When habitat complexity increases predation risk: experiments with invasive and neotropical native fishes

Alejandra F. G. N. Santos\textsuperscript{A,E}, Emili García-Berthou\textsuperscript{B}, Carmino Hayashi\textsuperscript{C} and Luciano N. Santos\textsuperscript{D}

\textsuperscript{A}Department of Zootechny and Sustainable Socioenvironmental Development, Fluminense Federal University, Niterói, Rio de Janeiro, Brazil.
\textsuperscript{B}Institute of Aquatic Ecology, University of Girona, E-17071, Girona, Catalonia, Spain.
\textsuperscript{C}Universidade Federal do Triângulo Mineiro, Uberaba, Minas Gerais, Brazil.
\textsuperscript{D}Department of Eology and Marine Resources, Federal University of Rio de Janeiro State, Rio de Janeiro, Brazil.
\textsuperscript{E}Corresponding author. Email: alejandrafilippo@hotmail.com

Abstract. We tested the predator–prey relationships between a native piscivore (\textit{Salminus brasiliensis}) and introduced and native fish species of the Paraná River, Brazil. We hypothesised that \textit{S. brasiliensis} can exert biotic resistance against invasive fishes but not at the same degree for all species. Three invasive (\textit{Cichla piquiti}, \textit{Oreochromis niloticus} and \textit{Ictalurus punctatus}) and two native (\textit{Astyanax altiparanae} and \textit{Prochilodus lineatus}) species were offered as prey to \textit{S. brasiliensis} in 300 L aquaria trials at three levels of cover (0\%, 50\% and 100\% of artificial macrophytes). \textit{S. brasiliensis} had a greater ability to capture prey in complex habitats, so predation success did not decrease with habitat complexity and even increased on \textit{I. punctatus}. Prey survival was variable through time and among species, being high for \textit{I. punctatus}. The three most consumed species (\textit{P. lineatus}, \textit{C. piquiti}, and \textit{O. niloticus}) were less active and occupied the aquaria surfaces, changing strongly their behaviour with habitat complexity. Except for \textit{P. lineatus} and \textit{C. piquiti}, \textit{S. brasiliensis} preferably preyed on smaller individuals of the other species. Our experiments support that \textit{S. brasiliensis} is an interesting candidate to resist the invasion by \textit{C. piquiti} and \textit{O. niloticus} but not to control the abundance of \textit{I. punctatus}.

Additional keywords: biotic resistance, invasive species, Paraná River basin, predator–prey interactions, \textit{Salminus brasiliensis}.

Introduction

Invasive species are one of the major threats to biodiversity and freshwater ecosystems are especially vulnerable to the introduction of non-native species (Clavero and García-Berthou 2005; Dudgeon et al. 2006). Consequently, freshwater organisms are among the most imperilled taxa world-wide and, according to the International Union for Conservation of Nature (IUCN), 25\% of freshwater fish species are expected to be threatened with global extinction by invasive fishes (Marr et al. 2010). Among the most important factors responsible for these levels of imperilment is the difficulty to eradicate or control the spread of non-native fishes through the conventional physical and chemical management measures (Santos et al. 2009; Marr et al. 2010). In such cases, biological control can, thus, provide a sustainable, long-term alternative to control the non-native fish populations (Sato et al. 2010; Santos et al. 2012). However, caution is necessary to avoid the recurrent failures of past biological control experiences and novel approaches should be tested to avoid the risks of introducing other non-native predators, parasites or competitors (Sato et al. 2010).

Predation is a key structuring force of many fish assemblages and also an important mechanism of impact of invasive species (Kovalenko et al. 2010b; Thompson et al. 2012). The effects of piscivorous fishes on prey populations have been extensively examined and the role of habitat complexity and behavioural attributes of predators and prey on fish predation is increasingly known (Persson and Eklöv 1995; Juanes et al. 2002; Almany 2004; Kovalenko et al. 2010a). However, most of the novel trophic interactions between native and invasive fishes are poorly understood, especially in the neotropics, where non-native fish introductions are largely succeeding (García-Berthou 2007; Kovalenko et al. 2010a; Santos et al. 2012). Invasive species typically face new ecological interactions in the invaded ecosystem, and thus their invasiveness may be affected by the biotic resistance exerted by competitors and predators (Bajer et al. 2012; Thompson et al. 2012). Despite its applied importance for aquatic ecologists and fisheries managers, very few studies have provided experimental evidences on the potential of native predators to control the abundance of invasive fish in natural ecosystems (but see Santos et al. 2009; Bajer et al. 2012; Santos et al. 2012).
Salminus brasiliensis (Cuvier, 1816), the largest characid endemic to the Paraná–Paraguay and Uruguay River basins, is a piscivorous and rheophilic fish that has been adversely affected by human activities and invasive species (Agostinho et al. 2007; Barletta et al. 2010). Since floodplain lakes and meandering rivers function as critical nursery grounds for *S. brasiliensis*, this species is particularly vulnerable to juvenile predation by the many large-sized (>300 mm TL) non-native piscivores mostly introduced from Amazon basin, which are preadapted to succeed at these structurally-complex lentic or semi-otic systems (Agostinho et al. 2007; Júlio Júnior et al. 2009; Barletta et al. 2010). This study aims to experimentally test how: (i) piscivory of juvenile *S. brasiliensis* affects the survival and behaviour of common 0+ year native and introduced fishes in Brazil; and (ii) how habitat complexity and species-specific prey behaviour and morphology mediates these predator–prey relationships. We predicted that *S. brasiliensis* would affect survival and behaviour of most prey species but that the responses would be species-specific and would depend on habitat complexity. Understanding how habitat complexity mediates the predator–prey interactions between native and invasive species is essential to help managers to attempt to control the abundance of invasive species in such diverse ecosystems as the Paraná River and so to preserve native biota. Our findings were compared to those of the few previous experiments with neotropical piscivores (Santos et al. 2009, 2012), and the potential of *S. brasiliensis* to exert biotic resistance against three fish species (*Cichla piquiti* Kullander & Ferreira, 2006, *Oreochromis niloticus* (Linnaeus, 1758) and *Ictalurus punctatus* (Rafinesque, 1818)) introduced into the Paraná River (Júlio Júnior et al. 2009; Britton and Orsi 2012) and invasive in many regions is also discussed.

**Materials and methods**

**Experimental trials**

Two native (*Astyanax altiparanae* Garutti & Britski, 2000 and *Prochilodus lineatus* (Valenciennes, 1837)) and three invasive (*Cichla piquiti*, *Oreochromis niloticus* and *Ictalurus punctatus*) species were offered as prey to juvenile *S. brasiliensis*. The predator was selected not only due to its wide distribution and high value as fishery resource in many South American rivers (Agostinho et al. 2007; Barletta et al. 2010) but also because of its piscivorous habit throughout the ontogenetic growth (Corrêa et al. 2009). Native prey species were chosen because they are widespread and among the most abundant fish in the Paraná River basin (Agostinho et al. 2007). *Prochilodus lineatus* is a large (>700 mm TL), migratory characiform of detritivorous habits (Barletta et al. 2010), whereas *A. altiparanae* is a small (<150 mm TL) and widespread characid that is able to colonise the reservoirs due to its feeding flexibility and its ability to reproduce in lentic habitats (Dias et al. 2005). Because they are very prolific, being usually found in large shoals in nature, and lack defensive morphological features (i.e. spineless fins), these two native species are important food resource for many piscivores in Paraná River (Bozza and Hahn 2010).

Invasive species were selected because of their presence in many South American ecosystems, the strong ecological impacts of tilapias and peacock-basses, and the increasing use of *O. niloticus* and *I. punctatus* in Brazilian aquaculture (Britton and Orsi 2012). *Cichla piquiti* is a >300 mm SL piscivorous cichlid native to the Araguaia and Tocantins basins but widely introduced into the Paraguay–Paraná basin and other Brazilian regions (Kullander & Ferreira 2006). *Oreochromis niloticus* is an omnivorous and very prolific cichlid, native to Africa, whereas *I. punctatus* is a catfish native to North America that attains >1000 mm TL and eats invertebrates and fish when adult (Vitule et al. 2009). These three invasive species are generally gregarious when juveniles, having moderate- (i.e. the two cichlid species) to well developed (i.e. *I. punctatus*) stout spines in pectoral, dorsal and anal fins (Santos et al. 2009, 2012). All the fishes used in the experiments were young-of-the-year (0+ year; 6 months-old *S. brasiliensis*; 6–8 weeks the other species) and came from local fish farms, from which they were acquired in January 2006. The nine individuals of *S. brasiliensis* used in the trials averaged 101.3 mm (s.e. = 0.02) TL and 0.4 g (s.e. = 0.05) on average.

Experimental trials were performed in microcosms (300 L glass aquarium, 100 cm x 50 cm x 60 cm) in a closed water recirculating system (i.e. renewal rate = 5 L per min; supplementary aeration was provided only at 1500 L storage-pumped tanks), following the same procedure as in Santos et al. (2009, 2012). Three treatments of habitat complexity were used (i.e. three replicates per treatment; *N* = 9 predation trials), by covering the aquaria floor with green plastic filaments (1 cm wide x 1 mm thick polypropylene ribbons) simulating submersed macrophytes: 0%, no plastic filaments; 50%, intermediate complexity, with plastic filaments covering one half of the aquaria floor; 100%, high complexity, with plastic filaments covering the entire aquaria floor. Plastic filaments encompassed in length from the bottom to surface of the aquaria and the density used was 250 filaments per m². This density was chosen because it easily allows the inspection of fish movement and behaviour, even at high complexity treatments (see Santos et al. 2009, 2012 for further details).

All fish were acclimated to aquaria conditions 15 days before performing the trials, and treated with 0.3% NaCl solution to prevent infections. All fish were anesthetized with Eugenol (5 mL per 20 L of water) 48 h before the experiments, to measure TL (mm) TW (g). In order to mimic natural conditions as well as to reduce the opportunistic predation over disoriented prey, all aquaria were stocked initially with prey whereas the predator was stocked 3 h after. Only one *S. brasiliensis* was stocked in each aquarium with six individuals of each prey species (i.e. a total of 30 prey individuals per aquaria). Fish density used in the treatments mimicked natural densities of juvenile fish in the floodplain lakes and littoral areas of the Paraná River (Pelicice et al. 2005; Bulla et al. 2011). Control treatments (*N* = 9; three replicates per habitat complexity treatment) were stocked with the same prey density but without predators to provide a baseline of prey survival and behaviour in predator’s absence (Prince et al. 2004). The aim of this experimental design was to provide not an absolute but a relative feeding preference of the predator in a multi–species assemblage and to assess the role of habitat complexity (see also Santos et al. 2009, 2012).

The three treatments (predator plus 0%, 50%, or 100% cover) and three paired predator-free controls were replicated three
times. Each treatment or control was assigned randomly across a set of 18 aquaria. All trials were carried out within 4 days, exposed to a 12D:12L light regime. Between 9:00 and 21:00 hours of each day, the number of surviving prey and the behavioural patterns of both predator and prey were recorded at time intervals of 4 h (9:00, 13:00, 17:00 and 21:00 hours). Fish behaviour was assessed directly through visual inspection as in Santos et al. (2009, 2012), and each visual census took \(-5\) min per aquarium. Three behavioural traits were measured for the predator: (i) microhabitat use (surface, water column, or bottom); (ii) refuge use (sheltered, hiding within submersed structures; partially sheltered, using the interface between structured-unstructured areas; or not-sheltered, occupying open water areas); and (iii) activity (immobile, swimming, pursuing, or attacking). For each prey species, four behavioural traits were measured (as for predators, except when specified): microhabitat use; refuge use; shoaling (yes \(-\) minimum of three fish swimming together, or no); and activity (immobile, swimming, or escaping). Because fish would be always not-sheltered or hidden within submersed structures at 0\% and 100\% habitat complexity treatments, respectively, refuge use of predator and preys was measured only at treatments with intermediate level of habitat complexity. Inspections of fish behaviour were performed according to the following routine: (i) the behaviour of predator was first assessed; (ii) then, all fishes of a single prey species were targeted, and the behaviour of each individual was evaluated; (iii) this procedure was subsequently applied for other prey species within the aquarium and, then, (iv) the overall routine was then repeated for other treatments. It was not complicated to assess predator and prey fish behaviour because a valuable experience was acquired by the observer from preliminary census performed during fish acclimation period and because the record of behavioural traits was greatly facilitated by the use of a codified writing tablet. The most frequent behaviour of each fish species in each aquarium was recorded at every visual census; the behaviours of the different individuals of each species were similar and thus an overall behavioural pattern was considered in order to avoid pseudoreplication (as in Santos et al. 2009, 2012). Subsequently to the first census (at 9:00 hours) of the fifth day, all aquaria were emptied and the TL and TW of the remaining fishes were measured.

**Data analyses**

The effects of experimental factors (predator presence and habitat complexity) on prey survival (proportion of individuals per species surviving between censuses in each aquarium) were tested with Cox proportional-hazards regression analysis, using the two factors as categorical covariates. Cox proportional-hazards regression is the most common tool for studying the effects of predictors on survival time, which is a right-censored variable (Fox and Weisberg 2010). Cox regression is a semi-parametric method, because the hazard function can take any form and method is thus broadly applicable.

Behavioural traits were analysed with generalized estimating equations (GEEs), which are an extension of generalised linear models to accommodate repeated-measures designs (Diggle et al. 2002). For polytomous behavioural traits (all except shoaling behaviour), we first identified the category that fluctuated most among treatments and used this category to recode variables as binary traits. We then used these recoded traits as response variables in the GEEs with binary errors logit link functions; although this procedure might underestimate the presence of significant variation (by pooling information in some categories), this is unimportant given the frequency of significant effects. Throughout these analyses, we used time and replicate as within-subject factors and predator presence and habitat structure as between subject factors, but we only report the experimental (between-subject) factors; for refuge use we omitted habitat structure as a factor and only analysed data at the intermediate level of habitat complexity (at 50\% structure covered). To compare the sizes (TL) of the surviving individuals with those initially stocked in each, we used a repeated-measure ANOVA, with predator presence and habitat structure as between-subject factors. An interaction of time (Before–After factor) with the between-subject factors indicates that the temporal differences are affected by them; note that since some replicates had no surviving fish, the degrees of freedom of these analyses varied with prey species. All statistical analyses were performed with SPSS 15 (SPSS Inc., Chicago, IL, USA).

**Results**

**Prey survival**

The presence of *S. brasiliensis* significantly affected survival of all prey species (Table 1), which at the end of the experiment was \(>97\%\) in predator-free trials (Fig. 1a) and generally \(<26\%\) (i.e. except for *I. punctatus* in predator’s presence (Fig. 1b). The invasive *C. piquiti* and *O. niloticus* and the native *P. lineatus* were the most consumed prey, particularly at the beginning of the experiment (Fig. 1b, 2a). The native *A. altiparanae* (consumed mostly at the end of the experiment) and particularly the invasive *I. punctatus* were the least consumed prey species. The effects of habitat complexity and the habitat complexity \(\times\) predation interaction were significant for all species except *A. altiparanae* and *P. lineatus* (Table 1). In presence of the predator, survival was similar in the different habitat complexity treatments for all species except for *I. punctatus*, which actually survived more in treatments without structure (94\% v. 50\%).

Table 1. Effects of predator presence (*S. brasiliensis*) and habitat complexity on prey survival: results of Cox proportional-hazards regression analysis

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>C. piquiti</th>
<th>O. niloticus</th>
<th>I. punctatus</th>
<th>A. altiparanae</th>
<th>P. lineatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predator</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Habitat complexity</td>
<td>***</td>
<td>***</td>
<td>0.001</td>
<td>0.935</td>
<td>0.811</td>
</tr>
<tr>
<td>Predator × Habitat complexity</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.400</td>
<td>0.773</td>
</tr>
</tbody>
</table>
Control of invasive fish by a neotropical native piscivore

Marine and Freshwater Research 755

Prey species were generally gregarious but shoaling increased in the 100% complexity treatments (Fig. 5). Similarly, prey species were generally swimming in predator’s absence, whereas in predation treatments they markedly increased the immobile and escaping behaviours, particularly in the 100% complexity treatments (Fig. 6).

Predator behaviour was similarly affected by habitat complexity and most measured variables showed significant effects of habitat complexity (Wald’s tests, $P < 0.01$). *Salminus brasiliensis* largely occupied the water column, particularly in the 50% complexity treatments. It was generally swimming, particularly in the structureless treatments, but increased the frequency of quiet and attacking behaviours in the 50% and 100% complexity treatments.

**Discussion**

In our experiment, the neotropical native *Salminus brasiliensis* reduced survival of all prey species. The effects of habitat

---

**Prey size**

The size of surviving individuals depended on predator presence for all five prey species but *P. lineatus* (repeated-measures ANOVAs, Before–After × Predator or Before–After × Predator × Habitat complexity: $P < 0.05$ for all species but *P. lineatus*). Mean size of surviving prey was greater for all prey species but *P. lineatus* (Fig. 2b). The interactions of Before–After with Habitat complexity were only significant for *C. piquiti* (Before–After × Predator × Habitat complexity, $P = 0.03$), so habitat complexity only affected the predator’s size-selectivity for *C. piquiti*. Mean species-specific prey survival (percentage) at the end of the experiment was not significantly correlated (Spearman’s $r = 0.49$, $N = 5$, $P = 0.40$) with the effect of predation on size structure (mean TL of survivors – mean TL of initial stocking).

**Predator and prey behaviour**

Prey behaviour was profoundly altered by predator’s presence and habitat complexity; most sources of variation and particularly interactions were significant (Table 2). Microhabitat use was species-specific in predator’s absence, with some species preferring bottom areas (*I. punctatus*), other the (intermediate) water column (*A. altiparanae*) and *C. piquiti* being the species that used surface areas more frequently (Fig. 3). Except for *I. punctatus*, all prey species increased their use of surface areas in presence of the predator. However, this increase was stronger in structure-less treatments, hence the significant interactions.

Three species significantly increased their use of refuge in predator-in treatments (Table 2; Fig. 4), whereas *I. punctatus* reduced it and differences were not significant for *C. piquiti*. Prey species were generally gregarious but shoaling increased in predator’s presence mostly in structure-less areas (Fig. 5). Similarly, prey species were generally swimming in predator’s absence, whereas in predation treatments they markedly increased the immobile and escaping behaviours, particularly in the 100% complexity treatments (Fig. 6).

Predator behaviour was similarly affected by habitat complexity and most measured variables showed significant effects of habitat complexity (Wald’s tests, $P < 0.01$). *Salminus brasiliensis* largely occupied the water column, particularly in the 50% complexity treatments. It was generally swimming, particularly in the structureless treatments, but increased the frequency of quiet and attacking behaviours in the 50% and 100% complexity treatments.

**Discussion**

In our experiment, the neotropical native *Salminus brasiliensis* reduced survival of all prey species. The effects of habitat
complexity on survival to predation clearly were species-specific and were not significant for some prey fish species. In contrast, habitat complexity (and predation treatments) strongly affected prey behavioural traits and in predator’s presence most prey increased their use of surface areas, refuges, and shoaling, particularly in structureless treatments. These results suggest that although the behavioural response of prey to predator’s presence depended on the structure of habitat available, overall predation rates were high irrespective of this. Our findings contrast those of Kovalenko et al. (2010a) who observed weak behavioural (i.e. foraging) responses of native prey fish in presence of the non-native piscivore Cichla kelberi, but predation rates were marginally lower at vegetated habitats than in structureless treatments. Santos et al. (2009), using the same prey species and experimental conditions than those in our current study but a different predator, found that the native characid Brycon orbignyanus (Valenciennes, 1850) reduced its predatory efficiency in high complexity treatments. Although previous studies have shown that most fish predators reduce their efficiency in high complexity treatments (e.g. Savino and Stein 1982; Persson and Eklöv 1995), predators that ambush (rather than chase) are less affected (Almany 2004).

### Table 2. Effects of predator presence (S. brasiliensis) and habitat complexity on prey behavioural traits: between-subjects factors of generalized estimating equations

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>C. piquiti</th>
<th>O. niloticus</th>
<th>I. punctatus</th>
<th>A. altiparanae</th>
<th>P. lineatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>MICROHABITAT USE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>–</td>
<td>***</td>
<td>0.084</td>
<td>0.78</td>
<td>***</td>
</tr>
<tr>
<td>Habitat complexity</td>
<td>–</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Predator × Habitat complexity</td>
<td>–</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>REFUGE USE</td>
<td>0.11</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>SHOALING</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>***</td>
<td>***</td>
<td>0.25</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>Habitat complexity</td>
<td>0.007</td>
<td>***</td>
<td>***</td>
<td>0.057</td>
<td>***</td>
</tr>
<tr>
<td>Predator × Habitat complexity</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
<tr>
<td>ACTIVITY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>–</td>
<td>***</td>
</tr>
<tr>
<td>Habitat complexity</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>0.048</td>
<td>***</td>
</tr>
<tr>
<td>Predator × Habitat complexity</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>–</td>
<td>***</td>
</tr>
</tbody>
</table>

### Fig. 3. Mean microhabitat use (%) of the different prey species in response to predator presence (S. brasiliensis) and levels of habitat complexity. White = surface areas, grey = water column, black = bottom areas. Top panel = predator-free; bottom panel = predator-in treatments.
et al. (2012) found that prey selection and consumption by *Pseudoplatystoma corrucans* (Spix & Agassiz, 1829), a neotropical nocturnal pimelodid that uses mainly sensory organs instead of visual detection to search and capture food, were also less dependent of habitat complexity. *Salminus brasiliensis* smaller than 200 mm TL are rarely found in the mainstem Paraná River but mostly in its floodplains, rich in macrophytes and highly structured habitats, which function as important nursery grounds for *S. brasiliensis* and other large, migratory fishes (Agostinho et al. 2007; Barletta et al. 2010). In our experiment, *S. brasiliensis* displayed excellent manoeuvring ability and great swimming strength during the trials (A. Santos, pers. observ.). Our findings also revealed that *S. brasiliensis* is able to shift its foraging strategy of active predator, at structureless treatments (i.e. 0% cover), to ambush its preys at structurally-complex habitats (i.e. 50% and 100% cover). Therefore, this species seems well adapted to highly structured habitats, in which it might be more efficient than other diurnal

**Fig. 4.** Mean refuge use (%) by prey species in response to predator presence (*S. brasiliensis*) and levels of habitat complexity. White = not sheltered; grey = partially sheltered; black = entirely sheltered within the artificial vegetation. Top panel = predator-free; bottom panel = predator-in treatments.

**Fig. 5.** Mean shoaling (%) of prey species in response to predator presence (*S. brasiliensis*) and levels of habitat complexity. White = dispersed; black = shoaling. Top panel = predator-free; bottom panel = predator-in treatments.
piscivorous species. However, our results should be viewed with caution since structural complexity of floodplain lakes at Paraná River basin is naturally much beyond of our plastic filaments resembling the ribbon-like leaves of Typha domingensis, comprising a highly-complex three-dimensional mosaic of floating, emerging and submerged macrophytes, woody debris and rocky banks, arranged in a myriad of varying proportions. Therefore, further studies should be conducted to test whether the predation success of *S. brasiliensis* at habitats of other materials, shapes, and complexities would validate our findings.

Surprisingly, the survival of *I. punctatus* significantly increased in predation treatments without structure. These results contrast with most previous literature, which has shown that predation risk generally decreases with habitat complexity (e.g. Savino and Stein 1982; Persson and Eklöv 1995; Santos et al. 2009). Some studies, however, suggest that both prey and predators often aggregate in structured environments (Newbrey et al. 2005; Santos et al. 2012), thus reducing predation events in open habitats (Sass et al. 2006). In addition, *I. punctatus* like other catfishes is known to have pectoral spines that deter gape-limited predators by making ingestion difficult and harmful (Fine and Ladich 2003; Bosher et al. 2006). Comparing to Santos et al. (2009), who found that *B. orbignyanus* preyed preferentially on *I. punctatus* and less efficiently in structured treatments, our results suggest that these two native characid predators differ in habitat-related predatory abilities and that *S. brasiliensis* is less able to learn preying on novel species with defensive spines such as *I. punctatus*. This hypothesis can be partially supported by the trend of tropical fishes (i.e. *S. brasiliensis*) to be more associated with submerged plant beds than temperate ones (i.e. *I. punctatus*), which are more strongly associated with free-floating plants at pelagic zone (Meerhoff et al. 2007). In addition, the contrasting predation success on *I. punctatus* found between *S. brasiliensis* and *B. orbignyanus* could be also associated with the differential ability of *I. punctatus* to recognize and respond to these predators (i.e. the prey naiveté hypothesis; see Kovalenko et al. (2010b) for further details). Santos et al. (2009) observed that, in addition to the high aggressiveness of *B. orbignyanus* when preying on *I. punctatus* (attributable to the stridulatory sounds produced by catfish pectoral spines), this invasive prey persisted in a scattering behaviour in presence of predator. On the other hand, we observed that *I. punctatus* displayed the strongest shoaling behaviour at structureless treatments in presence of *S. brasiliensis*, suggesting a greater ability of this prey in recognize *S. brasiliensis* than *B. orbignyanus* as a predator. Thus, the increase of shoaling behaviour by *I. punctatus* probably contributed to a decrease on predation success of *S. brasiliensis*, because the ability of the predator to distinguish, pursue and attack an individual prey often declines with numerous and aggregated shoals (Pitcher and Parrish 1993). Except for Kovalenko et al. (2010b) we are not aware of any other study that experimentally tested the naiveté hypothesis for neotropical fishes.

Fish size is a primary factor in predator–prey interactions that determines visual detection, swimming ability, gape limitation, and foraging success (Persson and Eklöv 1995; Juanes et al. 2002). We observed a clear size-selectivity in predation by *S. brasiliensis* on some prey species. The most vulnerable species (notably *P. lineatus*, but also *C. piquiti*) were consumed irrespective of size, whereas *I. punctatus*, *A. altiparanae*, and *O. niloticus* surviving at the end of the experiment were significantly larger. We believe these differences in prey-size-selectivity, with *S. brasiliensis* preying preferentially on smaller individuals of some species but unselectively on others, are an artefact arose from the high predation on *P. lineatus* and *C. piquiti*, masking the predator preference towards smaller preys. However, *B. orbignyanus* significantly preyed on larger fish (Santos et al. 2009), again suggesting species-specific predatory abilities. Since *S. brasiliensis* and *B. orbignyanus*

---

**Fig. 6.** Mean activity level (%) of prey species in response to predator presence (*S. brasiliensis*) and levels of habitat complexity. White = immobile; grey = swimming; black = escaping. Top panel = predator-free; bottom panel = predator-in treatments.
are two closely related characids, sharing similar ecological niches when juveniles (Agostinho et al. 2007; Barletta et al. 2010) and differences in prey size: predator size ratio were too small between the experiments (i.e. 1 : 3.2, this study; 1 : 3.5, Santos et al. (2009)), further studies are necessary to elucidate the deviations on prey-size-selectivity between these native predators. In this way, experiments addressing whether predator aggressiveness lead to differential predation towards particular prey sizes among neotropical native piscivores could provide interesting results. For example, B. orbignyanus displayed by far the most aggressive behaviour among the three native predators tested through this study and Santos et al. (2009, 2012).

The three species (P. lineatus, C. piquiti, and O. niloticus) most consumed by S. brasiliensis were less active and occupied largely the surfaces of the aquaria, and the effects of habitat complexity on their behaviour were more marked for them in predator treatments, compared with the other two prey species. In contrast, A. altiparanae was often swimming or escaping, a behaviour that was apparently effective in reducing predation. Swimming performance can crucially affect fish survival (Juanes et al. 2002; Wolter and Arlinghaus 2003) and although S. brasiliensis was often observed pursuing A. altiparanae, a successful attack was never recorded. Although a less active behaviour often reduces predation risk (Juanes et al. 2002; Teplitsky and Laurila 2007), S. brasiliensis was more effective preying on structure-dependent prey species, such as C. piquiti. This pattern was also observed in a similar experiment using the pimelodid P. corruscans as predator (Santos et al. 2012). A. altiparanae is amongst the most abundant species in several ecosystems of the Paraná River basin and seems well adapted to a high predation risk, given its small size ($<150$ mm TL at maximum) and the variety of its habitats (Agostinho et al. 2007; Barletta et al. 2010). Conversely, all other prey species tested attain larger sizes when adults ($\geq400$ mm TL), thus reducing their predation risk. Diet activity patterns, as observed by Santos et al. (2012), are another factor that could have influenced these predatory preferences of S. brasiliensis, preying more on diurnal prey species instead of on I. punctatus, the only with nocturnal habits.

Our results have some implications for the conservation of native fish and the management of invasive species in neotropical environments. Apart the complex interactive effects of behavioural and morphological traits of predator and prey species on predation, our findings revealed that juvenile S. brasiliensis can exert a biotic resistance to invasive fishes in neotropical ecosystems, but not at the same degree for all prey species. The potential of S. brasiliensis to help to control the abundance of invasive species is thus expected to be weak for I. punctatus but higher for the invasive C. piquiti and O. niloticus. While the potential of native predators to control the abundance of invasive fishes had been already stressed in our previous experiments (Santos et al. 2009, 2012), this is the first study to directly address the concept of biotic resistance for Neotropical fishes. Our microcosm results should, however, be viewed with caution if used for scaling-up initiatives. Preserving or restoring vegetated habitats and maintaining the natural flooding pulse seems likely to benefit in general S. brasiliensis and to increase the vulnerability to predation of I. punctatus. However, as commented before, our artificial macrophytes were comparatively much less structurally complex than the natural habitats found at nursery grounds (i.e. floodplain lakes) in the Paraná River basin. Second, all the fishes used in our experiments came from fish farms, so it is expected that they displayed some behavioural differences from those of natural stocks. As already emphasised in Santos et al. (2009, 2012), it is expected that predation rates of S. brasiliensis on the invasive cichlids, especially C. piquiti, would be lower in natural systems than those observed in our experiments, because of the intensive parental care. On the other hand, considering the low vulnerability of A. altiparanae to S. brasiliensis piscivory, the broad distribution of both A. altiparanae and P. lineatus in many river basins at the neotropics, and taking into account the premises of prey naiveté hypothesis (Kovalenko et al. 2010b), no severe effects of S. brasiliensis predation would be expected on these native prey species in the natural systems. In conclusion, our experiments overall demonstrate that the effects of habitat complexity and fish predation depend on species-specific features of predator and prey species and are thus complex to predict.

Acknowledgements

The experiments were carried out in agreement with the ‘Ethical Principal in Animal Research’ adopted by the Brazilian College of Animal Experimentation (COBEA). This work was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico, Brazil (graduate grant to AFGF Santos, code 210199/2006-7; Edital Universal, code 478541/2004-0), Programme Allian of the European Union (Programme of High Level Scholarships for Latin America, grant to LNS), and the Government of Catalonia (Distinction Award for University Research 2004 to EGB). We especially thank Drs. A. A. Agostinho, A. Bialetzki and H. F. Júlio Júnior, from Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura (UEM, Brazil), for providing the infrastructure for the laboratory experiments, and three anonymous reviewers for helpful comments on the manuscript.

References


www.publish.csiro.au/journals/mfr