**Diet and feeding ecology of non-native fishes in lentic and lotic freshwater habitats**

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**Abstract**

The Paranapanema River is most frequently invaded by non-native fish from the Upper Paraná River Freshwater Ecoregion. To understand how the diet of non-native fishes varies based on habitat type, we studied 12 populations of 6 non-native fish species with the aim of verifying whether diet, niche breadth, or trophic guild vary between lentic and lotic habitats. Fish were sampled in both habitats in the Paranapanema River basin between August 2014 and March 2016. A permutational multivariate analysis of variance – PERMANOVA was applied so that the composition of fish diet could be compared between habitats. Levin’s standardized index was used to evaluate the trophic niche breadth of the species, revealing differences in the diets of *Ossancora eigenmanni*, *Auchenipterus osteomystax* and *Trachelyopterus galeatus* based on habitats. Seven trophic guilds were identified, and those for *Serrasalmus marginatus*, *Loricariichthys platymetopon* and *T. galeatus* were the same (piscivores, detritivores, and omnivores, respectively) in both habitats. In contrast, the trophic guilds of *O. eigenmanni*, *A. osteomystax*, and *Plagioscion squamosissimus* varied between the habitats. Habitat-specific variability in the diet composition of the species and, for the most, the niche breadth in the lotic habitats increased; therefore, we conclude that this type of environment can provide access to a greater variety of food resources for non-native fishes.

**Key words:** allochthonous species, biological invasions, establishment, food resources, niche breadth, reservoir, upper Paraná river

**Introduction**

Invasive aquatic species have extended their distribution ranges in worldwide ecosystems as a result of barrier removal, canal construction, commercial and ornamental aquaculture, and human mobility (Leprieur et al. 2008; Gozlan et al. 2010; Seebens et al. 2017; Lima Junior et al. 2018). Aquatic invaders can disrupt ecosystem processes by reducing the abundance and diversity of native communities (Gallardo et al. 2016). Food web alterations can then occur because of influences on established trophic interactions in aquatic communities (Vitousek 1990; Shea and Chesson 2002; Gallardo et al. 2016). In addition to identifying the environmental, biological, and human factors responsible for the successful establishment of invasive species, it is important to discover features that are common among species and invaded areas (Shea and Chesson 2002).

Invasive fish species are particularly pervasive, causing food web disruption (Britton et al. 2010; Martin et al. 2010; Gallardo et al. 2016; Copp et al. 2017) and threatening biodiversity (Pelície e Agostinho 2009; Matsuzaki et al. 2016). However, food resources impact population fitness and define the permanence of non-native species (Zambrano et al. 2010). Furthermore, the spatial and temporal variability promoted by human activities (e.g., construction of dams) favors
non-native species with higher tolerances to changes in physicochemical characteristics and plasticity in life history traits (Marchetti et al. 2004; Gozlan et al. 2010).

Among the goals of biological invasion studies are predicting those environments most susceptible to invasion, defining species that will become invasive, and identifying factors that facilitate establishment (Marchetti et al. 2004; Fleming and Dibble 2015). Several factors are associated with the invasion success of a species. Among them are its life history characteristics, such as tolerance to environmental shifts (Moyle and Light 1996a), rapid growth (Graebner et al. 2012), reproductive investment (Lodge 1993; Simberloff and Rejmanek 2011), and feeding plasticity (Agostinho et al. 2015; Pander et al. 2016). In this context, improved knowledge of the feeding ecology of non-native fishes is needed to understand the invasion process (Moyle and Ellsworth 2004; Kornis et al. 2013) and to develop management strategies (García-Berthou 2007; Leuven et al. 2017). Therefore, it is important to describe the use of food resources under the influence of various environmental conditions so that habitats that are susceptible to species invasion can be identified, and information for controlling the spread of those species can be provided (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001; Sepulveda 2018).

Plasticity in life history traits is a feature of successful invaders; they can rapidly respond to new conditions (Gozlan et al. 2010). Some studies address fish escapes from aquaculture facilities, impacts on other species, or invasion success (Pelcice and Agostinho 2009; Vitule et al. 2009; Ortega et al. 2015; Xiong et al. 2015; Casimiro et al. 2018; Garcia et al. 2018). Other studies aim to understand the conditions that determine invasion success (Agostinho et al. 2015; Pazianoto et al. 2016; Casimiro et al. 2018; Franco et al. 2018; Tonella et al. 2018). The biology of Neotropical freshwater fishes comparing native and non-native ranges have been the focus of multiple other studies, including trophic ecology (Agostinho et al. 2015; Lima Junior et al. 2015; Tonella et al. 2018).

When a natural geographic barrier (Sete Quedas Falls) to movement of some fish species was flooded with the construction of the Itaipu Dam, a massive invasion of the Upper Paraná from the Lower Paraná basin resulted. After this event, more than 30 fish species colonized the Upper Paraná River floodplain and some of its tributaries (Júlio Júnior et al. 2009; Vitule et al. 2012). Some species became dominant (in terms of abundance) and have successfully invaded the new basin (Agostinho et al. 2004; Luiz et al. 2004; Bailly et al. 2011; Tonella et al. 2018).

Here, we describe diet composition, niche breadth, and trophic guild for six of these species based on samples from lentic and lotic habitats in the Paraná River watershed. The species chosen are typically the most abundant in the Upper Paraná River floodplain. In the invaded area, these species occur in multiple habitats that have differing hydro-geomorphological characteristics due to natural features and impacts promoted by dams. Environmental differences reflect food availability, and it is expected that the non-native fish populations will present different feeding behaviors. We tested the hypothesis that for specialist species, the diet will not vary as the resources consumed do not vary. The trophic niche breadth will be the same; however, for generalists, diet will be more variable in lotic habitats due to the incorporation of the allochthonous material that will increase the availability of feeding resources. Therefore, it is probable that lotic habitats with riparian vegetation on both margins may provide feeding resources that are more diverse.

Methods

Study area

The springs of the Paranapanema River are located in the Serra de Paranaípacity (southeastern Brazil) at 900 m altitude, flowing 930 km to the west before its confluence with the Paraná River (Figure 1). Originally, the Paranapanema River basin contained the Atlantic Rainforest and Brazilian Savannah biomes (hotspots) that have since been converted to agriculture and livestock uses.

This study was performed in two types of habitats in the Lower Paranapanema River basin: lentic (Lagoon 1 and Lagoon 2) and lotic (the Pirapozinho and Anhumas rivers, Figure 1, Supplementary material Table S1). The lagoons studied were formed after the Rosana Reservoir was filled in 1986. Lagoon 1 is located in the state of São Paulo and borders the Morro do Diabo State Park, whereas Lagoon 2 is located in the state of Paraná. The Pirapozinho and Anhumas rivers are located in the state of São Paulo and flow directly into the reservoirs of Rosana and Taquaruçu, respectively.

Sampling

Fishes were sampled quarterly from August 2014 to March 2016 by capturing with a seine (6.0 m², 0.5 cm mesh) and sieve (0.4 m², 0.5 cm mesh) over a time span of one hour by five people. Furthermore, 14 gillnets were used (2 to 14 cm meshes between opposing knots), 1,000 m² of net per site. Nets were placed near aquatic macrophytes, at sunset and removed the following morning, being exposed for approximately 12 hours. Fishes were anesthetized by

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immersion in a water solution of clove oil (Animal Ethics Committee of Universidade Estadual de Londrina n. 30992.2014.3). They were then fixed with 10% formalin buffered with calcium carbonate. In the laboratory, fishes were identified using specialized literature (Britski et al. 2007; Graça and Pavanelli 2007; Ota et al. 2018) and by specialists from the Museu de Zoologia of the Universidade Estadual de Londrina, then transferred to 70% ethanol.

A total of 290 individuals belonging to six successful non-native species were studied: *Serrasalmus margaritatus* Valenciennes, 1837 (Serrasalmidae; 27 individuals); *Loricariichthys platymetopon* Isbrücker and Nijsen, 1979 (Loricariidae; 51 individuals); *Ossancora eigenmanni* (Boulenger, 1895) (Doradidae; 26 individuals); *Auchenipterus osteomystax* (Miranda-Ribeiro, 1918) (Auchenipteridae; 27 individuals); *Trachelyopterus galetaus* Linnaeus, 1766 (Auchenipteridae; 98 individuals); and *Plagioscion squamosissimus* (Heckel, 1840) (Sciaenidae; 61 individuals). Stomachs were removed and deposited in 70% ethanol for additional analysis. The first quarter of the intestine of *L. platymetopon* was also used in the analysis.

**Data analysis**

Fish diets were determined by analyzing stomach contents through the use of stereoscopic and optical microscopes. Food items were identified to the lowest possible taxonomic level using specific identification keys. Dietary analysis was based on the volume of each food item (Hyslop 1980), obtained by displacing large items in water in a graduated cylinder (0.1 ml graduations) or small items on a glass millimeter plate (mm$^3$). The volume obtained (mm$^3$) was converted to milliliters when the volume was less than 0.1 ml (Hellawell and Abel 1971).

For each species, differences in dietary compositions between lentic and lotic habitats were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), which was applied to a matrix of food items per analyzed stomach. The Bray-Curtis distance was used as a measure of dissimilarity, and 9999 permutations were used to test the significance of the pseudo-$F$ statistic derived from PERMANOVA. Statistical analyses were conducted using the R Programming...

Trophic niche breadth was estimated for each species using Levin’s standardized index: $B_A = \frac{(B-1)}{(n-1)}$, where $B_A$ is Levin’s standardized index, $n$ is the number of items, and $B = \frac{1}{\sum_i p_i^2}$, where $B$ is the trophic niche breadth, and $p_i$ is the proportion of item $i$ in the diet (Krebs 1998). This calculates the evenness of distribution for any one item among the various food resources.

Trophic guilds were determined for each habitat because fishes can vary their feeding responses according to the environment. Trophic guilds were based on those described by Delariva et al. (2013) and adapted from Merona et al. (2001): detritivores: more than 50% detritus/sediment in the stomachs; planktivores: more than 50% plankton in the stomachs; terrestrial insectivores: more than 50% terrestrial insects in the stomachs; carcinophagous: more than 50% decapods (crab and shrimp) in the stomachs; invertivores: more than 50% others invertebrates in the stomachs; omnivores: none of the above but including items of animal and plant origins (leaf, flower, fruit, or seed of higher plants).

**Results**

**Diet composition**

The diets of *O. eigenmanni*, *A. osteomystax*, and *T. galeatus* differed between habitats (PERMANOVA, Pseudo-$F_{1,21} = 1.75$, $P = 0.042$; Pseudo-$F_{1,12} = 2.31$, $P = 0.004$; Pseudo-$F_{1,70} = 1.94$, $P = 0.005$, respectively), whereas those of *S. marginatus*, *L. platymetopon*, and *P. squamosissimus* did not (Pseudo-$F_{1,24} = 1.37$, $P = 0.205$; Pseudo-$F_{1,48} = 1.99$, $P = 0.100$; Pseudo-$F_{1,40} = 0.75$, $P = 0.602$, respectively). The diet of *O. eigenmanni* was composed predominantly of the Gastropoda, Ostracoda, Acari, and Trichoptera (larvae) in lentic habitats, but of Copepoda and Ostracoda with associated detritus (organic and inorganic) in lotic habitats (Figure 2, Table S2). Cladocera was the primary food item found in the stomachs of *A. osteomystax* in lentic habitats, but Coleoptera and other terrestrial insects dominated in lotic areas. Coleoptera and plant materials were predominant in diet of *T. galeatus* in lentic habitats, whereas plant materials (> 45% by volume), and the Decapoda, Aranae, terrestrial insects, and Orthoptera were dominant in lotic habitats.

The diet of *S. marginatus* was composed primarily of fish in both lentic and lotic habitats (Figure 2, Table S2). *Loricariichthys platymetopon* primarily fed on organic detritus (volume ~ 80%) in both habitats. The diet of *P. squamosissimus* was composed primarily of the Decapoda and fish in both habitats.

**Trophic niche breadth**

Wider niche breadths were verified for *A. osteomystax*, *S. marginatus*, *L. platymetopon*, and *P. squamosissimus* in lotic habitats, where the greatest richness and evenness of food items was found (Figure 2, Table S2). On the other hand, *O. eigenmannii* and *T. galeatus* demonstrated wider niche breadths in lentic habitats.

**Trophic guild**

Fish exhibited seven trophic guilds (Figure 2, Table S2). *Serrasalmus marginatus* (piscivore), *L. platymetopon* (detritivore), and *T. galeatus* (omniivore) maintained their feeding habits in both types of habitats. In contrast, there was a clear shift in *O. eigenmanni*, which was invertivorous and planktivorous in lentic and lotic habitats, respectively, in *A. osteomystax*, which was planktivorous in lentic habitats and terrestrial insectivorous in lotic habitats, and in *P. squamosissimus*, which presented the carcinophagous habit in lentic habitats and the piscivorous habit in lotic habitats (Figure 2, Table S2).

**Discussion**

Non-native species invade new areas once they overcome environmental barriers and become established (Colautti and Maclsaac 2004; Blackburn et al. 2011). The specialists *S. marginatus* (piscivorous) and *L. platymetopon* (detritivorous), and omnivorous *T. galeatus* are among the most abundant species in various biotopes of the Upper Paraná River floodplain (Agostinho et al. 2004; Luiz et al. 2004; Bailly et al. 2011), because they have feeding plasticity, and the environment provides greater availability of food resources (Tonella et al. 2018). In this study, these species maintained the same trophic guilds in lentic and lotic habitats. The ability to maintain large populations through the same food resource ingestion provides invasion success (Gido and Franssen 2007). In contrast, *O. eigenmanni*, *A. osteomystax*, and *P. squamosissimus* (generalist species) differed their trophic guilds in both habitats. These populations showed opportunistic diets, and most of them showed wider trophic niche breadth in lotic habitats. *Auchenipterus osteomystax*, for example, the wider trophic niche breadth in lotic habitats can be attributed to the greater availability of allochthonous resources in this environment. It is noteworthy that organisms...
Diet and feeding ecology of non-native fishes

Figure 2. Diet composition (% volume) of non-native fishes sampled in lentic and lotic habitats of the Paranapanema River basin, southern Brazil: *Serrasalmus marginatus* (A), *Loricariichthys platymetopon* (B), *Ossancora eigenmanni* (C), *Auchenipterus osteomystax* (D), *Trachelyopterus galeatus* (E), and *Plagioscion squamosissimus* (F). Cla = Cladocera; Cra = Crab; Shr = Shrimp; Cop = Copepoda; Ost = Ostracoda; Aca = Acari; Ara = Aranae; EpN = Ephemeroptera (nymph); EpA = Ephemeroptera (adult); OdN = Odonata (nymph); OdA = Odonata (adult); Ort = Orthoptera; Hom = Homoptera; Col = Coleoptera; Dip = Diptera; TrL = Trichoptera (larvae); Hym = Hymenoptera; Aqi = Aquatic insect; Tei = Terrestrial insect; Gas = Gastropoda; Fis = Fish; Pla = Plant material; Alg = Algae; Ode = Organic detritus; Ide = Inorganic detritus/sediment.

with hard parts may be over-represented compared to soft-bodied organisms that may digest faster.

The successful establishment of *S. marginatus* into the Upper Paraná River basin can be attributed to its behavioral and reproductive aspects (Agostinho 2003; Agostinho et al. 2004). The aggressive territorial behavior might be the reason for declines in populations of the native congener *Serrasalmus maculatus* Kner, 1858 in the Upper Paraná River basin (Agostinho and Júlio Júnior 2000; Agostinho 2003). The piscivorous habit of *S. marginatus* may also have facilitated the establishment (Pereira et al. 2016; Tonella et al. 2018). In this floodplain, a coexistence between the native *S. maculatus* and the non-native *S. marginatus* was created by trophic niche segregation (Alves et al. 2017). In this study, the species in lentic habitats showed high propensity (volume ~ 90%) to feed on fish, probably juveniles and small fish inhabiting the lagoons of the Lower Paranapanema River (Casatti et al. 2003). The highest trophic breadth in lotic habitats may be due to the greater consumption of plant material. This consumption
may occur due to accidental ingestion when catching fish that live close to aquatic macrophytes and riparian vegetation present in the both margins.

Detritivory is one of the most specialized fish trophic habits (Gerking 1994), possibly explaining why the diets were similar between the habitats used by _L. platymetopon_. The dominance of detritus and sediment in the diet of _L. platymetopon_ contributed to its low trophic niche breadth. However, species that feed at low levels in the food web tend to become integrated into the community (Gido and Franssen 2007) because detritus is rarely limited in aquatic environments (Moyle and Light 1996a; Winemiller and Kelso-Winemiller 2003). Therefore, detritivory is considered a useful food strategy for invasive species (Gido and Franssen 2007; Agostinho et al. 2015; Liew et al. 2016; Pazianoto et al. 2016). Furthermore, the environments studied are located in stretches of the Paraná River, whose dynamics includes periods of flooding and entry of this resource into the system.

_Ossancora eigenmanni_ showed an opportunistic habit in invertebrates in lentic habitats and in plankton (Copepoda and Ostracoda) with associated detritus in lotic habitats. The invertivorous habit adopted in lentic habitats resulted from the abundance of this resource in lagoon bottoms and morphological adaptations for feeding on benthic organisms. Its mouth is terminal with dentigerous plaques in both jaws (Graça and Pavanelli 2007). In lotic habitats, greater consumption of organisms associated with detritus resulted in narrower trophic niche breadth. Despite this, the planktivorous habit adopted by _O. eigenmanni_ in lotic habitats might indicate that the species can adopt this strategy to facilitate invasion (Gido and Franssen 2007; Agostinho et al. 2015). Therefore, bottom-feeder species such as _L. platymetopon_ and _O. eigenmanni_ are likely to establish wherever they are introduced because their resources are unlimited. The impacts of bottom-feeders include feeding on the eggs of invertebrates and other fishes and competing with bottom-dwelling fish for food (Chaichana and Jongphadungkiet 2012).

_Auchenipterus osteomystax_ fed primarily on the Cladocera in lentic habitats (planktivores) and on the Coleoptera and terrestrial insects in lotic habitats (terrestrial insectivores). This species is generally characterized as aquatic insectivorous (Hahn et al. 1998; Barili et al. 2012; Tonella et al. 2018) because these food items are highly available in reservoirs (Bonecker et al. 2001; Rocha et al. 2009).

The diet of _T. galeatus_ was highly diverse, showing that this species is better able to explore feeding resources in lentic habitats, where it had a wider niche breadth. Omnivorous fish have high food plasticity (i.e., they can shift food resources), and the broad diet of _T. galeatus_ is an advantageous strategy in the invasion process (Moyle and Light 1996b; Ruesink 2005). In the early stages of life, its diet is composed primarily of aquatic insects and microcrustaceans (Santin et al. 2015). Throughout its development, individuals continue to prefer insects (Andrian and Barbieri 1996; Hahn et al. 1998; Ximenes et al. 2011). Reportedly, _T. galeatus_ is opportunistic when feeding on fruit, which composed a large part of its diet, primarily in the lotic habitats. Opportunistic feeding is an attribute of invasive aquatic species that facilitates establishment (Ricciardi and Rasmussen 1998). In addition to the invasive detritivores, the omnivores promote increased turbidity and nutrient concentration (Mormul et al. 2012; Gallardo et al. 2016), possibly leading to a reduction in the abundance of submerged macrophytes, a result of changes in nutrient dynamics through excretion and bioturbation (Matsuzaki et al. 2007). Omnivorous fish can still decrease the abundance of benthic invertebrates by direct consumption, habitat disturbance, or uprooting of macrophytes (Matsuzaki et al. 2009; Gallardo et al. 2016).

_Plagioscion squamosissimus_ proved to be a shrimp specialist (carcinophageous) in lentic habitats. In contrast, the species shows a piscivorous habit (> 50% fish) and wider niche breadth in lotic habitats. In both native (Williams et al. 1998) and invaded areas (Hahn et al. 1997; Stefani and Rocha 2009; Capra and Bennemann 2009; Vidotto-Magnoni and Carvalho 2009), the diet of _P. squamosissimus_ varies among fish, crustaceans, plant materials, and insects (e.g., Ephemeroptera, Odonata, and Chironomidae). The variety of food items consumed by _P. squamosissimus_ indicates food plasticity; it can be considered a generalist (Stefani and Rocha 2009). Nevertheless, in most cases, when _P. squamosissimus_ eats shrimp, this is the only type of food item available (Bennemann et al. 2006). In the Upper Paraná basin, the carnivorous habit has important roles in the feeding patterns of the species, from early stages (feeding on the Cladocera and Copepoda) until adulthood (eating mainly shrimp and fish; Neves et al. 2015).

Although _O. eigenmanni_ and _T. galeatus_ showed greater abilities to exploit feeding resources in lentic habitats (wider trophic niche breadth), the riparian vegetation present in both margins in the lotic habitats
provided a broader food spectrum to aquatic communities and enlarged the niche breadth of the other species. The greater availability of food resources for fish occurs mainly during high-water periods (Junk et al. 1989; Walker et al. 2013). Here, the results partially support the hypothesis that wider niche breadth are expected in lotic environments without damming impacts.

In summary, the successful colonization of these non-native fish species in new areas is expected because they have diet plasticity as an adaptive advantage. While *S. marginatus*, *L. platytenon*, and *P. squamosissimus* (specialist species) did not vary their diet compositions according to habitats, *O. eigenmanni*, *A. osteomystax*, and *T. galeatus* did so. Furthermore, trophic niche breadth was wider in lotic habitats for most species (generalist), where the riparian vegetation provided higher allochthonous resources and opportunity windows for invasion. Thus, the greater availability of food resources in the invaded habitats provided conditions conducive for the establishment of non-native species. This study was restricted to invasive fishes, and further research is needed to assess competitions with native species in Neotropical freshwaters.

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References


Diet and feeding ecology of non-native fishes


Supplementary material

The following supplementary material is available for this article:

Table S1. Characterization of the sampling sites of the Paranapanema River basin, southern Brazil.

Table S2. Standard length range, diets composition, trophic niche breadth and trophic guilds of non-native fishes sampled in lentic and lotic habitats of the Paranapanema River basin, southern Brazil.

This material is available as part of online article from: http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Garcia_etal_SupplementaryTables.xlsx


