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Habitat selection and maturation of *Saccocoelioides nanii* (Digenea: Haploporidae) in *Prochilodus argenteus* (Actinopterygii: Prochilodontidae) from the São Francisco River, Brazil

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ABSTRACT. This work examined the possible preference of *Saccocoelioides nanii* Szidat, 1954 for the three major intestinal portions of *Prochilodus argenteus* Agassiz, 1829 and statistically evaluated whether the river water level dynamic interfered in the parasite's ecological parameters and in its transmission to the definitive host. One-hundred-fifty specimens of *P. argenteus* were collected in July, 2003 (dry season) and in January, 2004 (rainy season) in the upper São Francisco River, State of Minas Gerais, Brazil. Of the 150 hosts, 96 (64%) were parasitized by *S. nanii.* The mean intensity and abundance were 32.6 ± 34.8 and 20.8 ± 31.9, respectively, and the range of infection intensity was from 1 to 177. The abundance of *S. nanii* was higher in the middle intestine than in either the anterior or posterior portions. This selection could be evidence of niche restriction to facilitate mating. The proportion of non-pregnant specimens of *S. nanii* was higher in the dry season as well as the intensity and abundance. At least two hypotheses can be considered for elucidated this inference: the presence/absence or change in the quantity of some substance in the host body amending/inhibits the reproduction of the parasite or that non-pregnant specimens corresponds to newly recruited individuals who did not have time to reproduce.

KEY WORDS. Niche; parasite ecology, São Francisco Basin.

Species of *Saccocoelioides* Szidat, 1954 live in the intestine of freshwater and occasionally estuarine fish in North and South America (Overstreet & Curran 2005). Kohn (1985) presented new morphological data, measurements and figures of the syntypes of *Saccocoelioides nanii* Szidat, 1954. Dyer *et al.* (1999) described *Saccocoelioides agnostomun* Dyer, Bunkley-Williams & Williams Jr, 1999 and provided a summary of the genus *Saccocoelioides*. Lizama *et al.* (2006) analyzed the influence of seasonal and environmental patterns and host reproduction on *S. nanii* and other metazoan parasites of *Prochilodus lineatus* (Valenciennes, 1836). They showed that the abundance of the latter was higher during the reproductive period of the host, and that the prevalence was positively correlated with water temperature. There is no available information on the distribution of *S. nanii* and the species' preference for a particular portion of the host's intestine. Other aspects of the biology of *S. nanii* are also unknown, such as life cycles and the correlation between host and parasite reproductive periods. *Prochilodus argenteus* Agassiz, 1829, known popularly as the "curimatá-pacú", is a detritivorous species (Alvim & Peret 2004) that migrates long distances (Gomes & Verani 2003). It is endemic to the São Francisco River and makes up a considerable portion of the fish catch in the upper São Francisco region (Sato *et al.* 1996).

The rainy and dry seasons are well defined in the upper São Francisco basin. The beginning of the rainy season and the associated limnological changes trigger the start of reproduction of migratory spawning fish species (Lowe-McConnell 1987).

In this paper, the possible preference of *S. nanii* for some portions of the intestine of *P. argenteus* is evaluated, as well as whether the river water level dynamics interferes in with the parasite's ecology, and thus with its transmission to the definitive host.

MATERIAL AND METHODS

One-hundred and fifty specimens of *P. argenteus* were collected in July, 2003 (dry season – 89 specimens) and in January, 2004 (rainy season – 61 specimens) in the region of the upper São Francisco River, downstream from the Três Marias Dam (18°12'32"S, 45°15'41"W), in the municipality of Três Marias, State of Minas Gerais, Brazil. In the necropsies, the intestine was divided into three portions: anterior, middle and posterior. The specimens of Digenea found in the infected hosts were counted to compose the three infrapopulations based on each intestinal portion. Specimens were processed according to Amato *et al.* (1991) to obtain permanent slides, and identified according to Travassos *et al.* (1969).

The prevalence, intensity and abundance of *S. nanii* were calculated for all samples combined, and in separate, for the two rainfall periods (rainy and dry), and abundance was also calculated separately for the anterior (AI), middle (MI) and posterior intestinal (PI) portions. To determine whether the *S. nanii* parasites were more abundant at a particular portion of the intestine, the Friedman test (χ^2_r) and the Mann-Whitney (U) test were used to detect possible pair-wise differences in abundance. In the statistical analyses, all hosts included were parasitized in at least one intestinal region. The helminths of hosts that showed abundance greater than or equal to the mean of each season were separated into two groups: not pregnant (without eggs in the uterus) and pregnant (with eggs in the uterus). The Chi-square (χ^2) test was used to compare the proportion of pregnant and non-pregnant specimens of *S. nanii* between the two periods (rainy and dry). The Chi-square test with Yates' correction was used to verify if the prevalence (P) was influenced by the rainfall dynamic of the São Francisco River, and the Mann-Whitney test to evaluate the variation in intensity (I) and abundance (A) of parasites. The ecological terminology follows Bush *et al.* (1997) and the statistical tests followed Zar (1996), to the level of significance, $p < 0.05$. Voucher specimens of the host were deposited in the Museu de Zoologia of the Universidade de São Paulo (USP), São Paulo, Brazil (MZUSP 95167), and specimens of *S. nanii* in the Coleção Helmintológica do Instituto Oswaldo Cruz, Rio de Janeiro, Brazil (CHIOC 36917, 36918a, b).

RESULTS

Of the 150 hosts examined, 96 (64%) were parasitized by *S. nanii*. The prevalence, range, mean intensity and mean abundance of *S. nanii* are given for the total sample, and for the two rainfall periods (Tab. I). The abundance at the different intestinal portions (Tab. II), and the proportion of pregnant and non-pregnant individuals in each rainfall period (Tab. III) are also presented.

The intensity and abundance of the parasites were higher in the dry season (I = 41.21 ± 38.42, A = 30.56 ± 37.68) than in the rainy season (I = 13.50 ± 10.97, A = 6.64 ± 10.22) (U = 425.50, $p < 0.0001$ and U = 1472.00, $p < 0.0001$, respectively). There was no significant difference in the prevalence of *S. nanii* between the two sampling periods ($\chi^2 = 8.74$, p = 1.508).

Thirteen hosts had only parasites at one portion of the intestine: one in the anterior intestine (7.69%), ten in the middle intestine (76.92%) and two in the posterior intestine (15.38%). The abundance of *S. nanii* was higher in the middle intestine (A = 11.17 ± 20.77) than in the anterior (A = 5.23 ± 9.88) or posterior (A = 4.43 ± 0.10) of *P. argenteus* ($\chi^2_r = 23.93$, $p < 0.0001$) (AI – MI: U = -3.96, $p < 0.0001$; AI – PI: U = -1.11, p = 0.266; MI – PI: U = -4.84, $p < 0.001$), respectively. The proportion of non-pregnant specimens of *S. nanii* in the samples was higher in the dry season ($\chi^2 = 18.01$, $p < 0.0001$).

DISCUSSION

In general, helminths are highly specific (Stock & Holmes 1988), and are characterized by having habitat preferences within specific host sites. Each parasite occupies its own habitat, since the resources are limited in the host (Sukhdeo 1990). This study has shown that the middle intestine of *P. argenteus* is the region most commonly used by *S. nanii*. This preference could be a result of a niche restriction that facilitates mating (Rohde 1994). The anterior and posterior portions of the intestine were rarely infected by other adult helminths, and may be considered underexploited, thus constituting vacant niches available for colonization by *S. nanii*. Although the middle intestine was region most heavily parasitized by *S. nanii,* the distribution of individuals of this species along the entire intestine may represent a low level of specialization of this host

Table I. Prevalence, range, mean intensity, mean abundance of *S. nanii* of *P. argenteus*, from the São Francisco River, Três Marias, Minas Gerais, Brazil.

Seasons	Prevalence (%)	Range	Mean intensity	Mean abundance
Rainy season	49.18	1 – 50	13.50 ± 10.97	6.64 ± 10.22
Dry season	74.15	1 – 177	41.21 ± 38.42	30.56 ± 37.68
Total	64.00	1 – 177	32.55 ± 34.84	20.83 ± 31.93

Table II. Abundance of *S. nanii* in the different intestinal portions of *P. argenteus*, from the São Francisco River, Três Marias, Minas Gerais, Brazil.

Intestinal portion	Abundance
Anterior	5.23 ± 9.88
Middle	11.17 ± 20.77
Posterior	4.43 ± 0.10

Table III. Proportion of pregnant and non-pregnant specimens of *S. nanii* of *P. argenteus*, from the São Francisco River, Três Marias, Minas Gerais, Brazil, in the rainfall periods.

Rainfall periods	Pregnant (%)	Non-pregnant (%)
Dry	27.30	72.70
Rainy	41.55	58.45

regarding infection site, directly related to its high tolerance to the physiological conditions in each portion of the intestine (Stock & Holmes 1988). It is possible that the absence of other helminths allows *S. nanii* to expand its distribution to other areas with available resources to accommodate a greater number of parasites through occupation of a broader range of niches. The latter would be difficult in the presence of competitors (Poulin 2007).

Lizama *et al.* (2006) showed that the abundance of *S. nanii* in *P. lineatus* was higher during the rainy season the same is valid during the dry season for *S. nanii* in *P. argenteus*. Abiotic factors can interfere directly and/or indirectly in the development of parasites (Poulin 1996). Changes in water temperature, for example, can have a direct influence on the free-living larval stages of parasites, and can indirectly affect their growth, maturation, and reproduction inside their hosts (Pojmánska 1995). Alterations in the physical-chemical parameters of the water at the beginning of the rainy season trigger the start of the spawning season of *P. argenteus,* which occurs from November to January (Sato *et al.* 2003).The presence of non-pregnant individuals in both dry and rainy seasons suggests that the biological cycle of *S. nanii* was maintained in the two periods and that it was not synchronized with that of the host. Similarly, there were digenetic specimens with the uterus filled with eggs in both seasons. These results indicate a discrete seasonal maturation pattern for *S. nanii*. However, the proportion of non-pregnant digenetics in the infrapopulations was higher in the dry season, probably due to an increase in larval recruitment by the definitive host in this period. The presence of pregnant specimens of *S. nanii* in the two periods indicates that there is no synchronization between the reproduction of the parasite and the host. It also demonstrates that the intermediate and definitive hosts of *S. nanii* share the same environment both in the rainy and dry seasons, thus permitting the continuity of the parasite's biological cycle. The abundance of *S. nanii* in the dry season was a reflection of the greater number of non-pregnant specimens at infrapopulation, since the number of adults did not change significantly. From this observation, two hypotheses can be generated: 1) non-pregnant specimens may be a result of physiological changes in the host, which may have impacted the reproduction of the parasite. Hosts have mechanisms to maintain their homeostasis, i.e. their physical and chemical parameters within specified levels (Combes 2001). Changes in hormones and other substances related to sexual maturation and reproduction, however, may impact the egg production in *S. nanii*; 2) non-pregnant specimens can be considered newly recruited individuals who have not had enough time to mature. Studies on the life cycle of species of *Saccocoelioides* address only the developmental stages that occur in the aquatic environment and in the invertebrate host (see Martorelli 1988, Díaz & González 1990). Therefore, there is no information available about the time needed for sexual maturation and early reproduction in the definitive host. However, Díaz *et al.* (2009) elucidated the life cycle of *Culuwiya tilapiae* (Nazir & Marval, 1976) in Venezuela, and compared it to that of other living species *Culuwiya* Overstreet & Curran, 2005 and *Saccocoelioides tarpesensis* Díaz & González, 1990 (Haploporidae). They considered the life-cycle of all these species to be similar, at least in the early stages of development. *Culuwiya tilapiae* needs approximately 23 days inside the host to start reproduction (Díaz *et al.* 2009). If the cycle of *S. nanii* follows a similar pattern to that of other species in the family, non-pregnant specimens found in the gut of *P. argenteus* can correspond to newcomers who have not yet started eggs production.

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