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Metacercariae of *Austrodiplostomum compactum* (Trematoda, Diplostomidae) in non-native fish species in Brazil: a possible explanation for the high rate of parasitic infection

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Abstract: Metacercariae of Diplostomidae are widely distributed in America and may cause diplostomiasis, an ocular disease in fishes. The aim of this study is to report the occurrence of metacercariae of *Austrodiplostomum compactum* in *Plagioscion squamosissimus* (non-native fish species) from Nova Avanhandava Reservoir, Tietê River, Brazil and an explanation for the high infection rates with this parasite in the Paraná River Basin is proposed. Eyes of 70 hosts were examined, the metacercariae were preserved and identified. The prevalence (P), mean intensity of infection (MII) ± standard deviation, mean abundance (MA) ± standard deviation, were calculated and a bibliographic review was performed. There was no difference in parasitism between male and female hosts. The values of P = 80%, MII = 21.55 ± 3.25 and MA = 17.24 ± 2.91 were high, as in most studies in areas where *P. squamosissimus* were introduced, while these values were low in areas of natural occurrence. This may be explained by the genetic susceptibility of the host to the parasite. The entire population of *P. squamosissimus* from the Upper Paraná has been founded by a few specimens, resulting in very low genetic variability. Consequently, the population may be highly susceptible to *A. compactum*.

Key words: introduced species, fish parasite, eye-fluke, corvina, Sciaenidae, Tietê River Basin.

INTRODUCTION

Metacercariae of Diplostomidae are widely distributed in the Americas (Ramos et al. 2013, García-Varela et al. 2016). Ocular diplostomiasis is a parasitic disease that affects reared and wild fish (Pinto & Melo 2013) caused by metacercariae, which at high densities may result in blindness and retarded development, as well as facilitating predation by piscivorous birds (Shariff et al. 1980, Corrêa et al. 2014). They may also infect the cranial cavity of fish and induce changes in their swimming behavior (Corrêa et al. 2014). In South America, diplostomiasis is mainly caused by species of the genus *Austrodiplostomum* Szidat & Nani, 1951.

The adults of *Austrodiplostomum compactum* (Lutz, 1928) were recorded in several countries from America (Argentina, Brazil, U.S.A., Mexico and Venezuela) inhabit the intestine of the piscivorous birds *Nannopterum auritus* (Lesson, 1831) (=*Phalacrocorax auritus*) and *Nannopterum brasilianus* (Gmelin, 1789) (=*Phalacrocorax brasilianus*) (Szidat & Nani 1951, Dubois 1968, Ostrowski de Núñez 1982, 2017, Dronen 2009, Monteiro et al. 2011, O'Hear et al. 2014, Garcia-Varela et al. 2016, Rosser et al. 2016). Although, cercariae emerge from the tegument of gastropods such as: *Biomphalaria straminea* (Dunker, 1848), *Biomphalaria glabrata* (Say, 1818) (Pinto & Melo 2013), *Biomphalaria prona* (Martens, 1873) (Ostrowski de Núñez 1982), *Biomphalaria obstructa* (Morelet, 1849) (Rosser et al. 2016) and larval forms (metacercariae) can inhabit the eyes of several species of freshwater fishes (Yamada et al. 2008, Ramos et al. 2013). According to Ramos et al. (2013, 2016) and Campos et al. (in press), metacercariae of *A. compactum* have been reported in 38 Brazilian fish species belonging to 13 families of four orders, highlighting the high infection rates in *Plagioscion squamosissimus* (Heckel, 1840).

Plagioscion squamosissimus is a native species of the Amazon, Tocantins (Merona 1986), and Parnaíba Basins (Silva & Menezes 1950), with carnivorous food habits (Hahn et al. 1997, Stefani & Rocha 2009, Neves et al. 2015). The colonization of the Paraná River by this species may have begun in the decade of 1960, through an introduction conducted by the Companhia Energética de São Paulo (CESP) (Torloni et al. 1993). Introduced specimens came from the Nazaré Lake (municipality of Nazaré, State of Piauí, Brazil) and the Feitoria Lake (municipality of Oeiras, State of Piauí, Brazil) in 1949 (Fontenele & Peixoto 1978).

Since then, *P. squamosissimus* has colonized a wide variety of habitats in the Upper Paraná River Basin and it is considered the best example of introduced species successfully established in this basin according to Agostinho et al. (2008). Furthermore, this host presented the highest prevalence and mean intensity of infection values among fish species parasitized by *A. compactum* in the Upper Paraná River Basin.

The aim of the present study was to report the occurrence of metacercariae of *A. compactum* in *P. squamosissimus* from the Bonito River, in the Nova Avanhandava reservoir, Lower Tietê River, State of São Paulo, Brazil, and to propose an alternative explanation for the high rate of parasitic infection in areas where *P. squamosissimus* were introduced (non-natural occurrence).

MATERIALS AND METHODS

This study was conducted in the Bonito River (Nova Avanhandava reservoir, Lower Tietê River Basin) in the municipality of Glicério, State of São Paulo, Brazil (21°12'21.69" S 50°08'36.59" W) (Figure 1). Seventy fish specimens (31 males and 39 females) were collected by fishermen in April 2012, frozen, and transported to the laboratory, where they were weighed (total weight in grams of fish with viscera) and measured (standard length in centimeters measured from the tip of the snout to the final vertebra). Their eyes were removed and examined with the aid of a stereomicroscope. Metacercariae were collected from the aqueous humor and vitreous humor, fixed in alcohol-formalin-acetic acid solution (AFA) under slight pressure with a coverslip, preserved in 70% ethanol, and later stained with carmine and clarified with eugenol for identification (Eiras et al. 2006). Morphometric analysis of the metacercariae was carried out using a computerized system for image analysis with differential interference contrast (DIC) (Leica Application Suite, V3; Leica Microsystems, Wetzlar, Germany) and the identification of the parasite was based on Ostrowski de Núñez (2017). Specifically, for the pseudosuckers (right and left) the length and width measurements were randomly performed because they were symmetrical. Thus, the data presented for this morphological structure come from measurements of the two pseudosuckers grouped of all the samples evaluated. All measurements were described in micrometers

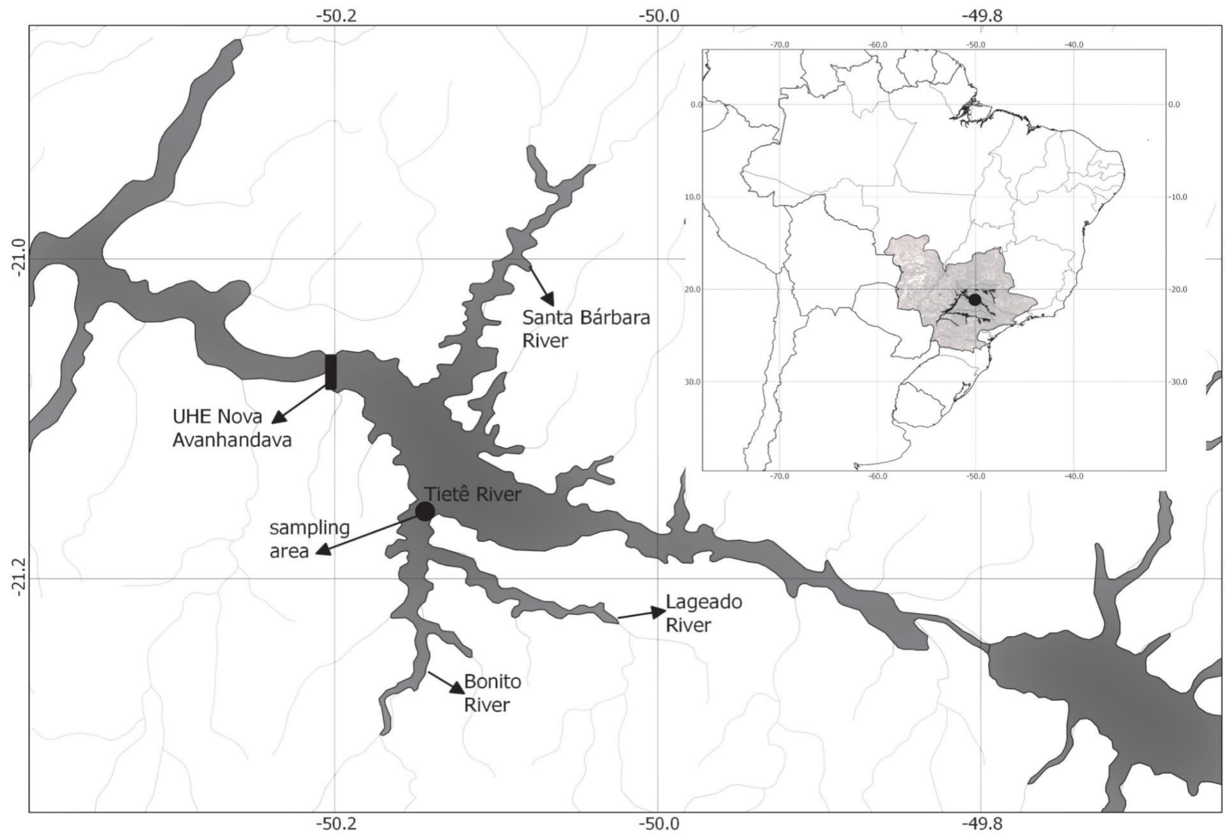

Figure 1. Nova Avanhandava reservoir (Lower Tietê Basin) indicating the sampling area in the Bonito River, State of São Paulo, Brazil.

and represented by mean followed by standard error, and range and number of specimens measured in parenthesis.

Prevalence (P), mean intensity of infection (MII), and mean abundance (MA) were calculated according to Bush et al. (1997), for all studies when possible (present and reviewed studies). Mean intensity of infection and mean abundance are expressed as mean, followed by standard deviation. The prevalence of males and females and the natural and non-natural areas were compared using the *G*-test, while the mean intensity of infection and mean abundance of male and female were compared using the Mann-Whitney test (*U*-test). The mean abundance among the natural and non-natural occurrence areas for *P. squamosissimus* was tested by Summary-*t* test. All statistical tests were performed using BioEstat version 5.3 software. The significance level used was $p<0.05$.

Parasite and host voucher specimens were deposited in the Coleção Helmintológica do Departamento de Bioestatística, Biologia Vegetal, Parasitologia e Zoologia (CHIBB 6723 and 6962) and the Coleção de Peixes do Laboratório de Biologia e Genética de Peixes (LBP 3493), respectively, both in the Instituto de Biociências of the Universidade Estadual Paulista (UNESP), located in the municipality of Botucatu, State of São Paulo, Brazil. A review of the studies on the infection of *P. squamosissimus* by *Austrodiplostomum* spp. in Brazil was carried out using Ramos et al. (2013) and a database search (SciELO, ISI, Scopus, and Google Scholar). Studies with a sample smaller than 20 animals were not considered due to the probability of the sample size influencing the results of the parasitological attributes (P, MII, and MA).

RESULTS

The morphology of the recovered metacercariae followed the redescription proposed by Ostrowski de Núñez (2017): body bipartite; forebody spatulate, slightly concave ventrally (1253.0 ± 41.3 (941.3–1583.3; n=21) long and 456.9 ± 17.1 (310.8–624.5; n=23) wide); hindbody very short, with a small conical segment (98.1 ± 5.5 (64.0–132.4; n=16) long and 88.5 ± 5.3 (52.5–130.9; n=19) wide). Oral sucker subterminal (40.5 ± 2.5 (29.2–59.2; n=13) long, and 52.9 ± 2.1 (32.2–72.1; n=22) wide), two lateral pseudosuckers well developed and symmetric, on each side of oral sucker (pseudosuckers 94.3 ± 3.8 (52.3–137.4; n=19) long and 69.3 ± 3.3 (42.3–120.5; n=19) wide); ventral sucker absent. Small pharynx (60.2 ± 5.0 (38.5–90.2; n=12) long and 54.9 ± 4.3 (37.7–90.2; n=12) wide), esophagus short (24.6 ± 2.9 (18.2–37.8; n=6) long), ceca simple, reaching until level of genital primordia. Holdfast organ (= tribocytic organ) elliptical and bilobed (321.0 ± 18.9 (201.8–538.3; n=20) long and 179.6 ± 9.6 (104.7–257.8; n=20) wide). Glandular cells most spread in the anterior region, extending from pseudosuckers to the region before of the tribocytic organ. Genital primordia poorly developed, differentiated in two small testes, ovary not distinct.

Seventy fish (standard length 14.1 ± 0.1 (11.4–16.3) cm; total weight 57.9 ± 1.6 (29.1–84.3) g), of which 39 males (standard length 13.8 ± 0.2 (11.4–16.0) cm, total weight of 54.6 ± 2.6 (33.7–81.9) g), and 31 females (standard length of 14.3 ± 0.1 (12.0–16.3) cm, total weight of 60.7 ± 2.0 (29.0–84.3) g) were examined. The length and weight of the males and females were similar (*U*-test $p>0.05$).

The overall prevalence was 80% (male 77.4% and female 82.1%), mean intensity of infection 21.6 ± 3.3 (male 16.8 ± 2.8 and female 25.2 ± 5.2), and mean abundance 17.2 ± 2.8 (male 13.0 ± 2.51 and female 20.6 ± 4.6). A total of 1207 (1–151 per host) parasites were collected from the eyes of 56 *P. squamosissimus* specimens, of which 402 (1–51 per host) were from males and 805 (1–151 per host) from females. No significant differences in prevalence (*G*-test $p>0.05$), mean intensity of infection, and mean abundance (*U*-test $p>0.05$) were observed between male and female hosts.

The prevalence, mean abundance and mean intensity of infection with metacercariae of *A. compactum* in the aqueous humor and vitreous humor of *P. squamosissimus* observed in the present study and others studies in non-natural occurrence area were higher than in the natural occurrence area ($p<0.05$) (Table I).

DISCUSSION

Metacercariae analyzed in the present study are morphologically similar to that redescribed by Ostrowski de Núñez (2017) (Table SI – Supplementary material), and therefore, assumed to belong to *A. compactum*. Similar prevalence, mean abundance and mean intensity of infection of the male and female fish were observed, as previously reported by Martins et al. (2002) and Machado et al. (2005). According to Machado et al. (2005), this fact can be related to similar physiological or behavioral patterns between male and female specimens of *P. squamosissimus*. We can, therefore, infer that sex is probably a non-determinant factor for infection with metacercariae of *A. compactum* in *P. squamosissimus*.

Table I. List of studies recording *Austrodiplostomum compactum* metacercariae in the eyes of *Plagioscion squamosissimus* in Brazil. Number of specimens examined (N), prevalence (P), mean intensity of infection (MII) and mean abundance (MA). Mean values followed by standard deviation when available; different small letter = significative difference (*p*<0.05) between the natural (Solimões River) and non-natural occurrence area; different capital letters = significative difference (*p*<0.05) between the natural (Tocantins River) and non-natural occurrence area. CF = area close to cage fish farm; CT = area not influenced by cage fish farms.

Studies	N	P (%)	MII	MA	State/River	Coordinates
Natural occurrence area						
Lacerda et al. (2012)	35	40.0a	10.8	4.3±7.8a	AM/Solimões	4°2'0"S, 63°15'16"W
Lacerda et al. (2012)	35	8.3A	2.9	0.1±0.5A	TO/Tocantins	10°66'55"S, 48°42'36"W
Non-natural occurrence area						
Martins et al. (1999)	68	45.6aB	7.1	3.2	MG/Grande	Volta Grande reservoir (uninformed)
Martins et al. (2002)	70	52.8aB	5.3	2.8	MG/Grande	Volta Grande reservoir (uninformed)
Souza-Santos et al. (2002)	61	91.8bB	42.0	38.5	SP/Paraná	NUPELIA Base (uninformed)
Machado et al. (2005)	81	95.1bB	38.9±64.3	37.0±63.2bB	PR/Paraná	33 different sites (uninformed)
Paes et al. (2010a)	378	94.2bB	21.7	20.4	SP/Tietê	21°07'S, 50°17'W
Paes et al. (2010b)	213	90.1bB	20.8	18.7	SP/Tietê	21°07'S, 50°17'W
Kohn et al. (2011)	61	36.1aB	-	-	PR/Paraná	25°32'52"S, 54°35'17"W
Lacerda et al. (2012)	35	88.6bB	98.8	87.5±153.3bB	PR/Paraná	22°46'11"S, 53°17'6"W
Souza-Santos et al. (2012)	57	98.0bB	42.7	41.9	PR/Paraná	21°45'48"S, 52°06'56"W
Ramos et al. (2013)	30	66.6bB	13.1±6.1	8.7±23.0bB	SP/ Paranapanema	23°07'36"S, 49°59.23'10"W
Ramos et al. (2014) CF	37	86.4bB	20.3±1.1	17.7±38.3bB	SP/ Paranapanema	23°07'37"S, 49°30.71'37.31"W
Ramos et al. (2014) CT	28	57.1aB	4.3±7.1	2.3±4.2	SP/ Paranapanema	23°07'36"S, 49°59.23'10"W
Present study	70	80.0bB	21.55±3.2	17.24±23.4*	SP/Tietê	21°12'21.69"S, 50°08'36.59"W

However, the mean intensity of infection of the fish analyzed in the present study (21.5 ± 3.2) was similar to that observed by Karvonen et al. (2004) for *Diplostomum spathaceum* (Rudolphi, 1819). Karvonen et al. (2004) reported that the fish harbored more than 20 metacercariae per eye, had cataracts coverage of 100%, causing vision problems. Hahn et al. (1997) affirmed that *P. squamosissimus* is a visual predator, has large eyes arranged laterally to the skull, and carnivorous. Therefore, it is possible to infer that infection with metacercariae of *A. compactum* can affect food intake, as described by Owen et al. (1993) for *Gasterosteus aculeatus* Linnaeus 1758, and Crowden & Broom (1980) for *Leuciscus leuciscus* (Linnaeus, 1758). These infections also alter fish behavior when metacercariae are found in the cranial cavity, as reported by Seppälä et al. (2004) for *Oncorhynchus mykiss* (Walbaum, 1792) and Corrêa et al. (2014) for *Hoplias malabaricus* (Bloch, 1794), with consequences for susceptibility to predation.

Another important fact observed is the maintenance of high rates of infection over time. In a previous study with *P. squamosissimus* in the Nova Avanhandava reservoir, Paes et al. (2010b) recorded a mean abundance of metacercariae of *A. compactum* in the aqueous humor of 18.7 and a mean intensity of infection of 20.8 parasites per host, similar to the results observed in the present study (mean abundance 17.2 ± 2.9 and mean intensity of infection 21.5 ± 3.2). Thus, local environmental conditions may not have changed over this period or did not influence the infection rates of metacercariae of *A. compactum* in *P. squamosissimus*.

Lacerda et al. (2012) suggested that *P. squamosissimus* in Upper Paraná River Basin may be acting as a new and very suitable host for a local *Austrodiplostomum* sp., i.e., a reservoir for native parasites from which infections flow back to native hosts, which firstly could be explained by the spillback. Parasite spillback process second Kelly et al. (2009), could occur when a non-native species is a competent host for a native parasite, with the presence of the additional host increasing disease impacts in native species. However, there is no data available for the incidence of *Austrodiplostomum* metacercariae in native fish species, anterior to the introduction of *P. squamosissimus* in non-natural occurrence area (Upper Paraná Basin).

The prevalence of metacercariae of *Austrodiplostomum* exceeds 20% in native fish species such as *Crenicichla britskii* Kullander, 1982, *Eigenmannia trilineata* López & Castello, 1966, *Hoplias malabaricus, Hypostomus iheringii* (Regan, 1908), *Hypostomus regani* (Ihering, 1905), *Hypostomus strigaticeps* (Regan, 1908), *Loricariichthys castaneus* (Castelnau, 1855) and *Pimelodus maculatus* Lacépède, 1803 (Ramos et al. 2013).

Additionally, to the hypothesis proposed by Lacerda et al. (2012), we present another fact that could also contribute to the high infection rates observed in *P. squamosissimus* in the Upper Paraná River Basin. We infer that non-native hosts with high prevalences such as *Cichla kelberi* Kullander & Ferreira, 2006, *Geophagus sveni* Lucinda, Lucena & Assis, 2010 (= *Geophagus proximus*), *Satanoperca pappaterra* (Heckel, 1840) and *P. squamosissimus* (Ramos et al. 2013) may be acting as parasitic amplifiers, and possibly contributing to increase the population of *A. compactum* metacercariae in the Upper Paraná River Basin. Moreover, the high infection rates and prevalence observed in *P. squamosissimus* may be related to the low genetic variability of non-native populations.

According to Lively (2010), the high genetic diversity of hosts is important to reduce the spread of disease in natural populations and would, therefore, reduce infection. This hypothesis is supported by studies from the plant (Zhu et al. 2000) and animal hosts for a several diseases/parasites (Dwyer et al. 1997, Baer & Schmid-Hempel 1999, Altermatt & Ebert 2008), in which the possibility of infection was related to the genetic variability of the host. The possible influence of the host genetic susceptibility to the parasite (*P. squamosissimus* x *A. compactum*) was previously proposed by Souza-Santos (2002) to explain the high infection rates, but without considering the genetic data of the hosts.

Plagioscion squamosissimus from the Upper Paraná River Basin shares a single haplotype with populations from the Parnaíba River, revealing that *P. squamosissimus* offspring from the Parnaíba River Basin occur only in the Paraná River Basin and have low kinship with the populations of the Amazon River Basin (Panarari-Antunes et al. 2012). According to Panarari-Antunes et al. (2012, 2015) and Diamante et al. (2017), the non-native populations of *P. squamosissimus* from the Upper Paraná River Basin and the native population of the Parnaíba River, have low polymorphism and high genetic similarity. These populations of *P. squamosissimus*, however, differ genetically from the Araguaia-Tocantins native population, which is the most basal and polymorphic population.

The high rate of prevalence and intensity of infection with *A. compactum* metacercariae in *P. squamosissimus* could be explained by the fact that the colonization in the Upper Paraná River Basin occurred with a small founding population, which was highly susceptible to this parasite. As the entire population of *P. squamosissimus* from the Upper Paraná River Basin was founded by few specimens, causing very low genetic dissimilarity and consequently high kinship, the entire population could be highly susceptible to infection with *A. compactum* metacercariae. This fact could also be applied to other non-native invasive species that have high rates of infection with *A. compactum* metacercariae and large populations in the Upper Paraná River Basin.

Other natural mechanisms not linked to genetic diversity could explain the higher rates of prevalence and infection in non-native species in the Upper Paraná River Basin. Larger populations of intermediate hosts, such as gastropods (specifically belonging to the genus *Biomphalaria*), and piscivorous birds, coupled to high temperatures and favorable hydrological conditions, could contribute to an increase in the rates of infection with *A. compactum* metacercariae. This fact was observed between *P. squamosissimus* and *A. compactum* metacercariae by Ramos et al. (2014) in areas close to cage fish farms when compared to areas without the influence of this type of aquaculture activity in the Upper Paraná River Basin. However, there are no population size data available for gastropods and piscivorous birds in natural and non-natural occurrence areas of *P. squamosissimus*.

It is possible to infer that the high infection rate observed in the Upper Paraná River Basin, may be related to the life and introduction history of *P. squamosissimus* in this basin, which has resulted in very low genetic variability contributing to the amplifier host process.

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SUPPLEMENTARY MATERIAL

Table SI.

How to cite

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Igor Paiva Ramos, as the main author, contributed to the laboratorial analysis, general structure of the manuscript, discussion of the results and interpretations contained in this manuscript. Cibele Diogo Pagliarini took part in the scientific discussions and interpretation contained in this manuscript. Lidiane Franceschini contributed to parasite identification and laboratorial analysis, and took part in the structuration, scientific discussions and interpretation contained in this manuscript. Reinaldo José da Silva took part in the scientific discussions and interpretation contained in this manuscript.