*Journal of Helminthology*

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## Research Paper

**Cite this article:** Lehun AL, Cavalcanti LD, Lizama MdelosAP, Santos Silva JO, Casali GP, Takemoto RM (2022). Temporal effects and changes in the parasitic community of *Prochilodus lineatus* (Valenciennes, 1837) (Characiformes: Prochilodontidae) in a floodplain. *Journal of Helminthology* **96**, e4, 1–8. https://doi.org/10.1017/S0022149X21000742

Received: 14 September 2021
Revised: 5 November 2021
Accepted: 4 December 2021

**Keywords:**
Dams; anthropogenic effects; digeneans; acanthocephalans; ichthyofauna

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# Temporal effects and changes in the parasitic community of *Prochilodus lineatus* (Valenciennes, 1837) (Characiformes: Prochilodontidae) in a floodplain

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### Abstract

The construction of dams causes several impacts on aquatic environments, altering the flow of rivers, environmental variables, and all biota present, including parasites. Little is known about how the parasitic community can be influenced in the long term by environmental changes. In this study, it was expected that the impacts caused by environmental disturbances will be directly reflected by the composition of the parasite populations. We evaluated the change in the structure of the *Prochilodus lineatus* endoparasite community between two periods sampled 15 years apart in the upper Paraná River floodplain. There was a significant difference in the weight–length relationship of *P. lineatus* between these periods and a total of 15 species of parasites were found: 11 species in Period 1 and nine species in Period 2 and five species occurred in both periods. The species richness and diversity were higher in Period 1, and we observed that the correlation of descriptors (richness, diversity and evenness) increased with fish length in this period. In both periods, digeneans numerically dominated the parasitic community, and we verified changes in the composition of parasites between periods. Both the host and the parasites were possibly affected by the environmental impacts resulting from the construction of dams over time, and it is noteworthy that complex life cycle parasites such as Digenea and Acanthocephala require intermediate hosts to complete their life cycle, and the population responds to fluctuations in the face of modified environments.

## Introduction

The degradation and homogenization of natural habitats are causes of the accelerated loss of biodiversity in the last decades (Brooks *et al.*, 2006). The intensities of the intermediate disturbances and other environmental fluctuations can reduce the dominance of some species, interfering in the dynamics of the evolutionary and ecological processes of aquatic ecosystems (Reid & Ogden, 2006), such as floodplains. The damming of rivers interferes in the hydrodynamics of the system of flood and drought pulses, and the connectivity between habitats (Junk *et al.*, 1989; Neiff, 1990; Agostinho *et al.*, 2004a, b).

Due to the increase in the number of dams and the resulting effects on the flooding of the main watercourses in the Paraná Basin, the local physical, chemical and biological characteristics have undergone various changes (Agostinho *et al.*, 2009; Santos *et al.*, 2017). The impacts caused by natural flooding oscillations or by anthropic influence cause high environmental modification and contribute to changes in the composition of species (Tombolini *et al.*, 2014; Ceschin *et al.*, 2015; Abati *et al.*, 2016; Winemiller *et al.*, 2016). This change in biodiversity is observed in the ichthyofauna of a specific region and directly reflects on the structure and composition of its parasite communities (Pavanelli *et al.*, 2004).

The interaction between biotic and abiotic factors in an ecosystem is essential to the composition and structure of parasite communities (Poulin, 2007). In a parasite community, some species undergo substantial changes and this has been explained primarily by parasite life cycles, environmental dynamics and host-specific immune responses (Fallon *et al.*, 2003; Violante-González *et al.*, 2008; Nagel *et al.*, 2009; Vital *et al.*, 2011). In dams, the distribution of parasites depends on the coverage of upper aquatic vegetation, the extent of shallow areas and the density of bird populations attracted to the reservoir (Iskov, 1976; Morley, 2007). The area closest to the dam is generally narrower and deeper, has slower water flow and relatively

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low temperatures, resulting in a low population density of invertebrates and fish, and consequently few parasites with complex life cycles (Markevich *et al.*, 1976; Izyumova, 1979; Morley, 2007). Thus, the definitive host and the intermediate hosts must co-occur in a stable community for the endoparasite to survive (Landsberg *et al.*, 1998) and changes in the host fauna can hinder the transmission of endoparasites and, thus, modify parasitic biodiversity (MacKenzie, 1999).

*Prochilodus lineatus* (Valenciennes, 1837), popularly known as curimba, is a species of fish that has always presented high biomass in the upper Paraná River floodplain (Gubiani *et al.*, 2007). Their diet consists of inorganic detritus and particles of organic matter that comprise the bottom body of aquatic environments, in addition to algae and benthic macroinvertebrates that are found in this environment (Fugi *et al.*, 1996; Lopes *et al.*, 2007). Considered medium-sized, their migratory habits are dependent on the flood pulses of floodplains because they migrate upstream during floods to spawn in tributaries (Lizama *et al.*, 2005; Oyakawa *et al.*, 2009; Piana *et al.*, 2017). After hatching, the larvae drift downstream, reaching floodplain lakes where they develop into the juvenile and adult stages, grow and mature until the flood pulses again when they are apt to reproduce. After the closing of the Engineer Sérgio Motta Dam in Porto Primavera (state of São Paulo, Brazil) in November 1998, which caused the interruption of the critical phase of the floods in this floodplain (Agostinho *et al.*, 2004a, b), the life cycle of the species underwent considerable changes, since the number of individuals in their populations has steadily decreased (Rosa & Lima, 2008; Oyakawa *et al.*, 2009).

In this study, it is expected that the impacts caused by environmental disturbances will be directly reflected in the composition of the parasite populations; thus, we evaluated the change in the structure of the *P. lineatus* endoparasite community between two periods sampled 15 years apart in the upper Paraná River floodplain.

## Material and methods

### Study area, host and parasite sampling

The upper Paraná River floodplain is situated between the Engineer Sérgio Motta Dam (North) and Itaipu Reservoir (South) and is the last remaining free-flowing stretch of this river (230 km long) within Brazil (fig. 1). This river stretch is regulated by the cascade of dams upstream (e.g., Muniz *et al.*, 2021), but receives large tributaries and still has marked water level variations, although not as intense and as frequent as before the dams were built (Gubiani *et al.*, 2007). The collections occurred in two periods, where Period 1 corresponds to the collections in the years 2000 and 2001, and Period 2 corresponds to the collections in the years 2016 and 2017.

Specimens of *Prochilodus lineatus* were collected using gillnets of different mesh sizes (2.4, 3, 4, 5, 6, 7, 8, 10, 12, 14 and 16 cm between opposite knots on 20 m long nets) for both periods. The nets were deployed for 24 h and checked at 8:00 h, 16:00 h and 22:00 h. It is fundamental to clarify that the sampling effort for fish collections was standardized and is part of the Long Term Ecological Research Program (LTER) that has been monitoring the upper Paraná river floodplain since 2000 (LTER PIARP-site 06). The captured fish were anaesthetized with 5% benzocaine, euthanized according to the LTER PIARP-06 protocol, measured, weighed and eviscerated. Each fish was identified based on specialized literature. The intestine was collected and screened in the laboratory, and the sampled endoparasites were collected, fixed (Eiras *et al.*, 2006) and identified according to Moravec (1998), Vidal-Martínez *et al.* (2000), Thatcher (2006) and Kohn *et al.* (2007). A total of 149 specimens of *P. lineatus* were collected in Period 1 and 40 specimens in Period 2 in the floodplain (table 1).

To test the sufficiency of samples (number of hosts collected), the species accumulation curve was performed for both periods (fig. 2) using the iNEXT package (Hsieh *et al.*, 2016). The number of hosts collected, even in Period 2, was sufficient to obtain a representative sample of the parasite species present in the infra-communities and both curves showed a trend towards stability.

### Data analysis

To assess whether individuals showed differences in weight and length between periods, we used the analysis of covariance (ANCOVA). We used the weight and length of individuals as the response variable and covariate in the model, respectively. The period was used as a fixed factor. At ANCOVA we tested the parallelism (homogeneous slope) assumption of standard ANCOVA through the interaction between period and length (García-Berthou & Moreno-Amich, 1993).

In addition, the relative condition factor (Le Cren, 1951) was performed for each analysed fish and the weight/length ratio was estimated using the equation ($Wt = a * Lt^b$), where $Wt =$ weight, $a =$ intercept, $Lt =$ total length, and the exponent b is derived from the weight-to-length ratio. The a and b values were used to calculate the expected weight ($We = a * Lt^b$) and then the relative condition factor (Kn) was calculated as the ratio of the observed weight to the theoretically expected weight ($Kn = Wt/We$). To assess the differences in condition factor between periods and parasitized and non-parasitized fish, the non-parametric Kruskal–Wallis (H) analysis was performed.

To describe the structure and quantitative analysis of the parasites found, we used the parasitic indices described by Bush *et al.* (1997). Four descriptors of the parasite infra-communities were calculated: abundance (the sum of all parasites); richness (number of species); species diversity (calculated using the Shannon index); and evenness (calculated using the Pielou index). As the parasite descriptors did not present normal distribution, we used non-parametric tests: the Mann–Whitney test to compare parasite descriptors between periods and Spearman's correlations to correlate parasitological variables and fish body length.

As an exploratory method, a non-metric multidimensional scaling (NMDS) (vegan package) was performed based on the Bray–Curtis dissimilarity matrices, in two dimensions, to visualize the differences in the parasite community between the sampled periods (Period 1 and Period 2). To detect significant differences in the parasite community between the periods a multivariate permutational analysis of variance (PERMANOVA) with 999 permutations was applied (vegan package) (Anderson, 2005). We used the indicator species analysis (IndVal) to determine the representative parasite species in each sample period (indicspecies package) (Dufrêne & Legendre, 1997). The level of statistical significance adopted was $P \leq 0.05$. All of these statistical procedures were performed using R 3.2.4 software (R Development Core Team, 2017).

## Results

In the ANCOVA performed for the host weight and length data, we found a significant effect of the period on the weight–length relationship, being that the individuals collected in Period 1 showed

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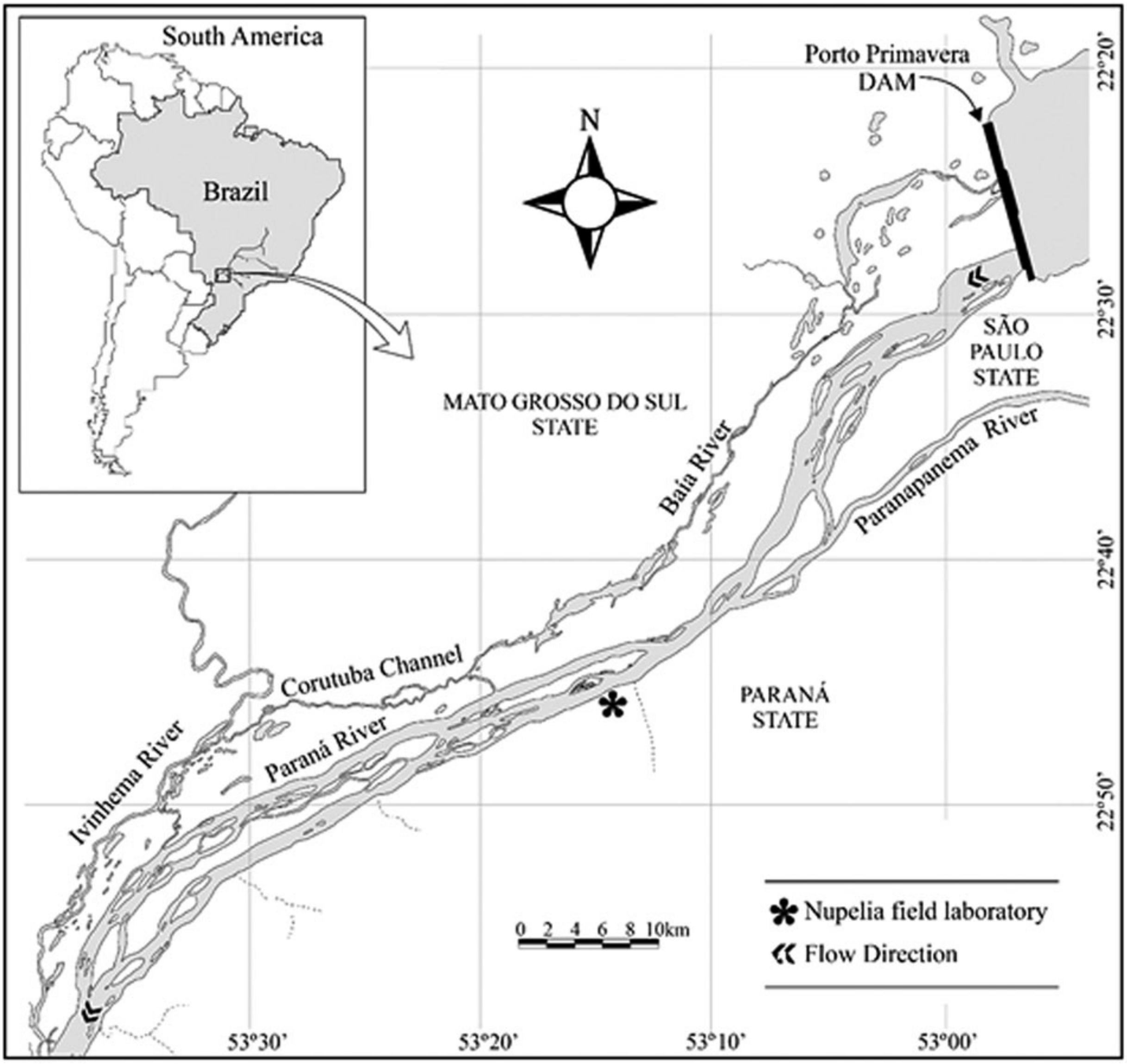


**Fig. 1.** Upper Paraná River floodplain. From Jaime Luiz Lopes Pereira.

greater investment in weight and length, compared to individuals collected in Period 2 (table 2) (fig. 3). Regarding the Kn, the mean of the values was similar between the periods (Period 1 Kn = 1.007 ± 0.17; Period 2 Kn = 1.007 ± 0.11), and there were no significant differences (H = 1.31; $P = 0.201$) between the parasitized individuals and non-parasitized in both periods (Period 1: non-parasitized Kn = 0.98 ± 0.13; parasitized Kn = 1.03 ± 0.17/Period 2: non-parasitized Kn = 0.96 ± 0.16; and parasitized Kn = 1.01 ± 0.1).

A total of 15 species of endoparasites were found: 11 in Period 1 and 9 in Period 2 (table 2), but only *Neoechinorhynchus curemai*, *Saccocoelioides* sp. 1, *Saccocoelioides magnorchis*, *Saccocoelioides nanii*, and *Saccocoelioides saccodontis* occurred in both periods. In Period 1, *S. magnorchis* and *S. nanii* were the most prevalent species among hosts. In Period 2, *N. curemai* was the most prevalent species among the hosts.

The abundance (U = 2566.5; $P = 0.16$) of the infra-communities did not differ between periods. However, species richness (U = 2072; $P = 0.001$) and diversity (U = 2457.5; $P =$ 0.04) were higher in Period 1, and equitability (U = 2425.5; $P =$ 0.02) was higher in Period 2 (table 4). Due to length being significantly correlated with fish weight (fig. 3), we considered it for correlations with parasite descriptors. In Period 1, we observed that the correlation of descriptors (richness, diversity and equitability) increased with length (table 4), though the correlation of abundance with length increased in Period 2 (table 3).

An NMDS ordered the variability of the species composition of parasites between the periods: even with the overlaps and sharing of species (fig. 4), the periods showed differences in the parasite infra-communities (PERMANOVA: F = 15.21; $P = < 0.05$). IndVal showed that *S. margnorchis* ($P = 0.001$) and *Saccocoelioides nanni* ($P = 0.001$) were the indicator species in Period 1 and *Colocladorchis ventrastomis* ($P = 0.001$), *Neoechinorhynchus prochilodorum* ($P = 0.001$) and *S. saccodontis* ($P = 0.02$) in Period 2.

## Discussion

The results of this study showed that there was a change in the structure of the parasitic community of *P. lineatus,* as some

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**Table 1.** Biometric data of the hosts *Prochilodus lineatus* collected during the two sampling periods in the upper Paraná River floodplain.

| | Period 1 (2000–2001) | | | Period 2 (2016–2017) | | |
|---|---|---|---|---|---|---|
| | *N* samples | Mean standard length (±SD) cm | Mean weight (±SD) g | *N* samples | Mean standard length (±SD) cm | Mean weight (±SD) g |
| Parasitized | 80 | 27 (6.45) | 569.20 (435.93) | 35 | 20.2 (3.73) | 227.3 (153.98) |
| Non-parasitized | 69 | 25.5 (7.41) | 504.20 (352.44) | 5 | 20.1 (2.50) | 202.5 (86.45) |
| Total | 149 | 26.5 (6.98) | 531.5 (403.4) | 40 | 20.2 (3.59) | 215.5 (147.42) |

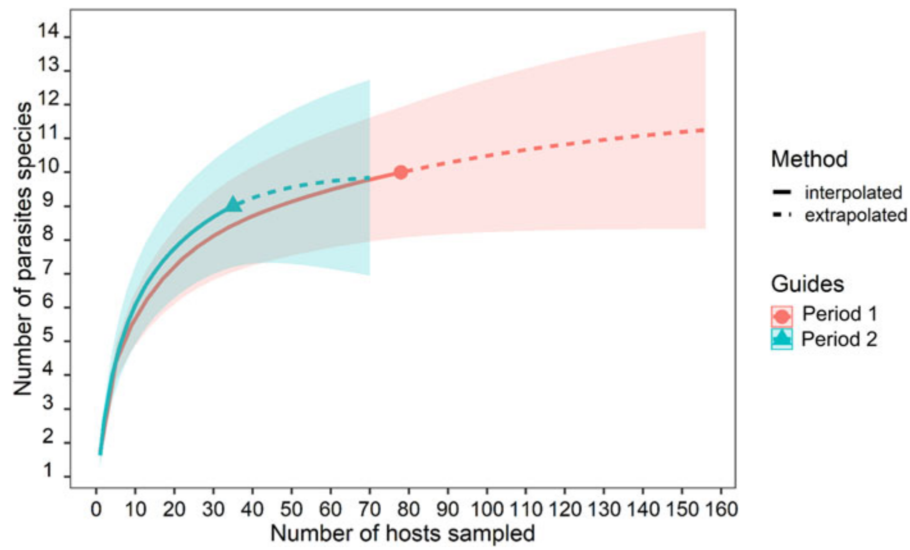


**Fig. 2.** Species accumulation curve for the parasitic community of *Prochilodus lineatus* in the upper Paraná River floodplain. (Period 1: 2000–2001 and Period 2: 2016–2017).

**Table 2.** Summary of the analysis of covariance of the weight–length relationship of *Prochilodus lineatus* between the periods (Period 1: 2000–2001 and Period 2: 2016–2017) in the upper Paraná River floodplain.

| | *Df* | *F* | *P*-value |
|---|---|---|---|
| length | 1 | 532.636 | **0.00*** |
| period | 1 | 1.17 | 0.28 |
| period × length | 1 | 5.56 | **0.02** |

*statistically significant correlations ($P \leq 0.05$) are indicate in boldface type.

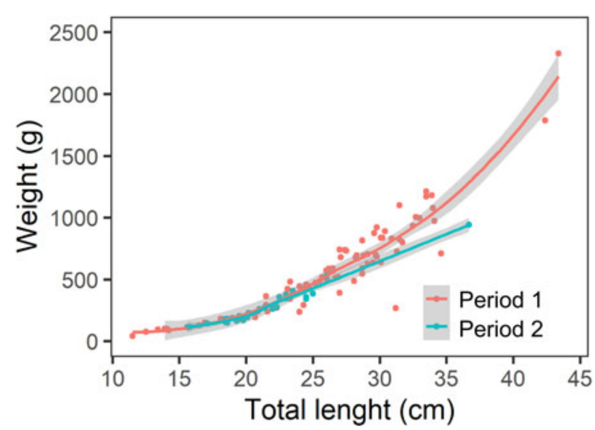


**Fig. 3.** Weight–length relationship of the host *Prochilodus lineatus* in the periods (Period 1: 2000–2001 and Period 2: 2016–2017) in the upper Paraná River floodplain.

species showed higher prevalence in Period 1, and others showed a decrease in prevalence in Period 2, such as *S. magnorchis*. Some species were recorded only in one of the periods, such as *N. prochilodorum* and *C. ventrastomis* in Period 2. Such variations seem to result from factors linked to environmental disturbances occurring in the floodplain, which directly affect the host and, consequently, the parasitic community.

The formation of a new dam destabilized the aquatic environment for several years which has serious implications for the aquatic wildlife of the affected area (Morley, 2007). With the construction of the Porto Primavera dam, the floodplain suffered changes in the structure and dynamics of aquatic communities that were influenced by the flood regime because the flow of the Paraná River redistributed and altered the hydrological regime (Agostinho *et al.*, 2009). Although changes in ecological conditions in dammed rivers depend on several factors (e.g., water quality, geomorphology and sediments) that are varied and complex, some changes that occur both upstream and downstream of dams are acute and irreversible (Arantes *et al.*, 2019).

Santos *et al.* (2017), studying a series of reservoirs in three different basins, demonstrated the role of dams as environmental filters, reducing the abundance of fish species. The reduction in the average size of migratory species in the Paraná, São Francisco, Iguaçu and Paranapanema rivers, which are rivers that have a cascade of reservoirs, is associated with characteristics that convey tolerance or vulnerability to the new ecological conditions of the impacted system (Arantes *et al.*, 2019). As the curimba is a

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**Table 3.** Species of parasites, periods (Period 1: 2000–2001 and Period 2: 2016–2017) and their parasitological indices found in *Prochilodus lineatus* in the upper Paraná River floodplain.

| | Prevalence (%) | | Mean intensity (±SD) | | Mean abundance (±SD) | |
|---|---|---|---|---|---|---|
| Parasites | Period 1 | Period 2 | Period 1 | Period 2 | Period 1 | Period 2 |
| Acanthocephala | | | | | | |
| *Neoechinorhynchus* sp. | 1.34 | 0 | 1 ± 0.3 | 0 | 0.01 ± 0.11 | 0 |
| *Neoechinorhynchus curemai* | 18.79 | 57.5 | 3.92 ± 2.43 | 2.34 ± 1.65 | 0.73 ± 2.37 | 1.35 ± 1.31 |
| *Neoechinorhynchus prochilodorum* | 0 | 17.5 | 0 | 2.14 ± 0.97 | 0 | 0.37 ± 0.89 |
| *Quadrigyrus* sp. | 3.35 | 0 | 1.6 ± 0.38 | 0 | 0.05 ± 0.32 | 0 |
| Cestoda | | | | | | |
| *Valipora* sp. | 5.36 | 0 | 1.62 ± 0.56 | 0 | 0.08 ± 0.53 | 0 |
| Digenea | | | | | | |
| *Colocladorchis ventrastomis* | 0 | 30 | 0 | 1.75 ± 1.14 | 0 | 0.52 ± 1.08 |
| *Megacoelium* sp. | 4.69 | 0 | 2.42 ± 0.79 | 0 | 0.11 ± 0.62 | 0 |
| *Saccocoelioides* sp. 1 | 0.67 | 5 | 6 | 1.5 ± 0.89 | 0.04 | 0.07 ± 0.34 |
| *Saccocoelioides* sp. 2 | 0 | 5 | 0 | 18 ± 15.55 | 0 | 0.9 ± 1.08 |
| *Saccocoelioides leporinodus* | 2.68 | 0 | 2.5 ± 0.7 | 0 | 0.06 ± 0.16 | 0 |
| *Saccocoelioides magnorchis* | 26.84 | 2.5 | 14.67 ± 11.96 | 5 | 3.93 ± 11.85 | 0.12 ± 0.79 |
| *Saccocoelioides nanii* | 26.84 | 12.5 | 33.27 ± 31.93 | 6.4 ± 5.12 | 8.93 ± 30.21 | 0.8 ± 2.67 |
| *Saccocoelioides saccodontis* | 0.67 | 10 | 2 | 2.5 ± 1 | 0.01 ± 0.16 | 0.25 ± 0.83 |
| Nematoda | | | | | | |
| *Contracaecum* larva tipo 1 | 0 | 2.5 | 0 | 1 | 0 | 0.02 ± 0.15 |
| *Raphidascaris* sp. | 0.67 | 0 | 1 | 0 | 0.006 ± 0.08 | 0 |

**Table 4.** Mean (± SD), minimum and maximum (Min-Max) values of parasite infra-community descriptors of *Prochilodus lineatus* between the periods (Period 1: 2000–2001 and Period 2: 2016–2017) in the upper Paraná River floodplain, Spearman rank correlation coefficients (rs) between these descriptors and total host body length (cm) and statistically significant values (*P*).

| Parasite descriptors | Mean (± SD) | (Min-Max) | rs | *P* |
|---|---|---|---|---|
| Period 1 | | | | |
| abundance | 14 ± 34.85 | 1-221 | 0.21 | **0.01*** |
| species richness | 0.91 ± 1.03 | 1-4 | 0.17 | **0.03** |
| diversity (Shannon–Wiener index) | 0.16 ± 0.31 | 0.07-1.37 | 0.20 | **0.01** |
| evenness (Pielou index) | 0.2 ± 0.34 | 0.10-1 | 0.20 | **0.01** |
| Period 2 | | | | |
| abundance | 4.27 ± 5.33 | 1-27 | 0.36 | **0.02** |
| species richness | 1.42 ± 0.91 | 1-4 | 0.09 | 0.55 |
| diversity (Shannon–Wiener index) | 0.3 ± 0.37 | 0.15-1.18 | 0.08 | 0.62 |
| evenness (Pielou index) | 0.38 ± 0.45 | 0.22-1 | 0.03 | 0.81 |

*statistically significant correlations ($P \leq 0.05$) are indicate in boldface type.

long-distance migratory species, gonad maturation, spawning, development and larval growth are strictly related to flooding. Moreover, recruitment success depends on the timing and duration of floods (Gomes & Agostinho, 1997). Lopes *et al.* (2020) reported in a floodplain study with curimba, smaller body size in a dammed river (Paraná River) when compared to a river without a dam (Ivinhema River).

For parasites, body size and host weight play an important role in determining host susceptibility to parasite infection, as host body size is considered a representation of the number of resources available (i.e., habitat area and nutrients or energy) for exploitation by the parasite (Luque *et al.*, 2004; Poulin *et al.*, 2011; Marcogliese *et al.*, 2016). In both periods, length did not play a key role in parasitological descriptors, but we observed

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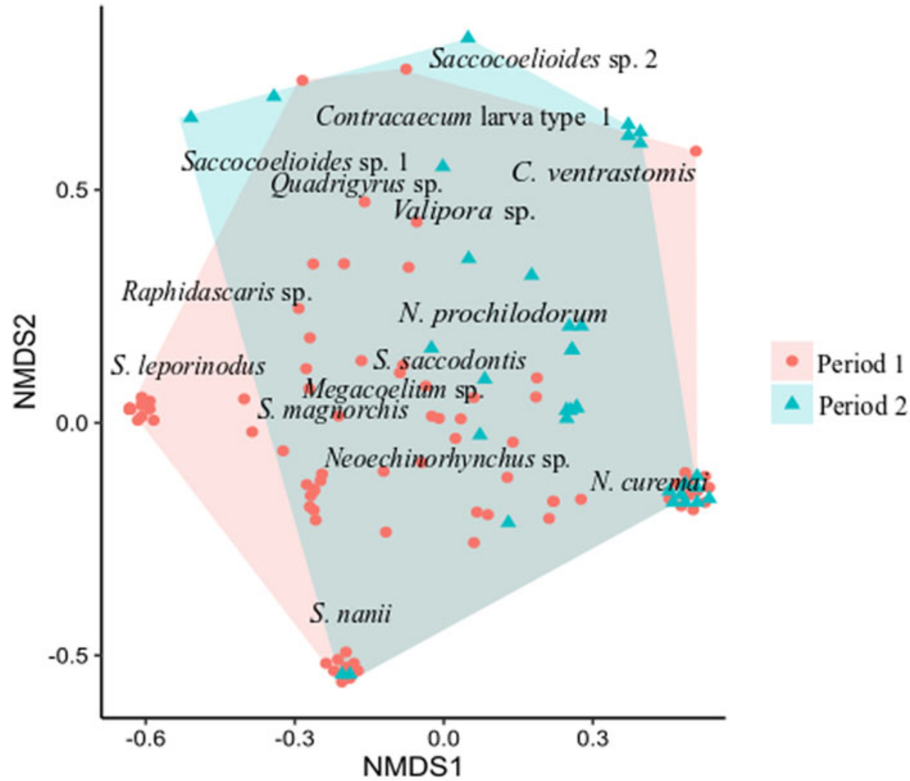


**Fig. 4.** Non-metric multidimensional scaling (NMDS) showing the variability in the composition of parasite species in *Prochilodus lineatus* between the periods (Period 1: 2000–2001 and Period 2: 2016–2017) in the upper Paraná River floodplain.

that in Period 1 the diversity and equitability remained constant across host lengths, meaning that the relative abundances of parasite species in each infra-community are constants relative to the length of the fish tested.

Many of these parasite communities experience temporal–structural or spatial–structural changes and this is related to seasonal variations in biotic and abiotic environmental factors and responds strongly to changes in host community composition. Over time these variations can reflect in parasite species' composition and density (Anderson & Gordon, 1982; Luque *et al.*, 2004; Hechinger & Lafferty, 2005; Gallegos-Navarro *et al.*, 2018). The species composition and structure of the parasite communities varied between periods, with species richness and diversity being highest in Period 1, although the endoparasites of *P. lineatus* exhibited similar distribution patterns in both periods, i.e., the low number of species, low diversity and numerical dominance of one parasite group.

Digenea species numerically dominated the parasite communities, accounting for 93% of the total parasites in Period 1 and 59% in Period 2, as well as *S. margnorchis* and *S. nanni*, were the representative species of Period 1, and *C. ventrastomis* and *S. saccodontis* were the representative species of Period 2. Transmission can occur when metacercariae encyst in aquatic vegetation or other surfaces (Al-Jahdali & Hassanine, 2012), and as the diet of *P. lineatus* is detritivorous and it feeds on the bottom, it facilitates infection by these parasites. Moreover, this is expected because, in tropical regions, Digenea is part of the most abundant and diverse group of fish parasitic helminths (Takemoto *et al.*, 1996; Luque & Poulin, 2008; Garcia-Prieto *et al.*, 2014). However, despite the dominance of the group for both periods, digenean parasites showed decreased infection levels in Period 2.

Acanthocephalans were the second most dominant group, mainly due to the high prevalence of *N. curemai* in both periods and the dominance of *N. prochilodorum* in Period 2. This dominance also can be explained by the feeding habits of the host, which includes a wide variety of invertebrates, presenting low food specificity, making it extremely susceptible to parasite acquisition through the trophic web (Fugi *et al.*, 2001; Lizama *et al.*, 2005). Other studies have already demonstrated the high prevalence of *N. curemai* in *P. lineatus* (Martins *et al.*, 2001; Leite *et al.*, 2018; Duarte *et al.*, 2020; Lehun *et al.*, 2020), which contributes to the high abundance in the present study, especially for Period 2.

The homogenization of the environment, caused by the construction of dams upstream of the reservoirs, directly affects the downstream river, with changes in the dynamics of fish assemblages, and may also cause a decrease in functional and taxonomic diversity, besides modifying the distribution and density of zoobenthos and zooplankton communities, which act as intermediate hosts for these parasites (Pinha *et al.*, 2013; Simões *et al.*, 2015; Petsch, 2016; Braghin *et al.*, 2018; Lopes *et al.*, 2020). These areas may not have all the hosts needed for the complex life cycles of certain parasites, which can reduce the chance of these populations becoming established (Minchella, 1985; Marcogliese & Cone, 1997; Torchin & Mitchell, 2004; Hechinger & Lafferty, 2005; Song & Proctor, 2020). Thus, due to the high dependence on the hosts, the parasites are also affected by the physical, chemical and environmental changes that have been occurring in the lowland, although this effect is indirect (Karling *et al.*, 2013).

As in all ecosystems and especially aquatic ecosystems (Winemiller *et al.*, 2016), environmental impacts have a strong negative effect on the life history of the host and, consequently, the parasite (Marcogliese & Cone, 1997; Tompkins *et al.*, 2002). The life stage of each parasite will generally have its own direct and indirect responses to a stressor, as the impact becomes more evident as life cycle complexity increases (Lafferty & Kuris, 1999). Moreover, some studies in recent years have observed that the local extinction of parasite species, changes in prevalence, diversity, composition and dominance of parasitic infra-communities, an increase of monoxenous parasites (monogenetic, protozoa and crustaceans), and reduction of heteroxenous parasites (digenetic, nematodes and acanthocephalans) due to biotic and abiotic changes in the ecosystem (Karling *et al.*, 2013; Yamada *et al.*, 2017). We found that, over the years, the composition of the parasitic fauna of *P. lineatus* changed, and the dominant species was different in the two periods. This can be influenced by the environmental characteristics of the floodplain that suffers constantly from the impacts caused by dam construction.

**Financial support.** This work was financially supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

**Conflicts of interest.** None.

## References

**Abati S, Minciardi MR, Ciadamidaro S, Fattorini S and Ceschin S** (2016) Response of macrophyte communities to flow regulation in mountain streams. *Environmental Monitoring and Assessment* **188(7)**, 1–12.

**Agostinho AA, Gomes LC, Veríssimo S and Okada EK** (2004a) Flood regime, dam regulation and fish in the upper Paraná River: Effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries* **14(1)**, 11–19.

**Agostinho AA, Thomaz SM and Gomes LC** (2004b) Threats for biodiversity in the floodplain of the upper Paraná River: effects of hydrological regulation by dams. *Ecohydrology & Hydrobiology* **4(3)**, 255–256.

**Agostinho AA, Bonecker CC and Gomes LC** (2009) Effects of water quantity on connectivity: the case of the upper Paraná River floodplain. *Ecohydrology & Hydrobiology* **9(1)**, 99–113.

**Al-Jahdali MO and Hassanine RES** (2012) The life cycle of *Gyliauchen volubilis* Nagaty, 1956 (Digenea: Gyliauchenidae) from the Red Sea. *Journal of Helminthology* **86(2)**, 165–172.

**Anderson M** (2005) *Permutational multivariate analysis of variance: A computer program*. Auckland, New Zealand, Department of Statistics, University of Auckland.

**Anderson RM and Gordon DM** (1982) Processes influencing the distribution of parasite numbers within host populations with special emphasis on parasite-induced host mortalities. *Parasitology* **85(2)**, 373–398.

**Arantes CC, Fitzgerald DB, Hoeinghaus DJ and Winemiller KO** (2019) Impacts of hydroelectric dams on fishes and fisheries in tropical rivers through the lens of functional traits. *Current Opinion in Environmental Sustainability* **37**, 28–40.

**Braghin LDSM, Almeida BDA, Amaral DC, Canella TF, Gimenez BCG and Bonecker CC** (2018) Effects of dam's decrease zooplankton functional β-diversity in river-associated lakes. *Freshwater Biology* **63(7)**, 721–730.

**Brooks TM, Mittermeier RA, da Fonseca GA, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD and Rodrigues AS** (2006) Global biodiversity conservation priorities. *Science* **313(5783)**, 58–61.

**Bush AO, Lafferty KD, Lotz JM and Shostak AW** (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83 (4)**, 575–583.

**Ceschin S, Tombolini I, Abati S and Zuccarello V** (2015) The effect of river damming on vegetation: Is it always unfavourable? A case study from the River Tiber (Italy). *Environmental Monitoring and Assessment* **187(5)**, 1–12.

**Duarte GSC, Lehun AL, Leite LAR, Consolin-Filho N, Bellay S and Takemoto RM** (2020) Acanthocephalans parasites of two Characiformes fishes as bioindicators of cadmium contamination in two neotropical rivers in Brazil. *Science of the Total Environment* **738**, 140339.

**Dufrêne M and Legendre P** (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* **67 (3)**, 345–366.

**Eiras JC, Takemoto RM and Pavanelli GC** (2006) *Métodos de estudo e técnicas laboratoriais em parasitologia de peixes* [Study methods and laboratory techniques in fish parasitology]. Maringá, Brazil, Eduem. [In Portuguese.]

**Fallon SM, Bermingham E and Ricklefs RE** (2003) Island and taxon effects in parasitism revisited: avian malaria in the Lesser Antilles. *Evolution* **57(3)**, 606–615.

**Fugi R, Hahn NS and Agostinho AA** (1996) Estilos alimentares de cinco espécies de peixes que se alimentam de fundo do alto rio Paraná [Food styles of five species of fish that feed on the upper Paraná River]. *Environmental Biology of Fishes* **46**, 297–307. [In Portuguese.]

**Fugi R, Agostinho AA and Hahn NS** (2001) Trophic morphology of five benthic-feeding fish species of a tropical floodplain. *Brazilian Journal of Biology* **61(1)**, 27–33.

**Gallegos-Navarro Y, Violante-González J, Monks S, García-Ibáñez S, Rojas-Herrera AA, Pulido-Flores G and Rosas-Acevedo JL** (2018) Factors linked to temporal and spatial variation in the metazoan parasite communities of green jack *Caranx caballus* (Günther 1868) (Pisces: Carangidae) from the Pacific coast of Mexico. *Journal of Natural History* **52(39–40)**, 2573–2590.

**García-Berthou E and Moreno-Amich R** (1993) Multivariate analysis of covariance in morphometric studies of the reproductive cycle. *Canadian Journal of Fisheries and Aquatic Sciences* **50(7)**, 1394–1399.

**Garcia-Prieto L, Mendoza-Garfias B and Perez-Ponce de Leon G** (2014) Biodiversity of parasitic Platyhelminthes in Mexico. *Revista Mexicana de Biodiversidade* **85(Suppl)**, 164–170.

**Gomes LC and Agostinho AA** (1997) Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná River, Brazil. *Fisheries Management and Ecology* **4(4)**, 263–274.

**Gubiani EA, Gomes LC, Agostinho AA and Okada EK** (2007) Persistence of fish populations in the upper Paraná River: effects of water regulation by dams. *Ecology of Freshwater Fish* **16(2)**, 191–197.

**Hechinger RF and Lafferty KD** (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. *Proceedings of the Royal Society B: Biological Sciences* **272(1567)**, 1059–1066.

**Hsieh TC, Ma KH and Chao A** (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* **7(12)**, 1451–1456.

**Iskov MP** (1976) The influence of training the river Dnieper, construction of water stops and hydroelectric plants on the parasitofauna of fish. *Wiadomości Parazytologiczne* **22(4–5)**, 451–453.

**Izyumova NA** (1979) The fish parasite fauna of the Volga. *Monographiae Biologicae (The Volga and its Life)* **33**, 340–345.

**Junk WJ, Bayley PB and Sparks RE** (1989) The flood pulse concept in river-floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences* **106**, 110–127.

**Karling LC, Isaac A, Affonso IP, Takemoto RM and Pavanelli GC** (2013) The impact of a dam on the helminth fauna and health of a neotropical fish species *Salminus brasiliensis* (Cuvier 1816) from the upper Paraná River, Brazil. *Journal of Helminthology* **87(2)**, 245–251.

**Kohn A, Fernandes BM and Cohen SC** (2007) *South American trematodes parasites of fishes*. Rio de Janeiro, Brazil, Imprinta Express Ltda.

**Lafferty KD and Kuris AM** (1999) How environmental stress affects the impacts of parasites. *Limnology and Oceanography* **44(3)**, 925–931.

**Landsberg JH, Blakesley BA, Reese RO, Mcrae G and Forstchen PR** (1998) Parasites of fish as indicators of environmental stress. *Environmental Monitoring and Assessment* **51(1–2)**, 211–232.

**Le Cren ED** (1951) The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *The Journal of Animal Ecology* **20(2)**, 201–219.

**Lehun AL, Hasuike WT, Silva JOS, *et al.*** (2020) Checklist of parasites in fish from the upper Paraná River floodplain: An update. *Brazilian Journal of Veterinary Parasitology* **29(3)**, 1–20.

**Leite LAR, Pelegrini LS, Agostinho BN, Azevedo RKD and Abdallah VD** (2018) Biodiversity of the metazoan parasites of *Prochilodus lineatus* (Valenciennes, 1837) (Characiformes: Prochilodontidae) in anthropized environments from the Batalha River, São Paulo State, Brazil. *Biota Neotropica* **18(3)**, 1–10.

**Lizama MAP, Takemoto RM and Pavanelli GC** (2005) Influence of host sex and age on infracommunities of metazoan parasites of *Prochilodus lineatus* (Valenciennes, 1836) (Prochilodontidae) of the upper Paraná River floodplain, Brazil. *Parasite* **12(4)**, 299–304.

**Lopes CA, Benedito-Cecilio E and Martinelli LA** (2007) Variability in the carbon isotope signature of *Prochilodus lineatus* (Prochilodontidae, Characiformes) a bottom-feeding fish of the neotropical region. *Journal of Fish Biology* **70(6)**, 1649–1659.

**Lopes TM, Peláez O, Dias RM, Oliveira AG, Rauber RG, Gomes LC and Agostinho AA** (2020) Temporal changes in migratory fish body size in a neotropical floodplain. *Oecologia Australis* **24(2)**, 489–504.

**Luque JL and Poulin R** (2008) Linking ecology with parasite diversity in Neotropical fishes. *Journal of Fish Biology* **72(1)**, 189–204.

**Luque JL, Mouillot D and Poulin R** (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* **128(6)**, 671–682.

**Mackenzie K** (1999) Parasites as pollution indicators in marine ecosystems: a proposed early warning system. *Marine Pollution Bulletin* **381(1)**, 955–959.

**Marcogliese DJ and Cone DK** (1997) Food webs: a plea for parasites. *Trends in Ecology & Evolution* **12(8)**, 320–325.

**Marcogliese DJ, Locke SA, Gélinas M and Gendron AD** (2016) Variation in parasite communities in spottail shiners (*Notropis hudsonius*) linked with precipitation. *Journal of Parasitology* **102(1)**, 27–36.

**Markevich AP, Iskov MP, Koval VP and Chernogorenko MI** (1976) Effect of hydraulic works on the parasite fauna of the Dnieper river. *Hydrobiological Journal* **2**, 1–6.

**Martins ML, Moraes FR, Fujimoto RY, Onaka EM and Quintana CL** (2001) Prevalence and histopathology of *Neoechinorhynchus curemai* Noranha, 1973 (Acanthocephala: Neoechinorhynchidae) in *Prochilodus lineatus* Valenciennes, 1836 from Volta Grande reservoir, MG, Brazil. *Brazilian Journal of Biology* **61(3)**, 517–522.

**Minchella DJ** (1985) Host life-history variation in response to parasitism. *Parasitology* **90(1)**, 205–216.

**Moravec F** (1998) *Nematodes of freshwater fishes of the neotropical region*. Czech Republic, Academia Praha, Academy of Sciences of the Czech Republic.

**Morley NJ** (2007) Anthropogenic effects of reservoir construction on the parasite fauna of aquatic wildlife. *EcoHealth* **4(4)**, 374–383.

**Muniz CM, García-Berthou E, Ganassin MJM, Agostinho AA and Gomes LC** (2021) Alien fish in Neotropical reservoirs: assessing multiple hypotheses in invasion biology. *Ecological Indicators* **121**, 107034.

**Nagel L, Robb T and Forbes MR** (2009) Parasite mediated selection amidst marked inter-annual variation in mite parasitism and damselfly life history traits. *Ecoscience* **16(2)**, 265–270.

**Neiff JJ** (1990) Aspects of primary productivity in the lower Paraná and Paraguay riverine system. *Acta Limnologica Brasiliensia* **3(1)**, 77–113.

**Oyakawa OT, Menezes NA, Shibatta OA, Lima FCT, Langeani F, Pavanelli CS, Nielsen DTB and Hilsdorf AWS** (2009) Peixes de água doce [Freshwater fish]. pp. 349–424 In Bressan PM, Kierulff MCM and Sugieda AM (Eds) *Fauna ameaçada de extinção no Estado de São Paulo* [Fauna threatened with extinction in the state of São Paulo]. Fundação Parque Zoológico de São Paulo. São Paulo, Brazil, Ministério do Meio Ambiente. [In Portuguese.]

**Pavanelli GC, Machado MH, Takemoto RM, Guidelli GM and Lizama MAP** (2004) Helminth fauna of the fishes: diversity and ecological aspects. pp. 309–329 In Thomaz SM, Agostinho AA and Hahn NS (Eds) *The upper Paraná River and its floodplain: Physical aspects, ecology and conservation*. Leiden, Brazil, Backhuys Publishers.

**Petsch DK** (2016) Causes and consequences of biotic homogenization in freshwater ecosystems. *International Review of Hydrobiology* **101(3–4)**, 113–122.

**Piana PA, Cardoso BF, Dias J, Gomes LC, Agostinho AA and Miranda LE** (2017) Using long-term data to predict fish abundance: the case of *Prochilodus lineatus* (Characiformes, Prochilodontidae) in the intensely regulated upper Paraná River. *Neotropical Ichthyology* **15(3)**, e160029.

**Pinha GD, Aviz D, Lopes Filho DR, Petsch DK, Marchese MR and Takeda AM** (2013) Longitudinal distribution of Chironomidae (Diptera) downstream from a dam in a neotropical river. *Brazilian Journal of Biology* **73 (3)**, 549–558.

**Poulin R** (2007) Are there general laws in parasite ecology? *Parasitology* **134 (6)**, 763–776.

**Poulin R, Guilhaumon F, Randhawa HS, Luque JL and Mouillot D** (2011) Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* **120(5)**, 740–747.

**R Core Team** (2017) *R: A language and environment for statistical computing*. Vienna, Austria, R Foundation for Statistical Computing.

**Reid MA and Ogden RW** (2006) Trend, variability or extreme event? The importance of long-term perspectives in river ecology. *River Research and Applications* **22(1)**, 167–177.

**Rosa RS and Lima FCT** (2008) Os peixes Brasileiros ameaçados de extinção [The Brazilian fishes threatened with extinction]. pp. 9–275 In Bressan PM, Kierulff MCM, Sugieda AMS (Eds) *Fauna ameaçada de extinção no Estado de São Paulo* [Fauna threatened with extinction in the state of São Paulo]. Fundação Parque Zoológico de São Paulo. São Paulo, Brazil, Secretaria do Meio Ambiente. [In Portuguese.]

**Santos NCL, Santana HS, Ortega JCG, *et al.*** (2017) Environmental filters predict the trait composition of fish communities in reservoir cascades. *Hydrobiologia* **802(5)**, 245–253.

**Simões NR, Nunes AH, Dias JD, Lansac-Tôha FA, Velho LFM and Bonecker CC** (2015) Impact of reservoirs on zooplankton diversity and implications for the conservation of natural aquatic environments. *Hydrobiologia* **758(1)**, 3–17.

**Song Z and Proctor H** (2020) Parasite prevalence in intermediate hosts increases with waterbody age and abundance of final hosts. *Oecologia* **192**, 311–321.

**Takemoto RM, Amato JFR and Luque JL** (1996) Comparative analysis of the metazoan parasite communities of leatherjackets, *Oligoplites palometa*, *O. saurus*, and *O. saliens* (Osteichthyes: Carangidae) from Sepetiba Bay, Rio de Janeiro. *Brazilian Journal of Biology* **56(4)**, 639–650.

**Thatcher VE** (2006) *Aquatic biodiversity in Latin America. Vol 1. Amazon fish parasites*. Sofia, Bulgaria, Pensoft Publishers.

**Tombolini I, Caneva G, Cancellieri L, Abati S and Ceschin S** (2014) Damming effects on upstream riparian and aquatic vegetation: the case study of Nazzano (Tiber River, Central Italy). *Knowledge and Management of Aquatic Ecosystems* **412(1)**, 1–15.

**Tompkins DM, Dobson AP, Arneberg P, *et al.*** (2002) Parasites and host population dynamics. pp. 45–62 In Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson PJ (Eds) *The ecology of wildlife diseases*. Oxford, Oxford University Press.

**Torchin ME and Mitchell CE** (2004) Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and the Environment* **2(4)**, 183–190.

**Vidal-Martínez VM** (2000) *Metazoan parasites in the neotropics: A systematic and ecological perspective*. México, Universidad Nacional Autonoma de Mexico.

**Violante-González J, Aguirre-Macedo ML and Vidal-Martinez VM** (2008) Temporal variation in the helminth parasite communities of the Pacific fat sleeper, *Dormitator latifron*s, from Tres Palos Lagoon, Guerrero, Mexico. *Journal of Parasitology* **94(2)**, 326–334.

**Vital JF, Varella AMB, Porto DB and Malta JCO** (2011) Seasonality of the metazoan fauna of *Pygocentrus nattereri* (Kner, 1858) in Piranha Lake (Amazonas, Brazil) and evaluation of its potential as an indicator of environmental health. *Biota Neotropica* **11(1)**, 199–204.

**Winemiller KO, McIntyre PB, Castello L, *et al.*** (2016) Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* **351(6269)**, 128–129.

**Yamada FH, Bongiovani MF, Yamada PO and Silva RJ** (2017) Parasite infracommunities of *Leporinus friderici*: a comparison of three tributaries of the Jurumirim Reservoir in southeastern Brazil. *Anais da Academia Brasileira de Ciências* **89(2)**, 953–963.