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Research Article

Non-lethal effects of a native and a non-native piscivorous fish on the interaction between a mesopredator and benthic and pelagic invertebrates

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Abstract

Predator presence may result in non-lethal costs to prey; these costs may be even larger if both predators and prey do not naturally co-occur. We experimentally evaluated the survival of two aquatic invertebrates from the upper Paraná River basin (*Chironomus sancticaroli* – benthic and *Daphnia magna* – pelagic) exposed to a native mesopredator fish (*Astyanax lacustris*) in three non-lethal predation treatments: (i) the absence of piscivorous fish, (ii) the presence of a native piscivorous fish (*Hoplias* aff. *malabaricus*), or (iii) the presence of a non-native piscivorous fish (*Astronotus crassipinnis*). The treatments were crossed with the absence and presence of vegetated habitats. We predicted that the mesopredator might not have adapted foraging strategies to eat in the presence of an unfamiliar predator while invertebrate prey use vegetated habitats for protection. Therefore, we expected that the combination of piscivorous fish presence and vegetated habitat would lead to a classical additive response on invertebrate survival, which will be higher in the presence of non-native piscivorous fish than in the presence of native piscivorous fish. The presence of vegetated habitat and piscivorous fish increased invertebrate survival, but together they did not promote an additive response. Instead, the non-lethal cascade effects of the native piscivorous fish was similar between vegetation treatments, whereas the non-native piscivorous fish led to higher survival of the invertebrates in non-vegetated *versus* vegetated habitats. Although refuges are understood as elements that enhance predator-prey stability, the effectiveness of submerged macrophyte stands as safe habitats is dependent on some predator traits, such as origin and hunting mode. Our results also indicate that the invasion of *A. crassipinnis* has the potential to change mesopredator prey selectivity from a diet based on pelagic prey with the native *H.* aff. *malabaricus* to the random consumption of pelagic and benthic prey, which may have important consequences for the stability of natural aquatic food webs.

Key words: anti-predator behaviour, evolutionary history, predation threat, predator-prey interaction

Introduction

The presence or absence of predators may lead to profound changes in trophic links and in the survival of species of a lower trophic level (Carpenter et al. 1985; Pace et al. 1999; Estes et al. 2011). According to cascade models of aquatic food webs, an increase in piscivorous biomass reduces both zooplanktivorous and benthivorous fish biomass, which in turn increases the abundance of aquatic invertebrates (Carpenter et al. 1985). Although there is empirical evidence for this traditional theoretical model (e.g., Benndorf et al. 2002), one of its main limitations is the consideration of only the lethal effects of predators. The simple presence of a predator may also provide a non-lethal cost to prey, which often spends more time in a vigilant state after perceiving the predation threat (Lima 1998; Werner and Peacor 2006; Ajemian et al. 2015). When prey display anti-predation behaviours (such as keeping in a vigilant state), they consequently reduce the time spent on feeding-related events (Abrahams et al. 2009; Rudman et al. 2016), ultimately impacting the prey reproduction and growth rates (McPeek 2004; Ahlgren et al. 2011). Therefore, the mere presence of predators may be as important as their consumption effect on the community assemblage (Romare and Hansson 2003).

Anti-predator behaviours that minimise the costs while maximising the benefits usually evolve in predator-prey interactions over co-occurrence time between predators and prey species (Abrahams et al. 2009; Lazzaro et al. 2009; Sih et al. 2010). The effects of predator presence may be more pronounced when the predator involved is a non-native species given the lack of prey adaptation to avoid being eaten (Salo et al. 2007; Martin 2014). Introduced predators might also be able to decrease prey populations not by a xenophobic effect (Simberloff 2003) but rather because invaders could present higher resource use efficiency than native species and have superior competitive ability (e.g., Vilà and Weiner 2004; Alexander et al. 2014). Conversely, species with high anti-predator plasticity behave cautiously towards any new threat (Sneddon et al. 2003; Mesquita and Young 2007); this trait may concede them some resistance to predator introduction. However, mesopredator species in a constant vigilant state usually decrease their foraging area and consumption rate, benefiting the trophic level below. Mesopredators may also feed on non-preferential prey types in safe areas to maintain their energy intake (Persson and Eklöv 1995). Although species origin does matter (Paolucci et al. 2013), differences in predator hunting modes might also affect the structure of trophic cascades because they lead to different prey responses (Miller et al. 2014). For example, the mayfly *Baetis bicaudatus* Dodds, 1923 (Insecta: Baetidae) hides under rocks when threatened by an active predator (trout) but tends to be more active and less timorous in the presence of a less active predator (stoneflies) (Peckarsky and McIntosh 1998). In this sense, the interaction between piscivorous (tertiary consumer) species origin and hunting mode may elicit more profound changes in prey fish behaviour (secondary consumer), which might end up affecting the consumption of invertebrates (primary consumer).

Hoplias aff. *malabaricus* Bloch, 1794 (Osteichthyes: Erythrinidae) is a native sit-and-wait predator (Montenegro et al. 2013) of the upper Paraná River floodplain, southern Brazil, where it is one of the most abundant and important piscivorous fishes. It feeds upon almost all fish species in the region (Peretti and Andrian 2008; Montenegro et al. 2013). Around the year 2000, an omnivorous predator fish with a high tendency for piscivory, *Astronotus crassipinnis* Heckel, 1840 (Perciformes: Cichlidae) (hereafter considered as a piscivorous fish), native to the Amazon River basin, was introduced into the upper Paraná River by fish-stocking programmes (Garcia et al. 2018). *Astronotus crassipinnis* is an active predator well-adapted to living in shallow lakes (Abujanra et al. 2009; Júlio-Júnior et al. 2009). Presently, there have been no reports regarding the extent of environmental alteration caused by *A. crassipinnis*. However, the effects of *A. crassipinnis* on native fish populations could be similar to that of *Cichla kelberi* Kullander and Ferreira, 2006 (Perciformes: Cichlidae), another recent non-native cichlid established in the region. *Cichla kelberi* was responsible for a 95% decline in native fish density and an 80% decline in fish richness in a reservoir located in the upper Paraná River basin (Pelicice and Agostinho 2009; Pelicice et al. 2015).

This relationship between the arrival of a new predator and the decline in native fish populations may have occurred because the prey was not prepared to recognise and avoid such a new threat (naiveté hypothesis, Cox and Lima 2006), and consequently it may have experienced higher rates of mortality compared with a condition without the exotic predator (Sih et al. 2010). Alternatively, the new top predator may have had few antagonistic trophic interactions in the new environment (enemy release hypothesis, Williamson 1996), which allowed it to have a high population growth rate. Therefore, *A. crassipinnis* can be a potential danger to native fish populations in lentic environments, as *C. kelberi* was. The negative impact caused by *A. crassipinnis* to native fish populations may be further intensified in environments with greater water transparency (e.g., Figueiredo et al. 2016), such as the current state of the upper Paraná River basin, generated by the increasing number of hydroelectric reservoirs (Stevaux et al. 2009).

Both *H.* aff. *malabaricus* and *A. crassipinnis* inhabit shallow lakes with large littoral areas, where vegetated habitats, such as macrophyte beds, are abundant. Vegetated habitats are recognised as crucial providers of refuge for prey because their structural complexity can limit the movement of large predators and reduce the likelihood of encounters between predators and prey (Diehl 1988; Padial et al. 2009). Thus, the presence of vegetated habitats might reduce the predation rates of mesopredators on invertebrates. However, in the presence of piscivorous predators, mesopredators could also move to vegetated habitats to decrease their susceptibility to predator strikes. This co-occurrence between invertebrates and mesopredators amid the interstices of the vegetation may increase the mesopredator feeding rate, decreasing the importance of vegetated habitats as a refuge for invertebrates. Hence, the presence of aquatic plants could either amplify or attenuate the non-lethal effect of piscivorous fish on the survival of aquatic invertebrates.

Our main objective was to verify how the interaction between an omnivorous mesopredator, *Astyanax lacustris* Lütken, 1875 (Characiformes: Characidae), and its prey, *Chironomus sancticaroli* Strixino and Strixino, 1981 (Insecta: Chironomidae) and *Daphnia magna* Straus, 1820, (Crustacea: Daphniidae) could be affected by the presence of a native (*H.* aff. *malabaricus*) and non-native piscivorous fish species (*A. crassipinnis*) in vegetated and non-vegetated habitats. We evaluated two main predictions. First, we expect that the combination of piscivorous fish presence and vegetated habitat would lead to a classical additive response on invertebrate survival because: i) invertebrates can decrease their risk of being eaten by hiding in aquatic plants and ii) *A. lacustris* may reduce its foraging behaviour in the presence of a piscivorous fish. Second, we predict that invertebrate survival is lowest in non-vegetated habitats with the presence of the non-native piscivorous fish and highest in vegetated habitats with the presence of the native piscivorous fish. This second expectation is based on the hypothesis that the mesopredator may not have adapted foraging strategies to eat in the presence of a new threat (e.g., Cox and Lima 2006) while invertebrate prey may still use vegetated habitats as protection. We also evaluated whether the feeding preference of *A. lacustris* (mesopredator) regarding the prey *C. sancticaroli* (benthic) and *D. magna* (pelagic) differs in the presence of different piscivorous fish, the native *H.* aff. *malabaricus* (sit-and-wait predator) and the non-native *A. crassipinnis* (active predator). The same approach was used to compare prey selection in the presence/absence of vegetated habitats.

Methods

Experimental design

Fish were collected in December 2014, when piscivorous fish (*H.* aff. *malabaricus*, Total Length – TL = 27.2 ± 0.35 cm; *A. crassipinnis*, TL = 25.6 ± 0.20 cm) were sampled using a hook and line and the mesopredator (*A. lacustris*; TL = 8.6 ± 1.1 cm) with trawls (long: 20 m; net mesh: 5 mm) in shallow lakes connected to the upper Paraná River, Brazil. Then, the fish were transported to the laboratory and kept in aquaria for 15 days to acclimate to the experimental water conditions. During the acclimation period, piscivores were fed with commercial fishing bait (cultivated *A. lacustris*), and mesopredators were fed with commercial dry food pellets. Larval stages of *C. sancticaroli* and adults of *D. magna*, which are known to be important prey of *A. lacustris* (Casatti et al. 2003; Gomiero and Braga 2008), were cultivated in tanks at a laboratory located at the State University of Maringá, Brazil. *Astyanax lacustris* was used due to its wide distribution in the upper Paraná River floodplain and because it forages in different compartments of the water column (Hahn et al. 2004; Peretti and Andrian 2008), influencing several populations of aquatic invertebrates.

We conducted the experiments in mesocosms using rectangular aquaria as experimental units (water volume 35 L; width = 25 cm; length = 45 cm; height = 35 cm). We exposed the aquatic invertebrates, seven midge larvae of *C. sancticaroli* (7 ± 1.6 mm) and fifteen adults of *D. magna* (2 ± 0.6 mm), to predation by three *A. lacustris* individuals in all aquaria. We used more than one mesopredator individual per aquarium to attenuate the influence of differences in individual feeding performance (Padial et al. 2009) and because the species forms schools. The different densities of invertebrates were set to simulate the real proportions of these organisms in nature (e.g., Thomaz et al. 2008). The relationship between the aquatic invertebrates and *A. lacustris* was evaluated in three non-lethal predation treatments: i) in the presence of the native piscivorous fish *H.* aff. *malabaricus*; ii) in the presence of the non-native piscivorous fish *A. crassipinnis*; and iii) in the absence of piscivorous fish. All three non-lethal predation treatments were crossed with the absence and presence of vegetated habitats, totalling six treatments. Vegetated habitats were simulated with sixteen artificial fragments of submersed aquatic plants (30 cm long), which have an architecture similar to the submersed macrophyte *Egeria najas* Planch, 1849. In the treatments without vegetated habitats, no other kind of potential refugia for the prey species was provided. All treatments were replicated five times (total n = 30).

Native and non-native piscivorous fish were fed immediately before the beginning of the trials to prevent the consumption of the mesopredators during the experiment. However, with this procedure, piscivores could not release any cues related to hunger in the water (Åbjörnsson et al. 1997), which could be identified as a predation threat by the mesopredator shoal (Figueiredo et al. 2015b). Thus, to resemble more realistic conditions, we inserted chemical cues from a hungry predator individual of *H.* aff. *malabaricus* or *A. crassipinnis* into their respective treatments. Following the protocol proposed by Figueiredo et al. (2015b), the chemical cues were obtained before the experiment by keeping the piscivorous fishes isolated in tanks of 100 litres without food for 48 hours. After this period, water samples with predator secretions were collected with a syringe and frozen, a process that prevents degradation of the secretion chemical and allows for its later use (e.g., Ferrari et al. 2008; Epp and Gabor 2008). Individuals of *A. lacustris* were starved for five days to standardise a hungry status and stimulate the consumption of invertebrate prey.

The experiment began with the introduction of the piscivorous fish into the experimental units together with their respective chemical cues (150 ml). The next step was the addition of invertebrates and mesopredators. A time gap of ~ 15 minutes between the addition of invertebrates and mesopredators was established to allow invertebrates to search for and use a safer habitat. One hour after the addition of the mesopredators, we removed all fish, filtered the water and counted the surviving invertebrates. We also counted the number of invertebrates in the mesopredators' stomach to ensure that during the experiment the piscivorous *H.* aff. *malabaricus* and *A. crassipinnis* did not ingest the aquatic invertebrates (i.e., ensure that there was no omnivory). Due to the scarce number of piscivorous fish, we conducted the experiment in two blocks. However, the block effect was not significant (Beta regression: Chi-square (1) = 0.187; P = 0.664), and we disregarded this effect in the subsequent analyses.

Data analysis

We tested hypotheses 1 and 2 using beta regressions (Ferrari and Cribari-Neto 2004). In both cases, we used the ratio between the number of invertebrate prey found at the end of the experimental period and the total number of invertebrate prey released at the beginning of the experiment as the response variable (hereafter named "invertebrate survival"). For hypothesis 1, the presence of the piscivorous fish (independent of species identity), the presence of vegetated habitats and the interaction of both of these terms were considered as independent variables. For hypothesis 2, the piscivorous identity (*H.* aff. *malabaricus* or *A. crassipinnis*), vegetated habitats and their interaction term were considered as independent variables. We opted to use beta regressions with dummy-coded independent variables instead of logistic regressions, as suggested by Warton and Hui (2011), due to overdispersion problems. Likelihood-ratio tests were used to assess the significance of the main factors in each beta regression model. Multiple comparisons among treatments in each beta regression were performed using Wald tests (asymptotic Chi-squared statistic; Fox 2008). The goodness of fit of each model was estimated using the pseudo-R-squared, and P values lower than 0.05 were considered significant.

To evaluate whether predation pressure of the mesopredator on benthic and pelagic prey follows the same pattern in all treatments, we used the Ivlev electivity index (Ivlev 1961). This electivity index was calculated using the initial and final numerical abundance of each type of prey in each experimental unit. The values of this index range from −1 to 1, where positive values indicate a preference for a given prey, zero indicates no preference, and negative values indicate rejection. We performed paired sample *t*-tests to compare the Ivlev electivity index values between *C. sancticaroli* and *D. magna* in each treatment. To avoid the inflation of a type I error due to the multiple paired *t*-tests performed (N = 6), we applied the Bonferroni correction (P value corrected = 0.008).

The beta regressions, likelihood-ratio tests, Wald tests, and the paired *t*-tests were performed in the R packages "betareg" (Cribari-Neto and Zeileis 2010), "lmtest" (Zeileis and Hothorn 2002), "car" (Fox and Weisberg 2011), and "stats" (R Core Team 2016), respectively.

Results

No individuals of the mesopredator *A. lacustris* and the invertebrates *C. sancticaroli* and *D. magna* were consumed by *A. crassipinnis* or *H.* aff. *malabaricus* during the experiments. The interaction term between the presence of non-lethal effects of piscivorous fish and vegetated habitat was significant (chi-square (1) = 11.96; P < 0.001) and explained 67% of the variation in invertebrate survival. Considering only the presence of piscivorous fish, we found a significant increase in the survival of aquatic invertebrates by 65% in the treatment without vegetation habitat (P < 0.001; Figure 1) and by 23% in the treatment with vegetation (P = 0.02; Figure 1). Considering only the vegetated habitat, we found a significant increase in the survival of invertebrates by 29% in the absence of piscivorous fish (P = 0.001; Figure 1). Interestingly, with the presence of piscivorous fish, the survival of invertebrates was 13% lower in the presence of vegetated habitats than in the absence of vegetation (P = 0.048; Figure 1). These results indicate no additive effect between the presence of piscivorous fish and vegetated habitat.

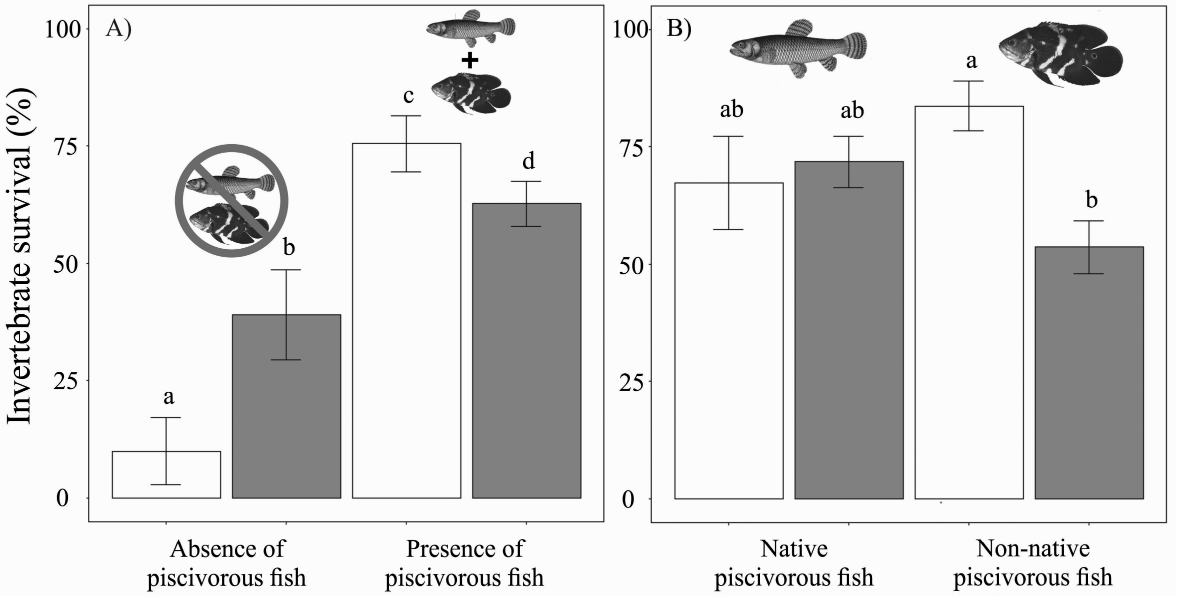

Figure 1. The mean and standard error of aquatic invertebrate survival after *Astyanax lacustris* predation (%) in the presence/absence of piscivorous fish and in the presence/absence of habitat vegetation are shown in panel A. In panel B, the invertebrate survival is shown just for treatments with the presence of piscivorous fish, highlighting the differences between the two species of piscivorous fish used in this study, the native *H.* aff. *malabaricus* and the non-native *Astronotus crassipinnis*. The pseudo R^2 was 0.67 and 0.37 in the model of the panel A and panel B, respectively. Different letters indicate significant differences in the post hoc tests. *White bars*: absence of vegetated habitats, *Grey bars*: presence of vegetated habitats.

The interaction term between the non-lethal effects of piscivorous identity and vegetated habitat was significant (chi-square (1) = 6.12; P = 0.01) and explained 37% of invertebrate survival variation. We did not find a significant difference in the invertebrates' survival between the treatments with *A. crassipinnis* and *H.* aff. *malabaricus* (vegetated treatment: P > 0.065, non-vegetated treatment: P = 0.055, Figure 1). The effect of vegetated habitat on the survival of invertebrates differed between treatments with different piscivorous fish (Figure 1). The presence of vegetated habitat did not significantly alter the survival of invertebrates in the treatments with *H.* aff. *malabaricus* (P = 0.812; Figure 1), but the survival decreased by 30% in the treatments with *A. crassipinnis* (P < 0.001; Figure 1).

In the absence of piscivorous fish and the presence of vegetation habitat, the mesopredator *A. lacustris* consumed the benthic prey *C. sancticaroli* and the pelagic prey *D. magna* in similar proportions (mean survival = 40.0% ± SD 18.6% for *C. sancticaroli*, and 38.7% ± 23.8% for *D. magna*, Table 1, Figure 2). Similar survival rates between both invertebrate types also occurred without both vegetated habitat and piscivorous fish (mean survival = 8.6% ± 19.2% for *C. sancticaroli*, and 10.7% ± 23.8% for *D. magna*, Table 1, Figure 2). In contrast, mesopredators significantly selected the pelagic prey *D. magna* instead of the benthic prey *C. sancticaroli* in the presence of the native piscivorous fish in the vegetated treatments (*t*(4) = −6.705, P = 0.002; Figure 2) but not in the non-vegetated treatments (*t*(4) = −2.334, P = 0.079; Figure 2). The survival rate of *C. sancticaroli* (mean survival = 94.3% ± 7.8%) was on average 33% higher than the survival rate of *D. magna* (mean survival = 61.3% ± 14.5%) in the treatments with vegetation and with *H.* aff. *malabaricus*. In the treatments with *H.* aff. *malabaricus* and without vegetation, the average

Table 1. Significance of paired sample *t*-tests comparing the Ivlev electivity index values between the types of aquatic invertebrate (benthic *Chironomus sancticaroli* and pelagic *Daphnia magna*) subjected to the predation of the mesopredator *Astyanax lacustris*. Bold values indicate significant differences after the Bonferroni correction (corrected P-value = 0.008).

Treatments	DF	*t*	P
Absence of piscivorous fish			
Absence of vegetated habitats	4	0.191	0.857
Presence of vegetated habitats	4	−0.029	0.978
Hoplias aff. *malabaricus*			
Absence of vegetated habitats	4	−2.33	0.079
Presence of vegetated habitats	4	−6.70	**0.002**
Astronotus crassipinnis			
Absence of vegetated habitats	3	0.27	0.804
Presence of vegetated habitats	4	0.16	0.878

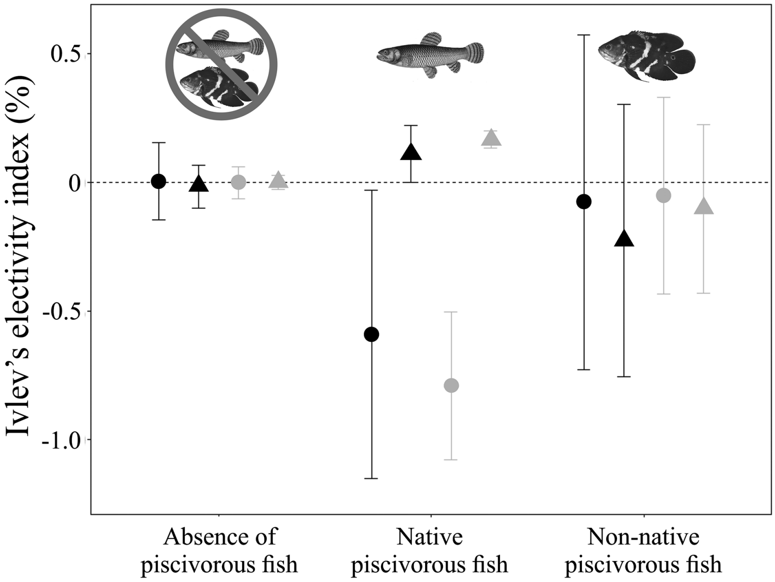

Figure 2. The mean and standard error of the Ivlev electivity index related to prey selection by *Astyanax lacustris* on benthic *Chironomus sancticaroli* (circles) and pelagic *Daphnia magna* (triangle) in treatments without piscivorous fish, with the native piscivorous fish *Hoplias* aff. *malabaricus* and with the non-native *Astronotus crassipinnis*. *Grey symbols*: absence of vegetated habitats, *Black symbols*: presence of vegetated habitats.

survival of *C. sancticaroli* was 88.6% (± 18.6%), and the survival of *D. magna* was 57.3% (± 33.2%). Mesopredators did not present any significant selection for benthic or pelagic invertebrate prey when co-occurring with the non-native piscivorous fish either in the presence or in the absence of vegetation (Table 1, Figure 2). In the vegetated treatments, 51.4% ± 29.6% of *C. sancticaroli* and 54.7% ± 26.8% of *D. magna* individuals survived. In the treatments without vegetation, 80.0% ± 21.7% of *C. sancticaroli* and 85.3% ± 15.2% of *D. magna* individuals survived. Therefore, the predation pressure on pelagic and benthic prey shifted according to the presence of piscivorous species and vegetation.

Discussion

The non-lethal effects of piscivorous fish had strong cascade effects on our experimental system, where the presence of piscivorous fish and the availability of vegetated habitats strongly increased the survival of benthic and pelagic invertebrates. However, the highest invertebrate survival was not observed in the treatment with piscivorous fish and vegetated habitats. Instead, in the presence of top predators, invertebrate survival was higher in non-vegetated than in vegetated habitats. This is an unexpected result considering that invertebrate survival is directly impacted by the mesopredator feeding efficiency, which tends to be reduced in the presence of top predators (Mazzeo et al. 2010; Estes et al. 2011) and when refuges are available (Savino and Stein 1989; Stansfield et al. 1997; Figueiredo et al. 2015a). Hence, it is expected that the presence of a piscivorous fish and the availability of vegetated habitats together would have an additive effect on invertebrate survival, which was not the case. The lack of an additive effect may have occurred because both the benthic and pelagic invertebrate (Grutters et al. 2015) and the mesopredator (Stansfield et al. 1997) use the same habitat as a refuge against predators. Thus, the basal prey and the mesopredator probably co-occurred in vegetated habitats, increasing the encounter rate between them (Ahlgren and Brönmark 2012) and, consequently, the predation rate on the mesopredator.

Although refuges are understood as elements that enhance predator-prey stability (Sih 1987), the effectiveness of submerged macrophyte stands as safe habitats for basal prey (primary consumers; e.g., benthic invertebrates) seems to be dependent on some piscivorous (tertiary consumer) fish traits, such as origin and hunting mode. For example, in the presence of non-native piscivorous fish, more invertebrates survived in the absence than in the presence of vegetated habitats; meanwhile, in the treatment with native piscivorous fish, the survival of invertebrates was similar regardless of vegetated habitat availability. Furthermore, without vegetation, a non-significant tendency towards higher invertebrate survival with non-native *versus* native piscivorous was uncovered. On the other hand, in the vegetation treatments, a non-significant tendency towards higher invertebrate survival with native *versus* non-native piscivorous was found. The tendency of invertebrate survival to be lower with than without vegetation is an unexpected result because the structural complexity generated by plants is supposed to reduce the visual range and manoeuvrability of predators, decreasing their effectiveness (Werner et al. 1983; Figueiredo et al. 2015a). We attributed this unexpected result to two independent events: (i) the increase in invertebrate concentration in vegetated habitats (Meerhoff et al. 2007) and (ii) the mesopredator inability to properly respond to a new predator (Sneddon et al. 2003). Several invertebrate species use macrophytes to avoid predators, which leads to higher invertebrate densities in these refuges (Thomaz et al. 2008; Cunha et al. 2012). If mesopredator shoal members increased their swimming activity to avoid being eaten by an active new predator (McPeek et al. 1996), then they could also enter vegetated habitats more frequently. In this scenario, mesopredators could find and eat hidden invertebrates more easily because after being detected, the small invertebrates require a short time to be captured and swallowed (i.e., handling time is short) (Kislalioglu and Gibson 1976). Therefore, the role of the macrophyte refuge as protection for invertebrates may be context specific (Meerhoff et al. 2006; Santos et al. 2013) and depend on indirect interactions with top predators.

Our findings indicate that piscivorous fish identity also determined the type of basal prey that was more vulnerable to mesopredator strikes. Mesopredators randomly ingested pelagic and benthic prey in treatments without piscivorous fish and with the non-native piscivorous fish, whereas they tended to select the pelagic prey in the presence of the native piscivorous fish (the high variation in the treatments without vegetated habitat led to a non-significant selection by the mesopredator). Mesopredators may forage more efficiently in the presence of native piscivorous fish (naïveté hypothesis; Cox and Lima 2006). If so, it is likely that in the treatments with the more sedentary native piscivorous fish, the mesopredator was able to avoid the bottom of the experimental units, where both the piscivorous fish and *C. sancticaroli* were usually located (authors' observation during the experiments). As a response to the co-occurrence of benthic prey and native piscivorous fish, mesopredator individuals could have focused their foraging on pelagic prey, offsetting the reduction in prey availability (Stuart-Smith et al. 2007; Figueiredo et al. 2015a). In contrast, when the more active non-native piscivorous fish is present, the mesopredator may show an unceasing swimming activity, leading to an environment where the basal prey is more homogenous in terms of predation vulnerability. In this situation, the constant movement of the studied non-native piscivorous fish (authors' observation in the field and in experiments) can generate an intense movement response by the mesopredator shoal, leading the shoal members to find and ingest both available prey indistinctly. Therefore, randomness in prey finding becomes the main factor underlying prey choice, which explains (i) the absence of prey preference and (ii) the huge variability in prey selectivity pattern uncovered in the presence of the non-native piscivorous fish.

Prey-shifting processes mediated by the introduction of a piscivorous fish may have important consequences in natural aquatic ecosystems because it affects the relative importance of the pelagic and benthic compartments as the main pathways of energy (Figure 3). Without predation threat, different mesopredator shoals (in distinct experimental units) ingested proportional amounts of the two prey types in both vegetated and unvegetated habitats. The absence of preferential prey was also observed in the presence of the non-native top predator. However, in this latter case, there was high variability in the proportion of prey types eaten by mesopredator shoals. These results may indicate that when non-native top predators are present, the selection for one invertebrate type becomes contingent. The active behaviour response of the mesopredators to the presence of the non-native top predator may have caused the random prey selection. For example, if mesopredator shoal members increase their swimming activity to avoid being eaten by an active new predator (McPeek et al. 1996), then they also would enhance the size of the explored area, improving the encounter rate with a potential prey (a behaviour observed for other tropical characid fish *Moenkhausia forestii* Benine, Mariguela and Oliveira, 2009 – Characiformes: Characidae) (Figueiredo et al. 2016). We suggest that after the introduction of a piscivorous fish, factors such as individual behaviour (e.g., shy/boldness of fish – Chapman et al. 2010) or even randomness of finding a prey type (Gal et al. 2015) may become more important to determining the outcomes of a predator-prey interaction.

An unbalanced strategy between foraging activity and hiding behaviour (e.g., caused by exposure to a new predator) may compromise the nutritional balance of the fish and, consequently, their fitness if the situation lasts over an extended period (Lima and Dill 1990; Chapman et al. 2010). Our findings indicate that *A. lacustris* can have similar predation rates in the presence of a native and non-native piscivorous fish, despite the differences in diet composition. Therefore, the flexibility in the feeding behaviour observed in omnivorous mesopredators, such as *A. lacustris*, together with efficient predator avoidance behaviour might attenuate the non-lethal effects caused by the introduction of a predator fish. However, similar behavioural adjustments to a novel

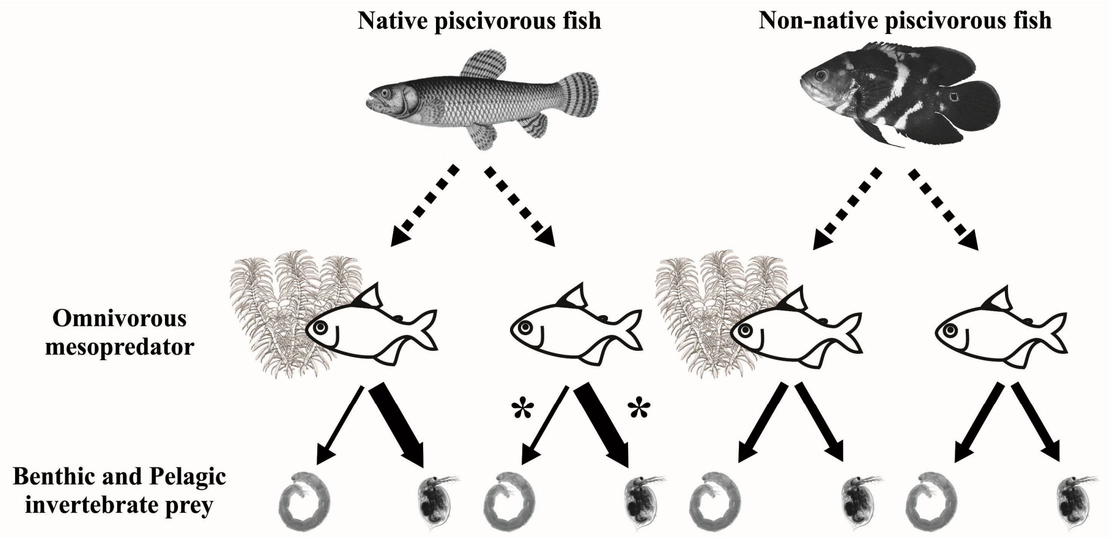

Figure 3. Conceptual model of the trophic cascades highlighting the non-lethal effects from the presence of native (*Hoplias* aff. *malabaricus*) and non-native piscivorous fish (*Astronotus crassipinnis*) on prey selection by an omnivorous mesopredator and the survival of aquatic invertebrates. *Full lines* indicate the lethal effects while *dashed lines* indicate the non-lethal effects. Line widths indicate the intensity of predation pressure (supported by our data) on aquatic invertebrates. Illustrations of aquatic plants denoted the treatments with vegetated habitat available. The invertebrate types selected in the treatment without predators showed a similar pattern to those found in the treatment with the non-native piscivorous fish. Asterisks denote non-significant tendencies.

top predator should not be expected for specialist mesopredator species (i.e., species that are able to live in a narrow range of environmental conditions or have a limited diet). As specialist mesopredators (e.g., zooplanktivorous and bottom-feeder species) have a limited capacity to shift their diet, the co-occurrence between their prey and an unknown top predator might cause long periods of starvation, diminishing their growth and reproductive potential (Lima 1998; Rudman et al. 2016).

In summary, our results demonstrate that the non-lethal effects of piscivorous fish may cause cascade effects on aquatic food chains. Our results also indicate that the invasion of *A. crassipinnis* has the potential to change the feeding selectivity of the mesopredator from a diet based on pelagic prey with the native *H.* aff. *malabaricus* to the random consumption of pelagic and benthic prey. This homogenisation of interaction strength may have important consequences for the stability of aquatic food webs (Rooney et al. 2006; McCann and Rooney 2009), and it deserves further investigation. Furthermore, this result corroborates with a recent view, usually referred to as the “Ecology of Fear,” which purports that non-lethal effects of predators may have strong consequences for population dynamics, species diversity and ecosystem processes (Ripple and Beschta 2004). Experimental studies such as ours are a powerful, easy and affordable approach to inferring how powerful non-lethal effects can be. They may be especially important for comprehending how significant non-lethal effects are for native prey after the introduction of non-native predators. A future challenge is confirming whether the non-lethal effects caused by non-native species can generate cascade effects on natural aquatic ecosystems as trophic cascade effects are supposed to be more prone to occur in simple low-diversity environments, such as mesocosms (Strong 1992; Polis and Strong 1996). Although demanding, the contribution of non-lethal effects of non-native predators can be isolated from their lethal effects and quantified in the field (e.g., Pangle et al. 2007), especially in regions extensively studied, such as the upper Paraná River basin (Agostinho et al. 2007). It is noteworthy that our results were obtained in a mesocosm with high water transparency to mimic the current conditions of the upper Paraná River basin (Stevaux et al. 2009), which may intensify the importance of the non-lethal effects of top predators (Figueiredo et al. 2016). In addition, our findings are based on the non-lethal effects of top predators on the food chain, and lethal effects may be more aggressive and deserve attention in further studies. Thus, we encourage future experiments to verify the lethal and non-lethal effects of top predators with different origins on food webs comprising omnivorous and specialist mesopredators.

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