Ecología Austral 33:439-454 Agosto 2023
Asociación Argentina de Ecología

The INVASS model, a conceptual framework to depict the invasion of the top-predator fish *Cichla ocellaris* in a large river floodplain

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Abstract. The peacock cichlid *Cichla ocellaris* is a piscivorous fish, native to the Amazon region and introduced throughout the Americas, leading to adverse impacts on native fish assemblages. Applying the INVASS model, an approach conceived primarily to structure knowledge on terrestrial plants, we systematically describe which mechanisms are critical at each step of *C. ocellaris* invasion in the floodplain of the Upper Paraná River (UPRF). Through invasion Step 1, it was found that both intentional introductions and accidental escapes from fish farms were the key factors for the arrival of *C. ocellaris* in the UPRF. Intensive bi-parental care and the invader ability to form aggressive shoals seem to be the most favorable traits that allowed *C. ocellaris* to surmount invasion Step 2. Multiple spawns and a long reproductive season, coupled with a quick growth to a reproductive maturity largely contributed to the continuous establishment of the invader in the UPRF, overcoming thus invasion Step 3. Since peacock cichlids have been favored by cascading reservoirs upstream and experienced few threats in the UPRF, we anticipated that *C. ocellaris* is now crossing Step 4 of the invasion process, considerably increasing the risk of other systems still preserved —but also interconnected— being invaded.

[Keywords: river-floodplain system, introduction, dispersal, invasion steps, non-native fish]

Resumen. El modelo INVASS, un marco conceptual para representar la invasión del pez depredador tope *Cichla ocellaris* en una gran llanura de inundación. El cíclido tucunaré, *Cichla ocellaris* es un pez piscívoro, nativo de la región amazónica e introducido en todo el continente americano, ha provocado impactos adversos en los distintos ensambles de peces nativos. Aplicando el modelo INVASS, un enfoque concebido sobre todo para estructurar el conocimiento sobre invasiones de plantas terrestres, describimos sistemáticamente qué mecanismos son críticos en cada paso de la invasión de *C. ocellaris* en la llanura de inundación del Alto Paraná (UPRF). A través del Paso 1 de la invasión, se encontró que tanto las introducciones intencionales como los escapes accidentales de las piscifactorías fueron los factores clave para la llegada de *C. ocellaris* a la UPRF. El cuidado biparental intensivo y la capacidad del invasor de formar cardúmenes agresivos parecen ser los rasgos más favorables que permitieron a *C. ocellaris* superar el Paso 2 de la invasión. Los múltiples desoves y una larga temporada reproductiva, junto con un crecimiento rápido hasta la madurez reproductiva, contribuyeron en gran medida al establecimiento continuo del invasor en la UPRF, superando así el Paso 3 de la invasión. Dado que los cíclidos del pavo real se vieron favorecidos por los embalses en cascada aguas arriba y experimentaron pocas amenazas en la UPRF, anticipamos que *C. ocellaris* está cruzando ahora el Paso 4 del proceso de invasión, aumentando de forma considerable el riesgo de que otros sistemas aún conservados —pero también interconectados— sean invadidos.

[Palabras clave: sistema de llanura aluvial, introducción, dispersión, pasos de invasión, peces no nativos]

Editora asociada: Irina Izaguirre

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Recibido: 30 de Agosto de 2022
Aceptado: 10 de Marzo de 2023

INTRODUCTION

Several approaches have been proposed in attempt to explain and predict biological invasions (Heger and Trepl 2003; Olden et al. 2006; Heger et al. 2013). These approaches rely on a variety of methods, such as climate matching, ecological niche modelling or statistical modelling (Welk et al. 2004; Thuiller et al. 2005; Moles et al. 2008), but they generally have critical pitfalls related to the lack of pre-invasion data or noninvaded sites. Especially in cases where quantitative data on the first invasion stages are lacking, conceptual and qualitative frameworks can be useful approaches to describe single cases of invasion and thus prepare the ground for explanation and prediction (Thomaz et al. 2012; Heger et al. 2015). Despite their usefulness for organizing knowledge on the factors driving invasions, conceptual and more qualitative models have largely failed to be appreciated as a valuable method, amongst others because they often do not consider the contingency of events (Heger and Trepl 2003; Heger et al. 2013).

Primarily conceived for invasive terrestrial plants, the model of invasion steps and stages (INVASS model) assumes a relational approach between specific characteristics of the invaders and those of the invaded systems to describe biological invasions (see Heger and Trepl 2003). Unlike other models, the INVASS model provides a unified and detailed scenario on the invasion process, pointing out those attributes of both invading species and invaded systems that are critical in a given period of time (step) in which the biological invasion would surpass the filter and reach another level (stage). By describing the invasion process in chronological periods, the model allows for a detailed presentation of all relevant factors to each stage, minimizing the chance of leaving behind important issues that govern the biological invasion as a whole (Heger and Trepl 2003; Heger et al. 2013). Despite its potential to guide in-depth analyses on the invasion process, the INVASS model has not been applied up to now to depict biological invasions in tropical environments.

Non-native fishes are increasingly introduced into the Neotropics and most fish introductions have succeeded in Brazil (Welcomme 1998). In this study, the peacock cichlid *Cichla ocellaris* (Kullander and Ferreira 2006), a piscivorous fish with visual acuity, native to the Amazonian Basin and introduced into many other South American basins, and also into Central and North America and Hawaii, was selected as target species. The detrimental effects of *C. ocellaris* on indigenous assemblages were documented (Zaret and Paine 1973; Latini and Petrere Jr. 2004; Sharpe et al. 2017), but peacock cichlids continue to be introduced into Brazilian freshwater, especially hydroelectric reservoirs, to improve fish production and angling (Agostinho et al. 2007; Marques et al. 2016; Santos et al. 2016). Since early 1990 *C. ocellaris* has been recorded in the Upper Paraná River floodplain (hereafter, UPRF), a habitat- and species-rich ecosystem that has been severely threatened by habitat alteration and invasive species (Agostinho et al. 1994). The precise arrival date of *C. ocellaris* is unknown and its success in establishment and spread seems to be rather variable through the peculiar habitats and environments within this floodplain (Pelicice and Agostinho 2009; Espínola et al. 2015). The UPRF is an important remnant free of dams for spawning and nursery habitat for more than 250 native fish species. It is important to maintain the economic value of fish stocks in the region. However, the effect of sediment retention prompted by damming (increasing water transparency) has favored the invasion of species that have a visual orientation like *C. ocellaris.* Therefore, this suite of conditions is an excellent opportunity to apply a conceptual framework based on a species × ecosystem of species, such as the INVASS model, to analyze the invasion of peacock cichlids in the UPRF.

The aim of this paper is to describe how functional traits of the invader interact with environmental characteristics of the invaded ecosystem to allow the invasion of *C. ocellaris* into the UPRF. We combined our own expertise with the published literature and data collected on UPRF and *C. ocellaris* to identify the critical factors that allow *C. ocellaris* to overcome a sequence of barriers (steps) in the course of its invasion. The results of this in-depth analysis of the invasion process was provided separately for each of the invasion steps. Future scenarios for *C. ocellaris* invasion are also hypothesized based on the step-and-stage model approach, which could help to understand and control the spread of this species into the UPRF and interconnected ecosystems.

Materials and Methods

Studied system: Upper Paraná River floodplain

Draining approximately 2.8x10^6 km^2, the Paraná River is the 10th longest river (4695 km) in the world, and the second largest river in South America, after the Amazon. Within the Brazilian territory, the UPRF is the longest remaining stretch of the Paraná River free of dams (extending over ~230 km between the Porto Primavera Dam and the Itaipú Reservoir (Figure 1). With an average declivity of 0.18 m/km, the UPRF can reach up to 20 km wide on the west margin of the Paraná River, exhibiting an intricate mosaic of aquatic and terrestrial biotopes (e.g., river channels, secondary channels, permanent and temporary fluvial lakes, wetlands, alluvial plains and islands).

However, the ecological function and integrity of the UPRF have been increasingly threatened by human activities, with flow alteration and establishment of invasive species as the main threats (Agostinho et al. 2004). Apart from the adverse impacts on large migratory fish, by blocking migration routes and reducing spawning and nursery grounds, flood control by dams also seems to favor the spreading and population growth of some invasive fish species currently recorded in the UPRF (Agostinho et al. 2005; Britton and Orsi 2012). By now, *Plagioscion squamosissimus*, *Astronotus crassipinnis*, *Cichla ocellaris* and *Cichla piquiti*, all native to the Amazon River Basin, are the leading invasive fishes established in the UPRF. Among those introduced species, the peacock cichlid *C. ocellaris* seems to show the highest population growth (Agostinho et al. 2004; Espínola et al. 2007; 2010; 2015). Regarding morphological analysis, *C. ocellaris* was split into five different species, including *C. kelberi*, *C. monoculus*, *C. nigromaculata*, *C. pleiozona* and *C. ocellaris* (Kullander and Ferreira 2006). However, further molecular analysis suggested that these five species

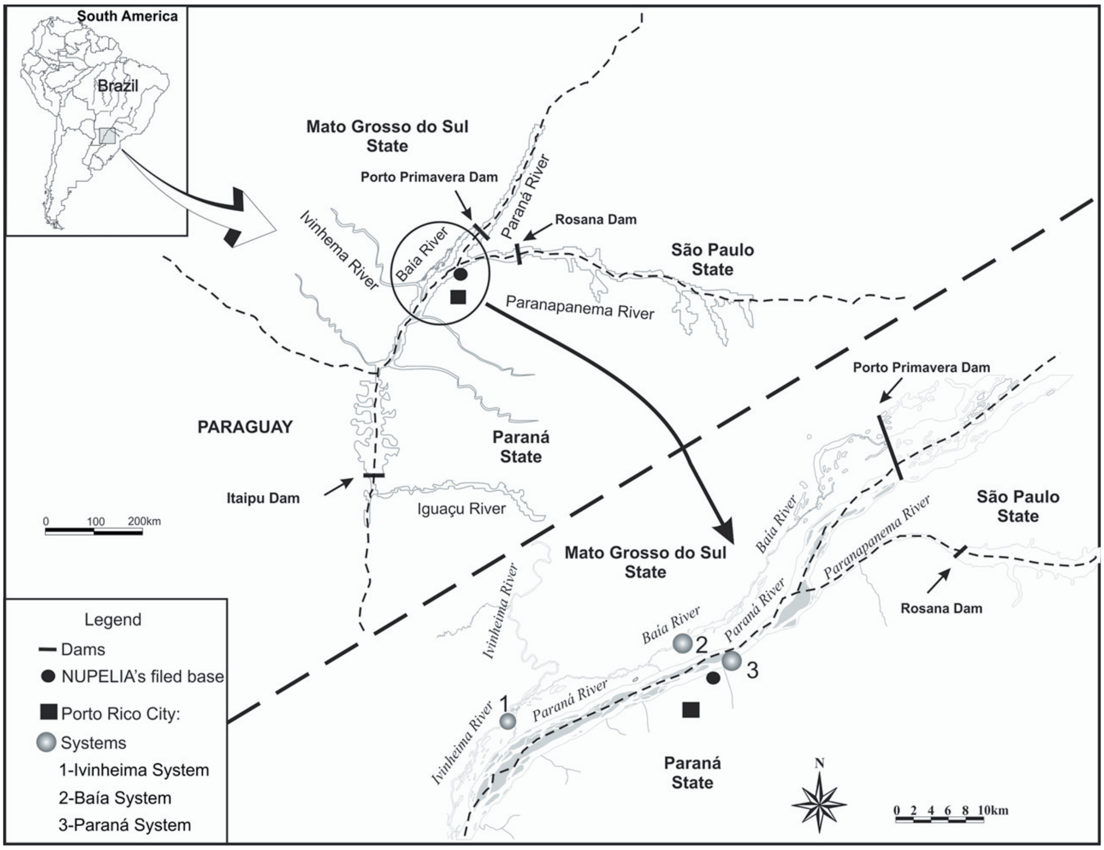

Figure 1. Geographic location of the Upper Paranaì River floodplain, between Porto Primavera Dam and Itaipú Reservoir, and the position of NUPELIA's field base, near Porto Rico city. Modified from Espínola et al. (2015).

Figura 1. Ubicación geográfica de la llanura de inundación del Alto Paraná, entre la presa de Porto Primavera y el embalse de Itaipú y la ubicación de la base de campo de NUPELIA, cerca de la ciudad de Porto Rico. Modificado de Espínola et al. (2015).

of peacock cichlids are actually a single one (i.e., *C. ocellaris*) with extensive genetic introgression among geographic variants showing varying degrees of morphological differentiation (Willis et al. 2012). Here, we follow the recommendation of Willis et al. (2012) and refer to the five species from the Tocantins-Araguaia basin as *C. ocellaris*. Although the impacts of invasive fish species on the native assemblages of UPRF are still not well known, many correlate studies have highlighted biodiversity loss and changes in the structure of the population of native species as effects of introduction and establishment of *C. kelberi* (Pelicice and Agostinho 2009; Pelicice et al. 2015; Sharpe et al. 2017).

Fish surveys and data analysis

Biological data were provided by the Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (NUPELIA, in Portuguese) at the Universidade Estadual de Maringá (UEM, in Portuguese), Brazil. The NUPELIA database includes data collected in floodplain lakes and rivers of the Ivinheima, Baía, and Paraná system (Figure 1) since 1986 until the present. However, only data belonging to the 1992-2007 period were considered in this work due to the fact that during that time, the same methodology and sample effort were applied in similar environments.

The 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 to 8 cm opposite knots). Nets were installed in each study site each three months during the whole studied period —15 years—, and were revised at 08:00, 16:00 and 22:00 h. The abundance of peacock bass recorded in each sample was indexed by capture per unit effort (CPUE; number of individuals per 1000 m^2 of gill nets in 24 h).

Generalized additive models (GAM) were fitted to evaluate the relationships of *C. ocellaris* CPUE with the sampling year (i.e., time) of the NUPELIA 1992-2007 data set. GAM are an extension of generalized linear models that, unlike more conventional regression methods, do not assume a particular functional relationship between the response variable and the predictors. The complexity of the GAM was chosen by the stepwise selection procedure using the AIC. GAM were applied for combined data of the three main riverine systems in the UPRF (i.e., Paraná, Baía, and Ivinheima rivers) and also for each river separately. All model-fitting procedures were performed with the CANOCO 4.5 software (Lepš and Šmilauer 2003).

Steps and stages invasion model (INVASS)

The model of invasion steps and stages (INVASS model) (Heger 2001, 2004), resembles other recent approaches used to explain the mechanisms of biological invasions (e.g., Lockwood et al. 2007; Catford et al. 2009; Davis 2009), but was designed to lead in-depth analyses of invasion processes through time, assuming that some functional traits of an invader will meet a series of environmental characteristics within each phase of the invasion process. Based on the suggested chronological dissection of an idealized course of an invasion, knowledge about different aspects of invasion cases (characteristics of the invading species, site or community characteristic and mode of transportation) can be easily synthesized. It was primarily conceived in the context of plant invasions, but since presenting nonstatic properties, it can be adjusted and applied to analyze invasion processes by other organisms (e.g., mammals) (Steil and Heger 2008). In this sense, the model can be used as a basis to develop a full and integrated scenario on the spread of any organism, especially when quantitative data on species introduction and its first invasion stages are lacking.

The INVASS model translates the invasion process into a staircase diagram, where four steps and stages are used as a basis for a chronological differentiation of an idealized invasion process (see Heger 2001). To reach subsequent stages (i.e., move upward in the 'staircase'), an invasive species must overcome several steps (i.e., biotic and abiotic constraints). The 'staircase' can be climbed up or down several times, depending on the level of suitability between the functional attributes of the invader and the environmental characteristics of the invaded ecosystem. Many individuals and populations may fail at the lower steps and never reach the upper ones, and shifts in the species-environment interaction may influence the status of a species within the invasion process.

The conceptual steps of the INVASS model differ in perspective. The first and second steps deal with single individuals, asking about the constraints during a biological invasion at the individual level. The third step stresses the founder population, which is confronted with problems of a different type, at the population level. The fourth step focuses on other types of problems, which are related to the further spreading and establishment of invading species in new habitats or ecosystems. For each of the steps, the problems that an invading organism might encounter are named explicitly, and possible solutions to them (species characteristics and favorable environmental conditions) are given (Heger and Trepl 2003).

Here, the INVASS model was applied for the first time to describe the invasion process of a freshwater fish, the peacock cichlid *Cichla ocellaris* (Kullander and Ferreira 2006), which was introduced into a habitat- and species-rich Neotropical ecosystem. The four tables provided in the original INVASS model list the critical problems a nonnative plant species might undergo during its invasion into a new area. Most of these problems are not restricted to plants, but may happen, as well, during a fish invasion process (e.g., occurrence of predators). There were few obstacles to invasion named in the original INVASS tables that were highly specific for plants (e.g., missing the necessary trigger for germination). Likewise, most of the species characteristics and favorable environmental conditions identified as 'solutions' for invading plant species can be easily transferred to fish invasions. Those potentially important difficulties a freshwater fish species might undergo during its invasion into a new environment, as well as species features that might help the invading fish to overcome these obstacles are provided in Table 1. Despite the possibility of some factors being relevant for two or more steps (e.g., competitive ability), they were listed only for the single and most critical step.

On the basis of Table 1, an in-depth analysis on the process of *Cichla ocellaris* invading the UPRF was conducted. Aiming at finding out

Table 1. Hypothetical threats to and favorable traits of freshwater invasive fish that involved with the probability of a successful invasion, related to the four steps proposed in the INVASS model (adapted from Heger [2004] for invasive plants).

Tabla 1. Amenazas hipotéticas y rasgos favorables de los peces invasores de agua dulce que intervienen con la probabilidad de una invasión exitosa, relacionados con los cuatro pasos propuestos en el modelo INVASS (adaptado de Heger [2004] para las plantas invasoras).

Invasion steps	Potential problems for invasive fish	Favorable traits of invasive fish
Step 1: Immigration	At this stage, success largely depends on anthropogenic activities (i.e., non-ecological factors are more important than ecological ones)	
Step 2: Early development, growth to maturity and independent reproduction	- Adverse abiotic conditions - Occurrence of predators or parasites - Occurrence of competitors - Shortage of resources - Lack of sexual partners (due to low density, or because only one sex is present in the new area)	- Broad ecological tolerance of environmental conditions - Defense against generalist predators or parasites - Competitive strength - Ecological requirements not partitioned by other species - Large ecological amplitude concerning resource use - Ability to change habitat conditions - Ability to generate a large founder population - Presence of functional traits enhancing reproductive success - Long life span
Step 3: Population growth	- Long-term probation to environmental stresses (biotic and abiotic) - Small size of initial population leading to demographic, genetic, and environmental stochasticity	- Potential for evolutionary adaptation - Ability to change habitat conditions - High genetic diversity of the populations - Presence of functional traits enhancing reproductive success - Short generation time - High intrinsic rates of somatic growth - Ability to form a large founder population - Tolerance of inbreeding - Hybridization and mating with formerly distant populations
Step 4: Colonisation of new localities	- Not enough descendants are produced - No effective transportation is possible - Lack of further suitable habitats	- Ability to produce many offspring - Ability to perform active migrations - Large ecological amplitude of the individuals - High genetic and/or phenotypic plasticity of the individuals - Genetic diversity of the metapopulation within the new area

which factors have been decisive throughout the four invasion steps and thus to be used as a proxy to anticipate the potential of spreading and establishment of this species into new environments, the literature on both native and introduced populations of *C. ocellaris* and also to its congeners were extensively searched. For the purpose of this study, only species characteristics were detailed and any further favorable environmental conditions (e.g., repeated secondary introductions or new suitable habitats resultant of environmental changes) were provided in the text whatever necessary. In this sense, published data on physical, chemical and biological characteristics of the UPRF, especially those from the various studies performed by NUPELIA that has spanned ca. 20 years (from providing information on fish assemblages, environmental variables and other aquatic organisms), were analyzed qualitatively to find out which obstacles the UPRF poses to *C. ocellaris* and which species characteristics enabled it to invade that ecosystem. A systematic search was performed on November 2022 with the Google Scholar database (scholar.google.com.br) to find published articles dealing with the occurrence of peacock cichlids in the UPRF. The search terms were as follows: peacock bass OR tucunaré OR pavón OR Cichla AND Upper AND Paraná AND River OR floodplain OR wetland OR basin, and the time period encompassed all years prior to this research. Further literature on the overall requirements and characteristics of *C. ocellaris* and congeneric species was also examined. Information gathered from literature was thus combined with the expertise of the authors (namely, L. A. Espínola, H. F. Júlio Jr. and L. N. Santos) on the invader and thus the studied system, and the INVASS model was used to structure the available evidence on the invasion of *C. ocellaris* in the UPRF, and to develop hypothetical predictions about its future expansion.

Results

Steps and stages of peacock cichlid invasion in the UPRF

The results of the in-depth analysis of available literature and data based on the INVASS model are summarized in Table 2, indicating those threats and favorable species characteristics which have been identified as potentially decisive for the invasion of *C. ocellaris* into the UPRF. In the following, the detailed results of our analysis of the available literature and the data for each invasion step were provided separately.

Step 1: Arrival of *C. ocellaris*. Despite the poor knowledge on the local species and ecosystem functioning, the introduction of non-indigenous fishes into Brazilian reservoirs was a common practice of hydroelectric companies during the 1980s, as an attempt to mitigate the adverse impacts of river impoundment on native fish assemblages (Agostinho et al. 1994). As a result, *C. ocellaris*, together with other non-native piscivorous species, was extensively translocated from the Amazonian basin (i.e., its native distribution range) into many other Brazilian hydrographic basins (see Agostinho et al. 2007). *C. ocellaris* may have, thus, spread out from the reservoirs in which it had successfully established, and then invaded the UPRF, which lies both downstream and upstream to such impoundments (Espínola et al. 2010, 2015). A similar pattern of introduction was reported by a study using molecular markers for the peacock cichlid *C. kelberi* in the Paraíba do Sul river, South-eastern Brazil (Marques et al. 2016). Since the practice of introducing nonnative fish by hydroelectric companies has been largely abandoned after the late 1990s, *C. ocellaris* might have also arrived in the UPRF through more recent accidental introductions and escapes. Individuals of greater size are likely to have invaded this ecosystem, after escaping from adjacent ponds and fish farms that are periodically connected to the UPRF during extreme flood pulse episodes (Orsi and Agostinho 1999).

Although the precise way in which *C. ocellaris* arrived in UPRF is unknown due to the lack of official records, both pathways described above appeared to have contributed together to the arrival of this species. *C. ocellaris* was first recorded at the Itaipú Reservoir in 1985, probably due to intentional stocking programs that were commonly undertaken by hydroelectric companies at that time (Agostinho et al. 1994). Since the chance for the peacock cichlid to spread out from invaded reservoirs to adjacent systems is high (Espínola et al. 2010; Marques et al. 2016), *C. ocellaris* took only seven years to reach the UPRF (i.e., 160 km upstream), but until 2001, this species remained at low densities (<5 individuals per sample) and restricted to floodplain lakes and secondary channels (Espínola et al. 2015). After that, *C. ocellaris* experienced a sharp population growth (Figure 2), broadening

Table 2. Hypothetical threats to the invasion of *Cichla ocellaris* into the Upper Paraná River floodplain (UPRF) and favorable species characteristics helping to avoid or overcome them.

Tabla 2. Amenazas hipotéticas a la invasión de *Cichla ocellaris* en la planicie de inundación del Alto Paraná (UPRF) y características favorables de la especie que ayudan a evitarlas o superarlas.

Invasion steps	Potential threats for *C. ocellaris* invasion into the UPRF	Favourable characteristics of *C. ocellaris*
Step 1: Immigration	The following anthropogenic activities probably have facilitated *C. ocellaris* immigration: 1) Intentional introduction (stocking programmes, sport fish associations) 2) Unintended introduction (accidental escapes)	
Step 2: Early development, growth to maturity and independent reproduction	- Adverse abiotic conditions[1] - Occurrence of predators or parasites - Occurrence of competitors - Shortage of resources - Lack of sexual partners	- Parental care - Parasite species loss through the invasion process[2] - Aggregation in aggressive shoals - Generalized top predator - Sexual dimorphism (increases the chance of the introduction of both sexes)
Step 3: Population growth	- Long-term probation to environmental stresses - Small size of initial population leading to environmentally-related demographic stochasticity	- Potential for evolutionary adaptation[3] - Multiple spawners - Short generation time
Step 4: Colonisation of new localities	- Not enough descendants are produced - No effective transportation is possible - Lack of further suitable habitats	- Ability to produce many offspring - Large oocyte diameter - Ability to migrate[4] - Tolerance to temperatures lower than in native range

[1] Adverse abiotic conditions may have prevented *C. ocellaris* establishment before 2000, see text. [2] There is no general agreement in literature, however, on whether enemy release has an influence on invasion success of *C. ocellaris*. [3] Data on the potential for evolutionary adaptation is missing. [4] Migratory abilities are probably restricted, see text

its distribution to virtually all habitats in the UPRF, probably due to synergetic effects of the founder individuals proceeding from the Itaipú Reservoir and new arriving individuals from accidental escapes and furtive introductions by anglers (Espínola 2009; Marques et al. 2016). Because of its great value as a game fish, there have been various initiatives carried out by sport fish associations or even by isolate anglers to buy and release young-of-the-year *C. ocellaris* into the UPRF and interconnected systems.

Step 2: Early development, growth to maturity and independent reproduction. *Cichla ocellaris*, like its close congeners, exhibits many physiological and behavioral traits that contribute to high survival and growth rates of the young in the UPRF. The survival of eggs and fry is enhanced by the habits of both parents of building nests and guarding eggs and brood. *C. ocellaris* always spawns on hard substrates (i.e., logs or rocks), and the eggs are constantly watched and defended by both parents (Winemiller 2001). As soon as the larvae hatch, they are moved by their parents into a nest (i.e., a hollow excavated at the bottom of the lake), which is often located close to other mock nests (i.e., similar hollows on the periphery, to mislead predators). The predators are a threat to juveniles only if their parents are unable to defend them (e.g., when they are removed by angling), and juvenile peacock bass have been recorded in the gut of adult *C. ocellaris* and other native piscivorous species in the UPRF systems (Pereira et al. 2014, 2017). Although no specific study has ever been conducted on this theme, there are evidences that few or no brood survives, when both parents are removed from nests, due to increased predation by other fish species or even by large cannibal *C. ocellaris* (Santos et al. 2001; Gomiero and Braga 2004; Santos et al. 2009, 2012, 2013, 2014).

The fry are kept under continuous vigilance until attain 60-70 mm of standard length (SL) and become totally independent, which can take more than three months (Zaret 1980). Juvenile *Cichla ocellaris* tend to group into

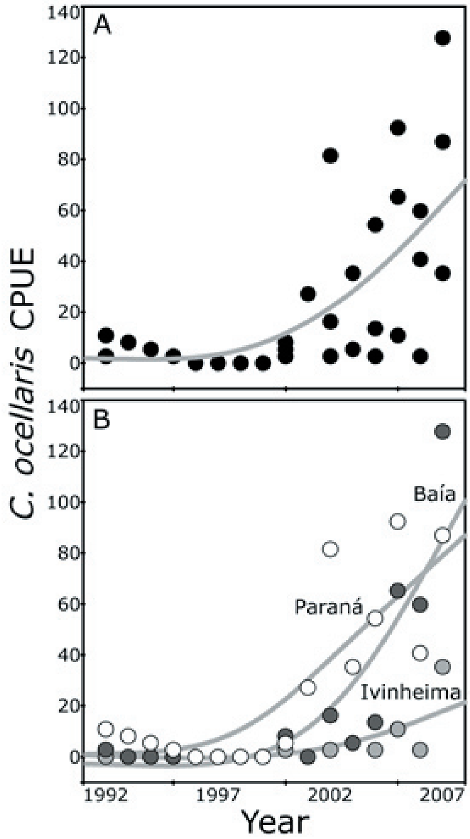

Figure 2. Relationship of *Cichla ocellaris* CPUE (number of fish per 1000 m^2 of gillnet per 24 h) with year for the three main rivers in the UPRF (i.e., Paranaì, Baiìa and Ivinheima rivers; A=combined data; B=for each river separately). Peacock cichlid abundances were retrieved from NUPELIA's 1992-2007 data set. Data before 1992 were omitted, since *C. ocellaris* was first recorded in this year in the UPRF. B) ○=Río Paraná; ●=Río Baía; ◍=Río Ivinheima. Lines represent predictions from generalized additive models selected by the Akaike information criterion (AIC). Modified from Espiìnola et al. (2015).

Figura 2. Relación de la CPUE de *Cichla ocellaris* (número de peces por 1000 m^2 de red de enmalle por 24 h) con los años para los tres principales ríos de la UPRF (es decir, los ríos Paraná, Baía e Ivinheima; A=datos combinados; B=para cada río por separado). Las abundancias de cíclidos del tucunaré se obtuvieron del conjunto de datos de NUPELIA de 1992 a 2007. Los datos anteriores a 1992 fueron omitidos, ya que *C. ocellaris* fue registrado por primera vez en este año en la UPRF. B) ○=Río Paraná; ●=Río Baía; ◍=Río Ivinheima. Las líneas representan las predicciones de los modelos aditivos generalizados seleccionados por el criterio de información de Akaike (AIC). Modificado de Espínola et al. (2015).

abundant shoals throughout their ontogenetic growth, which reduces the influence of competitors as well as predators (Santos et al. 2008, 2019).

During the first days of life, larvae rely on the vitelline sac to survive, but, after a week, the juveniles become largely zooplanktivorous-insectivorous until attaining 120-130 mm SL, when they start to include small fishes in the diet (Zaret 1980; Winemiller 2001). Pre-adults and adult-of-the-year are often found in copious and very aggressive shoals, preying largely on every fish small enough to be swallowed entirely by their protractile but toothless mouths. Considering the high abundance and diversity of aquatic invertebrates (i.e., zooplankton and insects) and small-sized fish species in the UPRF (Agostinho et al. 2005), the lack of resources was not a severe menace for *C. ocellaris* during its somatic growth in the invaded ecosystem.

The length by which *C. ocellaris* reaches its first maturation is quite variable, depending on the abiotic conditions of the invaded ecosystems. In the UPRF, *C. ocellaris* is unable to spawn until it attains 165 mm SL (Suzuki and Agostinho 2001), which approximately corresponds to one year of age and 250-350 g of total weight (TW). There are evidences that *C. ocellaris* can surpass 400 mm total length (TL) and 1000 g total weight (TW) in its second year of life (Suzuki and Agostinho 2001). Although the lack of sexual partners might be an obstacle for non-native fish during the early establishment phase, it does not seem to be the case for *C. ocellaris* in the UPRF, since there is a trend for all peacock cichlid species to group into abundant shoals (Santos et al. 2019; Winemiller et al. 2021).

In general, all *Cichla* species find the ideal conditions in nonturbulent, warm and transparent waters for feeding and reproduction, becoming frequently the dominant diurnal piscivorous of these habitats (Winemiller 2001). AIC and GAM selected a non-linear increase in *C. ocellaris* CPUE with time since its first record in the UPRF (AIC=23916.8; nonlinear F1, 28=10.5, P<0.01), suggesting an exponential population growth (Figure 2a). Historically, the typical environmental conditions of the UPRF appear to have hindered the establishment of *C. ocellaris* (Espínola et al. 2010), but, since 2000 (Figure 2a), this floodplain has experienced a decrease in sediment load and an increase in water transparency, coinciding with the beginning of Porto Primavera Dam operation, upstream (Agostinho et al. 2004; Thomaz 2022), which have probably provided better conditions for *C. ocellaris* to search and find food (Espínola et al. 2010; 2015). Other environmental changes in the UPRF, related to upstream reservoirs and especially the Porto Primavera Dam, such as decreases in flood duration and intensity due to dam operation routines (Thomaz et al. 2004; Thomas 2022), are likely to have a further synergic effect on the invasion process of *C. ocellaris*. More stable water levels favor macrophyte growth, which has probably increased both feeding and reproductive success of *C. ocellaris* in the UPRF (Santos et al. 2008; Kovalenko et al. 2010; Franco et al. 2018; 2022a). AIC and GAM also selected a nonlinear increase of *C. ocellaris* CPUE with time for the three main rivers in the UPRF, but the trends of population growth rates were not the same between the systems (Figure 2B). *Cichla ocellaris* undergone a sharp population growth in Paraná (AIC=6891.4; nonlinear F1, 13=5.4, P=0.04) and Baía (AIC=5159.1; nonlinear F1, 13= 21.4, P<0.001) rivers, the most transparent and regulated systems in the UPRF (Figure 2B). The lower population growth rate (AIC=712.7; nonlinear F1, 13=7.9, P=0.01) was recorded for C. ocellaris on the Ivinheima River (Figure 2B), one of the most preserved and least regulated systems in the UPRF, supporting the hypothesis that flood control and hydrological changes caused by dams are key factors for the invasion of *C. ocellaris* to be successful in the UPRF (Espínola et al. 2009, 2015; Thomas 2022).

Low water temperature is another environmental characteristic that might have constrained the invasion of *Cichla ocellaris* in the UPRF. Before the 1980s, there was a general belief that *Cichla* spp. would never invade Southern Brazilian ecosystems, because of the inability of peacock cichlids in surviving to water temperatures <15 °C (Swingle 1966). Until the early 1990s, water temperatures <15 °C were recorded in the UPRF during winter (Thomaz et al. 1997), but more recent studies have reported a current temperature range of 16-32 °C for this ecosystem (Rocha and Thomaz 2004; Thomaz et al. 2004). Therefore, no direct lethal effect of low water temperatures is expected to have occurred after the year 2000 on *C. ocellaris* in the UPRF. Nevertheless, *C. ocellaris* is most likely to be found in reservoirs of the Paraná River Basin (Espínola et al. 2010) and Southeastern Brazil (Franco et al. 2018) with temperatures between 21 and 30 °C. Although the temperature range found currently in the UPRF is very close to the conditions experienced by native (Winemiller 2001) or other introduced *Cichla* populations (Shafland 1995; Santos et al. 2008; Souza et al. 2008; Franco et al. 2018), we cannot evaluate whether temperatures lower than 21°C during the winter season would adversely affect reproductive success and somatic growth of *C. ocellaris* in the UPRF. Nevertheless, in Southeastern Brazil, this species appears to be more resistant to seasonal temperature differences than its close congener *Cichla piquiti* (Gomiero et al. 2009).

When juvenile (50-100 mm TL), *C. ocellaris* kept in aquaria seems to be prone to infestation by ectoparasite protozoans, especially *Ichthyophthirius multifiliis* (Guest 1983; Picón-Camacho et al. 2012), but there is no study on host vulnerability in natural systems. The eyes of large *C. ocellaris* (>200 mm TL) are often infected and injured by larvae of *Diplostomum* (*Austrodiplostomum*) *compactum* (Machado et al. 2005), which may decrease prey capture success or increase host susceptibility to predation. In fact, the fauna of metazoan parasites recorded for native and introduced populations of *C. ocellaris* is much more diverse, comprising at least 11 other species of ecto- and endoparasites belonging to the Monogenea, Digenea, Cestoda, and Nematoda groups (Yamada and Takemoto 2013). Despite the apparent mediating effects of environmental conditions on fish infection by parasites and the probable increased vulnerability of *C. ocellaris* to parasite infection during the low water temperatures of winter in southern Brazilian regions (Santos et al. 2012; Yamada and Takemoto 2013), no study has demonstrated whether parasitic infection could affect survival rates of *C. ocellaris*, neither for introduced nor native populations. Although the role of parasites as threats to the invasion success of *C. ocellaris* in the UPRF remains widely unclear, Yamada et al. (2011) suggest that the trend of parasite species loss through the invasion process may have contributed to the establishment of non-native *Cichla* populations in Brazilian reservoirs (i.e., the enemy release hypothesis). Such hypothesis was not supported for endoparasites of the congener *C. piquiti*, but Lacerda et al. (2013) found that increased infection of the Digenea *Austrodiplostomum* sp. over native piscivores and the lack of adverse physiological effects of the Cestoda *Sciadocephalus megalodiscus* only for non-native *C. piquiti* populations (i.e., escape from the parasites' effects) may contribute to alleviate agonistic interactions for this invader. Although further studies examining effects on host physiology and/or fitness in the native and introduced ranges are needed for peacock basses, it was thus assumed that parasite species may overall affect the fitness of *C. ocellaris* only at the organism scale, with few consequences at the population level. Therefore, except for overfishing, especially that performed on parents during the reproductive season, large (>200 mm TL) peacock cichlids are expected to not be severely threatened by predators in the invaded ecosystem (Gomiero et al. 2009; Santos et al. 2018).

Step 3: Population growth. *Cichla ocellaris* is a multiple spawning species with a long (i.e., over 6 months) reproductive season. A continuous (i.e., throughout the year) spawning has been reported for non-native *C. ocellaris* populations in many Brazilian reservoirs, with peaks of reproductive activity recorded during high water levels (Santos et al. 2008; Souza et al. 2008; Gomiero et al. 2009). Batch fecundity (i.e., the number of oocytes laid per spawning event) is not so high in *C. ocellaris*, with average values ranging from 5000 to 8000 oocytes (Souza et al. 2008; Gomiero et al. 2009; Normando et al. 2009), but since each individual is able to mature quickly (~1-year age) and to spawn several times per reproductive season, the total number of eggs produced in a population is quite high. *Cichla ocellaris* also has an apparent plasticity to change its feeding and reproductive strategies with the environmental conditions of invaded ecosystems. For example, *C. ocellaris* preyed unselectively on small characids, cichlids and catfishes during its early colonization phase in Corumbá Reservoir (Middle-West Brazil) but became largely cannibal just two years after the reservoir filling (Fugi et al. 2008). Preferential cannibal feeding was also recorded for most non-native peacock cichlid populations introduced into Southeastern Brazilian reservoirs (Durães et al. 2000; Santos et al. 2001; Gomiero and Braga 2004; Santos et al. 2011). Variations in fecundity (e.g., 487 to 13900 oocytes/batch) and the size of vitellogenic oocyte (e.g., 428.4 to 2485 m) also suggest flexible reproductive strategies from introduced *C. ocellaris* populations (Souza et al. 2008; Gomiero et al. 2009; Normando et al. 2009), and except for its probable vulnerability to low water temperatures, *C. ocellaris* generally has a broad tolerance to environmental conditions (Winemiller 2001; Kullander and Ferreira 2006; Espínola et al. 2010, 2015; Franco et al. 2022b).

This set of advantageous physiological traits has probably allowed, whenever environmental conditions were favorable, invasive *C. ocellaris* populations to grow rapidly to a critical size in which problems inherent to demographic and environmental stochasticity are avoided or widely minimized. Even the low genetic variability found for virtually all nonnative *C. ocellaris* populations in Brazil is apparently of minor importance to prevent its establishment and growth in the UPRF and other invaded systems, probably due to the increased occurrence of illegal, and untracked introductions of peacock cichlids and the potential of *C. ocellaris* to hybridize with other species of the genus *Cichla* (Oliveira et al. 2006; Marques et al. 2016; Santos et al. 2016a,b). The sharp demographic growth of this species in the UPRF following the change in the environmental conditions in 2000 (Figure 2) supports these assumptions.

Step 4: Colonisation of new localities. We are unaware of any study addressing the movement patterns of natural or introduced *Cichla ocellaris* populations. However, in Venezuelan rivers, a 52-month tagging-recapture program on its congeners *Cichla temensis*, *Cichla orinocensis* and *Cichla intermedia* revealed that most of the recaptures (73%) occurred within 1 km of the tagging location, except for a few large *C. temensis* that moved up to 21 km (Hoeinghaus et al. 2003). If similar results can be extended to *C. ocellaris*, a restricted movement within the UPRF. However, the potential of *C. ocellaris* for colonizing new localities seems to be higher than this expectation. For instance, today it is increasingly accepted that *C. ocellaris* invaded the UPRF due to spreading individuals from Itaipú Reservoir (Agostinho et al. 1994). Such hypothesis is somewhat corroborated by the genetic similarities among *C. ocellaris* populations in the UPRF and Itaipú Reservoir (Oliveira et al. 2006). However, if during the invasion process no lag phase is considered, *C. ocellaris* must have swum more than 20 km per year to spread from Itaipú Reservoir in 1985 (i.e., when the invader was first recorded) and reach the UPRF in 1992. Therefore, unintended introductions or accidental escapes from ponds and fish farms must be considered to not only explain the arrival of *C. ocellaris* in the UPRF, but also the potential of this peacock cichlid to colonize new adjacent or interconnected systems.

A potential hindrance for this invader could be the lack of suitable sites within its migratory range. *C. ocellaris* prefers nonturbulent, transparent and warm (>23 °C) waters (Espínola et al. 2010). Running waters together with low transparencies and temperatures should thus be real obstacles to the expansion of *C. ocellaris*, but within the study area these factors still seem to be tolerable for this species (Franco et al. 2018). Despite the lack of specific studies on the topic, a hypothesis which could not only explain the spread of *C. ocellaris* within the UPRF but also account for the recent establishment of this invader in southern Brazilian reservoirs, is the potential of invasive peacock cichlid populations for evolutionary adaptation (e.g., the apparent increasing tolerance to low temperatures). The lack of native predators and competitors to exert biotic resistance to alien piscivorous fish might have also complementary and positive effects to *C. ocellaris* invasion (see Santos et al. 2009, 2012, 2013). We cannot assert whether flood regulation by Porto Primavera Dam after 2000, recent climatic changes, the adaptability to environmental conditions, successive escapes and illegal introductions, acting individually or together, were the main reasons, but the fact is that *C. ocellaris* extended towards the southern limit of its distribution.

Discussion

According to Heger and Trepl (2003), the step and stage model offers a holistic view of the invasion process of chronologically defined stages of an idealized invasion process. In this sense, the model allows visualizing the differences between the different stages that a potentially invasive non-native species faces, having the possibility to make predictions considering the contingency of events at each stage of the invasion process. However, since the model assumes that the characteristics of the species must adapt at each step, depending on the conditions of the invading environment, detailed knowledge of the attributes of the non-native species and the environment is required, which in some cases is difficult to achieve.

The aim of this study was, through combining the information available in the scientific literature with authors' expertise, to summarize the critical factors allowing *C. ocellaris* to overcome a sequence of barriers (steps) in the course of its invasion into the UPRF. Invasive plants and freshwater fish obviously differ in many biological and ecological aspects, but by applying the INVASS model, a conceptual model originally conceived for plant invasions, we nevertheless were able to consider systematically the various threats that could hinder invasion into the floodplain, and species traits that enabled this invasive freshwater fish to overcome these problems. Our study thus indicates that the INVASS model can be helpful to illustrate the invasion process of several other groups of invasive organisms, beyond plants or freshwater fish.

By discriminating the invasion process in time, the INVASS model allowed profiling which mechanisms are critical at each step of the invasion of *C. ocellaris* in the UPRF (Figure 3). Through invasion Step 1, it is clear that intentional introductions together with furtive illegal introductions (by sport fish associations or even by isolate anglers) and accidental escapes from fish farms were the key factors causing the arrival of *C. ocellaris* in the UPRF. Intensive biparental care and the ability to form aggressive shoals seem to be the traits that allowed *C. ocellaris* to surmount invasion Step 2 in the UPRF. Multiple spawns and a long reproductive season, coupled with a quick growth to a reproductive maturity largely contributed to the continuous establishment of the invader in the UPRF, thus overcoming invasion Step 3. The question of which factors are the most important in allowing the species to colonize new localities is less clear. Nevertheless, the natural hydrological connection between different territories with varied policies in relation to peacock cichlids control (Espínola et al. 2022), increased propagule pressure (repeated introductions) (Lodge 1993; Colautti and et al. 2006) by recreational fishing organizations (Pelicice and Agostinho 2009), the elimination of natural geographic barriers (Siete Quedas waterfalls), as well as the construction of artificial canals (Piracema canal in Itaipu), have favored exchange and dispersal of this invader. In this sense, just as species have moved up within a river basin, it is also likely that they can move down, either actively or not (e.g., passively through natural river flow or reservoir turbines), thus facilitating the invasion process of several fish species (Júlio Jr et al. 2009). The invasion Step 4 is probably overcoming due to the interplay of many factors such as the ability of this species to produce many offspring, its tolerance of temperatures lower than in its native range, and changes in the environmental conditions. In this sense, the establishment of a nonnative species in a new area is fundamental for a successful invasion

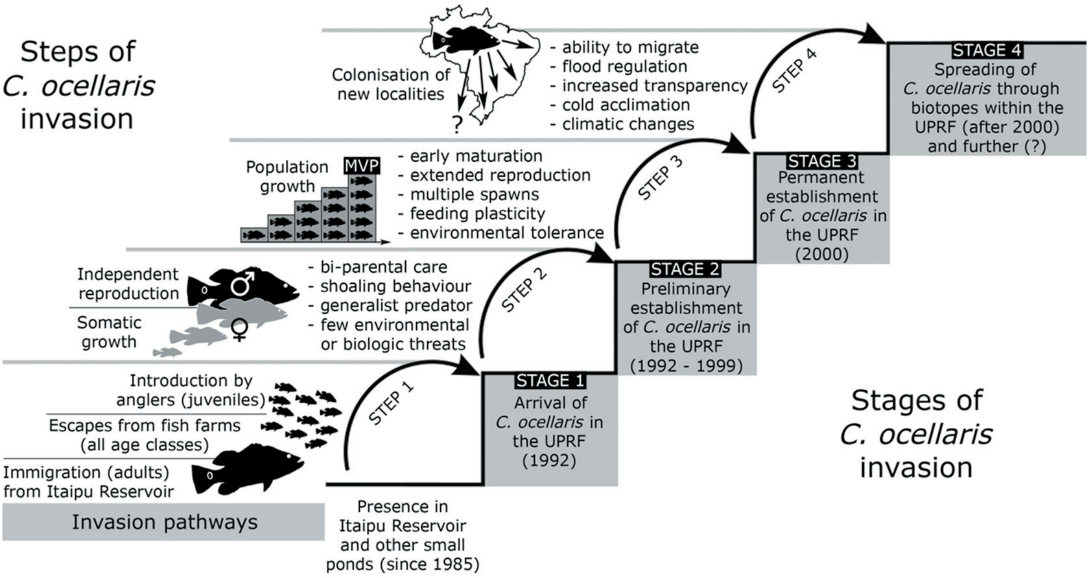

Figure 3. Integrated scenario on the invasion process of *Cichla ocellaris* into the Upper Paranà River floodplain (UPRF), illustrating the invasion pathways and the critical factors (functional traits of the peacock cichlid and environmental characteristics of the invaded ecosystem) that allowed the invader to surmount the four steps and stages proposed in the INVASS model. MVP: minimum viable population.

Figura 3. Escenario integrado del proceso de invasión de *Cichla ocellaris* en la planicie de inundación del Alto Paraná (UPRF), ilustrando las vías de invasión y los factores críticos (rasgos funcionales del cíclido tucunaré y características ambientales del ecosistema invadido) que permitieron al invasor superar los cuatro pasos y etapas propuestos en el modelo INVASS. MVP: población mínima viable.

process. This process basically depends on the biological attributes of the non-native species as well as the ecological characteristics (biota and environment) of the invaded environment (Colautti et al. 2006). The reproductive strategy (repeated spawns and parental care) of the peacock cichlids has contributed to turn them into aggressive invaders, becoming dominant in several environments, particularly reservoirs and semi-lotic systems, where they were successfully established (Winemiller et al. 2021; Franco et al. 2022a). The alteration of hydroclimatic patterns due to the global climate crisis is another problem, directly increasing anthropic pressure on the biological cycle, survival and distribution of fish (Comte and Olden 2017). In this sense, the potential establishment of *C. ocellaris* in Argentine territory could be facilitated by global warming, since the predicted increased temperatures (Barros et al. 2005) would cause a displacement of thermal barriers toward the south of the La Plata Basin (Barros et al. 2005; Camilloni et al. 2013), creating favorable conditions for the establishment of this species. Furthermore, a recent study (Franco et al. 2022b) also indicates that *C. ocellaris* is able to adapt to environmental conditions different from its native region, expanding its nonnative distribution across the Argentinian territory.

The INVASS model was especially helpful for structuring our analysis because it allowed to explicitly consider the interaction of environmental conditions and species traits. However, even after this an in-depth analysis of literature and data indicated that the precise environmental factors that led to the sharp demographic growth of *C. ocellaris* (Figure 2) still remain unclear. For example, decreases in sediment load have been argued as the primary cause for the spread and establishment of *C. ocellaris* in the UPRF (Thomas 2022) and the reservoirs of the Upper Paraná River Basin (Espínola et al. 2010, 2015), since prey consumption rates by visual and diurnal piscivores, such as peacock cichlids, are expected to increase with water transparency. However, changes in sediment load, although important, cannot be accounted for as the single mechanism that triggered the expansion of the *C. ocellaris* population throughout the UPRF. Other environmental changes in the UPRF, related to upstream reservoirs and especially the Porto Primavera Dam, such as decreases in flood duration and intensity due to dam operation routines (Thomaz et al. 2004; Thomas 2022), which also adversely affected the native predators and competitors (i.e., decreased the biotic resistance), should be considered as additional causes of the population expansion.

By applying the INVASS conceptual model, we suggest that *C. ocellaris* is now crossing Step 4 of the invasion process in the UPRF (see Figure 3). We have shown that *C. ocellaris* has many functional traits that help it avoid and overcome most of the environmental barriers it faces in the UPRF. Current obstacles for this species are only exceptional flood pulses, which significantly increase the turbidity and velocity of waters, and low water temperatures, asking for further studies to quantify the actual tolerance of *C. ocellaris* to those factors. Given that even the Ivinheima River —one of the least-regulated rivers in the UPRF— was permanently invaded after 2000 (Espínola et al. 2010; 2015) we anticipate that other still preserved but also interconnected systems in the UPRF are vulnerable of being invaded by *C. ocellaris*. Furthermore, since juveniles of this invader are already found below the Itaipú Reservoir, at the fluvial stretch of the Paraná River (LN Santos; personal observation) and have recently spread into the comparatively low water temperature reservoirs of the Iguaçu River (Daga et al. 2016), we expect that the southern limit of *C. ocellaris* distribution will continue to broaden. If water temperature does not limit its spread, there seems to be no other severe obstacle that could be able to prevent *C. ocellaris* from invading Paraguayan and Argentinean waters, especially if late anthropogenic activities continue to support its transportation and also adversely affect the stocks of native piscivores.

Acknowledgments. We would like to thank Dr. AA Agostinho, Dr. SM Thomaz, Dr. FM Pelicice and Dr. M Orsi for their valuable comments that significantly improved the manuscript. We would like to acknowledge the Núcleo de Pesquisa em Limnologia, Ictiologia e Aqüicultura (Nupelia, UEM, Brasil) and its several researchers and students that have been working since the 80's to assemble the long-term data set used in this study. This work benefited from funding by CNPq (PELD Programme 2000-2007; graduate grant to LAE), FUEM-PADCT-CIAMB (1992-1995) and FINEP (1986-1988).

References

Agostinho, A. A., H. F. Júlio-Júnior, and M. Petrere Júnior. 1994. Itaipú reservoir (Brazil): impacts of the impoundment on the fish fauna and fisheries. Pp. 171-184 *in* I. G. Cowx (ed.). Rehabilitation of Freshwater Fisheries. Fishing New Books, Bodmin.

Agostinho, A. A., L. C. Gomes, and F. M. Pelicice. 2007. Ecologia e manejo de recursos pesqueiros em reservatórios do Brasil. EDUEM, Maringá, Brazil. Pp. 501.

Agostinho, A. A., L. C. Gomes, S. Veríssimo, and E. K. Okada. 2004. Flood regime, dam regulation and fish in the Upper Paraná River: effects on assemblage attributes, reproduction and recruitment. Reviews in Fish Biology and Fisheries 14:11-19. https://doi.org/10.1007/s11160-004-3551-y.

Agostinho, A. A., S. M. Thomaz, and L. C. Gomes. 2005. Conservation of the biodiversity of Brazil's inland waters. Conservation Biology 3:646-652. https://doi.org/10.1111/j.1523-1739.2005.00701.x

Barros, V., M. Doyle, and I. Camilloni. 2005. Potential impacts of climate change in the Plata basin. Regional Hydrological Impacts of Climatic Variability and Change. Proceedings of symposium S6 held during the Seventh IAHS Scientific Assembly at Foz do Iguaçu, Brazil.

Britton, J. R., and M. L. Orsi. 2012. Non-native fish in aquaculture and sport fishing in Brazil: economic benefits versus risks to fish diversity in the upper River Paraná Basin. Reviews in Fish Biology and Fisheries 22:555-565. https: //doi.org/10.1007/s11160-012-9254-x.

Camilloni, I. A., R. Saurral, and N. B. Montroull. 2013. Hydrological projections of fluvial floods in the Uruguay and Paraná basins under different climate change scenarios. International Journal of River Basin Management 11(4):389-399. https://doi.org/10.1080/15715124.2013.819006.

Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity and distributions 15:22-40. https://doi.org/10.1111/j.1472-4642.2008.00521.x.

Colautti, R. I., I. A. Grigorovich, and H. J. MacIsaac. 2006. Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023-1037. https://doi.org/10.1007/s10530-005-3735-y.

Comte, L., and J. Olden. 2017. Climatic vulnerability of the world's freshwater and marine fishes. Nature Clima Change 7:718-722. https://doi.org/10.1038/nclimate3382.

Daga, V., T. Debona, V. Abilhoa, E. A. Gubiani, and J. Vitule. 2016. Non-native fish invasions of a Neotropical ecoregion with high endemism: a review of the Iguaçu River. Aquatic Invasions 11:209-223. https://doi.org/10.3391/ai.2016.11.2.10.

Davis, M. A. 2009. Invasion biology. Oxford University Press, Oxford, UK. Pp. 288. https://doi.org/10.1111/j.1654-1103.2010.01187.x.

Durães, R., G. B. Santos, and P. S. Formagio. 2000. Observações sobre a alimentação do tucunaré *Cichla monoculus* (Pisces, Cichlidae) em um reservatório do Sudeste brasileiro. Revista de Ictiología 8:53-56.

Espínola, L. A., and H. F. Júlio-Júnior. 2007. Espécies invasoras: conceitos, modelos e atributos. Interciencia 32:580-585.

Espínola, L. A., A. P. Rabuffetti, N. Carrara, E. Abrial, E. M. C. Ferlay, F. Yoya, M. C. M. Blettler, C. Baigún, and K. M. Wantzen. 2022. Increased geographical distribution and richness◎of non-native freshwater fish species in Argentina: evidence from a literature review. Biological Invasions 24:1611-1634. https://doi.org/10.1007/s10530-022-02742-5.

Espínola, L. A., C. V. Minte-Vera, and H. F. Júlio-Júnior. 2010. Invasibility of reservoirs in the Paraná Basin, Brazil, to *Cichla kelberi* Kullander and Ferreira, 2006. Biological Invasions 12:1837-1888. https://doi.org/10.1007/s10530-009-9598-x.

Espínola, L. A., C. V. Minte-Vera, H. F. Júlio-Júnior, L. N. Santos, and K. O. Winemiller. 2015. Evaluation of factors associated with dynamics of *Cichla ocellaris* invasion of the Upper Paraná River floodplain system, Brazil. Marine and Freshwater Research 66:33-40. https://doi.org/10.1071/MF13105.

Franco, A. C. S., L. N. dos Santos, A. C, Petry, and E. García-Berthou. 2018. Abundance of invasive peacock bass increases with water residence time of reservoirs in southeastern Brazil. Hydrobiologia 817:155-166. https://doi.org/10.1007/s10750-017-3467-x.

Franco, A. C. S., A. C. Petry, M. R. Tavares, F. T. R. Guimarães, and L. N. dos Santos. 2022. Global distribution of the South American peacock basses *Cichla spp*. follows human interference. Fish and Fisheries 23:407-421. https://doi.org/10.1111/faf.12624.

Fugi, R., K. D. G. Luz-Agostinho, and A. A. Agostinho. 2008. Trophic interaction between an introduced (peacock cichlid) and a native (dogfish) piscivorous fish in a Neotropical impounded river. Hydrobiologia 607:143-150. https://doi.org/10.1007/s10750-008-9384-2.

Gomiero, L. M., and F. M. S. Braga. 2004. Reproduction of species of the genus Cichla in a reservoir in southeastern, Brazil. Brazilian Journal of Biology 64:613-624. https://doi.org/10.1590/S1519-69842004000400008.

Gomiero, L. M., G. A. Villares-Junior, and F. Naous. 2009. Reproduction of *Cichla kelberi* Kullander and Ferreira. 2006, introduced into an artificial lake in southeastern Brazil. Brazilian Journal of Biology 69:175-183. https://doi.org/10.1590/S1519-69842009000100023.

Guest, C. W. 1983. Control of Ichthyophthirius in peacock bass fingerlings. Progressive Fish Culturist 45:57. https://doi.org/10.1577/1548-8659(1983)45[57:COIIPB]2.0.CO;2.

Heger, T. 2001. A model for interpreting the process of invasion: Crucial situations favouring special characteristics of invasive species. Pp. 3-10 *in* G. Brundu, J. H. Brock, I. Camarda, L. E. Child and P. M. Wade (eds.). Plant invasions: Species ecology and ecosystem management. Backhuys Publishers. Leiden, The Netherlands.

Heger, T. 2004. Zur Vorhersagbarkeit biologischer Invasionen. Entwicklung und Anwendung eines Modells zur Analyse der Invasion gebietsfremder Pflanzen. Neobiota 4:197.

Heger, T., A. T. Pahl, Z. Botta-Dukát, F. Gherardi, C. Hoppe, I. Hoste, et al. 2013. Conceptual frameworks and methods for advancing invasion ecology. Ambio 42:527-540. https://doi.org/10.1007/s13280-012-0379-x.

Heger, T., and L. Trepl. 2003. Predicting biological invasions. Biological Invasions 5:313-321. https://doi.org/10.1023/B:BINV.0000005568.44154.12.

Heger, T., S. Haider, W. Saul, and J. Jeschke. 2015. Species from different taxonomic groups show similar invasion traits. Immediate Science Ecology 3:1-13. https://doi.org/10.7332/ise2015.3.1.dsc.

Hoeinghaus, D. J., C. A. Layman, A. D. Arrington, and K. O. Winemiller. 2003. Movement of Cichla species (Cichlidae) in a Venezuelan floodplain river. Neotropical Ichthyology 1:121-126. https://doi.org/10.1590/S1679-62252003000200006.

Júlio Júnior, H. F., C. Dei Tós, A. A. Agostinho, and C. S. Pavanelli. 2009. A massive invasion of fish species after eliminating a natural barrier in the upper Rio Parana basin. Neotropical Ichthyology 7:709-718. https://doi.org/10.1590/S1679-62252009000400021.

Kovalenko, K. E., E. D. Dibble, A. A. Agostinho, G. Castanhêde, and R. Fugi. 2010. Direct and indirect effects of an introduced piscivore, *Cichla kelberi* and their modification by aquatic plants. Hydrobiologia 638:245-253. https://doi.org/10.1007/s10750-009-0049-6.

Kullander, S. O., and E. J. G. Ferreira. 2006. A review of the South American cichlid genus Cichla, with descriptions of nine new species (Teleostei: Cichlidae). Ichthyological Exploration of Freshwaters 17:289-398.

Lacerda, A. C. F., R. M. Takemoto, R. Poulin, and G. C. Pavanelli. 2013. Parasites of the fish *Cichla piquiti* (Cichlidae) in native and invaded Brazilian basins: release not from the enemy, but from its effects. Parasitology Research 112: 279-288. https://doi.org/10.1007/s00436-012-3135-z.

Latini, A. O., and M. Petrere-Júnior. 2004. Reduction of native fish fauna by alien species: an example from Brazilian freshwater tropical lakes. Fisheries Management and Ecology 11:71- 79. https://doi.org/10.1046/j.1365-2400.2003.00372.x.

Lepš, J., and P. Šmilauer. 2003. Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge. Pp. 360. https://doi.org/10.1017/CBO9781139627061.

Lockwood, J. L., M. F. Hoopes, and M. P. Marchetti. 2007. Invasion ecology. Blackwell Publishing, Oxford. Pp. 428.

Lodge, D. M. 1993. Biological Invasions: Lessons for Ecology. Trends in Ecology and Evolutions 8:133-137. https://doi.org/10.1016/0169-5347(93)90025-K.

Machado, P. M., R. M. Takemoto, G. C. Pavanelli. 2005. Diplostomum (Austrodiplostomum) compactum (Lutz, 1928) (Platyhelminthes, Digenea) metacercariae in fish from the floodplain of the Upper Paraná River, Brazil. Parasitology Research 97:436-444. https://doi.org/10.1007/s00436-005-1483-7.

Marques, A. C. P. B., A. C. S. Franco, F. Salgueiro, E. García-Berthou, and L. N. Santos. 2016. Genetic divergence among invasive and native populations of the yellow peacock cichlid *Cichla kelberi*. Journal of Fish Biology 89:2595-2606. https://doi.org/10.1111/jfb.13144.

Moles, A. T., M. A. M. Gruber, and S. P. Bonser. 2008. A new framework for predicting invasive plant species. Journal of Ecology 96:13-17. https://doi.org/10.1111/j.1365-2745.2007.01332.x.

Normando, F. T., F. P. Arantes, R. K. Luz, R. G. Thomé, E. Rizzo, et al. 2009. Reproduction and fecundity of tucunaré, *Cichla kelberi* (Perciformes: Cichlidae), an exotic species in Três Marias Reservoir, Southeastern Brazil. Journal of Applied Ichthyology 25:299-305. https://doi.org/10.1111/j.1439-0426.2008.01174.x.

Olden, J. D., L. Poff, and K. R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. Ecological Monographs 76:25-40. https://doi.org/10.1890/05-0330.

Oliveira, A. V., A. J. Prioli, S. M. A. P. Prioli, T. S. Bignotto, H. F. Júlio-Júnior, et al. 2006. Genetic diversity of invasive and native Cichla (Pisces: Perciformes) populations in Brazil with evidence of interspecific hybridization. Journal of Fish Biology 69:260-277. https://doi.org/10.1111/j.1095-8649.2006.01291.x.

Orsi, M. L., and A. A. Agostinho. 1999. Introdução de espécies de peixes por escapes acidentais de tanques de cultivo em rios da bacia do rio Paraná, Brasil. Revista Brasileira de Zoologia 16:557-560. https://doi.org/10.1590/S0101-81751999000200020.

Pelicice, F. M., and A. A. Agostinho. 2009. Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biological Invasions 11:1789-1801. https://doi.org/10.1007/s10530-008-9358-3.

Pelicice, F. M., J. D. Latini, and A. A. Agostinho. 2015. Fish fauna disassembly after the introduction of a voracious predator: main drivers and the role of the invader's demography. Hydrobiologia 746:271-283. https://doi.org/10.1007/s10750-014-1911-8.

Pereira, L. S., L. F. C. Tencatt, R. M. Dias, A. G. Oliveira, and A. A. Agostinho. 2017. Effects of long and short flooding years on the feeding ecology of piscivorous fish in floodplain river systems. Hydrobiologia 795:65-80 https://doi.org/10.1007/s10750-017-3115-5.

Pereira, L. S., A. A. Agostinho, and L. C. Gomes. 2014. Eating the competitor: a mechanism of invasion. Hydrobiologia 746:223-231. https://doi.org/10.1007/s10750-014-2031-1.

Picon-Camacho, S. M., M. Marcos-Lopez, J. E. Bron, and A. P. Shinn. 2012. An assessment of the use of drug and non-drug interventions in the treatment of *Ichthyophthirius multifiliis* Fouquet, 1876, a protozoan parasite of freshwater fish. Parasitology 139:149-190. https://doi.org/10.1017/S0031182011001867.

Rocha, R. R. A., and S. M. Thomaz. 2004. Variação temporal de fatores limnológicos em ambientes da planície de inundação do alto rio Paraná (PR/MS - Brasil). Acta Scientiarum 26:261-271. https://doi.org/10.4025/actascibiolsci.v26i3.1538.

Santos, A. F. G. N., C. Alcaraz, L. N. Santos, C. Hayashi, and E. García-Berthou. 2012. Experimental assessment of the effects of a Neotropical nocturnal piscivore (*Pseudoplatystoma corruscans*) on juvenile native and invasive fishes. Neotropical Ichthyology 10:167-176. https://doi.org/10.1590/S1679-62252012000100016.

Santos, A. F. G. N., E. García-Berthou, C. Hayashi, and L. N. Santos. 2013. When habitat complexity increases predation risk: experiments with invasive and neotropical native fishes. Marine Freshwater Research 64:752-760. https://doi.org/10.1071/MF12264.

Santos, A. F. G. N., L. N. Santos, and E. García-Berthou. 2009. Could native predators help to control invasive fishes Microcosm experiments with the Neotropical characid *Brycon orbignyanus*. Ecology of Freshwater of Fish 18:491-499. https://doi.org/10.1111/j.1600-0633.2009.00366.x.

Santos, A. F. G. N., L. N. Santos, and F. G. Araújo. 2011. Digestive tract morphology of the Neotropical piscivorous fish *Cichla kelberi* (Perciformes: Cichlidae) introduced into an oligotrophic Brazilian reservoir. Revista de Biología Tropical 59:1245-1255.

Santos, L. N., A. C. S. Franco, A. Marques, F. Nóbrega, and F. Salgueiro. 2016. Molecular analysis confirms the introduction of a second species of yellow peacock cichlid *Cichla monoculus* Spix and Agassiz 1831 (Cichliformes: Cichlidae) in the Southeast Atlantic Hydrographic province, Brazil. BioInvasions Records 5:277-284. https://doi.org/10.3391/bir.2016.5.4.13.

Santos, L. N., F. Salgueiro, A. C. S. Franco, A. Marques, and F. Nóbrega. 2016b. First record of the invasive blue peacock cichlid *Cichla piquiti* Kullander and Ferreira 2006 (Cichliformes: Cichlidae) in the Paraíba do Sul river basin, south eastern Brazil. BioInvasions Records 5:267-275. https://doi.org/10.3391/bir.2016.5.4.12.

Santos, L. N., A. F. González, and F. G. Araújo. 2001. Dieta do tucunaré-amarelo *Cichla monoculus* (Bloch and Schneider) (Osteichthyes, Cichlidae), no Reservatório de Lajes, Rio de Janeiro, Brasil. Revista Brasileira de Zoologia 18:191-204. https://doi.org/10.1590/S0101-81752001000500015.

Santos, L. N., F. G. Araújo, and D. S. Brotto. 2008. Artificial structures as tools for fish habitat rehabilitation in a neotropical reservoir. Aquatic Conservation 18:896-908. https://doi.org/10.1002/aqc.931.

Santos, A. F. G. N., E. García-Berthou, C. Hayashi, and L. N. Santos. 2019. Water turbidity increases biotic resistance of native Neotropical piscivores to alien fish. Hydrobiologia 817:293-305. https://doi.org/10.1007/s10750-018-3548-5.

Santos, R. S., N. Marchiori, V. A. Santarem, H. K. Takahashi, J. L. P. Mourino, et al. 2012. *Austrodiplostomum compactum* (Lutz, 1928) (Digenea, Diplostomidae) in the eyes of fishes from Paraná river, Brazil. Acta Scientiarum 34:225-231. https://doi.org/10.4025/actascibiolsci.v34i2.9337.

Shafland, P. L. 1995. Introduction and establishment of a successful butterfly peacock fishery in Southeast Florida Canals. American Fisheries Society Symposium 15:443-451.

Sharpe, D. M. T., L. F. De León, R. González, and M. E. Torchin. 2017. Tropical fish community does not recover 45 years after predator introduction. Ecology 98:412-424. https://doi.org/10.1002/ecy.1648.

Souza, J. E., E. N. Fragoso-Moura, N. Fenerich-Verani, O. Rocha, and J. R. Verani. 2008. Population structure and reproductive biology of *Cichla kelberi* (Perciformes, Cichlidae) in Lobo Reservoir, Brazil. Neotropical Ichthyology 6: 201-210. https://doi.org/10.1590/S1679-62252008000200007.

Steil, J., and T. Heger. 2008. Der Mink (Mustela vison Schreber 1777) in Deutschland - eine Bedrohung für heimische Arten? Natur und Landschaft 83:365-369.

Suzuki, H. H., A. A. Agostinho. 2001. Reprodução de peixes do reservatório Corumbá (GO). Pp. 227-323 *in* A. A. Agostinho, R. Fugi, S. Veríssimo and J. D. Latini (eds.). Estudos Ictiológicos na Área de Influência do AHE de Corumbá. Maringá. EDUEM, Brazil.

Swingle, H. S. 1966. Temperature tolerance of the peacock cichlid and a pond test of its value as a piscivorous species. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 20:297-299.

Thomaz, S. M., A. A. Agostinho, L. C. Gomes, M. J. Silveira, M. Rejmanek, et al. 2012. Using space-for-time substitution and time sequence approaches in invasion ecology. Freshwater Biology 57:2401-2410. https://doi.org/10.1111/fwb.12005.

Thomaz, S. M., M. C. Roberto, and L. M. Bini. 1997. Caracterização limnológica dos ambientes aquáticos e influência dos níveis fluviométricos. Pp. 73-102 *in* A. E. A. Vazzoller, A. A. Agostinho and N. S. Hahn (eds.). A planície de inundação do alto Rio Paraná: aspectos físicos, biológicos e socioeconômicos. Maringá, EDUEM, Brasil.

Thomaz, S. M., T. A. Pagioro, L. M. Bini, M. C. Roberto, and R. R. A. Rocha. 2004. Limnological characterization of the aquatic environments and the influence of hydrometric levels. Pp. 75-102 *in* S. M. Thomaz, A. A. Agostinho and N. S. Hahn (eds.). The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. Backhuys Publishers, Leiden, UK.

Thomaz, S. M. 2022. Propagule pressure and environmental filters related to non-native species success in river-floodplain ecosystems. Hydrobiologia 849:3679-3704 https://doi.org/10.1007/s10750-021-04624-8.

Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, et al. 2005. Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11:2234-2250. https://doi.org/10.1111/j.1365-2486.2005.001018.x.

Welcomme, R. L. 1988. International introductions of inland aquatic species. Fisheries Technical Paper 294:1-318.

Welk, E. 2004. Constraints in range predictions of invasive plant species due to non-equilibrium distribution patterns: Purple loosestrife (*Lythrum salicaria*) in North America. Ecological Modelling 179:551-567. https://doi.org/10.1016/j.ecolmodel.2004.04.020.

Willis, S. C., J. Macrander, I. P. Farias, and G. Ortí. 2012. Simultaneous delimitation of species and quantification of interspecific hybridization in Amazonian peacock cichlids (genus Cichla) using multi-locus data. BMC Evolutionary Biology 12:96. https://doi.org/10.1186/1471-2148-12-96.

Winemiller, K. O. 2001. Ecology of peacock cichlids (Cichla spp.) in Venezuela. Journal of Aquariculture and Aquatic Sciences 9:93-112.

Winemiller, K. O., L. C. K. Winemiller, and C. G. Montaña. 2021. Peacock bass: Diversity, ecology and conservation. Academic Press.

Yamada, F. H., and R. M. Takemoto. 2013. Metazoan parasite fauna of two peacock-bass cichlid fish in Brazil. Check List 9:1371-1377. https://doi.org/10.15560/9.6.1371.

Yamada, F. H., L. N. Santos, and R. M. Takemoto. 2011. Gill ectoparasite assemblages of two non-native Cichla populations (Perciformes, Cichlidae) in Brazilian reservoirs. Journal of Helminthology 85:185-191. https://doi.org/10.1017/S0022149X10000441.

Zaret, T. M. 1980. Life history and growth relationships of *Cichla ocellaris*, a predatory South American cichlid. Biotropica 12:144-157. https://doi.org/10.2307/2387730.