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Influence of the Seasonal and Environmental Patterns and Host Reproduction on the Metazoan Parasites of *Prochilodus lineatus*

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ABSTRACT

One hundred and forty-eight specimens of Prochilodus lineatus *(Valenciennes, 1836) were collected on the Upper Paraná River floodplain, Brazil.* Kritskyia boegeri *presented significant differences in the abundance according to the host stage of gonadal maturity.* Ergasilus *sp. presented negative correlation between the GSR of the females and parasite abundance.* K. boegeri *presented negative correlation between the GSR of the males and abundance.* Tereancistrum curimba *and* Saccocoelioides magnorchis *occurred in higher abundance in the open lagoons.* Rhinonastes pseudocapsaloideum *and* S. nanii *presented higher abundance in the channels and* Tylodelphis *sp. presented higher abundance in the closed lagoons and in the rivers.* K. boegeri *and* Amplexibranchius *sp. presented significant differences in their abundances between the months of the year.* Saccocoelioides nanii *presented higher abundances in February-March 2000. Only* Tylodelphys *sp. presented correlation between fluviometric level and abundance and* S. nanii *presented significant correlation between water temperature and prevalence.*

Key words: *Prochilodus lineatus*, parasite, Upper Paraná River floodplain, Brazil

INTRODUCTION

Prochilodus lineatus (Valenciennes, 1836) is a species that has always presented high biomass on the Upper Paraná River floodplain. After the closure of the reservoir of Sérgio Motta Hydroelectric Power Plant in Porto Primavera (São Paulo State) in November 1998, which caused the interruption of the critical phase of the floods on this floodplain (Veríssimo, 1999), the life cycle of the species underwent considerable change (Agostinho and Júlio Jr, 1999). This may have caused alterations in reproduction or the displacement of individuals in reproduction to other spawning grounds, with the consequent disappearance of young individuals from areas previously sampled. The impact that the species experienced has probably influenced the metazoan parasite community, modifying its structure. Few studies related to the parasite ecology of this species on the Upper Paraná River floodplain have been carried out (Ranzani-Paiva, et al., 2000). A recent work related to the parasite ecology of this species was developed by Martins et al. (2001).
Therefore, the study of the seasonal dynamics of parasitism levels serves as a tool to understand

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broad aspects that determine the population biology of the host-parasite system (Chubb, 1982). The objective of this work was the evaluation of the relationships between the host, *Prochilodus lineatus*, and its community of metazoan parasites regarding seasonal dynamics, as well as aspects referring to reproduction.

MATERIALS AND METHODS

One hundred and forty-eight specimens of *Prochilodus lineatus* were collected from February 2000 to May 2001 on the Upper Paraná River floodplain in the "Ilhas e Várzea do rio Paraná" Protected Area (Brazil) (Fig. 1). Fish captures were undertaken using gill nets. The total weight, standard length, gonad weight, sex and stage of gonadal maturity of each fish were recorded. The parasites were collected with the aid of a stereoscopic microscope (see Eiras et al., 2000).

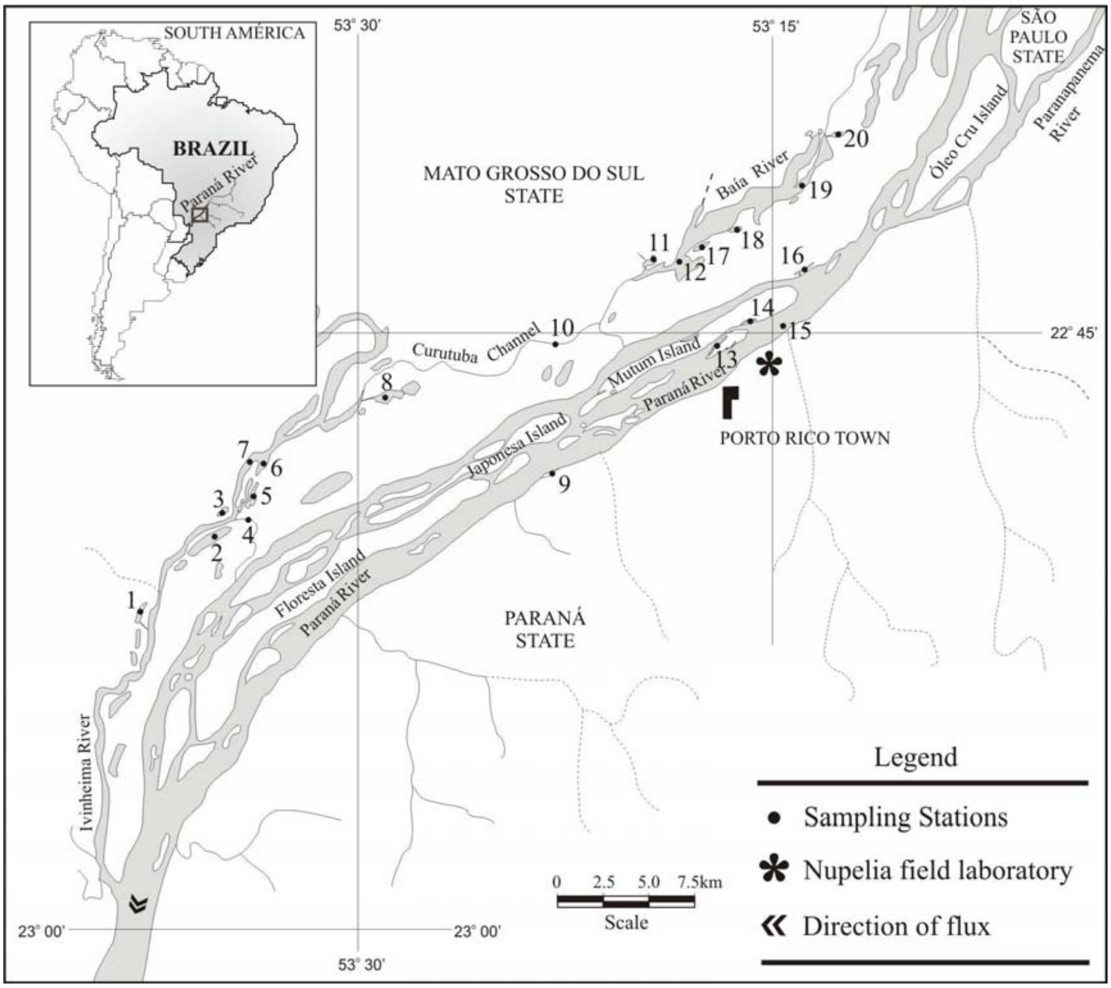

Figure 1 - Upper Paraná River floodplain. Sampling stations. 1. Peroba Lagoon, 2. Ventura Lagoon, 3. Zé do Paco Lagoon, 4. Ipoitã Channel, 5. Patos Lagoon, 6. Capivara Lagoon, 7. Ivinheima River, 8. Sumida Lagoon, 9. Cortado Channel, 10. Corutuba Channel, 11. Guaraná Lagoon, 12. Baia River, 13. Leopoldo Glades, 14. Pau Véio Glades, 15. Paraná River, 16. Garças Lagoon, 17. Fechada Lagoon, 18. Pousada das Garças Lagoon, 19. Baía Channel and 20. Onça Lagoon.

The metazoan parasites were identified according to Thatcher (1978, 1979, 1991 and 1993), Thatcher and Boeger (1984a and b); Thatcher and Varella (1981), Moravec (1998), Takemoto et al. (2002) and Lizama et al. (2004). The environments were divided into Open Lagoons, which included the sites Onça Lagoon (Number of fishes collected = 5), Peroba Lagoon (N = 3), Garças Lagoon (N = 19), Guaraná Lagoon (N = 1), Patos Lagoon (N = 4), Sumida Lagoon (N = 1), Leopoldo Glade (N = 13) and Pau Véio Glade (N = 5); Closed Lagoons, including Capivara Lagoon (N = 4), Ventura Lagoon (N = 4), Fechada Lagoon (N = 8), Zé do Paco Lagoon (N = 12) and Pousada das Garças Lagoon (N = 10); Channels, including Ipoitã Channel (N = 4), Baía Channel (N = 3), Cortado Channel (N = 9) and Corutuba Channel (N = 2); and Rivers Ivinheima (N = 5), Paraná (N = 9) and Baía (N = 27).

The bimonthly frequency data of the stage of gonadal maturity, as well as the bimonthly mean of the gonadosomatic index, or GSR (expression between gonad weight and body weight of the fish), were used as a tool to determine the reproduction period of the "curimba". The monthly water temperature values were recorded. The monthly means of the fluviometric levels were provided by the Agência Nacional das Águas (ANA). Data analysis was carried out using Pearson’s coefficient of correlation "r", with previous angular transformation of the prevalence values to determine possible correlation with water temperature and fluviometric level, in addition to Spearman’s rank coefficient of correlation "rs", used to determine possible correlation between abundance of infection/infestation and the GSR, water temperature and fluviometric level. The Kruskall-Wallis "H" test was used to observe the differences in parasitism abundance between each period of gonadal maturity (immature, maturation, in reproduction, spent and at rest), according to Vazzoler (1996), in order to observe the differences between the diverse environments of the Upper Paraná River floodplain, as well as the differences in the months of the year (Zar, 1996).

The tests were applied to the species of parasites that presented prevalence higher than 10% (Bush, et al., 1990). The statistical level of significance adopted was p $\leq$ 0.05.

The terminology related to parasite ecology was based on Bush et al. (1997).

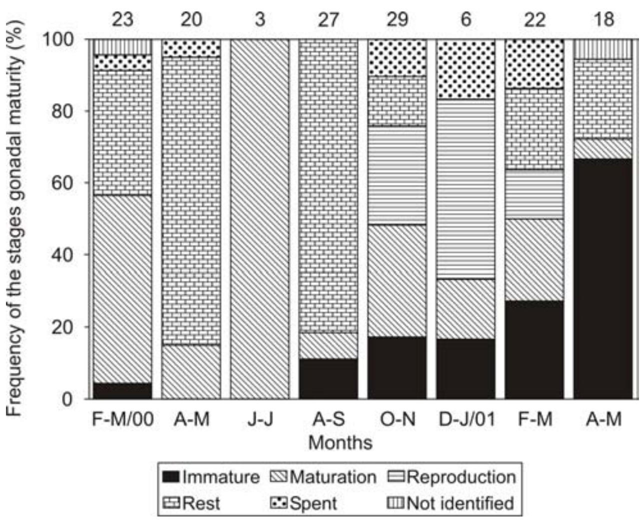

Figure 2 - Stages of gonadal maturity of the *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001. (Numbers in the superior part of the graph refer to the number of analyzed fish).

RESULTS

Reproduction

Out of a total of 148 fishes examined, 120 specimens were parasitized by at least one species of parasite. Thirty-three species of metazoan parasites were recorded. A total of 2,660 parasites were collected and the majority of the specimens were digeneans. Only 11 species presented prevalence higher than 10%. The study of the stage of gonadal maturity showed that the specimens of *P. lineatus* in reproduction occurred from October-November 2000 to February-March 2001, with the peak in December 2000-January 2001 (Fig. 2).

Kritskyia boegeri presented significant differences in the abundance values among the stages of host gonadal maturity (Table 1), with the lowest means in the immature stage (0.43) and the highest observed in the maturation and reproduction stages (2.17 and 2.36, respectively). The highest values of the mean gonadosomatic relation (GSR) of the females occurred between October-November 2000 and February-March 2001, with the GSR peak in December 2000- January 2001. The males, despite presenting lower GSR values than the females, showed the same tendency. The period in which the highest GSR values occurred coincided with the rising water temperature values and the beginning of the high water period (Fig. 3).

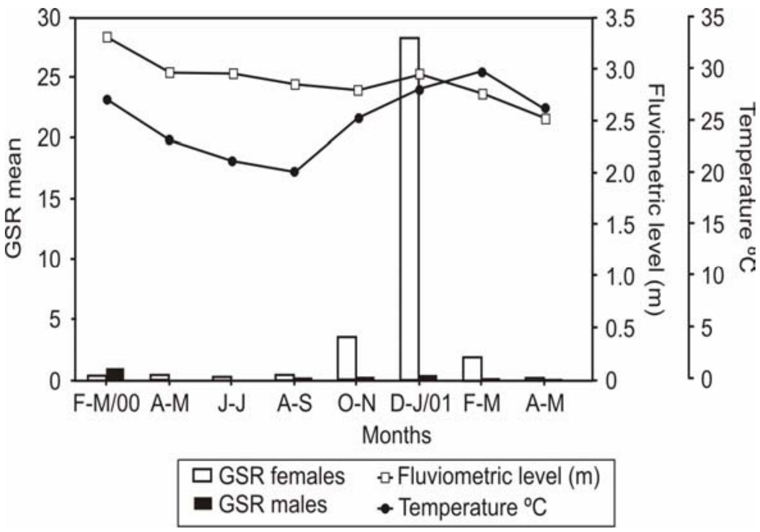

Figure 3 - Gonadosomatic Relation (GSR) of *Prochilodus lineatus*, temperature of the water (°C) and fluviometric level (m) in the Upper Paraná River floodplain, from February 2000 to May 2001.

Table 1 - Values of Kruskal-Wallis "H" test comparing the abundances of parasitism with the influence of stage of gonadal maturity of *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = level of significance)

Parasite	H	p
Monogenea		
Rhinonastes pseudocapsaloideum	5.937	0.2039
Kritskyia boegeri	10.210	0.0370*
Tereancistrum curimba	7.738	0.1017
Digenea		
Saccocoelioides magnorchis	3.161	0.5313
Saccocoelioides nanii	5.462	0.2431
Tylodelphis sp. (metacercariae)	7.675	0.1042
Acanthocephala		
Neoechinorhynchus curemai	4.038	0.4009
Copepoda		
Gamidactylus jaraquensis	3.900	0.4197
Gamispatulus sp.	4.713	0.3180
Amplexibranchius sp.	5.450	0.2441
Ergasilus sp.	3.317	0.5062

* Significant Values

Table 2 - Values of Spearman's rank coefficient correlation "rs", correlating the GSR of the males and females with the abundance of parasitism for *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = significance level)

Parasite	Females		Males	
	rs	p	rs	p
Monogenea				
Rhinonastes pseudocapsaloideum	- 0.0552	0.6450	- 0.2165	0.1123
Kritskyia boegeri	0.0818	0.4944	- 0.3258	0.0152*
Tereancistrum curimba	0.0067	0.9557	- 0.2624	0.0530
Digenea				
Saccocoelioides magnorchis	0.0155	0.8969	- 0.1453	0.2897
Saccocoelioides nanii	0.1915	0.1071	- 0.1159	0.3993
Tylodelphis sp. (metacercariae)	0.0347	0.7721	0.1345	0.3276
Acanthocephala				
Neoechinorhynchus curemai	0.2137	0.0715	- 0.1911	0.1623
Copepoda				
Gamidactylus jaraquensis	0.0306	0.7987	- 0.1992	0.1448
Gamispatulus sp.	- 0.1665	0.1621	- 0.0947	0.4918
Amplexibranchius sp.	0.0347	0.7721	- 0.0957	0.4871
Ergasilus sp.	- 0.2754	0.0192*	- 0.2200	0.1065

* Significant Values

The copepod *Ergasilus* sp. presented significant negative correlation between the GSR of the females and parasite abundance. In the male host, the monogenean *Kritskyia boegeri* presented significant negative correlation between the GSR and abundance. The monogenean *Tereancistrum curimba* also presented negative correlation; however, it was not very significant in the males (Table 2).

Influence of the environment

Several species of parasites presented significant differences among their abundances in the different environments of the Upper Paraná River floodplain. The monogenean *T. curimba* and the digenean *S. magnorchis* occurred in higher abundance in the hosts captured in the open lagoons (mean abundance = 1.31 and 5.57, respectively) in relation to the other environments sampled. The monogenean *R. pseudocapsaloideum* and the digenean *S. nanii* presented higher abundance in the channels (mean abundance = 2.00 and 28.75, respectively). The metacercaria *Tylodelphys* sp. presented higher abundance in the closed lagoons and in the rivers (mean abundance = 0.26 and 0.25, respectively) (Table 3).

Seasonality

Among the ectoparasites, the monogenean *K. boegeri* and the copepod *Amplexibranchius* sp. presented significant differences in their abundances between the months of the year (Table 4).

The most abundant months were: December 2000-January 2001 for *K. boegeri* and June-July 2000 for *Amplexibranchius* sp. Among the endoparasites, *Saccocoelioides nanii* and *Tylodelphis* sp. presented significant differences between the months of the year and parasite abundance, with higher abundances in February-March 2000 and December 2000- January 2001, respectively (Fig. 4 and Table 4).

Only the digenean *Tylodelphis* sp. presented significant positive correlation between fluviometric level and parasite abundance. No species presented significant correlation between fluviometric level and parasitism prevalence. Only *S. nanii* presented significant correlation between water temperature and parasitism prevalence (Tables 5 and 6).

Table 3 - Values of Kruskall-Wallis "H" tests comparing the abundance of parasitism of *Prochilodus lineatus* captured in different environments (open ponds, closed ponds, channels and rivers) in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = level of significance)

Parasite	H	p
Monogenea		
Rhinonastes pseudocapsaloideum	9.737	0.0209*
Kritskyia boegeri	3.218	0.3593
Tereancistrum curimba	8.526	0.0363*
Digenea		
Saccocoelioides magnorchis	10.199	0.0169*
Saccocoelioides nanii	8.583	0.0354*
Tylodelphis sp. (metacercariae)	9.540	0.0229*
Acanthocephala		
Neoechinorhynchus curemai	7.737	0.0518
Copepoda		
Gamidactylus jaraquensis	0.3042	0.9592
Gamispatulus sp.	6.594	0.0860
Amplexibranchius sp.	2.198	0.5323
Ergasilus sp.	1.049	0.7893

* Significant Values

Table 4 - Values of Kruskall-Wallis "H" tests to verify the seasonality of the abundance of parasitism of *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = level of significance)

Parasite	H	p
Monogenea		
Rhinonastes pseudocapsaloideum	13.623	0.0583
Tereancistrum curimba	13.109	0.0695
Kritskyia boegeri	22.567	0.0020*
Digenea		
Saccocoelioides magnorchis	13.431	0.0623
Saccocoelioides nanii	14.254	0.0468*
Tylodelphis sp. (metacercariae)	21.522	0.0031*
Acanthocephala		
Neoechinorhynchus curemai	5.324	0.6205
Copepoda		
Gamidactylus jaraquensis	10.067	0.1848
Gamispatulus sp.	6.584	0.4734
Amplexibranchius sp.	14.095	0.0495*
Ergasilus sp.	13.924	0.0525

* Significant Values

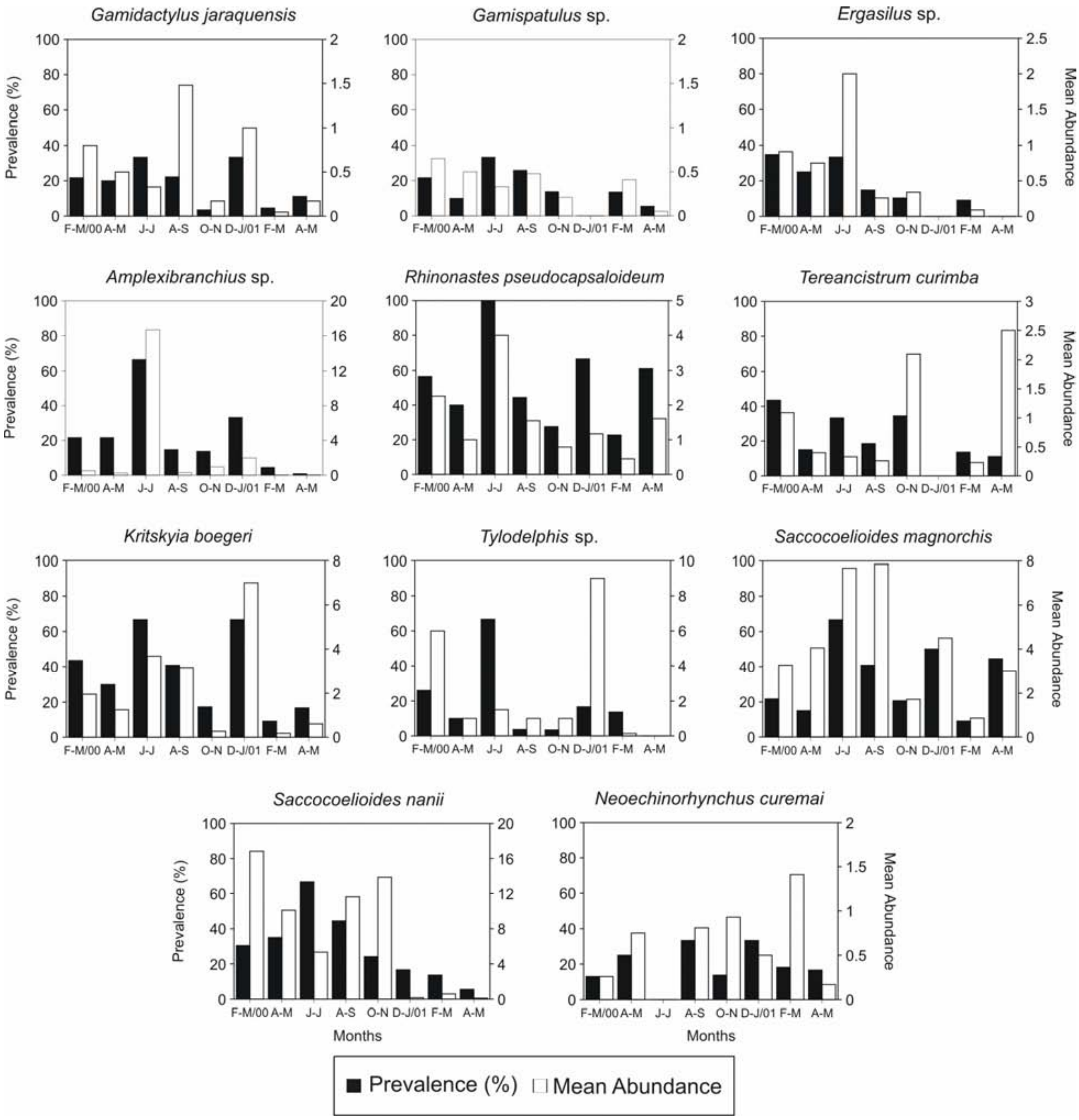

Figure 4 - Bimonthly values of de Mean Abundance and Prevalence of the metazoan parasites of the *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001.

DISCUSSION

Reproduction

The results of the study of the stage of gonadal maturity and the mean GSR showed that the reproduction of *Prochilodus lineatus* on the Upper Paraná River floodplain (Brazil) was from October to March, with the peak in December.

Table 5 - Values of Spearman's rank coefficient correlation "rs", correlating the fluviometric level and the abundance of parasitism and Pearson's coefficient correlation "r" between the fluviometric level and prevalence of parasitism for *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = significance level)

Parasite	Fluviometric level			
	rs	p	r	p
Monogenea				
Rhinonastes pseudocapsaloideum	0.4084	0.3268	0.1918	0.6490
Tereancistrum curimba	0.1190	0.7930	0.3627	0.3772
Kritskyia boegeri	0.5476	0.1710	0.5460	0.1615
Digenea				
Saccocoelioides magnorchis	0.4762	0.2431	-0.0907	0.8308
Saccocoelioides nanii	0.5476	0.1710	0.4970	0.2102
Tylodelphis sp. (metacercariae)	0.7563	0.0368*	0.5921	0.1220
Acanthocephala				
Neoechinorhynchus curemai	- 0.3333	0.4279	- 0.1173	0.7821
Copepoda				
Gamidactylus jaraquensis	0.5749	0.1511	0.5021	0.2049
Gamispatulus sp.	0.5952	0.1325	0.2694	0.5188
Amplexibranchius sp.	0.4762	0.2431	0.4769	0.2322
Ergasilus sp.	0.7186	0.0576	0.6860	0.0643

* Significant Values

Table 6 - Values of Spearman's rank coefficient correlation "rs", correlating the temperature of the water and the abundance of parasitism and Pearson's coefficient correlation "r" between the fluviometric level and prevalence of parasitism for *Prochilodus lineatus* captured in the Upper Paraná River floodplain, from February 2000 to May 2001 (p = significance level)

Parasite	Temperature of the water			
	rs	p	r	p
Monogenea				
Rhinonastes pseudocapsaloideum	- 0.3810	03599	- 0.4101	0.3129
Tereancistrum curimba	- 0.2143	0.6199	- 0.3384	0.4123
Kritskyia boegeri	- 0.3095	0.4618	- 0.3669	0.3713
Digenea				
Saccocoelioides magnorchis	- 0.6667	0.0831	- 0.4609	0.2504
Saccocoelioides nanii	- 0.3333	0.4279	- 0.7756	0.0237*
Tylodelphis sp. (metacercariae)	0.0244	0.9768	- 0.1793	0.6710
Acanthocephala				
Neoechinorhynchus curemai	0.2143	0.6191	0.2257	0.5910
Copepoda				
Gamidactylus jaraquensis	- 0.3713	0.3599	- 0.4056	0.3188
Gamispatulus sp.	- 0.2381	0.5821	- 0.5862	0.1267
Amplexibranchius sp.	- 0.2857	0.5008	- 0.4567	0.2554
Ergasilus sp.	- 0.4791	0.2431	- 0.4534	0.2592

* Significant Values

The results coincided with the findings of Vazzoler (1996) and Agostinho and Júlio Jr. (1999) on the Upper Paraná River floodplain and Terraes et al. (1999) in Argentina.
The frequency graph of the stage of gonadal maturity showed the presence of spent specimens starting in October. These results reinforced that the reproductive period of the species occurred between October and February. The presence of spent fish in February-March and April-May 2000 indicate was that in the previous year the reproductive period of the species altered by environmental changes on the floodplain.
The higher abundance of the monogenean *K. boegeri* coincided with the reproductive period of the host. This probably occurred because the

period caused stress in the fish, leaving it more susceptible to parasitism. Zaman and Seng (1989), showed that the increase in the parasitism abundance of *Clarias batrachus* and *C. macrocephalus* coincided with the increase in fluviometric level and the gonadosomatic indices, which are indicators of the reproductive period of the host.

The study of the gonadosomatic index is used as a tool to increase the knowledge of the reproductive biology of a fish population. Gil de Pertierra and Ostrowski de Nuñez (1990) used this index in relation to the life cycle of a parasite, since it was intimately related to the life cycle of the host. Their results showed that the GSR peak, characteristic of the reproductive phase of the fish *Rhamdia sapo*, coincided with the maximum egg production of the cestode *Proteocephalus jandia*, whereas the output of gonadotropin by the fish was in synchrony with the peak of the ovoposition of the parasite. The occurrence of negative correlation between the GSR of the hosts and parasitism abundance, as observed for *Ergasilus* sp. in females and *K. boegeri* in males of *P. lineatus*, was also observed by Zaman and Seng (1989) for the parasites of *C. batrachus* and *C. macrocephalus*. Thomas (1964) and Pennicuick (1971a and b) suggested that the low infection by parasites during the spawning period, which coincided with the rainy period, occurred because of the presence of estrogen, a hormone that appeared in the blood of fish during maturation. After spawning, the hormone decreased, and the opposite happened.

Influence of the environment

According to Yañes and Canaris (1988), the reproductive migration pattern of a host can be a determining factor in the composition and structure of parasite communities. Youngs of the "curimba" (up to one year old) remain exclusively in the lagoons. From the first to the second year of life, the "curimba" makes short migrations to the streams and small rivers in the ebbing period in search of food and shelter. From the second year, *P. lineatus* begins to carry out long upward migrations to reproduce and downward migrations to feed and/or recuperate (Resende et al., 1996). Youngs of the "curimba" between 7-12 cm long, and adults between 40-50 cm long are found in lateral lagoons (shallow lagoons that fill in the flood period) and channels. During the floods, when the river reaches countless lagoons and islands of the floodplain, the fish migrate to the rivers or lagoons. At the end of the ebbing period, the shallow lagoons dry up, imprisoning large numbers of fish and leading to high mortality at these sites (Agostinho and Júlio Jr, 1999).

Ectoparasites are considered typical of lentic environments because the free-swimming larval forms easily find their host in these environments. *Tereancistrum curimba* and *Rhinonastes pseudocapsaloideum* are examples. These species present eggs without filaments, typical of habitats with little water flow. However, they were found in higher abundance in semi-lotic and lotic (channels and rivers) environments. This may have occurred due to the migration pattern of the host. The short and long migrations that this species carries out over its lifetime permit the fish to exploit diverse environments, increasing the possibility of infection/infestation by diverse species of parasites. In this way, the "curimba" is able to become bearer and disseminator of parasites in the several environments of the Upper Paraná River floodplain.

Regarding endoparasites, their presence in higher abundance in the open lagoons and channels may be evidence of the presence of intermediate invertebrate hosts that serve as food for the "curimba", in addition to the detritus and sediment that compose its diet (Hahn et al., 1997). Takeda et al. (2000) found that in the diverse subsystems of the Upper Paraná River floodplain, many lagoons and glades were interconnected to the main channel, influenced by the fluviometric fluctuation of the river, which often turns the lentic environment into a lotic one, favoring the establishment of these species of intermediate hosts and consequently the parasites in these environments. This interconnection of subsystems also explained the dissemination of ectoparasites.

Seasonality

Not all parasite species of *P. lineatus* of the Upper Paraná River floodplain presented the same seasonal pattern. Of the species that presented significant seasonal variation, *Amplexibranchius* sp. presented the highest abundance in June-July, before the hosts left the lagoons for the river to form schools and later began reproductive migration (Agostinho and Júlio Jr., 1999). On the other hand, *Kritskyia boegeri* was more abundant in December 2000-January 2001, during reproductive period of the host.

Many abiotic factors affect the abundance and prevalence of parasites. Among these, temperature is one of the most important in the parasite-host-environment relationship (Kennedy, 1982). Williams and Jones (1994) observed that the development and reproduction of fish was directly related to temperature. Vazzoler et al. (1997) suggested that there was a synchrony between the abiotic factors, which functioned as triggers, causing the maturation of the gametes and consequently the reproduction of the species of fish. Among these triggers, temperature, fluviometric level and photoperiod are the most important. Thomas (1964) concluded that the spawning of *Salmo truta* was directly related to the flood period and the hormonal levels of the fish, and the parasitism levels were related to both. Works similar to these were carried out by Pennicuick (1971a and b) and Nie and Kennedy (1991).

Some studies showed that for most of the species of fish, the rise in temperature increased the intensity of infection by the parasites (Hanzelová and Zitnan, 1982, 1983; Gelnar, 1987). However, the results obtained in this work showed that the water temperature on the floodplain presented negative correlation only with the parasitism prevalence for *S. nanii*. Gil de Pertierra and Ostrowski de Nuñez (1995) suggested that each species of parasite used a range of specific ideal temperature, which triggered physiological development processes of the parasite. These patterns, in addition to temperature, are influenced by factors connected to the life cycle of the parasite (availability of cercariae, metacercariae and final host), host biology (diet during its development, and during the seasons and migrations) and other possible final hosts. Bauer (1959) showed that factors such as age, physiological condition, host migration and season were very important as regards parasitism levels.

The results obtained in this work suggested that fluviometric level directly influenced the *P. lineatus* population and indirectly influenced the community of metazoan parasites, as in the case of *Tylodelphis* sp., which presented positive correlation regarding abundance and fluviometric level. These results were in agreement with those observed by Stromberg and Crites (1974), who suggested that more than temperature, fluviometric level influenced the population of copepods, intermediate hosts of the nematodes, object of that study. Zaman and Seng (1989) also suggested that the extra peaks in abundance could be explained by the fact that in the dry period, the intermediate hosts were more congregated, thus increasing the chances of infection.

According to Veríssimo (1999), the intensity and duration of the flood period greatly influenced the reproductive success of the species of fish. In years in which the flood period was intense and lasting, the offspring of migratory species, as in the case of the "curimba", reached the lagoons in search of food and shelter, occurring in large numbers of specimens. In years in which the flood period was short, migratory species presented lower densities. With the closure of Sérgio Motta Reservoir in 1998, the floods were interrupted, resulting in migratory species (e.g. *P. lineatus*) recruitment failures (Júlio, Jr. et al., 2000). These failures caused reduction in the population existing in the region, and/or influenced the exit of part of the "curimba" population to other environments, which could have interfered with the metazoan parasite community of the Upper Paraná River floodplain.

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RESUMO

Cento e quarenta e oito espécimes de *Prochilodus lineatus* (Valenciennes, 1836) foram coletados na planície de inundação do Alto rio de Paraná, Brasil. *Kritskyia boegeri* apresentou diferenças significativas na abundância de acordo com os estágios de maturação de gonadal do hospedeiro. *Ergasilus sp* apresentou correlação negativa entre o RGS das fêmeas e a abundância parasitária. *K.*

boegeri apresentou correlação negativa entre o RGS dos machos e a abundância. *Tereancistrum curimba* e *Saccocoelioides magnorchis* ocorreram em abundância mais alta nas lagoas abertas. *Rhinonastes pseudocapsaloideum* e *S. nanii* apresentaram abundância mais alta nos canais e *Tylodelphis* sp. apresentou abundância mais alta nas lagoas fechadas. *K. boegeri* e *Amplexibranchius* sp. apresentaram diferenças significativas em suas abundâncias durante os meses do ano. *Saccocoelioides nanii* apresentou abundâncias mais altas nos meses de fevereiro-março de 2000. Somente *Tylodelphis* sp. apresentou correlação entre nível fluviométrico e abundância e *S. nanii* apresentou correlação significativa entre a temperatura da água e prevalência de parasitismo.

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