

Facilitation underpinning the success of the non-native catfish *Hoplosternum littorale* (Callichthyidae) in lakes of the Middle Doce River Basin, southeastern Brazil

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Abstract

Facilitation is defined as an interaction between two or more species, which benefits at least one of them and causes harm to neither. The establishment of non-native species in new areas is a global phenomenon that raises the question of how facilitation may help in successful biological invasions. We describe a possible facilitation process between the catfish *Hoplosternum littorale* (Tamboatá) and its predators: *Pygocentrus nattereri* (pirunha) and *Cichla cf kelberi* (tucunaré), all non-native fish that live in the lakes of the Middle Doce River Basin, southeastern Brazil. We found evidence of indirect facilitation, where non-native predators probably release *H. littorale* from competition, as they prefer to prey on native fish. Our main evidence in favor of this interpretation was a difference in the abundance of *H. littorale* between lakes where these species co-occur and lakes where *H. littorale* is the only non-native fish species. This difference was not associated with environmental differences between lakes or spatial segregation of age classes of *H. littorale*. Differences in peak activity among *H. littorale* and non-native predators are probably the main driver of co-occurrence.

Keywords: biological invasion, tropical lakes, fish, non-native species

Introduction

Ecology has been heavily influenced by ideas and theories related to interspecific competition, competitive exclusion, and niche and species packing, and there has been much less emphasis on mutualism and facilitation (Bruno *et al.* 2003). Studies on positive interactions are comparatively modest, and so is our knowledge of this phenomenon (Callaway 1995; 1997; Stachowicz 2001; Bruno *et al.* 2003).

Facilitation or positive interactions are encounters between organisms that benefit at

least one of them and cause harm to neither (Bruno *et al.* 2003). It may be considered a type of mutualism that can occur between native species, native species and non-native species, or non-native species (Richardson *et al.* 2000). This mechanism may occur in two different forms: (i) direct facilitation, when a species alters the environmental conditions to favor another species (e.g., reduction in temperature and wind incidence, increase in pollination rate or propagule dispersal rate); or (ii) indirect facilitation, which occurs when there is a positive indirect effect of one species on

another (e.g., reduction in predation pressure, increased opportunities for competition refuge, reduced competitor populations) (Levine 1999; Richardson et al. 2000; Stachowicz 2001).

New interactions between species in natural ecosystems stemming from the colonization of non-native species constitute real threats to native ecosystems worldwide (Vitousek et al. 1997; Mack et al. 2000; Clavero & García Bertou 2005) and drive global biodiversity toward homogenization (McKinney & Lockwood 1999; Olden 2006). To date, the best studied causes of biodiversity decline due to the invasion of non-native species are competition and predation (Barel et al. 1985; Baltz & Moyle 1993; Lodge 1993; Richardson et al. 1995; Johnson & Padilla 1996; Kitchell et al. 1997), but positive interactions among non-native species are an important factor in invasion processes (Simberloff & Von Holle 1999; Bruno et al. 2003; O'Dowd et al. 2003; Grosholz 2005; Green et al. 2011).

In Brazil, the lake system of the Middle Doce River Basin is well-suited for studying the effects of non-native fish establishment and facilitation on other non-native species. The region has approximately 140 natural lakes, and non-native fish have been introduced into these lakes in the 1970s (Sunaga & Verani 1985). Among seven non-native fish already established, stand out the red piranha *Pygocentrus nattereri* (Kner 1858) and the peacock bass *Cichla* cf. *kelberi* (Latini et al. 2004). The predatory behavior of these two fishes, which places them at top positions in the food webs of local lakes, as well as their parental care behavior, may explain their successful colonization of these lakes (Latini & Petrere Jr. 2004). The other five non-native species are the oscar *Astronotus ocellatus* (Agassiz, 1831), the African catfish *Clarias gariepinus* (Burchell, 1822), the Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758), the tambaqui *Colossoma macropomum* (Curvier, 1818), and the tamboatá *Hoplosternum littorale* (Hancock, 1828).

Hoplosternum littorale is a common catfish in most Cis-Andean South American river systems draining the northern region of Buenos

Aires (Froese & Pauly 2004; Berra 2007). This species does not occur naturally in the basins of Eastern Brazil (Oliveira & Moraes Júnior 1997) and was introduced in the 1990s after the introductions of *P. nattereri* and *C. kelberi* (Latini et al. 2004), probably as a bait for fishing in the Lakes District of the Rio Doce Basin (Latini et al. 2004). *Hoplosternum littorale* is a benthic species that preys on invertebrates and has a broad diet (Hahn et al. 1997; Froese & Pauly 2004). Its reproductive behavior includes the construction and guarding of a floating nest by males: the floating nest protects eggs and larvae against opportunistic predators. The male guarding behavior discourages intruders and larger predators (Hostache & Mol 1998; Nico & Muench 2004). In these lakes, *H. littorale* is either the only non-native species in a given lake, or it co-occurs with other non-native fish, such as *P. nattereri* and *C. kelberi* (Latini et al. 2004). In all cases, *H. littorale* only became established after the establishment of *P. nattereri* and *C. kelberi*. Although there are no studies on the negative impacts of *H. littorale* on native fish, field experiments in Florida (USA) have suggested that introduced *H. littorale* alter the structure of macroinvertebrate assemblages (Duxbury et al. 2010).

The previous colonization by non-native fish has reduced the abundance of native species and modified the assemblage structure (α and β diversity) of those lakes (Latini & Petrere Jr. 2004; Giacomini et al. 2011). As the lakes of the studied system have few native predators, we expected lakes with non-native predators to show a strong reduction in native fish diversity (Giacomini et al. 2011) and in the abundance of native competitors of *H. littorale* (i.e., species that feed on invertebrates). We expected reduced antagonistic pressure on *H. littorale* and thus less biotic resistance to its colonization (e.g., space free of competitors), thus we tested the hypothesis that colonization by *H. littorale* is facilitated by the prior establishment of non-native fish. Our predictions were as follows: (i) the abundance and biomass of *H. littorale* are higher in lakes where it co-occurs with *P. nattereri* or *C. kelberi* than in lakes where *H. littorale* is the unique non-native fish; (ii) *H. littorale* populations co-

occurring with *P. nattereri* and *C. kelberi* have higher condition factor, (iii) diet breadth is wider in *H. littorale* populations that co-occur with *P. nattereri* and *C. kelberi*.

Material and Methods

Study area

The Rio Doce Basin is located in southeastern Brazil and drains an area of approximately 83,500 km² (ANA 2013). Its middle portion consists of natural lake systems containing about 140 lakes formed approximately 4,000 to 10,000 years ago through tributary impoundment of the main river (Tundisi & De Meis 1985). This study was conducted at the Dionisio District (meridians 42°38'W and 48°28'W and parallels 19°41'S and 19°30'S) in the state of Minas Gerais, Brazil. The altitude varies between 236 and 515 m above sea level, and the climate is tropical with rainy summer (Nimer 1989). This region is near the Rio Doce State Park, an important protected area of the Atlantic Forest, one of the world's biodiversity hotspots (Myers et al. 2000).

Twenty-four lakes are located in areas owned by Companhia Agrícola Florestal Santa Barbara (CAF). For this study, we selected six lakes in CAF, which were sampled bimonthly between July 2002 and May 2003, and collected six samples from each lake. Lakes were divided into two groups: (1) where *H. littorale* was the only non-native fish species (Group I, formed by Poço Redondo, Romoalda, and Timburé Lakes), and (2) where *H. littorale* co-occurs with *P. nattereri* and *C. kelberi* (Group II, formed by Águas Claras, Ariranha, and Palmeirinha Lakes). A map of the studied area, including all studied lakes, is presented in Figure 1.

Fish sampling

Bimonthly sampling was carried out from July 2002 to May 2003 (a total of 6 samplings, except for Palmeirinha Lake, with only five because the gillnets were stolen). Sampling involved the use of six gillnets, each with a different mesh size (15, 20, 30, 40, 50, and 60 mm between adjacent knots). The six different gillnets represented a set. For each sample at each lake, we used three sets, totaling

18 gillnets per lake (three sets x six mesh size). All the gillnets were 1.6 m in height and 10 m long, except the 60 mm mesh gillnet, which was 2 m in height and 20 m long. Gillnets were deployed near the margin that included different habitat physiognomies, which consequently ensured a representative sample of the environmental heterogeneity. Moreover, nets were deployed for three hours, covering the peak activity of fish, which occurs at approximately 18:00 h (Sunaga & Verani 1985).

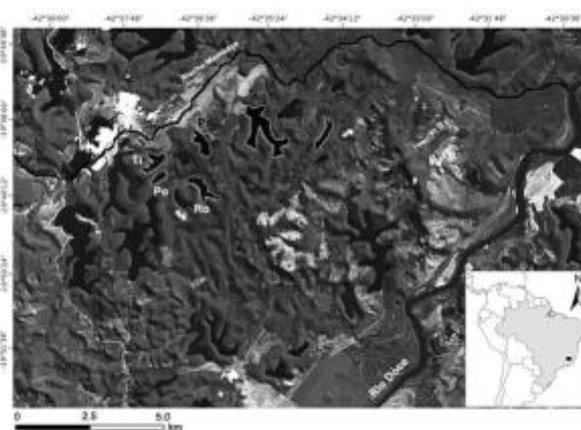


Figure 1 – Satellite image of the study area. In the bottom right, the location of the study region in South America. The studied lakes are numbered in the figure as Group I (Ti – Timburé; Po – Poço Redondo, and Ro – Romoalda) in white, where the catfish *H. littorale* is the only non-native fish species, and Group II (Pa – Palmeirinha, Ag – Águas Claras, and Ar – Ariranha) in black, where *H. littorale* co-occurs with *P. nattereri* and/or *C. kelberi*.

Gillnets were set between 16:00 h and 19:00 h (dusk), totaling 3 daily hours of sampling and a total effort of 160 m²h⁻¹ [(5 gillnets x 10 m x 1.6 m x 3 sets / 3 h) + (1 gillnet x 20 m x 2 m x 3 sets / 3 h)] per sample, and a sampling effort of 960 m²h⁻¹ for all six samples (160 m²h⁻¹ per each sample x 6 samples). We collected only five samples in Palmeirinha Lake, with a total sampling effort of 800 m²h⁻¹. Our total sampling effort was 5600 m²h⁻¹.

Diet analysis

All fish sampled were put in water with ice and later fixed in 10% formalin. Total length and weight were measured in the laboratory of

Parque Estadual do Rio Doce. For the diet analysis, we randomly selected 410 individuals, including 41 of *H. littorale*. Each individual was gutted, and the contents were identified and counted using a stereoscopic microscope. All items were weighted (g) using a precision balance. All analyses were performed at the Laboratory of Museu Zoologia João Moojen, at the Universidade Federal de Viçosa, MG, Brazil.

Environmental variables

Differences in the structure and composition between the local assemblages can be the result of local environmental conditions. Therefore, we assessed four environmental variables: the lake area (ha) and lake perimeter (m), both measured using GIS and remote sensing image processing system called Spring (available on: <http://www.dpi.inpe.br/spring/english/>) and a satellite image of the study region; and oxygen concentration (mgL^{-1}) and water turbidity (ntu – nephelometric turbidity units) obtained using specific electronic portable equipment.

Statistical analysis

We used a repeated measures ANOVA (Zar 1999) to test differences in abundance and biomass of *H. littorale* populations in the lakes where was the only non-native fish species (Group I) and compared to lakes where co-occurred with *P. nattereri* or *C. kelberi* (Group II) and the control temporal effects. In this analysis, the total abundance and biomass of *H. littorale* in each lake at each sampling were the dependent variables, and the lake group was the independent variable with two levels (with and without *P. nattereri* and *C. kelberi*). The homogeneity of variance was tested; and whenever necessary, we used log transformation to meet the assumptions required for the use of parametric statistics.

The condition factor is an estimator of the physiological status of fish and the relative well-being of fish populations (Bolger & Connolly 1989; Pope & Kruse 2007). We estimated the alpha and beta parameters by fitting linear regressions between logarithmic transformations of the standard length and

weight (continuous predictor) to assess whether the *H. littorale* populations between the lake groups (categorical predictor) show differences in their condition factor. We then checked for differences in the condition factor between the lake groups using an ANCOVA (Zar 1999).

We used the Smith's measure (Smith 1982) to obtain the *H. littorale* diet breadth in the two groups:

$$FT = \sum_{i=1}^R (\sqrt{p_j a_j})$$
, where FT is the Smith's measure of diet breadth, p_j is the proportion of individuals found in or using resource state j , a_j is the fraction of total resources constituted by resource j (expressed in weight), and R is the total number of possible resource states.

We used a 95% confidence interval, as suggested by Krebs (1999), to compare the *H. littorale* diet breadth between the two groups:

$$CI_{95\%} = \sin \left[x \pm \frac{1.96}{2\sqrt{y}} \right]$$
, where x is the arcsine (FT) and y is the total number of individuals studied ($\sum N_j$). Ontogenetic development is an important factor that influences the diet of fish (Gerking 1994). Therefore, we performed a t -test to assess whether the *H. littorale* individuals used for the diet characterization have different body sizes (standard length) between the groups of lakes. Lastly, we tested whether the environmental conditions were different between the lake groups using a non-parametric multivariate analysis of variance (MANOVA) (Anderson 2001). For all the statistical tests, the significance level was set at $\alpha=0.05$, and the statistical analyses were performed in the software R (R Development Core Team 2008).

Results

We sampled 893 individuals belonging to 18 fish species, with a total biomass of 103.37 kg. The abundance and biomass of *Hoplosternum littorale* was 125 individuals and 14.145 kg, respectively, showing no homogeneity of variance (Levene's test: $p<0.05$). Thus, data were log transformed. We removed sampling months was heteroscedastic from our dataset which corresponded to *H. littorale* biomass in the first sample and *H. littorale* abundance in the fourth sample. Only

one individual of *H. littorale* was sampled in abundance of non-native and native fish
 Águas Claras Lake during our study; then we sampled in the lakes.
 decided to remove this lake from our analysis.
 Table 1 shows the values of biomass and

Table 1 – Fish species sampled in six lakes of the middle Doce River Lake system in Dionisio District, Minas Gerais State, southeastern Brazil. We used gillnets to sample fish bimonthly from July 2002 through May 2003. Body size range (standard length), total abundance, and biomass (kg) are presented. Non-native species are identified by an X.

Species	Non-native	Standard length (cm)	Sample size	Total fish biomass
Order Characiformes				
Family Anostomidae				
<i>Leporinus steindachneri</i> Eigenmann, 1907		8.6-34.0	44	7.191
Family Characidae				
<i>Astyanax</i> sp.		4.5-14.0	168	2.315
<i>Moenkhausia doceana</i> (Steindachner, 1877)		5.0-8.6	15	0.128
<i>Oligosarcus solitarius</i> Menezes, 1987		8.2-19	115	2.620
<i>Pygocentrus nattereri</i> Kner, 1858	X	7.5-23.5	110	15.950
Family Curimatidae				
<i>Cyphocharax gilbert</i> (Quoy & Gaimard, 1824)		6.8-18.0	47	2.598
Family Erythrinidae				
<i>Hoplias malabaricus</i> (Bloch, 1794)		10.5-37.0	115	23.450
Family Prochilodontidae				
<i>Prochilodus vimboides</i> Kner, 1859		7.5-41.0	58	23.380
Order Siluriformes				
Family Auchenipteridae				
<i>Trachelyopterus striatulus</i> (Steindachner, 1877)		10.0-19.7	26	2.396
Family Callichthyidae				
<i>Hoplosternum littorale</i> (Hancock, 1828)	X	9-4-19.7	125	14.145
Family Clariidae				
<i>Clarias gariepinus</i> (Burchell, 1822)	X	30.5-55.0	3	3.165
Order Gymnotiformes				
Family Gymnotidae				
<i>Gymnotus carapo</i> Linnaeus, 1758		6.2-31.0	9	0.854
Order Perciformes				
Family Cichlidae				
<i>Astronotus ocellatus</i> (Agassiz, 1831)	X	13.5	1	0.15
<i>Cichla kelberi</i> Kullander & Ferreira, 2006	X	14.5-37.5	8	2.175
<i>Crenicichla lacustris</i> (Castelnau, 1855)		11.3-22.0	5	0.489
<i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)		5.4-18.0	28	1.993
Family Sciaenidae				
<i>Pachyurus adspersus</i> Steindachner, 1879		21.5-22.5	2	0.405
Order Clupeiformes				
Family Engraulidae				
<i>Lycengraulis</i> sp.		6.5-15.0	13	0.115

Hoplosternum littorale biomass was greater in the Group II ($F=41.192$; $df=1$; $p=0.023$, Figure 2) and not affected by time ($F=0.583$; $df=4$; $p=0.683$) or by interactions between the groups of lakes and time ($F=0.130$; $df=4$; $p=0.966$). In Group II, we also found higher abundances of *H. littorale* ($F=28.029$; $df=1$; $p=0.013$, Figure 3). Again, the effect of time was not significant ($F=1.345$; $df=4$; $p=0.309$) as well as the interaction between the lake group and time ($F=0.215$; $df=4$; $p=0.354$). The condition factor of the two groups of lakes were not significantly different ($F=1.3$; $df=1$; $p=0.25$). Figure 4 illustrates the relationship between the logarithm of weight (Log W (g)) and logarithm of standard length (Log SL(cm)) in the Groups I and II lakes.

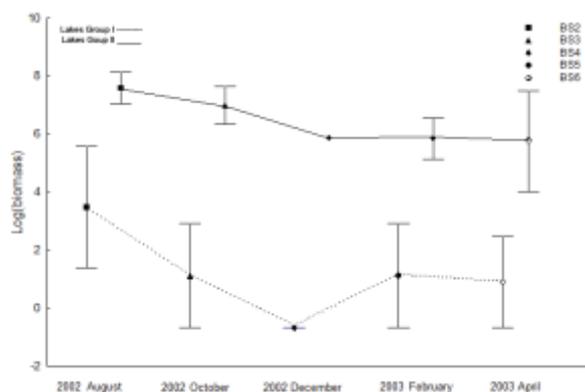


Figure 2 – Average biomass of the catfish *Hoplosternum littorale* (Log (g)/lake) from the two groups of lakes. In Group I, *H. littorale* is the only non-native fish ($N=5$); in Group II, *H. littorale* co-occurs with *P. nattereri* and *C. kelberi* ($N=5$). The intervals represent the standard error of the mean. BS indicates the bimonthly sampling.

A total of 34 (83%) out of 41 *H. littorale* guts examined contained some measurable content, indicating the high feeding activity of this species in the lakes under study. In the absence of *P. nattereri* and *C. kelberi* (Group I), *H. littorale* used five different food resources (including one unidentified; Figure 5A), whereas the number of food items increased to ten (including unidentified items; Figure 5B) in the presence of these species (Group II). Smith's measure of the diet breadth of *H. littorale* was also high in the Group II (Figure 6). These individuals presented a body size of

about 15 cm, whose standard length values were not significantly different between the groups of lakes ($t=-0.66$; $df=40$; $p=0.50$). Therefore, we can reject any effect of ontogenetic development on the diet of *H. littorale* between lake groups. Lastly, no differences in environmental conditions were found between lake groups ($F=1.127$; $p=0.40$).

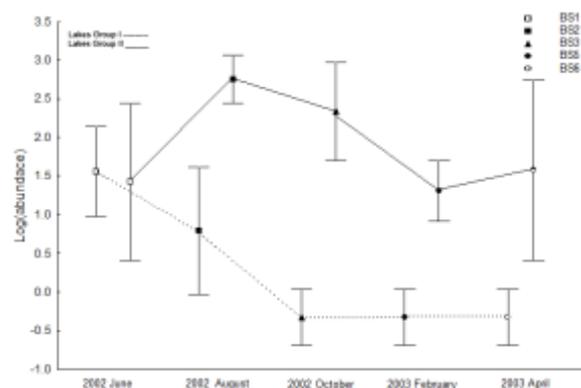


Figure 3 – Average abundance (Log abundance) of the catfish *H. littorale* in the two groups of lakes. In Group I, *H. littorale* is the only non-native fish ($N=5$); in Group II, *H. littorale* co-occurs with *P. nattereri* and *C. kelberi* ($N=5$). The intervals represent the standard error of the mean. BS indicates the bimonthly sampling.

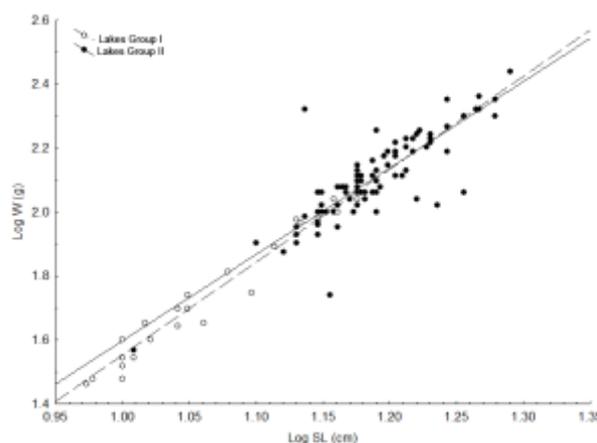


Figure 4 – Relationship between the logarithm of weight (Log W (g)) and logarithm of standard length (Log SL(cm)). The Group I lakes: (Log W(g) = $-1.3539+2.9067*x$; $R^2=0.95$; $n=30$), open circles, where the catfish *H. littorale* is the only non-native fish present. The Group II lakes: (Log W(g) = $-1.1076+2.7047*x$; $R^2=0.86$; $n=95$), black circles, where *H. littorale* co-occurs with *P. nattereri* and *C. kelberi*.

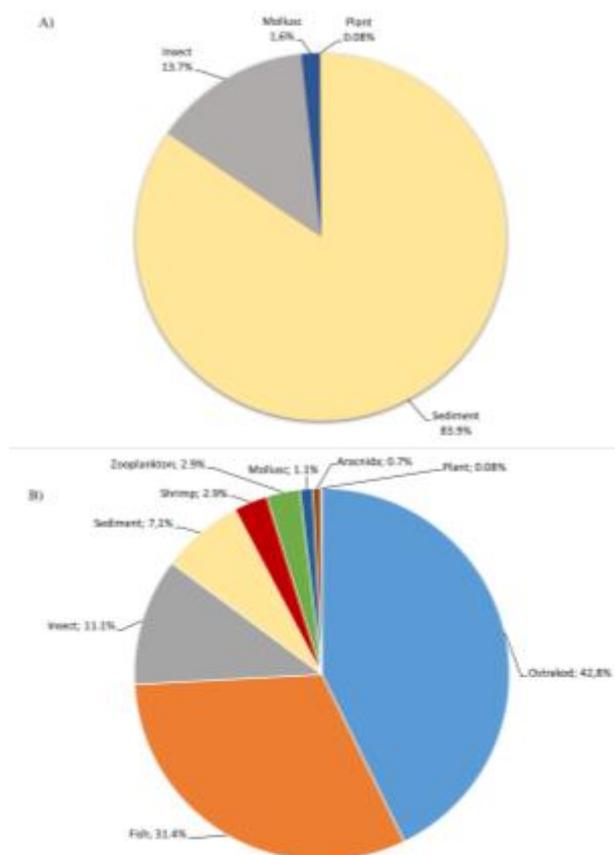


Figure 5 – Gut contents of the catfish *H. littorale* in the Group I lakes (Figure 5A, N=10) and Group II lakes (Figure 5B, N=31). Each specific item is followed by the mass percentage of the item in the total mass.

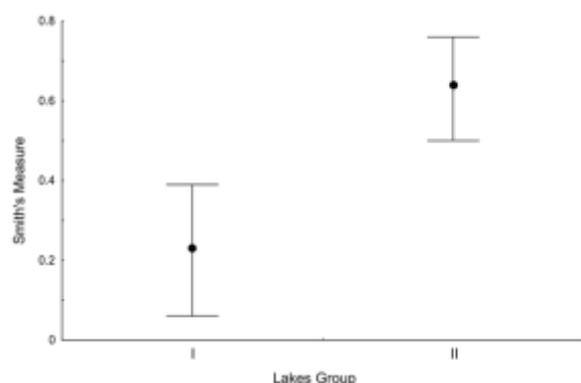


Figure 6 – Comparison between populations of the catfish *H. littorale* from lakes in Group I (N=10) or Group II (N=31) using the Smith metric of niche breadth. The point represents the Smith metric of niche breadth, and the interval around the metric is the 95% confidence interval. The lack of interval overlap indicates a significant difference between groups.

Discussion

Predation pressure by non-native species on native fish is the main driver of reduction in abundance and richness of native species and increase in the temporal variability in species composition in lakes (Latini et al. 2004; Giacomini et al. 2011). It may affect native fish assemblages and potentially provide resources to non-native fish, such as *H. littorale*. These effects may explain the higher abundance and biomass of *H. littorale* and the broader diet of this species in environments where it co-occurs with *P. nattereri* and *C. kelberi*. However, some issues need to be clarified. There is evidence that species of *Cichla* and *Pygocentrus* prey upon *H. littorale* in its native habitats (Nico & Taphorn 1988). Thus, it is possible that *C. kelberi* and *P. nattereri* are also preying on *H. littorale* in non-native habitats. Nevertheless, *H. littorale* remains were not found in gut contents of these predators in the studied lakes, which corroborates the hypothesis of facilitation.

There is a marked difference in *H. littorale* body size between lake groups (Figure 4); in other words, *H. littorale* individuals are smaller in lakes where this species is the only non-native fish. This result may indicate a possible spatial segregation between immature and mature sexual classes. Although we have not examined the reproductive biology of this species, we can assume that this type of segregation does not occur: (i) *Hoplosternum littorale* does not present reproductive migration, which can result in a spatial segregation between juvenile and adults; (ii) different studies have shown that *H. littorale* starts its reproductive period at about 8 cm standard length (Winemiller 1987; Hahn et al. 1997). All the individuals sampled in our study showed standard length above 10 cm. Therefore, it is plausible that the sampled individuals were adults.

Another explanation for the observed differences in body size between lake groups could be viewed as an antagonistic rather than facilitative process. Smaller species and/or individuals tend to suffer greater impacts of predation (Woodward & Hildrew 2002; Sinclair et al. 2003; Woodward et al. 2005) and are

frequently the first impacted by an introduced predator. In the same lakes, suggested a similar mechanism to explain a shift in the composition of native fish communities, from small native fish in non-invaded lakes to large native fish in invaded lakes (Giacomini *et al.* 2011). In this case, the non-native predator can select larger individuals of *H. littorale* via predator gap limitation. Conversely, differential survival does not explain why *H. littorale* is more abundant in lakes where it co-occurs with non-native predators; indeed, the opposite was expected.

If predation pressure from *P. nattereri* and *C. kelberi* are significant to the point where it reduces or excludes local native species (Latini & Petrere 2004), the question remains as to why it does not negatively affect *H. littorale* populations. First, *H. littorale* overlaps home range with *C. kelberi* and *P. nattereri* (Reis *et al.* 2003) and most likely already has mechanisms to avoid predation from these predator species. In contrast, native fish did not develop mechanisms to avoid predation, since predation by the congener species *C. kelberi* and *P. nattereri* did not occur in their evolutionary history. The native top predator in lakes of the current study area is *Hoplias malabaricus*, which is phylogenetically distant, morphologically dissimilar, and exhibits a different foraging behavior (ambush predator). Second, *P. nattereri* and *C. kelberi* are visually oriented, active predators that ambush their prey in daylight (Lowe-McConnell 1999). On the other hand, *H. littorale* displays a peak activity at night (Boujard *et al.* 1990; 1992; Hahn *et al.* 1997). Thus, it is probable that these differences in activity patterns may promote non-native co-occurrence. In fact, this behavior of *H. littorale* was reported as a strategy to avoid predation (Boujard *et al.* 1990). Furthermore, this strategy was also corroborated by the maintenance of native *H. malabaricus* in lakes where *P. nattereri* and *C. kelberi* are also present (Latini 2001); because both species are nocturnal (Machado 2003). At last, *H. littorale* exhibits parental care and aggressive behavior during its reproductive period (Winemiller 1987), and both biological characteristics impart success to the

establishment of non-native species (Holway & Suarez 1999; Drake 2007).

The studied lakes are very similar in environmental conditions and support similar fish communities (with the exception of invaded lakes). This finding was expected because the lakes have similar geological formation and are located in the same landscape (Sugio & Kohler 1992; Perônico & Castro 2008).

Other uncontrolled factor most likely influenced the system and contributed to the observed results. However, we think that indirect facilitation is a plausible mechanism responsible for the differences found in this study. Specifically, the presence of *C. kelberi* and *P. nattereri* caused negative impacts on the local communities, mainly with regard to small competitors of *H. littorale* and an increase in the temporal variability of the invaded communities (release of resources over time). With a decrease in the abundance of competitors, *H. littorale* was provided with access to additional feeding resources (as reflected in the different diet breadth). This increase in feeding resources is most likely reflected in its greater abundance and biomass in the lakes with co-occurrence of non-native predators.

Non-native invasions cause major ecological, social, and economical problems worldwide (USBC 1998; Pimentel *et al.* 2001), and detailed information is important for suggesting effective global control practices (Kolar & Lodge 2001; Marchetti *et al.* 2004) and different Brazilian ecosystems (Pelicice 2009; Zeni & Zillier 2011). Thus, despite earlier studied pointing out to facilitation among non-native species as important for biological invasions (Bruno *et al.* 2003), evidence found in our study suggest that facilitation may be occurring among non-native fish in the lakes of the Rio Doce Basin, which may intensify negative ecological impacts on the aquatic ecosystem. Potential mechanics responsible for positive interactions among non-native fish species should be further investigated in experimental studies.

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