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PRIMARY RESEARCH PAPER

Direct and indirect effects of an introduced piscivore, *Cichla kelberi* and their modification by aquatic plants

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Abstract The non-native peacock bass (*Cichla kelberi*) is causing freshwater fish extinctions in the tropical regions around the world, but there are very few studies on its interaction with native species. This study, based on a mesocosm experiment, examined direct and indirect effects of a non-native peacock bass on the native prey in Paraná River, Brazil, and tested whether these effects were mitigated by aquatic vegetation. Feeding activity of most prey was unaffected by the presence of peacock bass. All prey were consumed in the absence of vegetation; whereas a marginally significant decrease in mortality was observed in the vegetated habitats. Overall, peacock bass had minor indirect effects on prey foraging, but very significant direct effects on prey survival. As aquatic plants provide very limited protection to native prey, vegetated habitats are unlikely to slow down the decline in biodiversity resulting from this invasive species and conservation measures may need to consider other ways to ensure survival of the source populations.

Keywords Non-native species · Predator–prey interactions · Intimidation effects · Feeding activity · Refuge · Macrophyte

Introduction

Predator–prey interactions are important in defining structure and dynamics of food webs (e.g., Kerfoot & Sih, 1987). Direct or lethal effect of predators on prey population depends on the ratio of consumption rate to prey recruitment rate. In turn, prey can detect small changes in predation risk and modify their behavior to reduce the risk of attack or develop defenses against predators (e.g., Lima & Steury, 2005). The resulting indirect predator effects often include reduced prey activity, food intake, and reproduction (reviewed in Lima & Dill, 1990). Although historically more attention has been paid to direct predator effects, indirect effects are often stronger than direct and their proportional importance is even greater in aquatic than terrestrial environments, possibly because aquatic organisms are better able to recognize predation risk through the use of water-soluble cues (Preisser et al., 2005).

Invasive species threaten diversity and function of native ecosystems and magnify the impact of other anthropogenic assaults (e.g., Gordon, 1998, Wilcove

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et al., 1998; Simon & Townsend, 2003; Schläpfer et al., 2005). Invasive predators have caused great declines in biodiversity, especially in freshwater habitats (Zaret & Paine, 1973; Witte et al., 1992). However, despite evidence that indirect predator–prey interactions are important for community trophic structure, few studies have considered indirect behavioral effects of introduced predators (Sih et al., 2006 but see Nyström et al., 2001; Trussell et al., 2003, 2006; Mills et al., 2004). This is critical because a fundamental understanding of both types of effects is required before we can successfully predict the outcome of the invasion and mitigate the impacts on native prey.

Highly diverse and endemic fauna of the Paraná River, Brazil, is endangered by the hydrological alterations and invasive species (Agostinho et al., 2005). Among invasive fishes in the Paraná River basin, the peacock bass (*Cichla kelberi* Kullander and Ferreira, Cichlidae), native to the Amazon River, is dispersed throughout the region and, due to its highly predatory nature, is the greatest threat to the native fish diversity (Agostinho et al., 2008). Peacock bass was first observed in the Paraná River in 1985 and remained at a low density until recently, and its expansion coincided with changes in water clarity and flood cycle due to hydroelectric dams (Abujanra, 2007). In 2 years after peacock bass was detected in Rosana reservoir, there was a 95% decline in macrophyte-associated native fish density and 80% decline in richness and a complete assemblage extinction was predicted in this habitat by 2010 (Pelicice & Agostinho, 2009). Under this scenario, it is necessary to better understand the relationship between invasive predator and native prey to implement protective measures for the native species. For example, complex habitats provide spatial heterogeneity that acts to stabilize predator–prey interactions (Huffaker, 1958). In aquatic environments, macrophytes provide habitat complexity that serves as a refuge from predation to many fish (e.g., Sih, 1987; Dibble et al., 1996) and in particular they have been shown to reduce susceptibility of native fish to invasive predators (Stuart-Smith et al., 2007).

In this article, we examine the role of aquatic vegetation in mediating predator–prey interactions between the non-native peacock bass and its prey in order to understand whether macrophytes can protect the native species from this invasive predator. In addition, native macrophytes in the Upper Paraná floodplain are threatened due to a recent invasion by *Hydrilla* and, therefore, we also tested whether changes in macrophyte species would affect this relationship, because invasive plants are known to influence fish foraging behavior (Theel & Dibble, 2008). Overall, our hypotheses were: (1) peacock bass has indirect effects on prey feeding activity and direct effects on prey survival, (2) the direct effect of this predator is mitigated by aquatic macrophytes, and (3) observed direct and indirect effects are similar in native and non-native macrophytes.

Materials and methods

Experimental setup

The experiment was carried out in a mesocosm facility, which consisted of 1,000 l tanks with sandy substrate, continuous water flow, and indirect natural light (partly shaded). Prey fish were collected using cast nets and peacock bass were collected by angling from the upper Paraná River. Aquatic plants were collected from lagoons or the main channel of the Paraná River. *Eichhornia azurea*, or blue water hyacinth, is the dominant macrophyte in the floodplain (Bini et al., 2001). It is a stoloniferous aquatic plant with an extensive floating stem system only partly anchored in the sediments and with extensive roots in their nodes, known to provide habitat to a diverse fish community dominated by small characids (Agostinho et al., 2007). Preliminary analysis showed that *Eichhornia* densities averaged 2.7 stems or 16.7 nodes/m^2 and this stem and node density was recreated in each mesocosm tank. Variable *Hydrilla* coverage was observed in canals, backwaters, and the main channel of the Paraná River. For this experiment, we used an approximately 90% coverage to best represent corresponding backwater environments. *Hydrilla* was transported in water-filled containers to retain its natural structure and minimize loss of associated fauna. In the tanks, clumps of *Hydrilla* were rooted by digging the lower part of stems into the substrate, after which tanks were slowly filled with water and plants assumed their normal structure. Water hyacinth was very resilient and regained its normal position in less than a day after transplanting into the tanks.

Visual inspection of tanks several days after transplanting confirmed numerous invertebrates and thick epiphyton; however, a detailed assessment of the food resources was beyond the scope of this project and no assumption is made about their similarity between the two plant treatments. Water quality was monitored using YSI Model 556 portable meter (YSI Environmental, Yellow Springs, OH, USA).

Indirect effects of a non-feeding predator

The first part of the experiment was designed to examine whether feeding activity of prey was affected by the presence of a non-feeding peacock bass. In this experiment, 30 prey fish were stocked in each mesocosm tank and acclimated for approximately 2 h before adding the predator. In an attempt to accurately mimic natural conditions, we recreated a multi-species assemblage of macrophyte-associated species commonly occurring in vegetated lagoons, including *Serrapinnus notomelas* (Eigenmann), *Hemigrammus marginatus* (Ellis), and *Hemigrammus* sp. (previously identified as *H. marginatus*) and used small schools similar to those observed in natural macrophyte stands (Casatti et al., 2003; Pelicice & Agostinho, 2006). *S. notomelas* and *H. marginatus* also were very abundant in Rosana Reservoir and were observed declining after the peacock bass introduction (Pelicice & Agostinho, 2009). All individuals of the same species within a tank were treated as subsamples and averaged for analysis. One peacock bass (TL = 30–40 cm) was introduced in each predator treatment tank. Peacock bass did not attack prey due to stress from handling and unfamiliar surroundings. Treatments were assigned to the tanks using a coin toss. We designated five replicates for each of the four treatment combinations (peacock bass/no peacock bass crossed by *Hydrilla*/*Eichhornia* macrophyte habitats), but one tank was lost due to peacock bass jumping out of the tank, which resulted in a total of 19 tanks (10 *Hydrilla* and nine *Eichhornia*). After 24 h, tanks were drained, macrophytes were pushed aside and prey fish were retrieved with a net, anesthetized with Eugenol and preserved in 10% formalin. The strength of the indirect effect was determined as a change in prey feeding activity, estimated from stomach fullness, because small size of fish would make volumetric analysis difficult. Stomach fullness was measured on a scale from 0 to 3 (0—completely empty stomach, 1—25%, 2—25–75%, and 3—75–100% full; Fugi et al., 1996).

Indirect effects of a foraging predator

The second part of this study examined whether prey feeding activity, estimated from stomach fullness, was affected by the presence of a foraging predator. We used a setup similar to the one used in the previous experiment, except that a foraging peacock bass was used in the predator presence treatment. It was only possible to get peacock bass to feed under experimental conditions after a 3-week acclimation in relatively dark or vegetation-containing tanks and by avoiding pre-experimental disturbance (such as transfer into a different tank). Prey (*Hemigrammus* sp. and *Bryconamericus exodon*) were stocked at a density of 30 fish/tank. Presence of an observer for the first 15 min after stocking prevented predatory attacks and allowed prey to acclimate to the tanks. The gape size of peacock bass was sufficiently large to easily handle all prey species.

Direct predator effects

We compared prey survival with and without peacock bass in the two macrophyte types in the same tanks used for the indirect effects of foraging predator experiments and unvegetated tanks. Prey mortality observed within 2 h post-stocking (11%) was assumed to be related to handling stress and these fish were immediately replaced. After that, any dead fish were collected and counted as non-consumptive mortality but not replaced. This experiment was run for 48 h, after which tanks were drained and fish were harvested as described for experiment one. Macrophytes were removed and carefully searched for remaining fish. Since it was not possible to reliably distinguish the two prey species during stocking without incurring significant handling mortality, they were stocked together but analyzed separately after post-mortem identification.

Statistical analysis

Indirect predator effects (i.e., prey stomach fullness) were analyzed using a two-factor ANOVA (SAS 9.1, with predator presence/absence and the type of plant habitat as the two factors), separately for each prey species and for the feeding and non-feeding predator. Prey mortality was analyzed using Kruskal–Wallis test because these data did not meet the assumption of homogeneous variance. In addition, we tested whether there was significant intrapopulation variability in the antipredator response by comparing the within-tank variance in feeding behavior for treatments with and without predator.

Results

Indirect effects of a non-feeding predator

Presence of a non-feeding predator did not affect prey feeding activity (Fig. 1; $P > 0.05$ for each of the three species studied). There was no interaction between predator and plant treatments ($P > 0.05$). Feeding activity was not affected by the plant treatment ($P > 0.05$) despite significant differences in water quality between the two plant treatments (Table 1). Lower pH and dissolved oxygen were observed in *Eichhornia*, whereas water samples from the *Hydrilla* treatment did not differ from those obtained directly from the main channel of the Paraná River. In addition, there was no change in within-population variability in feeding activity in response to the predator ($P > 0.05$ for each species).

Indirect effects of a foraging predator

In the second experiment, *Hemigrammus* sp. feeding was unaffected by either the presence of a feeding predator or the plant habitat (Fig. 2a; $P > 0.05$). *B. exodon* reduced feeding activity in the presence of peacock bass in *Eichhornia* but did not have a similar decrease in *Hydrilla* (Fig. 2b; predator by plant interaction: $F_{1,13} = 5.72$, $P = 0.0405$; effect slices $P = 0.0046$ and 0.9163 for *Eichhornia* and *Hydrilla*, respectively). There was no predator effect on the number of fish observed dead (i.e., non-consumptive mortality; $P > 0.05$).

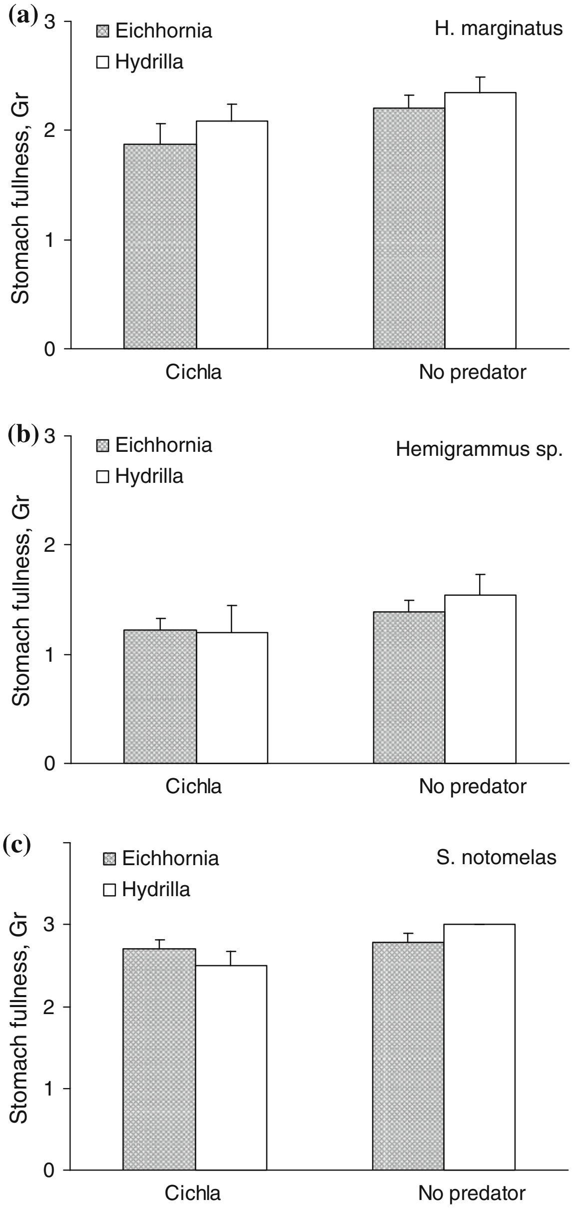

Fig. 1 Indirect effects of a non-feeding peacock bass on the foraging activity of **a** *Hemigrammus marginatus* ($n = 19$), **b** *Hemigrammus* sp. ($n = 20$), and **c** *Serrapinnus notomelas* ($n = 15$) in the two plant habitats, native *Eichhornia* and the non-native *Hydrilla* (mean ± SE). Note lack of differences in the intrapopulation variability with and without the predator

Direct predator effects

There was a significantly greater total mortality in the treatment containing peacock bass (Fig. 3; $F_{1,21} = 54.57$, $P < 0.0001$). All prey were consumed in the absence of plants, whereas partial mortality (average of 74%) was observed in the vegetated treatments (Kruskal–Wallis $P = 0.044$). Surviving individuals were observed in vegetation and they were not moving.

Table 1 Water quality in the two plant treatments as compared with the river

Parameter	Eichhornia	Hydrilla	River
Temperature	24.6 b	24.4 b	27.4 a
Conductivity	66.4 b	65.3 c	69.0 a
DO %	68.2 b	73.6 a	80.3 a
pH	6.6 b	7.1 a	7.1 a

Means with the same letter are not significantly different

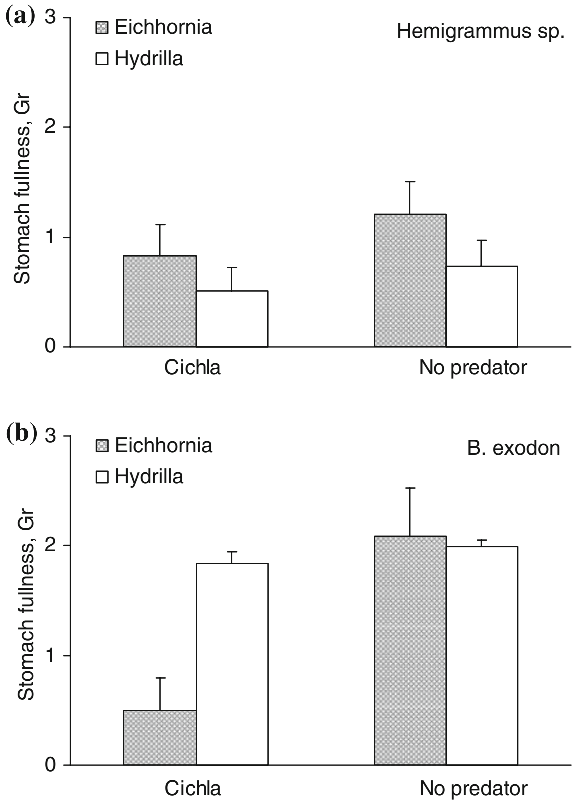

Fig. 2 Foraging activity of **a** *Hemigrammus* sp. ($n = 19$) and **b** *Bryconamericus exodon* ($n = 14$) with and without the non-native peacock bass in *Eichhornia* and the non-native *Hydrilla* (mean ± SE)

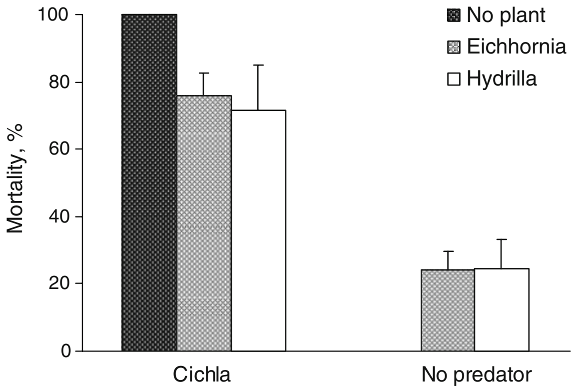

Fig. 3 Lethal effects of the peacock bass with and without macrophytes ($n = 21$, mean ± SE)

Discussion

Indirect predator effects

Reduced feeding activity of prey in high-risk situations is one of the most frequently observed and well-documented indirect predator effects (Schmitt & Holbrook, 1985; Lima & Dill, 1990), yet we did not observe a decrease in prey feeding activity in response to the peacock bass with the exception of *B. exodon* feeding in *Eichhornia*. Other studies have shown that some prey recognize non-native predators and adequately respond to the predation threat, often experiencing substantial indirect effects from invasive predators. For example, native least chub, *Iotichthys phlegethontis*, reduced activity and selected vegetated habitats in the presence of invasive predatory mosquitofish, *Gambusia affinis* (Mills et al., 2004). Cues from invasive green crab, *Carcinus maenas*, led to increased refuge use by snails (*Littorina littorea* and *Nucella lapillus*), which resulted in reduced feeding activity and decreased growth (Trussell et al., 2003, 2006). *Rana* tadpoles reduced their activity in the presence of cues of the introduced brown trout (Nyström & Åbjörnsson, 2000). The introduced brown trout induced a habitat shift in a native galaxiid but did not affect its feeding activity (Stuart-Smith et al., 2008). Lack of predator recognition, or prey naiveté is often evoked when prey fail to respond to non-native predators (Cox & Lima, 2006) and peacock bass may be a novel, visual predator in this system; however, our concurrent behavioral study demonstrated that prey recognized chemical and visual cues of peacock bass and displayed avoidance behaviors similar to those observed with a native predator (K. Kovalenko, unpublished data). Moreover, in the present study we observed several instances of prey jumping out of the tank which contained a predator immediately after being stocked in that tank. This indicates that prey were not naive to peacock bass in terms of being able to recognize it as a predator, yet they did not modify their feeding activity in its presence.

The nature and strength of predator–prey interactions can be affected by abiotic and habitat variables, and indirect effects can decrease in importance under certain conditions. For example, there is evidence that indirect effects of predators are weakened in the presence of vegetation (Woodley & Peterson, 2003), which could explain lack of changes in foraging activity observed in our study. In particular interest to our system is an observation that a predator-induced habitat shift of fathead minnow, *Pimephales promelas* was less pronounced in turbid environments (Abrahams & Kattenfeld, 1997). This implies limited effectiveness of the antipredator behavior in turbid water and means that under these conditions, the indirect effects are considerably less important than direct effects (Abrahams & Kattenfeld, 1997). Since the Paraná River was very turbid before the construction of dams (Abujanra, 2007), native fish may not have evolved this type of anti-predator behavior. When prey cannot accurately predict the level of risk or the direction of potential attack, they might be better off maximizing their foraging returns. In addition, small, relatively short-lived species as the ones used in our study may have greater constraints on their ability to wait out the predator in terms of the reproductive strategy and energy acquisition needs (Lima & Dill, 1990). Our behavioral experiments showed that prey decreased their overall activity after an acute exposure to peacock bass or its chemical cue (K. Kovalenko, unpublished data). A long-term reduction in activity would probably result in decreased stomach fullness, which was not observed in this study. It is possible that reduced activity in behavioral study was a response to a pulse of high risk which may not be sustained for long periods of time (Lima & Bednekoff, 1999).

This apparently maladaptive behavior may be viewed as an example of phylogenetic inertia because limited behavioral plasticity does not allow an immediate adaptation to the novel predation pressure (Sih et al., 2000). Alternatively, our assumption about the decrease in feeding activity as an adaptive antipredator response may not be correct. If prey fish do not have to venture out of the vegetated habitat in order to feed, as appears to be the case with these macrophyte-associated species (Pelicice & Agostinho, 2006), they would not incur foraging costs by avoiding the predator unless they are also trying to reduce within-habitat movement. Even though we did not observe any effects on prey feeding activity, peacock bass may have other indirect effects on prey growth and survival such as changes in gut retention time and food assimilation and increased stress (e.g., Trussell et al., 2006).

It is interesting that foraging activity was mostly unaffected by the macrophyte type despite the differences in their growth form. However, our water quality data show that if *Hydrilla* replaces *Eichhornia* as a dominant macrophyte, taking advantage of continuing decline in turbidity due to hydrological alteration by dams (Abujanra, 2007), it may result in significant changes in diel oxygen and pH dynamics in the lagoons. This change may affect fish communities presently dominated by characids, which are resistant to oxygen deficit (Agostinho et al., 2007). This effect, as well as the actual diet composition in the two plants, warrants further investigation to evaluate potential impacts of *Hydrilla* invasion on the fish community.

Direct predator effects

Although predator foraging efficiency is usually reduced in complex habitats (e.g., Denno et al., 2005 and references therein; Gotceitas & Colgan, 1987); vegetated habitats provided only marginal protection to native prey in the present study. As with indirect effects, there was no significant difference in prey responses between native and invasive macrophytes, despite the fact that each provided very different structural habitat. It is interesting that the same macrophyte as the one in our study, *E. azurea* provided very significant protection to invertebrate prey against predation by a small insectivore *Moenkhausia sanctaefilomenae* (Padial et al., 2009), and yet it had only a negligible effect on foraging of a much larger peacock bass, which apparently attacked its prey at vegetation densities capable of hindering its movement. However, the relationship between vegetation density and predator success is not as straightforward for the littoral zone piscivores, which may use several methods for capturing prey in macrophytes and even switch their foraging mode depending on the macrophyte density (Savino & Stein, 1989). Some predators may chase prey out of macrophytes: for example, largemouth bass, *Micropterus salmoides* was observed to make lunges into densely vegetated plots in an attempt to chase prey out of hiding (Gotceitas & Colgan, 1987). In addition, suction may be used to dislodge the remaining prey from vegetation, although it is only effective on very short distances, and peacock bass, *C. ocellaris* had one of the greatest ram and suction distances of several cichlid species examined (Wainwright et al., 2001).

Indirect evidence from previous studies indicates that vegetated habitats provide very limited protection to native prey against peacock bass predation. Reduction in native species richness in lakes with introduced peacock bass *C. monoculus*, oscar *Astronotus ocellatus*, and red piranha *Pygocentrus natterei* was observed in all areas of each lake regardless of the presence of macrophyte refugia (Latini & Petrere, 2004). On the contrary, Zaret & Paine (1973) speculated that one of the few fish that survived *C. monoculus* invasion in Lake Gatun, Panama, *Roeboides* sp., has probably done so by remaining in dense aquatic vegetation. More recently, Pelicice & Agostinho (2009) documented a nearly complete elimination of the native small fish fauna in the Rosana Reservoir, Brazil after peacock bass introduction despite the great abundance of macrophyte refugia (*Egeria* spp., a Hydrocharitacea with similar architecture of *Hydrilla*). However, this is the first study to experimentally demonstrate that neither submerged nor floating aquatic macrophytes provide substantial protection to the native species against peacock bass predation.

Dramatic effects of invasive predators are commonly associated with depauperate systems or systems with a history of evolutionary isolation (Cox & Lima, 2006), such as effects of Nile perch in Lake Victoria (Witte et al., 1992) or trout in many fishless lakes (Knapp et al., 2001). However, as this invasion shows, species-rich systems may also be vulnerable to non-native predators. In this case, native species may be so susceptible to this invader at least in part due to human-caused disruption of the hydrological regime, which may have eliminated critical release from predation during the high-water periods.

Few studies compared the direct and indirect effects of introduced predators and no experiments addressed those effects with peacock bass. We found that peacock bass had minor indirect effects on the native prey foraging activity. Direct effects, on the other hand, seemed overwhelmingly important and mortality observed in our mesocosm experiment corresponded well with the rate of species disappearance reported previously (Pelicice & Agostinho, 2009). Prey foraging activity and survival were similar in the native water hyacinth and invasive *Hydrilla*, even though distinct structural habitat was provided by each of these macrophytes. Since macrophyte refugia provide only limited protection to native prey, conservation measures may need to consider creating exclosures to make some macrophyte stands inaccessible to peacock bass to ensure survival of the source populations, especially in areas of high endemicity or where local extinctions jeopardize the survival of native species. Further research is necessary to understand what mitigates effects of peacock bass in its native range (where it was associated with increased diversity; Jepsen et al., 1997). Especially worth examining is the importance of flood-related environmental variability for persistence of predator–prey interactions, in particular, the protective role of turbidity and seasonally flooded habitats.

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