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Identification of spawning sites and natural nurseries of fishes in the upper Paraná River, Brazil

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Synopsis

We studied the timing of migratory fish spawning in the last dam-free stretch of the upper Paraná River and in Itaipu Reservoir. Eggs were more common in the Amambai and Ivaí Rivers, while larvae predominated in the Paraná River and in Itaipu Reservoir. Both eggs and larvae were more abundant at night. The highest abundance of eggs was in October and that of larvae in November. Migratory species predominated in the Amambai and Paraná Rivers, and non-migratory species in the Ivaí River and Itaipu Reservoir. The predominance of eggs in the upper and middle portions, and larvae in the lower, infer that there are spawning sites in the former and nurseries in the latter. The high nocturnal abundance of eggs is associated with spawning at sunset and that of larvae with feeding, avoidance of predators and nocturnal disorientation. The presence of tributaries such as the Amambai and Ivaí Rivers in the last dam-free stretch of the Paraná River is extremely important to the maintenance of regional fish diversity and fish stocks in both the Paraná River and Itaipu Reservoir.

Introduction

Many freshwater fish species carry out reproductive migrations from the lower parts of rivers to the headwaters (Lowe-McConnell 1987, Vazzoler 1996, Agostinho et al. 1997, Agostinho & Júlio 1999). They reproduce when reach the upper portions, and their fertilized eggs passively drift to regions where embryonic development occurs (Nakatani et al. 1997a, Gomes & Agostinho 1997). The drift exhibits an annual periodicity resulting from the reproductive cycle, and even a daily periodicity, which may be associated with larval feeding (Elliott 1966, Gale & Mohr 1978), predation avoidance (Naesje et al. 1986), and spawning at sunset (Graaf et al. 1999), or for reasons still unclear.

When dam construction interrupts the migratory route of many fish species, tributaries can serve as alternative routes, playing an important role in the maintenance of regional biodiversity and fish stocks. Seven of the 10 most important commercial fishes in Itaipu Reservoir depend on areas upstream from the reservoir to reproduce

(Agostinho et al. 1992). To maintain fish stocks it is essential to maintain the integrity of spawning areas, which are responsible for the dispersion of eggs and larvae to feeding and development sites, making satisfactory recruitment possible. Precise identification of these areas is fundamental to measures for the protection of the ichthyofauna, and management of fisheries (Hempel 1973, Nakatani et al. 2001).

Studies of the spatial distribution of eggs and larvae, and species descriptions of the fishes involved, have been carried out in the upper Paraná River floodplain (Baumgartner 1992, Baumgartner et al. 1997, 2003, Cavicchioli et al. 1997, Nakatani et al. 1997a, Bialetzki et al. 1998, 1999, 2002, Sanches et al. 1999, Castro et al. 2002), and Itaipu Reservoir (Nakatani et al. 1993, 1997b, 1998, Nakatani 1994, Makrakis et al. 2003). However, the stretch of the upper Paraná River between the mouth of the Ivinheima River and the beginning of Itaipu Reservoir (object area of this work), has been little studied regarding eggs and larvae. Only those studies carried out by FUEM/Itaipu Binacional[1] are available.

The objective of this study was to determine the location of fish spawning sites, in the last dam-free stretch of the upper Paraná River, preservation of which seems fundamental to maintenance of fish stocks and regional biodiversity. Specifically, this study evaluates the month, site and time of day at which fish spawning occurs in the upper Paraná River and Itaipu Reservoir. Additionally we evaluate the use of these environments as spawning sites or nurseries for migratory species (seasonal strategy; Winemiller 1989), which are important to upper Paraná River fish landings and considered susceptible to extinction because of the height of the dams in this river (Agostinho et al. 1997).

Study area

The Paraná River, one of the most important in Brazil, starts from the confluence of the Paranaíba and Grande Rivers and runs 4695 km from its source to its mouth in the Prata River estuary (Paiva 1982). The upper Paraná River is entirely within Brazil, and has an average gradient of 0.18 m km^{-1} and a wide floodplain, which can reach 20 km in width, mainly on its right bank. The last dam-free stretch (230 km) extends from the dam at Porto Primavera Hydroelectric Power Station (São Paulo – Minas Gerais States) and Itaipu Reservoir (Brazil-Paraguay) (Agostinho et al. 1995). We carried out sampling in the upper Paraná River (23°–25°S; 53°–55°W) at 12 sites located in the upper, middle and lower portions of the main channel of the Paraná River (Figueira, Morumbi and Saraiva), Itaipu Reservoir (Guaçu, Capivara and Ipiranga) one right bank tributary (Amambai River: Areia, Ponte and Bom Fim) and one left bank (Ivaí River: Bananeira, Tapira and Pontal do Tigre) (Figure 1).

Material and methods

We carried out collections monthly between October 1994 and January 1995 (spawning period) during 24 h cycles, with 4 h intervals between samplings. We used conical–cylindrical plankton nets (0.5 mm mesh), with a flow meter coupled to the mouth to measure the volume of filtered water for standardization purposes, to collect eggs and larvae. At sites located in tributaries (Amambai and Ivaí), we tied nets to a rope extended from one bank to the other and operated them for 30 min (except at Pontal do Tigre where, due to the low flow, we carried out sampling using a slow-moving boat). Due to the width and high water velocity of the Paraná River, we collected samples from an anchored boat. We made collections in Itaipu Reservoir from a slow-moving boat. We fixed samples in buffered 4% formaldehyde, and standardized the abundance of eggs and larvae to a volume of 10 m^3 of filtered water (modified from Tanaka 1973). We carried out identification of the eggs and larvae in accordance with the development sequence technique (Ahlstrom & Moser 1976, Nakatani et al. 2001).

We used Analysis of Variance (ANOVA) to evaluate the differences between the eggs and larvae (dependent variable) in the different environments (rivers and reservoir), portions (upper, middle and lower), months (October, November,

[1] FUEM/Itaipu Binacional. 1995. Estudos das áreas de desovas de peixes – no Reservatório e trecho a Montante. Maringá, 73 pp. (Annual Report – Project Report ITAIPU BINACIONAL).

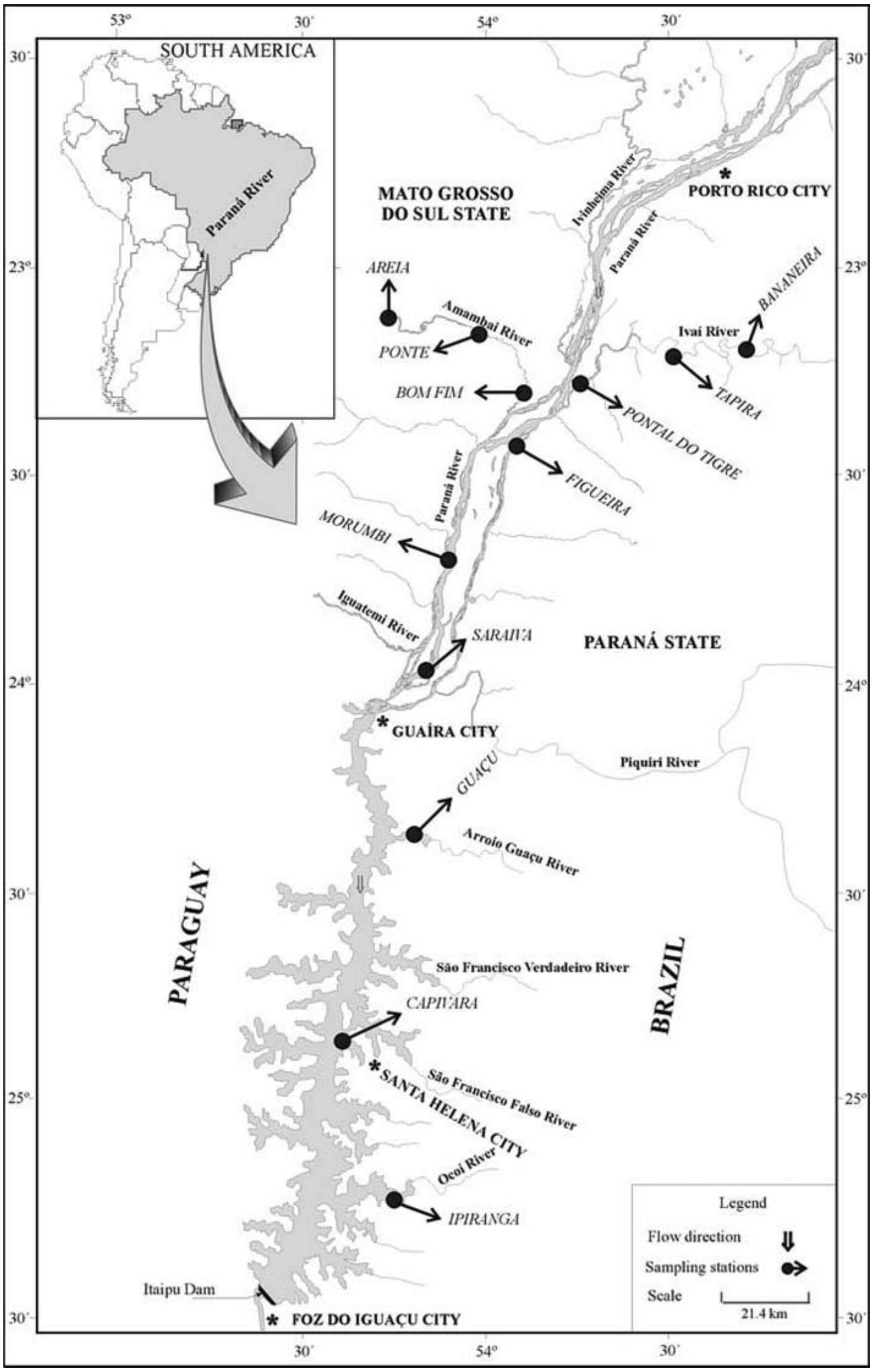

Figure 1. Location of the sampling sites in the upper Paraná River, Brazil.

December and January) and shifts (day and night) (independent variables). Our analyses were similar to those of Gido & Mathews (2000). To evaluate the most common reproductive strategy among the species that spawn in the different environments sampled, we grouped the identified larvae (specific level) into migrants and non-migrants, in accordance with Vazzoler (1996) and Agostinho et al. (2003). We examined differences between the densities of eggs and larvae at each sampling site (portions) (considering the environments separately) using the *t* test for paired samples. Due to the use of many tests with the same objective, we used a Bonferroni correction (0.05 number of $tests^{-1}$) to minimize the significant differences resulting from chance (many tests increase the probability of at least one of them being significant). In both analyses we transformed density data($\log(x + 1)$) to meet the assumptions of the analysis (normality and homogeneity of variance) (Peters 1986). Statistical significance is $p < 0.05$ in the ANOVA and $p < 0.004$ (Bonferroni correction) in the paired *t* test.

Results

Egg

During the study period, we collected 20 376 eggs (60.44% of all organisms registered in this study), with the highest densities recorded in the Amambai and Ivaí Rivers and the lowest in the Paraná River and Itaipu Reservoir. It should be emphasized that the high catch sites are located in the uppermost portions of this stretch of the basin (i.e. in the tributaries of the Paraná River). We observed the highest catches at night in the upper and middle portions and the lowest in the lower. The highest catches were in October, mainly in the Amambai and Ivaí Rivers (Figure 2). Variations in egg abundance, in relation to the four factors considered in the ANOVA, were significantly different ($p < 0.05$). The fourth order interaction was not significant ($F = 1.17$; $p = 0.29$), however, the third order interactions were significantly different ($F = 1.02$; $p = 0.02$), indicating that the effect of a determined factor on egg density depends on the other factors considered.

Larva

During the study period, we collected 13 338 larvae (39.56% of all organisms registered in this study). We observed the highest larval densities at night in the Paraná River and Itaipu Reservoir. Considering each environment separately, we observed the highest densities in the lower portion of the Amambai, Ivaí and Paraná Rivers and in the upper portion of the Reservoir. The nocturnal larval catches had higher densities than those carried out during the day in every month considered, with the highest densities in November (Figure 3). We also observed significant differences in larval density in relation to all factors considered ($p < 0.05$), except month ($p = 0.22$). The fourth order interaction was not significant ($F = 1.37$; $p = 0.15$), however, the third order interactions were ($F = 2.79$; $p = 0.01$), indicating that the effect of a determined factor on larval density depends on the other factors considered.

Reproductive strategy

We identified the larvae of 42 fish species during the sampling period. The reproductive strategy of 30 of these species had been determined in previous studies (Vazzoler 1996, Agostinho et al. 2003) (Figure 4). The 12 species that have not been studied are *Aphyocharax* cf. *anisitsi*, *Apteronotus albifrons*, *Bryconamericus* cf. *stramineus*, *Characidium* sp., *Crenicichla lepidota*, *Hemigrammus marginatus*, *Paravandellia* sp., *Pseudocetopsis gobioides*, *Rhamdia quelen*, *Roeboides paranensis*, *Synbranchus marmoratus* and *Tatia neivai*.

The most abundant species were *Leporinus elongatus*, *L. friderici* and *Pimelodus maculatus* (migrants) in the Amambai River; *Pimelodus maculatus* (migrant), *Auchenipterus osteomystax* and *Iheringichthys labrosus* (non-migrants) in the Ivaí River; *Pterodoras granulosus*, *Leporinus elongatus* (migrants) and *Bryconamericus* cf. *stramineus* (undetermined) in the Paraná River; and *Hypophthalmus edentatus* (non-migrant), *Bryconamericus* cf. *stramineus* (undetermined) and *Pterodoras granulosus* (migrant) in Itaipu Reservoir. In accordance with the reproductive strategy, larval abundance differed among the environments sampled. We observed a high density of migratory

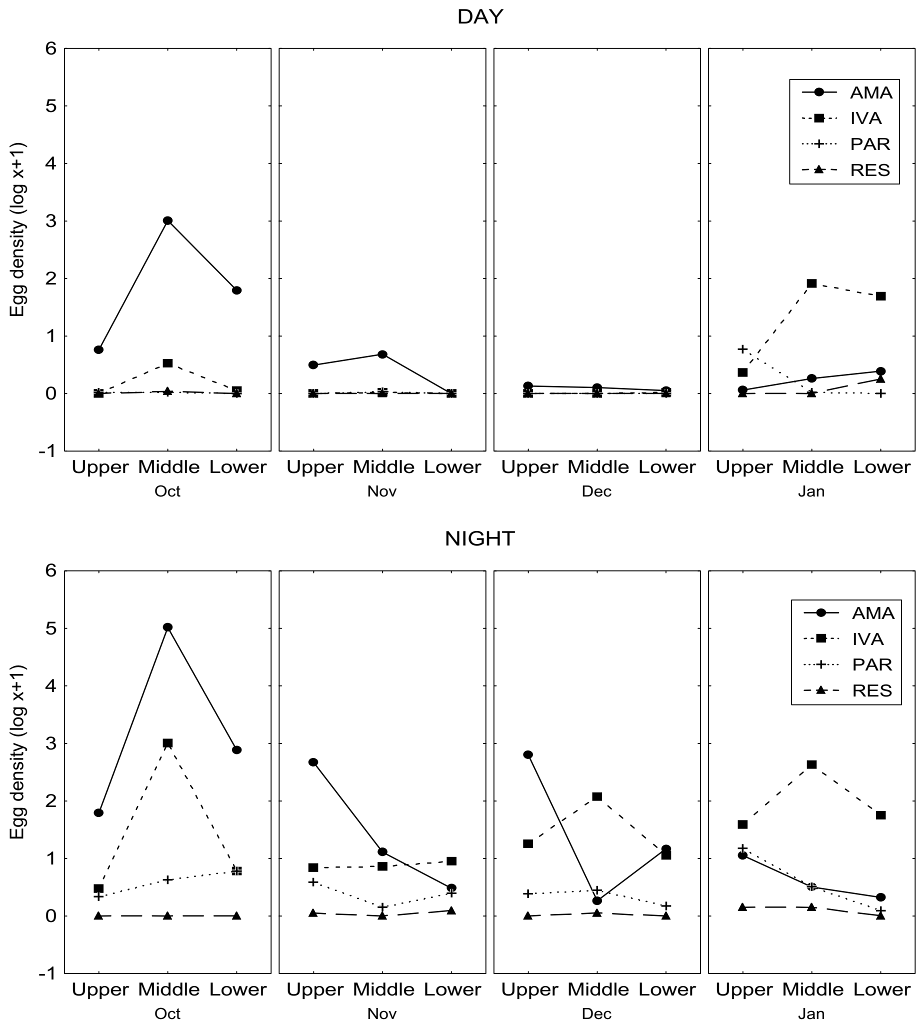

Figure 2. Diel variation in egg density (log $(x + 1)$) of samples collected in the upper, middle and lower portions of the Amambai (AMA), Ivaí (IVA) and Paraná (PAR) Rivers and Itaipu Reservoir (RES) from October 1994 to January 1995.

species larvae in the Amambai and Paraná Rivers. In the Ivaí River there was a modest predominance of non-migrators; whereas in Itaipu Reservoir, they were much more abundant (Figure 5).

Comparison of egg and larval densities

As the objective of this study was to verify if the upper portions of the various environments sampled are spawning sites, we analyzed them separately. In the Amambai River, we caught 16 674 eggs and 561 larvae, with significantly higher densities of eggs than larva occurring in the upper (Areia) and middle (Ponte) sites ($t > 3.6$, $p < 0.004$; Figure 6a). It should be emphasized that we observed a gradient along this river (upper to lower portion), showing a decrease in egg density and an increase in larval density. In the Ivaí River, we collected 1319 eggs and 1518 larvae. We found significant differences between eggs and larvae at all positions ($t > 2.10$, $p < 0.004$). There was a predominance of eggs at the upper (Bananeira) and middle (Tapira) sites, while larvae predominated at the lower site (Pontal do Tigre) (Figure 6b). The gradient of this river was similar to that in the Amambai River, with decreasing egg

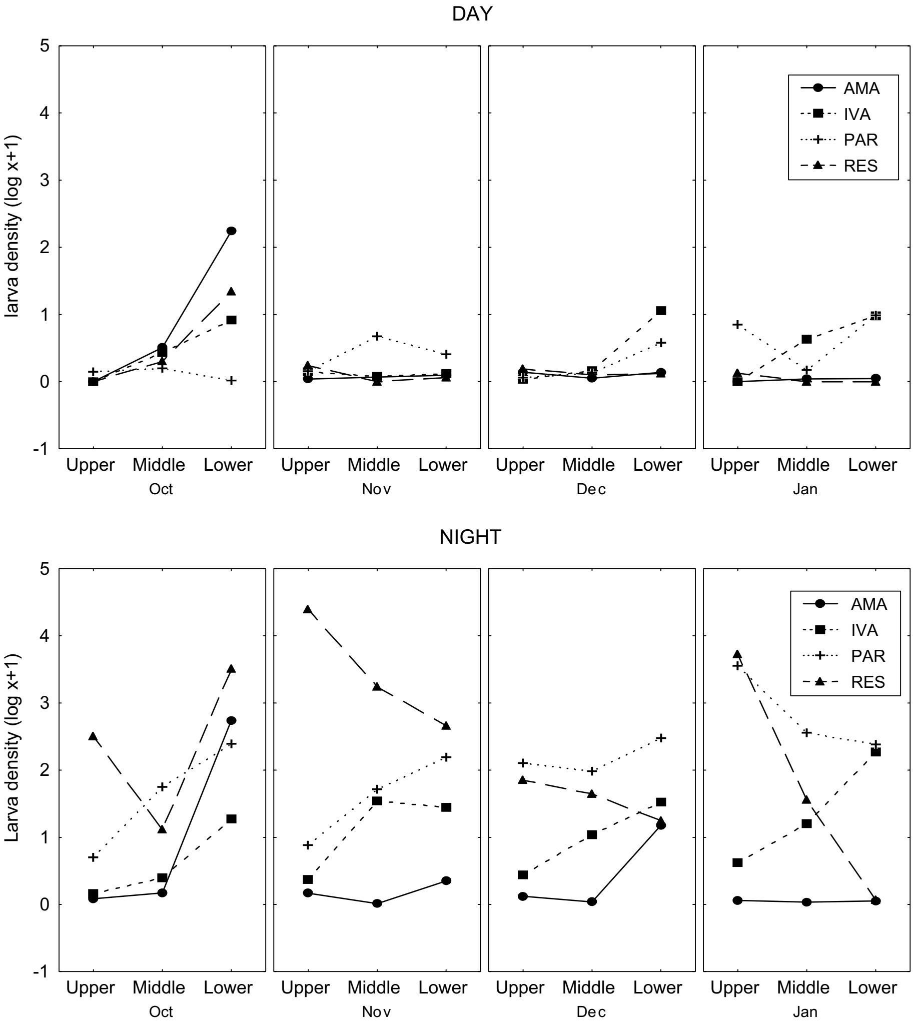

Figure 3. Diel variation in larva density (log($x + 1$)) of samples collected in the upper, middle and lower portions of the Amambai (AMA), Ivaí (IVA) and Paraná (PAR) Rivers and Itaipu Reservoir (RES) from October 1994 to January 1995.

density and increasing larval density toward the lower portion of these tributaries. We caught 483 eggs and 5864 larvae in the Paraná River, with the latter dominant at all positions ($t > 3.30$, $p < 0.004$; Figure 6c). We observed a gradient in which egg density decreased and larvae density increased from the upper to the lower portion. During the study period, we caught 20 eggs and 5395 larvae in Itaipu Reservoir. Larval densities were significantly higher than egg densities at every position ($t > 3.40$, $p < 0.004$; Figure 6d). We observed a reduction in larval densities toward the dam.

Discussion

High egg densities at sites located in the upper and middle portions of the Amambai and Ivaí Rivers are the result of spawning associated with the presence of geographic barriers (waterfalls or rapids). Rapids are appropriate environments for migratory species to spawn because they supply favorable conditions in terms of oxygen concentration and transport to areas where embryonic development can occur. Godoy (1954) noted that *Prochilodus scrofa* (a common migratory species in the neotropics) spawns in the middle of the river,

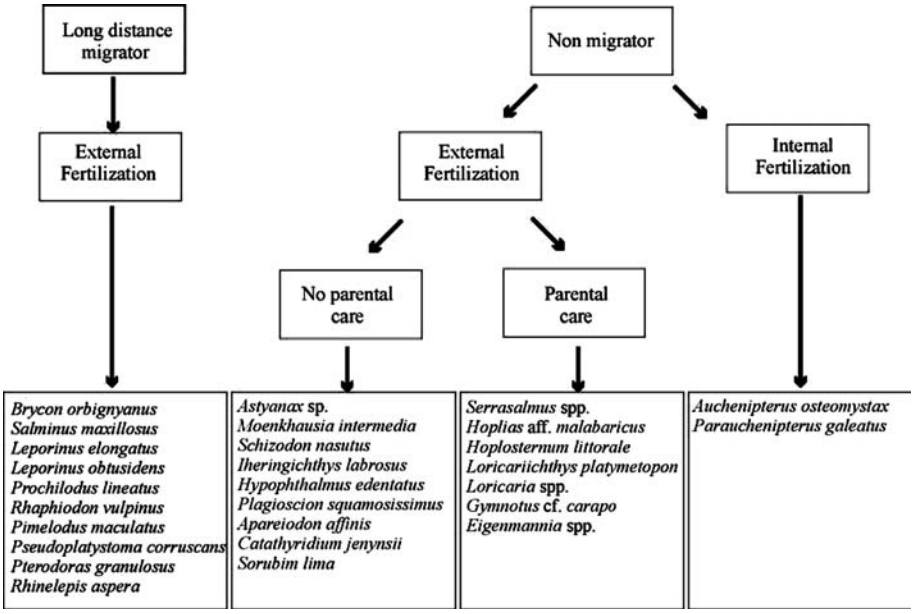

Figure 4. Reproductive strategy of the species whose larvae were caught during the study period (Adapted from Agostinho et al. 2003).

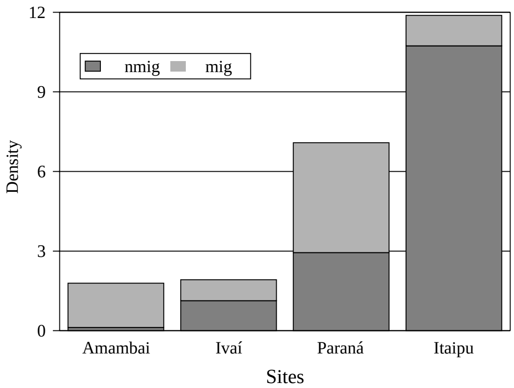

Figure 5. Larval density (larva10 m^{-3}) of migratory (mig) and non-migratory species (nmig) caught in the Amambai, Ivaí and Paraná Rivers and Itaipu Reservoir from October 1994 to January 1995.

in very strong current. High egg densities in the rapids emphasize the importance of preservation of these environment as spawning grounds. Damming of the river can significantly alter these sites, extinguishing lotic conditions or making access impossible, causing severe impacts on migratory species.

Despite the significant interactions in our ANOVAs, it was possible to determine that egg density was higher at night, which corresponds with daily periodicity in drift of organisms as suggested by Elliott (1966), Gale & Mohr (1978), Armstrong & Brown (1983) and Johnston et al. (1995). The most plausible explanation for the higher nocturnal egg density observed in this study is that spawning is induced by the reduction of light (Graaf et al. 1999). The general rule for tropical species is that they spawn at sunset, when water temperature is at its highest, which is reflected in higher nocturnal egg densities (Godoy 1975).

In addition to eggs, the presence of larvae is also strong evidence of spawning. Despite significant interactions in our ANOVAs, larval densities were determined to be higher at night, which may be associated with food strategies and predator avoidance. Baumgartner et al. (1997) observed that larvae drift on the surface at night and on the bottom during the day. They stay on the bottom during the day and leave at night in search of food, becoming more vulnerable to capture. In a study carried out by Lansac-Tôha et al. (1995) on the upper Paraná River floodplain, high concentrations of zooplankton (main food of the larvae) were registered on the surface at night and on the bottom during the day, which could lead to

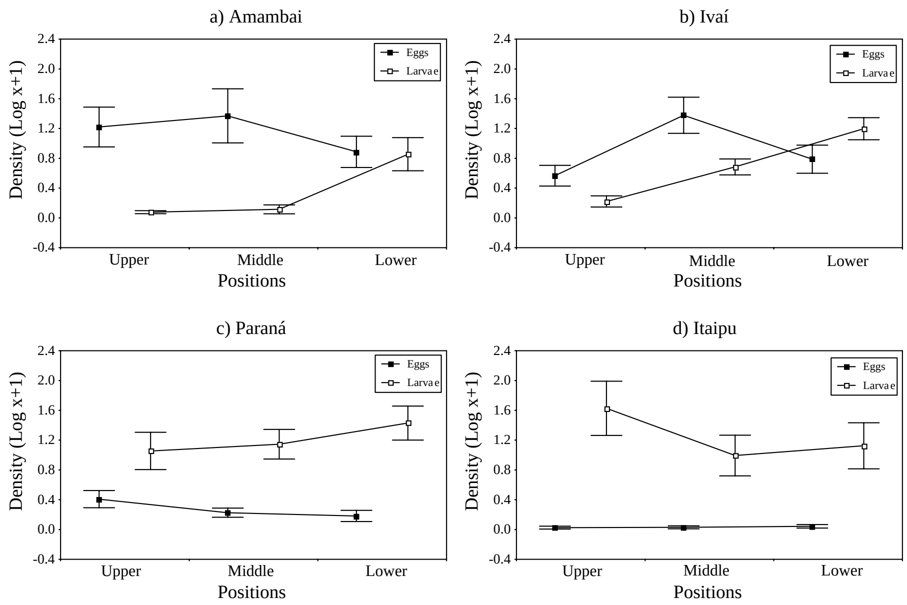

Figure 6. Average densities (log(x + 1)) and standard error of eggs and larvae for the different sites and environments sampled between October 1994 and January 1995.

feeding migrations. Therefore, it seems that a combination of factors influences the catch of larvae and that feeding is the trigger for the entire process.

High larval densities at sites located in the lower portions of the Amambai, Ivaí and Paraná Rivers may be the result of two processes: (1) eggs being transported by the current open along the way, and the emerging larvae are caught at the river mouth, or (2) environments which have littoral plant cover and reduced water flow supply appropriate conditions for development in the initial phases of these species , as is the case of the Pontal do Tigre and Saraiva sites. The longitudinal gradient in egg and larval densities (more eggs in upper portion and more larvae in lower portions), observed for the region as a whole (and especially in the Amambai and Ivaí Rivers), confirms that fertilized eggs are transported by the current and continue their development until they become larvae, in the lower portion, in marginal lagoons (when present), or at sites having aquatic macrophytes and low water flow.

High fish egg densities in Amambai and Ivaí Rivers (upper regions of the stretch sampled) coincide with results from other tributaries (Ivinheima, Piquiri and Iguatemi) of the upper Paraná River (Nakatani et al. 1997a). High water velocity in these environments transport the eggs to larval feeding and growth areas. Godoy (1954) emphasized that in southeastern Brazilian rivers, annual fish migrations (a phenomenon known as 'piracema') are directly related to spawning in their upper portions. Similar results were obtained in the upper Paraná River for *Prochilodus scrofa* (Agostinho et al. 1993). Evidently at least part of the fish stock of the upper Paraná River migrates into tributaries of the last dam-free stretch in order to spawn, due to disruption of the continuity of migration routes along the Paraná River.

The presence of larvae of migratory species such as *L. elongatus*, *P. granulosus*, *P. maculatus* and *S. maxillosus* in the Amambai, Paraná and, to a lesser degree, the Ivaí rivers allows us to determine such sites as spawning grounds of these species. The predominance of larvae of non-migratory species such as *H. edentatus*, *P. squamosissimus* and *I. labrosus* in the Ivaí River and Itaipu Reservoir demonstrates that these regions are spawning grounds of resident species and serve as natural nurseries for both migratory and non-migratory species.

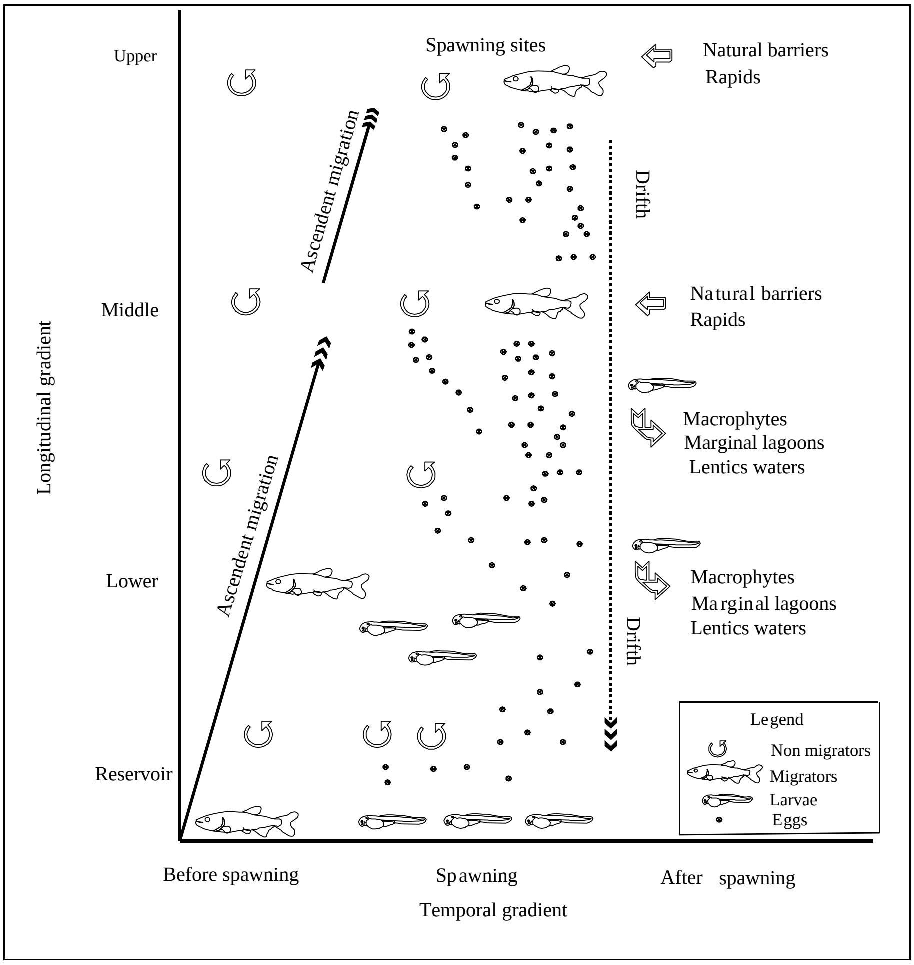

Figure 7. Conceptual model showing the process of migration and spawning for migratory and non-migratory species of the upper Paraná River.

The differences observed between the densities of larvae caught in the environments considered demonstrate the importance of the Paraná and Reservoir areas for their development. Both areas supply appropriate conditions for species development and function as nurseries. Baumgartner et al. (1997), studying ichthyoplankton in habitats immediately upstream from the upper Paraná River floodplain, observed a high larval catch in environments with lotic characteristics and the presence of macrophytes, which resemble the environments studied in the Paraná River. The lentic characteristic of the Itaipu Reservoir favors the development of certain species. This is evident from the specific composition of larvae in the Paraná and Reservoir areas. Larvae from migrants dominate in the former, whereas larvae from residents dominate in the latter. Nakatani (1994) recorded highest densities of *Plagioscion squamosissimus* larvae in the lateral extensions of Itaipu Reservoir tributaries.

Although our collection period was limited, the number of species identified in this study corresponds to 25% of those referred to by Agostinho et al. (2000) in a previous study in the upper Paraná River. It is important to emphasize that among the species captured, 11 are referred to by Vazzoler (1996) and Agostinho et al. (2003) as migrants, and that five sustain the commercial fishery of Itaipu Reservoir.

We can conclude that at least some upper Paraná River fish species migrate from the lower portions of the basin toward the headwaters of the tributaries before initiating spawning. The Amambai and Ivaí Rivers are spawning grounds, and the Paraná River and Itaipu Reservoir are development sites. Both migratory and non-migratory species spawn at dusk in these environments. Migratory species spawn in environments with rapids or natural barriers, promoting dispersal of developing young down river. Both eggs and larvae can: (1) be released in areas having reduced flow and aquatic macrophytes, (2) reach marginal lagoons (when present), and (3) be carried to the reservoir (Figure 7). In any of these environments, both eggs and larvae find appropriate conditions for development. We emphasize that not only tributaries of the upper portions, but also those nearer the reservoir can be used as alternative routes for migratory fish. Thus, the last dam-free stretch of the Upper Paraná River (Brazil) is extremely important to the maintenance of fish stocks and regional fish diversity.

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