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Tese de Doutorado

Ecologia do movimento de um pequeno peixe de riacho: padrões de movimento em pequena escala e efeito de cruzamentos riacho-estradas

[**Movement ecology of a small stream fish: small-scale movement patterns and effect of stream road-crossings**]

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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ecologia, do Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências com ênfase em Ecologia.

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Resumo

O entendimento dos padrões e processos do movimento em peixes pode ser útil em diversas situações, abrangendo muitos interesses básicos e aplicados em ecologia. Entretanto, quantificar a mobilidade e identificar quais são os fatores ambientais que influenciam o movimento não é uma tarefa fácil. Existem vários fatores abióticos e bióticos que podem influenciar o movimento em riacho. Infelizmente, por várias razões, a maioria dos estudos ainda não procurou entender por completo quais são as características de história de vida (p.ex., idade, período reprodutivo, tamanho de primeira maturação gonadal), variáveis intra e interespecíficas que podem estar relacionadas com a mobilidade individual em peixes de riachos Neotropicais, tanto em trecho livre quanto naqueles com a presença de barreira (p.ex. cruzamento-de-estrada). Baseado no contexto acima, o objetivo geral da minha tese, através de uma abordagem de marcação e recaptura, é entender os padrões de movimento de *Rineloricaria aequalicuspis*, e avaliar quais são os fatores bióticos e abióticos e as características de história de vida relacionados com a probabilidade de movimento em um riacho livre e outro com a presença de um cruzamento-de-estrada. A tese é desenvolvida ao longo de três capítulos: o primeiro traz um estudo descritivo sobre a idade e biologia reprodutiva para auxiliar no entendimento da biologia básica e dinâmica populacional da espécie; o segundo complementa o padrão de movimento da espécie em trecho livre e sua relação com fatores bióticos, abióticos e comprimento total; o terceiro traz um estudo de caso avaliando o efeito de um cruzamento-de-estrada sobre a mobilidade de *R. aequalicuspis*.

Palavras-chave: cruzamentos-de-estrada, habitat, idade, tabela de vida, marcação-recaptura, movimento*,* multi-estados*,* reprodução, *Rineloricaria aequalicuspis,* riacho.

Abstract

The understanding of patterns and processes of fish movement can be useful in a variety of situations, covering many basic and applied interests in ecology. However, quantifying mobility and identifying the environmental factors that influence movement is not an easy task. Several abiotic and biotic factors that can influence movement in the stream. Unfortunately, for several reasons (issues of time in the field and the need for greater availability of financial resources) most studies do not seek to fully understand what are the characteristics of life history (age, reproductive period, size of first gonadal maturation), intra and interspecific variables that may be related to individual mobility both in the free stretch and in those with the presence of a barrier (road crossings). The general objective of my thesis is to understand the movement patterns of *Rineloricaria aequalicuspis*, what are the biotic and abiotic factors and characteristics of life history that may be related to the probability of movement in free-flowing conditions and in the presence of a road crossing. The thesis is developed over three chapters: the first brings a study on the age and reproductive biology, to assist in understanding the basic biology and population dynamics of the species; the second deals with the movement pattern of the species in a free stream stretch and its relationship with biotic and abiotic factors, and total length; the third is a case study evaluating the effect of a road crossing on the mobility of *R. aequalicuspis*.

Keywords: age, habitat, life-table, mark-recapture, movement, multi-states, reproduction, *Rineloricaria aequalicuspis*, road-crossings, stream.

Sumário

Introdução geral

Pensando no projeto

Ecologia de peixes de água doce é uma área da biologia a qual sempre tive o interesse em conhecer e na qual venho estudando há aproximadamente 13 anos. Especificamente, entender o processo do movimento em peixes tanto em rios quanto em riachos sempre me cativou. Além de avaliar o efeito antrópico sobre a mobilidade de peixes, um dos principais interesses que tenho neste tema é procurar entender o quanto, como, por que e para onde os peixes se movimentam. Aparentemente, perguntas simples quando comparadas a outros temas de ecologia teórica, mas que na prática são muito difíceis de serem respondidas e extremamente importantes para a complementação do conhecimento nessas abordagens ecológicas mais teóricas (p.ex. metapopulações, metacomunidades).

O efeito da atividade humana sobre a biodiversidade é um dos temas mais relevantes da atualidade. Diversos estudos científicos no mundo demonstram que os efeitos negativos sobre biodiversidade podem ser irreversíveis caso nada seja feito exatamente agora. Por este motivo, acredito que os projetos de iniciação científica, conclusão de curso, mestrado ou doutorado são obrigados a terem um viés cada vez mais aplicado com questões envolvendo a sociedade, ambiente e conservação. Além disso, entendo que não realizamos ecologia aplicada sem a biologia básica. Dessa maneira, procurei desenvolver um projeto que englobasse tanto o meu interesse em ecologia do movimento de peixes de riachos quanto à necessidade de um estudo mais aplicado com um tema relacionado ao impacto da sociedade (cruzamentos de estradas que conectam pessoas) sobre o ambiente (riachos) e especificamente a conservação de peixes.

Contexto teórico

O movimento do organismo é um processo ecológico de mudança da posição do indivíduo dentro do espaço ao longo do tempo, fundamental para a dinâmica populacional, organização de comunidade e ecossistema (Nathan et al., 2008; Hohausová et al., 2010). Por exemplo, baseado na equação populacional básica na qual a abundância (N) num tempo (t) em uma população aberta ou sub-população é conjuntamente determinada pelo número de nascimentos (B), mortes (D), imigrantes (I) e emigrantes (E): $N_t = N_{t-1} + B + D + I-E$ (Begon *et al*., 2007). Assim, a redução ou eliminação do movimento de imigração resultará em uma diminuição proporcional do N (abundância) (Nislow et al., 2011). Além disso, quando a abundância de uma espécie particular resulta em zero, isso irá diminuir a riqueza de espécies local (Nislow et al., 2011). Geralmente, esta diminuição da abundância em escala local deve contribuir para um sinal de declínio populacional e perda da biodiversidade (Hanski, 1991). Outro exemplo está relacionado à estruturação de comunidades, onde processos do movimento de dispersão e migrações em grande escala funcionam como um filtro ambiental, determinando quanto e quais espécies são capazes de entrar numa comunidade particular e formar um *pool* de espécies local (Poff, 1997).

Peixes são organismos com ampla capacidade de movimento, utilizando diversos ambientes para suas atividades diárias (deslocamento para alimentação, reprodução, descanso e refúgio) (Uieda, 1984; Sabino & Castro, 1990; Schlosser, 1991; Sabino & Zuanon, 1998). Existem quatro tipos de padrões de movimento relevantes para peixes (Dingle, 2014; Rahel & McLaughlin, 2018): 1) *Station keeping*: movimentos repetidos dentro de um *home range* ou território; 2) *Migration*: movimentos de ida e volta para um novo habitat para realização da desova ou refúgio; 3) *Ranging*: movimento para fora do *home range* sem retorno (*dispersal*); 4) *Involuntary*: deslocamento por um distúrbio ou atividade humana. Entre todos esses padrões, o movimento relacionado com a migração e dispersão de espécies de grande porte que realizam grandes deslocamentos (> 1000 km; p. ex. espécies de salmão, curimbá, dourado, dourada) são os mais estudados na região Neotropical e no hemisfério norte (Agostinho et al., 2003; Barthem et al., 2017; Comte & Olden, 2018; Lopes et al., 2019; De Fries et al., 2019). O conhecimento da frequência e extensão do movimento para outras espécies de menor porte localizadas em riachos que não realizam movimentos extensos de migração ainda se mantém limitado (Mazzoni et al., 2012; Mazzoni et al., 2018).

Muitas espécies de peixes de riachos são tidas como espécies de movimento restrito (*home range* pequeno de 0 a 50 m). Essa ideia foi formalmente sintetizada por Gerking (1959), ficando conhecida como o "paradigma do movimento restrito". Gerking (1959) apresentou dados de que até 80% dos indivíduos marcados haviam sido recapturados dentro de um trecho de 100 m ao longo de 1 ano, e suas conclusões influenciaram a visão que muitos ecólogos de peixe adotaram sobre a real mobilidade de peixes de riachos. Entretanto, ao longo do tempo, os estudos mostraram uma diversidade de situações, colocando em cheque a generalização implícita do paradigma do movimento restrito. Especialmente após os anos 1990, começaram a surgir estudos com diferentes delineamentos amostrais e ferramentas metodológicas mais sofisticadas, rediscutindo diretamente o paradigma do movimento restrito em peixes de riachos (e.g. Gowan et al. 1994; Gowan & Faush, 1996; Smithson & Johnston, 1999; Rodríguez, 2002). Esses estudos mostraram padrões de deslocamento que incluem não apenas as espécies de movimento realmente restrito, mas sugerem uma gama muito maior de comportamentos.

Mais recentemente, o conceito de movimento heterogêneo foi elaborado, o qual indica que as populações de peixes podem apresentar componentes estacionários e móveis (Skalski & Gilliam, 2000; Rodríguez, 2002; Booth et al., 2014; Radinger & Wolter, 2014). Neste conceito, a distribuição da frequência do movimento é representada por uma distribuição leptokurtica (Gotelli & Ellison, 2004). Esta distribuição prediz que a maioria dos indivíduos são sedentários, com alta concentração de observações com distância igual ou próxima a zero. Já os indivíduos com maior mobilidade, localizados nas extremidades da cauda desta distribuição, apresentam reduzido número.

Em escala local, vários fatores ambientais podem estar associados com a mobilidade de peixes de riachos, destacando-se o comprimento total, densidade de indivíduos, velocidade da água, temperatura da água e profundidade (Bjorn, 1971; Crisp, 1993; Albanese et al., 2004; Aparicio et al., 2018; Rasmussen & Belk, 2017; Pennock et al., 2018). Entretanto, os estudos que procuram entender aspectos da história de vida (p.ex. idade e período reprodutivo) relacionados com o movimento são mais focados naquelas espécies migradoras que se deslocam entre diferentes manchas de habitat para desova, alimentação e refúgio e estão mais relacionadas com movimentos de escala regional (Crisp, 1993; Janowicz et al., 2018). Infelizmente, por questões de maior tempo de amostragem, maior tempo de procedimentos de laboratório e consequentemente maior disponibilidade de recurso financeiro, poucos estudos procuram entender quais são as características de história de vida (p.ex., idade, período reprodutivo, tamanho de primeira maturação gonadal) que podem estar relacionadas com a mobilidade de peixes de pequeno porte localizados em riachos. A identificação dos fatores ambientais que influenciam o movimento pode ter implicações diretas para a colonização e a persistência de determinadas populações (Albanese et al., 2004).

A biodiversidade aquática é uma das mais ameaçadas do mundo (Dudgeon et al., 2006) e a falta de conectividade para a continuidade do movimento individual é umas das principais causas de ameaça a conservação de peixes (Helfman, 2007; David et al., 2013; Rahel & McLaughlin, 2018). Em particular, a instalação de barreiras físicas como os cruzamentos de estrada (*culverts*) tem impactado negativamente o movimento de peixes de riacho (Warren & Pardew 1998; Gibson et al. 2005; Benton et al. 2008; Nislow et al. 2011; Favaro et al. 2014). Na região neotropical, onde os peixes apresentam maior diversidade de espécies e as suas características de história de vida diferem daquelas do Hemisfério Norte (Winemiller et al., 2008), poucos estudos publicados avaliam o efeito de barreiras sobre populações de peixes, causadas pela presença de cruzamentos em riachos (exceção de Mariano et al., 2012; Brejão et al., 2020). A compreensão de como ocorrem esses efeitos é importante para o desenho de estruturas físicas que atenuem os impactos de estradas sobre peixes.

Na tese aqui descrita, eu realizei três capítulos buscando entender padrões de movimento de uma espécie de peixe bentônico de pequeno porte, em um trecho livre de cruzamento de estrada, avaliar o possível efeito de barreira de um cruzamento de estrada sobre a mobilidade desta espécie e entender quais são os aspectos de história de vida e variáveis ambientais que podem estar relacionados tanto com o movimento em trecho livre quanto em trecho com a presença do cruzamento de estrada. Espero que esta tese contribua no mínimo para aumentar o conhecimento da ecologia do movimento de peixes de riachos, mostrar a importância da realização de estudos de biologia básica e auxiliar em planejamentos estratégicos para a conservação de peixes neotropicais localizados em riachos impactados por estradas.

Objetivo (s)

Entender os padrões de movimento de *Rineloricaria aequalicuspis*, quais são os fatores bióticos e abióticos e características de história de vida que podem estar relacionados com a probabilidade de movimento em um riacho livre e outro com a presença de um cruzamento-de-estrada. Para atingir estes objetivos, a tese foi desenvolvida ao longo de três capítulos: o primeiro traz um estudo descritivo sobre a idade e biologia reprodutiva para auxiliar no entendimento da biologia básica e dinâmica populacional da espécie; o segundo complementa o padrão de movimento da espécie em trecho livre e sua relação com fatores bióticos, abióticos e comprimento total; o terceiro traz um estudo de caso avaliando o efeito de um cruzamento-de-estrada sobre a mobilidade de *R. aequalicuspis*.

CAPÍTULO 1 - Life history traits of an armored catfish (*Rineloricaria aequalicuspis*, Loricariidae)

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Abstract

This study evaluated life history traits (reproductive period, size at first maturity, age, mortality, and survival) of a population of *Rineloricaria aequalicuspis*, a loricariid species inhabiting coastal streams in southern Brazil. In the first stream, fish samples were taken monthly for one year, to obtain reproduction data from 265 females and 242 males. In the second stream, in the same watershed, estimates of age, survival, and mortality were obtained from 247 recapture events, based on a 17-month photo-identification mark-recapture study. The studied species has a long reproductive period extending 7 months, between spring-summer; the female length at first maturity was 107.5 mm, and the mean absolute fecundity was of 137.5 ± 42 oocytes. The estimated life span was 7 years, with a growth constant estimate (K) = 0.41, and asymptotic length (Linf) = 193 mm. The annual survival rate (S_x = 0.42) was lower than the annual mortality rate (M_a = 0.58), and the estimated annual survival rate for younger fish (age $\leq$ 1; S1 = 0.036) was much lower when compared to older fish (age $\geq$ 2; S2 = 0.415), indicating that the pre-reproductive phase is more sensitive to changes in biotic or abiotic environmental factors. This study has performed a thorough assessment of the basic biology and population ecology of *R. aequalicuspis*, providing thus subsidies for the development and improvement of conservation policies regarding armored catfish populations in Neotropical streams.

Keywords: population parameters, life cycle, life-table, Siluriformes, Neotropical.

Introduction

Loricariidae is the largest family of Neotropical catfishes with approximately 1.000 species described so far (see Fricke *et al*., 2020), comprising the armored catfishes, which possess a highly specialized morphology to survive in water-flowing habitats having a moderate to high flow (Casatti and Castro, 2006). Most of loricariids species are benthic and detritivorous, important for stream ecosystem functioning, making an expressive contribution to the processing of matter and nutrient cycling (Bailly et al., 2011; Capps and Flecker, 2013; Flecker, 1992). Despite this high taxonomic diversity and ecological importance, several authors have pointed out that there is a lack of knowledge on loricariid ecology, and have called attention to the need for research on the basic biology of several species in this family (Alves et al., 2019; Figueiredo et al., 2019; Moodie and Power, 1982; Power, 2003; Suzuki et al., 2000).

Loricariids have a diversity of forms, behaviors, and reproductive strategies (Agostinho et al., 1995; Burges, 1989; Mas et al., 2019; Suzuki et al., 2000). For instance, while *Nannoplecostomus eleonorae* can reach up to 22 mm of body length (Ribeiro et al., 2012), other species such as *Pseudacanthicus major* can achieve more than 540 mm (Chamon and Silva, 2018). From a reproductive perspective, the number of oocytes (i.e., fish eggs) is usually low, from less than 200 oocytes (Alves et al., 2019; Barbieri, 1994) to approximately 2500 oocytes (Suzuki et al., 2000). Some form of parental care is relatively common in loricariids, and spawning can be either partial or total (Mas et al., 2019; Suzuki et al., 2000). However, information about loricariid life span, growth, mortality, and survival rate is still scarce, especially the latter two. Most age and growth studies were carried out between the 1980s and in the beginning of the 2000s, and indicated that some species may show a growth constant (K) ranging from 0.08 to 0.89 (Agostinho et al., 1991; Bruschi-Junior et al., 1997; Nomura, 1988). Their longevity may vary from 4 to 15 years, based on few studied species (Agostinho, 1991; Antoniutti et al., 1985; Barbieri, 1995; Barbieri and Santos, 1987; Braga et al., 2009; Goulart and Verani, 1992; Nomura , 1988; Trajano, 2001).

Age is one of the life history features with the greatest influence in population dynamics, affecting the rates of mortality, survival, movement, reproduction, age of maturity, and longevity (Campana, 2001; Haag and Rypel, 2011; Lorenzen, 2016; Stearns, 1983). However, in South America, little is known about the patterns of age, growth, and population dynamics of freshwater fish (Dei Tos et al., 2010; Santana et al., 2020). In most freshwater ecoregions, there is little information available or basic studies on age and growth (< 5% of species were investigated until now; Santana et al., 2020). For coastal freshwater ecoregions of the neotropics, such as the Tramandaí-Mampituba ecoregion (present study), there is age and growth information for only 4.12% of the fish species, demonstrating a need for improving research aimed at understanding freshwater fish population dynamics (Santana et al., 2020). Also, there is a low number of studies on age and growth of loricariids in streams (Santana et al., 2020), which is an important knowledge gap considering that this group is one of the main constituent of stream fish communities in neotropics (Bailly et al., 2011).

Hence, this study aimed to describe the growth, age, reproductive period, size of first maturation, mortality, and survival of *Rineloricaria aequalicuspis* Reis & Cardoso, 2001, which is an endemic loricariid to coastal drainages in Southern Brazil. To our knowledge, this is one of the few assessments of survival and mortality parameters for stream fish in the Neotropics (including Braga et al., 2009; Lobón-Cerviá et al., 1993; Penha et al., 2015), and it is the first study to use recapture data for this purpose (but see Trajano and Bichuette, 2007; Trajano, 1991, 1997, 2001 for cave fish).

Material and Methods

Study species

Rineloricaria aequalicuspis Reis & Cardoso, 2001 is an armored catfish (Loricariidae) endemic to streams of coastal drainages in southern of Brazil. *R. aequalicuspis* is abundant across the streams of the Maquine River Basin, and this species has not yet showed signs to be endangered (FZB, 2014; ICMBio, 2014). The total length (LT) of this species reaches up to 200 mm (Dala-Corte and De Fries, 2018; Dala-Corte *et al*., 2016). It is a typically benthic species, relatively widespread and abundant in shallow streams with medium to strong current and rocky bottom (Dala-Corte and De Fries, 2018; Malabarba *et al*., 2013).

Study area

For this study, we sampled fish in two 3rd order streams (at 1:50,000 scale). Reproduction data, were obtained from fish collected at the Forqueta river (29°32'18.26 "S; 50°14'46.96" W; catchment area = 97 km² and channel width = 80 m at the sampling site). Age, growth, mortality and survival data were obtained from a mark-recapture study at Encantado river (29°36'28"S; 50°12'48"W; catchment area = 12 km^2, channel width = 20 m, at the sampling site). These streams are located in the Maquiné river watershed, in southern Brazil, at the Tramandaí-Mampituba aquatic ecoregion (Abell et al., 2008). The Maquiné river has an area of 550.5 km² (Becker et al., 2004), with elevation ranging from 10 to 800 meters between the mouth and the head, forming a V-shaped valley and creating a gradient in elevation with high slopes that affect water velocity (Camana et al., 2016). The streams present clear water and a rocky substrate (Dala-Corte and De Fries, 2018). According to the Köppen-Geiger classification, the regional climate is humid subtropical, with hot summers and cold winters, and an average annual temperature of around 20 ° C. There is no defined dry season and rainfall is spread throughout the year (average annual rainfall = 1400-1800 mm; Hasenack and Ferraro, 1989).

Reproductive characteristics

Individuals of *R. aequalicuspis* were sampled monthly during 12 months between October 2018 and September 2019 in the Forqueta river. We captured fish by kick-sampling, using a rectangular dip-net (40 x 40 cm opening and 80 cm bag depth; 4 mm mesh). In each sampling month, we collected approximately 40 individuals, representing each size class equally, comprising small (Total length, LT < 70 mm), medium (70 mm < LT < 100 mm) and large (LT > 100 mm) sized fish. The collected specimens were fixed in 10% formaldehyde for further dissection in the laboratory. Voucher specimens (6 individuals) were deposited in the fish collection of the Department of Zoology, Universidade Federal do Rio Grande do Sul (UFRGS 27644).

From each specimen, we measured total length (mm) and total weight (g). Gonads were removed, weighted (0.01 g), and macroscopically inspected under a stereomicroscope for determination of sex and maturity stage. We classified the gonads in three categories only: immature, mature, and non-mature. The mature category included gonads in mature as well as early spawning stages (based on their macroscopical characteristics; Brown-Peterson *et al*., 2011; Vazzoler, 1996). Oocytes from mature ovaries were counted under a stereomicroscope to describe fecundity. Differences in the proportion of males and females in the samples were assessed using a chi-square test (χ^2).

The gonadosomatic index was calculated as GSI = $(W_g.W_t^{-1}) * 100$, where W_g is the gonad weight and W_t is the fish total weight (Vazzoler, 1996). Size at first maturity (L_{50}) was defined as the fish length where 50% of all individuals are predicted to be adults (Vazzoler, 1996). For each individual, L_{50} was estimated by logistic regression (Roa *et al*., 1999), with total length as the independent variable and life stage (either adult or non-adult), as the dependent variable. Individuals were classified as adult or non-adult according to their gonadal maturity stage (non-adult = immature gonads; adults = all other gonadal stages). Male gonads presented little variation in macroscopic characteristics, so that classifying them into maturity stages was not possible and therefore GSI and L_{50} values were not calculated for males.

Age, growth, and life table

Individuals of *R. aequalicuspis* were captured monthly during 17 months between January 2016 and August 2017 in the Encantado river. In each sampling event, the studied stream reach was divided into six consecutive sections of 10 meters. Fish were captured by kick-sampling using a rectangular dip-net (40 x 40 cm opening and 80 cm bag depth, with 4 mm mesh). In each 10-m stream section, kick-sampling was performed in the downstream-to-upstream direction, following an approximately zigzag route and screening all available habitats. Captured individuals were placed in 20 l plastic buckets filled with water from the stream. After sampling each 10-m section, individuals were measured (total length) and had their abdominal region photographed for later individual photo-identification as described in Dala-Corte *et al*. (2016). Subsequently, individuals were released into the same section they were captured.

Fish age was calculated by adjusting the von Bertalanffy growth model (Bertalanffy, 1938) with an growth constant estimate (K), the K variance, and the estimated longevity (*sensu* Taylor, 1962) for each asymptotic length (L_{inf}) selected. For this model, we used the MiniVar-Recap spreadsheet (Fontoura, 2016). For each row in the spreadsheet, the total length (mm) at the time of capture, total length (mm) at the recapture, and the interval (number of days) between mark and recapture were inserted. In the present study, the spreadsheet contained 247 recapture events.

Mortality of *R. aequalicuspis* was estimated as the instantaneous mortality rate (M), calculated as $\log M = -0.0066-0.279 * \text{Log}\ (\text{Linf}) + 0.6543 * \text{Log}\ (K) + 0.4634 * \text{Log}\ (T)$, where T = average temperature given in °C (see Pauly, 1980). Temperature values were measured *in situ* during each sampling, yielding an mean value of 16.1±2.8°C. Based on the mortality rate (M), fertility, and sexual proportion a time-specific life table was built. The annual survival rate (S) for age > 1 year was calculated as $S = e^{(-M)}$. Consequently, the annual mortality rate (M_a) was calculated as $M_a = 1 - S$, where S represents the annual survival rate. The survival rate of the first generation (S_1) was calculated using the Solver routine in Excel (www.solver.com) to obtain a net reproductive rate (R_0) equal to 1, representing thus a viable and stable population (Janowicz et al., 2018). The proportion of any given cohort surviving at age x (l_x) was calculated as $l_x = l_{(x-1)}S_x$, where l_{x-1} is the proportion of the cohort surviving at age x-1 and S_x is the estimated annual survival rate at age x. The expected fertility was calculated by multiplying the beta coefficient (derived from the relationship between fecundity and total weight) with the total weight at age x. The reproductive rate per generation (R_x) was calculated as $R_x = l_x b_x$, where b_x is the average fertility at age x. Generation time (t_{gen}) was estimated as $t_{gen} = \Sigma\, l_x b_x\, (\Sigma\, x\, l_x b_x)^{-1}$.

Results

Reproduction

In a total of 507 individuals captured for reproductive characteristics, 265 were females and 242 males. The sex ratio in the monthly samples was not different from 1:1 ($\chi^2 = 1.04$, df = 1, $p = 0.30$; Figure 1a), but the total length frequency distribution suggests that larger individuals tend to be male (Figure 1b). There was no significant difference between female and male length-weight relations (Table 1).

Monthly changes in female GSI indicated that *R. aequalicuspis* has a long reproductive period, with a few individuals showing high values already in winter (August and September). However, the higher frequency of high GSI values was observed in spring and summer, from December to February (Figure 2). The size at first maturity was 107.5 mm for females (Figure 3). The average number of oocytes in mature ovaries was 137.5 (min = 92; max = 209). The number of oocytes showed a positive linear relationship with total length ($n_{oocytes} = 5.062L_t - 632.63$; $p = 0.04$; $r^2 = 0.58$), but not with total weight ($n_{oocytes} = 5.342W_t + 11.672$; $p = 0.20$; $r^2 = 0.30$) (Figure 4).

Age, growth, and life-table

According to the lowest residual variance value (Table 2), individuals had longevity of approximately 7 years of age, with an estimated individual growth constant (K) of 0.41 and asymptotic length (L_{inf}) of 193 mm. Based on the mark-recapture data, calculated instantaneous mortality was -0.879, resulting in an annual survival rate of 41.48% ($S_x = 0.4148$). Accordingly, the annual mortality rate was 58.52% ($M_a = 0.5852$). Based on the validated sex ratio of 0.5 (sex ratio 1:1 = 50% of the population is female), the expected fecundity varied from 7 to 202 oocytes, between age 1 and age 8, respectively (Table 3). When establishing a constant 1-year mortality rate and assuming a constant population dynamic (net reproductive rate, $R_0 = 1$), the survival rate (S_x) was estimated at 3.6% for the first year of life ($S_1 = 0.0364$). Overall, the estimated generation time was of 3 years.

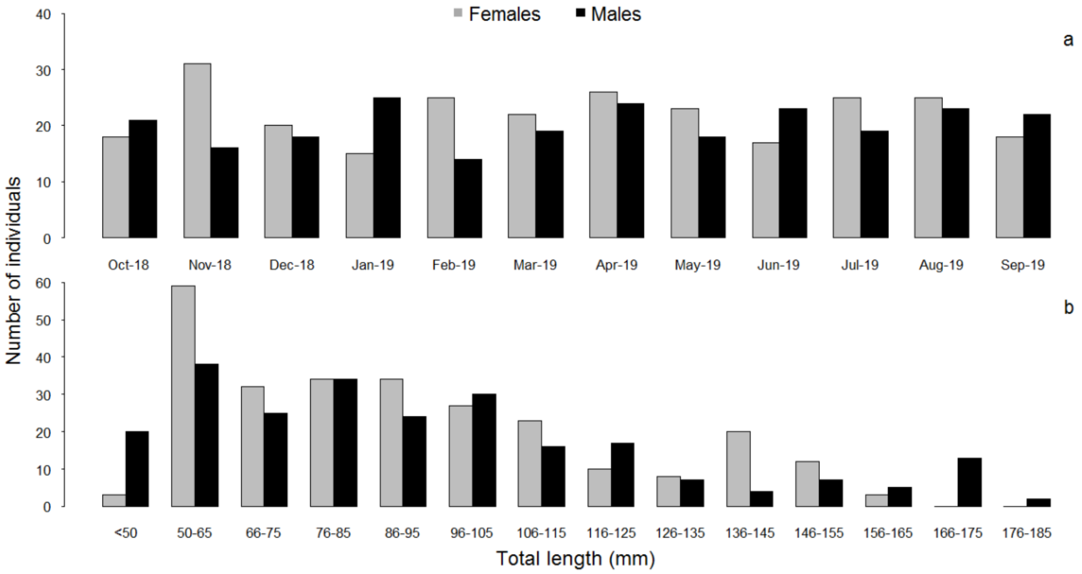

Figure 1. Proportion of females and males (a) and total length frequency distribution (b) of fish sampled in the Maquiné river basin.

Table 1. Length-weight relation for Rineloricaria aequalicuspis. Legend: n = number of individuals; Lt min and Lt max = minimum and maximum Total Length; a and b = parameters of the length-weight relation; r² = coefficient of determination.

Sex	N	Lt min - Lt max (mm)	a	b	r^2
F	265	46 - 164	0.0031	3.22	0.99
M	242	36 - 179	0.0038	3.14	0.96

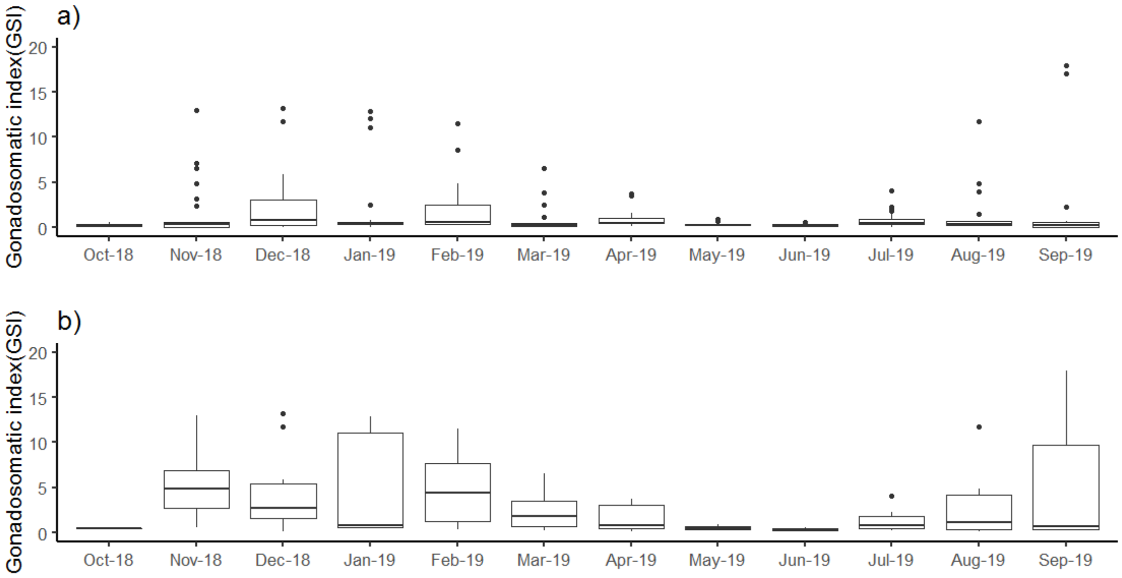

Figure 2. Monthly values of gonadosomatic index (GSI) in the total sample of female *Rineloricaria aequalicuspis* (a), and monthly values of GSI only for females larger than L50 (Lt = 107.5mm) (b). Legend: heavy horizontal line crossing the box is the median; bottom and top of the box are the lower and upper quartiles, respectively; the vertical lines are the minimum and maximum values of GSI; and black circle are potential outliers.

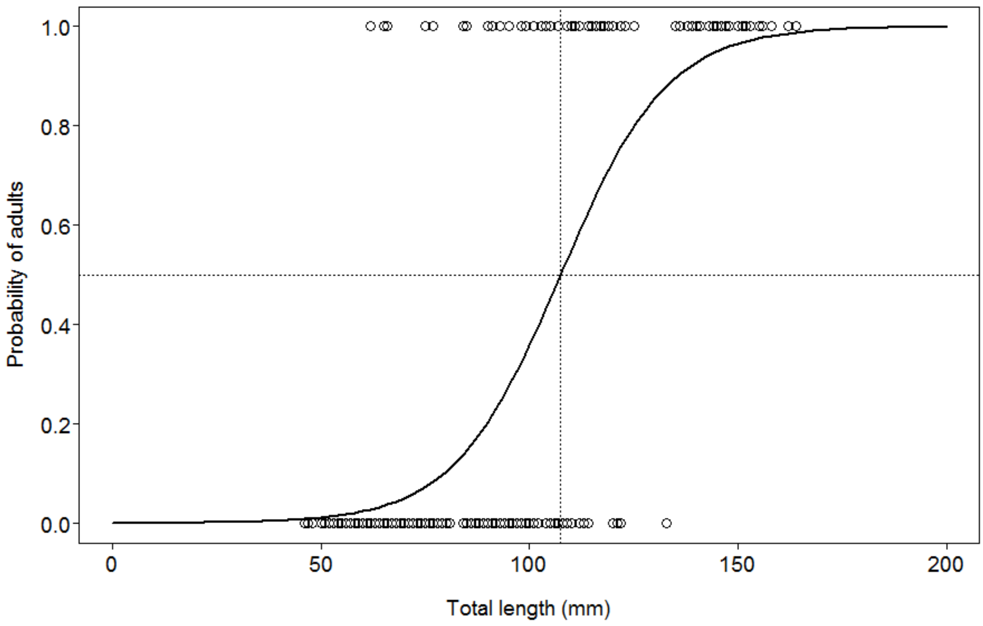

Figure 3. Logistic regression estimating the size at first maturity for female *Rineloricaria aequalicuspis* (a) (coef. beta = 0.07; standard error = 0.009; p < 0.001).

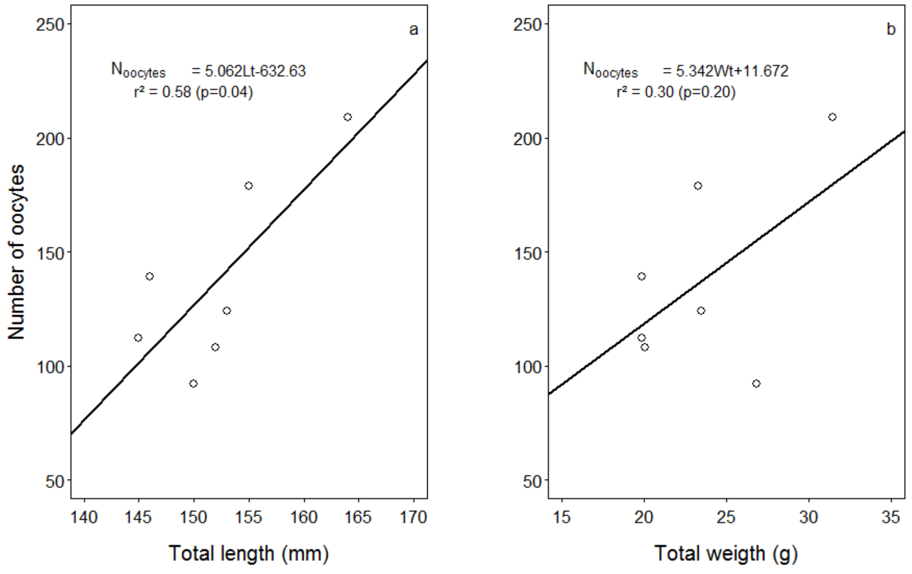

Figure 4. Relation between number of oocytes and total length (a) and total weight (b) for *Rineloricaria aequalicuspis*.

Table 2. Estimates of constant growth (k), k variance and estimated longevity (sensu Taylor, 1962) for each asymptotic length (Linf). The light grey line shows results with minor k residual variance.

Linf	**k**	**Residual Variance**	**Longevity**
18.8	0.439078635	0.370665751	6.822769389
18.9	0.43335298	0.370093741	6.9129149
19	0.427851582	0.369699053	7.001802489
19.1	0.422550753	0.369452958	7.089638943
19.2	0.417431424	0.369333031	7.17658543
19.3	0.412477936	0.369321431	7.262769742
19.4	0.407677207	0.369403724	7.348294742
19.5	0.403018136	0.369568056	7.433244334
19.6	0.39849118	0.36980457	7.517687771
19.7	0.394088039	0.370104967	7.601682819

Table 3. Life table for *Rineloricaria aequalicuspis* (Loricariidae) in the Encantado river, southern Brazil. TL = Total length; TW = Total weight; Sx = annual survival rate; lx = proportion of individuals surviving to age; Rx = annual reproductive rate; x.R = generation time at age x.

Age (x)	**TL (mm)**	**TW (g)**	**S_x**	**l_x**	**Maturity (Probability)**	**Expected Fecundity to age**	**Sex Ratio**	**R_x**	**$x.R_x$**
0	0	0		1	0	0	0.5	0.0092	0
1	65	1.3	0.0364	0.0364	0	7	0.5	0.1337	0.134
2	108	6.6	0.4149	0.0151	0.5	35	0.5	0.2753	0.551
3	137	14.1	0.4149	0.0063	0.9	75	0.5	0.2445	0.733
4	156	21.4	0.4149	0.0026	1	114	0.5	0.1576	0.63
5	168	27.5	0.4149	0.0011	1	147	0.5	0.0883	0.442
6	177	32.2	0.4149	0.0004	1	172	0.5	0.0476	0.285
7	182	35.5	0.4149	0.0002	1	190	0.5	0.0268	0.188
8	186	37.9	0.4149	0.0001	1	202	0.5	0.0170	0.136
Net Reproductive rate (Ro) =								1	3.099
							Generation time (tgen)	3	

Discussion

The armored catfish *R. aequalicuspis* had a long reproductive period, without differentiation between males and females, a mean fecundity of 137.5 oocytes, and first maturation size (L_{50}) equals to 107.5 mm (i.e., indicating that 50% of individuals were ready for breeding at the age of two years). Almost all individuals are capable of breeding at age three. Their longevity reached approximately seven years, with a generation time of three years. The estimated annual survival rate for younger fish (age $\leq$ 1; Lt <100 mm) was lower than in older age groups (age $\geq$ 2; Lt > 100 mm), suggesting that this stage of life (e.g., pre-reproductive) is much more sensitive to changes in biotic or abiotic factors.

The reproductive period of *R. aequalicuspis* was rather long (ranging from five to six months) and beginning during the winter time but having its peak between spring and summer (from November to February). Low average values of GSI occurred throughout the year, indicating that a reasonable portion of the population is in a non-reproductive stage at any given month, even during the reproductive period. Reproduction during spring-summer is common for most freshwater fish (Mathews, 1998), including loricariids occurring in streams (Alves et al., 2019; Braga et al., 2008, 2009) and rivers (Hirschman et al., 2011; Mazzoni and Caramaschi, 1997). The seasonal reproductive period of stream fish in the southern hemisphere (i.e., during spring and summer) may be related to the increase in temperature and photoperiod, probably resulting in extra favorable conditions for the development of the offspring (Vazzoler and Menezes, 1992).

The low absolute fecundity observed here (137.5 oocytes), has been also observed in other loricariids inhabiting streams (Alves et al., 2019; Braga et al., 2008; Figueiredo et al., 2019) and rivers (De Fries et al., 2018; Hirschman et al., 2011). These studies pointed out that low fecundity would be a characteristic associated to an equilibrium strategy (according to Winemiller, 1989; Winemiller and Rose, 1992), in which the reduced fecundity is compensated by the high investment in parental care and protection of eggs. A decrease in fecundity and an increase in the diameter of the oocytes (not measured in our study) can be interpreted as an advantage for a higher survival probability of eggs and larvae (Alves et al., 2019; Braga et al., 2008, 2009), specially for species living in spatially and temporally heterogeneous environments, such as tropical streams (Balon, 1975; Winemiller et al., 2008).

The increase in number of eggs with the fish size has been observed in other loricariids and other groups of fish (Figueiredo et al., 2019; Janowicz et al., 2018; Mazzoni and Caramaschi, 1997; Quinn et al., 2011). Because most fish grow indefinitely, annual fecundity is also expected to increase with age and body size (Tsoukali et al., 2016). Life-history theory predicts that the mortality rate should increase with a reproductive effort (e.g., fecundity and GSI) (Gunderson, 1997; Tsoukali et al., 2016). Therefore, the survival rate of bigger, older, and most fertile individuals should decrease as the total length and age increase. Our life table (proportion of individuals surviving to age) demonstrated the same patterns.

The length at first maturity (L_{50}) is a flexible reproductive strategy due to its closely relatedness to age and growth. Also, this trait presents intraspecific spatial and temporal variation related to the abiotic and biotic environmental conditions of a certain period or region (Vazzoler, 1996). We estimated the L_{50} for *R. aequalicuspis* females was about 107.5 mm, when individuals reach 2 years old. Our results were similar to those found by Barbieri (1994) for *Rineloricaria latirostris*, although their L_{50} was slightly lower for females (85 mm) and for males (101mm), both at the 2-years age class. Unfortunately, due to the lack of information on fish growth and age, the selective evolutionary forces that act on the L_{50} in Loricariidae are of little known (Mazzoni and Caramaschi, 1995). However, based on our results of high growth estimate (K = 0.41) for *R. aequalicuspis*, when compared to other loricariids (Agostinho et al., 1991; Antoniutti et al., 1985; Nomura, 1988) and other studies that indicated a negative relationship between Linf and K in Neotropic fish populations (Gubiani et al., 2012), we assumed that this high (K) value might indicate an accelerated growth rate at the beginning of life to reach the L_{50}. For most fish species, a fast early growth is necessary to escape from the risk of predation or other mortality factors, and to ensure that the minimum size for maturation is reached (Mathews, 1998).

Most of the studied South American freshwater fish attains maximum ages less than 15 years (Dei Tos et al., 2010). Our estimate of maximum longevity for *R. aequalicuspis* (7-years) is within the range described for other species of Loricariidae, where most studies indicated an estimated age range between 4 and 15 years of life (Agostinho, 1991; Antoniutti et al., 1985; Barbieri, 1995; Barbieri and Santos, 1987; Braga et al., 2009; Goulart and Verani, 1992; Nomura, 1988; Trajano, 2001). However, when we restrict comparisons to fish from Neotropical streams (excluding rivers, lakes, and reservoirs, for example), we found only one study comprising information on fish age (Braga et al., 2009). The authors, anazyling frequency distribution of body length, estimated that *Pareiorhina rudolphi* (a species with a maximum total length of 72 mm; approximately 2.5 times smaller than *R. aequalicuspis*), had an estimated life span of 8.6 years. For other species of loricariids such as *R. latirostris,* similar in size to *R. aequalicuspis*, but inhabiting rivers, the life span was estimated to be around six years (Barbieri, 1995).

In our study, the annual survival rate for young individuals (age ≤ 1) was much lower (3.6%, $S_x = 0.036$, see Table 3) compared to older individuals (41%, Sx = 0.41, see Table 3). In other words, there is a high initial mortality and subsequent higher survival rate for our focal species (*R. aequalicuspis*). This general pattern is represented in nature by a type III survival curve and it is commonly found in teleost fish (Wang et al., 2017). Usually, the mortality rate of fish appears to be inversely related to size and the cause of this mortality can be explained for different reasons (Janowicz et al., 2018; Wootton, 1998). Sources of mortality can be associated with density-dependent relationships such as intra and interspecific competition for resources or space, predation, and changes in abiotic factors (e.g., water temperature, pH, dissolved oxygen, water depth, and water velocity) (Bley, 1987; Heggenes and Borgstrom, 1988; Matte et al., 2020; Utz and Hartman, 2009). Also, another relevant factor is found in river basins having steep slopes (as the Encantado river basin where our study has taken place), where the effect of flash floods is stronger and potentially the cause higher mortality of fish, especially of early life stages (Harvey, 1987; Pearsons et al., 1992). Hence, young fish, at pre-reproductive stage of life might be more sensitive to changes in biotic or abiotic environmental factors, but mainly related to small body sizes.

Due to the high number of species of freshwater fish in South America (about 5160 but the estimate for the freshwater fish fauna alone points to a final diversity between 8000 and 9000 species, see Reis et al., 2016), understanding all the aspects related to the life history of Neotropical fish is a quite hard and impracticable task to be reached (the Raunkiæran shortfall, Hortal et al. 2015). For loricariids, studies on the reproductive characteristics (e.g., Suzuki et al., 2000) or attempting to identify reproductive patterns by phylogenetic group (Mas et al., 2019) have already been developed. However, most research so far has focused on descriptive aspects of single species (Alves et al., 2019; Braga et al., 2008; Figueiredo et al., 2019), and many species have been studied only in one of three aspects (reproduction, feeding habits, and age and growth; see Becker et al., 2010, for an assessment on reproductive aspects). Consequently, the understanding of general patterns of life history are incomplete due to their high fish diversity (approximately 1000 described species, see Fricke et al., 2020). According to Becker et al. (2010), improving general knowledge on fish populations and searching for general patterns of life history can benefit scientific strategies to direct study efforts to a representative sample of different taxonomic and phylogenetic groups, body sizes, and habitats, as also implied by Hortal et al. (2015). In this sense, our study add new information considering understudied fish group, habitat type, ecoregion, life history traits and population parameters.

A variety of methods used to estimate individual growth parameters can be utilized (e.g. length frequency and otoliths) (Campana, 2001). The mark and recapture method is one of the most rigorous one validating the age of fish, because the absolute age of the recaptured individual fish is known (Campana, 2001). However, despite its effectiveness, the use of mark-recapture methods was not found in a recent review study on age and growth of South American freshwater fish conducted by Santana et al. (2020). Thus, the present study is believed to be one of the few (except for cave fish, see Trajano and Bichuette, 2007; Trajano, 1991, 1997, 2001) using mark-recapture to estimate life traits of Neotropical stream fish (age, growth, survival). Furthermore, we believed that mark-recapture can be a promising approach because it has been recently used in fish movement ecology (De Fries et al., ver Cap 2, nesta Tese; Espírito-Santo et al., 2017; Mazzoni et al., 2012; Mazzoni et al., 2018), with potential application to understanding the effects of stream fragmentation by road crossings (De Fries et al., submetido, ver Cap 3, nesta Tese; Amtstaetter et al., 2017).

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CAPÍTULO 2 – Individual movement patterns of a small stream catfish (*Rineloricaria aequalicuspis*, Loricariidae)

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Abstract

Understanding the movement patterns of stream fish and their causes can be crucial in understanding the behavior of spatially structured populations and predicting how species respond to environmental changes. In this study, we used a mark-recapture approach to describe the individual movement of *Rineloricaria aequalicuspis* in a stream in southern Brazil. We assessed whether the species presents heterogeneous movement, the degree of mobility, and the relationship of individual fish movement with body size and local habitat variables. The study was carried out monthly from November 2018 to March 2019 and fish individuals were sampled in 10 stream sections of 20 m each, along a 430-m stream stretch. The movement frequency distribution was moderately leptokurtic (kurtosis = 3.31) indicating that the population has a heterogeneous movement with two groups of individuals, stationary and mobile. The maximum distance of movement downstream was -248 m and the maximum distance upstream was 208m. The mean and median movement distance (independent of the direction) was of 101.5 m (downstream Dm = 109.6 m, upstream Dm = 87.5 m) and 80 m, respectively. The density of individuals was the main factor affecting probability of movement, suggesting that the motivation to leave a given stream section may depend on the availability of resources and, potentially, on intraspecific competition. The heterogenous movement pattern observed in a non-migratory stream fish as *R. aequalicuspis* indicates that intra-populational variability occurs in a behavior that is usually assumed to be uniform in stream fish species. Finally, we suggest that assuming that a species is either sedentary or mobile may represent an oversimplification, weakening our understanding about stream fish ecology and its application to conservation and environmental impact analysis.

Keywords: Atlantic forest, benthic fish, Loricariidae, mark-recapture, movement ecology, stream

Introduction

The understanding of patterns and processes related to fish movement can be applicable in a variety of circumstances, covering from basic to applied interests in ecology (Petty & Grossman, 2004; Skalski & Gilliam, 2000). For instance, quantifying the mobility of a certain species can be used to determine its ability for colonization, recolonization, and population recovery after natural and anthropogenic changes in the environment (Albanese, Angermeier, & Dorai-Raj, 2004). However, only 1% of the worldwide riverine fish species have been considered in studies related to fish movement, and most of these studies were accomplished on salmoniform species (i.e., salmons, trout, and allies) from the Northern Hemisphere (Comte & Olden, 2018). Furthermore, for other groups of fish most studies focus on large species (Comte & Olden, 2018). Hence, the understanding of the frequency and extent of stream fish movement is still limited taxonomically and geographically (Roberts et al., 2008).

The restricted movement paradigm (Gerking, 1959; RMP, *sensu* Gowan et al., 1994) has historically influenced research on stream fish movement. According to the RMP, most stream fish species would be sedentary, with home ranges restricted to the same stream reach (e.g., ranging from 0 to 50 meters, Petty & Grossman, 2004). However, several studies have discussed the validity of the RMP because of the diversity of sampling protocols that have been used (e.g. Gowan et al., 1994; Gowan & Fausch, 1996; Rodriguez, 2002; Smithson & Johnston, 1999). Recently, the concept of *heterogeneous movement* has been developed for fish populations, to describe that populations may have both stationary and mobile components of movement (Booth, Flecker, & Hairston, 2014; Rodríguez, 2002; Radinger & Wolter, 2014; Skalski & Gilliam, 2000). In this concept, the frequency distribution of the movement is represented by a leptokurtic distribution. This distribution predicts that most individuals in a population are sedentary (a high concentration of observations corresponding to a movement distance equal or close to zero), while individuals with greater mobility comprise a small proportion of the population (observations corresponding to the tail extremity of a leptokurtic distribution). Hypothetically, highly mobile individuals would be the main responsible for dispersion, colonization, and recolonization, and consequently, for gene flow between populations within and between streams, and genetic diversity within populations in a watershed (Radinger & Wolter, 2014).

Previous investigations on stream ecosystems of North America, Europe, and Asia indicated that populations of benthic fish may show restricted movement, with most of individuals moving less than 50 meters (Martin-Smith et al., 1999; Ho & Dudgeon, 2016; Petty & Grossman, 2004). Other studies have found populations with heterogeneous movement, where some individuals can move more than 90 or even 260 m (Aparicio & De Sostoa, 1999; Dammeyer, Phillips, & Bonner, 2013; Knaepkens, Baekelandt, & Eens, 2005; Knaepkens, Bruyndoncx, & Eens, 2004; Mitsuo et al., 2013). In Neotropical streams, heterogeneous movement for small fish populations has been observed (Barbosa, 2019; Mazzoni et al., 2018), and some authors have stated that loricariid (armored catfish) species are sedentary, have a low swimming or dispersion ability (Casatti & Castro, 2006; Hirschmann, Fialho, & Grillo, 2012). Nonetheless, the few available studies have shown that individuals can have either low (0 to 50 meters; Mazzoni, 2018) or high mobility (more than 800 meters; Barbosa, 2019; Power, 2003). However, these studies were based on observations of few recaptured individuals (1 to 5), so that an in-depth assessment of movement heterogeneity was not possible.

At local scale, stream fish movement probabilities can occur both due to individual intrinsic characteristics or changes in the extrinsic environmental conditions

(Rasmussen & Belk, 2017; Winemiller & Jepsen, 1998). For example, previous studies have indicated that larger adult individuals may be more likely to move than younger individuals (Pennock et al., 2018; Radinger & Wolter, 2014). Yet negative relationships or even the absence of a relationship at all have also been found (Albanese, Angermeier, & Dorai-Raj, 2004; Petty & Grossman, 2004). Variables related to habitat quality such as depth, water velocity, and the density of individuals in the population can have a potential effect on individual fish movement (Albanese, Angermeier, & Dorai-Raj, 2004; Aparicio et al., 2018; Aparicio & De Sostoa, 1999; Mitsuo et al., 2013). Thus, studies characterizing and identifying the environmental factors underlying fish movement would have direct implications for the understanding of colonization-recolonization processes and persistence of stream fish populations (Albanese, Angermeier, & Dorai-Raj, 2004).

In this study, we used a mark-recapture approach to describe the individual movement of a benthic loricariid armored catfish (*Rineloricaria aequalicuspis*, Reis & Cardoso, 2001) in a stream in southern Brazil. This is a native, relatively abundant, and non-commercial species, endemic to Atlantic Forest streams (Malabarba et al., 2013; Reis & Cardoso, 2001). We assessed the type of movement in the population (heterogeneous or not), the mobility degree of individuals and the relationship between individual fish movement, body size and local habitat characteristics.

Material and Methods

Study species

Rineloricaria aequalicuspis is a siluriform fish (Loricariidae) endemic to streams of coastal drainages in southern of Brazil (Reis & Cardoso, 2001). This species can reach 200 mm in total length (Dala-Corte & De Fries, 2018; Dala-Corte, Moschetta & Becker, 2016). It is a typically benthic species occurring in shallow streams (1st to 5th order) with rocky bottom (Dala-Corte & De Fries, 2018; Malabarba et al., 2013). The reproductive period of *R. aequalicuspis* is relatively long, from late winter to summer (September to March), but mainly in summer (De Fries, Fontoura & Becker, see Chapter 1 in this Thesis).

Study site

The study was conducted in a 2nd order, 4-km stream in the Tramandaí-Mampituba freshwater ecoregion (Abell et al., 2008) (Fig. 1). The studied stream has a watershed area of 5 km², with elevation ranging from 880 to 60 meters from headwaters to the mouth (in the Maquiné river), forming a deep valley with steep slopes and strong runoffs (Camana, Dala-Corte, & Becker, 2016). The studied stream is shallow (mostly less < 30, with clear waters and a rocky substrate (Fig. 1). Rainfall is regular throughout the year, with average annual rainfall ranging from 1400 to 1800 mm (Hasenack & Ferraro, 1989).

Fish sampling and mark-recapture

The study was carried out monthly from November 2018 to March 2019. We sampled fish individuals in 10 stream sections of 20 m each, along a 430-m stream stretch (Fig. 1). Each 20-meter sampled section was intercalated by non-sampled stream sections of at least 20 m. Fish were captured by kick-sampling, using rectangular dip-net (40 x 40 cm, 80 cm deep, and mesh of 4 mm). In the last sampling month, we used electrofishing (EFKO model GmbH FEG 1500) to increase sampling efficiency. To prevent fish from moving out of the sampling section, we blocked both the beginning and the end of each section with gillnets (1.2 cm mesh size). Catches were conducted in upstream direction, following an approximately zig-zag path to screen all the habitats in each 10-m section. When an individual fish was captured, we immediately placed it in a 20-l plastic bucket containing water from the stream. After going through each section, all individuals were measured (total body length, TL, mm) and a photograph of the abdominal region was taken for individual identification, as described by Dala-Corte, Moschetta, & Becker (2016). Only individuals larger than 70 mm were photographed. After carefully handling each individual, we released the fish in the center of the same stream section where it was caught.

For determining recapture events, we used individual photo-identification and a semi-automated software assisted procedure to match pictures of the same specimen obtained in different sampling events. All images were analyzed using the Wild-ID software (Bolger et al., 2012) to individually identify each fish captured, assigning a unique identification number for each capture event. The images were then stored in an image bank. New images from subsequent samples were compared to those of previous sampling events, with a list of the ten most similar matches being provided by automated analysis. The final validation of a recapture event (a match between two pictures of the same individual, obtained in different sampling events) was made by two of the authors (L. De Fries and M. Camana) to ensure accuracy in identification. Firstly, validation was made independently by each observer. Then, the two observers compared their assessments and reassessed any inconsistency before a final decision.

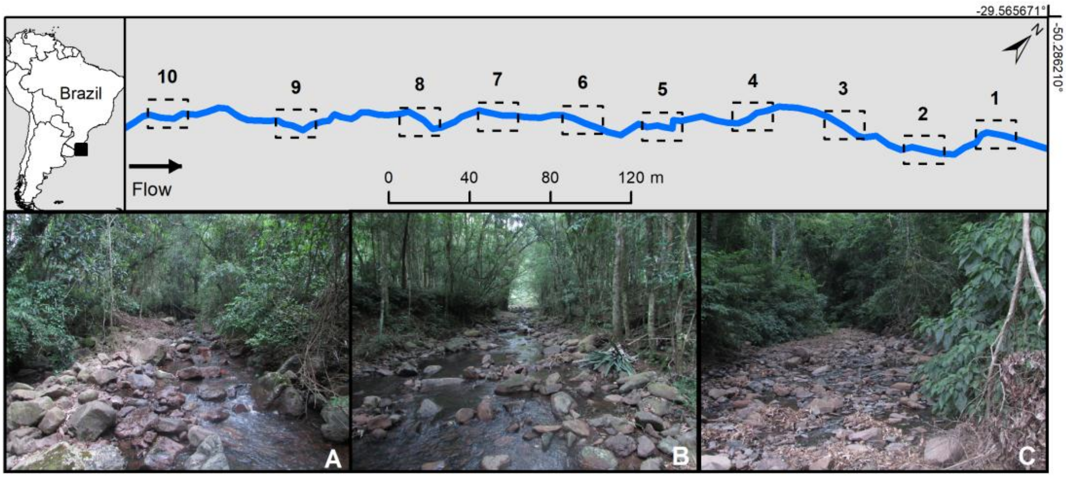

Figure 1. Study site location and sampling design. The dotted rectangles represent each sampled section (i.e., 20 meters). The black arrow indicates the flow direction in the stream. A) Image featuring habitat structure at the uppermost sampling section (section 10). B) Image illustrating an intermediate section (section 6). C) The first sampled section (section 1). Sampling was performed in upstream (from section 1 to 10) direction. Geographic coordinates of section 1 (29.5671°S, 50.2854°W) and ending in section 10 (29.5703°S; 50.2893°W).

Habitat characteristics

In each 10-m stream section, we measured habitat characteristics (e.g., depth and water velocity) to calculate four explanatory variables which were previously known to be related to fish movement in streams (Table 1). These variables included: 1) mean depth (Depth_M); 2) depth variation coefficient (Depth_CV); 3) mean water velocity (Water velocity_M); 4) individuals per m² (Density). Depth, water velocity, and wetted width were measured in two points in each section at distances of 5 and 15 meters from the downstream section limit. Water velocity was measured with a mechanical flow meter for 60 seconds (General Oceanics'). Density of individuals was measured as the number of individual fish (*R. aequalicuspis*; including individuals with TL < 70 mm) divided by the area of each sampled section (m^2). Area was measured as section length multiplied by mean wetted width.

Table 1. Description of habitat variables measured in each 10-m stream section. Mean depth (Depth_Me), depth coefficient of variation (Depth_CV), mean water velocity (Water velocity_Me), and density of individuals (Density).

Capture reach	**Mean**	**Standard Deviation**	**Minimum**	**Maximum**
Depth_Me (cm)	16.53	4.18	8.5	23
Depth_CV (cm)	0.35	0.34	0.1	1.29
Water velocity_Me (m/s)	0.44	0.16	0.17	0.8
Density (ind./m^2)	0.11	0.10	0.01	0.45

Data analysis

For every specimen that was recaptured, we estimated a movement distance (D_m), which was calculated as the distance from the central point of the recapture stream section to the central point of the previous capture stream section, including the 20-m non-sampled sections. Each individual recapture event was considered as unique movement event (so that if one given specimen was recaptured two or more times, there would be two or more movement records). Individuals captured and recaptured in the same stream section were classified as stationary and were represented by zero (0) in the data matrix. Individuals with $D_m \geq 40$ m were considered to be mobile and were assigned as one (1) in the data matrix. To assess direction of movement, negative values were assigned to downstream movement and positive values to upstream movement. We tested the difference between the number of observations for sedentary and mobile fish, as well as between the number of individuals moving upstream or downstream using a chi-square test.

Heterogeneous movement was assumed for a population when the frequency distribution of movement distance was leptokurtic (Skalski & Gilliam, 2000, 2003). We calculated the kurtosis value of the frequency distribution of movement distance to test for the presence of heterogeneous movement in *R. aequalicuspis*. For kurtosis values greater than zero, we accepted that the population had a leptokurtic distribution; and for values lower than or equal to zero, we assumed that the population had a platykurtic distribution (Gotelli & Ellison, 2013). Although kurtosis is not a very common index in ecological studies, it has been demonstrated to be very useful as an indicator of variation at the level of individual movement behavior (Skalski & Gilliam, 2000, 2003). This index has been used in studies that assessed movement patterns in stream fish (Aparicio et al., 2018; Fraser et al., 2001; Ho & Dudgeon, 2016). The statistical analyses were conducted using the *kurtosis* function to get kurtosis value of the frequency distribution of distance moved by *R. aequalicuspis* from the moments package (Komsta & Novomestky, 2015) in the R environment (R Core Team, 2018).

The mobility degree was assessed by the % of individuals with movement distance at the following classes: 0 (no movement between stream sections), 40 to 100 m, 101 to 200 m and larger than 200 m. We calculated the mean movement distance for all mobile individuals. In addition, the mobility degree was assessed by an analysis that predicts the movement parameters (i.e., stationary = mean movement distance of the stationary component, mobile = mean movement distance of the mobile component and *p* = share of the stationary component on the total population) of a leptokurtic distribution, based on a meta-analysis study on heterogeneous fish movement in rivers

(Radinger & Wolter, 2014). The stationary and mobile parameters for the population were calculated using the following data: mean length (L) for each individual captured between release and recapture; mean aspect ratio of the caudal fin (AR) set as 1.8 (minimum = 0.61; maximum = 3.02); stream order (SO) equal to two; study period (T) of 100 days (maximum number of days that an individual was recaptured between release and recapture). For calculating AR, we used 504 specimens in the laboratory (these specimens had been collected for the study of reproduction De Fries et al., ver Cap 1, nesta Tese). For each specimen, we measured the length and height of the caudal fin and then calculated the Caudal fin Area as A_c = (length x height)/2 and AR = $(\text{height})^2/A_c$. We used this analysis of fish movement (Radinger & Wolter, 2014) to test the predictions proposed by Oyanedel et al. (2018), based on three different scenarios, the existence of (i) a mobile population (1% stay in one territory for life, $p = 0.01$); (ii) intermediate mobility (50% stay in one territory for life, $p = 0.50$); (iii) sessile population (99% stay in one territory for life, $p = 0.99$). To test whether the movement of *R. aequalicuspis* was consistent with one of the three scenarios mentioned above, we estimated the probability of finding values equal to or greater than the average linear home range (101.5 m) over those three scenarios. A scenario was rejected if the *p*-value was significant ($p < 0.05$). The analyses were conducted using the *fishmove* function to calculate movement parameters of leptokurtic fish dispersal from the *fishmove* package (Radinger & Wolter, 2014) in the R environment (R core Team, 2018).

The relationship between environmental factors and movement in each sampled section was tested using a generalized linear mixed model (GLMM). The response variable included in the model was of binary nature (i.e., recapture in the release portion and without movement = 0; not recaptured in the release section and with movement = 1). The predictor variables were: mean depth, depth coefficient of variation, mean water velocity, and density (individuals / m²) as fixed effects; and the identification of each section was considered as a random effect. The most significant model was selected by an automated model selection, which we generated using the *dredge* function and a set of models with different combinations (Bartoń, 2020). Model selection was based on the Akaike's information criterion for small sample size (AICc), where models with higher weights were considered the most likely to be the best model for a given dataset (Burnham & Anderson, 2002). The relative importance of each predictor variable was extracted using the function *importance*, based on the sum of all Akaike's weights over all models. We used model averaging to estimate the coefficients and *p*-values of each variable inputted in the models, and in this procedure we selected the candidate models with $\Delta\text{AIC} < 2$ out of all possible combinations among the predictor variables (Burnham & Anderson, 2002). The relationship between probability of movement and total body length was analyzed separately by logistic regression (Generalized Linear Model). These analyses were conducted in the R environment (R Core Team, 2018) using the *lme4* package (Bates et al., 2015) and *glmer* function to fit a GLMM and the *MuMIn* package (Bartoń, 2020) for the functions *dredge* and *importance*.

Results

A total of 158 individuals were captured and 33 were recaptured (recapture rate = 20.9%). When accounting for repeated captures for the same individual, the total number of capture events was 198, of which 40 were recaptures (33 fish recaptured only once, 2 fish recaptured twice, and 1 fish recaptured three times). The mean total body length of the recaptured individuals was 102 mm (minimum = 71; maximum = 178; standard deviation = 28.7).

The frequency distribution of movement distance was moderately leptokurtic (kurtosis = 3.31) with 32.5% of the events corresponding to a movement distance of 0 m, while 45% of the movements corresponded to distances between 40 and 100 meters, 15% to distances between 101 and 200 meters, and 7.5% to distances greater than 200 meters (maximum distance downstream = -248 meters; maximum distance upstream = 208 meters) (Figure 2). This results suggests a population with heterogeneous movement, with two groups of individuals, stationary and mobile. The number of mobile individuals was greater than the stationary individuals and no difference between upstream and downstream movement frequency was found (Figure 3). The mean and median movement distance (independent of the movement direction) were 101.5 m (downstream D_m = 109.6 m, upstream D_m = 87.5m) and 80 m, respectively (Figure 4).

When we analyzed the mobility degree using the *fishmove* function, the movement in the stationary group was described by a mean (D_m) of 10.93 meters (with values ranging from 6.24 to 19.16), while in the mobile group the mean (D_m) was 144.26 meters (with values ranging from 93.58 to 222.40) (Figure 5). The prediction of low mobility was rejected ($p < 0.01$). On the other hand, intermediate and high mobility predictions were accepted ($p = 0.40$; $p = 0.18$, respectively) (Figure 6 shows the expected distribution of linear home range of *R. aequalicuspis* for the three mobility scenarios).

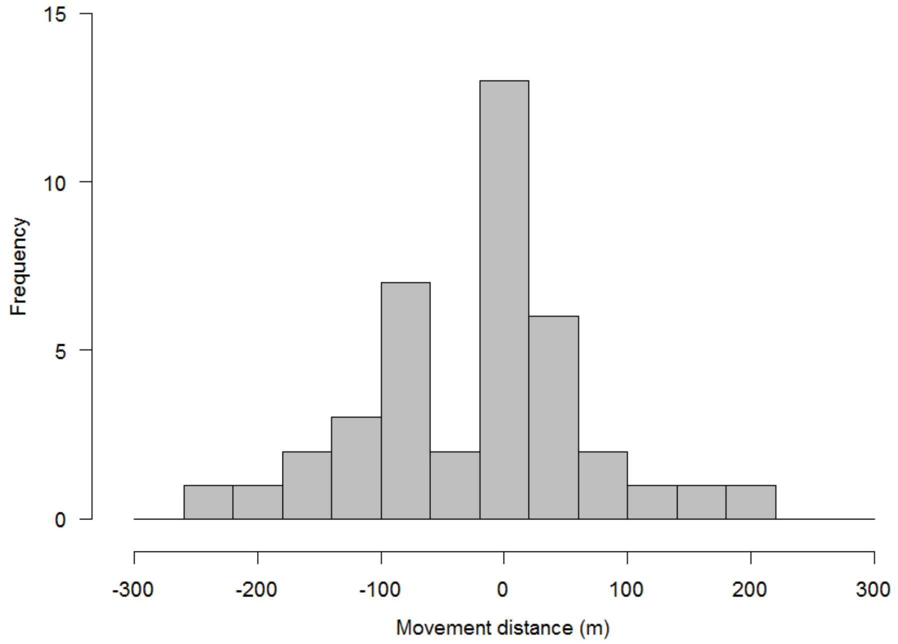

Figure 2. Distribution of movement displacement performed by recaptured individuals of *R. aequalicuspis*.

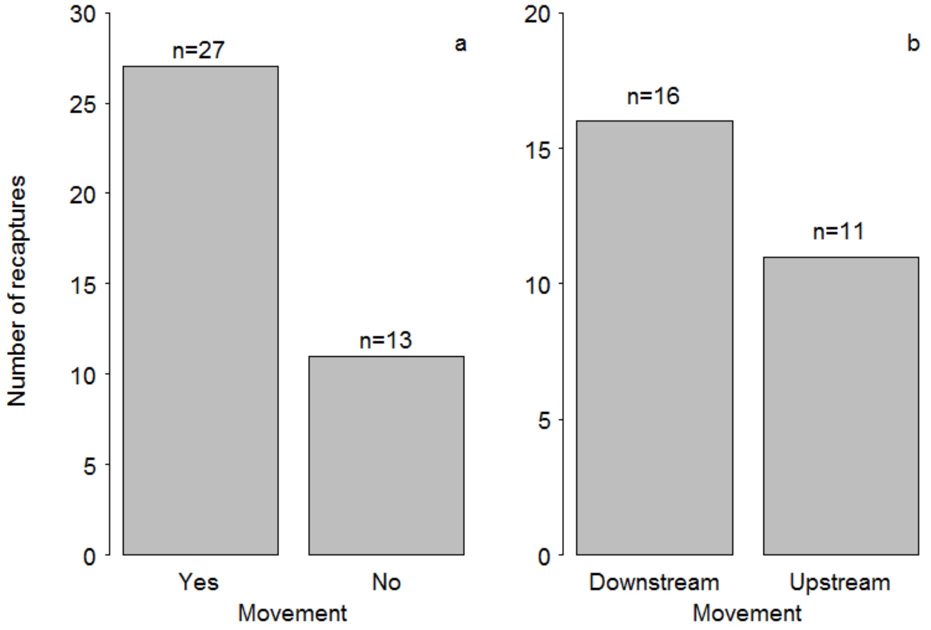

Figure 3. Movement of *Rineloricaria aequalicuspis*, according to recapture data: a) Frequency of movement (fish recaptured) and non-movement (fish that were captured and recaptured in the same section) events. b) Number of movement events in downstream or upstream direction. The frequency of movement and non-movement events was significantly different (2a; chi-squared = 4.9, df = 1; p = 0.02); but no statistical difference was found for frequency of downstream vs upstream movements (2b; x^2 = 0.92, df = 1; p = 0.33).

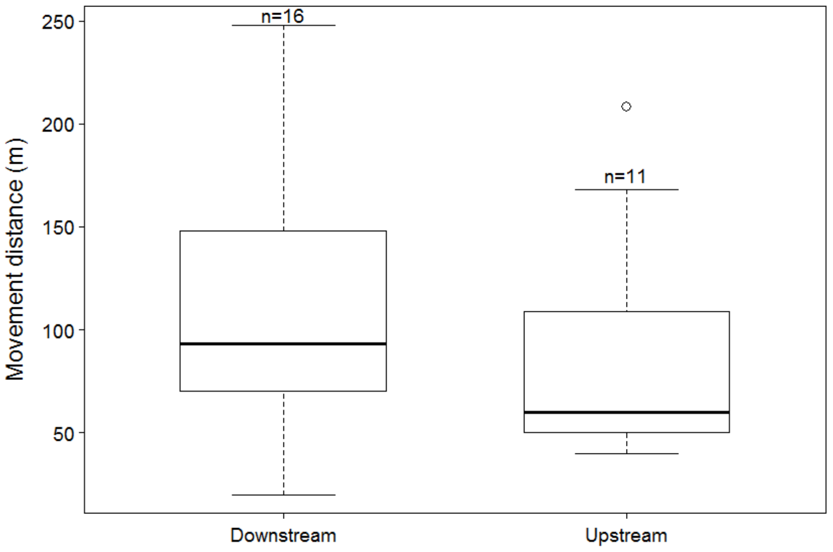

Figure 4. Boxplots of movement distance of *Rineloricaria aequalicuspis*. N = number of movement events recorded with capture-recapture data. Empty circles represent outlier values. The bold horizontal line crossing the boxes is denoted by the median values. The bottom and top box sides represent the lower and upper quartiles .The whiskers represent the minimum and maximum values.

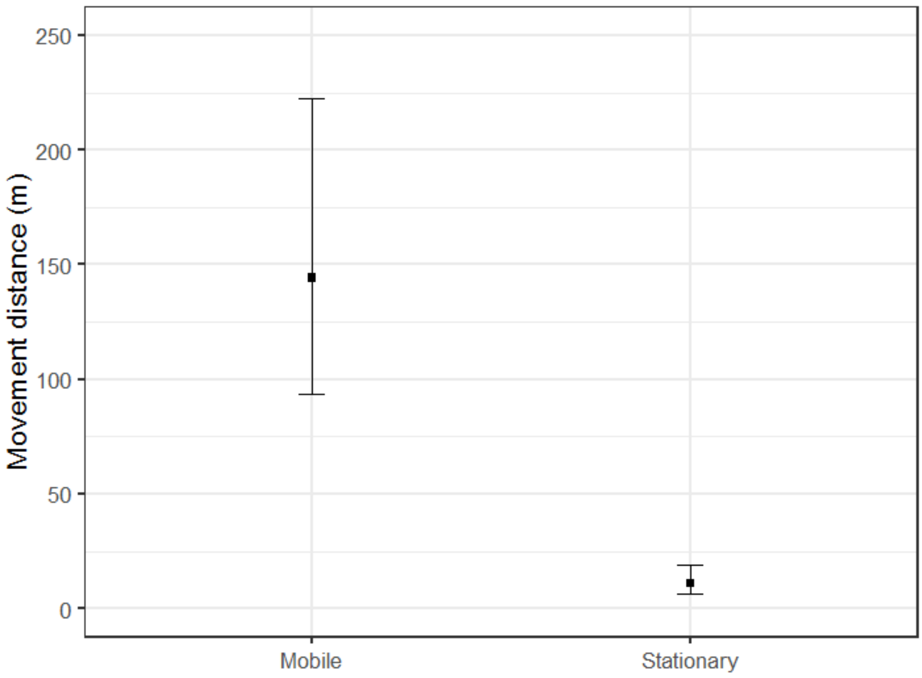

Figure 5. Movement distance calculated for mobile and stationary individuals. Movement distance was calculated utilizing the *fishmove* package (Radinger & Wolter, 2014) with the morphological values of the recaptured individuals, environmental stream features, and the study time. Black squares represent the mean distance value and the whiskers represent the standard error.

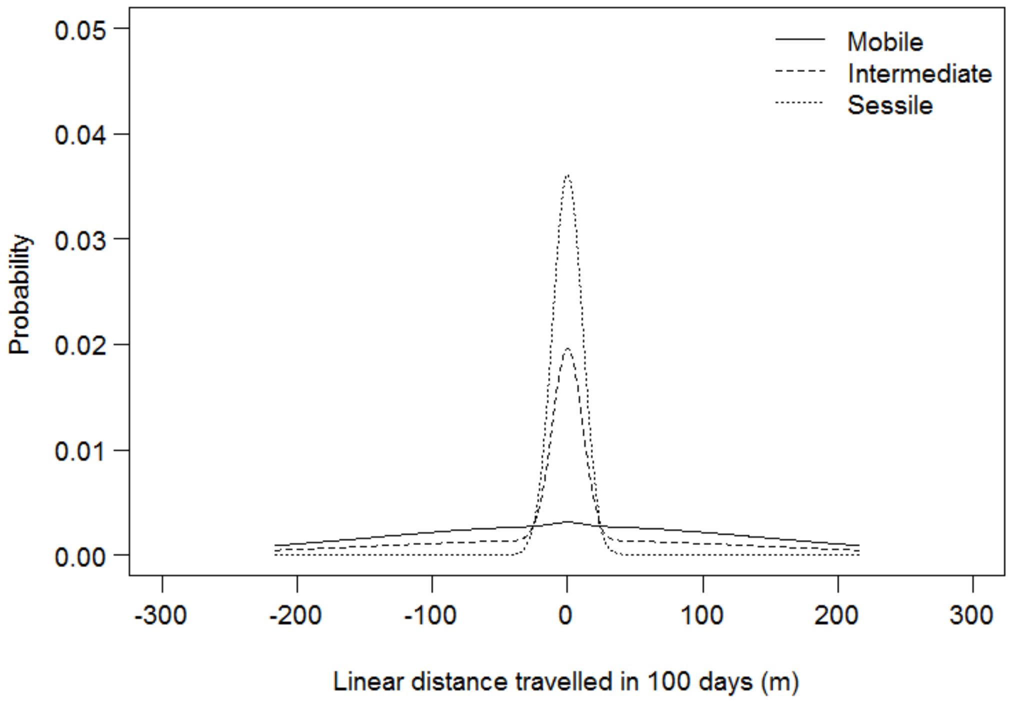

Figure 6. Probability distribution showing the expected linear home range distribution of individuals based on the three mobility scenarios: (i) full line = mobile population (1% site fidelity); (ii) dashed line = intermediate population (50% site fidelity); (iii) dotted line = sessile population (99% site fidelity). The sessile population scenario was rejected (p = 0.0051), and the other two scenarios, i.e., intermediate population (p = 0.4882) and mobile (p = 0.2243), were accepted.

The most important factors explaining movement of *R. aequalicuspis* were individual density and mean water velocity. These variables were included in the most parsimonious model explaining the probability of movement (Weight = 0.289, Table 2). In the final average model, fish movement was positively related to individual density (Density) (coef. beta = 28.43) and average water velocity (Water velocity_Me) (coef. beta = 6.86) (Table 3). Density was an important predictor (RI = 0.89; $p < 0.05$), followed by water velocity (RI = 0.78; p = 0.06) (Table 3). Movement was also weakly but positively related with mean body length (coef. beta = 0.05; *p* = 0.04) (Figure 7).

Table 2. Models (GLMM) of the influence of habitat variables on movement of *R. aequalicuspis*. AICc = Akaike information criteria for small sample size. ΔAIC = deviation for AICc compared with top model. Weight = AICc weight.

Model	**Variables**	**AICc**	**ΔAIC**	**Weight**
Capture reach	Density + Water velocity_Me	46.8	0	0.289
	Density + Depth_CV + Water velocity_Me	47.1	0.25	0.255
	Density	49.2	2.36	0.089
	Density + Depth_Me + Water velocity_Me	49.4	2.6	0.079
	Density + Depth_CV + Depth_Me + Water velocity_Me	49.8	2.98	0.065

Table 3. Parameters estimated by the model-averaging procedure that were included in the best models (ΔAIC < 2) and their respective *p* values.

Model	**Variables**	**Estimate**	***p***	**Relative Importance**
Capture reach	Density	28.43	0.04	0.89
	Water velocity_Me	6.86	0.06	0.78
	Depth_CV	1.86	0.23	0.42
	Depth_ME	0.005	0.97	0.23

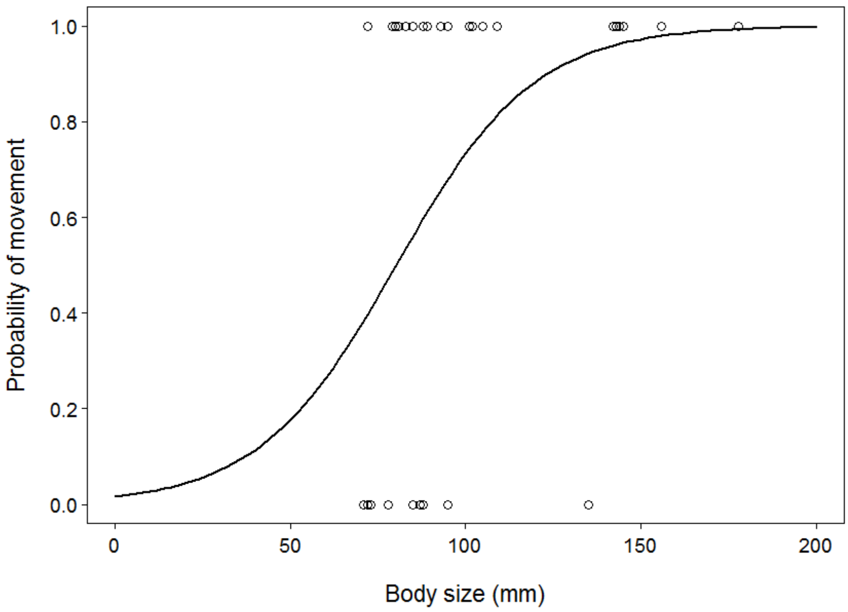

Figure 7. Results of the logistic regression estimating fish movement probability related to the mean total length of *R. aequalicuspis*.

Discussion

Our results support the concept of heterogeneous movement for *R. aequalicuspis*, a non-migratory small benthic stream fish. The degree of mobility indicated that this population has a large proportion of stationary individuals (movement distance < 50 meters), while a small proportion of mobile individuals has shown intermediate to high mobility, moving over distances greater than 200 m, between 20 and 50 days. Interestingly, the density of individuals was the variable that had the greatest effect on the probability of movement, indicating that the motivation to leave a given stream section may depend on the amount of resources available, the stream size and, potentially, on intraspecific competition. Water velocity had a marginally significant relationship related to the probability of movement, and the total body length did not have a great effect in fish mobility within the stream.

Heterogeneous movement and the degree of mobility showed by *R. aequalicuspis* was similar to that of other benthic species found in streams all over the world (Aparicio & De Sostoa, 1999; Dammeyer, Phillips, & Bonner, 2013; Knaepkens, Baekelandt, & Eens, 2005; Knaepkens, Bruyndoncx, & Eens, 2004; Mitsuo et al., 2013). In the Neotropical region, despite some evidence of heterogeneous movement in streams (Barbosa, 2019; Mazzoni et al., 2018), the most significant knowledge of fish movement patterns so far is still focused on larger non-benthic species, which perform extensive movements due to their reproductive migration patterns in rivers (Agostinho et al., 2003; Hahn et al., 2011; Lopes et al., 2019). Some authors have argued that the morphology of the loricariids fish is adapted to being able to remain fixed to the substrate against the water current (Casatti & Castro, 2006), and reproductive characteristics such as territorial behavior, parental care, and nesting sites would explain the restricted individual movement of loricariid species in streams (Hirschmann, Fialho, & Grillo, 2012; Mazzoni et al., 2018). However, our results indicate the occurrence of heterogeneous movement in *R. aequalicuspis*, with intraspecific variation in movement patterns, and not a simple "sedentary or not" definition of movement [as previously noted by other authors, such as Gowan et al. (1994) and Petty & Grossman (2004)].

Reproductive individuals engaged in activities such as guarding spawning sites, mating and parental care are likely to have restricted movement, in contrast to those not engaged in these activities. However, we found that the stationary group included specimens of all sizes, even those smaller than mean reproductive size (De Fries et al., see Chapter 1 in this thesis), and reproduction would not suffice for explaining their stationary behavior. Hence, heterogeneous movement cannot be explained solely by reproductive behavior and future research should consider a more complex set of situations, including genetic basis for different behaviors (Lamphere & Blum, 2012) and others factors like age, size, and individual variation (Knaepkens, Bruyndoncx, & Eens, 2004; Petty & Grossman, 2004; Radinger & Wolter, 2014).

The individual probability of movement in *R. aequalicuspis* was mainly influenced by the density of individuals, while physical habitat (only water velocity) and body size were weak factors. According to Rose et al. (2001), processes such as growth, survival, reproduction and movement are density-dependent if their rates change as a function of the density or number of individuals in a population. Our results thus suggest that movement pattern of *R. aequalicuspis* might be related to density-dependent mechanisms. This evidence has been observed for other teleost species localized in rivers and streams of others places of the world, including *Argyrosomus japonicas* (Taylor, Fairfax, & Suckers, 2013), *Cyprinidon macularius* (McMahon & Tash, 1988), *Oncorhynchus mykiss* (Keeley, 2001; Polivka, 2020), *Salmo trutta* (Crisp, 1993) and *Tilapia guineensis* (Louca, Lindasay, & Lucas, 2009). Density-dependent movement may be a function of habitat space, habitat quality, resource availability and the number of individuals (Rose et al., 2001). Thus, an increased population density can reduce individual fitness, resulting in movement of individuals to leave a given habitat patch due to competition for food and space (Bowler & Benton, 2005; Louca et al., 2009), spawning habitat (Maunder, 1997), or predation risk (Taylor, Fairfax, & Suckers, 2013). High density of individuals may force some individuals to occupy patches of inferior quality, reducing growth and survival rates (Rashleigh & Grossman, 2005).

Water velocity had a weak positive relationship and low relative importance for the movement of *R. aequalicuspis*. Generally, the number of mobile individuals increases with flow and can allow the fish to explore habitats that were previously inaccessible, or allow them to find shelters off those sections with higher water velocity

(Albanese, Angermeier, & Dorai-Raj, 2004). Our results indicate that, at some point, water velocity may stimulate individuals to leave the stream section. Despite the frequency of upstream and downstream movements not being significantly different, flash floods are common in the studied stream and can potentially cause greater downstream displacement of individuals, so that downstream displacement rate may possibly have two components, one of active movements, and another of passive movement (Chun et al., 2011; Pearsons, Li, & Lamberti, 1992).

The sample extent of streams is one of the main criticisms concerning the studies on the Restricted Movement Paradigm (RMP), particularly when they are not sensitive to fish sampled outside the studied area (Gowan et al., 1994; Rodríguez, 2002). We studied a 4-km stream, but 80% of this extension is either intermittent (in the headwaters), isolated by vertical waterfalls or with very steep channels with large rocks (> 50cm) in the channel, where *R. aequalicuspis* is absent or very rarely found (De Fries & Becker, personal observation). From the remaining stream stretch (800 m in length), we sampled a total of 430 m (53% of the extension effectively occupied by the studied species). The recapture rate of approximately 20% may indicate that 80% of fish may have left the study area, not detected or moved to those areas between the unsampled stream sections, or even suffered high rates of mortality. Perhaps if we would have increased the extension of our stream sections, or sampled over the entire stream site, we could have improved our results showing even a greater distance movement. For instance, a previous study (Barbosa, 2019) recorded a movement distance equals to 1760 m for an individual of *Hemiancistrus punctulatus* (Loricariidae) using a sample design with extension area of approximately 25 times greater than ours.

The choice of the streams to be sampled poses a significant challenge in understanding the ecology of movement in stream fish (Fausch et al., 2002). While a narrow stream with a small extension may allow greater efficiency in the number of recaptures, a greater spatial scale (i.e., greater stream width and length) would mean worse sampling efficiency (and higher sampling cost), making it difficult to understand fish mobility patterns. Therefore, we emphasize the need to develop study designs with longer sampling periods, higher sampling frequency, longer sampling segments, segment replication, and implementing the use of electronic tags (Cooke et al., 2013, 2016; Knaepkens, Baekelandt, & Eens, 2005; Knaepkens, Bruyndoncx, & Eens, 2004; Pennock et al., 2018). However, same with some limitations, our study increased the knowledge about patterns of movement in Neotropical streams.

Dispersal plays an important role in structuring stream fish metacommunities (see Dala-Corte, Becker, & Melo, 2017; Mozzaquattro et al., 2020). However, there is a knowledge gap on the home-range, movement distance and dispersal of stream fish in community ecology studies. One of the main challenges for a better understanding of community ecology and conservation of stream fish is to acknowledge what are the differences in dispersal between species and how this can influence sampling design (Erös, 2017), temporal turnover of fish assemblies (Hitt & Angermeier, 2008, 2011), and even the recovery time after a disturbance (Albanese et al., 2009). Our results can add to the notion of how loricariids move in streams, and which environmental variables may limit their mobility. Some loricariid species may be actively and constantly moving within a stream, having a high dispersal capacity, which is contrary to previously inferred by past studies.

A previous study (Mozzaquattro et al. 2020) have found evidence, at a watershed scale, that the height of a set of barriers, both natural (e.g., waterfalls) and anthropogenic (e.g., road crossings), can increase the dispersal resistance of benthic stream fish. In another study (De Fries et al., see Chapter 3 in this thesis), the authors have shown that culverts (i.e., tunnel structure constructed under roadways to provide cross drainage) can restrict the upstream movements of *R. aequalicuspis*. Therefore, as the number of culverts may increase along the streams, disrupting the connectivity within the fish distribution area, the effect of these barriers might accumulate and turn into a critical factor concerning the maintenance of fish population. For instance, without a source of immigrants in isolated subpopulations, stochasticity might be responsible for a higher probability of local or global extinction of species over time (Aparicio et al., 2018; Johnston, 2000).

Knowledge about movement ecology has management implications for species that are pressed by habitat loss and fragmentation, and climatic change (Bowler & Benton, 2005). For example, recolonization after disturbance may involve short distance exploratory movements that depend on species mobility (Meffe & Sheldon, 1990). Further, knowing the species mobility and its potential habitat occupancy may be useful for predicting the effects of artificial barriers on fish (Mazzoni et al., 2018). However, depending on the perspective on the type of a fish species movement (sedentary or mobile), management implications can be quite different (Smithson & Johnston, 1999). Our results suggest there is intraspecific variability in movement behavior even for species that are generally assumed to be sedentary, in accordance with the concept of heterogeneous movement (Aparicio & De Sostoa, 1999; Dammeyer, Phillips, & Bonner, 2013; Gowan & Fausch, 1996; Knaepkens, Baekelandt, & Eens, 2005; Knaepkens, Bruyndoncx, & Eens, 2004; Mitsuo et al., 2013). Thus, the habitat area necessary for a small benthic fish population persistence in a stream may be larger than expected (Smithson & Johnston, 1999). Lastly, we suggest that classifying stream fish species as either sedentary or mobile is probably an oversimplification that undermines our understanding of stream fish ecology and its application in environmental impact analysis and conservation.

Our study demonstrated that a population of *R. aequalicuspis* has a heterogeneous movement, an intermediate to high degree of mobility, and that their movement depends on the density of individuals. The degree of mobility indicated that individuals were not necessarily sedentary when analyzing the variation within the whole population. The density of individuals affecting fish movement suggests that movement patterns might vary across populations, depending on the resources available and the size of the stream. These results shed light on uncertainties concerning the mobility of stream fish species, with potential implications for conservation and management strategies.

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CAPÍTULO 3 – Road crossings and stream fish movement: a case study on a small benthic species

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Abstract

Crossings between roads and streams can negatively affect fish, especially when culverts prevent free movement along the stream. Understanding this effect is essential to design structures that can mitigate the impact of roads on fishes. Here, we used a capture-recapture study and multi-state open population models to investigate the influence of a culvert on the movement probability of the armored catfish *Rineloricaria aequalicuspis*, a small benthic species (total length ca. 180 mm) endemic to stream riffles in southern Brazil. Additionally, we tested whether environmental variables and body size affect movement probability through the culvert. Fish sampling and environmental data collection were carried out during 2016 and 2017, in a stream section crossed by a road and in the adjacent free-flowing stream sections upstream and downstream. Movement probability was higher within free sections than through the culvert. Water depth in the culvert positively influenced movement probability, whereas body size was not related to movement through the crossing. Our results indicate that the culvert hinders movement of *R. aequalicuspis* and that approximately 30 cm of depth inside the culvert results in an 8-fold increase in the passage probability. These results extend the evidence that culverts affect fish movement in streams, even for non-migratory, relatively small species adapted to environments with natural obstacles. That indicates the need to design road crossings that are more favorable to fish movement, especially in streams crossed by roads in multiple sites.

Keywords: Environmental impact, Freshwater, Loricariidae, Movement ecology, Road ecology.

Introduction

The movement of organisms has implications for the reproductive success and survival of individuals, and consequently for the distribution and persistence of populations (Nathan et al. 2008; Rasmussen and Belk 2017). In streams, fish must move across different habitats for spawning, growing, feeding, and sheltering (Schlosser 1991; Fausch et al. 2002). However, natural and artificial barriers can limit movement and consequently influence fish distribution, abundance, and persistence along streams. Such limitation may be caused by physical structures that restrict movement rate of individuals between stream segments, affecting not only access to different habitats (Tsuboi et al. 2020), but also the input of individuals through immigration, which is important for persistence of local populations with high mortality rates. Therefore, given the connection between stream fish movement and population dynamics (Tsuboi et al. 2020), understanding the potential effects of environmental changes that limit these movements is particularly important to predict population responses (Bowler and Benton 2005), and thus to guide proper environmental planning and management of crossings between roads and streams.

Crossings between roads and streams present different engineering structures (culverts), used to allow the passage of watercourses, usually under the road. Culverts can negatively impact fish by reducing or eliminating upstream or downstream movement (Warren and Pardew 1998; Gibson et al. 2005; Benton et al. 2008; Nislow et al. 2011; Favaro et al. 2014). As movement can be critical to support individuals and populations, barriers that hinder fish movements can be detrimental for species conservation (Bouska and Paukert 2010). Culverts can act as barriers when the structure design and/or problems with its maintenance result in physical changes (e.g., a large gap between the water outlet and stream, shallow depth, high water velocity, and debris accumulation) that can restrict upstream or downstream fish passage (Blank 2010; Timm et al. 2017). However, identifying whether a culvert acts as a barrier can be difficult because fish vary widely in their ability to overcome physical obstacles (Ficke et al. 2011; Anderson et al. 2012).

Several factors influence fish motivation and ability to swim, potentially affecting upstream movement through the culvert (Johnson et al. 2012). These can be species-specific, or vary within a species, including life stage, environmental conditions (water velocity, depth, temperature) and body size (Hoffman and Dunham 2007; Kemp and O'Hanley 2010; Goerig and Castro-Santos 2017). Organisms may need to pass through the culvert only in specific periods, for instance, when searching for spawning or foraging sites (Schlosser 1991; Fausch et al. 2002; Anderson et al. 2012; Goerig and Castro-Santos 2017). Environmental factors, such as season, water temperature, turbulence, and water velocity can also influence upstream movement (Goerig et al. 2015; Goerig and Castro-Santos 2017). For instance, changes in water temperature can alter the physiological condition and motivate individuals to move through the culvert upstream (Goerig and Castro-Santos 2017). Additionally, many culverts can temporarily change from passable to impassable due to variation in water flow and depth (Kemp and O'Hanley 2010; Diebel et al. 2014; Mahlum et al. 2014).

Movement capability in active dispersers is positively correlated with body size (Peters 1983), and larger individuals are expected to overcome obstacles such as culverts (Johnson et al. 2012) more easily than smaller, younger fish of the same species (Webb 1977). This trend has been observed in ascending movements, where individuals with large body sizes may be more successful (Castro-Santos 2004; Johnson et al. 2012; Peterson et al. 2013; Goerig et al. 2017). However, passability may also correlate negatively with body size, depending on the species and on the type of culvert evaluated

(Goerig et al. 2015). Overall, most knowledge about the correlation between movement through culverts and body size comes from studies with salmonids or larger fish species (Amtstaetter et al. 2017); while information on small fish species is still scarce (but see Ficke et al. 2011 and Amtstaetter et al. 2017).

The identification, prioritization, and mitigation of barriers created by culverts are crucial elements in the management of streams in the Northern Hemisphere (e.g., Poplar-Jeffers et al. 2009; Peterson et al. 2013), mainly to guarantee the passage of species that perform seasonal spawning or sheltering movements (migration movement, see Dingle 2014; Rahel and McLaughlin 2018). However, studies on species with other types of movement are still rare. For example, in Neotropical streams with many road crossings, culverts can act as obstacles to resident fish (Makrakis et al. 2012) that perform repeated movements within a territory or home range (*station keeping*, see Dingle 2014; Rahel and McLaughlin 2018). A large number of road crossings can become a significant problem due to cumulative effect along streams or stream networks, affecting fish movements in large geographical areas. For instance, Flores (2017) estimated that at least 78,173 stream-road crossings exist within a 281,189 km² area in Southern Brazil. This high frequency of road crossings added to the lack of technical specifications for culvert design to enhance the passage of freshwater fish (DNIT 2006; DNIT 2009), suggest that the potential impact on road-crossings on Neotropical freshwater fish should not be neglected.

Inferences about the impact of road crossings on Neotropical fish populations usually rely on indirect studies, which compare species abundance and richness between segments up and downstream from crossings (Mariano et al. 2012). On the other hand, there are few studies that directly measure the movement probability and that seek to describe the effect of road crossings on populational processes (such as dispersion) and behavior (movement), and to understand how these can be mediated by environmental (temperature, flow) and biological (size) factors (e.g., Goerig and Castro-Santos 2017). This information is not only useful to demonstrate undesired effects on fish but mainly to guide and develop new designs for road crossings that meet the proper requirements for fish passage (e.g., depth, velocity, perch height, body size).

In this study, we investigated the influence of a road crossing on the movement of *Rineloricaria aequalicuspis* (Reis and Cardoso 2001), a small armored catfish endemic to clear water, rocky bottom streams in southern Brazil. This armored catfish is a small benthic species, and the streams it inhabits can be characterized as riffle-run-pool habitat sequences, with occasional short rapids. Although *R. aequalicuspis* is capable of vigorous short distance (a few meters) bursts, it cannot jump or sustain continued swimming against strong currents (De Fries, personal observation). Therefore, we expect its movements through the culverts (Figure 1, see description in the Methods) to be more affected by perch height and water velocity inside the culvert, than by water depth in the culvert or the stream. The latter are features known to favor the passage of larger species or of species able to jump, such as *Oncorhynchus clarkii* (brook trout) (Kondratieff and Myrick 2006) or *Lepomis macrochirus* (sunfish) (Prenosil et al. 2016). We tried to answer two questions: 1) does the road crossing restrict the movement probability of *R. aequalicuspis*? 2) is the movement probability across the culvert affected by environmental characteristics (water temperature, velocity, perch height, and depth), season of the year, or body size?

Methods

Study area

This study was carried out in a third order stream (Strahler, 1:50000 map scale) in the Maquiné river basin (578 km²), at the Tramandaí-Mampituba freshwater ecoregion (Abell et al. 2008). The study site (-29.6079º; -50.2134º) is a stream reach of approximately 10 m wide, crossed by a local unpaved road. The study site has a 12 km² catchment basin and is located 7 km upstream from the Forqueta River confluence, and 6 km downstream the headwaters. The road-crossing has five rectangular culverts, each measuring 45 cm high, 155 cm wide, and 3.5 m long; the bottom of the structure is made of concrete, and the perch height averages 35.8 cm (Fig. 1).

Fig. 1. View of the study site. a) Upstream view of the road crossing. b) downstream view.

Study species

Rineloricaria aequalicuspis Reis and Cardoso, 2001 is a loricariid catfish endemic to small coastal river basins in southern Brazil (Reis and Cardoso 2001). It is a benthic fish, typical of shallow streams, small and medium-sized, with medium to strong water currents and rocky bottom (Dala-Corte and De Fries, 2018). According to Mazzoni et al. (2018), several species of stream Loricariidae are territorial, presenting parental care and probable spawning areas, having a small home range (up to 150 m). Our observations based on another mark-recapture study with *R. aequalicuspis* (De Fries et al., in preparation) indicate that individuals of this species can move up to 248 m, but usually not more than 100 m all year-round.

Fish sampling and photo-identification

Sampling was carried out during 17 months, between January 2016 and August 2017 (there was no sampling in April 2016, May and July 2017). In each sampling event, the sampled reach was divided in six consecutive 10-m sections. Three reaches were positioned immediately downstream, while the other three were upstream from the crossing. Sections were blocked with a gillnet (1,2 cm mesh size) (Fig. 2).

Fish were captured by kick-sampling, using a rectangular dip-net (40 x 40 cm opening and 80 cm deep, with 4 mm mesh). Kick-sampling was conducted in the downstream-upstream direction, following a zigzag route in each 10 m section. The captured individuals were placed in 20 l plastic containers with water from the stream. After sampling each 10-m section, captured individuals were measured (total length, TL, mm) and had their abdominal region photographed for later individual photo-identification, as described by Dala-Corte et al. (2016). After being photographed, we released the fish in the central portion of the stream section where they were caught. After completing this procedure, we moved on to sampling the next upstream section. Throughout the study, the average sampling effort (number of kicks per area) was approximately the same in the downstream (mean = 0.22, SE = 0.03) and upstream (mean = 0.23, SE = 0.03) sections.

The image files of each individual captured in a given sampling event received a unique identifying code associated to sampling section and date, and were stored for comparison with images taken in subsequent sampling months. A recapture was recorded whenever a picture from a given sampling date matched a picture from a previous sampling date. Image analysis (comparison and matching of pictures to determine recapture events) was software-aided (Wild-ID software, Bolger et al. 2012), while final decision on image matching was made by the authors (see detailed procedure in Dala-Corte et al., 2016).

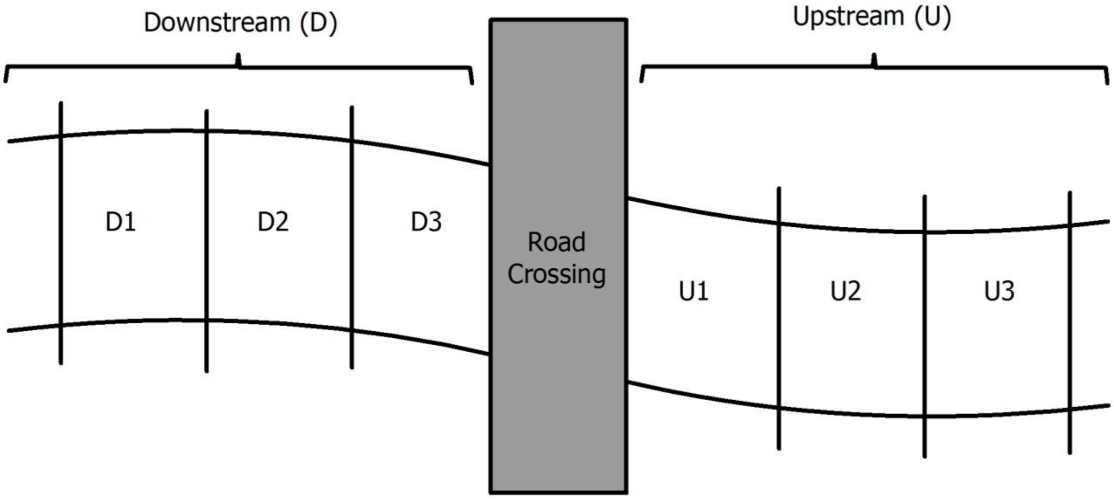


Fig. 2. Sample design for the mark and recapture study with *R. aequalicuspis*. Fish were caught by kick-sampling conducted in the downstream to upstream direction. Each 10-m free section was blocked with a gillnet. Letters represent the downstream (D) and upstream (U) reaches, free downstream sections (D1, D2, D3), and free upstream sections (U1, U2, U3).

Environmental variables

In each sampling month, water temperature was measured 5 meters upstream of the road crossing. Water depth at the culvert and perch height were measured with a ruler in three places at each culvert (right side, middle and left side). The maximum value of these two variables across all positions for each culvert was used in the data analysis. Water velocity (m/s) was measured once in the middle of each culvert, and the monthly average was calculated for the entire crossing. Water velocity was also measured in each 10 m free section in three positions (right, middle and left margin), and the mean value was calculated for each section. Water velocity was measured with a General Oceanics mechanical flow meter for 60 seconds. Depth was also measured in each 10 m free section at the right, middle and left margins, and the respective mean for each section was calculated. For characterizing stream substrate size, three measurements were made (right, middle and left margins) by visually evaluating the percentage coverage (0 to 25%; 25 to 50%; 50 to 75%; 75 to 100%) of different classes of substrate grain size (0.1 to 0.2 cm; 0.2 to 2 cm; 2 to 7 cm; 7 to 25 cm; 25 to 50 cm; 50 to 100 cm). The mean substrate size was calculated for each section. In the first three sampling months (February, March, and May) the variables mentioned above were not measured, however, in order to avoid the exclusion of individuals marked and recaptured in this period, we used the mean of each variable in the data matrix for the same period of the following study year.

Mark-recapture multi-state models

To estimate the probability of movement through the culvert and between the free sections, we used multi-state models (White et al. 2006) in Program MARK (White and Burnham 1999). The multi-state model is an extension of the open population model (Cormack 1964; Jolly 1965; Seber 1965). Among the main advantages, the multi-state model simultaneously estimate the probability of transition and survival, while accounting for capture probability (Williams et al. 2002; Norman et al. 2009). This model estimates apparent survival probability (phi), the capture probability (p) in each state (here, each stream section), and the transition probability (ψ) between states. This parameter represents the probability of movement between states, in which marked individuals can potentially be found assuming they are alive and in the given state.

Three different analyses were performed to answer the study questions. The first encompassed all individuals that were marked in two states (D and U; 178 individuals), with D including all individuals captured downstream of the crossing, no matter which section (D1, D2 or D3; Fig. 2), while U includes all individuals caught in the upstream section (U1, U2, and U3). This analysis aimed to estimate the probability of movement through the culvert (that is, between D and U). The other two analyses were designed to estimate the probability of movement between free upstream sections (inside U) and free downstream sections (inside D). In these last two analyses, recaptures were considered separately per section, respectively, upstream (three sections, U1, U2, U3; 47 individuals) and downstream (three sections, D1, D2, D3; 132 individuals) (Fig. 2). Given our main interest in evaluating movement probability while considering the effect of spatial variability on the capture probability, the survival probability parameter was considered constant in all models {phi (.)}.

To model the probability of movement through the culvert, we built 24 *a priori* models, including the environmental variables and the individual body size. All the proposed models were developed based on studies with other fish species. Overall, the models considered the relationship between the variables and the movement probability, as described below.

Water temperature. Fish are ectothermic animals, therefore seasonal variation in temperature can influence their body temperature and, therefore, their mobility. Species from cold regions are generally more active at higher temperatures (Lucas and Baras 2002). There is evidence that rising water temperatures may increase the likelihood of culvert passing. In the Neotropical region, fish motivation for ascending passage to overcome obstacles (e.g., fish ladder) increases at higher temperatures (Fernandez et al. 2007). Therefore, we tested the relationship between temperature and passage probability by the culvert. The temperature effect was considered to have the same effect on transition and recapture probabilities.

Depth. Depth variation inside the culvert can either facilitate or prevent movement through the culvert (Blank 2010; Kemp and O'Hanley 2010; Diebel et al. 2014). We expect that the greater the depth in the culvert, the higher the movement probability, both upstream and downstream. Depth was considered to have the same effect for each ψ parameter and was also considered in the recapture probability.

Perch height. Perch height, measured between the culvert outlet and the stream surface downstream, can negatively interfere in the likelihood of movement through the culvert (Burford et al. 2009; Blank 2010), especially in downstream-upstream direction. We expect that the higher the perch height, the lower should be the probability of moving in the direction D-U. On the other hand, in the U-D direction, we expected there would be no effect. Therefore, we considered different effects of perch height for each parameter of ψ (different intercepts for each parameter of ψ). This variable was not considered in the recapture probability.

Water velocity. High water velocity can increase the probability of fish moving in streams (Albanese et al. 2004). However, culverts can significantly increase the usual water velocity in streams, potentially preventing upstream movement (Blank 2010; Goerig et al. 2015). Therefore, we expect that the higher the water velocity inside the culvert, the lower the probability of movement from state D (downstream) to state U (upstream). This variable was considered to have different effects for each parameter of ψ and was not considered in the probability of recapture.

Body size. The probability of movement through the culvert increases with total body length (Castro-Santos 2004; Peterson et al. 2004; Johnson et al. 2012; Goerig and Castro-Santos 2017), so one can expect that larger fish, and particularly *R. aequalicuspis,* will be more likely to move through the culvert (mainly upstream) because they have a greater dispersion capacity (Peters 1983). However, shallow depth inside the culvert could favor small individuals. For this reason, we modeled the effect of body size, both independently and interacting with depth. The total length was included in the recapture probability and was considered to have different effects for each parameter of ψ and p.

Substrate: capture probability is expected to vary spatially according to differences in the stream structure (Peterson et al. 2004; Norman et al. 2009). Therefore, this effect should be more pronounced in segments with the presence of road crossings because they alter stream geomorphology (Norman et al. 2009). Dala-Corte and De Fries (2018) observed that the occurrence of *R. aequalicuspis* has a positive relationship with substrate size on a very fine spatial scale. Therefore, a relationship between substrate and capture probability can be expected, as well as a positive correlation with substrate size. This variable was considered to have different effects for each parameter of p and was not considered in the movement probability.

For analyzing the capture history with three states (three sections downstream and three sections upstream), the same variables were used (except perch height, intrinsic to the existence of the culvert), but measured in each section without a culvert. In all three movement probability analyses, interactions between depth and body size, velocity and body size, and depth and velocity were tested. All estimates and the 95% confidence intervals (CI) were extracted from the best model for each data analysis (movement through the culvert, free movement upstream, and free movement downstream). Model fit was evaluated by estimating the overdispersion parameter ($\hat{c}$), according to the goodness-of-fit procedure in the U-CARE software (Pradel et al. 2003). Estimates of $\hat{c}$ greater than 1 were used to adjust the variance estimates for all models using the QAIC (Burnham, K. P., Anderson 2002). The best models were selected using the adjusted Akaike information criterion for overdispersion (QAIC) and small sample size (QAICc), where models with the lowest QAIC value and the highest weights were considered to best explain the data (Burnham, KP, Anderson 2002).

Results

Movement through the culvert and individual movement

A total of 1,094 fish were individually photo-identified, 178 individuals were recaptured (16.3%), representing 261 recapture events (23.8%, recapture rate). Of the recaptured fish, 116 individuals were recaptured only once and 62 between two and six times. Only 24 fish (2.2%) passed the crossing (15 towards upstream and nine towards downstream).

The mean total length of captured individuals was 103 mm (min = 58 mm; max = 180 mm), and over 70% of the individuals measured between 60 and 119 mm (Fig. 3a). The mean total length of the recaptured individuals was 101 mm (minimum = 71.5 mm; maximum = 173.5 mm). The length frequency distribution of the individuals that passed the crossing upstream (Fig. 3b) is generally similar to that of the total number of captured individuals (Fig. 3a), suggesting that upstream movement is not related to body size. For downstream movement (Fig. 3c), the number of crossing events is too small for a pattern to be interpreted.

The individual movement data (originated from the recaptures) suggest that *R. aequalicuspis* movement is limited to small stretches of the stream, since most of the individuals were captured in the same location they were released (net movement = 0) or close (up to 10 m; Fig. 4), with fish generally being restricted 30 meters downstream or upstream of the release section.

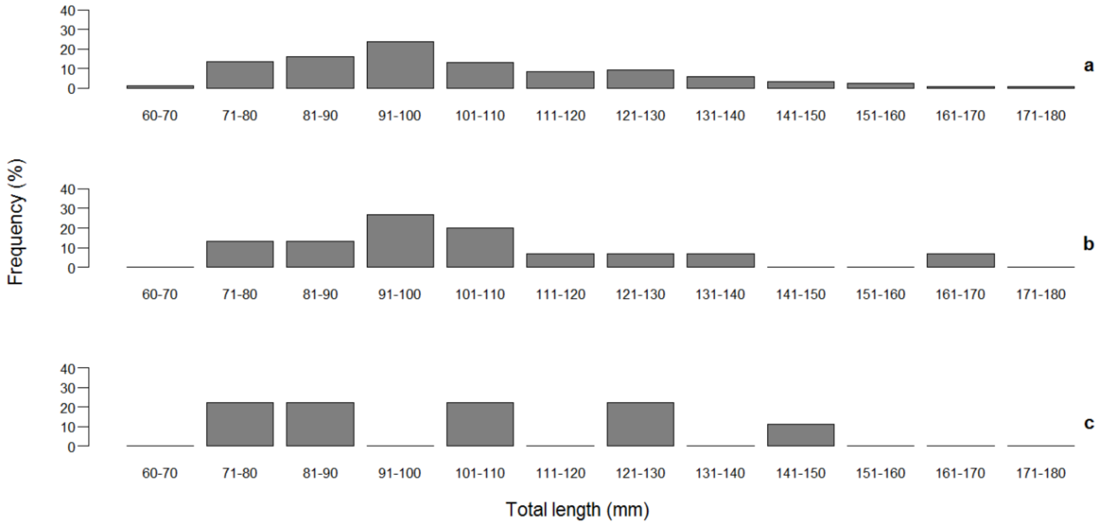


Fig. 3. Length frequency distribution of *Rineloricaria aequalicuspis* (a) in the whole sample; b) in only for individuals that passed upstream through the road crossing; c) in only for individuals that passed downstream through the road crossing.

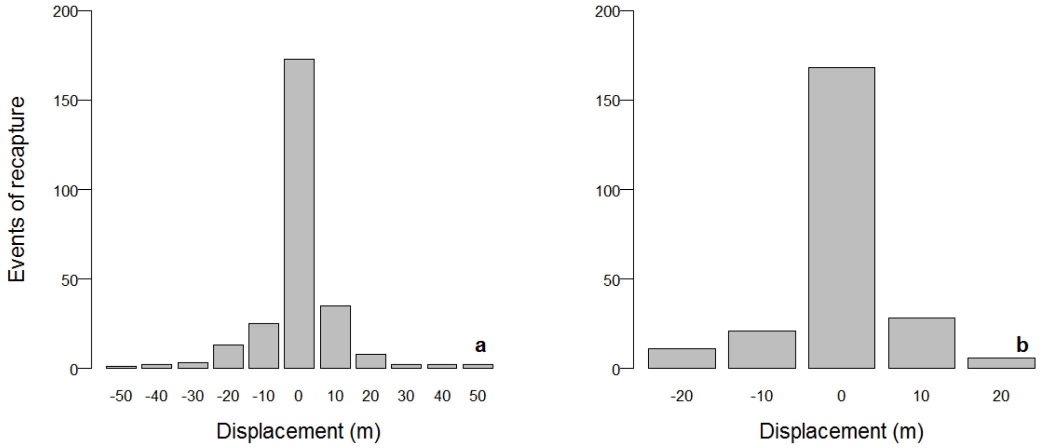


Fig. 4. Frequency distribution of movements extent between the release position and the subsequent recapture position. (a) All recorded movement events; (b) movement occurring only within the free-flowing sections downstream or upstream. The measure of movement does not represent the total individual movements that occurred between release and recapture, but only the distance between the release section and the recapture section.

Influence of environmental variables

All environmental variables used to evaluate the culvert passage analysis (C = crossing) varied across samplings (Fig. 5). The water temperature was the only variable with a clear seasonal pattern indicating a cold period (June to October, 11 to 16ºC) and a warm period (November to March, around 18 to 20ºC) (Fig. 5a). The other variables showed a non-seasonal pattern, with high fluctuations from one month to another, and no collinearity between variables. Overall, maximum culvert depth remained between 9 and 16 cm, but with three extreme values of about 30-35 cm in October and January-February (Fig. 5b). Despite showing higher values in state U, the mean depth had a similar variation among states D and U, with the highest values occurring in October and March (Fig. 5c, d). The mean depth variation of the water velocity inside the culvert fluctuated during the year, presenting the highest value in October (5.54 m/s) and the lowest values in November (0.26 m/s), December (0.25 m/s) and January (0.25 m/s) (Fig. 6a). Perch height varied between 18 and 35 cm throughout the year, except for a relatively higher value in August (51 cm; Fig. 6b). Mean substrate size variation was only slightly different between states D and U (Fig. 6c, d), ranging from 5 to 27 cm (Fig. 6c, d).

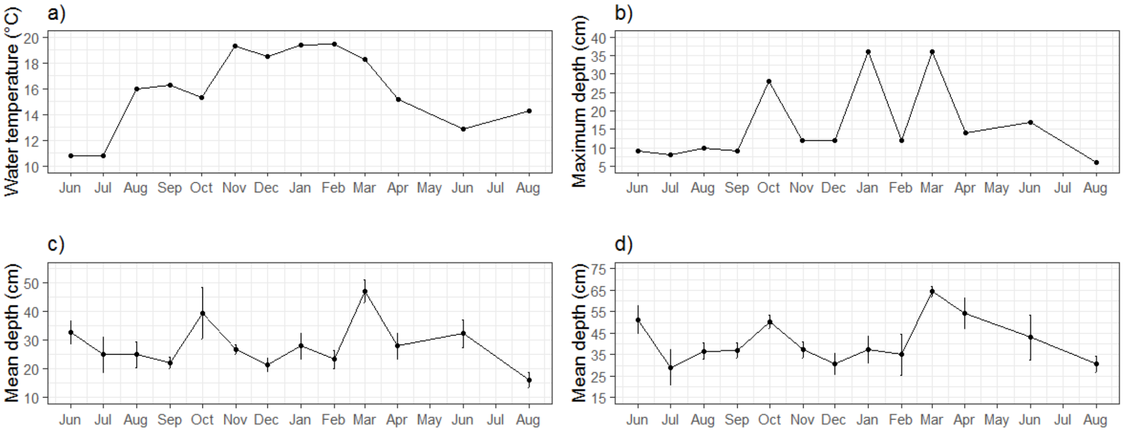


Fig. 5. Monthly values of the measured environmental variables used to assess the movement probability through the crossing. a) Water temperature (°C); b) maximum depth (cm); c) mean depth of water in section D; d) mean depth of water in the U section.

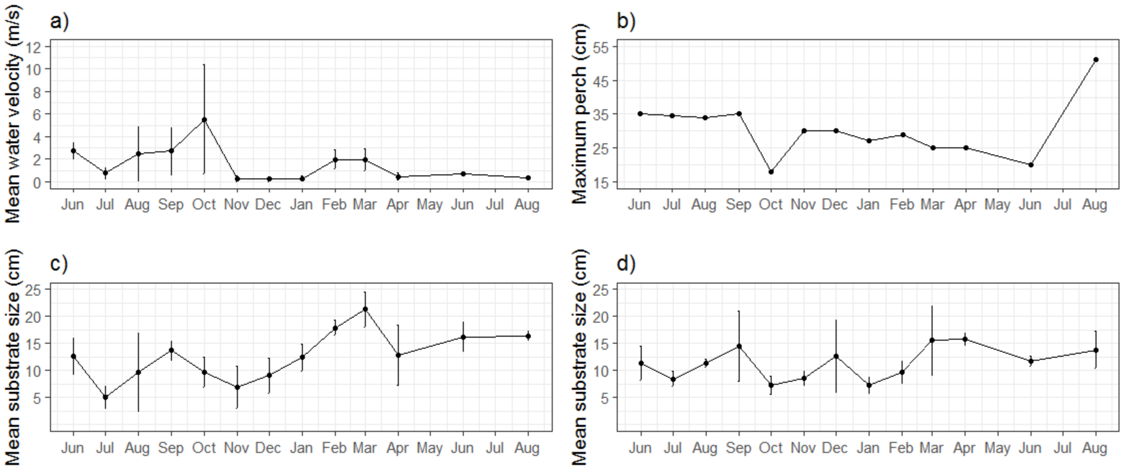


Fig. 6. Monthly values of the measured environmental variables used to assess the movement probability through the crossing. a) mean water velocity in the culvert (m / s); b) perch height (cm); c) mean size substrate size in section D; d) mean substrate size in the U section.

Probability of passing through the culvert

The movement probability estimated for the entire study period was higher among the free upstream (mean = 0.22) and downstream (mean = 0.10) sections, than through the culvert (mean = 0.04) (Fig. 7). The evaluation of movement probability through the culvert considering direction showed that movement up and downstream are similar (mean = 0.03; mean = 0.05, respectively) (Fig. 8a, b). In the free downstream sections, movement probability was lower upstream than downstream (mean = 0.08; mean = 0.12, respectively), and in the free upstream section, it was more likely to move upstream than downstream (mean = 0.25; mean = 0.17, respectively) (Fig. 8a, b). The probability of fish movement through the culvert was low throughout the entire study period (except for October, January, and March), and we found no difference between upstream and downstream movements (Fig. 9a). A similar pattern was found for movements within the free sections (D and U), except for the probability of movement in the upstream and downstream direction, during the fall and winter months, in the free section above the bridge (U1-U2-U3/U3 -U2-U1) (Fig. 9b, c).

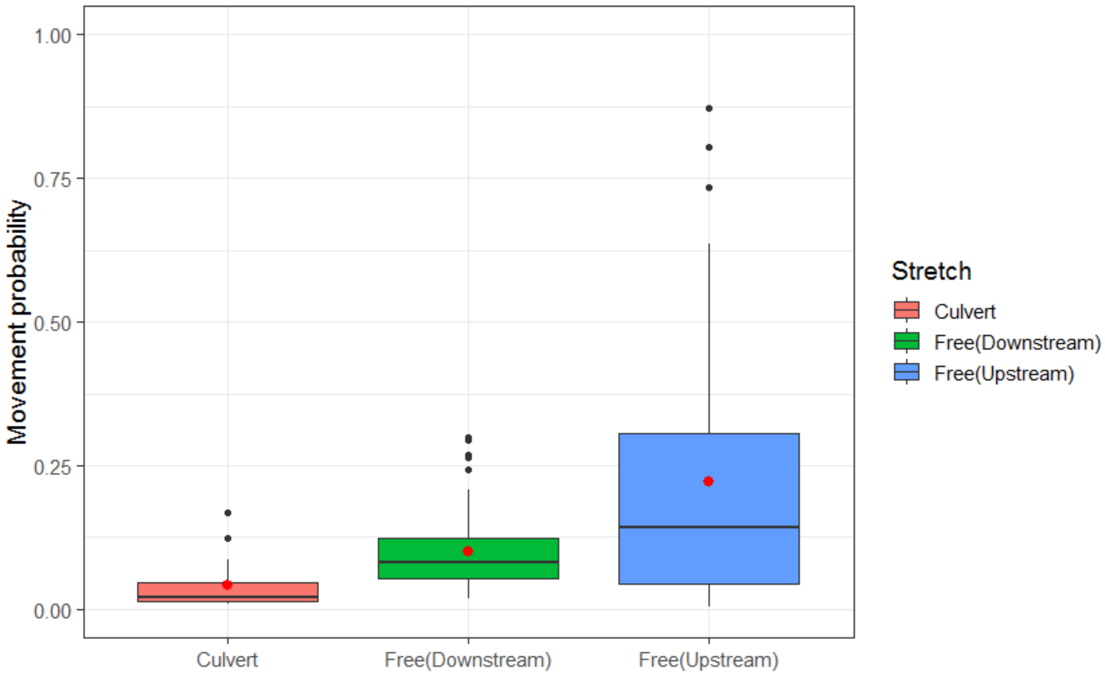
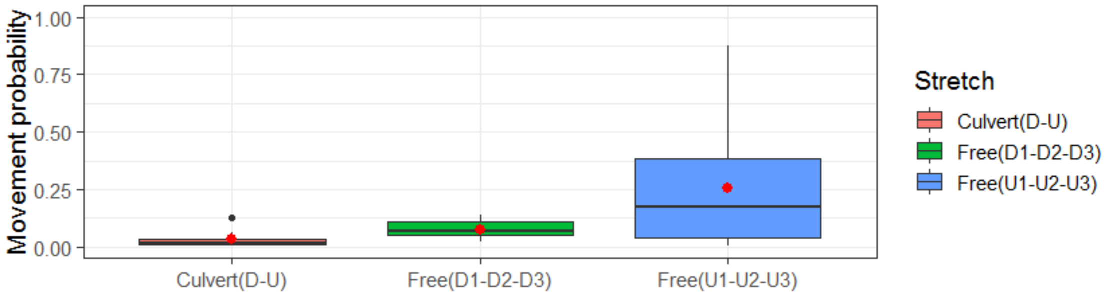


Fig. 7. Boxplot of the probability of movement through the culvert (D-U), in free sections downstream (D1-D2-D3), and in the free sections upstream (U1-U2-U3) for the entire study period. The red circle represents the mean, black circles represent outlier values; the thick horizontal line across the box is the median; the bottom and top of the box are the lower and upper quartiles, respectively; and the whiskers are the minimum and maximum values.

a) Upstream



b) Downstream

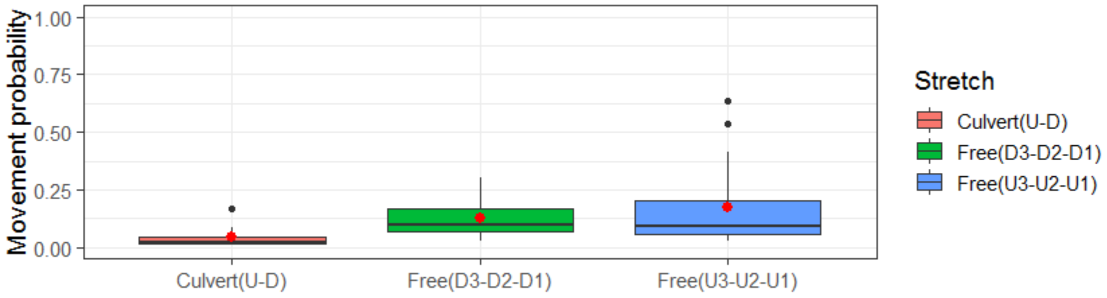


Fig. 8. (a) Boxplot representing the estimated probability of movement upstream, through the culvert (DU), through the free downstream sections (D1-D2-D3) and the free upstream sections (U1-U2-U3). (b) Estimated average probability of movement downstream through the culvert (U-D), downstream sections (D3-D2-D3), and upstream sections (U3-U2-U1). The red circle represents the mean, circles black represent outlier values; the heavy horizontal line crossing the box is the median; the bottom and top of the box are the lower and upper quartiles, respectively; and the whiskers are the minimum and maximum values.

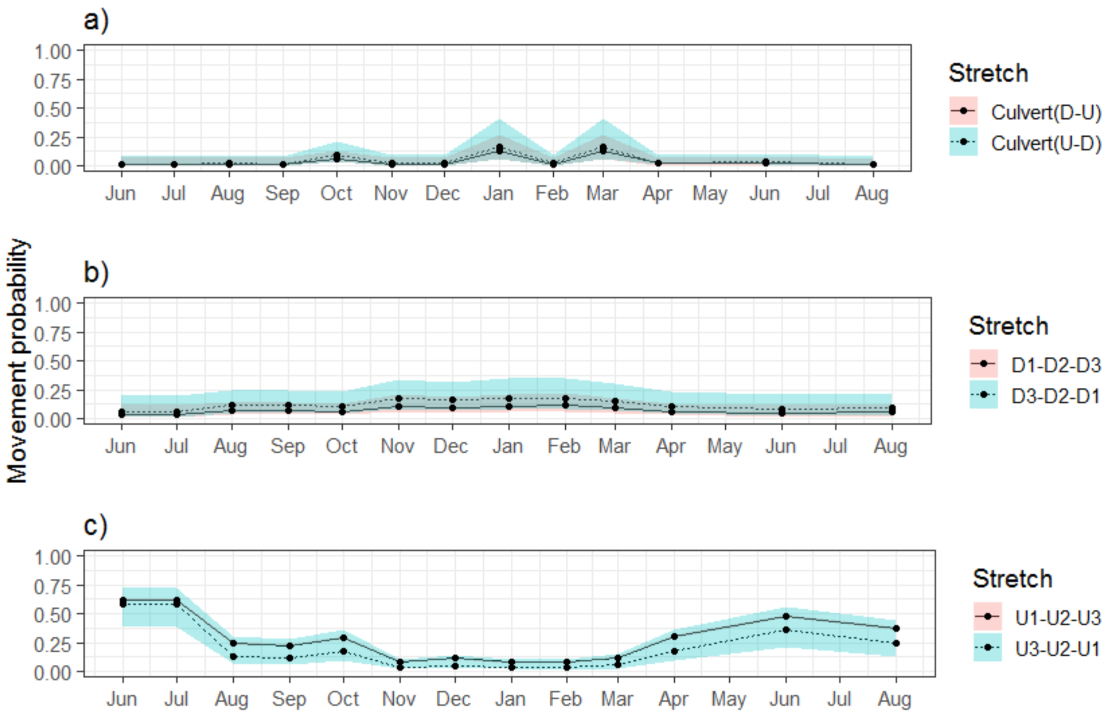


Fig. 9. (a) Monthly probability of movement through the road crossing in the upstream (D-U) and downstream (U-D) direction (for the entire study period). b) Monthly probability of movement through the free downstream section in the upstream direction (D1-D2-D3) and in the downstream direction (D3-D1-D2). c) Monthly probability of the movement through the free section in the upstream direction (U1-U2-U3) and in the downstream direction (U3-U2-U1). Blue and pink colors represent the lower and upper confidence intervals (95%).

Movement probability models

The 2-state model fitting (D and U), to estimate the probability of movement through the culvert, presented a value of ĉ = 1.8. For the models of movement through the free downstream and upstream sections, the values were 0.92 and 0.85. The best 2-state model (between D and U, that is, movement through the culvert), C1, showed that the depth inside the culvert was the main variable related to the probability of movement through the crossing (model weight = 0.272) (Table I). In this model, the probability of movement through the culvert, in both directions D-U and U-D, increased with the depth inside the culvert (beta coefficient = 0.093, CI 0.011, 0.176) (Fig. 10). The capture probability in section D increased with water temperature (beta coefficient = 0.095, CI 0.015, 1,174) and reduced with increasing total length (beta coefficient = -0.222, CI -0.414, -0.031). Two other equally plausible models (delta QAIC <2), indicate that passing through the crossing can be influenced, not only by the depth but also by the water velocity (models C2 and C3), especially when interacting with the depth (C3) (Table S1) with is a significant effect (beta coefficient = 0.031; CI 0.005, 0.058).

In the free sections downstream of the crossing, the selection of 3-state movement models (D1, D2, D3) indicates that the measured variables had no effect on movement (Table I). Between the two best-ranked models (FD1 and FD2), FD2 did not include any of the variables, while FD1 included variables whose confidence interval included zero (see Table S2).

In the free sections upstream of the crossing (U1, U2, U3), the best model (smaller Delta AICc) indicated that movement probability was positively influenced by body size (beta coefficient = 0.695; CI 0.691, 0.698) and negatively by water temperature (beta coefficient = -0.433, CI -0.436, -0.430) (Table I). The capture probability was significantly related to water temperature (beta coefficient = 0.230, confidence interval (95%) = 0.076, 0.385) and depth (beta coefficient = 0.033, confidence interval (95%) = 0.003, 0.062). The total length had no significant effect on the capture probability (Table S3).

Table I. Result of the model selection estimating the survival probability (phi), capture probability (p), and movement probability (ψ) between the sections referring to each data matrix. The survival probability was kept constant (.), and the intercepts for each parameter of phi, p and ψ were considered different for each section. Variables analyzed included water temperature (WT), water velocity (WV), depth (D), perch height (P), substrate size (S), and body size (BS). Only the five best models are presented. Models represent movements through the crossing (C1 to C5), in the free section downstream of the crossing (free downstream section, FD1 to FD5) and in the free section upstream of the crossing (free upstream section, FU1 to FU5).

States D and U	**QAICc**	**Delta QAIC**	**Weight**	**No par**
C01.{$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(D)}$}	822.385	0.000	0.240	10
C02.{$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WV+D)}$}	823.059	0.674	0.171	12
C03.{$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WV*D+WT)}$}	823.485	1.099	0.138	12
C04.{$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WV+D+BS)}$}	825.153	2.768	0.060	14
C05.{$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+D+BS)}\ \boldsymbol{\psi}_{(D)}$}	825.393	3.007	0.053	12
States D1, D2 and D3	**AICc**	**Delta AIC**	**Weight**	**No par**
FD01. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WT)}$}	1224.020	0.000	0.163	13
FD02. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT)}\ \boldsymbol{\psi}_{(WT)}$}	1224.343	0.322	0.139	12
FD03. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WT+BS)}$}	1225.441	1.420	0.080	14
FD04. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+BS)}\ \boldsymbol{\psi}_{(WT+D*BS)}$}	1225.607	1.587	0.073	14
FD05. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT)}\ \boldsymbol{\psi}_{(WT)}$}	1225.618	1.598	0.073	12
States U1, U2 and U3	**AICc**	**Delta AIC**	**Weight**	**No par**
FU01. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+S+D+BS)}\ \boldsymbol{\psi}_{(WT+BS)}$}	377.549	0.000	0.274	15
FU02. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+S+BS)}\ \boldsymbol{\psi}_{(WT+WV+BS)}$}	378.419	0.869	0.177	15
FU03. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+S+D+BS)}\ \boldsymbol{\psi}_{(WT+WV+D+BS)}$}	378.457	0.908	0.174	17

FU04. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+S+BS)}\ \psi_{(WT+WV*D+BS)}$}	379.105	1.556	0.126	15
FU05. {$\boldsymbol{phi}_{(.)}\ \mathbf{p}_{(WT+S+BS)}\ \psi_{(WV+BS)}$}	379.740	2.191	0.091	14

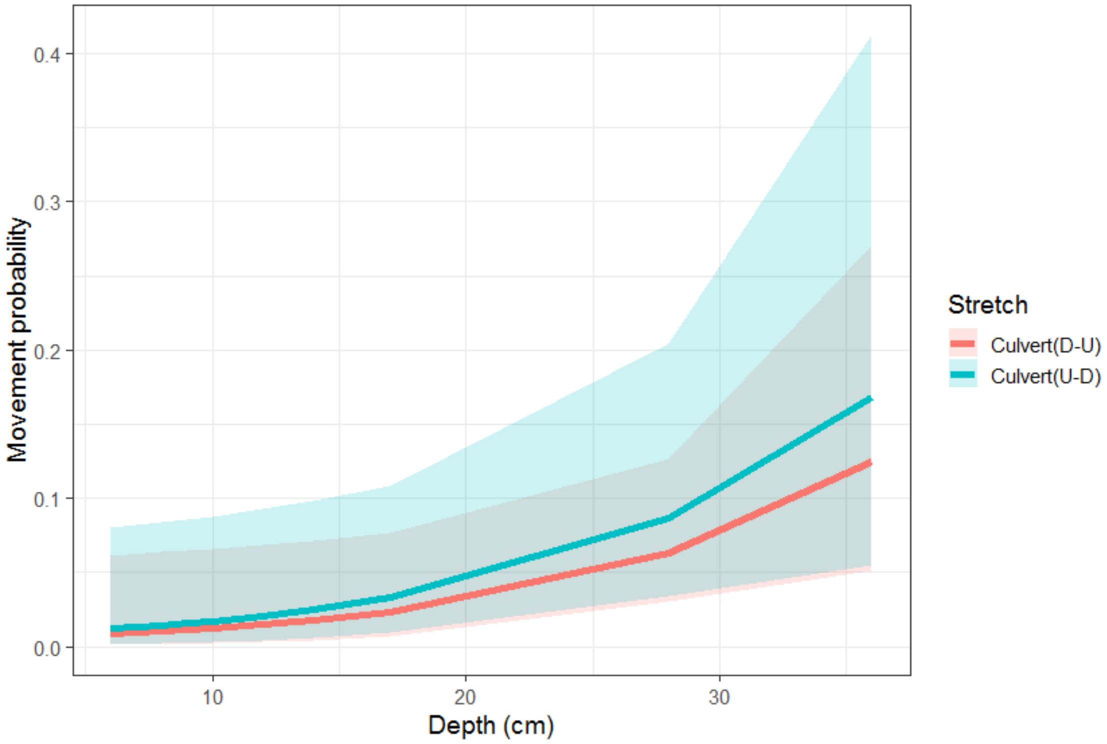


Fig. 10. Relationship between the probability of movement through the culvert and the maximum depth in the culvert. Blue and pink colors represent the lower and upper confidence intervals (95%).

Table S1. Models elaborated to evaluate the movement probability by the crossing and relationship with environmental variables and body size.

Model	QAICc	Delta QAICc	AICc Weights	Num. Par
C01. {*phi*(.) p(WT+BS) ψ(D)}	822.3852	0	0.2404	10
C02. {*phi*(.) p(WT+BS) ψ(WV+D)}	823.0593	0.6741	0.17162	12
C03 {*phi*(.) p(WT+BS) ψ(WV*D+WT)}	823.4851	1.0999	0.13871	12
C04. {*phi*(.) p(WT+BS) ψ(WV+D+BS)}	825.1536	2.7684	0.06023	14
C05. {*phi*(.) p(WT+D+BS) ψ(D)}	825.393	3.0078	0.05343	12
C06. {*phi*(.) p(WT+BS) ψ(WV*BS+D)}	825.4426	3.0574	0.05212	12
C07. {*phi*(.) p(WT+BS) ψ(WV*D)}	825.4952	3.11	0.05077	11
C08. {*phi*(.) p(WT+BS) ψ(WV*D+WT+BS)}	825.8719	3.4867	0.04205	14
C09. {*phi*(.) p(WT+D+BS) ψ(WV+D)}	826.217	3.8318	0.03539	14
C10. {*phi*(.) p(WT+BS) ψ(WV)}	826.2741	3.8889	0.03439	11
C11. {*phi*(.) p(WT+BS) ψ(BS*D+WT+WV)}	826.9735	4.5883	0.02424	14
C12. {*phi*(.) p(WT+BS) ψ(WT+WV+D+BS)}	827.2246	4.8394	0.02138	15
C13. {*phi*(.) p(WT+BS) ψ(WV*D+BS)}	827.4036	5.0184	0.01955	13
C14. {*phi*(.) p(WT+S+BS) ψ(.)}	827.578	5.1928	0.01792	11
C15. {*phi*(.) p(WT+BS) ψ(WV*BS+WT+D)}	828.9573	6.5721	0.00899	13
C16. {*phi*(.) p(WT+BS) ψ(WV*BS+WT)}	829.6991	7.3139	0.00621	12
C17. {*phi*(.) p(.) ψ(.)}	829.9401	7.5549	0.0055	6
C18. {*phi*(.) p(WT) ψ(WT+WV+D+P+BS)}	830.3212	7.936	0.00455	15
C19. {*phi*(.) p(D) ψ(D)}	830.8066	8.4214	0.00357	9
C20. {*phi*(.) p(WT+S+D+BS) ψ(.)}	831.0922	8.707	0.00309	13
C21. {*phi*(.) p(WT+S) ψ(WT+WV+D+P+BS)}	831.7041	9.3189	0.00228	17
C22. {*phi*(.) p(WT+S+BS) ψ(WT+WV+D+P+BS)}	832.0845	9.6993	0.00188	19
C23. {*phi*(.) p(.) ψ(WT+WV+D+P+BS)}	832.6486	10.2634	0.00142	14
C24. {*phi*(.) p(WT+S+D+BS) ψ(WT+WV+D+P+BS)}	835.773	13.3878	0.0003	21

Table S2. Models elaborated to evaluate the movement probability by the free sections downstream of the crossing.

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Num. Par**
FD01. {*phi*(.) p(WT+BS) ψ(WT)}	1224.0207	0	0.16362	13
FD02. {*phi*(.) p(BS) ψ(WT)}	1224.3432	0.3225	0.13926	12
FD03. {*phi*(.) p(WT+BS) ψ(WT+BS)}	1225.4411	1.4204	0.08043	14
FD04. {*phi*(.) p(WT+BS) ψ(WT+D*BS)}	1225.6079	1.5872	0.07399	14
FD05. {*phi*(.) p(WT) ψ(WT)}	1225.6189	1.5982	0.07359	12
FD06. {*phi*(.) p(BS) ψ(WT+D*BS)}	1225.9229	1.9022	0.06321	13
FD07. {*phi*(.) p(WT+D+BS) ψ(WT)}	1226.0035	1.9828	0.06071	14
FD08. {*phi*(.) p(WT+BS) ψ(WT+WV*D)}	1226.0129	1.9922	0.06043	14
FD09. {*phi*(.) p(WT+BS) ψ(BS)}	1227.1246	3.1039	0.03466	13
FD10. {*phi*(.) p(WT+BS) ψ(D*BS)}	1227.5694	3.5487	0.02775	13
FD11. {*phi*(.) p(.) ψ(.)}	1227.5725	3.5518	0.02771	10
FD12. {*phi*(.) p(WT+BS) ψ(WT+WV+BS)}	1227.6507	3.63	0.02664	15
FD13. {*phi*(.) p(WT+BS) ψ(WV*D)}	1227.7524	3.7317	0.02532	13
FD14. {*phi*(.) p(WT+BS) ψ(D)}	1227.7773	3.7566	0.02501	13
FD15. {*phi*(.) p(D) ψ(WT)}	1228.0252	4.0045	0.02209	12
FD16. {*phi*(.) p(WT+BS) ψ(WT+WV*BS+D)}	1228.2299	4.2092	0.01994	15
FD17. {*phi*(.) p(WT+BS) ψ(WV)}	1228.6723	4.6516	0.01599	13
FD18. {*phi*(.) p(WT+BS) ψ(WV*D+BS)}	1229.321	5.3003	0.01156	14
FD19. {*phi*(.) p(WT+S+D+BS) ψ(.)}	1229.4494	5.4287	0.01084	14
FD20. {*phi*(.) p(WT+BS) ψ(WT+WV*D+BS)}	1229.6112	5.5905	0.01	15
FD21. {*phi*(.) p(WT+BS) ψ(WT+WV+D*BS)}	1229.8869	5.8662	0.00871	15
FD22. {*phi*(.) p(WT+BS) ψ(WV+D)}	1229.9756	5.9549	0.00833	14
FD23. {*phi*(.) p(WT+BS) ψ(WT+WV+D+BS)}	1231.9853	7.9646	0.00305	16
FD24. {*phi*(.) p(WT) ψ(WT+WV+D+BS)}	1232.0019	7.9812	0.00303	15
FD25. {*phi*(.) p(.) ψ(WT+WV+D+BS)}	1232.9997	8.979	0.00184	14
FD26. {*phi*(.) p(WT+S+BS) ψ(WT+WV+D+BS)}	1233.2243	9.2036	0.00164	17
FD27. {*phi*(.) p(WT+S+D+BS) ψ(WT+WV+D+BS)}	1235.0943	11.0736	0.00064	18

Table S3. Models elaborated to evaluate the movement probability by the free sections upstream of the crossing.

Model	**AICc**	**Delta AICc**	**AICc Weights**	**Num. Par**
FU01. {*phi*(.) p(WT+S+D+BS) ψ(WT+BS)}	377.5495	0	0.27461	15
FU02. {*phi*(.) p(WT+S+BS) ψ(WT+WV+BS)}	378.4192	0.8697	0.17777	15
FU03. {*phi*(.) p(WT+S+D+BS) ψ(WT+WV+D+BS)}	378.4577	0.9082	0.17438	17
FU04. {*phi*(.) p(WT+S+BS) ψ(WV*D+WT+BS)}	379.1057	1.5562	0.12612	15
FU05. {*phi*(.) p(WT+S+BS) ψ(WT+BS)}	379.7407	2.1912	0.09181	14
FU06. {*phi*(.) p(WT+S+BS) ψ(WT+BS)}	379.7433	2.1938	0.09169	14
FU07. {*phi*(.) p(WT+S+BS) ψ(WT+D+BS)}	381.4882	3.9387	0.03832	15
FU08. {*phi*(.) p(WT+S+BS) ψ(WV*D)}	384.1592	6.6097	0.01008	12
FU09. {*phi*(.) p(WT+S+BS) ψ(BS)}	386.0445	8.495	0.00393	12
FU10. {*phi*(.) p(WT+S+BS) ψ(WV)}	386.3189	8.7694	0.00342	14
FU11. {*phi*(.) p(.) ψ(WT+WV+D+BS)}	387.297	9.7475	0.0021	13
FU12. {*phi*(.) p(WT) ψ(WT+WV+D+BS)}	387.3235	9.774	0.00207	15
FU13. {*phi*(.) p(WT+S+BS) ψ(WV+D+BS)}	388.6255	11.076	0.00108	15
FU14. {*phi*(.) p(WT+S+BS) ψ(WV+D)}	389.2147	11.6652	0.0008	15
FU15. {*phi*(.) p(WT+BS) ψ(WV+D)}	389.8191	12.2696	0.00059	13
FU16. {*phi*(.) p(WT+BS) ψ(WT+WV+D+BS)}	390.8621	13.3126	0.00035	16
FU17. {*phi*(.) p(WT+S+BS) ψ(WT+WV+D*BS)}	390.8697	13.3202	0.00035	16
FU18. {*phi*(.) p(WT+S+BS) ψ(WV*D+BS)}	391.1193	13.5698	0.00031	14
FU19. {*phi*(.) p(WT+S+BS) ψ(D)}	392.3499	14.8004	0.00017	14
FU20. {*phi*(.) p(WT+S+D+BS) ψ(.)}	397.6311	20.0816	0.00001	14
FU21. {*phi*(.) p(WT+S+D+BS) ψ(BS)}	398.5564	21.0069	0.00001	15
FU22. {*phi*(.) p(WT+S+BS) ψ(WT+WV+D)}	399.9603	22.4108	0	16
FU23. {*phi*(.) p(.) ψ(.)}	402.1903	24.6408	0	9
FU24. {*phi*(.) p(WT+S+BS) ψ(D+WT)}	404.3723	26.8228	0	15
FU25. {*phi*(.) p(WT+S+BS) ψ(WT+D+WV*BS)}	406.1604	28.6109	0	16

Discussion

The results indicate that the movement of *R. aequalicuspis* is affected by the road crossing. Movement probability was consistently higher in the free sections downstream (2.5 times higher) and upstream (5.5 times higher) in relation to the section with the road crossing, as indicated by the overall low movement probabilities throughout the year, even in the free sections. In addition, upstream movements through the culvert were more affected than the downstream movements, indicating that the culvert effect limits dispersion mainly to the upper portion of the stream.

Contrary to what we expected, among all the environmental variables that could potentially affect the passage of *R. aequalicuspis* through the road crossing, depth had the greatest effect, with values below 30 cm significantly reducing passage probability. Depth inside the culvert changes over time depending on streamflow, and debris accumulation (sand, rocks, branches, etc.), which implies that controlling the minimum depth can be crucial when designing stream-road crossings and managing the culverts (removal of accumulated material). The latter could be performed periodically, especially in drier periods and after natural or anthropogenic events that lead to the accumulation of material in the culverts, reducing its depth. Examples of anthropic activities that imply in culvert monitoring and management include construction work done upstream or agricultural activities that lead to increased sediment or debris input to the streams and potential accumulation in the culverts.

Water depth can influence fish perception of the available physical space within the culvert (Goerig et al. 2015) and consequently affecting its swimming potential inside the structure and the chance of overcoming the obstacle. For *R. aequalicuspis*, the information that individuals passed the crossing only when culvert depth was between 28 and 36 cm could at least serve as an initial reference to guide culvert design and management. Ideally, studies on other species (including experimental studies, for example, Johnson et al. 2012), particularly species relevant for conservation, would be essential to guide management actions. For large and long-distance migratory species (e.g., salmonids), the minimum recommended depth to ensure passage varies between 15 to 30 cm and must follow the natural stream depth (BCMF 2002; CDFG 2002). Since these species have distinct swimming behavior and morphology when compared to *R. aequalicuspis* (that presents flattened and elongated body, with caudal fin height up to 3 cm), one would expect the minimum depth threshold for the passage of *R. aequalicuspis* to be less than what we observed. An important implication of our results is that the proposal of culvert characteristics must consider species with different swimming behaviors and morphologies, as previously suggested by others (Ficke et al. 2011; Prenosil et al. 2016). This problem is analogous to that of fish passage to overcome dams, where transposition mechanisms that are designed for one or a few species do not necessarily benefit all other species (Fernandez et al. 2004; Oldani et al. 2007; Noonan et al. 2012).

Regarding water velocity, most studies indicate that the increase in water velocity hinders upstream movement through the crossing (Johnson et al. 2012; Peterson et al. 2013; Goerig et al. 2015). In our study, water velocity appeared in two of the three most plausible candidate models (QAIC < 2) explaining the probability of movement through the crossing. However, water velocity had a weak positive correlation with movement probability in the upstream to downstream direction, and only when interacting with water depth. That may be explained, at least in part, by the fact that the water velocity was not measured at the time of the individual passage through the road crossing, but at the time of recapture. Still, the relationship between water velocity and the probability of passing through the crossing shows the need for a more accurate approach to measuring water velocity within the culvert (increasing sampling frequency, or using data loggers) or for an experimental approach, with manipulation of different water velocities in the culvert and testing the effect on individual movement (e.g., Johnson et al. 2012; Peterson et al. 2013).

In contrast with the literature, we did not observe a relationship between total body length and movement through the culvert. Most studies show that larger individuals of the same species (Johnson et al. 2012; Peterson et al. 2013; Goerig and Castro-Santos 2017) are more successful in ascending through culverts than smaller individuals. However, due to differences in jumping and swimming skills, and movement behavior between larger and smaller species (Ficke et al. 2011), studies with a diverse range of species are necessary to understand the extent to which the probability of passage is species-specific or, can otherwise be predicted from size and morphology.

In summary, our results indicate that culverts can limit the movement of *Rineloricaria aequalicuspis*, a non-migratory small benthic fish species endemic to southern Brazil coastal drainages. The number of road crossings can be high along a stream (e.g., 11 road crossings along 13 km in the studied stream) and also across the stream network (161 road crossings in the streams of the Maquiné basin; 78,173 in the state of Rio Grande do Sul, Brazil, Flores (2017); 268,818 in the Great Lakes basin, North America, Januchowski-Hartley et al. 2013). Thus, the effects of this limitation to movement and dispersal can accumulate, affecting the local or global species persistence, especially if road crossings affect the whole species distribution area. A major implication of our results is that, even for small benthic species, which are less dependent on the water column for swimming, water depth in the culvert can limit the passage through the road crossing. Therefore, the design and management of road crossings can be valuable as a practice of minimizing impact and conserving riverine fish. The design of these structures must be planned to specify a minimum water depth based on the requirements of the most sensitive species, thus ensuring that a depth-related barrier is not created (Ottburg and Blank 2015). Regarding those culverts already present throughout existent road networks, perhaps one possible solution for mitigating impact on fish is the use of structures that guarantee the minimum depth for the fish passage, or that attenuate water velocity through the culvert, such as baffles (Amtstaetter et al. 2017), ropes (David et al. 2014) or other fish-ladder designs, like Denil fish pass (Ottburg and Blank 2015). We also consider that approaches with a broader scale, evaluating the cumulative effect of multiple road crossings on different populations and species with different movement behaviors, can help the definition of management and restoration actions in streams crossed by roads (Poplar-Jeffers et 2009; Kemp and O'Hanley 2010).

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Considerações finais

Enquanto os padrões de movimento de peixes migradores de longa distância no Brasil são cada vez mais estudados e conhecidos, principalmente pelo apelo que se tem frente ao impacto de hidrelétricas por espécies de grande porte e com interesse para a pesca comercial, o conhecimento sobre os padrões do movimento de peixes pequenos de riachos é bem menos documentado na literatura. Esta lacuna do conhecimento torna-se mais preocupante se considerarmos que 36% das espécies ameaçadas distribuídas na mata atlântica são de pequeno porte (comprimento padrão < 150mm, ver Castro & Polaz, 2020). E conforme estes autores, a falta de informação sobre a biologia e ecologia dessas espécies é um dos principais problemas enfrentados ao se analisar os diferentes impactos antrópicos que afetam as populações de peixes. Além disso, a ausência de experimentos que tentam utilizar ferramentas tecnológicas mais sofisticadas como marcadores eletrônicos (p.ex. PIT-tags), contribui para termos uma resposta de padrões mais lenta ao longo do tempo, visto que no método de marcação-recaptura, precisamos recapturar os indivíduos e a maioria daqueles peixes marcados nunca mais são recapturados. Assim, além de termos um baixo número de recapturas para indicarmos padrões, para a maioria dos indivíduos não sabemos para onde eles vão e nem o quanto realmente se deslocam ao longo do riacho.

O efeito de barreira ocasionado por cruzamentos de estradas vem sendo estudado por no mínimo 20 anos em países da América do Norte e Europa. No Brasil esta preocupação de que cruzamentos de estradas afetam o movimento de pequenos peixes de riachos é mais recente (a partir de 2012). Esta lacuna é bem preocupante pelo alto número de cruzamentos que existem em estradas pavimentandas e não pavimentadas no Brasil. Por exemplo, apenas no RS, foram contabilizados 78,173 cruzamentos (Flores, 2017) que podem funcionar como efeito de barreira a movimentação de peixes. Além disso, infelizmente, até o momento, todas essas estruturas foram e talvez ainda sejam construídas sem nenhum critério para garantir a passagem de peixes e demais organismos aquáticos.

Teoricamente para entendermos o efeito de estruturas antrópicas sobre a mobilidade de uma espécie ou várias espécies temos que entender quais são os requisitos básicos dessas espécies na natureza. Portanto, apesar de ser cada vez mais ausente os estudos de história de vida, por questões de inviabilidade de demanda de maior tempo com coleta de campo e demora para publicação (ver Santana et al., 2020), é importante retomarmos os esforços para termos o mínimo de conhecimento sobre a dinâmica populacional tanto relacionados a capacidade de movimento quanto idade, período reprodutivo, tamanho de primeira maturação, fecundidade, tempo de geração, sobrevivência e mortalidade.

Acredito que todos os capítulos da tese (1, 2 e 3) podem ser replicados para outras espécies ou diferentes grupos de peixes de pequeno porte distribuídas em riachos. Enquanto o capítulo 1, contribuiu para entender as características da história de vida da *R. aequalicuspis*, mostrando que é uma espécie que atinge 7 anos, período reprodutivo longo entre a primavera e verão, tamanho de primeira maturação superior a 100 mm, fecundidade média absoluta menor do que 140 ovócitos, tempo de geração curto (≤ 3 anos) e uma sobrevivência dos indivíduos jovens (< 2 anos) muito menor do que os indivíduos adultos (> 2 anos). O capítulo 2 demonstra que esta espécie, apesar de não apresentar um comportamento migratório de longa distância (>100km, ver Agostinho et al., 2003) como os peixes de grande porte, apresenta um padrão de movimentação heterogênea com uma possível variabilidade intra-populacional ocorrendo em um comportamento que geralmente é assumido a ser uniforme em peixes de riachos. Por último, o capítulo 3 representou a abordagem mais próxima da ecologia aplicada na qual tanto gostaria de ter executado no inicio do projeto. Este capítulo, através de uma ferramenta metodológica mais robusta como os modelos multi-estados, demonstrou que a diminuição da profundidade dentro do bueiro (*culvert*) é a principal variável que pode impedir a movimentação pelo cruzamento de estrada. Além disso, demonstrou que a probabilidade de movimento pelo cruzamento aumenta durante o mês de outubro, janeiro e março, período que pode estar relacionado à busca por procura de ambientes de desova visto que são meses que a espécie reproduz. Os resultados deste último capítulo demonstram a necessidade de uma comunicação direta aos órgãos responsáveis pela construção de estradas, mostrando que o desenho destas estruturas também deve levar em consideração a passagem da fauna aquática e não apenas o escoamento da vazão. Por último, sugerir a reformulação de cruzamentos de estradas já construídos e propor que os futuros garantam a passagem de todos os organismos aquáticos;

Ao fim da tese, pensei em algumas sugestões que possam vir a auxiliar futuras pesquisas tanto para história de vida quanto aqueles que busquem entender os padrões de movimento e sua relação com fatores bióticos e abióticos, bem como avaliar os efeitos de cruzamentos de estradas sobre a movimentação de peixes de riachos. Alguns dos tópicos abaixo já foram escritos nas discussões de cada capítulo, mas outros são sugestões novas.

Capítulo 1

1) Devido a alta diversidade de peixes de água doce, é necessário pensar em estratégia cientifica que não precise avaliar todas as espécies quanto aos aspectos de história de vida, mas em uma amostragem representativa de diferentes grupos taxonômicos e filogenéticos, tamanho do corpo e habitats (proposto por Becker et al., 2010 e Hortal et al., 2015);
2) Aumentar os esforços de publicação em estudos de história de vida, aproveitando o método de marcação e recaptura (que tem como objetivo avaliar padrões de movimento em riachos) para estimar a idade e construir tabelas de vida

Capítulo 2

1) Avaliar o comportamento de movimento heterogêneo para outras espécies de peixes que apresentam morfologia diferente de *R. aequalicuspis* e que provavelmente tenham outra capacidade de movimentação ao longo de um riacho (p.ex. lambaris);
2) Aumentar a escala espacial do estudo para inferir padrões de movimento em escala maior (entre 1 a 10 km), buscando realizar o método de marcação e recaptura em pelo menos 60% do trecho amostrável do riacho;
3) Caso não seja possível realizar o item 2, pensar num delineamento amostral que diminua o intervalo entre os eventos de recaptura, assim

poderia aumentar as chances de recaptura para cada indivíduo e talvez identificar que a distância de movimento acumulada pode ser maior do que a amplitude do trecho total estudo;

4) Avaliar a viabilidade de utilização de marcadores eletrônicos (Passive integrated transponder - PIT tags, ver Jørgensen et al., 2017), realizando testes envolvendo o implante em diferentes espécies para verificar os efeitos na mobilidade e sobrevivência dos peixes de riachos;
5) Desenvolver parcerias de projetos em diferentes bacias hidrográficas, entretanto, com os mesmos delineamentos amostrais e ferramentas metodológicas para conseguirmos responder as mesmas perguntas relacionadas a ecologia do movimento

Capítulo 3

1) Replicar um delineamento amostral semelhante para outras espécies e diferentes tipos de bueiros, entretanto, utilizar riachos controle sem a presença de cruzamentos;
2) A partir dos resultados evidenciados no Capítulo 2 de que a densidade é importante na probabilidade de movimento, incluir esta variável nos modelos multi-estados e avaliar se esta variável pode ter influência na probabilidade de passagem pelo cruzamento;
3) Realizar experimentos com estruturas físicas (tanto natural do próprio riacho quanto artificial) que possam auxiliar na passagem do peixe pelo cruzamento. Assim, avaliar que tipo de estrutura pode auxiliar no manejo e consequentemente no aumento da probabilidade de passagem;
4) Realizar experimentos em laboratório ou *in situ* para verificar a probabilidade de passagem, submetendo os peixes a diferentes níveis

de velocidade de água, profundidade e outras variáveis que geralmente estão relacionadas com o aumento ou diminuição da passagem pelo cruzamento

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