Limnologica 52 (2015) 89–102

Contents lists available at ScienceDirect

Limnologica

journal homepage: www.elsevier.com/locate/limno

Dietary–morphological relationships of nineteen fish species from an Amazonian *terra firme* blackwater stream in Colombia

Fernando Ramírez[a,*], Thomas Lee Davenport[b], José Iván Mojica[c]

[a] *Facultad de Ciencias Sociales, Universidad Colegio Mayor de Cundinamarca, Calle 28# 5B-02, Bogotá, Colombia*
[b] *University of Florida, TREC, 18905 SW 280 St., Homestead, FL 33031, USA*
[c] *Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Carrera 45 No 26-85, Bogotá, Colombia*

A R T I C L E   I N F O

Article history:
Received 23 October 2014
Received in revised form 16 April 2015
Accepted 16 April 2015
Available online 29 April 2015

Keywords:
Ecomorphology
Tropical
Stream
Amazon
Diet

A B S T R A C T

Small, oligotrophic Amazonian streams support an extremely rich fish fauna. The aim of the current study was to elucidate the relationship between diet and morphology in fishes from an Amazonian *terra firme* stream in the Colombian Amazon River basin near the city of Leticia. Fish specimens were collected from two locations at the Yahuarcaca *terra firme* stream. All fish species selected in the morphological analyses were used in the dietary analyses. We analyzed 10–60 adult individuals per species based on availability. Morphology and diet were correlated by direct observation (description) of morphological structures and food items found in gut. Only morphological variables presumed to be associated with prey capture and feeding were recorded for each individual. Species diets were classified into six food categories based on stomach content analysis. By comparing morphological characteristics, and dietary data, it was possible to find a relationship between structures and feeding habits. Morphological and dietary specializations were found among some fishes inhabiting the examined stream. Internal morphological characteristics such as gill rakers, pharyngeal teeth, pyloric caeca and stomach form should be used more often in ecomorphological studies because they are directly associated with resource utilization and linked to feeding habits.

Introduction

Neotropical fishes exhibit great morphological and ecological diversity (Vari and Malabarba, 1998). Based on the theory of ecomorphology (Wainwright, 1994), an organism's morphology can be related to its ecology. The idea of correlating morphological characteristics of fish with habitat and feeding variables has been tested in various aquatic ecosystems including streams (Wikramanayake, 1990), rivers (Hugueny and Pouilly, 1999; de Mérona et al., 2008), flood plains (Pouilly et al., 2003), and lakes (Winemiller and Adite, 1997; Xie et al., 2001). Amazonian fishes exhibit great morphological and dietary diversity, suggesting the two are closely related (Pouilly et al., 2003; Galvis et al., 2006). This diversity is seen in dentition type (Goulding et al., 1988), gill-raker architecture (Goulding, 1980), stomach and intestine organization (Delariva and Agostinho, 2001).

Dietary diversity of Amazonian fishes is displayed in various feeding guilds, e.g. algaevores, detrivores, pescivores, omnivores and carnivores (Val and de Almeida-Val, 1995; Pouilly et al., 2003). The diet of fishes inhabiting Amazon streams has been characterized by a number of investigators (Knöppel, 1970; Ibañez et al., 2007; Tedesco et al., 2007). The diet of fishes inhabiting streams near Manaus in the Brazilian Amazon has been classified by items that came from the aquatic medium, i.e. fish, algae, or aquatic insects and separating them from the terrestrial sources, such as terrestrial insects, seeds of terrestrial plants, and vegetation (Knöppel, 1970). Most species exhibited great variability in food items consumed, and this trend was observed throughout all fish families examined. Distinct specialists in food ingestion were not found in the study (Knöppel, 1970). Other investigators classified the diet of Amazonian stream fishes from the Bolivian Amazon into eight trophic guilds: mud feeders, algivorous, aquatic invertivorous, general invertivorous, terrestrial invertivorous, omnivorous, herbivorous and piscivorous (Ibañez et al., 2007). Their study strongly suggested a high degree of dietary specialization for species at almost all trophic levels. However, these authors did not specify the food items found within each food category e.g. if invertivorous species include Diptera or Hymenoptera larvae, etc.

* Corresponding author. Tel.: +57 3019409.
E-mail addresses: framirezl@unicolmayor.edu.co, fermp44@yahoo.com (F. Ramírez), tldav@ufl.edu (T.L. Davenport), jimojicac@unal.edu.co (J.I. Mojica).

http://dx.doi.org/10.1016/j.limno.2015.04.002
0075-9511/

Another study, classified Amazonian stream fish trophic groups as detritivores, omnivores, invertivores, or piscivores. In this classification, species belonging to the detritivorous, invertivorous, and piscivorous trophic groups were considered as specialized species (i.e. species having specialized diets), whereas species belonging to the omnivorous trophic group were considered as generalist species (Tedesco et al., 2007).

Several ecomorphological studies have focused on dietary–morphological relationships of Amazonian fishes. These works have been conducted in different Amazonian environments such as flood plains (Pouilly et al., 2003), rivers (de Mérona et al., 2008), and streams (Ibañez et al., 2007). The relationships between diet and morphology has been studied in 30 fish species from forested tropical streams of the Bolivian Amazon (Ibañez et al., 2007). This study reported that fishes belonging to the algivorous and detritivorous guilds displayed long relative gut lengths. Benthic fishes from the algivorous and mud feeder guilds were also characterized by relatively narrow heads and a ventral (Loricariidae) or oblique (Curimatidae) mouth orientation. Fishes from the herbivorous and piscivorous guilds generally displayed a large standard length and size whereas species from the aquatic invertivorous guild were mostly characterized by their small sizes. Relative intestinal length and mouth orientation appear to be the most useful descriptors of diet (Ibañez et al., 2007). Other studies have provided evidence describing the relationship of diet and morphology in Amazon streams (Knöppel, 1970). Forms, position and number of teeth were associated with shearing and holding leafy remains or insects. Fish feeding on detritus lacked teeth e.g. Curimatidae. Large mouth *Gymnotus* and *Sternopygus* fed on Malacostraca and fishes. Smaller mouthed species *Eigenmannia* fed on Entomostraca larvae and adults. Tubular-mouthed species *Gymnorhamphichthys* fed on annelids and insect larvae. Stomach and intestine length were also related to diet (Knöppel, 1970).

Terra firme streams are here defined as small and oligotrophic (nutrient poor) Amazonian streams supporting a rich fish fauna and are stable enough to maintain fish populations. Some of these streams support an extremely high diversity of fish species. This is the case of the Yahuarcaca *terra firme* stream, home to 171 fish species (Mojica et al., 2009). In Amazonian streams, tree canopies prevent light from reaching the water surface directly, nutrient salts are scarce, and aquatic plant life is virtually non-existent. Furthermore, food webs are highly influenced by resources coming from the nearby terrestrial environment (Lowe-McConnell, 1987). They are low primary productivity systems with high concentrations of humic and fulvic acids caused by the decomposition of forest-derived organic matter over podzolic soils, which generate a low pH, dark water coloration as in blackwater streams and poor nutrient conditions (Sioli, 1967; McClain and Elsenbeer, 2001). Blackwater *terra firme* streams in the Amazon are variable systems wherein abiotic conditions, such as water level, can dramatically fluctuate within a matter of hours due to local, heavy rainfall events. The fishes inhabiting these streams are relatively small in size (Mojica et al. 2009). Most of these fishes are opportunists with respect to diet and consume a variety of foods that come from the aquatic system (i.e. other fish and aquatic invertebrates) or from terrestrial sources (i.e. terrestrial insects, vegetation and seeds).

The aim of the current study was to elucidate the relationship between diet and morphology in fishes from an oligotrophic Amazonian stream in the Colombian Amazon River basin near the city of Leticia. The nature of this study is descriptive, focusing on the ecological relationships between diet and morphological structures in the 19 fish species studied. The research question we ask is if there are specialists in respect to diet and morphology, or are generalists more common.

Materials and methods

Fish samples and study sites

Fish specimens were collected from two locations in the Yahuarcaca *terra firme* stream situated 8 and 11 km northwest of Leticia (see Mojica et al., 2009, sites 1 and 2). The stream flows into the seasonal lake, Yahuarcaca, which connects with the Amazon River.

Fish were sampled during late afternoon and nighttime hours for 6 days each in April, July and November, 1999. Samplings were performed by groups of four people for a mean of 4 h per day per person for a total of 288 man-hours over the year. A variety of sampling methods were used including cast nets, gill nets, drag seines, and hand seines with different mesh sizes. All fish specimens were immediately preserved in 10% formaldehyde and stored until morphological analysis. Different numbers of nineteen fish species of different sizes were used in the study (Table 1). The same fish specimens that were used for morphological measurements were also assessed for gut content (Table 2).

Morphological measurements

All fish species selected in the morphological analyses were also used in the dietary analyses. We analyzed 10–60 adult individuals per species based on availability from the samples (Table 1). Following the definitions of Lagler et al. (1977), Motta et al. (1995) and Xie et al. (2001), only morphological variables presumed to be associated with prey capture and feeding were recorded for each individual (Table 1). Dimension and length measurements reported in mm, including fish length, were made to the nearest 0.1 mm using digital calipers (Minitutoyo AZW 120). They included:

(1) Standard length (LS). Measured from tip of snout to tip of tail.
(2) Relative head length (HEAD), the ratio between the head (distance from the tip of snout to the posterior end of the operculum and standard length) (Pouilly et al., 2003).
(3) Eye diameter (EYE). Eye size was assumed to be positively correlated with the importance of vision for feeding (Gatz, 1979; Pouilly et al., 2003).
(4) Eye position (EPO) is the proportion of head depth measured at the middle of the eye (Watson and Balon, 1984). It is expected that benthic fishes have more dorsally located eyes, whereas those of nektonic fishes are laterally located (Hugueny and Pouilly, 1999).
(5) Mouth orientation (MTYPE) was designated as 1 for inferior, 2 for sub-inferior, 3 for terminal and 4 for superior. Variables associated with the position of the mouth were assumed to indicate the general position of food relative to the fish (Gatz, 1979; Hugueny and Pouilly, 1999; Pouilly et al., 2003).
(6) Teeth type, i.e. number of cusps on each tooth (TEETH), coded 1 for unicuspid teeth, 2 for bicuspid teeth, and so on. See Table 1.
(7) Number of tooth rows on the premaxilla (NTR) was noted. The number and shape of the premaxillar and mandibular teeth describe the mode of intake of the diet (Pouilly et al., 2003).
(8) Gill raker dimensions, i.e. length of upper gill arch of fish's left gill (UGL) divided by HEAD length.
(9) Length of lower gill arch for fish's first left gill (LGL) divided by HEAD length.
(10) Number of gill rakers of the upper arch (NGU) were noted.
(11) Number of gill rakers of the lower arch (NGL) were noted.
(12) Mean length of gill rakers from the upper arch (LRU) divided by upper gill arch length.
(13) Mean length of gill rakers from the lower arch (LRL) divided by lower gill arch length.