

Auto-ecological responses of rainbow trout populations to ecoregional differences in a neotropical Andean river

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Received: 30/11/18

Accepted: 20/12/19

ABSTRACT

Auto-ecological responses of rainbow trout populations to ecoregional differences in a neotropical Andean river

We assessed changes in auto-ecological traits of Rainbow Trout (*Oncorhynchus mykiss*) in a river flowing through two ecoregional belts. Besides the temperature and elevation, these ecoregional belts mainly differed in terms of the presence or absence of riparian forest (high-Andean and páramo regions, respectively). Our results indicated that fish populations in the páramo attained sexual maturity at a smaller size and fed mainly on autochthonous small aquatic invertebrates such as chironomid midges and caddisflies. In the high-Andean reach, Rainbow Trout attained larger sizes and there was a segregation in the use of food resources; adults fed primarily on allochthonous resources and juvenile fish on autochthonous prey items. Overall, our results suggested that limited availability of resources did not constrain the successful establishment of Rainbow Trout in Andean streams but appeared to have a direct effect on some auto-ecological characteristics such as sexual maturity, size and diet. The variability of the evaluated traits seemed to be linked to the presence or absence of resources provided by a well-developed riparian forest, instead of variability in temperature, water quality or flow regime.

Key words: allochthonous, autochthonous, diet, high-Andean stream, Páramo, Colombia

RESUMEN

Respuestas auto-ecológicas de las poblaciones de trucha arcoíris a las diferencias ecorregionales en un río andino Neotropical

En este estudio evaluamos los cambios en los rasgos auto-ecológicos de la trucha arcoíris (*Oncorhynchus mykiss*) en un río que fluye a través de dos cinturones ecorregionales (Altoandino y Páramo). Además de la temperatura y la altitud, estos cinturones ecorregionales difieren principalmente en términos de la presencia y ausencia "natural" de bosques de ribera (altoandino y páramo, respectivamente). Nuestros resultados indicaron que las poblaciones del páramo alcanzan la madurez sexual a un tamaño más pequeño y se alimentan principalmente de pequeños invertebrados acuáticos, como larvas de quironómidos y frigáneas. En la región altoandina, por otra parte, las truchas arcoíris alcanzaron tamaños mayores y evidenciamos una segregación en el uso de los recursos alimenticios, donde los adultos se alimentaron principalmente de recursos alóctonos y los juveniles de presas autóctonas. En términos generales, nuestros resultados sugieren que una disponibilidad limitada de recursos no limita el establecimiento de la trucha arcoíris en los ríos altoandinos, sino que parece tener un efecto directo sobre algunas de sus características autoecológicas como la madurez sexual, el tamaño y la dieta. Esta variabilidad observada en los rasgos auto-ecológicos parece estar vinculada a la presencia y ausencia de recursos provistos por un bosque ribereño bien desarrollado, en lugar las características de temperatura, calidad del agua o régimen hidrológico de cada ecorregión.

Palabras clave: alóctono; autóctono, dieta, río altoandino, Páramo, Colombia

INTRODUCTION

The Rainbow Trout (*Oncorhynchus mykiss*, Walbaum 1792) is a species native to the west coast of North America, ranging from northwest Mexico to southwest Alaska and the Kamchatka Peninsula in eastern Russia (Behnke, 1992). The species has been introduced worldwide for aquaculture purposes and recreational fisheries (Rahel, 2000; Fausch, 2007). Its introduction has reduced several populations of native fishes and altered the natural dynamics of invertebrate populations in New Zealand, Australia, Japan, South Africa, Chile and Argentina (Macchi *et al.*, 1999; Cambray, 2003; Simon & Townsend, 2003; Kitano, 2004; Soto *et al.*, 2006). In light of its potential impact, understanding which factors affect trout ecology and population dynamics has been a priority for researchers for the past several years (e.g. Flecker & Townsend, 1994; Townsend, 2003; Fausch, 2007; Soto *et al.*, 2006). Nevertheless, while the Rainbow Trout was introduced in the 1930s to “repopulate” Andean streams in the Neotropical region (Segnini & Bastardo, 1995; Pascual *et al.*, 2002; Pineda *et al.*, 2004), few studies have addressed how the auto-ecology of trout populations might change as a consequence of the distinctive features of these ecosystems.

Generally, most high-altitude streams flow through two distinct ecoregional belts in the tropical Andes, the páramo and high-Andean ecoregions. These ecoregions differ mainly in terms of elevation and climate, as first noted by Alexander Von Humboldt (Humboldt & Bonpland, 1805). The high-Andean ecoregion is located below 3000 m s.a.l., which is usually where the Andean Forest belt ends (IDEAM, 2010). This ecoregion has relatively stable temperature conditions throughout the year, and its riparian forests are composed mainly of shrubs and leafy trees (Rangel-Ch *et al.*, 1997; Morales *et al.*, 2007). The páramo ecoregion has extreme temperature variations, soils with high water retention capacity as well as endemic vegetation assemblages. The páramos vegetation, beginning above 3000 m a.s.l., is chiefly comprised of giant rosette plants (*Espeletia* spp.), shrubs, and grasses (Buytaert *et al.*, 2006).

The patchy riverscape emerging from these ecoregional differences can be appreciated in a longitudinal dimension: high-altitude streams flow throughout the páramo regions and have no canopy cover before entering the well-forested zones characteristic of high-Andean regions. To date, few studies have addressed how these ecoregional differences might affect the structure and dynamics of riverine populations.

Streams and riparian forest are ecosystems closely linked by the input of allochthonous material (Baxter *et al.*, 2004, 2005). The terrestrial arthropods that accidentally fall into streams, for instance, represent not only high-quality food resources for fishes (Wipfli, 1997) but also energy inputs for maintaining food-web structure (Nakano *et al.*, 1999). The input of allochthonous material, associated with a well-developed riparian forest, appear to be the most relevant factors for explaining trout distribution in forested streams (Polis *et al.*, 1997; Vimos *et al.*, 2015). However, in the natural absence of allochthonous inputs, such as in the páramo ecoregion, fish might be deprived of these energetic sources, limiting their development and survival opportunities. Therefore, the increasing quality and quantity of allochthonous inputs as rivers enter to the high-Andean ecoregion could be one of the major factors influenc-

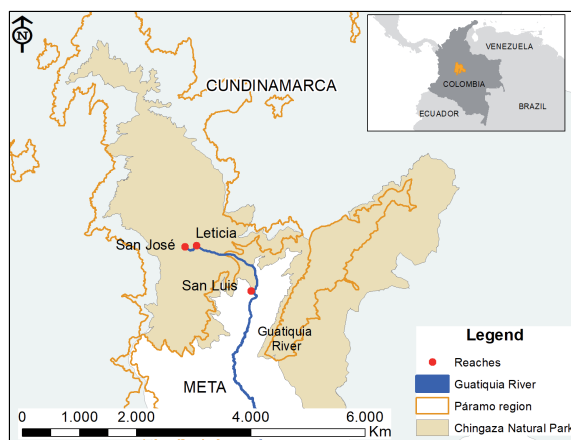


Figure 1. Map of sampled reaches, showing the páramo region at Chingaza Natural Park. *Mapa de los tramos muestreados, mostrando la región de Páramo en el Parque Nacional Chingaza.*

ing the auto-ecology and distribution of fishes along high-Andean rivers.

The aim of this study was to assess how auto-ecological traits of Rainbow Trout change due to ecoregionally-driven differences along a high-Andean river. This assessment included the description of some auto-ecological features (i.e., diet, feeding strategy, and sexual maturity) and their possible relationships with the presence of a well-developed forest in the high-Andean ecoregion. We expected that the diet and related auto-ecological traits of Rainbow Trout would change among sites on páramo and high-Andean reaches responding to differences in the input of allochthonous material, mostly terrestrial invertebrates.

MATERIALS AND METHODS

Study site

The Guatiquía River is a Strahler third order stream formed by the union of three small streams at an elevation of 3500 m. The river flows through the páramo ecoregion for approximately 20 km until it enters the high-Andean ecoregion. In the páramo, two reaches were sampled, “San José” (3180 m a.s.l.; 04° 32' 19.5" N, 73° 44' 40.5" W) and “Leticia” (3030 m a.s.l.; 04° 32' 24.1" N, 37° 43' 51.4" W) (Fig. 1). The riverbed of these two reaches is dominated by boulders, cobble and gravel, and their riparian vegetation consists mainly of shrubs, such as *Polylepsis sp.* (Rosaceae), *Hypericum sp.* (Hypericaceae) and *Chusquea tessellate* (Poaceae), grasses like *Calamagrostis sp.* (Poaceae) and mosses such as *Sphagnum sp.* (Sphagnaceae). A third reach was sampled in the high-Andean ecoregion: “San Luis” (1850 m a.s.l.; 04° 29' 9.6" N, 73° 39' 58.2" W) (Fig. 1). Its riverbed is also composed by gravel, boulders and sand, but its riparian vegetation comprises primarily two strata: a tree layer composed of *Ficus sp.* and *Cecropia sp.*, shrub species of Melastomataceae and Moraceae, and a ground layer composed of species of Araceae, Ericaceae and ferns. The three reaches are generally exposed to low anthropogenic stress because they are inside a protected area (Chingaza National Natural Park).

Fish sampling

At each reach, we sampled the fish communities during daylight (from 8 to 16 h) in three occasions: July and November 2013 and January 2014 (high, intermediate and low water flows, respectively). Sampling reaches were approximately 80 – 100 m in length. We measured temperature, dissolved oxygen, conductivity and pH using a HACH Hq multiparameter probe upon arrival (early morning) and departure (dawn) from each reach. The number of reaches and their length were constrained by difficult access to the river. Inside the park, few reaches are accessible without compromising the security and integrity of the field crew because of the steep topography of the river margins. We used non-parametric Kruskal-Wallis tests (with a significance level of $\alpha = 0.05$) to assess the significance of the differences between reaches in terms of environmental characteristics.

We collected samples by electrofishing (Smith-Root 1.5 KVQ and Honda generator 3 Kw) with three passes per reach. The reaches were not blocked because of the river's high flow (minimum of 3 m³/s). Following capture, we sacrificed all fish using a MS-222 overdose. We measured fish standard length (0.01 mm) and weight (0.01 g) in the field. After measurements, we preserved fish in 96 % ethanol and transported them to the ichthyology laboratory at the Instituto de Ciencias Naturales (“ICN” - Universidad Nacional de Colombia). In the laboratory, sex and gonadal development (juvenile or adult) were determined by direct observation of the gonads after gut removal. A one-way ANCOVA was conducted to determine statistically significant difference between páramo and high-Andean reaches on the somatic condition of trout individuals controlling for length. An $\alpha < 0.05$ was established to determine a significant effect.

Aquatic invertebrate sampling

We sampled invertebrate assemblages before fishing. Samples were taken in gravel and boulder substrates to complement fish diet characterization. We took five random samples in each type of substrate with a Surber (0.09 m², 200 μ m

mesh size). The area of the sampled boulders was equal or inferior to a Surber sampling area. We took a total of 90 samples (3 occasions x 3 reaches x 2 substrates x 5 samples) and preserved each sample individually in 96 % ethanol. In the laboratory, we sorted all individuals and identified them to family level following Domínguez and Fernández (2009) and Prat *et al.* (2011). We carried out the sampling of aquatic invertebrates, fish community, and water physical and chemical properties in parallel during all sampling occasions.

Diet characterization

In the laboratory, we dissected the fish specimens to remove their complete digestive system. We gathered food items from each stomach and preserved each item in 96 % ethanol. We identified all arthropods from the stomachs to family level following Domínguez and Fernández (2009) and Prat *et al.* (2011) for aquatic invertebrates, and Johnson and Tripplehorn (2005) for terrestrial invertebrates.

We described diet composition in terms of prey occurrence (F_i , eq.1) and prey-specific abundance (P_i , eq.2) of prey items (Hyslop, 1980; Amundsen *et al.*, 1996):

$$F_i = N_i/N \quad (\text{equation 1})$$

Where, N_i is the number of stomachs with the prey item i , and N is the total number of stomachs with at least one prey item.

$$P_i = (\sum S_i / \sum S_{ti}) \times 100 \quad (\text{equation 2})$$

Where, P_i is the prey-specific abundance of prey i , S_i the number comprised by prey i , and S_{ti} the total content in only those predators with prey I in their stomach (Amundsen *et al.*, 1996).

Data analysis

We explored diet composition differences among reaches through a non-metric multidimensional scaling (nMDS) using the Morisita-Horn index (Morisita, 1959; Horn, 1966). We used this index because it is a measure weighted towards the dominant species (Jost *et al.*, 2011). Therefore, we could compare diet composition without giving too much importance to incidental prey items such as some allochthonous taxa that occasionally fell into the river. We did not include families with five or less individuals in the ordination analysis. We performed analyses and graphical outputs using the statistical program R v3.2.1 (R Core Team 2015 – software available at <http://www.R-project.org>). We performed the nMDS by using the ‘metaMDS’ function of the ‘vegan’ package. We set all parameters of this function as default. We used the program ArcGIS 10.3 to create Fig 1.

Table 1. Physical and chemical values of the water of the studied reaches. Mean value and standard error in parenthesis. Only comparisons with p -values < 0.05 were considered as statistically significant. KW: Kruskal-Wallis test. *Valores físicos y químicos del agua en los tramos estudiados. Valor promedio y error estándar en paréntesis. Solo las comparaciones con valores $p < 0.05$ fueron considerados estadísticamente significativas. KW: análisis Kruskal-Wallis.*

	San José	Leticia	San Luis	
Temperature (°C)	10.95 (0.26)	14.22 (0.06)	12.13 (0.64)	KW Chi-squared = 6.6, df=2, p -value = 0.05
Dissolved Oxygen (mg/L)	7.57 (0.14)	7.33 (0.04)	8.13 (0.03)	KW Chi-squared = 0.62, df=2, p -value = 0.73
Conductivity (µS/cm)	36.33 (2.94)	40.93 (3.72)	76.50 (3.84)	KW Chi-squared = 8, df=2, p -value = 0.02
pH	7.30 (0.07)	7.30 (0.04)	7.30 (0.03)	KW Chi-squared = 5.9, df=2, p -value = 0.10

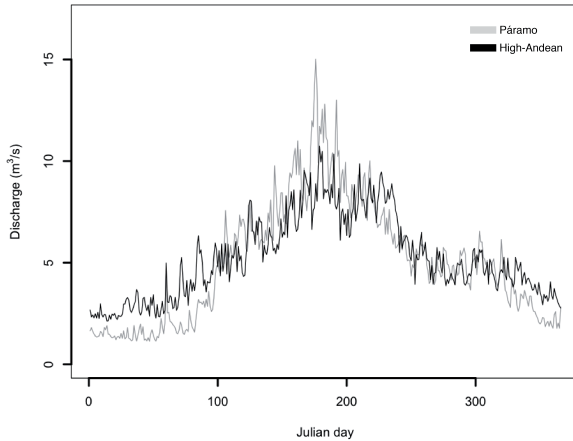


Figure 2. Daily average discharge of páramo (grey) and high-Andean reaches from the Guatiquía River. Data series from 2000 to 2013, were provided by the “Empresa de Acueducto y Alcantarillado de Bogotá”. *Promedio diario del caudal de los tramos de Páramo (gris) y alto-andinos del río Guatiquía. Serie de datos desde 2000 hasta 2013, provisto por la “Empresa de Acueducto y Alcantarillado de Bogotá”.*

RESULTS

Water conductivity was statistically different among the three sampled reaches (Table 1). The temperature tended to be higher at Leticia, on the páramo ecoregion, but its mean value was not statistically different from the other reaches: San Jose (páramo) and San Luis (high-Andean) (Table. 1). Dissolved oxygen, pH and flow history were similar between the selected reaches (Table. 1, Fig. 2). We only observed differences in the base-flow magnitude during the dry season (December to February); the base-level of the high-Andean reach was slightly greater than in the páramo reaches.

Fish sampling efforts captured a total of 138 individual trout: 78 at the páramo reaches (mean standard length = 104.01 ± 32.07 mm, mean weight = 19.96 ± 13.41 g) and 60 at the high-Andean reach (mean standard length = 121.6 ± 29.25 mm, mean weight = 39.32 ± 29.25 g). Two individuals of the small catfish - locally known as *Barbillo* (*Astroblepus micrescens*, Eigenmann 1918) were also captured at the high-Andean reach. The direct observation of gonadal development showed that trout reach sexual maturity

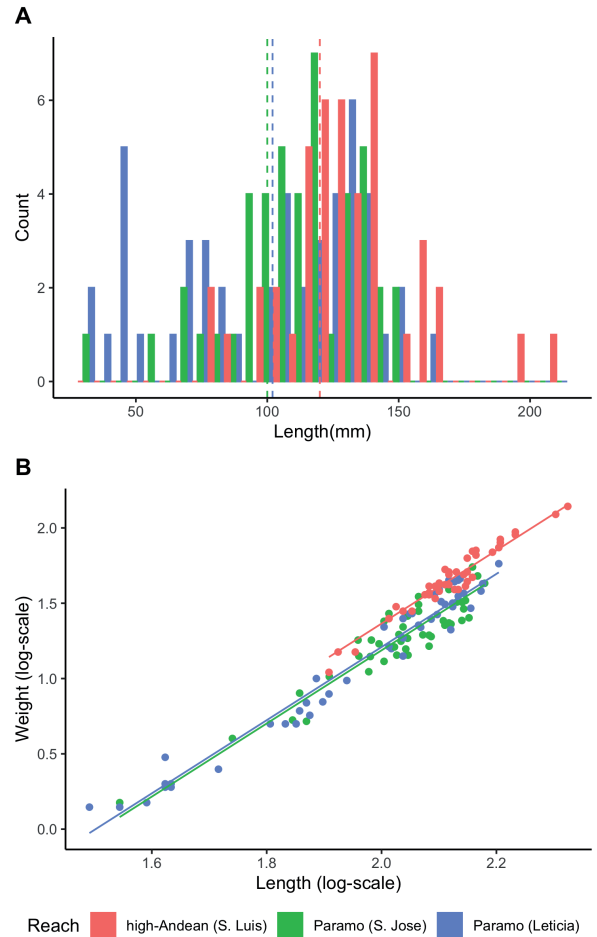


Figure 3. Size (A) distributions of Rainbow Trout populations at the three reaches. The dotted line highlights the size-at-maturity values of trout at each reach. C- Linear relationships between the logarithmically transformed weights and lengths of trout at the three studied reaches. *Distribución de tallas (A) de las poblaciones de trucha arcoíris en los tres tramos. La línea punteada señala la talla de maduración de las truchas en cada uno de los tramos. C- Relaciones lineales entre los pesos y longitudes de las truchas, transformados logarítmicamente en los tres tramos estudiados.*

at a short standard length. Sexual maturation was reached at 100 mm in the páramo reaches and at 120 mm in the high-Andean reach. Mature females presented well-developed ovaries containing fully formed oocytes, immature females presented long string-like ovaries without oocytes. On the other hand, mature males presented extended testes, while immature males presented long and thin testes. We observed pres-

ence of milt in two mature males during the intermediate water flow season (November 2013).

The distribution of trout sizes varied across ecoregions. Populations from the páramo were composed mainly of adult individuals that rarely exhibited standard lengths over 150 mm. Meanwhile, the number of juvenile individuals was higher in the high-Andean reach, where less than half of the captured trout had reached adulthood. This is because size-at-maturity is very different among reaches, being notably larger in the high-Andean reach (Fig. 3A). Adult individuals reached significantly bigger sizes than in the páramo. Indeed, the biggest individual was found in this reach (210 mm and 138 g). Trout inhabiting the high-Andean reach had a significantly higher somatic condition than in those occupying

páramo reaches ($F(1,2) = 46.65, p < 0.01$; Fig. 3B). This shows that there is a significant effect of ecoregion type on the trout weight after controlling for individuals' length.

Diet Composition

We identified a total of 70 families from the gut contents of Rainbow Trout populations. Trout diet included a broad array of aquatic and terrestrial invertebrates. However, trout did not consume all the aquatic families that inhabit each reach. In the páramo region (S. José and Leticia reaches), trout fed primarily on aquatic larvae of Diptera (mainly chironomids) and Trichoptera, while in the high-Andean region trout diet was dominated by allochthonous invertebrates and

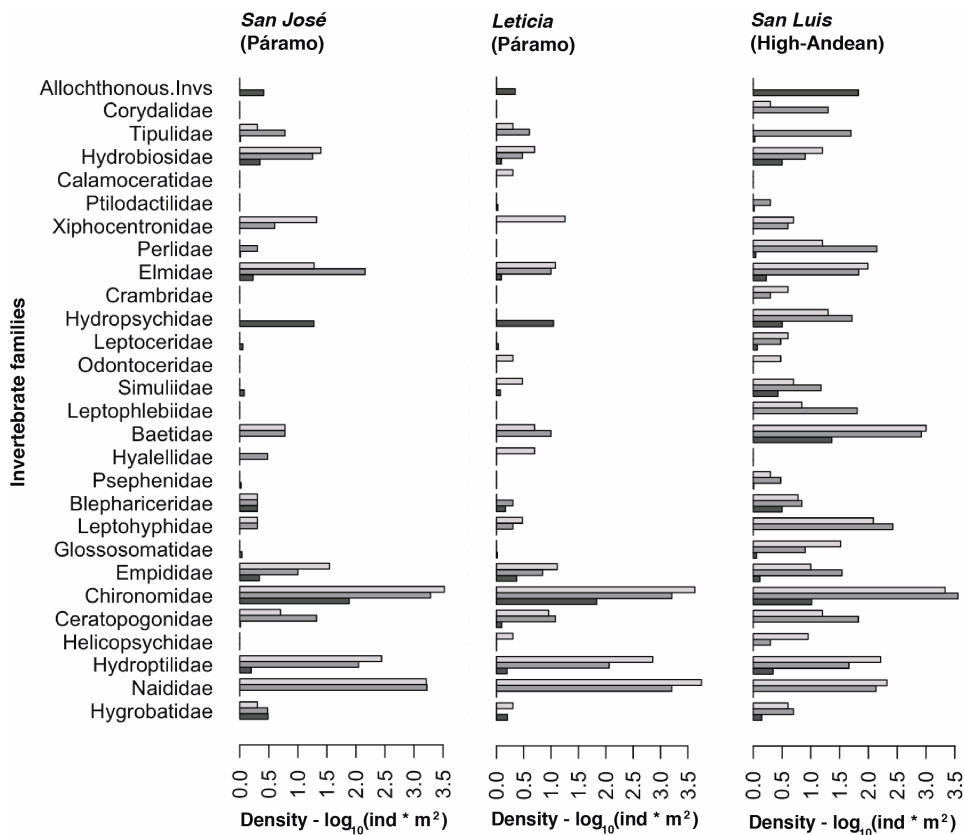


Figure 4. Mean density of invertebrate families (*individuals per square meter - log10 transformed*) found on two distinct substrates of the river (*Boulder – light-grey; Gravel – dark-grey*) and in the trout stomach (*individuals per stomach – black*). *Densidad promedio de las familias de invertebrados (individuos por metro cuadrado – transformado por log10) encontradas en dos substratos diferentes (Rocas – gris claro; Grava – gris oscuro) y en el estómago de las truchas (individuos por estómago – negro).*

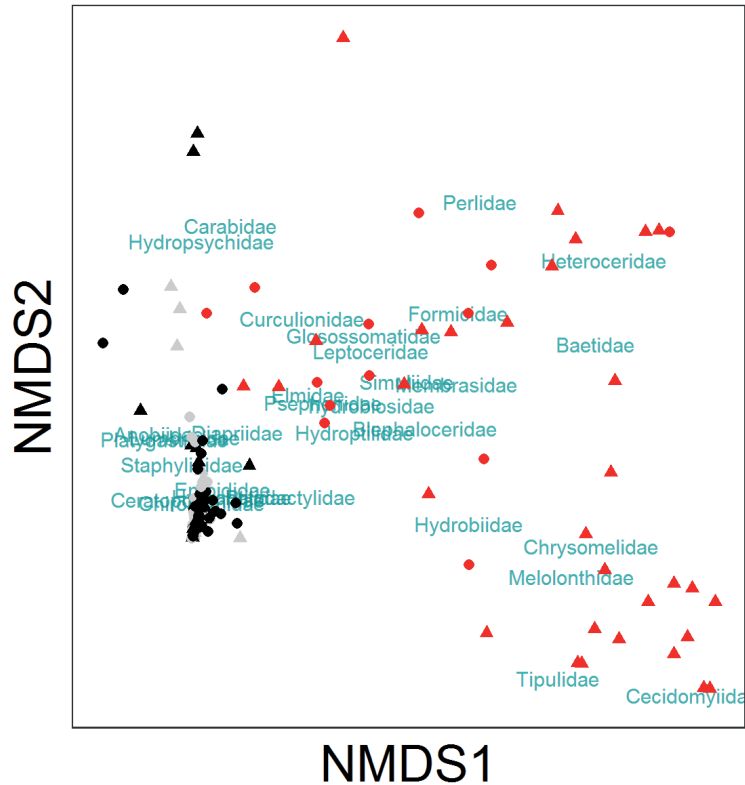


Figure 5. Ordination plot of trout according to their diet composition using a non-Metric Multidimensional Scaling (nMDS) technique. Páramo reaches are represented in black and grey, the high-Andean reach in red. Triangles represent mature trout and circles refer to immature trout. *Stress = 0.1018. Distance = Horn-Morisita. Ordenación de las truchas de acuerdo a la composición de la dieta usando un Escalamiento Multidimensional no Métrico (nMDS). Los tramos de páramo están representados en negro y gris, el tramo alto-andino en rojo. Los triángulos representan las truchas maduras y los círculos las truchas inmaduras. Estrés = 0.1018. Distancia = Horn-Morisita.*

larvae of Diptera, Trichoptera and Ephemeroptera (Fig. 4). Some highly abundant invertebrates were rarely found in trout stomachs (Fig. 4). This result might be a consequence of several invertebrate characteristics, including small size (e.g. Naididae, Ceratopogonidae and Hydroptilidae), sclerotized exoskeleton (e.g. Elmidae), or protective cases or cocoons (e.g. Xiphocentronidae).

Trout diets differed between ecoregions. Overall, the occurrence of allochthonous invertebrates in trout stomachs was greater in the high-Andean region than in the páramo region, where trout diet was mainly composed of aquatic invertebrates (e.g. Chironomidae, Hydropsychidae, Empididae) and, to a minor degree, by terrestrial families. The greatest distances among trout individuals (points) on the nMDS plot suggest

generalist behaviors in the high-Andean region (Fig. 5). Importantly, there was no trace of piscivory, such as scales, bones, fins, rays or muscle in the dissected stomachs.

Most of the prey items had similar contributions to the trout diet (Fig. 5). Overall, both adult and juvenile trout exhibited a notable similarity in their feeding strategies in the páramo reaches. There was a generalized feeding strategy with a presumable preference for Chironomidae midges (Fig. 5). At the high-Andean reach, adults had a slightly different feeding strategy from juveniles. Adults did not show a bias towards a specific invertebrate and their diet was composed mainly by mid- or low-occurrence taxa (except for Cecidomyiidae). Juveniles fed on a lesser quantity of taxa and their diet tended to be composed of

aquatic invertebrates such as Chironomidae and Baetidae (Fig. 5).

DISCUSSION

The distribution of the ecoregional belts has been the basis of studies that seek to understand the drivers of biodiversity patterns in the Neotropical Andes. Several studies have demonstrated that ecoregional features (e.g. evolutionary history and contemporary environmental conditions) determine species distributions and, therefore, the composition of species in local communities and metacommunities (Nottingham *et al.*, 2018; González-Trujillo *et al.*, 2019). Our study emphasizes that ecoregional features might also determine individual- and population-level responses of Rainbow Trout. Particularly, we observed that the diet, maximum size, sexual maturation, and feeding behavior might change depending on the ecoregion through which the river flows. Our overall results suggest that the changes in trout auto-ecology might respond to the natural absence of a riparian forest instead of river's water quality or flow conditions, since forest presence affects resource availability and water temperature (Allan *et al.*, 2003; Lorion & Kennedy, 2009; Eros *et al.*, 2012).

It is known that water temperature affects the growth, physiology, development, locomotion and digestive efficiency of aquatic ectotherms such as salmonids (Azevedo *et al.*, 1998; Myrick & Cech., 2000; Ojanguren *et al.*, 2001; Stiller *et al.*, 2017). Rainbow Trout populations at the sampled reaches thrive among the acceptable ranges for this species and other salmonids (10 to 18 °C, Austreng *et al.*, 1987; Bendiksen *et al.*, 2003; Amin *et al.*, 2014). Although there were no differences in terms of water temperature among reaches, this parameter tended to be higher in one of the páramo reaches (Leticia), where the trout population was close to the optimal culture temperature (14 to 16 °C, Table 1; Hardy 2002; Wing-Keong *et al.*, 2010). Trout within this reach attained smaller sizes and earlier sexual maturity compared to those at the high-Andean reach. This can be explained by the temperature-size rule, which states that higher temperatures result in faster growth to a smaller size (Atkinson, 1995;

Angilletta & Dunham, 2003). However, there are other environmental variables that can affect growth rate such as food availability and size at maturity (Angilletta & Dunham, 2003; Angilletta *et al.*, 2004; Arendt, 2011). Páramo reaches can present extreme changes in weather conditions throughout the day, especially of radiation and temperature (Buytaert *et al.*, 2006; Morales *et al.*, 2007). Thus, water temperatures between day and night and amongst ecoregions might be significantly different. Further studies should contemplate these important conditions that impose biological stress and can affect the auto-ecological characteristics such as those analyzed here.

Considering that neither the flow regime nor the physical and chemical stream properties (except conductivity) varied considerably between ecoregions, it could be hypothesized that the characteristics of the riparian forest in terms of the quantity and quality of resources that they provide probably drive the observed variability in auto-ecological characteristics. The herbaceous riparian vegetation of páramo does not provide the same broad spectrum of allochthonous prey as the high-Andean reach. Thus, it is reasonable that aquatic invertebrates – in special Chironomidae – were the main components of the trout diet in the páramo reaches. Meanwhile, the broad spectrum of allochthonous prey could explain the mixed diet and feeding strategy (varying between specialization and generalization) observed in the individuals inhabiting the high-Andean reach (Amundsen, 1995; Amundsen *et al.*, 1996).

Despite the fact that the daily and seasonal temperature regimes might have a considerable effect, it appears that the lower availability and quality of resources may have a relevant role explaining why páramo populations attain sexual maturity at shorter standard lengths compared to other rivers of the world (Bastardo, 1994; Dedual & Collier., 1995; Oscoz *et al.*, 2005; Arismendi *et al.*, 2011). Slower growth of salmonids is thought to occur due to the lack of suitable prey that are sufficiently large to sustain further growth (Keeley & Grant., 2001). According to Kawaguchi and Nakano (2001) and Webster and Hartman (2005), terrestrial prey is paramount for fish bioenergetics at headwater streams and represents nearly half of the prey consumed on a yearly basis.

The scarce allochthonous inputs might have driven trout populations to maintain a diet of small benthic invertebrates that represent a low-quality resource compared to the larger invertebrates coming from the riparian forest. Therefore, the páramo region trout could be allocating energy towards sexual maturity instead of towards biomass accumulation, as was suggested for trout inhabiting rivers with extreme environmental conditions and lack of resources (e.g. high-altitude streams; Barros & De Gonzo, 2004).

The partition of resources reduces trophic competition and facilitates habitat segregation (Elliott, 1973). The larger average trout size in the high-Andean population compared to populations in the páramo may be linked to behavioral partitioning of resources driven by differences in the amount of allochthonous input. Juvenile trout might take advantage of the higher diversity of benthic invertebrates in the high-Andean reach. Meanwhile, adults feed mainly on allochthonous invertebrates originating from the riparian forest. As reported by Eros *et al.* (2012), large dominant salmonids forage in the water column where they find and consume drifting terrestrial or aquatic invertebrates. Although we only sampled benthic invertebrates, a diet composed of allochthonous insects and aquatic invertebrates not occurring in benthic samples partially supports that larger trout fed primarily in the water column of the high-Andean reach. Epibenthic feeding requires active seeking of prey, while drift feeding relies more on current to deliver the prey to the trout. Thus, drift feeding presumably requires less energy for prey capture, allowing high-Andean trout to allocate more energy towards the individual growth (Tippets & Moyle, 1978). Drift feeding might be an important energy source for trout (Wipfli, 1997; Romaniszyn *et al.*, 2007; Vimos *et al.*, 2015). However, Flecker (1992) reported a change from diurnal to nocturnal drift of macroinvertebrates in Neotropical Andean streams as a way to avoid predation from introduced Rainbow Trout. Further research should address the relationship between feeding strategies and invertebrate drift patterns, and how changes in this relationship may affect Rainbow Trout auto-ecological traits.

Andean rivers and mountain headwaters in general are oligotrophic ecosystems where the

resources for maintaining high-trophic levels come from allochthonous pathways (Encalada *et al.*, 2010). Therefore, it has been asserted that the diversity and distribution of fish communities, and other high-trophic level species are closely linked to the characteristics of the rivers' riparian forest (Polis *et al.*, 1997; Nakano *et al.*, 1999; Syrjänen *et al.*, 2011; Vimos *et al.*, 2015). Overall, our results suggest that limited availability of resources linked to ecoregional characteristics may not constrain successful trout establishment at high-Andean streams but may have a direct effect over some trout auto-ecological features such as feeding behavior, sexual maturation and maximum size. We observed that the expression of these auto-ecological features changed in parallel to the higher availability of allochthonous resources in the high-Andean ecoregion. The observed patterns could be helpful for modeling the distribution of Rainbow Trout abundance and biomass in the tropical Andean mountains, since they are closely related to the auto-ecological features examined in this paper, as has been reported and used in other countries (Jowett, 1990). Nevertheless, future studies are needed to disentangle the possible effects of changes in the thermal regime and invertebrate drift patterns on the auto-ecological traits of Rainbow Trout.

ACKNOWLEDGEMENTS

We wish to thank Universidad Nacional de Colombia, Bogotá, Parques Nacionales Naturales de Colombia (PNN) and Empresa de Acueducto y Alcantarillado de Bogotá (EAAB). Thanks to J. Donato, J. Mojica, J. Morales, Y. Abuhatab and K. Chacón for field trip assistance, and to D. Symonds and A. DeMillo for comments and suggestions. This research was approved by the ethics committee of Nacional de Colombia and all animal care guidelines were followed.

FUNDING

This study was developed as part of the Scientific and Technological Agreement (No. 1-07-24300-0832-2012 EAAB-ESP – UNAL) between Empresa de Acueducto y Alcantarillado de Bogotá (EAAB) and Universidad Nacional de Colombia.

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