

Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir

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Abstract In South America, the introduction of peacock-bass (*Cichla*), a voracious predator fish, has been an underestimated threat for native fish communities. Although this predator is widespread in many reservoirs, few studies have explored its impact on biodiversity. To investigate the relationship between invasion and fish diversity, the present study followed a natural experiment in the Rosana Reservoir (Paraná River basin), where *Cichla kelberi* were introduced in 2004. We monitored fish assemblages associated with submerged macrophytes between 2003 and 2007, using a 1 m² throw trap. In the years following the introduction, fish diversity dramatically changed. For example, in March 2007, mean fish density and richness were reduced by ca. 95 and 80%, respectively, and many small-sized species had vanished. One aspect was the gradual change of

biodiversity, which unfolded at two times during each year: (1) impacts during summer/autumn periods, which coincided with large shoals of young *C. kelberi* in the patches; and (2) assemblage recovery during the spring. The sequence of extinction-colonization events, however, might not be able to maintain fish assemblages due to the decrease in recovery intensity each spring; assuming a constant decline rate in the coming years, we predict complete assemblage extinction by the summer of 2010. Results from this natural experiment provided evidence supporting the collapse of fish assemblages soon after the introduction of *C. kelberi*. Such rapid destruction (2 years) reveals an important homogenizing force behind this predator and stresses the need for control measures that prevent new transferences among South American basins.

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Introduction

The processes of transferring and introducing non-native species have increased with improvements in transport systems around the world and the globalization of economic activities (Mack et al. 2000; Rahel 2007). The activity became widespread over

the last century and, together with habitat destruction, is presently one of the major threats to biodiversity (Simberloff 2003; Clavero and García-Berthou 2005). Very disparate points of view about the topic still exist among stakeholders, particularly due to the lack of a comprehensive theoretical framework and the consequent inability to predict future colonization and environmental impacts (Moyle and Light 1996; Kolar and Lodge 2002; Lodge and Shrader-Frechette 2002; Cambray 2003). As a consequence, new introductions are still common, and education programs designed to prevent new releases or control established populations have faced several difficulties (e.g., ornamental trade, aquaculture and catch and release fishery). Only recently, for example, has the theme reached social groups other than scientists and conservationists, which have begun to realize economical, environmental and social costs of introductions (Kaufman 1992; McKaye et al. 1995; Simberloff 2003; Eby et al. 2006).

An emblematic example of this conflicting issue has been the frequent transfer of peacock-bass species (*Cichla* spp.) among freshwater watersheds in Brazil, predatory fishes naturally restricted to the Amazon basin (Kullander and Ferreira 2006). Their introduction is forbidden by law in Brazil, but the lack of information on impacts, together with its strong appeal to sport fisherman and commercialization, have motivated clandestine introductions all over the country (Agostinho et al. 2007a). Some *Cichla* species, together with other Amazon piscivores, have thrived in basins regulated by dams and, at present, they are integrated to the fish fauna of many Neotropical reservoirs (Paiva et al. 1994; Chellappa et al. 2003; Oliveira et al. 2006; Agostinho et al. 2007b). Because the peacock-bass is an exceptionally voracious predator, its introduction may seriously threaten native fish diversity (Godinho et al. 1994; Santos et al. 1994) or even act as a major force of biotic homogenization (Zaret and Paine 1973; Latini and Petrere 2004).

There is, therefore, an urgent need to understand the environmental consequences of *Cichla*, mainly because introductions are still occurring in Brazilian reservoirs. For instance, this predator had not been registered in the Rosana Reservoir, Paraná River Basin, until 2003 (Casatti et al. 2003; Pelicice et al. 2005). In 2005, large shoals of *Cichla kelberi* Kullander and Ferreira were observed occupying

the beds of *Egeria* spp., a submerged macrophyte with wide distribution in this reservoir. These plants create important microhabitats for a fish assemblage composed primarily of minute characin species (Casatti et al. 2003; Pelicice et al. 2005), so the presence of non-native predators may pose a significant threat. The conditions in the Rosana Reservoir provide an excellent opportunity for measuring the eventual impacts associated with the presence of *C. kelberi*, especially since the introduction was recent and there is information about the fish fauna associated with *Egeria* before the introduction.

The present study followed a natural experiment (sensu Diamond 1986) in the Rosana Reservoir in order to describe and quantify changes in fish assemblages that followed the introduction of *C. kelberi*. In particular, the study monitored fish assemblages associated with *Egeria* patches during 2 years after the first record of the non-native predator, and investigated patterns of species composition, richness and density. Because there was information about the fish fauna before the introduction, we were able to (1) directly compare the assemblage structure before and after the introduction, (2) follow the assemblage trajectory over time, and (3) investigate the pattern of changes that led to the fish assemblage destruction. Although South America is intensely impounded and *Cichla* spp. are widespread in many reservoirs, this is the first paper describing temporal patterns in fish assemblages that immediately follow the introduction of these predators.

Materials and methods

Study area

Rosana Reservoir is the last of a series that regulates the discharge of the Paranapanema River, one of the main tributaries of the upper Paraná River (22°36'S and 52°52'W). The dam was closed in 1986 for hydroelectric production and created a shallow reservoir with 276 km² of surface area. Submerged macrophytes, especially *Egeria densa*, are very abundant in terms of spatial distribution and coverage (depths <5 m). Other species commonly found are: *E. najas*, *Eichhornia azurea*, *E. crassipes*, *Salvinia herzogii*, *Echinodorus tenellus*, *Nymphaea amazonum*, *Typha domingensis*, and various grass species.

A smaller number of fish introductions have occurred in the Paranapanema River basin (Luiz et al. 2005; Agostinho et al. 2007a). Until recently, *C. kelberi* was only recorded in the Capivara Reservoir, where it was introduced a decade ago (~1998). In Rosana, this predator was not registered in the intensive samplings that used seines and gill-nets with different meshes, which operated in three different zones of the reservoir between 2000 and 2001 (Luiz et al. 2005; A. A. Agostinho, unpublished data). Similarly, other studies did not register the predator between 2000 and 2003 (Casatti et al. 2003; Pelicice et al. 2005). Local fishermen informed the researchers that *C. kelberi* appeared in captures around 2004. Its dispersal from the Capivara Reservoir (~150 km upstream), or even new clandestine fish releases, are possible causes for the introduction of *C. kelberi* in Rosana.

Sampling of fish and macrophytes

Fish assemblages were monitored in an arm of the transition zone of the reservoir (22°34'07"S; 52°33'34"W), upstream from Euclides da Cunha Paulista district, São Paulo state (Fig. 1). The arm is ~40 ha, with littoral areas massively colonized by *Egeria densa*.

Sampling was carried out over six periods between 2003 and 2007 during warm months (>30°C). The first sampling period occurred in the summer of 2003, when *C. kelberi* was absent from the Rosana Reservoir (hereafter Before). Other sampling periods

started about 1 year after the introduction, and occurred between 2005 and 2007, during the summer/autumn and spring seasons (hereafter After-1, 2, 3, 4 and 5) (Table 1).

Fish were collected in mixed patches of *E. densa* and *E. najas*, distributed among both margins of the arm. Sampling was done with a 1 m² throw trap (Pelicice et al. 2005), handled during the day (7:00 a.m.–6:00 p.m.). The trap has a rectangular aluminum frame (1.0 × 1.0 × 1.5 m) with small mesh covering all sides (0.5 cm mesh), except for top and bottom ends.

A boat was silently positioned above *Egeria* patches and used as a platform for trap deployment. Immediately following boat positioning, the trap was quickly thrown into the water and pressed to the bottom. Macrophytes were then removed from the trap with a metal fork and were washed and weighed in the field (fresh mass, g). Next, fish inside the trap were collected with a big sieve (0.90 × 1.5 m) and a dip-net (49 × 49 cm), both with 0.5 cm mesh. We used both methods to ensure that all fish inside the trap were recovered. The sieve was handled until three procedures captured no fish. The dip-net was hauled inside the trap area until ten successive hauls resulted in no additional capture. All fish were preserved in 10% formalin and taken to the laboratory, where they were identified, counted, measured (standard length, cm; SL) and eviscerated to evaluate gonad development (immature or adult). Species identification was based on Graça and Pavanelli (2007).

Fig. 1 Map of the Rosana Reservoir, the last hydroelectric impoundment of the Paranapanema River. The arrow and circle indicate the arm monitored between 2003 and 2007

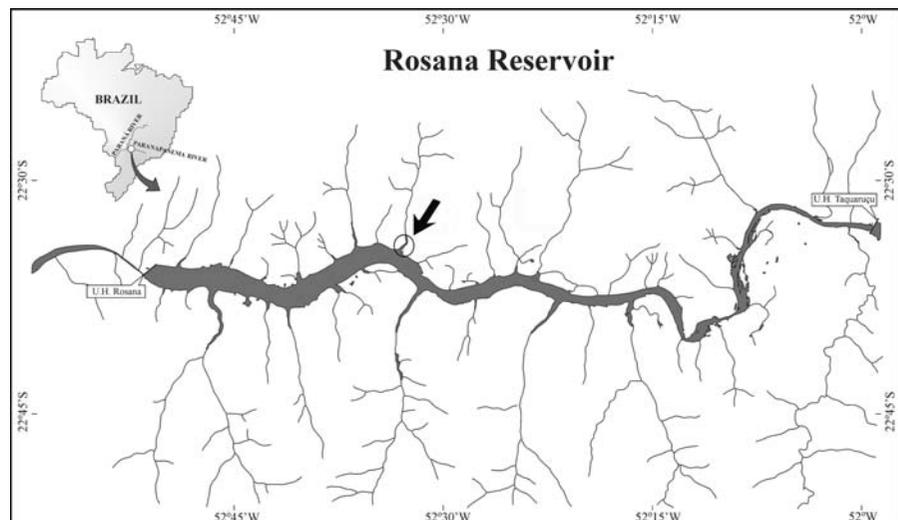


Table 1 Sampling schedule in Rosana Reservoir, indicating date, season and sample size (throw traps) of each period

	Date	Season	Sample size	Periods
1	Jan 2003	Summer	19	Before
2	Mar–Apr 2005	Summer–autumn	20	After-1
3	Nov 2005	Spring	23	After-2
4	Mar–Apr 2006	Summer–autumn	20	After-3
5	Dec 2006	Spring	21	After-4
6	Mar–Apr 2007	Summer–autumn	20	After-5

Periods: Before = prior to the introduction of *C. kelberi*; After = after the introduction

Each throw trap sample represented an independent sampling unit. About 20 samples were taken each period and were distributed at least 50 m apart in order to cover both margins of the arm. A total of 123 samples (thrown traps) were obtained in the study area between 2003 and 2007 (Table 1).

Data analysis

A covariance analysis (ANCOVA) was used to test differences in fish assemblage attributes (density and species richness) among the six sampling periods (Before, After-1...After-5), considering macrophyte biomass as covariable. In this case, the relationship between plant dry biomass and fresh biomass (Pelicice et al. *in press*) was used to estimate total dry biomass (g/m^2) for each sample. Fish density and richness were $\log(+1)$ transformed to correct for problems with heterocedasticity.

To evaluate changes in total species richness along the periods, rarefaction curves were calculated based on sampling effort. In this case, sample order in the original matrix was randomized 1,000 times. The first-order Jackknife estimator (non-parametric) was used to estimate total species richness expected for each period, and the software EstiMateS 5.0 (Colwell 1997) was used for these analyses. Additionally, we used mean (\pm SD) Jackknife estimates to test for significant differences in expected richness between Before and After-periods. Fitting a normal Z-distribution to data, we calculated the probability to find After estimates within the distribution of Before.

A dissimilarity matrix was calculated to assess changes in species composition along the periods.

Due to the high variability in composition within periods, we pooled samples and calculated a general species matrix (presence/absence) for each period. Sorensen distance was used as a dissimilarity index (McCune and Mefford 1997).

Alterations in fish size structure (assemblage-level) were assessed by evaluating the distribution of abundances within different size classes. Such classes were arbitrarily defined in 1 cm intervals: class 1 (0–1 cm); class 2 (1.1–2 cm); class 3 (2.1–3 cm); class 4 (3.1–4 cm); class 5 (4.1–5 cm); class 6 (5.1–6 cm); class 7 (6.1–7 cm); class 8 (7.1–8 cm); class 9 (8.1–9 cm); class 10 (9.1–10 cm); class 11 (>10.1 cm). Due to low fish abundance in last summer/autumn periods (After-3 and 5), the frequency distribution was calculated only for Before and After, which was divided into summer/autumn (After-1, 3 and 5) and spring (After-2 and 4). Changes in frequency distribution among periods (Before, After summer/autumn and After spring) were tested by non-parametric correlation (Spearman rank).

Because fish density notably declined between 2003 and 2007, and because some studies have reported fish extinctions after the introduction of other *Cichla* species (Zaret and Paine 1973; Latini and Petrere 2004), we projected the trajectory of assemblages through time to predict the moment of extinction. The rate of decline was then calculated between periods based on the equation:

$$e = \frac{D_{t+1}}{D_t}$$

where, e = decline rate; D_{t+1} = fish density in the subsequent period; D_t = fish density in the previous period.

Because density declined in a non-linear fashion (see Fig. 6), e was calculated separately for recovery periods (in the case: Before–After-2–After-4) and suppression periods (in the case: After-1–After-3–After-5). By calculating mean e values for recovery and suppression events, we were able to estimate fish density over time until assemblage extinction ($D_t = 0$). In this case, we assumed that the decline rate will remain constant in the coming years.

Except for rarefaction curves and the dissimilarity matrix, all analyses were performed with the software STATISTICA 7.1 (Statsoft 2005). Statistical differences implied an $\alpha = 0.05$.

Results

The fish fauna

A total of 577 fish, belonging to 25 species, were captured in patches of *Egeria* between 2003 and 2007 (Table 2). The assemblages were primarily composed of small-sized species, with a predominance of Characiformes. Five species represented about 80% of the total capture and are presented here in decreasing order of importance: *Roeboides descalvadensis* (previously identified as *R. paranensis*), *Hyphessobrycon eques*, *Serrassalmus marginatus*, *Hemigrammus marginatus* and *Satanoperca pappaterra*.

A total of 256 individuals (17 species) were captured in the period that preceded the introduction of *C. kelberi* (Before), while 321 individuals (21 species) were caught in all subsequent periods (After-1...After-5) (Table 2). Considering the relevant difference in sampling effort between Before ($n = 19$) and After ($n = 104$), some of the most abundant species before the introduction showed remarkable reduction in After, such as *H. eques*, *H. marginatus* and *Serrapinus notomelas* (Table 2).

Fish density and species richness

The relationship between fish density and macrophyte biomass significantly differed among periods (ANCOVA; interaction Biomass \times Period; $F_{5,110} = 4.10$; $p < 0.0019$) (Fig. 2). After the introduction, the slope of relationships decreased in subsequent summer/autumn seasons (After-1, 3 and 5), until the weak relationship observed in After-5. During summer/autumn seasons, higher density values (>10 fish/m²) occurred only in After-1. Density tended to increase during the spring seasons (After-2 and 4), accompanied, however, with a progressive reduction in the slope of relationships.

Similarly, the relationship between fish species richness and macrophyte biomass significantly differed among periods (ANCOVA, interaction biomass \times period; $F_{5,110} = 3.05$; $P < 0.013$) (Fig. 3). After the introduction, fish species richness declined with the same pattern of seasonal fluctuation: strong slope reduction in each subsequent summer/autumn season, with a recovery trend during the spring. Again, during summer/autumn seasons, higher

richness values (>3 species/m²) were observed only in After-1.

When analyzing total fish richness associated with *Egeria* patches, rarefaction curves indicated that species number declined progressively along the summer/autumn periods (Fig. 4). Total richness was reduced by 71 and 82% in the last two summer/autumn seasons (After-3 and 5) when compared to Before, and the rarefaction curves tended to reach an asymptote after the 15th sample. In contrast, total richness had higher values in Before and the After springs (After-2 and 4), and rarefaction curves did not reach an asymptote during these periods, suggesting underestimation. Total richness estimated by Jackknife supported this trend, since springs were more underestimated than summer/autumn periods (Fig. 4). All estimates followed the same oscillatory trend, with accentuated decreases in each subsequent summer/autumn. In addition, total richness estimated in Before was statistically higher than richness estimated in all other periods ($0.039 < P > 0.00001$), except for After-2 ($P = 0.247$).

Assemblage composition and structure

Dissimilarity analysis (Sorensen) showed that assemblage composition changed after the introduction of *C. kelberi*. Considering the composition observed in Before, there was a progressive loss of assemblage similarity in each following summer/autumn season (After-1, 3 and 5). The loss of similarity also occurred during the springs (After-2 and 4), but to a lesser degree (Table 3).

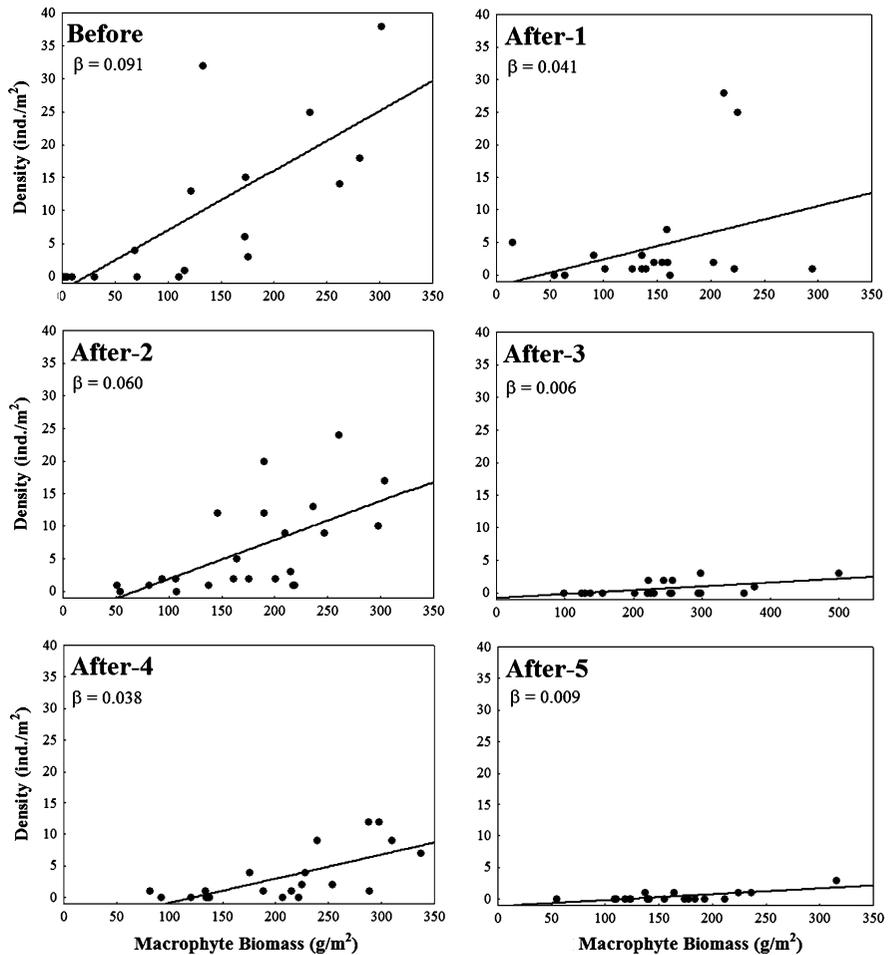
Fish assemblages before the introduction had a prevalence of length class 3 ($>70\%$; Fig. 5), consisting mainly of the adults of *H. eques*, *H. marginatus*, *R. descalvadensis*, *S. notomelas* and the juvenile of *S. marginatus*. After the introduction of *C. kelberi*, abundance in class 3 declined during the summer/autumn seasons (After-1, 3 and 5), when class 2 prevailed ($>60\%$; Fig. 5). These assemblages were composed of juvenile *Satanoperca pappaterra*, *S. marginatus* and *Metynnis lippincottianus* (previously identified as *M. maculatus*). It is interesting to note that small-size classes found in After-1 (classes 2, 3 and 4) virtually disappeared in the following summer-
autumn seasons. Class 3 reappeared in springs of After (Fig. 5), but was constituted predominantly of juvenile *R. descalvadensis*, *S. marginatus* and *S. pappaterra*.

Table 2 Fish species associated with *Egeria* patches before (2003; 19 samples) and after (2005–2007; 104 samples) the introduction of *C. kelberi* in Rosana Reservoir

Taxa	Before		After	
	<i>N</i>	<i>N%</i>	<i>N</i>	<i>N%</i>
<i>CHARACIFORMES</i>				
<i>CURIMATIDAE</i>				
<i>Steindachnerina brevipinna</i> (Eigenmann & Eigenmann, 1889)	0	0.00	5	1.56
<i>ANOSTOMIDAE</i>				
<i>Leporinus</i> sp.	2	0.78	0	0.00
<i>Schizodon borellii</i> (Boulenger, 1900)	1	0.39	0	0.00
<i>Schizodon nasutus</i> Kner, 1858	1	0.39	2	0.62
<i>CHARACIDAE</i>				
<i>Astyanax altiparanae</i> Garutti & Britski 2000	0	0.00	2	0.62
<i>Hemigrammus marginatus</i> Ellis, 1911	46	17.97	16	4.98
<i>Hyphessobrycon eques</i> (Steindachner, 1882)	100	39.06	5	1.56
<i>Metynnis lippincottianus</i> (Cope, 1870)	3	1.17	24	7.48
<i>Oligosarcus pintoii</i> Campos, 1945	2	0.78	3	0.93
<i>Roeboides descalvadensis</i> Fowler, 1932	25	9.77	144	44.86
<i>Serrapinnus notomelas</i> (Eigenmann, 1915)	17	6.64	2	0.62
<i>Serrasalmus marginatus</i> Valenciennes, 1837	34	13.28	49	15.26
<i>ACESTRORHYNCHIDAE</i>				
<i>Acestrorhynchus lacustris</i> (Lütken, 1875)	0	0.00	4	1.25
<i>ERYTHRINIDAE</i>				
<i>Hoplias</i> sp.	0	0.00	1	0.31
<i>SILURIFORMES</i>				
<i>LORICARIIDAE</i>				
<i>Loricariichthys platymetopon</i> Isbrücker & Nijssen, 1979	1	0.39	3	0.93
<i>HEPTAPTERIDAE</i>				
<i>Pimelodella gracilis</i> (Valenciennes, 1835)	0	0.00	1	0.31
<i>DORADIDAE</i>				
<i>Oxydoras eigenmanni</i> Boulenger, 1895	0	0.00	2	0.62
<i>GYMNOTIFORMES</i>				
<i>GYMNOTIDAE</i>				
<i>Gymnotus</i> sp.	0	0.00	1	0.31
<i>STERNOPYGIDAE</i>				
<i>Sternopygus macrurus</i> (Block & Schneider, 1801)	2	0.78	0	0.00
<i>Eigenmannia trilineata</i> López & Castello, 1966	14	5.47	6	1.87
<i>RHAMPHICHTHYIDAE</i>				
<i>Rhamphichthys hahni</i> (Meinken, 1937)	1	0.39	0	0.00
<i>PERCIFORMES</i>				
<i>CICHLIDAE</i>				
<i>Crenicichla britskii</i> Kullander, 1982	1	0.39	4	1.25
<i>Satanoperca pappaterra</i> (Heckel, 1840)	5	1.95	33	10.28
<i>Cichlasoma paranaense</i> Kullander, 1983	1	0.39	3	0.93
<i>Cichla kelberi</i> Kullander and Ferreira, 2006	0	0.00	11	3.43
Total	256		321	

N = total abundance; *N%* = relative abundance

Fig. 2 The relationship between macrophyte biomass (g/m^2) and fish density ($\text{ind.}/\text{m}^2$) in *Egeria* patches, before and after the introduction of *C. kelberi* in the Rosana Reservoir (β = slope). Data are not transformed



The correlation using class frequencies demonstrated that Before was significantly correlated with the spring season (Spearman; $R = 0.72$; $t = 3.12$; $P < 0.012$) but not with summer/autumn periods ($R = 0.27$; $t = 0.85$; $P < 0.42$). Both seasons in After were intermediately correlated, however without statistical significance ($R = 0.58$; $t = 2.14$; $P < 0.062$).

Fish assemblage extinction

As evidenced in all analyses, the temporal trajectory in fish density had moments of severe suppression (summer/autumn; After-1, 3 and 5) followed by recovery phases (spring; After-2 and 4), with decreasing density at each step (Fig. 6). Assuming that the decline rate (e) between moments of suppression ($e = 0.345$) and recovery ($e = 0.483$) remain constant in future periods, we estimated fish density until

the spring of 2011 (After-14; Fig. 6). Based on such projection, assemblage extinction is likely to occur in the summer/autumn of 2010 (After-11).

Discussion

The introduction of *C. kelberi* in the Rosana Reservoir coincided with a striking reduction in fish diversity associated to *Egeria* patches. The existence of information before the introduction, together with the monitoring carried out soon after the introduction, allowed for the observation of swift changes in the structure of fish assemblages. In this case, biodiversity declined progressively over time, and the most important result was the nearly complete loss of fish assemblages in the few years after the introduction. Although the present study is limited to the description of community-level patterns, causal relationships

Fig. 3 The relationship between macrophyte biomass (g/m^2) and fish species richness ($\text{spp.}/\text{m}^2$) in *Egeria* patches, before and after the introduction of *C. kelberi* in the Rosana Reservoir (β = slope). Data are not transformed

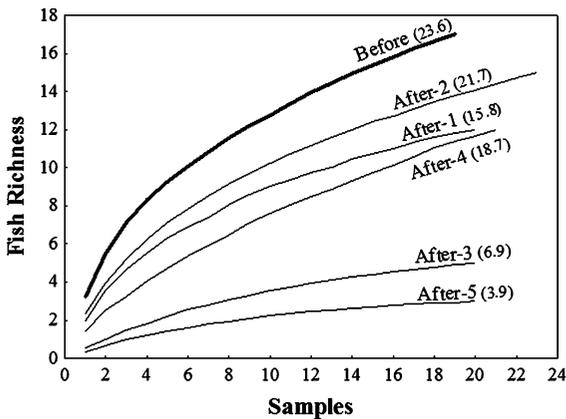
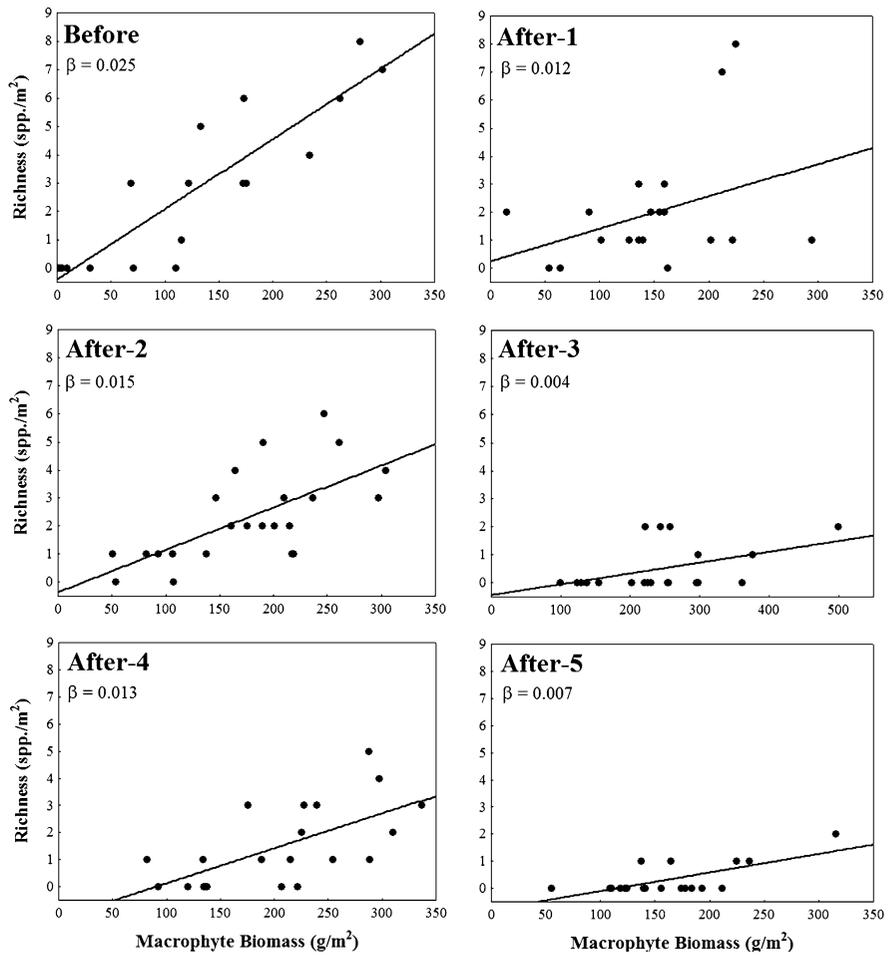


Fig. 4 Total fish species richness observed in *Egeria* patches, before and after the introduction of *C. kelberi* in the Rosana Reservoir. Rarefaction curves were calculated after 1,000 randomizations of the original matrix, and numbers in parentheses indicate total richness estimated by the first-order Jackknife estimator

Table 3 Dissimilarity (Sorensen) in fish assemblage composition before and after the introduction of *C. kelberi* in the Rosana Reservoir

	Before	After-1	After-2	After-3	After-4
Before					
After-1	0.45				
After-2	0.31	0.41			
After-3	0.64	0.41	0.50		
After-4	0.51	0.42	0.33	0.65	
After-5	0.80	0.60	0.67	0.25	0.73

behind invasion and biodiversity loss are analyzed in a forthcoming article, which investigated the relationship among fish assemblage structure, *C. kelberi* abundance and habitat quality in the Rosana Reservoir. Based on field surveys and a field experiment, this article clearly states *C. kelberi*, together with its

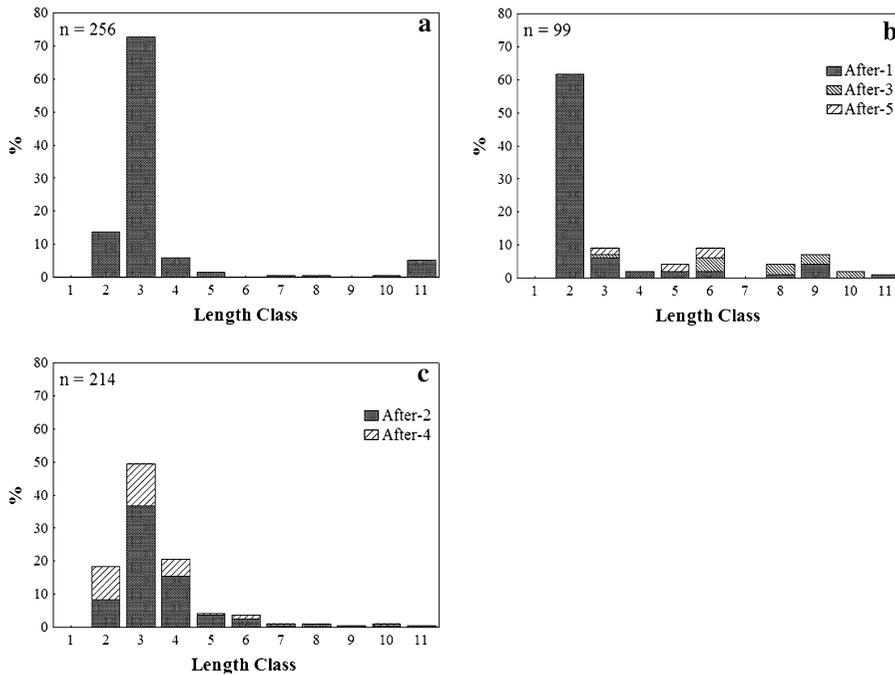


Fig. 5 Frequency distribution of size classes before the introduction of *C. kelberi* (a), and in the summer/autumn (b) and spring (c) seasons that followed introduction. Classes were

contained within 1 cm intervals of fish standard length (see “Materials and methods”)

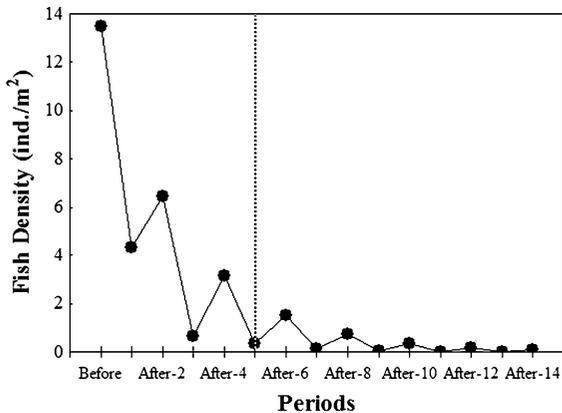


Fig. 6 Mean fish density (ind./m²) in *Egeria* patches along the periods, before and after the introduction of *C. kelberi*. After-5 is the last observed period (vertical dotted line); fish density in the following periods was estimated based on its decline rate (e) measured between Before and After-5

reproductive dynamics (demography), as the main drivers behind the fish fauna collapse (details in Pelicice 2007).

The significant changes observed in the Rosana Reservoir support a general trend: non-native predators causing catastrophic consequences on the native

biota (Zaret and Paine 1973; Kaufman 1992; Moyle and Light 1996; Gratwicke and Marshall 2001; Townsend 2003; Eby et al. 2006; Macchi et al. 1999). Two years after the first record of *C. kelberi* in Rosana, mean fish density and species richness had declined 97.5 and 82%, respectively, and rarefaction curves tended to reach an asymptote after few samples. The small-size of fishes associated to *Egeria* probably increased the predatory effect of *C. kelberi*, if we consider that the five most abundant species before the introduction (87% of total capture), all small-sized (Table 4), were not captured during the last sampling period. At this time, only three species were recorded, two belonging to the original assemblage (*M. lippincottianus* and *S. pappaterra*), plus *C. kelberi*. Studies have reported that many *Cichla* species, including *C. kelberi* (= *C. monoculus*), ingest preferentially small-sized preys, usually smaller than 10 cm SL (Jepsen et al. 1997; Novaes et al. 2004). The invasion of *C. kelberi*, therefore, can promote local extinctions in a short time scale (2 years), and the loss of small-sized species is the first negative consequence—a pattern also observed in other reservoirs and natural lakes in Brazil (Santos et al. 1994;

Table 4 Most abundant fish species in *Egeria* patches before the introduction of *C. kelberi* (2003), which were not registered in 2007

Species	Abundance Rank	Adults (%)	SL (mean)	SL (range)
<i>H. eques</i>	1	99.0	2.76	1.9–3.2
<i>H. marginatus</i>	2	93.5	2.52	1.4–2.9
<i>S. marginatus</i>	3	0.0	1.92	1.3–2.9
<i>R. descalvadensis</i>	4	40.0	2.62	1.7–4.4
<i>S. notomelas</i>	5	94.1	2.62	1.7–3.0

SL standard length (cm)

Gomieiro and Braga 2004; Latini and Petrere 2004). Considering this result, it is possible to predict that homogenization effects caused by *C. kelberi* will be more likely in headwater environments or in basins with high endemic diversity of small-bodied species (e.g., the unique Iguacu River, where this predator has been introduced but not yet studied).

The relationship between fish assemblages and habitat complexity was also affected. Before the introduction, the amount of submerged macrophytes determined patterns of fish diversity in small spatial scales, a result of habitat availability for shelter and feeding provided by high plant coverage (Casatti et al. 2003; Pelicice et al. 2005; Pelicice and Agostinho 2006). Macrophyte biomass, for example, alone could predict more than 50% of variability in fish density and richness in 1 m² plots (Pelicice et al. in press). After the introduction, however, macrophyte biomass was no longer related to the structure of fish assemblages. For instance, mean fish density decreased more than 90% in patches with high structural complexity (plant biomass ~250 g/m²), and mean species richness declined from 6 to 1 spp./m². Despite several studies pointing out the role of macrophytes as refuges for small-sized fish (Savino and Stein 1989; Jacobsen and Perrow 1998; Stuart-Smith et al. 2007), *Egeria* patches failed to provide shelter in the presence of a non-native predator adapted to forage in littoral environments, as in the case of *Cichla* (Winemiller et al. 1997). Latini and Petrere (2004) also observed the irrelevance of refuges in the presence of introduced predators that efficiently use littoral habitats for feeding and protection. These results illustrate, therefore, two important aspects related to the invasion of *C. kelberi* (or related species). First, predator behavior is a key factor determining the extension of impacts (Holway and Suarez 1999; Shea and Chesson 2002), in relation to voracity and habitat

preferences. Second, these results suggest the difficulty in minimizing the influence of *C. kelberi* once introduced, given that even a high availability of refuges (e.g., submerged macrophytes) was unable to reduce its influence.

An interesting aspect is the non-linear (oscillatory) loss of diversity over time; the collapse of fish assemblages unfolded at two different times within each year. The first occurred during summer/autumn periods, with remarkable decreases in fish density and richness. Such decline in fish diversity coincided with the presence of large shoals of young *C. kelberi* throughout the patches (fish <13 cm SL, data not shown; see Pelicice 2007). The reproduction of *C. kelberi* during warm months (starting in October and November), with the outbreak of juveniles during the summer, must increase predation pressure along littoral zones of the reservoir. Several studies emphasize that these young predators include fish in the diet, limited only by gape size (Santos et al. 1994, 2001; Bachelier et al. 2004; Novaes et al. 2004). Indeed, small-sized classes were the most affected in Rosana Reservoir, especially classes 2, 3 and 4 (fish ranging from 1 to 4 cm SL). The second period occurred during spring, when fish assemblages showed trends of recovery (i.e., significant increases in density and richness). In this season, juvenile *C. kelberi* were virtually absent in the patches (data not shown; see Pelicice 2007). Therefore, fish populations reassembled in the patches when young *C. kelberi* were no longer present, and the fast re-colonization of the whole area (~8 months) characterizes high resilience in these fish assemblages. We hypothesize that remnant populations living in *Egeria* or other habitats work as sources for community reassembly. Other macrophyte life forms may play a different role as a refuge, like *Eichhornia azurea*, *Typha domingensis* and *Eleocharis* spp.,

plants usually present in shallow areas of the arm and surrounding environments. Field observations, for example, revealed a few small-sized species (e.g., *H. eques* and *H. marginatus*) associated to *E. azurea* in March 2007, a moment when fish assemblages had disappeared from *Egeria* patches.

The sequence of extinction-colonization events, however, seems to be unable to maintain fish assemblages in the patches because the intensity of recovery has decreased at each period. It is likely that the presence of young *C. kelberi* in successive summers is promoting an additive impact on the resident fauna. Assuming a constant decline in the coming years (if no external factor control *C. kelberi* populations, such as extreme cold seasons, diseases or shortage of preys), we expect that fish assemblages will reach a critical structure in the summer of 2010, with populations becoming virtually extinct. The consequences to the functioning of the ecosystem are uncertain. The disappearance of invertivorous fish—the main trophic group associated to *Egeria* habitats (Pelicice and Agostinho 2006)—would interrupt the flow of matter and energy between invertebrates and top predators (Zaret and Paine 1973). In addition, the decreasing predation pressure upon microcrustaceans and insect larvae may significantly change top–down and bottom–up controls (Eby et al. 2006), or even interfere in the process of macrophyte colonization (Jones and Sayer 2003; Ward and Newman 2006). The removal of an important link in the food web, formed by minute invertivorous fish, will create a dangerous gap in the trophic connections that support the reservoir's biota in littoral areas.

An important question behind *C. kelberi* invasion is why its harmful potential increases so much in impounded rivers. Some authors have discussed that colonization and impacts caused by non-native species emerge from complex processes, usually in association with other environmental disturbances (Moyle and Light 1996; Byers 2002; Shea and Chesson 2002). The impounding of rivers, in particular, seems to facilitate the colonization and dispersion of non-native invaders (Gido and Brown 1999; Godinho and Ferreira 2000; Havel et al. 2005; Light and Marchetti 2007), as evidenced by the widespread colonization of *Cichla* spp. in several Brazilian reservoirs (Agostinho et al. 2007b). In addition, impacts can be magnified by modifications in hydrology, physical structure, habitat diversity or

the flow of matter/energy in rivers (Byers 2002). For example, *C. kelberi* was introduced in the upper Paraná River floodplain, a conservation unit located about 40 km downstream of the Rosana Dam, more than 20 years ago. Its density remained low for more than 15 years and there was no evidence that the native fish community was under threat (Agostinho et al. 2004). In this case, natural river conditions, such as low water transparency and the seasonal flood pulse, have controlled *C. kelberi* populations below harmful thresholds (Abujanra 2007). Although this situation has changed with the construction of the Porto Primavera Dam upstream to the floodplain, the short distance between both environments (floodplain–Rosana Reservoir), together with clear differences in colonization and impact exerted by *C. kelberi*, suggest that the impoundment has played an enhancing role in colonization and impact. A future challenge is to understand the factors behind these patterns and the environmental conditions that make *C. kelberi* so noxious.

In conclusion, the conservation of fish diversity in South America is currently at stake. In addition to other anthropogenic impacts (Agostinho et al. 2005), (1) the ongoing introduction of *Cichla* spp. into different environments, (2) the damming of all large rivers, and (3) the vulnerability of Neotropical fish fauna to invasions (Rodríguez 2001), increase the chance of environmental catastrophes in aquatic ecosystems. The upper Paraná River basin, for example, is extremely affected by large impoundments (>140). Small to medium-sized sedentary species, such as those associated to *Egeria* spp., are among the few fish able to flourish in reservoirs (Agostinho et al. 2007a); formerly widespread all over the basin, they currently represent an important component of fish diversity in impounded areas (Agostinho et al. 2007a). Considering that the main river channel and nearly all large tributaries are modified by impoundments, the conservation of fish diversity in this basin depends largely on the maintenance of fish populations in reservoirs. All these concerns sharply contrast with the lack of specific studies evaluating the impacts caused by *Cichla* species, and new efforts are necessary so that biodiversity loss can be inferred at different spatial scales. Future decisions concerning new introductions, including any eventual benefits they can bring for sport fishing and local economies, should take

into account the swift loss of biodiversity reported here.

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