Pontificia Universidad JAVERIANA Bogotá

Univ. Sci. 27(3): 234–252, 2022
doi: 10.11144/Javeriana.SC273.fsof

ORIGINAL ARTICLE

Feeding strategy of fish that colonize reservoirs in the Magdalena River basin

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Received: 24-01-2022
Accepted: 15-07-2022
Published online: 01-09-2022

Citation: Restrepo-Santamaría D, Navia AF, Palacios J, Jimenez-Segura LF. Feeding strategy of fish that colonize reservoirs in the Magdalena river basin., *Universitas Scientiarum*, 27(3): 234–252, 2022.
doi: 10.11144/Javeriana.SC273.fsof

Funding: This research is part of the baseline study "Ecología de la comunidad íctica en el río Porce, en el área de influencia de los embalses Porce II y Porce III (2011- 000558) entre la Universidad de Antioquia y Empresas Públicas de Medellín".

Electronic supplementary material:
Supp. 1, Supp. 2, Supp. 3

OPEN ACCESS

Abstract

The construction of dams for hydropower in the Andean rivers of Colombia is leading to a loss of regional fish species. Fish species that persist in these artificial ecosystems are those that find favorable new conditions for their recruitment. Suitable feeding strategies allow these fish to persist and thrive in reservoirs. We analyzed the stomach contents of the species present in two cascade reservoirs in the Magdalena River basin. The objectives were to describe fish diets, determine their feeding strategies, and evaluate if seasonal factors, like rain or spatial distribution, affect the diet of these fish species. Our results indicate that the fish species *Brycon henni* and *Astyanax microlepis* feed on a wide range of resources available within the systems and adopt a generalist feeding strategy. Also, opportunistic species such as *Roeboides dayi* and *Hoplosternum magdalenae* lived in the reservoirs. The fish species living in the two reservoirs showed different feeding behaviors. The rainy season in these reservoirs was beneficial for opportunistic fish species because it allowed them to diversify their eating behavior. Knowledge of the feeding habits of the studied fish species is a priority for strengthening the environmental management capacity of Andean aquatic resources.

Keywords: neotropical fish; freshwater fish diet; andean rivers; generalist strategy

1. Introduction

The increase of hydroelectrical projects in the Andean region of north-western South America has been favored by its water availability and landscape [1, 2]. A water reservoir is created as a hybrid system between a river and a lake. After damming, the composition of pre-existent riparian biota in the source river changes, especially in the reservoir area, and the species persisting are those that find favorable new conditions within the reservoir [3]. Such infrastructure projects may consist of dams in different basins, some of them serially located along the longitudinal axis of the same river and are known as cascade reservoirs [4].

Changes in the composition of fish fauna in dammed rivers have been reported [5]. In these reservoirs, fish assemblages shift from a set of riverine fishes to a group of lake fishes. Changes in the environmental conditions for spawning, incubation, and recruitment are the main causes for the decline of riverine fish populations in reservoirs [6]. Riverine fishes require not only the right conditions for spawning and recruitment but also for feeding. When a stream is dammed, the new flow conditions of the aquatic system change the fishes' diet, which can lead to the proliferation of some species and the disappearance of others [7].

Neotropical fishes possess an enormous set of feeding strategies. These range from feeding solely on fruits and seeds or fish scales [8] to broader diets [9]. In Andean rivers, some fish species can change their diet to consume allochthonous and autochthonous resources present in the water column, depending on the climate season. These species are naturally adapted to live in a variable environment where annual hydrological fluctuation causes major shifts in the availability of food and other resources [10]. The elevation gradient also influences feeding habits [11]. At lower elevations, the trophic composition of fish assemblages is more diverse with detritivore, algivore, and piscivore species dominating the community; as elevation increases, trophic structures become less diverse and insectivore fishes dominate [11].

The main food resources utilized by fish in neotropical water reservoirs are generally heterogeneous and of autochthonous origin (*i.e.*, plant material, aquatic insects, algae, and other fish), and their availability depends on seasonal variables and on water level oscillations, including these driven by the reservoir's energy generation processes [12]. This is the reason why the fish species of the original river that remain in these systems are those with plastic or diverse feeding strategies [13, 14] who can use the resources offered by the reservoir [15]. Therefore, highly specialized species without the ability of adapting to the new food sources offered in the reservoir tend to disappear in the first years of the new system [7].

Research on the fish fauna associated with reservoirs is a priority for strengthening the environmental management of aquatic resources in the Andes. These constitute an important natural renewable resource of great biological and social importance [10, 16]. Unfortunately, these fishes are among the least studied vertebrates in Colombia and entail one of the most endangered species groups [17, 18, 19]. In the Andes, fish species richness and their trophic structure are influenced by patterns along altitudinal gradients. There, the greatest species richness and trophic guilds are found at altitudes between 250 and 1300 meters above sea level (msl) [11, 20]. Currently, water reservoirs in the Andean region of Colombia are located at altitudes higher than 500 msl [4] and boast high fish species richness, with 68 % endemism [21]. This situation increases the probability of fish species loss in the region. Thus, investigating these fishes' feeding habits, will lead to an understanding of the trophic interactions within these modified ecosystems, which is central to promote the development of relevant environmental management and conservation strategies.

Two water reservoirs along the Porce River (Porce II and Porce III) have been built in the Colombian Andes, between 500 msl and 900 msl. These two systems are species-poor, even though their remaining aquatic fauna includes some of the species from the original riverine assemblage [4]. Based on previous studies from these reservoirs and our current understanding of fish trophic dynamics, we hypothesize that climate seasonality influences the feeding habits of the fish inhabiting these reservoirs, conditions their prey availability, and drives the dominance of generalist predators in both reservoirs. Therefore, in the present study we set out to: (i) describe the diet of the fish species inhabiting Porce II and Porce III reservoirs, (ii) determine their feeding strategies, and (iii) evaluate whether the season (dry and rainy) and/or spatial distribution (Porce II vs Porce III), affects the diet of these fish species.

2. Materials and Methods

2.1. Study area

The Porce River is located in the northwestern corner of South America. Its source is located on the Andes at 2660 msl and after flowing 247 km northward, it joins the Nechi River, at 170 msl, which eventually joins the Cauca River and then the Magdalena River before emptying into the Caribbean Sea (**Figure 1**). With an average annual rainfall of 2458.1 mm, a temperature range of 19 °C to 24 °C, and an average relative humidity greater than 80 %, the Porce River basin covers 5227 km^2. This river basin experiences two rainy seasons (May-June, October-November) and two dry seasons (January-March, July-September) every year. Upstream of the Porce II reservoir, the Porce River basin drains soils highly transformed by agriculture, livestock farming, and urban, suburban, and ex-urban housing development. It also receives the sewage discharge from the city of Medellín, an urban center with six million inhabitants [22]. In the middle section of the Porce River, there are two reservoirs for hydropower: Porce II (year 2002) and Porce III (year 2011). The Porce III reservoir receives water from the Porce II reservoir and the Guadalupe-Troneras reservoirs system. The Porce II and Porce III reservoirs are sourced by an important network of small creeks [22]. In terms of biological productivity, the Porce II reservoir is considered hypereutrophic and the Porce III reservoir is considered eutrophic. Environmental variables such as temperature, dissolved oxygen, pH, and conductivity differ between these two reservoirs [22, 23].

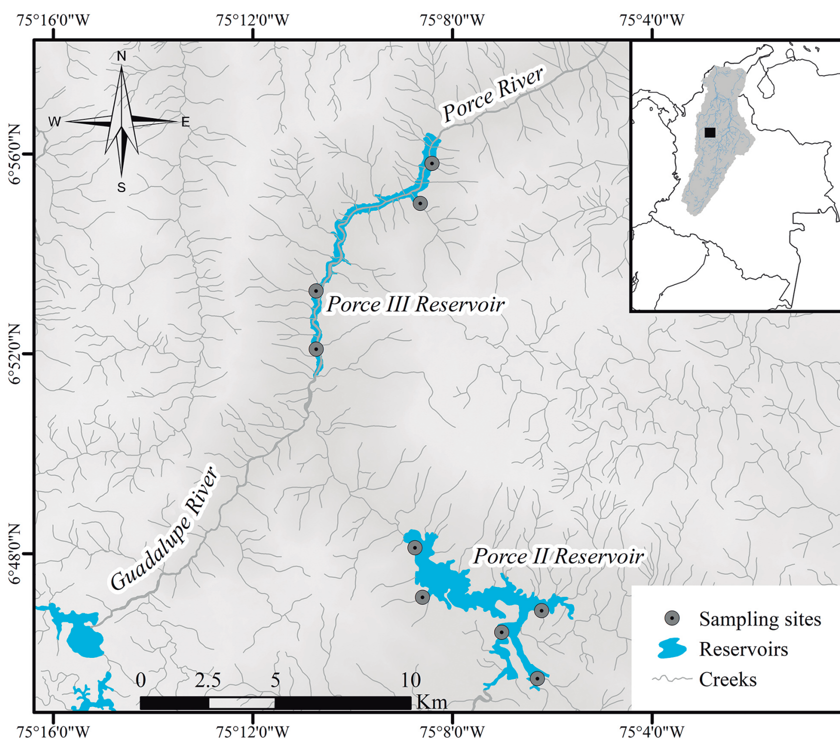

Figure 1. Area of study depicting the Andean region of Colombia where the Porce II and Porce III cascade reservoirs are located.

2.2. Sampling design

Fish sampling was approved for this study's sake by the Colombian Fishery Authority (through resolution number 03703-2011). Fish samples were taken in the two rainy and two dry seasons during three consecutive years (2011-2013) from nine sites in the Porce II and Porce III reservoirs. Three gillnets (each one 100 m long and 3 m high) were located at each site; each net had ten types of mesh size (1 cm to 10 cm between opposite knots) to increase the probability of catching fish of different species. Gillnets were located only in littoral areas twice a day (06:00 to 08:00 and 12:00 to 14:00). Of the fish caught, 10 % were anaesthetized with eugenol [24] and preserved in 10 % formaldehyde. In the laboratory each fish specimen was identified to species level and its stomach was removed for posterior analysis. We only considered for analysis those stomachs that with food inside. The content of each stomach was inspected under a stereoscope and a microscope, then, food items were grouped by taxonomic category and identified to the lowest possible taxonomic category.

2.3. Data analyses

The percentage of occurrence and volumetric index of food items in the stomach content of each fish species were recorded [25]. Frequency of occurrence, expressed as a percentage (%), was defined as the number of stomachs containing a given prey item divided by the total number of stomachs inspected for a specific predator species [25]. Volumetric stomach content analyses were done directly and indirectly. In the first, the displacement of each food item, or group of food items, from a given stomach content was measured in a graduated measuring cylinder, and the displaced volume was equated to that of the food item or group thereof [25]. The indirect volumetric estimation consisted of comparing food items with blocks of a known volume and depended on the three-dimensional shape of the item being measured [25].

2.3.1. Reservoir resources used as food by fish

To determine whether a sample size was enough for describing with accuracy the diet of a predator, a cumulative prey curve (or Cole rarefaction) was used [26]. Cortés [27] states that the construction of this curve should be a random process. The Sample-based rarefaction (species cumulative curve) tool of the program EstimateS 9.1 [28] was used to build these curves, iterating 500 times the item richness values of the analyzed stomachs. To prove the asymptote of the curves, a linear regression was done using the last four points of each curve to test if the slope of the line of best adjustment was significantly different from a line with slope zero (H0: $m = 0$ and HA: $m \neq 0$). The obtained slopes were compared using a t-student test, as follows:

$$t = \frac{b - 0}{S_b}. \tag{1}$$

Where, b = slope of the line of best adjustment (linear regression coefficient) and S_b = the standard error of the slope [29]. The slopes were not different if $P > 0.05$, indicating that the curve reached its asymptote [30].

To evaluate the precision of the cumulative curves, the slope of the line generated with the standard errors of the four final points was tested in a similar way, namely testing if variation around the mean is stabilized ($P > 0.05$). Finally, to obtain a standard measure of accuracy, the mean coefficient of the variation of the final points was calculated (CV = standard deviation/mean $*$ 100) [30].

2.3.2. Feeding strategies

The Shannon diversity index (H') was used to assess how diverse a fish species' diet was. Calculation followed this formula:

$$H' = \sum_i p_i i\ (\ln \rho_i)\,. \qquad (2)$$

Where p_i is the proportion of individuals found of i in relation to the total of identified prey items. This index equals near-zero values when there is just one type of consumed prey, indicating a specialized diet, whereas increased index values suggest a generalist feeding behavior [31].

Significant differences ($\alpha = 0.05$) in the diversity of the diet among species from the same reservoir, between species occurring in both reservoirs and differences between reservoir (all species of the Porce II versus all species of the Porce III reservoirs, and vice-versa) were evaluated by applying the Hutchenson's t test (1970) to the Shannon diversity index values. The null hypothesis stated that the diversity of the samples where not different. The test is calculated as follows:

$$t = (H'_1 - H'_2) \cdot (\text{Var } H'_1 + \text{Var } H'_2) - 0.5 \qquad (3)$$

Where H'_1 is the Shannon diversity index of sample 1, H'_2 is the Shannon diversity index of sample 2, Var H'_1 is the variance of H'_1 and Var H'_2 is the variance of H'_2 [31].

To define the contribution of each prey to a fish species' diet and to evaluate the food strategy of each species, a graphical analysis per species was conducted. This analysis is based on a two-dimensional representation of the abundance of a prey (P_i) and its frequency in the diet of the fish species x. The specific abundance of each prey was expressed as its percentage to the total volume ($\sum$ volume $i \ldots n$) of the sample and it is expressed as:

$$P_i = \sum \frac{S_i}{\sum St_i} \cdot 100. \qquad (4)$$

Where P_i is the specific abundance of prey i, S_i is the represented volume by the prey i and St_i is the total volume of the stomach content ($\sum$ volume $i \ldots n$) in the sample [32].

2.4. Spatial and temporal variation of a fish's diet

Prior to performing multivariate analyses, volumetric percentage (VP) data for dietary categories of each species (*i.e.*, replicate) were square root-transformed and used to construct a Bray-Curtis resemblance matrix for non-metric Multidimensional scaling (nMDS) ordination and a one-way ANOSIM test [33]. This nMDS was used to know a fish species' feeding scheme in relation to the reservoirs, using the clustering procedure and to illustrate the relationships between species in a two-dimensional space. The nMDS procedure was computed with 10 random restarts to reach a minimum stress value.

Analyses of similarities (one-way analysis of similarities [ANOSIM], with 999 permutations) were employed to test whether dietary compositions differed significantly among species, among reservoirs (Porce II, Porce III), and among seasons (dry and rainy months). The resulting R statistic ($-1 < R < 1$) describes the similarity between the groups defined according to the previously mentioned factors. Objects that are more dissimilar between groups than within groups will get an R statistic value greater than 0. An R value of 0 indicates that the null hypothesis is true. A level of significance (p value) also was obtained in this analysis [33]. A Bonferroni correction to the significance level was applied to decrease type I error probability, due to multiple comparisons [34]. A SIMPER analysis [33] was used to identify the food categories that contribute most to the dissimilarity of fish species' diets between seasons (dry and rainy months). The PAST software, version 3.04, was employed to conduct the multivariate analyses nMDS, ANOSIM and SIMPER [35].

3. Results

3.1. Reservoir resources used as food by fish

In total, 334 individuals in four fish species were analyzed (further information in **Suppl. 1**). All of the obtained accumulation curves reached the asymptote (**Figure 2**). These curves showed low variability and low coefficients of variation (Figure 2). These results suggest that sufficient precision was obtained for a thorough description of the diet of these fish species.

A total of 17 food categories identified as prey of different species with a larger number of eaten items identified in Porce II (Suppl. 1). With regard to the frequency of occurrence of these items, in Porce II the most frequent prey were terrestrial insect fragments (23.1 %), leaves (17.6 %), fish scales (14.1 %), and seeds (12.6 %). In Porce III, even though terrestrial insect fragments were slightly less frequent than in Porce II (22.02 %), this eaten item is also the highest in frequency of occurrence prey items in this reservoir and is followed by leaves (21.8 %), seeds (12.8 %), and Decapoda (11.8 %) (Suppl. 1).

3.2. Feeding strategies

The Shannon index values for Porce II reservoir showed that the stomach contents of the fishes *Astyanax microlepis* Eigenmann, 1913 and *Hoplosternum magdalenae* Eigenmann, 1913 entailed a similar diversity of prey items ($H' = 1.64$, $H' = 1.62$ and $H' = 1.42$ respectively), whereas *Roeboides dayi* (Steindachner, 1878) stomachs had the lowest trophic diversity ($H' = 0.94$). Based on t-Hutchenson test results, within this reservoir the diversity of *R. dayi* stomach contents differed significantly from that in *A. microlepis* stomachs (further information is available in **Suppl. 2**). Although in Porce II *A. microlepis* and *H. magdalenae* had a similar H' values, the graphic analysis of their diets revealed different feeding strategies (**Figure 3**). With regard to *A. microlepis* ($H' = 1.62$), this species had a more generalist strategy because no prey items of high individual specialization were identified, moreover only leaves showed a high frequency of consumption (Figure 3). Finally, the stomach contents of *H. magdalenae*, revealed a food strategy based on two prey items, suggesting a trophic behavior with a tendency towards population specialization (decapoda and terrestrial insect fragments) as well as many prey items of occasional consumption.

The Shannon index values for the stomach contents of fish in the Porce III reservoir showed that *A. microlepis* and *Brycon henni* Eigenmann, 1913 had a similar diversity of prey items ($H' = 1.43$ and $H' = 1.61$ respectively), whereas *R. dayi* had the lowest trophic diversity ($H' = 1.14$). With respect to t-Hutchenson test, no significant differences in prey diversity items within the stomachs of these three species in this reservoir were observed (further information is available in Suppl. 2). The graphic analysis of the diet of these fish species in Porce III revealed different feeding strategies. *A. microlepis*, had a more generalist strategy because no preys of high individual or population specialization were identified, but there were many occasional prey items (Figure 3). On the other hand, *B. henni* had a food strategy dominated by prey with low frequencies of consumption and, in some cases, high abundance (Fish bone or muscle, Decapoda) being classified as individual specialization strategy (Figure 3). Furthermore, *B. henni* also consumed the prey item "leaves" in intermediate frequencies and abundances. For *R. dayi*, the obtained low H' value indicates a

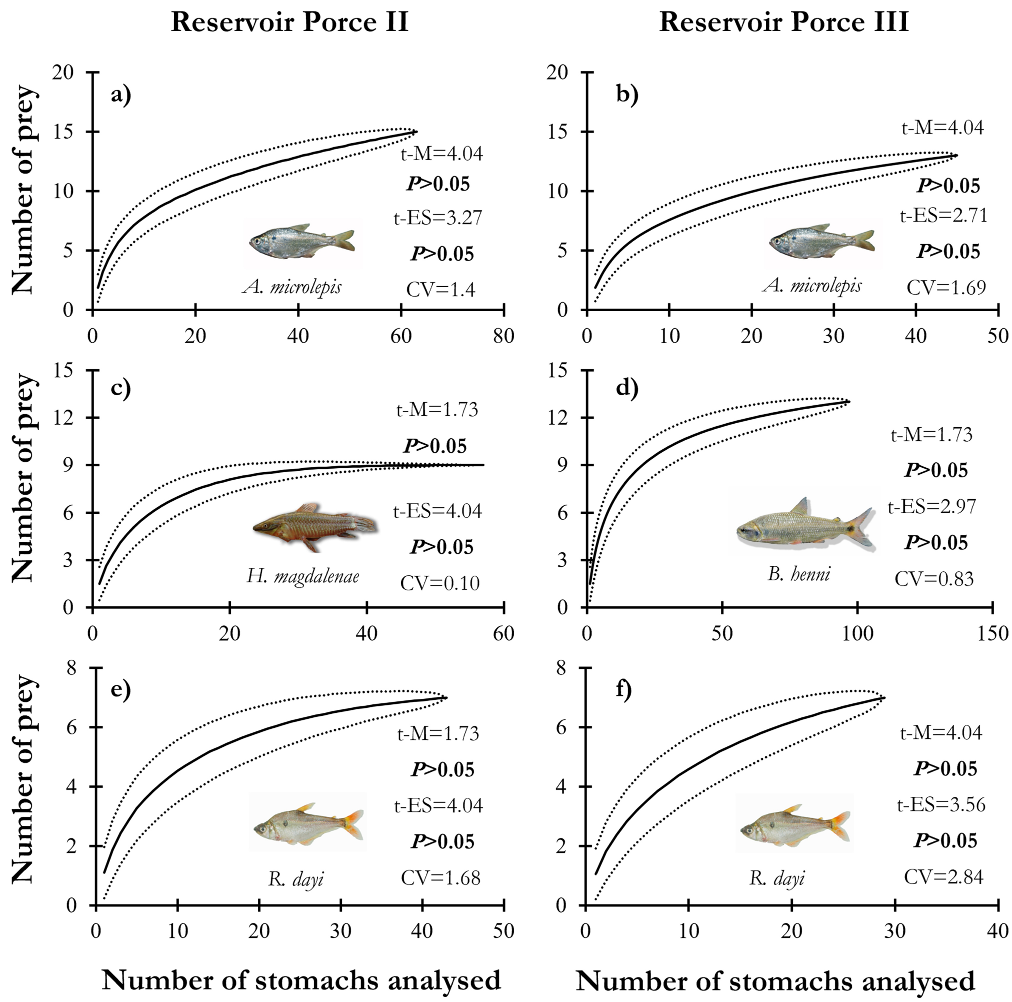

Figure 2. Cumulative prey curves for four fish species living in the reservoirs Porce II (a, c, e) and Porce III (b, d, f). The plots depict Cole's rarefaction or the cumulative prey curves (—) and their respective standard deviation S.D. (···). Each plot presents the obtained t-student values for the mean (t-M) and the standard error (t-ES) of the four final points of each cumulative prey curve, as well as their respective coefficient of variation (CV) values. $P > 0.05$ indicates slopes equal to zero.

feeding strategy with very abundant and infrequent prey items (leaves, diptera larvae, decapoda), which suggests specialization on these prey items for some individuals of the species, however, the stomach contents of a group of individuals of this fish species revealed specialization for a single prey item (*i.e.*, fish scales) (Figure 3).

When comparing t-Hutchenson test results on the diversity values of the stomach contents of the fish species occurring in both reservoirs (*A. microlepis* and *R. dayi*), no significant differences were observed (further information is available in Suppl. 2). However, the graphic analysis of their food strategies revealed diet composition disparities. *A. microlepis* stomachs from Porce III revealed a number of occasional preys greater than in stomachs of the same fish species in Porce II. Moreover, prey that were considered of low or medium relevance (terrestrial insect fragments, decapoda, leaves) in Porce II, were consumed more frequency and in grater abundance in Porce III. Finally, *R. dayi* revealed contrasting feeding strategies between reservoirs. In Porce II, this species

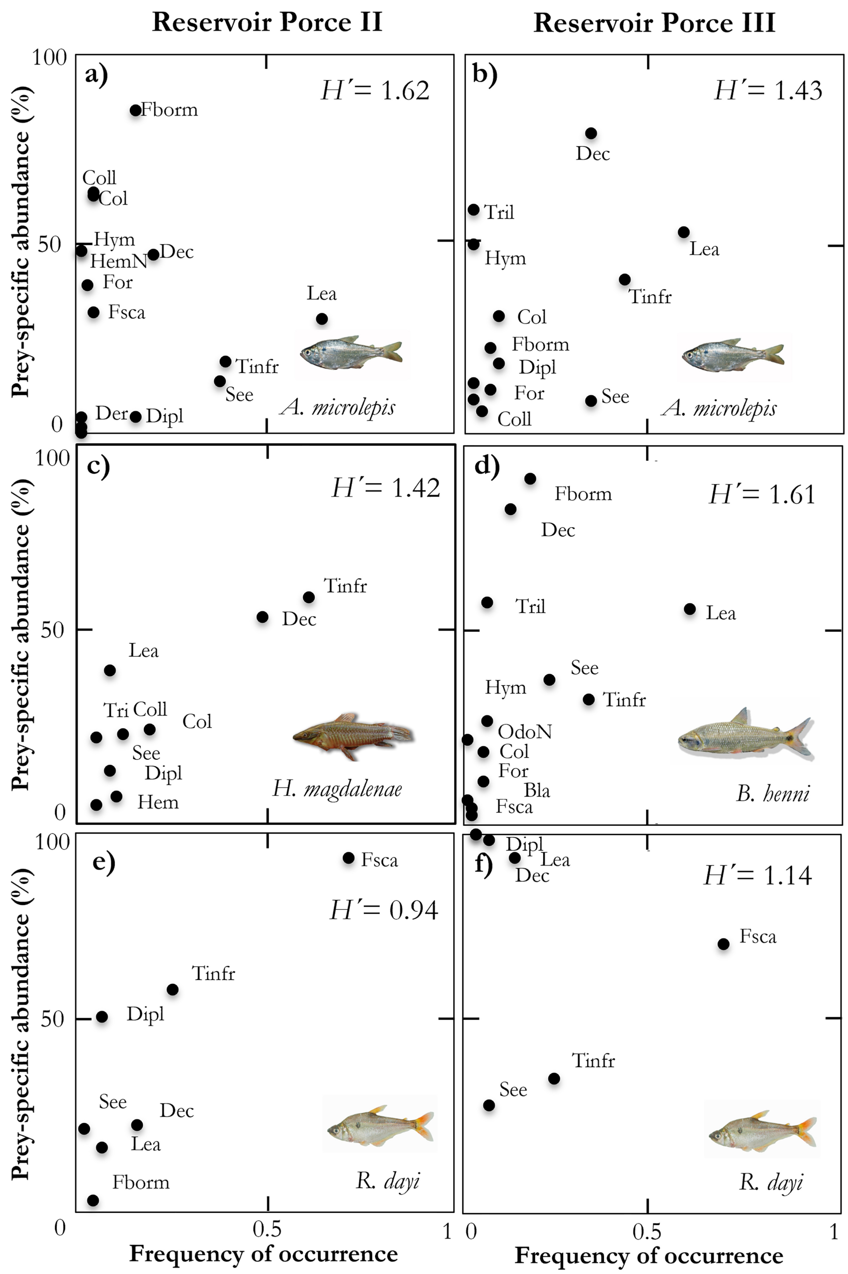

Figure 3. Graphic analysis of the feeding strategy of the species of fish present in the Porce II (a, c, e) and Porce III (b, d, f), following Amundsen and collaborators (1996), Ara = Aranae, Bla = Blattodea, Col = Coleoptera, Coll = Coleoptera (larva), Dec = Decapoda, Der = Dermaptera, Dipl = Diptera larvae, EphN = Ephemeroptera (nynph), Fborm = Fish bone or muscle, For = Formicidae, Fsca = Fish scales, Hem = Hemiptera, HemN = Hemiptera (ninph), Hym = Hymenoptera, Lea = Leaves, OdoN = Odonata (nymph), See = seed, Tinfr = Terrestrial insect fragments, Tri = Trichoptera, TriL = Trichoptera (larva).

showed a high population consumption of fish scales and an absence of individual specialization, whereas in Porce III their stomach contents revealed less fish scales and the occurrence of three prey items, indicating a shift towards individual specialization (Figure 3).

Table 1. Analysis of similarities (ANOSIM) among fish species diets within Porce II between climate seasons. R values (lower left) and P significance values (top right, values in bold significant) for diet similarity analyses for tests food choice of fish species in Porce II reservoir and among the rainfall seasons. Asmi = *A. microlepis*, Homa = *H. magdalenae*, Roda = *R. dayi*.

Specie/Climatic season	Asmi Dry	Asmi Rains	Homa Dry	Homa Rains	Roda Dry	Roda Rains
Asmi Dry		1	0.613	**0.016**	**0.002**	**0.005**
Asmi Rains	0.005		0.053	**0.002**	**0.008**	**0.022**
Homa Dry	0.340	0.508		1	1	0.210
Homa Rains	0.417	0.669	0.170		**0.044**	**0.030**
Roda Dry	0.679	0.824	0.376	0.729		1
Roda Rains	0.711	0.747	0.564	0.848	0.108	

3.3. Spatial and temporal variation in fish diets

The conducted multivariate analysis identified differences among fish species diets in Porce II. *A. microlepis* and *H. magdalenae* had the most differentiated diets (ANOSIM, $R_{\text{global}} = 0.44$, $p = 0.0001$) (**Figure 4**). Likewise, climate season-driven differences in diet were identified between fish species (**Table 1**). Most of these differences (8 out of 12) were associated with the dry period (Figure 4), with *R. dayi* having the most divergent diet (Table 1). The SIMPER analysis showed that in Porce II, fish scales, leaves, terrestrial insect fragments, and decapoda were the prey items with the greatest contribution to the trophic differences identified (further information is available in **Suppl. 3**).

In Porce III, differences in diet compositions between fish species were also observed (ANOSIM, $R = 0.30$, $p = 0.0001$). These differences are attributed to *R. dayi'* diet, which differed significantly from that of the other two fish species in the two climate seasons (**Table 2**). The SIMPER analysis showed that, as in Porce II, in Porce III, fish scales, leaves, terrestrial insect fragments, and decapoda were the prey items with the greatest contribution to the trophic differences identified (further information is available in Suppl. 3)

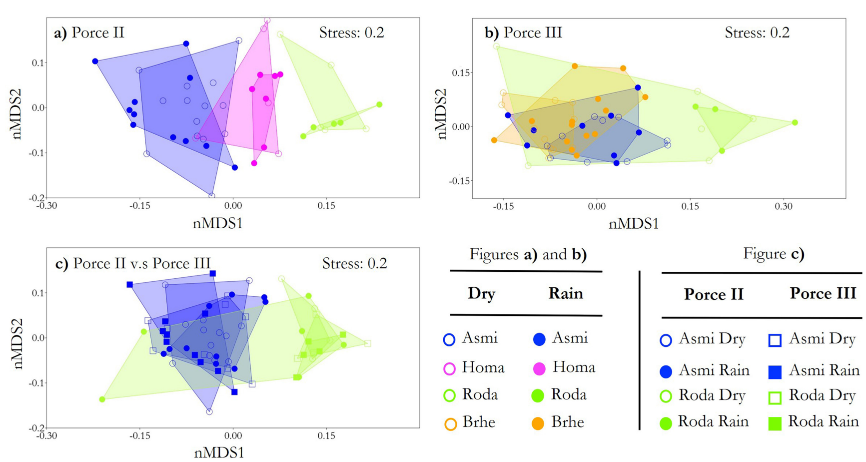

Figure 4. Non-metric multidimensional scaling (nMDS) plots for each sampling period for known fish feeding schemes in relation to reservoir (Porce II and Porce III). a) Among all fish species in Porce II and in rainfall seasons; b) Among all fish species in Porce III and in rainfall seasons; and c) Between the species shared by both reservoirs. Asmi = *A. microlepis*, Brhe = *B. henni*, Homa = *H. magdalenae*, Roda = *R. dayi*. PII = Porce II reservoir, PIII = Porce III reservoir.

Table 2. Analysis of similarities (ANOSIM) among fish species diets within Porce III between climate seasons. R values (lower left) and P significance values (top right, values in bold significant) for diet similarity analyses for tests food choice of fish species in Porce III reservoir and among the rainfall seasons. Asmi = *A. microlepis*, Brhe = *B. henni*, Roda = *R. dayi*.

Specie/rainfall season	Asmi Dry	Asmi Rains	Brhe Dry	Brhe Rains	Roda Dry	Roda Rains
Asmi Dry		1	0.094	1	**0.018**	**0.022**
Asmi Rains	-0.055		0.606	1	**0.039**	**0.031**
Brhe Dry	0.239	0.150		1	**0.007**	**0.019**
Brhe Rains	0.098	0.002	0.050		**0.003**	**0.010**
Roda Dry	0.446	0.441	0.654	0.669		1
Roda Rains	0.776	0.760	0.956	0.841	–0.206	

Differences were identified in the diet composition of *A. microlepis* and *R. dayi* between Porce II and Porce III (Figure 4), regardless of their distribution in these reservoirs and climatic temporality (ANOSIM, $R = 0.43$, $p = 0.0001$) (**Table 3**). The SIMPER analysis showed that the most frequent prey categories that contributed to the differences in diet composition between these two fish species and reservoirs were fish scales, terrestrial insect fragments, decapoda, leaves, and fish bone or muscle (further information is available in Suppl. 3).

4. Discussion

The wide variety of food resources consumed by the fish living in the Andean Porce II and Porce III reservoirs exemplifies these fish species' ability to exploit available food resources in these ecosystems. Our analyses revealed that the fish species that colonized these reservoirs have a generalist feeding behavior and are capable of changing their feeding strategies. These strategies depend on these fishes' ability to capture their food and is also determined by prey availability, which is associated with different biotic and abiotic features of the ecosystem [8, 36].

The fish species living in the Porce II reservoir, essentially fed on autochthonous resources (*e.g.*, aquatic arthropods and fish scales). This feeding behavior matches that observed in other reservoirs in tropical South American [12]. The Porce III reservoir differed from Porce II because of a high frequency of occurrence of allochthonous food items, such as vegetal material and a large variety of terrestrial insects and seeds. These are the same food resources consumed by fish in Andean rivers [37, 38]. This aspect of Porce III can be explained by its young age and river-like morphology, which allow this reservoir to retain the features that contribute to the presence of food items of allochthonous origin. In newly dammed tropical rivers, the incorporation of organic

Table 3. Analysis of similarities (ANOSIM) among the diets of the two fish species common to Porce II and Porce III between climate seasons. R values and P significance values for diet similarity analyses for tests food choice between *A. microlepis* and *R. dayi* in both reservoirs and among the rainfall seasons. Asmi = *A. microlepis*, Roda = *R. dayi*.

		Porce III			
		Asmi Dry	Asmi Rains	Roda Dry	Roda Rains
Porce II	Asmi Dry	R= 0.13; P= 1.00	$R = 0.07$; $P = 1.00$	$R = 0.64$; $P = 0.01$	$R = 0.95$; $P = 0.002$
	Asmi Rains	$R = 0.22$; $P = 0.07$	$R = 0.13$; $P = 0.86$	$R = 0.56$; $P = 0.01$	$R = 0.93$; $P = 0.01$
	Roda Dry	$R = 0.70$; $P = 0.002$	$R = 0.68$; $P = 0.01$	$R = -0.18$; $P = 1.00$	$R = -0.07$; $P = 1.00$
	Roda Rains	$R = 0.91$; $P = 0.0056$	$R = 0.90$; $P = 0.02$	$R = -0.03$; $P = 1.0$	$R = -0.03$; $P = 1.00$

material to the system during the filling phase can produce a stark increase in the availability of allochthonous resources; consequently, fish in these systems can expand their diet to new items [39].

The fish species *A. microlepis* and *B. henni* consumed a wide diversity of prey as a feeding resource in the two reservoirs, their diets consisted of a wide variety of terrestrial and aquatic invertebrates, as well as vegetal material and seeds. The generalist feeding behavior observed in these species can be seen as an adaptive trait, allowing them to inhabit environments as diverse and dynamic as the aquatic systems of the Colombian Andes [10, 40]. These species (*A. microlepis*, and *B. henni*) have similar foraging strategies in natural Andean ecosystems such as rivers, brooks, and small swamps [41, 42], usually feeding on aquatic insect larvae found in the water column [43], elements of allochthonous origin from shore areas such as ants and beetles [44], and incorporating items of vegetal origin such as seeds and leaves [41].

In these reservoir ecosystems the two fish species *R. dayi* and *H. magdalenae* consume specific prey. This is a feeding strategy that allows these fish to inhabit these environments. Under the conditions provided by reservoirs in the Andes, the species *R. dayi* shows specialized trophic habits mainly based on fish scales, which provide the necessary nutrients for their development [45]. The presence of external teeth in this species allows access to this specialized resource [46]. Such lepidophagous behavior of this species in the Andean reservoirs has been observed in fishes of lotic and semi-lentic aquatic systems [47]. However, an opportunistic feeding behavior has been seen in *R. dayi,* as evidenced by the presence, in stomach contents, of other items such as invertebrates or other abundant ones in the aquatic system [47, 48]. The high specialization of *H. magdalenae* to feed on decapods and terrestrial insects in Porce II suggests that in this reservoir there is a high availability of these prey organism or that *H. magdalena* individuals are successful predators, outcompeting other fish in consuming these food items. The feeding behavior of *H. magdalenae* in the studied reservoirs differs from that reported in natural environments like the floodplains of the Magdalena River, where this fish species acts as a generalist, consuming a wide variety of terrestrial and aquatic insects and incorporating vegetal material, such as leaves and seeds, into its diet [49].

The feeding behavior of the studied fish species varied both within and between Porce II and PorceIII, this is closely related to the availability of prey organisms and the characteristics of each reservoir. In Porce II, there were diet composition disparities among the fish species *A. microlepis*, *H. magdalenae,* and *R. dayi*, suggesting differential exploration of the available resources; perhaps this reservoir, having a higher flooded area with numerous internal bays, boasts a large diversity of food sources. In the Porce III reservoir, *R. dayi* was the species with the most divergent feeding habits, whereas the other two species (*A. microlepis*, *B. henni*) fed on similar prey. The potential for the fish species in both reservoirs to exploit the available resources is similar to that reported in other reservoir systems [7, 15], where the main food resources are generally the most abundant, and their availability depends on the condition of the reservoir [13, 50]. For this reason, the fish species that remain in these systems are those whose diet is flexible and diverse [51].

Rainfall in these reservoirs was advantageous for opportunistic species (*i.e.*, *R. dayi* and *H. magdalenae*). Rain influenced fish feeding behavior, allowing them to take advantage of abundant seasonal resources. This feeding plasticity, elicited as a response to the seasonal availability of food, underlays opportunistic diets [7, 13, 14]. The variation in the feeding behavior of these species responds to climate seasonality; the arrival of rains results in an abundant inflow of diverse, chiefly allochthonous, prey items from the tributary streams of both reservoirs [8]. In contrast, during the dry seasons, allochthonous food elements become scarce, leading to a higher intake of aquatic organisms [52].

Water level dynamics, depending on the reservoir's energy-production operation, are also likely to trigger changes in the availability of food resources. Frequent floods caused by high water levels tend to expand the aquatic environment including the diversity and abundance of allochthonous resources [50], whereas during the dry seasons a decrease in allochthonous food items is observed, leading to a higher intake of organisms native to the reservoir [13]. The change of food availability in a fluctuating environment is favorable for highly opportunistic fish with dietary flexibility [52]. Our results are similar to those reported for rivers with naturally driven water dynamics (*i.e.*, without damming), where opportunistic fish increase their trophic niche breadth to take advantage of abundant resources during the rains, and when these end, the fish turn to a more specialized diet [53]. This indicates that these changes in the ecosystem cause the development of new strategies in the fish so that they take advantage of available resources and are not restricted to feeding on the most recurring ones [37, 53].

We conclude that the studied reservoir fish species are those that can consume a wide spectrum of food resources, opting for a generalist strategy. In addition, both reservoirs revealed differences in the feeding behavior of their fish species, and climate seasonality benefited opportunistic species because it influenced their eating behavior. These species expanded their feeding habits to take advantage of abundant seasonal resources. Understanding the feeding habits of fish is a fundamental aspect in the ecology of aquatic systems and could help to predict which fish species can survive in rivers modified by dams and reservoirs.

5. Acknowledgments

We acknowledge S. López-Casas for her advising role in this investigation, and D. C. Taphorn for his orientation on manuscript style. We are thankful to the members of the group of fish fauna from Universidad de Antioquia (GIUA) for their support in the field and in the laboratory. We thank D. Castaño for sharing his knowledge about the fish in the study region. Finally, we thank the two anonymous reviewers of the manuscript for their suggestions.

6. Conflict of interest

The authors declare that they have no conflict of interest.

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Estrategias alimentarias de peces que viven en dos reservorios de agua en la cuenca del Río Magdalena

Resumen: La construcción de represas para generación de energía eléctrica en los ríos andinos de Colombia está conduciendo a una pérdida regional de especies de peces. Las especies que persisten en estos ecosistemas artificiales son aquellas que encuentran favorables las nuevas condiciones para su reclutamiento. Estrategias de alimentación apropiadas permiten a estos peces persistir y prosperar en reservorios. Se analizaron los contenidos estomacales de las especies presentes en dos reservorios en cascada de la cuenca del río Magdalena. Los objetivos fueron describir la dieta de los peces, determinar sus estrategias alimenticias y evaluar si factores estacionales, como lluvia o distribución espacial afectan la dieta de estas especies. Los resultados indican que las especies *Brycon henni* y *Astyanax microlepis* se alimentan de un amplio rango de recursos que el sistema ofrece y adoptan una estrategia alimenticia generalista. Por otra parte, en los reservorios viven especies oportunistas como *Roeboides dayi* y *Hoplosternum magdalenae*. Las especies que viven en los dos reservorios presentan diferentes comportamientos alimenticios. La estación lluviosa en estos reservorios fue benéfica para las especies oportunistas porque les permitió diversificar su comportamiento alimenticio. El conocimiento de los hábitos alimenticios de las especies de peces es una prioridad para el fortalecimiento del manejo ambiental de los recursos acuáticos de Los Andes.

Palabras Clave: peces neotropicales; dieta de peces de agua dulce; ríos andinos; estrategia generalista

Estratégias de alimentação de peixes de dois reservatórios de água na bacia do rio Magdalena

Resumo: A construção de barragens para hidrelétricas nos rios andinos da Colômbia está levando à perda de espécies regionais de peixes. As espécies de peixes que conseguem sobreviver nesses ecossistemas artificiais são aquelas que encontram novas condições favoráveis para seu recrutamento. Estratégias de alimentação adequadas permitem que esses peixes persistam e prosperem em reservatórios. Neste estudo, analisamos o conteúdo estomacal das espécies presentes em dois reservatórios de cachoeira na bacia do rio Magdalena. Os objetivos foram descrever a dieta dos peixes, determinar a estratégias de alimentação e avaliar se fatores estacionais, como chuva ou distribuição espacial, afetavam a dieta dessas espécies de peixes. Nossos resultados indicam que as espécies de peixes *Brycon henni* e *Astyanax microlepis* se alimentam de uma ampla gama de recursos que o sistema oferece e adotam uma estratégia de alimentação generalista. Adicionalmente, achamos espécies oportunistas como *Roeboides dayi* e *Hoplosternum magdalenae* vivendos nos reservatórios. As espécies de peixes que vivem nos reservatórios apresentaram comportamentos alimentares diferentes. A estação chuvosa beneficiou ás espécies de peixes oportunistas, pois lhes permitiu diversificar seu comportamento alimentar. Entender os hábitos alimentares das espécies de peixes é uma prioridade para fortalecer do manejo ambiental dos recursos aquáticos dos Andes.

Palavras-chave: peixes neotropicais; dieta de peixes de água doce; ríos andinos; estratégia generalista

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