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Distribution pattern of crustacean ectoparasites of freshwater fish from Brazil

Padrão de distribuição de crustáceos ectoparasitos de peixes de água doce do Brasil

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Abstract

The purpose of this study was to use the informations relating to parasite crustaceans species that was published over the course of one century (1913 to 2013), in order to search for infestation and distribution patterns among these ectoparasites in Brazilian freshwater fish species. This search was carried out on 445 samples of 119 host fish of 27 families within the orders Characiformes, Perciformes, Clupeiformes, Mugiliformes, Osteoglossiformes, Symbranchiformes, Tetraodontiformes and Siluriformes from various regions of Brazil. We organized different host-parasite systems into matrices grouping species at different taxonomic and infestation levels and according to host parameters. Five families of parasites (Ergasilidae, Argulidae, Lernaecidae, Lernaecopodidae and Cymothoidae) distributed into 76 species of 27 genera were analyzed in the host samples, which presented dominance of Ergasilidae species, mainly from the genus *Ergasilus*. Some crustaceans are host and site-specific, especially in relation to fish in particular habitats and lifestyles (e.g. *Perulernaea gamitanae*, *Anphira branchialis* and *Riggia paranensis*), while other parasites frequently have no preference (e.g. *Lernaea cyprinacea* and *Braga patagonica*). We found broadly similar distribution patterns for some crustacean species among the different localities, whereas other species showed well-defined geographical patterns, and these findings were discussed.

Keywords: Amazon, Branchiura, Copepoda, host, Isopoda, parasite.

Resumo

O objetivo deste estudo foi utilizar as informações relacionadas com espécies de crustáceos parasitas, que foram publicados durante um século (1913 a 2013), para procurar padrões de infestação e distribuição desses ectoparasitos em espécies de peixes de água doce do Brasil. Esta pesquisa foi realizada em 445 amostras de 119 peixes hospedeiros de 27 famílias de Characiformes, Perciformes, Clupeiformes, Mugiliformes, Osteoglossiformes, Symbranchiformes, Tetraodontiformes e Siluriformes das diversas regiões do Brasil. Foram organizados em matrizes de agrupamento diferentes sistemas parasito-hospedeiros em diferentes níveis taxonômicos, níveis de infestação e parâmetros dos hospedeiros. Cinco famílias (Ergasilidae, Argulidae, Lernaecidae, Lernaecopodidae e Cymothoidae) de parasitos, distribuídos em 76 espécies de 27 gêneros, foram analisados em amostras dos hospedeiros, que apresentaram dominância de espécies Ergasilidae principalmente do gênero *Ergasilus*. Alguns crustáceos são hospedeiros e sítios-específicos no hospedeiro, especialmente peixes de determinados hábitat e estilo de vida (por exemplo, *Perulernaea gamitanae*, *Anphira branchialis* e *Riggia paranensis*), enquanto outros parasitos não têm qualquer preferência (por exemplo, *Lernaea cyprinacea* e *Braga patagonica*). Foram encontrados padrões muito semelhantes na distribuição de algumas espécies de crustáceos entre as diferentes localidades, enquanto outras espécies mostraram um padrão geográfico bem definido, o que foi discutido aqui.

Palavras-chaves: Amazônia, Branchiura, Copepoda, hospedeiro, Isopoda, parasitas.

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Introduction

Species of Crustacea Brünich, 1722, present wide-ranging morphophysiological variations, which provide this group with presence in diverse habitats with a variety of lifestyles, from planktonic species to parasites (MARTIN & DAVIS, 2001; BOXSHALL & DEFAYE, 2008; WILSON, 2008; LUQUE et al., 2013). However, the parasitic species need a host during at least one phase of their life cycle. Parasitic crustaceans present diversity estimated as around 5,400 species (POULIN & MORAND, 2004; LUQUE et al., 2013), comprising species of Branchiura Thorell, 1818; Copepoda Milne-Edwards, 1940; and Isopoda Latreille, 1871. Many representative species of these three groups parasitize fish in freshwater, brackish and marine environments, and most of them are ectoparasites (THATCHER, 2006; LUQUE & POULIN, 2007).

Ectoparasitic crustaceans attack the gills, oral cavity, nostrils and/or integument of fish (FRYER, 1968; DOUELLOU & ERLWANGER, 1994; CARVALHO et al., 2004; TAVARES-DIAS et al., 2014), which may give rise to a variety of damage to their hosts. Some species of these parasites may have both direct and indirect effects on fish populations, especially through causing reductions in the hosts' growth and reproduction rates, along with mortality among these fish. These factors may lead to significant economic losses for fisheries and aquaculture (FRYER, 1968; POLY, 2008; TAVARES-DIAS et al., 2014). Consequently, parasitism by crustacean species has been recognized as a significant factor that may affect wild natural fish and farmed fish populations (CARVALHO et al., 2004; THATCHER, 2006; TAVARES-DIAS et al., 2011, 2014).

In South America, around 744 species of copepods, 187 species of isopods and 133 species of branchiurians are known to parasitize marine and freshwater fish (LUQUE & POULIN, 2007). This region includes the Amazon River basin, which is one of the most extensive River basins in the world, occupying 40.2% of South America and partially encompassing the territories of eight countries. The Amazon River begins as streams in the Andes Mountains in Peru and flows into the Atlantic Ocean (ANA, 2014). Thus, the Amazon River basin and other major Rivers of South America are significant hot spots for the fish-parasite group of crustaceans (LUQUE & POULIN, 2007; WILSON, 2008), thus reflecting the diversity of their hosts in this region.

In Brazil, crustacean species within the taxa Isopoda, Branchiura and Copepoda that are found in freshwater fish have been listed over recent decades (BRASIL-LIMA & BARROS, 1998; MALTA, 1998; MALTA & VARELLA, 1998; THATCHER, 2006; LUQUE & TAVARES, 2007; EIRAS et al., 2011). Recently, Luque et al. (2013) provided a checklist of the brackish, marine and freshwater crustaceans that had been described up to early 2013, which include 53 species of Isopoda, 29 of Branchiura and 207 of Copepoda that showed associations with environments or fish species. Since then, further species have been recorded, thereby providing more evidence of the richness of the parasitic crustacean fauna of this large Neotropical country, which presents more than 4,000 freshwater fish species distributed in more than 50 families (EIRAS et al., 2011; FROESE & PAULY, 2014), occurring in the systems between the major watersheds.

Despite this known diversity of parasitic crustaceans in Brazil, their distribution has been little addressed. Thus, this paper had the aim of characterizing the distribution of crustaceans associated with freshwater fish in Brazil. This study is of great importance and interest, given that better knowledge of the diversity and richness of crustacean species in this particular region could also contribute towards worldwide estimates for the diversity and distribution of parasitic crustaceans of freshwater fish, which have been little addressed in comparison with marine crustaceans. From the viewpoint of biogeography, this study is also important because it records what is known on the distribution of these ectoparasites in different fish species, because many of them have been translocated inside in Brazil, and also exported to different places worldwide.

Materials and Methods

A dataset of crustacean species parasitizing freshwater fish populations in Brazil was compiled using taxonomic descriptions of species and surveys on occurrences of these parasites published between 1913 and 2013. These data comprised surveys on parasitic crustaceans of native fish in rivers, lakes, lagoons and reservoirs distributed across the Brazil, except for 13 samples of cyprinids (*Cyprinus carpio*, *Hypophthalmichthys molitrix* and *Ctenopharyngodon idella*) and 11 samples of cichlids (*Oreochromis niloticus* and *Tilapia rendalli*), which are non-native fish present in Brazil. All of these surveys were chosen because they represent the various ecosystems found in Brazil and thus might aid in answering the primary questions of this study regarding the distribution of parasitic crustacean species in native fish. We used sample data on prevalence, intensity and abundance obtained during different seasons.

In addition, given that in some regions fish farming is linked to natural water bodies (rivers, lakes, streams and floodplains), and because non-native fish species have been translocated between the regions of this country, samples of farmed fish were also included. It was thought that these data might answer the secondary question on the distribution of exotic parasites in the native fish and of native parasites in exotic fish. Non-statistical comparison was performed between the parasite samples of wild fish (N = 387) and aquaculture fish (N = 58), since most of the samples were from wild fish populations.

Each sampling unit was defined as a number of individuals parasitized by a crustacean species at a certain location and time. Some of the information used in the sample included data on more than one host species. The ensuring data were organized in a data frame (extension ".txt") with a listing of the following variables: (i) number of fish examined, (ii) number of fish parasitized, (iii) parasite species, (iv) infection site, (v) mean prevalence, (vi) mean intensity and (vii) mean abundance; along with categorical factors such as: (i) host fish species, (ii) sample collection locality and (iii) mean length of the hosts. These variables and factors were analyzed with the aim of producing a classification according to groups of parasites, using R with "package bipartite" (DORMANN et al., 2008; DORMANN, 2011; R DEVELOPMENT CORE TEAM, 2014) or similarities for the variables. Pearson's correlation coefficient

(r_s) was also used with data transformation (\log_{10}). Studies with inconsistent data or outliers relating to the host and/or parasite (i.e. parasite infestation site and/or host collection locality) were not included in any of the analyses. To draw up a map with the geographical distribution, shapes that took into consideration the seven largest continental hydrographic basin systems of Brazil were used (<http://hidroweb.ana.gov.br/HidroWeb.asp?TocItem=4100>). The mean variance ratio was also calculated in order to determine the aggregation index (POULIN, 2013) in samples that contained information on mean abundance, number of hosts examined and number of hosts parasitized. Thus, one of the criteria for eliminating some of the samples that were excluded was the absence of data suitable for assessing this index. The ecological terms used were those recommended by Rohde et al. (1995) and Bush et al. (1997). The systematic classification used for the crustaceans was as described by Martin & Davis (2001) and Boxshall & Halsey (2004).

Results

A total of 445 samples of species of Copepoda, Branchiura and Isopoda (Table 1) parasitizing 119 fish of different families distributed into 35 host genera were used. A total of 76 species of parasite crustaceans, among Branchiura, Copepoda and Isopoda were analyzed (Figure 1). Copepoda was the most prevalent taxon among the samples, due to the dominance of species of the families Ergasilidae von Nordmann, 1832 and Lernaeidae Cobbold, 1879. However, the parasite family with greatest richness of species was Ergasilidae, followed by Argulidae Leach, 1819, while Lernaeopodidae Milne-Edwards, 1840 was the family with lowest richness of species. The richness of Isopoda species was also low, and these were strictly concentrated in the family Cymothoidea Leach, 1814 (Table 1). Among the hosts of the different families, the greatest number of parasite-host

Table 1. Number of Crustacea parasites of the network in 445 samples of freshwater fishes from Brazil.

Groups	Parasites samples	Parasites family	Parasites samples	Parasites species number
Branchiura	179	Argulidae	179	15
Copepoda	237	Ergasilidae	140	44
	-	Lernaeidae	94	8
	-	Lernaeopodidae	1	1
Isopoda	29	Cymothoidea	29	8

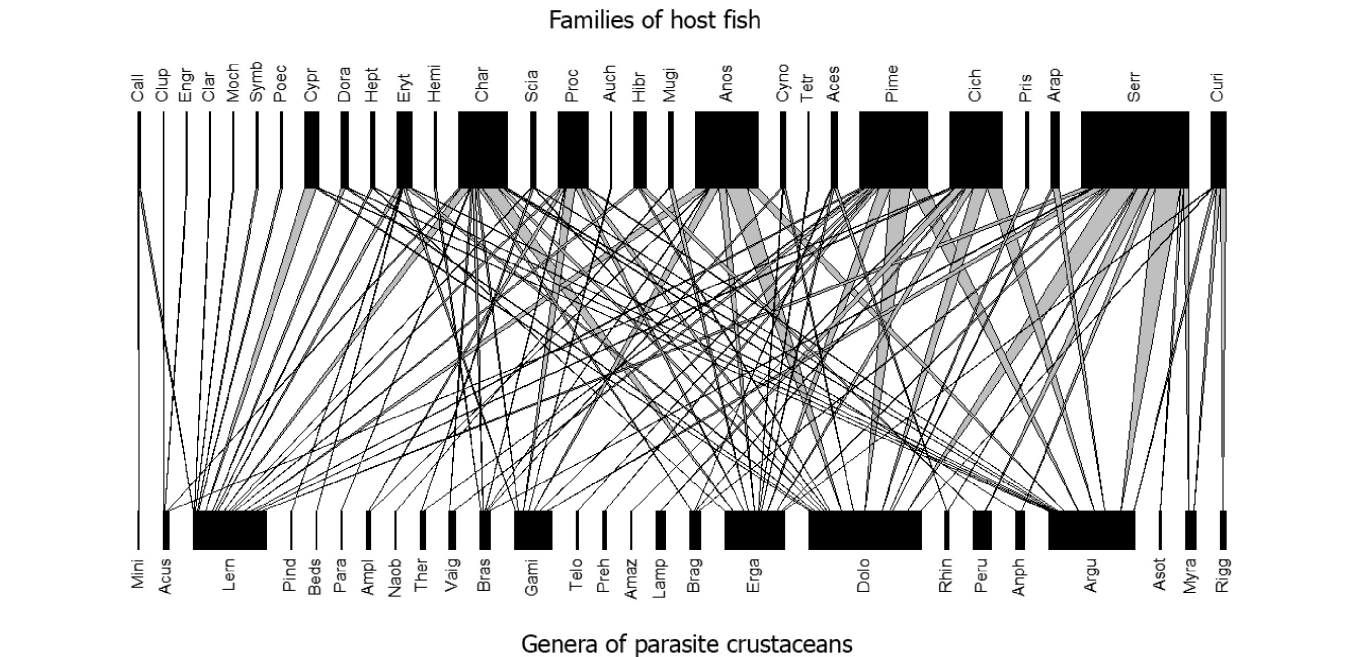


Figure 1. Network of interactions between families of host fish (N= 344) and Crustacea genera from Brazil. Calli: Callichthyidae, Clup: Clupeidae, Engr: Engraulidae, Poec: Poeciliidae, Moch: Mochokidae, Symb: Symbranchidae, Clar: Clariidae, Cypr: Cyprinidae, Dora: Doradidae, Hept: Heptapteridae, Eryt: Erythrinidae, Hemi: Hemiodontidae, Char: Characidae, Scia: Sciaenidae, Proc: Prochilodontidae, Auch: Auchenipteridae, Hibr: Híbridos, Mugi: Mugilidae, Anos: Anostomidae, Cyno: Cynodontidae, Tetr: Tetraodontidae, Aces: Acestrorhynchidae, Pime: Pimelodidae, Cich: Cichlidae, Pris: Pristigasteridae, Arap: Arapaimidae, Serr: Serrasalminae, Curi: Curimatidae. Mini: *Minilernaea*, Acus: *Acusicola*, Lern: *Lernaea*, Beds: *Bedsylernaea*, Pind: *Pindapixara*, Para: *Paracymothoa*, Ampl: *Amplexibranchius*, Naob: *Naobranchia*, Ther: *Therodamas*, Vaig: *Vaigamus*, Bras: *Brasergasilus*, Gami: *Gamidactylus*, Gapi: *Gamispinus*, Gapa: *Gamispatus*, Telo: *Telotha*, Preh: *Prehendorastrus*, Lamp: *Lamproglana*, Amaz: *Amazolernaea*, Brag: *Braga*, Erga: *Ergasilus*, Dolo: *Dolops*, Rhin: *Rhinergasilus*, Peru: *Perulernaea*, Amph: *Anphira*, Argu: *Argulus*, Asot: *Asotana*, Myra: *Myracetyma*, Rigg: *Riggia*.

associations were among species of Serrasalmidae, Characidae, Pimelodidae and Cichlidae (Table 2), which are considered to be the most abundant taxa of Brazilian fish species. In farmed fish, only one isopod (*Braga patagonica* Schiödt and Meinert, 1884) and two lernaeids (*Lamproglana monodi* Capart, 1944 and *Lernaea cyprinacea* Linnaeus, 1758) were found, and argulid species of the genera *Argulus* Müller, 1785 and *Dolops* Audouin, 1837 (*Dolops carvalhoi* Lemos de Castro, 1949) predominated.

Dolops Audouin, 1837 and *Argulus* Muller, 1785 (Argulidae); *Lernaea* Linnaeus, 1758 (Lernaeidae); and *Ergasilus* Nordmann, 1832 (Ergasilidae), were the genera with greatest occurrence in the samples analyzed. Among these, *Dolops* and *Argulus*, which were the ones with highest prevalence, occurred in hosts of a variety of families, but especially in species of Anostomidae, Pimelodidae, Cichlidae and Serrasalmidae. Species of *Lernaea* occurred in hosts of different families, especially *L. cyprinacea*; while species of *Ergasilus* frequently infested species of Characidae, Pimelodidae, Anostomidae and Cichlidae. Species of *Gamispatus* Thatcher & Boeger, 1984 (Ergasilidae), mainly infested Prochilodontidae and Anostomidae; while Thatcher & Boeger, 1984 (Ergasilidae), occurred in Prochilodontidae and Characidae (Figure 1). Isopods were mainly found in species of Characiformes of the families Serrasalmidae, Characidae, Acestrorhynchidae and Curimatidae; while *Riggia paranensis* Szidat, 1948 was limited to the curimatids *Cyphocharax gilbert* and *Curimata platana*.

Table 2. Richness of parasites crustacean species by taxonomic groups in 118 freshwater hosts from Brazil.

Host Order	Host family	Species richness
Characiformes	Acestrorhynchidae	3
Characiformes	Anostomidae	12
Osteoglossiformes	Arapaimidae	2
Siluriformes	Auchenipteridae	1
Siluriformes	Callichthyidae	2
Characiformes	Characidae	18
Perciformes	Cichlidae	16
Siluriformes	Clariidae	1
Clupeiformes	Clupeidae	1
Characiformes	Curimatidae	6
Characiformes	Cynodontidae	3
Cypriniformes	Cyprinidae	4
Siluriformes	Doradidae	3
Clupeiformes	Engraulidae	1
Characiformes	Erythrinidae	9
Characiformes	Hemiodontidae	1
Siluriformes	Heptapteridae	4
Siluriformes	Mochokidae	1
Mugiliformes	Mugilidae	4
Siluriformes	Pimelodidae	17
Cyprinodontiformes	Poeciliidae	1
Clupeiformes	Pristigasteridae	1
Characiformes	Prochilodontidae	12
Perciformes	Sciaenidae	5
Characiformes	Serrasalmidae	21
Synbranchiformes	Synbranchidae	1
Tetraodontiformes	Tetraodontidae	1

The highest number of host-parasite associations was recorded for *Pygocentrus nattereri* (Serrasalmidae); which had 29 records of infestation by *Anphira branchialis* Thatcher, 1993; *Argulus chicomendesi* Malta & Varela, 2000; *Argulus elongatus* Heller, 1857; *Argulus juparanaensis* Lemos de Castro, 1950; *Argulus multicolor* Stekhoven, 1937; *B. patagonica*; *Dolops bidentata* Bouvier, 1899; *D. carvalhoi*; *Ergasilus yumaricus* Malta and Varela, 1995; *Myracetyma etimaruya* Malta, 1993; *Myracetyma kawa* Malta, 1993; *Myracetyma piraya* Malta, 1993, *Argulus* sp., *Dolops* sp. and *Myracetyma* sp. For *Colossoma macropomum* (Serrasalmidae), there were 23 records of infestation by *A. multicolor*; *B. patagonica*; *Gamidactylus jaraquensis* Thatcher and Boeger, 1984; *L. cyprinacea* and *Perulernaea gamitanae* Thatcher & Paredes, 1985. For *Prochilodus lineatus* (Prochilodontidae), there were 15 records of infestation by *G. jaraquensis*, *Dolops geayi* Bouvier, 1897, *L. cyprinacea*, *Amplexibranchius* sp, *Ergasilus* sp. and *Gamispatus* sp.

The species of Isopoda parasitized the integument, mouth and gills, but higher prevalences were observed in the mouth, or the gills, or the integument and gills. There was greater variation in intensity in the gills and integument of the hosts. The species of Branchiura were found in the mouth, integument, gills and, occasionally, in the nostrils. The mean prevalence of infestation in the gills and integument was similar in the samples, while the intensity varied between all the parasite infestation sites. Copepoda were found at all the different sites in the hosts. The lowest variation in prevalence and intensity of infestation occurred when the gills, mouth and nostrils or the gills, mouth, nostrils and tongue were simultaneously parasitized. However, these results were caused by the low number of hosts in the samples investigated (Figure 2).

The prevalence, intensity and abundance of Copepoda species presented greater variation than those of Branchiura and Isopoda, and this was influenced by the greater presence of species of the families Ergasilidae and Lernaeidae (Figure 3), which were the most abundant parasites in the samples analyzed. The prevalence presented weak positive correlation with the intensity ($r = 0.004$, $p = 0.001$, $N = 251$) and with the abundance ($r = 0.004$, $p = 0.001$, $N = 190$), while the correlation between intensity and abundance ($r = 0.904$, 0.0001 , $N = 182$) was strongly positive (Figure 4).

It was observed a positive correlation between the number of hosts examined and the parasitized ($r = 0.560$, $p = 0.001$, $N = 188$) (Figure 5), and also in relation to the aggregated pattern ($r = 0.576$, $p = 0.001$, $N = 188$) of parasites distribution (Table 3). However, the analysis on the residuals of this correlation showed that, independent of the size of fish population sample, there was a loss of regression factor. In other words, the error tended to increase with increasing sample size, thus suggesting that there was probably no defined pattern for this specific parameter. Among the Ergasilidae of the samples, the species of *Gamispatus* Thatcher & Boeger, 1984; *Gamispinus* Thatcher & Boeger, 1984; *Brasergasilus* Thatcher & Boeger, 1983; *Myracetyma* Malta, 1993; *Gamidactylus* Thatcher & Boeger, 1984; *Rhinergasilus* Boeger & Thatcher, 1988; *Therodamas* Kroyer, 1863; *Amplexibranchius* Thatcher & Paredes, 1985; and *Vaigamus* Thatcher & Robertson, 1984, are distributed in several basins in Brazil. However, *Acusicola* Cressey, 1970, showed distribution in the basins of the Paraná and Amazon Rivers. The genera *Prebendorastrus* Boeger & Thatcher, 1990 and *Pindapixara* Malta, 1993 which only include a few

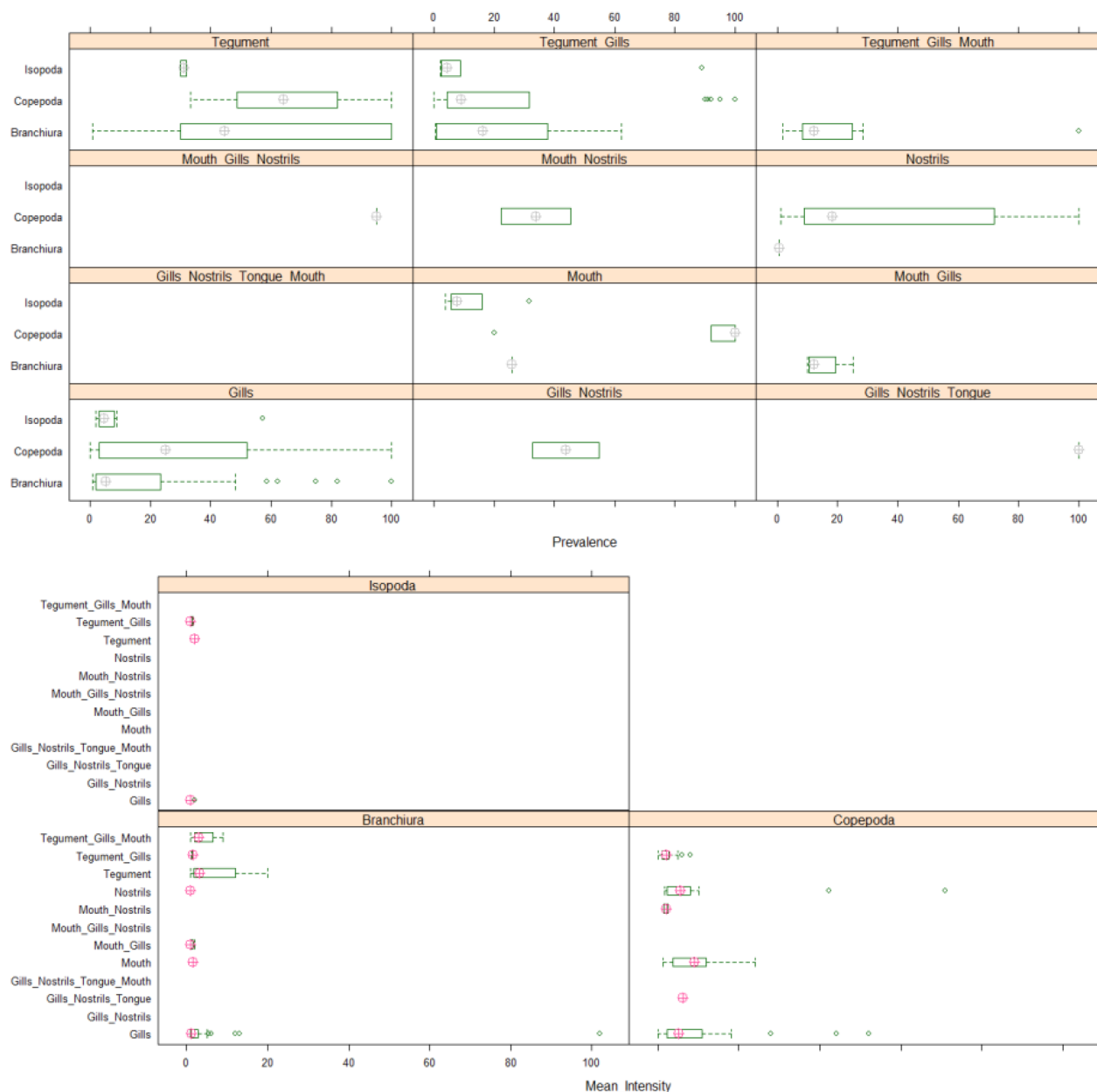


Figure 2. Infestation sites in freshwater fish from Brazil for three taxa of parasitic crustaceans found and according to prevalence and intensity of infestation. (Box plots represents medians, interquartile ranges (25-75%), minimum-maximum ranges and outliers).

species in the Amazon River system, seem so far to have limited geographical distribution. *Ergasilus* Nordmann, 1832 is a genus with greater frequency in the Amazon River system, but some species only occur in other basins (Figure 6).

Naobranchia lizae Kroyer, 1863, was the only species of Lernaepodidae found in the samples. Among the Lernaecidae, *Bedsylernaea* Thatcher & Williams, 1998 and *Amazolernaea* Thatcher & Williams, 1998 seem to occur only in the Amazon River basin; while *Minilernaea* Thatcher & Huergo, 2005 seems to occur only in basins outside of the Amazon region. However, these three did not show defined patterns because of the small number of samples examined. *Lamproglana* Nordmann, 1832 presents distribution in

the Paraná River and Atlantic Ocean systems. *Lernaea* Linnaeus, 1757 is distributed in all the hydrographic basins except in the Amazon River basin; while *Perulernaea* Thatcher & Paredes, 1985 occurs only in the Amazon River system (Figure 6).

Among the Isopoda, species of the genera *Anphira* Thatcher 1993, and *Braga* Schiodte & Meinert, 1881 have widespread distribution in the Amazon and Paraná River basins. Species of the genus *Riggia* Szidat, 1948 present distribution in the basins of the Amazon and Paraná River systems and the Atlantic Ocean rivers systems. However, species of the genera *Asotana* Schiödt & Meinert, 1881 and *Paracymothoa* Lemos de Castro, 1955 did not show any defined pattern because of the small number of

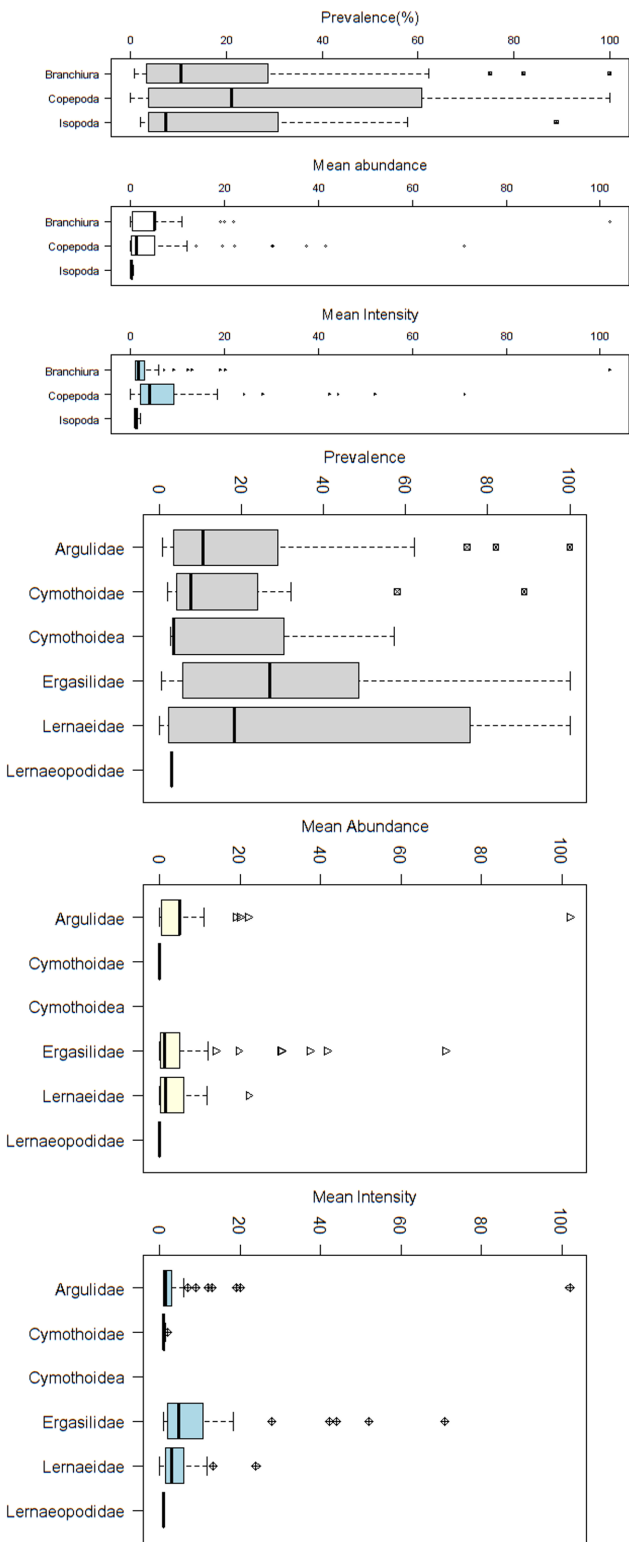


Figure 3. Quantitative descriptors of parasites crustacean populations for 334 freshwater fish species from Brazil (Box plots represents medians, interquartile ranges (25-75%), minimum–maximum ranges and outliers).

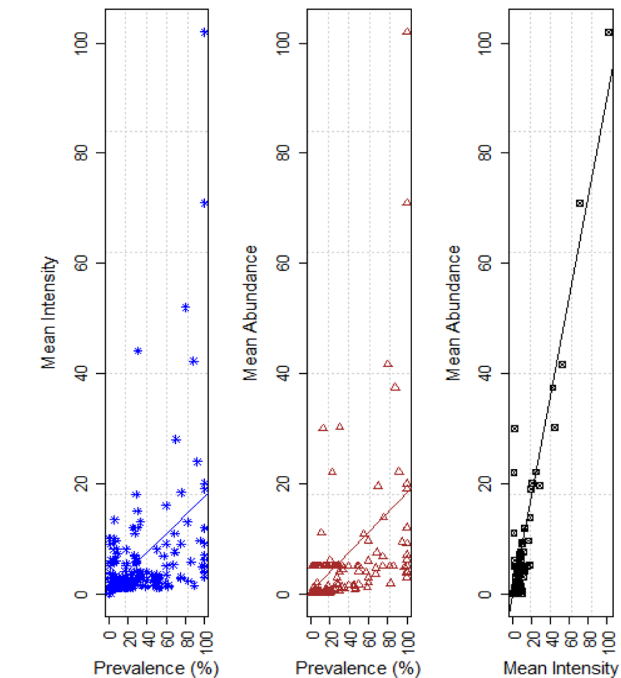


Figure 4. Relationship between the quantitative descriptors of parasites crustacean populations in freshwater fish species from Brazil

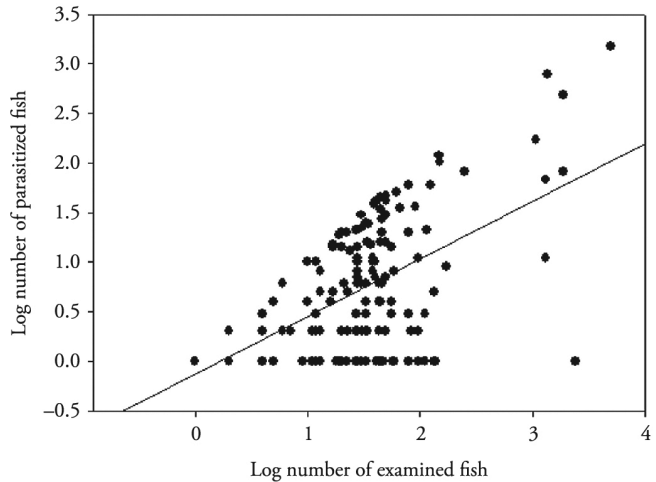


Figure 5. Relationship between examined fish and parasitized fish by parasites crustacean populations from Brazil.

Table 3. Aggregation levels for the main parasite crustaceans in freshwater fish species from Brazil.

Parasites	Samples number	Variance-to-mean ratio, mean (range)
<i>Argulus</i> spp.	18	17780.4 (40.8-149700.2)
<i>Dolops</i> spp.	49	94649.0 (81.4-830285.4)
<i>Brasergasilus</i> spp.	5	369696.0 (1549.8-1484190.2)
<i>Ergasilus</i> spp.	29	35812.6 (124.9-179156.1)
<i>Gamidactylus</i> spp.	5	1.9 (0.3-5.3)
<i>Gamispatulus</i> spp.	15	478.6 (10.7-4000.0)
<i>Myracetyma</i> spp.	6	23.3 (4.3-43.4)
<i>Vaigamus</i> spp.	9	460.4 (3.1-1600.0)
<i>Lamproglena monodi</i>	4	42.1 (1.4-101.3)
<i>Perulernaea gamitanae</i>	13	855.1 (59.8-3303.3)

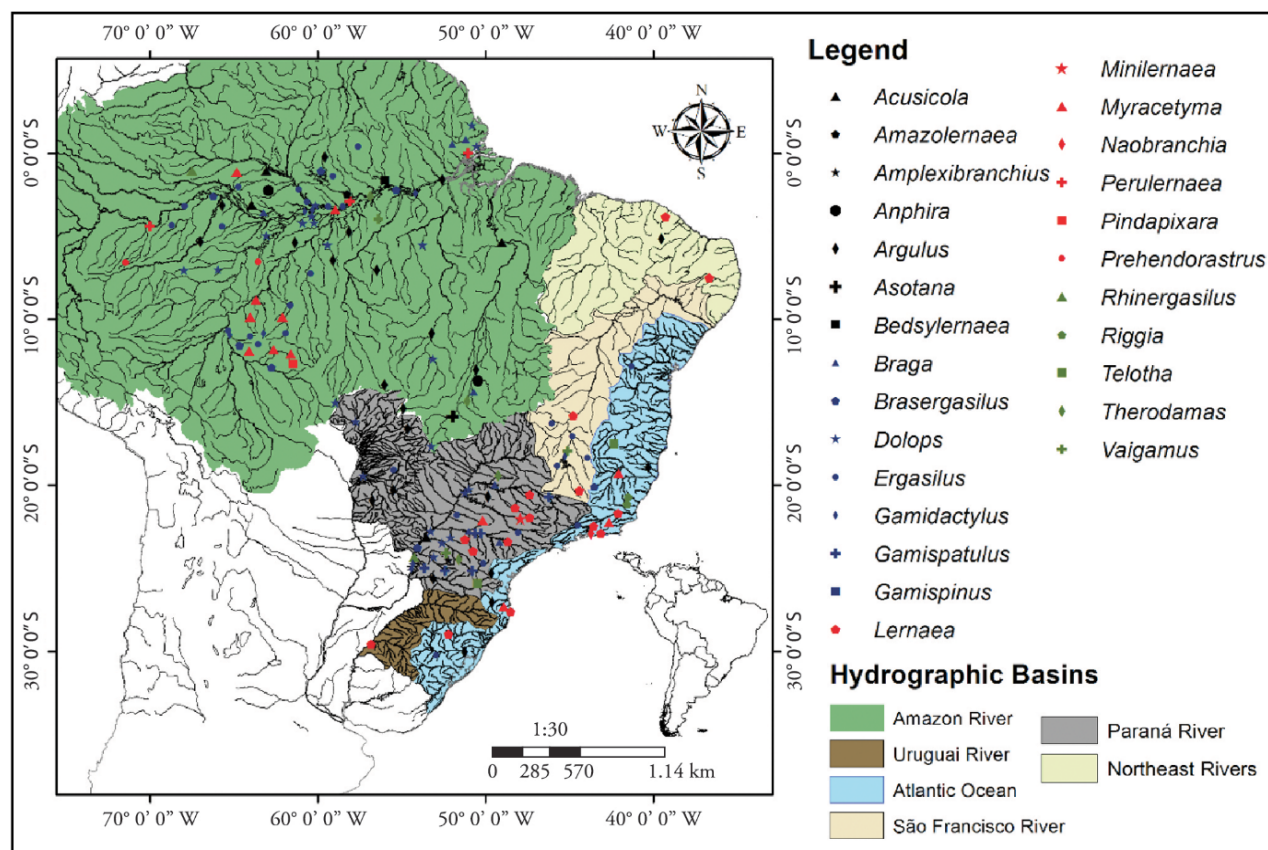


Figure 6. Distribution of the genera of parasitic crustaceans in freshwater fish of Rivers systems from Brazil.

reports available. The genera *Argulus* and *Dolops* showed wider distribution than all the others, such that they were present in the Amazon, Paraná, São Francisco and Uruguai River basins (Figure 6). However, some species had patterns limited to only one or two basins, as expected.

Discussion

Host-parasite distribution pattern

In this study, a search for patterns of parasitic crustacean distribution in freshwater fish in Brazil was carried out. We found 53 species of Copepoda, 15 species of Branchiura and 8 species of Isopoda. Several species of these taxa are also components of assemblages of ectoparasites of freshwater fish in other regions of the world (FRYER, 1968; DOUELLOU & ERLWANGER 1994; BOXSHALL & HALSEY, 2004; POLY, 2008; BOXSHALL & DEFAYE, 2008). However, most of these parasitic crustacean species occurred in hosts within Characiformes and Siluriformes, especially in species within Characidae, Serrasalminae and Pimelodidae. Characiformes comprise the majority of freshwater fish in Brazil (LACERDA et al., 2007; FROESE & PAULY, 2014) and Siluriformes is another group with abundant species (FROESE & PAULY, 2014). Among the hosts of the different families, the greatest number of host-parasite associations was among species of

Serrasalminae, Characidae, Pimelodidae and Cichlidae (Table 2), which are the most abundant taxa of Brazilian fish species.

Nearly 330 species of freshwater Copepoda are parasites, and most of them use fish and mollusk species as hosts (BOXSHALL & DEFAYE, 2008). Copepoda was the parasitic taxon most frequently associated with freshwater fish in Brazil, among the samples examined, with 43 species in the family Ergasilidae and dominance of *Ergasilus* spp., along with the presence of eight species in the family Lernaeidae. Many species of copepods have free-living infective stages, thus possessing morphological and behavioral adaptations that increase the likelihood of transmission (FRYER, 1968; DOUELLOU & ERLWANGER, 1994; THATCHER, 2006). In the Neotropical region, Copepoda is the third largest taxon of crustaceans parasitizing freshwater fish of different environments and ecosystems (LUQUE & POULIN, 2007). Fryer (1968) also found dominance of species of *Ergasilus* among fish species in Africa, especially in Cichlidae. Species of Lernaeidae occur in freshwater fish in Brazilian natural systems and aquaculture environments. They are notorious killers, specifically of small fish, and are the cause of great economic losses to aquaculture (THATCHER, 2006; TAVARES-DIAS et al., 2011). Although aggregation of *L. cyprinacea* at body sites induces severe local damage with adverse consequences to host function and survival, there are no official reports of fish mortality induced by this parasite in Brazil.

In Brazil, *L. cyprinacea* is the most common species of lernaeids, which has spread to fish farms and natural ecosystems

because of its lack of parasitic specificity (GABRIELLI & ORSI, 2000; MAGALHÃES, 2006; TAVARES-DIAS et al., 2011). This non-native ectoparasite was introduced into this country together with Hungarian carp and it does not yet occur in fish in the Brazilian Amazon region because of the geographical barrier of the Amazon River. Although aggregation of *L. cyprinacea* at body sites induces severe local damage with adverse consequences to host function and survival, there are no official reports of fish mortalities induced by this parasite in the country. However, the only native *Lernaea* species is *Lernaea devastatrix* Boxshall, Montú & Schwarzbald, 1997 which parasites wild native fish as well as farmed exotic fish. *Lamproglana monodi* is another non-native parasite that was introduced together with farming of Nile tilapia (*Oreochromis niloticus*) and it also infests natural populations of cichlids such as *Astronotus ocellatus* and *Cichla ocellaris*, as well as *Tilapia rendalli*, another exotic cichlid of natural ecosystems (AZEVEDO et al., 2012). Therefore, *L. monodi* is an emerging parasite with pathogenic potential that occurs in the southeastern and southern regions of Brazil. So far, neither of these non-native lernaeid species has been recorded in fish species in the Amazon region, while the native lernaeid species *P. gamitanae* is limited to serrasalmid hosts of this region. There was low representation of species of Lernaeopodidae, given that only *Naobranchia lizae* was found parasitizing *Mugil liza*. There are few known representatives of Lernaeopodidae in Brazil (LUQUE et al., 2013), unlike in other regions (FRYER, 1968; BOXSHALL & DEFAYE, 2008).

Isopods are a diverse group of crustaceans, with more than 10,300 species found in all realms from the deepest oceans to montane terrestrial habitats. Only around 950 described species (9%) live in freshwater environments. Thus, they live in widely varying habitats (WILSON, 2008). Out of the 95 families of Isopoda, only a few are parasites of fish: among these are the Cymothoidae, which are parasites of marine and freshwater fish, and have 40 recognized genera worldwide (SMIT et al., 2014). Isopods may cause morbidity in farmed and wild fish populations when their feeding and attachment activities cause tissue damage and blood loss (THATCHER, 2006; TAVARES-DIAS et al., 2014). The richness of isopod species in the samples analyzed was considered to be low, with only eight species concentrated solely in the family Cymothoidea. *Anphira branchialis* Thatcher, 1993 was found infesting piranhas of the genera *Serrasalmus* and *Pygocentrus* (Serrasalmidae). *Riggia paranensis* Szidat, 1948 was observed parasitizing species of the curimatids *Cyphocharax gilbert* and *Curimata platana*, while *Braga cigarra* Szidat & Schubart, 1960 parasitized the characid *Galeocharax knerii*. Smit et al. (2014) also suggested that most cymothoids are highly host-specific. *Braga patagonica* did not show any pattern of parasitic specificity, because of insufficient numbers in the samples analyzed here. In contrast, *B. patagonica* has been reported to have low parasitic specificity, since it seems to be the most widespread isopod of this genus, infesting species of Erythrinidae, Serrasalmidae, Characidae, Cichlidae, Cynodontidae, Curimatidae, Acestrorhynchidae and Sciaenidae in the Amazon region (TAVARES-DIAS et al., 2014). Hence, fish isopods present biological and economic importance.

In the hosts analyzed, among the two genera of Branchiura, 20 genera of Copepoda and six genera of Isopoda that were found, only four genera of these taxa were dominant. Their dominance

was due to the high occurrence of species of *Argulus* and *Dolops* in Serrasalmidae, Cichlidae, Pimelodidae and Anostomidae in the samples, along with species of *Ergasilus* in Characidae, Pimelodidae, Cichlidae and Anostomidae. Another frequently observed genus was *Lernaea*, influenced by the presence of *L. cyprinacea*, in more than 50% of the families of hosts. Among the species of argulids, *Argulus multicolor* Stekhoven, 1937 has been observed parasitizing Cichlidae, Serrasalmidae, Characidae and Pimelodidae. *Dolops bidentata* Bouvier, 1899 has parasitized Cichlidae, Anostomidae, Serrasalmidae and Prochilodontidae and *Dolops discoidalis* Bouvier, 1899 has parasitized Cichlidae, Pimelodidae, Arapaimidae and Erythrinidae. *Dolops carvalhoi* Lemos de Castro, 1949 is an argulid with lower parasitic specificity and has been correlated with hosts in almost 26% of the families analyzed. Furthermore, we observed that in 48.7% of the samples of *Argulus* (out of a total of 78 samples) and 15.8% of the samples of *Dolops* (out of a total of 101 samples), the species were not identified. Among the species of *Ergasilus*, the *Ergasilus bryconis* Thatcher, 1981 was found parasitizing Characiformes of the families Characidae and Anostomidae; while *Ergasilus coatiarius* Araujo & Varella, 1998 only parasitized Perciformes of the family Cichlidae. Therefore, it can be considered that some crustacean species prefer hosts from particular habitats or with particular behavior, while most are opportunist parasites. Moreover, in 17.8% of the samples of Ergasilidae (out of a total of 148 samples), the species were not identified and it was not possible to gain any understanding of patterns of parasitic specificity. However, because no species of the genera *Ergasilus*, *Argulus* or *Dolops* were identified, a relatively large number of these parasites are still awaiting taxonomic description.

Many parasitic crustacean species have preferences for particular sites on hosts in comparison with others (FRYER, 1968; DOUELLOU & ERLWANGER, 1994; CARVALHO et al., 2004; THATCHER, 1998, 2006; TAVARES-DIAS et al., 2011, 2014; SMIT et al., 2014), but this degree of restriction varies among parasite species. Thus, we found that while the lernaeid *P. gamitanae* infested only the oral cavity and gills of its host characids, *L. cyprinacea* is a parasite with low specificity that prefers the integument and gills of its hosts. Argulid species of the genera *Argulus* and *Dolops* have shown preferences for the integument and gills of their hosts. Among ergasilid species, parasites of the genera *Ergasilus*, *Acusicola* and *Myracetyma* have shown preference for the gills of their hosts. Species of the genus *Gamidactylus* have shown a preference for the nostrils, while species of the genera *Brasergasilus* and *Gamispatululus* have infested the gills and nostrils of their hosts. With regard to the habitat of cymothoid species on their hosts, the gills and integument have been found to be the major sites of attachment for *Anphira junki*, *A. branchialis* and *R. paranensis*, while species of the genus *Braga* seem to have a preference for the gills and mouth of hosts. Tavares-Dias et al. (2014) investigated the presence of *B. patagonica* in diverse freshwater fish in the Amazon region and found that both the mouth and the ventral part of the gill chamber were parasite attachment sites. In addition, they reported unusual fixation of *B. patagonica* on the dorsal area of the body near the fin of *Colossoma macropomum*, which caused destruction of the scales and severe inflammation at this attachment site. These results clearly showed a change of site preference in *C. macropomum*, for some unknown reason. Both

feeding and attachment sites probably play important roles in the distribution of native ectoparasite crustaceans in host fish (FRYER, 1968; DOUELLOU & ERLWANGER, 1994; THATCHER, 1998, 2006; CARVALHO et al., 2004; SMIT et al., 2014). Thus, one important reason why parasites prefer specific sites may relate to more effective use of resources such as food, the host species available and the vulnerability of the attachment site. Although one widely accepted view is that the primary function of site restriction is to avoid interspecific competition (CARVALHO et al., 2004; ANEESH et al., 2013), e.g. for space and food, competition seems to have minor importance among parasitic crustaceans. Most of the species of freshwater fish analyzed here harbored few parasitic crustacean species, and the abundance of infestation was low. Consequently, many vacant niches are available and therefore the resources are in a situation of oversupply and there is no need for competition among the species. However, the factors controlling distribution on hosts have not yet been well established for parasitic crustacean species.

Among fish parasitologists, there has always been a consensus that the precision of parasite infestation parameters (i.e. prevalence, mean intensity and mean abundance) is influenced by various factors such as sampling (i.e. method, design and number of samples obtained). Marques & Cabral (2007) demonstrated recently that only the prevalence of parasitic metazoans in fish, including crustacean species, was not affected by the sample size used, while the intensity and abundance are strongly influenced by sampling size. Here, we found a strong positive correlation between the number of fish examined and the number of fish parasitized. This initially suggested that the sample size of the fish examined has a large contribution towards the parasite prevalence levels among crustacean species found in the host population. However, analysis on the residuals confirmed that in fact prevalence was not influenced by the number of fish examined in the host-crustacean species system. Therefore, the proportion of hosts infected and the number of fish examined might not be predictable at the current stage of scientific knowledge.

Many parasite species commonly show overdispersion in different host fish (RÓZSA et al., 2000; MARQUES & CABRAL 2007; POULIN, 2013). This phenomenon occurs mainly due to processes that produce variability in host exposure, host acceptability by the parasite and host immune response. These parasites' overdispersion may also be influenced by the number of hosts examined in the sample, as well as by species-specific and study-specific effects (POULIN, 2013). For example, hyperparasitism of the ergasilid *Brasergasilus guaporensis* Malta, 1993, was reported in the gills of only two specimens of *Leporinus fasciatus* (mean intensity of 449 and range of 8-2400 parasites) out of five hosts examined (MALTA, 1993). Parasitic branchiuran and copepod species also showed an aggregated dispersion in the host populations investigated here. This is a common pattern for many taxa of fish parasites, including Crustacea (ROHDE et al., 1995; POULIN, 2013).

In many ecological systems, the distribution of infestation parameters varies with spatial and temporal scales, as do the processes that structure the parasitic populations and communities. For ectoparasitic crustaceans in fish populations, infestation levels are determined by factors operating during and after transmission, particularly those relating to the characteristics of the host, parasite

and environment (FRYER, 1968; DOUELLOU & ERLWANGER, 1994; THATCHER, 1998; CARVALHO et al., 2004; MARQUES & CABRAL, 2007; ANEESH et al., 2013). A significant positive correlation between the mean intensity and the mean abundance was found in the dataset analyzed here, whereas prevalence only showed weak positive correlations with the mean intensity and mean abundance of infestation. Poulin (2006) also reported this same pattern of correlation between mean intensity and mean abundance, from an analysis on fish parasite species in Canada, such as monogeneans, trematodes, cestodes, nematodes and copepods. However, the mean intensity and mean abundance of parasites have been found to vary independently of prevalence (RÓZSA et al., 2000).

Infestations of parasitic crustaceans are common among fish, affecting them in a variety of ways (DOUELLOU & ERLWANGER, 1994; ANEESH et al., 2013; SMIT et al., 2014; TAVARES-DIAS et al., 2014), and they are among the key threats to the sustainability of fisheries that feed millions of people worldwide, providing them with sources of protein and income. Some parasitic species may cause severe pathological effects and mortality among wild and farmed fish populations. Not surprisingly, the prevalence of infestations of parasitic crustaceans in the dataset analyzed was extremely variable, while the mean intensity and mean abundance were less irregular. This dataset mainly contained copepod and branchiuran species, along with a few samples of isopod cymothoids. Poulin (2006) also found exactly this in analyzing fish parasite species in Canada, thus finding that the intensity and abundance of infection showed little inter-population variation, while prevalence varied more widely, due to the characteristics of the parasite species. Smit et al. (2014) also noted that in some studies on wild marine fish populations, the prevalence of cymothoids was up to 73%, while in farmed fish, it was as high as 98%. In contrast, the prevalence of the cymothoid *B. patagonica* in *C. macropomum*, a freshwater fish farmed in Brazil, was registered as only 30%. Obviously, these results occur because certain host species are characterized by higher infection levels, by any parasite species, in comparison with other host species (POULIN, 2006). Indeed, branchiuran and copepod species have lower host specificity than do isopod species, and this therefore increases the availability of potential hosts for both taxa. Thus, differences in reproduction or mortality rates during the dispersal phase will cause the rates of establishment to differ among species of parasitic crustaceans.

Brazil is known to have a rich diversity of freshwater parasitic crustaceans (BRASIL-LIMA & BARROS, 1998; MALTA, 1998; MALTA & VARELLA, 1998; THATCHER, 2006; LUQUE et al., 2013), especially in the Amazon River basin system (THATCHER, 2006). The Amazon River basin and its diverse tributaries are characterized by extensive forested areas that become flooded every rainy season. Every year, the Amazon River rises and floods the surrounding forests, known as the varzea area ("flooded forests"). The Amazon region's flooded forests are the most extensive example of this habitat type in the world. Although the water temperature does not vary much in this basin during the year, the water levels, pH and dissolved oxygen levels can change dramatically, thereby influencing the floodplains, lakes and aquatic communities, including fish, parasites, vegetation, etc. Thus, when the water level in the Rivers is low and the

floodplains are exposed and lakes become shallow, the aquatic animals, including crustaceans and fish, become concentrated (THATCHER, 1998, 2006). Therefore, it can be expected that these environmental factors will also have a strong influence on parasite diversity, including that of parasitic crustacean species. Almost two-thirds of Brazilian territory lies within the area covered by the Amazon basin. In addition, there are more than 4000 species of fish (EIRAS et al., 2011; FROESE & PAULY, 2014) distributed across the different networks of Brazil's major basins and most of them are in the Amazon basin. This network of basins can be divided in three main biotopes, with Rivers and streams that contain fish of lengths ranging from a few millimeters to 3 meters in length. Therefore, many parasitic crustacean species still remain undescribed. Because of the high diversity of fish in these basins, a large number of species are very important for a variety of reasons, including economic interest (EIRAS et al., 2011).

Pattern of geographical distribution of parasite species

Among the diverse universal questions relating to the patterns of distribution of parasitic crustaceans in freshwater fish, the geographical pattern has been not addressed with much regularity in comparison with the situation regarding marine fish. A few studies have attempted to identify geographical patterns in the distribution of these parasites within particular regions, e.g. for Africa (FRYER, 1968) or in relation to a single taxon of parasites, e.g. for Brazil (LACERDA et al., 2007). Nonetheless, the results suggest that the distribution patterns of parasitic crustaceans result from complex host-parasite interactions, compounded by factors acting in either direction. The biology of the parasites and hosts, physiographic changes and ecological barriers are factors of prime importance within these interactions. Consequently, these host-parasite interactions may evolve into some associations comprising host specificity, latitudinal gradients and diversity of communities.

There are around 173 freshwater species of Ergasilidae, presenting widespread distributed. The species of the genus *Ergasilus* are distributed mainly in Africa and the Americas (BOXSHALL & DEFAYE, 2008). In Brazil, around 53 freshwater species of Ergasilidae are known, of which 17 are *Ergasilus* spp. (LUQUE et al., 2013). These occur most frequently in hosts in the Amazon River system, although only *Ergasilus bryconis* Thatcher, 1981 presents wide geographical distribution. Among the other 11 genera of Ergasilidae known to parasitize fish in Brazil, the genera *Prehendorastrus* and *Pindapixara* are endemic to the Amazon region. Species of *Therodamas* may have wide distribution in Brazilian aquatic ecosystems, since they have both freshwater and marine representatives (LUQUE et al., 2013). Species of the genus *Amplexibranchius* have not been recorded in hosts in the Amazon River basin system. Nor have species of the genera *Brasergasilus* and *Gamidactylus*, such as *Brasergasilus bifurcatus* Santos, Thatcher & Brasil-Sato, 2007 and *Gamidactylus piranhus* Santos Thatcher & Brasil-Sato, 2008. However, species of the genus *Gamispatulus* parasitize hosts within Prochilodontidae, Erythrinidae, Anostomidae and Serrasalminidae in several hydrographic basins in Brazil. Species of *Gamispinus* and *Myracetyma* Malta, 1993

have wide geographical distribution, given that they parasitize Siluriformes (Auchenipteridae and Pimelodidae) and Characiformes, respectively. The genus *Rhinergasilus* so far comprises only the species *Rhinergasilus piranhus* Boeger & Thatcher, 1988 that also have wide geographical distribution. The few known species of the genus *Acusicola* (three species) have been found infesting species of Engraulidae, Clupeidae and Cichlidae in the Amazon River basin, while the species parasitizing Characidae in the Paraná River basin has not yet been identified. The variations among parasitic crustacean species generally show one regular pattern, i.e. the species-area relationship. Hosts with more widespread geographical ranges usually tend to have more parasite species than do endemic hosts with smaller geographical ranges, because greater ranges may allow hosts to come into contact with more parasite species.

Parasitic isopods are typically marine and the species that live in freshwater have an adaptation to freshwater (WILSON, 2008). Recently, Smit et al. (2014) argued that there is no apparent distribution pattern for the cymothoid species that parasitize freshwater fish, because out of their 23 species, approximately 13 species occur in the Amazon region (South America) and six species are distributed in various localities in Asia or are only known in central Africa. However, the number of species in the Amazon region is much higher than this, given that Luque et al. (2013) recently listed 23 species of cymothoids known only in freshwater fish in Brazil, which include some in the Amazon region. Among the Cymothoidae, the isopods that most frequently parasitize freshwater fish in Brazil, i.e. species of *Riggia*, *Braga* and *Telotha* seem to have widespread distribution (LUQUE et al., 2013). However, *B. patagonica* occurs only in fish in the Amazon River system and *Riggia paranensis* Szidat, 1948 occurs only in the other basins of Brazil. Species of the genus *Anphira* present distribution in the Paraná and Amazon River basins. Wilson (2008) argued that the Amazon and other major Rivers of South America are significant hot spots for the Cymothoidae that parasitize fish, with more than 40 species in this family, therefore reflecting the diversity of the hosts in this Neotropical region.

In the Neotropical region, it has been estimated that there are six species of Lernaeidae, of which five are endemic species (BOXSHALL & DEFAYE, 2008). However, this number is certainly an underestimate, given that in Brazil alone, five native species are currently known (LUQUE et al., 2013). In Brazil, *P. gamitanae* is distributed only in the Amazon River system, while *L. devastatrix* so far presents distribution only in the Atlantic Ocean River systems. The non-native lernaeid *L. cyprinacea* has wide geographical distribution, but it does not occur in the Amazon River. *Lamproglana monodi* is distributed only in the Paraná, Uruguay and Atlantic Ocean River systems. However, the genera *Bedsylernaea*, *Amazolernaea* and *Minilernaea* only have one species in each of them and are therefore little known.

Three genera of Neotropical Argulidae are known, i.e. *Argulus*, *Dipteropeltis* and *Dolops* (POLY, 2008), and they are also found in Brazil (MALTA, 1998; LUQUE et al., 2013), but with variable distribution, mainly comprising species of *Argulus* and *Dolops*. *Argulus amazonicus* Malta & Santos-Silva, 1986 and *Argulus pestifer* Ringuelet, 1948 are found in the Amazon River basin,

while *Argulus elongatus* Heller, 1857 is distributed in the Paraná River basin. However, *Argulus multicolor* Stekhoven, 1937; *Argulus chicomendesi* Malta & Varela, 2000; *Argulus juparanaensis* Lemos de Castro, 1950; *Dolops bidentata* Bouvier, 1899; *D. carvalhoi*; *Dolops discoidalis* Bouvier, 1899; *Dolops geayi* Bouvier, 1897; *Dolops nana* Lemos de Castro, 1950; and *Dolops longicauda* Heller, 1857 have widespread distribution in the systems of these two hydrographic basins. On the other hand, *Dolops striata* Bouvier, 1899 is distributed in the Amazon, Paraná and Uruguay River basins; and *Argulus spinulosus* Silva 1980 in the Paraná and Uruguay River basins. Among the species of *Dolops*, *D. carvalhoi* has shown greatest geographical distribution.

Conclusions

The distribution pattern of parasitic crustaceans is the result of many factors that are not the same for all crustacean species, because besides physiographic changes and ecological barriers, they include the biology of these parasites, which may vary among the species. Among the biological factors, host preference is obviously of prime importance in cases of parasite specificity, although many species have been found to be generalists for Brazilian fish. Nevertheless, other external factors may also play an important role. Therefore, there are no crustacean species that parasitize all the host fish species. Some parasite genera and species have been found to be restricted to one or a few host species in a given region, although this is most likely due to the paucity of studies available in the literature or to the greater research effort expended among fish species of commercial interest, in comparison with studies on non-commercial fish. However, such information is useful for distinguishing host ranges and host specificity. Thus, we highlight the need for more quantitative data in order to assess the parasitic crustacean fauna of fish because these studies may lead to greater knowledge of their diversity, richness and distribution among fish in Brazil.

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