

Reproductive strategies of Red-bellied Piranha (*Pygocentrus nattereri* Kner, 1858) in the white waters of the Mamirauá flooded forest, central Brazilian Amazon

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Abstract Despite being an important member of neotropical fish assemblages, as well as a species with an unenviable reputation, little is known about the reproductive ecology of Red-bellied Piranha, *Pygocentrus nattereri*, in the wild. We tracked the reproductive activity of piranhas in the flooded forests of Mamirauá Reserve, Central Brazilian Amazon, for 2 years, in an investigation that included over 3,000 individual fish. Contrary to expectation piranhas had not one, but rather two annual reproductive seasons, tuned to water level fluctuation and the flooding pulse. Females were found to have up to 30,000 oocytes, little more than one third of which were mature and available for spawning in a single batch. Sexual maturation (of both males and females) occurred at around 160 mm. At this point sexually active individuals (of both sexes) became dark and lost most of their red coloration. Ontogenetic changes in habitat selection were strongly associated with the spawning behavior of mature adults. We also found

that flooded marginal vegetation and marginal grasses inside lakes were the preferred spawning areas. In contrast, non-reproductive individuals were found in open water and under floating meadows.

Keywords Red-bellied Piranha · *Pygocentrus* · Serrasalminae · Reproductive biology · Life-history strategies · Amazon

Introduction

The Neotropical Region supports probably the most diverse freshwater fish fauna in the planet (Lowe-McConnell 1987). The Characidae fish belonging to the subfamily Serrasalminae form a unique, non-migratory component this fauna, and often have piscivorous feeding habits (Machado-Alison 1983). The piranhas, fish from the genera *Serrasalmus* and *Pygocentrus*, are one of the most widely known representatives of this subfamily. Despite their notoriety, there is surprisingly little information on the ecology and life history of piranhas (Magurran and Queiroz 2003).

Pygocentrus nattereri is the piranha species with the largest geographic range, encompassing most of the Neotropical Region. This species is present in all the important tributaries of the Solimões-Amazon, but also in the Orinoco, the São Francisco, Plata and Paraná river basins (Machado-Alison 1983; Lowe-McConnell 1987; Machado-Alison and Fink 1995;

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Hubert and Renno 2006). This species has been introduced at other parts of the American continent, usually with negative consequences for the local fish fauna (Latini and Petrere 2004). Despite its wide distribution, it is believed that the species is particularly abundant in more productive waters (Fink 1993; Duponchelle et al. 2007), such as the white waters of the Amazon basin.

The popular impression of Red-bellied Piranha as pack-hunting fish living in the jungles of South America (Schulte 1988) is an over-simplification of the truth. In fact, the primary function of their shoaling behaviour is as a defence against predation (Magurran and Queiroz 2003; Queiroz and Magurran 2005). In spite of having captured the public imagination, these animals are rarely the focus of scientific investigation (Duponchelle et al. 2007). Red-bellied Piranha feed primarily on other fish, small invertebrates and plant material, though they may also scavenge the bodies of dead vertebrates (Goulding 1980; Sazima and Guimarães 1987; Winemiller 1989; Sazima and Machado 1990; Pauly 1994).

To date there are only a handful of studies describing the reproductive biology of piranhas (Pauly 1994; Duponchelle et al. 2007). Available data on the seasonal reproduction of the species of this group suggest that Serrasalminae species have a long reproductive period, usually during the rainy season (Rodrigues et al. 1978; Leão et al. 1991; Vazzoler and Menezes 1992; Ferreira et al. 1996). One species, *Serrasalmus spilopleura*, is known to spawn in marginal aquatic vegetation (Quaggio-Grassiotto and Guimarães 2003), and to be a multiple spawner (Lamas and Godinho 1996). *Pygocentrus nattereri* has been reported as defending territories, building nests in the marginal flooded vegetation, and showing parental care of the nest and young (Uetanabaro et al. 1993; Lowe-McConnell 1999). Uetanabaro et al. (1993) also described the formation of mating pairs, nuptial swimming display, and guarding of nests.

Drawing primarily on information from captive animals, Pauly (1994) described nest building by *P. nattereri* males, and the defence of the eggs and young, initially by both male and female, and subsequently only by the male. Pauly (1994) also calculated reproductive loads—the relationship between the asymptotic size and the size of sexual maturation—for this species. His analysis was based solely on scattered information in anecdotal accounts

from the literature. In a more recent investigation on the reproduction and growth of *P. nattereri*, the species was studied in two connected rivers of the Bolivian Amazon, where about 1,000 piranhas were captured and analyzed (Duponchelle et al. 2007). These authors documented the reproductive season, the sexual maturation, the size of first reproduction, and the fecundity of the species. They concluded that life-history traits are linked to the productivity of the local environment in which a population is located.

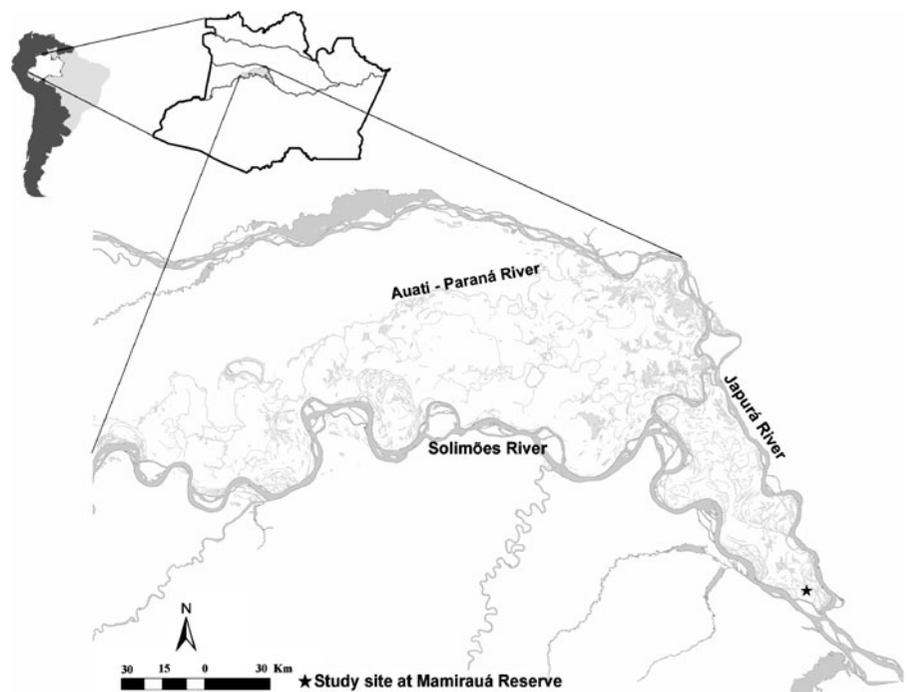
Here we provide the results of a long-term investigation of the reproductive ecology of Red-bellied Piranha in the Brazilian Amazon. Our study system is the *várzea* (flooded forest associated with white water rivers) of the Central Amazon floodplain (Goulding 1980; Lowe-McConnell 1987; Saint-Paul et al. 2000). In this particular environment Red-bellied Piranha are exceptionally abundant, and important as both predators and prey within the local aquatic food web (Queiroz and Magurran 2005). We conducted a longitudinal investigation of the species during which we monitored reproductive status, maturation and recruitment across two complete years. Our prediction, based on data collected for other characins (Machado-Alison 1983; Lowe-McConnell 1987, 1999) was that there would be a single spawning season per annum for Red-bellied Piranha, and that this would be linked to the annual rise in water level and the flooding of the marginal vegetation, that occurs from February to March in the part of the Amazon where this work took place (Ramalho et al. 2009).

Materials and methods

Site description

This study was carried out at the Mamirauá Sustainable Development Reserve (MSDR), in the Brazilian Central Amazon floodplain (Fig. 1). Mamirauá Reserve, the largest protected area of *várzea* in Brazil, covers 1,124,000 ha all of which are completely flooded for 3 to 6 months every year during the flooding pulse (Ramalho et al. 2009). Water levels fluctuate by 9 to 11 m annually. Different types of flooded forests form the reserve (Wittmann et al. 2006) and its mosaic of water bodies, lakes, channels and forest types is typical of the Amazonian *várzea*

Fig. 1 The location of the study site, at Mamirauá Sustainable Development Reserve, Amazonas State, Brazil



environment (Junk 1997; Junk et al. 2000). In general, white waters in the Amazon originate in the Andean slopes and foothills, and carry a considerable load of sediments plus a great deal of nutrients (Sioli 1984; Junk 1997). The aquatic environment is very diverse, and there is a rich fish fauna associated with each of the aquatic habitats (Henderson and Hamilton 1995; Henderson and Crampton 1997; Henderson and Robertson 1997; Crampton 1999; Saint-Paul et al. 2000). Some of the fish species present at Mamirauá Reserve are among the most economically important species currently under exploitation in the Amazon basin (Queiroz 1997).

Fish collection and analysis

A total of 3,046 individual piranhas were captured and measured with the help of local fishermen during the period of February 2003 to March 2005. Piranhas were sampled in three major habitats: the open water of channels and lakes, under the floating meadows and from the marginal vegetation of the flooded forest. Different types of fishing gears were used in each of these habitats since they present different structures and different seasonal availability.

The floating meadows are a particularly important habitat for piranhas (Petry et al. 2003). Here a seine

net (multifilament; 2 mm mesh size, 30 m long and 3 m wide) was used to sample the floating vegetation every month for an entire annual cycle (September 2003 to August 2004). The sampling effort was kept constant, and consisted of five samples of 16 m² per month per lake, in five different lakes. Total effort was of 400 m² of floating meadows per month.

The marginal vegetation and flooded grasses at the banks of the lakes were sampled using the same seine net, and also with line and hook (small pieces of dead chicken were used as bait), only during the months when these flooded habitats were present (early flooding seasons, Feb–Apr, and early droughts, Oct–Nov, in 2003, 2004 and 2005).

During the remaining months (Dec–Feb and May–Sep 2003, 2004 and 2005), only the open water was sampled, using three types of fishing gear. In addition to the seine net and the line-and-hook method, as above, a chicken wire cage (2 m×2 m×2 m) without a lid, was also used to sample this habitat. The cage was baited using pieces of dead chicken, and lowered 1 to 2 m deep in the water, for periods of between 30 s to 2 min, after which the trap was quickly removed from the water.

All fish caught were identified and all *P. nattereri* present in the samples (1,664 individuals in the floating meadows, 121 in the marginal vegetation

and 1,261 in the open water) were processed (measured and weighted). In most cases animals were collected, measured and weighted were returned alive to the water. However fish that would be eaten by the local fishermen, as well as those captured during the breeding season, were killed by quickly severing the spinal cord, just behind the head. These formed a sample of 347 individuals that were sexed and had their gonads analyzed. A sub sample of 92 gonads was collected and preserved for subsequent analysis of seasonality of maturation, fecundity and spawning strategy, to track egg development, and to calculate the gonadosomatic index (GSI), defined here as the percentage of gonad weight relative to total weight of the fish.

The relationship between the reproductive activity of piranhas and the seasonal hydrological cycle was deduced from the macroscopic analysis of gonad morphology, and also by the frequency and abundance of larvae (>50 mm total length) captured every month. Ovaries were classified using the well-established classification of fish gonad development (Vazzoler 1996). The monthly frequencies of mature gonads and of piranha larvae were correlated with the height of the water level, measured daily in the study site (Ramalho et al. 2009).

All animals sampled were allocated to 1 cm size classes. The frequency of mature animals of both sexes (stages 3, 4, 5 and 6 for females, and stages 3 and 4 for males) in each size class allowed us to estimate first sexual maturation (L_{50}), defined as the point when at least 50% of males or females in the population were sexually active (Vazzoler 1996). This information was subsequently fitted to a logistic model.

Finally, in each reproductive season, the ovaries of a subsample of mature females were removed and examined. After weighing and measuring the ovary, a tissue sample of 10% of the organ weight was taken. All oocytes present in these samples were removed from the ovarian matrix and counted. The fertility for each female studied was established by means of extrapolation from the total number of mature oocytes in each sample. These data were used to establish the relationship between fecundity and total length of females as well as with mature ovary size. A random sub-sample of 20–25% of the volume of these oocytes was taken after agitation and homogenization. The diameters of all sub-sampled oocytes were measured with a paquimeter. Frequency distributions of oocyte

diameter for each analyzed female were also constructed in order to establish their spawning strategy (Vazzoler 1996).

Results

Seasonality of reproduction

The observed seasonal variation in gonad development is consistent with two annual peaks of sexual activity at Mamirauá (Fig. 2). The first of these was observed during the rising of the water level, around March and April, when water starts to flood the marginal vegetation. The second peak was detected in the low water level periods, usually in November and December, when there is a sudden but temporary increase in the water level. The same pattern was observed in 2003, 2004 and early 2005. Gravid ovaries were particularly common in April and December in all years of this study. The seasonality of the reproduction of Red-bellied Piranha was also apparent from the seasonal recruitment of the population. A strong seasonal pattern was found in the abundance of larvae *P. nattereri*, (<50 mm in total length) in the floating meadows inside lakes of Mamirauá. There is a highly significant correlation between the presence of piranha larvae in the floating meadow and the monthly frequency of mature gonads in the sample of adult fish (r_s (Spearman) = 0.9128; $p=0.0014$; $N=12$ months). We also observed that mature individuals changed color during reproductive season. Red-bellied Piranha typically have silvery backs and flanks, and, as implied by their common name, red bellies. However, when sexually active, adults tend to be very dark in all parts of their bodies, and very little red coloration remains.

P. nattereri recruitment peaked shortly after the water level in the lakes reached its lowest level in the season. These events were recorded twice in each sampled year. The first was the extreme of the drought, in October. The second event was occurred when the water level was rising, (February and March), at a time known locally “*repiquete*”. This short period of sudden increase in the water level, with no substantial rain, is observed almost every year. Figure 2 illustrates the relationship between variation of the water level and recruitment. This distribution confirms the results from the visual

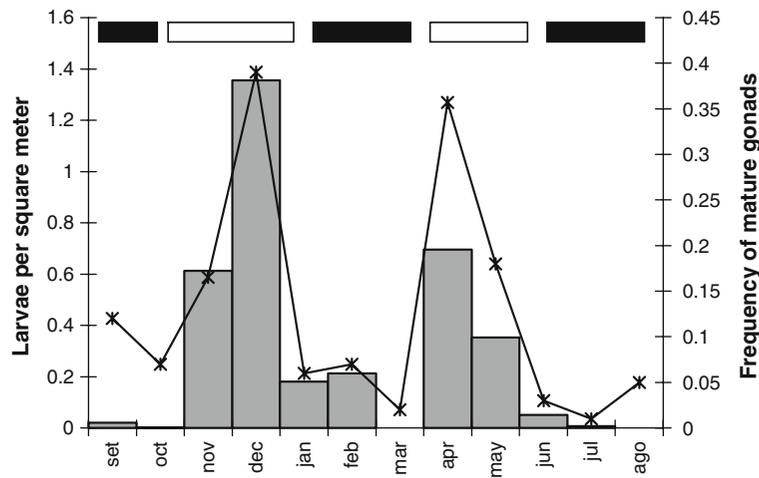


Fig. 2 Monthly distribution of larvae (<50 mm) *P. nattereri* collected in 400 m² in the floating meadows of five lakes (solid vertical gray bars) and frequency of mature gonads in adult females (N=195) during the same period at the Mamirauá

Reserve (solid line). The horizontal bars above represent periods of high water levels, when the forests were flooded (solid black bars) and periods of low water levels (open bars)

inspection of the gonads and the bimodal annual activity in the reproduction of *P. nattereri*. In fact, there is a strong negative correlation between the relative abundance of larvae piranhas in each month and the water level observed 2 months previously ($r_s = -0.78$; $p < 0.01$; $N = 12$ months).

in the form of gametes available for spawning each reproductive season.

Gonad development and fertility

Sexual maturation and size at first reproduction

When sexually mature females (stages 3, 4, 5 and 6) were analyzed, both ovaries were equally developed and at the same developmental stage. The gonadosomatic index of virgin females (stage 1) was 0.2% on average, increasing before the spawning season (stages 4 and 5), when it reached about 4%, while GSI of mature males never exceeded 0.2%. Egg counts from mature females (stages 4 and 5 only) ranging from 180 to 240 mm total length confirmed that the total number of oocytes varied with the size of the female and with the size of the mature ovary. Simple linear models describe this variation:

Both males and females exhibited similar developmental patterns. The sizes at first reproduction of males and females were estimated based on a frequency of mature gonads for each 10 mm size class. Values were as follows: females $L_{50} = 159.9$ mm ($r = 1.167$; $R^2 = 0.75$); males $L_{50} = 162.2$ mm ($r = 2.175$; $R^2 = 0.81$). Despite the fact that males apparently mature more quickly than females ($r_m = 2.175 > r_f = 1.167$), there was no significant difference between their size at first reproduction in a *t*-Test ($t = -0.0759$; $p < 0.001$). The data, fitted to a logistic model, are shown in Fig. 3(a and b) for females and males, respectively. All Red-bellied Piranha of both sexes are sexually mature (L_{100}) before reaching 180 mm in total length. Based on the reported asymptotic length for the species, 26 cm (Pauly 1994: 425), and on the size of sexual maturation reported above, 16 cm, the reproductive load for Red-bellied Piranha at Mamirauá was established as 0.61.

$$[\text{fertility}] = 308.97 * [\text{female length}] - 42\,700 (R^2 = 0.78) \text{ and}$$

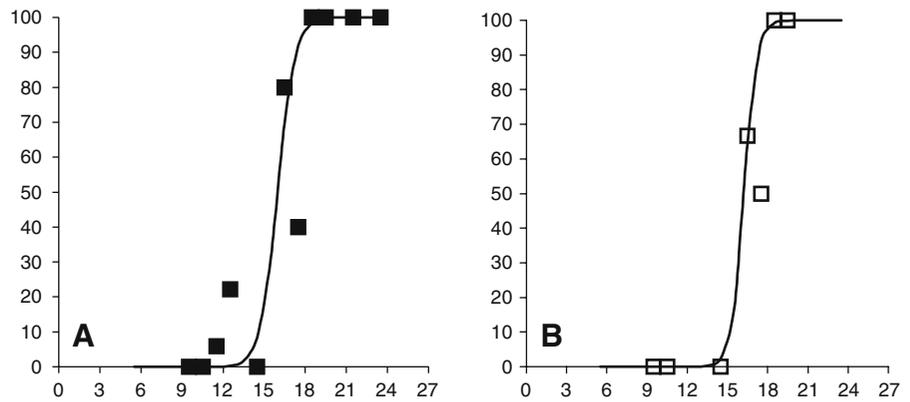
$$[\text{fertility}] = 839.3 * [\text{ovary length}] - 27\,728 (R^2 = 0.81)$$

Based on the counts in samples from the ovaries, the total number of oocytes per female varied from circa 9,000 to circa 33,000. However, in each ovary only 45–56% of the oocytes were mature (>0.9 mm of egg diameter). Consequently, a mature female produced a batch of circa 5,000–16,000 mature oocytes

Type of spawning and differential habitat use

The bi-modal frequency distribution of oocyte diameter observed in every mature female examined reveals that the egg load is always divided in two groups. Unripe

Fig. 3 Logistic models of the sexual maturation of (a) females ($N=201$) and (b) males ($N=146$) of *P. nattereri* at Mamirauá Reserve from 2003 to 2005, with adjusted data represented by closed (females) or open (males) squares



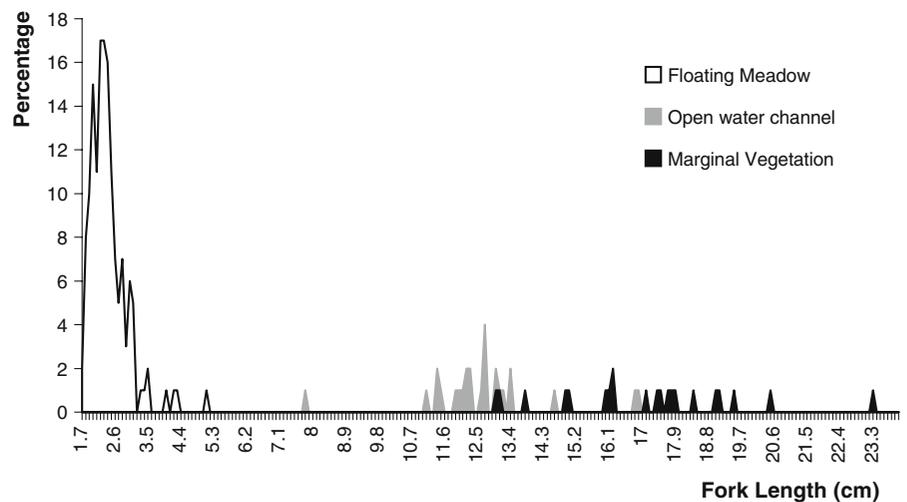
eggs and ripe eggs are separated by size. Egg maturation takes place at around 0.9 mm in diameter. The first mode, ranging from 0.3 to 0.5 mm in diameter, represents undeveloped oocytes, cells that will be retained and developed in the next reproductive seasons. The second mode, with peaks varying from 1.2 to 1.5 mm in diameter, represents ripe oocytes, and those will probably be spawned in one single batch in the current reproductive season. This diameter distribution suggests that *P. nattereri* is a total spawner. The mature, reproductive animals were found only among grasses and other marginal flooded vegetation, always inside lakes, during the periods of active reproduction identified in this study. These periods always occurred in the low water level phases in the *várzea* environment. In a distribution of sizes of Red-bellied Piranha caught at the three different environments sampled (floating meadows, open water and marginal vegetation at lakes), presented in Fig. 4, it is clear that reproductive animals are highly selective, and found

only inside lakes, in marginal vegetation. Juvenile and non-reproductive adult piranhas also differ in their use of the habitat. Thus, the marginal vegetation of lakes is used for reproduction, the floating meadows as nurseries, whereas the open water habitat is occupied by juveniles and by non-reproductive adults.

Discussion

The reproductive ecology of Red-bellied Piranha at Mamirauá is probably unique among the Serrasalminae subfamily. Contrary to expectation for the Red-bellied Piranha and for other piranhas studied elsewhere (Rodrigues et al. 1978; Leão et al. 1991; Vazzoler and Menezes 1992; Uetanabaro et al. 1993; Pauly 1994; Ferreira et al. 1996, Duponchelle et al. 2007), Red-bellied Piranha at Mamirauá Reserve have two seasonal peaks of sexual activity and recruitment per year. However, in accordance with previous work

Fig. 4 Size distribution of *P. nattereri* caught at floating meadows (white), open water (grey) and at the flooded marginal vegetation (black) at *várzea* lakes in Mamirauá Reserve, during the reproductive season



(Vazzoler and Menezes 1992; Ferreira et al. 1996), the seasonal peaks of reproductive activity appear to be related to the local pattern of rainfall, which in turn is closely related to the variation of the water level in the rivers, channels and lakes at Mamirauá (Queiroz and Crampton 1999) as in all *várzea* sites in the Amazon. A different trend was observed at the Bolivian Amazon, where Duponchelle et al. (2007) found a strong relationship with photoperiod, a trait that does not vary significantly in a site so close to the Equator as Mamirauá.

P. nattereri males and females appear to reach sexual maturation at similar sizes, around 16 cm in total length. This is in accordance with other observations on this species carried out at the Rupununi Savana, in Guyana (Lowe-McConnell 1964), but is different from the two related rivers studied at the Bolivian Amazon (Duponchelle et al. 2007), where males mature significantly sooner than females. In the few studies where the size of piranhas at first sexual maturation was described, animals reached maturity at 16 cm (both sexes) and at 11–14 cm and at 10.8–12.9 cm (males and females, in high and low productive waters, respectively) of standard length (Pauly 1994; Duponchelle et al. 2007). In the present study, L_{50} was established at 15.9–16.2 cm (for females and males, respectively) of total length. The small difference of circa 3 mm may be the result of the way the measures were taken or a sampling bias. We did not examine growth patterns but other investigators (Pauly 1994; Duponchelle et al. 2007) agree that the size at which first reproduction takes place is reached at the end of the first year of age.

This “size at first reproduction” is about 70% of the size of the largest animal in the sample collected at Mamirauá, and suggests a late maturation strategy. The reproduction load of 0.61 calculated here for Mamirauá is also similar to that previously calculated by Pauly (1994) for the species, but somehow higher than those obtained from data reported for the Bolivian Amazon (Duponchelle et al. 2007), where reproductive load varies from 0.49 (females in less productive waters) to 0.53 (females in more productive waters). These figures suggest that *P. nattereri* adjust their reproductive strategy to key aspects of the environment, such as the richness of nutrients in the water, the availability of food and their natural abundances, as noted by Duponchelle et al. (2007). Based on this assumption, it is suggested that Red-bellied Piranha mature comparatively later and larger

in the *várzeas* at Mamirauá, which are exceptionally rich in sediments, nutrients and food items, than in places where aquatic productivity is not as high.

In the present study, total fertility ranges from 9,000 to 33,000 oocytes, similar to 3,500–35,600 oocytes described by Duponchelle et al. (2007) for the Bolivian Amazon. However, only about 45% of the oocytes recorded at Mamirauá were made of mature cells, ready to be fertilized. In the present work and in the only other investigation where oocytes were counted and measured (Duponchelle et al. 2007), a bimodal distribution of diameters was described. It is here alternatively interpreted as a “two-groups synchronic oocyte development” strategy (Vazzoler 1996). In such a strategy, the first group is made of underdeveloped cells, which will not be spawned in the current season, while the second group is formed by mature eggs ready for spawning. Consequently, in contrast to other species within the larger group of piranhas species (Lamas and Godinho 1996), the Red-bellied Piranha *P. nattereri* is probably a total spawner. However, like other species in the Serrasalminae group, mature Red-bellied Piranha at Mamirauá use marginal vegetation for spawning (Uetanabaro et al. 1993). This assumes that no bias was introduced by the use of different sampling gears in different seasons and habitats, but the comprehensive nature of the study makes this unlikely.

Our findings suggest that *P. nattereri* at Mamirauá, and at other sites, have a life-history strategy that combines comparatively low fertility with some degree of parental care. This is not a common strategy for the group of Serrasalminae, in which the typical pattern is medium to very high fertility, with unprotected, pelagic eggs and larvae (Araújo-Lima and Goulding 1997). Fertility in the Characidae family usually ranges from around 30,000 (Sato et al. 2006) to up to 800,000 (Lowe-McConnell 1999) or even 1,200,000 (Araújo-Lima and Goulding 1997) mature oocytes annually.

Whether or not the biannual reproductive activity of *P. nattereri* described here is unique to the flooded environs of Mamirauá Reserve remains to be evaluated by further studies. But we concur with Duponchelle et al. (2007) that environmental variables shape the life-history patterns of Red-bellied Piranhas. It is clear that in some places spawning is linked to a change in photoperiod. In Mamirauá by contrast variation of the water level is probably the

main driver. We suggest that food availability (associated in turn with high aquatic productivity and nutrient abundance) is probably the key to understanding variation in sexual maturation and development in Red-bellied Piranha.

If our proposition is true, highly productive sites, such as the *várzeas* of Mamirauá Reserve are placed at one end of a spectrum, and clear water localities, such as those described by Duponchelle et al. (2007) at the other. Mamirauá is characterized by high abundances of prey and predators, and Red-bellied Piranhas exhibit late sexual maturation and low fertility, consistent with Pauly's (1994) conclusions. This idea need to be tested in further studies of this species in different kinds of environments, with other patterns of rainfall, water level variation, nutrient load and aquatic production.

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