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INVASIVE SPECIES

# Ecological and life history traits of *Hemiodus orthonops* in the invasion process: looking for clues at home

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**Abstract** The understanding of the environmental preferences and life history of a species in its native range provides insights for assessing its potential success in a novel area. *Hemiodus orthonops* is a migratory fish from the Paraguay and Middle Paraná rivers that invaded the Upper Paraná River through a fish pass, constructed in 2002. The invasion of this fish was analyzed based on habitat attributes and its life history in the native range and in the novel habitats. The native and novel habitats presented similar features. The population showed exponential growth in the years following the invasion, with relevant alterations in somatic growth, proportions of items in the diet, and in reproductive investment. The successful invasion appears to be related to similarities in water chemistry and habitat types between the native and novel range and the species' high dispersion ability. The species also showed earlier maturation and use of poor quality, but highly available feeding resources. Comparing life histories there was indication of a trade-off between investment in reproduction and somatic growth, with an increase in the latter in the novel habitats. In addition, the reproductive investment was more associated with offspring survival (oocyte size) than fecundity.

**Keywords** Non-native fish species · Species introduction · Fish pass dispersion · Establishment · Allochthonous species

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## Introduction

Biological invasions and hydrological alterations are currently considered the two largest threats to freshwater biota (Rahel, 2007; Johnson et al., 2008). These man-mediated actions are usually aggravated by the synergism between them. Habitat alterations that are induced by the control of flow with dams, for example, disrupt the structure of the aquatic biota and facilitate the establishment of invasive species (Havel et al., 2005). Damming can also eliminate natural barriers and promote the massive dispersal of species to upstream stretches (Júlio Júnior et al., 2009; Vitule et al., 2012). Furthermore, human actions to mitigate the effects of damming can further aggravate these impacts (Agostinho et al., 2007).

The installation of facilities for the passage of fish in dams, with the aim to preserve migratory species, may pose an additional threat to the biota of the upstream stretches by the dispersal of non-native species. This possibility occurs when the dam separates distinct native faunas along the watershed, either by the presence of non-native species in the downstream stretch, as occurs in coastal rivers in the Southeast of Brazil, or by the isolation processes determined by natural barriers, as occurs in the Paraná River or in the tributaries of the Amazon River (Torrente-Vilara et al., 2011). In the case of the Paraná River, the Itaipu Reservoir, filled in 1982, covered the Sete Quedas Falls, which separated distinct ichthyofauna provinces. Initially, this enabled the upstream movement of several fish species (Júlio Júnior et al., 2009). Some of these species became abundant to the point of replacing native congeneric species (Agostinho, 2003; Alexandre et al., 2004); whereas, other species were not able to establish themselves. During the next 20 years, approximately 17 species remained restricted to the stretch downstream from the dam. With the operation of a natural-like canal for fish transposition, called the “Canal de Piracema”, in the Itaipu Dam, other species dispersed to the upstream stretches of the watershed (Makrakis et al., 2007; Júlio Júnior et al., 2009; Vitule et al., 2012). Among the species that succeed in ascending the fish pass is *Hemiodus orthonops* (Eigenmann & Kennedy, 1903), which is a species endemic to the Paraná-Paraguay watershed that, until recently, was absent from the Upper Paraná River basin, an approximately 1,700 km segment of the watershed. The invasion of this species was noteworthy for both its fast colonization of the new environment and for its abundance, reaching approximately 8% of the total catch at the upstream plain, in less than five years.

The invasion process involves characteristics of the life history of the invasive species in addition to the biotic and abiotic environment invaded, which act as filters that may or may not be determinant of the success of the invasion (Davis, 2005; Quist et al., 2005). Among the most important aspects of the life history of the invasive species are tolerance to environmental variations, reproductive and feeding strategies, somatic growth rate, and morphometric aspects, especially those related to locomotion. Then, physiological tolerance, reproductive flexibility, high fecundity, omnivorous/detritivorous diet, rapid early growth, and swimming ability are some features related to dispersal and establishment in new areas (Lodge, 1993; Moyle & Light, 1996; Bøhn et al., 2004; Moyle & Ellsworth, 2004; Colautti et al., 2006). In terms of the environment, the limitation is related to the degree of biotic integrity, the intensity and nature of the environmental variations (seasonal or stochastic), and the presence of other species (interspecific relationships). Understanding the factors that facilitate the invasion process is necessary to implement measures for the prevention and management of invasive species in sustainable management (Garcia-Berthou, 2007), such as subsidizing environmental agencies in risk analysis to issue licenses. Several studies have been performed in the last decades that focus on invasive fish species; however, most of these studies address fish escapes, the impacts on other species or the invasion status (Orsi & Agostinho, 1999; Latini & Petrere Junior, 2004; Figueredo & Gian, 2005; Pelicice & Agostinho, 2009; Capra & Bennemann, 2009; Vitule et al., 2009; Vitule et al., 2012; Pelicice et al., 2014). There are not enough research efforts to understand the mechanisms that cause a given invasive species to be successful in the Neotropical zone. This study seeks this understanding and is a pioneer in South America in the search for the responses of a species in its natural distribution area. To that end, the aim is to describe the invasion process and the ecological and life history aspects of *H. orthonops* that may have favored its fast proliferation in the Upper Paraná River, based on samples from the native and invaded areas. Furthermore, this study summarizes the variations displayed in the life strategy of this species during the colonization process.

## Materials and methods

### Study area

The stretch selected for the evaluation of aspects related to the dispersal and colonization success of *H. orthonops* in the Upper Paraná River included the Cuiabá River watershed (natural distribution area of *H. orthonops*) and the floodplain of the Upper Paraná River (novel area)—Fig. 1. Additional data obtained

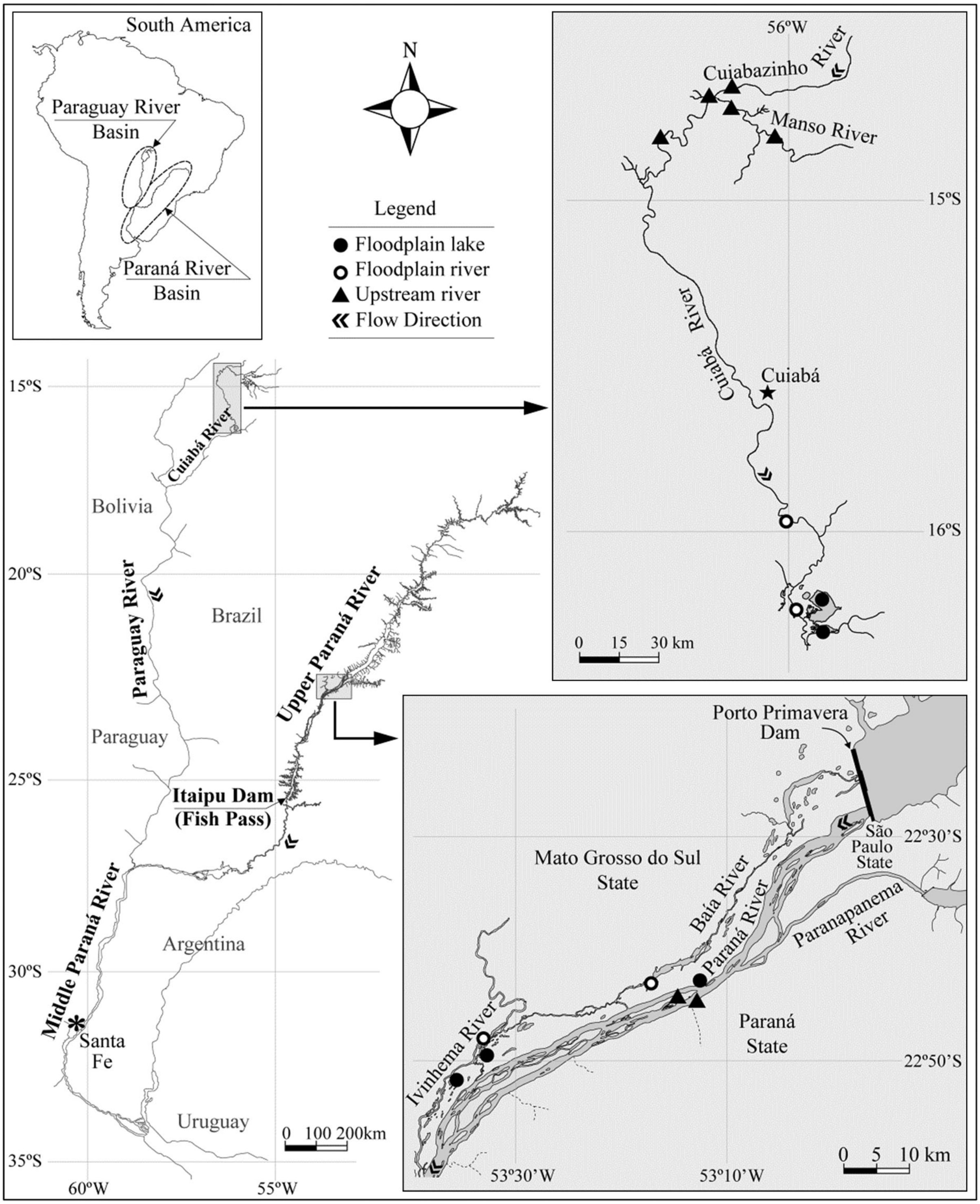

**Fig. 1** Map of the native (Paraguay and Middle Paraná River) and invaded area (Upper Paraná River) with details of the sampling sites in both regions. *Additional data on the physical and chemical variables of the water

at different times during the last 25 years from the Itaipu reservoir, in the stretch downstream of the dam, and in the fish pass that was installed more recently in the dam, were used to understand the invasion process.

The Cuiabá River, with an extension of approximately 850 km and a drainage watershed of approximately 100,000 km$^2$, is formed by the union of the Manso and Cuiabazinho Rivers. The Cuiabá River and the Paraguay River are the main watercourses forming the Pantanal of Mato Grosso. The climate of the Pantanal is marked by a dry season, which occurs from May to September, and a rainy season, which occurs from October to April. The study area was located between the Manso River and the municipality of Barão do Melgaço (14°41′S/56°13′W and 16°21′S/55°57′W) and included the channel of the Cuiabá River and the lower stretches of the Manso and Cuiabazinho Rivers, in addition to lakes located in the lowest parts of the studied stretch.

The river-floodplain system of the Upper Paraná River was originally 480 km long, located between the municipalities of Três Lagoas (Mato Grosso do Sul State) and Guaíra (Paraná State), with a similar, but less pronounced hydrologic peak. However, half of this area was taken away by the filling of the Porto Primavera Reservoir (Sérgio Motta Hydropower). Currently, the river-floodplain system of the Upper Paraná River covers 230 km between the Porto Primavera Dam and the Itaipu Reservoir, representing the last lotic stretch of the Upper Paraná River that is exclusively inside the Brazilian territory. The studied area was located between the mouths of the Paranapanema and Ivinheima Rivers (22°43′S/53°13′W and 22°47′S/53°32′W), including the main channel of the Paraná, Baía, and Ivinheima Rivers and lakes.

The Itaipu Reservoir (24°15′S/54°00′W and 25°33′S/54°37′W) was formed in October 1982 in the Paraná River and covered the Sete Quedas Falls, a natural barrier that separated two ichthyofauna provinces. The reservoir dam, located approximately 150 km downstream from the former natural barrier, became a new barrier for fish dispersal. It has an area of 1,350 km$^2$ and a water residence time of approximately 40 days (Thomaz et al., 2009a).

In 2002, a natural-like canal for fish passage ("Canal de Piracema") was built, which connected the Paraná River downstream from the Itaipu dam and the reservoir to allow the ascension of long-distance migratory fish. The "Canal de Piracema" extends for 10 km and levels a difference of 120 m between the Paraná River and the reservoir (Makrakis et al., 2007).

## Fish samplings

Fish were sampled in the native range (Cuiabá River basin) and in the novel area (Upper Paraná River basin). In the Cuiabá River basin, the fish were sampled from March 2000 to February 2004 along the river channel (7 sampling stretches distributed along 350 km and grouped in floodplain and upstream channel) and floodplain lakes (2 sampling sites). In the Upper Paraná River, the fish were sampled from March 2000 to March 2014 along the river channel (4 sampling sites distributed along 80 km and grouped in floodplain and upstream channel) and floodplain lakes (3 sampling sites). A set of gillnets composed of different mesh sizes were exposed for 24-hour periods, with harvests at 8:00 a.m., 4:00 p.m., and 10:00 p.m. The sampling was standardized by a constant effort and time (368 m$^2$ of gillnet operated during 24 hours).

Measures of total and standard length (cm), total weight (g), and gonad weight (g) were performed for each fish captured. Stomachs containing food were used to identify the diet. The reproductive cycle phases were determined using the terminology proposed by Brown–Peterson et al. (2011), including the phases immature, developing, spawning capable, regressing, and regeneration.

Measures of the temperature ($^o$C), transparency (m; Secchi depth), dissolved oxygen (mg l$^{-1}$), pH, and conductivity (μS cm$^{-1}$) of the water in the native and novel areas were performed. The invaded area was located in intermediate latitudes (Upper Paraná River: 22°45′S), with the native distribution of the species having an upper latitude in the Cuiabá River (14°41′S) and a lower latitude in the Middle Paraná River (31°43′S), near Santa Fe, Argentina.

## Data analysis

### *Dispersal, colonization, and population growth*

Historic data of the samplings performed in the Paraná River, which were obtained from technical reports (CETESB-Itaipu Binacional, 1981) or from the databases of the Center for Research in Limnology, Ichthyology and Aquaculture of the State University of Maringá (Nupélia—Universidade Estadual de

Maringá; from 1983 to March 2014), were used to describe the occurrence and abundance of *H. orthonops* in the native and invaded areas.

The population growth of *H. orthonops* in the Upper Paraná River was modeled, based on the following two scenarios: (i) exponential growth, representing the initial colonization phase, and (ii) logistic growth (complete series: 2008–2014), representing the long-term establishment. The parameters of the exponential and logistic growth models were determined according to Turchin (2003) and Forsyth et al. (2013).

The exponential growth model is given by the following equation:

$$N_{t+1} = N_t e^{(r_m)},$$

where $N_t =$ abundance of *H. orthonops* in the year $t$ and $r_m$ is the maximum population growth rate.

The logistic growth model is given by the following equation:

$$N_{t+1} = N_t e^{\left(r_m\left(1-\left(N_t/K\right)\right)\right)},$$

where $K$ is the carrying capacity.

The annual abundance of *H. orthonops* was defined as the total number of individuals captured in the standardized samplings (annual samplings during the month of March in seven locations, with a constant effort per sample of 368 $\mathrm{m}^2$ of gillnets operated for 24 h and seine nets with 220 $\mathrm{m}^2$ of area swept). The models were adjusted by the least squares method.

## Ecological and life history traits

### *Aquatic variables*

The limnological variables were used with the aim of testing whether the conditions in the invaded area are within the variation found in the native distribution area of this species. The extreme values (maximum and minimum) of the limnological variables in the native area (Cuiabá and Middle Paraná Rivers) were juxtaposed with the minimum, maximum, and median values and with the 25th and 75th percentiles by biotope of the novel area.

### *Somatic growth*

Based on the curve of the von Bertalanffy growth equation, the growth parameters were separately estimated for the males and females from the composition of length data. The parameter $L_\infty$ (asymptotic length) was obtained according to Pauly (1983), as follows: $L_\infty = L_{\max}/0.95$. The parameter k (growth rate) was estimated by the Shepherd's length-composition analysis (SLCA) (Shepherd, 1987).

### *Diet composition*

The feeding characteristic of *H. orthonops* was evaluated by examination of the stomach contents (79 stomachs from Cuiabá River and 110 from Upper Paraná River), using the frequencies of occurrence and dominance methods (Hyslop, 1980). To determine whether the diet composition differed between the native (Cuiabá River) and non-native (Upper Paraná River) sites, a permutational multivariate analyses of variance (Anderson, 2005) was employed using the data matrix of the occurrence of food items. We used the Jaccard distance as a measure of dissimilarity and 9999 permutations to assess the significance of the pseudo-F statistic derived from PERMANOVA.

### *Reproduction and migration*

The reproductive activity was evaluated with the Index of Reproductive Activity (IRA—Bailly et al., 2008). With the aim of evaluating the potential of this species to perform reproductive migrations, the frequencies of the lengths and reproductive activities in the different biotopes were analyzed. Additionally, the swimming ability (a surrogate of migration) of *H. orthonops* was evaluated by considering two morphological attributes related to locomotion, as follows: (i) Shape factor (the ratio between the total body length and the maximum height) and (ii) Swim factor (a ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin) (Webb, 1984; Olden et al., 2006). The measures of 40 individuals (20 from the Cuiabá River watershed and 20 from the Upper Paraná River watershed) were taken, and these values were compared with the data obtained from the literature for several species (Olden et al., 2006), with and without fluvial dependence (a surrogate of migration), and tested with a one-way analysis of variance.

The oocyte development and fecundity were evaluated based on the analysis of the ovaries of 23 females from the Cuiabá River watershed and 8

**Table 1** The chronology, dispersal route, and relative abundance (% of the total captures) of *Hemiodus orthonops* in the Upper Paraná River stretches

| Chronology | 1977–1981 | 1986–2001 | 2002–2006 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 |
|---|---|---|---|---|---|---|---|---|---|
| Downstream (Pre-impoundment) | ≪0.5 | | | | | | | | |
| Downstream (post-impoundment)[a] | | 1.9 | – | – | – | – | – | – | – |
| Fish pass[b] | | | <0.5 | – | – | – | – | – | – |
| Itaipu Reservoir (sampling) | | | ≪0.5 | <0.5 | <0.5 | 1.6 | – | – | – |
| Itaipu Reservoir (fisheries) | | | | | ≪0.5 | <0.5 | 0.5 | – | – |
| Upstream (river-floodplain) | | 0.0 | 0.0 | 0.14 | 1.0 | 1.1 | 3.3 | 8.1 | 10.4 |

'–' not available data

[a] Itaipu Reservoir was closed in 1982

[b] Fish pass was open in 2002

females from the Upper Paraná River watershed. The oocytes from ovaries in the spawning-capable phase were counted and measured. The oocytes in the primary growth phase, less than 0.28 mm, were not measured. The fecundity (F) estimate was based on the number of fully yolked oocytes present in the ovary samples obtained in the spawning-capable phase.

The sex ratio was analyzed with the $\chi^2$ test. The standard length at maturation was calculated based on DeMaster (1978). The comparisons of these and other ecological and life history differences of the populations of *H. orthonops* in the native and invaded areas were summarized in a table.

## Results

### Dispersal, colonization, and population growth

The natural distribution area of *H. orthonops* is restricted to the Paraná–Paraguay watershed. In the Paraná River, the distribution of *H. orthonops* in the upper stretches of the watershed was limited by a natural barrier (Sete Quedas Falls); thus, this species occurred sporadically in captures performed immediately downstream of this barrier. After the construction of the Itaipu hydroelectric dam (in 1982), which was 150 km downstream, this species continued to be restricted to a stretch downstream from this new obstacle; however, its abundance increased (Table 1). However, after the installation of a fish pass in 2002 (the "Canal de Piracema"), this species was recorded in the canal and in the upstream reservoir. Its presence in commercial fish landings was initially recorded in 2008, reaching 4.8 annual tons in 2013 (0.5% of the total). The first captures in the floodplain of the Upper Paraná River were observed in 2008, and this species reached more than 10% of the total of captures in six years.

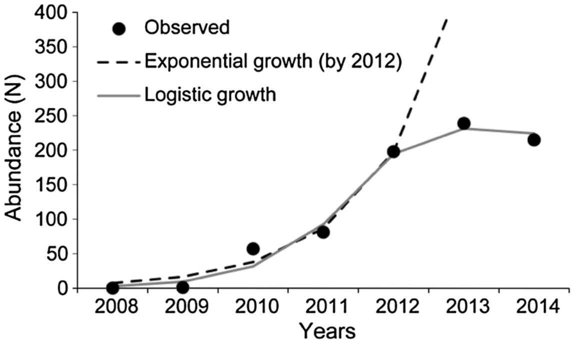

**Fig. 2** The number of individuals observed in standardized samples performed annually in March in the upper Paraná River watershed, with adjustments from the exponential growth model until 2012 (*dashed line*) and from the logistic growth model until 2014 (*continuous line*)

The total number of *H. orthonops* individuals captured annually in the standardized samples in the Upper Paraná River increased from 8 individuals in 2008 to 753 in 2013, when it reached 10.4% of the total fish captures in the samples (Table 1). Considering only the standardized samples performed in March of each year, the total number of individuals increased from 1 in 2009 to 239 in 2013, decreasing to 215 in 2014 (Fig. 2).

In the first population growth scenario (exponential growth, 2008–2012), representing the initial colonization phase, the maximum growth rate was estimated at 0.827; whereas, the maximum growth rate estimated for the second scenario (logistic growth, 2008–2014),

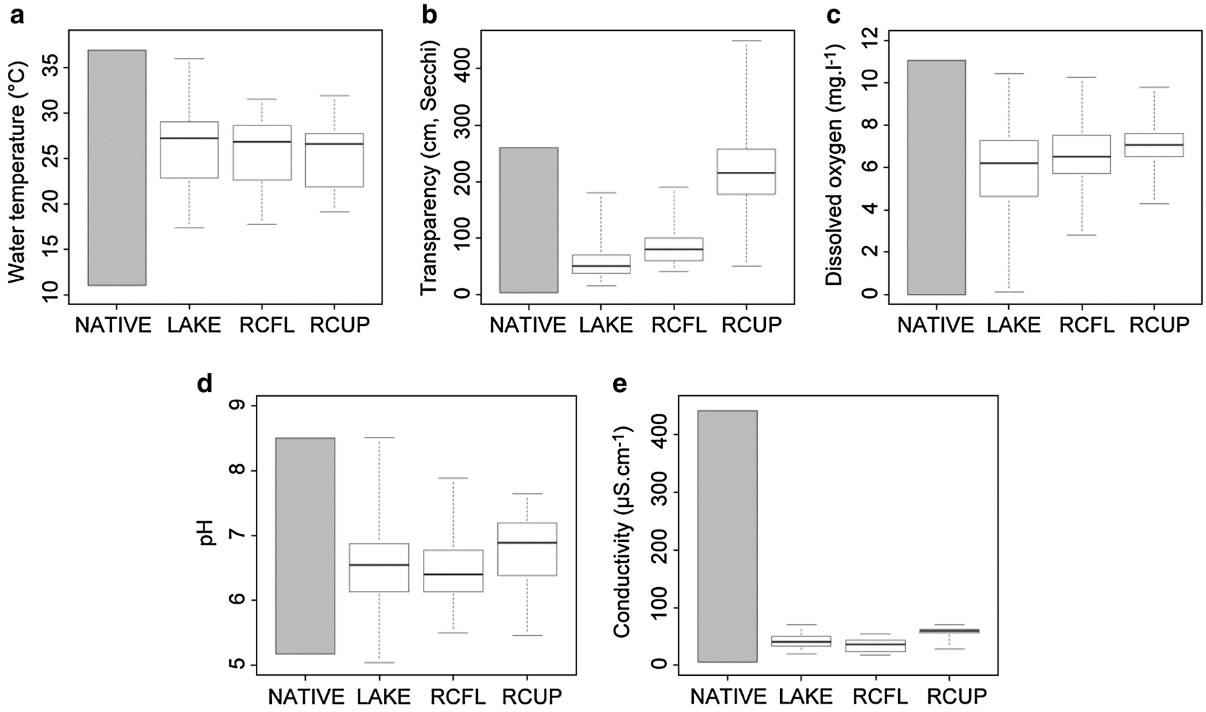

**Fig. 3** The variation of temperature (**a**), transparency (**b**), dissolved oxygen (**c**), pH (**d**) and conductivity (**e**) of the water in the natural (*gray column* maximum–minimum) and invaded (*box plot* with median, percentiles and maximum–minimum values) habitats. Invaded biotopes: *LAKE* floodplain lakes; *RCFL* river channel floodplain; *RCUP* river channel upstream

representing the long-term establishment, was 1.258, and the carrying capacity (K) was estimated at 226 individuals (Fig. 2). When considering the partial adjustments from 2008 to 2012, the exponential model was the best adjusted model, with a sum of squares of 692, in comparison to a partial sum of squares of 833 for the logistic model. However, when considering the complete series, the sum of squares is 716,913 in the exponential model and 1,024 in the logistic model. These results show that the population growth of the non-native *H. orthonops* displayed exponential growth during the initial colonization phase but later stabilized in an asymptote (carrying capacity), indicating that the population displayed logistic growth over the long term.

## Ecological and life history traits

### *Aquatic variables*

Comparisons among the abiotic variables evaluated in the natural distribution area of *H. orthonops* and in the biotopes of the invaded area in the Upper Paraná River indicate that the predominant values of these variables in the Upper Paraná River (25th and 50th percentiles) are contained in the total variation observed in the area of origin (Cuiabá River and Middle Paraná River)—Fig. 3. The extreme values of transparency and pH observed in the invaded area were higher (450 cm; Fig. 3b) and lower (5.0; Fig. 3d), respectively, than those from the natural distribution area.

### *Somatic growth rate*

The results of the somatic growth rate indicate two important characteristics, as follows: (i) high somatic growth rates for the species *H. orthonops*, in comparison to the rates of other species of the Upper Paraná River watershed, compiled by Lizama & Takemoto (2000) (Table 2) and (ii) flexibility in the somatic growth rate, considering that the somatic growth rates for *H. orthonops* varied from 0.56 to 1.16 (Table 2).

### *Diet composition and plasticity*

Detritus and algae were the most important food resources consumed by *H. orthonops* in both the native

**Table 2** Parameters of the somatic growth curve of *Hemiodus orthonops* populations in the Cuiabá River (native area) and Upper Paraná River (invaded area)

| Species | River basin | Male | | Female | |
|---|---|---|---|---|---|
| | | $L_\infty$ | $K$ | $L_\infty$ | $k$ |
| *Hemiodus orthonops* | Cuiabá | 27.3 | 0.56 | 30.5 | 0.64 |
| | Upper Paraná | 27.3 | 1.16 | 30.5 | 0.9 |
| Detritivorous species[a] | Upper Paraná | | 0.31 | | 0.26 |
| Other species[a] | | | 0.33 | | 0.28 |

[a] *Source* Lizama and Takemoto (2000)

**Table 3** Occurrence (Fi) and dominance (D) of dietary items of *Hemiodus orthonops* in the Cuiabá River (native area) and Upper Paraná River (invaded area)

| Food items | Cuiabá River | | Upper Paraná River | |
|---|---|---|---|---|
| | Fi | *D* | Fi | *D* |
| Algae | 97.5 | 35.4 | 85.4 | 39.4 |
| High plants | 22.8 | | 49.1 | 18.4 |
| Invertebrates | 21.5 | 5.1 | 17.3 | 5.5 |
| Detritus | 93.7 | 59.5 | 80.9 | 36.7 |

and invaded sites (Table 3). However, significant differences were found among them, even when only the occurrence is considered (PERMANOVA: pseudo-$F_{1,187} = 6.72$; $P < 0.001$), indicating diet plasticity.

### *Reproduction and migration*

The values of the Index of Reproductive Activity (IRA) showed that the reproduction of the species in both the native and invaded areas occurs in the river channel in the stretches upstream of the sampled area (Fig. 4c) and is incipient (IRA $< 5.0$) in plain areas (Fig. 4a, b). In addition, the frequency distribution of the lengths in the different biotopes reveals that, in both the native (Fig. 4d–f) and invaded (Fig. 4g–i) areas, juveniles predominate in the floodplain lakes while adults predominate in the upstream stretches, indicating migratory movements related to reproduction.

The long-distance migration ability of *H. orthonops*, inferred from the comparison of its morphometry with the data in the literature (Olden et al., 2006), showed that the body shape of *H. orthonops* differed significantly from that of species with no fluvial dependence ($F_{2,127} = 41.256$; $P < 0.001$) but did not differ from the shape of species with fluvial dependence (Fig. 5). The value of the swim factor of *H. orthonops*, however, was significantly lower than that of species with and without fluvial dependence ($F_{2,127} = 0.318$; $P < 0.001$), indicating that *H. orthonops* is a strong swimmer.

The values of the Index of Reproductive Activity for the *H. orthonops* females in their natural distribution area indicate that this species displays high seasonality in its reproduction, with intense reproduction (IRA $>$ 10) occurring only in October and November (Fig. 6a), during the beginning of the floods. The frequency distribution of oocyte diameters in the ovaries in the spawning-capable phase reveals that only one batch of fully yolked oocytes is present, indicating total spawning, which is compatible with the high seasonality in spawning. This trend was observed in both the natural and invaded distribution areas, even when considering the differences in the maximum diameters recorded between these areas (Fig. 6b, c).

### *Reproductive investments*

The evaluation of the aspects related to the reproductive investment of *H. orthonops* in the natural distribution area reveals that the species displays small oocytes (diameter <0.8 mm) in large numbers (maximum fecundity = 188,000) and a high relative weight of the ovaries (GSI = 21.5)—Fig. 7 and Table 4. The values obtained in the invaded area indicate that the species displays a considerable phenotypic plasticity regarding these reproductive aspects (Fig. 7).

## Variations in ecological, morphological and life history traits

The environments invaded by *H. orthonops* displayed ranges of the physical and chemical environmental variables that rarely exceeded the limits recorded in the natural distribution area and, in general, had similar extremes. The exceptions were the high conductivity values (maximum of 442 $\mu S\ cm^{-1}$ in the native area, compared to 117.8 $\mu S\ cm^{-1}$ in the invaded area) and the transparency, which had larger

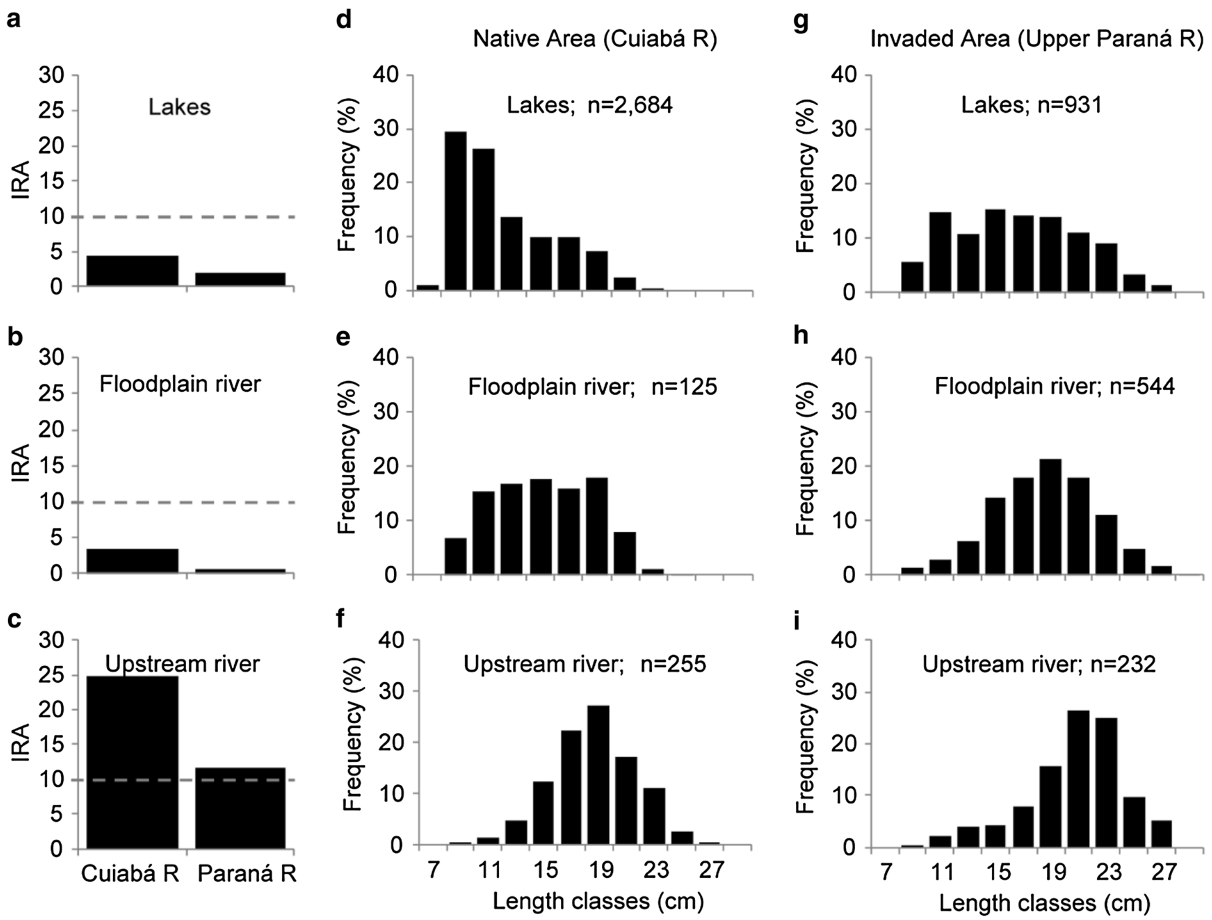

**Fig. 4** Values of the Index of Reproductive Activity (IRA; **a–c**) and frequency of standard length classes in different biotopes (floodplain river, floodplain lakes, and river channel upstream) of the native range (Cuiabá River, **d–f**) and invaded area (upper Paraná River; **g–i**). $n$ = sampling size

maximum values in the newly occupied environment compared to the native one (Table 4; Fig. 3).

Considering the life history traits, *H. orthonops* displays higher somatic growth rates in the invaded area for both genders. Although the maximum sizes are similar between the two areas, the frequency of individuals in the larger length classes is higher in the invaded area. Conversely, older ages are reached in the native area.

The analysis of the sexual proportion, which was of 1:1 in the native area, showed a predominance of males (1:1.3) in the invaded area. The females reached maturity at larger sizes, while males reached maturity at smaller sizes, in the invaded area. However, there was no difference in the age of the first maturation (1 year). The reproductive investment, inferred from the higher relative weight of the ovaries (GSI) and the larger number of oocytes (fecundity), is higher in the native area. However, the diameter reached by the mature oocytes is higher in the invaded area (Table 4; Fig. 7).

Regarding the diet, although detritus, algae, and higher aquatic plants were the most frequent items, higher aquatic plants is a dominant item only in the invaded area, where the dominance of algae is slightly higher.

## Discussion

In this study, we demonstrated that the installation of fish pass that establish connections between historically

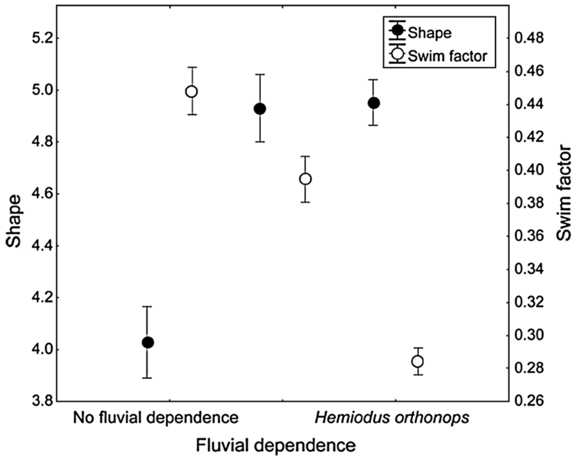

**Fig. 5** The mean (±standard error) of the shape of the body (ratio between the total length and the maximum height) and of the swim factor (ratio between the height of the caudal peduncle and the height of the caudal fin) for fish with and without fluvial dependence (compiled from Olden et al., 2006) and for *Hemiodus orthonops* in the floodplains of the Upper Paraná and Cuiabá Rivers

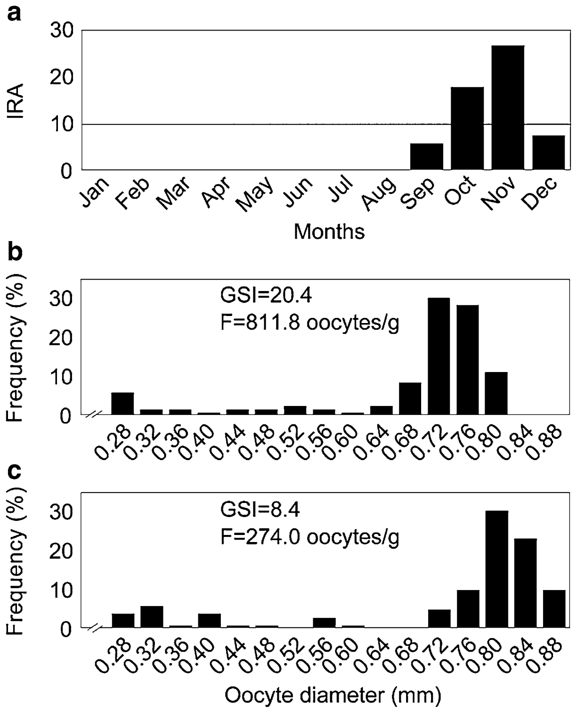

**Fig. 6** The monthly Index of Reproductive Activity (IRA) for *H. orthonops* in the native area (**a**), frequency distribution of oocyte diameters from ovaries in the spawning-capable phase for the Cuiaba River basin (**b**) and upper Paraná River Basin (**c**)

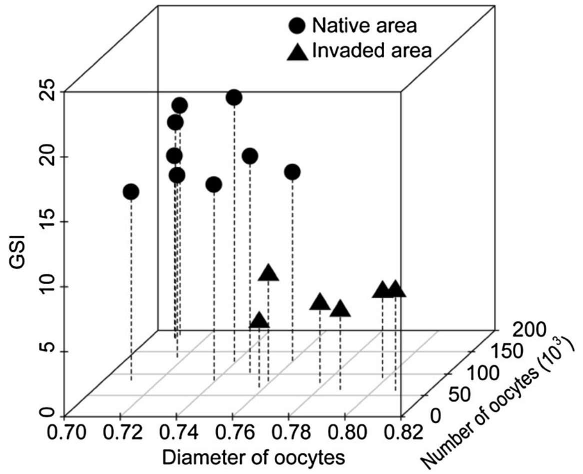

**Fig. 7** The relationship between the Gonadosomatic Index (GSI), diameter, and number of oocytes of *H. orthonops*, considering the females in the spawning-capable phase and their standard lengths in the natural and invaded areas

separated ichthyofauna enables the invasion and fast occupation of upstream environments by *H. orthonops*, which displays peculiar life history traits including migration, high reproductive seasonality, single batch spawning, and differential occupation of distinct biotopes (lentic and lotic) during the life cycle (seasonal strategy, sensu Winemiller, 1989). Sometimes, these characteristics are opposite to those considered more appropriate for invasion. Biological invasions have been better predicted by parental care, spawning in multiple batches, prolonged reproductive periods, egg with abundant reserves, moderate mobility, or sedentarism (equilibrium or opportunistic strategies, sensu Winemiller, 1989; Marchetti et al., 2004; Ruesink, 2005; Moyle & Marchetti, 2006). In addition to these characteristics, other life history traits have been related to success in dispersal and colonization, with an emphasis on propagule pressure, success in the colonization of other areas, maximum size of adults, size and distance of the native area, physiological tolerance, and trophic status (Marchetti et al., 2004; Lockwood et al., 2009). Although the role of propagule pressure in the process of dispersal and colonization was not evaluated in this study, the fish passage stays open constantly, which enables the continuous access of fish to the upstream stretches. Other aspects not analyzed in this study were biological interactions, such as predation and competition, which were considered important in the invasion process (Dick, 1996; Simberloff & Von

**Table 4** Comparison of the ecological and life history traits of the *Hemiodus orthonops* populations in the Cuiabá River (native area) and the Upper Paraná River (invaded area)

| Traits | Cuiaba River | Upper Parana River |
|---|---|---|
| Ecological | | |
| Abiotic "tolerance" | Higher conductivity | Higher transparency |
| Life-history | | |
| Somatic growth | | |
| Female growth rate ($year^{-1}$) | 0.64 | 0.90 |
| Male growth rate ($year^{-1}$) | 0.56 | 1.16 |
| Female maximum SL (cm) | 29 | 29 |
| Male maximum SL (cm) | 25.5 | 26 |
| Female maximum age (year) | 5 | 3 |
| Male maximum age (year) | 5 | 3 |
| Reproduction | | |
| Sex ratio F:M (total) | 1:1 | 1:1.3 |
| Female length at maturity (cm) | 17.1 | 19.4 |
| Male length at maturity (cm) | 15.8 | 15.2 |
| Age at maturity (year)—both sexes | 1 | 1 |
| Female maximum GSI | 21.55 | 8.46 |
| Male maximum GSI | 2.45 | 2.43 |
| Oocyte diameter (mm) | 0.73 | 0.79 |
| Mean relative fecundity (no. oocyte/g) | 759.3 | 217.3 |
| Maximum fecundity | 188,410 | 79,653 |
| Spawning type | Total | Total |
| Diet and feeding | | |
| More frequent items | Algae, detritus, plant | Algae, detritus, plant |
| More dominant items | Detritus, algae | Algae, detritus, plant |
| Trophic guild | Detritivore/ algivore | Algivore/ detritivore |

Holle, 1999; DeRivera et al., 2005; Fugi et al., 2008). An evaluation of the invasion potential of this species based on the history of other invasions was not possible because there are no other known attempts to introduce this species in other environments, in part because this species has little economic interest and is not an object of cultivation or fishing (Terraes et al., 1999). Although *H. orthonops* is abundant in artisanal fishing in the Itaipu reservoir, it is not a target species for this activity, especially because of its size and consumption acceptance (A.A. Agostinho, personal observation). Its maximum size (29.0 cm), however, is in the intermediate length range, which is a characteristic considered less susceptible to invasion failure by Moyle & Marchetti (2006). Conversely, the geographic proximity and the landscape similarity between the native and invaded areas observed in this study appear to have been decisive for the invasion process. In this sense, geographically closer areas are more similar in terms of hydrological conditions and seasonality than more geographically distant areas, increasing the probability of success by the invader (Moyle & Light, 1996; Marchetti et al., 2004; Gherardi, 2007). Furthermore, a supposed absence of floodplain lakes and rivers in the invaded area could have restricted the colonization of the species, considering that these biotopes are essential for the initial development of *H. orthonops*. Some species that coexist with *H. orthonops* and have similar traits (reproductive migration, use of different biotopes during their life cycle), such as *Pterodoras granulosus, Sorubim lima, and Leporinus macrocephalus*, also reached the upper Paraná River (Júlio Júnior et al., 2009) and became abundant. Moyle & Marchetti (2006) reported that the environmental resistance to the invasion of a given species is most likely lower when the characteristics of the new area are similar to those of the area of origin.

A tolerance to variations in the environmental conditions has been considered an important aspect for the invasion success (Moyle & Light, 1996; Jiguet et al., 2006). An evolutionary explanation for this process is provided by the "ecological fitting" concept (Agosta & Klemens, 2008). An indicator of high tolerance and potential fitness can be the width of the native geographic area. For the species studied, this area extends between the latitudes of 14°S and 33°S, and the invaded area is within this native area (22°43′S–25°33′S). However, the use of the extension of the native geographic area as a predictor of invasion success was not corroborated in the studies of Moyle & Marchetti (2006). In our study, the tolerance range of *H. orthonops* was determined from the variations in the chemical and physical variables of the water in the biotopes of the native area occupied by this species, including the sites closer to the latitudinal extremes of its natural distribution. The results showed that the variations in these water quality conditions in the native area were also within the range of the extremes of each variable considered, which must have contributed to the dispersal and colonization of the species in the invaded area. In their studies on streams in North America, Moyle & Light (1996) showed that abiotic resistance is a more important factor for the colonization of new areas than the resistance imposed by native biota. The real tolerance range of *H. orthonops*, both native and invaded area, may be narrower than the field measurements (e.g., anoxic conditions or temperatures of 36°C), given that individuals could avoid these conditions by seeking refuge in more favorable parts of the environment.

However, the similar biotopes between the areas (lakes, channels, and river channel) allows for the assumption that the species may use the same strategy in the invaded area. In addition to the climatic similarity, the success rate in the occupation of the new area should reflect a similarity in the flood regime, which is a seasonal disturbance that regulates the functioning of both watersheds studied (Thomaz et al., 2007; Bailly et al., 2008). In this context, Moyle & Marchetti (2006) attribute the success of the occupation of a watershed by species from adjacent watersheds to the higher similarity of these conditions.

The population of *H. orthonops* of the Upper Paraná River displayed fast growth, and the dynamics of this growth in the complete series (2008–2014) were better explained by the logistic model, which is considered the most realistic model to explain the long-term population growth of invasive species (Gilpin & Ayala, 1973; Turchin, 2003; Forsyth et al., 2013). However, invasive species may reach high growth rates in the initial period of their expansion, approaching the exponential model (Bedarf et al., 2001; Crooks, 2005), which occurred in the population of *H. orthonops* in the invaded area. The absence of restrictions imposed by density-dependent factors, at first, and the exacerbation of these restrictions after a given population size is reached explain the changes in the growth rates.

Côté et al. (2013) attribute the colonization success of invasive species to the following: (i) mechanisms that facilitate dispersal, such as the ability to overcome natural barriers, larval dispersal, reproduction type, high fecundity, high survival of eggs and larvae, and post-settlement dispersal and (ii) mechanisms that facilitate population growth, such as a fast life history, competitive ability, and enemy release. The colonization success of *H. orthonops* in the Upper Paraná River watershed was facilitated by the access provided by the Itaipu dam fish passage, followed by the environmental conditions of this watershed stretch and by the life history traits that are characteristic of this species. Some noteworthy strategies that facilitated the dispersal of this species are migration, which was inferred by its morphological characteristics (shape and swim factors), and spatial variations in reproductive activity, in addition to size stratification by biotopes. The spawning type, another life history characteristic related to invasion success, was identified as total spawning in both the native and invaded areas. However, this result is not consistent with the literature; in the middle Paraná River, this species displays multiple spawning (Flores & Hirt, 1998), which was determined by the analysis of only 50 oocytes in histological sections. Although the migration and total spawning (highly seasonal and in the river channel) are not peculiar characteristics of a species with invasion vigor, they provide a higher dispersal power for both the larvae and adults. Although *H. orthonops* does not display prolonged reproduction, this trend must have been compensated by the constant propagule pressure from the downstream stretches resulting from the fish passage, with the migratory ability of this species being fundamental in this process. Furthermore, the presence of spawning schools for a short time in the spawning area may reduce predation by other large size migrants that also reproduce in the upstream stretches of the plain. The predation of *H. orthonops* by large carnivorous fish has been reported for the downstream stretches of the Paraná River (Flores & Hirt 1998/1999). However, in the invaded area, this species was recorded in just one stomach (of 1,480 stomachs) of the 12 piscivorous species examined (L.Strictar-Pereira, unpublished data).

The values estimated in other traits related to the reproductive investment (GSI and number and size of oocytes), somatic growth rate, size at maturity, and diet, and the flexibility of these traits, as evidenced by the differences in their values between the populations of native and invaded areas, may be considered life history attributes related to invasion success, especially in the population growth (Denney et al., 2002; Polacik et al., 2009; Brandner et al., 2013; Kirankaya

& Ekmekçi, 2013). However, the increased number of oocytes and relative weight of the gonads (GSI) were not maintained in the invaded area, where they reached half of the values in the native area. Conversely, the somatic growth rates for both genders were higher in the invaded area. A negative relationship between the fecundity and population growth was reported in the studies of Denney et al. (2002) in marine environments, where higher somatic growth rates were also observed in the populations with high growth. Brandner et al. (2013) recorded high somatic growth rates and lower GSI values in recently invaded areas and suggested that somatic performance appears to be more important than investment in reproduction during the initial invasion phases. It is likely that these alterations in life history parameters represent tactical changes during the occupation of the new area related to inter and intraspecific pressures such as predation, competition and/or density-dependent mechanisms. We emphasize, however, that the diameter of oocytes was higher in the invaded area. Larger oocytes usually produce larger larvae with higher survival chances (Marteinsdottir & Steinarsson, 1998), indicating a greater emphasis of the reproductive effort on larval viability.

Although omnivory is considered a favorable strategy for the invasion success of fish (Ruesink, 2005), the diet of *H. orthonops* is based on food items of a low trophic level and is composed mainly of detritus and algae, thus showing a considerable level of specialization. However, the ability to forage resources of low trophic levels has been considered a trait that favors the success of invasive fish (Koehn, 2004; Gido & Franssen, 2007). Indeed, the success of omnivorous/detritivorous invasive fish can be positively associated with the availability of feeding resources, which are rarely limiting in aquatic ecosystems during the establishment phase (Moyle & Light, 1996). Therefore, omnivorous fish may have an advantage during the invasion stage because they find food resources capable of sustaining the propagules. However, species that are able to sustain growth and reproduction with a diet based on low quality resources tend to become integrated into the local community (Gido & Franssen, 2007), such as the case of detritivorous species. The differences in diet between the native and invaded areas were restricted to a slight dominance of algae followed by detritus in the invaded area. The consumption of aquatic plants, although recorded in the diet of the species in the natural area, predominated only in the invaded area. These changes likely occur because of the high transparency values of the invaded area, a condition that is not found in the native area. The high transparency values of the Upper Paraná River have facilitated the colonization of plain habitats by submerged aquatic plant species (Thomaz et al., 2009b), which may have also contributed to the establishment of new species of periphytic algae (Murakami et al., 2009). Therefore, the finding that *H. orthonops* consumes basically detritus and algae, which are highly available resources in aquatic environments, may have facilitated its fast colonization and expansion into the habitats associated with the Upper Paraná River.

In conclusion, the invasion success of *H. orthonops* was related to its dispersal ability, favorable environmental conditions (similar to the native area) in the new environment, ability to explore a food resource with high availability, early maturation, and high somatic growth rate. Therefore, the dispersal of *H. orthonops* to the Upper Paraná River stretches, which was enabled by the construction of a fish passage in the Itaipu dam, was due to the swimming capacity of this species. Its establishment, however, was favored by the similarity of the physiographic and limnological conditions between the native and invaded areas and by the plasticity of the life history traits related to trophic status, reproduction and growth.

Our results demonstrate that abiotic conditions have high predictive power in determining the success of invasive species in new environments. Then, species confined to part of a basin by the existence of natural barriers or present in neighboring basins have more chance to be successful due to a reduction in abiotic resistance. This draws attention to the importance of considering barrier elimination by impoundments or fish passage facilities built close to dams in fish introduction. This is true even on the route used by *H. orthonops* to arrive in the upper Paraná River: 25 species recorded in the fish passage at the Itaipu Dam (Makrakis et al., 2007) were still not found upstream. However, the continuous source of propagules represented by the fish passage suggests that the discovery of new species upstream is just a matter of time.

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