component community across a gradient of anthropogenic pressures of the Guaraguaçu River, south Brazil, a Neotropical river of central importance for biodiversity conservation. **Methods:** After fish sampling, all fish were identified, measured, weighed and eviscerated. The viscera and gills were inspected for parasite screening and subsequent identification. Parasite diversity estimators were calculated for the most abundant host species. **Results:** A total of 159 host specimens from 12 species were examined, being 140 (88.05%) found to be infected with at least one parasite, including 14 new parasite occurrences. The most widely distributed parasite was the nematode *Contracaecum sp.*, found in 8 host species. The highest mean infection intensity and mean abundance was observed for the monogenean *Aphanoblastella mastigatus*, infecting the Silver catfish *Rhamdia quelen*. The Shannon-Wiener, Jost and Simpson indexes were higher for the more abundant fishes, except for the Trahira *Hoplias malabaricus*. Most host species harbored parasites in poorly aggregated distribution, according to the discrepancy index. The Berger-Parker index showed monogenean dominance in all hosts except for *H. malabaricus*. We found little evidence for parasite infracommunity changes across the gradient of the river. **Conclusions:** We described the infection patterns in an important Neotropical river. The new parasite occurrences highlight the contribution of our study. Fish-parasite interactions changed throughout the river stretches, and we argue that it does not necessarily mean changes in diversity and abundance of parasite within species, but the rearrange of interactions. Moreover, it seems that parasites are more abundant in most impacted sites, another reason to continue the monitoring.

Keywords: neotropical tidal river; parasite community; biodiversity conservation; host species; anthropogenic pressures.



Resumo: Objetivo: A comunidade componente de parasitas da ictiofauna foi investigada ao longo de um gradiente de pressões antropogênicas no Rio Guaraguaçu, sul do Brasil, um rio Neotropical com grande importância para a conservação da biodiversidade. **Métodos:** Após a coleta, todos os peixes foram identificados, medidos, pesados e eviscerados. As vísceras e brânquias foram inspecionadas para coleta e subsequente identificação de parasitas. Estimadores de diversidade de parasitas foram calculados para as espécies de hospedeiros mais abundantes. **Resultados:** Um total de 159 espécimes de hospedeiros de 12 espécies foram examinados, sendo 140 (88,05%) infectados com pelo menos um parasita, incluindo 14 novas ocorrências de parasitas. O parasita mais amplamente distribuído foi o nematoide *Contracaecum* sp., encontrado em 8 espécies de hospedeiros. As maiores intensidades de infecção e abundância foram observadas para o monogenético *Aphanoblastella mastigatus*, infectando o Jundiá *Rhamdia quelen*. Os índices de Shannon-Wiener, Jost e Simpson foram maiores para os peixes mais abundantes, exceto para a Traíra *Hoplias malabaricus*. A maioria das espécies de hospedeiros abrigava parasitas com distribuição pouco agregada, de acordo com o índice de discrepância. O índice de Berger-Parker mostrou a dominância de monogenéticos em todos os hospedeiros, exceto *H. malabaricus*. Encontramos poucas evidências de mudanças nas infracomunidades de parasitas ao longo do gradiente do rio. **Conclusões:** Descrevemos os padrões de infecção em um importante rio Neotropical. As novas ocorrências de parasitas destacam a importância de nosso estudo. Interações entre parasitos e peixes mudaram ao longo dos setores do rio, e isso não necessariamente resulta em mudanças na diversidade e abundância de parasitos dentro de cada espécie, mas um rearranjo das interações. Além disso, parece que os parasitas são mais abundantes na maioria dos locais impactados, o que é mais uma razão para continuar o monitoramento.

Palavras-chave: rio neotropical de maré; comunidade parasitária; conservação de biodiversidade; espécie hospedeira; pressão antropogênica.

1. Introduction

Aquatic ecosystems are facing severe global threats (Dudgeon, 2019). There are more than 4,000 fish species in South America (Reis, 2013), and Brazil harbors one of the world's richest freshwater ichthyofauna (Abell et al., 2008). Nonetheless, the parasites associated with this extraordinary fish diversity are still poorly known (Brasil, 2003). It is consensus that parasite diversity in South America is underestimated (Luque et al., 2017), and only 17.3% of fish species known in Brazil have had their parasite fauna investigated (Luque & Poulin, 2007). That is because it is extremely hard to measure the existing parasite diversity on the planet, given the ubiquity of parasites across ecosystems (Price, 1980), the existence of cryptic species (Nadler & Pérez-Ponce, 2011; Poulin, 2011), the lack of information regarding parasite occurrence in their hosts (Poulin & Morand, 2004), and the lack of parasite taxonomists (Brooks & Hoberg, 2001). Therefore, any attempts to estimate total parasite diversity on the planet are intrinsically incomplete (Poulin, 2014).

Parasites can produce effects from the individual to the community level, and can also play an important role in the functioning and structure of ecosystems, as well as in trophic dynamics (Marcogliese & Cone, 1997; Studer et al., 2010). Additionally, parasites also serve as indicators of host's biological aspects and environmental quality (Minchella & Scott, 1991; Marcogliese & Cone, 1997; Marcogliese, 2005, 2003; Sures et al., 2017).

Due to their long evolutionary history, parasites are highly diverse in aquatic systems (Rohde, 2005). Indeed, freshwater hosts are related to greater parasite diversity when compared to ocean-dwelling hosts, since continental aquatic environments have greater sampling efforts (Luque & Poulin, 2007) and parasite diversification (Poulin, 2016). This pattern can be even more pronounced for estuarine and coastal systems, which represent transitional environments between freshwater and marine systems.

We conducted this study on the Guaraguaçu River, a tidal and coastal river located in the state of Paraná, Brazil. This is the most important freshwater watercourse of 'Lagamar', a set of estuaries in the Atlantic Forest biome (a biodiversity hotspot *sensu* Myers et al., 2000), considered a Biosphere Reserve by the World Heritage Site (UNESCO, 1999). The Guaraguaçu River has a conspicuous environmental gradient ranging from near-pristine areas to polluted regions, ending in a transition between freshwater and saltwater in an extensive mangrove area (see Galvanese et al., 2022). A recent study demonstrated that the modularity of the fish-parasite networks varies along the gradient of the river (Costa et al., 2023), and the present study is the first to describe the database cited above on fish parasite community of the Guaraguaçu River. We aimed to identify the metazoan parasitic diversity of fish species along the river continuum and analyze the ecological aspects of the parasite community of the most abundant host species.

As demonstrated for biodiversity of other biological groups (e.g. Galvanese et al., 2022), and for the structure of the host-parasite networks (Costa et al., 2023), we expected that abundance, diversity, and infection patterns of fish parasitic fauna will vary along the gradient of the river.

2. Material and Methods

2.1. Study region

The Guaraguaçu River has 60 km of extension, being located between the coordinates: -25.598896 S; -48.491263 W and -25.775462 S; -48.557954 W. Its source is located in pristine mountains surrounded by Atlantic Forest, flowing into the Atlantic Ocean in the Coastal Bay of Paraná State, Brazil. In addition to its ecological significance, the Guaraguaçu River represents great relevance for economic sustainability and coastal population well-being (Paraná, 2016). It surrounds two indigenous lands, harbors three protected areas, and is utilized for public water supply and sewage depuration. According to previous studies (Araújo et al., 2021; Sato et al., 2021; Galvanese et al., 2022), this river can be divided into different environmental regions. The upstream area is characterized as a semi-lotic habitat in near-pristine conditions; the intermediate section of the river is marked by severe pollution due to domestic sewage discharge, human settlement in its margins, and water supply for nearby cities. The downstream area is characterized by a transitional zone from freshwater to saltwater in a well-preserved extensive mangrove under state protection. This final stretch is connected to the Paranaguá Bay, which plays a role as a fish nursery and an ecological corridor for birds

and mammals (see Araújo et al., 2021; Sato et al., 2021; Galvanese et al., 2022 for a comprehensive description of the Guaraguaçu River).

2.2. Data sampling

Fish sampling was conducted in September 2018, April, and September 2019, as part of the ongoing Guaraguaçu River Monitoring Project, initiated in 2016 (see UFPR, 2023a). Samplings were done under a SISBio/ICMBio/MMA license for biological material samplings (number: 24779-6, see ICMBio, 2023). The sampling method employed a set of 20 meters gill nets, with meshes of five different sizes (2, 4, 6, 8 cm; and a net combining 2 and 4 cm), in addition to 10 modified traps (an adaptation of drum nets of 20 m long, 0.8 m height, 1.2 m half-arch diameter, and 3 mm mesh, see Figure 1). This sampling method was arranged along the four distinct sectors of the river, each with an average length of 5 km, characterized by distinct environmental features (Figure 1). The sampling sectors were categorized according to the different environmental characteristics of each river stretch. Sector 1, corresponding to the river's source area, is characterized by a preserved and pristine environment; Sector 2 is heavily impacted by anthropogenic disturbances, such as water subtraction, effluent release, and a sanitary landfill in the intermediate regions; Sector 3 is an area of pollutant dilution and depuration, bearing protected areas and hence few pollution sources; Sector 4 is highly influenced by tides, with a characteristic mangrove environment and higher degrees of salinity. The complete ichthyofauna sampling methodology is available in Occhi (2020).

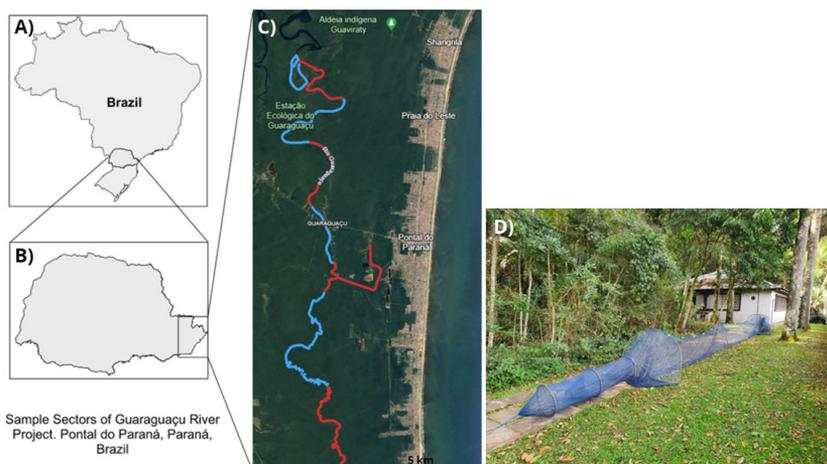


Figure 1. (A), (B) and (C) Map describing the locality of Rio Guaraguaçu, Paraná, Brazil. The highlighted stretches along the river correspond to each sector sampled; (D) Picture of the modified traps used in fish samplings.

In the field, fish were identified, measured for total and standard length, weighted, and eviscerated. The organs were fixed in 5% formaldehyde and transported to the Analysis and Synthesis in Biodiversity laboratory, “Universidade Federal do Paraná”, for later inspection. In the laboratory, with the aid of a stereomicroscope, the intestines, eyes, gills, and viscera were inspected for ecto and endoparasite. The parasites found were stored in 1.5 ml microtubes with 70% alcohol (following Eiras et al., 2006). Identification procedures were established based on different groups methodologies; monogeneans were mounted using Gray and Wess for clarification of the sclerotized structures; nematodes and copepods were placed into lactic acid solution for clarification and mounted on semi-permanent slides; trematodes and acanthocephalans were stained with Langeron’s hydrochloric carmine and mounted in Canadian balsam. The identification of the parasites was carried out to the lowest possible taxonomic level, using specific literature (Thatcher & Varella, 1981; Thatcher & Boeger, 1984a, b; Moravec, 1998; Thatcher, 2006; Kohn et al., 2006, 2007).

2.3. Data analysis

The parasite’s prevalence, mean intensity of infection, mean abundance, and respective confidence intervals were determined using the software Quantitative Parasitology, version 1.0.15 (Reiczigel et al., 2019). Prevalence refers to the ratio between the number of hosts infected by a particular species of parasite and the number of hosts examined, expressed as a percentage. Mean intensity is the number of individuals of a particular parasite species divided by the number of hosts infected by that parasite species, and the mean abundance is the number of specimens of a parasite species divided by the number of hosts analyzed (Bush et al., 1997).

Only the host species with more than three sampled specimens were used to assess information about parasite diversity, through the species accumulation curve and biodiversity estimators as Chao, Jack1, and Jack2. Furthermore, Shannon-Wiener, Jost, and Simpson diversity indexes were calculated for hosts - the latter ranging from 0 (low diversity) to 1 (high diversity). The Berger-Parker index (Berger & Parker, 1970) was used to determine the dominance of each parasite species in each host species; and the discrepancy index (Poulin, 1993) was used to determine the distribution of the parasite community within each host species, the latter ranging from 0 (all hosts of a given species have a similar abundance of parasites) to 1 (a single host of a given species has all the parasites found for that host species).

The sectors of the river were compared considering the parasite diversity and abundance: abundance of parasites, parasite species richness, Shannon-Wiener, Jost, and Simpson diversities, using Kruskal-Wallis tests. We also compared parasite species composition among sectors using Multivariate Permutational Analyses of Variance (Anderson, 2001) and Principal Coordinate Analyses (Gower, 1966) based on Bray-Curtis distances. In these cases, we considered each host individual as a community unit of parasites (i.e. the infracommunity, *sensu* Bush et al., 1997). We are aware that parasite community highly depends on both the number of infected hosts and the diversity of hosts (e.g. Lafferty, 2012). Indeed, there is a high turnover of fish composition and differences in abundances among sectors (see complete dataset in Occhi, 2020 and Table 1 in results), and the possible spatial variation may correlate with host variation. Here, we used all infected hosts to compare sectors considering the parasite community; analytical comparisons were conducted only for the host species that occurred in more than one sector with at least three individuals per sector.

Table 1. Fish taxonomic classification, common names, abundance per sector (N per sector) of the river, and total abundance (TN) (see Methods).

Family	Species	Common name	N per sector	TN
Ariidae	<i>Genidens barbatus</i> Lacépède, 1803	White sea catfish	S1 = 0; S2 = 0; S3 = 1; S4 = 0	1
	<i>Genidens genidens</i> Cuvier, 1829	Guri sea catfish	S1 = 0; S2 = 0; S3 = 0; S4 = 9	9
Centropomidae	<i>Centropomus parallelus</i> Poey, 1860	Fat snook bass	S1 = 0; S2 = 0; S3 = 2; S4 = 6	8
Characidae	<i>Oligosarcus hepsetus</i> Cuvier, 1829	Pike characin	S1 = 4; S2 = 2; S3 = 1; S4 = 0	7
Cichlidae	<i>Geophagus iporangensis</i> Haseman, 1911	Pearl cichlid	S1 = 9; S2 = 13; S3 = 9; S4 = 8	39
Erythrinidae	<i>Hoplias malabaricus</i> Bloch, 1974	Trahira	S1 = 12; S2 = 13; S3 = 13; S4 = 6	44
Guerreidae	<i>Eugerres brasiliensis</i> Cuvier, 1830	Brazilian mojarra	S1 = 0; S2 = 0; S3 = 0; S4 = 2	2
Gymnotidae	<i>Gymnotus carapo</i> Linnaeus, 1758	Banded knifefish	S1 = 0; S2 = 1; S3 = 0; S4 = 0	1
Heptapteridae	<i>Rhamdia quelen</i> Quoy & Gaimard, 1824	Silver catfish	S1 = 6; S2 = 6; S3 = 7; S4 = 1	20
Mugilidae	<i>Mugil curema</i> Valenciennes, 1836	White mullet	S1 = 0; S2 = 0; S3 = 0; S4 = 3	3
Scianidae	<i>Bairdiella ronchus</i> Cuvier, 1830	Ground croaker	S1 = 0; S2 = 0; S3 = 1; S4 = 7	8
	<i>Cynoscion acoupa</i> Lacépède, 1801	Acoupa weakfish	S1 = 0; S2 = 0; S3 = 0; S4 = 1	1

Even so, we also plotted the rank of parasite abundance for the most common parasites, identifying its abundance per sector of the river. All the diversity estimators, statistical analyses and graphs were calculated using the R software (version 4.1.1). The script of all analyses, as well as the analyzed matrices of fish individuals, their parasites and sectors in which they were sampled, are available at UFPR (2023b). The Berger-Parker and discrepancy indexes were calculated using *Microsoft Excel*.

3. Results

A total of 159 fish specimens were examined for parasites, being 143 (89.94%) infected by at least one parasite, totaling 4749 parasites. Infected fish belong to 12 different species and, most of them, had a clear spatial variation among sectors. Table 1 summarizes the infected sampled fish taxonomic classification and authors, common names, acronyms, and abundance (per sector of the river and total along the river). The total and mean abundance of parasites in each of their hosts, prevalence of infection, mean infection intensity, as well as the new occurrence records are available in Table 2. Ten out of the 14 new parasite occurrences involved Copepods, followed by Monogenea (3 new occurrences), and Nematoda (1 new occurrence, see Table 2).

A total of 67 parasite taxa were identified: Monogenea ($S = 24$, 35.82% of the total parasite diversity; $N = 2926$, 61.61% of the total parasite abundance), Nematoda ($S = 14$, 20.90% of the total parasite diversity; $N = 133$, 2.80% of the total parasite

abundance), Copepoda ($S = 13$, 19.40% of the total parasite diversity; $N = 950$, 20.00% of the total parasite abundance), Digenea ($S = 11$, 16.42% of the total parasite diversity; $N = 670$, 14.11% of the total parasite abundance), Acanthocephala ($S = 4$, 5.97% of the total parasite diversity; $N = 69$, 1.46% of the total parasite abundance), and Cestoda ($S = 1$, 1.49% of the total parasite diversity; $N = 1$, 0.02% of the total parasite abundance). At least, 10 taxa occurred in more than one host species: *Aphanoblastella mastigatus* (Suriano, 1986) Kritsky, Mendoza-Franco & Scholz, 2000, *Chauhanellus neotropicalis* Domingues & Fehlaue, 2006, *Chauhanellus* sp., and *Urocleidoides cuiabai* Rosim, Mendoza-Franco & Luque, 2011 (Monogenea); *Ergasilus jaraquensis* Thatcher & Robertson, 1982; and *Ergasilus* sp. (Copepoda); *Polyacanthorhynchus* sp. (Acanthocephala); *Contracaecum* sp.; and *Hysterothylacium* sp. (Nematoda); and Diplostomidae gen. sp. (Digenea). The most widely spread parasite was *Contracaecum* sp. (Nematoda), found in 8 host species, followed by the copepod *Ergasilus* sp. in 6 host species, while the digenean Diplostomidae gen. sp. had the third widest distribution, being found in 5 host species. The monogenean *A. mastigatus*, found in the silver catfish *R. quelen*, had the highest mean infection intensity (MII) and highest mean abundance (MA) of all taxa. The most abundant parasite species was *A. mastigatus* ($n = 1786$), followed by *Diplostomidae metacercariae* ($N = 498$, 10.49% of total parasite abundance) and *Ergasilus* sp. ($N = 366$, 7.71% of total parasite abundance), both occurring in hosts mainly in sectors 2 and 3 (Figure 2).

Table 2. Parasites and their hosts.

Parasite family	Parasite species or lower taxa	Host	ABD	P (%)	B-P	MII	MA	Or
Acanthocephala	Acanthocephala gen. sp.	Ground croaker	15	40	0.098	3.75 [1, 5.5]	1.5 [0.2, 3.6]	I
	Echinorhynchidae gen. sp.	Guri sea catfish	1	8.33	0.024	1	0.08 [0, 0.25]	I
	<i>Neoechinorhynchus</i> sp.	Pearl cichlid	35	15.38	0.062	5.83 [3.17, 8.5]	0.9 [0.28, 1.87]	V, I
	<i>Polyacanthorhynchus</i> sp.	Pearl cichlid	2	2.56	0.004	2	0.05 [0, 0.15]	I
		Trahira	16	6.25	0.015	5.33 [1, 7.67]	0.33 [0.02, 0.98]	I
Cestoda	Cestoda fam. gen. sp. (blastocyst)	Ground croaker	1	10	0.007	1	0.1 [0, 0.3]	I

ABD = Parasite abundance; P (%) = Prevalence of infection; B-P = Berger-Parker index; MII = Mean infection intensity; MA = Mean parasite abundance; Or = Organ of infection. The values inside square brackets are the 95% confidence levels. When the MII and MA are equal, it means that there is only one single host specimen infected, hence there are no confidence intervals. When there are no confidence intervals for MII, it means that there is only one individual of the host species infected by that parasite species. G = Gills; I = Intestine; E = eyes; C = Cavity; V = Viscera. *New occurrence record. Host species are identified by common names, see Table 1 for a complete taxonomic classification of hosts.

Table 2. Continued...

Parasite family	Parasite species or lower taxa	Host	ABD	P (%)	B-P	MII	MA	Or	
Copepoda	<i>Acusicola</i> sp. 1	Fat snook bass	106	75	0.344	17.67 [7.33, 38.5]	13.25 [5, 31.3]	G	
	<i>Acusicola</i> sp. 2	Ground croaker	1	10	0.007	1	0.1 [0, 0.3]	G	
	<i>Ergasilus atafonensis</i> Amado & Rocha, 1996	White mullet	17	100	0.185	5.67 [2, 8.33]	5.67 [2, 8.33]	G	
	<i>Ergasilus caraguatatubensis</i> Amado & Rocha, 1996	White mullet	6	66.67	0.065	3 [2, 4]	2 [0, 3.33]	G	
	<i>Ergasilus jaraquensis</i> Thatcher & Robertson, 1982	*White sea catfish	4	100	0.085	4	4	G	
		*Guri sea catfish	10	41.67	0.244	2 [1, 3]	0.83 [0.25, 1.74]	G	
	<i>Ergasilus leporinidi</i> Thatcher, 1981	*Pearl cichlid	23	7.69	0.041	7.67 [2, 13.3]	0.59 [0.05, 2.49]	G	
		<i>Ergasilus</i> sp.	*Fat snook	21	62.5	0.068	4.2 [2, 7]	2.63 [0.88, 5.16]	G
	<i>Ergasilus</i> sp.	*Pearl cichlid	28	20.51	0.050	3.5 [1.25, 9.62]	0.72 [0.18, 2.95]	G	
		*Trahira	366	45.83	0.349	16.64 [8.36, 39.2]	7.63 [3.4 18]	G	
	<i>Ergasilus</i> sp.	*Banded knifefish	100	100	0.980	100	100	G	
		*Silver catfish	42	27.27	0.019	7 [3.17, 15.6]	1.91 [0.55, 5.47]	G	
	<i>Ergasilus</i> sp.1	Ground croaker	1	10	0.007	1	0.1 [0, 0.3]	G	
		*Pearl cichlid	25	10.26	0.044	6.25 [2, 13.8]	0.64 [0.1 2.1]	G	
	<i>Ergasilus thatcheri</i> Engers, Boeger & Brandon, 2000	Silver catfish	92	31.81	0.041	13.14 [6.71, 22.9]	4.18 [1.55, 9.27]	G	
	<i>Gauchergasilus</i> sp.	Pearl cichlid	2	2.56	0.004	2	0.05 [0, 0.15]	G	
	<i>Therodamas elongatus</i> Thatcher, 1986	*Pearl cichlid	70	28.21	0.125	6.36 [3.55, 9.82]	1.79 [0.77, 3.49]	G	
	<i>Therodamas frontalis</i> El-Rashidy & Boxshall, 2001	White mullet	35	100	0.380	11.67 [4, 16.7]	11.67 [4, 16.7]	G	
	<i>Therodamas</i> sp.	White sea catfish	1	100	0.021	1	1	G	
	Digenea	<i>Acanthocolaritrema umbilicatum</i> Travassos, Freitas & Bührnheim, 1965	Fat snook bass	4	25	0.013	2	0.25 [0, 1]	I
		<i>Acanthostomum gnerii</i> Szidat, 1954	Silver catfish	13	9.09	0.006	6.5 [1, 6.5]	0.59 [0, 2.27]	I
		<i>Crassicutis</i> sp.	Pearl cichlid	17	5.13	0.030	8.5 [1, 8.5]	0.44 [0, 1.72]	I
		Cryptogonimidae gen. sp.	Silver catfish	5	4.55	0.002	5	0.23 [0, 0.68]	I
Digenea fam. gen. sp.		Pearl cichlid	88	25.64	0.157	8.8 [5.8 10]	2.26 [1.1 3.77]	G	
Diplostomidae gen. sp.		Pearl cichlid	3	2.56	0.005	3	0.08 [0, 0.24]	E	
		Trahira	498	56.25	0.475	18.44 [14.9 24]	10.38 [7.19, 14.3]	E, G	
<i>Hysterolecitha</i> sp.		White mullet	2	33.33	0.022	2	0.67 [0, 1.33]	E	
		Silver catfish	6	4.55	0.003	6	0.28 [0, 0.82]	E	
<i>Lobatostoma</i> sp.		Ground croaker	1	10	0.007	1	0.1 [0, 0.3]	E	
		White mullet	4	33.33	0.043	4	1.33 [0, 2.67]	I	
<i>Pseudoacanthostomum floridensis</i> Nahhas & Short, 1965		Pearl cichlid	6	7.69	0.011	2 [1, 3]	0.15 [0.03, 0.53]	I, G, C	
<i>Pseudocryptogonimus</i> sp.		Guri sea catfish	12	8.33	0.293	12	1 [0, 3]	I	
<i>Thometrema overstreeti</i> Brooks, Mayes & Thorson, 1979		Fat snook bass	10	12.5	0.032	10	1.25 [0, 3.75]	I	
<i>Thometrema</i> sp.		Trahira	1	2.08	0.001	1	0.02 [0, 0.06]	I	

ABD = Parasite abundance; P (%) = Prevalence of infection; B-P = Berger-Parker index; MII = Mean infection intensity; MA = Mean parasite abundance; Or = Organ of infection. The values inside square brackets are the 95% confidence levels. When the MII and MA are equal, it means that there is only one single host specimen infected, hence there are no confidence intervals. When there are no confidence intervals for MII, it means that there is only one individual of the host species infected by that parasite species. G = Gills; I = Intestine; E = eyes; C = Cavity; V = Viscera. *New occurrence record. Host species are identified by common names, see Table 1 for a complete taxonomic classification of hosts.

Table 2. Continued...

Parasite family	Parasite species or lower taxa	Host	ABD	P (%)	B-P	MII	MA	Or
Monogenea	<i>Anakohnia brasiliiana</i> Bravo-Hollis, 1986	Fat snook bass	3	25	0.010	1.5 [1, 2]	0.38 [0, 1]	G
	<i>Aphanoblastella mastigatus</i> (Suriano, 1986) Kritsky, Mendoza-Franco & Scholz, 2000	*Pike characin	1	8.33	0.011	1	0.08 [0, 0.25]	G
		Silver catfish	1786	72.72	0.802	111.63 [56.6 188]	81.18 [40.8, 149]	G
	<i>Aphanoblastella</i> sp.	Silver catfish	5	4.55	0.002	5	0.23 [0, 0.68]	G
	<i>Aristocleidus</i> sp.	Brazilian mojarra	9	50	0.118	9	4.5 [0, 4.5]	G
	<i>Characithecium longianchoratum</i> Rossin & Timi, 2014	Pike characin	54	50	0.607	9 [6.17, 16.2]	4.5 [1.84, 9.17]	G
	<i>Characithecium</i> sp.	Pike characin	10	16.66	0.112	5 [4, 5]	0.83 [0, 2.17]	G
	<i>Characithecium</i> sp.1	Pike characin	11	25	0.124	3.67 [2, 4.67]	0.91 [0.17, 2.17]	G
	<i>Chauhanellus boegeri</i> Domingues & Fehlaue, 2006	Guri sea catfish	1	8.33	0.024	1	0.08 [0, 0.25]	G
	<i>Chauhanellus neotropicalis</i> Domingues & Fehlaue, 2006	White sea catfish	21	100	0.447	21	21	G
		Guri sea catfish	2	16.67	0.049	1	0.17 [0, 0.34]	G
	<i>Chauhanellus</i> sp.	White sea catfish	21	100	0.447	21	21	G
		Guri sea catfish	3	25	0.073	1	0.25 [0, 0.42]	G
	Diplectanidae gen. sp.	Brazilian mojarra	65	100	0.855	32.5 [4, 32.5]	32.5 [4, 32.5]	G
	<i>Diplectanum</i> sp.	Acoupa weakfish	4	100	1.000	4	4	G
	<i>Ligophorus</i> sp.	White mullet	25	66.67	0.272	12.5 [6, 12.5]	8.33 [0, 14.7]	G
	Microcotylidae (post-larvae)	Fat snook bass	17	12.5	0.055	17	2.13 [0, 4.25]	G
	<i>Rhabdosynochus guanduensis</i> Abdallah, Azevedo & Luque, 2012	Fat snook bass	139	87.5	0.451	19.86 [11.6 25.0]	17.38 [8.5 23.2]	G
	<i>Rhamnocercus margaritae</i> Fuentes-Zambrano, 1997	Ground croaker	107	60	0.699	17.83 [5.67, 43.5]	10.7 [3, 32]	G
	<i>Rhamnocercus rhamnocercus</i> Monaco, Wood & Mizelle, 1954	*Ground croaker	25	40	0.163	6.25 [2, 10.5]	2.5 [0.4, 8.2]	G
	<i>Sciadicleithrum frequens</i> Bellay, Takemoto, Yamada & Pavanelli, 2008	Pearl cichlid	208	46.15	0.370	11.56 [7, 18.6]	5.33 [2.9 9.44]	G
	<i>Sciadicleithrum</i> sp.	Pearl cichlid	41	12.82	0.073	8.2 [4.4, 11.4]	1.05 [0.34, 2.4]	G
	<i>Urocleidoides brasiliensis</i> Rosim, Mendonza-Franco & Luque, 2011	Trahira	41	27.08	0.039	3.15 [2.08, 4.84]	0.85 [0.42, 1.56]	G
	<i>Urocleidoides cuiabai</i> Rosim, Mendonza-Franco & Luque, 2011	*Pearl cichlid	1	2.56	0.002	1	0.03 [0, 0.08]	G
		Trahira	43	20.83	0.041	4.3 [2.5, 6.5]	0.9 [0.38, 1.77]	G
	<i>Urocleidoides brasiliensis</i> Rosim, Mendonza-Franco & Luque, 2011	Trahira	5	4.17	0.005	2.5 [1, 4]	0.1 [0, 0.4]	G
	<i>Urocleidoides</i> sp.	Trahira	9	12.5	0.009	1.5 [1, 2.17]	0.19 [0.06, 0.38]	G
	<i>Vancleaveus</i> sp.	Silver catfish	269	40.91	0.121	29.88 [11.4 79.5]	12.23 [4, 35.8]	G

ABD = Parasite abundance; P (%) = Prevalence of infection; B-P = Berger-Parker index; MII = Mean infection intensity; MA = Mean parasite abundance; Or = Organ of infection. The values inside square brackets are the 95% confidence levels. When the MII and MA are equal, it means that there is only one single host specimen infected, hence there are no confidence intervals. When there are no confidence intervals for MII, it means that there is only one individual of the host species infected by that parasite species. G = Gills; I = Intestine; E = eyes; C = Cavity; V = Viscera. *New occurrence record. Host species are identified by common names, see Table 1 for a complete taxonomic classification of hosts.

Table 2. Continued...

Parasite family	Parasite species or lower taxa	Host	ABD	P (%)	B-P	MII	MA	Or	
Nematoda	<i>Contracaecum</i> sp.	*Guri sea catfish	1	8.33	0.024	1	0.08 [0, 0.25]	C	
		Fat snook bass	8	37.5	0.026	2.67 [1, 3.67]	1 [0.13, 2.25]	I, C	
		Pike characin	1	8.33	0.011	1	0.08 [0, 2.25]	C	
		Pearl cichlid	1	2.56	0.002	1	0.03 [0, 0.08]	C	
		Trahira	33	29.16	0.031	2.36 [1.71, 3.21]	0.69 [0.38, 1.17]	C	
		Banded knifefish	1	100	0.010	1	1	C	
		Silver catfish	2	9.09	0.001	1	0.09 [0, 0.23]	C	
		Ground croaker	2	20	0.013	1	0.2 [0, 0.4]	I	
		<i>Cucullanus</i> sp.1	Brazilian mojarra	2	50	0.026	2	1 [0, 1]	C
		<i>Cucullanus</i> sp.2	White mullet	3	33.33	0.033	3	1 [0, 2]	I
	<i>Cystidocoloides izecksohni</i> Fabio, 1982	Trahira	9	12.5	0.009	1.5 [1, 1.83]	0.19 [0.06, 0.35]	I, G	
		<i>Eustrongylides</i> sp.	Trahira	2	4.17	0.002	1	0.04 [0, 0.1]	C
	<i>Heliconema</i> sp.	Pike characin	9	8.33	0.101	9	0.75 [0, 2.25]	C	
	<i>Hysterothylacium</i> sp.1	Guri sea catfish	11	41.67	0.268	2.2 1, 2.8]	0.92 [0.25, 1.92]	I, C	
	<i>Hysterothylacium</i> sp.	Banded knifefish	1	100	0.010	1	1	I	
		Silver catfish	4	18.18	0.002	1	0.18 [0.05, 0.32]	C	
	Nematoda fam. gen. sp. 1	Pike characin	3	16.67	0.034	1.5 [1, 1.5]	0.25 [0, 0.67]	C	
	Nematoda fam. gen. sp. 2	Silver catfish	3	13.64	0.001	1	0.14 [0, 0.27]	I	
	<i>Procamallanus</i> sp.1	Pearl cichlid	7	10.26	0.012	1.75 [1, 2.5]	0.18 [0.03, 0.44]	I	
	<i>Procamallanus</i> sp.2	Pearl cichlid	1	2.56	0.002	1	0.03 [0, 0.08]	I	
	<i>Pseudoterranova</i> sp.	Trahira	25	16.67	0.024	3.13 [1.84, 4.62]	0.52 [0.19, 1.04]	C	
	<i>Rhabdochona</i> sp.1	Pearl cichlid	4	2.56	0.007	4	0.1 [0, 0.31]	I	

ABD = Parasite abundance; P (%) = Prevalence of infection; B-P = Berger-Parker index; MII = Mean infection intensity; MA = Mean parasite abundance; Or = Organ of infection. The values inside square brackets are the 95% confidence levels. When the MII and MA are equal, it means that there is only one single host specimen infected, hence there are no confidence intervals. When there are no confidence intervals for MII, it means that there is only one individual of the host species infected by that parasite species. G = Gills; I = Intestine; E = eyes; C = Cavity; V = Viscera. *New occurrence record. Host species are identified by common names, see Table 1 for a complete taxonomic classification of hosts.

The overall host infection prevalence, number of parasite taxa and abundance of parasites, as well as biodiversity indexes of parasites per host with more than 3 specimens sampled (see Table 1) is available in Table 3. The Guri sea catfish had the lowest abundance of parasites (N = 41, Table 3). For this host, there were two new parasitic records: *E. jaraquensis* (Copepoda), and *Contracaecum* sp. (Nematoda). On the other hand, the Silver catfish

harbored the highest abundance of parasites (N = 2227, Table 3), and the only new parasite record for this host was *Ergasilus* sp. (Table 2). The Trahira, the most abundant fish of all hosts (Table 1), had the second-highest abundance of parasites; and more than 90% specimens infected (Table 3). This was the only host species that reached the *plateau* of the parasite species accumulation curve (Figure 3), which means that the estimated

parasite richness is equal to or very close to the observed. For the Trahira, one new parasite record was found: the generalist copepod *Ergasilus* sp. (Table 2). Considering the other hosts, any of them seems to have reached a *plateau* in the parasite species accumulation curve (Figure 3). The host that harbors the highest parasite diversity, considering almost all indexes but Discrepancy, was the Pearl cichlid (Table 3).

Parasite diversity indexes could be compared for the following hosts: the Silver catfish (sectors 1 vs. 2 vs. 3), the Trahira, and the Pearl

cichlid (all sectors) (see Table 1). The diversity of parasites did not differ among sectors for most indexes. Only abundance ($H = 8.68$; $P = 0.013$) and species richness ($H = 5.91$; $P = 0.052$) of the silver catfish differed among sectors, with higher values in sectors 2 and 3 (Figure 4). The parasite community composition differed significantly among sectors for the Trahira and the Pearl cichlid (PERMANOVA; $P < 0.05$) but not for the Silver catfish. Apart from P -values, it is clear that differences are low for all hosts, with high compositional overlap (Figure 5).

Table 3. Number of hosts (N), infection prevalence (P, in percentages), number of parasite taxa (NPT), parasite total abundance (PTA), mean parasite abundance per host (MPA), diversity estimators Chao and Jackknife (Jack1 and Jack2), diversity indexes of Simpson (SI), Shannon-Wiener (SW) and Jost (J) and discrepancy index (D). Complete taxonomic description of hosts is available in Table 1.

Hosts species (common name)	N	P (%)	NPT	PTA	MPA	Chao	Jack1	Jack2	SI	SW	J	D
<i>Bairdiella ronchus</i> (Ground croaker)	10	80	8	153	15.3	15	11.5	13.86	0.47	0.96	2.62	0.63
<i>Centropomus parallelus</i> (Fat snook bass)	8	100	8	308	38.5	8.88	9.75	9.96	0.67	1.38	3.96	0.37
<i>Genidens genidens</i> (Guri sea catfish)	12	75	8	41	3.42	15.11	11.5	13.86	0.77	1.67	5.3	0.52
<i>Geophagus iporangensis</i> (Pearl cichlid)	39	92.3	18	562	14.4	41.82	24.81	30.5	0.81	2.05	7.74	0.46
<i>Hoplias malabaricus</i> (Trahira)	48	91.7	12	1048	21.8	12.24	12.98	12.06	0.65	1.37	3.92	0.41
<i>Oligosarcus hepsetus</i> (Pike characin)	12	58.3	7	89	7.42	8.93	9.57	10.52	0.59	1.25	3.5	0.53
<i>Rhamdia quelen</i> (Silver catfish)	22	90.9	11	2227	101	13.14	13.85	14.84	0.34	0.74	2.09	0.63

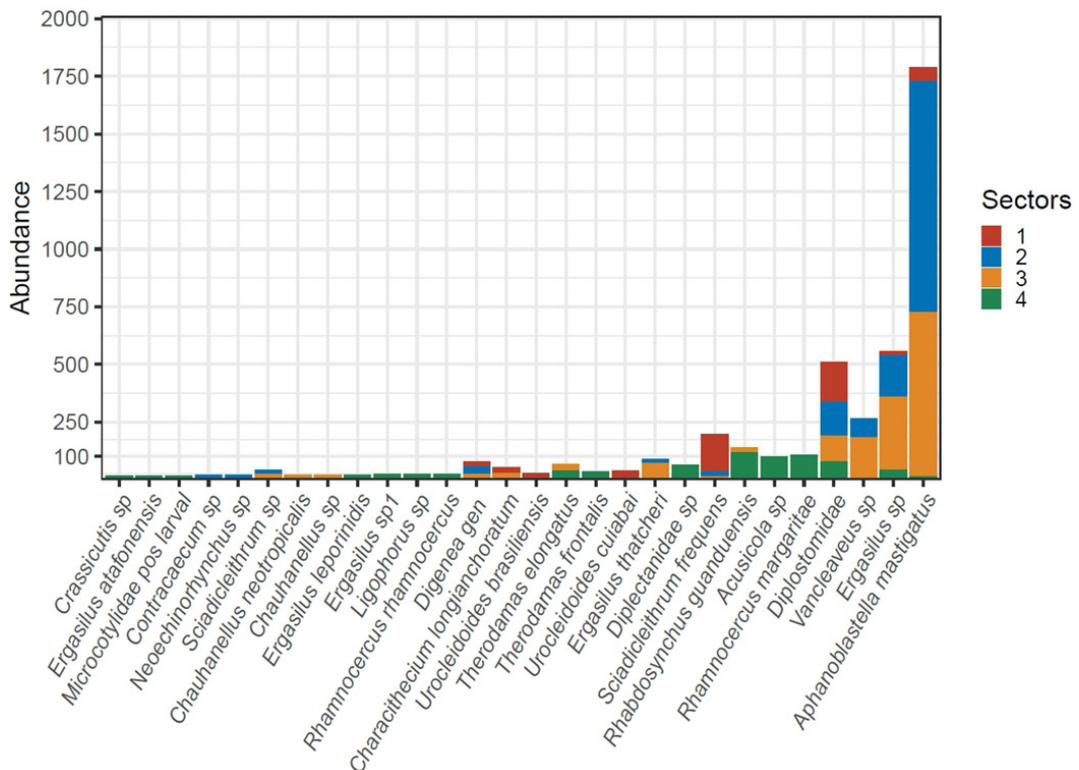


Figure 2. Abundance of parasites for the most common parasite species, identifying the abundance per sector of the river (see Methods). See Table 2 for taxonomic classification of parasite species.

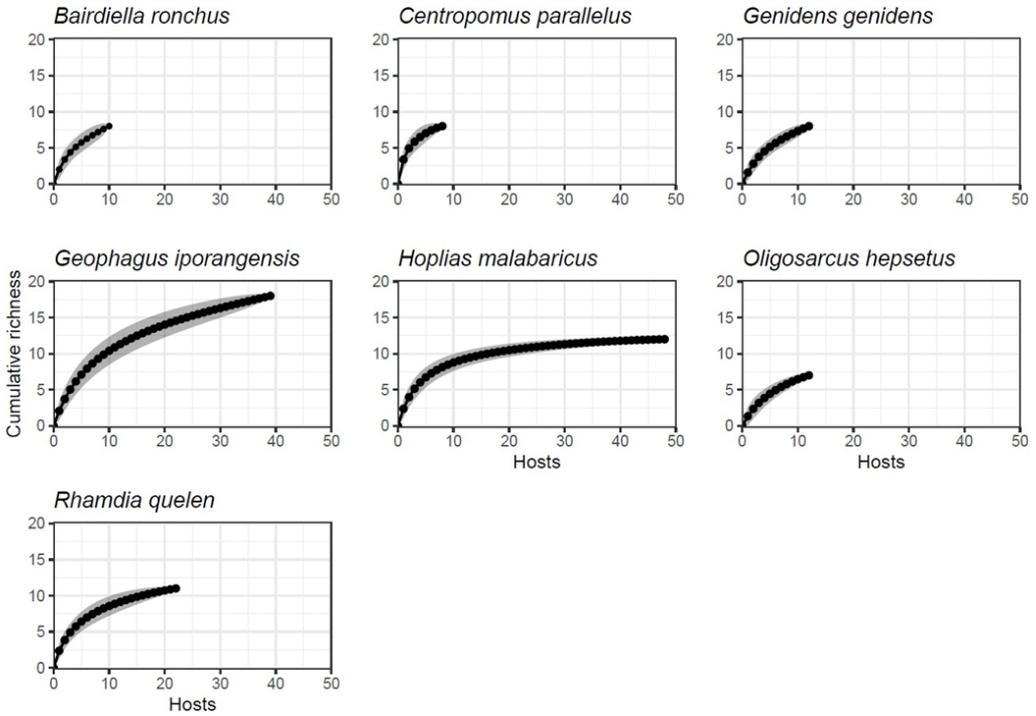


Figure 3. Parasite species accumulation curve in each of the seven host fish with more than three specimens sampled. Complete taxonomic description of hosts is available in Table 1.

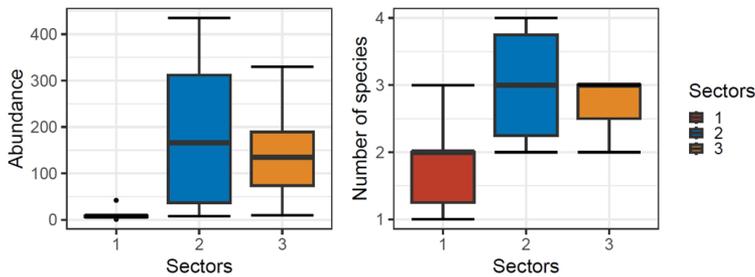


Figure 4. Abundance and species richness of parasites from the Silver catfish host *Rhamdia quelen* Quoy & Gaimard, 1824 among sectors of the river (see Methods). Sector four is not available for these comparisons given only one specimen of this host was sampled there (see Table 1).

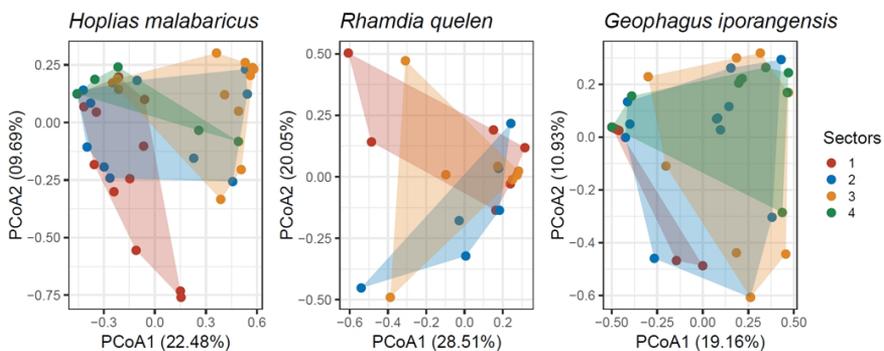


Figure 5. Principal coordinate analysis showing compositional differences/similarities of parasites for the following hosts: the Trahira *Hoplias malabaricus* Bloch, 1974, the Silver catfish *Rhamdia quelen* (Quoy & Gaimard, 1824) and the Pearl cichlid *Geophagus iporangensis* Haseman, 1911 among sectors of the river (see Methods).

4. Discussion

In this study, we shed light on the metazoan parasite diversity from the Guaraguaçu River ichthyofauna. Notably, certain parasite species, particularly monogenean parasites such as *A. mastigatus*, display a marked dominance within this ecosystem. As a consequence, Berger-Parker indexes and infection intensities were high only for a few species, and low for most of them. We have also described infection patterns and variation among hosts and localities along the river with different human impacts. Through the systematic monitoring of this river system, the resulting data will provide valuable insights into the underlying causal mechanisms and dynamics governing the complex host-parasite interactions in this unique and ecologically important transitional zone between freshwater and estuarine habitats. Indeed, our effort recorded 14 new interactions, making a valuing contribution to the biodiversity of unknown groups such as freshwater fish parasites.

The highest diversity and abundance of Monogenea is consistent with prior research in the Upper Paraná River (Lima et al., 2016; Acosta et al., 2020). Despite this group being composed usually of specialist parasites, infecting only one or few host species (Poulin, 1992; Dobson et al., 2008), the parasite *C. neotropicalis* was found in the two *Genidens* host species (estuary catfishes) in our study; and it has been previously recorded in other five sea catfish species from the same family (Ariidae): the Bressou sea catfish, *Aspistor quadriscutis* Valenciennes, 1840; the Softhead sea catfish *Amphiarus rugispinis* Valenciennes, 1840; the Thomas sea catfish *Notarius grandicassis* Valenciennes, 1840; the Passany sea catfish *Sciades passany* Valenciennes, 1840; and the Crucifix sea catfish *S. proops*, Valenciennes, 1840 (Domingues et al., 2016). In contrast, the monogenean *Chauhanellus boegeri* Domingues & Fehlaue, 2006 was found exclusively in the Guri sea catfish, although it was described when collected from the White sea catfish in the coastal region of Paraná (Domingues & Fehlaue, 2006).

Nematoda was the second most diverse group in this study, consistent with the findings of Acosta et al. (2020), in the Upper Parana River. The fact that the hosts Trahira, Pearl cichlid and Silver catfish were the most infected by this parasite taxon is potentially due to their diet and foraging habits. There are diet shifts related to Trahira (Meschiatti & Arcifa, 2002; Mello et al., 2006) and Pearl cichlid ontogenies (Abelha & Goulart, 2004;

Dias et al., 2005). Such hosts are highly generalist when adults, which is an explanation for harboring the greatest diversity for this group. Previous studies on *Geophagus brasiliensis* (Quoy & Gaimard, 1824) (now recognized as a species complex that included the Pearl cichlid studied here, *G. iporanguensis*, see Argolo et al., 2020), demonstrated that the fish feeds on macrophytes, and later shifts to an opportunistic diet, consuming sediment, benthic animals, seeds, fruits, fish, zooplankton, and other items (Abelha & Goulart, 2004; Dias et al., 2005). Conversely, Trahira juveniles primarily feed on insects, shifting to a piscivorous diet as adults, becoming generalists and top chain predators (Winemiller, 1989; Meschiatti & Arcifa, 2002; Mello et al., 2006). The Silver catfish is a benthic omnivore and generalist predator, feeding on fish, crustaceans, insects, detritus, and plant fragments (Casatti, 2002; Gomiero et al., 2007). Their different foraging methods and food sources can be used to explain why those hosts harbor only one parasite species in common: *Contraecaecum* sp. The host's diet and habitat are important factors in the acquisition of parasites (Guidelli et al., 2003), in addition to the generalist nature of *Contraecaecum* sp. The reason why this was the only shared nematode is potentially explained by the low abundance of the other nematode species, but it still lacks more evidence.

Nematode parasites have an indirect life cycle, with fish being intermediate or definitive hosts (Moravec, 1998). This study found larvae and adult nematodes. *Contraecaecum* nematodes were found infecting eight host species, across all sectors. This species is opportunistic and globally distributed (Anderson, 2000), being the only Anisakidae Railliet & Henry, 1912 capable of infecting terrestrial and aquatic animals in its life cycle (Shamsi, 2019). The fact that piscivorous birds are usually their definitive hosts (Vicente et al., 1995; Torres et al., 2000; Saad et al., 2018) contributes to their widespread distribution. Nevertheless, there are records of marine mammals as their definitive hosts (Anderson, 2000; Shamsi, 2019). Relatedly, it is not uncommon to find *Contraecaecum* nematodes in more than one host species.

Only two copepod parasite species were found in more than one host: *E. jaraquensis* and *Ergasilus* sp. The copepod *E. jaraquensis* was found in both *Genidens* species (the estuary catfishes) which is expected due to the phylogenetic proximity of both hosts, probably having similar immunological and physiological characteristics (Poulin, 1997; Morand, 2000).

In contrast, *Ergasilus* sp. displayed a broader host range and was found in six host species from different families, a common trait characteristic of generalist parasites (Lima et al., 2016). In addition, we highlight the fact that *Ergasilus* sp. had a higher prevalence and mean abundance in the Trahira than in other hosts. This observation indicates that Trahira may be an important connector in the Guaraguaçu River, and its movement and abundance along the river increases the likelihood of host switching. Even so, we must admit that *Ergasilus* sp. can be composed of more than one species, given difficulties in parasite taxonomy.

Digenea was one of the groups with fewer species in our study. Digenean species have a complex life cycle (Lefebvre & Poulin, 2005). For instance, *Acanthocolaritrema umbilicatum* Travassos, Freitas & Bührnheim, 1965 involves three host species, as described for the first time by Simões et al. (2008). This parasite belongs to Cryptogonimidae, which is composed of species that have gastropods as their first intermediate hosts (Miller & Cribb, 2008). In this study, we found it in the Fat snook bass, its definitive host, following the life cycle described by Simões et al. (2008). About the other parasites: *Acanthostomum gnerii* Szidat, 1954 has catfishes as its definitive hosts, other fishes as its second intermediate hosts, and gastropods as its first intermediate hosts (Núñez & Pertierra, 1991), which denotes the presence of these invertebrates in the ecosystem. Finally, there were ten specimens from the genus *Pseudocryptogonimus*, which were found in the intestines of the Fat snook bass. Even though there is little knowledge available about this parasite genus, it was previously found in other host species of *Centropomus* (snooks), and in other marine/estuarine fish genera such as the Grunt fish *Pomadasys* and the Snapper fish *Lutjanus* (Castañeda et al., 2003). We also found previously known digenean parasitism: *Lobatostoma* in Pearl cichlid. Such parasites been reported in other *Geophagus* species, and since this fish genus has recently been revised, their parasite fauna will also need review (Rassier et al., 2015; Argolo et al., 2020).

The only Acanthocephalan species that infect multiple host species was *Polyacanthorhynchus* sp., which was found in the Pearl cichlid and the Trahira in its encysted stage, consistent with previous reports for Trahira parasites (Amin et al., 1996). Despite the scarcity of information regarding the life cycle of acanthocephalans in Brazil (Gouveia et al., 2021), it is established that these organisms require intermediate hosts, typically insects or crustaceans

(mainly ostracods), to reach their definitive hosts, which include a diverse range of animals such as birds, mammals, reptiles, amphibians, and fishes (Crompton & Nickol, 1985; Kennedy, 2006). The *Polyacanthorhynchus* sp. specimens were recovered from four hosts of two distinct species. They occurred in sector 3 and particularly in sector 4, the one in the transition zone between freshwater and mangrove. Moreover, the only host specimen from sector 3 was Trahira, which is capable of reaching all sectors. The available data suggest that an estuarine crustacean could serve as the intermediate host. As already described, Trahira is a top chain predator with a shifting diet throughout its ontogeny (Winemiller, 1989; Novaes & Carvalho, 2011) which likely increases the chance of acquiring parasites that are trophic transmitted, since the host's diet is a critical determinant of endoparasite acquisition (Poulin, 1995).

As expected, the most infected host species were also the most abundant (except for the Fat snook bass, potentially due to its low sample size), and all hosts had its parasite infracommunity not similarly distributed among the host population. Indeed, the most abundant host – Trahira – was the only host in which parasite species accumulation curve reached *plateau*, so we can estimate that parasite species richness for this host is 12 parasite species. The fact that Pearl cichlid harbored the greatest parasite diversity (for most indexes) is probably due to its presence along the entire river and its very diverse diet (discussed earlier). The third most abundant host – Silver catfish – exhibited the highest parasite abundance because the abundance of *A. mastigatus*. The high dominance of one parasite species is likely responsible for the high Discrepancy index for this host species, since this parasite represents 80% of all the parasite infracommunity inside the silver catfish. The reason for such abundance remains unclear due to the scarcity of studies regarding the parasite biology. Even so, this parasite species was already found infecting Silver catfish from the Gandu River, Rio de Janeiro (Azevedo et al., 2010), also showing aggregate distribution (Negrelli et al., 2021).

For two out of the three most abundant hosts above-mentioned, we found little evidence that parasite species composition varies over the spatial gradient, and that diversity correlates with human impacts. Significant increases of parasite diversity and abundance in the most impacted sectors were observed only for Silver catfish. We add to the results of Costa et al. (2023), that used the same database described here and suggest that the structure of the interaction networks vary over the gradient.

In this case, we advocate that the restructuration of the networks does not necessarily involves changes in composition and diversity. Indeed, network structure of parasites may change both because of parasite species turnover among hosts and interaction rewiring. Here, we compared variation of the parasite infracommunity, i.e., within a host species (see Bush et al., 1997). Yet, diversity and abundance of parasites are expected to be higher in most impacted sites, since parasitism is an opportunistic interaction, particularly in impacted sites (Budria, 2017; Costa et al., 2023). While it is evident that most of the highly abundant parasites occurred in sectors 2 and 3, the sectors most impacted (see Figure 2), further investigation encompassing a broader spectrum of hosts, with more individuals in each sector, is imperative to draw definitive conclusions.

We must assume that the still low host sample size for most species may compromise the inference about the true parasite diversity present in fish from the Guaraguaçu River and possibly the interpretation of spatial patterns. Nonetheless, the significant evidence of the large parasite diversity in this environment suggests the existence of potentially undetected species in most hosts. We suggest that more studies are needed to increase the sample size and, hence, the accuracy of inferences. We also highlight that Trahira and Pearl cichlid may be the most important parasite links along the river. As both hosts were present in all sectors and very generalist, they are likely to play a crucial role in the parasite transmission dynamics.

5. Conclusions

This study has provided valuable insights into the parasite community of the ichthyofauna in the Guaraguaçu River ecosystem. The discovery of 14 new parasite occurrences and the exploration of infection patterns among hosts are important contributions to the understanding of this complex ecosystem. We highlighted the critical need for continuous monitoring of biodiversity, in order to gain a deeper understanding of the potential impacts of anthropogenic disturbances on local biodiversity and long-term ecosystem functioning.

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