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Simple assumptions predicts prey selection by piscivorous fishes

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ABSTRACT

Studies on trophic interactions permits the use of community-wide network analyses to evaluate the consequences of human interventions in natural communities. In this paper, we aimed to get insights into the underlying mechanism of prey selection for four piscivorous species, and evaluate behavioral responses to prey selection after an impoundment. We assemble six food web models to search for the hypothesis that best predict observed prey selection pattern of piscivorous fishes combining the following assumptions: (*i*) predation window, defined as the size range of prey species consumed by a piscivorous fish; (*ii*) prey strategies to avoid predation (*iii*) and prey abundance. We tested the probability of each hypothesis to reproduce two empirical data, one before and one after an impoundment with minimum assumptions. Before impoundment, we found that predators presented switching behavior, preying preferably on abundant prey; while after impoundment, predators consumed prey within its predation window. Those results explained better than the null hypotesis and all other assumptions; and corroborate with both theoretical and empirical studies. We conclude that different assumptions drives piscivorous fish behavior in different environments; and modelling procedures can be used to assess gaps in trophic interactions of fish communities.

1. Introduction

Impoundments of large rivers produce major interventions in the landscape (Nilsson et al., 2005). They cause physical, chemical, geomorphological and hydrological modifications to the river; alters the structure and dynamics of primary producers, and impacts fish assemblage's composition and abundance (Petts, 1984). This process is so intense that results in the creation of a new ecosystem (Baxter, 1977). In these unfavorable conditions, fish species usually adjust their behavior to achieve a greater availability and heterogeneity of feeding resources, shelter and habitats (Delariva et al., 2013). Those who do not successfully adapt to these conditions are selected against it (Gomes and Miranda, 2001).

In order to address the effects of impoundment into trophic interaction, studies in ichthyology have been focusing on describing diet shifts of fish species (Delariva et al., 2013). Piscivorous fish species, specifically, are an important trophic guild to fish assemblages and it highly contributes to the biomass in stock assessment surveys (Gomes and Miranda, 2001). They have been defined as apex predators, since they usually occupy the top trophic position in a community, and acts on populations of smaller predators, suppressing the impacts on prey species, sustaining biodiversity and preventing strong trophic cascades (Blanchard et al., 2003; O'Gorman et al., 2008).

Several modelling procedures in food web theory aimed to reproduce a predators' foraging behavior based on specific assumptions: predator-prey length ratios; one-dimensional niche interval; multi-dimensional niche intervals; non-fixed probability of consumption; phylogenetic constraints and adaptation, and group formation (Stouffer, 2010; Staniczenko et al., 2014). These concepts substantially improved our knowledge of the regulating mechanisms in natural communities, integrating biodiversity, community structure, and population dynamics into a single conceptual framework (Dunne, 2006; Thompson et al., 2012; Borrett et al., 2014).

In this study, we aimed to get insights into the underlying mechanism of prey selection for four piscivorous species, and evaluate behavioral responses to prey selection after an impoundment. In this way, we developed six hypothesis for the behavior of prey selection before and after an impoundment in accordance to three ecological assumptions from literature: size range of prey species consumed by a piscivorous fish, prey strategies to avoid predation and prey abundance. For each hypothesis, we assembled a modelling procedure to simulate the piscivorous' prey choice – either based on food web theory models or adjusting the existing

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models to attend the assumptions. Finally, through observed diet patterns, we searched for the hypothesis that best reproduced the scenarios before and after the impoundment with minimum assumptions.

2. Methods

2.1. Piscivorous fish diet description

To evaluate the effect of habitat modification caused by an impoundment in the Iguaçu River Basin (Paraná, Brazil) Delariva et al. (2013) assessed the variation in food-resource availability for the fish community, on both temporal and spatial scales. They sampled fish species throughout the reservoir region before and after the impoundment; analyzed the stomach contents; and recorded food items into broad categories: detritus, algae, terrestrial and aquatic plants, terrestrial and aquatic insects, decapods, microcrustaceans, microinvertebrates, macroinvertebrates and fishes.

Novakowski et al. (2007), following the same idea, evaluated the effects of the impoundment on the diets of the piscivores. They identified the food items of four piscivorous fish species in the region before and after the impoundment and assembled predation matrices – were an entry represented the piscivores in column consuming the prey in row.

We used this database to predict the interactions in the predation matrices of Novakowski et al. (2007) before the impoundment (Matrix Before Dam – BD) and after it (Matrix After Dam – AD), using the species listed in Delariva et al. (2013) as potential prey (see Supplementary material for more information).

2.2. Modeling procedures

In network theory, the first and simplest way to model an interaction between two elements is through the Erdös-Rényi random graph (Erdös and Rényi, 1959). We used this **Random Model** as null hypothesis to simulate piscivorous fish prey assuming that all prey have the same probability (*p*) of being consumed (Fig. 1).

Increasing the complexity in prey's choice behavior, we inserted a model assuming allometric constrain between the piscivorous and its prey. Studies demonstrated that the ability of piscivorous species to capture and handle its prey is dependent on its body size: a large predator has better visual accuracy, better swimming ability, and a larger mouth (Lundvall et al., 1999; Mittelbach and Persson, 1998). In fact, the variation in the diet of a piscivorous fish is more likely related to the prey-predator length ratio than to the piscivorous morphology. This pattern has been defined has the concept of "predation window": the size range of prey species consumed by a piscivorous fish (Mittelbach and Persson, 1998; Claessen et al., 2002). To test this hypothesis – of piscivorous consuming only within an interval of prey sizes – we used the **Niche Model** (Williams and Martinez, 2000) which employs a single niche dimension from 0 to 1, with both prey and piscivorous fish having a single niche position (*s*). A Piscivorous fish *i* consume its prey within an interval (predation window) of length $r_i = Xs_i$, were *X* is a random variable from a Beta-distribution (see Supplementary Material for more information on the Beta-distribution). The interval center (λ) is sampled from a uniform distribution between $r_i/2$ and $\min(s_i, 1 - r_i/2)$, and represent the optimal ratio between prey and predator size. Piscivorous fish consume all prey that falls in niche position between $\lambda - r_i/2$ and $\lambda + r_i/2$ (Fig. 2).

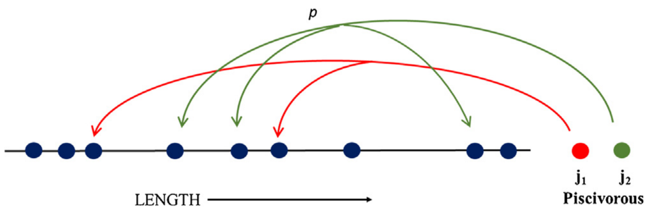

Fig. 1. Prey selection in the Random Model. All interactions are sampled with a fixed probability and both j_1 and j_2 can consume any prey with the same probability *p*.

However, fitting the predation window does not guarantee that prey-piscivorous interaction happens. Prey species have developed strategies to make themselves unavailable, unpalatable or difficult to locate, diminishing the predator's probability of consumption (Thompson, 1976). We used the **Generalized Cascade Model** (Stouffer et al., 2005) to test the hypothesis of prey selection contingent only to non-fixed predation probabilities – consumption efficiency of predators. This model also assumes a species ordering within a single niche dimension; however, each predator can prey all species with lower niche value with a predator-specific probability (*p*). This probability is sampled from a Beta-distribution (1,β) (Fig. 3).

To couple both assumptions (predation window and non-fixed predation probability given by prey strategies to avoid predation) we used the **Probabilistic Niche Model**, which inserts a Gaussian formulation to the Niche Model (Williams et al., 2010). In this way, each predator has a higher probability of eating preys that are close to the predation window center (λ), and have lower probability in the distribution tails (Fig. 4). Specifically, the predator *j* eats each prey *i* with a probability given by:

$$P(i,j) = \alpha exp\left\{-\left(\frac{s_{i-\lambda_j}}{r_i/2}\right)^2\right\} \qquad (1)$$

where P(i,j) is the probability that *j* eats *i*, s_i is the scaled length of prey *i*, λ is the optimal prey length ratio for the predator *j*, and r_i is the predation window. We maintained the predation window as a function of connectance trough the beta distribution function, but set λ as a free parameter between $r/2$ and $\min(s_i, 1-r/2)$. The Gaussian formulation ensures that the predation probability has an approximate exponential decay as the prey length gets far from λ (Fig. 3).

Consumption rate on prey species can also be a consequence of prey abundance. Food web theory suggests that the interplay between a predator's prey preference and the variation in the abundance of an alternative prey species acts in synergism with strong and weak interactions, decreasing interaction strengths and promoting stability in population dynamics and food webs (McCann et al., 1998; Post et al., 2000; Faria and Costa, 2009). We used the Generalized Cascade Model as a starting point to assemble a new model – **Abundance Model** – which employs the assumptions of non-fixed predation probabilities and prey abundance. In this model, we also sampled non-fixed probabilities from the Beta distribution (1,β), but we set each *prey* with a

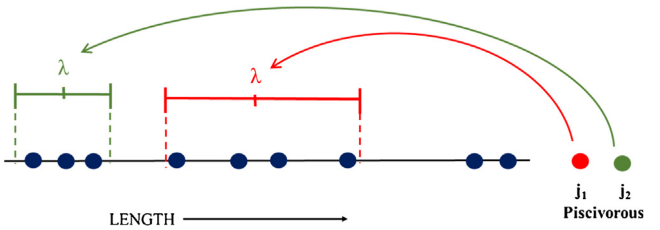

Fig. 2. Prey selection in the Niche Model. Each piscivorous have a predation window interval (i.e. a range of prey sizes consumed by a piscivorous of a given size) centered on the optimal prey size. All prey that fall within this interval is automatically consumed.

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