

Variation in the parasite community of the sardine fish *Triportheus nematurus* (Actinopterygii: Characidae) from the Medalha lagoon in the Pantanal wetland, Brazil

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Abstract

In July 2009 and July 2010 (two dry periods separated by an atypically large flood in the Pantanal wetland of Brazil), 34 and 33 specimens of the sardine fish *Triportheus nematurus* were collected, respectively, for the study of the metazoan parasite community of this species. Parasite ecological and community descriptors were calculated for both host samples, and possible similarities were tested statistically. Five species of metazoan parasites were identified, four of which were common to both host samples. A total of 61 metazoan parasites were collected from all fish hosts (17 specimens in July 2009 (mean: 0.5 ± 0.66 parasites/fish) and 44 specimens in July 2010 (mean: 1.33 ± 1.41 parasites/fish)). The nematode *Procamallanus hilarii* and the monogenean *Anacanthorus* sp. were the most prevalent and abundant species in 2009 and 2010, respectively. The mean total abundance and species richness were significantly higher in 2010. Parasite communities in both samples of *T. nematurus* were characterized by species with low prevalence, abundance, mean total abundance and species richness, thus indicating low parasite diversity. Significant differences in the prevalence and abundance of *P. hilarii* and *Anacanthorus* sp. between the two samples allowed the discrimination of infracommunities, which were united in two distinct groups. This appears to be the first evidence that the peculiar hydrological dynamics of the southern Pantanal wetland (Brazil) exert an important influence over the structure of the parasite community.

Introduction

Parasites are representative components of global biodiversity (Mouritsen & Poulin, 2005). However, the determination of overall patterns in parasite ecology is hindered by the scarcity of basic data on the parasite communities of a large number of host species (Poulin, 2007; Kennedy, 2009). This is particularly evident in Neotropical ichthyofauna, for which parasite communities

have been studied in less than 10% of potential host species (Luque & Poulin, 2007). The number of studies taking an ecological approach is even more limited.

The interaction between biotic and abiotic factors is essential to the composition and structure of parasite communities (Poulin, 2007). Variations in parasite communities on the temporal scale are usually related to environmental changes over time (Kennedy, 2009). However, the few eco-parasitological studies that have addressed temporal variations have produced contrasting results. In a parasite community, some species undergo substantial changes associated with the season,

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while others do not. 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; Carvalho *et al.*, 2010; Li *et al.*, 2010; Pech *et al.*, 2010; Vital *et al.*, 2011).

Wetlands are propitious to the study of the dynamics of parasite communities, as the well-defined seasonal variations in these systems act on both environmental characteristics and biotic relationships (Thomas *et al.*, 1997). However, the taxonomic and ecological knowledge of parasites in these environments is limited (Junk *et al.*, 2006).

The genus *Triporthesus* (Actinopterygii: Characidae) includes small fish species that reach 200 mm in length, and is widely distributed in South America. The sardine fish *Triporthesus nematurus* is abundant in the Paraguay River basin. In oxygen-poor floodplain water, this species develops barbels on its lower lips to direct the oxygenated surface water to its mouth (Malabarba, 2004). The small, upwardly turned mouth is associated with an omnivorous diet, primarily including allochthonous food items such as insects, fruits and seeds. However, this species also feeds on other items, such as algae, plankton and microcrustaceans (Resende & Pereira, 2000; Galina & Hahn, 2003), some of which (Cladocera, Copepoda, Ostracoda and Conchostraca) are recognized as potential hosts of many fish parasites (Eiras, 1994).

Studies that have recorded the occurrence of metazoan parasites in *T. nematurus* are summarized by Machado-Filho (1959), Pinto & Noronha (1976), Thatcher (1991, 2006), Moravec (1998), Kohn & Paiva (2000), Kohn *et al.* (2007), Santos *et al.* (2008), Eiras *et al.* (2010) and Luque *et al.* (2011). Some of these studies reported the host species to be *T. paranensis*, which is now considered to be a junior synonym of *T. nematurus* (Malabarba, 2004). Domingues & Boeger (2005) described *Rhinoxenus anaclaudiae* as parasitizing the nasal cavities of *T. cf. nematurus*, *Triporthesus* sp. and *Brycon* sp. from the Pantanal wetland, including fish specimens collected from the Medalha lagoon. However, these studies were focused on taxonomic surveys, and ecological approaches have not yet been explored.

The aim of the present study was to evaluate and compare the parasite communities of *T. nematurus* in two dry periods separated by an atypically large flood in the Pantanal wetland, Brazil.

Materials and methods

Collection and examination of fish

The Medalha lagoon (locally known as 'Baía da Medalha') is a perennial lagoon with an approximate area of 6 ha in the dry season, located near the Pantanal Study Base (19°34'36"S; 57°01'06"W) of the Universidade Federal de Mato Grosso do Sul in the Miranda-Abobral sub-region, municipality of Corumbá, state of Mato Grosso do Sul, Brazil. This lagoon is subject to fluctuations in water level depending on the annual hydrological cycle in the southern Pantanal wetland. In the dry period (May to September), the lagoon remains isolated from the Miranda River. From October to March, local rainfall and, secondarily, rainfall on the northern Pantanal wetland

cause a significant increase in water level in the Miranda River, with flooding to adjacent areas, which creates a connection between the Medalha lagoon and the Miranda River and floodplain. After reaching its maximum, the water level begins to drop until the lagoon is isolated again, which generally occurs from March to May. This seasonal environment with its annual hydrological cycle is propitious to the study of the temporal dynamics of biological populations and communities.

Two field collection campaigns were carried out in consecutive dry seasons (July 2009 and July 2010). The amount of rainfall between November 2009 and March 2010 was the largest in the previous 15-year period, flooding a wide plain area in the Pantanal wetland. Local data on the monthly cumulative rainfall and maximum and minimum temperatures between January 2009 and December 2010 were obtained from the meteorological station at São Bento Farm, located in the same municipality and sub-region. In the same period, the depth of the Miranda River was determined twice a day using a rigid meter rule immersed in the river in front of the Pantanal Study Base.

A total of 67 specimens of *T. nematurus* (34 in 2009 and 33 in 2010) were captured with cast nets with mesh sizes of 150 and 200 mm between opposing knots. The standard length was measured with a digital calliper (precision: 0.02 mm) and body mass was determined on a digital scale (precision: 0.1 g). All fish underwent necropsy under a stereomicroscope, in which the body surface and all organs and body cavities were examined for metazoan parasites. Licence number SISBIO 22 119-1/Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) was issued for collection of biological material.

Data analysis

Morphometric data on the hosts and the indices of parasite infrapopulations and infracommunities did not exhibit normal distribution (Shapiro-Wilk) and were therefore log-transformed to enable parametric analysis. Student's *t*-test was used to determine possible significant differences in standard length and body mass among hosts captured in the two different samples (July 2009 and July 2010). Pearson's correlation coefficient was calculated to determine possible correlations between the standard length and body mass of the hosts.

The following ecological descriptors of parasitism were calculated: prevalence, mean parasite abundance and mean parasite intensity (Bush *et al.*, 1997). Other infrapopulation analyses were only performed for parasite species with prevalence values greater than 10% (Bush *et al.*, 1990). The index of discrepancy (*D*) was calculated for each parasite species (Poulin, 1993). Pearson's correlation coefficient was calculated and used to determine possible correlations between the standard length of hosts and parasite abundance. Differences in abundance and prevalence values between the two samples were determined using Student's *t*-test and the chi-square (χ^2) test, respectively (Zar, 1999). The mean total parasite abundance and mean parasite species richness were calculated, and differences between the two samples were determined using Student's *t*-test (Zar, 1999). Pearson's correlation coefficient was calculated to

determine whether the standard length of the hosts was correlated with the mean total parasite abundance and the mean species richness (Zar, 1999). A discriminant analysis based on the Mahalanobis distance in square root-transformed data was used to detect possible differences in infracommunities between the two sample periods and to determine which metazoan species were responsible for these differences (Ludwig & Reynolds, 1988; Valentin, 2000).

Results

Figure 1 displays the data on cumulative rainfall, maximum and minimum temperature and the depth of the Miranda River between January 2009 and December 2010.

Specimens collected in 2009 measured 7.7 ± 1.8 cm (range: 5.1–11 cm) in standard length and weighed 10.8 ± 7.3 g (3–22 g). The specimens collected in 2010 measured 7.1 ± 0.9 cm (6–9.3 cm) in standard length and weighed 11.9 ± 4.9 g (5–24 g). The standard length and body mass values did not differ significantly between the two samples ($t = 1.5$, $P = 0.07$; $t = 1.7$, $P = 0.05$, respectively). As standard length and body mass values were positively correlated in the two samples ($r = 0.93$, $P < 0.01$; $r = 0.94$, $P < 0.01$, respectively), only the data on standard length were used to determine possible correlations with infrapopulation and infracommunity indices.

Sixty-one metazoan parasites were collected from the host specimens (mean: 0.91 ± 1.18 parasites/fish). A total of 53.7% of the host specimens were parasitized by at least one metazoan parasite species. *Anacanthorus* sp. was the most prevalent and abundant species, occurring in 34.3%

of the hosts and accounting for 70.5% of the total number of parasite specimens collected.

In the first sample (2009), 41.2% of the fish were parasitized, from which 17 specimens of metazoan parasites were collected (mean: 0.5 ± 0.66 parasites/fish). The nematode *Procamallanus hilarii* was the most prevalent and abundant species in this sample (table 1). In the second sample (2010), 67% of the fish were parasitized, from which 44 metazoan parasites were collected (mean: 1.33 ± 1.41 parasites/fish). The monogenean *Anacanthorus* sp. was the most prevalent and abundant species in the second sample. All the other species had prevalence values of less than 10% (table 1). The prevalence and mean abundance values for *P. hilarii* were significantly higher in the first sample ($\chi^2 = 6.2$; $P = 0.01$; $t = 2.6$, $P < 0.01$), whereas the prevalence and mean abundance values for *Anacanthorus* sp. were significantly higher in the second sample ($\chi^2 = 19.9$; $P < 0.01$; $t = -5.2$, $P < 0.01$). No correlations were found between the standard length of the hosts and the mean parasite abundance.

Anacanthorus sp. and *P. hilarii* exhibited typical aggregated distribution within the hosts (*Anacanthorus* sp.: $D = 0.886$ in the first sample and $D = 0.565$ in the second sample; *P. hilarii*: $D = 0.709$ in the first sample and $D = 0.969$ in the second sample).

In the first sample, mean total abundance and mean species richness were 0.5 ± 0.66 and 0.47 ± 0.62 , respectively. In the second sample, these values were 1.33 ± 1.43 and 0.73 ± 0.57 , respectively. Significant differences were found in the mean total abundance ($t = -2.97$, $P < 0.01$) and mean species richness ($t = -1.94$, $P = 0.03$) between the two samples. Standard length of the hosts was not

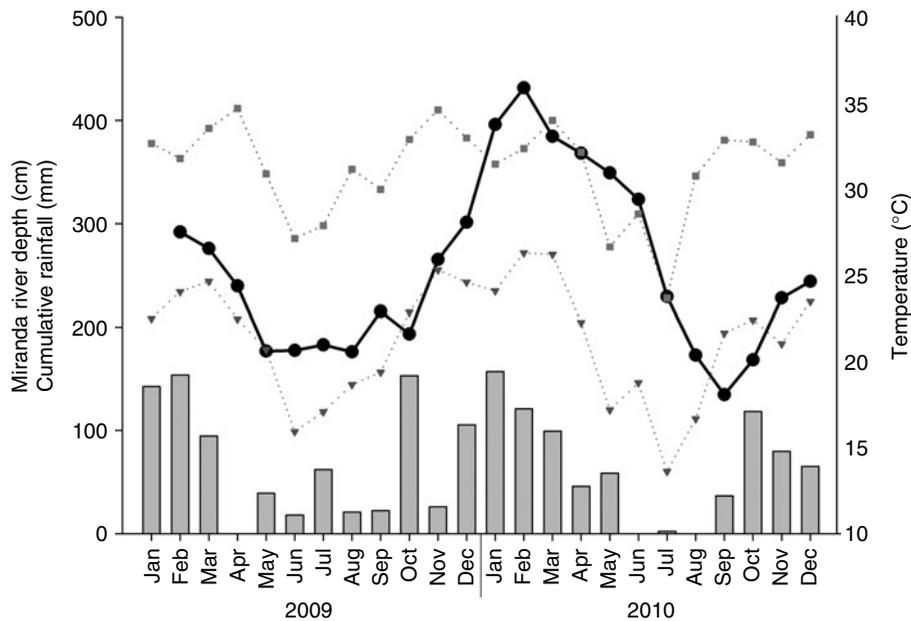


Fig. 1. Cumulative rainfall, temperature and depth of the Miranda River between January 2009 and December 2010 in the Miranda-Abobral sub-region, municipality of Corumbá, state of Mato Grosso do Sul, Brazil. Bars = cumulative rainfall; black line = river depth; grey dotted lines = maximum and minimum temperatures.

Table 1. Site of infection, prevalence (P), mean abundance (MA) and mean intensity (MI) of metazoan parasites of *Triportheus nematurus* from the Pantanal wetland, state of Mato Grosso do Sul, Brazil; SD = standard deviation.

Parasites	July 2009 (<i>n</i> = 34)			July 2010 (<i>n</i> = 33)			Site of infection
	P (%)	MA ± SD	MI ± SD	P (%)	MA ± SD	MI ± SD	
Monogenea							
<i>Anacanthorus</i> sp.	8.8	0.088 ± 0.288	1	60.6*	1.212 ± 1.409*	2 ± 1.298	Gills and opercular chambers
Nematoda							
<i>Contracaecum</i> sp. (larval stage)	2.9	0.029 ± 0.171	1	3.03	0.03 ± 0.174	1	Intestine
<i>Goezia</i> sp. (larval stage)	2.9	0.029 ± 0.171	1	3.03	0.03 ± 0.174	1	Intestine
<i>Procamallanus hilarii</i>	29.4*	0.324 ± 0.535*	1.1 ± 0.316	6.06	0.061 ± 0.242	1	Stomach and intestine
Copepoda							
<i>Ergasilus</i> sp.	2.9	0.029 ± 0.171	1	–	–	–	Gills

*Significant difference between parasite abundance (*t*) and prevalence (χ^2); $P < 0.05$.

significantly correlated with the mean total parasite abundance or the mean species richness in either sample.

The first discriminant variable explained 100% of the variance (eigenvalue = 0.547). The difference between the centroids of the groups was significant (Wilk's lambda = 0.65, $F_{5,61} = 6.68$, $P < 0.01$), and infracommunities constituted two distinct groups ($\chi^2 = 27.3$, $P < 0.01$) (fig. 2). A 76.12% rate of correct classification in the two host samples was achieved for the parasite infracommunities (94.12% in the first sample and 57.58% in the second sample). *Anacanthorus* sp. and *P. hilarii* contributed the most to the determination of the position of infracommunities on the first two discriminant axes, accounting for 90% and 51.6% of the values, respectively.

Discussion

The parasite communities of *T. nematurus* from the two samples (July 2009 and July 2010) were both characterized by the presence of species with low prevalence (without core species *sensu* Bush & Holmes, 1986), abundance and species richness, thereby indicating low parasite diversity. Moreover, the standard length of the hosts was not correlated with ecological or community descriptors. Four species were common to both samples, and *T. nematurus* constitutes a new host record for the nematode *P. hilarii* as well as for the larval stages of the nematodes *Contracaecum* sp. and *Goezia* sp. To date, 21 nominal species from the genus *Anacanthorus* have been reported as parasitizing species of *Triportheus*: six species in *T. albus*, 12 species in *T. angulatus* (9 of which have only been reported in *T. angulatus*) and 11 species in *T. elongatus* (4 of which have only been reported in *T. elongatus*) (Thatcher, 2006; Eiras *et al.*, 2010). However, reports of species of *Anacanthorus* parasitizing *T. nematurus* were previously unknown. Reports on crustacean species parasitizing *Triportheus* spp. are scarce and restricted to the isopod *Amphira junki* in *T. albus*, the brachyuran *Dolops* sp. and the copepod *Ergasilus* sp., both parasitic to *T. elongatus* (Thatcher & Boeger, 1983; Thatcher, 2006; Eiras *et al.*, 2010).

Despite the common characteristics in both samples, such as similar species composition, and the low values of ecological and community descriptors, with no signi-

ficant correlations to the standard length of the hosts, significant differences were found between samples with respect to the mean total abundance and the mean species richness as well as the alteration of the dominant species: *P. hilarii* was the most prevalent and abundant species in 2009, whereas *Anacanthorus* sp. was the most prevalent and abundant species in 2010. The significant differences in the prevalence and abundance of these species allowed the discrimination of infracommunities, which formed two distinct groups.

Studies on seasonal variation in the composition and structure of parasite communities have employed different time scales and have explained this variation in different ways (Kennedy, 1997, 2009; Li *et al.*, 2010). For example, Olson *et al.* (2004) observed a substantial change in the prevalence of metazoan parasites in two estuarine fish species between two temporally separated

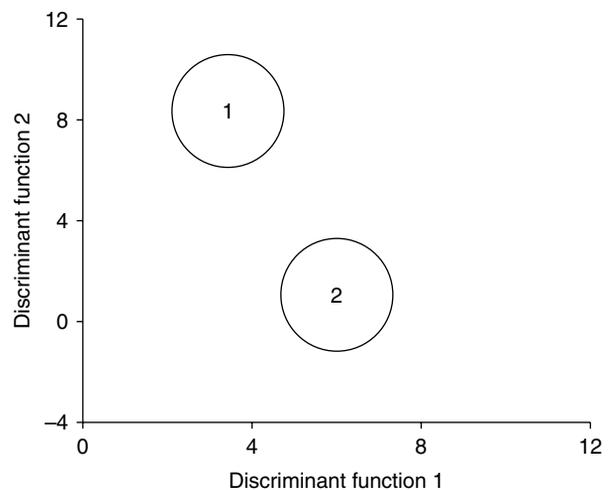


Fig. 2. Sample scores of the first two discriminant axes for parasite infracommunities of *Triportheus nematurus* from the Medalha lagoon, Miranda-Abobral sub-region, municipality of Corumbá, state of Mato Grosso do Sul, Brazil. Numbers represent groups of respective samples: 1, July 2009; 2, July 2010. Circles around groups represent 95% tolerance region, e.g. 95% of observations in a group are expected to lie within this region.

sampling periods in Yaquina Bay, Oregon, USA, in the early 1970s and at the end of the 1990s. These authors suggested that the climate-associated phenomenon known as El Niño, as well as the increase in populations of marine mammals and implications from the change in local ichthyofauna, are associated with the changes observed in host–parasite ecology. On a refined seasonal scale, Carvalho *et al.* (2010) studied the variation in communities of the metazoan parasites of *Geophagus brasiliensis* in the Guandu River, state of Rio de Janeiro, Brazil, between seasons of the year, and related this variation to climate changes throughout the year. The present study had a short temporal range, with the same climate conditions in both sampling campaigns. It is therefore suggested that the primary reason for the discrimination of the two groups was the large flood that occurred between the sampling campaigns, and its biotic and environmental consequences.

Host body size is considered to be a representation of the amount of available resources (i.e. habitat area and nutrients or energy) for parasite exploitation (Luque *et al.*, 2004; Poulin *et al.*, 2011) and has therefore been widely used to determine possible correlations with parasite ecological and community descriptors. Some studies have been carried out to determine whether host body size may be a predictor of parasite species richness. However, there is as yet no consensus on this issue. Luque *et al.* (2004) and Luque & Poulin (2007) found that fish size was strongly and positively correlated with parasite species richness, while Takemoto *et al.* (2005) and Poulin *et al.* (2011) did not find such a correlation. The lack of difference in host body size between the two samples and the lack of correlation between host standard length and ecological and community descriptors in the present study may be an indication that this intrinsic host factor (i.e. standard length and body mass) does not exert a fundamental influence over the variation in these parasite infracommunities between years, which may be explained by the action of environmental dynamics on shifts in parasite communities.

Features of the habitat (i.e. local abiotic factors such as water temperature, pH and lake size) and certain traits of the host population (size and density) could facilitate the transmission and establishment of fish parasites (Bagge *et al.*, 2004; Takemoto *et al.*, 2005; Poulin, 2006). Monogeneans have a direct life cycle and their transmission could be facilitated by proximity between hosts (Bagge *et al.*, 2004). Studying the seasonality of metazoan parasites of *Pygocentrus nattereri* in Piranha Lake, state of Amazonas, Brazil, Vital *et al.* (2011) found a significant increase in the mean intensity of monogeneans in the dry season. The Medalha lagoon becomes reduced in area in the dry period, which may favour the proximity between hosts and, consequently, favour monogenean transmission between hosts. In 2009, the cumulative rainfall and depth of the Miranda River were lower than in 2010. Thus, the area of the Medalha lagoon was smaller in 2009 than in 2010. However, the prevalence and mean intensity of *Anacanthorus* sp. were significantly higher in 2010, as were the mean total abundance and mean species richness.

Flooding in the Pantanal wetland connects a large number of habitats, such as perennial and ephemeral lagoons on the floodplain, enabling individuals to flow

between different fish populations that are usually exposed to different environmental and ecological pressures. A great number of fish species, including *T. nematurus*, move to the floodplain to feed and breed (Lowe-McConnell, 1991). This seasonal flow of fish between habitats may be an important mechanism associated with seasonal alterations in the dynamics of parasite communities in the Pantanal wetland.

This seems to be the first evidence that the peculiar hydrological dynamics in the southern Pantanal wetland exert an important influence over the structure of parasite communities, with seasonal floods serving as the major event that is associated with the discrimination of parasite infracommunities. However, further data are needed to confirm this on temporal, phylogenetic and spatial scales. Future studies should focus on variations in the parasite communities of fish communities or address a target fish species on a refined scale and over a long time period in the Pantanal wetland, Brazil.

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References

- Bagge, A.M., Poulin, R. & Valtonen, E.T. (2004) Fish population size, and not density, as the determining factor of parasite infection: a case study. *Parasitology* **128**, 305–313.
- Bush, A.O. & Holmes, J.C. (1986) Intestinal helminths of lesser scaup ducks: an interactive community. *Canadian Journal of Zoology* **64**, 142–152.
- Bush, A.O., Aho, J.M. & Kennedy, C.R. (1990) Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* **4**, 1–20.
- Bush, A.O., Lafferty, K.D., Lotz, J.M. & Shostak, A.W. (1997) Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* **83**, 575–583.
- Carvalho, A.R., Tavares, L.E.R. & Luque, J.L. (2010) Variação sazonal dos metazoários parasitos de *Geophagus brasiliensis* (Perciformes: Cichlidae) no rio Guandu, Estado do Rio de Janeiro, Brasil. *Acta Scientiarum Biological Sciences* **32**, 159–167.
- Domingues, M.V. & Boeger, W.A. (2005) Neotropical Monogenoidea 47. Phylogeny and coevolution of species of *Rhinoxenus* (Platyhelminthes, Monogenoidea, Dactylogyridae) and their Characiformes hosts (Teleostei, Ostariophysi) with description of four new species. *Zoosystema* **27**, 441–467.
- Eiras, J.C. (1994) *Elementos de ictioparasitologia*. 339 pp. Porto, Fundação Eng. Antônio de Almeida.
- Eiras, J.C., Takemoto, R.M. & Pavanelli, G.C. (2010) *Diversidade dos parasitas de peixes de água doce do Brasil*. 333 pp. Maringá, Editora Clivetec.
- Fallon, S.M., Bermingham, E. & Ricklefs, R.E. (2003) Island and taxon effects in parasitism revisited: avian malaria in the Lesser Antilles. *Evolution* **57**, 606–615.

- Galina, A.B. & Hahn, N.S.** (2003) Comparação da dieta de duas espécies de *Triportheus* (Characidae, Triporthetinae), em trechos do reservatório de Manso e lagoas do rio Cuiabá, Estado do Mato Grosso. *Acta Scientiarum Biological Sciences* **25**, 345–352.
- Junk, W.J., Brown, M., Campbell, I.C., Finlayson, M., Gopal, B., Ramberg, L. & Warner, B.G.** (2006) The comparative biodiversity of seven globally important wetlands: a synthesis. *Aquatic Sciences* **68**, 400–414.
- Kennedy, C.R.** (1997) Freshwater fish parasites and environmental quality: an overview and caution. *Parassitologia* **39**, 249–254.
- Kennedy, C.R.** (2009) The ecology of parasites of freshwater fishes: the search for patterns. *Parasitology* **136**, 1653–1662.
- Kohn, A. & Paiva, M.P.** (2000) Fishes parasitized by Monogenea in South America. pp. 25–60 in Salgado-Maldonado, G., Aldrete, A.N.G. & Vidal-Martínez, V.M. (Eds) *Metazoan parasites in the tropics: a systematic and ecological perspective*. Mexico, Universidad Nacional Autónoma (UNAM).
- Kohn, A., Fernandes, B.M.M. & Cohen, S.C.** (2007) *South American trematodes parasites of fishes*. 318 pp. Rio de Janeiro, Imprinta Express Ltda.
- Li, W.X., Wang, G.T., Yao, W.J. & Nie, P.** (2010) Frequency distribution and seasonal dynamics of intestinal helminths in the yellowhead catfish, *Pelteobagrus fulvidraco*, from Liangzi Lake, China. *Comparative Parasitology* **77**, 31–36.
- Lowe-McConnell, R.H.** (1991) *Ecological studies in tropical fish communities*. 382 pp. Cambridge, Cambridge University Press.
- Ludwig, J.A. & Reynolds, J.F.** (1988) *Statistical ecology: a primer on methods and computing*. 337 pp. New York, Wiley-Interscience Publications.
- Luque, J.L. & Poulin, R.** (2007) Metazoan parasite species richness in Neotropical fishes: hotspots and the geography of biodiversity. *Parasitology* **134**, 865–878.
- Luque, J.L., Mouillot, D. & Poulin, R.** (2004) Parasite biodiversity and its determinants in coastal marine teleost fishes of Brazil. *Parasitology* **128**, 671–682.
- Luque, J.L., Aguiar, J.C., Vieira, F.M., Gibson, D.I. & Santos, C.P.** (2011) Checklist of Nematoda associated with the fishes of Brazil. *Zootaxa* **3082**, 1–88.
- Machado-Filho, D.A.** (1959) Echinorhynchidae do Brasil II. *Memórias do Instituto Oswaldo Cruz* **57**, 195–198.
- Malabarba, M.C.S.L.** (2004) Revision of the Neotropical genus *Triportheus* Cope, 1872 (Characiformes: Characidae). *Neotropical Ichthyology* **2**, 167–204.
- Moravec, F.** (1998) *Nematodes of freshwater fishes of the Neotropical region*. 464 pp. Praha, Academy of Sciences of the Czech Republic.
- Mouritsen, K.N. & Poulin, R.** (2005) Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects. *Oikos* **108**, 344–350.
- Nagel, L., Robb, T. & Forbes, M.R.** (2009) Parasite-mediated selection amidst marked inter-annual variation in mite parasitism and damselfly life history traits. *Ecoscience* **16**, 265–270.
- Olson, R.E., Pierce, J.R., Jacobson, K.C. & Bureson, E.M.** (2004) Temporal changes in the prevalence of parasites in two Oregon estuary-dwelling fishes. *Journal of Parasitology* **90**, 564–571.
- Pech, D., Aguirre-Macedo, M.L., Lewis, J.W. & Vidal-Martínez, V.M.** (2010) Rainfall induces time-lagged changes in the proportion of tropical aquatic hosts infected with metazoan parasites. *International Journal for Parasitology* **40**, 937–944.
- Pinto, R.M. & Noronha, D.** (1976) *Procamallanus* brasileiros (Nematoda, Camallanoidea): considerações finais, com chave para determinação das espécies. *Memórias do Instituto Oswaldo Cruz* **74**, 133–136.
- Poulin, R.** (1993) The disparity between observed and uniform distributions: a new look at parasite aggregation. *International Journal for Parasitology* **23**, 937–944.
- Poulin, R.** (2006) Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. *International Journal for Parasitology* **36**, 877–885.
- Poulin, R.** (2007) Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.
- Poulin, R., Guilhaumon, F., Randhawa, H.S., Luque, J.L. & Mouillot, D.** (2011) Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. *Oikos* **120**, 740–747.
- Resende, E.K. & Pereira, R.A.C.** (2000) *Peixes onívoros da planície inundável do rio Miranda, Pantanal, Mato Grosso do Sul, Brasil*. 44 pp. Corumbá, Embrapa Pantanal.
- Santos, C., Gibson, D.I., Tavares, L.E.R. & Luque, J.L.** (2008) Checklist of Acanthocephala associated with the fishes of Brazil. *Zootaxa* **1938**, 1–22.
- Takemoto, R.M., Pavanelli, G.C., Lizama, M.A.P., Luque, J.L. & Poulin, R.** (2005) Host density as a major determinant of endoparasite species richness in fishes of floodplain of the upper Parana River, Brazil. *Journal of Helminthology* **79**, 75–84.
- Thatcher, V.E.** (1991) Amazon fish parasites. *Amazoniana* **6**, 263–572.
- Thatcher, V.E.** (2006) *Amazon fish parasites*. 508 pp. Sofia, Pensoft.
- Thatcher, V.E. & Boeger, W.A.** (1983) Patologia de peixes da Amazônia brasileira, 3. Alterações histológicas em brânquias provocadas por *Ergasilus*, *Brasergasilus* e *Acusicola* (Crustacea: Cyclopoida: Ergasilidae). *Acta Amazonica* **13**, 441–451.
- Thomas, F., Crivella, A., Cezilly, F., Renaud, F. & De Meeus, T.** (1997) Parasitism and ecology of wetlands: a review. *Estuaries and Coasts* **20**, 646–654.
- Valentin, J.L.** (2000) *Ecologia numérica. Uma introdução à análise multivariada de dados ecológicos*. 117 pp. Rio de Janeiro, Interciência.
- Violante-González, J., Aguirre-Macedo, M.L. & Vidal-Martínez, V.M.** (2008) Temporal variation in the helminth parasite communities of the Pacific fat sleeper, *Dormitator latifrons*, from Tres Palos Lagoon, Guerrero, Mexico. *Journal of Parasitology* **94**, 326–334.
- Vital, J.F., Varella, A.M.B., Porto, D.B. & Malta, J.C.O.** (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**, 199–204.
- Zar, J.H.** (1999) *Biostatistical analysis*. 663 pp. Upper Saddle River, Prentice-Hall.