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LUCAS ADRIANO PACHLA

REPRODUÇÃO E RECRUTAMENTO DE PEIXES MIGRADORES DO MÉDIO RIO URUGUAI

CERRO LARGO

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Dissertação de Mestrado, apresentada ao Programa de Pós-Graduação em Ambiente e Tecnologias Sustentáveis da Universidade Federal da Fronteira Sul, como requisito parcial para a obtenção do título de Mestre em Ambiente e Tecnologias Sustentáveis.

Linha de Pesquisa: Qualidade Ambiental

Orientador: Prof. Dr. David Augusto Reynalte-Tataje

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DEDICATÓRIA

A minha Família.

E ao Jurandir Paulo Radiuc (Boca).

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RESUMO

Estudos ecológicos voltados a entender o ciclo de vida dos peixes migradores em ambientes ainda preservados são de fundamental importância para a proteção e a conservação dos estoques naturais, pois estas espécies possuem um grande valor socioêconomico, e ainda fornecem importantes funções ecológicas nos ecossistemas que habitam. Nesse sentido este estudo investigou a reprodução e o recrutamento de espécies de peixes migradores ao longo de um gradiente extensivo fluvial, dividido em quatro estações amostrais no trecho do Médio rio Uruguai entre os países Brasil e Argentina. Onde no primeiro estudo, registrou-se pela primeira vez o comportamento de desova do surubim-pintado *Pseudoplatystoma corruscans* em ambiente natural. Onde constatou-se a reprodução em cardumes, numa proporção de cinco machos para cada fêmea. No agrupamento de desova, existe uma organização social, onde a fêmea de maior tamanho lidera o cardume seguido pelas outras fêmeas e com os machos posicionados nas laterais. Neste estudo foi observado poligamia dos machos e das fêmeas e uma grande disputa dos machos por fertilizar os ovos. No segundo estudo, foram realizadas coletas com apetrechos variados de pesca, abrangendo o rio principal e o tributário de cada um dos quatro trechos selecionados para a região do médio rio Uruguai, juntos os trechos abrangeram cerca 650 km aproximadamente. Através do conjunto de dados de coletas, realizadas entre os anos de 2015 a 2019, avaliou-se os padrões de distribuição na composição, abundância e comprimento total dos juvenis de peixes migradores. Além disso, dentre os principais resultados deste estudo destaca-se o aumento gradativo da abundância de juvenis de migradores dos trechos encaixados de montante para os trechos de planície a jusante e um aumento no comprimento dos jovens de jusante a montante. Além disso, foi verificado um maior número de peixes de menor tamanho nos tributários do que no rio principal. Revelando desta forma que a planície e os rios tributários são fundamentais como áreas de berçário, e que com o decorrer do crescimento há uma migração ascendente que distribui os jovens em toda a sub-bacia. Ambos os estudos mostram que o estado de conservação do Médio rio Uruguai ainda proporciona um ambiente favorável para que as espécies migradoras completem seu ciclo reprodutivo.

Palavras chave: Peixes migradores, juvenis e comportamento reprodutivo.

ABSTRACT

Ecological studies aiming to understand the life cycle of migratory fish in still conserved environments are of fundamental importance for protection and preservation of natural stocks, since these species have a great socio-economic value and provide important ecological functions for the ecosystems in which they develop. In this sense, this study investigated the reproduction and recruitment of migratory fish species along an extensive river gradient in the Middle Uruguay River sub-basin, RS, Brazil. Sampling was carried out with varied fishing equipment, covering the main river and the tributary of each of the four selected sections for middle area Uruguay River, covering together approximately 650 km. Using a data set of sampling made between the years of 2015 and 2019, an assessment of distribution patterns in the composition, abundance and total length of juvenile migratory fish was performed. In addition, a second study that registers for the fist time the spawning behavior of spotted surubim *Pseudoplatystoma corruscans* in natural environment was carried out. Among the main results of the first study, the gradual increase in the abundance of migratory juveniles from the stretches located upstream to the downstream plain stretches and an increase in the length of juveniles from downstream to upstream can be highlighted. Furthermore, there was a greater number of smaller fishes in the tributaries than in the main river. Showing in this way that the plains and tributary rivers are fundamental as nursery areas, and that in the course of growth, there is an upward migration that distributes juveniles across the whole sub-basin. On the other hand, in the second study, it was verified that *P. corruscans* reproduces in shoals, in a proportion of five males for each female. In the spawning group, there is a social organization, where the larger female leads the shoal, followed by the other females and with the males positioned on the sides. In this study, polygamy of males and females, as well as a great dispute between males to fertilized the eggs were observed. Both studies show that the conservation status of the Middle Uruguay River still allows migratory species to successfully complete their reproductive cycle.

Keywords: Migratory fish, juveniles and reproductive behavior.

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LISTA DE ABREVIATURAS E SIGLAS

VU - Vulnerável

EM - Em perigo

CR - Criticamente ameaçado

T - Rio Tributário

P - Rio Principal

Mobt - *Megaleporinus obtusidens*

Sbr - *Salminus brasiliensis*

Plin - *Prochilodus lineatus*

Slim - *Sorubim lima*

Rvul - *Rhaphiodon vulpinus*

SUMÁRIO

1. INTRODUÇÃO GERAL

Em rios maiores, que preservam seus trechos longitudinais, os padrões reprodutivos tendem a se tornar mais complexos (WELCOMME, 1985; TRIBUZY-NETO et al., 2018), reunindo um grande conjunto de características fisiológicas, morfológicas e comportamentais que atuam juntamente com estímulos ambientais, promovendo o deslocamento de animais ao longo de grandes distâncias com diferentes objetivos biológicos (DINGLE, 2006; DINGLE; DRAKE, 2007), entender estes padrões é uma forma de assegurar a preservação e a abundância das espécies, tornando o conhecimento do ciclo reprodutivo de fundamental importância, tanto para proteção de estoques naturais quanto para o cultivo (GODINHO; KYNARD, 2009).

Apesar das espécies migradoras da América do Sul apresentarem táticas reprodutivas semelhantes, alguns aspectos comportamentais são bem distintos, de acordo com a bacia e a espécie. Lacunas no conhecimento de aspectos da biologia, ecologia e comportamento, extensivas a várias espécies tornam alguns atributos os segredos mais bem guardados da natureza (AGOSTINHO et al., 2003; CAROLSFELD et al., 2003).

O grande porte é uma das principais características em comum às espécies migrátorias, o que lhes proporciona grande importância econômica tanto para a pesca comercial como para a pesca esportiva (CAROLSFELD et al., 2003; BARBIERI et al., 2004). Além disso, possuem importantes funções ecológicas nos ecossistemas, pois proporcionam o transporte de energia e nutrientes ao longo de regiões com diferentes condições tróficas (ALLAN et al., 2005). Dessa forma, dado os serviços que prestam aos ecossistemas, a conservação dessas espécies e a manutenção de seus estoques são de grande importância socioeconomica e ecológica.

Entre os principais fatores que podem interferir nos padrões migrátorios estão as hidrelétricas, suas barragens representão obstáculos que causam modificações nas estruturas fisícas dos rios, vêm interferindo no padrão reprodutivo da ictiofauna em diversas bacias no mundo (HOEINGHAUS; WINEMILLER; AGOSTINHO, 2008; LOURES; POMPEU, 2018; PELICICE; AGOSTINHO; GOMES, 2018). Os peixes migrátorios, em particular, são aqueles que mais podem sofrer com esses obtáculos, pois demandam áreas criticas, por vezes distantes entre si, para completar satisfatoriamente o seu ciclo de vida (SUZUKI; AGOSTINHO, 1997; AGOSTINHO et al., 2016). Está adequação pode não se realizar se existe falhas no recrutamento, condição esta que se repetitiva por muito tempo, pode levar a depleção dos estoques (SPARRE; VENEMA, 1997; AGOSTINHO et al., 2016; ARANTES et al., 2018).

Desta forma, entender os padrões reprodutivos em escala espacial, tem grande importância para o conhecimento dos locais de desenvolvimento das populações de peixes migradores, visto que usam distintas areas da bacia para completarem seu ciclo de vida (AGOSTINHO et al., 2003; RESENDE, 2003; ZANIBONI-FILHO; SCHULZ, 2003; GODINHO; LAMAS; GODINHO, 2010). Estudos voltados a comprensão dos padrões reprodutivos de peixes migradores na bacia do rio Uruguai, são oriundos principalmente da sub-bacia do Alto rio Uruguai (REYNALTE-TATAJE; ZANIBONI-FILHO, 2008; HERMES-SILVA; REYNALTE-TATAJE; ZANIBONI-FILHO, 2009; REYNALTE-TATAJE et al., 2012a, 2012b), onde se encontra o trecho mais impactado por barramentos.

O trecho Médio do rio Uruguai, ainda concentra um longo trajeto de fluxo livre sem barramentos, com mais de 800km de extensão, o que torna possível o desenvolvimento de várias espécies migratórias (ZANIBONI-FILHO; SCHULZ, 2003). Em geral pouco se sabe sobre a biologia, distribuição e exigências ecológicas dessas espécies neste trecho, que apresenta características únicas e é composta pelos biomas Mata Atlântica e Pampa. Desta forma, existe uma carência muito grande sobre o ciclo de vida destas espécies na região, principalmente na reprodução e recrutamento, informações essas de fundamental importância para nortear medidas de conservação para esta região.

Nesse sentido, o presente estudo investigou na sub- bacia do Médio rio Uruguai: o comportamento de desova do surubim-pintado *Psedoplatystoma corruscans* (Estudo disposto na secção dos resultados I). E os padrões de distribuição no recrutamento de espécies migrátorias (Estudo disposto na secção de resultados II).

2. REFERENCIAL TEÓRICO

2.1 MIGRAÇÃO E REPRODUÇÃO DE PEIXES MIGRADORES NEOTROPICAIS

A migração é um movimento realizado por vários grupos de animais (DINGLE, 1996), em especial este tipo de comportamento é observado para diferentes espécies de peixes, que realizam movimentos longitudinais e laterais ao longo dos principais corpos d’água (WELCOMME, 1985). Essas migrações tem como estratégia a procura de recursos favoráveis para alimentação, reprodução e sobrevivência (NORTHCOTE, 1978; FERNANDES, 1997; WINEMILLER; JEPSEN, 1998). De acordo com Northcote (1978), as espécies podem utilizar diferentes hábitats de uma bacia ao longo de sua vida, principalmente as espécies migradoras que realizam contínuos deslocamentos relacionados a fatores intrínsecos da espécie e a fatores ambientais. Desta maneira, são considerados três tipos funcionais de migração: (i) Migração reprodutiva; (ii) Migração alimentar; (iii) Migração para refúgio.

Em geral cada espécie possui suas particularidades em relação a estratégia reprodutiva. Agostinho et al., (2007) em uma concepção espacial em relação á estas estratégias, denomina dois tipos de modalidades: Espécies sedentárias e espécies migradoras. Onde as espécies sedentárias se adaptaram a realizar seu ciclo de vida em areas restritas, já as migradoras reconhecidas pela segregação, no tempo e no espaço entre habitats, necessitam de uma extensa área para completar seu ciclo de vida (WINEMILLER, 1989).

Os peixes migradores neotropicais, que fazem sua migração inteiramente em água doce, são denominados potamódromos, e podem percorrer grandes extensões longitudinais de caráter ascendente e/ou descendente ao longo do seu ciclo de vida (LUCAS; BARAS, 2001; AGOSTINHO; GOMES; PELICICE, 2007). As características gerais compartilhadas entre essas espécies migradoras, são corpo grande, maturação tardia, alta fecundidade e desova nas estações de cheia (ARAUJO-LIMA, 1994; WINEMILLER, 1989), onde suas migrações iniciam em condições ambientais especificas, tais como aumento da temperatura, nível do rio e turbidez o que funciona com estimulante para a maturação gonadal (VAZZOLER, 1996).

Para a bacia do Prata considera-se que as migrações são ascendentes, e que a desova em sua maioria acontece no período de chuvas da bacia, principalmente nos trechos altos da calha do rio principal ou nos trechos a montante dos seus principais tributários (NAKATANI; BAUMGARTNER; CAVICCHIOLI, 1997; AGOSTINHO et al., 2003; GOMES et al., 2012). Posteriormente, os ovos e as larvas tendem a derivar na correnteza, onde a elevação dos níveis dos rios juntamente com os vórtices e outros movimentos d’água formam o ambiente necessário à eclosão dos ovos e a primeira fase do desenvolvimento larval (NAKATANI, 2001), assim as larvas em deriva pela correnteza, são direcionadas para as áreas de jusante, até encontrarem as planícies de inundação, onde os variados habitats (lagoas marginais, várzeas, igapós, charcos, pântanos e alagadiços), fornecem alimentos e refúgio para os estágios iniciais (AGOSTINHO et al., 1993; AGOSTINHO; ZALEWSKI, 1995; POMPEU; GODINHO, 2003).

2.2 PEIXES MIGRADORES DO RIO URUGUAI

A maioria das espécies de peixes da América do Sul são conhecidas por realizar deslocamentos ascendentes ao longo do rio para se reproduzir, as espécies que efetuam tal migração são chamadas de espécies de piracema, ou simplesmente espécies migradoras (VAZZOLER; MENEZES, 1992; CAROLSFELD et al., 2003). O Rio Uruguai tem destaque como formador da principal bacia hidrográfica da região sul do Brasil, junto com os rios Paraná e Paraguai, seu trajeto longitudinal é dividido em três regiões distintas (Alto, Médio e Baixo Uruguai), que são separadas por barreiras físicas (ZANIBONI-FILHO; SCHULZ, 2003).

A região do Médio rio Uruguai, local deste estudo, é caracterizada por preservar uma longa seção de fluxo livre, formada por um mosaico de manchas hidrogeomórficas (canais restritos com corredeiras ou piscinas profundas) e trechos preservados como a região do Parque Estadual do Turvo, o que permite entender os padrões de diversidade de peixes em corredores lógicos da Bacia do Prata (MASSARO et al., 2019), em especial os migradores, que precisam de diferentes habitats para se desenvolverem, amadurecerem sexualmente e reproduzirem-se (AGOSTINHO; GOMES; PELICICE, 2007).

Dentre as 275 espécies registradas para a bacia do rio Uruguai (BERTACO et al., 2016), 15 são citadas como migradoras (AGOSTINHO; GOMES; PELICICE, 2007). As principais espécies migradoras presentes no Médio rio Uruguai estão elencadas no Tabela 1 abaixo:

Tabela 1- Principais espécies migradoras encontradas no Médio rio Uruguai. As fotos de cada uma destas espécies estão dispostas no tópico apêndice.

FAMÍLIA	ESPÉCIE	NOME POPULAR
Anostomidae	*Megaleporinus obtusidens* (Valenciennes, 1847)	Piava
Bryconidae	*Brycon orbignyanus* (Valenciennes, 1850)	Piracanjuba Bracanjuva
	Salminus brasiliensis (Cuvier, 1816)	Dourado
Cynodontidae	*Rhaphiodon vulpinus* Spix e Agassiz , 1829	Cachorra Facão
Doradidae	*Pterodoras granulosus* (Valenciennes, 1821)	Armau Armado
Prochilodontidae	*Prochilodus lineatus* (Valenciennes, 1847)	Grumatã Curimbatá
Pimelodidae	*Pseudoplastystoma corruscans* (Spix & Agassiz, 1829)	Surubim-pintado Pintado
	Steindachneridion scriptum (Miranda Ribeiro, 1918)	Suruvi, Bocudo
	Sorubim lima (Bloch & Schneider, 1801)	Surubim bico-de-pato Tamanco

Algumas destas espécies se encontram em risco de extinção tais como: *Salminus brasiliensis* (Cuvier, 1816) que está na situação de VU (Vulnerável), *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) na situação de EN (em perigo), *Brycon orbignyanus* (Valenciennes, 1850) e *Steindachneridium scriptum* (Miranda Ribeiro,1918) na situação de CR (criticamente ameaçado) segundo o DECRETO N.º 51.797, DE 8 DE SETEMBRO DE 2014 do GOVERNADOR DO ESTADO DO RIO GRANDE DO SUL.

Estas espécies de peixes migradores, são atualmente as mais sucetivéis a pressões ambientais (PELICICE; AGOSTINHO; GOMES, 2018), como perda de habitat, poluição, espécies invasoras, esforço de pesca sobre os seus cardumes na época da reprodução e especialmente alterações hidrológicas, visto que necessitam de longos trajetos de fluxo livre para conexão de suas áreas de reprodução e alimentação, assim a implantação de hidrelétricas e a construção de barramentos se tornam uma das principais ameaças, exercendo efeitos drásticos a suas populações (AGOSTINHO; THOMAZ; GOMES, 2005).

3. RESULTADOS

Os resultados deste estudo estão apresentados na língua inglesa sob a forma de dois artigos científicos. Os referidos artigos são apresentados na seção 3. Na seção 3.I. está o *short communication* intitulado: "**First record of the mating behavior of the spotted surubim *Pseudoplatystoma corruscans* (Spix & Agassiz 1829) in the Uruguay River**" formatado nas normas da revista JOURNAL OF FISH BIOLOGY e na seção 3.II está o artigo intitulado: "**Spatial variation in the distribution of recruitment of juvenile migratory fish in the Middle Uruguay River, between Brazil and Argentina**" o qual esta preparado para ser submetido após os ajustes na revista RIVER RESEARCH AND APPLICATIONS.

3.1 RESULTADOS I

First record of the mating behavior of the spotted surubim *Pseudoplatystoma corruscans* (Spix & Agassiz 1829) in the Uruguay River

Abstract

Pseudoplatystoma corruscans is a large migratory catfish native to the La Plata and São Francisco basins. Its life cycle involves long distance displacements between refuge, feeding and spawning sites. However, there is limited information about reproductive dynamics, especially spawning and mating behavior. In this short note, we provide the first record of the mating behavior of *P. corruscans* in the wild. This event was observed in the Middle Uruguay River (Brazil), during the austral summer (January 2019), early in the evening, when the river water level was level rising. A school of approximately 25 fish was video recorded, being five females (protuberant abdomen and larger body size) and twenty males. The largest female led the school, followed by other females and males. Polygamy characterized the mating behavior of *P. corruscans*. Spawning activity lasted for approximately 10 minutes, when males disputed insistently the posterior region of the females. Eventually, some males, apparently exhausted, turned upside down as they were pushed away by competitors. During this event, fish were in a date of pronounced agitation, and males had abrasions in the head.

Keywords: Female; Catfish; Polygamy; School; Spawning.

Resumo

Pseudoplatystoma corruscans é um grande bagre migratório nativo das bacias do Prata e São Francisco. Seu ciclo de vida envolve deslocamentos de longa distância entre locais de refúgio, alimentação e desova. No entanto, há informações limitadas sobre a sua dinâmica reprodutiva, especialmente sobre o comportamento de acasalamento e desova. Nesta breve nota, fornecemos o primeiro registro do comportamento de acasalamento de *P. corruscans* na natureza. Este evento foi observado no rio Uruguai Médio (Brasil), durante o verão austral (janeiro de 2019), no início da noite, quando o nível do rio estava subindo. Um cardume de aproximadamente 25 peixes foi gravado em vídeo, sendo cinco fêmeas (abdômen protuberante e tamanho corporal maior) e vinte machos. A maior fêmea liderou o cardume, seguida por outras fêmeas e machos. A poligamia caracterizou o comportamento de acasalamento de *P. corruscans*. A atividade de desova durou aproximadamente 10 minutos, quando os machos disputaram insistentemente a região posterior das fêmeas. Eventualmente, alguns machos, aparentemente exaustos, viraram de ventre para cima quando foram empurrados pelos concorrentes. Durante este evento, os peixes estavam em estado de agitação pronunciada e os machos sofreram abrasões na cabeça.

Palavras chaves: Fêmea, bagre, poligamia, cardume e desova.

Introduction

The diversity of potamodromous fishes in South America is remarkable (CAROLSFELD et al., 2004; LEVÊQUE et al., 2007), and it includes a wide variety of morphological, physiological, and behavioral traits (TOUSSAINT et al., 2016). Migratory fishes are among the most iconic, since they reach large sizes, display complex life cycles, and move periodically between distant habitats (CAROLSFELD et al., 2004). They are valued by inland fisheries (HOEINGHAUS; WINEMILLER; AGOSTINHO, 2008; HALLWASS; SILVANO, 2016). And historically attracted the attention of the scientific community. However, basic and important aspects about their ecology remain poorly understood, especially the reproductive behavior of large catfishes. Even some migratory patterns have been unraveled recently (BARTHEM et al., 2017; HAUSER et al., 2019), however, mating and spawning behaviors in the wild remain largely unreported.

This is the case of the spotted surubim *Pseudoplatystoma corruscans* (Spix, Agassiz, 1829), the largest potamodromous catfish in the La Plata and São Francisco basins. This predator grows up to 2.0 m and 100 kg, and migrates over hundreds of kilometers to complete its life cycle (AGOSTINHO et al., 2018). Long-distance displacements occur between refuge, feeding and spawning sites (GODINHO; KYNARD; GODINHO, 2007), with reproduction restricted to the rainy season (austral summer). The spotted surubim is a total spawner, releasing small yellowish eggs (1.6 mm diameter) in the water current (SATO, 1999); females are larger than males, however, information about spawning and mating behavior of males and females remains anecdotal (GODINHO et al., 1997; BRITO; BAZZOLI, 2003). Direct observation is impaired by environmental conditions, since spawning is ephemeral and takes place in turbulent waters with reduced transparency (GODINHO; KYNARD; GODINHO, 2007; REYNALTE-TATAJE et al., 2012a).

Understanding the reproductive behavior of the spotted surubim is essential to inform conservation and management plans, especially because overfishing and hydropower expansion have negatively affected migratory fish stocks in all basins (PELICICE et al., 2017). In this short note, we describe, for the first time, the mating and spawning behavior of *P. corruscans* in the Middle Uruguay River, where the species is now endangered (EN) and rare. We performed direct observation and video recording of males and females displaying spawning activity in the river, and presented information about the environmental conditions under which this event occurred.

Results and discussion

The mating behavior of *P. corruscans* was observed on 19 January 2019, in a river section of the Uruguay River (27°11'43.63"S and 53°59'29.16"O) located within two protected areas, the Turvo State Park (Derrubadas, Rio Grande do Sul, Brazil) and the Yabotí Biosphere Reserve (Missiones, Argentina) (Fig. 1). In this segment, the river flows across a narrow channel embedded in a steep valley, with well-preserved banks, rapids and deep pools (Ziober et al. 2015); depth ranges between 2 and 20 m. Turbulent waters characterize this river section, where small swirls eventually come up to the surface. On the observed day, the river water lervel was 2.16 m above its average level and rising rapidly, under rainy and cloudy weather. Water transparency was low (Secchi depth = 49 cm) and temperature was 26.2 °C.

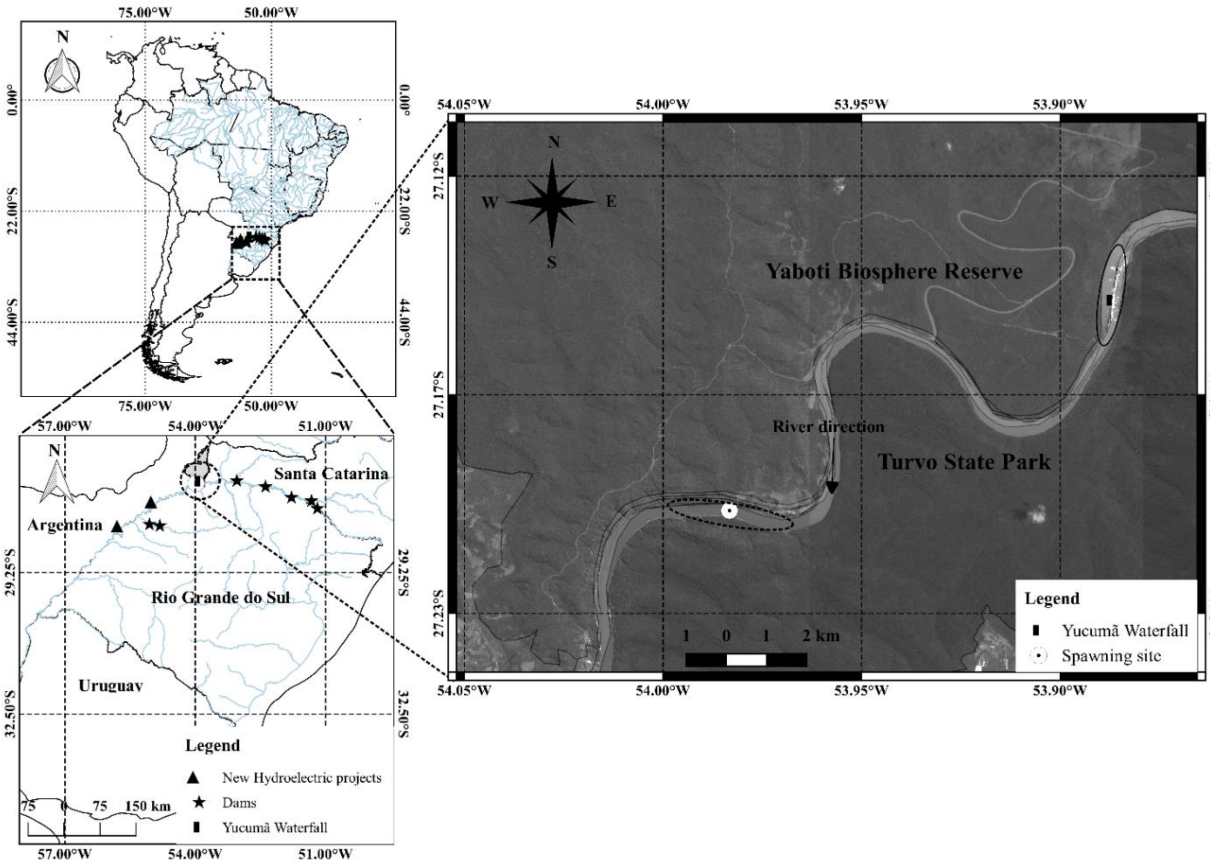

Figure 1 - Locality where the mating event was recorded.

We followed (on a boat) a small school of *P. corruscans* early in the evening (21 h). The school was moving slowly in the main channel near the water surface. Besides this school, other groups (between 7 and 10) were also observed in a stretch of approximately 5 km.

The studied aggregation was composed of at least 25 individuals, being five females and twenty males. Females were identified by their protuberant abdomen and larger body size, with estimated weights between 25 to 60 kg – based on body lengths observed in the recorded video. Males had smaller body sizes and estimated weights between 7 to 13 kg. The largest female led the school, followed by other females and males (**Figure 2 A**).

Spawning time lasted for approximately 10 minutes, and part of this event was filmed. Males disputed contact with the posterior region of the females, but other males continuously repelled them. Displaced males submerged and reemerged near the caudal fin of females, competing again for the position (**Figures 2BC)**. Eventually, some males floated belly up, apparentely exhausted, as they as they were pushed away from the posterior region of females. Furthermore, males had abrasions in the head. During this event, fish were in state of pronounced agitation.

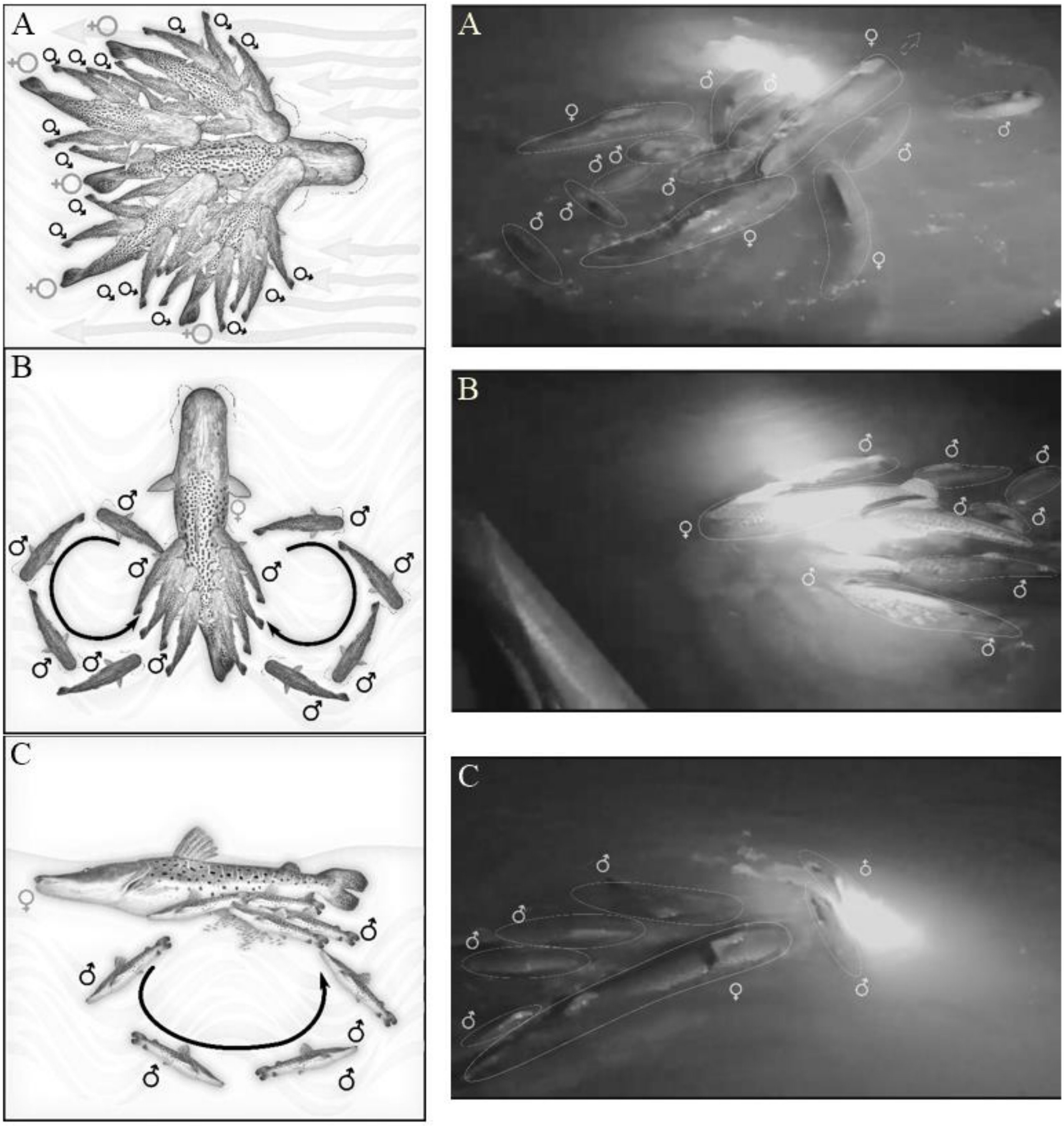

Figure 2 - School of *P. corruscans* engaged in a “mating and spawning cycle”, as recorded in the main channel of the Uruguay River, southern Brazil.

The overall reproductive behavior of the spotted surubim matches patterns reported for Neotropical potamodromous species (DE GODOY, 1975; VAZZOLER, 1996). It included the formation of aggregations (SATO; GODINHO, 2003), spawning early in the evening (DE GRAAF et al., 1999; BAUMGARTNER et al., 2004), in rapids (SATO et al., 1997), and during floods (WELCOMME, 1985). These conditions may increase offspring survival, because low light and high turbidity protect eggs against visual predators, while turbulent currents increase the fertilization rate and disperse young toward nursery areas.

The recorded spawning event indicated polygamy, since many males disputed a single female to fertilize released eggs. Males predominated in the school, in the proportion of five males to one female. Brito and bazzoli (2003) observed a lover ratio in the São Francisco River, with three males to one female. The spotted surubim is highly fecund, and a single female is capable of releasing hundreds of thousands eggs, i.e., more than 2,500 eggs/gram of weight (SATO, 1999). Under these conditions, with several males simultaneously releasing gametes in the water current, the number of fertilized eggs and genetic variability tend to increase. Brito and Bazzoli (2003) also reported that fishermen of the São Francisco River observed large schools of the spotted surubim during reproduction, where females float belly up during spawning. We did not record this behavior, but males kept agitated during the event and many had injuries in the head; after spawning, they floated belly up, possibly exhausted. It is likely, therefore, that males, and not females, drift exhausted as soon as the spawning happens.

Traditionally, it was believed that fish schools are indistinct aggregations with no leadership (BREDER JR, 1959; HUTH; WISSEL, 1992). However, new studies suggest that fish may play different functions in the school (PITCHER; WYCHE; MAGURRAN, 1982; KIFLAWI; MAZEROLL; GOULET, 1998), with leaders that coordinate movement and direction (PITCHER; WYCHE; MAGURRAN, 1982; BUMANN; KRAUSE, 1993). In the present study, shortly before spawning, the spotted surubim formed aggregations where a large female led the way, followed behind or laterally by other females and males. This ephemeral group is probably driven by reproductive stimuli, but we do not rule out the possibility that larger females can identify favorable environments for spawning, which would make it the leader of the school (WARNER, 1988).

According to Zaniboni-filho and Schulz (2003), some potamodromous fishes reproduce in the main channel while others use tributaries. We recorded the spawning of the spotted surubim in the main channel of the Uruguay River. Reynalte-Tataje, et al., (2017). observed the presence of early stages larvae of *P. corruscans* approximately 200 km downstream from the study site, confirming its preference for the main channel. These findings indicate that the Yabotí Biosphere Reserve and Turvo State Park work as spawning grounds for the spotted surubim in the Middle Uruguay River basin.

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3.2 RESULTADOS II

Spatial variation in the recruitment distribution of juvenile migratory fish in the Middle Uruguay River, Brazil

Abstract

Especially in fish, studies regarding recruitment in population organization models are an important tool to understand the dynamic process of several fish species' reproduction. Neotropical migratory fish species, besides the socio-economic value, play important ecological functions in ecosystems. In this study we investigated the recruitment of migratory fish species along an extensive river gradient in the sub-basin of the Middle Uruguay River, betweem Brazil and Argentina. For sampling, we used several fishing equipment to cover the main river and the tributaries of each of the four sections selected for the sub-basin, these sections were selected spatially in order to abrager various environments, such as valleys embedded in headland regions such as floodplain areas, together these sections covered approximately 650 km traveled. Through the set of sample data, obtained between 2015 and 2019, distribution patterns in composition, abundance and total length of juveniles were evaluated. Through the sampled data set, which was obtained between the 2015 and 2019, distribution patterns in the composition, abundance and total length of the juveniles were evaluated. A total of 768 individuals of migratory juvenile fish were sampled, belonging to nine species, where specimens of the order Characiformes predominated (98.01%). The spatial distribution of juveniles was characterized by a gradual increase in the abundance from upstream to downstream. In contrast, an increase in the length of juveniles from downstream to upstream was observed. In addition, there was a higher number of smaller fish in the tributary streams than in the main river. The observed patterns reveal that floodplains and tributary rivers are fundamental as recruitment areas, and that as growth progresses, there is an upward migration that distributes juveniles along the whole sub-basin.

Keywords: unregulated stretch, floodplain, river channel, fish reproduction.

Resumo

Especialmente em peixes, estudos de recrutamento em modelos de organização populacional, são uma importante ferramenta para entender o processo dinâmico da reprodução. Principalmente as espécies migradoras neotropicais, que além de possuirem valor socioêconomico, fornecem importantes funções ecológicas nos ecossistemas que se desenvolvem. Nesse contexto, este estudo investigou o recrutamento de espécies de peixes migradores ao longo de um gradiente extensivo fluvial na sub-bacia do Médio rio Uruguai, RS, Brasil. Foram realizadas coletas com apetrechos variados de pesca, abrangendo o rio principal e tributário de cada um dos quatro trechos selecionados para a sub-bacia, juntos os trechos abrangeram cerca 650 km aproximadamente. Através do conjunto de dados de coletas, realizadas entre os anos de 2015 a 2019, foram avaliados padrões de distribuição na composição, abundância e comprimento total dos juvenis. Foram coletados um total de 768 indivíduos de juvenis de peixes migradores, pertencentes a nove espécies, onde predominaram indivíduos da ordem Characiformes (98,01%). A distribuição espacial dos juvenis das principais espécies, foi caracterizada por um gradativo aumento da abundância dos trechos encaixados de montante para os trechos de planície a jusante. Na contramão foi observado um aumento no comprimento dos jovens de jusante a montante. Além disso, foi verificado um maior número de peixes de menor tamanho nos tributários do que no rio principal. Revelando desta forma que a planície e os rios tributários são fundamentais como áreas de berçário, e que com o decorrer do crescimento há uma migração ascendente que distribui os jovens em toda a sub-bacia.

Palavras Chaves: trecho não regulado, planície de inundação, canal de rio, reprodução de peixes.

Introduction

Ecologists increasingly see the importance of incorporating recruitment studies into models of population dynamic (CONNELL, 1978; CONNOR; SIMBERLOFF, 1983; FONTELES-FILHO, 2011). The influence of environmental variable on recruitment and population structure has been especially well documented among marine fish (CARR, 1991; MILICICH; MEEKAN; DOHERTY, 1992; AULT; JOHNSON, 1998; TOLIMIERI, 1998; SALE et al., 2005; PONDELLA; HORN, 2006) and temperate freshwater fish (COPP, 1990; GORSKI et al., 2011; HOGBERG; PEGG, 2016; REINHOLD et al., 2016; SIRIWAN; BOONSATIEN, 2018). Interactions among temporal and spatial aspects of physical disturbance, production and dispersion of individuals, play critical roles in determining colonization dynamics, population age structure, and community pattern among these organisms (POFF et al., 1997; THORP; THOMS; DELONG, 2006). Evaluating the role of these interactions in regulating the population pattern of, e.g. migratory fish, is essential for the theoretical development of population ecology (KARR; FREEMARK, 1985; THOMAZ et al., 2001; THOMAZ; BINI; BOZELLI, 2007). In this sense, evaluating the distribution and abundance of juveniles, the new recruits, can be important to know where they develop and to determine the number of individuals that will be added to the breeding stock (MYERS, 1998; FONTELES-FILHO, 2011).

A principal pattern for reproductive and recruitment of migratory fish in neotropical rivers is an upstream spawning movement followed by a downstream dispersion of eggs, larvae and juveniles into floodplain habitats (CAROLSFELD et al., 2003). Survival are directly related to the integrity of main river and it tributary river, since the possibility of lateral migration into tributaries that are often very important for reproduction and can serve as rearing areas for young fishes (COWX; WELCOMME, 1998). Moreover, connections between the river and floodplains habitats are essential in the life history of many migratory fishes that have evolved to use the inundated areas for initially developing and feeding (AGOSTINHO; GOMES; PELICICE, 2007). Neotropical rivers have become increasingly regulated by dams as a consequence of hydroelectricity demand. This disturbance have affected fish diversity especially when they induce fragmentation along the river (PELICICE et al., 2017), causing negative effects on the different stages of the life cycle and lead to the population declines and species losses (ARANTES et al., 2018). Migratory fishes, in particular, have been significantly affected by river regulation and fragmentation, and populations are currently suppressed or extirpated from some stretches or even the whole basins (LOURES; POMPEU, 2018; PELICICE; AGOSTINHO; GOMES, 2018).

In La Plata basin, few large rivers preserve their pristine fluvial conditions. Notables exceptions are the Paraguai-Paraná axis (RABUFFETTI et al., 2017) and the Uruguay river (MASSARO et al., 2019), which still preserve long unregulated sections. Both systems offers the possibility to understand how fish reproduction and recruitment take place along the river. The Uruguay river is currently subjected to several disturbances (e.g., dams, pollution, deforestation), but the Middle reach still preserves significant lotic segments with riparian vegetation a long fluvial stretch (ca. 900 km) is found between Foz do Chapecó and Salto Grande reservoir. The presence of this free-flowing section, with its constricted section and its floodplain area, provides essential elements the recruitment of migratory fish of the La Plata Basin.

In this scenario, we investigated the migratory recruitment along an extensive fluvial gradient (ca. 650 km) in the Middle Uruguay River. In particular, we analyzed the distribution of juveniles along the Middle Uruguay, a section characterized by different hydro-geomorphological conditions and landscape structure i.e., the presence of constricted channels, floodplain areas and tributaries rivers. Variation in flow, depth, channel width and the presence of riparian vegetation, for example, could be important for recruiting of migratory fish. In this sense, based on models applied to neotropical floodplain rivers (VAZZOLER et al., 1996; AGOSTINHO et al., 1997; SUZUKI et al., 2009; MOUNIC-SILVA et al., 2019), we predict spatial variation in recruitment a long of the basin. In this sense, we expect higher number of juveniles in floodplain patches, where food production is highest and habitat diversity is high (JUNK, 1997). Moreover, we expect there to be spatial variation in the different size classes within juveniles. Since some authors show that fish have different optimal habitats for each moment of their development (COWX; WELCOMME, 1998; STONER; MANDERSON; PESSUTTI, 2001).

Material and Methods

Study area

The Plata basin is the main hydrographic basin in the southern region of Brazil with 3,170,000 km^2 drainage area, and is composed of the Paraguay River, Paraná River and Uruguay River. The Uruguay River is divided into three regions: Upper, Middle and Lower Uruguay, which are separated by natural and antropical barriers. Yucumã Fall, located inside the Turvo State Park, Brazil, is the division between the Upper and Middle Uruguay. The Salto Grande Dam, located in the border between Argentina and Uruguay, divides the Middle from the Lower Uruguay. In the last 20 years a series of small and large dams have been built on the Upper Uruguay River.

The Middle Uruguay River is characterized by a long fluvial segment, a free area that, in addition to the small remaining section downstream of the Upper Uruguay River, can reach 900 km. This segment still has areas with riparian forests in both margins (Brazil-Argentina border) mainly within two conservation units, the Yaboti Biosphere Reserve (Argentina) and the Turvo State Park (Brazil); Human activities, however, have induced some disturbances, including the loss of riparian vegetation, urbanization and overfishing. This sub-basin is characterized by a width that varies from 280 m in the upstream section, to 2,000 m in the river section near the Salto Grande HPP. It has an average slope of 9 cm/km, which is more marked in the upper region, where the Atlantic Forest Biome predominates. The lower reach, downstream from the municipality of São Borja, contains a floodplain area and belongs to the Pampa Biome (ZANIBONI-FILHO; SCHULZ, 2003).

Samplings were realizated at four sampling stations, which included collections from two points the principal river (P) and the tributaries river (T), to cover a spatial extent of 650 km (Fig. 1) and to encompass a long river gradient with different hydro-geomorphic patches: constricted channel with shallow rapids and deep pools, and a floodplain. The characterization of the sampling stations is show in Tab. 1.

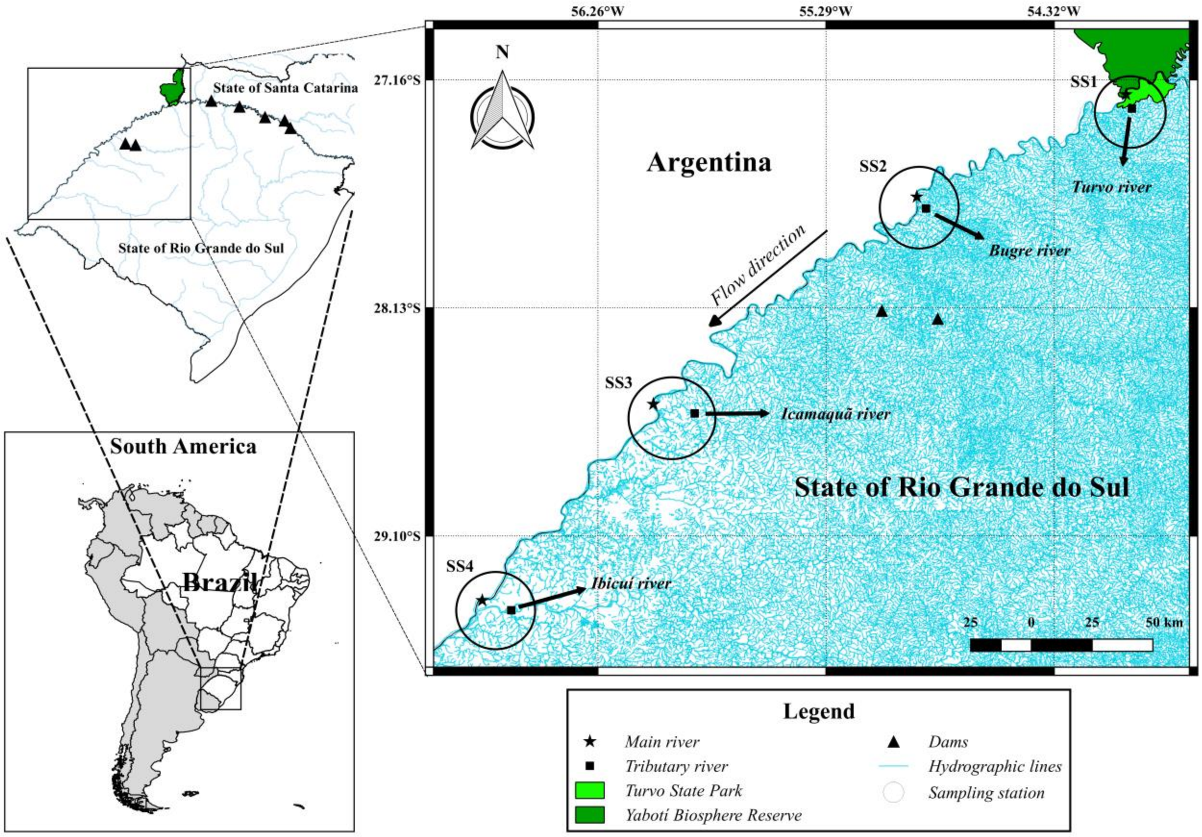


Figure 1 - Location of sampling station along the Middle Uruguay River, RS, Brazil. Derrubadas (SS1), Porto Vera Cruz (SS2), São Borja (SS3) and Itaqui (SS4).

SS1: This sampling station is located between the municipalities of Derrubadas and Esperança do Sul, RS and includes the Turvo River. This section, in general, presents little anthropized, riparian vegetation due to being located between two conservation units, Turvo State Park (Brazil) and the Yaboti Biosphere Reserve (Argentina) where the Atlantic Forest Biome predominates. This station is characterized by a series of rapids with deep wells. Where some of these wells can reach more than 40 m in depth. It is a stretch of narrow river where the average width is 280 m.

SS2: This sampling station is located between the mucipalities of Porto Vera Cruz and Porto Lucena, RS, and includes the Bugre River. This stretch is already associated with floodplains. This station is characterized by a series of rapids with deep wells, where the Atlantic Forest Biome starts to decline. It presents anthropogenic alterations, with little riparian forest, a depth that can vary between 2 and 60 m in depth and an average width of 900m in length.

SS3: This sampling station is located in the municipality of São Borja, RS, and includes the Icamaquã River. This stretch of the river is located at the beginning of the Pampa biome and is characterized by having river edges that are quite impacted by the presence of rice cultivation. It has a moderate lotic stretch, with an average depth of 2 meters and 1,200 meters wide. In this sector, some lowland areas are already found.

SS4: This sampling station is located in the municipality of Itaqui, RS, and includes the Ibicuí River. This stretch located in the Pampa Biome has a moderate lotic stretch, with an average depth of 2 meters and 1,500 meters wide. The small slope in this region allows the formation of floodplain areas on both sides of the Uruguay River. The sandy bottom of the tributary river has yet to be highlighted.

Table 1 - Information about sampling stations along the Middle Uruguay River, Brazil. P= Principal river, T= Tributary river, (*) Distance from the beginning of the Middle Uruguay River Basin.

Sampling Station	Municipalities	Coordinates	Distance*	Altitude (m)	River	Width (m)
SS1	Derrubadas	27º10’64”S 53º54’31”W	16 (Km)	135	P T	350 50
SS2	Porto Vera Cruz	27º42’.01”S 54º53’47”W	217(Km)	91	P T	900 50
SS3	São Borja	28 º34’.15”S 56º0.9’51”W	450 (Km)	52	P T	1250 70
SS4	Itaqui	29°25'.23"S 56°46'27.55"W	650 (km)	41	P T	1300 200

Data collection

In order to evaluate the composition of juvenile migratory fish and the size distribution in different sampling stations, data from collections that were carried out between the years 2015 and 2019 were used. These collections did not have a periodicity, because years monthly collections were made and others in which seasonal collections were made. Despite this, the sampling effort in the use of the sampling equipment between the sampling stations was equal.

To assess the abundance of juveniles in the different sampling stations and relationship with environment variables, standardized collections were carried out from October 2018 to March 2019. For this survey, two monthly collections were made at each sampling station and two sets of equal equipment were used at each point in the sample. Each sampling station had two collection points, one on the principal river (P) and the other on the lower tributary region (T).

Different fishing gears were employed to maximize fish capture, covering littoral, benthic and pelagic habitats. Fish were collected using a set of gillnets with different mesh sizes (25, 30, 40 mm between adjacent knots), 100 m long and 2.0 high and sizes (15 and 20 mm between adjacent knots), 20 m long and 2.0 high. Using 720 m^2 of network per point. All set of fishing gears remained deployed for 12 hours, mainly overnight. Additionally, we hauled a seine (5 mm mesh-size, 20 m long and 2 m high) and cast net (30 mm mesh-size, 20 m diameter and 12 mm mesh-size, 20 m diameter) over littoral areas, totaling five samples at each point for day for equipament.

Specimens were fixed in 10% formalin and preserved in 70% ethanol. Species were identified according to Zaniboni-Filho et al. (2004) and Da Graça and Pavanelli (2007). Voucher specimens will be deposited in the Fish Collection at the State University of Maringá, Paraná, Brazil. This study is part of Project 534 entitled “Fish Ecology of the Middle Uruguay” carried out under permits 55011-2 (ICMBio) and 104/2017 (Secretaria do Meio Ambiente e Infraestrutura do Estado do Rio Grande do Sul). This last permit allowed fish sampling in protected áreas (Turvo State Park).

We characterized habitat condition at each point by measuring limnological, land cover, spatial and geomorphological variables. The following limnological variables were recorded during each sampling occasion: water temperatura (°C), dissolved oxygen ($mg.l^{-1}$), current velocity ($m.s^{-1}$), pH, electrical conductivity ($uS.cm^{-1}$), transparency (cm) and water level (m). Water transparency was measured with a Secchi disk, current velocity with flowmeter and water level with registered through the website of the Naval Prefecture and PCD Manager (website of ANA - National Water Agency). Other water quality variables with a multiparameter. For each point, we recorded the following geomorphological descriptors: river width, altitude and distance of each point to the beginning of the sub-basin (Middle Uruguay). These descriptors were measured from georeferenced satellite images in Google Earth Pro (Google, Menlo Park, California). Finally, we calculated the percentage of riparian vegetation covering each point. For this, an area of 10 km^2 (10 km long and 0.5 km of each river side) was considered at each margin of the sampling point. This calculation was permormed using the program Fragstats package v. 4.0.

Individuals were classified as juvenile according to the total length of the first maturation (Lt 100) (VAZZOLER et al., 1996; CAROLSFELD et al., 2004; FEITOZA et al., 2004; ARAYA et al., 2005; VICENTIN et al., 2012). Juveniles were further divided into three size classes: C1= small juveniles; C2= middle juveniles and C3= large juveniles.

Data analyses

For the total data set of the collections carried out between the years 2015 to 2019, an analysis of the proportion of monthly catches was applied, for the total of young fish and for the three most abundant species (*Salminus brasiliensis, Prochilodus lineatus* and *Megaleporinus obtusidens*), the period of greatest concentration of young fish is verified, in different size classes. For this same set of data, a non-parametric analysis of variation (Kruskall-Wallis) was also performed to assess the variations in total length (mm) of juveniles between sampling stations and rivers, followed by the Dunn test for multiple comparisons. This non-parametric test was chosen because a variation was not homogeneous.

For the data set of the collections carried out between November 2018 and March 2019, they were applied as analyzes; Non-parametric analysis of variation (Kruskall-Wallis) to assess differences in the number of juveniles between sampling stations and rivers, followed by the Dunn test for multiple comparisons. This non-parametric test was chosen because a variation was not homogeneous.

To test differences in taxonomic composition between sampling stations and river and tributaries (Principal vs. Tributary), a two-way PERMANOVA was applied to the utilization matrix using the Bray-Curtis index with 4999 permutations (ANDERSON, 2005). Post-hoc comparisons in pairs were made using the t test.

Canonical Correspondence Analysis (CCA) was used to assess the connection between the assembly of juvenile fish and the set of environmental variables (TER BRAAK, 1995). The abiotic data were transformed into a log ($\log_{10} x + 1$), with the exception of pH. The inclusion of the environmental variables in the CCA was based on a *forward selection* procedure. Statistical significance of the juvenile species-environment relationship was tested using the Monte Carlo method (999 randomizations). Statistical significance implied $\alpha = 0.05$. All analyzes were performed using PCORD version 5 and Statistic version 7.1.

Results

Taxonomic Composition

Between the years 2015 and 2019, juveniles of migratory fish belonging to two orders six families, eight genera and nine species were collected (Table 2), The order of the Characiforms represented 97.91% (752) of the captured individuals. Distributed in the following proportions respectively, *Prochilodus lineatus* the most abundant species with 75.00% (576), *Salminus brasiliensis* with 11.19% (86), *Megaleporinus obtusidens* 8.59% (66), *Brycon orbignyanus* 1.69% (13) and *Rhaphiodon vulpinus* 1.43% (11). Siluriformes, on the other hand, represented only 1.95% (15) of the individuals caught, being distributed in the following species, *Sorubim lima* 1.43% (11), *Pterodoras granulosus* 0.39% (3), *Pseudoplatystoma corruscans* 0.13% (1) and *Steindachneridion scriptum* 0.13% (1).

Table 2 - List of juvenile captured between february 2015 and march 2019 in the sampling station (SS) of Middle Uruguay River, RS, Brazil. P= Principal river; T= Tributary river.

TAXA	SS1		SS2		SS3		SS4	
	P	T	P	T	P	T	P	T
CHARACIFORMES								
Anostomidae								
Megaleporinus obtusidens (Valenciennes, 1837)	2				19	4	2	39
Bryconidae								
Brycon orbignyanus (Valenciennes , 1850)						13		
Salminus brasiliensis (Cuvier , 1816)	11		21	1	30	14	2	7
Cynodontidae								
Rhaphiodon vulpinus Spix e Agassiz , 1829	5		2		4			
Prochilodontidae								
Prochilodus lineatus (Valenciennes , 1837)				3	6	140	19	408
SILURIFORMES								
Doradidae								
Pterodoras granulosus (Valenciennes , 1821)						3		
Pimelodidae								
Pseudoplatystoma corruscans (Spix & Agassiz , 1829)								1
Sorubim lima (Bloch & Schneider , 1801)							6	5
Steindachneridion scriptum (Miranda Ribeiro, 1918)			1					

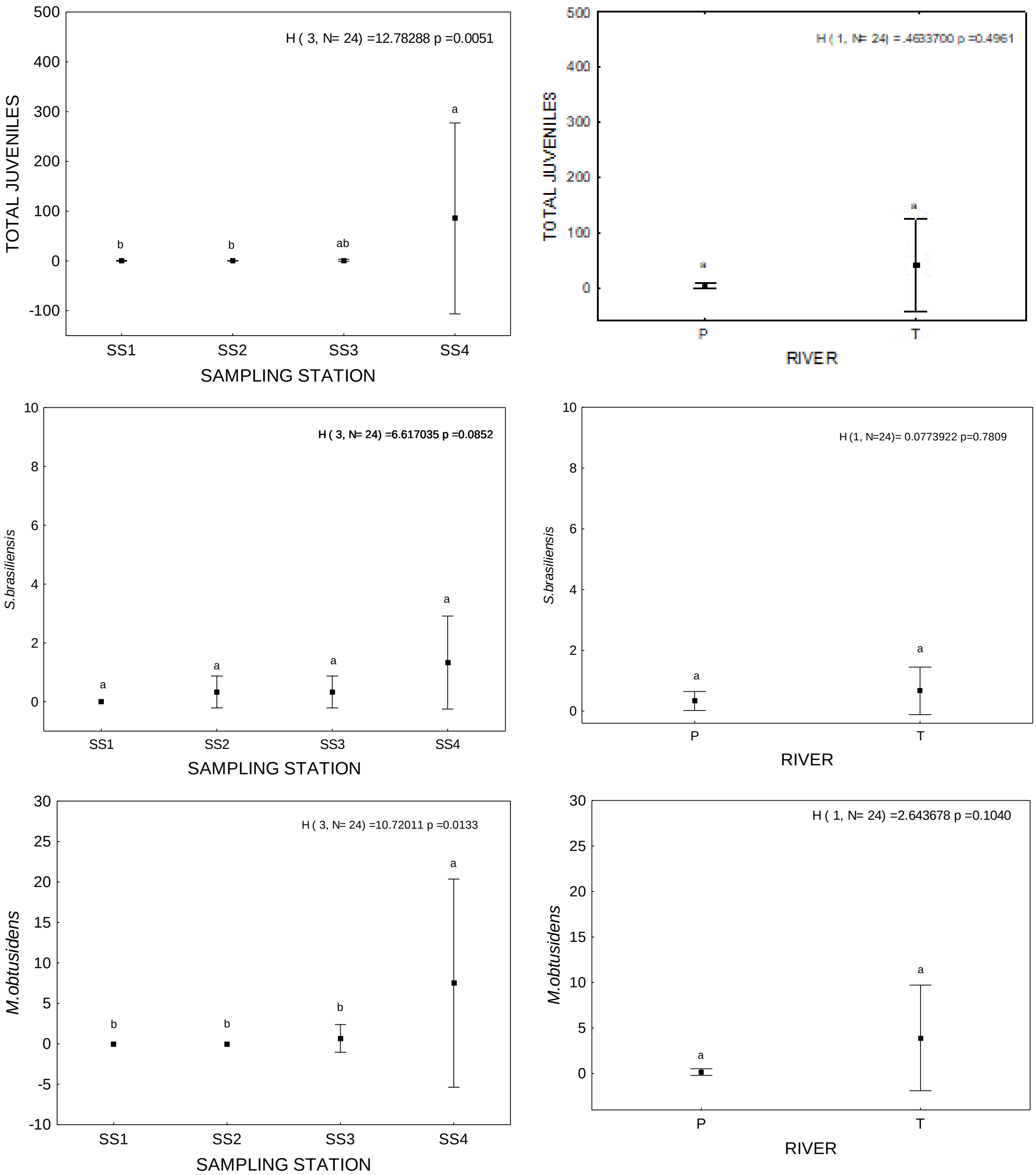
Considering only this period, there was a significant difference in the juvenile composition of species between sampling station (PERMANOVA; pseudo-F=337.22; p<0.05) and between river P and T (PERMANOVA; pseudo-F=415.43; p<0.05). No statistical difference was found in the interaction between sampling stations and rivers P e T (PERMANOVA; pseudo-F=-80.31; p>0.05). These results are probably related to the significant variation in composition species observed between sampling station and also between rivers. *P. lineatus* was more abundant in the tributary of SS4 and *M. obtusidens* in the tributary of SS3 and SS4. S*. brasiliensis* was mainly captured in SS1 and SS2 in the principal river (Table 2). Results of the paired comparison of composition species at sampling stations are shown in Table 3 and it shows that only SS3 and SS4 have a similar composition of juvenile species (P> 0.05).

Table 3 - Result of the t-test evaluating for paired comparisons of the composition of juvenile species captured at the different sampling stations in the Middle River Uruguay in the period 2018 to 2019. Bold t-values indicate statistical difference (p<0.05).

	Sampling station			
	SS1	SS2	SS3	SS4
SS1		**78.15**	**60.65**	**21.06**
SS2			**30.42**	**15.05**
SS3				9.42

Spatial distribution of juvenile abundande

Kruskal-Wallis showed significant differences between the distribution of total juveniles (H=12.78; P=0.005), *P*. *lineatus* (H=13.66; P=0.003) e *M*. *obtusidens* (H=10.72; P=0.013) in the station sampling. Only *S*. *brasiliensis* no showed significant differences (H=6.61; P=0.085). Kruskal-Wallis applied to assess the spatial variation of juvenile abundance between the principal and tributary rivers did not show significant differences, except in SS4 (P>0,05; Figura 2).


H (3, N= 24) =12.78288 p =0.0051
TOTAL JUVENILES
SAMPLING STATION
SS1
SS2
SS3
SS4
H (1, N= 24) =.4633700 p =0.4961
RIVER
P
T
H (3, N= 24) =6.617035 p =0.0852
S.brasiliensis
H (1, N=24)= 0.0773922 p=0.7809
H (3, N= 24) =10.72011 p =0.0133
M.obtusidens
H (1, N= 24) =2.643678 p =0.1040

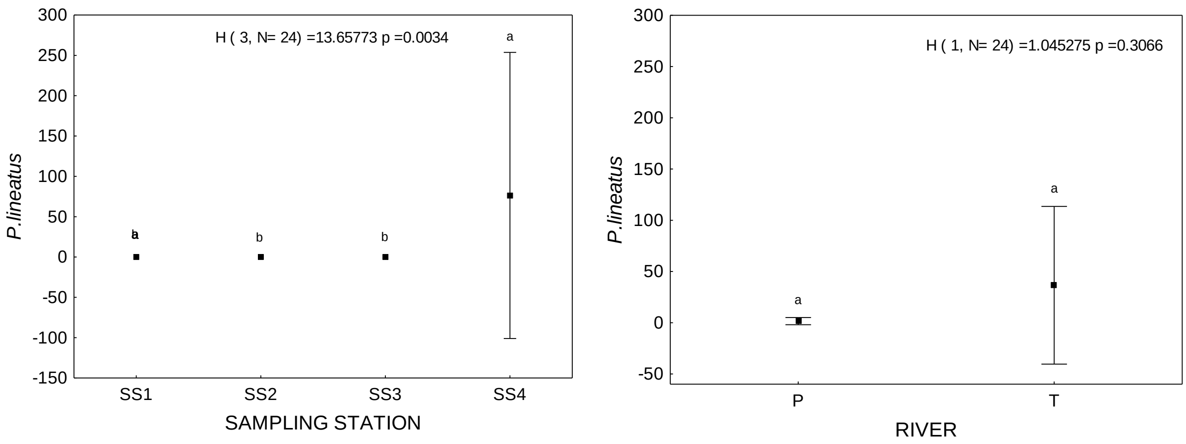
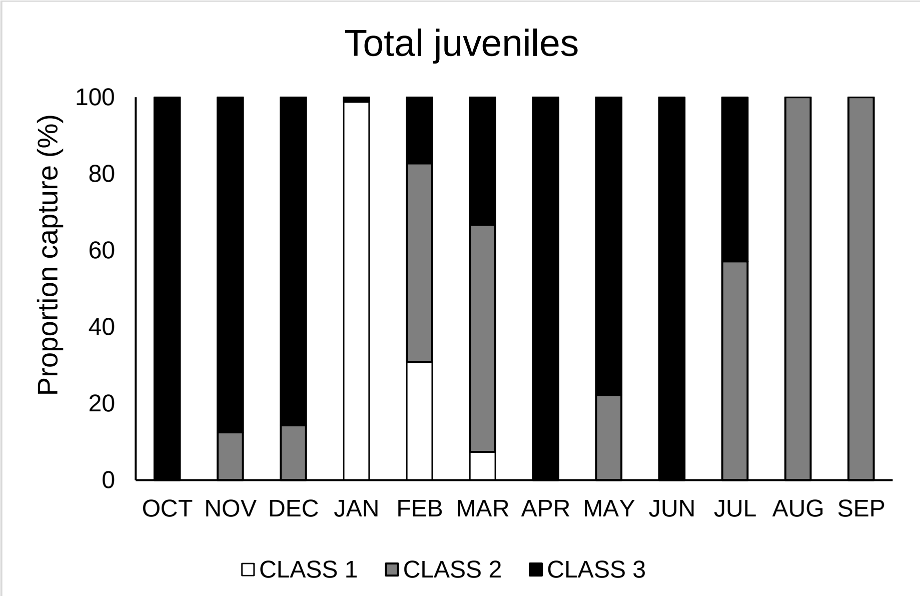
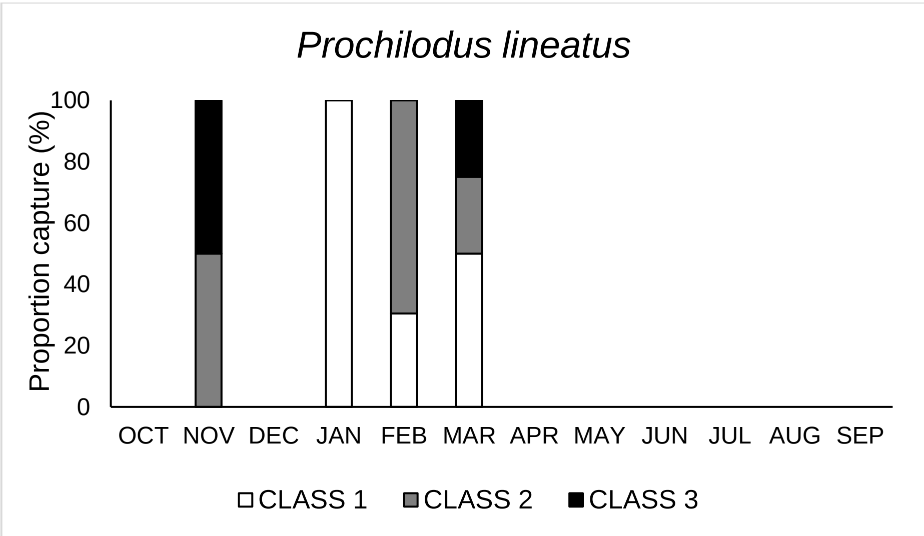
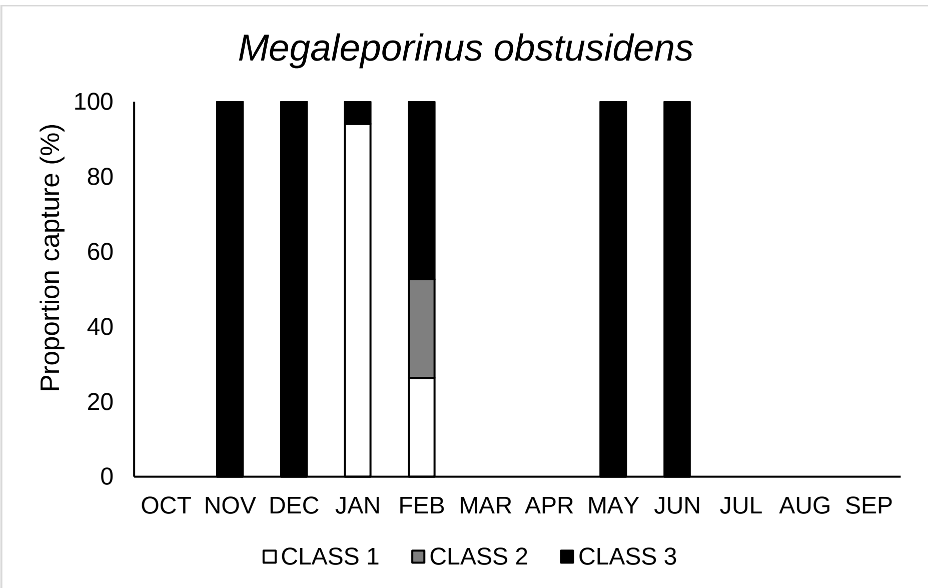


Figure 2 - Kruskal-Wallis results, average density and standard error for total juveniles, *Salminus brasiliensis*, *Prochilodus lineatus* and *Megaleporinus obtusidens* captured in each sampling station and river. Different letters represent significant differences.

In figure 3, evaluating the proportion of monthly catch, the total of juveniles and the three most abundant species (*S*. *brasiliensis*, *M*. *obtusidens* and *P*. *lineatus*) relating to three size classes, determined according to the Lt 100 of each species, is it is possible to observe that class 1, to which the smaller individuals belong, is restricted to the months of January, February and March, with the month of January presenting the highest proportion of class 1 juveniles, for all species. Classes 2 and 3, on the other hand, are randomly distributed in most months of the year. In February for *M*. *obtusidens* and *S*. *brasiliensis*, and in March for *P*. *lineatus*, there is a very similar proportion between the three size classes.


Total juveniles
Proportion capture (%)
100
80
60
40
20
0
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP
CLASS 1 CLASS 2 CLASS 3


Prochilodus lineatus
Proportion capture (%)
100
80
60
40
20
0
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP
CLASS 1 CLASS 2 CLASS 3


Megaleporinus obstusidens
Proportion capture (%)
100
80
60
40
20
0
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP
CLASS 1 CLASS 2 CLASS 3

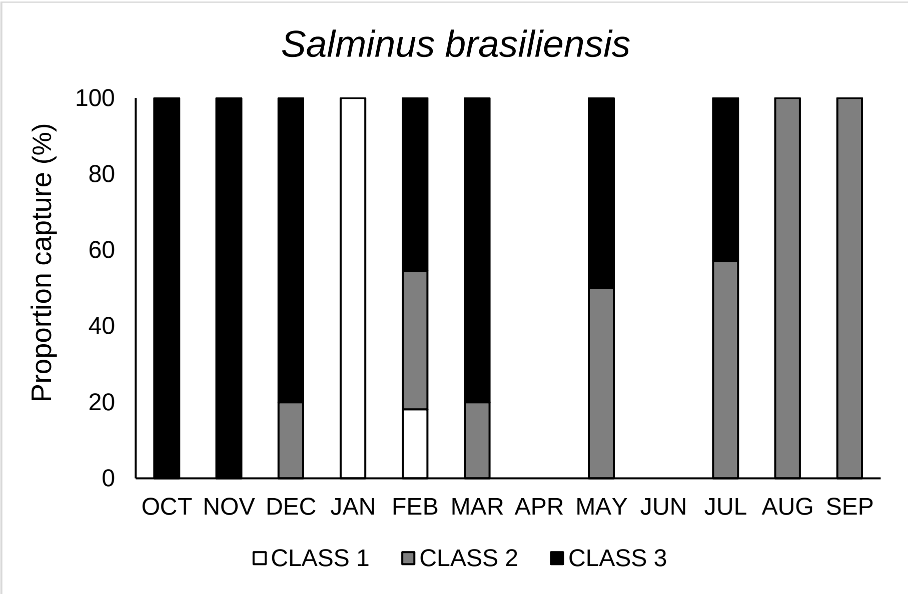
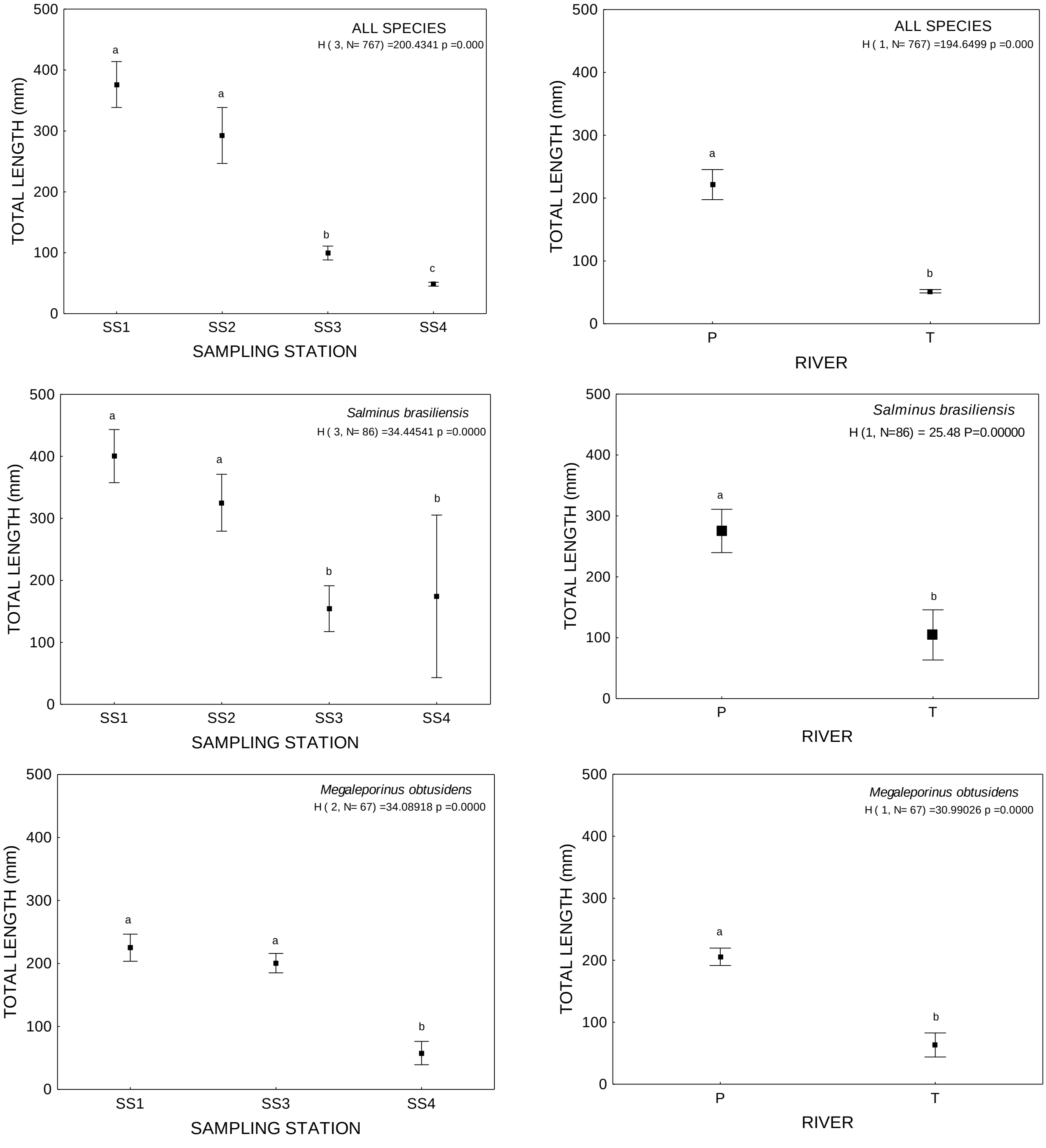


Figure 3 - Proportion of monthly capture of juvenile fish of *Salminus brasiliensis*, *Megaleporinus obtusidens* and *Prochilodus lineatus*, collected in the different sampling station in the Middle Uruguay River, Brazil, in the period from February 2015 to March 2019.

Kruskal Wallis showed statistically significant differences in the total length of juveniles of *S. brasiliensis* (H=34.44; P=0.000), *P. lineatus* (H=45.61; P=0.000), *M. obtusidens* (H=34,08; P=0.000) and total juveniles (H=200.43; P=0.000) captured at different sampling stations. In general, the results show a size gradient over the sampling stations, where the smallest individuals are found downstream and the largest upstream (P<0.05; Figure 4).

Kruskal-Wallis applied to assess the spatial variation in the total length of juvenile between the principal and tributary rivers also show significant differences of total juveniles (H=194.65; P=0.000), *P*. *lineatus* (H=10.58; P=0.001), *M*. *obtusidens* (H=30.99; P=0.000) and *S*. *brasiliensis* (H=25.48; P=0.000). In general, a greater presence of small juveniles can be seen in the tributaries and the largest in the principal river (P <0.05; Figure 4).


ALL SPECIES
H (3, N= 767) =200.4341 p =0.000
TOTAL LENGTH (mm)
SAMPLING STATION
SS1 SS2 SS3 SS4
ALL SPECIES
H (1, N= 767) =194.6499 p =0.000
TOTAL LENGTH (mm)
RIVER
P T
Salminus brasiliensis
H (3, N= 86) =34.44541 p =0.0000
TOTAL LENGTH (mm)
SAMPLING STATION
SS1 SS2 SS3 SS4
Salminus brasiliensis
H (1, N=86) = 25.48 P=0.00000
TOTAL LENGTH (mm)
RIVER
P T
Megaleporinus obtusidens
H (2, N= 67) =34.08918 p =0.0000
TOTAL LENGTH (mm)
SAMPLING STATION
SS1 SS3 SS4
Megaleporinus obtusidens
H (1, N= 67) =30.99026 p =0.0000
TOTAL LENGTH (mm)
RIVER
P T

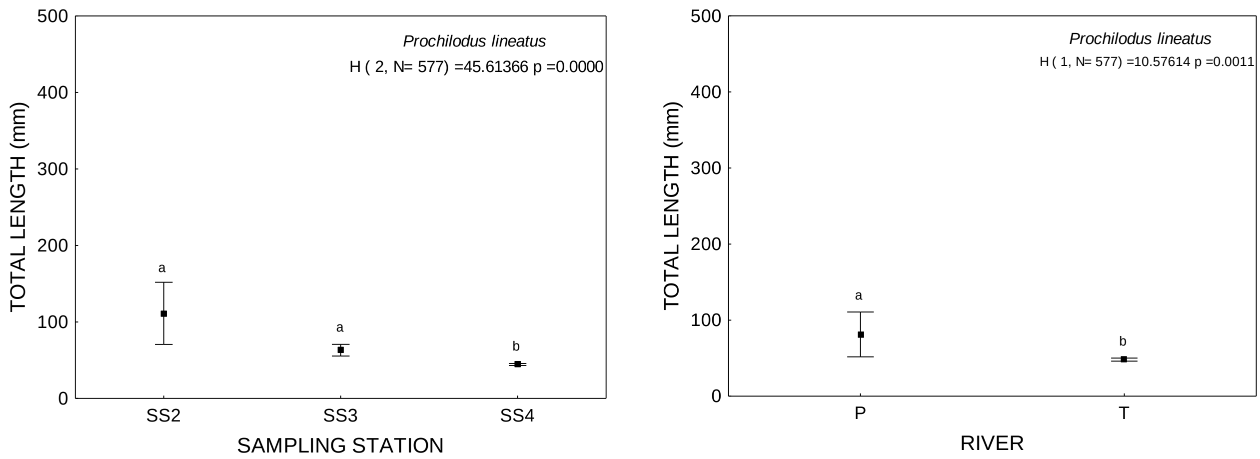


Figure 4 - Kruskal-Wallis results, averagem of total length and standard error for total juveniles, *Salminus brasiliensis*, *Prochilodus lineatus* and *Megaleporinus obtusidens* captured in each sampling station and river.

Association with environmental variables

The process of *forward selection* included two spatial variables (distance and width) and three limnological variables (electric conductivity, dissolved oxygen and water level).

The CCA considering the limnological and spatial variables indicated by the *forward selection* exhibit 55.4% of the explanation for the variation of the data (Figure 5) and showed a significant correlation with the species abundance (Monte Carlo test; $p<0.05$). The distribution of sampling station along the CCA1 axis was influenced by distance (r= 0.72), while the distribution along the CCA2 axis was affected mainly by electric conductivity (r= -0.65) and width (r= -0.80). *M*. *obtusidens* (r= 0.53), *P*. *lineatus* (r=0.64) and *S*. *lima* (r= 0.48) were directly associated with distance, being more present in floodplain station SS4. *S*. *brasiliensis* (r= 0.50) and *M*. *obtusidens* (r= 0.69) were inversely related to river width and electrical conductivity, typical tributary conditions, opposite to that observed with *R*. *vulpinus* (r=-0.76).

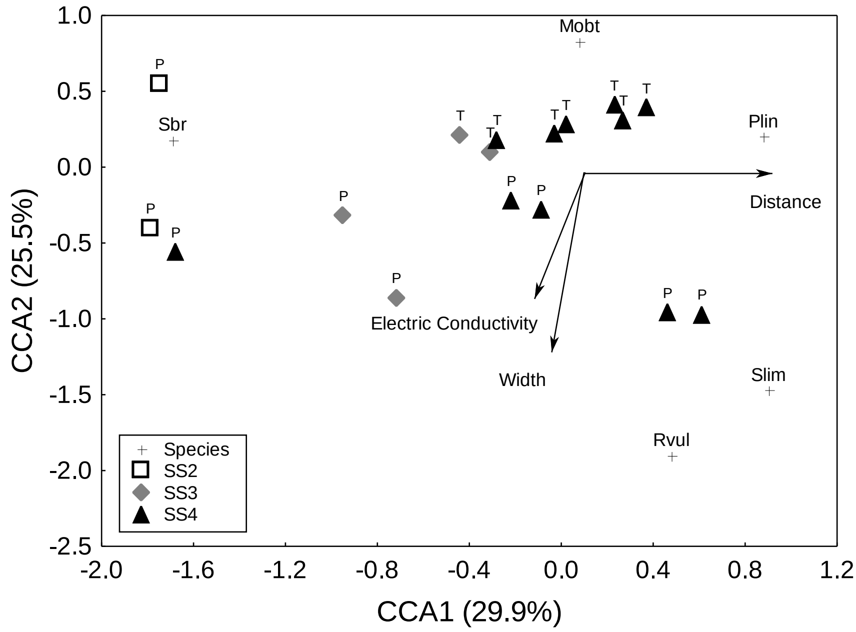


Figure 5 - Canonical Correspondence Analysis (CCA) applied to investigate the association between juvenil fish assemblage and environmental variables along the Middle Uruguay River.

Discussion

The longest free stretch on the Uruguay River is in its Middle section, where it has a long fluvial segment of approximately 800 km. This study, which is one of the few carried out in this sub-basin evaluating the distribution of juvenile migratory fish, covered a stretch of approximately 650 km, with distinct geomorphological characteristics and landscape that , including part of the Atlantic Forest and Pampa biomes, where different types of environments were observed, especially docked regions and floodplain areas. We assume that there is a spatial variation in the abundance of juveniles and their size classes along the Middle Uruguay River, and the results obtained confirm our hypothesis. In addition, the work reveals the importance of distance from the beginning of the sub-basin and river width, as well as the limnological variable electrical conductivity. It is also important to highlight a great diversity of juvenile migratory fish species, including some threatened with extinction, as well as a greater abundance of juveniles in floodplain areas.

Floodplains play a fundamental role in the life cycle of many fish species, especially in relation to the recruitment of migratory fish in different parts of the world (TURNER et al., 1994; LOWE MC CONNEL, 1995; KILLGORE; BAKER, 1996; AGOSTINHO et al., 2003; KING; HUMPHRIES; LAKE, 2003; MOUNIC-SILVA; LEITE, 2013; MOUNIC-SILVA et al., 2019), because recruitment is more successful under condiction great habitat diversity, abundant food and shelter against predators, both for larvae and juveniles (LEITE, 2000; SÁNCHEZ-BOTERO; ARAÚJO-LIMA, 2001; LEITE, 2004). In this sense, our results for the Middle Uruguay River reveal a gradual increase in the abundance of juvenile migratory fish, from the upstream stretches towards downstream and floodplain areas. As well as an upward migration of juveniles towards upstream, where sub-adult individuals are usually found. These results are in agreement with others found in the Plata basin (GODOY, 1972; BONETTO; CASTELLO, 1985; AGOSTINHO et al., 1993).

Our study also shows the importance of the Middle Uruguay River as an environment for migratory fish species recruitment, which are dispersed in search of food in other stretches of the basin, where the reproduction and recruitment of these species is reduced, especially due to the inadequate environmental condition, such as short tributary streams and the presence of landforms or due to anthropic impacts such as reservoirs and environmental pollution (ZANIBONI-FILHO; SCHULZ, 2003; REYNALTE-TATAJE et al., 2012a; LOPES et al., 2019). The relevance this medium stretch as a recruitment area had also been verified by Mounisc et al. (2019), who found a significantly higher number of juveniles in the Middle sub-basin than in the Upper Uruguay River.

In Neotropical rivers, there is a predominance of species of the orders Characiformes and Siluriformes (VARI; MALABARBA, 1998; REIS; KULLANDER; FERRARIS, 2003). This directly reflects in the composition of migratory fish from the Uruguay River, where these orders share similar proportions of these species. For this reason, an aspect that drew attention in this study was the discrepancy in the abundance of individuals between these two orders, since 98% of the sampled fish belong to the order Characiformes. Massaro et al. (2019), evaluating the diversity and structure of the fish assemblage in the Middle Uruguay River, described a higher abundance of migratory Siluriformes fish in the upper stretches of the basin, relating the abundance of these fishes to the presence of a docked river with deep wells, while the migratory characiforms were distributed throughout the sub-basin. A spatial segregation between Siluriformes and Characiformes was also verified by Martine (2019), who observed that Siluriformes larvae, unlike Characiformes larvae, were more present in the main river than in the tributaries, and by Reynalte-Tataje et al. (2017)

who found that Siluriformes larvae are more abundant in the upper section of Middle Uruguay than in the downstream section.

Several authors have suggest that macro and microhabitats throughout a basin imply strong effects on diversity and abundance (ARANTES et al., 2018; FOUBERT et al., 2018; LOPES et al., 2019). It is possible that the spatial segregation observed in larvae and adults of Characiformes and Siluriformes fish also applies to the recruitment areas, and that Characiformes and Siluriformes are recruiting in different environments. In addition to spatial differences, time differences have also been observed between Characiformes and Siluriformes in the Plata basin. The later reproductive migration seems to be a common pattern among the Siluriformes. An opposite trend was verified among the Characiformes that started migration earlier (OLIVEIRA et al., 2015). In the present study, we believe that while migrating Characiformes may be recruiting in the tributaries streams of the downstream region, Siluriformes are recruiting in the upper stretch of the main river, an environment that, due to geomorphological characteristics (such as steep slopes and deep wells) may have limited the use of sampling techniques used in this study, preventing an effective capture of Siluriformes' juveniles.

Variations in the composition of migratory species in the different sampling stations were also verified, indicating that there are ecospecific preferences for each species. Studies of recruitment and reproduction generally group fish species into reproductive guilds to address one of the largest problems in ecosystem management: the difficulty of examining several species simultaneously (WINEMILLER, 1989; OLIVEIRA et al., 2015). Although the formation of guilds is an important tool, there can be significant variation among species grouped into the same guild, which must be considered when proposing management actions. Thus, the results of our study demonstrate that species that comprise the guild of migratory respond differently to certain the spatial and limnological characteristics of the environment; so, some species prefer the floodplain environments more than others, and there are species that are more related to the principal river than to the tributary. In the present study, *M. obtusidens* and *P. lineatus* were more associated with tributary rivers of lowland stations, while *R. vulpinus* was more related to the upstream stations of the principal river.

During sampling, we captured juvenile fish of different sizes, however there was a significant difference in the size of the individuals between sampling stations, where the sampling stations within the Atlantic Forest biome (SS1 and SS2) presented larger individuals than the ones sampled in stations located further down the Pampa biome (SS3 and SS4). According to Barthem et al. (2017), who evaluated the distribution of *Brachyplatystoma* juvenile size classes in the Amazon basin, there is a migration already at this stage of life. Wallace (1985) describes that some species of freshwater fish migrate laterally and longitudinally from the floodplain towards the main channel, probably in order to avoid unfavorable conditions in the floodplain. In this sense, we assume, according to our results, that there is an upward migration behavior among juveniles, especially among migratory Characiformes.

It is important to highlight the segregation of juveniles' size classes found between the principal river and its tributary streams, where the tributaries showed a higher abundance of smaller individuals than the principal river. Thus, the tributary rivers of the Pampa biome, where the plain areas are found, were the ones in which we found smaller individuals of different migratory species, when comparing with the ones found in tributary rivers of the Atlantic Forest region (SS1 and SS2).

According to Zaniboni-Filho; Schulz (2003), the lower regions of the tributary streams show characteristics that may favor the first stages of fish life, since these confluence regions assume lentic characteristics when the main river floods it, thus providing temporary micro habitats that support favorable conditions for larvae and juvenile development. On the other hand, some authors have highlighted the importance of floodplain areas as nursery areas for young migrants, due to its great availability of nutrients and refuges (SÁNCHEZ-BOTERO; ARAÚJO-LIMA, 2001; PETRY; BAYLEY; MARKLE, 2003; ANJOS; DE OLIVEIRA; ZUANON, 2008). Our results are in agreement with the above-mentioned literature, since almost all juveniles of the first size class were captured in the lower region of tributary streams from floodplain areas.

According to several authors, the best habitat for breeding rarely coincides with the best habitat for feeding, that is, fish search for different habitats with suitable ecological conditions for their development (NAKATANI; BAUMGARTNER; CAVICCHIOLI, 1997; COWX; WELCOMME, 1998; REYNALTE-TATAJE; ZANIBONI-FILHO, 2008), as tributary streams, which often present little water volume, and downstream floodplain regions, tend to present adverse conditions at some times of the year, such as reduced water level, increased temperature, low dissolved oxygen and acidification, especially near from the bottom (MATSUMURA-TUNDISI et al., 1991; DE FILIPPO et al., 1999; THOMAZ et al., 2001; AGOSTINHO; PELICICE; GOMES, 2008). Such conditions have been observed in the floodplain areas of Middle Uruguay in late summer, as well as an increase in the predatory abundance of fish, such as piranhas (personal observation). Thus, this new dynamic has direct implications for the distribution of migratory fish, leading individuals to search for suitable environments such as lotic areas and free-flow upstream (AGOSTINHO; GOMES; PELICICE, 2007).

Among the studied species, *Salminus brasiliensis* showed the most evident spatial segregation, with small individuals (Class 1) occurring in the tributary streams of floodplain regions, and a consistent increase in size towards the principal river. The spatial segregation of piscivorous fish in the juvenile stage has also been recorded for catfish of the *Brachyplatystoma* genus (BARTHEM et al., 2017). In addition, Winemiller and Jepsen (1998) describe, for neotropical migratory fish, a spatial segregation arising from breeding behavior for different juvenile cohorts, and between adults and juveniles. The main hypothesis for this segregation is that piscivorous fish segregate spatially in order to avoid intraspecific cannibalism, since differences in individuals' size within a cohort can lead to this behavior (SMITH; REAY, 1991; PRADO; GOMIERO; FROEHLICH, 2006; RUDOLF, 2006; MOSS, 2013).

The spatial segregation of size observed in *S*. *brasiliensis* was also verified in *P*. *lineatus* and *M*. *obtusidens* in a less evident way. Many juvenile individuals (Classes 2 and 3) of these species continued to be captured in the floodplain region, which is characterized by the a greater availability of detritus and insects/vegetables, which are typical food resources for *P*. *lineatus* and *M*. *obtusidens*, respectively (AGOSTINHO et al., 1993; AGOSTINHO; ZALEWSKI, 1995; FUGI; HAHN; AGOSTINHO, 1996; POMPEU; GODINHO, 2003; BARTHEM; GOULDING, 2007).

By assessing the proportion of monthly catches over time, we can highlight the peak of Class 1 juveniles in the beginning of the southern summer (January), followed by the months of February and March, in a smaller proportion of Class 1 juveniles, along with juveniles of classes 2 and 3, indicating the existence of a common recruitment peak among the most abundant migratory species analyzed in this study (*S*. *brasiliensis*, *M*. *obtusidens* and *P*. *lineatus*). Even though in the Uruguay River rains and floods occur discontinuously and at different intensities, differently from the other Plata basins (CAROLSFELD et al., 2003), these species seem to identify these oscillations and establish spawning peaks.

This study contributes to the knowledge of the life cycle of migratory fish species in the Middle Uruguay River. According to the known panorama about these species' life cycle, reproduction occurs mainly in the upstream stretch of Middle Uruguay, in regions bordering the Conservation Units of the Turvo State Park and the Biosfera do Yabotí Reserve (ZIOBER; REYNALTE-TATAJE; ZANIBONI-FILHO, 2015), as well as in regions of confluence with the principal tributary streams distributed throughout this sub-basin (SOARES, 2018). Eggs and larvae descend downstream to encounter floodplain areas. In this region, larvae find suitable feeding areas, which allow their development (HARTMANN, 2020). After a first moment, some species such as *S. brasiliensis* leave the tributary streams and migrate upstream, while other species such as *M. obtusidens* and *P. lineatus* remain feeding in tributary streams for longer, but later, also migrate upward to disperse along the basin (ZANIBONI-FILHO; SCHULZ, 2003; MASSARO et al., 2019; MOUNIC-SILVA et al., 2019) (Figure 6).

The Middle section of the Uruguay River is an important segment for the recruitment of several migratory fish species. So the conservation of the connectivity within this region is of great importance for the maintenance of fish stocks. Among the main threats of this area, there is the possible fragmentation caused by the construction of dams, since the Uruguay River sub-basin has one of the greatest potential for hydroelectric energy generation in the Plata River Basin (POPESCU et al., 2012; CUYA et al., 2013). Furthermore, there are political and economic pressures to install these projects on the main channel. If these projects are implemented, we predict a significant reduction in the recruitment rates of migratory fish, since these species depend on the entire sub-basin to complete the life cycle (AGOSTINHO; PELICICE; GOMES, 2008; HOEINGHAUS; WINEMILLER; AGOSTINHO, 2008; LOURES; POMPEU, 2018; PELICICE; AGOSTINHO; GOMES, 2018). In this sense, the maintenance of the Middle Uruguay River integrity, as well as its geomorphological variations, are crucial for the conservation of these species.

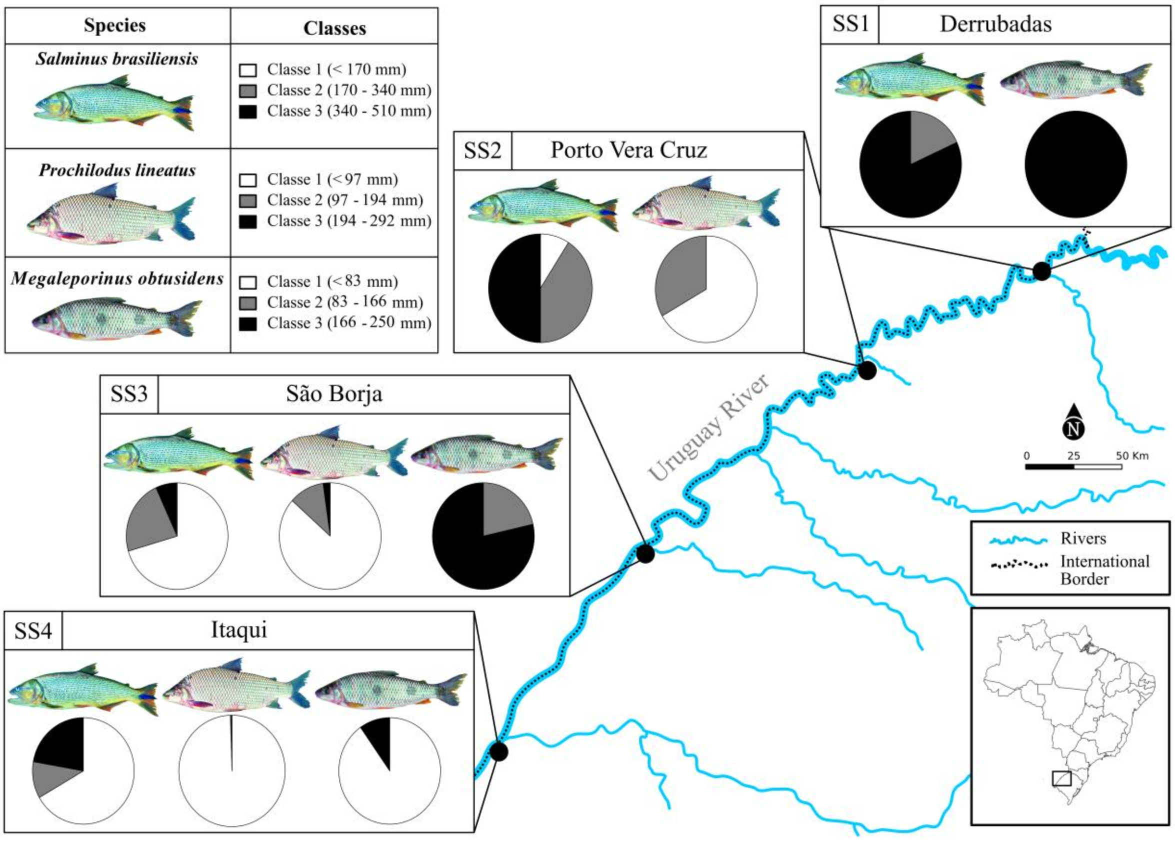


Figure 6 - Schematic illustration, informing the presumed distribution of juveniles of the main migratory fish species collected, and their respective size classes, in the middle of the Uruguay River.

Conclusion

From this study, we conclude that the lower section of the study area, where the floodplain is located within the Middle Uruguay, along with tributary watercourses, shelter fundamental recruitment environments for migratory fish. Demonstrating the importance of connectivity between these environments for effective recruitment. In addition, juveniles of these species, as they grow, migrate to different areas of the sub-basin, which highlights the importance of the conservation of these areas.

4. CONSIDERAÇÕES FINAIS E PERSPECTIVAS

(a) As espécies de peixes migradores utilizam toda extensão do trecho estudado, em alguma fase de suas vidas, nesse sentido a fragmentação da sub-bacia ou algum outro impacto antrópico em qualquer trecho do Médio Uruguai terá impacto no ciclo de vida destas espécies.

(b) Regiões de tributários e de planície de inundação são os principais ambientes de criação de juvenis de peixes migradores, visto que as maiores abundâncias de indivíduos menores foram registradas nestas regiões.

(c) Pelos registros de desova de *Pseudoplatystoma corruscans* e da presença de juvenis quase adultos na região de montante do Médio rio Uruguai, podemos afirmar que o trecho dentro do Bioma Mata Atlântica é importante como local de desova e alimentação. E que o trecho dentro do Parque Estadual do Turvo e da Reserva da biosfera Yabutí, são essenciais para o desenvolvimento inicial das espécies migradoras.

(d) O conjunto de dados apresentados neste trabalho, fornecem informações essenciais para o entendimento dos processos de reprodução e ocupação da bacia do médio rio Uruguai de várias espécies migradoras, contudo os planejamentos de futuras instalações de empreendimentos hidrelétricos nesta sub-bacia, devem levar em consideração estas informações, visando a preservação e manejo dos locais importantes para desova e recrutamento destas espécies.

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APÊNDICES

Figura 1 - Nome cientifico: *Prochilodus lineatus.* Nome popular*: Grumatã e* Curimbatá*.* Fonte imagem: Repósitorio do autor.

Figura 2 - Nome cientifico: *Rhapiodon vulpinus.* Nome popular*:* Facão e Cachorra. Fonte imagem: Repósitorio do autor.

Figura 3 - Nome científico: *Megaleporinus obtusidens.* Nome popular: Piava. Fonte imagem: Repósitorio do autor.

Figura 4 - Nome científico: *Salminus brasiliensis.* Nome popular*:* Dourado. Fonte imagem: Repósitorio do autor.

Figura 5 - Nome científico: *Brycon orbygnianus.* Nome popular*:* Piracanjuva e Bracanjuva. Fonte imagem: Fish base*.*

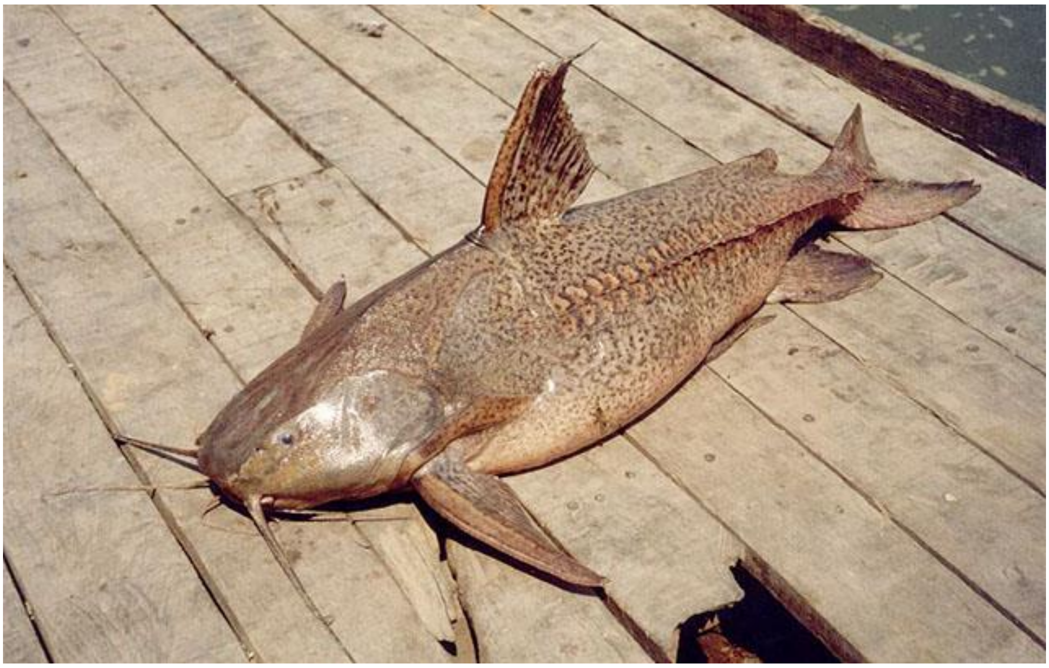

Figura 6 - Nome científico: *Pterodoras granulosos.* Nome popular*:* Armado e Armau*.* Fonte imagem: Fish base.

Figura 7 - Nome cientifico: *Surubim Lima.* Nome popular: *Tamanco e* Surubim Bico-de-pato. Fonte imagem: Repósitorio do autor.

Figura 8 - Nome cientifico:*Steindachneridion scriptum.* Nome popular*:* Suruvi e bocudo*.* Fonte imagem: Repósitorio do autor.

Figura 9 - Nome cientifico: *Pseudoplatystoma corruscans.* Nome popular*:* Surubim - pintado e Pintado*.* Fonte imagem: Repósitorio do autor.