Revista Brasileira de Parasitologia Veterinária
Brazilian Journal of
Veterinary Parasitology
ISSN 1984-2961 (Electronic)
www.cbpv.org.br/rbpv

Original Article

Distribution patterns of *Procamallanus* (*Spirocamallanus*) *inopinatus* (Nematoda: Camallanidae) and its interactions with freshwater fish in Brazil

Padrões de distribuição de *Procamallanus* (*Spirocamallanus) inopinatus* (Nematoda: Camallanidae) e suas interações com peixes de água doce do Brasil

Lígia Rigôr Neves[1]; Luís Mauricio Abdon Silva[2]; Alexandro Cezar Florentino[1]; Marcos Tavares-Dias[1,3]*

[1] Programa de Pós-graduação em Biodiversidade e Biotecnologia – Rede Bionorte, Universidade Federal do Amapá – UNIFAP, Macapá, AP, Brasil
[2] Grupo de Pesquisa Aquática – NUPAq, Instituto de Pesquisas Cientificas e Tecnológicas do estado do Amapá – IEPA, Macapá, AP, Brasil
[3] Empresa Brasileira de Pesquisa Agropecuária – Embrapa Amapá, Macapá, AP, Brasil

How to cite: Neves LR, Silva LMA, Florentino AC, Tavares-Dias, M. Distribution patterns of *Procamallanus* (*Spirocamallanus*) *inopinatus* (Nematoda: Camallanidae) and its interactions with freshwater fish in Brazil. *Braz J Vet Parasitol* 2020; 29(4): e012820. https://doi.org/10.1590/S1984-29612020092

Abstract

This study used information about *Procamallanus* (*Spirocamallanus*) *inopinatus* Travassos, Artigas & Pereira, 1928 that had been published over a period of more than 90 years to investigate the infection and distribution patterns of this nematode in teleost freshwater fish in Brazil. This study was carried out using 181 samples from 82 fish species in 19 families within the five orders, with predominance of Characiformes species (71.6%). We organized a matrix-based parasite-host system in which the fish species were classified in different trophic levels and parasitic infection parameters according data available on host fish species with different life histories and geographic distributions across Brazilian hydrographic basins. *Procamallanus* (*S.*) *inopinatus* showed prevalence ranging from low to moderate, low abundance, low intensity, typically aggregated dispersion, and preferential infection of the hosts' gastrointestinal tract. There was difference in prevalence between detritivorous, omnivorous, carnivorous and piscivorous hosts, but no difference in intensity and abundance was found due to similarity in the communities of this endoparasite among the host fish species. The geographic distribution of this parasite encompasses the river of the Amazon, Paraná, São Francisco, North Atlantic, South Atlantic and Eastern basins. Lastly, suggestions regarding the life cycle of *P.* (*S.*) *inopinatus*, with its potential intermediate hosts, were discussed.

Keywords: Endoparasite, freshwater fish, infection, nematode.

Resumo

O objetivo deste estudo foi utilizar as informações sobre a *Procamallanus* (*Spirocamallanus*) *inopinatus* Travassos, Artigas & Pereira, 1928, publicadas ao longo de mais de 90 anos (1928 e 2019), para a busca de padrões de infecção e distribuição desse nematoide em peixes de teleósteos de água doce, no Brasil. Este estudo foi realizado usando-se 181 amostras de 82 espécies de peixes de 19 famílias, distribuídas em cinco ordens, com predominância de espécies de Characiformes (71.6%). Foi organizado um sistema parasito-hospedeiro em matrizes com espécies de peixes de acordo com cinco níveis tróficos. Foram usados parâmetros de infecção parasitária (prevalência, intensidade e abundância), conforme os dados disponíveis para peixes hospedeiros com diferentes histórias de vida e distribuição geográfica em diferentes bacias do Brasil. *Procamallanus* (*S.*) *inopinatus* mostrou prevalência variando de baixa a moderada, baixa abundância, baixa intensidade, dispersão tipicamente agregada e infecção preferencial pelo trato gastrointestinal dos hospedeiros. Houve diferença na prevalência entre hospedeiros detritívoro, onívoro, carnívoro e piscívoro, mas não foram encontradas diferenças na intensidade e abundância de *P.* (S.) *inopinatus*, devido a uma similaridade na comunidade desse endoparasito entre os hospedeiros. Esse parasito tem distribuição geográfica nos sistemas das bacias do Rio Amazonas, Rio Paraná, Rio São Francisco, Atlântico Norte, Atlântico Sul e Leste, e esses achados foram discutidos. Por fim, o ciclo de vida de *P.* (*S.*) *inopinatus,* com potenciais hospedeiros intermediários, foi finalmente sugerido e discutido.

Palavras-chave: Endoparasito, peixes de água doce, infecção, nematoide.

Received May 28, 2020. Accepted September 11, 2020.
*Corresponding author: Marcos Tavares-Dias. E-mail: marcos.tavares@embrapa.br

Introduction

Over recent years, parasites have been recognized as important components of global biodiversity (Luque & Poulin, 2007; Luque et al., 2017). There is now a consensus that parasites play a key role in ecosystems (Azevedo et al., 2010; Gonçalves et al., 2016; Hoshino et al., 2016), since they can control the density of host fish communities and keep the food web stable. Among these parasite groups is the phylum Nematoda Rudolphi, 1808, which consists of numerous species distributed across the various zoogeographic regions of the world.

Nematoda is a taxon of endoparasites that has high diversity in South American fish, with a total of 303 known species, of which 143 species are known to infect Brazilian hosts (Luque et al., 2017). In Brazil, although the freshwater fish nematode fauna has been studied since the beginning of the 20th century (Luque et al., 2017), inventories that also include the diversity of this helminth taxon have only recently been published. Such studies were carried out on different species of fish in certain locations in the country: for example, the region of the middle and upper Paraná River, in the state of Paraná (Takemoto et al., 2009; Kohn et al., 2011), and Guandu River, in the state of Rio de Janeiro (Azevedo et al., 2010). This information is useful in aiding understanding of the biodiversity and geographic distribution of parasite species and the interactions of the host-parasite system. However, there are still several unresolved questions about the distribution patterns of the most abundant taxa of nematodes in freshwater fish throughout their geographic distribution in Brazil.

Nematodes are important endoparasites that infect freshwater, brackish and marine fish. They constitute a significant part of the parasite fauna in different ecosystems around the world. Associations of these parasites with their host fish usually include larval or adult stages, as components of their parasitic communities (Travassos et al., 1928; Moravec, 1998; Takemoto et al., 2009; Kohn et al., 2011; Gonçalves et al., 2016; Almeida-Berto et al., 2018). These endoparasites are equipped with an alimentary canal and, therefore, they are free to circulate through the intestine of the host fish. In general, they can inhabit particularly the digestive tract beside other viscera of the hosts, but some species seem to have a preference for certain infection sites in their hosts and show pathogenicity depending on the levels of parasitism. High levels of infection can affect the growth of host fish and cause mortality (Geets & Ollevier, 1996; Moravec, 1998; Gaines et al., 2012; Fujimoto et al., 2018).

Camallanidae Railliet & Henry, 1915, is a monophyletic family of Nematoda with three known genera, including *Procamallanus* Baylis, 1923, which infects marine and freshwater fish and has worldwide distribution. *Procamallanus* (*Spirocamallanus*) *inopinatus* Travassos, Artigas & Pereira, 1928, is a camallanid that was initially described as *Leporinus* spp., in the Mogi-Guaçu River, in the state of São Paulo, Brazil (Travassos et al., 1928). This nematode species of freshwater fish has distribution in South American countries such as Brazil, Argentina, Peru, Paraguay and Venezuela (Moravec et al., 1997; Moravec, 1998; Hamann, 1999; Takemoto et al., 2009; Chemes & Takemoto, 2011; Kohn et al., 2011; Gonçalves et al., 2016; Almeida-Berto et al., 2018; Rivadeneyra et al., 2020). Despite this wide biogeographic distribution, the life cycle of *P.* (*S.*) *inopinatus* remains unknown, since no detailed studies on the association between this nematode and its host fish have yet been carried out.

In fish in the Amazon River basin system, infection by *P.* (*S.*) *inopinatus* has been found to be higher during the rainy season (Gonçalves et al., 2016; Fujimoto et al., 2018), because during this season the hosts have highest access to food containing infective stages of this nematode species. In the Paraná River system, *P.* (*S.*) *inopinatus* was found infecting *Astyanax paranae* Eigenmann, 1914 only in highly polluted areas, thus indicating that this nematode can be used as a bioindicator (Ribeiro et al., 2013). This nematode feeds on nutrients that have been processed by the host fish and it can cause intestinal damage due to inflammation, desquamation, hypertrophy, formation of fibrous capsules, loss of villi and necrosis in the muscle, mucous and submucous layer. These processes can lead to host fish malnutrition and anemia (Gaines et al., 2012; Rivadeneyra et al., 2020). Infections by *P.* (*S.*) *inopinatus* can affect both wild and farmed fish populations (Takemoto et al., 2009; Kohn et al., 2011; Gaines et al., 2012).

In Brazil, *P.* (*S.*) *inopinatus* has been reported infecting several fish species in the Paraná River system (Takemoto et al., 2009; Kohn et al., 2011) and Amazon River system (Gonçalves et al., 2016; Hoshino et al., 2016; Fujimoto et al., 2018; Ferreira et al., 2019), but only a few of these studies have addressed the interactions of the host-parasite system. Vicente et al. (1985) listed 21 species of freshwater fish infected by *P.* (S.) *inopinatus*. Subsequently, Luque et al. (2011) listed 56 species of freshwater fish infected by this nematode species. Despite this knowledge about *P.* (*S.*) *inopinatus*, its patterns in fish in Brazil remain unknown.

Studies on ecological patterns and parasite distribution should be the second step in seeking to understand the patterns and processes of parasitic infections in wild fish populations. The first step is the determination of infection rates of the parasite species in the host fish populations (Chemes & Takemoto, 2020). Considering the complexity and diversity of the different Brazilian aquatic ecosystems, which are occupied by different species of fish, these investigations need to be conducted in order to better understand the factors that determine these patterns and processes for the different species of parasites, including the nematode *P.* (*S.*) *inopinatus*. In addition, these studies are also important because many aquatic ecosystems are threatened; thus, for many species of parasites, there is a potential risk of extinction. Thus, the aim of the present study was to investigate the patterns and distribution of *P.* (*S.*) *inopinatus* in freshwater teleost fish in Brazil. Our hypothesis was that for different host fish species with different life histories and geographic distributions across Brazilian hydrographic basins, the infection parameters (prevalence, intensity and abundance) and parasite-host interactions vary according to trophic level of hosts.

Materials and Methods

A review on *P.* (*S.*) *inopinatus* in freshwater teleost fish in Brazil was carried out using searches in different databases (SciELO, ISI, Scopus, Science Direct, Zoological Records, CAB Abstracts Lilacs, Periódico Capes and Google Scholar). Data from 88 available scientific papers were used. A data set on *P.* (*S.*) *inopinatus* in freshwater fish populations in Brazil was compiled using taxonomic descriptions and surveys of occurrences and infection parameters of this nematode that were published between 1928 and 2019. These data included research on *P.* (*S.*) *inopinatus* in native fish species in rivers, lakes, ponds and reservoirs across Brazil, with the exception of three samples (two relating to *Colossoma macropomum* Cuvier, 1818 and one to the hybrid *C. macropomum* x *Piaractus brachypomus* Cuvier, 1818 from cultivation. No statistical comparison was carried out between the samples of parasites of wild fish (N = 177) and aquaculture fish (N = 4), since the majority of the samples were from wild fish populations. All of these surveys were chosen because they represented the various ecosystems found in Brazil and, therefore, would be able to help answer the main questions of this study about the pattern and distribution of *P.* (*S.*) *inopinatus* in freshwater fish across Brazil. The systematic classification used for fish species was based on Froese & Pauly (2019).

The trophic level for each species of host fish was obtained from Froese & Pauly (2019). Each sampling unit was defined as a number of individuals parasitized by *P.* (*S.*) *inopinatus* at a given site. The data were organized in a spreadsheet (".xl") with a list of the following variables: (i) number of fish examined, (ii) number of parasitized fish, (iii) infection site in the host fish, (iv) mean prevalence, (v) mean intensity and (vi) mean abundance. The following category factors were also used: (i) host fish species, (ii) trophic level of the host fish (herbivorous, detritivorous, omnivorous, carnivorous or piscivorous) and (iii) collection site of each sample (Supplementary Material - S1). These variables and factors were analyzed in order to produce a classification of patterns for *P.* (*S.*) *inopinatus*, using the R software with the "bipartite package" (Dormann et al., 2008; Dormann, 2011; R Development Core Team, 2017) or similarities for the variables. In addition, aggregation distribution pattern, correlation of abundance with body size (length and weight) of host fish and association with other endoparasite infracommunities in the hosts were investigated. No studies with inconsistent or discrepant data relating to the host and/or parasite (e.g. host infection site and/or host fish collection site) were included in the data analyses. To produce a map showing the geographic distribution of *P.* (*S.*) *inopinatus* across Brazil, the seven largest continental river basin systems in the country were taken into account (ANA, 2020).

Statistical analyses

Data on the mean prevalence, mean intensity and mean abundance that were available in scientific papers were used to characterize the parameters of infection, as recommended by Bush et al. (1997). These data were firstly evaluated with regard to assumptions of normal distribution and homoscedasticity using the Shapiro-Wilk and Bartlett tests, respectively. Since these data were found not to present normal distribution, the Kruskal-Wallis test was then used, to compare medians between the trophic levels (i.e. detritivorous, omnivorous, carnivorous and piscivorous) of the host fish and multiple comparisons performed by Dunn's test, with Bonferroni correction of significance level (Zar, 2010).

To evaluate similarities between the trophic levels of the hosts, a data matrix was constructed using the abundance of *P.* (*S.*) *inopinatus* for the population of fish. The data matrix was subjected to cluster analysis using the Bray-Curtis index (Krebs, 1999), to test the null hypothesis of no difference in the composition of parasite communities between host fish, using the R software. Non-metric multidimensional scaling (NMDS) with Bray-Curtis similarity distances was also performed using abundance data on *P.* (*S.*) *inopinatus* for populations of detritivorous, omnivorous, carnivorous and piscivorous hosts, with the aim of evaluating the general pattern of similarity between these host fish. In this analysis, we used the R statistical environment (R Development Core Team, 2017) and the "Vegan" library (Oksanen et al., 2017).

Results

A total of 181 samples of *P.* (*S.*) *inopinatus* in 81 species of freshwater fish at different trophic levels and one sample of tambatinga hybrid (*C. macropomum* x *P. brachypomus*) were analyzed. The host fish belonged to 19 families in five orders and were infected at different sites (Table 1).

Table 1. Species of freshwater fish (N= 81) from the Brazil infected by *Procamallanus* (*Spirocamallanus*) *inopinatus*, infection sites and trophic levels of hosts.

Orders	Families	Host species	Trophic level*	Infection sites
Characiformes	Bryconidae	*Brycon amazonicus* Spix & Agassiz, 1829	Omnivorous	Intestine
		Brycon melanopterus Cope, 1872	Omnivorous	Intestine
		Brycon hilarii Valenciennes, 1850	Omnivorous	Intestine and caecum pyloric
		Brycon orthotaenia Günther, 1864	Omnivorous	Intestine
		Salminus brasiliensis Cuvier, 1816	Omnivorous	Stomach and intestine
		Brycon falcatus Müller & Troschel, 1844	Omnivorous	Intestine
		Brycon orbignyanus Valenciennes, 1850	Omnivorous	Mesentery
	Erythrinidae	*Hoplerythrinus unitaeniatus* Spix & Agassiz, 1829	Carnivorous	Intestine, abdominal cavity, caecum pyloric and stomach
		Hoplias malabaricus Bloch, 1794	Carnivorous	Intestine, abdominal cavity, caecum pyloric and stomach
	Acestrorhynchidae	*Acestrorhynchus lacustris* Lütken, 1875	Piscivorous	Intestine
		Acestrorhynchu falcatus Bloch, 1794	Piscivorous	Intestine
		Acestrorhynchus falcirostris Cuvier, 1819	Piscivorous	Intestine
	Anostomidae	*Leporinus* sp.	Omnivorous	Intestine
		Leporinus copelandii Steindachner, 1875	Omnivorous	Intestine
		Schizodon nasutus Kner, 1858	Herbivorous	Intestine
		Schizodon borelli Boulenger, 1900	Herbivorous	Intestine
		Leporinus elongatus Valenciennes, 1850	Omnivorous	Intestine and caecum pyloric
		Leporinus fasciatus Bloch, 1794	Omnivorous	Intestine
		Leporinus striatus Kner, 1858	Omnivorous	Intestine
		Leporinus macrocephalus Garavello & Britski, 1988	Omnivorous	Intestine
		Leporinus obtusidens Valenciennes, 1837	Omnivorous	Intestine and caecum pyloric
		Leporinus friderici Bloch, 1794	Omnivorous	Intestine, caecum pyloric, mesentery and stomach
		Leporinus lacustris AmaralCampos, 1945	Omnivorous	Intestine and caecum pyloric
		Leporinus taeniatus Lütken, 1875	Omnivorous	Intestine, caecum pyloric and stomach
		Leporinus piau Fowler, 1941	Omnivorous	Intestine, caecum pyloric and stomach
		Leporinus reinhardti Lütken, 1875	Omnivorous	Intestine, caecum pyloric and stomach
		Schizodon knerii Steindachner, 1875	Omnivorous	Intestine, caecum pyloric and stomach
		Leporellus vittatus Valenciennes, 1850	Omnivorous	Intestine, caecum pyloric and stomach
	Characidae	*Astyanax lacustris* Lütken, 1875	Omnivorous	Intestine, caecum pyloric and stomach
		Astyanax fasciatus Cuvier, 1819	Omnivorous	Intestine
		Astyanax sp.	Omnivorous	Intestine
		Astyanax paranae Eigenmann, 1914	Omnivorous	Intestine
		Galeocharax humeralis Valenciennes, 1834	Omnivorous	Intestine
		Astyanax schubarti Britski, 1964	Omnivorous	Intestine
		Hyphessobrycon takasei Géry, 1964	Omnivorous	Intestine
		Hemibrycon surinamensis Géry, 1962	Omnivorous	-
		Cynopotamus kincaidi Schultz, 1950	Carnivorous	-
	Serrasalmidae	*Pygocentrus nattereri* Kner, 1858	Piscivorous	Intestine and caecum pyloric
		Pygocentrus sp.	Piscivorous	Intestine
		Serrasalmus spilopleura Kner, 1858	Piscivorous	Intestine
		Serrasalmus marginatus, Valenciennes, 1837	Piscivorous	Intestine and caecum pyloric
		Serrasalmus maculatus Kner, 1858	Piscivorous	Caecum pyloric
		Serrasalmus altispinis Merckx, Jégu & Santos, 2000	Piscivorous	-
		Serrasalmus brandtii Lütken, 1875	Piscivorous	Intestine, caecum pyloric and stomach
		Myloplus asterias Müller & Troschel, 1844	Carnivorous	Intestine
		Metynnis lippincottianus Cope, 1870	Carnivorous	Intestine, and stomach
		Metynnis hypsauchen Müller & Troschel, 1844	Carnivorous	Intestine, caecum pyloric and stomach
		Colossoma macropomum Cuvier, 1816	Carnivorous	Intestine, caecum pyloric and stomach
		Mylossoma duriventre Cuvier, 1818	Carnivorous	Caecum pyloric
	Cynodontidae	*Rhaphiodon vulpinus* Spix & Agassiz, 1829	Carnivorous	-
	Iguanodectidae	*Bryconops melanurus* Bloch, 1794	Omnivorous	Intestine, caecum pyloric and stomach
	Prochilodontidae	*Semaprochilodus insignis* jardine, 1841	Detritivorous	Intestine
		Prochilodus lineatus Valenciennes, 1837	Detritivorous	Intestine
	Triportheidae	*Triportheu rotundatus* jardine, 1841	Omnivorous	Intestine and abdominal cavity
		Triportheus angulatus Spix & Agassiz, 1829	Omnivorous	Intestine, caecum pyloric and liver
		Triportheus curtus Garman, 1890	Omnivorous	Intestine, caecum pyloric and stomach

*Based on Froese & Pauly (2019).

Table 1. Continued...

Orders	Families	Host species	Trophic level*	Infection sites
Siluriformes	Loricariidae	*Squaliforma emarginata* Valenciennes, 1840	Detritivorous	-
		Loricaria prolixa Isbrücker & Nijssen, 1978	Detritivorous	Intestine
	Auchenipteridae	*Trachelyopterus galeatus* Linnaeus, 1766	Omnivorous	-
		Auchenipterus nuchalis Spix & Agassiz, 1829	Carnivorous	-
	Callichthyidae	*Corydoras melanistius* Regan, 1912	Omnivorous	Intestine
		Corydoras spilurus Norman, 1926	Omnivorous	Intestine
		Corydoras amapaenses Nijssen, 1972	Omnivorous	Intestine
		Corydoras ephippifer Nijssen, 1972	Omnivorous	Intestine
	Pimelodidae	*Pimelodus* sp.	Omnivorous	-
		Pimelodus maculatus Lacepède, 1803	Omnivorous	-
		Calophysis macropterus Lichtenstein, 1819	Omnivorous	Intestine
		Zungaro zungaro Humboldt, 1821	Piscivorous	Intestine
		Pseudoplatystoma corruscans Spix & Agassiz, 1829	Piscivorous	Intestine
		Pseudoplatystoma punctifer Castelnau, 1855	Piscivorous	-
	Doradidae	*Pterodoras granulosus* Valenciennes, 1821	Omnivorous	Intestine
		Trachydoras paraguayensis Eigenmann & Ward, 1907	Omnivorous	Intestine
		Geophagus brasiliensis Quoy & Gaimard, 1824	Omnivorous	-
		Cichlasoma amazonarum Kullander, 1983	Omnivorous	Intestine
		Cichlasoma bimaculatum Linnaeus, 1758	Omnivorous	Intestine
		Astronotus ocellatus Agassiz, 1831	Omnivorous	Intestine
		Crenicichla haroldoi Luengo & Britski, 1974	Piscivorous	Intestine
		Cichla kelberi Kullander & Ferreira, 2006	Piscivorous	Intestine
		Cichla ocellaris Bloch & Schneider, 1801	Piscivorous	Intestine and stomach
Osteoglossiformes	Arapaimidae	*Arapaima gigas* Schinz, 1822	Piscivorous	Intestine
Pleuronectiformes	Achiridae	*Catathyridium jenynsii* Günther, 1862	Piscivorous	-

*Based on Froese & Pauly (2019).

Table 2. Parameters of infection by *Procamallanus* (*Spirocamallanus*) *inopinatus* in samples with 50 species of freshwater fish in Brazil.

Parameters	N	Median	25th percentile	75th percentile	Minimum	Maximum
Prevalence (%)	87	21.2	8.9	39.3	0.04	100
Intensity	76	1.8	1.3	3.0	0.06	411.1
Abundance	81	0.4	0.1	1.1	0.01	411.1

N: Sample number.

The prevalence, intensity, and abundance of *P.* (*S.*) *inopinatus* in the host fish samples analyzed are shown in Figure 1 and Table 2. The prevalence was greater than or equal to 40% in some species: *Leporinus friderici* Bloch, 1794; *Leporinus obtusidens* Valenciennes, 1837 and *Leporinus macrocephalus* Garavello & Britski, 1988 (Anostomidae); *Astyanax lacustris* Lütken, 1875; *Metynnis lippincottianus* Cope 1780; *Metynnis hypsauchen* Müller & Troschel, 1844 and *Hyphessobrycon takasei* Géry, 1964 (Characidae); *Auchenipterus nuchalis* Spix & Agassiz, 1829 (Auchenipteridae); *Bryconops melanurus* Bloch, 1794 (Iguanodectidae); *Triportheus rotundatus* Jardine, 1841 (Triportheidae); *Hoplerythrinus unitaeniatus* Spix & Agassiz, 1829 (Erythrinidae); *Pygocentrus nattereri* Kner, 1858 and *Serrasalmus altispinis* Merckx, Jégu & Santos, 2000 (Serrasalmidae); and *Corydoras ephippifer* Nijssen, 1972, *Corydoras amapaensis* Nijssen, 1972 and *Corydoras spilurus* Norman, 1926 (Callichthyidae). However, most host fish had low prevalence, low intensity and low abundance of *P*. (*S.*) *inopinatus*.

In the host fish samples, the intensity and abundance of *P.* (*S.*) *inopinatus* were similar ($p>0.05$) according to trophic levels, since the numbers of samples from detritivorous (N = 4), carnivorous (N = 10), omnivorous (N = 52) and piscivorous (N = 19) fish hosts were low, while omnibus test showed that the prevalence between detritivorous, carnivorous, omnivorous and piscivorous had some difference ($p = 0.027$), identified with Dunn's test (Figure 2).

The Bray-Curtis cluster analysis between the host fish species showed a co-phenetic coefficient of 0.960 with 1,000 permutations. The results showed that there were three well-defined clusters. The first group included detritivorous hosts (*Semaprochilodus insignis* Jardine, 1841; *Squaliforma emarginata* Valenciennes, 1840; *Loricaria prolixa* Isbrücker & Nijssen, 1978 and *Prochilodus lineatus* Valenciennes, 1837), omnivorous hosts (*A. nuchalis*) and carnivorous hosts (*H. unitaeniatus*, *Hoplias malabaricus* Bloch, 1794; *Rhaphiodon vulpinus* Spix & Agassiz, 1829 and *Salminus brasiliensis* Cuvier, 1816). The second cluster only included omnivorous hosts and the third cluster only included only piscivorous hosts, with higher similarity (Figure 3).

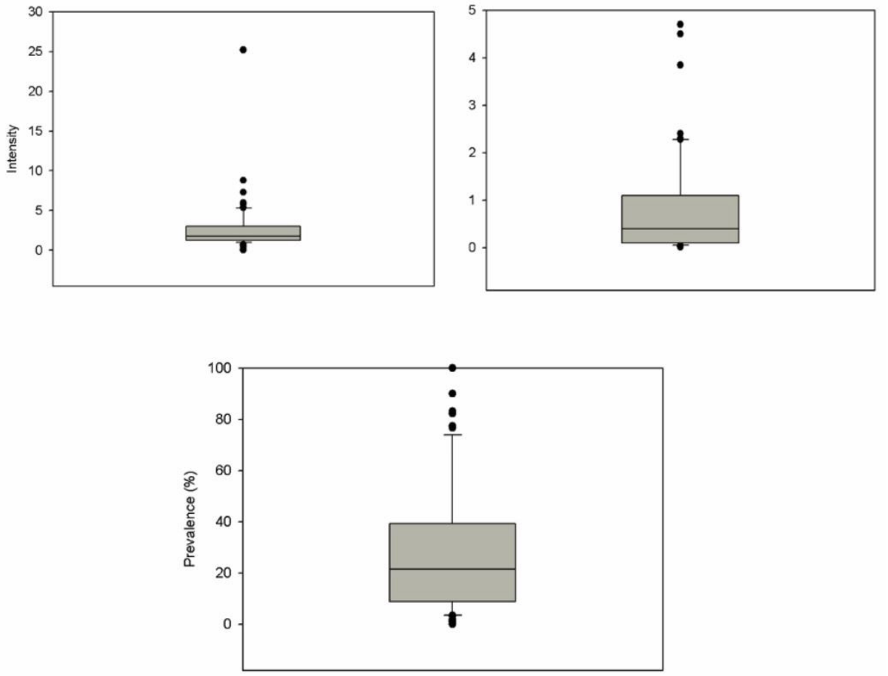

Figure 1. Quantitative descriptors of infection by *Procamallanus* (*Spirocamallanus*) *inopinatus* in 87 samples with 50 species of freshwater fish in Brazil (Box plots represent medians, interquartile ranges 25-75%, minimum-maximum values and outliers).

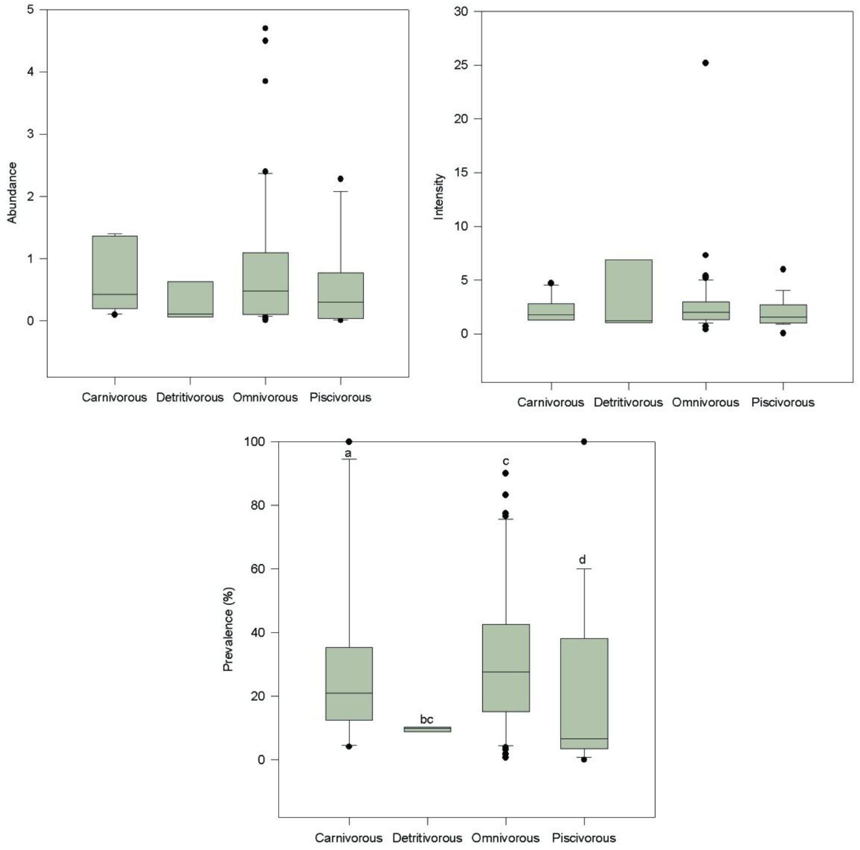

Figure 2. Quantitative descriptors of infection by *Procamallanus* (*Spirocamallanus*) *inopinatus* in 85 samples with 50 species of freshwater fish in Brazil, according to the trophic level of the hosts (Box plots represent medians, interquartile ranges 25-75%, minimum values and outliers). Kruskal-Wallis test for prevalence (H = 1.283, gl = 3, p = 0.005) indicate differences among trophic levels of hosts. Different letters indicate differences between trophic level for prevalence according to Dunn test (p = 0.027). There was no difference among trophic levels of hosts according to Kruskal-Wallis test for intensity (H = 2.068, gl = 3, p = 0.558) and abundance (H = 4.619, gl = 3, p = 0.202).

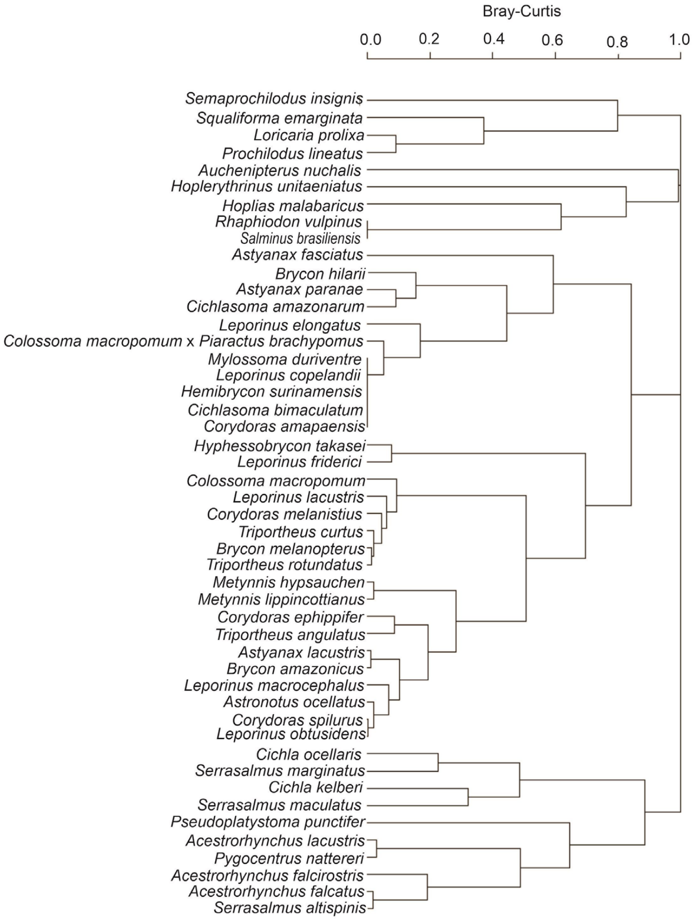

Figure 3. Dendogram of Bray-Curtis similarity for the community of *Procamallanus* (*Spirocamallanus*) *inopinatus* in 87 samples with 48 freshwater fish species in Brazil.

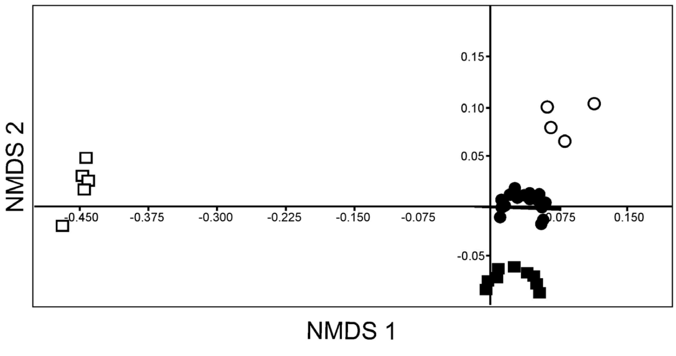

Figure 4. Non-metric multidimensional scaling (NMDS) for the abundance of *Procamallanus* (*Spirocamallanus*) *inopinatus* in 4 samples of detritivorous (☐), 52 samples of omnivorous (●), 10 samples of carnivorous (○) and 16 samples of piscivorous (■) host fish populations of freshwater in Brazil.

The NMDS analysis indicated that there was no difference in the abundance of *P.* (*S.*) *inopinatus* between detritivorous, omnivorous, carnivorous and piscivorous hosts (stress = 0.440). There was a high stress value in relation to the number of axes (Figure 4), although a distinct separation between the hosts at these four trophic levels could be seen.

The geographic distribution of *P*. (*S.*) *inopinatus* was observed to encompass the basin systems of the Amazon River, Paraná River, São Francisco River, North Atlantic and South and East Atlantic, but there were no reports of this parasite in the basins of the Tocantins River and Uruguay River (Figure 5).

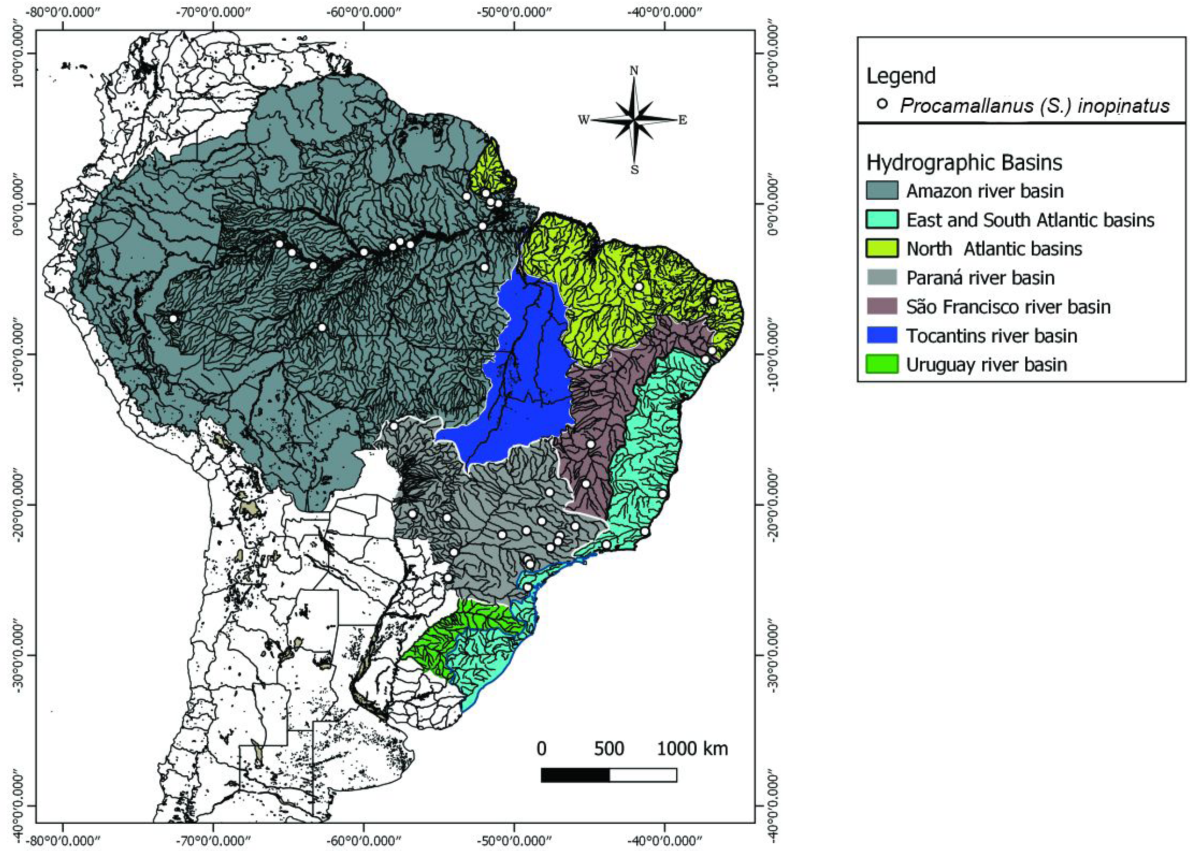

Figure 5. Geographic distribution of *Procamallanus* (*Spirocamallanus*) *inopinatus* in host fish of hydrographic basin systems from the Brazil.

Discussion

Distribution pattern of host-parasite interaction

In this study, we carried out a search for patterns of infection by *P.* (*S.*) *inopinatus* and distribution parameters in 82 host fish in 19 families and five orders in Brazil, which were mainly species of Characiformes (71.6%), Erythrinidae (20.9%), Serrasalmidae (14.8%) and Characidae (11.1%). Characiformes accounts for around 75% of freshwater fish in the Neotropical region, with approximately 234 genera and 2,000 species, distributed in different families at different trophic levels, including herbivorous, omnivorous and piscivorous species, which ingest a wide variety of food items and range from generalists to specialists, due to their differing body sizes (Bonato et al., 2017; Froese & Pauly, 2019). Therefore, these results may reflect greater effort on studies on the parasites of these host fish taxa and may also reflect local priorities for parasitological research on these host fish taxa. Nonetheless, despite these studies on the presence and infection of *P.* (*S.*) *inopinatus* in freshwater fish in different Brazilian aquatic systems, the distribution patterns were unknown until now.

We detected the following patterns within *P.* (*S.*) *inopinatus*-host interactions in the different basins in Brazil: (a) prevalence ranging from low to moderate, with low abundance and low intensity; (b) distribution pattern typically aggregated and occasionally random; (c) positive or negative correlation of abundance with body size (length and weight) of host fish at the infracommunity level; and (d) association with other endoparasite infracommunities at different infection sites in the hosts, mostly in the intestine and stomach. In these host fish, occurrences of *P.* (*S.*) *inopinatus* together with other endoparasite infracommunities and occupation of different infection sites (e.g. intestine, stomach, pyloric caecum and abdominal cavity) in the same population of fish, with different levels of infection together and with an aggregated dispersion pattern, seems allow coexistence of parasite species that would be excluded. Therefore, these findings corroborate the suggestion that the levels of different parasites shared by the same host may favor coexistence of more species of parasites, since large phylogenetic differences allow potentially competing parasites to consume the same resources without being sensitive to other parasite species (Geets & Ollevier, 1996; Bellay et al., 2013; Bhuiyan et al., 2014; Salgado-Maldonado et al., 2016, 2019). The findings from the present study are in line with this, because in most of the parasite-host systems investigated here, the gastrointestinal tract was the site most frequently infected by *P.* (*S.*) *inopinatus*.

In the samples of freshwater host fish from Brazil that we analyzed, we found low prevalence, low abundance and low intensity of abundance of *P*. (*S*.) *inopinatus*. This low parasitism level may be attributed, in part, to the fact that this nematode has a complex life cycle, with transmission through prey-predator interactions. Thus, the presence or absence of copepods (intermediate hosts), containing infective stages of *P.* (*S*.) *inopinatus* in different environments, determines the levels of their infection in populations of definitive hosts, i.e. the fish species. In addition, variations in the levels of endohelminth infection are, in general, strongly dependent on the population densities of intermediate and definitive hosts, overlapping in time and space in the same ecosystem (Blasco-Costa et al., 2015). It is also important to highlight that we analyzed host fish from different Brazilian hydrographic basin systems, which are environments with different dynamics due to the diverse characteristics of their water (Agostinho et al., 2005; Brasil, 2006; Takemoto et al., 2009; Barletta et al., 2010; Carvalho & Albert, 2011; Junk, 2013; Val, 2019). These characteristics strongly influence the invertebrate and fish communities that are intermediate and definitive hosts for *P.* (*S*.) *inopinatus*, respectively. In addition, accessibility to the definitive hosts is also related to the evolutionary strategies of endohelminths, given that some species in the adult stage are more dependent on the particular characteristics of the host fish (Bellay et al., 2013). Nevertheless, *P.* (*S*.) *inopinatus* is a species of camallanid whose strategies and life history were little known until now.

Several studies on wild fish populations have emphasized the importance of the hosts' diet and trophic level in relation to the diversity and parameters of endohelminth parasite infections (Choudhury & Dick, 2000; Simková et al., 2001; Timi et al., 2011; Poulin & Leung, 2011; Gonçalves et al., 2016; Hoshino et al., 2016; Ferreira et al., 2019; Baia et al., 2018; Negreiros et al., 2019; Ferreira et al., 2019). Endohelminth larvae complete their life cycles when ingested by their definitive hosts and are therefore dependent on prey-predator interactions (Choudhury & Dick, 2000; Timi et al., 2011; Poulin & Leung, 2011; Bhuiyan et al., 2014; Gonçalves et al., 2016; Hoshino et al., 2016; Baia et al., 2018). For this reason, fish at higher trophic levels (e.g. carnivorous and piscivorous fish) are exposed to higher numbers of infective endohelminth larvae than are those at lower trophic levels (e.g. insectivorous, herbivorous, detritivorous and omnivorous fish). The latter have lower richness and abundance of these parasites (Geets & Ollevier, 1996; Choudhury & Dick, 2000; Simková et al., 2001; Timi et al., 2011; Gonçalves et al., 2016). In the parasite-host systems investigated here, cluster analysis (Bray-Curtis) showed that host fish at the same trophic level had well-defined groups with high similarity. Consequently, the intensity and abundance of *P.* (*S*.) *inopinatus* were also similar for detritivorous, omnivorous, carnivorous and piscivorous hosts, influenced by the low levels of parasitic infection and predominant sampling of omnivorous hosts. However, the prevalence was higher in omnivorous hosts following by carnivorous hosts. In contrast, in a study on an assemblage of host fish in the Igarapé Fortaleza basin, a tributary of the Amazon River in Brazil, the prevalence of endohelminths in detritivorous hosts was reported to be lower than in carnivorous, omnivorous and piscivorous hosts, while the intensity and abundance were higher in carnivorous and omnivorous hosts (Baia et al., 2018). It has also been shown that the richness of endoparasite species in carnivorous fish is higher than in herbivorous fish (Simková et al., 2001). Choudhury & Dick (2000) reported that herbivorous fish had poorer endohelminth communities than benthivorous fish that feed on invertebrates. Moreover, the endohelminth communities in planktivorous and benthivorous fish were qualitatively different, since in planktivorous hosts the community was dominated by cestode species and in benthivorous fish by trematode species. These patterns were correlated with differences in the transmission strategies of these parasite taxa. Additionally, these authors found that carnivorous fish with diets based on invertebrates and fish and omnivorous fish with diets containing only invertebrates had higher richness of endohelminth communities than herbivorous and planktivorous fish. Therefore, these results demonstrate that omnivorous diet was a factor that was as determinant for accumulation of endoparasites as was accumulation through predation.

In the host fish analyzed, the nematode *P.* (S.) *inopinatus* was found in the adult stage. Since host-parasite interactions depend on mechanisms that provide parasites with a greater chance of completing their life cycle, the adaptations of generalist parasites such as *P.* (*S*.) *inopinatus* are not necessarily related to co-evolutionary processes in the parasites and hosts. They may also be related to low specificity to the intermediate hosts that are prey for the definitive hosts, i.e. the fish. Hence, in this trophic transmission system, *P.* (*S.*) *inopinatus* may have a greater chance of reaching its definitive hosts, because of its wide distribution in different host fish species (Bellay et al., 2013).

Although the life cycle of *P.* (*S.*) *inopinatus* remains unknown, studies on *Procamallanus* species have shown that different copepod species are the intermediate hosts for these camallanid nematodes. After ingestion by copepods, the first-stage larvae of *Procamallanus* spp. penetrate the hemocele of these intermediate hosts (e.g. *Mesocyclops* spp. and *Diaptomus* spp.) and reach the infective stage. Fish (the definitive hosts) acquire the infection from camallanids through feeding on copepods containing the infective stages of these camallanids (Pereira et al., 1936; De, 1995; Moravec et al., 1995; De & Maity, 2000).

In Brazil, it has been reported that the biological cycle of *Procamallanus* (*Spirocamallanus*) *hilarii* Vaz & Pereira, 1934 [= *Procamallanus* (*Spirocamallanus*) *cearensis* Pereira, Dias & Azevedo, 1936] takes place in the copepods *Diaptomus* Herbst, 1955, which are the intermediate hosts, and in *Astyanax lacustris* Lütken, 1875, which are the definitive hosts (Pereira et al., 1936). Therefore, it is possible to suggest that in the life cycle of *P. (S.) inopinatus*, the newly-hatched larvae are released into the feces of the definitive hosts (fish) in the water and are also ingested by copepod species (e.g. *Diaptomus* spp.), the intermediate hosts of this nematode species. Lastly, the larvae of this nematode invade the body cavity of the copepods and develop to reach the infective stages that are ingested by a fish, thereby reaching the adult stage. Nevertheless, detailed knowledge of this association between *P*. (*S.*) *inopinatus* and its intermediate hosts will only become possible when its biological cycle has been completely studied in the laboratory.

Geographic distribution pattern in freshwater fish in Brazil

In ecosystems, because of the potential role played by parasites, identification of critical points with high parasite diversity and areas of relatively low diversity is crucial for understanding the functioning of the biosphere. However, parasite biodiversity estimates for any geographic area can only be carried out after the parasite species and their host species are well known (Luque & Poulin, 2007).

As knowledge about parasite biodiversity increases, efforts towards mapping this diversity of parasites can also be developed. The aim will be to identify potential geographic hotspots for emerging diseases and to predict and mitigate the impacts of climate change on pathogen distribution. However, data limitations impede establishment of global biodiversity distribution maps for most parasite taxa (Jorge & Poulin, 2018). Thus, currently, geographic distribution is one of the several universal issues relating to the processes and patterns of the parasite species harbored by freshwater fish harbor that need to be addressed. This has already been done in some locations and regions: for instance, in the Canary Islands (Thorsen et al., 2000), Mexico (Pérez-Ponce De León & Choudhury, 2005), Asia, Africa and South America (Pariselle et al., 2011) and Europe (Thieltges et al., 2011).

González et al. (2006) investigated the geographic distribution of endohelminths in *Sebastes capensis* Gmelin, 1789, from the coasts of Peru, Chile, Argentina and South Africa. They concluded that the geographic patterns were a consequence of the biogeographic patterns exhibited by their prey, which were used as intermediate hosts. This was a determining factor in the structure of endohelminth communities throughout their distribution range. The specificity of hosts therefore strongly influences the biogeography of parasites, since there is close relationship between the hosts, as well as between them and the environment. These are determining factors in the characteristics of the regional fauna of endohelminth species (Thieltges et al., 2011; Salgado-Maldonado et al., 2016).

In Brazil, the geographic patterns of parasite distribution in freshwater fish have been little reported. Tavares-Dias et al. (2015) studied these patterns in relation to species of Crustacea in 119 hosts within 27 families in eight orders, distributed across the different Brazilian hydrographic basins. Pinheiro et al. (2019) reported on the geographic patterns of larvae of *Contracaecum* Railliet & Henry, 1912, among 140 fish species within 49 families in 16 orders. The geographic patterns of parasite species among 45 Loricariidae species were studied by Borges et al. (2018). Valladão et al. (2019) reported on the geographic patterns of *Neoechinorhynchus buttnerae* Golvan, 1956, in *C. macropomum*, across this country. Information of this nature is useful for gaining greater understanding of the biodiversity and geographic distribution patterns of host-parasite systems. However, many questions remain to be answered regarding the distribution patterns of the most abundant Nematoda taxa in fish, across Brazil.

The distribution patterns of endohelminth species result from several factors. In addition to physiographic changes and differences in habitats, the biology of these parasites can vary between species. Most parasites are closely associated with their hosts, through sharing their co-evolution history, and their biogeographic distribution generally reflects that of their hosts. Ecological factors also influence the parasite’s biogeography, mostly regarding the local diversity of the parasite communities. However, the co-evolution link between parasites and their hosts is a more important factor in this relationship (Poulin & Mouillot, 2003). Therefore, among biological factors, host specificity is also a determining factor for endohelminth species, which strongly influences the characteristics of the regional endohelminth fauna.

Given that *P*. (*S*.) *inopinatus* has low specificity to hosts and high adaptability to different freshwater habitats in Brazil, this nematode species has wide geographic distribution in the basin systems of the Amazon River, Paraná River, São Francisco River and North, South and East Atlantic (Figure 5). These results also suggest that the intermediate hosts of *P.* (*S*.) *inopinatus* have wide geographic distribution in these hydrographic basin systems. This is a prerequisite for establishment of this parasitic nematode in different environments. Parasites like *P.* (*S*.) *inopinatus*, which infect a wide range of host fish in the hydrographic basin systems of Brazil, are strongly resistant to environmental changes, which thus increases their chances of expanding their geographic distribution and use of resources (Poulin, 1992; Blasco-Costa et al., 2015). Furthermore, we have identified areas with the greatest deficit in sample effort for description in occurrence of *P.* (*S.*) *inopinatus*; hence, such information provides clear guides for a better allocation of future research effort this toward *P.* (*S*.) *inopinatus* prospecting across Brazilian basins.

In conclusion, the present study on *P.* (*S*.) *inopinatus* supports the understanding of the patterns and processes of infections caused by this endoparasite that is widely distributed in Brazilian host fish populations. It therefore fills a gap in the knowledge of this nematode species. In the parasite-host interaction network, there was no link with any trophic level occupied by the host fish. Thus, analysis on greater quantities of samples is required in order to reach more conclusive results in this regard. *Procamallanus* (*S.*) *inopinatus* uses a wide variety of fish as definitive hosts to complete its biological cycle, and thus has a wide distribution in the hydrographic ecosystems of Brazil. However, in the basin systems of the Tocantins River and Uruguay River, the lack of occurrence of *P*. (*S*.) *inopinatus* was caused by the lack of studies. Therefore, a concentrated and focused sampling effort is required in order to elicit information that has been neglected. Hence, we believe that the diversity of host fish used by *P.* (*S*.) *inopinatus* is much greater and with wider geographic range than what is documented here. Lastly, since this information is needed in order to understand the geographic distribution capacity of *P*. (*S*.) *inopinatus* and the parasite-host relationship, we highlight that further studies are required, for greater knowledge about this nematode species in Brazilian fish to be obtained.

Acknowledgements

The authors thank the National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq), Brazil for the research productivity grant to M. Tavares-Dias (Grant N^{o} 303013/2015-0).

References

Agostinho AA, Thomaz SM, Gomes LC. Conservação da biodiversidade em águas continentais do Brasil. *Megadiversidade* 2005; 1(1): 70-78.

Almeida-Berto MFC, Monteiro CMM, Brasil-Sato MC. Parasitic helminths of the non-native serrasalmid fish *Metynnis lippincottianus* from the Três Marias Reservoir, southeast Brazil. *Rev Bras Parasitol Vet* 2018; 27(3): 289-294. http://dx.doi.org/10.1590/s1984-296120180040. PMid:30133590.

Agência Nacional de Águas - ANA. [Online]. 2020. [cited 2020 June 4]. Available from: http://hidroweb.ana.gov.br/ HidroWeb .asp? TocItem = 4100

Azevedo RK, Abdallah VD, Luque JL. Acanthocephala, Annelida, Arthropoda, Myxozoa, Nematoda and Platyhelminthes parasites of fishes from the Guandu river, Rio de Janeiro, Brazil. *Check List* 2010; 6(4): 659-667. http://dx.doi.org/10.15560/6.4.659.

Baia RRJ, Florentino AC, Silva LMA, Tavares-Dias M. Patterns of the parasite communities in a fish assemblage of a river in the Brazilian Amazon region. *Acta Parasitol* 2018; 63(2): 304-316. http://dx.doi.org/10.1515/ap-2018-0035. PMid:29654690.

Barletta M, Jaureguizar AJ, Baigun C, Fontoura NF, Agostinho AA, Almeida-Val VMF, et al. Fish and aquatic habitat conservation in South America: a continental overview with emphasis on Neotropical systems. *J Fish Biol* 2010; 76(9): 2118-2176. http://dx.doi.org/10.1111/j.1095-8649.2010.02684.x. PMid:20557657.

Bellay S, Oliveira EF, Almeida-Neto M, Lima DP Jr, Takemoto RM, Luque JL. Developmental stage of parasites influences the structure of fish-parasite networks. *PLoS One* 2013; 8(10): e75710. http://dx.doi.org/10.1371/journal.pone.0075710. PMid:24124506.

Bhuiyan AI, Bushra J, Ghani O. Abundance and distribution of endoparasitic helminths in *Anabas testudineus* (Bloch, 1792) from a polluted beel of Bangladesh. *Bangladesh J Zool* 2014; 42(1): 1-10. http://dx.doi.org/10.3329/bjz.v42i1.23331.

Blasco-Costa I, Rouco C, Poulin R. Biogeography of parasitism in freshwater fish: spatial patterns in hot spots of infection. *Ecography* 2015; 38(3): 301-310. http://dx.doi.org/10.1111/ecog.01020.

Bonato KO, Burress ED, Fialho CB. Dietary differentiation in relation to mouth and tooth morphology of a neotropical characid fish community. *Zool Anz* 2017; 267: 31-40. http://dx.doi.org/10.1016/j.jcz.2017.01.003.

Borges WF, Oliveira MSB, Santos GG, Tavares-Dias M. Parasites in Loricariidae from Brazil: checklist and new records for fish from the Brazilian Amazon. *Acta Sci Biol Sci* 2018; 40(1): e40621. http://dx.doi.org/10.4025/actascibiolsci.v40i1.40621.

Brasil. Ministério do Meio Ambiente, Secretaria de Recursos Hídricos – MMA. *Plano Nacional de Recursos Hídricos. Panorama e estado dos recursos hídricos do Brasil*. Brasília: MMA; 2006.

Bush AO, Lafferty KD, Lotz JM, Shostak AW. Parasitology meets ecology on its own terms: margolis et al. revisited. *J Parasitol* 1997; 83(4): 575-583. http://dx.doi.org/10.2307/3284227. PMid:9267395.

Carvalho TP, Albert JS. The Amazon-Paraguay divide. In: Albert JS, Reis RE, editors. *Historical biogeography of Neotropical freshwater fishes*. London: University of California Press; 2011. p. 193-202. http://dx.doi.org/10.1525/california/9780520268685.003.0011.

Chemes SB, Takemoto RM. Diversity of parasites from middle Paraná system freshwater fishes, Argentina. *Int J Biodivers Conserv* 2011; 3(7): 249-266.

Chemes SB, Takemoto RM. Nuevos registros de helmintos parásitos de peces Pimelodidae, en el sistema Paraná medio (Argentina). *Neotrop Helminthol* 2020; 14(1): 19-34. http://dx.doi.org/10.24039/rnh2020141611.

Choudhury A, Dick TA. Richness and diversity of helminth communities in tropical freshwater fishes: empirical evidence. *J Biogeogr* 2000; 27(4): 935-956. http://dx.doi.org/10.1046/j.1365-2699.2000.00450.x.

De NC, Maity RN. Development of *Procamallanus saccobranchi* (Nematoda: Camallanidae), a parasite of a freshwater fish in India. *Folia Parasitol (Praha)* 2000; 47(3): 216-226. http://dx.doi.org/10.14411/fp.2000.040. PMid:11104150.

De NC. On the development and life cycle of *Spirocamallanus mysti* (Nematoda: camalanidae). *Folia Parasitol (Praha)* 1995; 42(2): 135-142.

Dormann CF, Gruber B, Fründ J. Introducing the bipartite package: analysing ecological networks. *R News* 2008; 8(2): 8-11.

Dormann CF. How to be a specialist? Quantifying specialisation in pollination networks. *New Biol* 2011; 1(1): 1-20.

Ferreira MM, Passador RJ, Tavares-Dias M. Community ecology of parasites in four species of *Corydoras* (Callichthyidae), ornamental fish endemic to the eastern Amazon (Brazil). *An Acad Bras Cienc* 2019; 91(1): e20170926. http://dx.doi.org/10.1590/0001-3765201920170926. PMid:30785499.

Froese R, Pauly D. *FishBase. Version (12/2019)* [online]. USA: FishBase; 2019 [cited 2020 June 1]. Available from: www.fishbase.org

Fujimoto RY, Couto MVS, Sousa NCS, Madi RR, Eiras JC, Martins ML. Seasonality of *Procamallanus* (*Spirocamallanus*) *inopinatus* (Nematoda: Camallanidae) infection in *Bryconops melanurus* (Characiformes: Iguanodectidae). *Bol Inst Pesca* 2018; 44(4): 331-338. http://dx.doi.org/10.20950/1678-2305.2018.44.4.334.

Gaines APL, Lozano LES, Viana GM, Monteiro PC, Araújo CSO. Tissue changes in the gut of *Arapaima gigas* (Schinz, 1822), infected by the nematode *Spirocamallanus inopinatus* (Travassos, 1929). *Neotrop Helminthol* 2012; 6(2): 147-157.

Geets A, Ollevier F. Endoparasitic helminths of the whitespotted rabbitfish (*Siganus sutor* (Valenciennes, 1835) of the Kenyan coast: distribution within the host population and microhabitat use. *Belg J Zool* 1996; 126: 21-36.

Gonçalves RA, Oliveira MSB, Neves LR, Tavares-Dias M. Seasonal pattern in parasite infracommunities of *Hoplerythrinus unitaeniatus* and *Hoplias malabaricus* (Actinopterygii: Erythrinidae) from the Brazilian Amazon. *Acta Parasitol* 2016; 61(1): 119-129. http://dx.doi.org/10.1515/ap-2016-0016. PMid:26751882.

González MT, Barrientos C, Moreno CA. Biogeographical patterns in endoparasite communities of a marine fish (*Sebastes capensis* Gmelin) with extended range in the southern hemisphere. *J Biogeogr* 2006; 33(6): 1086-1095. http://dx.doi.org/10.1111/j.1365-2699.2006.01488.x.

Hamann MI. Population biology of *Spirocamallanus inopinatus* (Travassos, Artigas et Pereira, 1928) (Nematoda, Camallanidae) in *Serrasalmus spilopleura* Kner, 1860 (Pisces, Characidae) from Corrientes, Argentina. *Res Rev Parasitol* 1999; 59(1-2): 1-6.

Hoshino MDFG, Neves LR, Tavares-Dias M. Parasite communities of the predatory fish, *Acestrorhynchus falcatus* and *Acestrorhynchus falcirostris*, living in sympatry in Brazilian Amazon. *Rev Bras Parasitol Vet* 2016; 25(2): 207-216. http://dx.doi.org/10.1590/S1984-29612016038. PMid:27334822.

Jorge F, Poulin R. Poor geographical match between the distributions of host diversity and parasite discovery effort. *Proc Biol Sci* 2018; 285(1879): 20180072. http://dx.doi.org/10.1098/rspb.2018.0072. PMid:29848643.

Junk WJ. Current state of knowledge regarding South America wetlands and their future under global climate change. *Aquat Sci* 2013; 75(1): 113-131. http://dx.doi.org/10.1007/s00027-012-0253-8.

Kohn A, Moravec F, Cohen SC, Canzi C, Takemoto RM, Fernandes BMM. Helminths of freshwater fishes in the reservoir of the Hydroelectric Power Station of Itaipu, Paraná, Brazil. *Check List* 2011; 7(5): 681-690. http://dx.doi.org/10.15560/7.5.681.

Krebs CJ. *Ecological methodology*. New York: Addison-Wesley Educational Publishers; 1999.

Luque JL, Aguiar JC, Vieira FM, Gibson DI, Santos CP. Checklist of Nematoda associated with the fishes of Brazil. *Zootaxa* 2011; 3082(1): 1-88. http://dx.doi.org/10.11646/zootaxa.3082.1.1.

Luque JL, Pereira FB, Alves PV, Oliva ME, Timi JT. Helminth parasites of South American fishes: current status and characterization as a model for studies of biodiversity. *J Helminthol* 2017; 91(2): 150-164. http://dx.doi.org/10.1017/S0022149X16000717. PMid:27855726.

Luque JL, Poulin R. Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology* 2007; 134(Pt 6): 865-878. http://dx.doi.org/10.1017/S0031182007002272. PMid:17291392.

Moravec F, Mendonza- Franco E, Vargas-Vázquez J, Vivas-Rodríguez C. Studies on the development of *Procamallanus* (*Spirocamallanus*) *rebecae* (Nematoda: Camallanidae), a parasite of cichlid fishes in México. *Folia Parasitol (Praha)* 1995; 42(4): 281-292.

Moravec F, Prouza A, Royero R. Some nematodes of freshwater fishes in Venezuela. *Folia Parasitol (Praha)* 1997; 44(1): 33-47. PMid:9188173.

Moravec F. *Nematodes of freshwater fishes of the Neotropical region*. Prague: Academia; 1998.

Negreiros LP, Florentino AC, Pereira BF, Tavares-Dias M. Long-term temporal variation in the parasite community structure of metazoans of *Pimelodus blochii* (Pimelodidae), a catfish from the Brazilian Amazon. *Parasitol Res* 2019; 118(12): 3337-3347. http://dx.doi.org/10.1007/s00436-019-06480-x. PMid:31664517.

Oksanen JF, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, et al. 2017. *Vegan: community ecology package. R Package version 2.4-3* [online]. USA: Vegan Development Team; 2017 [cited 2017 July 10]. Available from: https://CRAN.R-project. org/package=vegan

Pariselle A, Boeger WA, Snoeks J, Bilong Bilong CF, Morand S, Vanhove MP. The monogenean parasite fauna of cichlids: a potential tool for host biogeography. *Int J Evol Biol* 2011; 471480: 471480. http://dx.doi.org/10.4061/2011/471480. PMid:21869935.

Pereira C, Dias MV, Azevedo P. Biologia do nematoide "*Procamallanus cearensis*" n. sp. *Arch Inst Biol* 1936; 7: 209-226.

Pérez-Ponce de León G, Choudhury A. Biogeography of helminth parasites of freshwater fishes in Mexico: the search for patterns and processes. *J Biogeogr* 2005; 32(4): 645-659. http://dx.doi.org/10.1111/j.1365-2699.2005.01218.x.

Pinheiro RHS, Furtado AP, Santos JN, Giese EG. *Contracaecum* larvae: morphological and morphometric retrospective analysis, biogeography and zoonotic risk in the Amazon. *Rev Bras Parasitol Vet* 2019; 28(1): 12-32. http://dx.doi.org/10.1590/s1984-29612019002. PMid:30892463.

Poulin R, Leung TLF. Body size, trophic level, and the use of fish as transmission routes by parasites. *Oecologia* 2011; 166(3): 731-738. http://dx.doi.org/10.1007/s00442-011-1906-3. PMid:21249395.

Poulin R, Mouillot D. Host introductions and the geography of parasite taxonomic diversity. *J Biogeogr* 2003; 30(6): 837-845. http://dx.doi.org/10.1046/j.1365-2699.2003.00868.x.

Poulin R. Determinants of host-specificity in parasites of freshwater fishes. *Int J Parasitol* 1992; 22(6): 753-758. http://dx.doi.org/10.1016/0020-7519(92)90124-4. PMid:1428509.

R Development Core Team. *R: a language and environment for statistical computing* [online]. Vienna: R Foundation for Statistical Computing; 2017 [cited 2019 Sept 10]. Available from: http://www.R-project.org/

Ribeiro TS, Ghisi NC, Prioli AJ, Oliveira EC, Takemoto RM. Diversity of nematodes of red-tail-lambari *Astyanax* aff. *paranae* (Teleostei: Characidae) from polluted sites of a tropical river system. *Neotrop Helminthol* 2013; 7(2): 271-281.

Rivadeneyra NLS, Mertins O, Cuadros RC, Malta JCO, de Matos LV, Mathews PD. Histopathology associated with infection by *Procamallanus* (*Spirocamallanus*) *inopinatus* (Nematoda) in farmed *Brycon cephalus* (Characiformes) from Peru: a potential fish health problem. *Aquacult Int* 2020; 28(2): 449-461. http://dx.doi.org/10.1007/s10499-019-00474-3.

Salgado-Maldonado G, Mendoza-Franco EF, Caspeta-Mandujano JM, Ramírez-Martínez C. Aggregation and negative interactions in low-diversity and unsaturated monogenean (Platyhelminthes) communities in *Astyanax aeneus* (Teleostei) populations in a Neotropical river of México. *Int J Parasitol Parasites Wildl* 2019; 8: 203-215. http://dx.doi.org/10.1016/j.ijppaw.2019.02.005. PMid:30891400.

Salgado-Maldonado G, Novelo-Turcotte MT, Caspeta-Mandujano JM, Vazquez-Hurtado G, Quiroz-Martínez B, Mercado-Silva N, et al. Host specificity and the structure of helminth parasite communities of fishes in a Neotropical river in Mexico. *Parasite* 2016; 23: 61. http://dx.doi.org/10.1051/parasite/2016073. PMid:28004635.

Simková A, Morand S, Matejusová I, Jurajda P, Gelnar M. Local and regional influences on patterns of parasite species richness of central European fishes. *Biodivers Conserv* 2001; 10(4): 511-525. http://dx.doi.org/10.1023/A:1016658427730.

Takemoto RM, Pavanelli GC, Lizama MAP, Lacerda ACF, Yamada FH, Moreira LHA, et al. Diversity of parasites of fish from the upper Paraná River floodplain, Brazil. *Braz J Biol* 2009;69(2 Suppl.): 691-705. http://dx.doi.org/10.1590/S1519-69842009000300023. PMid:19738975.

Tavares-Dias M, Dias-Júnior MBF, Florentino AC, Silva LMA, Cunha AC. Distribution pattern of crustacean ectoparasites of freshwater fish from Brazil. *Rev Bras Parasitol Vet* 2015; 24(2): 136-147. http://dx.doi.org/10.1590/S1984-29612015036. PMid:26154954.

Thieltges DW, Hof C, Borregaard MK, Dehling DM, Brandle M, Brandl R, et al. Range size patterns in European freshwater trematodes. *Ecography* 2011; 34(6): 982-989. https://doi.org/10.1111/j.1600-0587.2010.06268.x.

Thorsen DH, Mille KJ, Van Tassell JL, Hajagos JG. Infestation of the parrotfish *Sparisoma cretense* (Scaridae) by the fish louse *Anilocra physodes* (Isopoda: Cymothoidae) in the Canary Islands. *Cybium* 2000; 24(1): 45-59.

Timi JT, Rossin MA, Alarcos AJ, Braicovich PE, Cantatore DMP, Lanfranchi AL. Fish trophic level and the similarity of non-specific larval parasite assemblages. *Int J Parasitol* 2011; 41(3-4): 309-316. http://dx.doi.org/10.1016/j.ijpara.2010.10.002. PMid:21081133.

Travassos L, Artigas P, Pereira C. Fauna helmintológica dos peixes de água doce do Brasil. *Arq Inst Biol (Sao Paulo)* 1928; 1: 5-82.

Val AL. Fishes of the Amazon: diversity and beyond. *An Acad Bras Cienc* 2019; 91(Suppl. 3): e20190260. http://dx.doi.org/10.1590/0001-3765201920190260. PMid:31166477.

Valladão GMR, Gallani SU, Jerônimo GT, Seixas AT. Challenges in the control of acanthocephalosis in aquaculture: special emphasis on *Neoechinorhynchus buttnerae. Rev Aquacult* 2019; 12(3): 1360-1372. http://dx.doi.org/10.1111/raq.12386.

Vicente JJ, Rodrigues HO, Gomes DC. Nematóides do Brasil. 1ª parte: nematóides de peixes. *Atas Soc Biol* 1985; 25: 1-79.

Zar JH. *Biostatistical analysis*. 5th ed. New Jersey: Prentice Hall; 2010.

Supplementary Material

Supplementary material accompanies this paper.

Table S1. Collection of data on *Procamallanus (Spirocamallanus) inopinatus*.

This material is available as part of the online article from https://www.scielo.br/rbpv e conferir se a página da rbpv na scielo abre corretamente