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ORIGINAL PAPER

Are non-native species larger in their invaded range? A test with tropical floodplain fish assemblages following inundation of a biogeographic barrier

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Abstract There is a purported tendency for non-native species to have larger body sizes in their introduced range, commonly attributed to mechanisms such as enemy release or reduced competition. However, results are equivocal and this tendency may also result from ecosystem differences and/or the selective introduction of larger individuals. For most invasions it is difficult to separate the human from biological influences on body size. In this study, we utilize a natural experiment caused by the elimination of a semi-porous biogeographical barrier to test for body size differences in 12 Neotropical fish species in native and invaded ranges, unbiased by human influence in selecting introduced individuals. Our analyses include an additional 25 fish species native to both basins, enabling tests of consistency of body size patterns across native and non-native species in both ecosystems. Twenty-two species (9 non-native, 13 native), irrespective of life-history or trophic guild, had an interaction of population length-weight relationships which indicated inconsistency in relative body sizes in donor and recipient regions across age classes. Of the 15 species with similar slopes of the length-weight relationships between basins, all non-native species (n = 3) and five species native to both basins exhibited significantly larger body sizes (i.e. body mass at a given length) in the more

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productive donor ecosystem, and the remaining native species were either larger in the recipient system (n = 3) or were not significantly different between basins (n = 4). Our findings contribute to the growing literature that suggests perceived tendencies of larger body sizes in invaded ranges should not be generalized, especially when environmental conditions differ greatly among regions and when dealing with populations that exhibit significant age structure.

Keywords Body size · Productivity · Enemy-release hypothesis · Natural experiments

Introduction

Successful establishment of non-native species is determined by interactions among environmental, biological and human factors (Shea and Chesson 2002; Thuiller et al. 2006). Given the numerous intervening factors, an important issue associated with biological invasions is determining characteristics common to non-native species and invaded areas, and from them inferring mechanisms likely influencing invasion success as well as establishing effective prevention, management, and control measures of non-native species (Forsyth et al. 2004; Ruensink 2005). For example, body size is an important biological characteristic related to different physiological and ecological processes, such as metabolic rates (Brown et al. 2004), patterns of distribution and abundance (White et al. 2007), trophic position of species (Woodward and Warren 2007) and vulnerability to extinction (Olden et al. 2007). Considering biological invasions, a reported tendency, regardless of taxonomic group, is that non-native species have larger body sizes in invaded areas when compared with native habitats (Blossey and Nötzold 1995; Roy et al. 2002; Grosholz and Ruiz 2003; Leger and Rice 2003; Ebeling et al. 2008; Darling et al. 2011). However, other studies have found contradictory patterns or have identified significant variability among species (Thébaud and Simberloff 2001; Miller et al. 2002; Vilà et al. 2005; Parker et al. 2013).

In most cases, it is difficult to distinguish among ecological (e.g. release of natural enemies, positive relationship between body size and dispersal rates, increased competitive ability) and anthropogenic factors (e.g. selection and introduction of larger individuals of the species of interest; Miller et al. 2002) affecting the establishment of non-native species. This separation between ecological and human factors is even more difficult for species of cultivation, as there is often selection of larger individuals which causes a sampling bias that may confound the interpretation of body size patterns in native and non-native ranges (Miller et al. 2002, Colautti et al. 2006). Moreover, environmental conditions can influence species' relative body size among habitats. For example, lower resource availability may select for smaller individual body size and hence a smaller average size of the population (Brown and Sibly 2006). These possibilities are generally neglected when explaining the difference in body size between populations of a species in native and non-native areas. Instead, differences in body size are more frequently interpreted as the result of, or release from, negative biotic interactions (e.g. competition, parasitism, predation; see Torchin et al. 2001, Grosholz and Ruiz 2003).

Comparative studies that include many species with diverse ecological traits and evolutionary histories may help assess the probability of ecological vs. anthropogenic influences on body size patterns in native and non-native ranges (van Kleunen et al. 2011; Parker et al. 2013). In particular, some events of introduction and establishment of non-native species may work as unplanned experiments, unintentionally controlling part of these influences (Sax et al. 2007). The introduction of species made possible by the elimination of biogeographical barriers enables evaluation of the differences in biological characteristics (e.g. body size) without direct human influence in selecting the introduced individuals. In this way, such studies may only measure the ecological component of body size variation between native and non-native areas. A second type of comparative control is possible when the two biogeographic regions of interest (i.e. donor and recipient regions) share other species native to both regions (Thébaud and Simberloff 2001). Specifically, if the status of being non-native is an important factor promoting ecological success in the non-native region (e.g. due to the lack of natural enemies) it is expected that non-native species respond differently when compared with native species shared by both regions.

This study takes advantage of the unintentional colonization and establishment of fish species between two Neotropical floodplains made possible by inundation of a biogeographic barrier. We address the following questions: (i) do body sizes of non-native species differ between native and non-native regions?; (ii) do differences in body sizes of species native to both the donor and recipient regions show similar patterns to those of non-native species?

Materials and methods

Study areas

Data were collected from two regions: the Upper Cuiabá River basin (UCR) and the Upper Paraná River Floodplain (UPRF). The Upper Cuiabá River basin, located in Mato Grosso State, Brazil, has a total area of about 29,162 km^2. Its major tributary is the Manso River with a catchment area of approximately 11,000 km^2. The Cuiabá River drains an extensive area until the confluence with the Paraguay River in the Northern Pantanal. In turn, the Paraguay River is one of the major tributaries of the Lower Paraná River, and there are no natural barriers that geographically isolate the lower from the upper basins (Fig. 1).

The Upper Paraná River basin is approximately 880,000 km^2, draining more than 10 % of Brazilian territory (Agostinho et al. 2007). The basin is heavily impounded, and the last free-flowing stretch of this basin, approximately 230 km in length, is located between Porto Primavera Dam and Itaipu Reservoir (Agostinho et al. 2004). This stretch is accompanied by a wide floodplain (Upper Paraná River Floodplain—UPRF) and is of high ecological importance for maintenance of regional biodiversity, ecological functions and ecosystem services (e.g. Hoeinghaus et al. 2009). Upstream impoundments, especially Porto Primavera Reservoir immediately upstream of the floodplain, retain sediments and cause oligotrophic conditions in the floodplain (Roberto et al. 2009). A series of waterfalls (Sete Quedas, Fig. 1) located down-river from the floodplain historically functioned as a semi-permeable biogeographic barrier that separated the fish faunas of the Upper Paraná River from the rest of the Paraná-Paraguay basin. This natural biogeographic barrier was flooded by the filling of Itaipu Reservoir in 1982, which allowed the colonization of the Upper Paraná basin by species from the Lower Paraná and Paraguay Rivers (Júlio et al. 2009; Vitule et al. 2012). Species native to the Lower Paraná and Paraguay basins are still able to colonize the Upper Paraná basin through a fish passage facility located at Itaipu dam (e.g. Agostinho et al. 2015). Additional details on the UPRF can be found in Thomaz et al. (2004).

These two regions have conditions interesting for the study of biological invasions. The first is that these regions share at least 45 fish species, belonging to different families and representing diverse life-history strategies and trophic ecologies. Among them, 15 are native to the UCR and colonized and established in the UPRF following the flooding of the biogeographic barrier (Júlio et al. 2009; Vitule et al. 2012). Many of these non-native species are currently abundant. The other 30 species present in both study systems have broad distributions and are native to both regions. There are no records of non-native species in the UCR that are native to the UPRF.

Data collection

For both locations, water temperature, transparency, conductivity, dissolved oxygen, and pH were measured at the same time as each fish collection (i.e. quarterly from 2000 to 2004). The quarterly sampling regime yields samples from all of the major river phases (i.e. flood, dry and transitional seasons) and thus the data are representative of the range of conditions in these two study areas. Water transparency was measured using a Secchi disk and the other parameters were measured with handheld probes. Additional variables related to ecosystem productivity [i.e. turbidity and concentrations of total phosphorus, phosphate (PO_4^{3-}), nitrate (NO_3^{-}), total nitrogen, and ammonia nitrogen (NH_4^{+})], were measured at 10 sampling sites for the two studied systems during the same time period for a total of 380 samples. Water samples for analysis of dissolved nutrients were stored on ice in the field and frozen (−20 °C) for subsequent analysis following standard methods (e.g. Golterman et al. 1978). Data were obtained from the database of the Long Term Ecological Research Program for the UPRF and from the Brazilian National Water Agency (Agência Nacional de Águas 2011) for the UCR.

Data for fish species common to both regions were compiled for the period between 2000 and 2004 from databases of the Research Nucleus in Limnology Ichthyology and Aquaculture (Nupélia) at the State University of Maringá, Brazil. Fishing effort was

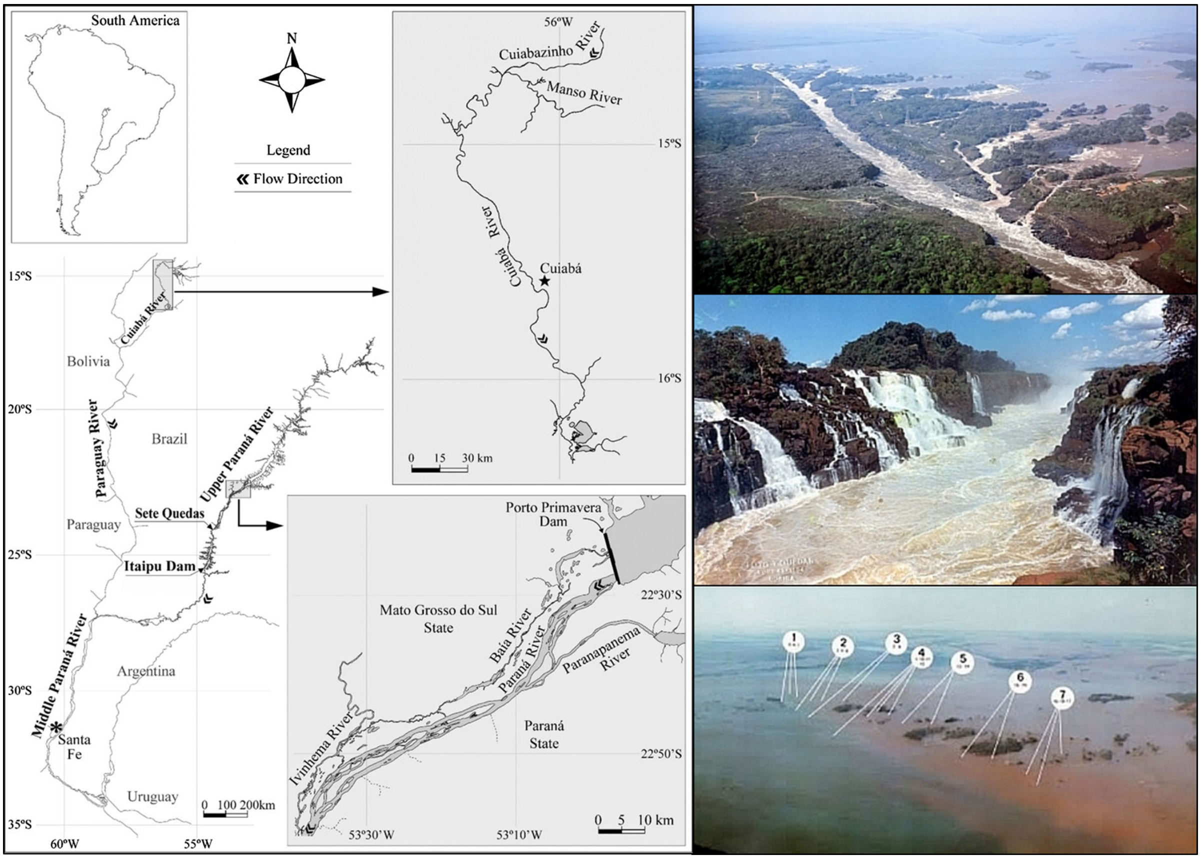

Fig. 1 Map of South America indicating the Paraná River basin (inset *top left*) and study regions within the Paraguay River basin (Upper Cuiabá River, upper shaded inset) and Upper Paraná River basin (Upper Paraná River Floodplain, lower shaded inset). Note the locations of 'Sete Quedas' (Seven Falls) and 'Itaipu Dam' in the main map, just downstream of the Upper Paraná study area. The *top two images* at the right depict the semi-porous biogeographic barrier formed by Sete Quedas prior to filling of Itaipu Reservoir. The *lower image* depicts the flooding of the falls (*1–7* identifying the former locations; compare with the *top image*) during filling of the reservoir

standardized for both areas, allowing for control of sampling bias, and consisted of both passive (gill nets, long-lines) and active capture techniques (seines, rod and reel). Most captures were achieved using experimental gill nets with multiple mesh sizes (2.4, 3.0, 4.0, 5.0, 6.0, 7.0, 8.0, 9.0, 10.0, 12.0, 14.0 and 16.0 cm between opposite knots). Gill nets were exposed for 24 h and checked in the morning (08:00 h), evening (16:00 h) and at night (22:00 h). Seines (20 m long, 0.5 cm mesh) were operated in littoral zones of lentic environments during the night and morning. Long-lines were operated only in lotic environments, baited with live baits in the evening and inspected the next morning. Sampling locations in both study areas represent the diversity of aquatic habitats in each system (i.e. multiple locations broadly distributed within the inset study area panels in Fig. 1) and include primary and secondary river channels as well as floodplain lakes that are perennially connected to channels or seasonally connected by rising water levels. For both study areas, all individuals collected were taken to the laboratory and measured for standard and total length (cm), weighed (g), and eviscerated for classification of reproductive stage and weighing of the gonads and stomachs. We classified the species' life-history strategies and trophic ecologies according to Suzuki et al. (2004) and Corrêa et al. (2009), respectively.

Dataset and statistical analyses

To test for potential effects of environmental conditions and ecosystem productivity on body-size patterns between study regions, we first calculated the annual mean of environmental variables to control for effects of seasonality. Mean values were subsequently standardized and tested for differences in environmental conditions between regions using a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001). Euclidean distance was used to build a dissimilarity matrix, with 10^3 permutations to calculate the statistical significance. In order to indicate which variables were most influential in distinguishing between locations, we used a Principal Coordinates Analysis (PCoA) based on the standardized Euclidean distance matrix.

After excluding species with fewer than 20 individuals collected in each study region (to control for effects of small sample sizes on body size patterns) and quality control, our dataset includes 26,236 individuals collected in the UPRF and 79,651 individuals collected in the UCR during the study period. This study includes 37 of the 45 species known to occur in both regions, 12 of which are non-native to the UPRF and 25 are native to both regions. The species list for our analyses, including species sample sizes and ranges of standard length, is provided in Table S1.

To test the hypothesis of larger body size in invaded ranges, we used an analysis of covariance (ANCOVA; Cone 1989; García-Berthou 2001; Sokal and Rohlf 2012) with weight as the response variable, standard length as the covariate and region (UCR and UPRF) as the categorical variable. This analytical approach tests for differences between populations in weight at a given length, and thus is useful for comparing body condition between populations of the same species in our two study regions while controlling for the effect of body length or age structure (e.g. Hoeinghaus et al. 2006). The quantitative variables weight (Wt, g) and standard length (SL, mm) were log-transformed to yield a linear relationship and meet statistical assumptions. For species with no difference in the slope of the length-weight relationships between regions (i.e. homogeneity of regression slopes, no significant interaction between 'region' and 'LogSL'), weight was compared between regions using the adjusted means (Quinn and Keough 2002; Sokal and Rohlf 2012). Sample sizes are unequal for all species, thus we used Type III sum of squares and critically evaluated the assumption of homogeneity of variance using a combination of residual spread and Q–Q plots, Levene's test and the ratio of the largest to smallest group variance (large departures in group variance combined with unequal sample sizes can affect Type I error rates or reduce power)(Quinn and Keough 2002; Gotelli and Ellison 2004). Violations of homogeneity of variances were very minimal, only for a few species, and never combined with disparate group variances (all ratios <3.0 and most <2.0).

To test for independence of species' body size patterns from native/non-native status and trophic and life-history guilds, results from ANCOVAs were used as responses in contingency tables after being classified into five categories [i.e. significantly larger in donor region (i.e. UCR), significantly larger in recipient region (i.e. UPRF), no significant difference between regions, significant interaction and greater regression slope in the donor region, and significant interaction and greater regression slope in the recipient region]. Contingency tables were compiled using counts for ANCOVA result categories across each of three predictor variables: native status (i.e. native or non-native to UPRF), trophic guild (i.e. detritivore/herbivore, insectivore/invertivore/planktivore, omnivore, or piscivore) and life-history strategy (i.e. equilibrium, periodic, or opportunistic). Trophic categories were grouped into the four categories described above due to the excessively large number of unique combinations and zero cells when using all seven guilds separately. Contingency tables were also compiled to test for independence of native status and trophic and life-history guilds. For each contingency table, the likelihood ratio (i.e. *G*-test) was calculated using Williams' correction for small sample sizes (Gotelli and Ellison 2004). All analyses were performed using R, and the significance level was set at $P \leq 0.05$ for all tests.

Results

Environmental conditions were significantly different between the two regions ($F = 25.12, P < 0.001$), with the first two principal coordinates explaining 81.75 % of the total variation (Fig. 2). The variables Secchi depth and concentrations of phosphate, ammonium and total phosphorus contributed the most to the difference between regions. Secchi depth was approximately seven-fold greater in the UPRF than in UCR. On the other hand, nutrient concentrations were higher

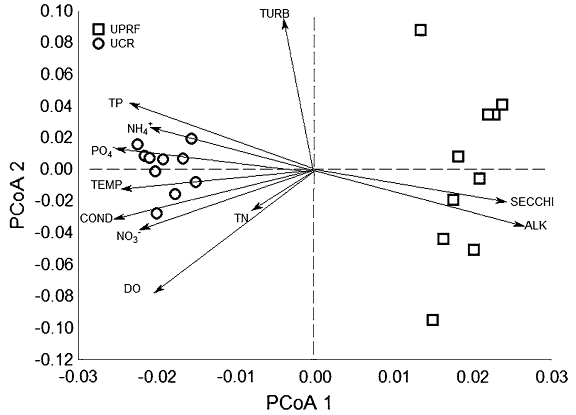

Fig. 2 Sample scores and loadings for the first two axes of Principal Coordinates Analysis of environmental data from the Upper Paraná River Floodplain and the Upper Cuiabá River. Summary values and abbreviations are in Table 1

in the UCR (Table 1). Thus, if ecosystem productivity has a strong effect on body sizes between systems, individuals from the UCR should be larger than those from the UPRF.

Of the 37 studied species, 22 presented significant interactions between regions in their length-weight relationships (Table S1), i.e. the difference in weight among individuals of those species between regions was not consistent over their range of lengths. Of those 22 species, exactly half had higher slopes for the length-weight relationship in each region. Considering only those species with interactions and non-native to the UPRF ($n = 9$), five species had higher slopes in UPRF and four had higher slopes in UCR. Furthermore, the type of interaction (e.g. in the middle, at either extreme or outside of the length distribution) was not consistent across taxa, but no species had a consistently higher weight across the entire length distribution (regardless of regression slope) in one basin. Therefore, for the 22 species with a significant interaction, the lack of parallelism of slopes is enough to reject our initial hypothesis of larger individuals in the invaded range.

Slopes of the length-weight relationships were parallel between regions for the remaining 15 species (Table 2, Table S1), which allowed us to test the null hypothesis that adjusted mean weight was not different between regions. Of those 15 species, the three species non-native to UPRF all had adjusted mean weight significantly higher in their native region (Table 2; Fig. 3). The same pattern of higher adjusted mean weight in the UCR was observed for five species native to both regions (Table 2; Fig. 4). *Gymnotus inaequilabiatus, Leporinus obtusidens, Pseudoplatystoma corruscans* and *Salminus brasilensis*, species native to both regions and of wide geographic distribution, had no significant differences in body size between the studied regions. Only three species native to both regions (*Hyphessobrycon eques*, *Pyrrhulina australis* and *Schizodon borelli*) presented higher adjusted mean body weight in the UPRF (Fig. 4).

Species non-native to UPRF were primarily equilibrium or opportunistic strategists (vs. primarily periodic and opportunistic strategists for natives) and were more evenly represented among trophic guilds (vs. dominance by invertivores and underrepresentation of

Table 1 Mean (± standard deviation) of environmental variables from the Upper Paraná River Floodplain (UPRF) and Upper Cuiabá River (UCR)

Variable	Units	UPRF	UCR
Alkalinity (ALK)	(mEq/L)	243.1 (76.39)	38.59 (10.70)
Conductivity (COND)	µS/cm	43.0 (10.97)	85.0 (19.10)
Phosphate (PO_4^-)	µg/L	7.2 (2.97)	36.2 (6.73)
Total Phophrus (TP)	µg/L	50.4 (29.23)	145.2 (21.67)
Nitrate (NO_3^-)	µg/L	64.6 (42.06)	103.1 (12.95)
Ammonia nitrogen (NH_4^+)	µg/L	18.2 (16.36)	76.3 (41.84)
Total Nitrogen (TN)	µg/L	411.7 (140.7)	358.0 (61.28)
Dissolved oxygen (DO)	µg/L	5.8 (0.92)	6.9 (0.35)
pH		6.6 (0.32)	7.5 (0.12)
Water temperature (TEMP)	°C	25.0 (0.68)	27.9 (0.29)
Transparency (SECCHI)	cm	318.5 (50.43)	43.1 (7.13)
Turbidity (TURB)	NTU	17.8 (12.43)	19.4 (2.99)

Variable abbreviations correspond with Fig. 2

Table 2 ANCOVA results comparing the adjusted mean body weight [Log(g)] of species with slopes not significantly different in each pairwise comparison (i.e. no interaction between LogSL and 'region')

Species	Status	Guilds	F_1	*P*	Figures
Ageneiosus inermis	NN	E-Pisc	164.36	**<0.001**	Fig. 3a
Auchenipterus osteomystax	NN	E-Inv	148.01	**<0.001**	Fig. 3b
Trachydoras paraguayensis	NN	O-Inv	384.42	**<0.001**	Fig. 3c
Gymnotus inaequilabiatus	N	E-Ins	0.30	0.588	Fig. 4a
Hyphessobrycon eques	N	O-Inv	114.18	**<0.001**	Fig. 4b
Hypostomus regani	N	E-Ins	42.30	**<0.001**	Fig. 4c
Iheringichthys labrosus	N	O-Inv	34.53	**<0.001**	Fig. 4d
Leporinus obtusidens	N	P-Omn	0.01	0.986	Fig. 4e
Pyrrhulina australis	N	O-Her	22.44	**<0.001**	Fig. 4f
Pseudoplatystoma corruscans	N	P-Pisc	1.84	0.175	Fig. 4g
Pimelodella gracilis	N	O-Ins	31.76	**<0.001**	Fig. 4h
Pinirampus pirinampu	N	P-Pisc	14.12	**<0.001**	Fig. 4i
Schizodon borellii	N	P-Her	453.26	**<0.001**	Fig. 4j
Salminus brasiliensis	N	P-Pisc	3.68	0.055	Fig. 4k
Serrasalmus maculatus	N	E-Pisc	407.65	**<0.001**	Fig. 4l

Species are classified as native to both basins (N) or non-native in the UPRF (NN), and according to life-history strategy (*E* equilibrium, *O* opportunistic, *P* periodic) and trophic guild (*Det* detritivore, *Her* herbivore, *Ins* insectivore, *Inv* invertivore, *Omn* omnivore, *Pisc* piscivore, *Pla* planktivore) following Suzuki et al. (2004) and Corrêa et al. (2009), respectively

Bold values are significant at $P < 0.05$

omnivores for natives). However, species' trophic and life-history guilds were independent of native or non-native status ($G_3 = 1.66$, $P = 0.65$ and $G_2 = 3.15$, $P = 0.21$, respectively). Similarly, species' body size patterns were independent of native/non-native status ($G_4 = 5.73$, $P = 0.22$), trophic guild ($G_{12} = 16.85$, $P = 0.16$), and life-history strategy ($G_8 = 9.85$, $P = 0.28$), but there was a trend of detritivores/herbivores either being larger or having higher regression slopes in UPRF, and the opposite for invertivores, and non-natives were never larger in the recipient region.

Discussion

The invasion of the Upper Paraná River basin by species from the Lower Paraná and Paraguay basins (Júlio et al. 2009) may be considered an unplanned experiment that controls for the direct human effect of selection on introduction because species were able to colonize the Upper Paraná due to inundation of a biogeographic barrier. This unplanned experiment allowed us to isolate the ecological effects of invasion on patterns of body size of non-native fishes as well as to compare body size patterns for species native to both basins. As pointed out by Parker et al. (2013), the availability of such comparative data from the native ranges of invasive species is often a limitation facing invasion biologists. The hypothesis that species have larger body sizes in invaded ranges has been tested and supported in several studies with different taxonomic groups (Roy et al. 2002; Grosholz and Ruiz 2003; Leger and Rice 2003; Darling et al. 2011), but our results are consistent with studies that did not support the proposed relationship (Thébaud and Simberloff 2001; Miller et al. 2002; Vilà et al. 2005) or that identify significant variability among species (e.g. Parker et al. 2013). Specifically, most of the species in our study exhibited an interaction between body mass and length between the two locations, suggesting that ecological mechanisms affecting body mass vary with age or life stage in a different manner in the two regions and among species. Of the remaining 15 species with similar length-weight regression slopes between basins, eight had higher body mass in the more productive UCR ecosystem regardless of whether they were non-native in the UPRF, and four native species had similar sizes in both basins.

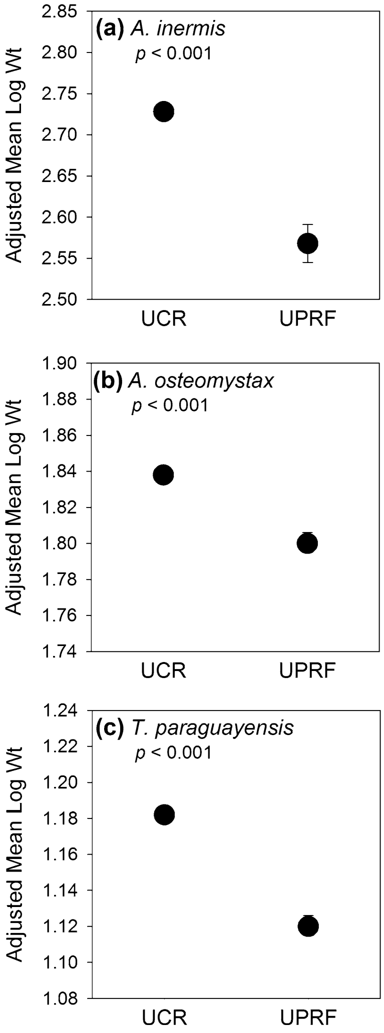

Fig. 3 Adjusted mean (±95 % confidence interval) log weights [Log(g)] of non-native species in the Upper Paraná River Floodplain (UPRF—invaded region) and Upper Cuiabá River (UCR—native region). Plots have the same relative scaling as those in Fig. 4 (though with different magnitudes among species) to facilitate direct comparability among species, with the exception of *A. inermis* (i.e. greatest pairwise difference between basins, exceeds the scaling in the other plots). ANCOVA results are provided in Table 2

The interaction between regions for the length-weight relationships, detected for more than half of the analyzed species, indicates that the rate of weight increase as a function of standard length (i.e. body condition) differs between regions. Because the length-weight regressions for each species crossed within the distribution of measured lengths (i.e. in contrast with different regression slopes but with individuals of one region larger in mass at all lengths), our results indicate that species did not have consistently larger body sizes in the invaded region. Importantly, our approach takes into account a wide range of standard lengths (i.e. incorporates age structure) for each population, and thus we are able to test for consistent patterns in body size across different age classes within each population. That is, for each of the 22 species with a significant interaction in the ANCOVA models, some age classes were larger (i.e. greater relative body mass) in the invaded range whereas others were smaller, and no general patterns were detected in terms of which age classes were larger. For example, five species non-native to UPRF had greater body mass in UCR at smaller standard lengths (and the opposite at larger lengths) and four non-native species exhibited the opposite pattern. Even within taxonomic groups, such as for catfishes non-native to UPRF, species exhibit a variety of responses (Table S1). Similarly, body size patterns were independent of life-history strategies and feeding guilds.

For species without an interaction in the length-weight regressions between basins, the pattern exhibited by all non-native species and five species native to both regions was larger body size (i.e. body mass at a given length) in the more productive UCR ecosystem. Only three species, all native to UPRF, were larger in that ecosystem. Consistent with Thébaud and Simberloff (2001), this result suggests a strong effect of differences in attributes of the ecosystems, likely due to differences in ecosystem productivity in this study, rather than release of antagonistic interactions in invaded ranges in determining body size. Higher ecosystem productivity should result in better condition or growth rates within species and larger body sizes among species at multiple scales (Huston and Wolverton 2011). Concomitantly, low productivity environments may exert selective pressure favoring decreases in body size (Brown and Sibly 2006). The effects of ecosystem productivity on body size are evident regardless of whether the species is native or non-native. Because non-native species and species native to both regions largely exhibited similar responses, we can reject the hypothesis that being non-native is an important factor promoting enhanced ecological success (compared with native species) in the non-native region (Thébaud and Simberloff 2001).

In addition to differences in productivity, water transparency differs greatly between the two study

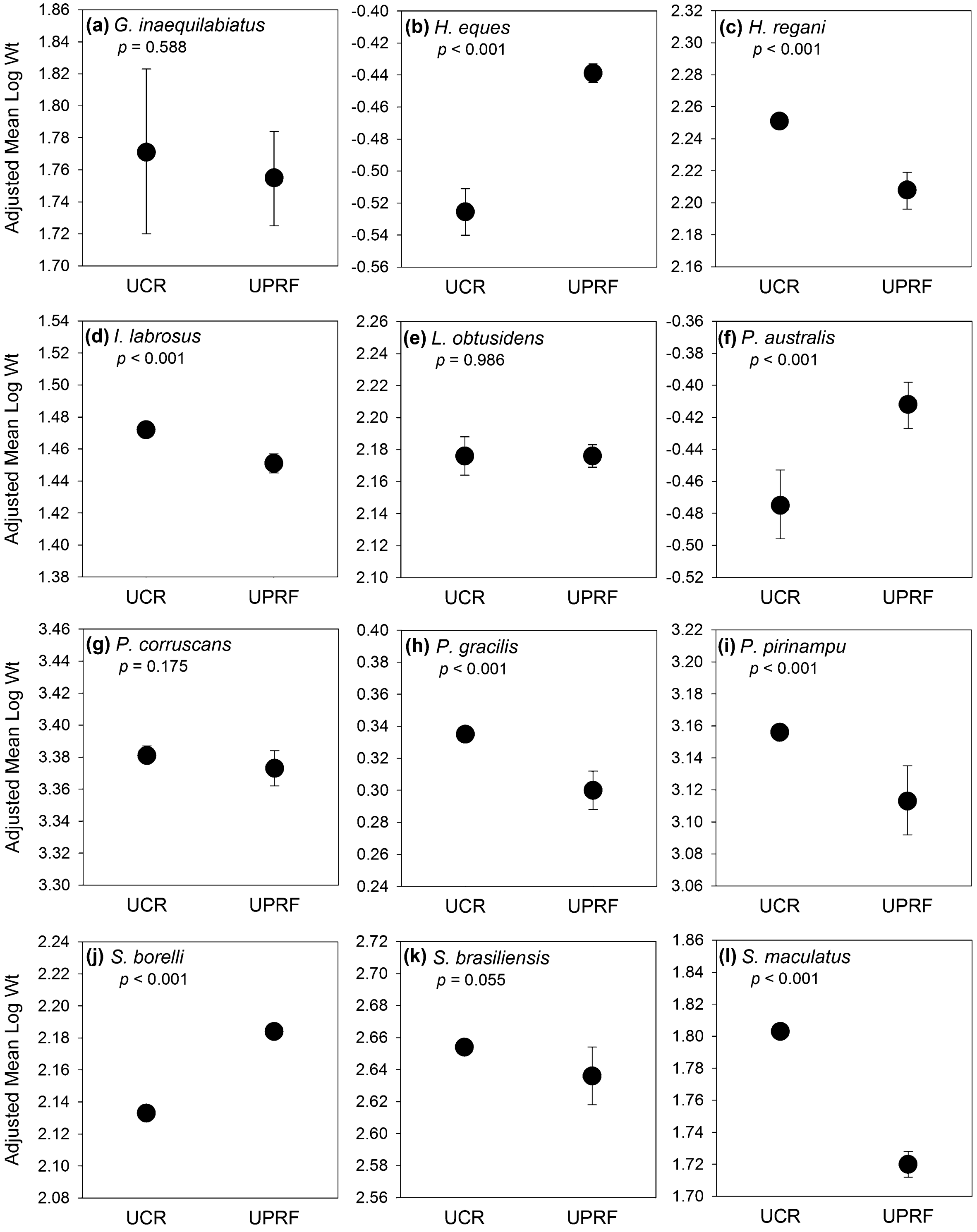

Fig. 4 Adjusted mean (±95 % confidence interval) log weights [Log(g)] of species native to both the Upper Paraná River Floodplain (UPRF) and Upper Cuiabá River (UCR). Plots have the same relative scaling (though with different magnitudes among species) to facilitate direct comparability among species. ANCOVA results are provided in Table 2

systems. The construction of dams upstream of the UPRF dramatically changed the limnological conditions of this stretch, increasing transparency and lowering nutrient concentrations, due to retention of sediments and nutrients in the upper stretches of the basin (Agostinho et al. 2004; Roberto et al. 2009). Increased water transparency is implicated as an important factor mediating establishment success and ecological impacts of visually-oriented non-native predators in this basin (e.g. peacock bass *Cichla* spp.; Pelicice and Agostinho 2009; Espínola et al. 2010). Thus, we might expect this trophic guild in particular, and especially for non-natives, to exhibit larger body sizes in UPRF. To the contrary, body size patterns were independent of trophic guild, and the visually-oriented predators without an interaction in the ANCOVA models exhibited no difference among systems (*S. brasiliensis*) or were larger in UCR (*S. maculatus*), and those species with an interaction (e.g. *C. jenynsii*, *S. marginatus*, *R. vulpinus*) did not present a consistent pattern in body size relationships between basins. That being said, this particular guild may be somewhat underrepresented in our analysis due to their ability to avoid passive sampling techniques such as gill nets, and our analyses did not include any peacock bass species, which are non-native to both regions.

Significantly higher adjusted mean body mass in the UPRF involved only three species (*H. eques*, *P. australis*, *S. borelli*), none of which are non-native. Two of these three species are herbivorous (*S. borelli* and *P. australis*), and the other two herbivorous species in our dataset, *L. lacustris* and *Hemigrammus marginatus*, exhibited greater slopes in UPRF. Previous research in the UPRF (Abujanra et al. 2009) verified a unique positive relationship between nutritional status of herbivorous species (e.g. *S. borelli*, *L. lacustris*) and water level variability. The authors demonstrated that frequent daily variations in river level, due to operational procedures of upstream hydroelectric dams that vary in response to energy demand, provide access to marginal vegetated areas providing feeding opportunities for herbivorous species (Abujanra et al. 2009). Concomitantly, *P. australis* and *H. eques* are the smallest (in length) of the taxa collected in this study, reaching sexual maturity a few months after hatching and at less than 2.2 cm SL (Suzuki et al. 2004). Previous studies suggested that opportunistic species such as these, characterized by small size, early maturation, and high mortality during juvenile stages but often with multiple reproductive bouts per year, are favored in habitats with higher environmental variability such as described above for the UPRF (Winemiller 2005; Agostinho et al. 2007). That being said, this pattern did not hold for other opportunistic species that were either native to both basins or non-native to the UPRF, and body size patterns were independent of life-history strategy.

Several factors act synergistically to determine establishment success, impacts to invaded ecosystems, and potentially also body sizes of non-native species. For example, propagule pressure plays a key role in population establishment (Colautti et al. 2006) and invasional meltdown (Simberloff and Von Holle 1999) may exacerbate that effect. Some evidence suggests that ecosystem productivity does not limit establishment success of non-native species (Schröder et al. 2009) and native communities impacted by disturbances are more vulnerable to invasion (e.g. Marchetti and Moyle 2000). Larger body size may increase establishment success due to a reduction of negative biotic interactions (mainly predation) with increased body size (Schröder et al. 2009). Nevertheless, both non-native species and native species with wide distributions in our study presented similar patterns in body size between regions in spite of the above-mentioned factors and in contrast to the expectation of larger body sizes in the non-native range. Furthermore, our analytical approach that focused on body condition (i.e. body mass at a given length) as the measure of size should correlate directly with the relative acquisition of resources (i.e. role in the food web and potential impact) as well as reproductive potential of the populations (e.g. Duponchelle et al. 2007). That being said, other attributes of invasion success not examined directly in this study, especially abundance, may not follow similar patterns to body size between native and invaded ranges (Parker et al. 2013) and requires further investigation.

In many instances, a sampling bias (e.g. selection for individuals being introduced or selection of taxa with high activity rates) may explain patterns of larger body size in non-native regions, without the need to propose any ecological mechanism such as absence of enemies, increased competitive ability or differences in ecosystem productivity (Simons 2003). This may be plausible for cases where humans directly influence the invasion process or if there is a positive intraspecific relationship between body size and dispersal rate. A further bias may affect studies that utilize databases that integrate large amounts of data not necessarily collected for the purpose of biogeographic comparisons (Parker et al. 2013). For example, Parker et al. (2013) found differences in response ratios for sizes of invasive plants in non-native versus native ranges based on data compiled from different researchers across the ranges or standardized data intended for biogeographic comparisons. The aforementioned sampling biases should not be present in our study due to the natural experiment provided by the inundation of the biogeographical barrier and standardized methodologies across sampling locations.

Taking advantage of a unique opportunity caused by the flooding of a semi-porous biogeographic barrier, we found that ecosystem productivity, irrespective of non-native status, likely results in larger relative body sizes for many species across these taxonomically and functionally diverse Neotropical fish assemblages. However, many taxa also exhibited interactions in relative body size between systems depending on age class or stage of ontogenetic development. Our findings contribute to the growing literature (e.g. Thébaud and Simberloff 2001; Miller et al. 2002; Vilà et al. 2005; Parker et al. 2013) that suggests perceived tendencies of larger body sizes in invaded ranges should not be generalized, especially when environmental conditions differ greatly among regions and when dealing with populations that exhibit significant age structure.

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References

Abujanra F, Agostinho AA, Hahn NS (2009) Effects of the flood regime on the body condition of fish of different trophic guilds in the Upper Paraná River floodplain, Brazil. Braz J Biol 69:469–479

Agência Nacional das Águas (2011) Portal da Qualidade das Águas. URL:http://pnqa.ana.gov.br/default.aspx

Agostinho AA, Thomaz SM, Gomes LC (2004) Threats for biodiversity in the floodplain of the Upper Paraná River: effects of hydrological regulation by dams. Ecohydrol Hydrobiol 4:255–268

Agostinho AA, Pelicice FM, Petry AC, Gomes LC, Júlio-Junior HF (2007) Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquat Ecosyst Health Manage 10:174–186

Agostinho AA, Suzuki HI, Fugi R, Alves DC, Tonella LH, Espindola LA (2015) Ecological and life history traits of *Hemiodus orthonops* in the invasion process: looking for clues at home. Hydrobiologia 746:415–430

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889

Brown JH, Sibly RM (2006) Life-history evolution under a production constraint. Proc Natl Acad Sci USA 103:17595–17599

Brown JH, Gilloolym JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. Biol Invasions 8:1023–1037

Cone RS (1989) The need to reconsider the use of condition indices in fishery science. Trans Am Fish Soc 118:510–514

Corrêa CA, Petry AC, Hanh NS (2009) Influência do ciclo hidrológico na dieta e estrutura trófica da ictiofauna do rio Cuiabá, Pantanal Mato-Grossense. Iheringia Série Zoologia 99:456–463

Darling ES, Green SJ, O'Leary JK, Côté IM (2011) Indo-Pacific lionfish are larger and more abundant on invaded reefs: a comparison of Kenyan and Bahamian lionfish populations. Biol Invasions 13:2045–2051

Duponchelle F, Lino F, Hubert N, Panfili J, Renno JF, Baras E, Torrico JP, Dugue R (2007) Environment-related life-history trait variations of the red-bellied piranha *Pygocentrus nattereri* in two river basins of the Bolivian Amazon. J Fish Biol 71:1113–1134

Ebeling SK, Hensen I, Auge H (2008) The invasive shrub *Buddleja davidii* performs better in its introduced range. Divers Distrib 14:225–233

Espínola LA, Minte-Vera CV, Júlio HF Jr (2010) Invasibility of reservoirs in the Paraná Basin, Brazil, to *Cichla kelberi* Kullander and Ferreira, 2006. Biol Invasions 12:1873–1888

Forsyth DM, Duncan RP, Bomford M, Moore G (2004) Climatic suitability, life-history traits, introduction effort, and the establishement and spread of introduced mammals in Australia. Conserv Biol 18:557–569

García-Berthou E (2001) On the misuse of residuals in ecology: testing regression residuals versus the analysis of covariance. J Anim Ecol 70:708–711

Golterman HL, Clymo RS, Ohmstad MAM (1978) Methods for physical and chemical analysis of freshwater. Blackwell Scientific, Oxford

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Sunderland

Grosholz ED, Ruiz GM (2003) Biological invasions drive size increases in marine and estuarine invertebrates. Ecol Lett 6:700–705

Hoeinghaus DJ, Winemiller KO, Layman CA, Arrington DA, Jepsen DB (2006) Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river. Ecol Freshw Fish 15:398–407

Hoeinghaus DJ, Agostinho AA, Gomes LC, Pelicice FM, Okada EK, Latini JD, Kashiwaqui EAL, Winemiller KO (2009) Effects of river impoundment on ecosystem services of large tropical rivers: embodied energy and market value of artisanal fisheries. Conserv Biol 23:1222–1231

Huston MA, Wolverton S (2011) Regulation of animal size by eNPP, Bergman's rule, and related phenomena. Ecol Monogr 81:349–405

Júlio HF Jr, Dei Tós C, Agostinho AA, Pavanelli CS (2009) A massive invasion of fish species after eliminating a natural barrier in the upper rio Paraná basin. Neotrop Ichthyol 7:709–718

Leger EA, Rice KV (2003) Invasive California poppies (Eschscholzia californica Cham.) grow larger than native individuals underreduced competition. Ecol Lett 6:257–265

Marchetti MP, Moyle PB (2000) Effects of flow regime on fish assemblages in a regulated California stream. Ecol Appl 11:530–539

Miller AW, Hewitt CL, Ruiz GM (2002) Invasion success: does size really matter? Ecol Lett 5:159–162

Olden JD, Hogan ZS, Vander Zanden MJ (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. Glob Ecol Biogeogr 16:694–701

Parker JD, Torchin ME, Hufbauer RA, Lemoine NP, Alba C, Blumenthal DM, Bossdorf O, Byers JE, Dunn AM, Heckman RW, Hejda M, Jarošík V, Kanarek AR, Martin LB, Perkins SE, Pyšek P, Schierenbeck K, Schlöder C, van Klinken R, Vaughn KJ, Williams W, Wolfe LM (2013) Do invasive species perform better in their new ranges? Ecology 94:985–994

Pelicice FM, Agostinho AA (2009) Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol Invasions 11:1789–1801

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Roberto MC, Santana NF, Thomaz SM (2009) Limnology in the Upper Paraná River floodplain: large-scale spatial and temporal patterns, and the influence of reservoirs. Braz J Biol 69:717–725

Roy K, Jablonski D, Valentine JW (2002) Body size and invasion success in marine bivalves. Ecol Lett 5:163–167

Ruensink JL (2005) Global analysis of factors affecting the outcome of freshwater fish introductions. Conserv Biol 19:1883–1893

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastinings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471

Schröder A, Nilson KA, Person L, van Kooten T, Reichstein B (2009) Invasion success depends on invader body size in a size-structured mixed predation–competition community. J Anim Ecol 78:1152–1162

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invasions 1:21–32

Simons AM (2003) Invasive aliens and sampling bias. Ecol Lett 6:278–280

Sokal RR, Rohlf FJ (2012) Biometry, 4th edn. W.H Freeman and Company, New York

Suzuki HI, Vazzoler AEAM, Marques EE, Lizama MAP, Inada P (2004) Reproductive ecology of the fish assemblages. In: Thomaz SM, Agostinho AA, Hahn NS (eds) The Upper Paraná River and its floodplain: physical aspects, ecology and conservation. Backhuys Publishers, Leiden, pp 230–257

Thébaud C, Simberloff D (2001) Are plants really larger in their introduced ranges? Am Nat 157:231–236

Thomaz SM, Agostinho AA, Hahn NS (2004) The Upper Paraná River and its Floodplain: physical aspects, ecology and conservation. Backhuys Publishers, Leiden

Thuiller W, Richardson DM, Rouget M, Proches S, Wilson JRU (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. Ecology 87:1755–1769

Torchin ME, Lafferty KD, Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biol Invasion 3:333–345

van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2011) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. Ecol Lett 13:947–958

Vilà M, Maron JL, Marco L (2005) Evidence for the enemy release hypothesis in *Hypericum perforatum*. Oecologia 142:474–479

Vitule JRS, Skóra F, Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. Divers Distrib 18:111–120

White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends Ecol Evol 22:323–330

Winemiller K (2005) Life history strategies, population regulation, and implications for fisheries management. Can J Fish Aquat Sci 62:872–885

Woodward G, Warren P (2007) Body size and predatory interactions in freshwaters: scaling from individuals to comunities. In: Raffaelli DA, Edmonds-Brown R, Hildrew AG (eds) Body size: the structure and function of aquatic ecosystems. Cambridge University Press, São Paulo, pp 98–118