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EVIDENCE SUPPORTING THE IMPORTANCE OF TERRESTRIAL CARBON IN A LARGE-RIVER FOOD WEB

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Abstract. Algal carbon has been increasingly recognized as the primary carbon source supporting large-river food webs; however, many of the studies that support this contention have focused on lotic main channels during low-flow periods. The flow variability and habitat-heterogeneity characteristic of these systems has the potential to significantly influence food web structure and must be integrated into models of large-river webs. We used stable-isotope analysis and IsoSource software to model terrestrial and algal sources of organic carbon supporting consumer taxa in the main channel and oxbow lakes of the Brazos River, Texas, USA, during a period of frequent hydrologic connectivity between these habitat types. Standardized sampling was conducted monthly to collect production sources and consumer species used in isotopic analysis. Predictability of hydrologic connections between habitat types was based on the previous 30 years of flow data. IsoSource mixing models identified terrestrial C_3 macrophytes (riparian origin) as the primary carbon source supporting virtually all consumers in the main channel and most consumers in oxbow lakes. Small-bodied consumers (<100 mm) in oxbow lakes assimilated large fractions of algal carbon whereas this pattern was not apparent in the main channel. Estimates of detritivore trophic positions based on $\delta^{15}N$ values indicated that terrestrial material was likely assimilated via invertebrates rather than directly from detritus. High flows in the river channel influenced algal standing stock, and differences in the importance of terrestrial and algal production sources among consumers in channel vs. oxbow habitats were associated with patterns of flooding. The importance of terrestrial material contradicts the findings of recent studies of large-river food webs that have emphasized the importance of algal carbon and indicates that there can be significant spatial, temporal, and taxonomic variation in carbon sources supporting consumers in large rivers.

Key words: Brazos River, Texas, USA; floodplain; food web; IsoSource; isotopes; oxbow lakes.

Introduction

Several conceptual models have been proposed to describe sources of organic carbon supporting aquatic consumers in large river-floodplain systems. The flood-pulse concept (FPC; Junk et al. 1989) has been widely cited in the ecological literature and is generally recognized as a good approximation of ecological function in large rivers. This model emphasizes the importance of lateral connectivity between the main channel and floodplain habitats, and predicts that terrestrial materials originating on floodplains provides the majority of organic carbon supporting aquatic fauna in the main river channel. Thorp and Delong (1994) proposed the riverine-productivity model (RPM) that states carbon transported from upstream reaches and the floodplain is difficult for consumers to assimilate directly. Algal carbon sources (e.g., benthic algae, phytoplankton) are more labile and may be assimilated by consumer taxa in greater proportions despite the lower abundance of these carbon sources in their environment (Thorp et al. 1998).

Advances in methodologies for studying food webs, especially stable isotope analysis, have provided opportunities to quantitatively evaluate predictions of these conceptual models. Increasingly, studies utilizing stable isotopes have identified algal carbon as the primary source of organic carbon supporting aquatic consumers in large rivers, confirming predictions of the RPM (Thorp and Delong [2002] and references therein, Winemiller 2005). These studies have primarily focused on aquatic fauna in lotic main-channel habitats during low-flow periods. Off-channel aquatic habitats, such as oxbow lakes, are recognized as areas of high biological productivity in large river systems, yet they have received comparatively little attention with regards to the sources of carbon supporting consumers in these habitats. Aditionally, food webs are dynamic in space and time, and their structure can change in response to environmental drivers, species interactions, or a combination of these factors (Winemiller 1996, Woodward and Hildrew 2002, de Ruiter et al. 2005). Fluctuations in water level cause variation in connectivity between different habitat units within the main channel and

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floodplain and have the potential to significantly influence food-web structure by facilitating movement of potential source materials and consumer taxa (Pringle 2003, Winemiller 2005). The dynamic nature of large river-floodplain systems must be integrated into food-web studies to provide more accurate and holistic estimates of carbon sources supporting aquatic food webs at spatial and temporal scales that are relevant to these systems.

In North America, the fluvial dynamics of most large river-floodplain systems have been significantly altered, which complicates attempts to examine ecological dynamics under natural conditions (Sparks 1995, Michener and Haeuber 1998). Here we use stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to examine proportional contributions of algal and terrestrial primary-production sources to aquatic consumer taxa in the main channel and floodplain habitats of the Brazos River, Texas, USA, over a five-month period in which several flood events exceeded 90th-percentile flow values. The hydrology of the lower Brazos River is less modified than most other North American floodplain systems, and provides a unique opportunity to examine food-web structure in a lowland river with frequent connections between the main channel and off-channel habitats.

Research goals were to identify the principal terrestrial and algal carbon sources supporting consumer taxa representing three trophic guilds in the main channel of the Brazos River and two oxbow lakes with different flood-recurrence intervals in order to test the applicability of current conceptual models during a high-flow period. In our study region, high temperatures and dry conditions during summer result in the domination of C_4 macrophytes ($\sim$70%) on the floodplain (Teeri and Stowe 1976), and many of the row crops are also C_4 (corn and sorghum). Thus, we defined the *floodplain* as the region dominated by C_4 macrophytes. Due to their poorer water-use efficiency, C_3 macrophytes are most abundant in riparian zones, especially deciduous trees that can contribute large amounts of material to the main channel regardless of water level. Here we define the *riparian zone* as the 5–20 m strip of vegetation along the banks of oxbows and the river channel where C_3 macrophytes are dominant. The riparian zone was well defined in most of the reach, where agricultural fields and pasture usually extended up to the riparian buffer. This spatial distribution of plants utilizing different photosynthetic pathways facilitates differentiation of carbon contributions to aquatic food webs from floodplain (primarily C_4) vs. riparian zones (primarily C_3). Additionally, we use $\delta^{15}N$ values to compare vertical trophic structure among the three habitats surveyed to reveal direct vs. indirect assimilation of carbon from primary producers.

We predicted that hydrology would significantly influence carbon sources supporting consumer taxa. Several studies that support the importance of algal carbon were conducted during low-flow periods (Thorp et al. 1998, Bunn et al. 2003, Delong and Thorp 2005), whereas studies conducted during different hydrologic periods (both high flow and low flow) or within habitats with different flow regimes have inferred that terrestrial carbon sources may significantly contribute to consumer biomass (Huryn et al. 2001, Wantzen et al. 2002, Herwig et al. 2004, Hoeinghaus et al. 2007). We predicted that terrestrial sources (C_4 and C_3 macrophytes) would be important for consumers in the main channel following high flows that import these materials from the floodplain and adjacent riparian zone, and reduce the availability of algal sources via scouring and sedimentation (Huryn et al. 2001). Oxbow lakes have small catchments and hydrologic disruptions are much less frequent and tend to be more gradual compared to those affecting the main channel (Winemiller et al. 2000, Zeug et al. 2005). We predicted that algal carbon sources would support a larger fraction of consumer biomass in oxbows than the main channel, and both terrestrial sources (C_3 and C_4 macrophytes) would be relatively unimportant to oxbow food webs. Greater fractions of terrestrial material were predicted to be assimilated by consumers in oxbows with shorter flood-recurrence intervals.

Methods

Study site

The Brazos River is the 11th-longest river in the United States draining a 116 000-km^2 catchment from its headwaters near the Texas–New Mexico border to its mouth near Freeport, Texas, USA. In the study region, located between 30°37′ and 30°27′ N, the Brazos River consists of a single channel without braids, side channels, or bays. Agriculture and grazing lands are dominant in the basin (81%), and remnant areas of native post oak (*Quercus stellata*) savanna are present (Dahm et al. 2005). The river is regulated by dams above the city of Waco, Texas, USA; however, the middle and lower regions of the Brazos lack dams and levees. Consequently, the actively meandering channel continues to form aquatic floodplain features such as oxbow lakes. Large-scale flood events that inundate wide areas of the floodplain have been reduced due to regulation; however, there is sufficient hydrologic variability that high-water periods result in inundation of low-lying agricultural lands and connections between the main channel and oxbow lakes. Flood dynamics are primarily driven by regional precipitation patterns that are less seasonal relative to other floodplain rivers in South America and Africa (Winemiller 1996).

To characterize the seasonality of flooding during the study period, we calculated the predictability of flows required to connect two oxbow lakes at different elevations on the floodplain, based on the previous 30 years of flow data. Predictability was calculated using the methodology of Colwell (1974) as recommended by Resh et al. (1988) for evaluation of stream flow. This

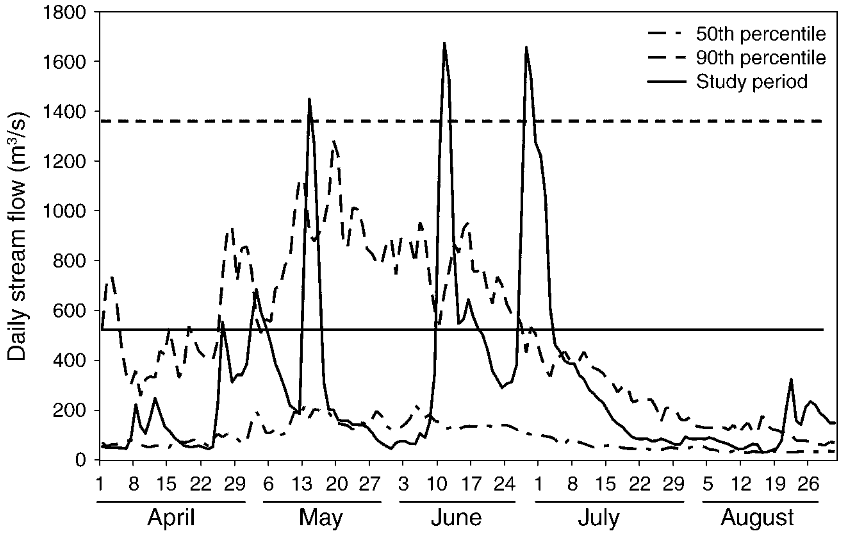

FIG. 1. Daily stream-flow hydrograph of the Brazos River (Texas, USA) during the 2004 study period, together with the 50th- and 90th-percentile daily values based on the previous 30 years of record. The solid horizontal line indicates flows required to connect OxFreq (the oxbow lake 200 m from the main channel, with flood-recurrence interval of 1.1 yr) with the river, and the dashed horizontal line indicates flows needed to connect OxRare (the oxbow lake 1200 m from the main channel, with flood-recurrence interval of ~2 yr) with the river.

methodology produces a measure of predictability between 0 and 1, where 0 is total unpredictability and 1 is total predictability. Two additional measures partition the amount of predictability accounted for by constancy (the predictability of flow across all time periods), and contingency (the degree to which time determines flow). Additionally, we plotted 50th- and 90th-percentile daily flow values for the past 30 years with daily flows during the study period (Fig. 1).

Samples of basal sources and consumer taxa for analysis of stable isotope ratios were collected from two oxbow lakes with different flood-recurrence intervals and from the main channel of the middle Brazos River. One of the oxbows, located 200 m from the main channel, connects to the river frequently (recurrence interval = 1.1 years) at moderate levels of river discharge (>75th-percentile flow for all days) and is hereafter referred to as OxFreq (Fig. 1; see also Plate 1). The other oxbow, located 1200 m from the main channel, connects to the river channel at high levels of discharge (>90th-percentile flow for all days) with a recurrence interval of ~2 years and is hereafter referred to as OxRare (Fig. 1). Samples from the main river channel were collected from a 7-km reach located near OxRare. Both oxbow lakes were located on cattle ranches but retained relatively unaltered riparian buffers (5–20 m) surrounded by pasture. Willow trees (*Salix nigra*) were the dominant riparian tree at both sites, and sycamores (*Platanus occidentalis*) also were common at OxRare. Willows dominated the riparian zone of the river channel, and the floodplain contained row crops (primarily corn, sorghum and cotton) and pasture with sparse areas of native post oak savanna. Aquatic macrophytes were rare in the channel and sparse in oxbow lakes.

Sample collection

A previous survey of one Brazos oxbow found significant seasonal variation in isotopic ratios of primary producers (Jepsen 1999). In order to capture this temporal variability for modeling contributions of production sources to consumer species that integrate variability in source materials over time, production sources were collected monthly at each site from September 2003 to August 2004. Samples of dominant riparian vegetation (*S. nigra*, *P. occidentalis*) were collected when live leaves were available (early fall, spring, and summer). Leaves were clipped, placed in plastic bags, and frozen for later processing. Samples of grasses from adjacent pastures were collected during flood periods (May and June) when water inundated these areas. Benthic algae were scraped directly off the mud substrate using a metal spatula. Samples were rinsed with distilled water to remove sediment and large particles of detritus and then examined under a microscope to remove small particles and microorganisms. Because this collection and processing technique was unlikely to produce pure samples, we hereafter refer to this source as *phytomicrobenthos* (benthic algae with associated microorganisms). Samples of phytomicrobenthos were not collected in the river channel during certain months due to scouring and sediment deposition. Water samples were collected in two 1-L opaque bottles and transported to the laboratory on ice. Samples were passed through a 64-mm sieve to remove zooplankton and then examined under a microscope to ensure the sample primarily contained phytoplankton. Sieved

PLATE 1. Aerial photograph of OxFreq (1.1-yr flood recurrence interval) during a period of isolation from the main channel. Riparian buffer zones and common land-use types are clearly visible. The main channel of the Brazos River is located in the lower right corner. Photo credit: K. O. Winemiller.

samples were filtered onto precombusted (450°C for 24 hr) Whatman GF/F filters and frozen for later analysis. Samples contained both phytoplankton and suspended organic matter and are hereafter referred to as *seston*. Seston samples could not be collected in the river channel during high-flow periods due to heavy sediment loads.

Fish and invertebrates were collected monthly from April 2004 to August 2004. Small-bodied species (<100 mm long) were collected with a 10 × 2 m bag seine and large-bodied species (>100 mm) were collected with experimental gill nets. Abundance estimates of consumer taxa were standardized by the total number of meters traveled for seine hauls and the total hours for each gill-net set. For a more detailed description of the collection methodology see Zeug and Winemiller (2007). Species collected for isotopic analysis were selected based on previous surveys that identified them as dominant consumers (Winemiller et al. 2000, Zeug et al. 2005) and their representation of different trophic guilds. In oxbow lakes, gizzard shad (*Dorosoma cepedianum*), smallmouth buffalo (*Ictiobus bubalus*), grass shrimp (*Palaemonetes kadiakensis*), and crayfish (cambaridae) represented the detritivore/omnivore guild. Western mosquitofish (*Gambusia affinis*), red shiner (*Cyprinella lutrensis*), and bluegill (*Lepomis macrochirus*) represented the insectivore guild. White crappie (*Pomoxis annularis*) and spotted gar (*Lepisosteus oculatus*) represented the piscivore guild. Species assemblage structure of the river channel is significantly different than that of oxbow lakes (Zeug et al. 2005), and several lotic-associated species were dominant guild members in the main channel. In the river channel, gizzard shad, river carpsucker (*Carpiodes carpio*), and Ohio River shrimp (*Macrobrachium ohione*) represented the detritivore/omnivore guild. Red shiner, bullhead minnow (*Pimephales vigilax*), and longear sunfish (*Lepomis megalotis*) represented the insectivore guild. Longnose gar (*Lepisosteus osseus*) represented the piscivore guild. During each month we attempted to collect three individuals of each species, however, in certain months three replicates were not available. When more than three specimens were collected, individuals were selected to represent the minimum, maximum, and approximate mean size in the sample. All samples were placed in plastic bags and frozen for later processing.

In the laboratory, fish and invertebrate samples were defrosted, measured to the nearest 0.1 mm (standard length for fishes and total length for decapods) and weighed to the nearest gram. Samples of dorsal muscle were used for fishes, and abdominal muscle for decapods. For some small species (mosquitofish and grass shrimp), composite samples of up to three similar-sized individuals were used to ensure adequate sample mass. Muscle tissue was removed using a scalpel, rinsed with distilled water, and inspected to ensure samples were free of bone, scales, or exoskeleton fragments. Samples of muscle and processed basal source materials were placed in individually labeled, acid-washed Petri dishes and dried for 48 h at 60°C. Dried samples were ground to a fine powder and subsamples were weighed to the nearest 0.01 mg on an analytical balance. Subsamples were sealed within Ultra-Pure tin capsules (Costech Analytical Technologies, Valencia, California, USA) and then sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens, Georgia, USA, for analysis of carbon and nitrogen isotope ratios. Isotopic results for carbon and nitrogen were quantified as deviations relative to isotopic standards (delta notation):

$$\delta^{13}\text{C or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. For carbon isotopes, the standard was Pee Dee Belemnite limestone, and atmospheric nitrogen was the nitrogen standard.

Some samples were destroyed due to equipment malfunctions during isotopic analysis. Destroyed consumer samples were reanalyzed when additional processed material was available however, samples of phytomicrobenthos and seston usually did not contain enough additional material to be reanalyzed.

Data analysis

The IsoSource procedure described by Phillips and Greg (2003) was performed to model the contribution of source materials to consumer taxa. Plots of carbon and nitrogen ratios of source materials indicated that baseline nitrogen values (average δ^{15}N of all production sources) may have been different among the three habitats surveyed. A one-way ANOVA indicated that differences among habitats were significant ($F_{2,86}$ = 32.19, $P < 0.001$), and Tukey's multiple comparisons test indicated that differences were significant between each habitat. Because of these differences, models were run for each habitat separately using source and consumer taxa collected only in that habitat. Plots revealed that some sources could be combined. In OxRare, willow and sycamore had similar isotopic ratios and were combined into the variable C_3 terrestrial plants. Grasses collected along the river channel and OxFreq were C_3. In the river channel, C_3 grasses had signatures similar to willow and were combined into the variable C_3. Grasses in OxFreq did not overlap with willow isotope ratios and these sources were not combined. Although C_3 grasses appeared to be dominant in the riparian zone of the section of the Brazos channel that was surveyed, C_4 plants dominate the floodplain therefore, isotopic values for Brazos River C_4 grasses collected previously by K. O. Winemiller (*unpublished data*) were included in the Brazos River model.

A four-source dual-isotope δ^{13}C/δ^{15}N model was run for consumer species in each habitat. Sources in the river channel and OxRare models included C_3 macrophytes, C_4 macrophytes, phytomicrobenthos, and seston. Because C_4 macrophytes used in the river-channel model were not collected during the study period and δ^{15}N values were higher than other production sources, an additional model was run for the Brazos using only δ^{13}C values. The OxFreq model included C_3 trees, C_3 grasses, phytomicrobenthos, and seston. Nitrogen values were corrected for trophic fractionation using the value of 2.54‰ calculated from a meta-analysis of fractionation studies (Vanderklift and Ponsard 2003). Each model examined source contributions in 1% intervals with a tolerance of 0.1‰.

Trophic position (TP) of each species was estimated based on fractionation of δ^{15}N between consumers and basal production sources (Vander Zanden and Rasmussen 1999, Post 2002). Calculations were performed using the methodology described in Jepsen and Winemiller (2002), and the trophic position of each consumer was calculated as

$$\text{TP} = [(\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{reference}})/2.54] + 1$$

where $\delta^{15}\text{N}_{\text{ref}}$ was the mean δ^{15}N of basal sources (C_3 macrophytes, C_4 macrophytes, phytomicrobenthos, and seston), and 2.54‰ was the mean trophic fractionation value from a meta-analysis of trophic fractionation studies (Vanderklift and Ponsard 2003). Reference nitrogen values were calculated separately for each habitat due to the significant spatial difference in nitrogen ratios of basal sources discussed above. Because reference values were calculated separately, estimates of consumer trophic positions were directly comparable among the three habitats surveyed.

Results

A total of 378 consumer and basal-source samples was analyzed for carbon and nitrogen isotopic ratios, with 85, 151, and 142 samples analyzed in the Brazos River, OxFreq (the oxbow lake 200 m from the river), and OxRare (the oxbow lake 1200 m from the river), respectively. Predictability of flows that connect oxbows with the main channel was low (P = 0.35) as was constancy, the predictability of flow across all time periods (C = 0.32), and contingency, the degree to which time determines flow (M = 0.03). A large proportion of predictability was accounted for by constancy (91%) rather than contingency (9%), indicating that high-flow periods do not exhibit a seasonal pattern. The months during which consumer taxa were sampled (April–August 2004) represented a period of frequent channel–oxbow connections, and there was not a prolonged low-flow period in the main channel (Fig. 1). Five separate flood connections occurred between the river channel and OxFreq (normal recurrence interval = 1.1 years), and OxRare was connected to the river channel on three occasions (normal recurrence interval = 2 years). In total, the river channel was hydrologically connected with at least one of the study oxbows for a total of 24 days (Fig. 1).

Mean δ^{13}C values of basal sources were relatively well differentiated within each habitat, however some sources had different isotopic ratios between habitats. Terrestrial C_3 macrophytes had relatively light carbon ratios and had similar mean δ^{13}C values among habitats (Brazos = −29.40‰, OxFreq = −29.13‰, and OxRare = −28.86‰). Terrestrial C_4 macrophytes contained greater proportions of ^{13}C and had similar values in the two habitats where they were collected (Brazos = −13.32‰, OxRare = −12.78‰). Seston samples had similar values in the two oxbow lakes, and these ratios were intermediate between those of the two terrestrial sources (OxFreq = −25.00‰, OxRare = −26.37‰), whereas seston in the river channel had greater proportions of ^{13}C (−15.36‰) relative to oxbow samples. Samples of phytomicrobenthos had mean values of −20.15‰, −25.50‰, and −17.63‰ in the river channel, OxFreq and OxRare, respectively. Factors such as current velocity, CO_2 concentration and temperature can influence the $\delta^{13}C$ values of benthic algae (Finlay et al. 1999), and may have contributed to the spatial variation observed in our study. Coefficients of variation for $\delta^{13}C$ of sources sampled over one year (September 2003–August 2004) were generally greater for aquatic production sources (0.07–0.36) relative to terrestrial sources (0.04–0.11), a result similar to that found by Jepsen (1999).

$\delta^{15}N$ values of sources were significantly different between habitats as discussed above (see *Methods: Data analysis*). Within habitats, the range of mean $\delta^{15}N$ values between sources was greater in the Brazos River (7.21–12.12‰) relative to OxFreq (5.91–6.94‰), and OxRare (3.78–4.90‰). Coefficients of variation for source $\delta^{15}N$ were generally greater than $\delta^{13}C$, which supported results reported by Jepsen (1999) that there is considerable seasonal variation in nitrogen ratios of production sources in Brazos oxbows.

Carbon sources supporting aquatic consumers

Consumer taxa in the Brazos River channel had a narrow range of $\delta^{13}C$ values (1.28‰) that were intermediate relative to the range of mean values of production sources (Fig. 2). IsoSource model solutions (1st–99th percentile ranges) indicated that C_3 macrophytes were the most important production source supporting biomass of all seven taxa examined, and C_4 macrophytes also accounted for a significant fraction of assimilated carbon (Table 1). Model results suggested that the two aquatic production sources (phytomicrobenthos and seston) probably made minor contributions, although 99th percentile values were greater for phytomicrobenthos relative to seston (Table 1). Solutions from the carbon-only model supported the importance of C_3 macrophytes to consumer biomass, however ranges for other sources had first-percentile values of zero.

Species in OxFreq had a greater range of $\delta^{13}C$ vales relative to the river channel (3.31‰), and, on average, had lighter carbon ratios (Fig. 2). IsoSource solutions indicated assimilation of material from a mixture of production sources. Phytomicrobenthos accounted for a large fraction of crayfish and mosquitofish biomass, with seston also being an important contributor (Table 2). Terrestrial production sources appeared to contribute little to crayfish, whereas greater, although relatively minor, contributions were possible for mosquitofish. Terrestrial C_3 trees accounted for a large fraction of grass shrimp, white crappie, bluegill, and smallmouth buffalo biomass (Table 2). Seston contributions for these species also were important (1st-percentile values > 0), although 99th-percentile values were relatively low for white crappie and smallmouth buffalo, suggesting that seston was a minor yet consistent contributor to biomass of these species (Table 2). For bluegill and grass shrimp, large contributions from terrestrial C_3 grasses were also possible, although ranges of potential contributions were broad (Table 2). Red shiner and gizzard shad seemed to assimilate material from all four sources, although only the two aquatic sources had 1st-percentile values > 0, indicating they were consistent contributors

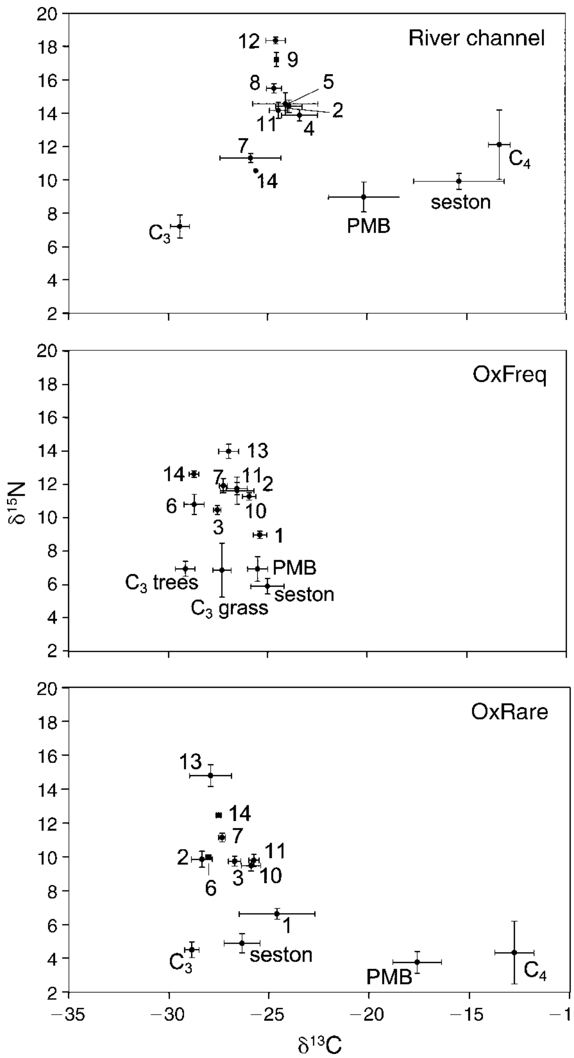

FIG. 2. Carbon and nitrogen isotope-ratio ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) biplots of production sources and consumer taxa in each habitat. Species codes are as follows: PMB = phytomicrobenthos, 1 = crayfish, 2 = gizzard shad, 3 = grass shrimp, 4 = Ohio River shrimp, 5 = river carpsucker, 6 = smallmouth buffalo, 7 = bluegill, 8 = bullhead minnow, 9 = longear sunfish, 10 = mosquitofish, 11 = red shiner, 12 = longnose gar, 13 = spotted gar, 14 = white crappie.

Table 1. Means and 1st–99th percentile ranges (in parentheses) of source contributions to Brazos River consumer biomass from IsoSource models.

Species†	C_4	C_3	Phytomicrobenthos‡	Seston§
Fish				
Red shiner (15)	0.28 (0.27–0.31)	0.68 (0.66–0.69)	0.02 (0.00–0.07)	0.01 (0.00–0.05)
River carpsucker (3)	0.27 (0.23–0.33)	0.64 (0.59–0.67)	0.06 (0.00–0.16)	0.04 (0.00–0.11)
Gizzard shad (9)	0.25 (0.21–0.32)	0.62 (0.56–0.66)	0.08 (0.00–0.21)	0.05 (0.00–0.14)
Longnose gar (11)	0.29 (0.28–0.30)	0.69 (0.68–0.70)	0.01 (0.00–0.04)	0.01 (0.00–0.02)
Longear sunfish (2)	0.29 (0.27–0.30)	0.69 (0.67–0.70)	0.02 (0.00–0.05)	0.01 (0.00–0.03)
Bullhead minnow (12)	0.29 (0.29–0.30)	0.70 (0.70–0.70)	<0.01 (0.00–0.01)	<0.01 (0.00–0.01)
Invertebrates				
Ohio River shrimp (2)	0.21 (0.15–0.27)	0.55 (0.47–0.61)	0.15 (0.00–0.35)	0.10 (0.00–0.22)

Note: The IsoSource procedure is described by Phillip and Greg (2003).
† Sample sizes for consumers are in parentheses next to species names.
‡ Phytomicrobenthos = samples of benthic algae with associated microorganisms.
§ Seston = samples with phytoplankton and suspended organic matter, from sieved water samples.

(Table 2). Model results did not suggest a dominant production source for spotted gar. As apex predators with broad diets, spotted gar likely feed on a prey assemblage that assimilates material from multiple aquatic and terrestrial sources.

Carbon ratios of consumers in OxRare had a similar range (3.76‰) as those in OxFreq (Fig. 2). A large fraction of all consumer biomass was accounted for by terrestrial C_3 macrophytes, with a 1st-percentile value range of 47–84%, and 99th-percentile value range of 67–98% (Table 3). Terrestrial C_4 macrophytes likely contributed little to most consumers. Similar to patterns in OxFreq, phytomicrobenthos accounted for significant fractions of mosquitofish and crayfish biomass, and this also was an important source for red shiner. Phytomicrobenthos also accounted for a smaller, yet similar, fraction of spotted gar, bluegill, white crappie, and grass shrimp biomass. Seston seemed to be a minor contributor for most consumers, although a relatively large fraction was possible for spotted gar (Table 3).

Trophic position of consumers

$\delta^{15}N$ data indicated ~5 trophic levels in the river channel and OxRare, and 4 trophic levels in OxFreq (Fig. 3). In the river channel, no consumers had a trophic level below 3, suggesting that trophic-level 2 may be dominated by aquatic insects that were not well sampled in our survey. The third trophic level contained species in the detritivore/omnivore guild (gizzard shad, Ohio River shrimp, and river carpsucker) and two species in the insectivore guild (red shiner and bullhead minnow), although the trophic position (TP) of bullhead minnow approached level 4 (3.7). Longear sunfish and longnose gar comprised the fourth trophic level, and the longnose gar value approached trophic-level 5 (TP = 4.8).

Trophic-level 2 in OxFreq included crayfish, grass shrimp and smallmouth buffalo. Crayfish had a trophic position slightly less than 2.0 (TP = 1.9) which may have resulted from seasonal variation in $\delta^{15}N$ of sources. Five species approximated trophic level 3 (gizzard shad, bluegill, mosquitofish, red shiner, and white crappie), and spotted gar approached trophic level 4 (TP = 3.8). In OxRare, crayfish were the only species in trophic-level 2, and, similar to crayfish in OxFreq, crayfish trophic position was slightly less than 2.0 (TP = 1.9). Gizzard shad, grass shrimp, smallmouth buffalo, mosquitofish, red shiner, and bluegill comprised trophic-level 3. White crappie was the only species in trophic-level 4, and spotted gar approximated trophic-level 5 (Fig. 3).

Table 2. Means and 1st–99th percentile ranges (in parentheses) of sources contributions to OxFreq consumer biomass from IsoSoure models.

Species	C_3 grasses	C_3 trees	Phytomicrobenthos	Seston
Fish				
Red shiner (8)	0.33 (0.00–0.67)	0.16 (0.00–0.34)	0.28 (0.04–0.50)	0.24 (0.13–0.34)
Gizzard shad (17)	0.32 (0.00–0.66)	0.16 (0.00–0.34)	0.27 (0.03–0.49)	0.25 (0.14–0.35)
Mosquitofish (12)	0.15 (0.00–0.34)	0.08 (0.00–0.17)	0.53 (0.36–0.70)	0.24 (0.14–0.34)
Smallmouth buffalo (10)	0.07 (0.00–0.24)	0.83 (0.71–0.93)	0.03 (0.00–0.10)	0.07 (0.03–0.14)
Spotted gar (14)	0.35 (0.00–0.81)	0.26 (0.01–0.45)	0.15 (0.00–0.37)	0.24 (0.13–0.36)
Bluegill (11)	0.29 (0.00–0.73)	0.36 (0.12–0.52)	0.12 (0.00–0.31)	0.23 (0.13–0.36)
White crappie (25)	0.05 (0.00–0.16)	0.84 (0.76–0.91)	0.02 (0.00–0.07)	0.09 (0.07–0.14)
Invertebrates				
Crayfish (13)	0.02 (0.00–0.08)	0.01 (0.00–0.04)	0.68 (0.57–0.82)	0.28 (0.17–0.36)
Grass shrimp (14)	0.20 (0.00–0.54)	0.49 (0.29–0.61)	0.08 (0.00–0.23)	0.23 (0.14–0.36)

Note: Format is as in Table 1.

TABLE 3. Means and 1st–99th percentile ranges (in parentheses) of sources contributions to OxRare consumer biomass from IsoSource models.

Species	C_4	C_3	Phytomicrobenthos	Seston
Fish				
Red shiner (11)	0.01 (0.00–0.03)	0.71 (0.67–0.74)	0.26 (0.23–0.28)	0.02 (0.00–0.06)
Gizzard shad (15)	0.01 (0.00–0.04)	0.92 (0.84–0.98)	0.02 (0.00–0.06)	0.04 (0.00–0.11)
Mosquitofish (9)	0.01 (0.00–0.04)	0.73 (0.69–0.75)	0.24 (0.21–0.27)	0.02 (0.00–0.06)
Smallmouth buffalo (15)	0.02 (0.00–0.06)	0.89 (0.79–0.95)	0.04 (0.00–0.09)	0.05 (0.00–0.15)
Spotted gar (12)	0.07 (0.00–0.21)	0.57 (0.36–0.72)	0.23 (0.07–0.26)	0.12 (0.00–0.34)
Bluegill (15)	0.02 (0.00–0.06)	0.84 (0.77–0.89)	0.11 (0.06–0.15)	0.03 (0.00–0.10)
White crappie (17)	0.01 (0.00–0.03)	0.87 (0.81–0.90)	0.11 (0.08–0.13)	0.02 (0.00–0.07)
Invertebrates				
Crayfish (2)	0.04 (0.00–0.11)	0.59 (0.47–0.67)	0.31 (0.21–0.38)	0.07 (0.00–0.19)
Grass shrimp (15)	0.03 (0.00–0.08)	0.79 (0.70–0.84)	0.15 (0.08–0.20)	0.04 (0.00–0.13)

Note: Format is as in Tables 1 and 2.

DISCUSSION

Isotopic mixing-model estimates indicated that terrestrial carbon from the riparian zone (C_3 macrophytes) was the primary source supporting consumer biomass in the main channel and the rarely flooded oxbow, and accounted for a large fraction of biomass of certain consumers in the frequently flooded oxbow. In the river channel, terrestrial C_4 macrophytes (primarily from the floodplain) made a consistent, yet smaller contribution relative to C_3 macrophytes. C_4 macrophytes only had the potential for minor contributions to oxbow consumers. Isotopic studies of other temperate and subtropical rivers have found that C_4 macrophytes are relatively unimportant as an energy and nutrient source contributing to consumer biomass (Thorp et al. 1998, Clapcott and Bunn 2003, Herwig et al. 2004); however, these studies were conducted during low-flow periods. Surveys of tropical-river food webs indicate relatively minor contributions from C_4 macrophytes, and their importance tends to be greater during high-water periods or in high gradient rivers with greater flow velocity (Leite et al. 2002, Wantzen et al. 2002, Hoeinghaus et al. 2007). The large estimated contribution of terrestrial carbon (C_3 riparian macrophytes) to consumers within the Brazos River ecosystem contradicts recent studies reporting the importance of algal carbon to large river food webs (Lewis et al. 2001, Thorp and Delong 2002, Douglas et al. 2005).

Hydrologic dynamics during the study likely influenced the importance of terrestrial (C_3 riparian) relative to aquatic (algal) primary-production sources. Our current study was conducted during a period of

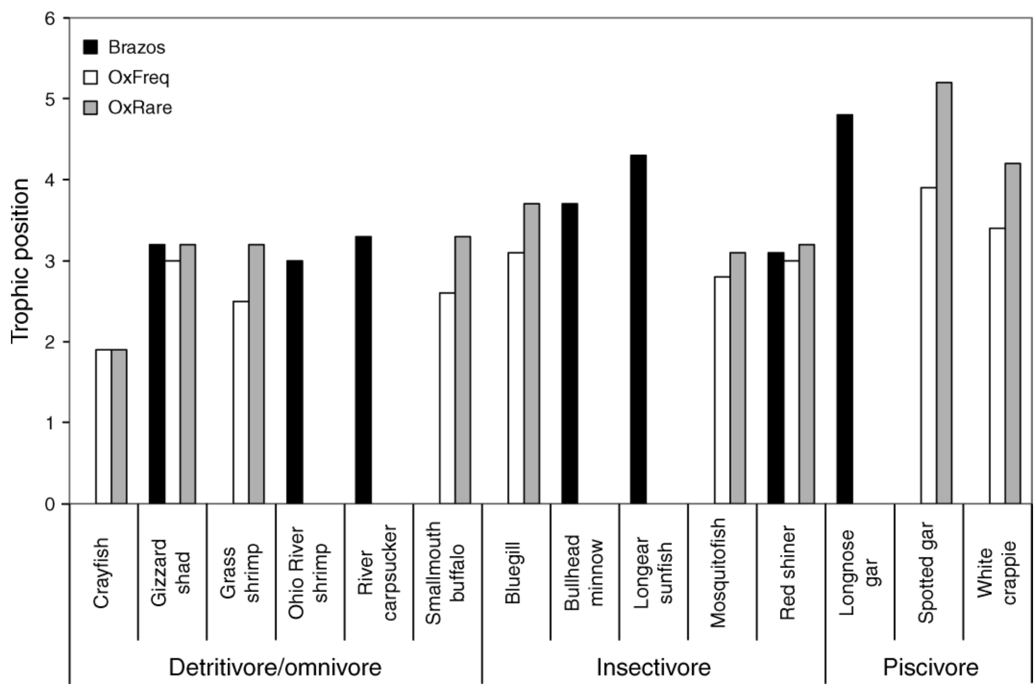

FIG. 3. Trophic positions of main-channel and oxbow-lake consumers based on $\delta^{15}N$ values.

greater-than-average (50th percentile) flows in the middle Brazos River. High flows in the main channel resulted in scouring of benthic algae from shallow areas and/or deposition of large volumes of sediment that prevented collection of algal samples during certain periods. IsoSource model results for certain consumer taxa in oxbow lakes, where flow disruptions were less frequent, indicated significant contributions from algal carbon (phytomicrobenthos and seston). Mosquitofish, red shiner, and crayfish in oxbows potentially had assimilated large amounts of carbon derived from benthic algae (phytomicrobenthos). These species are small bodied (<100 mm) and exploit shallow littoral habitats where benthic algae are most abundant. Thus, benthic algae may be a more ephemeral resource relative to terrestrial material from the riparian zone during high-flow periods in the channel. Greater contributions of algal carbon to certain consumers in the channel may be observed during extended low flows. Delong et al. (2001) reported little change in carbon sources supporting consumers in response to a flood in the Upper Mississippi River (USA); however, the flow regime of the Brazos is much less predictable within and among years relative to other floodplain systems (Winemiller 1996). Shifts in the contribution of terrestrial and algal carbon sources to consumers based on resource availability, as mediated by river hydrology, were reported for a New Zealand river by Huryn et al. (2001). Bunn et al. (2003) found that benthic algae were the primary carbon source supporting consumers in isolated water holes during a low-flow period in Cooper Creek, Australia.

The flood-pulse concept (FPC) predicts that production sources supporting consumers in the main channel are primarily terrestrial materials originating on the floodplain (Junk et al. 1989). Our results support the importance of terrestrial material to consumer biomass; however, these sources were primarily C_3 macrophytes (riparian origin), and contributions of C_4 macrophytes (floodplain origin) were less important. The FPC is vague regarding whether the riparian zone is included in their definition of the floodplain, whereas the riverine-productivity model (RPM) defines the riparian zone as part of the channel. Floods in the Brazos River are of short duration (maximum of nine days in the current study) compared to the rivers used to formulate the FPC (e.g., Amazon and upper Mississippi) and may not provide the time needed for decomposition and/or invertebrate processing of floodplain-derived material that can then enter metazoan food webs; in contrast, C_3 materials from the riparian zone can enter the channel during both high- and low-flow periods. Additionally, aquatic organisms may not exploit inundated areas due to the risk of stranding during rapid declines in water level (Humphries et al. 1999). A concurrent study investigating gar diets in the Brazos found that terrestrial invertebrates (Orthoptera) increased in importance during periods of connectivity (Robertson et al. 2008), and this may be the primary pathway of floodplain (C_4) carbon to aquatic consumers given the short duration of flooding.

The riverine-productivity model (Thorp and Delong 1994) emphasizes the importance of algal–grazer pathways to consumer biomass production in the channel of large rivers. Direct terrestrial inputs from the riparian zone are included as a potential, yet less important, source in the original formulation of the RPM; however, revisions of the model have increasingly emphasized the importance of algal carbon, with riparian inputs considered to be of little importance (Thorp et al. 1998, Thorp and Delong 2002, Delong and Thorp 2006). Even though our results conflict with the revised RPM, certain consumers in oxbow lakes assimilated large fractions of algal carbon, indicating that there can be significant spatial and taxonomic variation in production sources supporting consumers.

Given the hydrologic, geomorphic, and taxonomic diversity of large river systems world wide (Puckridge et al. 1998), it is unlikely that a single conceptual model of carbon dynamics can apply to all rivers, or even all habitat units and consumer taxa within a particular river. Hoeinghaus et al. (2007) found that landscape-scale hydrologic characteristics significantly influenced the sources of carbon supporting food webs in Brazilian rivers and that the FPC and RPM could not be uniformly applied to all systems. Floods in the Brazos can occur during any month of the year and are characterized by a rapid rise and fall in water level that may occur several times in succession (as observed in our study). These dynamics appear to provide poor conditions for production of benthic algae in the main channel and may not allow enough time for decomposition and invertebrate processing of floodplain vegetation. Thus, it is more difficult for floodplain and algal carbon to enter aquatic food webs relative to terrestrial material from the riparian zone. These hydrologic characteristics may account for the conflict of our results with studies conducted in rivers with more predictable (seasonal) hydrology or during low-flow periods.

Estimates of consumer trophic positions indicated ~5 trophic levels in the main channel and OxRare, and 4 levels in OxFreq. Longnose and spotted gars were the only species that approximated trophic-level 5. Differences in prey assemblages among habitats may have influenced gar trophic positions. Beaudoin et al. (1999) reported that trophic positions of northern pike (*Esox lucius*) could vary up to one trophic level in relation to consumption of invertebrate versus fish prey. Analysis of gar stomachs revealed that individuals in OxFreq primarily consumed crayfish (TP = 1.9), whereas gar in OxRare consumed more shad (TP = 3.2) and sunfish (TP = 3.7), and longnose gar consumed large volumes of catfish (Robertson et al. 2008). Few consumers in the detritivore/omnivore guild had trophic positions below three, and trophic-level 2 is likely composed of aquatic invertebrates that were not well sampled in this study. Species in this guild consume large amounts of detritus but may assimilate greater fractions of animal matter despite the lower abundance of the latter in consumer diets (Mantel et al. 2004, Winemiller et al. 2007).

Stable isotopes are effective tracers of material assimilated by consumers because they integrate diet over relatively long time periods compared to stomach-content analysis. Our current study examined the isotopic composition of consumers over five months, a period potentially insufficient to characterize the contribution of different production sources in relation to the long-term hydrologic dynamics of the Brazos River. Seasonal variation in production sources supporting food webs can be significant, especially in floodplain systems that experience large fluctuations in water level and associated changes in species-assemblage structure and availability of production sources (Winemiller 1990, Huryn et al. 2001). Additionally, aggregation of potential sources can result in a loss of information (Phillips et al. 2005). Seston and phytomicrobenthos are both aggregate sources, and further refinement of living and detritus fractions could potentially reveal greater contributions of algal material for certain consumers (Delong and Thorp 2006).

Identification of the trophic pathways supporting species in large-river floodplain systems is essential for their management and restoration (Winemiller 2005). Our results indicate that multiple terrestrial and algal production sources support aquatic consumer taxa. Contributions from individual sources varied considerably among habitat units and consumer species, which reinforces the need to examine the interaction among habitat heterogeneity, flow variability, and taxonomic diversity for the maintenance of essential ecological functions in lotic systems (Poff et al. 1997, Bunn and Arthington 2002). The relative importance of different production sources can be affected by the spatial and temporal scale of collections as well as the choice of species used in isotopic analysis, and these factors should be addressed in future studies of large-river food webs.

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