Acta Oecologica 35 (2009) 513–522

Contents lists available at ScienceDirect

Acta Oecologica

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

Original article

Consistent trophic patterns among fishes in lagoon and channel habitats of a tropical floodplain river: Evidence from stable isotopes

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A R T I C L E I N F O

Article history:
Received 8 July 2008
Accepted 30 March 2009
Published online 21 April 2009

Keywords:
Fish
Flood pulse
Food web
Hydrological connectivity
IsoSource
Venezuela

A B S T R A C T

The relationship between food web dynamics and hydrological connectivity in rivers should be strongly influenced by annual flood pulses that affect primary production dynamics and movement of organic matter and consumer taxa. We sampled basal production sources and fishes from connected lagoons and the main channel of a low-gradient, floodplain river within the Orinoco River Basin in Venezuela. Stable isotope analysis was used to model the contribution of four basal production sources to fishes, and to examine patterns of mean trophic position during the falling-water period of the annual flood cycle. IsoSource, a multi-source mixing model, indicated that proportional contributions from production sources to fish assemblages were similar in lagoons and the main channel. Although distributions differed, the means for trophic positions of fish assemblages as well as individual species were similar between the two habitats. These findings contradict recent food web studies conducted in temperate floodplain rivers that described significant differences in trophic positions of fishes from slackwater and floodplain versus main channel habitats. Low between-habitat trophic variation in this tropical river probably results from an extended annual flood pulse (ca. 5 mo.) that allows mixing of sestonic and allochthonous basal production sources and extensive lateral movements of fishes throughout the riverscape.

1. Introduction

Studies using stable isotope analysis increasingly have stressed the importance of algal carbon in supporting river food webs (Hamilton et al., 1992; Forsberg et al., 1993; Thorp and Delong, 1994, 2002; Douglas et al., 2005; Winemiller, 2005), but recent research indicates that sources of organic matter supporting consumers vary spatially and temporally (e.g., Herwig et al., 2004; Zeug and Winemiller, 2008). In some temperate floodplain rivers, environmental conditions related to seasonal changes in hydrological connectivity affect the availability of alternative basal production sources for secondary consumers (Fisher and Willis, 2000; Fisher et al., 2001; Herwig et al., 2004). Such seasonal and temporal changes in hydrological connectivity can contribute to significant variation in the trophic position of secondary consumers (Zeug and Winemiller, 2008; Zeug et al., in press).

The relationship between food web dynamics and hydrological connectivity is influenced both by the passive movement of basal production sources and active movement of consumer taxa (Pringle, 2003; Winemiller, 2005), which in turn are affected by components of the flow regime. Tropical floodplain rivers experience predictable annual flood pulses that have been hypothesized to mix production sources (e.g., Junk et al., 1989); however, a synthesis of research conducted on the Orinoco River floodplain in South America concluded that export of organic carbon sources to the main channel is low due to restricted net lateral movement of water (Lewis et al., 2000). Annual flood pulses also restructure local assemblages of fishes and other aquatic organisms across heterogeneous riverscapes, which may result in significant lateral and longitudinal transport of organic matter (Lowe-McConnell, 1964; Lagler et al., 1971; Welcomme, 1985; Fernandez, 1997; Winemiller and Jepsen, 1998).

In the present study, we used stable isotope analysis (δ^{13}C and δ^{15}N) to examine food web patterns during the descending phase of the annual hydrological cycle in connected lagoons and the main channel of the Cinaruco River. The Cinaruco River is a meandering lowland river in the llanos (savanna) region of southwestern

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1146-609X/$ – see front matter
doi:10.1016/j.actao.2009.03.007

Venezuela with strongly seasonal hydrology and an annual flood pulse of approximately 5 months duration (a detailed description appears in Montoya et al., 2006). Here, we modeled differences in the relative importance of the four most important basal production sources supporting fish biomass in floodplain lagoons and the river channel (i.e., benthic algae, seston, terrestrial C_3 plants, and terrestrial C_4 plants), and examined how trophic positions of fishes varied between these habitats.

2. Methods

2.1. Study site

The Cinaruco River is a tributary of the Orinoco River located in the Venezuelan llanos (6°32′N, 67°24′W) and forms the southern boundary of Santos Luzardo National Park (Fig. 1). This black-water floodplain river has oligotrophic and acidic waters, low conductivity, low concentrations of suspended sediments, high amounts of humic acid, and sandy substrates (Montoya et al., 2006). Hydrological regime is strongly seasonal, and the drainage basin is ca. 10,000 km^2. In our study region, aquatic habitats of the Cinaruco River consist of the main channel and numerous floodplain lagoons. Hydrological connectivity of lagoons varies with the hydrological regime, geomorphology, and distance from the main channel, but most lagoons are connected by floodwaters from May to December. In July and August, floodwaters extend into the gallery forest and across hundreds of square kilometers of the llanos. During the period of water recession, from January to April, the aquatic habitat is greatly reduced. More than 280 fish species have been documented in the river, and this assemblage encompasses a great diversity of ecological niches (e.g., Jepsen and Winemiller, 2002). A previous analysis of stable isotope ratios in fish tissues in the Cinaruco River concluded that fishes are mostly dependent upon autochthonous primary production from benthic algae and phytoplankton, and that little carbon is assimilated from C_3 macrophytes and C_4 grasses (Jepsen and Winemiller, 2007).

2.2. Sample collections

Samples of fishes and basal sources for organic matter were collected from lagoons and the main channel during the falling-water period of the dry season (November–April) from 1999 to 2005. Most lagoon samples were from Laguna Larga, a large floodplain lake that is connected to the main channel throughout the annual hydrological cycle. Ecological dynamics are strongly influenced by the highly predictable annual flow regime of the Cinaruco River, and this interannual consistency justifies pooling seasonal samples across years (Layman et al., 2005b; Arrington and Winemiller, 2006; Cotner et al., 2006; Montoya et al., 2006; Winemiller et al., 2006). Additionally, among-year variation in stable isotope signatures was low for the majority of species (Table 1).

The Cinaruco River supports little aquatic macrophyte growth, especially during the low-water period (Cotner et al., 2006). Thus, we assume this production source is relatively unimportant in supporting consumer biomass, a conclusion supported by Jepsen and Winemiller's (2007) analysis. Elimination of this source pool greatly increased resolution for the other four principal production sources in the IsoSource modeling. Replicate samples of fresh leaves from abundant terrestrial C_3 plants were collected from the riparian zone of lagoons and the main channel ($n = 44$). Twenty-seven of these samples were from the dominant riparian trees *Campsiandra angustifolia* and *Bactris* sp. A single sample of C_4 grass (*Trachypogon plumosus*) was collected from the savanna near the shoreline of a lagoon. The δ^{13}C value of our C_4 grass sample (-11.8) was very similar to the δ^{13}C value of C_4 grass from a previous study in the Cinaruco River (-11.5; Jepsen and Winemiller, 2007) and is also within the range of C_4 plants sampled extensively along the Amazon River (-11.6 to -13.6; Martinelli et al., 1991). Samples of filamentous algae ($n = 16$) were removed from substrates (rocks, woody debris) in the lagoons and the river channel and filtered onto pre-combusted (450° for 24 h) Whatman GF/F filters following Zeug and Winemiller (2008). This collection technique was unlikely to produce pure samples, therefore this basal production source, composed of attached filamentous algae and probably other materials (e.g., fine particulate organic matter [FPOM], diatoms, and other microorganisms) is referred to as "benthic algae." Phytoplankton samples ($n = 4$) were collected by filtering water from the lagoon and the main channel onto pre-combusted GF/F filters following Zeug and Winemiller (2008). Samples probably contained both phytoplankton and suspended organic matter; hereafter this source is referred to as "seston." Basal production source samples were frozen and then transported on ice until processing in the laboratory.

Fishes were collected with seines, cast nets, experimental gill nets, and hook and line. Following euthanasia via emersion in a 1% solution of tricaine methanesulfonate, a sample of muscle tissue from each individual was removed from the dorso-lateral region using a scalpel, and then rinsed and preserved in salt. This preservation technique causes minimal isotopic shifts in tissue samples (Arrington and Winemiller, 2002). In order to account for ontogenetic shifts in diet, only tissues from adult consumers were sampled. All samples were transported to the laboratory at Texas

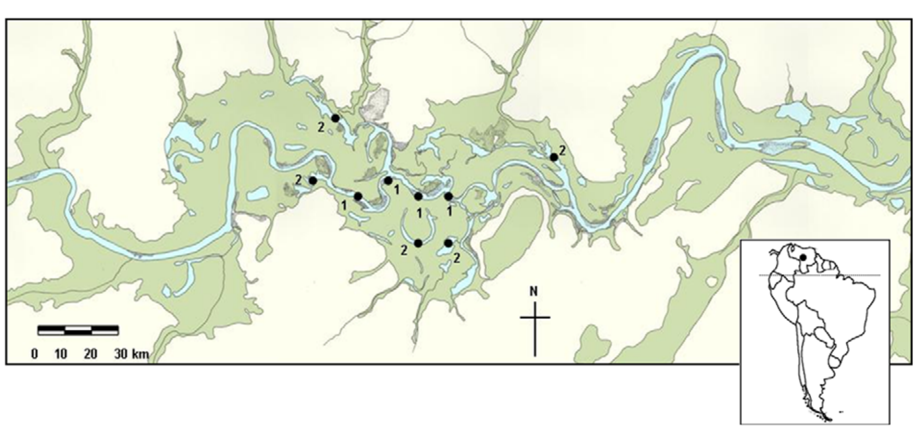

Fig. 1. Map of the Cinaruco River in the llanos savanna region of southwestern Venezuela. The main channel (1), floodplain lagoons (2), and the forested littoral zone are visible (in green). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)