An Acad Bras Cienc (2024) 96(Suppl. 1): e20240291 DOI 10.1590/0001-3765202420240291
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ANIMAL SCIENCE

Spatial distribution, host specificity, and affinity of Branchiura for surface and macrohabitat types in fish species from the Brazilian Amazon

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Abstract: This study investigated the spatial distribution, parasite interactions, and affinities of Branchiura parasites according to macrohabitat and surface type on fish from the Araguari River, Amapá State, in the Brazilian Amazon. This study presents novel information on the interactions of branchiuran species with host fish, and how the morphology of their attachment structures is associated with different host surface morphologies, with and without scales. A total of 558 fish specimens of 26 species were collected, of which 109 fish (10 species) were parasitized by at least one branchiuran parasite; these were selected for further study. The parasites were collected from the buccal cavity, gills, fins, and integument of the host fish. Parasites with suction discs (*Argulus*) were mainly associated to hosts with small scales and no scales, while parasites with hooks (*Dolops*) were mainly associated to hosts with large scales. Overall, parasites with suction discs were more specialized per site than those with hooks.

Key words: Araguari River, crustacea, ectoparasites, functional morphology.

INTRODUCTION

To adapt to the parasitic lifestyle, animals that were formerly free-living have undergone a series of reproductive, feeding, and morphological adaptations, which influence their exploitation of hosts (Kearn 1994, Poulin 2007). One of the main adaptive characteristics of parasites are the structures that facilitate attachment to their hosts. These structures are usually among the main characteristics used for ontogeny and systematic classification of such invertebrates (Suárez-Morales 2020, Møller et al. 2008, Thatcher 2006, Lemos de Castro 1985). Therefore, the morphology of parasitic attachment structures varies in terms of size and shape, depending on the attachment site (Kearn 1994, Oliveira et al. 2022, Poulin 2007).

Crustacean parasites of fish are distributed across three major groups: Isopoda, Copepoda, and Branchiura (Tavares-Dias et al. 2015, Luque et al. 2013, Thatcher 2006). The family Argulidae of the subclass Branchiura has four genera: *Argulus* Müller, 1785; *Dipteropeltis* Calman, 1912; *Chonopeltis* Thiele, 1900, and *Dolops* Audouin, 1837, with approximately 164 known species in this family (WoRMS 2023). *Argulus*, *Dipteropeltis*, and *Chonopeltis* species attach to the host using the first jaw, which has been modified into suction discs, while *Dolops* species attach to hosts using the first jaw modified into sharp-pointed hooks (Møller et al. 2008). Possibly, these morphological variations are responsible for the wide variety of niches that these ectoparasites exploit on host fishes, as well as their different attachment sites in hosts. Branchiurans can be found on the integument, buccal cavity, fins, and gills of host fish because they can move across the outside of the fish body (Oliveira et al. 2017, Lemos de Castro 1985, Tavares-Dias et al. 2015, Thatcher 2006).

The morphology of the surface to which branchiurans adhere potentially plays an important role in the distribution and affinity of these parasites to the host. Based on this principle, it is possible that differences in host macrohabitat affinities occur according to the two functional groups, (1) one that has a suction disc, (2) and the other that has hooks to attach to the host. Thus, we question whether the morphology of these attachment structures plays a role in the spatial distribution, specificity, or differences in the use of fish as hosts on a taxonomic or functional level. Therefore, our hypotheses are: (1) Branchiura ectoparasites that use suction discs (genera *Argulus* and *Dipteropeltis*) and hooks (*Dolops*) to attach to the host have affinities for different infestation sites on fish because of their attachment structure morphology and specialization to exploit different surfaces on hosts; (2) Branchiurans that use suction discs (*Argulus* and *Dipteropeltis*) and hooks (*Dolops*) for attachment parasitize different groups of hosts depending on the type of integument (large-, small-, or no scales), because the divergence of these parasites is associated with the sites they exploit on the host fish; (3) Branchiura species with hooks (*Dolops*) are generalists and species with a suction disc (genera *Argulus* and *Dipteropeltis*) are specialists, because phylogenetically, Branchiura species with suction discs are an early lineage that diverged to exploit specific sites on the host; and (4) Branchiuran abundance is higher in larger host fish because they have a larger area of integument for simultaneous attachment of parasites. Thus, this study aimed to determine differences in host use in relation to the morphology of fish parasitized by branchiuran ectoparasites to determine parasitism patterns in relation to macrohabitat in the host fishes.

MATERIALS AND METHODS

Location of fish and parasite collection

This study used samples collected during expeditions by the project Monitoring Fishing Activity in the upper Araguari River (Protocol number 004/2013), funded by the Fundação de Amparo à Pesquisa do Amapá (FAPEAP) (Protocol number 004/2013). Fish collection was authorized by ICMBio (Protocol number 42203-1), and the Ethics Committee on Animal Use of the Laboratório de Biologia de Peixes da Universidade Federal do Amapá (UNIFAP) approved the procedures involving animals (Protocol number 47757715.5.0000.0003).

Fish were collected in the upper stretch of the Araguari River, between the cities of Serra do Navio and Ferreira Gomes, Amapá State, Northern Brazil, at geographic coordinates 1°4’26.11”N 51°59’1.94”W; 1°7’16.50”N 51°58’59.64”W; 1°12’43.59”N 52°0’8.70”W; 1°13’50.97”N 51°59’59.53”W; 1°16’52.75”N 51°59’47.51”W and 1°18’8.54”N 51°58’52.28”W (Figure 1), during several different periods (January 2012; February and December 2013; and January, February, March, and June 2014). Gillnets of different mesh sizes (30, 40, 50, 60, 70, 80, 90, and 100 mm between knots) were set for 24 h and were inspected every 4 h in order to collect fish, as well as lines and fishhooks. In terms of fish biometry, weight (g) and total length (cm) were measured.

A total of 558 fish specimens of 26 species were collected. Only fish parasitized by branchiurans of the Argulidae family were selected (Table I).

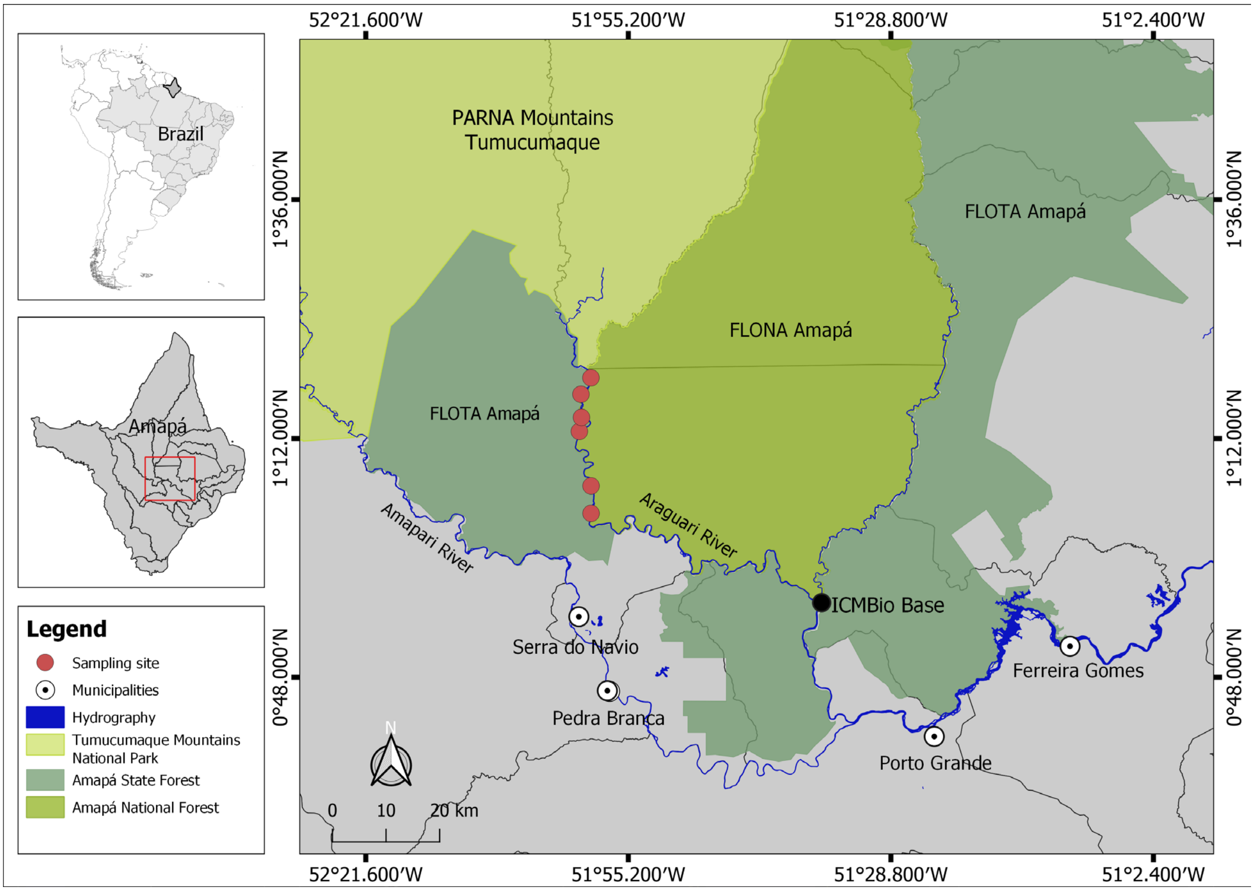

Figure 1. Location of the fish collection sites in the upper Araguari River, Amapá state, Brazil.

Parasite collection and analysis

After capture, each fish was transferred to a plastic tray and the integument, buccal cavity, gills, and fins were immediately analyzed to verify the presence of Branchiura. The branchiurans were clarified in 5% potassium hydroxide then transferred into a petri dish and placed on a heating plate at 50 °C until complete clarification. The specimens were then mounted on a permanent slide with pure glycerin, sealed with paraffin and examined under a light microscope (Oliveira et al. 2022). Specialized literature on the taxonomy of branchiuran in fish was used for identification of the parasite species (Suárez-Morales 2020, Lemos de Castro 1985, Thatcher 2006).

Data analysis

To test hypotheses 1 and 2, we applied principal coordinates analysis (PCoA) using a matrix of branchiuran species abundance data from the “vegan” R package (Oksanen et al. 2020). For PCoA and PERMANOVA we used the Bray-Curtis distance method. Interactions were defined based on qualitative and quantitative information, including species and attachment structure morphology (suction disc or hooks), and the type of host integument surface (small scales, large scales, and no scales). In addition, we used the envfit function of the vegan package (Oksanen et al. 2020) to assess the relationship between branchiuran groups (group I = suction disc) and (group II = hooks) with sites on the

Table I. **Fish species parasitized and not parasitized by Branchiura, collected from the upper Araguari River, Amapá, Brazil.**

Species of fish	N	Length (cm)	Weight (g)	Parasitized
Acestrorhynchus falcirostris (Acestrorhynchidae)	2	26.7 ± 1.8	205.5 ± 17.7	No
Acestrorhynchus microlepis (Acestrorhynchidae)	13	21.8 ± 1.9	114.3 ± 23.1	Yes
Ageneiosus inermis (Auchenipteridae)	57	31.8 ± 6.0	484.3 ± 311.7	Yes
Boulengerella cuvieri (Auchenipteridae)	21	47.5 ± 8.7	1008.9 ± 593.4	Yes
Charax sp. (Characidae)	29	17.1 ± 2.6	107.0 ± 41.3	Yes
Cichla sp. (Cichlidae)	3	38.1 ± 9.8	1297.0 ± 971.2	No
Hoplias aimara (Erythrinidae)	42	44.7 ± 11.7	2075.5 ± 1698.4	Yes
Hoplias sp. (Erythrinidae)	3	29.5 ± 2.8	475.0 ± 114.0	No
Hypostomus sp. (Loricariidae)	2	16.3 ± 1.1	136.0 ± 29.7	No
Leporinus maculatus (Anostomidae)	13	21.8 ± 3.3	245.1 ± 110.5	No
Leporinus melanostictus (Anostomidae)	1	22.5	268.0	No
Leporinus pellegrini (Anostomidae)	7	22.8 ± 10.9	337.7 ± 221.5	No
Mylesinus paraschomburgkii (Serrasalmidae)	4	21.3 ± 1.9	364.3 ± 117.3	No
Prosomyleus rhomboidalis(Serrasalmidae)	26	29.1 ± 3.0	1082.5 ± 285.5	Yes
Myloplus asterias (Serrasalmidae)	50	14.6 ± 2.7	152.5 ± 53.2	Yes
Myloplus sp. (Serrasalmidae)	12	21.7 ± 6.7	566.0 ± 446.9	No
Myloplus ternetzi (Serrasalmidae)	29	18.2 ± 2.2	259.0 ± 48.3	Yes
Pimelodus sp.1 (Pimelodidae)	1	28.0	378.0	No
Pimelodus sp.2 (Pimelodidae)	2	25.5 ± 2.1	285.5 ± 43.1	No
Satanoperca sp. (Cichlidae)	1	19.0	200.0	No
Serrasalmus eigenmanni (Serrasalmidae)	6	13.1 ± 2.7	82.3 ± 63.1	No
Serrasalmus elongatus (Serrasalmidae)	12	14.4 ± 3.7	104.4 ± 92.6	No
Serrasalmus rhombeus (Serrasalmidae)	25	30.9 ± 5.1	1045.8 ± 478.3	Yes
Tometes trilobatus (Serrasalmidae)	67	36.1 ± 6.6	2170.0 ± 883.3	Yes
Triportheus angulatus (Tripotheidae)	98	18.0 ± 2.4	103.9 ± 41.5	No
Triportheus brachipomus (Serrasalmidae)	32	19.7 ± 2.8	141.9 ± 49.2	No

hosts (fins, buccal cavity, gills, and integument), and surface types (large-, small-, and no scales).

To test hypothesis 3, i.e. aiming to determine parasite-host relationships at the species and functional group level (suction disc and hooks), we devised two interaction networks using the "bipartite" R package, calculating the C-score, number of compartments, species range and strength, and species specificity index (SSI) (Dormann et al. 2009, 2008, Dormann 2011). The C-score is an index that measures the co-occurrence rate of species in the network and is an indicator of the degree of specificity of the species that compose it. Its value ranges from 0 (high co-occurrence) to 1 (low co-occurrence). Compartments are independent groups of ectoparasites and hosts within the network and are indicators of specificity patterns. Range is the number of fish species with which an ectoparasites species interacts. Finally, species strength is the sum of the proportions of a species' participation in all network interactions. The bipartite figure shows all connections between organisms at two levels. The volume of the connection bars and lines represents the proportion of interactions performed by each species and between species, respectively.

To test hypothesis 4, we used Spearman's correlation (*rs*) in the "tidyverse" R package (Wickham et al. 2019), in which we correlated the abundance of all Branchiura species (sum of all species) and correlated it with the total length (cm) and weight (g) of the host fish.

The database was organized using Excel, Microsoft Office 2019. Figures were plotted using the "ggplot2" R package (Wickham 2016). All analyses were performed using R software (R Core Team 2021). Differences were deemed statistically significant at $p < 0.05$.

RESULTS

A total of 109 fish of 10 species were selected for this study, from which a total of 261 branchiuran specimens of the genera *Argulus*, *Dipteropeltis*, and *Dolops* were collected, attached to four different sites on the hosts (Table II).

Hypotheses 1 and 2

PERMANOVA showed that the attachment structure of the Branchiura parasites (suction disc and hooks) affects the choice of infestation site on the fish ($F = 22.54$; R^2 0.298; $p = 0.001$). The envifit test indicated that parasites with suction discs were mainly associated with the fins and buccal cavity, while those with hooks were mainly associated with the integument of the host (Table III).

In the PCoA, axes 1 and 2 explained 90.2% of the variation in the data. The figure showed the formation of two groups of ectoparasites, which correspond to the morphological characteristics of hooks and suction discs, as well as a gradient of separation between the macrohabitats of attachment, including the

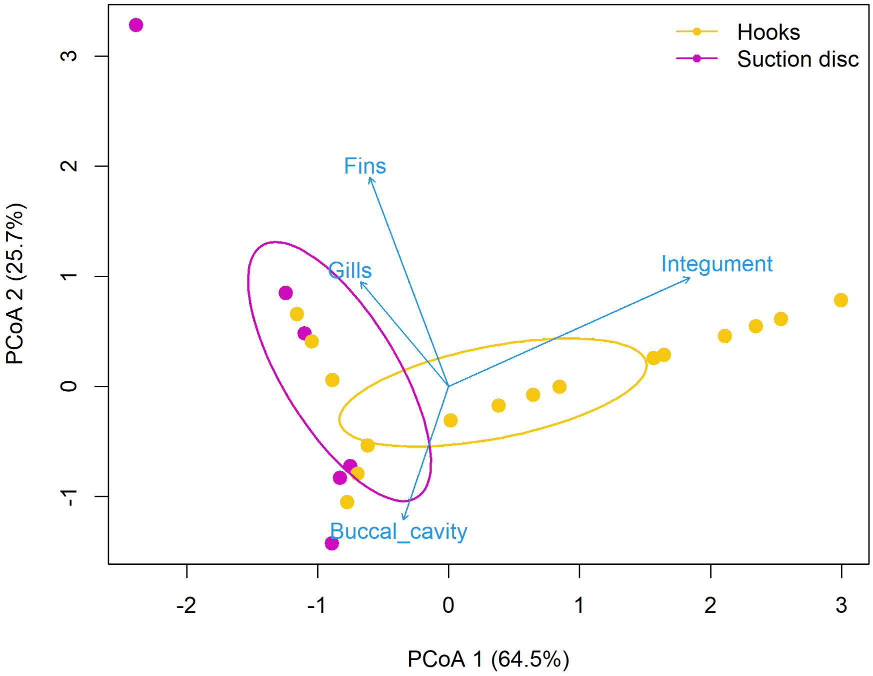

Figure 2. Principal coordinate analysis (PCoA) using a Bray-Curtis distance matrix for macrohabitat preferences of Branchiura from the upper Araguari River, Amapá state, Brazil in relation to their attachment structure. The percentage of variation explained by the principal coordinates is indicated on axes 1 and 2. Arrows correspond only to sites where $p < 0.05$.

Table II. **Branchiura ectoparasites collected from fish of the upper Araguari River, Amapá state, Brazil.**

Parasitized fish species	Parasite species	TNP	Site of infestation
Acestrorhynchus microlepis (n = 13)	*Argulus* sp.1	1	Buccal cavity
	Argulus multicolor	2	Gills
	Argulus multicolor	2	Buccal cavity
	Argulus sp.2	10	Buccal cavity
	Dolops bidentata	1	Buccal cavity
	Dolops striata	4	Integument
Boulengerella cuvieri (n = 5)	*Argulus* sp.1	1	Buccal cavity
	Argulus sp.1	1	Gills
	Dolops bidentata	31	Integument
Charax sp. (n = 4)	*Argulus* sp.2	2	Integument
	Dipteropeltis sp.	1	Integument
	Dolops bidentata	1	Integument
Myloplus asterias (n = 7)	*Dolops bidentata*	2	Integument
	Argulus sp.3	3	Fins
	Argulus sp.3	2	Gills
Myloplus ternetzi (n = 10)	*Dolops bidentata*	4	Integument
	Dolops bidentata	2	Fins
	Dipteropeltis sp.	4	Fins
Myloplus rhomboidalis (n = 9)	*Dolops bidentata*	3	Buccal cavity
	Dolops bidentata	19	Integument
	Dolops bidentata	2	Fins
Serrasalmus rhombeus (n = 12)	*Dolops bidentata*	1	Buccal cavity
	Dolops bidentata	4	Integument
	Dolops striata	1	Integument
Tometes trilobatus (n = 17)	*Dolops bidentata*	54	Integument
	Dipteropeltis sp.	2	Fin
Hoplias aimara (n = 16)	*Dolops striata*	10	Integument
	Dolops bidentata	3	Integument
	Argulus sp.2	73	Fins
	Dipteropeltis sp.	2	Fins
Ageneiosus inermis (n = 16)	*Argulus* sp.2	1	Integument
	Argulus sp.2	3	Fins
	Argulus sp.2	1	Gills

TNP: Total number of parasites.

integument, buccal cavity, gills, and fins (Figure 2). However, considering axis 1, no groups were formed where ectoparasites with hooks occur in all three macrohabitats but with a particular affinity for the integument. In terms of axis 2, ectoparasites with suction discs show an affinity for the buccal cavity, gills, and fins.

PERMANOVA showed the host surface (small-, large-, and no scales) affected the macrohabitat of branchiuran parasites as a function of the attachment structure (suction disc or hooks) (F = 7.221; R^2 0.144; p = 0.003). The envfit test indicates that parasites with suction discs were mainly associated with small-scaled and scale-free hosts, while parasites with hooks were mainly associated with large-scaled hosts (Table IV and Figure 3).

In the PCoA, axes 1 and 2 explained 99.9% of the data variation. The Figure 3 show the formation of three groups (small, large, and no scales), which correspond to morphological characteristics of the surfaces that the parasites use to attach to the host. The analysis also shows a gradient of separation between the parasite attachment structures (suction disc and hooks). On axis 2, parasites with suction discs were mainly associated with small-scaled fish, and parasites with hooks were mainly associated with large-scaled fish. Scale-free fish were not strongly associated with parasite attachment structure, but the parasites collected from the integument had suction discs. However, considering axis 1, no groups were formed (Figure 3).

Hypothesis 3

Of the total possible connections between parasites and host fish (n = 100), 35% were made. No compartments were formed and the co-occurrence rate of ectoparasites was high at the network level (C-score = 0.44) indicating that most parasites share the same host species (Figure 4). Evaluation of the interaction between parasites with suction discs and hooks showed low co-occurrence (C-score = 1.00).

Only *Argulus multicolor* Stekhoven, 1937 and *Argulus* sp. 3 had a high SSI and were associated with a single host species: *Acestrorhynchus microlepis* (Jardine, 1841) and *Myloplus asterias* (Müller & Troschel, 1844), respectively. The remaining parasite species were found in at least two host species. The most generalist ectoparasite was *Dolops bidentata* (Bouvier,

Table III. Envfit test with 999 permutations using the distance matrix of parasite samples to test the effect of attachment morphology of Branchiura ectoparasites on the choice of macrohabitat on fish from the upper Araguari River, Amapá state, Brazil. p <0.001 indicated by '***'.

Attachment structure	PCoA1	PCoA2	R^2	p
Suction disc	-0.52002	-0.85416	0.8810	0.001***
Hooks	0.83570	-0.54919	0.8338	0.001***

Table IV. Envfit test with 999 permutations using the distance matrix of parasite samples to test the effect of Branchiura ectoparasite preference for macrohabitat on fish from the upper Araguari River, Amapá state, Brazil. p <0.001 and p <0.05 are indicated by '***' and '*', respectively.

Macrohabitat	PCoA1	PCoA2	R^2	p (> R)
Buccal cavity	-0.27581	-0.961221	0.2562	0.028*
Gills	-0.57848	0.81570	0.2179	0.024*
Integument	0.88112	0.47289	0.7027	0.001***
Fins	-0.30245	0.95316	0.6395	0.001***

1899), which parasitized nine host species and participated in a large proportion of the interactions in the network. Regarding hosts, *A. microlepis* was the most parasitized, comparable only to *Hoplias aimara* (Valenciennes, 1847) (Table V and Figure 4).

The range of hosts was similar for both groups of parasites, with nine host species parasitized by those with hooks, and eight by those with suction discs. The group with suction discs had a higher SSI (Table VI and Figure 5).

Hypothesis 4

Spearman's correlation testing showed that there was a significant positive correlation between branchiuran ectoparasites abundance with host weight (R = 0.42, p = 0.001), but not with host length (R = 0.46, p = 0.001) (Figure 6).

DISCUSSION

In fish, branchiurans are found mainly on the integument, fins, buccal cavity, and gills (Luque et al. 2013, Tavares-Dias et al. 2015, Oliveira et al. 2017). In general, these parasites exploit different sites on the host fish, which is a reflection of several evolutionary and ecological processes (Kearn 1994, Poulin 2007). The exploitation of various sites on a host fish by different branchiuran lineages may be closely associated with the morphology of their attachment structures, the attachment surface, and water drag force, as it is for ergasilids (Oliveira et al. 2022). In the present study, we recorded branchiurans on the body surface, fins, buccal cavity, and gills of host fish. Similar results were reported for branchiurans from other regions of South America (Tavares-Dias & Oliveira 2017, Mamani et al. 2004, Carvalho et al. 2003, Malta 1984, Oliveira et al. 2017, Tavares-Dias et al. 2015, Fontana et al. 2012). To better understand the dynamics of site exploitation by branchiurans, we evaluated spatial distribution patterns of these parasites on freshwater fish, and our results propose a particular pattern of distribution on the host fish examined.

Branchiura species that use suction discs (*Argulus* and *Dipteropeltis*) to attach to host fish

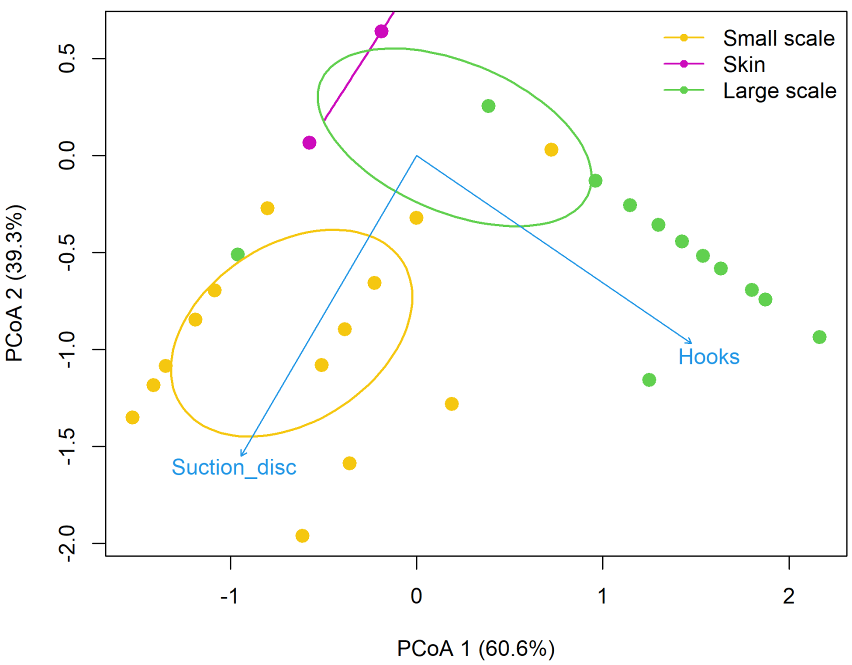

Figure 3. Principal coordinate analysis (PCoA) using a Bray-Curtis distance matrix for Branchiura attachment structures in relation to integument type in fish from the upper Araguari River, Amapá state, Brazil. The percentage of variation explained by the principal coordinates is indicated on axes 1 and 2. Arrows correspond only to sites where p < 0.05.

were mainly found in the buccal cavity, gills, and fins (only two individuals were collected from the surface of a host with scales), while species with hooks (*Dolops*) were mainly collected from the surface of fish with scales. The evolution of parasites is associated with the infestation sites they exploit on their hosts (Kearn 1994, Poulin 2007). It is possible that the divergence of the lineage of parasitic crustaceans with a suction disc is associated with expansion of ecological niches (Møller et al. 2008, Kearn 1994). Therefore, we suggest that the ancestral lineage of *Dolops* species, which have attachment organs with strong, fine-pointed chitinous hooks, are inefficient at remaining attached to or moving across smooth surfaces (e.g. the buccal cavity or fins). Therefore, they are mainly associated with surfaces with scales as such keratinous structures have tiny fissures (Dey et al. 2014) that allow *Dolops* species to adhere to their hosts more easily using their hooks. Furthermore, the diversification of attachment structures constitutes strong evidence for the establishment efficiency of parasites *Argulus* on other host groups, such as salamanders, tadpoles, and crocodiles (Tanzola & Villegas-Ojeda 2017, Poly 2003, Møller 2009). Similarly, studies show that the spatial distribution of ergasilids *Therodamas longicollum* Oliveira, Correa, Adriano & Tavares-Dias, 2021 and *Ergasilus* sp. on the gills of *Leporinus fasciatus* was mainly influenced by the morphology of their attachment structures. These studies suggest that the evolutionary processes of these species were influenced by abiotic factors, such as water flow in the host gills (Oliveira et al. 2022). Therefore, we can assume that for Branchiura species, water flow also plays an important role in the choice of attachment sites on host fish, since hook-bearing ectoparasites (*Dolops*) are ancestral and mainly attach to the fish integument, where water drag is great. However, branchiurans that have suction discs for attachment diverged early and possibly evolved to parasitize sites where water drag is lower, such as the buccal cavity, gills, and muscular subdivisions of the fins.

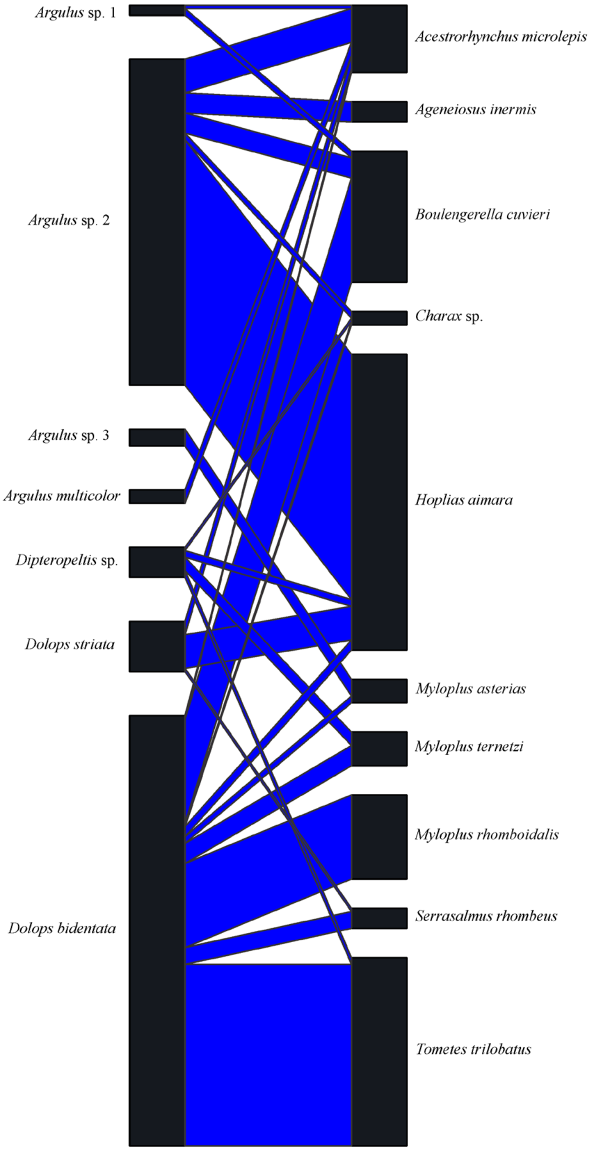

Figure 4. Interaction network of Branchiura with fish species in the upper Araguari River, Amapá state, Brazil.

At some point in the evolutionary history of branchiurans, competition for resources in hosts or reduction of predation may have been the precursor to the divergence of the branchiuran lineage, which has the first modified suction disc jaw, similar to the proposal by Kearn (1994) for Monogenea ectoparasites. In this study, branchiuran species with a suction disc showed a greater affinity for the buccal cavity and fins of fish with smooth surfaces, i.e., without scales. This suggests that the function of this attachment organ (adhering to the suction cup-like surface) is more efficient on smooth structures, such as the inner region of the buccal cavity, gills, and fins of the host fish (Yashpal et al. 2006). Moreover, the buccal cavity of the host is a site that makes predation difficult, because it is inaccessible, while the fins are difficult to see, also offering protection, as the fins have muscular subdivisions (similar to a fan); this is where the parasite adheres, for example, *Argulus* sp.2 (a parasite with a suction disc) in *H. aimara*. Therefore, the pressure exerted on the integument-favoring parasites throughout evolutionary history may have been a precursor to the exploration of new sites in host fish, such as predation by other animals, even other fish species with omnivorous and carnivorous feeding habits (Genovez et al. 2008, Sazima & Machado 1990, Kearn 1994).

Studies show that branchiuran parasites have low host specificity, since many species have been reported to parasitize several fish species (Luque et al. 2013, Tavares-Dias et al. 2015, Oliveira et al. 2017). In the present study, the C-score of the bipartite analysis shows moderate levels of co-parasitization, indicating that Branchiura species share the same host species, particularly *D. bidentata*, the most generalist ectoparasites, which parasitized nine fish species, followed by *Argulus* sp. 2 that parasitized five species of host fish. In contrast, *A. multicolor* parasitized only *A. microlepis*, while *Argulus* sp. 3 parasitized only *M. asterias*, indicating that both are specialists. This high host specificity is potentially a reflection of the high species richness of the fishes of the Araguari River harbor, since specificity levels

Table V. Specificity indices of Branchiura on fish from the upper Araguari River, Amapá state, Brazil.

Parasite species	Degree	Normalized degree	Species strength	SSI	Proportional generality
Argulus sp.1	2	0.2	0.101	0.711	0.293
Argulus sp.2	5	0.5	2.983	0.734	0.356
Argulus sp.3	1	0.1	0.714	1.000	0.155
Argulus multicolor	1	0.1	0.200	1.000	0.155
Dipteropeltis sp.	4	0.4	0.708	0.481	0.554
Dolops striata	3	0.3	0.480	0.683	0.346
Dolops bidentata	9	0.9	4.812	0.446	0.714

SSI: Species specificity index.

Table VI. Specificity indices of Branchiura groups with suction discs and hooks on fish from the upper Araguari River, Amapá state, Brazil.

Groups	Degree	Normalized degree	Species strength	SSI	Proportional generality
Suction disc	8	0.8	4.707	0.606	0.567
Hooks	9	0.9	5.292	0.385	0.850

SSI: Species specificity index.

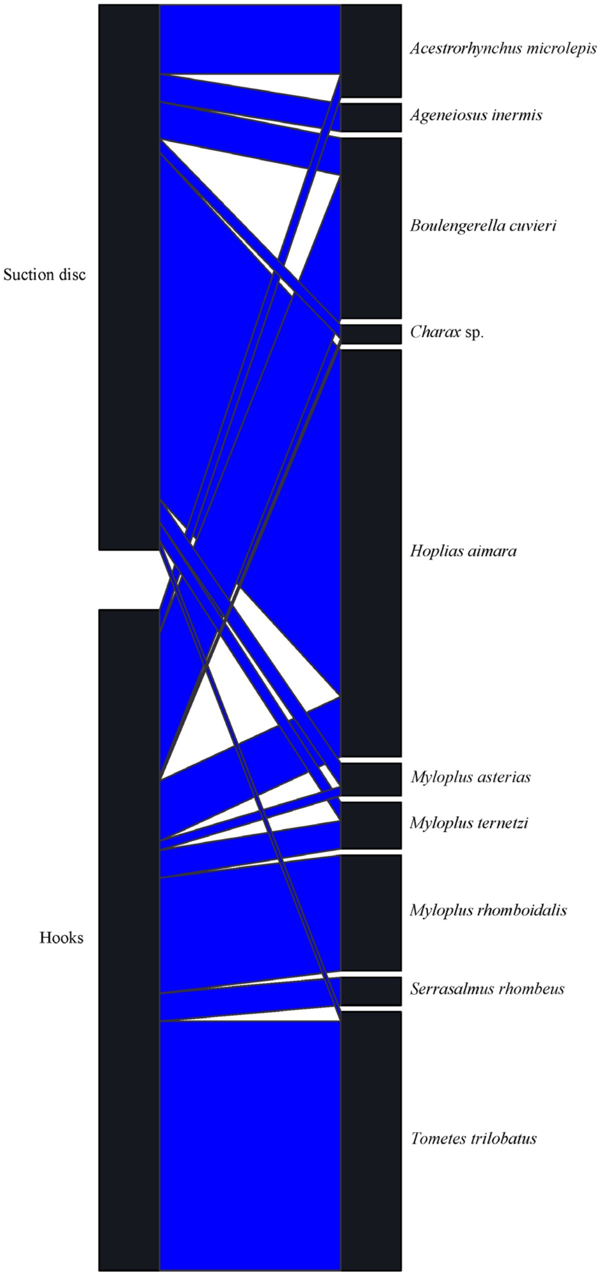

Figure 5. Interaction network of Branchiura functional groups (suction discs and hooks) with fish species of the upper Araguari River, Amapá state, Brazil.

are influenced by host species richness (Poulin 2007). Therefore, we suggest that interspecific competition contributed to this specificity, where the low richness and abundance of these ectoparasites could have provided another interaction scenario, such as a higher number of fish species hosting more than one crustacean parasite species. It is possible that the population density of branchiurans is closely associated with the abundance of host species and, consequently, to parasite-host interactions.

In this study, we grouped branchiuran species according to attachment structures and observed that the group with hooks (*Dolops*) was more of a generalist than the group with suction discs (*Argulus* and *Dipteropeltis*). Host specificity is a reflection of ancestral or ecological conditions (Johnson et al. 2009, Poulin 2007). Traditional ecological theory predicts that interspecific competition selects for an increase in ecological specialization (Futuyma & Moreno 1988, Poulin 2007). Our findings support this hypothesis, as the group of hooked parasites (*Dolops*) are generalists and ancestral in relation to *Argulus* and *Dipteropeltis*, whereas the group with suction discs (*Argulus* and *Dipteropeltis*) are specialists and diverged early (Møller et al. 2008).

Host body size is a variable that partially explains the abundance and species composition of parasites in host fish (Poulin & Leung 2011, Poulin 2007), including fish from the Amazon region (Baia et al. 2018, Tavares-Dias & Oliveira 2017, Oliveira & Tavares-Dias 2016). This relationship has been poorly documented for branchiuran species, possibly due to the low abundance of these crustaceans in the parasitic community of natural fish populations. In this study, a positive correlation was observed between the total abundance of branchiurans and the weight and length of host fish. This increase in the abundance of Branchiura with the growth of host fish is likely due to the increase in the body surface area of the hosts, which constitutes an abundant resource with high capacity to support many parasites (Poulin 2007, Baia et al. 2018). The correlation coefficient of weight better explains this correlation (46% of data) than length (42% of data). It is possible that fish weight is the more important because heavier fish theoretically have better body condition and also a better immune system, increasing the capacity of these fish to house more parasites without affecting their health (Jones et al. 1999, Lagrue & Poulin 2015). In addition, larger fish are easier targets for branchiurans, driven mainly by their swimming abilities when searching for hosts in the environment.

In conclusion, the parasite-host relationship is indeed very close, and the morphological attributes of the parasites and host determine certain patterns. This gives us an understanding of the interaction between branchiurans and their host fish on a broader scale, where these parasites evolved according to the sites they exploit on fish, and this interspecific interaction provided lineages that are more specialized. Assessing the relationship between parasite attachment structures may answer important questions of parasite ecology and may assist researchers in broad inquiries into the evolutionary history of parasites and their host fish. Finally, our hypothesis was that branchiurans that use suction discs and hooks for attachment to host fish parasitize different fish species depending on integument (large-, small-, and no scales). Furthermore, we hypothesized that Branchiura species with hooks (*Dolops*) are generalists and those with suction discs (*Argulus* and *Dipteropeltis*) are specialists, and that branchiuran abundance is greater in larger fish, especially those with greater body weight.

Acknowledgments

(1) Fundação de Amparo à Pesquisa do Amapá (FAPEAP) for its financial support under the project Monitoramento da Atividade Pesqueira no Médio Rio Araguari; (2) Conservação Internacional do Brazil (CI); (3) Walmart Brazil; (4) Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), for their support under the Biology and Ethnoecology of Ichthyofauna in the Amapá National Forest (FLONA) project; (5) Conselho Nacional de Pesquisa e Desenvolvimento Tecnológico

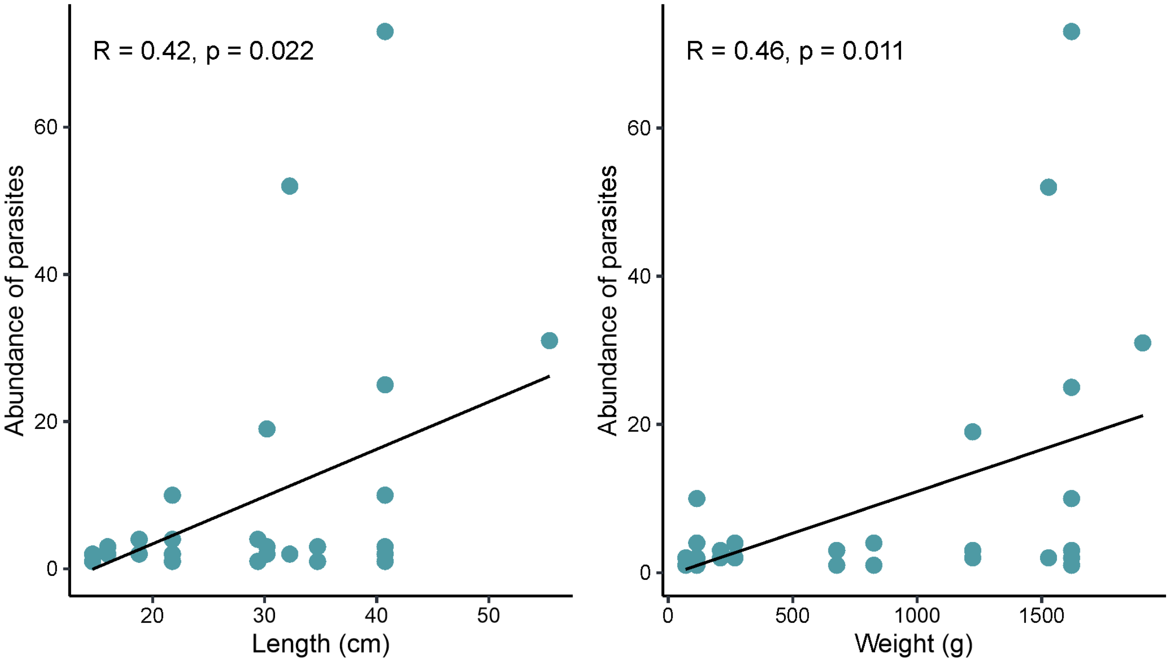

Figure 6. Spearman's correlation between Branchiura species abundance with fish length and weight in the upper Araguari River, Amapá state, Brazil.

(CNPq), for the productivity grant to Tavares-Dias, M., and the Financiadora de Estudos e Projetos, Brazil (the Studies and Projects Funding) (FINEP); (6) Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for granting a doctoral scholarship to Oliveira, MSB and Paulo Mejia, and for granting a master degree scholarship to Ferreira, DO.

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How to cite

FERREIRA DO, OLIVEIRA MSB, MEJIA P, TAVARES-DIAS M & VIDEIRA MN. 2024. Spatial distribution, host specificity, and affinity of Branchiura for surface and macrohabitat types in fish species from the Brazilian Amazon. An Acad Bras Cienc 96: e20240291. DOI 10.1590/0001-3765202420240291.

Manuscript received on March 20, 2024;
accepted for publication on May 4, 2024

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