

Evaluation of factors associated with dynamics of *Cichla ocellaris* invasion of the Upper Paraná River floodplain system, Brazil

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Abstract. Invasion by *Cichla ocellaris* was studied in the Upper Paraná River floodplain. Generalised linear models and the Akaike Information Criterion (AIC) were applied to standardised gill-net catch data (CPUE), with years, rivers, secchi depth, and their respective interactions. Generalised additive models and AIC were used to evaluate relationships of CPUE for *C. ocellaris* with standard length, sampling year and secchi depth. *C. ocellaris* was first recorded in 1992 in the Paraná and Ivinheima Rivers. Nevertheless, the CPUE of individuals was very low in the latter until 2000, and the species was not recorded from the Baía River until 2000. In 2001, CPUE of *C. ocellaris* greatly increased (from 20 to 140) in all three rivers, and this coincided with changes in hydrology and suspended sediment. Greater secchi depth is thought to benefit foraging by these visually oriented, diurnal piscivores. The estimated annual growth rate for local populations was 21% for the Paraná, 42% for the Ivinheima, and 73% for the Baía Rivers. Consequently, relative to other populations, *C. ocellaris* of the Baía River and, to a lesser degree, the Ivinheima River, appear to be less influenced by density-dependent factors given their more recent invasions of those areas.

Additional keywords: body size, invasive species, piscivore, population density, population dynamics, secchi depth.

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Introduction

The introduction of non-native fish is one of the leading threats to freshwater biodiversity (Mack *et al.* 2000; Kolar and Lodge 2001; Rahel 2002; Clavero and García-Berthou 2005). Impacts of non-native freshwater fishes on native species and ecosystems have been documented in the Neotropical region, mainly in Brazil (Orsi and Agostinho 1999; Latini and Petrere 2004; Vitule *et al.* 2012; Pelicice *et al.* 2014). Research on spatial and temporal dynamics of non-native populations is urgently needed in order to improve understanding of causal relationships that could assist management (García-Berthou 2007).

The peacock cichlid (*Cichla ocellaris*) is a piscivorous fish native to the Amazon and Essequibo Basins of South America. Based on morphological analysis, Kullander and Ferreira (2006) split *C. ocellaris* into several species, including *C. kelberi*, a species they recognised within the Tocantins–Araguaia Basin. Further analysis based on genetics suggested that several of the species described by Kullander and Ferreira (2006) are actually

C. ocellaris (Willis *et al.* 2012), a single species with extensive genetic introgression among geographic variants showing varying degrees of morphological differentiation. Here we follow the recommendation of Willis *et al.* (2012) and refer to the species from the Tocantins–Araguaia Basin as *C. ocellaris*.

Cichla ocellaris has been translocated into several river basins in Brazil as well as to other rivers in other parts of the world, including Central and North America, Hawaii and Southeast Asia. The detrimental effects of *C. ocellaris* on native fish have been documented for Gatún Lake in Panama (Zaret and Paine 1973) and for reservoirs in southern Brazil (Latini and Petrere 2004; Pelicice and Agostinho 2009). Currently, *C. ocellaris* is established in several hydroelectric reservoirs and rivers in southern Brazil (Agostinho *et al.* 2007). The potential for *C. ocellaris* to invade reservoirs is influenced by environmental conditions such as temperature, water quality, and lake size and depth (Espínola *et al.* 2010). Zaret and Paine (1973) examined the spatial and temporal dynamics of

successful invasions by *C. ocellaris* in Lake Gatún, Panama. They recorded how the species had invaded this reservoir in the Panama Canal Zone from the Chagres River and had spread through nearly the entire lake in just two years. The *Cichla* invasion was followed by major changes in native fish populations and food web structure. Near Barro Colorado Island, seven of eight native fish species declined by 50–100%, and sites invaded by *Cichla* yielded seven native fish species in surveys compared with 13 at sites where *Cichla* were not present. Documentation of invasion processes and their consequences for native communities and ecosystems is needed in order to understand causal mechanisms for impacts of invasive species and their management.

Here, we address the spatial and temporal processes of invasion by non-native *C. ocellaris* in three rivers within the Upper Paraná River floodplain, a species-rich ecosystem that is also affected by altered hydrology and habitat as well as other invasive species (Agostinho *et al.* 1994, 2008). The specific objectives of this study were: (1) to model the population growth of *C. ocellaris* during the two decades after its first appearance in the Upper Paraná River; (2) to compare the relative growth rates

among *C. ocellaris* populations in three major tributaries of this ecosystem; and (3) to assess the potential for environmental factors and possible anthropogenic disturbances to have an impact on the establishment and population growth of *C. ocellaris* in this system.

Material and methods

The Upper Paraná River floodplain

Approximately 4695 km in length, the Paraná River is the tenth longest river in the world and the second largest river in South America. Within Brazilian territory, the Upper Paraná River floodplain (UPRF) reach extends ~230 km between Porto Primavera Dam and Itaipu Reservoir, and is the longest stretch without a dam (Fig. 1). The UPRF comprises a mosaic of aquatic, terrestrial, and transitional biotopes and supports more than 250 native fish species (including migratory *Brycon orbignyanus*, *Piaractus mesopotamicus*, *Prochilodus lineatus*, *Pseudoplatystoma corruscans* and *Salminus brasiliensis*) that depend on the floodplains as nursery grounds (Agostinho *et al.* 2004).

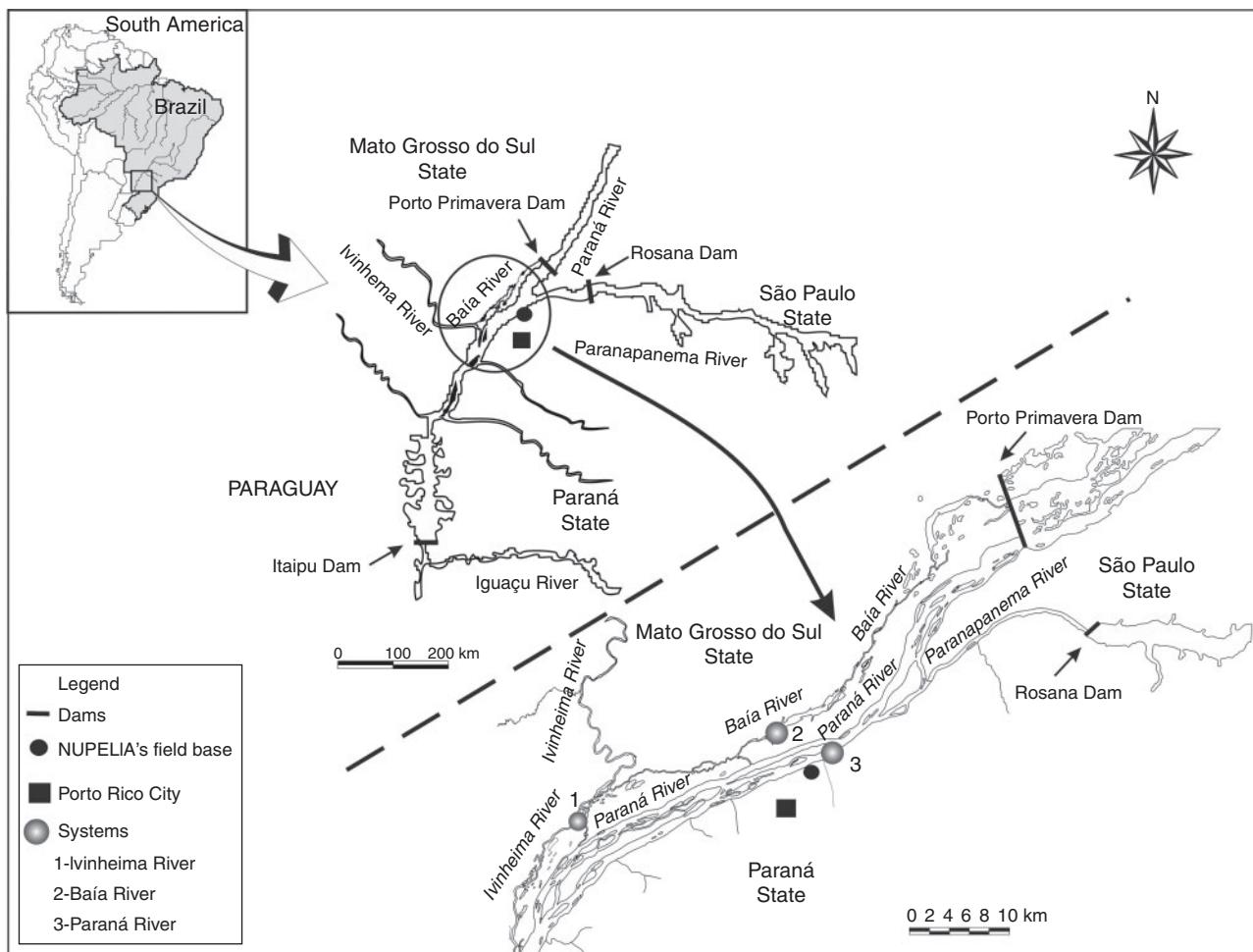


Fig. 1. Map of the Upper Paraná River Floodplain (UPRF) showing locations of the Porto Primavera Dam, Itaipu Reservoir, NUPELIA's field station (●) near the city of Porto Rico (■), and the Upper Paraná mainstem, Baía River, and Ivinheima River.

The ecological integrity of the UPRF has been increasingly altered by human actions, especially flow alteration from dams and establishment of invasive species from the Amazon Basin. Several fish species native to the Rio Paraguay sub-basin, within the Paraná River Basin invaded the UPRF when the Itaipu Dam and Reservoir flooded the Sete Quedas Falls and allowed upstream migration past this barrier. *Plagioscion squamosissimus*, *Astronotus crassipinnis*, *Cichla ocellaris* and *Cichla piquiti*, all native to the Amazonian Basin, have become well established in the UPRF following accidental escapes as well as intentional stockings undertaken by hydroelectric companies. *C. ocellaris* probably arrived to the UPRF in the early 1990s from the Itaipu Reservoir (Agostinho *et al.* 1994, 2008), but subsequent escape from fish farms and intentional introductions by anglers have contributed to its dispersal in the region (Espínola *et al.* 2010). *C. ocellaris* is abundant in lentic habitats of the UPRF, and particularly in shallow floodplain lakes with high densities of submerged macrophytes (Agostinho *et al.* 2008).

Fish surveys and data analysis

Since 1986, the Nucleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (NUPELIA) at Universidade Estadual de Maringá (UEM), Brazil, has collected physical, chemical and biological data from stations located in floodplain lakes, channels, and river habitats distributed among the Ivinheima, Baía, and Paraná Rivers (Fig. 1). This long-term research program is focussed on causal relationships among environmental variables, fish, other aquatic organisms, and aquatic and riparian vegetation. Fish surveys within this program are conducted with variable frequencies, degrees of effort, and gear types; however, for this study, only data from standardised station surveys conducted in each study river using the same methods, effort, and gear were analysed.

Fish were captured using monofilament gill-nets of different mesh sizes (ranging from 3 to 16 cm opposite knots) and trammel nets (internal mesh of 6-, 7- and 8-cm opposite knots). Nets were retrieved at 0800, 1600, and 2200 hours on the dates of deployment. Species abundances in each sample were indexed by capture per unit effort (CPUE; number of individuals per 1000 m² of gill-nets in 24 h). Data for secchi depth (m) and the CPUE and size (millimetres standard length) of *C. ocellaris* captured in the Paraná, Ivinheima and Baía Rivers during 1986–2007 were included in the present analyses. Surveys from 1989 to 1991 and 1996 to 1999 were not included in the analysis. In addition to being the three major rivers of the UPRF, the Ivinheima, Baía, and Paraná Rivers contain diverse habitats that appear to be suitable for *Cichla* (i.e. backwaters along the main channel, floodplain lakes, floodplain creeks).

Population growth rates of *C. ocellaris* were estimated by fitting generalised linear models to density data in the form of CPUE. An exponential growth model using population size data taken at the same time each year (Eberhardt and Simmons 1992) was assumed to provide the best approximation of the annual rate of change during the initial phase of invasion:

$$N_t = N_0 \lambda^t, \quad (1)$$

where N_0 = initial population size, N_t = population size in the time t , and λ = annual population change rate. This equation

can be linearised (i.e. log-transformed) and a simple linear regression can be thus applied to calculating the parameter λ (Eqn 2):

$$\log N_t = \log N_0 + t \log \lambda \quad (2)$$

It is important to note that, in this case, N_t indicates the relative size of the population, since models were derived from temporal data series of relative density (CPUE). Multiple hypotheses (i.e. concurrent statistical models as in Hobbs and Hilborn 2006) were tested to explain population densities of *C. ocellaris* in the UPRF. Eleven models were tested by replacing independent variables in Eqn 2 with the variables *year*, *river*, *secchi depth* and interactions between these variables. These variables were added in a hierarchical manner that allowed inference of the best fit for predicting population growth of *C. ocellaris* based on the complete interannual regional dataset (Burnham and Anderson 2004).

Given that multiple concurrent models can be fitted to the dataset, the Akaike's Information Criterion (AIC), which considers not only goodness of fit but also parsimony (i.e. penalising more complex models), was used to select the best model (Burnham and Anderson 1998). Two variables were taken into account to select the best model: (1) the adjusted AIC ($= AIC_c$), which should be used whenever the ratio between the number of observations and the number of parameters in the model is < 40 (i.e. best model = lowest AIC_c values), and (2) the difference ($= \Delta AIC_c$) between the AIC_c value calculated for a specific model and the minimum AIC_c value calculated among all the 11 concurrent models (i.e. best model = lowest ΔAIC_c values) (see Burnham and Anderson (1998) for further details). All model-fitting procedures were performed with the R statistical software (R Development Core Team 2011).

Generalised additive models (GAMs), as available in CANOCO 4.5 (Lepš and Šmilauer 2003), were fitted to evaluate relationships of *C. ocellaris* CPUE with standard length, sampling year and secchi depth, as well as relationships between standard length and secchi depth with sampling year. GAMs are an extension of generalised linear models that, unlike more conventional regression methods, do not assume a particular functional relationship between the response variable and the predictors (Lepš and Šmilauer 2003). The model complexity of GAMs was chosen by the stepwise selection procedure using the AIC, also available in CANOCO 4.5.

Results

Although *C. ocellaris* was first recorded in the UPRF in 1992, only a few individuals (< 5 per sample) were caught sporadically until 2001. However, catches increased greatly in surveys conducted thereafter. AIC and GAM revealed non-linear increases in CPUE (non-linear $F_{1,26} = 4.1$, $P = 0.05$), consistent with an interpretation of exponential growth (Fig. 2a). AIC also selected a positive linear trend in body size ($F_{1,26} = 2.8$, $P = 0.10$), with individuals larger than 200 mm being more common after 2000 (Fig. 2b).

Patterns of colonisation by *C. ocellaris* differed between the three rivers. After its first appearance in 1992 within the Paraná River, the species was consistently present in samples, and,

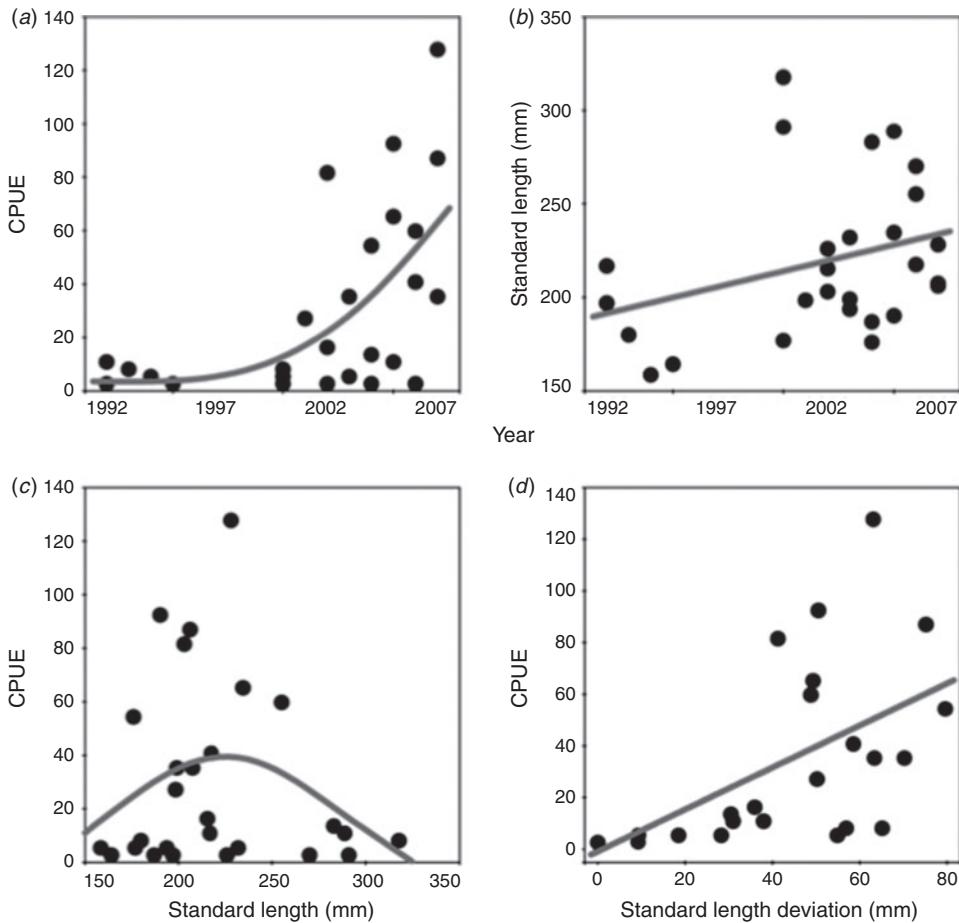


Fig. 2. Relationship of (a) CPUE for *C. ocellaris* (fish per 1000 m² of gill-net per 24 h) and (b) body size of *C. ocellaris* (L_s) with year; and relationships of CPUE with (c) mean body size and (d) standard deviation of body size of *C. ocellaris* in the UPRF (pooled data for the Paraná, Baía and Ivinheima Rivers). Lines represent predictions from generalised additive models selected by the Akaike information criterion.

although a range of size classes was consistently present in the Paraná River most individuals were larger than 150 mm. Fish of 50–100 mm were recorded in 1994, 2000 and 2003, but many individuals with intermediate sizes (100–150 mm) were consistently recorded after 2001. Apart from a single 200-mm individual in 1992, *C. ocellaris* was not captured from the Ivinheima River until 2000, but captures were consistent after 2002. In the Baía River, *C. ocellaris* was not captured until 2000, and all were juveniles <50 mm. Individuals spanning a broad range of body sizes were captured after 2000. GAMs indicated a unimodal relationship between CPUE and L_s ($F_{1,26} = 4.0, P = 0.05$) (Fig. 2c) and a positive linear relationship between CPUE and the standard deviation of L_s ($F_{1,26} = 14.3, P < 0.01$) (Fig. 2d).

Models selected by AIC to predict CPUE for *C. ocellaris* appear in Table 1. The model that best explained density changes included the variables *year*, *river*, and their interaction. The second-best model also included *secchi depth*, but its high ΔAIC_c value indicated that this variable had a relatively weak influence. The response curves (GAMs) revealed minor interannual temporal changes during the survey period in secchi depth for the Baía and Ivinheima Rivers (AIC; non-linear $F_{1,11} = 8.2, P = 0.02$; non-linear $F_{1,11} = 3.5, P = 0.09$,

respectively) but not for the Paraná River (AIC; non-linear $F_{1,11} = 4.3, P = 0.07$), with a sharp increase in secchi depth after 2000 (Fig. 3a). AIC selected a response curve of CPUE for *C. ocellaris* with secchi depth for the Paraná River only (non-linear $F_{1,11} = 3.2, P = 0.10$), suggesting a population increase of *C. ocellaris* until secchi depth reached ~3.0 m, and thereafter a stabilisation of population growth (Fig. 3b). Hence, even when secchi depth was selected for the model, it was a relatively weak predictor of the abundance of *C. ocellaris*.

The estimated parameters from the best-fit linear regression model (Model 1) were used to formulate population growth equations for *C. ocellaris* populations in each study system of the UPRF (Fig. 4). The intercept, a , was 0.86 (± 0.28 , s.e.) for all three populations. The value for b was 0.19 (± 0.11 , s.e.) for the Paraná, 0.55 (± 0.08 , s.e.) for the Baía, and 0.35 (± 0.07 , s.e.) for the Ivinheima Rivers. With these values in the exponential equation of population growth (Eqn 1), the annual rate of population change (λ) was 1.21, 1.73, and 1.42, respectively for the Paraná, Baía and Ivinheima Rivers. Nearly a decade separates the estimated time of initial invasion by *C. ocellaris* of the Paraná and Ivinheima Rivers (1992 versus 2000, respectively). The estimated population growth rate is much higher

Table 1. Concurrent models, number of parameters added and values of *AIC*, *AICc* and $\Delta AICc$ for the population growth of *Cichla ocellaris* in the UPRF

Symbol code follows Wilkinson and Rogers (1973): \sim = as a function of; ~ 1 = intercept; + = main effects; * = interaction; log = natural logarithm; co = no. of *C. ocellaris*. The best-fit model is shown in bold

Selected models: variations of $\log N_t = \log N_0 + t \log \lambda$	No. of parameters	Adjusted R^2	<i>AIC</i>	<i>AICc</i>	$\Delta AICc$
1-Log co ~years + years*systems	5	0.7	57.99	61.32	0
2-Log co ~years + years*systems + secchi depth	6	0.69	59.52	64.46	3.13
3-Log co ~years*systems	7	0.69	59.52	67.12	5.79
4-Log co ~years*systems + secchi depth	8	0.69	61.01	70.6	9.27
5-Log co ~years + systems	5	0.67	60.4	63.74	2.41
6-Log co ~systems* secchi depth	7	0.48	72.91	79.91	18.52
7-Log co~systems	4	0.07	84.63	86.77	25.44
8-Log co ~years	3	0.39	73.37	74.57	13.25
9-Log co~1	2	—	84.56	85.13	23.8
10-Log co~secchi depth	3	0.12	62.23	83.54	22.21
11-Log co ~years*systems + secchi depth* systems	10	0.68	62.23	79.15	17.82

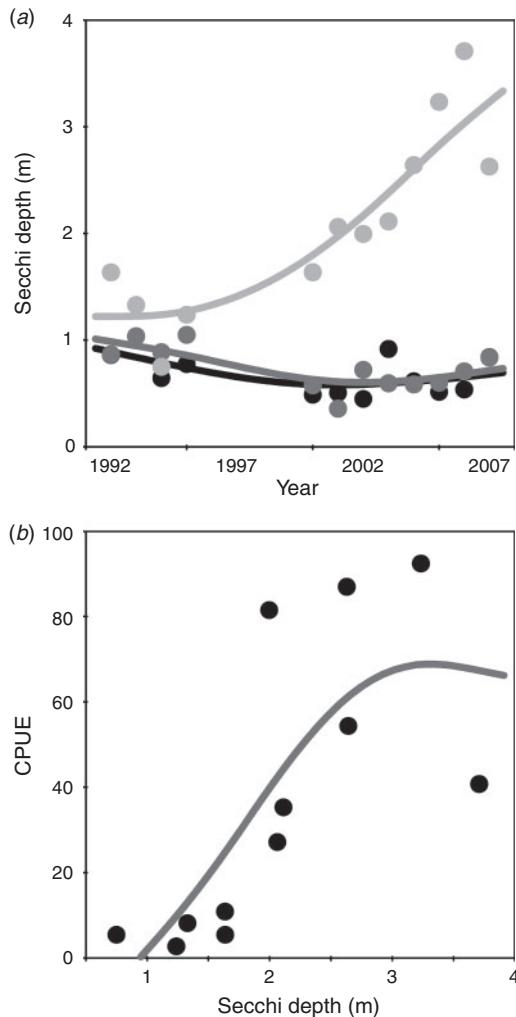


Fig. 3. Responses of (a) Secchi depth with time for the Paraná, Baía and Ivinheima Rivers (light grey, grey and black circles, respectively) and relationship of (b) CPUE for *C. ocellaris* (fish per 1000 m² of gill-net per 24 h) with Secchi depth for the Paraná River. Lines are the generalised additive models selected by the Akaike information criterion.

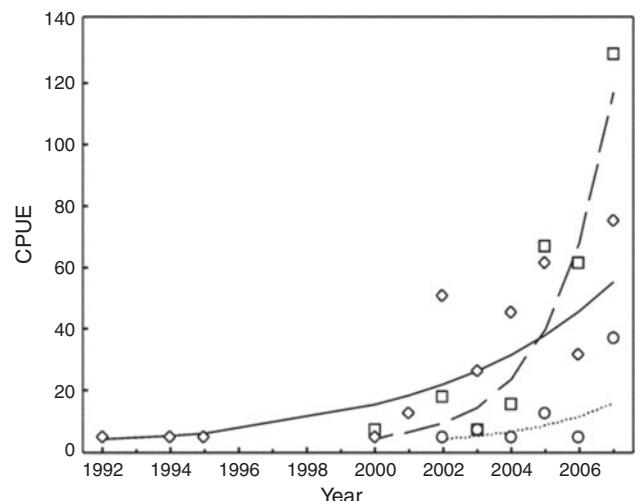


Fig. 4. Relative growth of *Cichla ocellaris* population predicted for the three study systems of the UPRF (i.e. Paraná (\diamond ; dotted lines), Ivinheima (\circ ; solid lines) and Baía (\square ; dashed lines) Rivers). Symbols: CPUE for *C. ocellaris* (fish per 1000 m² of gill-net per 24 h); Lines: adjusted growth model. Samples devoid of fish were omitted from the figure.

for the Ivinheima River (42% per year) than the Paraná River (21% per year). *C. ocellaris* appeared in the Baía River surveys for the first time in 2000, and this population has an even higher estimated growth rate (73% per year).

Discussion

Our findings revealed that although *C. ocellaris* was first recorded in 1992 in the Paraná and Ivinheima Rivers, it remained in low numbers and was not recorded in the Baía River until 2000, suggesting that this species took at least eight years (i.e. its lag-phase) to become established in the Upper Paraná River floodplain. After 2000, CPUE for *C. ocellaris* increased dramatically in the three rivers, probably in response to the filling and operation of Porto Primavera Dam upstream, which decreased flood pulse intensity and frequency and also reduced

suspended sediment. Although our GAM results support the general hypothesis that increased secchi depth is critical for the invasion process of a visually oriented and diurnal piscivore such as *C. ocellaris*, differences in annual growth rates recorded for peacock cichlid populations in the Paraná (21%), Ivinheima (42%), and Baía (73%) Rivers suggest the influence of density-dependent factors. They also stress the importance of knowing as much as possible about the ecological attributes of the invader and the environmental conditions of the invaded ecosystem to fully understand the invasion process of *C. ocellaris* across a Neotropical floodplain with high species and habitat diversity.

The precise date and location of the introduction of *C. ocellaris* into the UPRF remains unclear, although introducing this species as a stocking strategy and to support sport fishing activities was quite common until 1990 (Agostinho *et al.* 2005), mostly led by hydroelectric companies (Orsi and Agostinho 1999; Pelicice and Agostinho 2009; Vitule *et al.* 2012). Moreover, there could have been accidental escapes from ponds at fish farms and pay-to-fish businesses (Agostinho *et al.* 1994, 2008). Those introductions, intentional or accidental, not only established *C. ocellaris* in the UPRF, but also could have facilitated dispersal throughout the interconnected systems (Lockwood *et al.* 2005). *C. ocellaris* was first recorded in 1985 from Itaipu Reservoir, where it was probably stocked by the hydroelectric company (Agostinho *et al.* 1994). The filling of Itaipu Reservoir submerged the Sete Quedas Falls and allowed the upstream spread of fish species previously restricted to the Lower Paraná River Basin (Júlio *et al.* 2009; Vitule *et al.* 2012), and consequently increased fish diversity of the Upper Paraná River Basin (Britton and Orsi 2012). In addition to the direct adverse effects on native fish assemblages, such as habitat changes, blockage of migratory routes, and disturbances on ecosystem functioning (Agostinho *et al.* 2005, 2008; Gubiani *et al.* 2007; Júlio *et al.* 2009), the presence of Itaipu Reservoir and other impoundments in the basin probably have also contributed to the invasion and establishment of many non-native fish species, including *C. ocellaris*, in the UPRF (Santos *et al.* 2009, 2012, 2013). *C. ocellaris* took seven years to invade the UPRF, where it remained at low densities (<5 individuals per sample) in floodplain lakes and secondary channels of all three rivers until 2001 (Fig. 2a). During the initial phase of regional colonisation, population densities in most habitats were probably influenced most strongly by dispersal dynamics (i.e. differential propagule pressure from intentional or accidental introductions) as opposed to recruitment derived from local reproduction.

The variable *river* was a significant predictor of CPUE for *C. ocellaris*, indicating that populations of the Paraná, Baía and Ivinheima Rivers had different growth patterns. Local recruitment probably influenced population densities to a greater extent after 2001, the period when young fish smaller than 50 mm were first captured along with adults of variable body sizes. However, recruitment success did not appear to be the same in all rivers. Recruitment appeared to be particularly successful in the Baía River during the period 2005–07. In the Ivinheima River, few individuals <100 mm were captured during this study. Together with local recruitment, differences among local fisheries also could have influenced the population dynamics of *C. ocellaris* in different rivers. Since the Ivinheima

River and its floodplain (~700 km²) lie entirely within a State Conservation Park where fishing is prohibited, *Cichla* population dynamics in this river were mostly affected by local recruitment. On the other hand, sport and commercial fisheries probably influenced population dynamics in the Paraná and Baía Rivers. Whether population dynamics of *C. ocellaris* in these two rivers were influenced by humans in ways that were adverse (i.e. increased mortality by sport or commercial fisheries) or positive (i.e. increased propagule pressure from releases by sport fishers) remains unclear because data are lacking with regard to the latter.

In addition to the influence of time, place, and propagule pressure associated with initial and subsequent colonisation events, environmental changes that occurred in the UPRF after 2000 also could have influenced recruitment success and population density changes. The closure of the Porto Primavera Dam, the filling of the reservoir, and the initiation of hydroelectricity generation changed the hydrology and sediment dynamics of the UPRF downstream from the dam (Agostinho *et al.* 2004; Souza Filho *et al.* 2004). The reduced loads of suspended sediments has been proposed as the principal factor facilitating the spread and increase in abundance of *C. ocellaris* in the UPRF and nearby reservoirs (Espínola *et al.* 2010). *Cichla* species are visual, diurnal piscivores (Winemiller 2001), and their foraging success should increase with greater secchi depth (Luz-Agostinho *et al.* 2008). However, our results revealed that secchi depth, though important, accounts for a minor proportion of the density changes of *C. ocellaris* populations in rivers of the UPRF. Other environmental changes caused by the Porto Primavera Dam, such as decreases in duration and magnitude of the annual flood pulse, probably act in concert with secchi depth to influence the population dynamics of *C. ocellaris*. Stabilised water levels resulting from the operation of the Porto Primavera Dam appeared to stimulate the growth of aquatic macrophytes, and this could have influenced the aquatic food web as well as the recruitment of species such as *C. ocellaris* that nest and guard before abandoning their brood within littoral habitats.

With respect to the three rivers studied here, the Ivinheima River has experienced the lowest impact from hydrologic regulation and, following initial invasion in 2000, *C. ocellaris* had a lower estimated population growth rate in this river compared with the population in the Baía River, established at about the same time. If accurate, this difference in invasion dynamics supports the hypothesis that alteration of the natural flood regime somehow facilitated the invasion of *C. ocellaris* in the UPRF (cf. Bunn and Arthington 2002). The high estimate for the growth rate of the Baía River population could have been associated with density-independent growth dynamics given its recent establishment, but would also have been influenced by high secchi depth during most of the year. In contrast, the lower growth rate estimated for the Paraná River population could have been associated with stronger density-dependent influences on population dynamics following its establishment in this region more than a decade before establishment of populations in the other two rivers.

Once a non-indigenous fish has invaded a freshwater ecosystem, it is virtually impossible to eliminate it (Myers *et al.* 2000; Simberloff 2009; Britton *et al.* 2011). The goal should be to manage the impact of the invader on the native communities so

that influential ecosystem features and processes can be maintained at relatively natural levels to maintain native biota and ecosystem services. Given the extensive hydroelectric infrastructure established within the basin, efforts should be undertaken to restore key components of the natural hydrological regime of the UPRF. Additionally, efforts should be made to limit further expansion of *Cichla ocellaris* populations using methods such as promotion of fisheries with liberal harvest regulations for the species.

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