Species of the *Hoplias* aff *malabaricus* complex (Characiformes: Erythrinidae): An investigation of coexistence in a Neotropical floodplain

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ABSTRACT. This study assessed the coexistence of three species of thraira present in the Upper Paraná River floodplain, using population structure as an investigation tool. The species were designated as: *Hoplias* sp. 1, introduced after the construction of the Itaipu reservoir, and *Hoplias* sp. 2 and *Hoplias* sp. 3, native species that have been identified as *Hoplias* aff. *malabaricus*. We tested the hypothesis that those species in fact differ from each other in respect of population abundance, sex ratio, relative frequency of adults and juveniles, length structure and weight-length relationship. Additionally, possible effects of the flood pulse on the first four of these parameters were investigated. Samples were collected quarterly from March 2006 to December 2007 from nine collection sites on the floodplain. *Hoplias* sp. 1 presented a greater balance of sex ratio and length structures over the seasons, as well as a higher allometric coefficient. The population attributes of *Hoplias* sp. 2 and *Hoplias* sp. 3 showed a high responsiveness to hydrological seasonality, indicating that these species exploit available resources in a conspicuous flood period with greater efficiency. These differences, beyond reflecting possible mechanisms that allow closely related species to coexist, indicate the importance of understanding the life strategies adopted by each species which, as part of a complex system, are considered key elements of the aquatic community structure in the region, providing important information for habitat management and biodiversity conservation.

KEY WORDS. Dams; flood pulse; species introduction; structure population; thraira.

Technological advances have increased the demand for electricity in Brazil, and this has been reflected in the construction of new dams, implying the establishment of reservoirs (Souza *et al.* 2008). These reservoirs transform the structure of the entire aquatic environment, causing important changes in the ichthyofauna not only in the flooded area, but also upstream and downstream of it (Agostinho *et al.* 2007).

In spite of the superior stretch of the Paraná River, which is located between the Paranapanema River mouth and the Itaipu reservoir and which includes an extensive floodplain and the last dam-free stretch of the Upper Paraná River, this area suffers the effects of both upstream and downstream impoundments. As a consequence of the reservoir cascade located upstream of the Upper Paraná River floodplain, the current flow in this ecosystem has been controlled, including control of the period, frequency and intensity of the flood pulse. These changes were intensified after the construction of the Porto Primavera reservoir (Petry *et al.* 2003, Agostinho *et al.* 2004). Although the effects of the impoundment are less pronounced in the upstream region, aquatic fauna in the basins, which are naturally fragmented by large waterfalls, may be mixed by the impoundments there, as occurred in the basin of the Upper Paraná River floodplain after the formation of the Itaipu reservoir (Agostinho *et al.* 2007). This impoundment inundated the Sete Quedas Falls of the Paraná River, the limit of two hydrographic ecoregions, and moved this natural barrier 150 km downstream, allowing a remarkable dispersal of species from the Middle Paraná River to superior stretches, including individuals from the *Hoplias* aff. *malabaricus* complex (Bloch 1794), known as thraira (Júlio Júnior *et al.* 2009).

According to some authors (Dergam & Bertollo 1990, Dergam *et al.* 1998, Vicari *et al.* 2005), *H.* aff. *malabaricus* exhibits some of the highest known inter- and intrapopulation karyotypic diversities, with seven identified cytotypes in South America which, due to the absence of gene flow, suggests a species complex (Bertollo *et al.* 2000). Pazza & Júlio Júnior (2003), studying this complex in the Upper Paraná River, reported the presence of three cytotypes (A, C, D) coexisting in sympatry separated by a large genetic distance, one cytotype (C) being introduced after the formation of the Itaipu Reservoir, and the other two cytotypes (A, D) being native to the region. Graça & Pavanelli (2007) classified these cytotypes as

three distinct species based on specific morphological traits and designated them as *Hoplias* sp. 1, *Hoplias* sp. 2 and *Hoplias* sp. 3 (cytotypes C, D and A, respectively).

The *H.* aff. *malabaricus* complex exhibits a wide geographical distribution (GERY 1977, BARBIERI *et al.* 1982, MELLO *et al.* 2006, VICARI *et al.* 2006, GOMES *et al.* 2007) and is commonly found in the biotopes of the Upper Paraná River floodplain (BIALETZKI *et al.* 2002), where this complex is important among piscivorous fish species with a high contribution to both number and biomass (LUIZ *et al.* 2004).

PETRY *et al.* (2007), analysing the complex as a single species, verified its key role in the Upper Paraná River floodplain in structuring assemblages of fish in isolated lagoons. However, despite the importance of thraira to the dynamics of freshwater ecosystems, the structure of its population is poorly known in the region, being restricted to results obtained from the Itaipu reservoir after its impoundment.

Understanding the population structures of species is one of the greatest objectives of biology, especially for teleost fishes, which present great variability in strategies and practices for survival (WINEMILLER 1989, ORSI *et al.* 2004). ODUM (1988) reports that population parameters offer components that may be used to determine patterns of strategy and survival of species, as they allow the elucidation and interpretation of several responses to their ecology (VAZZOLER & AMADIO 1990).

Thus, considering that most studies of *Hoplias* aff. *malabaricus* focus on the complex without distinguishing between the species that it is composed of, our study aimed to determine the population structure of the three species of *Hoplias* Gill, 1903 present in the Upper Paraná River floodplain. Additionally, due to the fact that the regularity of variation in the hydrometric level may function as a key factor in establishing complex relationships of dependence between the organisms and the floodplains (POFF *et al.* 1997), we also examined the possible effects of the flood pulse on the population structure of these species. According to BEGON *et al.* (2007), congener species must at least exhibit different behavioral strategies to coexist. Considering that morphological and reproductive differences have already been identified for these three species of *Hoplias*, the hypothesis of this study was that these species differ in several population parameters: abundance, sex and adult/juvenile ratio, length structure and weight-length relationship.

MATERIAL AND METHODS

The Paraná River is the second longest in South America (AGOSTINHO & JÚLIO JÚNIOR 1999). Its upper portion, designated the Upper Paraná, is represented by the following hydroelectric dams (HEDs): the Itaipu (downstream) and the Porto Primavera (upstream) (SOUZA FILHO & STEVAUX 2004). The study area consisted of a section of the braided floodplain of the Upper Paraná River (22°40'S and 22°50'S latitude and between 53°10'W and 53°40'W longitude), located between the mouths of the

Paranapanema and Ivinheima rivers and representing the last undimmed stretch of the Paraná River in Brazil. Since 1999, this region has been included in the Long-Term Ecological Research Program (LTER) developed by the Universidade Estadual de Maringá (Fig. 1).
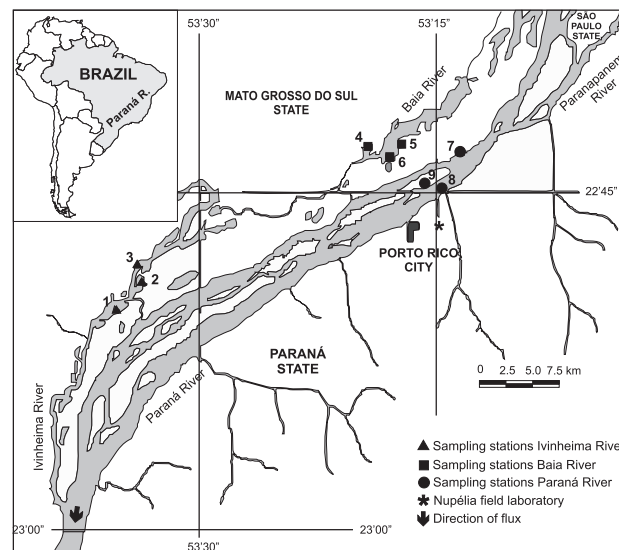

Figure 1. The study area, with the location of the sampling stations in the Upper Paraná River floodplain: PR (1 – Paraná River, 2 – Garças lagoon, 3 – Pau Véio backwater); BA (4 – Baía River, 5 – Fechada lagoon, 6 – Guaraná lagoon); IVI (7 – Ivinheima River, 8 – Patos lagoon, 9 – Ventura lagoon).

To determine the flood period in the study area, hydrologic data from the Paraná River were obtained from the Fluviometric Station of Porto São José (state of Paraná) and from the Itaipu Binacional. A quota of 3.5 m was considered the limit for overflow of the Paraná River, and a flood period was designated when the hydrometrical level exceeded this value (CUNICO *et al.* 2002, THOMAZ *et al.* 2004) (Fig. 2).

Species samples were collected quarterly between March 2006 and December 2007 from nine stations belonging to three subsystems: Baía – BA (Baía River, Fechada lagoon and Guaraná lagoon); Paraná – PR (Paraná River, Garças lagoon and Pau Véio backwater); and Ivinheima – IV (Ivinheima River, Ventura lagoon and Patos lagoon) (Fig. 1). Specimens were collected using gill nets (2.4 to 16 cm mesh) with standardized fishing effort exposed for a period of twenty-four hours and verified every eight hours. After sampling, the specimens were anaesthetized and killed as described for fishes in AVMA (2007). The following were also measured for each specimen: standard length (L_s) (cm), total weight (W_t) (g), sex and gonadal maturation stage (immature, rest, maturation, in reproduction, spent; adapted from VAZZOLER 1996).
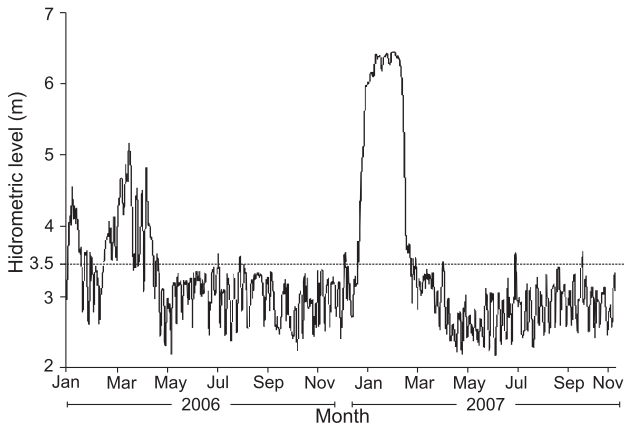
Figure 2. Hydrological regime of the Paraná River measured at Porto São José municipality. Stippled line = water level required for initial inundation of the floodplain (Source: Fluviometric Station's Porto São José-PR).

Individuals were classified according to Graça & Pavanelli (2007) as *Hoplias* sp. 1, *Hoplias* sp. 2 and *Hoplias* sp. 3, and vouchers were deposited in the ichthyologic collection of the Museum of Nupélia at the Universidade Estadual de Maringá (*Hoplias* sp. 1 voucher specimen: NUP3456, *Hoplias* sp. 2: NUP3457, *Hoplias* sp. 3: NUP3458).

Species abundance was determined using the absolute frequency, i.e., the total number of individuals, considering the standardized sampling effort. Sex ratio was obtained by observing the frequency of males and females and comparing to the expected proportion (1:1), while the proportion of juveniles to adults was analyzed using the relative frequency of these individuals. Specimens with immature gonads were considered to be juveniles, whereas all other stages of gonadal maturity were deemed adults (Vazzoler 1996). For both analyses of proportion, the results were tested whenever possible using a 'G' test to determine significant differences. The three above-mentioned population attributes were estimated for the three species of *Hoplias* and analyzed monthly and to standard length class. The amplitude of these classes was established using Sturges' rule (Vieira 1991), obtained using the difference between the smallest and largest standard length sampled, for both 2006 and 2007.

Froese (2006) indicates that a reliable length-weight relationship, which allows for evaluation of the 'b' exponent, requires at least 10 small, medium and large specimens. Thus, considering the low number of individuals of *Hoplias* sp. 3 collected during the study period, its length-weight relationship was established by pooling individuals of both sexes, whereas for *Hoplias* sp. 1 and *Hoplias* sp. 2, this was determined for males and females separately. These relationships were determined using the equation: $W_t = a.L_s^b$, where W_t = total weight, L_s = standard length, a = linear coefficient and b = slope coefficient

(Le Cren 1951). The parameters of these relationships were estimated after logarithmic transformation of the values of weight and standard length and subsequent adjustment of a straight line to the points using the least squares method (Vanzolini 1993).

To test for possible differences between the population parameters using the adjusted curves for males and females, an analysis of covariance (ANCOVA) (Goldberg & Scheiner 1993) was applied to the coefficients of the linear regressions of standard length and total weight ($\log_{10}$). To investigate the development patterns of these fishes, a Student's test was employed on the slope coefficient (b) of species to evaluate the null hypothesis (H_0): b = 3, using the equation: %b-3%/standard error of the 'b' (Zar 1996).

The significance level adopted for all statistical analyses was 5%, and the parameters from the length-weight relationship and ANCOVA were determined using Statistica™software for Windows 7.1. (StatSoft 1996).

RESULTS

During the two annual cycles, we captured and evaluated 434 individuals of *Hoplias* sp. 1 (221 females and 213 males), 604 individuals of *Hoplias* sp. 2 (280 females and 324 males) and 15 individuals of *Hoplias* sp. 3 (7 females and 8 males). In 2006, *Hoplias* sp. 1 and *Hoplias* sp. 2 exhibited similar absolute frequencies, with a small predominance of the first species between September and December. In 2007, *Hoplias* sp. 2 was more abundant between June and December, especially in June, when it presented more than twice the number of individuals found for *Hoplias* sp. 1. *Hoplias* sp. 3 was found to have the lowest frequency, with a higher occurrence in March and September 2007 (Fig. 3).

In 2006, more than 80% of individuals of *Hoplias* sp. 1 and *Hoplias* sp. 2 ranged from 19 to 26 cm standard length, with similar absolute frequencies of these two species (Fig. 3). In 2007, there was a verified increase in the number of individuals for all three species, especially *Hoplias* sp. 2, which were widely distributed among the standard length classes (Fig. 3).

For annual sex ratio only, *Hoplias* sp. 2 and *Hoplias* sp. 3 exhibited a significant difference in 2006, when the males were more frequent (p < 0.05) (Tab. I). *Hoplias* sp. 1 did not exhibit significant differences in the monthly sex ratio, whereas *Hoplias* sp. 2 showed significant predominance of males in March (G = 5.01) and June (G = 4.97) of 2006 and in December of 2007 (G = 4.35) (Fig. 4). For both species, significantly more adults were collected than juveniles during the entire period (p > 0.05), except in March 2007 (G = 0.51 for *Hoplias* sp. 1 and G = 0.34 for *Hoplias* sp. 2). However, we recorded an increase in juveniles in 2007, especially for *Hoplias* sp. 2 (Fig. 4). For *Hoplias* sp. 3, only males were collected in 2006 and only females in March 2007, while in June and September of 2007, the frequency of occurrence was 1:1 for each sex. All sampled individuals were adults (Tab. I and Fig. 4).
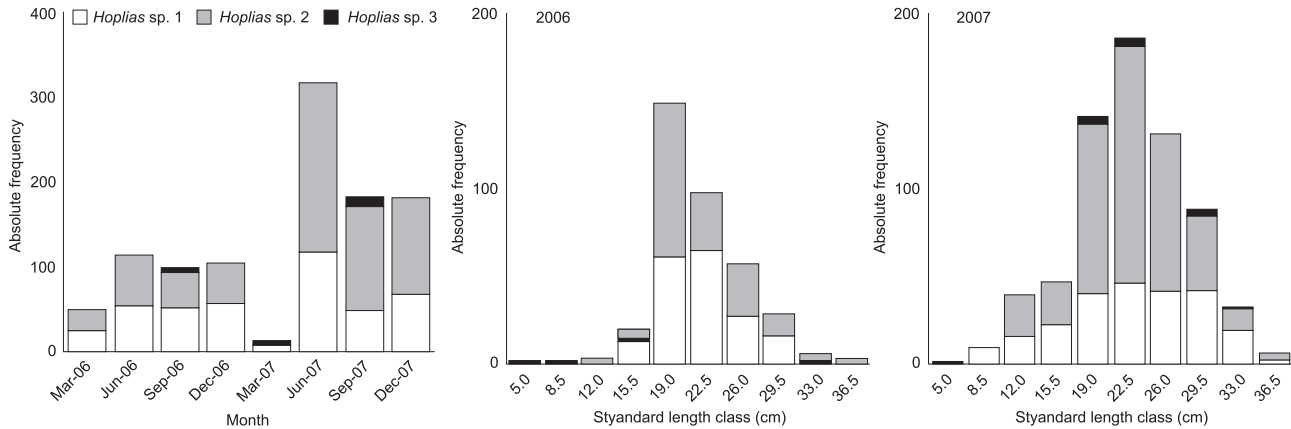
Figure 3. Absolute frequency of *Hoplias* sp. 1, *Hoplias* sp. 2 and *Hoplias* sp. 3 by month and by standard length class, in 2006 and 2007, in the Upper Paraná River floodplain

Table I. Sex ratio of the species of *Hoplias* by year. (N) Number of specimens, (%) frequency percentage, (*) significant at the level of 5%, (Δ) impossible to calculate G.

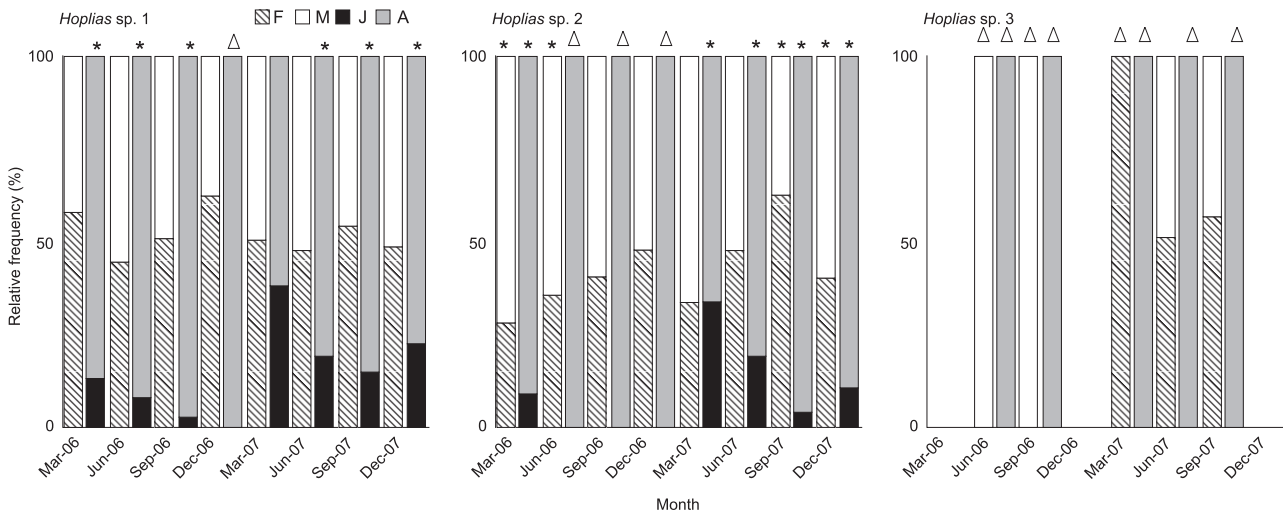| Species	2006					2007				
	Female		Male		G	Female		Male		G
	N	%	N	%		N	%	N	%	
Hoplias sp. 1	101	53.4	88	46.6	0.89	120	49.0	125	51.0	0.10
Hoplias sp. 2	67	39.0	105	61.0	8.47*	213	49.3	219	50.7	0.08
Hoplias sp. 3	0	0	3	100.0	Δ	7	58.3	5	41.7	0.33

Figure 4. Quarterly variation in the relative frequencies of males (M) and females (F) and juveniles (J) and adults (A) of *Hoplias* sp. 1, *Hoplias* sp. 2 and *Hoplias* sp. 3 in the Upper Paraná River floodplain. * significant at the level of 5%; Δ = impossible to calculate G.

Considering the length class, in 2006 there was a predominance of females among the smaller (8.5 and 12 cm) and larger individuals (33 cm) (p < 0.05) for *Hoplias* sp. 1. In 2007, there were no significant differences in sex ratio, except for

the class of 26 cm standard length, where males prevailed (G = 4.76) (Fig. 5). In contrast to *Hoplias* sp. 2, males still exhibited a higher occurrence in the 12, 22.5, 29.5, and 36.5 cm size classes (p < 0.05), with this sex being exclusive to the first and

last classes in 2006. However, in 2007, the proportion of the sexes was almost 1:1 in most of the size classes, except among individuals larger than 36.5 cm standard length, in which only males occurred. We also observed only females among individuals of less than 12 cm standard length (Fig. 5). For *Hoplias* sp. 1, we recorded juveniles up to 19 cm in 2006 which were exclusive in the two lower standard length classes (p < 0.05). Individuals larger than 22.5 cm were all adults. In 2007, there was an increase in the size of juveniles and adults, reaching 26 and 36.5 cm, respectively (Fig. 5). For *Hoplias* sp. 2, we recorded only adults, with the exception of the 19 cm size class in 2006. However, there was an increased frequency of juveniles in 2007, observed between 8.5 and 29.5 cm, despite the majority of adults measuring over 19 cm in standard length (Fig. 5). For *Hoplias* sp. 3, we exclusively found males in the size class

ranging from 22.5 to 29.5 cm in 2006. In the following year, we sampled only females in the size class from 15.5 to 29.5 cm, and only males in the 33 cm size class, with a sex ratio of 1:1 in the intermediate size classes (Fig. 5).

The equations that relate the W_t x L_s relationship for *Hoplias* sp. 2 were $W_t = 10^{-1.80}. L_s^{3.14}$ for females and $W_t = 10^{-1.67}. L_s^{3.03}$ for males (Fig. 6). The allometric coefficient related to the growth form of individuals and the 'a' parameter, attributed to the degree of fattening, exhibited significant differences between the sexes (ANCOVA, p < 0.05). The females presented a 'b' value significantly different from 3 (p < 0.05), indicating positive allometric development, while the males exhibited isometric growth. For *Hoplias* sp. 1, the following relationships were determined: $W_t = 10^{-1.79}. L_s^{3.06}$ for females and $W_t = 10^{1.92}. L_s^{3.16}$ for males. However, the parameters from the length-weight
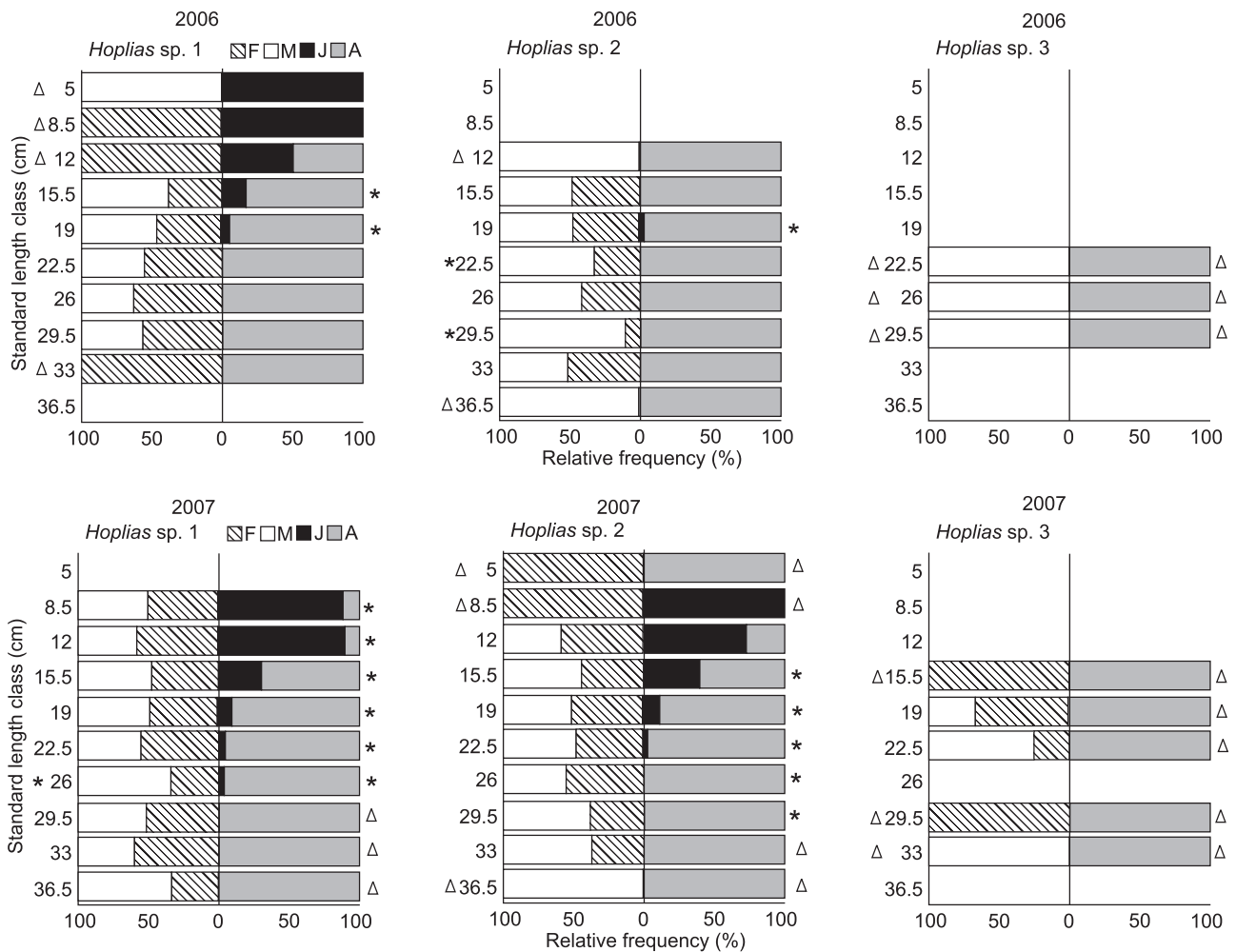

Figure 5. Relative frequency of males (M) and females (F) and juveniles (J) and adults (A) of *Hoplias* sp. 1, *Hoplias* sp. 2 and *Hoplias* sp. 3 for standard length class (cm) in the Upper Paraná River floodplain in 2006 and 2007. * significant at the level of 5%; Δ = impossible to calculate G.

relationship ('a' and 'b') showed no significant differences between the sexes (ANCOVA, p > 0.05), exhibiting a single relationship represented by $W_t = 10^{-1.86}. L_s^{3.10}$ (Fig. 6), with all individuals expressing positive allometric development, (b > 3, p < 0.05). Due to the low number of individuals of *Hoplias* sp. 3, we obtained only one relationship: $W_t = 10^{-1.03}. L_s^{2.56}$ (Fig. 6) for the pooled sexes, indicating isometric development for this species (b = 3, p > 0.05).

DISCUSSION

In general, *Hoplias* sp. 1 and *Hoplias* sp. 2 presented the same seasonal trend of length structure regarding the abundance data, while we did not observe any pattern in *Hoplias* sp. 3 due to the low number of sampled individuals. So, populations of *Hoplias* sp. 1 and *Hoplias* sp. 2 were stable, as more than 80% of the first species (larger than 18 cm standard length)

and 90% of the second species (larger than 15.3 cm standard length) were adult.

According to the seasonal similarity noted for *Hoplias* sp. 1 and *Hoplias* sp. 2, the higher abundance observed in June and September is probably due to higher feeding activity and preparation for breeding, factors that induce greater movement of individuals, favouring their capture (HOLZBACH *et al.* 2005). According to some authors (BARBIERI *et al.* 1982, BARBIERI 1989), the best feeding conditions for *H.* aff. *malabaricus* are in the period previous to and during the breeding season, which occurs between September and March in the studied floodplain. Moreover, PAIVA (1974) asserts that the period between June and December shows the highest growth, when more specimens from this species complex are collected with full stomachs in the dams from north-eastern Brazil.

In contrast, the lower capture rate of individuals in March in both study years, especially in 2007, may be related to the
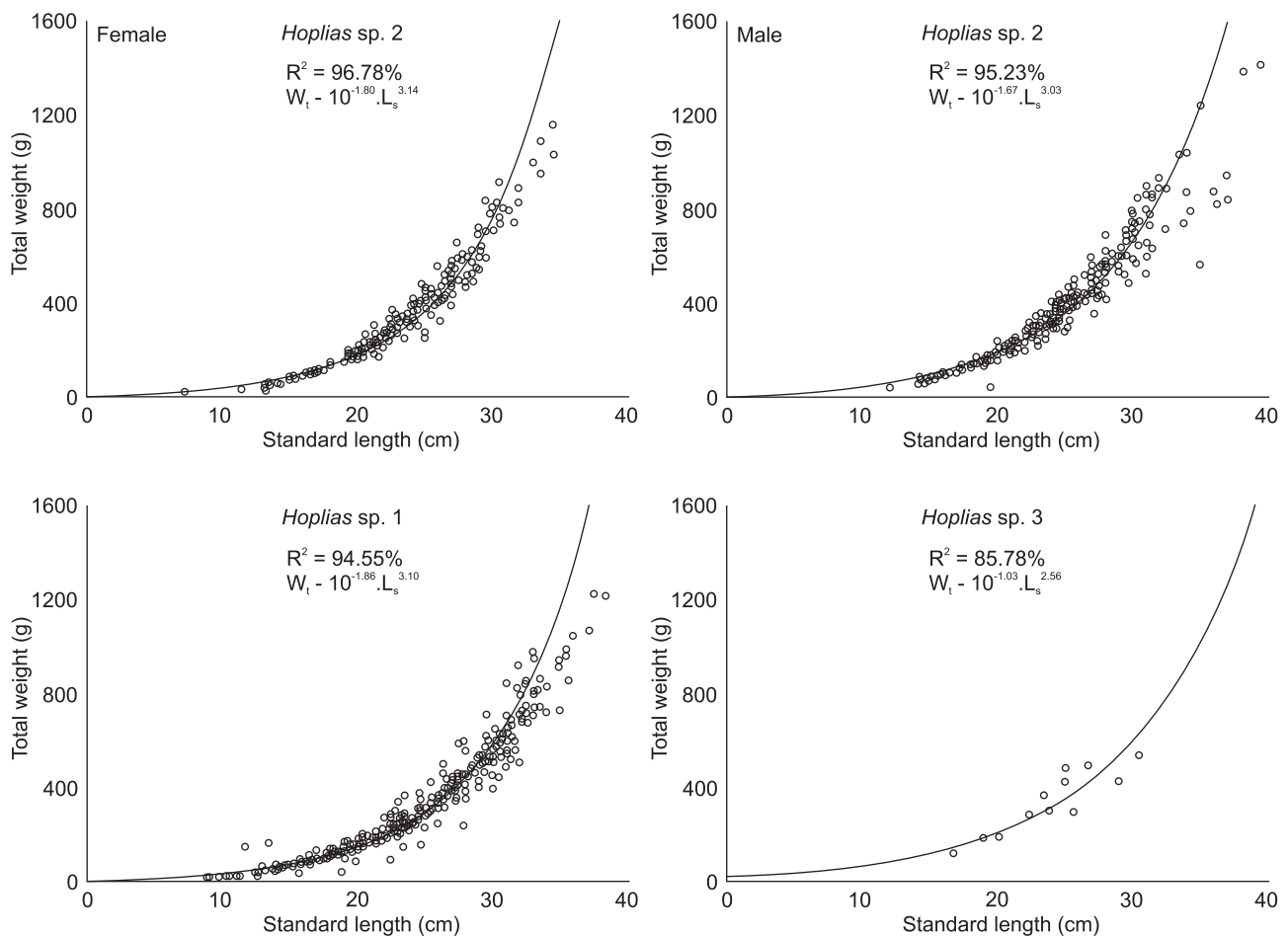

Figure 6. Total weight – standard length relationship for females alone and males alone of *Hoplias* sp. 2 and for the grouped sexes of *Hoplias* sp. 1 and *Hoplias* sp. 3 sampled between March of 2006 and December of 2007, in the Upper Paraná River floodplain.

high hydrometric level in this month, a factor which promotes a habitat increase, allowing greater availability of shelter (Agostinho *et al.* 2004) and dispersal opportunities (Sousa & Freitas 2008). Amadio & Bittencourt (2005) also report the same predictions for Amazonian fish, which exhibit a wide range of responses in life history associated with the flood-drought cycle and major morphophysiological and behavioral adaptations (Zaret & Rand 1971, Menezes & Vazzoler 1992).

However, the slight change in absolute frequency of *Hoplias* sp. 1 shows the lower dependence of this species on the flood-drought cycle. Luz-Agostinho *et al.* (2008) observe that *H.* aff. *malabaricus* is one of the species least affected by flood control in the Upper Paraná River floodplain. According to the authors, this is likely to be associated with the significant concentration of prey in years with smaller flood pulses, whereas in years with intense and prolonged floods, certain food items dominate the diet of thraira, reflecting a narrow niche. Jepsen *et al.* (1999) also affirmed that these predators increase their feeding activity and development during low-water periods. Agostinho *et al.* (2001) verified that the capture fish with mature and semi-spent gonads in the studied floodplain are more successful in dry years for sedentary species because the large flooded area during years of prolonged floods affects the absolute density and capture of individuals which exhibit this reproductive tactic, as observed for the thraira.

In this context, the sex ratio reflects an adaptation to the food supply, with a predominance of males in dams and oligotrophic rivers, and of females when there is abundant food available (Nikolsky 1969, Raposo & Gurgel 2001). The higher abundance of *Hoplias* sp. 1 females in 2006 possibly reflects the better feeding conditions in this year due to the less pronounced flood conditions. Moreover, as competition in this period was potentially stronger (Lowe-McConnell 1999), it is possible that this species is a better competitor than either *Hoplias* sp. 2 or *Hoplias* sp. 3. Some authors argue specifically that aggression and foraging voracity are basic behaviours that promote the competitive superiority of exotic over native species (Holway & Suarez 1999, Rehage & Sih 2004, Pintor *et al.* 2008). Nevertheless, this last observation should be carefully considered, because confirmation of the specific competitive mechanisms must rely on preliminary feeding analyses.

Considering the seasonal similarities between *Hoplias* sp. 1 and *Hoplias* sp. 2, the remarkable increase in the native species in 2007, mainly in the number of females, may reflect a greater dependence of these species on the seasonal hydrological cycle compared to *Hoplias* sp. 1 (Hauser *et al.* in press). According to Gaspar da Luz *et al.* (2001), piscivorous fish in the lakes from the Upper Paraná River floodplain seem to be favoured by flood conditions, when a greater number of juveniles reach these biotopes, and also by the gradual retraction of the water, which concentrates individuals closer together and increases their availability to predators. Studies in terrestrial (Norrdahl *et al.* 2002) and aquatic environments (Menge

2000, Piraino *et al.* 2002) also demonstrate the influence of climatic and hydrological seasonality on the performance of key species.

Furthermore, according to Mazzoni & Iglesias-Rio (2002), there is a great heterogeneity of habitats in periods with intense floods, which may intensify the proliferation of fish and aquatic invertebrates, increasing the availability of food resources for the thraira (Agostinho *et al.* 2004). In addition, the low oxygen levels of the water during this period, due to the incorporation of a greater biomass in the aquatic environment (Agostinho & Júlio-Júnior 1999), may favour *Hoplias* sp. 2, considering the greater tolerance to water chemical variation of this species in the *H.* aff. *malabaricus* complex (Menni *et al.* 1996).

Considering the possible impact of *Hoplias* sp. 1 on native species, a second hypothesis we considered was that the increase in females represents a mechanism employed by *Hoplias* sp. 2 and *Hoplias* sp. 3 that restores the population balance, as this mechanism results in a greater recruitment rate of juveniles (Nikolsky 1969, Barbieri *et al.* 2004). This increase occurred mainly during the reproductive period, corroborating the results of Gurgel (2004), who attributes this result to behavioral differences between the sexes as the females become more susceptible to capture in this period due to gonad weight.

In contrast, the greater proportion of males of the native species in 2006 may be related to differences in the environmental variables that favor the ability of each sex to find more suitable locations, given that variation in population parameters of fish is probably associated with the hydrological changes imposed by the seasonal regime (Abilhoa 2007). Several studies find a strong relationship between the abundance of juveniles and hydrometric level in the neotropics (Lowe-McConnel 1969, Jepsen *et al.* 1997, 1999). Thus, the low number of these individuals, especially in 2006, may be explained by the less pronounced flood in that year, which affects species' recruitment and increases the death rate of juveniles (Mérona & Gascuel 1993). Gomes & Agostinho (1997) assert that, for most fish, flow regulation by dams caused a drastic reduction in population size due to the changes in recruitment. Another factor to be considered is that these species, in particular native species, may use other areas to complete their development (Ramos & Konrad 1998/99), given the remarkable swimming ability of their larvae (Paiva 1974).

The greater occurrence of juveniles in December and March is probably related to the intense reproduction observed in September associated with the high temperatures and feeding activity (Bialetzki *et al.* 2008). According to Bialetzki *et al.* (2002), thraira reproduce in the period prior to the flood season, which allows the larvae to reach later stages of development while most of the other trophic guilds have not yet spawned, minimizing predation and maximizing their use of available resources, with consequent improvement in offspring survival. Ikeziri *et al.* (2008) observe the same strategy in several piscivorous species in the Amazon region.

The larger standard length of males of the native species may be ascribed to their superior voracity and foraging ability relative to females of the same age classes, in addition to the low production cost of sperm (Paiva 1974). According to Gurgel (2004), the economy in the elaboration of sex processes explains the larger size reached by the males, since testicle development may be more related to fish growth than to the annual cycle. Dei Tos *et al.* (1997) verify that species exhibits paternal care from the males, they reach larger sizes, as is also observed for thraira (Prado *et al.* 2006).

Regarding their length-weight relationships, both sexes of *Hoplias* sp. 1 (b > 3) exhibited a rounded body shape, while *Hoplias* sp. 2 showed sex dimorphism, with robust females (b > 3) and isometric males (b = 3). Isometric growth has also been reported for *Hoplias* sp. 3. Divergence in these coefficients between undescribed species may supply relevant information for their future discrimination (Santos & Novaes 2008). Santos *et al.* (2004) indicated that the parameters of this relationship may differ not only between species but also between stocks of the same species, considering that the growth coefficient depends on genetic, nutritional and environmental differences (Le Cren 1951, Bagenal & Tesh 1978). Considering that the thraira were sampled in the same environments, the differences in the relationships between them probably reflect genetic dissimilarities inherent to each species.

These relationships also indicate eventual changes in body shape over ontogenetic development (Costa & Araújo 2003). According to Froese (2006), if b = 3, small specimens in the sample exhibit the same shape and condition as the adults, but if b > 3, then the adults increase more in width than in length. Inversely, if b < 3, then the adult fish change their body shape to be more elongated or the juveniles exhibit better nutritional condition. Therefore, adult individuals of *Hoplias* sp. 1, independent of sex, may experience good conditions in the Upper Paraná River floodplain, corroborating the results of Hauser *et al.* (in press), who verify greater factor conditions for the females of *Hoplias* sp. 1 compared to *Hoplias* sp. 2. Thus, the introduced species is well-adapted in the study area, partially explaining its occupation success in the region (Prioli *et al.* 2004).

The higher allometric coefficient of females from *Hoplias* sp. 2 compared to the males may be related to their intense reproductive effort and heavier gonads. The development of the female organs occurs at a more intense rhythm than the increase in length or weight, and this is reflected in the more pronounced change in body shape throughout the lifecycle (Isaac-Nahum & Vazzoler 1983). Environmental particularities that establish better or worse conditions for feeding or reproduction may also influence this coefficient (Araújo & Vicentini 2001). Craig *et al.* (2005) argued that the occurrence of this sex dimorphism is expected, and the population age is a determining factor of the length-weight relationship. According to Motta *et al.* (2005), morphological variation leads to functional and performance differences, resulting in divergence in resource use. Consequently, it is pos-sible that such morphometric differences between the males and females of *Hoplias* sp. 2 reflect differences in habitat use and niche occupation, and may affect the production of offspring.

Despite the observation that *Hoplias* sp. 3 exhibits isometric development, it is not possible to affirm that this species maintains the same body shape throughout its life cycle or whether any differences exist between the sexes, which, due to the low number of individuals, were analyzed together.

Our results suggest that the complex of species recognized as *Hoplias* aff. *malabaricus* present in the Upper Paraná River floodplain shows differences in some of the population attributes investigated here, especially in *Hoplias* sp. 1 and *Hoplias* sp. 2, as the number of sampled specimens allowed a more reliable evaluation. In general, the native species exhibits higher dependence on hydrological seasonality and apparently explored the available resources more efficiently during periods of conspicuous floods. *Hoplias* sp. 1 seems to exhibit a higher degree of population balance, given the absence of sexual dimorphism in the allometric coefficient, and little variation between males and females regarding seasonality and length structure, and both genders have a low dependence on hydrometric levels. These characteristics probably allow this species to occupy the Upper Paraná River floodplain. In this way, these differences reflect the genetic aspects of each species, reasserting the need to discriminate between the species that comprise the *Hoplias* aff. *malabaricus* complex and, especially, to denote the importance of understanding the life strategies adopted by each since they, as part of a complex, are important to the structure of the aquatic community in the study region. In addition, these species are directly related to measures of habitat management and biodiversity conservation. Consequently, further studies on the autoecology of these individuals, mainly focusing on behavioral and foraging aspects as well as the relationship between abiotic factors and their population dynamics, would be indispensable for a better understanding of how these closely-related species are able to coexist in the same environment.

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