Limnologica 46 (2014) 22–30

Contents lists available at ScienceDirect

Limnologica

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

Food webs of the Paraná River floodplain: Assessing basal sources using stable carbon and nitrogen isotopes

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ARTICLE INFO

Article history:
Received 24 February 2013
Received in revised form
23 November 2013
Accepted 25 November 2013
Available online 11 December 2013

Keywords:
Carbon sources
Detritivores
Herbivores
Isotopic niche
Benthic–pelagic food webs

ABSTRACT

Food webs in floodplain ecosystems may be based on a variety of aquatic, terrestrial or amphibious food resources. Here, we determined which of the basal resources mostly contribute to the food webs in a floodplain lake of the Middle Paraná River using isotopic composition of C and N (δ^{13}C and δ^{15}N) of potential food sources in the Paraná floodplain (Argentina). We analyzed if organic matter sources isotope of C and N differ between flooding and low water seasons, and analyzed the isotopic niche representations of consumers in order to characterize niches width and intraguilds overlapping. To estimate the contribution of different sources of carbon to primary consumers, we measured the stable isotopic compositions of bottom sediment organic matter, coarse particulate organic matter, biofilm, suspended particulate organic matter, epiphyton, phytoplankton, C3 and C4 macrophytes and riparian tree leaves, benthic macroinvertebrates, aquatic orthopterans and fishes in dry and flooding seasons. The packages Stable Isotope Analysis and the Stable Isotope Bayesian Ellipses algorithm in R were calculated to compare the C and N isotopic variability between the primary consumers and their sources. The energy sources available for benthic organisms mainly originated from autochthonous sources based on the C3 photosynthesis pathway. The isotopic signatures of sources and primary consumers did not differ significantly between low and high water seasons. Our results demonstrated a higher contribution to primary consumers of C3 macrophytes and low contributions of C4 for herbivores; biofilm and benthic organic matter for gatherer collectors (Oligochaeta and Chironominae); epiphyton for ephemeropterans, amphipods and fishes, whereas biofilm was the most important source for mussels.

Introduction

Classical concepts for the functioning of riverine systems are generally based on organic matter flows and carbon pathways. In the River-Continuum Concept (Vannote et al., 1980) the importance is given to the gradual transformation of allochthonous inputs from the terrestrial part of the catchment (e.g., leaves, wood, riparian and upland trees, shrubs, and grasses) into fine particulate organic matter (FPOM) and dissolved organic matter (DOM), and an increasing production of autochthonous algae along with the increasing stream order. The Flood Pulse Concept (Junk et al., 1989) focuses on the importance of the floodplain as productive areas, whereas the Riverine Productivity Model (Thorp and Delong, 1994) stresses the importance of benthic production even in lower river section.

In this context, the study of the relative importance of the different food sources in freshwater food webs stand as a key issue to understand the ecosystem functioning. For example, whereas C_4 grasses mainly represent the river bank production, C_3 macrophytes make up most of lakes primary production in Paraná River system (Sabattini and Lallana, 2007). In a similar way the benthic production is held by detritus inputs (particulate organic matter) and by biofilm which is a complex of primary producers (diatoms mainly) and microbes.

The Stable Isotopes Analysis (SIA) in ecological research allows a quantification of the importance of the individual compartments of organic matter (Fry, 2006). Indeed, this analytical tool is increasingly used to trace energy flow and describe food web structures because it integrates both the variation across spatial

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0075-9511/$ – see front matter
http://dx.doi.org/10.1016/j.limno.2013.11.004

and temporal scales, providing important information to understand food web dynamics (Peterson and Fry, 1987; Paetzold et al., 2005, 2006; O'Callaghan et al., 2013). Moreover, in recent years, mixing models have been developed and applied to SIA in order to determine sources contribution to consumers (Phillips and Gregg, 2003), being carbon and nitrogen isotope ratio commonly used in food webs studies (Minagawa and Wada, 1984; Post, 2002; Rubenstein and Hobson, 2004; Kurle, 2009).

The calculation of proportional contributions of the basal resources to food webs in floodplain lakes is challenging because existing isotopic mixing model approaches are generally sensitive to the number of sources they can accommodate, based on the number of isotopic tracers used (Phillips and Gregg, 2003). The models (e.g., MixSIR and SIAR) that have recently emerged based on stable isotope data combined with Bayesian analysis techniques (Moore and Semmens, 2008; Parnell et al., 2010; Solomon et al., 2011) incorporating many sources of variability within the model can be adequate tools for quantifying such sources of uncertainty and for estimating the contribution of multiple sources to floodplain lake food webs. The isotopic values of consumers may be represented in δ-space and has been used to explore questions traditionally resided within the domain of ecological niche theory, formalized in the concept of "isotopic niche" by Newsome et al. (2007, 2012). Thus, the isotopic axes provide quantitative information on both resource (bionomic) and habitat (scenopoetic) factors commonly used to define ecological niche space (Newsome et al., 2007; Martínez del Rio et al., 2009).

Stable isotope studies have tested patterns of food web structure in large rivers of the neotropics (Araújo-Lima et al., 1986a,b; Hamilton and Lewis, 1992; Hamilton et al., 1992; Martinelli et al., 1994; Thorp et al., 1998; Lewis et al., 2001; Wantzen et al., 2002, 2011; Benedito-Cecílio et al., 2004; Jepsen and Winemiller, 2002, 2007; Lopes et al., 2009; Correa and Winemiller, in press) and a point of view arising from these studies is that river food webs have a strong watershed signal embedded in consumer isotopic compositions (Fry and Allen, 2003). The organic matter sources of aquatic food webs are highly diverse in space and time in large river-floodplain-systems. During rising inundation (the rising limb of the flood pulse), differently organic matter is driven into the floodplain area (Junk and Wantzen, 2004, 2006; Wantzen and Junk, 2006). On the other hand, autochthonous material (e.g., biomass resulting from primary production by attached algae, phytoplankton and aquatic macrophytes) produced or accumulated during the dry period is fundamental for energy flow and carbon stocks in floodplains of large rivers (Martinelli et al., 1994; Benedito-Cecílio et al., 2000). Although many studies have documented the major role of allochthonous detritus in low order streams (Füreder et al., 2003), autochthonous production is also a valuable food resource because of its high nutrient and energy contents (Forsberg et al., 1993; Thorp and Delong, 2002; Jepsen and Winemiller, 2007). Recent works on stable isotopes has proved the importance of algal primary production even for smaller streams in the tropics (Brito et al., 2006; Dudgeon et al., 2010).

Based on this conceptual background, our goals were to determine the basal resources that mostly contributed to the food webs in a floodplain lake of the Middle Paraná River, to analyze if isotopic signatures (C and N) of organic matter sources differ between flooding and low water seasons, and to analyze the isotopic niche representations of consumers to characterize niches width and intra-guilds overlapping. To address these questions, we collected different potential energy sources and primary consumers in a floodplain lake during two hydrological phases.

Materials and methods

Study site

Samplings were carried out during high (November 2009 and March 2010) and low water seasons (September and December 2010) in a floodplain lake connected to the main channel of the Middle Paraná River (31°41′ S, 60°43′ W). Water temperature ranged from 24.6 to 27.7 °C during the study period. The floodplain lake was characterized by low conductivity (62.0–70.3 μS/cm), water transparency did not exceed 0.8 m, and dissolved oxygen varied between 3.2 and 7.2 mg/l. The benthic particulate organic matter ranged from 10.0 to 17.4% (Mesa et al., 2012).

Sample collection and isotope analyses

We collected different energy sources and primary consumers in a floodplain lake during two hydrological seasons, such as bottom sediment organic matter (BSOM), coarse particulate organic matter (CPOM), biofilm, suspended particulate organic matter (SPOM), epiphyton (filamentous green algae attached to macrophytes), phytoplankton, macrophytes and riparian tree leaves, benthic macroinvertebrates, aquatic orthopterans, and fish for SIA.

Benthic macroinvertebrates were sampled with a Tamura grab (sampled surface: 322 cm^2), the bivalves with a dredge and the orthopterans with a D-net. After allowing time for gut clearance, the individuals were rinsed with distilled water to remove attached inorganic and organic materials. Depending on the body mass of taxa, samples of multiple individuals (same location, same sampling date) were pooled to provide 3–4 mg samples for replicated analysis. The legs of orthopterans and the foot muscle in mollusks were selected for SIA.

The dominant and more frequent C_3 and C_4 plants in the Paraná River system were selected to analyze the relative contribution as sources of energy. Several leaves (10–15) of the dominant C_3 floating macrophytes such as, *Eichhornia crassipes*, *Pistia stratiotes*, *Salvinia biloba*, *Limnobium laevigatum*; rooted plants, such as *Ludwigia peploides*, *Nymphoides indica*, *Polygonum* sp.; submerged plants, such as *Ceratophyllum demersum* and C_4 grass *Paspalum repens* and *Echinochloa* sp. were handpicked. Stable isotope data of riparian vegetation consisted in values of fresh leaves of dominant riparian plants in the floodplain of the Middle Paraná River, such as *Salix humboldtiana* and *Sapium haematospermum*. CPOM was represented by samples of leaf litter collected from the bottom of the lake and sorted with sieves (>1000 μm). Water-column SPOM samples were collected from integrated subsurficial water samples and filtered onto precombusted (450 °C) glass fiber filters (Whatman® GF/F). Then, filters were frozen until isotope analysis. Bottom sediment organic matter (BSOM), which is mainly associated with silt and clay, was taken with a Tamura grab in the upper 2–3 cm of sediment depositions. Stable carbon isotope analysis was performed separately for epiphytic and planktonic algae. The epiphyton filamentous algae were scraped from aquatic plant stems, whereas phytoplankton was collected with a net of 25 μm mesh. In order to separate epiphytic and planktonic algae from detritus, we performed density fractionation in colloidal silica Ludox©AM-50 (density 1.210 g/cm^3) diluted with deionized water according to Hamilton et al. (2005).

Biofilm was sampled with an ooze sucker sampler (Welch, 1963), collecting the interstitial water layer between the bottom sediment and the water column. The biofilm consisted in amorphous non-living organic matter, mixed with adhering bacteria and fungi, diatoms, protozoans, and mineral particles. The selected invertebrates were identified to the lowest possible taxonomic level, and then associated with different