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INVASIVE SPECIES

Invasion of an Amazonian cichlid in the Upper Paraná River: facilitation by dams and decline of a phylogenetically related species

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Abstract Biological invasions and damming are currently considered the main threats to aquatic biota. This is aggravated by the facilitative effect of damming on dispersal and establishment of non-native species. In this study, the invasion process by *Geophagus proximus*, an Amazonian Cichlid fish, was examined in different environments of the Upper Paraná River floodplain and Itaipu Reservoir. The effect of sediment retention prompted by damming (increasing water transparency) in the invasion process was investigated, in addition to the possible effects on the phylogenetically related *Satanoperca pappaterra*. The invasion process of *G. proximus* began in upstream reservoirs (source of propagules), then this species occupied the floodplain and later dispersed into the Itaipu Reservoir, being most successful (greater abundances) in environments with high water transparency (most above 200 cm). Increased abundances of the invasive species coincide with declined abundances of *S. pappaterra*. Diet overlap between these species was high, but apparently related to their omnivorous–detritivorous habits. Reproductive strategies were also similar. Therefore, it appears that the main factor that favored the invasive species was the increased transparency resulted from river damming, and that some interaction with *S. pappaterra* may be occurring.

Keywords Non-native species · Dispersion · Facilitation · Species introduction · Damming · Non-native impacts

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Introduction

Species introductions are an important threat to ecosystem functioning (Mack et al., 2000; Simberloff, 2003). Biological invasions have become a problem for freshwater ecosystems on a global scale and are considered, along with hydrological changes, the greatest threats to freshwater biota (Rahel, 2007; Johnson et al., 2008). The synergism between these two stressors is highlighted because river damming tends to disrupt resident communities, facilitating the establishment of new species (Gido & Brown, 1999; Havel et al., 2005; Pelicice & Agostinho, 2009).

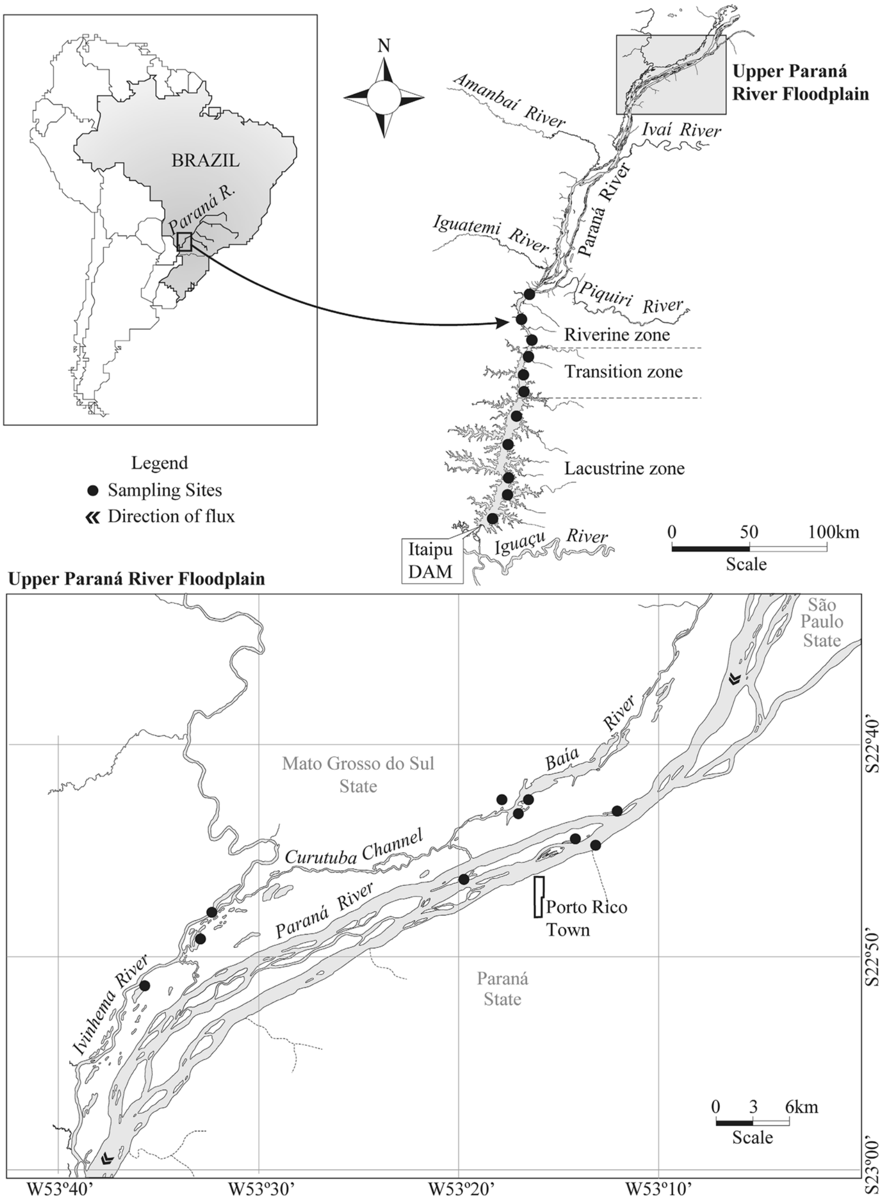
The Paraná River basin, in South America, is a special case because it holds over 130 large operating hydroelectric plants (dam height >10 m) (Agostinho et al., 2008). All of the river segments in the upper area of the river basin are under the direct influence of dams; thus, the Paraná River channel and its major tributaries are fragmented by a long series of dams. In this context, the Paraná River basin may illustrate well the relationship between the building of dams and the introduction of exotic fish. The flooding of natural barriers (Julio et al., 2009), operation of fishways (Makrakis et al., 2007; Julio et al., 2009), hydro-limnological changes (Roberto et al., 2009; Espínola et al., 2010), and human activities associated with fisheries production (stocking and aquaculture programs; Agostinho et al., 2007; Azevedo-Santos et al., 2011) contribute to the dispersal and establishment of exotic species in different parts of this river basin. Many exotic fish species have successfully colonized different river basin environments and established populations in the resident communities; only a few river segments have no invasive species (Agostinho et al., 2008). As a result of this complex scenario, the upper Paraná River basin has the highest richness of exotic species in Brazil (Smith et al., 2005a).

Some Amazonian species successfully colonized the upper Paraná River basin, such as the corvina (*Plagioscion squamosissimus* Heckel, 1840) and the peacock basses (*Cichla* spp.), which are present in almost all the major reservoirs of the basin (Agostinho et al., 2007). Recently, the caratinga or porquinho (*Geophagus proximus* Castelnau, 1855), an Amazonian cichlid, colonized the basin and developed high abundance. This species displays sedentary behavior and parental care and, in its native range, reaches its highest densities in lakes and flooded forests (Cerdeira et al., 2000). *Geophagus proximus* has been recorded in reservoirs of the Upper Paraná River since the beginning of the last decade (CESP, 2005a, Vidotto & Carvalho, 2007; Moretto et al., 2008) and is becoming increasingly important in artisanal and sport fishing landings in these environments (CESP, 2005b; Marques et al. 2008; UEM-Itaipu Binacional, 2009). The species is of reduced interest for aquaculture, yet it is highly attractive for aquarium hobbyists, an activity that may have caused the introduction of *G. proximus* in the river basin (Graça & Pavanelli, 2007).

It is not possible to say which factors enabled the colonization of *G. proximus* in the Paraná River basin. However, Moretto et al. (2008) suggest that the high abundance of *G. proximus* in the last reservoir of the Tietê River basin (Três Irmãos Hydropower) may be a result of the better adaptation of the species to environments with low trophic states (i.e., oligotrophic). High water transparency may have played an important role in this process because cichlids tend to be visually oriented. Knowing the relationship between water transparency and the invasion process of *G. proximus* will enable a better understanding of the role of dams in facilitating species establishment. It will also help to predict the establishment of new exotic species and subsidize measures that prevent the spread of other invasive species. In addition, little is known about the eventual impacts caused by the introduction of *G. proximus*. The colonization of reservoirs and adjacent environments may have affected the community structure of the resident fauna, especially species with similar behavior. Evidence of species changes in this river basin exists, although the occurrence of competition is difficult to estimate in the field (Agostinho & Julio, 2002). However, laboratory experiments revealed a strong competitive interaction between native and exotic cichlids (Sanches et al., 2012).

Based on this information, this study aimed to evaluate the distribution and abundance of *G. proximus* in different environments of the Upper Paraná River floodplain and along the Itaipu reservoir and, based on a large spatial and temporal dataset, investigate its colonization process and its relationship with the variation in water transparency. This variable was selected because cichlids are visually oriented and dams, due to retention of sediments by the reservoir, tend to increase transparency downstream. In this sense, we hypothesize that changes in water transparency mediate the colonization of this invasive cichlid fish, i.e., they have the advantage in clear water environments. Additionally, this study compared the colonization of *G. proximus* with variations in the abundance of a phylogenetically related species, *Satanoperca pappaterra* Heckel, 1840, to begin clarifying the relationship between *G. proximus* and the preexisting resident fish fauna. The indigenous

Fig. 1 Study area comprising the Itaipu reservoir and the Upper Paraná River floodplain



status of *S. pappaterra* is still uncertain (Julio et al., 2009), but this species was abundant in samples taken 20 years before the arrival of *G. proximus* in the upper Paraná River. *Satanoperca pappaterra* and *G. proximus* have similar morphology and behavior (Cassemiro et al., 2008), creating a situation in which strong biological interactions (e.g., competition) are expected. To this end, this study investigated the trophic interactions and reproductive behavior of the two cichlids in addition to their temporal variation in abundance.

Materials and methods

Study area

Sampling was conducted in the Upper Paraná River floodplain and along the Itaipu reservoir. The Upper Paraná River floodplain (Fig. 1) extends for approximately 230 km and is located between the Itaipu Reservoir (downstream limit) and the Porto Primavera Dam (upstream limit). This stretch has an area of 5,268 km^2 containing many secondary channels, lakes, and tributary rivers (some large, such as the Ivaí and Ivinhema rivers) and is the last non-dammed segment of considerable length in the Paraná River located within Brazil. This region encompasses a wide floodplain (20 km wide) on the west bank that experiences predictable seasonal hydrological pulses despite hydrological effects of the upstream dams (Agostinho et al., 2009). The high variability of aquatic and terrestrial habitats confers this segment of the Paraná River with a high diversity of terrestrial and aquatic species (Agostinho & Julio, 2002; Thomaz et al., 2007). *Geophagus proximus* was captured for the first time in the Paraná River floodplain in 2005 (in backwater environments).

The Itaipu reservoir (Fig. 1), located downstream from the floodplain, was completed in October 1982 and is located on the Paraná River along the Brazil-Paraguay border (24°05′–25°33′S, 54°00′–54°37′W). The artificial lake has a length of approximately 150 km (reaching up to 170 km when full), with an area of 1,350 km^2. The mean depth is 22 m (reaching 170 m near the dam), and the mean residence time is 40 days (Okada et al., 2005). The first record of *G. proximus* in this reservoir was in 2007; the species was observed in the riverine zone of the reservoir.

Data collection

Data from experimental fishing catches in the floodplain and artisanal fishing catches in the Itaipu reservoir were analyzed to investigate the colonization of *G. proximus* in the area between Itaipu Dam (Foz do Iguaçu, Paraná State) and Porto Primavera Dam (Porto Primavera, São Paulo State). These data were also used to analyze temporal variations in the abundance of *G. proximus* and the co-occurring *S. pappaterra*. Diet, niche breadth, and food overlap analyses relied exclusively on individuals from the Itaipu Reservoir. The Upper Paraná River floodplain was sampled quarterly from January 2005 to December 2009 at ten sampling stations: three in the Paraná, Baia, and Ivinhema river channels, four in lakes permanently connected to these rivers, and three in seasonally connected lakes. The experimental fishing in the floodplain area was carried out using an array of gill nets (set in littoral habitats) with mesh of different sizes (24, 30, 40, 50, 60, 70, 80, 100, 120, 140, and 160 mm between opposite knots). Both species were caught in mesh sizes ranging from 24 to 80 mm. Gill nets were deployed for 24 h, and fish were removed at dawn (8 am), dusk (4 pm), and night (10 pm). Captured fish were identified to species level, measured and weighed. Voucher specimens are deposited at the Ichthyological Collection of the Center for Research in Limnology, Ichthyology and Aquaculture (Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura—Nupélia), State University of Maringá (Universidade Estadual de Maringá—UEM), Paraná State.

The Itaipu Reservoir was sampled monthly from January 2005 to December 2009 at twelve fishing areas grouped into three different zones (riverine, transition, and lacustrine; Fig. 1) taking into account longitudinal gradients of sedimentation rate, limnological characteristics, and ichthyofauna composition (Thornton et al., 1990; Okada et al., 2005). The data obtained along the Itaipu Reservoir were based on the fish-landing monitoring carried out by the State University of Maringá and Nupélia in association with Itaipu Binacional Hydropower Company. The total number of fish caught per fishing day per fisherman at each zone was calculated. Water transparency (Secchi disk, cm) was measured during each sampling event in both studied regions.

All *S. pappaterra* and *G. proximus* individuals captured during the monitoring at Itaipu were eviscerated, and the filled stomachs were preserved in 4% formalin. The stomach contents were identified to the lowest possible taxonomic level. The diet composition was analyzed using the volumetric and occurrence methods (Hyslop, 1980). For the volumetric method, the volume (ml) of each food item was obtained to calculate its contribution (percentage) to the total volume. These measurements were made using a graduated plate, in which volume is obtained by compressing the material against a glass slide to a known height (1 mm). The results were then converted to ml (1 mm^3 = 0.001 ml) following Hellawel & Abel (1971). For the occurrence method, the percentage of the stomachs in which each item occurred was calculated.

To investigate and qualitatively compare the reproductive characteristics of the two species, information on their reproductive behavior, including the type of fertilization, nesting, and parental care, was obtained from the literature.

Data analysis

Transparency data were graphically summarized (mean ± standard error), and statistical differences were tested using a two-way ANOVA according to the factors of interest (Years and Rivers for the floodplain data; Years and reservoir Zones for the Itaipu data) and their interaction. Inter-annual variation in the abundance of *G. proximus* was evaluated through ANOVA considering fish caught in both regions and factors of interest (Years and Rivers of the floodplain; Years and reservoir Zones for Itaipu) and their interaction. We also used ANOVA to evaluate trends in abundance (number of individuals captured per 24 h of sampling) of the two species in the Upper Paraná River floodplain to investigate patterns of replacement of *S. pappaterra* (preexistent) by *G. proximus* (invasive) in the years studied (Species and Years and their interaction were the factors of the ANOVA). We chose to restrict this analysis to the floodplain area because fish sampling was standardized in this region (i.e., scientific monitoring with the same effort in every sampling), and the sampling design included the broad environmental heterogeneity of the area. Whenever the ANOVA was significant, the Tukey test was applied to identify which levels of the factors differed.

To investigate the trophic interactions between the species, frequency of occurrence and the relative volume of consumed resources were combined to calculate a feeding index (FI) (Kawakami & Vazzoler, 1980). Trophic niche breadth, based on the volumetric proportion of items, was calculated based on Levin's Index (Krebs, 1999) following the equation

$$B = \frac{1}{\sum P_j^2},$$

where B is the trophic niche breadth and P_j is the proportion of item j in the total diet.

Levin's index values were transformed according to the equation

$$B_A = \frac{B - 1}{n - 1},$$

where n is the number of items, to standardize the niche measurement on a scale from 0 to 1.

The items were grouped into 12 categories (higher plants, algae, protozoa, microcrustaceans, crustaceans, aquatic insects, terrestrial insects, aquatic invertebrates, terrestrial invertebrates, mollusks, fish, and detritus/sediment) to analyze all the trophic aspects. Based on FI values, we evaluated food overlap using the Pianka's Index. The significance of the observed index was tested through randomization (Randomization Algorithm 3; 1,000 iterations) using the software Ecosim (Entsminger, 2012). We also used Spearman correlation (ρ) to evaluate possible differences in the total volume of the items consumed between *S. pappaterra* before and after the invasion and both with *G. proximus*. The purpose of this analysis was to determine if there were indications of changes in the items consumed (low correlation indicates changes; high correlation indicates the same rank of the items consumed).

To investigate possible interactions in reproductive activities (i.e., similarity in behavior), we qualitatively described the behavior of each species in regard to the type of fertilization, nesting, and parental care.

Results

Water transparency

In the floodplain, the two-way ANOVA applied to the transparency data showed significant interaction ($F = 3.87$; $P < 0.001$), indicating that variation among years depended on the river considered. However, it is clear that the Paraná River environments had the most transparent waters among the sites analyzed in the region (averages always above 172.0 cm; Fig. 2a); the Ivinhema and Baia tributaries have more turbid waters. In the Itaipu Reservoir, the interaction between Years and Zones was not significant ($F = 0.49$; $P = 0.86$), but there was a significant difference among years ($F = 13.20$; $P < 0.0001$). Most pronounced water transparency differences occurred in 2005, 2008, and 2009 (Fig. 2b). For the Zones, mean water transparency was highest in the lacustrine zone, followed by the transitional and riverine (Fig. 2b). In 2009, the mean transparency was the lowest for each Zone, with 159, 57, and 87 cm in the lacustrine, riverine, and transition zones, respectively.

Invasion by *G. proximus*

The ANOVA applied to evaluate the variations in the abundance of *G. proximus* captured in the floodplain,

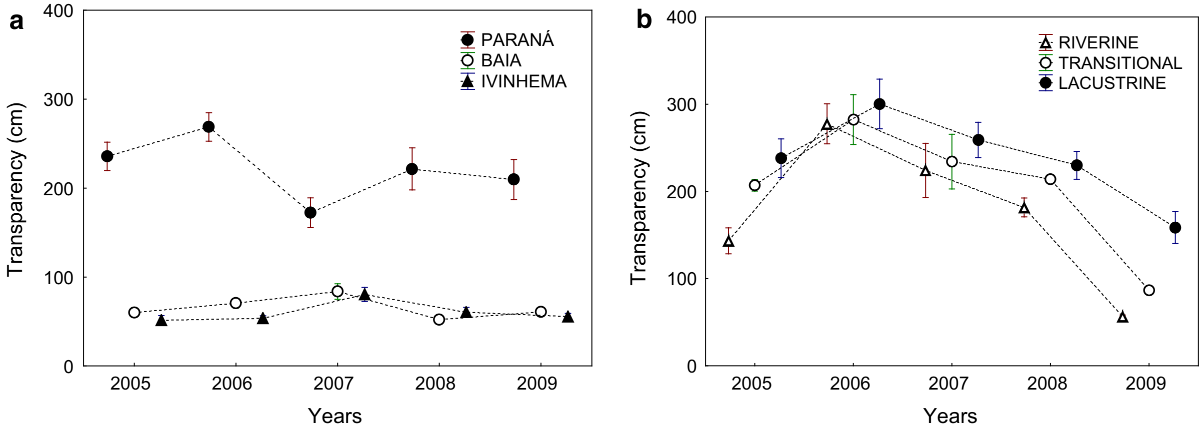


Fig. 2 Spatial and temporal water transparency variations in the Upper Paraná River floodplain (**a**) and in the Itaipu reservoir (**b**), including environments and zones under different damming influences (floodplain: Paraná, Baia, and Ivinhema rivers; Itaipu reservoir: riverine, transition, and lacustrine zones; *vertical lines* standard error)

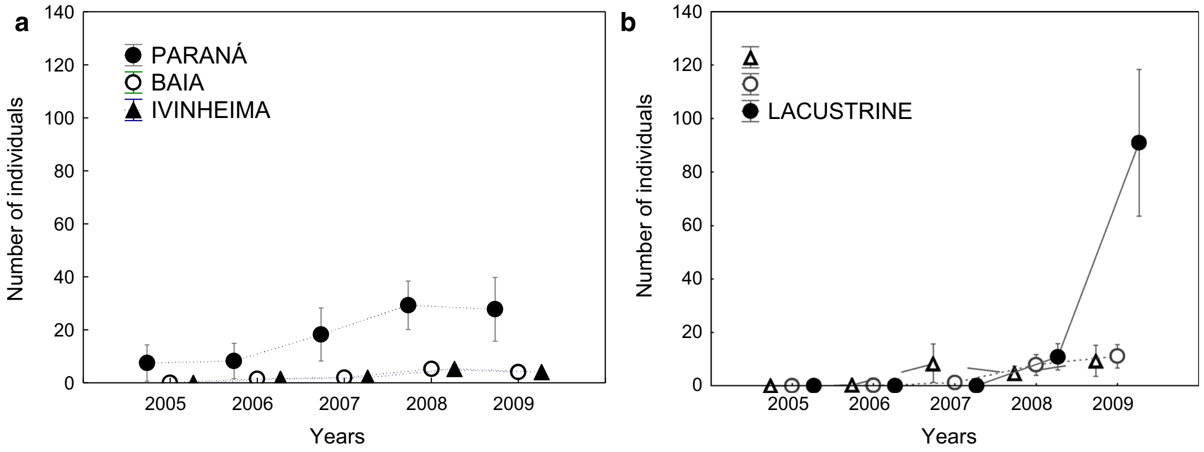


Fig. 3 Spatial and temporal variation in the abundance (monthly number of individuals) of *G. proximus* in the Upper Paraná River floodplain (**a**) and the Itaipu reservoir (**b**), including environments and zones under different damming influences (floodplain: Paraná, Baia, and Ivinhema Rivers; Itaipu reservoir: riverine, transition, and lacustrine zones; *vertical lines* standard error)

according to the factors Years and Rivers, presented a non-significant interaction ($F = 0.81$; $P = 0.60$), which allowed interpreting the main factors. The factor year was not significant ($F = 2.36$; $P = 0.07$) due to the low values registered in some rivers (Fig. 3a). However, after the initial capture of the species in the floodplain in 2005, its abundance quadrupled until 2009 (Fig. 3a). On the other hand, the factor River was significant ($F = 14.12$; $P < 0.001$) with higher mean abundance in the Paraná River (vs. Baia and Ivinhema; $P < 0.0001$). In fact, *G. proximus* initially colonized the backwaters connected to the Paraná River channel (Pau Véio backwater), *G. proximus* became predominant in a lake environment (Lagoa das Garças, Paraná River) in the following years, where fish captures during the last two years accounted for 83% of all the captures since it was first recorded. In the Ivinhema and Baia tributaries, which had the lowest transparency values, *G. proximus* occurred sporadically since its first record in 2006.

At the Itaipu Reservoir (Fig. 3b), the ANOVA applied to evaluate variations between the factors Years and Zones presented a significant interaction ($F = 6.35$; $P < 0.001$), which did not allow to

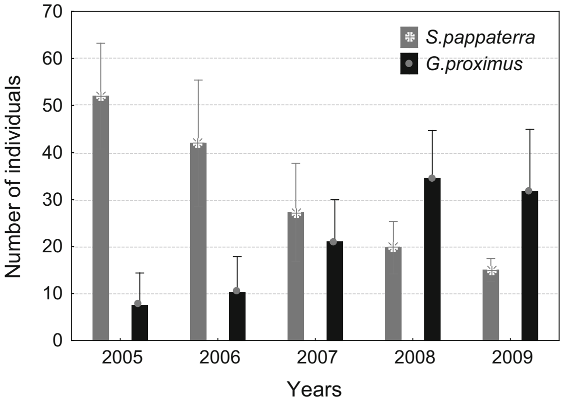


Fig. 4 Annual variation in abundance (mean monthly number of individuals captured) of *G. proximus* and *S. pappaterra* in the Upper Paraná River floodplain (*vertical lines* standard error)

interpret the main factors. The significant interaction was due to the fact that most *G. proximus* captures occurred in the lacustrine zone (highest average transparency), especially in 2009 (Tukey test only identified difference in the lacustrine zone, where the year 2009 differed from the others; $P < 0.0001$). In the lacustrine zone, the mean catch per fisherman-day increased from 10 in 2008 to 90 individuals in 2009. In the riverine zone, where the first *G. proximus* invasion in the Itaipu reservoir was recorded (in 2007), the abundance was low and constant in the following years. A similar trend was recorded in the transitional zone of the reservoir, where *G. proximus* was recorded since 2008.

Interaction between *G. proximus* and *S. pappaterra*

In 2005, when *G. proximus* was first recorded in the floodplain, an average of approximately 50 *S. pappaterra* individuals was captured per sample. This value decreased in the following years and reached the mean value of 20 individuals per sample in 2009. However, there was a significant interaction between the Species and Years ($F = 4.10$; $P = 0.009$), which did not allow to interpret the variation in the main factors. Thus, *S. pappaterra* and *G. proximus* presented significant differences in abundances in 2005, 2006 (in these years, *S. pappaterra* had higher abundance; $P < 0.0001$), and in 2009 (in this years, *G. proximus* had higher abundance; $P < 0.0001$). In fact, there were opposite trends in the abundance of the two species across time (Fig. 4).

The analysis of 494 stomach contents (*G. proximus* = 140; *S. pappaterra* = 354) sampled from the Itaipu reservoir revealed an omnivorous diet for both species, with a large predominance of detritus/sediment, mollusks, and aquatic insects based on both volume and occurrence (Table 1). The estimated niche breadth value was slightly higher for *S. pappaterra* before the arrival of *G. proximus*. The value then decreased after invasion, resembling values estimated for *G. proximus* (Table 1). Eleven of the twelve groups of items consumed by *S. pappaterra* before *G. proximus* invasion were still being ingested after the invasive species was recorded, nine of which also composed the diet of *G. proximus*. To better explore the results of diet analyses, we correlated the volume of consumed items between species. There was a low correlation between *S. pappaterra* before (Pre) and *S. pappaterra* after (Post) ($\rho = 0.49$; $P = 0.09$) and between *S. pappaterra* before (Pre) with *G. proximus* (after the invasion) ($\rho = 0.26$; $P = 0.32$). However, the correlation between *S. pappaterra* and *G. proximus* post-invasion was high (0.92; $P < 0.001$). The relevant changes in diet composition of *S. pappaterra* were restricted to reduction in the ingestion of fish, terrestrial insects, and algae consumed in the post-invasion period, but the invasive species was not found to consume fish or terrestrial insects.

In the Itaipu reservoir, food overlap between *S. pappaterra* and *G. proximus* was greater (Index of Pianka = 0.85) than the overlap among *S. pappaterra* individuals before (Index of Pianka = 0.76) and after (Index of Pianka = 0.80) the arrival of the invasive species. All observed indices differed significantly from the simulated ones ($P < 0.02$), indicating a high feeding niche overlap. There were several differences in the ingestion of less important (secondary) food items and a higher importance of detritus/sediments in the pre-invasion period (Table 1).

The reproductive behavior of the two species is similar. *Satanoperca pappattera* (L_s max = 19.2 cm) nests in the substrate (bottom) has external fertilization and exhibits female parental care (http://www.fishbase.org). Published reports describe that males actively defend breeding territories and may even confront piranhas, charging toward them with the mouth open and the dorsal fin extended (http://www.fishbase.org; Sazima & Machado, 1990). *Geophagus proximus* (L_s max = 22.5 cm) also nests in the substrate has external fertilization and displays parental

Table 1 Overall composition of the diet of *S. pappaterra* and *G. proximus* in the Itaipu Reservoir, Paraná River

Items	*S. pappaterra*						*G. proximus*		
	Pre ($n = 184$)			Post ($n = 170$)			($n = 140$)		
	%V	%O	%FI	%V	%O	%FI	%V	%O	%FI
Algae	9.59	17.53	11.64	1.68	15.07	1.80	1.06	15.59	1.10
Crustaceans	0.44	0.20	0.06						
Detritus/sediment	26.98	30.44	56.84	25.16	18.18	32.57	21.27	19.77	28.05
Aquatic insects	10.37	16.93	12.15	24.19	21.17	36.57	18.44	18.81	23.13
Terrestrial insects	16.27	2.62	2.94	0.19	0.11	<0.01			
Aquatic invertebrates	0.93	1.21	0.07	1.12	3.33	0.26	0.74	2.41	0.11
Terrestrial invertebrates	0.55	7.86	0.30	1.73	15.07	1.86	1.32	13.83	1.22
Microcrustaceans	0.83	1.61	0.92	8.35	10.12	6.02	7.00	4.50	2.10
Mollusks	13.45	13.90	12.94	20.17	9.32	13.38	34.55	14.95	34.44
Fish	15.94	0.80	0.88	1.30	0.11	0.01			
Protozoa	<0.01	0.20	<0.01	0.06	0.80	<0.01	0.04	0.64	<0.01
Plants	4.52	6.65	2.07	16.00	6.67	7.60	15.54	9.49	9.82
Niche Breadth (Ba)	0.46			0.41			0.42		

pre pre-invasion, *post* post-invasion, *n* number of stomachs analyzed, *V* volume, *O* occurrence, *FI* feeding index

care. The difference is that both sexes may care for eggs and juveniles, and it is common for the male to defend territory, while the female cares for the brood. Some males may become aggressive after spawning and dispel the female, thus caring for the brood alone (Palicka, 1992; Moretto et al., 2008; http://www.seriouslyfish.com/species/geophagus-proximus).

Discussion

Geophagus proximus, a cichlid fish native to the Amazon River basin, was first recorded in the Paraná River basin at the beginning of the last decade. As of 2000, the species was already abundant in Ilha Solteira Reservoir, comprising 23% of all fish landings, and was listed among the top three most abundant species (CESP, 2005b). In 2001, this species was caught in Três Irmãos and Jupiá reservoirs and in 2002 was caught in Porto Primavera Reservoir. Both Vidotto & Carvalho (2007) and Moretto et al. (2008) caught this species in 2003 in independent samples from different reservoirs of the Tietê River basin (Três Irmãos, Nova Avanhandava and Ibitinga). From 2003 to 2004, *G. proximus* made up 22% of commercial fishery landings from Três Irmãos Reservoir, being the second most abundant in this reservoir (Maruyama et al., 2010). In contrast, Smith et al. (2005a, b) argue that the species was most likely introduced between 1980 and 1990 and attribute its arrival to concerns about improving fishing. However, it is unlikely that *G. proximus* was deliberately introduced for this purpose because this species is small (<20 cm), and its importance for fisheries is determined by its high abundance. Escapes, deliberate releases by aquarists or accidental introductions during stockings of other species seem to be more plausible explanations for the presence of *G. proximus* in the river basin.

The chronology of the first occurrence of *G. proximus* in the study region indicates that it dispersed from upstream reservoirs. The species was found in the Paraná River and its floodplain environments downstream from Porto Primavera in 2005 (Thomaz et al., 2012), in tributaries of the Paraná River in 2006, in the riverine zones of the Itaipu reservoir in 2007, and in internal zones of the reservoir in 2008. Thus, the dispersal of this exotic species along 380 km between Porto Primavera and Itaipu dams took at least four years, at an average speed of approximately 95 km per year. Because *G. proximus* is small, sedentary and has low migratory-displacement ability, it is possible that it disperses by progressive diffusion via colonization of adjacent environments. The presence of suitable environments is essential in this process because invasive species is more dependent on successive colonization events than on dispersal per se. The presence of lentic environments with high water transparency (reservoirs and floodplain lakes connected to the Paraná River) in the study area may have enabled the invasion process, acting as stepping-stones (sensu Havel et al., 2005). High transparency (or Secchi depth or low turbidity) has already been mentioned as important in determining the success of invasion of several species in impoundments (see examples in Havel et al., 2005; Johnson et al., 2008; and Brown et al., 2012). However, this effect appears to be also true for lotic systems where dams play important role in determining environmental variables, such as the one studied here (increased water transparency; Agostinho et al., 2008), which facilitates the species arriving to a new reservoir. It is worth noting that *G. proximus,* in its original river basin (Amazon), is mainly captured in lakes and, to a lesser extent, in flooded forests (Cerdeira et al, 2000), which explains its better success in and dependency on lentic environments.

Geophagus proximus seemed to have difficulty in colonizing floodplain lakes of tributaries of the Upper Paraná River (Ivinhema and Baia rivers), which are characterized by environments (lakes and channels) with low water transparency, suggesting that transparency is affecting the invasion process. Reservoirs modify transport and material sedimentation processes by (i) retaining suspended solids and nutrients in the dammed area, which leads to high water transparency downstream, and (ii) changing water dynamics in the reservoir, which increases sedimentation rates and reduces trophic states in the innermost areas (Agostinho et al., 2008). The two processes lead to increased water transparency in both the dammed (i.e., Itaipu) and downstream areas (Paraná River lakes downstream from Porto Primavera Dam), an environmental change that seems to have enabled colonization by *G. proximus*. In the study area, the species proliferated in most lentic environments with high transparency levels (c.a. >200 cm), that is, marginal lakes of the Paraná River and internal zones of the Itaipu Reservoir. Monitoring of fish landings and water quality carried out in reservoirs of the Upper Paraná River confirmed that *G. proximus* (=*G. surinamensis*) makes up a larger part of the fishing yield in reservoirs with higher mean transparency (CESP, 2005b), which supports the trend found in this study. However, the mechanism by which transparency benefits the invasive species is not yet clear. It is likely that *G. proximus* requires high transparency conditions to locate food resources and complete its reproductive cycle, which involves brood guarding and active territory defense, because it is visually oriented. Studies have reported the effect of increased light intensity on the behavior of cichlids (e.g., Carvalho et al. 2012; Carvalho et al., 2013). Laboratory experiments have shown that cichlid species, including *G. proximus* (=*G. surinamensis*), became more aggressive with increased light intensity (Palicka, 1992; Carvalho et al. 2012), indicating that the colonization success in Paraná River environments may be related to increased aggressiveness due to increased water transparency.

It is difficult to detect impacts caused by the invasion and colonization of *G. proximus* in the studied area. A recent evaluation in the floodplain, based on a combination of approaches, showed that this species invaded sites with higher fish diversity (non-invaded sites presented lower diversity), suggesting that biotic and/or abiotic factors favoring natives were also important for the invasion success (Thomaz et al., 2012). However, the diversity of native species increased in invaded and non-invaded sites from 2001 (before) to 2010 (after invasion), indicating that an independent factor contributed to this increase, probably linked to flood pulses and connectivity (Thomaz et al., 2012). However, the present study presented evidence that the invasion of *G. proximus* may have caused negative effects on some preexisting species; the increase in *G. proximus* abundance coincided with *S. pappaterra* decline in this floodplain. Although the decline of *S. pappaterra* population can be attributed to predation by other non-native species that arrived in the area together with *G. proximus*, there is no record of other non-native species invading concurrently. *Cichla kelberi*, a voracious non-native predator, has been recorded in the area for a long time. In addition, a study carried out by Pelicice & Agostinho (2009) showed that *S. pappaterra* was one of the few species that became more abundant after the invasion of *C. kelberi*, indicating that *S. pappaterra* is less affected by this predator. On the other hand, *G. proximus* and *S. pappaterra* are phylogenetically related (Cichlidae, Geophaginae, tribe Geophagini; Lopez-Fernandez et al., 2005; Ribeiro, 2007), so there may be overlap in life-history characteristics (Olden et al., 2006). Opposing catch trends were evident, and the possibility of competitive exclusion of *S. pappaterra* by *G. proximus* should not be discarded, even considering the short co-occurrence time between the two species in the Upper Paraná River. This trend was also reported in the monitoring of commercial fishing landings in the other three reservoirs of the Upper Paraná River basin (Três Irmãos, Ilha Solteira and Jupiá; CESP, 2005b; Marques et al., 2008), where *G. proximus* became prevalent.

Diet composition was highly similar between the species when they co-occurred, with the same items comprising over 80% of the resources consumed (i.e., detritus, invertebrates, and plants). A similar pattern was reported at Nova Avanhandava, one reservoir upstream, in the Tietê River, where *G. proximus* was also introduced and the two cichlids shared the same major food items (Vidotto & Carvalho, 2009). However, in this study, the niche breadth was similar between the species when they co-occurred (*G. proximus*: 0.41; *S. pappaterra*: 0.42) but was not so similar at Nova Avanhandava (0.37 and 0.26, respectively; Vidotto & Carvalho, 2009). Garrone-Neto & Sazima (2009) illustrate the trophic relationships between the two species by describing their association with freshwater stingrays of the Upper Paraná River. *Geophagus proximus* and two other cichlid species are attracted by hunting stingrays, when the stingrays feed on the substrate and form clouds of sediment. These cichlids stay near the undulating ray disc, with an angled body, attentively observing and capturing small prey, mainly insect larvae. Hahn & Cunha (2005) characterized *S. pappaterra* as detritophagous-invertivorous (bottom feeders) in an analysis of feeding and trophic morphology in the Manso Reservoir (Cuiabá River basin). The authors report that *S. pappaterra* shows no selection in gill rakers, thus ingesting any available food type, having only its narrow mouth opening as a limitation (Hahn & Cunha, 2005). Given the phylogenetic and morphological proximity between *S. pappaterra* and *G. proximus* and the similarity in diet, it is likely that the two species display similar behaviors in resource acquisition, and strong competitive interactions may develop under such a scenario.

Although niche overlap may hinder the colonization of invasive species (biotic resistance hypothesis; Coulatti & McIsaac, 2004; Price & Partel, 2013), resident species are most affected by an invasion when niche overlap is significant (Olden et al., 2006). Strong competitive interactions may emerge if species overlap in the use of resources for feeding and breeding. Modification in the use of resources to avoid competition (i.e. niche packing) may be an important mechanism for coexistence, particularly if the resources consumed are limited and if *G. proximus* is competitively superior in foraging compared to *S. pappaterra*. In this study, however, high food overlap between the two species when co-occurring, and the lack of niche packing by *S. pappaterra*, suggests competition for resources. It is likely, therefore, that the invader is displacing *S. pappaterra* in the study area. In a recent laboratory study, Sanches et al. (2012) demonstrated how an invasive cichlid (*Oreochromis niloticus*) competitively displaced a native cichlid species (*Geophagus brasiliensis*) by direct interaction. In that case, the aggressive behavior of the invasive species intimidated the native species, even though the native had a larger body size. A similar pattern was observed between interacting native and exotic piranha species (i.e., *Serrassalmus*) in the Upper Paraná River, and the aggressive behavior of the invasive species was suggested as a mechanism of competitive superiority (Agostinho & Julio 2002). Thus, future experimental studies may clarify the role of trophic competition between *G. proximus* and *S. pappaterra* in the decline of populations of the latter, and investigate how underwater light intensity is influencing interactions.

More detailed studies of the relationship between this exotic species and the preexisting fish fauna should examine, in addition to the trophic dimension, characteristics of the reproductive behavior (parental care; Agostinho et al., 2007), and competition for space. According to Lowe-McConnell (1999), competition for space among Cichlidae may be stronger than competition due to insufficient food because this group is territorial and may compete for sites for reproduction. In the present study, we qualitatively recorded high similarity in reproductive patterns between the two species: both build nests and actively defend brood and territory. This behavior, when mating pairs (mainly the males) mark territory for reproduction, promotes competition for space and spawning sites. If the exotic species has competitive advantages, such as being more aggressive, the preexisting species may be displaced or unable to establish territories. Additionally, *G. proximus* becomes more aggressive in light-intense environments (Palicka, 1992; Carvalho et al., 2012), common in the Paraná River and its surroundings due to the high water transparency. The agonistic behavior of *G. proximus* should play a central role in its invasion dynamics and affect the resident fauna via the acquisition of food resources and territory defense.

The real possibility of depletion of native populations (as occurred for *S. pappaterra*) with the proliferation of *G. proximus* makes it important to understand the processes that lead to such impacts. Moreover, the relationship between the invasive species and the native fauna may be mediated by environmental changes caused by human activities. Changes imposed by damming, for example, impact existing communities, alter community dynamics and water quality, and create opportunities for other species to succeed in colonization (Havel et al., 2005). The high percentages of Amazonian species that succeed in the upper Paraná River basin, likely the most dammed basin in the world, illustrate this scenario well. Greater knowledge of species introductions and their interactions with native communities will improve the success of measures aimed at containing new species introductions and controlling species that are already established.

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