Larvae of migratory fish (Teleostei: Ostariophysi) in the lotic remnant of the Paraná River in Brazil

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ABSTRACT. Fish larvae and adults are morphologically distinct from each other and have different ecological requirements. Research on the dynamics of ichthyoplankton provides valuable information about the early stages of the life cycle of fish. This study analyzed the temporal and spatial distribution of the larval stages of three migratory species – \textit{Salminus brasiliensis} (Cuvier, 1816), \textit{Prochilodus lineatus} (Valenciennes, 1836) and \textit{Pseudoplatystoma corruscans} (Agassiz, 1829) – to identify possible spawning areas in the last lotic remnant of the upper Paraná River, in the Brazilian territory. A total of 26 points were sampled monthly from October 2003 to November 2004. The PERMANOVA detected significant differences between the months only for \textit{S. brasiliensis} (Pseudo-F = 3.88, p = 0.0021) and \textit{P. corruscans} (Pseudo-F = 3.35, p = 0.004).

Among the environmental variables, temperature was the most important and the Mantel test detected a significant correlation between temperature and the densities, only for \textit{P. lineatus} (r = 0.09, p = 0.03). The species in our data chose for spawning tributaries that are not dammed, of which most are outside conservation areas. Therefore, recruitment, maintenance and possible actions aiming to recover the stocks of these species are dependent on the conservation of tributaries and floodplain lakes in the region, in addition to monitoring to prevent fishing during the reproductive period.

KEY WORDS. Ichthyoplankton; \textit{Prochilodus lineatus}; \textit{Pseudoplatystoma corruscans}; \textit{Salminus brasiliensis}; Upper Paraná River.

Fish colonize all types of habitats, which are subjected to various environmental conditions. They have various shapes, sizes and life cycles (\textit{Wootton} 1991). The life strategy of these organisms is associated with favorable conditions to the early development of eggs and larvae, highlighting sites and seasons with higher availability of food and shelter (\textit{Nakatani} et al. 2001). Nevertheless, larvae and adults are morphologically and behaviorally distinct, and thus have different ecological requirements, such as habitat and food (\textit{Sanches} et al. 2001, \textit{Nakatani} et al. 2001).

Reproduction is one of the most important aspects of the biology of a species, since the maintenance of viable populations depends on its success (\textit{Suzuki} \& \textit{Agostinho} 1997). Reproductive failure in consecutive years, mainly caused by changes in hydrological cycles (flow regulation and change in the timing of high flows) (\textit{Vazzoler} 1996, \textit{Agostinho} et al. 2003, 2004a), may result in depletion or even extinction of natural populations (\textit{Welcomme} 1979, \textit{Gomes} \& \textit{Agostinho} 1997, \textit{Suzuki} \& \textit{Agostinho} 1997, \textit{Ali} \& \textit{Wootton} 1999, \textit{Agostinho} et al. 2004b).

The Paraná River is intensely impacted by dams. A conservative count that takes into consideration only dams that are 10 m high above the water level (\textit{Agostinho} et al. 1995, 2007) totals 130 dams, transforming the river course into a cascade of dams.

The Sêrgio Motta Dam, built in 1998 (known as Porto Primavera), has deeply affected the dynamics of the ichthyoplankton in the upper Paraná River floodplain (\textit{Sanches} et al. 2006), located immediately downstream from it. This study was conducted in this area (above the Porto Primavera Dam and the Itaipu Reservoir), which represents the lotic rem-
nant of the Paraná River inside the Brazilian territory. Despite the fact that three conservation units (Ilha Grande National Park, State Park of the Várzeas of the Ivinhema River, and Environmental Protection Area of the Islands and Várzeas of the Paraná River) are present in the area, the local fish fauna is especially impacted by the dams (Agostinho et al. 2000, Sanches et al. 2006), which directly impact water quality, spawning, and recruitment of populations (Gomes & Agostinho 1997, Peiry et al. 2003, Agostinho et al. 2004b).

Species of great commercial value in professional fishing, such as Salminus brasiliensis (Cuvier, 1816), Prochilodus lineatus (Valenciennes, 1836) and Pseudoplatystoma corruscans (Agassiz, 1829), are among the most vulnerable to habitat changes in the Paraná River basin (Agostinho et al. 1997). These species are migratory. Consequently, restrictions to water flow and changes in the seasonality of the hydrological cycle of the river, imposed by the dams, impair their reproduction, which depends on seasonal variations in river tide (Agostinho et al. 2003). According to the Red List of Threatened Fauna of the state of Paraná (Ablhoa & Duboc 2004), S. brasiliensis and P. corruscans are no longer abundant in the Paraná River basin. However, these species are still found in this stretch of the river where there are several tributaries, many of which are outside the conservation units. These tributaries are still not dammed, and can be used by migratory species as alternative migration routes, particularly for reproduction (Sanches et al. 2006).

The identification of fish eggs and larvae, combined with data on their distribution provide considerable evidence about the spawning season, sites for reproduction, and natural breeding areas (Nakatani et al. 1997, Nakatani et al. 2001). With this information, we can implement guidance and protection measures in these areas, preventing the capture of young individuals to maximize recruitment and maintenance of fish stocks (Baumgartner et al. 2004).

This study aimed to evaluate the temporal and spatial distribution (indication of preferred areas and season for spawning) of larvae of three migratory species (S. brasiliensis, P. lineatus and P. corruscans) in the region of the upper Paraná River, located in the lotic remnant of the Paraná River in the Brazilian territory. We intended to answer the following questions: i) Do larval abundances vary in the temporal and spatial scales considered (temporal and spatial)? ii) Does the abundance of larval stages (yolk-sac larvae, preflexion and flexion) differ between sampled stretches and the stretches chosen for spawning; and iii) is there any relationship between larval density and selected environmental variables (pH, dissolved oxygen, electric conductivity, water temperature, and river water level)?

**MATERIAL AND METHODS**

The study area is located in the Paraná River, in a 230 km stretch that divides the states of Paraná and Mato Grosso do Sul. It is delimited upstream by the Porto Primavera Dam (Sérgio Motta Hydroelectric Power Plant), and downstream by the Itaipu Reservoir. In this stretch there is still a river-floodplain system, which currently encompasses three important conservation units (Ilha Grande National Park, Ivinhema River State Park, and Environmental Protection Area of the Islands and ‘Várzeas’ of the Paraná River).

The area is mainly represented by the Ilha Grande archipelago, which divides the Paraná River into two channels, and is composed of a fluvial complex with about 157 islands of variable sizes. The presence of these islands transforms the river into an anastomosed channel, with backwater areas and secondary channels (Gogola et al. 2010). These characteristics promote great habitat heterogeneity, which in turn is associated with great biological diversity of terrestrial and aquatic organisms (Agostinho et al. 2000, 2004b).

Although under the influence of the dams, the stretch chosen for this research has several tributaries, such as the Piquiri and Ivaí rivers, located on the left (East) bank of the Paraná River (Paraná State), and Amambai, Iguatemi and Ivinhema, on the right (West) bank (Mato Grosso do Sul State), all free of dams, with their flow characteristics exclusively dependent on the hydrological cycle (local rains). In addition to these tributaries, the region still has several floodplain lakes, with constant or intermittent connection with the Paraná River or secondary channels (Gogola et al. 2010).

The 26 sampling sites selected were distributed in the main channel of the Paraná River along the Ilha Grande National Park, tributaries (Ivinhema, Amambai, Piquiri and Iguatemi), marginal lakes (Saraiva Lake) and channels (Canal Ipoitã and Boca do Ipoitã), including the mouth of the major tributaries. For analysis, these sampling stations were categorized into three sections, according to the position of the main tributaries: i) Upper section, with sampling sites influenced by the rivers Ivinhema and Amambai (Boca do Ipoitã; Ipoitã Channel; Mouth of Ivinhema River; Channel of Paraná River; Bandeirantes Right Channel; Amambai; Bandeirantes Left Channel; Ilha Grande Pontal); ii) Middle section corresponding to sampling sites located in the main channel of the Paraná River (Triângulo; Porto Santo Antonio; Peruzzi; Paraná/Iguatemi; Alvarenga; Esmeralda; Três Coqueiros; São João), with only a few tributaries; iii) Lower section, with sampling sites influenced by the rivers Piquiri and Iguatemi (Iguatemi; Paraná/Saraiva; Saraiva Middle; Saraiva Channel; Ilha Grande Right Channel; Porto Cerâmica; Piquiri; Porto Terra Roxa; Ilha Grande Left Channel) (Fig. 1). Samples were taken during the spawning season, from October 2003 to March 2004 (Vazzoler 1996). A cylindrical-conical plankton net (0.5 mm mesh size), with a flowmeter coupled to the mouth opening to obtain the volume of filtered water, was employed. In the sampling sites with lotic characteristics, the nets were submerged approximately 10 cm against the water current for 10 minutes. In the lentic sites, the depth and time used for sampling was the same as in lotic sampling, but the net was towed at a lower speed. We obtained
one sample per collection point, which was fixed with formaldehyde solution (4%) buffered with calcium carbonate (CaCO₃). During sampling we also measured the following environmental variables using digital portable equipments: pH, dissolved oxygen (mg.l⁻¹), electric conductivity (µS.cm⁻¹) and water temperature (°C). Fluviometric level data were supplied by Nupélia/Fluviometric Station of the Advanced Research Base in Porto Rico, Paraná State.

After sorting the larvae from the rest of the plankton, the larvae were identified according to Nakatani et al. (2001) and classified into three categories according to Ahlstrom & Ball (1954) and modified by Nakatani et al. (2001): yolk-sac larval, preflexion and flexion stages. Larval abundance was standardized to 10 m³ of filtered water according to Tanaka (1973), modified by Nakatani et al. (2001). Specimens of P. corruscans, S. brasiliensis, and P. lineatus were deposited at Coleção Ictiológica da Universidade Estadual de Maringá, Paraná, Brazil (Nupélia vouchers numbers NUP 17332, NUP 1733, NUP 17330, respectively).

In order to test for significant differences between the means of larval abundance and considering the factors Month (Temporal variation: October, November, December, January, February and March) and Section (Spatial variation: Upper, Middle, and Lower) and their interaction, we used a distance-based analysis of variance, but the significance based on a permutation test, the PERMANOVA, employing the software PRIMER and PERMANOVA+. This software performs the permutational analysis of variance (Anderson 2001, McArdle & Anderson 2001) on the values of any distance measure, using permutation procedures to obtain the probability to reject the
null hypothesis for the test (Pseudo – F). Whenever the PERMANOVA was significant, a pairwise test was applied a posteriori to identify which mean values of each level of the factor were different.

In this study, the matrix of original data (larval density) contained many zero values, which prevent calculating the similarity matrix (in the case using the Bray-Curtis similarity index). To minimize this problem, a constant value (1) was added to all the cases, thus allowing calculating the matrix. In this way, all empty cells were forced to have overall similarity (100%) (Clarke et al. 2006) and we sought for differences between the less similar samples, which presented greater abundance. For the evaluations of the possible spawning sites, only the graphs were inspected, given the low densities of larval stages (yolk-sac larvae, preflexion and flexion) when they were analyzed separately.

The association between the matrices of the environmental variables (one for each variable) and the matrices of larval density (one for each species) was evaluated through the Mantel tests. The metrics used to generate the matrices were: Bray-Curtis for the data of larval abundance (added the constant 1) and the Euclidean distance for the environmental variables. Since the sampling sites are distant from each other (most downstream and upstream most sites) they could represent very heterogeneous abiotic data, invalidating the use of the Mantel tests. To evaluate the homogeneity of the environmental variables among the sampling sites, a permutation test of multivariate homogeneity of group dispersions (Anderson 2006, Anderson et al. 2006) was carried out. This analysis was performed using the R software, package vegan (Oksanen et al. 2013) by the functions betadisper using vegan (Oksanen et al. 2013) by the functions betadisper using Euclidean distance to generate distance from centroids to each stretch followed by the permutest.betadisper function to test the mean distance from centroids among the stretches. In addition, scatter plots were built to explore possible patterns between the data of larval abundance and selected abiotic variables selected. The Mantel test was conducted using the PC-ORD version 4.01 (McCune & Mefford 1999) and the graphs in the software 7.0 (StatSoft 2005).

**RESULTS**

**Variations in the water level of Paraná River**

The floods in the studied stretch usually occur from October to March, coinciding with the greatest reproductive activity of fish, especially migratory species. However, higher values were observed at the river level in October, November, December and March. Lower values were verified (Fig. 2) in January, which corresponds to the peak of the reproductive activity.

With regard to environmental variables, during the study period the pH ranged from 5.9 to 8.0, electrical conductivity varied from 42.4 to 68.3 μS/cm, water temperature varied between 26.5 °C and 30.6°C and dissolved oxygen was between 2.2 and 9.2 mg/l (Fig. 3).

Spatial and temporal variations in the abundance and identification of preferred section for spawning

During the study period, were captured a total of 169 larvae of long-distance migratory species. Among them, 53 were Salminus brasiliensis and its higher density was collected in section 20 (Piquiri), 40 larvae were Pseudoplatystoma corruscans and the highest density of this species was collected in section 24 (Mouth of Ivinhema River) and only 13 Prochilodus lineatus and its higher density was collected in section 11 (Ilha Grande Right Channel) (Table 1).

These low values may be due to the low levels of the river during the reproductive period, mainly in January, 2004. High densities of S. brasiliensis were verified in October and November. In October, the highest mean value was registered in the Upper section, whereas in November, at the Lower section (Fig. 4). The mean values of larval density were generally low. However, they were lower from January to the end of the sampled period. The PERMANOVA detected significant differences between the months (Pseudo-F = 3.88, p = 0.0021). The mean values obtained in October and November were not different according to the pairwise test (p = 0.79), but they were different from the other months (p < 0.03).

Yolk-sac larvae (YL) were found in the three sections, with higher densities in the Lower stretch; preflexion larvae (PF) were only captured in the Middle and Upper stretches. Flexion larvae (FL) had the lowest densities, with no capture in the Lower section (Fig. 5). Thus, it can be stated that S. brasiliensis has reproduced in the vicinities of the sampling sites located in the Upper and Lower sections, due to the capture of larvae at the yolk-sac stage.

In the sampled stretches, higher captures of P. coruscans occurred in December (Fig. 6). However, the highest mean was registered in the Upper section sites. No record of this species...
was verified in February and March, which can be result from the low levels of the Paraná River in January 2005. The PERMANOVA also evidenced significant differences only between the months (Pseudo-F = 3.35, p = 0.004), and December differed from the others (pairwise test, p < 0.05).

*Pseudoplatystoma corruscans* was not captured at yolk-sac larval stage. The stages of pre-flexion (PF) and flexion (FL) were only registered in the Upper and Middle sections (Fig. 7).

*Prochilodus lineatus* was captured in almost all studied months, but in low mean densities. The highest mean density of this fish was registered in the Lower stretch, followed by the Upper stretch, in October and November, respectively (Fig. 8). The PERMANOVA revealed no significant difference between the months and stretches (Pseudo-F < 0.75, p > 0.60). Yolk-sac larvae (YL) were found in the three sections of the stretch, with higher densities in the Upper and Middle ones. The pre-flexion stage larvae (PF) were captured only in the Middle and...
Larvae of migratory fish in the lotic remnant of the Paraná River in Brazil


Lower sections, with the highest abundance in the latter section. Nevertheless, no larvae at flexion stage (FL) were captured (Fig. 9).

**Relationship between larval abundance and environmental variables**

The relationships between the densities of the selected migratory species and the environmental variables measured were not clear (Fig. 10). However, temperature was an important variable, mainly for *S. brasiliensis*, whose larvae were captured only when the temperature was below 28°C. This was shown by the lack of significance between the matrices (abundance and abiotic) obtained for this species (Mantel $r = 0.08$, $p = 0.06$). There was also no significant correlation between the matrices constructed for *P. corruscans* ($r = -0.06$, $p = 0.09$). However, for *P. lineatus* the correlation was significant ($r = 0.09$, $p = 0.03$), but the larval densities of this species were quite low. The distance to the centroid was 4.749 to the superior, 6.307 to the middle and 4.543 to the lower stretches and the mean distance comparing the stretches were 0.554 to the upper-middle, 0.912 to the superior-lower, 0.482 to the middle-lower comparisons. The test homogeneity of groups dispersions to environmental variables among the sampling sites are not significant ($F = 0.3567$, $p = 0.713$), validating the use of Mantel tests.

**DISCUSSION**

Studies performed in La Plata River basin have shown that the reproduction of migratory fish occurs from October to March (BAUMGARTNER et al. 1997, 2004, ZANIBONI-FILHO & SCHULZ 2003, BIALETZKI et al. 2005, REYNAUT-TATAJE et al. 2008, TONDATO et al. 2010). In this study, larvae of the three species studied were captured in the same period, but the density of *S.*...
brasiliensis and P. coruscans decreased from February on. Likewise, considering the low levels of the Paraná River, the migratory fish species studied did spawn, strengthening the close relationship between their reproduction and the fluviometric level (VAZZOLER 1996). These data also demonstrate the importance of the studied area for the migratory species, as there was an indication that at least two of them (S. brasiliensis and P. lineatus with record of yolk-sac larval stage) have spawning areas near the sampled sites.

The distribution pattern found for the larvae of the three species is consistent with the results of NAKATANI et al. (1997) and AGOSTINHO et al. (2003). These authors described that during the spawning season, migratory species moved towards the headwaters of the tributaries, their pelagic eggs developed and

Figure 10. Relationship of environmental variables with densities of Salminus brasiliensis, Pseudoplatystoma coruscans and Prochilodus lineatus in the Upper Paraná River floodplain.

hatched while drifting, and the larvae were conducted to the marginal aquatic environments, which are connected to the rivers during the flood season. Thus, the greater abundances of yolk-sac stage (YL) larvae of *S. brasiliensis* in the sampling sites of the Lower and Upper stretches are possibly the result of the influence of the rivers Iguatemi (tributary on the right bank) and Piquiri (tributary on the left bank); and from the rivers Ivinhema and Amambai (tributaries on the right bank) respectively, indicating that the species is using these environments as spawning areas. However, we cannot rule out the possibility that spawning had occurred in the main channel of the river as well, as observed for *P. lineatus*. Prochilodus lineatus larvae at the yolk-sac stage (YL) were captured in the sampling sites located in the main channel of Paraná River (Middle stretch). Although migratory species use the headwaters to spawn (Nakatani et al. 1997), this species may also be spawning at this site (considered as a drift area), since it has high reproductive plasticity, as observed in hormone-induced spawning studies (Britski 1972, Godoy 1975, Castro 1993).

The absence of *P. corruscans* larvae at the yolk-sac larval stage is not evidence that it does not spawn in the studied area. This is because a great number of pre-flexion larvae were registered in the Upper stretch, indicating that the species uses the vicinities of the area for spawning and uses the main channel of the river too (Godinho et al. 2007). Its reproductive period is relatively short, covering the rainy months (November to January); the spawning is total or single (Bazzoli 2003, Sato & Godinho 2003).

Surveys carried out by Nakatani et al. (2004) demonstrate the importance of the tributaries for fish reproduction in the Upper Paraná River floodplain. These rivers are still not dammed, and their water level variations are exclusively controlled by their hydrological cycle (rain on the watersheds). Moreover, they present several marginal lakes and extensive flooding areas along their courses, providing favorable conditions for spawning and larval growth (Baumgartner et al. 2004, 2008, Daga et al. 2009, Gogola et al. 2010). The results obtained in our analysis of distribution of developmental stages reinforce their importance. Some studies performed in Ivinhema River suggest that this is one of the main environments for fish reproduction in the Upper Paraná River (Baumgartner et al. 1997, Nakatani et al. 1997, Sanches et al. 2006), probably due to the pristine characteristics of this river (part of this river is located in a State Park and most of it is a Protect Area), with intense riparian vegetation and extensive flooded areas (Souza Filho & Stevaux 1997).

The capture of *S. brasiliensis* larvae only occurred between October and December, at the three stages of development (yolk-sac larvae, pre-flexion and flexion). The record of flexion larvae suggests that the reproductive period of the species may have started in September, when an increase in the level of the river was registered (data not shown), leading to spawning. On the other hand, *P. corruscans* was captured from October to January, with higher larval density at the pre-flexion stage recorded in December, with occurrence also in October, which may indicate that this species, as well as *S. brasiliensis*, also started its reproductive period in September. Nakatani et al. (1997) observed high numbers of eggs and larvae in September in the region of the Upper Paraná River floodplain. This occurrence deserves further attention, since the strategy to protect these species in the region consider the period between November and February as their main spawning season.

Unlike these species, *P. lineatus* presented the lowest larval density. This result is unexpected, since this species has greater reproductive activity when the values of flow and water level increase (Agostinho et al. 2004b). Again, the low values of the river level registered in January may have influenced these values, also indicating that *P. lineatus* starts reproducing later.

The study period, between October and March, is characterized by high values of temperature and precipitation that seem to be the main triggers for reproduction (Vazzoler 1996) and also appear to affect larval abundance in several habitats (Araújo-Lima & Oliveira 1998). Studies conducted at the Upper Paraná River also identify these variables as determinants of the distribution of abundances of eggs and larvae of fish (Nakatani et al. 2001, Castro et al. 2002, Bialecki et al. 2005, Sanches et al. 2006, Baumgartner et al. 2008, Reynalte-Tataje et al. 2011a). However, despite certain trends in fish communities, the differences among the reproductive strategies within a community enable the populations to respond differently to environmental variables at the regional level (Reynalte-Tataje et al. 2011b). Although the three species studied herein have a limited biological plasticity (Agostinho et al. 1993), there was no significant influence of the environmental variables on the abundance of their larvae. However, an increase in photoperiod and temperature determine the start of gonad maturation in tropical fish, which is intensified during the reproductive period (Vazzoler 1996). This was observed in the present study, primarily for *S. brasiliensis* and *P. corruscans*, which had already been recorded as spawning in October. Nevertheless, the real importance of each of these variables for reproduction is not completely clear.

Temperature probably was a limiting factor for *S. brasiliensis*, since in general larvae of this species were registered in the sampled months with lower temperatures. Meanwhile, it is worth mentioning again that the Mantel test was not significant, pointing to the weak associations between the matrices of larval abundance and abiotic variables. In addition, it should be remembered that the levels of the river were low in the warm months (January and February). Indeed the predominance of larvae of *S. brasiliensis* and *P. corruscans* between October and December reveals that this species has reproductive activity in this period.

The low levels of the river recorded in January may result from the absence of rainfall or water retention by the up-
stream dams. The presence of dams creates irreversible impacts, mainly changing the natural pulses of flood and drought and their timing, which is detrimental to the spawning of species with reproductive cycles that depend on the rising of the fluviometric level (Agostinho et al. 2004a, Sanches et al. 2006). Nonetheless, the impact would be worse if there were no tributaries, along with the Saraiva Lake, which are important for fish reproduction and growth (nursery) (Gogola et al. 2010). We should also point out that this study may have been hampere by low flows. However, periods like this tend to become more frequent with the predicted climate change.

Based on the results obtained in this study, we conclude that S. brasiliensis, P. corruscans and P. lineatus seek the dam-free tributaries for spawning. However, we cannot rule out the hypothesis that they also spawn in the lotic stretch of the main river. Godinho et al. (2007) observed spawning sites of P. corruscans in the lotic stretch of the São Francisco River. The reproductive dynamics, recruitment, maintenance, and possible attempts to recover the stocks of these species are directly dependent on the preservation of tributaries, especially the Piquiri, Iguatemi and Amambaí rivers and lakes in the region, and also of a close monitoring to prevent fishing during the reproductive period.

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Larvae of migratory fish in the lotic remnant of the Paraná River in Brazil


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