

# The role of the predatory trahira (Pisces: Erythrinidae) in structuring fish assemblages in lakes of a Neotropical floodplain

Ana Cristina Petry · Luiz Carlos Gomes ·  
Pitágoras Augusto Piana ·  
Angelo Antonio Agostinho

Received: 8 June 2009 / Revised: 19 April 2010 / Accepted: 26 April 2010 / Published online: 15 May 2010  
© Springer Science+Business Media B.V. 2010

**Abstract** We performed an experimental manipulation of trahira *Hoplias* aff. *malabaricus* in a series of isolated lakes of the upper Paraná River floodplain to evaluate its short-term impact on the structure of fish assemblages. The effects of trahira density (treatment groups: addition, removal, and reference) in two habitat categories (open and macrophyte-covered areas) on attributes of the fish assemblage structure were evaluated (using rm-ANOVA) over 120 days. Reductions in species richness were recorded in all

assemblages and were more pronounced at the end of the experiment within macrophyte-covered areas of the lakes where *H. aff. malabaricus* was removed. In these lakes, the number of fish was also significantly smaller and evenness was significantly higher than in those in which trahira were added or maintained at natural densities. The increase of the relative abundance of all size classes over the first 60 days on the assemblages where trahira was present, and the decrease of the small-sized fish where trahira was absent contributed to the lack of pronounced alterations in total biomass. The absence of the predator from its preferred habitat was found to negatively affect the less abundant species, which seemed to be highly sensitive to the effects of interspecific competition among prey species. In addition to the well-known effects of hydrological seasonality, the role played by native predators might be important in determining the persistence of local species in the fish assemblages of Neotropical floodplains.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-010-0281-0) contains supplementary material, which is available to authorized users.

Handling editor: D. Dudgeon

A. C. Petry (✉)  
Universidade Federal do Rio de Janeiro, Nupem,  
R. Rotary Club, sn, CP: 119331, Macaé, RJ 27910-970,  
Brazil  
e-mail: ac\_petry@yahoo.com.br

L. C. Gomes · A. A. Agostinho  
Universidade Estadual de Maringá, Nupélia, Av.  
Colombo, 5790, Maringá, PR 87020-900, Brazil  
e-mail: lcgomes@nupelia.uem.br

A. A. Agostinho  
e-mail: agostinhoaa@nupelia.uem.br

P. A. Piana  
Universidade Estadual do Oeste do Paraná, R. da  
Faculdade, 2550, Toledo, PR 85903-000, Brazil  
e-mail: pitapiana@yahoo.com.br

**Keywords** *Hoplias* aff. *malabaricus* · Predation · Whole-lake experiment

## Introduction

The identification of mechanisms through which some species can assume greater importance within their assemblages has been the basis for research aiming conservation of species and ecosystems,

especially in temperate regions (Power et al., 1996a; Creed, 2000). For example, predators may affect prey in several ways, such as on its number, habitat use, period and intensity of foraging, with direct effects on intra- and inter-specific dynamics (e.g., growth, reproduction, and interactions) (Werner et al., 1983; Fraser & Gilliam, 1992; Miyasaka et al., 2003). Paine (1969) used the term *keystone* to identify species, such as the sea star *Pisaster ochraceus*, that, when present, promoted the coexistence of a larger number of species than expected relative to its abundance (Paine, 1966, 1969; Power et al., 1996b). In tropical regions, however, factors such as high environmental complexity, high species diversity, high potential interactions among species, and a limited understanding of food web dynamics (Lowe-McConnell, 1987; Flecker, 1992) have hampered investigations of the keystone concept.

Based on the conclusions of several descriptive studies, a strong candidate for this status is the trahira *Hoplias* aff. *malabaricus* (Bloch, 1794), an opportunistic and sedentary predator that is widespread in Neotropical aquatic environments (Oyakawa, 2003). Controlled investigations of the trahira's effects on other species are restricted to those which experimentally examined only one (Mazzeo et al., 2010) or two prey species (Fraser & Gilliam, 1992; Gilliam et al., 1993; Fraser et al., 1999; Gilliam & Fraser, 2001). However, other fish and some invertebrate taxa, e.g., the crab *Pseudothelphusa garmani*, appear to undergo behavioral shifts in their habitat use patterns in the presence of this strong predator (D.Fraser, pers. comm.). Alterations in the distribution patterns of small-sized fish species in Caribbean streams, increasing fishery yields in large northeastern Brazilian reservoirs, and strong cascading effects in subtropical mesocosms have been associated with the presence of trahira (Fraser & Gilliam, 1992; Paiva et al., 1994; Mazzeo et al., 2010). *H. aff. malabaricus* represents a species complex in several Brazilian riverbasins, since at least seven cytotypes have been identified (Bertollo et al., 2000). In the upper Paraná River floodplain, trahira are found in almost all biotopes, such as river channels, secondary channels, permanent and temporary lakes (Petry et al., 2003a). Despite the unsolved taxonomic problems, and the fact that ecological reports may involve more than one species, all trahiras studied have strong impacts in their local communities, which is also true for

*H. aff. malabaricus*, which appears to play an important role in structuring fish assemblages either in temporary disconnected lakes of the upper Paraná River floodplain over time. There, densities of trahira were used to explain variations in the density of prey species in recent studies, especially in macrophyte-covered areas (Okada et al., 2003; Piana et al., 2006).

This study evaluated the short-term impact of the strong piscivore trahira in modifying the dynamics of fish assemblage structure of isolated lakes in the upper Paraná River floodplain. The ichthyofauna of these lakes is essentially composed of sedentary, small-sized species whose life history characteristics [e.g., short life span, early maturation (<12 months)] reflect in high population growth rates (Winemiller, 1989; Vazzoler, 1996; Okada et al., 2003; Froese & Pauly, 2008). The expected reduction in consumption and the simplification of food webs during droughts (from autumn to spring) suggests that, if competition exists, it should be more intense during these periods. Aquatic macrophytes play an important role in floodplain lakes by increasing habitat heterogeneity, providing food resources and refuge for prey species, and lessening the forage efficiency of pelagic and aerial predators (Agostinho et al., 2007), but not reducing predation from trahira (Piana et al., 2006). Therefore, we tested the hypothesis that by piscivory, trahira determines assemblage structure and, therefore, is able to mediate fish species coexistence. If the hypothesis is true, the addition and removal of *H. aff. malabaricus* will alter species richness, abundance, evenness, biomass, and body size structure of the fish assemblages. We also tested whether any effects depended upon habitat structure, once trahira may be successful in capturing fish in macrophyte-covered areas.

## Materials and methods

The biology of the trahira *H. aff. malabaricus*

*Hoplias* aff. *malabaricus* is commonly found in the upper Paraná River floodplain (Bialecki et al., 2002; Petry et al., 2003b), where it is the main predator. The absence of pronounced floods in recent years has prevented access for other large piscivores (Petry et al., 2003b; Agostinho et al., 2004). The species exhibits multiple spawning and an extended reproductive period (from September to February) (Bialecki et al.,

2002; Suzuki et al., 2004). The sedentary and solitary trahira preferentially inhabits macrophyte-covered areas that favor its ambush feeding strategy (Almeida et al., 1997; Luz-Agostinho et al., 2008), and as larvae, juveniles, and adults, respectively, feeds on plankton, insects, and primarily fishes (Oliveros & Rossi, 1991; Hahn et al., 2004). Although there is evidence of a positive relationship between trahira and prey size, small-sized fish are the trahira's most important food resource (Loureiro & Hahn, 1996).

### Whole-lake experiment

The experiment was conducted over 120 days during autumn and winter of 2002. This period was selected based on the low water levels of the Paraná River, which caused the lakes to remain isolated (no fish movement between lakes). The experimental design consisted of six lakes (Canal do Meio, Carioca, Cidão, Zé Marinho, Genipapo, and Tião), all with open and macrophyte-covered areas (herein named habitats) and a single initial disturbance (manipulation of trahira density). We opted to test habitat effect because trahira has behavioral adaptations to thrive in macrophyte-covered areas (Piana et al., 2006). In addition, fish species that inhabit macrophyte-covered areas are distinct than those that inhabit opened areas (Delariva et al., 1994), but may present similar response to trahira predation. The lakes were similar in shape (elongated form and <1.6 m maximum depth) and in structural complexity [macrophyte cover >50% of the area and dominance of the floating *Eichhornia crassipes* (Mart.) Solms and the emergent *Paspalum repens* Berg.] (Table 1). Predator density (treatment groups: addition, HM+; removal, HM–; and natural density, named reference, REF) was randomly assigned for each lake (Fig. 1). Before running the experiment, each lake was sampled in order to determine the trahira density and to obtain baseline data for the fish assemblage (Table 1).

To better evaluate the effect of the trahira on the fish assemblages, we added trahira (size ranging from 8.3 to 33.3 cm in SL) to two lakes, Canal do Meio and Carioca, based on the mean density registered in regular 4-year surveys carried out in the region by the Nucleus of Research in Limnology, Ichthyology and Aquaculture of Maringá State University (see Petry et al., 2003b for details). Hooks and seine nets were used to remove trahira from Cidão and Zé Marinho

lakes (HM– treatment). Despite the fact that the experimental removal did not assure complete predator exclusion, the trahira density was kept near zero in these lakes. Predator density manipulation was carried out 2 days after the first sampling. At the beginning of the experiment, SL did not differ significantly between HM+ treatment lakes (Student *t* test,  $t_{(52)} = 0.53$ ,  $P = 0.60$ ).

All samplings (before and after the manipulations) were carried out bimonthly (from April to August) during the morning (from 07:00 to 11:00). Seine nets (50 m × 2.4 m, 0.5 cm mesh) were used to isolate ca. 112 m<sup>2</sup> in two selected sampling areas (open and macrophyte-covered) in every lake. These nets were set on the bottom and were attached to the edges 24 h prior to sampling. Immediately before each sampling, the nets were raised to completely enclose the areas in order to block fish passage, and fish were collected inside the areas by seine nets (open area) (5 mm mesh) and a sieve (macrophyte-covered area) until successive five sweeps did not capture any fish. The large sieve consisted of a rectangular metal frame with a 1 mm mesh sized net, dimensions of 1.5 m × 1.0 (1.5 m<sup>2</sup>) following Nakatani et al. (2001). After identification and measurement (SL, cm) all fish were returned to the water, except those that were collected in the first sampling. Fish sampled in April were weighed and coefficients of species weight–length regressions were further used to estimate fish biomass of June and August samplings.

### Response variables and data analysis

Species richness, abundance (number of fish m<sup>-2</sup>), evenness [ $E = H'/\ln$  (species richness)] (Pielou, 1969), biomass (g m<sup>-2</sup>, determined from weight–length regressions of the fish collected in the first sampling), and body size structure (relative abundance of fish in four size classes) were considered as attributes of the fish assemblage structure. To reduce the effects of the initial differences of the fish assemblage attributes (Table 1), analyses were carried out on percentage values in relation to the April measurements. This allowed us to determine variations from the beginning of the experiment attributable to treatment effects.

Repeated measures analyses of variance (rm-ANOVA, procedure GLM of the software Statistica<sup>®</sup> 7.1, Stat Soft Inc., Tulsa, OK, USA) were applied to

**Table 1** Surface area (SA, m<sup>2</sup>) at the beginning (April) and end (August) of the experiment of the six isolated lakes of the upper Paraná River floodplain, initial fish assemblage attributes [SR, species richness; AB, abundance (ind m<sup>-2</sup>); EV, evenness;

BI, biomass (g m<sup>-2</sup>); SCA, size classes abundance (% individuals)]; and initial manipulated trahira *H. aff. malabaricus* density (ind m<sup>-2</sup>)

Treatment lakes	SA		Initial fish assemblage attributes					Trahira density
	April	August	SR	AB	EV	BI	SCA	Addition
HM+								
Canal do Meio	1330	273	14	27.53	0.54	4724.98	1: 94 2: 5 3: <1 4: 2	0.01
Carioca	3800	1184	18	5.57	0.71	33068.31	1: 49 2: 42 3: 5 4: 5	0.01
HM-								
Cidão	660	228	7	7.41	0.28	2685.06	1: 83 2: 16 3: <1 4: 1	
Zé Marinho	4580	3806	14	2.12	0.70	9361.27	1: 49 2: 23 3: 27 4: <1	
REF								
Genipapo	230	162	21	7.37	0.72	3066.70	1: 63 2: 26 3: 3 4: 8	
Tião	840	285	12	5.37	0.60	1668.17	1: 93 2: 4 3: 2 4: 1	

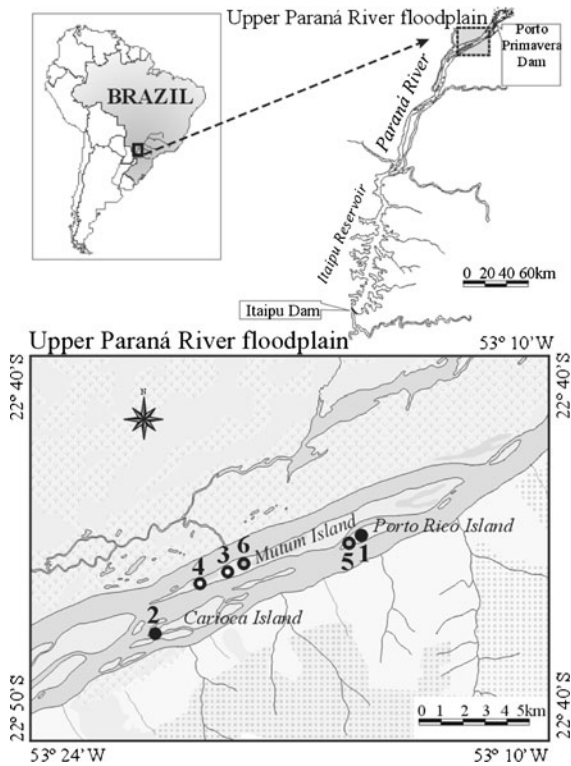
HM+, HM-, and REF refer to addition, removal, and reference of *H. aff. malabaricus* treatments, respectively

test the temporal variation of species richness, abundance, evenness, biomass (two-way rm-ANOVA), and assemblage body size structure (three-way rm-ANOVA). Predator density (addition, HM+; removal, HM-; and reference, REF) and habitat categories (open and macrophyte-covered areas) were considered treatments, whereas samplings (June and August) were the repeated measures. For the assemblage body size structure analysis, size classes (1: <3.0 cm; 2: 3.1–4.5 cm; 3: 4.6–6.5 cm; 4: >6.5 cm) were also considered a treatment. Assumptions of normality and

homoscedasticity were met in all tests and significance was implied at  $P < 0.05$ .

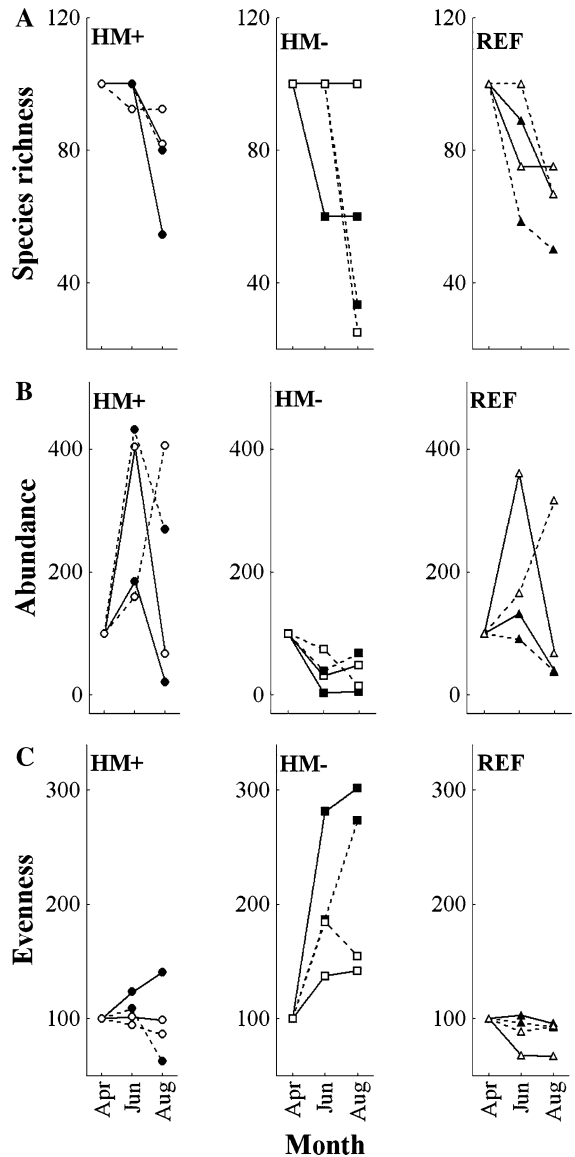
## Results

All lakes exhibited a substantial reduction in area between April and August (average 54.38%, SE = 10.20) (Table 1). Immediate mortality resulting from prey handling (i.e., biometry) was less than 5%. A total of 40 fish species was recorded, with



**Fig. 1** Study area and location of the lakes in the upper Paraná River floodplain where *H. aff. malabaricus* were added (1 Canal do Meio, 2 Carioca), removed (3 Cidão, 4 Zé Marinho), or maintained at natural density (5 Genipapo, 6 Tião)

most of them being opportunists (sensu Winemiller, 1989) that were characterized by small size and short sedentary life cycles. Species such as *Aphyocharax anisitsi* Eigenmann & Kennedy, 1903, *Astyanax altiparanae* Garutti & Britski, 2000, and *Serrapinnus notomelas* (Eigenmann, 1915) dominated the assemblage of almost all open and macrophyte-covered areas and comprised almost 65.3 and 30.05% of the initial abundance and biomass, respectively. On the other hand, some species were so rare on the initial sampling, that their occurrence (overall relative density ranging from 0.01 to 0.09) was detected only in June and/or August [such as *Hypheosbrycon* sp., *Acestrorhynchus lacustris* (Lütken, 1875), *Characidium aff. zebra* Eigenmann, 1909, *Characidium* sp., and *S. maculatus* Kner, 1858] (Appendix—Electronic Supplementary Material). In general, the effect of predator density was stronger than habitat or time, and significant differences for the assemblage attributes were detected only in those lakes where trahira was removed (Fig. 2).



**Fig. 2** Fish species richness (percentage of the number of species in relation to initial values) (A), abundance (percentage of the number of individuals in relation to initial values) (B), and evenness (percentage of evenness in relation to initial values) (C) in open (solid line) and macrophyte-covered (broken line) areas over 120 days in lakes of the upper Paraná River floodplain where *H. aff. malabaricus* was added (HM+: closed circle Canal do Meio; open circle Carioca), removed (HM–: closed square Cidão; open square Zé Marinho), or kept at natural density (REF: closed triangle Genipapo; open triangle Tião). Manipulations were performed after the April sampling

Species richness decreased during the experiment in all lakes and habitat categories. The species number in August represented, on average, 73%

(SE = 7.20) of that observed in April (Fig. 2A). Because ANOVA detected significant interactions among factors, the influence of predator density depended on the habitat category and time after *H. aff. malabaricus* manipulation (Table 2). Reductions in species richness were significantly different in August in macrophyte-covered areas and in the absence of the predator compared to other conditions. Species loss was associated with low abundance, e.g., *Hyphessobrycon eques* (Steindachner, 1882), *Erythrinus erythrinus* (Bloch & Schneider, 1801), *Eigenmannia trilineata* López & Castello, 1966, *Hoplosternum littorale* (Hancock, 1828) and *Crenicichla niederleini* (Holmberg, 1891) among others (see Appendix—Electronic Supplementary Material).

In lakes where the trahira was added or kept at its natural density (HM+; REF, respectively), fish abundance experienced an overall increase in June, followed by a sharp reduction in August, except in the macrophyte-covered areas of the Carioca and Tião lakes. These results were attributed to the increase of small-sized Characins *H. eques*, *Pyrrhulina australis* Eigenmann & Kennedy, 1903, *Moenkhausia sanctae-filomenae* (Steindachner, 1907) and *A. altiparanae* Garutti & Britski, 2000. However, this trend was not observed in lakes where trahira was removed and where other piscivores [*A. lacustris*, *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829), *Astronotus crassipinnis* (Heckel, 1840), and *Cichla kelberi* Kullander & Ferreira, 2006] were naturally absent. Significant reductions in abundance were only observed for the treatment predator density (Table 2). On average, only 37% (SE = 5.79) of the initial number of fishes were registered 60 days after trahira removal (Fig. 2B).

A strong effect of predator density was also observed on evenness, which was marked by significantly higher values in the assemblages where trahira was removed (Table 2; Fig. 2C). An overview of species abundances revealed a plausible mechanism underlying this pattern of evenness: trahira removal caused a differential effect on the populations of the more abundant species such as *A. altiparanae* and *Laetacara* sp., which were drastically reduced in number after the initial sampling (see Appendix—Electronic Supplementary Material).

Size classes changed substantially in some lakes during the experiment (Fig. 3). Although small-sized fish (Classes 1 and 2; smaller than 4.5 cm) predominated in

all assemblages (40–99% of total abundance) at the beginning of the experiment, Zé Marinho, Genipapo, and Carioca lakes exhibited the most heterogeneous fauna in terms of standard length at the April sampling (Fig. 3, first and fourth columns). Over the initial 60 days of the experiment, the ichthyofauna inhabiting these lakes and also Cidão exhibited the most pronounced alterations in size class structure: an intense reduction in the relative contribution of fish of Class 1 and greater participation of fish of Classes 2, 3, and 4 (>3 cm) (Fig. 3, first and second; fourth, and fifth columns). Except in Zé Marinho and Genipapo (at a lesser extent), however, the relative contribution of size classes at the end of the experiment resembled that verified in April. Independently of the habitat, the abundance of fish on each size class in June in the presence of the trahira (HM+) was significantly higher than those verified in all other assemblages (Table 2). The spatio-temporal trends in size classes mentioned above may explain the fact that biomass did not significantly differ according to predator density, habitat category, and the interaction among them.

## Discussion

The importance of biotic interactions in structuring fish assemblages was first recognized in the beginning of the last century, but intense experimentation did not begin until the 1960s (Sih et al., 1985). Whole-lake manipulations of density demonstrated that some species (usually predators) can play distinct roles that influence the persistence of assemblages (Mittelbach et al., 1995). Therefore, this study experimentally addresses the importance of the trahira in structuring fish assemblages in floodplain lakes. Manipulative field experiments are well suited for examining such multi-species responses and follow general and growing trends in ecological studies (Tilman, 1989; Demers et al., 2001). Although they suffer from some important limitations, such as a lack of replication (i.e., at large spatial scale) and the influence of confounding variables (i.e., differences of initial species composition and physical structure), these whole-system studies allow measurement of how variables of interest respond to altered levels of predictor variables (i.e., predator density, habitat, and time, herein called treatments), while either maintaining or altering system complexity. Considering the multi-species



**Table 2** Results of the rm-ANOVA applied to the species richness, abundance, evenness, biomass, and assemblage body size structure

Fish assemblage attributes	SS	GL	MS	<i>F</i>	<i>P</i>
<b>Species richness</b>					
<u>P</u>	1,231.20	2	615.60	1.38	0.32
<u>H</u>	170.50	1	170.50	0.38	0.56
<u>P</u> × <u>H</u>	521.30	2	260.70	0.59	0.59
Error	2,667.00	6	444.50		
<u>T</u>	3,484.70	1	3,484.70	35.86	<0.01
<u>P</u> × <u>T</u>	408.60	2	204.30	2.10	0.20
<u>H</u> × <u>T</u>	575.00	1	575.00	5.92	0.05
<u>P</u> × <u>H</u> × <u>T</u>	2,218.90	2	1,109.50	11.42	<0.01
Error	583.00	6	97.20		
<b>Abundance</b>					
<u>P</u>	172,385.00	2	86,192.50	7.28	0.02
<u>H</u>	20,865.30	1	20,865.30	1.76	0.23
<u>P</u> × <u>H</u>	24,156.00	2	12,078.00	1.02	0.42
Error	71,069.60	6	11,844.90		
<u>T</u>	21,454.50	1	21,454.50	1.80	0.23
<u>P</u> × <u>T</u>	10,709.20	2	5,354.50	0.45	0.66
<u>H</u> × <u>T</u>	43,238.10	1	43,238.10	3.62	0.11
<u>P</u> × <u>H</u> × <u>T</u>	29,039.70	2	14,519.90	1.22	0.36
Error	71,631.70	6	11,938.60		
<b>Evenness</b>					
<u>P</u>	68,293.90	2	34,147.00	7.11	0.03
<u>H</u>	782.10	1	782.10	0.16	0.70
<u>P</u> × <u>H</u>	1,440.90	2	720.50	0.15	0.86
Error	28,796.50	6	4,799.40		
<u>T</u>	51.50	1	51.50	0.08	0.79
<u>P</u> × <u>T</u>	985.60	2	492.80	0.76	0.51
<u>H</u> × <u>T</u>	32.90	1	32.90	0.05	0.83
<u>P</u> × <u>H</u> × <u>T</u>	687.50	2	343.80	0.53	0.61
Error	3,907.50	6	651.30		
<b>Biomass</b>					
<u>P</u>	472,456.00	2	236,228.00	1.12	0.39
<u>H</u>	1,163.00	1	1,163.00	<0.01	0.94
<u>P</u> × <u>H</u>	597,325.00	2	298,663.00	1.42	0.31
Error	1,252,526.00	6	210,421.00		
<u>T</u>	51,176.00	1	51,176.00	1.16	0.32
<u>P</u> × <u>T</u>	85,463.00	2	42,732.00	0.97	0.43
<u>H</u> × <u>T</u>	5,194.00	1	5,194.00	0.12	0.74
<u>P</u> × <u>H</u> × <u>T</u>	182,817.00	2	91,408.00	2.07	0.21
Error	264,898.00	6			
<b>Body size structure</b>					
<u>P</u>	550,113.00	2	275,056.00	3.52	0.05
<u>H</u>	334,211.00	1	334,211.00	4.27	0.05
<u>Size class</u>	171,401.00	3	57,134.00	0.73	0.54

**Table 2** continued

Fish assemblage attributes	SS	GL	MS	<i>F</i>	<i>P</i>
$\underline{P} \times \underline{H}$	426,780.00	2	213,390.00	2.73	0.09
$\underline{P} \times \underline{Sc}$	344,177.00	6	57,363.00	0.73	0.63
$\underline{H} \times \underline{Sc}$	105,948.00	3	35,316.00	0.45	0.72
$\underline{P} \times \underline{H} \times \underline{Sc}$	307,420.00	6	51,237.00	0.66	0.69
Error	1,877,298.00	24	78,221.00		
<u>Time</u>	509,218.00	1	509,218.00	11.65	<0.01
$\underline{P} \times \underline{T}$	392,249.00	2	196,125.00	4.49	0.02
$\underline{H} \times \underline{T}$	130,823.00	1	130,823.00	2.99	0.10
$\underline{Sc} \times \underline{T}$	234,344.00	3	78,115.00	1.79	0.18
$\underline{P} \times \underline{H} \times \underline{T}$	269,273.00	2	134,636.00	3.08	0.06
$\underline{P} \times \underline{Sc} \times \underline{T}$	232,452.00	6	38,742.00	0.89	0.52
$\underline{H} \times \underline{Sc} \times \underline{T}$	128,794.00	3	42,931.00	0.98	0.42
$\underline{P} \times \underline{H} \times \underline{Sc} \times \underline{T}$	81,750.00	6	13,625.00	0.31	0.92
Error	1,048,876.00	24	43,703.00		

Predator density (addition, HM+; removal, HM–; and reference, REF) and habitat categories (open and macrophyte-covered areas) were considered the treatments, whereas samplings (June and August) were the repeated measures. For the assemblage body size structure analysis, size classes (1: <3.0 cm; 2: 3.1–4.5 cm; 3: 4.6–6.5 cm; 4: >6.5 cm) were also considered a treatment

character of the studied assemblages, the adopted framework was feasible and the complexity of the results was less than expected in a short-term of 4 months. We are unaware of any other whole-lake experiment in the Neotropics involving assemblage-level responses to a strong piscivore.

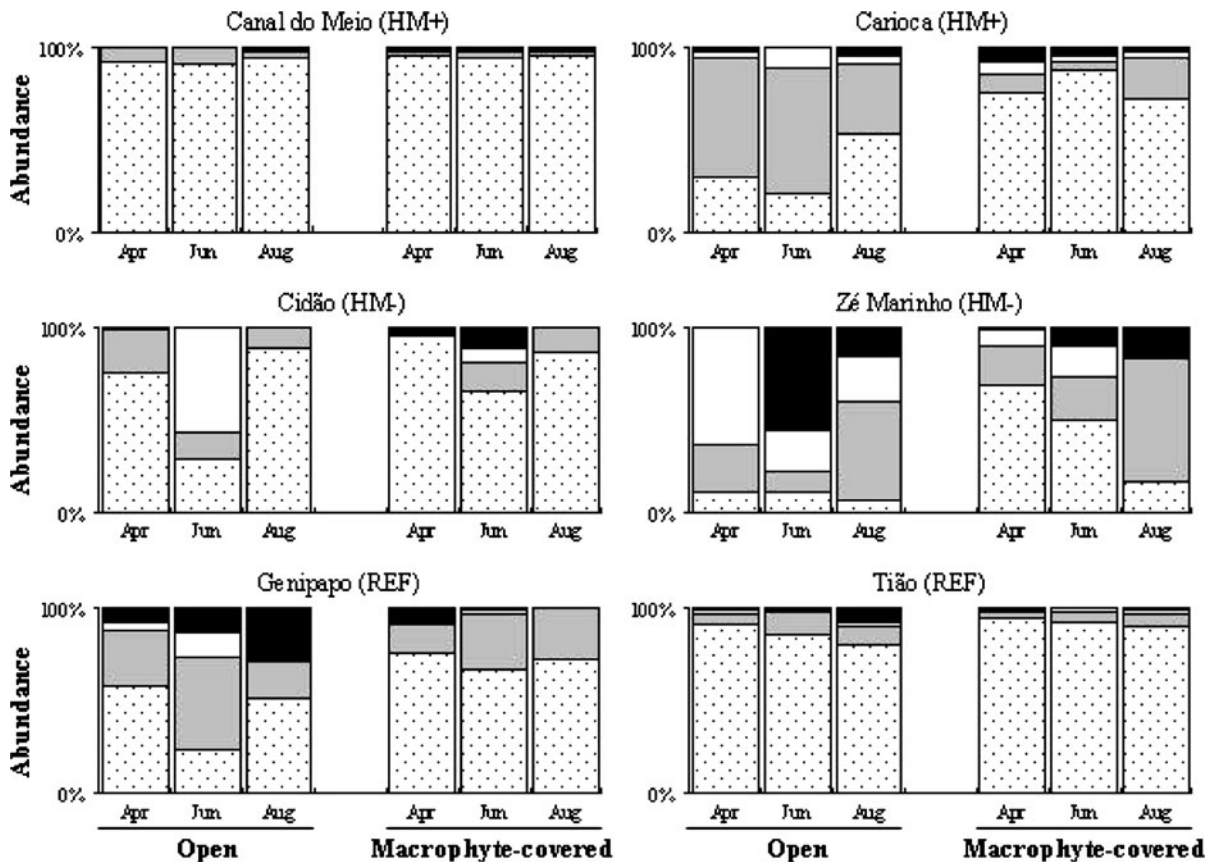
In our study, the effects of the absence of trahira on fish abundance and evenness were more severe than those related to its presence (e.g., predation). For species richness and assemblage body size structure, however, the significance of the interaction highlights the fact that the effect of predator density was dependent on habitat category and/or time. Lakes were characterized by high species richness, and fish elimination was greater among the rare species. Although decreases in species number occurred in all assemblages and was strongly affected by drought, the relevance of these sharp alterations was restricted to macrophyte-covered areas in August. Therefore, trahira could be influencing the persistence of organisms in its preferred habitat through the mechanism of predator-mediated coexistence (sensu Caswell, 1978).

According to other studies, environments structured by vegetation are recognized to promote species coexistence because they offer shelter and protection, especially to small-sized fish (Jacobsen & Berg, 1998; Pelicice et al., 2008). However, the manipulated

species represents a typical ambush predator in macrophyte stands in the investigated system, where it takes advantages from its behavioral and morphological adaptations (Okada et al., 2003; Piana et al., 2006). In our study fish abundance was negatively affected by predator absence, independent of habitat category and time. It is important to note, however, that other piscivores may also feed on small fish, such as a non-*Hoplias* erythrinid and some cichlid species which were naturally absent in Zé Marinho and Cidão lakes. Therefore, we are aware that our results may depend, at some level, on the absence of species other than trahira. We suspect that the sharp decreases in the number of the more abundant species (which consequently increased evenness) in the HM– treatment lakes would either lead to local extinctions if the experiment has been extended until the beginning of the rainy season. Reductions in food availability during the dry period intensified competitive interactions in streams in Panama (Zaret & Rand, 1971) as well as diet overlapping of fish species in the marginal lakes of the upper Paraná River basin (Esteves & Galetti, 1995). Therefore, we suggest extending this approach to other independent floodplain lakes to validate the patterns observed here.

The general increase of fishes of all size classes following the April sampling by predator presence, as





**Fig. 3** Relative contribution of size classes [Class 1 (dotted): <3.0 cm; Class 2 (gray): 3.1–4.5 cm; Class 3 (white): 4.6–6.5 cm; Class 4 (black): >6.5 cm] over 120 days in lakes

where *H. aff. malabaricus* were added (HM+), removed (HM–), or kept at natural density (REF). Manipulations were performed after the April sampling

well as the sharp reduction in the small-sized fish (Class 1) in HM– lakes may non-exclusively explain the absence of treatment effects (predator density, habitat, and time) on biomass. We postulate that the alterations in small-sized fish species abundance, which represents 77.42% of the total, would not necessarily reflect a trend of similar variation in biomass, since fish of less than three cm in length represented only 23.22% of the total biomass. The effect of size on prey species susceptibility has been assessed in studies that involve the effect of predators on their assemblages (Chase, 2003; Layman & Winemiller, 2004). According to Bayley (1988), consumption tends to increase with fish size. However, small-sized fishes (<1.5 cm) feeding on zooplankton seem to display more intense inter-specific competitive ability (Connell, 1983) by their higher capacity to deplete food resources (Hjelm & Persson, 2001).

The intensity of the trahira's impact on fish assemblages has been discussed for decades (Azevedo & Gomes, 1943; Gilliam et al., 1993; Paiva et al., 1994; Piana et al., 2006; Jeppesen et al., 2007). Although this experiment revealed indirect effects of trahira density, the intensity of direct effects (predation, for example) might have been underestimated due to the period of the year when it was carried out (Petry et al., 2007), as observed in studies of other animal groups (Sanford, 1999; Norrdahl et al., 2002). Feeding studies of trahira in a variety of systems and regions have revealed high occurrences of empty stomachs during the period from May to August (Barbieri et al., 1982; Bistoni et al., 1995). However, the species does not stop feeding during the reproductive period (Barbieri et al., 1982).

From a conservation perspective, the investigation of the influence of native predators on species

persistence is crucially important. In spite of not being evaluated in this study, the potential effect of non-piscine piscivores on the fish assemblages of the study area cannot be ignored. Fish-eating mammals (e.g., otters, puma) and especially aquatic birds are diverse groups that use these floodplain areas for foraging and breeding (Okada et al., 2003; Gimenes & dos Anjos, 2004). At least 15 species of Ciconiiforms live closely associated to aquatic environments of the upper Paraná River floodplain. During low water season, however, they exhibit habitat preference for lakes permanently connected to the main river and secondary channels, which are greater in size and perimeter (Gimenes & dos Anjos, 2006). The reference sites (REF) were included in our experimental design to overcome a possible effect of these non-piscine piscivorous, in addition to control for trahira density manipulation (either addition, HM+ as removal, HM−). For this reason, and considering the strong effect of predator density in most of the response variables, it seems not reasonable to believe that our randomly chosen and similar in habitat feature sampling sites would exhibit differential patch quality for fish-consumers other than the trahira. Thus, the hypothesis that the existence of competition is capable of promoting species exclusion in the absence of predators is a rich subject for further exploration in floodplain lakes.

## Conclusion

Our results supported the hypothesis that the trahira may mediate the short-term coexistence in fish assemblages of the upper Paraná River floodplain lakes. The dynamics of fish abundance and evenness was similar between assemblages with the addition of trahira and the reference assemblages, whereas alterations were observed with removal of the species. However, the negative effect on species richness and assemblage body size structure depended on habitat category and/or elapsed time since predator removal. The loss of the less abundant species, as well the life history traits of trahira (e.g., feeding tactics, preferences for macrophyte-covered areas) may account for this apparent contradiction of more intense competition among prey species in structurally complex habitats.

**Acknowledgments** This study is part of the PhD dissertation of ACP, in the Program of Environmental Sciences, of the Maringá State University, in the long-term program PELD Site-6. Authors acknowledge many people and institutions: several students of Maringá State University assisted in field and lab work; logistical support was supplied by the Nucleus of Research in Limnology, Ichthyology and Aquaculture (Nupélia), and financial support was provided by the National Council of Scientific and Technological Development (CNPq) to PELD Site-6, to ACP (Process 142220/2001-9), and to LCG, AAA, and ACP (research productivity scholarship). We particularly acknowledge the critical reading and suggestions of E. K. Okada, L. M. Bini, and C. S. Agostinho. The constructive comments of G. Grossman and other five anonymous referees substantially contributed to the improvement of earlier versions of the manuscript.

## References

- Agostinho, A. A., L. C. Gomes, S. Veríssimo & E. K. Okada, 2004. 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: 11–19.
- Agostinho, A. A., S. M. Thomaz, L. C. Gomes & S. L. S. M. A. Baltar, 2007. Influence of the macrophyte *Eichhornia azurea* on fish assemblage of the Upper Paraná River floodplain (Brazil). *Aquatic Ecology* 41: 611–619.
- Almeida, V. L. L., N. S. Hahn & A. E. A. M. Vazzoler, 1997. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecology of Freshwater Fish* 6: 123–133.
- Azevedo, P. & A. L. Gomes, 1943. Contribuição ao estudo da traíra *Hoplias malabaricus* (Bloch, 1794). *Boletim de Indústria Animal* 5: 15–64.
- Barbieri, G., J. R. Verani & M. C. Barbieri, 1982. Dinâmica quantitativa da nutrição de *Hoplias malabaricus* (Bloch, 1794), na represa do Lobo (Brotas—Itirapina/SP), (Pisces, Erythrinidae). *Revista Brasileira de Biologia* 42: 295–302.
- Bayley, P. B., 1988. Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology of Fishes* 21: 127–142.
- Bertollo, L. A. C., G. G. Born, J. A. Dergam, A. S. Fenocchio & O. Moreira-Filho, 2000. A biodiversity approach in the neotropical Erythrinidae fish, *Hoplias malabaricus*: karyotypic survey, geographic distribution of cytotypes and cytotoxic consideration. *Chromosome Research* 8: 603–613.
- Bialezki, A., K. Nakatani, P. V. Sanches & G. Baumgartner, 2002. Spatial and temporal distribution of larvae and juveniles of *Hoplias* aff. *malabaricus* (Characiformes, Erythrinidae) in the upper Paraná River floodplain, Brazil. *Brazilian Journal of Biology* 62: 211–222.
- Bistoni, M. A., J. G. Haro & M. Gutiérrez, 1995. Feeding of *Hoplias malabaricus* in the wetlands of Dulce river (Córdoba, Argentina). *Hydrobiologia* 316: 103–107.
- Caswell, H., 1978. Predator-mediated coexistence: a nonequilibrium model. *The American Naturalist* 112: 127–154.

- Chase, J. M., 2003. Strong and weak trophic cascades along a productivity gradient. *Oikos* 101: 187–195.
- Connell, J. H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist* 122: 661–696.
- Creed, R. P. Jr., 2000. Is there a new keystone species in North American lakes and rivers? *Oikos* 91: 405–408.
- Delariva, R. L., A. A. Agostinho, K. Nakatani & G. Baumgartner, 1994. Ichthyofauna associated to aquatic macrophytes in the upper Parana river floodplain. *Revista UNIMAR* 16: 41–60.
- Demers, E., D. J. McQueen, C. W. Ramcharan & A. Pérez-Fuentetaja, 2001. Did piscivores regulate changes in fish community structure? *Archiv für Hydrobiologie* 56: 49–80.
- Esteves, K. E. & P. M. J. R. Galetti, 1995. Food partitioning among some characids of a small Brazilian floodplain lake from the Paraná river basin. *Environmental Biology of Fishes* 42: 375–389.
- Flecker, A. S., 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. *Ecology* 73: 927–940.
- Fraser, D. F. & J. F. Gilliam, 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73: 959–970.
- Fraser, D. F., J. F. Gilliam, M. P. MacGowan, C. M. Arcaro & P. H. Guillozet, 1999. Habitat quality in a hostile river corridor. *Ecology* 80: 597–607.
- Froese, R. & D. Pauly, 2008. FishBase. World Wide Web electronic publication. [www.fishbase.org](http://www.fishbase.org), version (09/2008).
- Gilliam, J. F. & D. F. Fraser, 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* 82: 258–273.
- Gilliam, J. F., D. F. Fraser & M. Alkins-Koo, 1993. Structure of a tropical stream fish community: a role for biotic interactions. *Ecology* 74: 1856–1870.
- Gimenes, M. R. & L. dos Anjos, 2004. Spatial distribution of birds on three islands in the upper River Paraná, Southern Brazil. *Ornitologia Neotropical* 15: 71–85.
- Gimenes, M. R. & L. dos Anjos, 2006. Influence of lagoons size and prey availability on the wading birds (Ciconiiformes) in the upper Paraná River floodplain, Brazil. *Brazilian Archives of Biology and Technology* 49: 463–473.
- Hahn, N. S., R. Fugi & I. F. Andrian, 2004. Trophic ecology of the fish assemblages. In Thomaz, S. M., A. A. Agostinho & N. S. Hahn (eds), *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation*. Backhuys Publishers, Leiden: 247–269.
- Hjelm, J. & L. Persson, 2001. Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. *Oikos* 95: 520–532.
- Jacobsen, L. & S. Berg, 1998. Diel variation in habitat use by planktivores in field enclosure experiments: the effect of submerged macrophytes and predation. *Journal of Fish Biology* 53: 1207–1219.
- Jeppesen, E., M. Meerhoff, B. A. Jacobsen, R. S. Hansen, M. Sondergaard, J. P. Jensen, T. L. Lauridsen, N. Mazzeo & C. W. C. Branco, 2007. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* 581: 269–285.
- Layman, C. A. & K. O. Winemiller, 2004. Size-based prey responses to piscivore exclusion in a Neotropical river. *Ecology* 85: 1311–1320.
- Loureiro, V. E. & N. S. Hahn, 1996. Dieta e atividade alimentar da traíra *Hoplias malabaricus* (Bloch, 1794) (Osteichthyes, Erythrinidae), nos primeiros anos de formação do reservatório de Segredo—PR. *Acta Limnologica Brasiliensia* 8: 195–205.
- Lowe-McConnell, R. H., 1987. *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge.
- Luz-Agostinho, K. D. G., A. A. Agostinho, L. C. Gomes & H. F. Júlio Jr, 2008. Influence of flood pulses on diet composition and trophic relationships among piscivorous fish in the upper Paraná River floodplain. *Hydrobiologia* 607: 187–198.
- Mazzeo, N., C. I. Iglesias, F. T. de Mello, A. Borthagaray, C. Fosalba, R. Ballabio, D. Larrea, J. Vilches, S. Garcia, J. P. Pacheco & E. Jeppesen, 2010. Trophic effects of *Hoplias malabaricus* (Characiformes, Erythrinidae) in subtropical lakes food webs: a mesocosm approach. *Hydrobiologia* 644: 325–335.
- Mittelbach, G. G., A. M. Turner, D. J. Hall, J. E. Retting & C. W. Osenberg, 1995. Perturbation and resilience: a long-term whole-lake study of predator extinction and reintroduction. *Ecology* 76: 2347–2360.
- Miyasaka, H., M. Genkai-Kato, N. Kuhara & S. Nakano, 2003. Predatory fish impact on competition between stream insect grazers: a consideration of behaviorally- and density-mediated effects on an apparent coexistence pattern. *Oikos* 101: 511–520.
- Nakatani, K., A. A. Agostinho, G. Baumgartner, A. Bialetzki, P. V. Sanches, M. C. Makrakis & C. Pavanelli, 2001. Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação. EDUEM, Maringá, Brazil.
- Norrdahl, K., T. Klemola, E. Korpimäki & M. Koivula, 2002. Strong seasonality may attenuate trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos* 99: 419–430.
- Okada, E. K., A. A. Agostinho, M. Petrere Jr. & T. Penczak, 2003. Factors affecting fish diversity and abundance in drying ponds and lagoons in the upper Paraná river basin, Brazil. *Ecohydrology & Hydrobiology* 3: 97–110.
- Oliveros, O. B. & L. K. Rossi, 1991. Ecologia trófica de *Hoplias malabaricus malabaricus* (Pisces, Erythrinidae). *Revista de la Asociacion de Ciencias Naturales del Litoral* 22: 55–68.
- Oyakawa, O. T., 2003. Family Erythrinidae. In Reis, R. E., S. O. Kullander & C. J. Ferraris Jr. (eds), *Check List of the Freshwater Fishes of South and Central America*. EDI-PUCRS, Porto Alegre, Brazil: 238–240.
- Paine, R. T., 1966. Food web complexity and species diversity. *The American Naturalist* 100: 65–75.
- Paine, R. T., 1969. A note on trophic complexity and community stability. *The American Naturalist* 103: 91–93.
- Paiva, M. P., M. Petrere Jr., A. J. Petenate, F. H. Nepomuceno & E. A. Vasconcelos, 1994. Relationship between the number of predatory fish species and fish yield in large north-eastern Brazilian reservoirs. In Cowx, I. G. (ed.), *Rehabilitation of Freshwater Fisheries*. Fishing News Books, Oxford: 120–129.

- Pellicice, F. M., S. M. Thomaz & A. A. Agostinho, 2008. Simple relationships to predict attributes of fish assemblages in patches of submerged macrophytes. *Neotropical Ichthyology* 6: 543–550.
- Petry, A. C., A. A. Agostinho & L. C. Gomes, 2003a. Spatial variation of the fish assemblage structure from the upper Rio Paraná floodplain, Brazil, in a dry year. *Acta Limnologica Brasiliensia* 15: 1–13.
- Petry, A. C., A. A. Agostinho & L. C. Gomes, 2003b. Fish assemblages of tropical floodplain lagoons: exploring the role of connectivity in a dry year. *Neotropical Ichthyology* 1: 111–119.
- Petry, A. C., A. A. Agostinho, P. A. Piana & L. C. Gomes, 2007. Effects of temperature on prey consumption and growth in mass of juvenile trahira *Hoplias aff. malabaricus* (Bloch, 1794). *Journal of Fish Biology* 70: 1855–1864.
- Piana, P. A., L. C. Gomes & A. A. Agostinho, 2006. Comparison of predator–prey interaction models for fish assemblages from the neotropical region. *Ecological Modelling* 192: 259–270.
- Pielou, E. C., 1969. *An Introduction to Mathematical Ecology*. John Wiley & Sons, New York.
- Power, M. E., M. S. Parker & J. T. Wootton, 1996a. Disturbance and food chain length in rivers. In Polis, G. A. & K. O. Winemiller (eds), *Food Webs: Integration of Patterns & Dynamics*. Chapman & Hall, New York: 286–297.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, D. Daily, J. C. Castilla, J. Lubchenco & R. T. Paine, 1996b. Challenges in the quest for keystones: identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience* 46: 609–620.
- Sanford, E., 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283: 2095–2097.
- Sih, A., P. Crowley, M. McPeck, J. Petranka & K. Strohmeier, 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Reviews of Ecology and Systematics* 16: 269–311.
- Suzuki, H. I., A. E. A. de M. Vazzoler, E. E. Marques, M. A. P. Lizama & P. Inada, 2004. Reproductive ecology of the fish assemblage. In Thomaz, S. M., A. A. Agostinho & N. S. Hahn (orgs), *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation*. Backhuys Publishers, The Netherlands: 271–291.
- Tilman, D., 1989. Ecological experimentation: strengths and conceptual problems. In Likens, G. E. (ed.), *Long-term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, New York: 207–228.
- Vazzoler, A. E. A. de M., 1996. *Biologia da reprodução de peixes teleosteos: teoria e prática*. EDUEM, Maringá, Brazil.
- Werner, E. E., J. F. Gilliam, D. J. Hall & G. G. Mittelbach, 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540–1548.
- Winemiller, K. O., 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81: 225–241.
- Zaret, T. M. & A. S. Rand, 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52: 336–342.