Universidade Estadual de Londrina

DIEGO AZEVEDO ZOCCAL GARCIA

CARACTERÍSTICAS DA INVASÃO DE PEIXES NÃO NATIVOS NA BACIA DO RIO PARANAPANEMA, ECORREGIÃO DO ALTO PARANÁ, BRASIL

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Programa de Pós-Graduação Ciências Biológicas

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Enfim, pode-se dizer que aqui se derruba uma gigantesca perobeira para em seu lugar se plantar quatro grãos de milho. Se a isso se dá o nome de lavoura, eu não sei então, o que seja destruição.”

Theodoro F. Sampaio, 1890

GARCIA, Diego Azevedo Zoccal. **Características da invasão de peixes não nativos na bacia do rio Paranapanema, Ecorregião do Alto Paraná, Brasil.** 2018. 82 f. Tese (Doutorado em Ciências Biológicas) – Universidade Estadual de Londrina, Londrina, 2018.

RESUMO

Detectar os vetores e os impactos de espécies não nativas é necessário para prevenir novas introduções. Além disso, estudar as condições em que tais espécies se estabelecem são importantes para conhecer o processo de invasão e propor ações de manejo. Portanto, nesta tese são apresentados três capítulos, e com eles objetivou-se: (i) investigar os peixes não nativos no rio Paranapanema (capítulo 1); (ii) descrever a composição da dieta, a guilda trófica e a amplitude de nicho trófico (capítulo 2); (iii) avaliar traços reprodutivos (capítulo 3) de peixes não nativos em lagoas (habitat lêntico) e rios livres de barragens (habitat lótico). O rio Paranapanema é um dos maiores afluentes e um dos mais invadidos por peixes do alto rio Paraná (sudeste/sul do Brasil). O Paranapanema percorre 930 km para o oeste com 11 usinas hidrelétricas em seu leito. Os locais de estudo foram selecionados para representar habitats lênticos e lóticos. As lagoas possuem conexão direta com o canal principal do rio e estão localizadas no reservatório de Rosana. Os rios Pirapozinho e Anhumas fluem diretamente para os reservatórios de Rosana e Taquaruçu, respectivamente. Os peixes foram capturados sazonalmente de agosto de 2014 a março de 2016, com o uso de rede de arrasto (6,0 m^2, 0,5 cm de malha) e peneira (0,4 m^2, 0,5 cm de malha). Além disso, 14 redes de espera (2 a 14 cm de malha entre nós opostos, com 1.000 m^2 de rede por local) foram dispostas ao anoitecer e removidas ao amanhecer. Os peixes foram anestesiados por imersão em solução com óleo de cravo. Após, os peixes foram fixados com formalina 10% tamponada com carbonado de cálcio. Em laboratório, os peixes foram identificados e transferidos para etanol 70%. No capítulo 1 estão apresentados dados de 47 espécies de peixes não nativos, das quais 24 vieram do baixo rio Paraná após a construção da barragem de Itaipu. Estocagem, aquicultura e pesca também contribuíram com novas introduções. As espécies pertenceram principalmente à Cichlidae e Characidae; e a maioria é originária de outras ecorregiões da América do Sul. No capítulo 2 foi demonstrado que peixes invasores tem a capacidade de explorar diferentes recursos alimentares e aumentar o nicho trófico de acordo com o tipo de habitat. Por fim, no capítulo 3 concluiu-se que as espécies podem variar seu esforço reprodutivo de acordo com o habitat. O cuidado parental apresentado por *Serrasalmus marginatus* e *Loricariichthys platymetopon*, e a fertilização interna por *Auchenipterus osteomystax* e *Trachelyopterus galeatus* parecem ter sido características importantes para o sucesso na invasão.

Palavras-chave: América do Sul. Biodiversidade. Conservação. Invasões Biológicas. Rio Paraná.

GARCIA, Diego Azevedo Zoccal. **Invasion characteristics of non-native fish in the Paranapanema River basin, Upper Paraná Ecoregion, Brazil.** 2018. 84 f. Thesis (Doctorate in Biological Sciences) – State University of Londrina, Londrina, 2018.

ABSTRACT

Detecting vectors and impacts of non-native species is necessary to prevent new introductions. In addition, studies about the conditions under which non-native species are established are important to know the invasion process and propose management issues. Therefore, in this thesis three chapters are presented, with the aim of: (i) to investigate non-native fish in the Paranapanema River (Chapter 1); (ii) to describe the composition of the diet, the trophic guild and the trophic niche breadth (Chapter 2); (iii) to evaluate reproductive traits (Chapter 3) of non-native fish in lagoons (lentic habitat) and free of dams rivers (lotic habitat). The Paranapanema River is one of the largest tributaries and one of the most invaded by fish from the Upper Paraná River (southeast/south Brazil). The Paranapanema River runs 930 km to the west with 11 hydroelectric power plants in its channel. The sampling sites were selected to represent lentic and lotic habitat. The lagoons have direct connection with the main channel of the river and are located in the Rosana Reservoir. The Pirapozinho and Anhumas rivers flows directly into the Rosana and Taquaruçu reservoirs, respectively. The fish were captured seasonally from August 2014 to March 2016, using a seine (6.0 m^2, 0.5 cm mesh) and a sieve (0.4 m^2, 0.5 cm mesh). In addition, 14 nets (2 to 14 cm of mesh between opposing knots, with 1,000 m^2 of net per site) were disposed at the sunset and removed the following morning. The fish were anesthetized by immersion in solution with clove oil. After, the fish were fixed with 10% formalin buffered with calcium carbonate. In the laboratory, the fish were identified and transferred to 70% ethanol. Chapter 1 presents data from 47 non-native fish species, of which 24 came from the Lower Paraná River after the construction of the Itaipu Dam. Stocking, aquaculture and fishing also contributed with new introductions. The species belonged mainly to Cichlidae and Characidae; and most of them were from other South American ecoregions. In Chapter 2 it was shown that invading fishes have the ability to exploit different food resources and to enlarge the trophic niche according to the type of habitat. Finally, in chapter 3 it was concluded that species can vart their reproductive effort according to the habitat. The parental care presented by *Serrasalmus marginatus* and *Loricariichthys platymetopon*, and the internal fertilization by *Auchenipterus osteomystax* and *Trachelyopterus galeatus* seem to have been important characteristics for invasion success. Finally, in chapter 3 it was concluded that species can vary their reproductive effort according to habitat. The parental care presented by *Serrasalmus marginatus* and *Loricariichthys platymetopon*, and the internal fertilization by *Auchenipterus osteomystax* and *Trachelyopterus galeatus* seem to have been important characteristics for invasion success.

Keywords: Biodiversity. Biological invasions. Conservation. Paraná River. South America.

SUMÁRIO

1. INTRODUÇÃO GERAL

O número de espécies introduzidas no mundo cresce rapidamente, devido ao aumento da globalização, do comércio e da mobilidade humana (GOZLAN, 2008; LEPRIEUR et al., 2008; SEEBENS et al., 2017). As invasões biológicas são consideradas um problema ambiental de interesse público (GOZLAN et al., 2010). Diante disto, os estudos sobre invasões têm aumentado (LOWRY et al., 2013), principalmente pelo crescimento da dispersão geográfica de muitas espécies (SEEBENS et al., 2017). Espécies invasoras comumente alteram a funcionalidade dos ecossistemas e interferem em mecanismos como predação, competição, parasitismo e mutualismo (FULLER; NICO; WILLIAMS, 1999; GALLARDO et al., 2016). Além disso, hibridizam com espécies nativas, transmitem doenças e geram impactos sócio-econômicos (PIMENTEL; ZUNIGA; MORRISON, 2005; GOZLAN et al., 2010; SIMBERLOFF et al., 2013; BLACKBURN et al., 2014).

O processo de invasão é variável e dependente de fatores bióticos, abióticos, e da capacidade adaptativa dos organismos (MARCHETTI et al., 2004). Deve-se considerar que toda espécie introduzida é potencialmente invasora, porém, nem toda espécie introduzida conseguirá invadir. Isto dependerá de possíveis interações da espécie introduzida com a área invadida e de suas próprias características (WILLIAMSON; FITTER, 1996; MARCHETTI et al., 2004).

Os peixes estão entre os grupos de vertebrados mais introduzidos do mundo (GOZLAN, 2008; SEEBENS et al., 2017), bem como entre os mais ameaçados (IUCN, 2017). Apesar das consequências já conhecidas, muitas espécies de peixes ainda são translocadas entre ecossistemas aquáticos sem que seus impactos sejam considerados (PASCUAL et al., 2002; LOWRY et al., 2013). Neste sentido, os vetores de introdução de peixes, as condições em que as espécies se encontram, suas relações com os fatores bióticos, abióticos e condições ambientais devem ser avaliadas de forma integrada. Avaliar se tais espécies podem exercer efeitos diretos na ictiofauna nativa é importante para entender os mecanismos gerais de controle biológico (ROSS, 1991). Neste contexto é relevante a análise das consequências das introduções das espécies de peixe sobre a comunidade nativa, assim como a divulgação de resultados em linguagem acessível para o público em geral.

A fauna de peixes de água doce na América do Sul é a mais diversa do mundo (BARLETTA et al., 2010; REIS et al., 2016; VITULE et al., 2017). Neste continente, os estudos sobre invasões biológicas ainda são poucos, principalmente em água doce (LOWRY et al., 2013; SCHWINDT; BORTOLUS, 2017). No Brasil, a maioria dos estudos em ambientes de água doce abordam a aquicultura e novos registros de espécies não nativas. Em seguida, estão os estudos sobre biologia e ecologia (SCHWINDT; BORTOLUS, 2017). Para se entender quais características podem ter facilitado o processo de invasão, é importante comparar traços de história de vida das espécies entre as áreas nativa e invadida (THOMAZ et al., 2015). Alguns trabalhos já compararam dados de crescimento, dieta e reprodução de algumas espécies de peixes entre as duas áreas (GARCIA et al., 2014, AGOSTINHO et al., 2015; LIMA JUNIOR et al., 2015; TONELLA et al., 2018). Como se não bastassem as invasões que já ocorrem no país, a política brasileira ainda ameaça a biodiversidade e os serviços ecossistêmicos de água doce ao permitir a criação e incentivar o uso de peixes não nativos (PELICICE et al., 2014; AZEVEDO-SANTOS et al., 2016; PADIAL et al., 2017; PELICICE et al., 2017; ALVES et al., 2018).

Nesta tese, estão descritas a distribuição espaço-temporal e as possíveis interações em diferentes habitat de peixes não nativos no rio Paranapanema, Ecorregião do Alto Paraná, estados de São Paulo e Paraná. O capítulo 1 é um manuscrito publicado no periódico *Biological Invasions* sobre taxas, padrões e manejo de peixes não nativos na bacia do rio Paranapanema. Foi verificado que o principal vetor de introdução de peixes não nativos na bacia foi a inundação do Salto de Sete Quedas em 1982 para a formação do reservatório de Itaipu (JÚLIO JR. et al., 2009; VITULE et al., 2012). Esta invasão no rio Paranapanema ocorreu até 1987, quando foi concluída a barragem de Rosana, sem sistema de transposição de peixes. A barragem de Capivara, já construída em 1978, conteve a maior dispersão de peixes não nativos para montante da bacia. Portanto, os dois últimos reservatórios são os mais invadidos por peixes no rio Paranapanema. Além da inundação de Sete Quedas, a estocagem, a aquicultura, a pesca esportiva e a soltura de peixes ornamentais e iscas-vivas também estão entre os principais vetores. No segundo capítulo ‘Dieta e ecologia alimentar de espécies de peixes invasores sob diferentes condições de habitat’, é avaliada a dieta de peixes invasores em ambientes lênticos e lóticos. No terceiro capítulo, intitulado ‘Traços reprodutivos de peixes invasores de água doce em uma grande bacia Neotropical’, são descritos traços reprodutivos de peixes invasores na seca e na cheia em lagoas e tributários.

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3. CAPÍTULO 1

INTRODUCTIONS OF NON-NATIVE FISHES INTO A HEAVILY MODIFIED RIVER: RATES, PATTERNS AND MANAGEMENT ISSUES IN THE PARANAPANEMA RIVER (UPPER PARANÁ ECOREGION, BRAZIL)

(INTRODUÇÕES DE PEIXES NÃO NATIVOS EM UM RIO ALTAMENTE MODIFICADO: TAXAS, PADRÕES E QUESTÕES DE MANEJO NO RIO PARANAPANEMA (ECORREGIÃO DO ALTO PARANÁ, BRASIL))

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Introductions of non-native fishes into a heavily modified river: rates, patterns and management issues in the Paranapanema River (Upper Paraná ecoregion, Brazil)

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Abstract Understanding the pathways and impacts of non-native species is important for helping prevent new introductions and invasions. This is frequently challenging in regions where human activities continue to promote new introductions, such as in Brazil, where aquaculture and sport fishing are mainly dependent on non-native fishes. Here, the non-native fish diversity of the Paranapanema River basin of the Upper Paraná River ecoregion, Brazil, was quantified fully for the first time. This river has been subject to considerable alteration through hydroelectric dam construction and concomitant development of aquaculture and sport fishing. Through compilation of a non-native fish inventory by literature review, with complementary records from recent field studies, analyses were completed on the timings of introduction, and the taxonomy, origin and introduction vectors of the non-native fishes. A total of 47 non-native fishes are now present across the basin. Of these, 24 invaded from the Lower Paraná River following construction of Itaipu Dam that connected previously unconnected fish assemblages. Activities including fish stocking, aquaculture and sport angling continue to result in new introductions. Discounting Itaipu invasions, the introduction rate between 1950 and 2014 was approximately one new introduction every 3 years. Introduced fish were mainly of the Cichlidae and Characidae families; most species were from other South American ecoregions, but fishes of African, Asian, North American and Central American origin were also present. These introductions have substantially modified the river's fish fauna; when coupled with altered lentic conditions caused by impoundment, this suggests that the river's native fishes are increasingly threatened.

Keywords Biodiversity · Invasion · Aquaculture · Hydroelectric dams · Hydropower

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Introduction

Quantifying the extent of introductions of non-native species into different biogeographic regions is important for identifying how anthropogenic activities modify natural patterns of biodiversity (Villéger et al. 2011; Magurran et al. 2015). As introductions of non-native species result in global biotic homogenization (Rahel 2000; Olden et al. 2004), it is important to understand the pathways and rates of introductions between biogeographic regions, especially in this era of globalization (Jackson and Grey 2013). Introductions of non-native species are often coincident with the anthropogenic modification of natural habitats that can increase invasion risk (McKinney 2006; Poff et al. 2007). Thus, the interaction of introduction pressure and environmental change frequently exacerbates the issues faced by managers when attempting to limit new introductions and then prevent invasions (Britton et al. 2011).

In freshwaters, river basins are frequently considered as biogeographic islands in which opportunities for new species to invade are primarily from introductions that result from anthropogenic activities, such as aquaculture (Gozlan et al. 2010). Introduction rates into river basins can be high with, for example, 96 introduced species now present in the River Thames, England (Jackson and Grey 2013). In developing inventories of non-native species, the identification of vectors and pathways enables development of proactive management approaches that can focus efforts on preventing further introductions via greater surveillance and regulation (Zieritz et al. 2017). In some countries, pro-active approaches to prevent introductions and manage introduced species are, however, confounded by environmental and societal factors that promote the likelihood of new invasions, albeit often unintentionally. In Brazil, for example, a combination of measures to increase hydropower provision via river impoundment, the promotion of the aquarium trade using ornamental fish, and the use of intensive aquaculture is substantially increasing the rate of introduction and establishment of non-native species (Britton and Orsi 2012; Lima Júnior et al. 2015a, b; Xiong et al. 2015; Padial et al. 2016; Tófoli et al. 2016). Indeed, there is a long legacy of introductions of non-native fishes into many Brazilian river basins (Agostinho et al. 2007; Pelicice et al. 2015; Frehse et al. 2016), including numerous translocations between South American ecoregions that are diverse in their species richness (Reis et al. 2016). Therefore, understanding the respective contributions of these human activities (vectors) to the non-native fish fauna of specific Brazilian river basins and ecoregions is important in determining how future introductions could be prevented (Britton and Orsi 2012; Ortega et al. 2015).

The vectors responsible for the introduction of non-native freshwater fish in Brazil, in areas such as the Upper Paraná freshwater ecoregion, include aquaculture (Azevedo-Santos et al. 2011; Ortega et al. 2015), fish stocking to support sport angling (Britton and Orsi 2012), releases of live-bait fishes used by anglers (Garcia et al. 2015), the aquarium trade (Magalhães and Jacobi 2013; Magalhães and Vitule 2013), and the use of fish as biological control agents (Azevedo-Santos et al. 2016). Moreover, the elimination of a natural barrier to fish movement via construction of the Itaipu Dam has already resulted in a mass invasion of the Upper Paraná from the Lower Paraná basin (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015). The Upper Paraná ecoregion is in one of the most inventoried areas of Brazil (Graça and Pavanelli 2007; Langeani et al. 2007), facilitating analysis of the origin and vectors of the non-native fishes. These data then provide more precision and quality on current knowledge of the introduced species that can then be applied to developing policy and practice for their management.

The Paranapanema River is a major tributary of the Upper Paraná River that has undergone considerable hydro-geomorphological alteration via the construction of 11 hydropower reservoirs. Correspondingly, the river is a highly representative habitat in South America where the interactions of human activities and environmental changes are substantially altering the composition of the fish fauna. Such profound hydro-geomorphological disturbances to rivers tend to promote the likelihood of invasions (Johnson et al. 2008; Britton and Orsi 2012). Correspondingly, the aim here was to investigate the non-native fishes that are now present in the Paranapanema River, with compilation of an inventory of the species present, and analysis of their timings of introduction, current distribution, origins and vectors. Their taxonomy was also determined, with analysis of the orders and families of non-native fishes most frequently introduced.

Methods

Study area

The Upper Paraná Freshwater ecoregion is located upstream of the Itaipu Reservoir and Lower Paraná River, with the Rivers Paranapanema, Grande, Paranaíba and Tietê being its main tributaries (Castro et al. 2003). The ecoregion is almost entirely in Brazil, except for its southwest region in Paraguay, and it is the most industrialized and urbanized region of Brazil, with large number of cities with over 1 million inhabitants. Originally, this area contained the Atlantic Rainforest and Brazilian Savannah biomes that have now largely been converted to agriculture and livestock. In addition, the Upper Paraná River basin had its watercourses transformed into reservoirs, primarily for electricity production (Agostinho et al. 2007, 2016).

The Paranapanema River basin extends from the southwest of the state of São Paulo (SP) to the northwest of the state of Paraná (22°–26°S and 47°–54°W) (Fig. 1). Its sources are in the Serra de Paranapiacaba at 900 m altitude, and it flows 930 km to the west before its confluence with the Paraná River. Its course is subdivided into three main stretches: Upper Paranapanema, formed from the sources to the confluence of the Apiaí-Guaçu River, which together with the Itapetininga River are the main tributaries of this section; Middle Paranapanema, where the main tributaries are Itararé and Pardo rivers; and Lower Paranapanema, with the Rivers Cinzas, Tibagi and Pirapó being the main tributaries (Sampaio 1944) (Fig. 1). The hydroelectric development of the Paranapanema River began in 1936, with 11 dams now present that have modified the main river channel into a succession of cascading reservoirs (Fig. 1; Orsi et al. 2016). Cage and tank aquaculture is practised in and around some reservoirs (Orsi and Agostinho 1999; Ramos et al. 2013). The naturally high fish species richness of the basin (at least 127 species, e.g. Castro et al. 2003; Duke Energy 2008) is threatened by these reservoirs, with considerable declines in native fish species richness being recorded in, for example, the Capivara Reservoir (Orsi and Britton 2014). For the purposes of this study, the presence of non-native fishes within the basin was considered across 11 locations that covered the major hydroelectric reservoirs, the main river channel and river tributaries (Fig. 1; Table 1).

Fish species inventory and data analysis

In the study, a species was considered to be non-native in the Paranapanema River if literature suggested it should not have naturally occurred in the river due to biogeographical factors. The non-native fishes in the river thus included species from other ecoregions of South America, as well as from other continents. They also included species from the Lower Paraná River that, prior to construction of the Itaipu Dam, were biogeographically isolated from the Upper Paraná River (Vitule et al. 2012).

To compile the inventory list of non-native fishes, the principal method was literature review. The review was based on searches completed in Web of Science, and supplemented by Google Scholar, starting with the river name (‘Paranapanema’) or ecoregion (‘Upper Paraná’) in ‘title’ searches, and then using these within Boolean logic search terms with words including ‘alien’, ‘non-native’, ‘invasive’, ‘non-indigenous’, ‘introduced’ and ‘allodiversity’. Searches were then completed using the same terms but searching for ‘topic’. These searches provided an overall list of articles that, following their review, provided a final list of relevant articles from which data for the study were extracted. In addition to these published sources, grey literature was also sourced; this literature primarily comprised of books, PhD theses and documents produced and archived by power companies in charge of the hydroelectric dams. The latter provided details on intentional introductions of non-native fish into the reservoirs that were not available from any other source (e.g. CESP 1997). This review process and data extraction thus provided a list of non-native fishes that have been introduced into the Paranapanema River basin. Complementary data extracted from the literature covered the timing of detection of the non-native fishes (and, in some cases, their introduction) and their taxonomy, native origin and introduction vector. Where taxonomic and native origin information was not available then it was collated from other literature sources; these were primarily Reis et al. (2003), Britski et al. (2007), and Eschmeyer et al. (2016).

The introduction vector of each species was assessed from information provided in the original

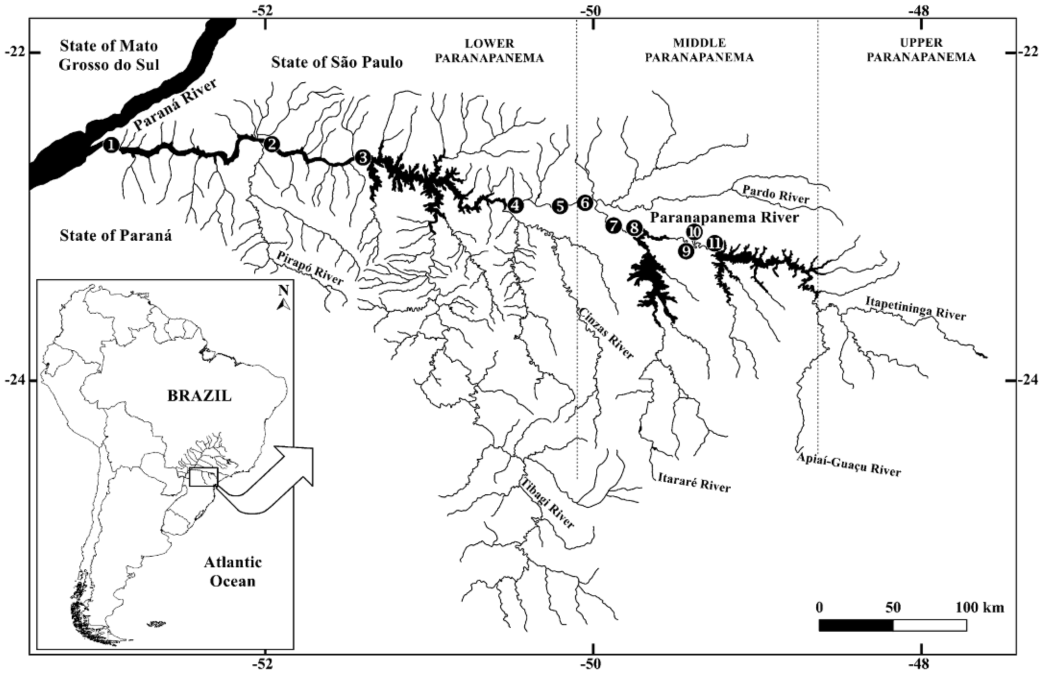

Fig. 1 Inset: Location of the study area in Brazil. Main: the Paranapanema River basin located in the Upper Paraná ecoregion, where the numbers represent the locations of the hydroelectric reservoirs: (1) Rosana; (2) Taquaruçu; (3) Capivara; (4) Canoas I; (5) Canoas II; (6) Salto Grande; (7) Ourinhos; (8) Chavantes; (9) Paranapanema; (10) Piraju; and (11) Jurumirim

Table 1 Number of individuals of non-native fish species stocked in reservoirs of the Paranapanema River between 1978 and 1992, from stocking programs conducted by 'Companhia Energética de São Paulo' (CESP 1997)

Species	Reservoir					Total
	Rosana	Capivara	Salto Grande	Chavantes	Jurumirim	
Astronotus crassipinnis	0	26,300	34,000	17,000	24,000	101,300
Cyprinus carpio	0	390,000	135,000	265,646	819,557	1,610,203
Sorubim lima	10,000	9000	0	0	0	19,000
Schizodon borellii	0	30,000	38,000	60,144	90,000	218,144
Triportheus angulatus	0	1,075,000	52,642	80,000	305,000	1,512,642
Oreochromis niloticus	0	1,935,000	615,000	1,243,000	5,694,200	9,487,200
Hoplias lacerdae	0	188,280	27,800	50,000	169,300	435,380
Total	10,000	3,653,580	902,442	1,715,790	7,102,057	13,383,869

literature source; when this information was not present, then the vector was interpreted from subsequent literature on that species (e.g. whether it is primarily a species used in aquaculture or sport angling). Where even this information was lacking then author knowledge was used. The vectors that were identified were: (1) fish stocking via sport-angling; (2) live-bait fishes used in sport angling; (3)

aquaculture ('fish farming'); (4) biological control (primarily of mosquito); (5) Itaipu Dam, where the non-native fish was present in the river only as a direct consequence of their upstream movement that was enabled by the dam flooding the natural biogeographic barrier of the Sete Quedas Falls; and (6) the aquarium trade (Júlio Júnior et al. 2009; Britton and Orsi 2012; Vitule et al. 2012; Azevedo-Santos et al. 2016).

To provide an up-to-date inventory of non-native species in the river, the literature review was complemented by field samples. These samples had been collected quarterly between 2012 and 2014 as part of a monitoring project within the Paranapanema River basin to detect natural fish spawning and nursery areas. Data from these samples were used here to only provide new information on the presence of non-native fishes that had yet to be reported in the literature. The samples were collected from the major habitats of the Rosana, Taquaruçu, Capivara, Canoas I, Canoas II and Salto Grande reservoirs, and their river tributaries (Fig. 1). Adult and juvenile fishes were captured by seine nets (6.0 m^2, 2.0 mm of mesh) and complemented by samples of juvenile and larval fishes collected by sieves (0.4 m^2, 0.5 mm of mesh). As any identified new species would have no supporting information on their native origin and vector, these were determined through literature review and author opinion, as described above.

Following compilation of the inventory list of the non-native fishes and their associated information (taxonomy, timing of introduction, native origin, and vector), these data were evaluated to determine their main patterns. To assess the temporal and spatial pattern of non-native fish introductions, the year of their first detection/introduction was identified (where detection was used as a proxy of the year of introduction). This enabled calculation of the proportion of non-native species that were introduced over time, their introduction rate per year, the cumulative number present, and the spatial variation in the number of species present across the basin (Fig. 1). If the introduced species was South American, then their geographic origin was given as the donor freshwater ecoregion (Abell et al. 2008); if its origin was from outside of South America then their continent was given (e.g. Africa, Asia, North America and Central America). Analysis of the vectors of introduction was determined as the proportion of species that were introduced via that vector. In addition, information on fish stocking rates in the reservoirs was provided where this was available. Note that the species lists and associated information generated by the study and used in the analyses are provided in full in Appendices 1 and 2 of the Supplementary Material.

Results

Literature review

The initial 'title' search in the 'Web of Science' database, using 'Paranapanema' as the search term, returned 86 articles; whilst these articles were published between 1992 and 2017, 58 (67%) were published between 2008 and 2017. The search of 'Upper Paraná' returned 328 papers that were published between 1968 and 2017, with 208 (63%) published since 2008. The use of these words with other key words within Boolean search terms (*cf.* Methods) resulted in a total of 20 articles from which data on the introduced fishes of the Paranapanema River basin could be extracted (Appendix 1, 2). This information was then supplemented by data extracted from 10 articles in non-ISI journals that were located by searches in Google Scholar using the same search terms (Appendix 1, 2). Finally, a combination of online searches (e.g. for books), and sourced documents from power companies (e.g. for historical stocking records) and universities (e.g. PhD theses), provided a further 15 literature sources from which data were also extracted (Appendix 1, 2). Thus, the literature review was based on 30 peer-reviewed papers and 15 items of grey literature (*cf.* Supplementary Material).

Initial non-native fish introductions

Literature review revealed that the first recorded non-native fish in the Paranapanema River occurred in the 1950s, with the North American largemouth bass, *Micropterus salmoides* Lacepède, 1802, reported (Fig. 2; Appendix 2). Further deliberate introductions of non-native fishes occurred between 1978 and 1992 through fish stocking programmes conducted by 'Companhia Energética de São Paulo' (CESP 1997), with seven non-native species released (Table 1; Appendix 2). A major introduction event was then

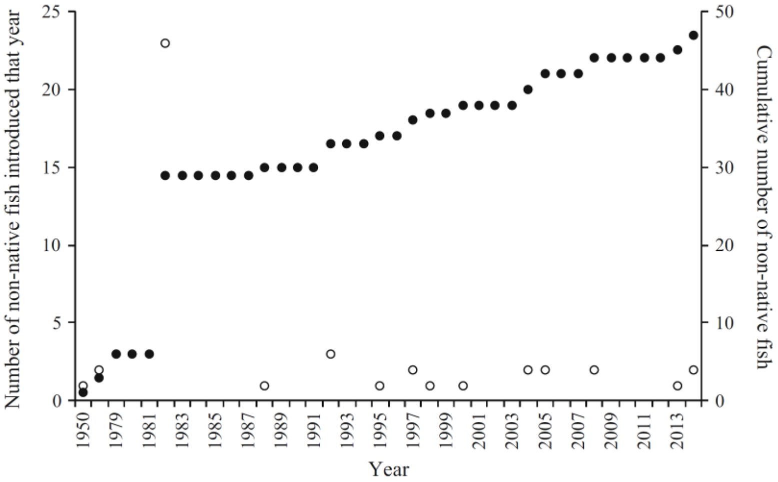

Fig. 2 Number of non-native fish species introduced in the Paranapanema River basin per year between 1950 and 2014 (clear circles) and the cumulative number of non-native fishes that have been introduced (filled circles)

the flooding of the natural biogeographic barrier of the Sete Quedas Falls during the formation of the Itaipu Reservoir. This enabled 24 fishes originating from the Lower Paraná ecoregion to disperse upstream into the Paranapanema River (Júlio Júnior et al. 2009; Vitule et al. 2012; Daga et al. 2015), with these new species resulting in a major peak in the introduction rate (Fig. 2).

Non-native fish composition and distribution

A total of 45 non-native fish species were recorded in the literature as having been introduced into the Paranapanema River between 1950 and 2014 (Table 2; Appendix 1). The field sampling conducted between 2012 and 2014 in a number of reservoirs and their tributaries (*cf*. Methods) increased this total to 47 non-native fishes (Table 2; Appendix 1). This represents an overall rate of 0.72 new species per year; if the 24 fishes associated with the construction of the Itaipu Dam are removed from the data then this reduces to 0.35 new species per year. The 47 non-native fishes were from eight orders and 21 families. The orders were primarily Characiformes (8 families, 13 species), Siluriformes (6 families, 12 species), and Perciformes (3 families, 12 species) (Appendix 1).

The two new non-native fishes added to the non-native fish inventory from the field sampling were *Ossancora eigenmanni* (Boulenger 1895) and *Laetacara araguaiae* Ottoni & Costa, 2009. Note that although *O. eigenmanni* has previously been recorded in the basin, it had only been recorded as unidentified Doradidae (Duke Energy 2008), with these new samples now enabling their identification to species level. Conversely, *L. araguaiae* has not reported previously but was present in field samples collected from the Rosana Reservoir in 2013 and was subsequently identified to species level in the laboratory.

Information gathered from the published literature revealed that in terms of distribution in the Paranapanema River, the non-native fishes that have been detected in at least 9 of the 11 evaluated habitats of the basin were *Hyphesobrycon eques* (Steindachner, 1882) (mato-grosso), *Metynnis lippincottianus* (Cope, 1870) (pacu-cd), *Plagioscion squamosissimus* Heckel, 1840 (corvina), and *Oreochromis niloticus* (Linnaeus, 1758) (Nile tilapia) (Fig. 1; Table 2; Appendix 1). Most of the non-native fishes were recorded within the hydropower reservoirs, with only a small proportion recorded in the main river channel (Fig. 3). Of the reservoirs, the Rosana, Taquaruçu and Capivara reservoirs had the highest numbers of introduced non-native fishes (Fig. 3).

Native origin and vectors

Nine South American freshwater ecoregions provided 38 of the 47 non-native fishes present in the basin (83% of all introductions) (Fig. 4a). The regions of native origin of these species were primarily Paraguay

Table 2 Composition and distribution of the non-native fish species introduced into the Paranapanema River basin between 1950 and 2014, where 'X' denotes introduced and '-'denotes absence in that location

Species	Location within the Paranapanema River basin										
	Ros	Taq	Cap	Tib	Can I	Can II	Sgr	Our	Cha	Jur	Upper
Aphyocharax dentatus	X	X	X	–	X	X	–	–	–	–	–
Apteronotus caudimaculosus	–	–	X	–	–	–	–	–	–	–	–
Astronotus crassipinnis	X	–	X	–	X	X	X	X	–	–	–
Auchenipterus osteomystax	X	X	–	–	–	–	–	–	–	–	–
Brachyhypopomus pinnicaudatus	–	–	–	–	–	–	X	–	–	–	–
Bryconamericus exodon	–	–	–	X	–	–	–	–	–	–	–
Catathyridium jenynsii	X	X	–	–	–	–	–	–	–	–	–
Cichla kelberi	X	–	X	–	–	–	X	–	X	–	–
Cichla monoculus	–	–	X	–	X	X	–	–	–	X	–
Cichla ocellaris	–	–	–	–	–	–	–	X	–	–	–
Cichla piquiti	–	–	–	–	–	–	X	–	X	–	–
Cichla temensis	–	–	–	–	–	–	–	X	–	–	–
Clarias gariepinus	–	X	X	X	–	–	–	–	–	–	–
Coptodon rendalli	X	–	X	X	–	–	–	X	–	X	–
Ctenopharyngodon idella	–	–	–	X	–	–	–	–	–		–
Cyprinus carpio	–	–	X	X	–	–	–	–	–	X	X
Erytrhinus erythrinus	X	–	X	–	–	–	–	–	–	–	–
Hoplias lacerdae	–	–	–	–	–	–	–	–	–	X	–
Hyphessobrycon eques	X	X	X	X	X	X	X	X	–	X	–
Hypophthalmus edentatus	X	X	–	–	–	–	–	–	–	–	–
Ictalurus punctatus	–	–	X	–	–	–	–	–	X	–	–
Laetacara araguaiae	X	–	–	–	–	–	–	–	–	–	–
Leporinus macrocephalus	–	–	X	X	X	–	X	–	–	–	–
Loricariichthys platymetopon	X	X	X	X	X	X	–	–	–	–	–
Metynnis lippincottianus	X	X	X	X	X	X	X	–	–	X	–
Micropterus salmoides	–	–	–	X	–	–	–	–	–	–	–
Misgurnus anguillicaudatus	–	–	–	–	–	–	–	–	–	–	X
Oreochromis niloticus	X	X	X	X	X	X	X	–	X	X	X
Ossancora eigenmanni	X	X	–	–	–	–	–	–	–	–	–
Pimelodus ornatus	X	X	–	–	–	–	–	–	–	–	–
Plagioscion squamosissimus	X	X	X	X	X	X	X	X	X	–	–
Poecilia reticulata	X	X	X	X	–	–	X	X	–	–	–
Potamotrygon cf. *motoro*	X	X	–	–	–	–	–	–	–	–	–
Pterodoras granulosus	X	X	–	–	–	–	–	–	–	–	–
Pterygoplichthys ambrosettii	X	–	X	–	–	–	–	–	–	–	–
Rhamphichthys hahni	X	X	–	–	–	–	–	–	–	–	–
Roeboides descalvadensis	X	X	–	–	–	–	–	–	–	–	–
Satanoperca pappaterra	X	–	–	–	–	–	–	–	–	–	–
Schizodon borellii	X	X	X	–	–	–	–	–	–	–	–
Serrasalmus marginatus	X	X	–	–	–	–	–	–	X	–	–
Sorubim lima	X	X	X	X	–	X	–	–	–	–	–
Steindachnerina brevipinna	X	–	–	–	–	–	–	–	–	–	–
Trachelyopterus galeatus	X	X	–	–	–	–	–	–	–	–	–

Table 2 continued

Species	Location within the Paranapanema River basin										
	Ros	Taq	Cap	Tib	Can I	Can II	Sgr	Our	Cha	Jur	Upper
Trachydoras paraguayensis	X	X	–	–	–	–	–	–	–	–	–
Triportheus angulatus	–	–	X	X	–	–	–	–	–	–	–
Triportheus nematurus	–	X	X	–	–	–	X	–	X	X	–
Xiphophorus hellerii	X	–	–	–	–	–	–	–	X	–	–
Total number of species by location	30	23	22	15	9	9	11	7	8	8	3

Locations are shown in Fig. 1 and are represented here as: *Ros* Rosana Reservoir, *Taq* Taquaruçu Reservoir, *Cap* Capivara Reservoir, *Tib* Tibagi River; *Can I* Canoas I Reservoir, *Can II* Canoas II Reservoir, *Sgr* Salto Grande Reservoir, *Our* Ourinhos Fish Ladder, *Cha* Chavantes Reservoir, *Jur* Jurumirim Reservoir, *Upper* Tributaries of the Upper Paranapanema River. For taxonomic details by species and the sources of information on the introduction, please see Appendix 1 of Supplementary Material

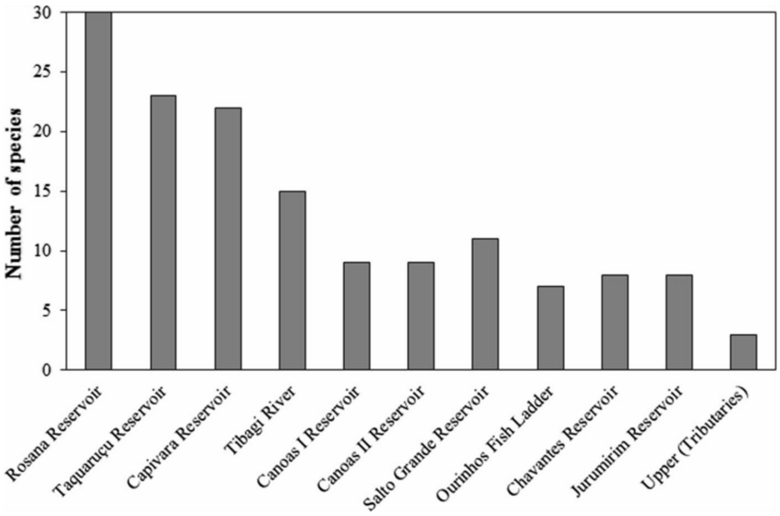

Fig. 3 The number of non-native fish present in each hydroelectric reservoir and river tributary of in the Paranapanema River basin. Information gathered from literature and field samples

and the Lower Paraná ecoregions, the Amazonas, Orinoco, Guianas, and Uruguay River basins. The importance of the Lower Paraná ecoregion as a donor region is reflected in the main introduction vector being the flooding of the Sete Quedas Falls via Itaipu Dam construction (24 of the 47 non-native fishes) (Fig. 4b). The native origins of the introduced fishes from outside of South America were Africa, Asia, North America and Central America, with their vectors primarily mainly being aquaculture, fish stocking and the release of ornamental fish (via the aquarium trade) (Fig. 4b).

Discussion

The number of non-native fishes in the Paranapanema River basin of the Upper Paraná ecoregion has increased over time, with at least 47 non-native fishes now present. When the influence of the Itaipu Dam is removed from the data, there was a new fish species recorded in the river approximately every 3 years. These results also represent the highest numbers of non-native fish recorded in the Paranapanema River basin to date. In the riverine habitats, three non-native fishes have been recorded previously (Castro et al.

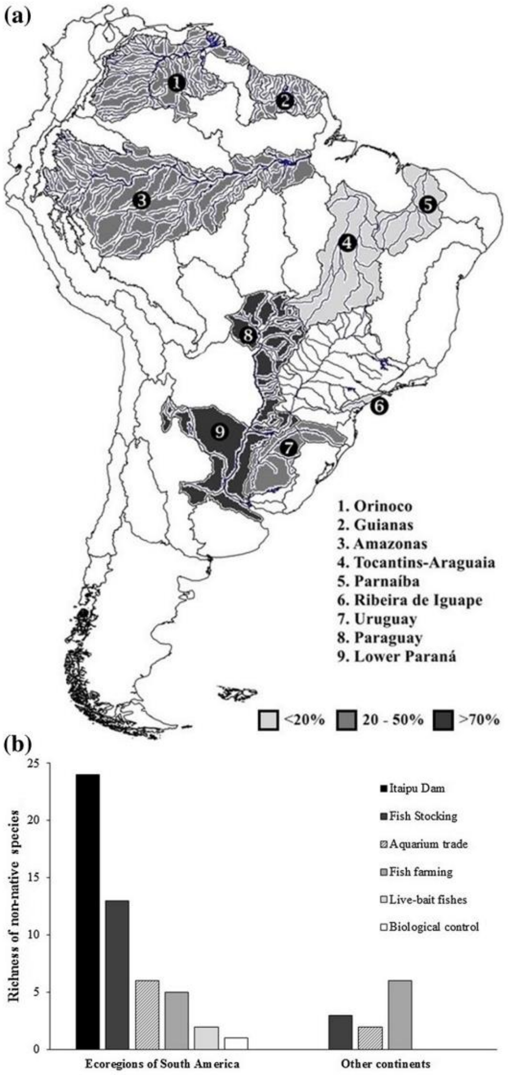

Fig. 4 **a** Origin of the non-native fish species (N = 47) introduced into the Paranapanema River according to South American ecoregions (Abell et al. 2008); **b** origins of the non-native fish species introduced into the Paranapanema River according to the vector of introduction

2003), whereas in reservoirs and the tributaries, previous recordings were 13 species (Carvalho et al. 2005) through to 27 (Orsi et al. 2016), 31 (Duke Energy 2008), and finally up to 39 species (Ortega et al. 2015). The families now contributing most to the introduced fish fauna are the Cichlidae and Characidae; of the 10 cichlids present, five have been recorded as *Cichla* species (peacock basses).

The Paranapanema River has a relatively low native fish species richness compared to other rivers in the Upper Paraná ecoregion (e.g. compared to the Paraná, Paranaíba, Grande and Tietê rivers) (Agostinho et al. 1997). It is now apparent that the Paranapanema has a relatively high number of introduced fishes compared with other rivers in the ecoregion (Ortega et al. 2015), suggesting it can be considered as a regional fish invasion hotspot. In other areas of the world that have been studied for their non-native taxa, 15 non-native fish species were recently recorded in the River Thames, England (of 96 non-native species recorded in total) (Jackson and Grey 2013) and in Lake Naivasha, Kenya, 11 non-native fish were introduced between the 1920s and 2000s (Gherardi et al. 2011). Kolar and Lodge (2002) identified 45 non-native fishes in the North American Great Lakes for development of their invasion predictions and risk assessment. As each of these freshwater systems were described as highly invaded (Kolar and Lodge 2002; Gherardi et al. 2011; Jackson and Grey 2013) then the Paranapanema River can also be considered as a highly invaded freshwater system at the global scale.

The construction of the Itaipu Dam was responsible for over 50% of the non-native fish present in the Paranapanema River basin. The construction of this dam flooded the Sete Quedas Falls in 1982. These falls had historically functioned as a semi-permeable biogeographic barrier (a small number of large-bodied migrant fishes could pass under high discharge conditions) via its sequence of 19 groups of waterfalls that physically separated the fish fauna of Upper and Lower Paraná basins (Bonetto 1986; Vitule et al. 2012; Lima Júnior et al. 2015b). Its flooding thus enabled the upstream dispersal of a number of fishes from the Lower Paraná basin into the Upper Paraná basin (Júlio Júnior et al. 2009). The movement of these fishes through the Paranapanema River was restricted by the Capivara Dam, built in 1978 without fish passage. However, species such as *Pterygoplichthys ambrosettii* (Holmberg, 1893) and *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 have since moved above this dam following their rescue from its hydropower turbines and their subsequent release into the reservoir upstream (Casimiro et al. 2017). In addition, the 11 hydroelectric reservoirs now present along the Paranapanema River has resulted in increased use of cage aquaculture and sport fishing (Britton and Orsi 2012). Both activities are heavily reliant on non-native fishes, especially *O. niloticus* (aquaculture) and *Cichla* fishes (sport fishing) (Britton and Orsi 2012). In addition, at least 13 million fish across seven non-native species were released in the reservoirs in stocking events between 1978 and 1992 to mitigate the effects of impoundment, with these fishes now having established populations (CESP 1997). This number of released fishes could be considered as representing high propagule pressure, an important factor that tends to increase the probability of introduced species establishing (Lockwood et al. 2005, 2009). In entirety, these findings strongly suggest that the major engineering of the Paranapanema basin specifically, and the Paraná River more generally, has been the primary reason for most of the non-native fish introductions occurring, with the other introduction vectors secondary to this.

Although this study has documented 47 introduced fish in the basin, the status of these fishes, such as whether they were established or invading, was not always apparent. However, with their repeated reporting in the literature and/or recording in field samples, it was assumed that most of the fishes have at least established sustainable populations. The high proportion of these fishes within the reservoirs, rather than the main river channel, suggests that these impoundments are important habitats in their establishment and colonisation of the basin. Indeed, studies generally suggest that impoundments enhance the probability of non-native fishes establishing populations (e.g. Johnson et al. 2008). The high proportion of invasive cichlids in the Paranapanema reservoirs is also supported by other studies suggesting Neotropical impoundments are prone to dominance by introduced cichlids (e.g. Agostinho et al. 2007; Langeani et al. 2007; Ortega et al. 2015). The relative importance of *Cichla* fishes in the altered hydro-geomorphic conditions might also relate to the shift in abiotic conditions caused by river impoundment, for example, the initial reduction in water turbidity in the reservoirs when compared to the river channel. This is because increased water clarity can assist *Cichla* fishes in their prey detection and capture, even when macrophytes are present that usually provide effective prey refugia (Pelicice and Agostinho 2009). A potentially important factor in the success of *Cichla* fishes in the reservoirs is also their reproductive plasticity. For example, the spawning of *Cichla piquiti* Kullander & Ferreira, 2006 is seasonal in their native Amazonian rivers, with increased reproductive activity at the beginning of the rainy season (Muñoz et al. 2006). In contrast, in their invasive population of the Itumbiara Reservoir (Paranaíba River basin, Southeast Brazil), their reproduction occurred throughout the year and was asynchronous with rainfall and temperature patterns (Vieira et al. 2009). This plasticity in reproductive behaviour potentially facilitates establishment through elevated annual recruitment. Indeed, plasticity in life history traits is a general feature of many successful invaders, as it usually enables rapid adaptive responses to new conditions (Gozlan et al. 2010).

The high number of non-native fishes introduced into the Paranapanema River means it is important to consider their ecological impacts, especially as the river also has a relatively high native fish species richness (at least 127 fishes; Castro et al. 2003; Duke Energy 2008). In the reservoirs, there has been an increased number and abundance of invasive piscivores, especially *Cichla* fishes (Orsi and Britton 2014). The impacts of introduced *Cichla* fishes have already received considerable attention in the Paraná basin more generally, where deleterious impacts on native fish species richness have been consistently recorded (e.g. Pelicice and Agostinho 2009; Menezes et al. 2012; Pelicice et al. 2015). A study documenting temporal changes in the fish assemblage of the Capivara Reservoir between 1992 and 2010 revealed that of 50 native fishes present in the initial samples, there were only 23 remaining in final samples, with an additional 11 non-native fish present by 2010 (Orsi and Britton 2014). However, as this native fish diversity started to decrease prior to *Cichla* establishment, then it was most likely driven initially by the substantial alterations to the hydro-geomorphology of the river, with losses only then exacerbated by high *Cichla* predation pressure (Orsi and Britton 2014).

The importance of vectors such as the Itaipu Dam for non-native fish introductions in the Paranapanema River was reflected in the origin of most introduced fishes being other Neotropical basins and South American ecoregions. Indeed, this is typical of the non-native fish fauna of Neotropical reservoirs more generally (Ortega et al. 2015; Latini et al. 2016). However, non-native fishes were also present in the Paranapanema River from four other continents, revealing how globalization of activities such as the ornamental fish trade and aquaculture has resulted in some fishes, such as *Cyprinus carpio* Linnaeus, 1758 and *O. niloticus*, achieving a global distribution (Gozlan et al. 2010; Britton and Gozlan 2013). Moreover, given the propensity of fish farmers to diversify their cultured fishes using fish from different countries and continents (Gozlan 2008), it is probable that more non-South American fish will be introduced into the Paranapanema basin via this vector in future.

From a management perspective, the increased non-native fish diversity and decrease in native fish diversity in the Paranapanema River basin raises substantial conservation concerns. The results here suggest that strategies that prevent new introductions via better regulation of the important introduction vectors should be considered. For example, the aquaculture sector is an important economic activity in the Paranapanema basin and is a key introduction vector (Agostinho et al. 2007; Ortega et al. 2015; Latini et al. 2016). Non-native fishes, including *Clarias gariepinus* (Burchell, 1822) and *O. niloticus* are cultured (Orsi and Agostinho 1999); both are highly invasive and harmful to native fish diversity (Forneck et al. 2016; Latini et al. 2016; Padial et al. 2016). Brazilian aquaculture also tends to prefer cultivating non-native species (Agostinho et al. 2007), with a proposed bill (Law 5989/09) encouraging this further (e.g. Pelicice et al. 2014). In combination, this suggests there is a pressing requirement for increased education of fish farmers on the risks their activities pose to native fish diversity. This should be allied with enhanced biosecurity of aquaculture sites to prevent fish escapes, with a concomitant shift towards farming indigenous fishes (Britton and Orsi 2012; Forneck et al. 2016). It is also recommended that all policies that promote introducing non-native fishes in reservoirs (e.g. for sport angling) are terminated, with increased regulation and supervision on the keeping and release of ornamental fishes by the public. Unfortunately, given the large spatial distribution of many of the non-native fishes that have already been introduced into the Paranapanema River basin, there are few management options available that would be effective at preventing their further dispersal and impact (Britton et al. 2011). Consequently, management priorities should aim to prevent new introductions and implement mitigation actions to promote the protection and restoration of native fish diversity.

In summary, the Paranapanema River is a highly altered river system due to the construction of hydroelectric reservoirs. These altered conditions, in conjunction with human activities, such as aquaculture and sport angling, have facilitated the introduction and subsequent invasion of non-native fishes. Thus, it is apparent that the fish fauna of this river within the Upper Paraná ecoregion has been heavily modified due to a range of human activities that have altered its physical and biological characteristics, and facilitated the introduction and invasion of many non-native fishes.

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4. CAPÍTULO 2

DIET AND FEEDING ECOLOGY OF INVASIVE FISH UNDER DIFFERENT HABITAT CONDITIONS

(DIETA E ECOLOGIA ALIMENTAR DE PEIXES INVASORES SOB DIFERENTES CONDIÇÕES DE HABITAT)

Capítulo elaborado e formatado conforme as normas da revista *Aquatic Invasions*
(http://www.aquaticinvasions.net/submissions.html)

Diet and feeding ecology of invasive fish under different habitat conditions

Running title: **Diet and feeding ecology of invasive fish**

Paranapanema River is most frequently invaded by non-native fish from the Upper Paraná River Freshwater Ecoregion. To understand how the diet of invasive species varies by different habitat types, we studied 12 non-native populations belonging to: *Serrasalmus marginatus*, *Loricariichthys platymetopon*, *Ossancora eigenmanni*, *Auchenipterus osteomystax*, *Trachelyopterus galeatus*, and *Plagioscion squamosissimus*. The feeding was described in the lentic and lotic habitat of the Paranapananema River basin between August 2014 and March 2016. The fish were caught with a seine and gillnets. PERMANOVA revealed differences between habitat in the diet of *O. eigenmanni* (Pseudo-$F_{1,21} = 1.75$; $P = 0.042$), *A. osteomystax* ($F_{1,12} = 2.31$; $P = 0.004$) and *T. galeatus* ($F_{1,70} = 1.94$; $P = 0.005$). Eight trophic guilds were identified, and *S. marginatus*, *L. platymetopon*, and *T. galeatus* have the same trophic guild (piscivorous, detritivorous and omnivorous, respectively) in both habitat. In contrast, the trophic guilds of *O. eigenmanni*, *A. osteomystax* and *P. squamosissimus* varied according to the habitat. Most populations of the lotic habitat have wider trophic niche breadth, except for *O. eigenmanni* and *T. galeatus*. All populations have specialist habit. In conclusion, invasive fish species have the ability to explore different food resources and increase the niche breadth according to habitat.

Keywords. Biodiversity, Biological invasions, Food resources, Niche breadth, Reservoir, Stomach contents, Upper Paraná River.

Introduction

Aquatic invasive species have extended their range distribution in the worldwide ecosystems by the barrier removal, increasing trade and human mobility (Leprieur et al. 2008; Panov et al. 2009; Gozlan et al. 2010; Thomaz et al. 2015; Seebens et al. 2017). Aquatic invaders have the capacity to disrupt ecosystem processes by the reduction in the abundance and diversity of native communities (Gallardo et al. 2016). The disturbance occurs because of the influence on established trophic interactions in aquatic communities (Vitousek 1990; Shea and Chesson 2002; Gallardo et al. 2016). In addition to environmental, biological and human factors responsible for the successful establishment of invasive species, it is important to determine the features common to species and invaded areas (Shea and Chesson 2002).

Invasive fish species are particularly pervasive and may cause food web disruption (Khan and Panikkar 2009; Britton et al. 2010; Gallardo et al. 2016; Copp et al. 2017) and threats biodiversity (Pelicice and Agostinho 2009; Matsuzaki et al. 2016). However, food resources affect the fitness of populations and define the permanence of the non-native species (Zambrano et al. 2010). Furthermore, the spatial and temporal variability promoted by human activities favors non-native species with higher tolerances to changes in physicochemical characteristics and plasticity of life history traits (Marchertti et al. 2004; Gozlan et al. 2010).

Among the goals of the biological invasion studies is to predict which environments are most susceptible to invasion and to identify which factors facilitate establishment (Marchetti et al. 2004). Improved knowledge of feeding ecology of invasive fishes and their variations is needed to understand the invasion process (Moyle and Ellsworth 2004; Kornis et al. 2013) and to elaborate management strategies (García-Berthou 2007; Guinan Jr. et al. 2015; Leuven et al. 2017). Therefore, to describe the use of food resources under the influence of different environmental conditions is important to predict susceptible habitat to species invasion and provide information to control their spread (Ricciardi and Rasmussen 1998; Kolar and Lodge 2001; Sepulveda 2017).

Plasticity in life history traits is a feature of successful invaders, due to its rapid ability to respond to new conditions (Gozlan et al. 2010). In Brazil, although several studies address fish escapes, impacts on other species or the invasion status (Pelicice and Agostinho 2009; Vitule et al. 2009; Pelicice et al. 2014; Ortega et al. 2015; Garcia et al. 2017; Padial et al. 2017; Casimiro et al. in prep) few aim to understand the mechanisms and conditions that determine the invasion success (Agostinho et al. 2015; Pazianoto et al. 2016; Cassemiro et al. 2017; Franco et al. 2017; Tonella et al. 2018). Some studies on the biology of Neotropical fish species have focused on the comparison between its native and invasive ranges (Garcia et al. 2014; Agostinho et al. 2015; Lima Junior et al. 2015; Tonella et al. 2018). Thus, the limited information available on food ecology for most invasive fish species makes it even more difficult to assess the stability of populations and their ability to interfere with the availability of prey (Charlebois et al. 2001). Therefore, with this study we aimed to describe the diet composition, trophic guild, and niche breadth of invasive fish species based on samples of damming (lentic) and free from dam (lotic) habitat of a same watershed. The species occur in different habitat in the invaded area in relation to hydro-geomorphological characteristics due to natural features and types of impacts. Environmental differences may reflect food disponibility, and it is expected that the invasive fish populations will present different feeding behavior. It will be tested the hypothesis that invasive fish populations present wider trophic niche breadth in lotic habitat without damming impact. It is expected that lotic environments provide more food resources and are more susceptible to the establishment of non-native species.

Methods

Study area

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

The study was performed in two types of habitat of the Lower Paranapanema River basin: lentic (Lagoon 1 and Lagoon 2) and lotic (Pirapozinho and Anhumas rivers) (Figure 1; Table 1). Lagoons are environments that were formed after the filling of the Rosana Reservoir in 1986. Lagoon 1 is located in the state of São Paulo and borders of the Morro do Diabo State Park, whereas Lagoon 2 is located in the state of Paraná. 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 seasonally from August 2014 to March 2016. Fishes were captured with seine (6.0 m^2, 0.5 cm mesh) and sieve (0.4 m^2, 0.5 cm mesh) which were operated for one hour by five people. Furthermore, 14 gillnets were used (2 to 14 cm meshes between opposing knots), with 1,000 m^2 of net per site. Nets were disposed at the sunset and removed the following morning, with approximately 12 hours of exposure. Fishes were anesthetized by immersion in water solution with clove oil (Animal Ethics Committee of Universidade Estadual de Londrina n. 30992.2014.33). After this procedure, fishes were 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) and by specialists from the Museu de Zoologia of the Universidade Estadual de Londrina (MZUEL), and then transferred to 70% ethanol.

A total of 290 individuals belonging to six invasive species were studied: *Serrasalmus marginatus* Valenciennes, 1837 (Serrasalmidae) (27 individuals analysed; standard length [SL] range = 8.8 - 29.5 cm); *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 (Loricariidae) (51 individuals analysed; SL = 13.4 - 26.5 cm); *Ossancora eigenmanni* (Boulenger, 1895) (Doradidae) (26 individuals analysed; SL = 6.4 - 9.5 cm); *Auchenipterus osteomystax* (Miranda-Ribeiro, 1918) (Auchenipteridae) (27 individuals analysed; SL = 12.0 - 24.0 cm); *Trachelyopterus galetaus* Linnaeus, 1766 (Auchenipteridae) (98 individuals analysed; SL = 10.7 - 18.0 cm); and *Plagioscion squamosissimus* (Heckel, 1840) (Sciaenidae) (61 individuals analysed; SL = 8.0 - 47.0 cm). Stomachs were removed and deposited in 70% ethanol for later analysis in the laboratory. The first quarter of the intestine of *L. platymetopon* was also used in the analysis.

Data analysis

Fish diet was determined from the analysis of stomach contents with 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), which was obtained by displacing the item in the water column using a graduated cylinder (0.1 ml) for large items and a glass millimeter plate (mm^3) for smaller items. The volume obtained in mm^3 was converted to ml when the volume was less than 0.1 ml (Hellawel and Abel 1971).

Differences in the diet composition of the species between lentic and lotic habitat were tested by permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008), which was applied to a matrix of food items per analyzed stomach, with volume values of items for each species separately. The Bray-Curtis distance was used as a measure of dissimilarity, and 9999 permutations to test the significance of the pseudo-*F* statistics derived from PERMANOVA. Statistical analyzes were conducted in the R Programming Environment using the Vegan package (Oksanen et al. 2007) (The R Project for Statistical Computing, http://www.r-project.org/).

Trophic guilds were based in Delariva et al. (2013) adapted from Mérona et al. (2001): detritivorous: more than 50% detritus/sediment in the stomachs; planktivorous: more than 50% plankton in the stomachs; detritivorous-planktivorous: more than 50% detritus/sediment and plankton in the stomachs; terrestrial insectivorous: more than 50% terrestrial insects in the stomachs; carcinophagous: more than 50% decapods (crab and shrimp) in the stomachs; invertivorous: more than 50% invertebrates in the stomach; piscivorous: more than 50% fish (including scales and ray of fish fin) in the stomachs; omnivorous: none of the above statements and adding items of animal and plant origins (leaf, flower, fruit and seed of higher plants).

Trophic niche breadth was estimated for each species by the Levin's standardized index (B_A): $B_A = (B-1)/(n-1)$, where B_A is the Levin's standardized index by the number of items (n) and $B = 1/(\sum_{i=1}^{n} pi^2)$, where B = trophic niche breadth, pi = proportion of item i in the diet and n = number of food items (Krebs 1998), which calculates the evenness of distribution of items among the various food resources. The values were established as: low (< 0.4), intermediate (0.4 to 0.6) and high (> 0.6). Low values indicate a specialized diet (S), while intermediate and high values indicate generalist diet (G) (Levins 1968).

Results

Diet composition

Diet of *O. eigenmanni*, *A. osteomystax* and *T. galeatus* was different between the types of habitat, whereas the diet of *S. marginatus*, *L. platymetopon* and *P. squamosissimus* did not varied (PERMANOVA, Table 2). Diet of *S. marginatus* was composed mainly of fish in lentic and lotic habitat (Figure 2A, Table 3).

Loricariichthys platymetopon primarily fed on organic detritus (volume ~ 80%) in both habitat (Figure 2B, Table 3). Diet of *O. eigenmanni* was composed predominantly by Gastropoda, Ostracoda, Acari and Trichoptera (larvae) in the lentic habitat, whereas organic detritus, inorganic detritus and Copepoda predominated in the lotic habitat (Figure 2C, Table 3).

Cladocera was the main food item of *A. osteomystax* in the lentic habitat, whereas Coleoptera and terrestrial insect (non-identified) dominated in the lotic areas (Figure 2D, Table 3). *Trachelyopterus galeatus* had the highest richness of food items. Coleptera and plant material predominated in the lentic habitat, whereas plant material (volume > 45%), Decapoda, Aranae, terrestrial insects (non-identified) and Orthoptera in the lotic habitat (Figure 2E, Table 3). Diet of *P. squamosissimus* was composed primarily by Decapoda and fish in both habitat (Figure 2F, Table 3).

Trophic guild

Fish exhibited eight trophic guilds (Table 4). *Serrasalmus marginatus* (piscivorous), *L. platymetopon* (detritivorous) and *T. galeatus* (omnivorous) maintained their trophic habits in both types of habitat. In contrast, there was a clear shift in: *O. eigenmanni* was invertivorous and detritivorous-planktivorous in lentic and lotic habitat, respectively; *A. osteomystax* planktivorous and terrestrial insectivorous; *P. squamosissimus* carcinophagous and piscivorous (Figure 2; Table 4).

Trophic niche breadth

Wider niche breadth was verified for *A. osteomystax*, *S. marginatus*, *L. platymetopon*, and *P. squamosissimus* in lotic habitat, where there was highest richness and evenness of food items (Table 4). On the other hand, *O. eigenmanni* and *T. galeatus* presented wider niche breadth in lentic habitat. All species were characterized with specialist habit in both habitat (TH < 0.4) (Table 4).

Discussion

Non-native species invade new areas when they overcome environmental barriers and establish (Colautti and MacIssac 2004; Blackburn et al. 2011). The piscivorous *Serrasalmus marginatus,* detritivorous *L. platymetopon* and omnivorous *T. galeatus* are among the most abundant species in different biotopes of the Upper Paraná River floodplain (Agostinho et al. 2004; Luiz et al. 2004; Bailly et al. 2011), due to their feeding plasticity and the greater availability of food resources (Tonella et al. 2018). In this study, such species maintained the same trophic guild in lentic and lotic habitat. The ability to maintain large populations through the same food resources ingestion provide the invasion success (Gido and Franssen 2007). In contrast, *O. eigenmanni*, *A. osteomystax* and *P. squamosissimus* differed their trophic guild in both types of habitat. All populations showed a specialized diet and most of them wider trophic niche breadth in lotic habitat. In addition, the specialist habitat has been shown to be advantageous in the colonization of new environments.

The success of the establishment of *S. marginatus* into Upper Paraná River basin can be attributed to its piscivorous habit (Pereira et al. 2016; Tonella et al. 2018). In the lentic habitat, the species showed high ability (volume ~ 90%) to feed on fish, probably of juveniles and small fish that inhabit the studied lagoons (Casatti et al. 2003). Individuals of *S. marginatus* feed on fish parts and fins that are nutritious and high availability in the environment (Winemiller 1989). Therefore, high food availability and its aggressive territorial behavior may be responsible for the population decline of its native congener *Serrasalmus maculatus* Kner, 1858 in the Upper Paraná River basin (Agostinho and Júlio Júnior 2000; Agostinho 2003).

Detritivory is one of the most specialized fish trophic habits (Gerking 1994) and may explain the similarity of diet among the habitat used by *L. platymetopon.* The dominance of detritus and sediment in the diet of *L. platymetopon* contributed to the 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), since 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).

Ossancora eigenmanni showed a specialist habit in invertebrates in lentic habitat and in detritus/sediment and plankton (Copepoda) in lotic habitat. The invertivorous habit adopted in lentic habitat is due to the abundance of this resource in lagoons bottoms and morphological adaptations to fed on benthic organisms (Fugi et al. 1996) and contributed to wider trophic niche breadth. On the other hand, in lotic habitat there was higher consumption of detritus and associated organisms, resulting in narrower trophic niche. Despite this, detritivorous/planktivorous habit adopted by *O. eigenmanni* in lotic habitat may be an indication that the species has the ability to adopt this strategy and facilitate the invasion (Gido and Franssen 2007, Agostinho et al. 2015). So, bottom-feeders species, like as *L. platymetopon* and *O. eigenmanni*, have high probability of establishing in areas where they are introduced since their resources are unlimited. The impacts of detritivorous species include feeding on eggs of invertebrates and other fish, and competition with bottom-dwelling fish for food (Chaichana and Jongphadungkiet 2012).

Auchenipterus osteomystax fed mainly on Cladocera in lentic habitat (planktivorous), and Coleoptera and terrestrial insects (non-identified) in lotic habitat (terrestrial insectivorous). The species is generally characterized as aquatic insectivorous (Hahn et al. 1998; Barili et al. 2012; Tonella et al. 2018). The presence of riparian vegetation interfered positively in the diet of *A. osteomystax* due to the contribution of allochthonous materials as food items (Coleoptera and terrestrial insect). On the other hand, its ability to eat aquatic and terrestrial insects, and microcrustaceans (e.g., Cladocera) guaranteed success in the colonization of reservoirs of the Upper

Paraná basin (Barili et al. 2012; Tonella et al. 2018), since these food items are highly available in reservoirs (Bonecker et al. 2001; Rocha et al. 2009).

The diet of *Trachelyopterus galeatus* was composed by high diversity of food items. The species showed more ability to explore the food resources in lentic habitat, where it had wider niche breadth. Omnivorous fish have high food plasticity, i.e., the ability to 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, the diet of *T. galeatus* is composed mainly of aquatic insects and microcrustaceans (Santin et al. 2015). With ontogenetic development, individuals continue to have insect preference (Andrian and Barbieri 1996; Hahn et al. 1998; Ximenes et al. 2011). Here, it was reported the opportunism of *T. galeatus* when feeding on fruit (i.e., plant material) (Gerkin 1994), which composed a large part of the diet, mainly in the lotic habitat. The opportunistic feeding is an attribute of invasive aquatic species which facilitates the establishment (Ricciardi and Rasmussen 1998). Invasive omnivorous promote increased turbidity and nutrient concentration (Gallardo et al. 2016). This may lead to a reduction in the abundance of submerged macrophytes due to changes in nutrient dynamics through excretion and bioturbation (Matsuzaki et al. 2007). In addition, omnivorous fish can decrease the abundance of benthic invertebrates by direct consumption, habitat disturbance and uprooting of macrophytes (Matsuzaki et al. 2009; Gallardo et al. 2016).

Plagiosgion squamosissimus proved to be a shrimp specialist (carcinophagous) in lentic habitat. In contrast, the species show piscivorous habit (fish > 50%) and wider niche breadth in lotic habitat. Both in the native (Williams et al. 1998) and in the invaded range (Hahn et al., 1997; Stefani and Rocha 2009; Capra and Bennemann 2009; Vidotto-Magnoni and Carvalho 2009) the diet of *P. squamosissimus* varies from fish, crustaceans, plant material, and insects (e.g., Ephemeroptera, Odonata and Chironomidae). The variety of food items consumed by *P. squamosissimus* proves its food plasticity and can be considered generalist (Stefani and Rocha 2009). Nevertheless, in most cases when *P. squamosissimus* eats shrimp, this is the only type of food item that occurs (Bennemann et al. 2006). In the Upper Paraná basin, the carnivorous habit has important roles on feeding patterns of the species, from the early stages (feeding on Cladocera and Copepoda), until adult fase (eating mainly shrimp and fish) (Neves et al. 2015). Therefore, the species has the ability to present trophic specialization in areas where it is introduced and increase its niche breadth according to the habitat.

Although *O. eigenmanni* and *T. galeatus* showed greater ability to exploit food resources in lentic habitat (wider trophic niche breadth), the riparian vegetation present in the lotic habitat 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 the high-water period (Junk et al. 1989, Walker et al. 2013). Thus, the results support the hypothesis that wider niche breadth would be expected in the lotic environments without damming impact and offers better conditions for establishment of some non-native fish species.

In summary, the success colonization of these non-native fish species in new areas is expected, due to the diet plasticity be an adaptive advantage of successful fish invaders. Whereas *S. marginatus*, *L. platymetopon* and *P. squamosissimus* did not vary their diet composition according to the habitat, *O. eigenmanni*, *A. osteomystax* and *T.*

galeatus differed their diet. Furthermore, trophic niche breadth was wider in lotic habitat for most species, where the riparian vegetation provided higher allochthonous resouces. Thus, the high availability of food resources in the invaded habitat provide conditions for the establishment of invasive species. This study was restricted to invasive fishes, and further research is needed to assess the competition with native species in Neotropical freshwater.

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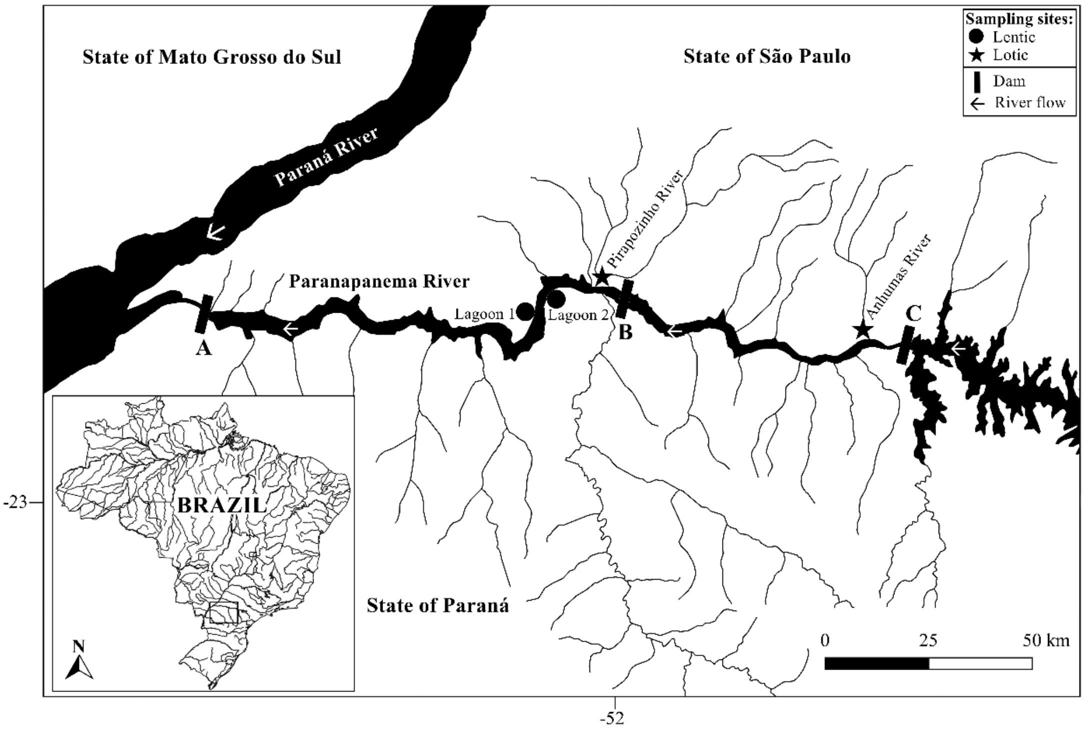

Figure 1. Map of the sampling sites of the Paranapanema River basin, southeast/southern Brazil. A = Rosana Dam; B = Taquaruçu Dam; C = Capivara Dam.

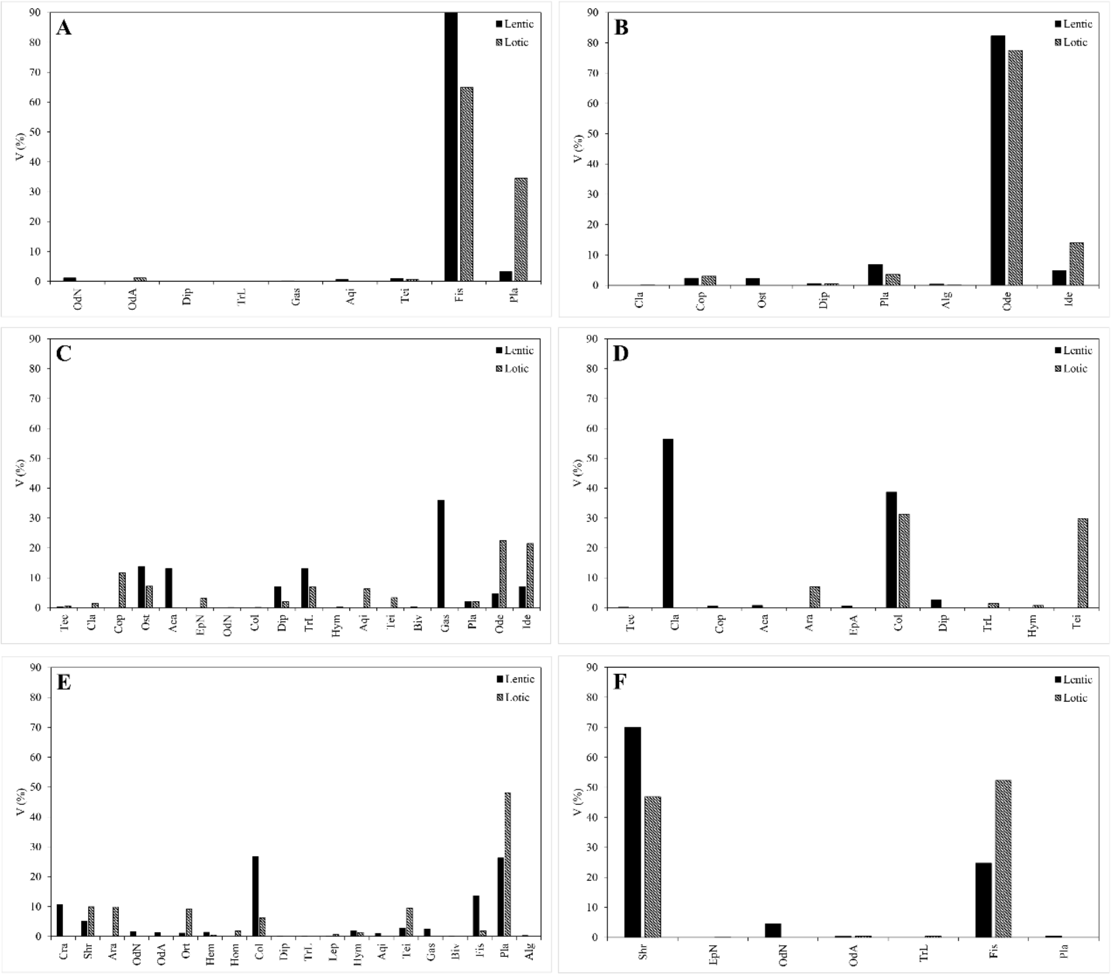

Figure 2. Diet composition (% volume) of invasive fish species caught in lentic and lotic habitat of the Paranapanema River basin, southern Brazil: *Serrasalmus marginatus* (A), *Loricariichthys platymetopon* (B), *Ossancora eigenmanni* (C), *Auchenipterus osteomystax* (D), *Trachelyopterus galeatus*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

Table 1. Characterization of the sampling sites of the Paranapanema River basin, southern Brazil.

Sites	Coordinates	Habitat	Diameter/ width (m)	Depth (m)	Average flow rate (m.s^{-1})	Riparian vegetation	Occupation of margins
Lagoon 1	22º38’04.52” S / 52º09’40.86” W	Lentic	143.7	2.63	0	Present	-
Lagoon 2	22º36’42,27” S / 52º09’31.81” W	Lentic	138.9	2.27	0	Absent	Pasture
Pirapozinho River	22º3’27.47” S / 52º09’05.92” W	Lotic	20.7	4.34	0.37	Present	-
Anhumas River	22º38’47.55” S / 51º26’43.54” W	Lotic	24.5	2.77	0.23	Present	-

Table 2. Results of permutational multivariate analysis of variance (PERMANOVA) applied to the data on diet of invasive fish species caught in lentic and lotic habitat of the Paranapanema River basin, southern Brazil.

Species	PERMANOVA
S. marginatus	Pseudo-$F_{1,24}$ = 1.37; P = 0.205
L. platymetopon	Pseudo-$F_{1,48}$ = 1.99; P = 0.100
O. eigenmanni	Pseudo-$F_{1,21}$ = 1.75; P = 0.042
A. osteomystax	Pseudo-$F_{1,12}$ = 2.31; P = 0.004
T. galeatus	Pseudo-$F_{1,70}$ = 1.94; P = 0.005
P. squamosissimus	Pseudo-$F_{1,40}$ = 0.75; P = 0.602

Table 3. Diet composition (% volume) of invasive fish species caught in lentic and lotic habitat of the Paranapanema River basin, southern Brazil. (Number of total stomachs/number of stomachs with content).

	S. marginatus		*L. platymetopon*		*O. eigenmanni*		*A. osteomystax*		*T. galeatus*		*P. squamosissimus*	
Food items/Habitat	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic	Lentic	Lotic
	(19/19)	(8/7)	(25/25)	(26/26)	(12/10)	(14/13)	(8/6)	(19/9)	(69/55)	(29/18)	(42/31)	(19/16)
Tecameba					0.31	0.50	0.13					
Phylum Arthropoda												
Subphylum Crustacea												
Class Branchiopoda												
Order Diplostraca												
Suborder Cladocera				0.02		1.38	56.34					
Class Malacostraca												
Order Decapoda												
Crab									10.66			
Shrimp									5.02	9.89	69.95	46.84
Class Maxillopoda												
Subclass Copepoda			2.31	2.95		11.66	0.48					
Subclass Ostracoda			2.26	0.46	13.79	7.14						
Subphylum Cheliceriformes												
Class Chelicerata												
Order Acari					13.05		0.72					
Order Araneae								6.95		9.88		

Subphylum Hexapoda												
Class Insecta												
Order Ephemeroptera (nymph)						3.10						0.004
Order Ephemeroptera (adult)							0.64					
Order Odonata (nymph)	1.10					0.02			1.52		4.49	
Order Odonata (adult)	0.41	1.11							1.35		0.33	0.46
Order Orthoptera									1.12	9.19		
Order Hemiptera									1.40	0.45		
Homoptera										1.87		
Order Coleoptera	0.04					0.09	38.71	31.27	26.68	6.28		
Order Diptera (larvae)									0.085			
Order Diptera (adult)	0.003		0.55	0.39	7.05	2.00	2.51					
Order Trichoptera (larvae)	0.01				13.03	6.89		1.34	0.003			0.38
Order Lepidoptera									0.17	0.67		
Order Hymenoptera						0.17		0.71	1.87	1.36		
Aquatic insetc	0.64					6.31			0.99			
Terrestrial insect	0.91	0.66				3.32		29.88	2.81	9.49		
Phylum Mollusca												
Class Bivalvia					0.23				0.05			
Class Gastropoda					35.96				2.45			
Phylum Chordata												

Class Osteichthyes												
Fish	90.62	64.90							13.61	1.89	24.73	52.32
Plant material	3.22	34.45	6.81	3.49	1.96	1.99			26.30	48.10	0.51	
Algae			0.33	0.04					0.28			
Organic detritus			82.22	77.55	4.60	22.46						
Inorganic detritus/sediment			4.87	13.90	6.99	21.48						

Table 4. Trophic guild (TG, Delariva et al. 2013 modified from Mérona et al. 2001), niche breadth (B), and trophic habits (TH, based on Levins 1968) for invasive fish species caught in lentic and lotic habitat of the Paranapanema River basin, southern Brazil. S = specialist.

Species/Habitat	Lentic			Lotic		
	TG	B	TH	TG	B	TH
S. marginatus	Piscivorous	0.02	S	Piscivorous	0.30	S
L. platymetopon	Detritivorous	0.06	S	Detritivorous	0.11	S
O. eigenmanni	Invertivorous	0.32	S	Detritivorous-planktivorous	0.22	S
A. osteomystax	Planktivorous	0.19	S	Terrestrial insectivorous	0.39	S
T. galeatus	Omnivorous	0.23	S	Omnivorous	0.08	S
P. squamosissimus	Carcinophagous	0.15	S	Piscivorous	0.25	S

5. CAPÍTULO 3

TRAÇOS REPRODUTIVOS DE PEIXES INVASORES DE ÁGUA DOCE EM UM GRANDE RIO NEOTROPICAL

(REPRODUCTIVE TRAITS OF INVASIVE FRESHWATER FISHES IN A LARGE NEOTROPICAL RIVER)

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Traços reprodutivos de peixes invasores de água doce em um grande rio Neotropical

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Estudos sobre biologia reprodutiva podem fornecer explicações sobre o sucesso na colonização de uma nova área, dado que muitos traços biológicos associados a espécies invasoras podem conferir vantagem na invasão. Deste modo, objetivou-se avaliar variações de traços reprodutivos de cinco espécies de peixes invasores em lagoas e rios livres de barragens. Foram estudadas populações de *Serrasalmus marginatus*, *Loricariichthys platymetopon*, *Ossancora eigenmanni*, *Auchenipterus osteomystax* e *Trachelyopterus galeatus* em habitat lêntico (Lagoas 1 e 2) e lótico (rios Pirapozinho e Anhumas) durante as estações seca e chuvosa. Fêmeas predominaram na maioria das populações (χ^2, $P < 0{,}05$). Fêmeas de *L. platymetopon* e *T. galeatus* apresentaram maior índice gonadossomático durante a estação chuvosa no rio Anhumas e na Lagoa 2, respectivamente (teste de Mann-Whitney, $P < 0{,}05$). Populações de *S. marginatus*, *L. platymetopon*, *O. eigenmanni* e *T. galeatus* apresentaram atividade reprodutiva muito intensa na Lagoa 1. *Auchenipterus osteomystax* apresentou maior abundância de larvas nos rios Pirapozinho e Anhumas. *Trachelyopterus galeatus* apresentou atividade reprodutiva muito intensa nas duas lagoas e no rio Pirapozinho, e intensa no rio Anhumas. Enquanto algumas espécies exibem alto investimento reprodutivo, independentemente do tipo de habitat (por exemplo, *T. galeatus*), outras podem apresentar variações entre eles (*S. marginatus* e *L. platymetopon*). Fêmeas em maiores razões sexuais, alto investimento reprodutivo, cuidado parental (*S. marginatus* e *L. platymetopon*) ou fertilização interna (*A. osteomystax* e *T. galeatus*), e desova parcelada podem ser características reprodutivas responsáveis pelo sucesso na invasão da bacia do alto rio Paraná. Portanto, espécies não nativas com alta sobrevivência da prole podem ter mais sucesso no estabelecimento de novos ambientes.

Palavras-chave: América do Sul; barragem; espécie não nativa; invasão biológica; recrutamento; reprodução.

Introdução

Os ecossistemas de água doce estão entre os mais ameaçados no mundo (Gozlan 2009; Olden et al. 2010). A modificação de rios por atividades antropogênicas (Nilsson et al. 2005; Liermann et al. 2012) aliada à intensificação na mobilidade humana facilita a transferência de espécies e contribui para a crise da biodiversidade (Clavero e García- Berthou 2005; Vitule et al. 2009; Wilson et al. 2009). A introdução de espécies é uma das principais ameaças à biodiversidade e intensificou-se nos últimos anos (Leprieur et al. 2008, Gozlan et al. 2010; Seebens et al. 2017). Em reservatórios brasileiros, os principais vetores da introdução de peixes não nativos são escapes de pisciculturas, pesca e soltura de peixes ornamentais por aquaristas (Agostinho et al. 2007; Ortega et al. 2015). Além disso, o alagamento promovido por barragens pode eliminar barreiras geográficas naturais e conectar diferentes províncias ictiofaunísticas (Júlio Júnior et al. 2009; Vitule et al. 2012).

Muitas espécies introduzidas que se tornam invasoras têm a capacidade de tolerar condições e características de ambientes diferentes (Williamson e Fitter 1996; Marchetti et al. 2004a; Gutierre et al. 2014). Enquanto muitas espécies falham na invasão, outras têm maior potencial para invadir (Olden et al. 2006; Simberloff e Rejmánek 2011).

Características reprodutivas associadas às relações biológicas e ecológicas entre as espécies e os ambientes podem auxiliar no entendimento do sucesso das invasões. Assim, o conhecimento da história de vida das espécies em relação à reprodução, o crescimento, e a manutenção de população viável é importante para prever o sucesso e o impacto de novas invasões (Moyle e Marchetti 2006). Apesar da atenção que as espécies invasoras recebem, poucos dados sobre a plasticidade reprodutiva estão disponíveis (Sakai et al. 2001; Peterson et al. 2004; García-Berthou 2007).

Portanto, objetivou-se avaliar traços reprodutivos de cinco espécies de peixes invasores em lagoas e rios livres de barragens da bacia do rio Paranapanema, sudeste/sul do Brasil. As espécies estudadas foram: piranha *Serrasalmus marginatus* Valenciennes 1837 (Serrasalmidae), cascudo-chinelo *Loricariichthys platymetopon* Isbrücker & Nijssen 1979 (Loricariidae), armado *Ossancora eigenmanni* (Boulenger 1895) (Doradidae) e os bagres palmitinho *Auchenipterus osteomystax* (Miranda-Ribeiro 1918) e cangati *Trachelyopterus galeatus* L. 1766. (Auchenipteridae).

Métodos

Área de estudo

O rio Paranapanema é um dos maiores afluentes da Ecorregião do alto rio Paraná, e sua bacia hidrográfica localiza-se entre as coordenadas 22-26ºS e 47 a 54ºW. Suas nascentes estão no Planalto Atlântico (município de Capão Bonito, estado de São Paulo). O rio percorre por 930 km para oeste e seu desnível é de 900 m até o rio Paraná. Esta variação de altitude é importante, pois permitiu a construção de 11 hidrelétricas que alteraram o curso do rio para uma série de trechos lênticos e lóticos.

Os locais de estudo foram selecionados para representar esses ambientes lênticos e lóticos dentro do rio Paranapanema (Fig. 1). Lagoa 1 e Lagoa 2 (denominados L1 e L2, respectivamente) foram localizadas nas margens do reservatório de Rosana. Ambas as lagoas têm conexão direta e permanente com o canal principal do rio. Os ambientes lóticos foram os rios Pirapozinho e Anhumas (denominados PZ e AN, respectivamente). Ambos são afluentes livres de barragens do Paranapanema e fluem diretamente para os reservatórios de Rosana e Taquaruçu, respectivamente (Tabela 1).

Amostragem

Amostras de larvas e juvenis foram capturadas durante os períodos reprodutivos (outubro de 2012 e março de 2015) como parte de um projeto de monitoramento na bacia do rio Paranapanema para detectar áreas de desova e criadouros naturais de peixes (Orsi et al. 2016). Estes dados foram utilizados apenas para fornecer informações sobre a presença das fases iniciais das espécies invasoras nos locais de amostragem. Larvas e juvenis foram capturados com o uso de redes de plâncton cônicas (0,5 mm de malha), rede de arrasto (6,0 m^2; 0,5 mm de malha) e peneira (0,4 m^2; 0,5 mm de malha), operadas por cinco pessoas durante uma hora. Os peixes adultos foram capturados no meio e no final das estações seca e chuvosa entre agosto de 2014 e março de 2016. Os peixes foram capturados com 14 redes de emalhar (malhas de 2 a 14 cm entre nós opostos), com 1.000 m^2 de rede por local. As redes foram dispostas ao pôr-do-sol e removidas na manhã seguinte, com aproximadamente 12 horas de exposição. Os espécimes foram anestesiados por imersão em solução aquosa com óleo de cravo (Comitê de Ética Animal da Universidade Estadual de Londrina n. 30992.2014.33). Após este procedimento, os peixes foram fixados com 10% de formalina tamponada com carbonato de cálcio. No laboratório, os espécimes foram transferidos para etanol a 70% e identificados por meio de literatura especializada (Britski et al. 2007; Graça e Pavanelli 2007) e por especialistas do Museu de Zoologia da Universidade Estadual de Londrina (MZUEL). Os peixes foram então medidos (comprimento padrão, L_S, 0,1 cm), pesados (W_T, 0,1 g) e dissecados para identificação sexual a partir da observação macroscópica de gônadas, que também foram pesadas (W_G, 0,01 g). Os estágios do desenvolvimento gonadal foram definidos como: 1) desenvolvimento (amadurecimento), indivíduos que iniciam desenvolvimento gonadal, mas não estão preparados para gerar gametas; 2) adultos capazes de gerar gametas (amadurecidos), prontos para reprodução; 3) regressão (gasto), após a fase de desova; 4) regeneração (em repouso), sexualmente maduros, mas reprodutivamente inativos (Vazzoler 1996; Brown-Peterson et al. 2011).

Análise de dados

A captura por unidade de esforço (CPUE) padronizou quantos peixes adultos foram capturados em 1.000 m^2 de rede por 12 horas de exposição. O método do qui-quadrado foi aplicado para avaliar a proporção sexual entre fêmeas e machos (χ^2, P <0,05). O comprimento padrão mínimo na maturidade foi determinado de acordo com o comprimento de primeira maturação como o menor tamanho onde ocorrem indivíduos em estádio avançado de maturação gonadal, de acordo com Sato e Godinho (1988). O índice gonado-somático (I_G) foi estabelecido para fêmeas e machos por estações seca e chuvosa com base na relação percentual entre o peso gonadal (W_G) e o peso total (W_T) para determinar o estado reprodutivo ($I_G = 100\ W_G\ W_T\ \text{-}1$). Os valores médios do índice gonado-somático para as fêmeas em estádios capazes de desova nas duas estações (seca e chuvosa) foram comparados com o teste não paramétrico de Mann-Whitney ($P < 0,05$). O índice de atividade reprodutiva (I_R) foi estabelecido apenas para fêmeas (Agostinho et al. 1993), e classificada como nula ($I_R \leq 2$), incipiente ($2 < I_R \leq 5$), moderada ($5 < I_R \leq 10$), intensa ($10 < I_R \leq 20$) e muito intensa ($I_R > 20$).

Os seguintes traços reprodutivos foram obtidos a partir da literatura, a fim de complementar e comparar com os dados do presente estudo: comprimento padrão de primeira maturação de fêmeas e machos (Suzuki et al. 2004), guilda reprodutiva (Agostinho et al. 2007), período reprodutivo, tipo de desova, diâmetro dos oócitos maduros (Vazzoler 1996) e fecundidade absoluta de fêmeas (Vazzoler 1996; Suzuki et al. 2000; Marcucci et al. 2005;

Bailly et al. 2011; Melo et al. 2017). Todos os estudos foram realizados na bacia do alto rio Paraná, ou seja, na área invadida.

Resultados

As maiores abundâncias de larvas foram apresentadas por *S. marginatus* e *A. osteomystax* nos rios Pirapozinho e Anhumas (Orsi et al. 2016, Tabela 2). A maior captura por unidade de esforço foi apresentada por *A. osteomystax* também no rio Anhumas durante a estação chuvosa, com baixa ou nenhuma captura nos demais locais (Tabela 3). *Serrasalmus marginatus* foi capturada essencialmente durante a estação chuvosa na maioria dos locais. As demais espécies variaram suas capturas durante as estações e os locais de amostragem.

Em geral, as proporções sexuais foram maiores para as fêmeas nas amostras e, além de *S. marginatus* no rio Pirapozinho, *L. platymetopon* no rio Anhumas e *T. galeatus* em todos os locais, desviaram-se significativamente de 1F:1M (Tabela 4). A maioria das espécies apresentou comprimento padrão mínimo na maturidade maior que o já registrado na literatura (Suzuki et al. 2004, Tabelas 4 e 5), exceto para *O. eigenmanni*, cujo comprimento padrão mínimo na maturidade é aqui estimado pela primeira vez.

As populações de *L. platymetopon* no rio Anhumas e *T. galeatus* na Lagoa 2 apresentaram fêmeas com maiores valores de I_G durante a estação chuvosa ($P < 0,05$, Mann-Whitney) (Tabela 4). Houve mais indivíduos com atividade reprodutiva muito intensa na Lagoa 1 (Tabela 4). *Trachelyopterus galeatus* teve atividade muito intensa na maioria dos locais (Lagoa 1, Lagoa 2 e rio Pirapozinho).

Os dados da literatura revelaram que *S. marginatus* tem o período reprodutivo mais longo (oito meses) (Vazzoler 1996, Tabela 5). Nenhuma das espécies estudadas realiza migração reprodutiva e todas possuem desova parcelada e sazonal. Além disso, *S. marginatus* e *L. platymetopon* possuem cuidado parental, enquanto que em *A. osteomystax* e *T. galeatus* a fertilização é interna (Agostinho et al. 2007). Dentre as espécies aqui estudadas, *Loricariichthys platymetopon* tem o maior diâmetro de oócitos maduros.

Discussão

Fêmeas em maiores razões sexuais, alto investimento reprodutivo, cuidado parental e/ou fertilização interna podem ser traços biológicos responsáveis pelo sucesso na invasão de peixes na bacia do alto rio Paraná. Além disso, enquanto algumas espécies exibem alto investimento reprodutivo, independentemente do tipo de habitat onde ocorrem (por exemplo, *T. galeatus* nas lagoas e rio Pirapozinho), outras podem apresentar acentuada variação espacial (*S. marginatus* e *L. platymetopon*). Ambientes lênticos (tais como as lagoas) criados pelo represamento facilitam a invasão de peixes (Johnson et al. 2008). Muitos traços biológicos associados a espécies invasoras podem conferir vantagem no estabelecimento (Williamson e Fitter 1996; Sakai et al. 2001; Moyle e Marchetti 2006). Aquelas que se tornam invasoras, apresentam indivíduos que se dispersam, sobrevivem, reproduzem em diferentes tipos de habitat e possuem extensa área de ocorrência (Blackburn et al. 2011). Além disso, certas características da área invadida podem aumentar a chance da invasão, tais como a semelhança entre a área de origem e a área invadida, o alto nível de perturbação humana (por exemplo, reservatórios), e a menor riqueza de espécies nativas na área invadida (Elton 1958; Moyle e Light 1996; Havel et al. 2005; Johnson et al. 2008).

Serrasalmus marginatus, *L. platymetopon*, *O. eigenmanni*, *A. osteomystax* e *T. galeatus* invadiram a bacia do alto rio Paraná após a inundação da barreira natural do Salto de Sete Quedas para o enchimento do reservatório de Itaipu (Júlio Júnior et al. 2009; Vitule et al. 2012). Assim, além da província ictiofaunística do baixo rio Paraná (área doadora) possuir relativa semelhança com o Alto Paraná (área receptora), este é altamente modificado por reservatórios hidrelétricos (Agostinho et al. 2008; 2016). A alta abundância de *S. marginatus*, *L. platymetopon* e *T. galeatus* na planície de inundação do Alto Paraná (Agostinho et al. 2004; Luiz et al. 2004) pode ser atribuída às características tanto do invasor (invasividade) como dos ambientes invadidos (invasibilidade) (Moyle e Marchetti 2006). Ainda, o rio Paranapanema possui a menor riqueza de espécies nativas de peixes dentre os grandes afluentes da bacia do Alto Paraná (Agostinho et al. 1997).

A plasticidade reprodutiva é uma característica da história de vida necessária para a colonização e a estabilidade das espécies em diferentes habitat, visto que os colonizadores devem se adaptar às condições dos novos ambientes (Williamson e Fitter 1996; Moyle e Marchetti 2006). Após a colonização inicial, as espécies introduzidas investem fortemente em atributos reprodutivos, tornando a população auto-sustentável e conferindo sucesso no estabelecimento (Blackburn et al. 2011). As fêmeas de *L. platymetopon* apresentaram maiores valores de índice gonadossomático no rio Anhumas durante a estação chuvosa. Na bacia do rio Cuiabá (área nativa) as intensas enchentes favorecem o desenvolvimento gonadal de espécies com cuidado parental (Bailly et al. 2008), tais como *S. marginatus* e *L. platymetopon*.

Ao contrário de muitas espécies nativas, as invasoras são capazes de se reproduzir em diferentes ambientes (Sakai et al. 2001; Williamson e Fitter 1996; Moyle e Marchetti 2006; Olden et al. 2006). Assim, após o estabelecimento em áreas lênticas, *S. marginatus* e *L. platymetopon* conseguiram colonizar ambientes lóticos. Enquanto a espécie de piranha nativa do Alto Paraná *Serrasalmus maculatus* Kner 1858 possui maior atividade reprodutiva apenas em ambientes lênticos (Agostinho e Júlio Jr. 2002; Agostinho 2003), a invasora *S. marginatus* apresentou alto investimento reprodutivo tanto em habitat lêntico (Lagoa 1) quanto em lótico (rio Anhumas). Foram necessários seis anos após a introdução para que *S. marginatus* ultrapassasse *S. maculatus* em abundância na planície de inundação do alto rio Paraná, e desde então manteve sua dominância (Alves et al. 2017). Além disso, a ausência de captura de *S. marginatus* na estação seca sugere que a espécie não permanece todo seu ciclo de vida dentro dos locais amostrados.

O cuidado parental ou a fertilização interna (i.e., esperma depositado dentro do corpo da fêmea com gonopódio do macho) provaram ser características de espécies invasoras mais bem sucedidas na bacia do Alto Paraná (Agostinho e Júlio Jr. 1999). Embora os peixes com qualquer estratégia de história de vida possam invadir, o sucesso na invasão é mais provável em espécies com cuidado parental (Marchetti et al. 2004b; Moyle e Marchetti 2006). Espécies com cuidado parental realizam desova parcelada por um longo período, tem baixa fecundidade e ovos grandes e adesivos (Vazzoler 1996). Estas espécies investem grande quantidade de energia por indivíduo em sua prole (Bailly et al. 2008). *Serrasalmus marginatus* é capaz de atacar um predador potencial para defender sua prole e estabelecer seu território (Agostinho 2003). Por outro lado, os machos de *L. platymetopon* carregam a massa de ovos sob os lábios durante a incubação, sendo esta uma estratégia eficiente em ambientes que apresentam variações nas condições limnológicas e no nível da água, como em reservatórios (Marcucci et al. 2005). Dentre as espécies estudadas, *L. platymetopon* possui oócitos maduros com os maiores diâmetros (3.197,1 µm) (Vazzoler et al. 1996). Apesar de espécies com cuidado parental ou fertilização interna possuírem menor fecundidade do que as demais espécies, elas possuem maiores diâmetros de oócitos maduros (Vazzoler 1996; Suzuki et al. 2000). *Loricariichthys platymetopom* totaliza com cerca de 17% de outras espécies que possuem oócitos maduros entre 2.000 e 5.000 µm de diâmetro no rio Paraná (Suzuki 1992). Isto confere ovos maiores que originam larvas mais desenvolvidas (precociais) no momento da primeira alimentação exógena (Balon 1984), e eclodem em estágio de pós-flexão (Nakatani et al. 2001). Portanto, espécies não nativas com alta sobrevivência da prole podem ter maior sucesso no estabelecimento de novos ambientes (Olden et al. 2006).

As características reprodutivas intrínsecas, como a atividade reprodutiva e o cuidado parental, podem ter beneficiado a colonização de diferentes tipos de habitat por *L. platymetopon* na bacia do alto rio Paraná. *Loricariichthys platymetopon* é capaz de apresentar alta abundância em todos os tipos de biótopos e sua atividade reprodutiva é considerada maior em habitat lêntico e semi-lótico (Dei Tós et al. 1997; Marcucci et al. 2005; Bailly et al. 2011). Esse fato pode ser atribuído ao hábito de indivíduos em estádios iniciais que se abrigam na vegetação aquática para evitar a predação (Baumgartner et al. 1997). Esses ambientes oferecem maior disponibilidade de alimento e abrigo, bem como menores restrições no transporte dos ovos (Dei Tós et al. 1997; Bailly et al. 2011).

No reservatório de Rosana, as maiores capturas de espécies com fertilização interna são de *A. osteomystax* e *T. galeatus.* Outros representantes de Auchenipteridae nativos do rio Paranapanema são o bocudinho *Tatia neivai* (Ihering, 1930) e o manduvê *Ageneiosus militaris* Valenciennes, 1835. As espécies invasoras tiveram suas abundâncias aumentadas no reservatório de Rosana e na planície de inundação do alto rio Paraná, especialmente em áreas lênticas e no reservatório de Itaipu (Suzuki et al. 2005). As fêmeas de Auchenipteridae fertilizadas são capazes de transportar oócitos maduros e espermatozóides antes da fertilização e da desova (Meisner et al. 2000). Assim, esta estratégia permite que as fêmeas aguardem até que as condições ambientais sejam favoráveis à desova (Pusey e Stewart 1989). *Auchenipterus osteomystax* e *T. galeatus* possuem fecundidade relativamente baixa e geralmente escondem sua prole (Bailly et al. 2008). Suas larvas apresentam desenvolvimento relativamente rápido e são bem desenvolvidas quando eclodem (Sanches et al. 1999; Bialetzki et al. 2001). Apesar da ausência de adultos entre 2014 e 2016, as maiores capturas de larvas de *A. osteomystax* foram no rio Pirapozinho entre 2012 e 2015, e indicam que este rio é utilizado como local de atividade reprodutiva (Orsi et al. 2016).

Auchenipterus osteomystax demonstrou utilizar o rio Anhumas como área de reprodução. Dentre as demais espécies, *A. osteomystax* possui o período reprodutivo mais curto e a maior fecundidade registrada (Vazzoler 1996). Por outro lado, as populações da Lagoa 1 possuem mais indivíduos em atividade reprodutiva muito intensa (Agostinho et al. 1993). *Trachelyopterus galeatus* apresentou atividade reprodutiva muito intensa nas lagoas e no rio Pirapozinho, e intensa no rio Anhumas. Ainda, ressalta-se o maior índice gonadossomático em machos de *T. galeatus*, como observado em outros Auchenipteridae (Becker 2001; Mazzoldi et al. 2007). Na área nativa, as enchentes são menos importantes para espécies com fertilização interna. Porém, a ocorrência de inundações parece ser crucial para a sobrevivência de juvenis das duas estratégias, porque tais inundações aumentam a chance de sobrevivência durante o desenvolvimento inicial (Bailly et al. 2008).

As cinco espécies avaliadas possuem desova parcelada e sazonal (Vazzoler 1996; Nakatani et al. 2001; Orsi 2010). A desova de vários lotes por período reprodutivo (desenvolvimento oocitário sincrônico em mais de dois grupos) favorece o estabelecimento por aumentar a probabilidade de envolver uma janela de oportunidade em um ambiente variável (Agostinho et al. 2007). Assim, deve haver uma vantagem adaptativa na produção de vários grupos de oócitos, uma vez que o primeiro grupo pode apresentar riscos devido a flutuações no nível da água (Lowe-McConnell 1999), como nas lagoas estudadas, cujo nível pode variar de acordo com o controle do nível do reservatório de Rosana.

A baixa captura de *Ossancora eigenmanni* pode estar relacionada ao mesmo que ocorreu com a invertívora *Trachydoras paraguayensis* (Eingenmann & Ward, 1907) (Doradidae) (Tonella et al. 2018). No início da invasão, *T. paraguayensis* era abundante na planície do alto rio Paraná. Porém, ao longo dos anos houve uma queda drástica e não se manteve abundante. A disponibilidade de organismos bentônicos pode ter influenciado a queda de *T. paraguayensis* após a redução no aporte de nutriente e sedimento pelo reservatório de Porto Primavera, construída em 1998 (Tonella et al. 2018). Os reservatórios de Rosana e Taquaruçu são os últimos de uma sequência de 11 no canal principal e também podem não estar recebendo aporte de sedimento suficiente para manter populações abundantes de *O. eigenmanni*.

Em resumo, não há um conjunto de características capazes de prever quais espécies de peixes terão sucesso na invasão (Moyle e Marchetti 2006). Contudo, tanto os traços biológicos (i.e. invasividade) quanto a área invadida (invasibilidade) podem facilitar o estabelecimento e a dispersão. O cuidado parental de *S. marginatus* e *L. platymetopon*, e a fertilização interna de *A. osteomystax* e *T. galeatus* parecem ser características importantes para o estabelecimento e manutenção de populações abundantes. Portanto, traços de vida de peixes invasores devem ser estudados sob diferentes aspectos para entender a dinâmica populacional e assim se propor ações para se evitar novas introduções.

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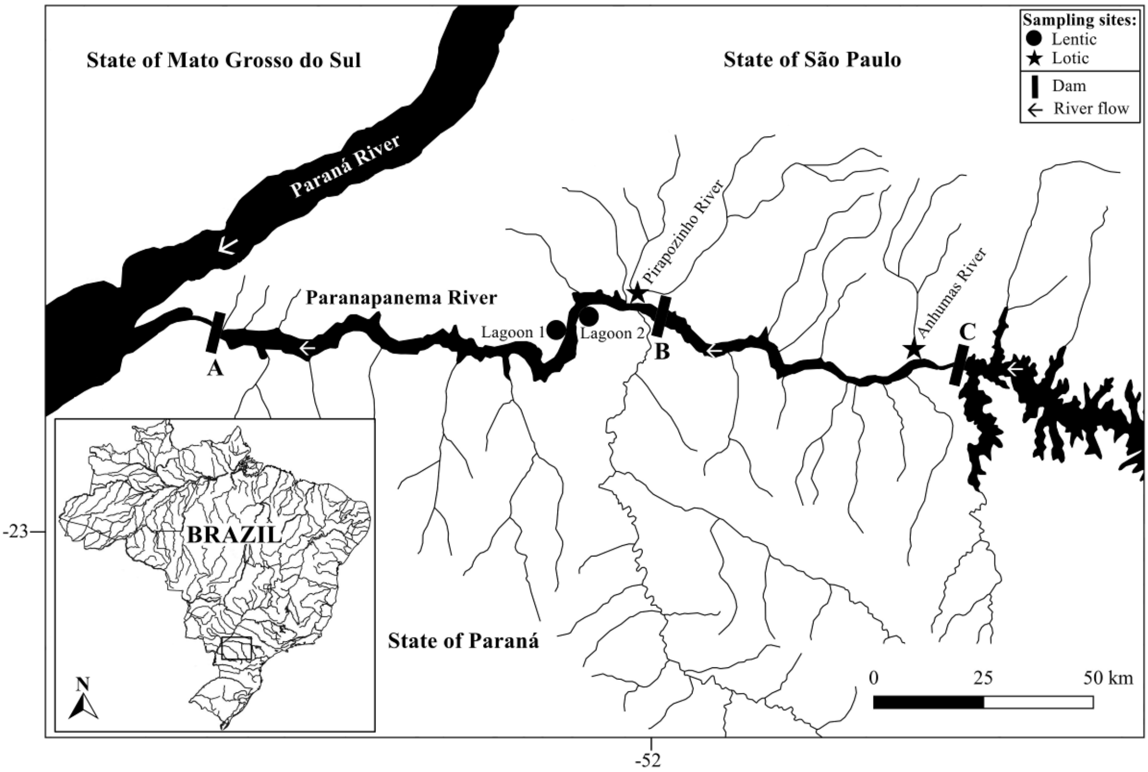

Figura 1 Mapa dos locais de amostragem da bacia do rio Paranapanema. A: barragem de Rosana; B: barragem de Taquaruçu; C: barragem de Capivara

Tabela 1 Caracterização dos locais de amostragem na bacia do rio Paranapanema

Local	Coordenadas	Habitat	Diâmetro /Largura (m)	Profundidade (m)	Fluxo médio (m s^{-1})	Vegetação ripária	Ocupação das margens
Lagoa 1 (L1)	(22º38’04,52” S / 52º09’40,86” O)	Lêntico	143,7	2,63	0	Presente	-
Lagoa 2 (L2)	(22º36’42,27” S / 52º09’31,81” O)	Lêntico	138,9	2,27	0	Ausente	Pastagem
Rio Pirapozinho (PZ)	(22º32’01,11” S / 52º01’38,29” O)	Lótico	20,7	4,34	0,37	Presente	-
Rio Anhumas (AN)	(22º38’47,55” S / 51º26’43,54” O)	Lótico	24,5	2,77	0,23	Presente	-

Tabela 2 Abundâcia de larvas e juvenis de espécies de peixes invasores na bacia do rio Paranapanema durante os períodos reprodutivos entre outubro de 2012 e março de 2015 (Orsi et al. 2016). ‘-‘ indica que não houve captura

Espécies	Lagoa 1		Lagoa 2		Rio Pirapozinho		Rio Anhumas	
	Larva	Juvenil	Larva	Juvenil	Larva	Juvenil	Larva	Juvenil
S. marginatus	7	-	-	2	39	1	12	-
L. platymetopon	-	-	2	-	-	-	2	-
O. eigenmanni	-	-	-	-	-	-	-	-
A. osteomystax	1	-	2	-	116	-	35	-
T. galeatus	3	-	-	-	-	-	-	-

Tabela 3 Captura por unidade de esforço (CPUE) e comprimento padrão médio (cm) de espécies de peixes invasores na bacia do rio Paranapanema entre agosto de 2014 e março de 2016. A variação fornecida representa o desvio padrão

Espécies	L1		L2		PZ		AN	
	Seca	Chuvosa	Seca	Chuvosa	Seca	Chuvosa	Seca	Chuvosa
S. marginatus								
CPUE	1,4	3,6	0	1,4	0	1,4	0	3,6
Comprimento médio	17,9±4,2	18,7±4,0	-	14,0±8,2	-	16,8±4,4	-	23,5±3,8
Variação do comprimento	15,2–22,8	10,3–22,5	-	8,8–23,5	-	13,7–21,8	-	18,0–29,5
L. platymetopon								
CPUE	9,5	19,1	7,3	3,6	1,4	0,9	21,8	12,3
Comprimento médio	21,7±2,7	22,6±2,2	21,7±1,8	21,1±2,7	21,8±2,9	20,8±0,7	17,0±2,5	21,5±2,9
Variação do comprimento	15,3–25,2	18,3–26,5	18,3–24,7	17,5–25,5	19,8–25,2	20,3–21,3	13,4–22,3	16,0–25,7
O. eigenmanni								
CPUE	0,5	2,3	0	1,8	0	0	3,6	3,2
Comprimento médio	7,4	8,9±0,6	-	7,4±0,7	-	-	6,9±0,4	7,6±1,0
Variação do comprimento	-	8,0–9,5	-	6,6–8,2	-	-	6,4–7,4	6,5–9,0
A. osteomystax								
CPUE	0	0	0,5	0,9	0	0	1,4	40,0
Comprimento médio	-	-	19,4	22,0±2,8	-	-	13,0±0,9	16,8±1,1
Variação do comprimento	-	-	-	20,0–24,0	-	-	12,0–13,7	14,5–19,6
T. galeatus								
CPUE	6,8	23,6	4,1	15,5	0	7,3	2,3	3,6
Comprimento médio	14,1±1,3	14,6±1.0	13,1±1,0	14,1±1,3	-	14,4±1,3	14,1±1,2	14,8±1,6
Variação do comprimento	12,7–16,7	11,4–17,7	11,0–14,4	10,7–18,0	-	12,5–17,2	12,5–15,5	12,0–17,0

Tabela 4 Valores de qui-quadrado (χ^2) aplicado à razão sexual, índice gonadossomático (I_G), resultado do teste de Mann-Whitney, e índice de atividade reprodutiva (I_R) de peixes invasores na bacia do rio Paranapanema. $L_{S\ <adu}$, comprimento padrão mímino na maturidade; *, indica diferença significativa entre estações seca e chuvosa. A variação fornecida representa o desvio padrão. '-' indica poucos valores para a análise

Espécies	Local	Razão sexual	χ^2	I_G							I_R
				Fêmeas				Machos			Fêmeas
				$L_{S\ <adu}$	Seca	Chuvosa	Teste de Mann-Whitney	$L_{S\ <adu}$	Seca	Chuvosa	
S. marginatus	L1	2:1	7,44*	18,5	4,29 (±0,00)	4,21 (±1,39)	-	15,6	0,22 (±0,17)	0,40 (±0,27)	38,20 – muito intensa
	L2	2:1	11,11*	-	-	2,79 (±2,98)	-	-	-	0,48 (±0,00)	0,00 – nula
	PZ	1:2	11,11*	21,8	-	3,46 (±0,00)	-	15,0	-	0,66 (±0,35)	0,00 – nula
	AN	7:1	56,25*	18,0	-	6,94 (±2,60)	-	-	-	0,44 (±0,00)	62,78 – muito intensa
L. platymetopon	L1	2:1	5,67*	21,1	2,80 (±1,28)	3,54 (±2,63)	$P = 0,5208$	20,7	0,18 (±0,06)	0,18 (±0,10)	26,49 – muito intensa
	L2	2:1	6,25*	22,5	0,86 (±0,32)	5,73 (±3,43)	$P = 0,0777$	-	0,09 (±0,04)	0,25 (±0,16)	11,46 – muito intensa
	PZ	2:1	4,00*	20,3	1,58 (±0,00)	5,87 (±0,27)	-	-	0,09 (±0,02)	-	5,62 – moderada
	AN	1:1	1,44	19,3	0,93 (±1,29)	7,34 (±2,95)	$P < 0,0001$*	19,5	0,10 (±0,06)	0,19 (±0,19)	10,55 – intensa
O. eigenmanni	L1	2:1	11,11*	8,6	-	6,79 (±6,39)	-	8,9	0,17 (±0,00)	1,42 (±0,00)	25,26 – muito intensa
	L2	3:1	25,00*	-	-	1,10 (±0,44)	-	-	-	0,85	2,61 – incipiente
	PZ	-	-	-	-	-	-	-	-	-	-
	AN	2:1	4,00*	7,4	0,72 (±0,23)	6,38 (±0,53)	$P = 0,0556$	-	0,09 (±0,00)	1,69 (±1,19)	4,96 – incipiente
A. osteomystax	L1	-	-	-	-	-	-	-	-	-	-
	L2	3:0	100,00*	-	0,45 (±0,00)	1,57 (±0,10)	-	-	-	-	0,00 – nula
	PZ	-	-	-	-	-	-	-	-	-	-
	AN	6:1	51,02*	14,6	-	5,37 (±2,73)	-	14,5	0,11 (±0,09)	2,80 (±1,41)	19,25 – intensa
T. galeatus	L1	1:2	8,04*	12,7	3,89 (±2,04)	4,60 (±2,21)	$P = 0,6088$	13,5	4,09 (±1,15)	4,90 (±2,71)	43,35 – muito intensa
	L2	1:1	0,49	12,7	1,30 (±1,58)	4,72 (±2,82)	$P = 0,0077$*	14,0	0,98 (±0,98)	2,42 (±2,53)	30,33 – muito intensa
	PZ	1:1	0,00	12,5	-	6,19 (±1,14)	-	14,5	-	6,77 (±3,21)	36,47 – muito intensa
	AN	1:1	0,59	13,2	4,85 (±3,80)	4,92 (±1,97)	$P > 0,9999$	14,5	0,52 (±0,003)	5,46 (±2,84)	15,13 – intensa

Tabela 5 Traços reprodutivos de espécies de peixes invasores baseados em dados de litetatura. * indica espécie com poucos dados na literatura

Espécies	Comprimento padrão de primeira maturação (cm)	Período reprodutivo	Guilda reprodutiva	Tipo de desova	Diâmetro de oócitos maduros (µm)	Fecundidade (número de oócitos)	Referências para fecundidade
S. marginatus	Fêmea: 12,2 Macho: 11,5	De setembro a abril	Não migradora, fertilização externa, cuidado parental	Parcelada	1.816,3	Máxima: 752 Média: 584	Melo et al. (2017)
L. platymetopon	Fêmea: 15,7 Macho: 14,5	De outubro a março	Não migradora, fertilização externa, cuidado parental	Parcelada	3.197,1	Máxima: 1.451 Média: 962,1	Suzuki et al. (2000)
						Máxima: 850	Marcucci et al. (2005)
						Máxima: 1.594,6 Média: 663,95	Bailly et al. (2011)
O. eigenmanni	*	*	Não migradora, fertilização externa, sem cuidado parental	Parcelada	*	*	
A. osteomystax	Fêmea: 15,3 Macho: 14,7	De setembro a novembro	Não migradora, fertilização interna, sem cuidado parental	Parcelada	1.315,9	14.950	Vazzoler (1996)
T. galeatus	Fêmea F: 10,8 Macho: 11,3	De novembro a fevereiro	Não migradora, fertilização interna, sem cuidado parental	Parcelada	1.615,3	10.330	Vazzoler (1996)

6. CONSIDERAÇÕES FINAIS

O rio Paranapanema situa-se em uma das regiões mais populosas do Brasil e seu curso principal encontra-se altamente modificado por reservatórios hidrelétricos. Tais condições foram facilitadoras para que este rio seja um dos mais invadidos da Ecorregião do alto rio Paraná. Ressalta-se que o Paranapanema é uma bacia representativa na América do Sul onde as atividades humanas e as alteraçãos ambientais estão modificando a composição da fauna de peixes há décadas. Ao comparar diferentes tipos de habitat (lêntico e lótico) na área invadida, as espécies mostraram plasticidade tanto na dieta quanto em traços reprodutivos. A conscientização da população em geral deve ser priorizada, uma vez que esta medida tem custo mais baixo do que qualquer ação de controle ou erradicação. Estudos sobre traços de vida de peixes invasores no alto rio Paraná irão contribuir para o conhecimento de características importantes para prever espécies mais invasivas e locais mais sucetíveis à invasão. Novos tipos de habitat devem ser estudados, tais como riachos e regiões lótica, semi-lótica e lêntica de reservatórios. Por último, poderão ser determinados padrões que ajudem a explicar o sucesso das invasões de peixes no alto rio Paraná.

7. ANEXO – MATERIAL SUPLEMENTAR DO CAPÍTULO 1

Introductions of non-native fishes into a heavily modified river: rates, patterns and management issues in the Paranapanema River (Upper Paraná Ecoregion, Brazil)

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Supplementary material

Appendix 1 Composition and distribution of the non-native fish species introduced into the Paranapanema River basin between 1950 and 2014 (Ros = Rosana Reservoir; Taq = Taquaruçu Reservoir; Cap = Capivara Reservoir; Tib = Tibagi River; Can I = Canoas I Reservoir; Can II = Canoas II Reservoir; Sgr = Salto Grande Reservoir; Our = Ourinhos Fish Ladder; Cha = Chavantes Reservoir; Jur = Jurumirim Reservoir; Upper = Tributaries of the Upper Paranapanema River). Distribution was based in CESP (1994)[1], Shibatta et al. (2002)[2], Barrella and Petrere Jr. (2003)[3], Carvalho et al. (2003)[4], Casatti et al. (2003)[5], Luiz et al. (2003)[6], Carvalho et al. (2005)[7], Pelicice et al. (2005)[8], Britto and Carvalho (2006)[9], Shibatta et al. (2007)[10], Duke Energy (2008)[11], Brandão et al. (2009)[12], Vidotto-Magnoni (2009)[13], Orsi (2010)[14], Zanatta et al. (2010)[15], Ferrareze and Nogueira (2011)[16], Kipper et al. (2011)[17], Arcifa and Esguícero (2012)[18], Garcia et al. (2012)[19], Pagotto et al. (2012)[20], Souto et al. (2012)[21], Britto and Carvalho (2013)[22], Galindo (2014)[23], Garcia et al. (2014)[24], Kurchevski and Carvalho (2014)[25], Orsi and Britton (2014)[26], Frantine-Silva et al. (2015)[27], Garcia et al. (2015)[28]; Hoffmann et al. (2015)[29]; Vidotto-Magnoni et al. (2015)[30], Cerqueira et al. (2016)[31], and Cetra et al. (2016)[32].

Species	**Ros**	**Taq**	**Cap**	**Tib**	**Can I**	**Can II**	**Sgr**	**Our**	**Cha**	**Jur**	**Upper**	**References**
CHONDRICHTHYES												
Myliobatiformes												
Potamotrigonidae												
Potamotrygon cf. *motoro* (Müller & Henle, 1841)	X	X	-	-	-	-	-	-	-	-	-	11, 16
OSTEICHTHYES												
Cypriniformes												
Cobitidae												
Misgurnus anguillicaudatus (Cantor, 1842)	-	-	-	-	-	-	-	-	-	-	X	32
Cyprinidae												
Cyprinus carpio Linnaeus, 1758	-	-	X	X	-	-	-	-	-	X	X	3, 4, 6, 7, 23
	-	-	-	X	-	-	-	-	-		-	6, 31

Ctenopharyngodon idella (Valenciennes, 1844)												
Characiformes												
Curimatidae												
Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)	X	-	-	-	-	-	-	-	-	-	-	20
Anostomidae												
Schizodon borellii (Boulenger, 1900)	X	X	X	-	-	-	-	-	-	-	-	1, 3, 8, 9, 26
Leporinus macrocephalus Garavello & Bristki, 1988	-	-	X	X	X	-	X	-	-	-	-	2, 12, 14, 22, 27
Characidae												
Bryconamericus exodon Eigenmann, 1907	-	-	-	X	-	-	-	-	-	-	-	11
Hyphessobrycon eques (Steindachner, 1882)	X	X	X	X	X	X	X	X	-	X	-	2, 4, 5, 12, 14, 18, 22, 25, 26, 30
Triportheus angulatus (Spix & Agassiz, 1829)	-	-	X	X	-	-	-	-	-	-	-	2, 3, 7, 26
Triportheus nematurus (Kner, 1858)	-	X	X	-	-	-	X	-	X	X	-	7, 9, 11, 13, 14, 25, 27
Metynnis lippincottianus (Cope, 1870)	X	X	X	X	X	X	X	-	-	X	-	2, 7, 9, 11, 12, 14, 16, 22, 25, 26
Serrasalmus marginatus Valenciennes, 1837	X	X	-	-	-	-	-	-	X	-	-	1, 4, 5, 7, 9, 13
Aphyocharax dentatus Eigenmann & Kennedy, 1903	X	X	X	-	X	X	-	-	-	-	-	11, 23, 30
Roeboides descalvadensis Fowler, 1932	X	X	-	-	-	-	-	-	-	-	-	3, 4, 5, 9, 11, 30
Erythrinidae												
Erytrhinus erythrinus (Bloch & Schneider, 1801)	X	-	X	-	-	-	-	-	-	-	-	20, 28
Hoplias lacerdae Miranda-Ribeiro, 1908	-	-	-	-	-	-	-	-	-	X	-	3, 7
Siluriformes												
Loricariidae												
Loricariichthys platymetopon Isbrücker & Nijssen, 1979	X	X	X	X	X	X	-	-	-	-	-	2, 7, 9, 11, 14, 16, 21, 26, 30
Pterygoplichthys ambrosettii (Holmberg, 1893)	X	-	X	-	-	-	-	-	-	-	-	11, 14, 19, 26

Pimelodidae												
Hypophthalmus edentatus Spix & Agassiz, 1829	X	X	-	-	-	-	-	-	-	-	-	3, 11, 17
Pimelodus ornatus Kner, 1858	X	X	-	-	-	-	-	-	-	-	-	1, 9, 11
Sorubim lima (Bloch & Schneider, 1801)	X	X	X	X	-	X	-	-	-	-	-	1, 9, 10, 11, 14, 27
Doradidae												
Ossancora eigenmanni (Boulenger, 1895)	X	X	-	-	-	-	-	-	-	-	-	1, 11, field sampling
Pterodoras granulosus (Valenciennes, 1821)	X	X	-	-	-	-	-	-	-	-	-	9, 11
Trachydoras paraguayensis (Eingenmann & Ward, 1907)	X	X	-	-	-	-	-	-	-	-	-	9, 11
Auchenipteridae												
Auchenipterus osteomystax (Miranda-Ribeiro, 1918)	X	X	-	-	-	-	-	-	-	-	-	1, 7, 9, 11, 17
Trachelyopterus galeatus (Linnaeus, 1766)	X	X	-	-	-	-	-	-	-	-	-	1, 3, 9, 11, 16, 30
Clariidae												
Clarias gariepinus (Burchell, 1822)	-	X	X	X	-	-	-	-	-	-	-	2, 7, 9, 11
Ictaluridae												
Ictalurus punctatus (Rafinesque, 1818)	-	-	X	-	-	-	-	-	X	-	-	7, 15
Gymnotiformes												
Rhamphichthyidae												
Rhamphichthys hahni (Meiker, 1937)	X	X	-	-	-	-	-	-	-	-	-	9, 11, 16
Hypopomidae												
Brachyhypopomus pinnicaudatus (Hopkins *et al.* 1990)	-	-	-	-	-	-	X	-	-	-	-	12
Apteronotidae												
Apteronotus caudimaculosus Santana, 2003	-	-	X	-	-	-	-	-	-	-	-	23
Cyprinodontiformes												
Poeciliidae												
Poecilia reticulata Peters, 1859	X	X	X	X	-	-	X	X	-	-	-	2, 12, 18, 20, 23, 29, 30
Xiphophorus hellerii Heckel, 1848	X	-	-	-	-	-	-	-	X	-	-	13, 20

Perciformes												
Centrarchidae												
Micropterus salmoides (Lacepède, 1802)	-	-	-	X	-	-	-	-	-	-	-	24
Sciaenidae												
Plagioscion squamosissimus Heckel, 1840	X	X	X	X	X	X	X	X	X	-	-	1, 2, 3, 7, 9, 11, 12, 13, 14, 16, 18, 26, 27
Cichlidae												
Astronotus crassipinnis (Heckel, 1840)	X	-	X	-	X	X	X	X	-	-	-	12, 14, 18, 22, 26
Cichla kelberi Kullander & Ferreira, 2006	X	-	X	-	-	-	X	-	X	-	-	12, 13, 16
Cichla monoculus Spix & Agassiz, 1831	-	-	X	-	X	X	-	-	-	X	-	11, 14, 25, 26
Cichla ocellaris Block & Schneider, 1801	-	-	-	-	-	-	-	X	-	-	-	18
Cichla piquiti Kullander & Ferreira, 2006	-	-	-	-	-	-	X	-	X	-	-	12, 13
Cichla temensis Humboldt, 1821	-	-	-	-	-	-	-	X	-	-	-	3, 18
Laetacara araguaiae Ottoni & Costa, 2009	X	-	-	-	-	-	-	-	-	-	-	Field sampling
Oreochromis niloticus (Linnaeus, 1758)	X	X	X	X	X	X	X	-	X	X	X	2, 3, 6, 7, 11, 12, 13, 14, 20, 22, 26, 27, 29, 30, 31
Satanoperca pappaterra (Heckel, 1840)	X	-	-	-	-	-	-	-	-	-	-	4, 5, 11
Coptodon rendalli (Boulenger, 1897)	X	-	X	X	-	-	-	X	-	X	-	2, 6, 7, 14, 18, 20, 25
Pleuronectiformes												
Achiridae												
Catathyridium jenynsii (Günther, 1852)	X	X	-	-	-	-	-	-	-	-	-	3, 11, 17
Total	30	23	22	15	9	9	11	7	8	8	3	

Appendix 2 List of the non-native fish species introduced into the Paranapanema River basin betwen 1950 and 2014, from different continents (*) and freshwater ecoregions of South America (i. e., ecoregions where the species was considered a native species, Abell et al. (2008)). The identification of the year and vector of introduction was based in CESP (1997), Orsi and Agostinho (1999), Bennemann et al. (2000), Graça and Pavanelli (2007), Langeani et al. (2007), Pelicice and Agostinho (2009), Júlio Jr. et al. (2009), Britton and Orsi (2012), and Ortega et al. (2015). The identification of the native range of occurrence was based in Reis et al. (2003), Britski et al. (2007), and Eschmeyer et al. (2016).

Species	**Year**	**Vector**	**Native Freshwater Ecoregion**
CHONDRICHTHYES			
Myliobatiformes			
Potamotrigonidae			
Potamotrygon cf. *motoro*	1982	Itaipu Dam	Orinoco, Amazonas, Uruguay, Paraguay and Lower Paraná River basins
OSTEICHTHYES			
Cypriniformes			
Cobitidae			
*Misgurnus anguillicaudatus**	2014	Aquarium trade	Asia
Cyprinidae			
*Cyprinus carpio**	1979	Fish stocking/Fish farming	Black, Caspian and Aral Sea basins (Asia)
*Ctenopharyngodon idella**	1995	Fish farming	China and Russia (Asia)
Characiformes			
Curimatidae			
Steindachnerina brevipinna	1982	Itaipu Dam	Uruguay, Paraguay and Lower Paraná River basins
Anostomidae			
Schizodon borellii	1982	Itaipu Dam/Fish stocking	Paraguay and Lower Paraná River basins
Leporinus macrocephalus	1997	Fish farming/Fish stocking	Paraguay and Lower Paraná River basins
Characidae			
Bryconamericus exodon	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Hyphessobrycon eques	1992	Aquarium trade	Amazonas, Paraguay and Lower Paraná River basins
Triportheus angulatus	1978	Fish stocking	Amazonas River basin
Triportheus nematurus	1982	Itaipu Dam/Fish stocking	Paraguay and Lower Paraná River basins
Metynnis lippincottianus	1982	Itaipu Dam/Fish farming	Guianas, Amazonas, Paraguay and Lower Paraná River basins
Serrasalmus marginatus	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Aphyocharax dentatus	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Roeboides descalvadensis	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Erythrinidae			
Erythrinus erythrinus	1982	Itaipu Dam/Bait	Orinoco, Guianas, Amazonas, Paraguay and Lower Paraná River basins
Hoplias lacerdae	1978	Fish stocking	Ribeira de Iguape and Uruguay River basins

Siluriformes Loricariidae			
Loricariichthys platymetopon	1982	Itaipu Dam	Uruguay, Paraguay and Lower Paraná River basins
Pterygoplichthys ambrosettii	1982	Itaipu Dam/Aquarium trade	Uruguay, Paraguay and Lower Paraná River basins
Pimelodidae			
Hypophthalmus edentatus	1982	Itaipu Dam	Orinoco, Guianas, Amazonas, Paraguay and Lower Paraná River basins
Pimelodus ornatus	1982	Itaipu Dam	Orinoco, Amazonas, Paraguay and Lower Paraná River basins
Sorubim lima	1982	Itaipu Dam/Fish stocking	Orinoco, Amazonas, Parnaíba, Paraguay and Lower Paraná River basins
Doradidae			
Ossancora eigenmanni	1982	Itaipu Dam	Amazonas, Paraguay and Lower Paraná River basins
Pterodoras granulosus	1982	Itaipu Dam	Guianas, Amazonas, Paraguay and Lower Paraná River basins
Trachydoras paraguayensis	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Auchenipteridae			
Auchenipterus osteomystax	1982	Itaipu Dam	Amazonas, Tocantins-Araguaia, Uruguay, Paraguay and Lower Paraná River basins
Trachelyopterus galeatus	1982	Itaipu Dam	Orinoco, Guianas, Amazonas, Paraguay and Lower Paraná River basins
Clariidae			
*Clarias gariepinus**	1992	Fish farming	Africa
Ictaluridae			
*Ictalurus punctatus**	1997	Fish farming	North America
Gymnotiformes Rhamphichthyidae			
Rhamphichthys hahni	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Hypopomidae			
Brachyhypopomus pinnicaudatus	2005	Bait	Orinoco, Guianas, Amazonas, Uruguay, Paraguay and Lower Paraná River basins
Apteronotidae			
Apteronotus caudimaculosus	1982	Itaipu Dam	Paraguay and Lower Paraná River basins
Cyprinodontiformes Poeciliidae			
Poecilia reticulata	1988	Biological control/Aquarium trade	Orinoco, Guianas, Amazonas (Northern South America) and Barbados and Trinidad (Caribbean Islands)
*Xiphophorus hellerii**	2004	Aquarium trade	Central America

Perciformes			
Centrarchidae			
*Micropterus salmoides**	1950	Fish stocking	North America
Sciaenidae			
Plagioscion squamosissimus	1992	Fish stocking/Fish farming	Orinoco, Guianas and Amazonas River basins
Cichlidae			
Astronotus crassipinnis	1979	Itaipu Dam/Fish stocking/Fish farming/Aquarium trade	Amazonas, Paraguay and Lower Paraná River basins
Cichla kelberi	2004	Fish stocking	Tocantins-Araguaia River basin
Cichla monoculus	1998	Fish stocking	Amazonas River basin
Cichla ocellaris	2008	Fish stocking	Guianas River basin
Cichla piquiti	2005	Fish stocking	Tocantins-Araguaia River basin
Cichla temensis	2008	Fish stocking	Orinoco and Amazonas River basins
Laetacara araguaiae	2013	Aquarium trade	Tocantins-Araguaia River basin
*Oreochromis niloticus**	1979	Fish stocking, Fish farming	Africa
Satanoperca pappaterra	2000	Fish farming/Aquarium trade	Amazonas, Paraguay and Lower Paraná River basins
*Coptodon rendalli**	1993	Fish farming	Africa
Pleuronectiformes			
Achiridae			
Catathyridium jenynsii	1982	Itaipu Dam	Uruguay, Paraguay and Lower Paraná River basins

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