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ECOLOGY

The role of habitat complexity in the survival rates of migratory (native) and sedentary (non-native) species of fish larvae

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ABSTRACT. The increasing losses of original features of many riverine environments and the consequent decline of native aquatic species are now a widely recognized problem. The main river basins of South America have been undergoing constant changes in their communities of fish, with native migratory species disappearing and the rising of sedentary exotic ones. However, few studies report experiments that qualify and/or quantify this correlation. Three experiments were conducted to evaluate the predation mortality of two species of fish larvae (native and non-native) regarding their habitat features. The hypothesis that natural features of habitat (aquatic vegetation and water turbidity) controls the survival rates of fish larvae was tested. The experiments highlight the importance of community structure on population dynamics. The native fish larvae showed to be more adapted than the non-native to using the aquatic plants for refuge. The habitat complexity can be closely related to the persistence of native migratory fish species.

Keywords: biodiversity; habitat loss; optimal foraging; predator-prey; aquatic plants; water turbidity.

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Introduction

The large river basins of South America travel thousands of kilometers across the continent and debouch into the Atlantic Ocean (Junk, Bayley, & Sparks, 1989; Junk & Wantzen, 2004; Lasso et al., 2004; Agostinho, Gomes, & Pelicice, 2007; Maldonado-Ocampo, Vari, & Usma, 2008). These ecosystems are characterized by presenting migratory fish species at the top of their food chains. Many of these species use the flood pulse for reproduction, with larval development in coastal nursery habitats along the flooded vegetation and lagoons (Agostinho et al., 2007).

Studies (Agostinho et al., 2007; Barletta et al., 2010; Palmer, Hondula, & Koch, 2014) have demonstrated how human actions like farming, dams, urban and industrial activities lead to disturbances in these ecosystems (e.g., through deforestation, sediment flow, water eutrophication, habitat loss, exotic species), affecting some features such as water turbidity and spatial complexity, crucial in determining patterns of species interaction and community structure (Stein, 1977). These changes, reported in the main basins of South America, are related to the decline of many fish populations. In such basins, changes in fish communities followed the same pattern, with native migratory species being replaced by exotic sedentary ones (Agostinho et al., 2007; Barletta et al., 2010).

Nursery habitats often are established in the river banks and coastal zones, a complex and highly productive ecotone (Esteves, 1998). These marginal habitats are essential for fish larvae and invertebrate species (Rodrigues, Thomaz, Agostinho, & Gomes, 2005; Thomaz, Pagioro, Bini, & Roberto, 2005), which find protection against predators in the shallow waters and natural refuges offered by the flooded vegetation, riparian plants and macrophytes (Esteves, 1998; Lacerda, Hayashi, Galdioli, & Fernandes, 2010). In such ecosystems, habitat alterations related to human activities tend to promote changes in the dynamics of some environmental factors such as sediment flow and macrophytes. The way in which these factors can contribute to the persistence of native species of migratory fish larvae, as well as, the establishment of exotic species, are investigated.

Fish larvae are not only the most critical phase for the success of a species, but also present themselves as different organisms from adults in respect to ecological requirements, essential in understanding species autoecology and population dynamics (Nakatani et al., 2001). Three experiments were conducted to evaluate the predator-prey relationship between two species of fish larvae (native and non-native) and an important fish larvae predator (Odonate larvae). The hypothesis tested was that the natural feature of nursery habitats in continental water bodies, such as water turbidity and structural complexity promoted by aquatic plants, affect the survival rates of native and non-native species of fish larvae in different ways.

Material and methods

Species studied

Predator *Pantala flavescens* (Insecta - Libellulidae) is a circumtropical species known on all continents except Antarctica, commonly found in different regions of South America (Boudot et al., 2016).

Preys - One of Odonata's preys is the larva of *Piaractus mesopotamicus* (Actinopterigii – Characidae) (Prey 1 – native), a Brazilian migratory fish species that has shown a decrease in its natural populations (Agostinho, Pelicice, & Júlio Júnior, 2005; Agostinho et al., 2007). Another potential prey of *P. flavescens* are the larvae of *Oreochromis niloticus* (Actinopterigii – Cichlidae) (Prey 2 – non-native), an African fish species with sedentary behavior, introduced in Brazil in the nineteen-fifties aiming to develop freshwater aquaculture and now commonly found in Brazilian water bodies (Agostinho et al., 2007).

Aquatic plants - To simulate habitats with different structural complexities, we used three species of aquatic plants common in Brazilian water bodies, being two free-floating (*Salvinia auriculata* and *Pistia stratiotes*) and one rooted submerged (*Egeria najas*) (Thomaz et al., 2005). The specimens were collected from the field on the local research base of Nupélia (*Núcleo de Pesquisa em Ecologia, Limnologia e Aquicultura*), in the Paraná River floodplain (22°45´54´´S – 53°15´26´´W).

Experiments - The methodology used to obtain the larvae of *P. flavescens*, *P. mesopotamicus* and *O. niloticus* are described in Lacerda et al. (2010). Survival rate (%) of prey and the biomass (g) consumed by predators were analyzed. To estimate the mean biomass of preys (1 and 2), samples of each species were weighed (N = 50, *P. mesopotamicus* = 0.00147g and *O. niloticus* = 0.01639g). Both prey species were the same age (5 days old in the first experiment and 7 in the last).

For all experiments, randomized designs were conducted in aquaria with 12 L, filled with water from an artesian well. The predators were always placed in aquaria one hour before prey, at the start of the experiments. Eighteen hours later, the predators were removed and the number of preys remaining in each aquarium was counted. The aquaria had constant illumination by incandescent lamps (25W) at 55 cm from the bottom.

Suspended sediment - This experiment tested the influence of different levels of suspended sediment in the survival rates (by predation) of fish larvae. For this study 560 larvae of prey 1 were used, the same quantity of prey 2, and 32 predator larvae (*Lt* = 14.33 - 16.50 mm). The predators were distributed in 32 aquaria, being one predator per aquarium in a factorial design with four levels of suspended sediment (T1, 0.000; T2, 0.035; T3, 0.070; T4, 0.105 g L^{-1}) and two prey species. The clay previously weighed was first diluted in 100 L of water. The turbidity levels used in treatments are compatible with natural conditions (Thomaz et al., 2005; Pagioro, Thomaz, & Roberto, 2005). This experiment had eight treatments and four replicas. The difference between treatments is the prey species (Prey 1 and 2) and the levels of suspended sediment (T1–T4). Each aquarium containing a predator and 35 specimens of one of the preys (1 or 2) was considered an experimental unit (EU).

Structural complexity - This study used three species of aquatic plants to create habitats with different structural complexities. Plants were selected by species, size, washed in running water and weighed, to ensure that each replica presented similar biomass of aquatic plants. This experiment utilized 480 larvae of each prey (1 and 2) and 32 larvae of predators, distributed in 32 aquaria being one predator per aquarium in a factorial design with four treatments [control (no plants), *S. auriculata*, *P. stratiotes* and *E. najas*)] and two prey species with eight treatments and four replicas. The treatments differ depending on prey species and aquatic plants, or their absence (control). Each aquarium containing a predator and 30 specimens of prey was an EU.

Optimal foraging - This experiment evaluated the predator-prey interactions (prey survival rate and biomass of consumed prey) with both prey species (native and non-native) representing the ichthyoplankton community under four levels of spatial complexity (presence of *E. najas*, *P. stratiotes*, *S. auriculata* and no plant). For this, we used 16 EU consisting of an aquarium with one predator and 15 larvae of each prey species I (e.g., 240 larvae of each prey and 16 larvae of predators distributed in 16 aquaria). The experiment had four treatments and four replicas, with treatments differing in relation to the structural complexity (aquatic plants).

Water physical-chemical variables - The chemical parameters of water such as pH, electrical conductivity (μS cm^{-1}) and dissolved oxygen (mg L^{-1}) were measured at the beginning and end of each experiment, and the water temperature (°C) was monitored at 8:00 and 17:00.

Statistical analysis - In experiment 1, to analyze the effect of suspended sediment on prey consumption by predators, data (number of preys consumed and total biomass consumed) was submitted to an analysis of variance (ANOVA) as well as a Tukey test at 5% probability to detect statistical differences. Moreover, a polynomial regression analysis (equation 1) was used to investigate possible correlations between clay concentration and survival values (%) of different prey species (Quinn & Keough, 2002). To test the effect of prey species and levels of turbidity on survival values, a covariance analysis (ANCOVA) was performed, according to the procedure described by Dowdy and Wearden (1985). For experiments 2 and 3, to verify the effect of aquatic plants on the survival rates of prey species an analysis of variance (ANOVA) was used as well as a Tukey test at 5% probability (Quinn & Keough, 2002). The SAS program was used for statistical analyses.

Ethical standards

The present study is original research developed by the authors, in accordance with the content of the manuscript and its submission to the journal. This study was made without violating the ethical standards of work with animals or the Brazilian bioethical laws.

Results

Physical-chemical water characteristics – In all experiments, two-way MANOVA did not detect any significant effect ($p > 0.05$) of suspended sediment and aquatic plants on water temperature, pH, dissolved oxygen and electrical conductivity (Table 1). The values of the physical-chemical water characteristics measured in the experiments closely matched the values found in natural Brazilian ecosystems (Rodrigues et al., 2005).

Suspended sediment - In the first experiment, *Oreochromis niloticus* (prey 2) showed a higher survival rate (%) than prey 1 for all suspended solids levels ($p < 0.05$) (Figure 1A). The control treatment promoted the lowest survival rates for both preys ($p < 0.05$). For prey 1 the survival on the treatment T4 was higher than T3 ($p < 0.05$), and the biomass consumption (g) by predators did not differ between treatments (Figure 1B). For prey 2 in the control treatment the consumption (g) was higher than the others treatments ($p < 0.05$).

Table 1. The mean values of physical and chemical water parameters in all experiments.

Experiments	Physical and chemical parameters			
	Temperature (°C)	pH	O_2 (mg L^{-1})	Cond. (µS cm^{-1})
1	23.85	7.06	4.5	0.14
2	23.66	7.23	4.25	0.15
3	23.72	7.13	3.89	0.14

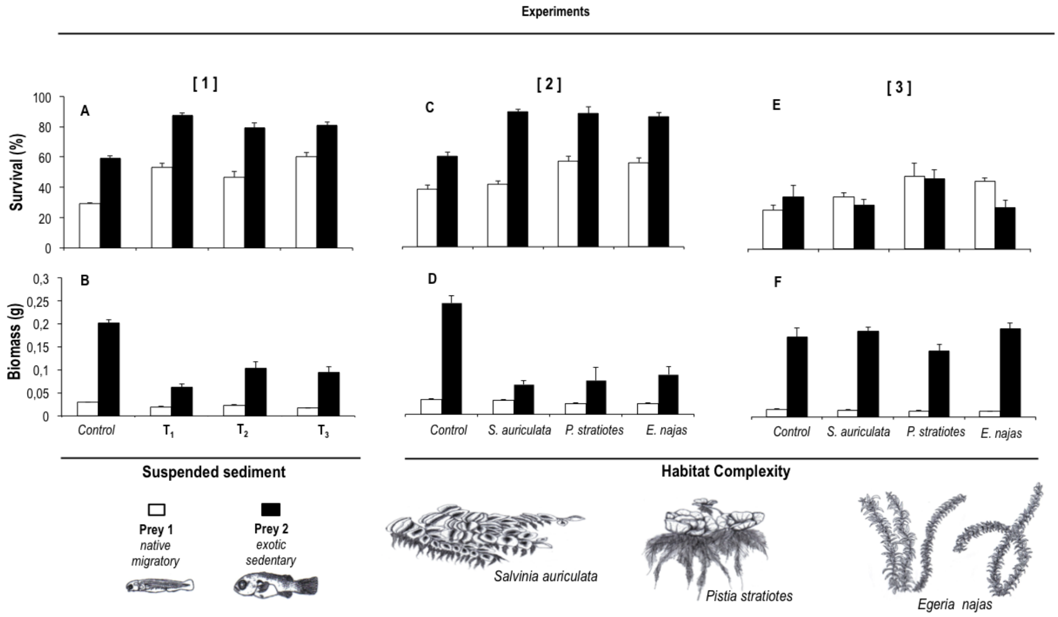

Figure 1. Prey survival rate (%) and prey biomass (g) consumed by predators (mean ± standard error), in treatments with different clay concentrations in water (T1-T4) (experiment 1) and spatial complexity levels promoted by different species of aquatic plants (L – low complexity (*Salvinia auriculata*), M – moderate complexity (*Pistia stratiotes*) and H – high complexity (*Egeria najas*). □ Prey 1 (*Piaractus mesopotamicus*), ■ Prey 2 (*Oreochromis niloticus*).

Regression analysis showed a non-linear effect between the clay levels and prey survival (Equation 2 and 3, ε = *error*; Figure 2):

Prey 1 = 31.7+ 477.4 Clay (g L^{-1}) - 2210.9 Clay (g L^{-1})2+ ε (Eq. 2; r^2=0,649)

Prey 2 = 61.5+ 733.3 Clay (g L^{-1})- 5442.2 Clay (g L^{-1})2 + ε (Eq. 3; r^2=0,662)

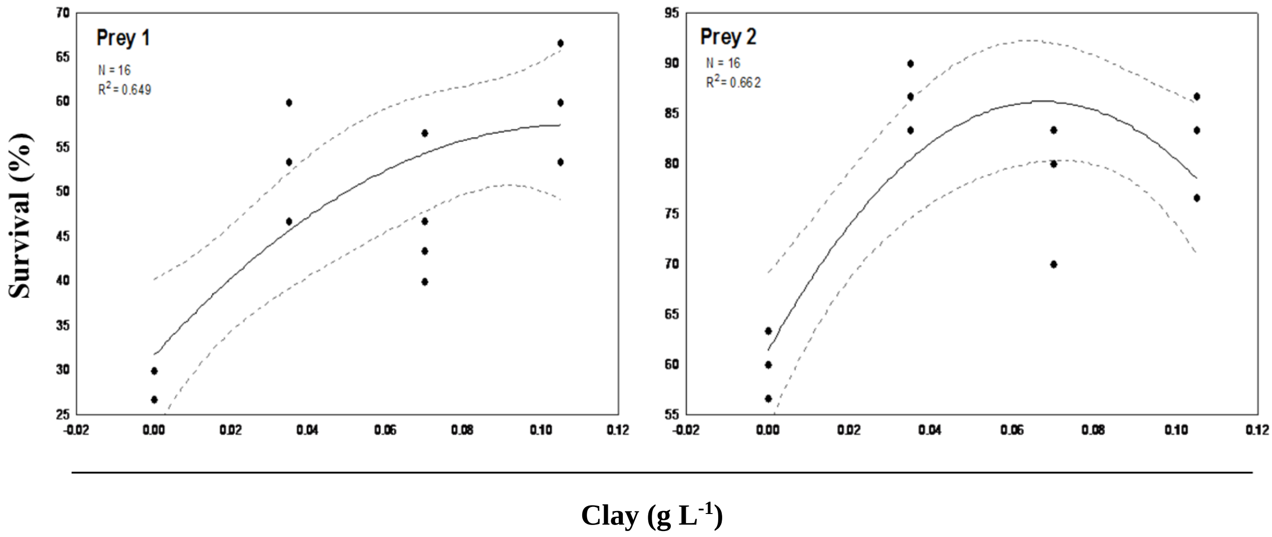

Figure 2. Polynomial regression analyses. Non-linear effect of clay concentration in the survival values (%) of the different prey species.

Structural complexity - Once again prey 2 showed highest survival rates (Figure 1C) with lowest values in the control treatment ($p < 0.05$). Treatments with more structural complexity (*P. stratiotes* and *E. najas*) promoted a significant increase (~20%, $p < 0.05$) in survival rates of prey 1 compared with the *Salvinia auriculata* treatment, which did not differ ($p > 0.05$). The prey consumption (g) by predators did not differ between treatments for prey 1, whereas highest consumption (g) in the control treatment occurred for prey 2 ($p < 0.05$) (Figure 1D).

Optimal foraging – When both prey species were tested together in the same aquarium, the survival rates of the two prey species differed only in the *E. najas*' treatment (Figure 1E). For the first time prey 1 showed a higher survival rate. No differences in survival rates according to treatments were observed for prey 2. Prey consumption (g) did not differ between treatments for each prey species and prey 2 was more consumed (g) by predators (Figure 1F).

Discussion

Prey size - The differences in size between prey species are probably responsible for the differences in survival rates (experiments 1 and 2). The larvae of *O. niloticus* (prey 2) present bigger size (and biomass) at birth than *P. mesopotamicus* (prey 1) (Nakatani at al., 2001; Lacerda et al., 2010), satiating predators with fewer preys. However, this reasoning applies only to those treatments where predators only have a single prey option. In the last experiment (3), the larger size of prey 2 could have contributed to their lowest survival rates.

Suspended sediment (turbidity) - The role of water turbidity in several processes (e.g., trophic relationship and species persistence) in aquatic ecosystems are widely studied (Souza-Filho, Rocha, Comunello, & Stevaux. 2004; Agostinho et al., 2007; Gubiani, Gomes, Agostinho, & Okada, 2007; Abujanra, Agostinho, & Hahn, 2009; Luz-Agostinho, Agostinho, Gomes, Júlio-Jr, & Fugi. 2009). Turbidity can determine the behavior of prey and predators, decreasing the interaction and distance among them (Abrahams & Kattenfeld, 1997). According to McCafferty (1983), Odonata larvae are carnivorous and opportunistic, finding their prey visually.

The data suggest that predators had their predatory potential reduced by the water turbidity, which affected their vision and reduced the information received by prey. The prey, in turn, may have shown a less aggregated distribution in treatments with turbid water, a characteristic already observed in experimental tanks of fish hatchery stations (Snickars, Sandström, & Mattila. 2004; Meag & Batty, 2007), which can affect prey availability. The non-linear relation between water turbidity levels and prey survival were also shown in other studies (Boehlert & Morgan, 1985; Vandenbyllaardt, Ward, Braekevelt, & McIntyre, 1991; Meag &

Batty, 2007). In natural water bodies, water turbidity can be affected by different causes such as silting from deforestation, dams, primary production, eutrophication from farms, industries and urban runoff. This study validates the effect of water turbidity in the predator-prey relationship, determinant in the structure of aquatic communities (Stein, 1977).

Habitat complexity and optimal foraging - In the second experiment, in the treatments with *E. najas* and *P. stratiotes* (major complexity), both preys showed an increase in their survival rates. However, in treatments with low complexity (*S. auriculata*) prey 1 showed survival rates similar to the control treatment (no complexity), while prey 2 showed their highest values. The data suggests differences in larval behavior between prey species in the aquaria with *S. auriculata*.

Based on daily observations, it was evident that prey 2 (*O. niloticus*) had a tendency to remain in a single shoal, probably by genetic influence from the parental care existent in this specie and many other sedentary fishes (Agostinho et al., 2007). According to the results observed in the treatments with *S. auriculata*, prey 2 specimens probably remained at the bottom of the aquaria to facilitate the shoal behavior. In such manner, prey 2 avoided the predators which were hidden in the roots to ambush the prey. On the other hand, prey 1 (*P. mesopotamicus*) although sometimes organized in small groups, occupied the whole tank independently. This difference in behavior is acceptable considering the strategies of each species, sedentary with parental care (prey 2) and migratory (prey 1).

In the last experiment (optimal foraging), both prey species occupied the same EU and the predator started counting on two options of prey. Compared to the previous experiments a dramatic change in survival patterns of prey 2 was observed. Under the major complexity level, the survival rates of prey 2 were numerically lower, and did not differ from the control treatment (no complexity). In the treatments with *S. auriculata* and P. stratiotes, survival rates of prey 2 were 43% and 61% lower than values found in their respective treatments (Habitat complexity experiment). On the other hand, the survival values of prey 1 were similar in both experiments.

The shoal behavior of prey 2, in addition to its larger size, probably drew more attention to the predator and according to the optimal foraging theory (Macarthur & Pianka, 1966), it becomes a more attractive prey. Migratory species were probably more susceptible to predators (than sedentary species) and better adapted to the predator-prey relationship. For *P. mesopotamicus* larvae (prey 1) this adaptation can be related to habitat occupation, exploring more efficiently the natural refuges, many represented by macrophyte and riparian vegetation.

Then, the loss of original features of aquatic habitats and consequently this heterogeneity, can affect the competition (survival) between native and non-native fish species directly during their early stages of life. This way, the integrity of the marginal structural complexity of aquatic nursery habitats becomes crucial, and a basic step in the conservation of native species. Changes in fish community are reported in many river basins of South America (Barletta et al., 2010). In these ecosystems migratory species of fish are being replaced by exotic sedentary species, introduced accidentally by aquaculture farms installed in deforestation areas adjacent to the river systems (Agostinho et al., 2007).

In the Magdalena Basin (Colombian), the main cause of the depreciation of native fish species has been attributed to the loss of nursery habitats by farming development areas. In that region, exotic species introduced by government projects have totally established themselves. In the Orinoco basin (Colombia and Venezuela) the main root of the environmental problems is related to the constant demand for services and space, to live and cultivate food and other agro-industrial products. Deforestation, water pumping for irrigation, aquaculture and the petroleum industry are the main sources of anthropogenic impact in that basin. Exotic species (e.g., *Oreochromis* spp.) were reported and related to the depletion of the natural fish fauna. Moreover, in La Plata Basin (almost 90% of continental fish production for Argentina, Uruguay and Paraguay), studies suggest the disappearance of migratory species (including *P. mesopotamicus*) could be a consequence of the loss of nursery habitats. Among exotic species, *Cyprinus carpio* (L. 1758) (sedentary species) is considered the most abundant in this basin and *Tilapia zillii* (Gervais, 1848) have occasionally been reported in the Paraná and Uruguay Rivers (Barletta et al., 2010).

Therefore, developing countries, like the South American nations, must be more careful with their development strategies involving the use of areas and resources from their river basins that suffer from similar problems.

Conclusion

The structural complexity proved to be a crucial feature for the prevalence of *P. mesopotamicus*. The integrity of coastal areas around the continental water bodies are essential for many ecological processes, as well as the persistence of native migratory fish species larvae, which in this study shows to be more adapted to interact with the natural refuges.

The predatory efficiency being reduced by study factors, which can determine the communities' structure. Data also suggests that the larger size at birth can act in different ways on the survival rate of the larvae species, based on the habitat and community features.

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