

Hydrologic regime and turbidity influence entrance of terrestrial material into river food webs

Katherine A. Roach and Kirk O. Winemiller

Abstract: We used stable isotope signatures of deuterium (δD) and a Bayesian stable isotope mixing model to estimate contributions of algae versus terrestrial plants to consumers during different hydrologic phases in three Texas rivers spanning a gradient of turbidity and light penetration. In the two rivers where high-flow pulses increased turbidity, assimilation of source material by consumers varied according to discharge stage. In these rivers, algae made greater contributions to macroinvertebrates and fish biomass following low-flow periods, and terrestrial plants made greater contributions following high-flow pulses. In the river with greatest loads of suspended sediments, contributions of material from terrestrial plants also increased slightly following an extended low-flow period, possibly because of increased abundance of inedible cyanobacteria. During flow pulses, lower algal biomass and production, combined with increased inputs of terrestrial organic matter from watersheds and riparian habitats, can result in greater inputs of terrestrial material into aquatic food chains. These patterns most closely match predictions of the River Wave Concept, which posits that flow is the key process determining the source of organic matter assimilated by higher consumers in rivers. Incorporation of interactions between hydrology and turbidity into river ecosystem models should facilitate more accurate predictions of food web dynamics.

Résumé : Nous avons utilisé les signatures isotopiques du deutérium (δD) et un modèle bayésien de mélange d'isotopes stables pour estimer les apports respectifs des algues et des plantes terrestres aux consommateurs durant différentes phases hydrologiques dans trois rivières du Texas couvrant un gradient de turbidité et de pénétration de la lumière. Dans les deux rivières où des débits élevés transitoires accroissent la turbidité, l'assimilation de matières brutes par les consommateurs variait selon le niveau de débit. Dans ces rivières, les apports des algues aux macroinvertébrés et à la biomasse de poissons étaient plus grands après des périodes d'étiage, et les apports des plantes terrestres étaient plus grands après des épisodes de débit élevé transitoire. Dans la rivière présentant la plus grande charge de sédiments en suspension, les apports de matières des plantes terrestres augmentaient aussi légèrement après une longue période d'étiage, possiblement à cause de la plus grande abondance de cyanobactéries non comestibles. Durant les débits élevés transitoires, la biomasse et la production plus faibles d'algues, combinées à des apports accrus de matière organique terrestre provenant des bassins versants et des habitats riverains, peuvent se traduire par de plus grands apports de matériel terrestre dans les chaînes trophiques aquatiques. Ces motifs s'apparentent le plus aux prédictions du concept d'ondes fluviales (« River Wave Concept »), qui postule que l'écoulement est le processus clé qui détermine la source de la matière organique assimilée par les consommateurs de niveau supérieur dans les rivières. L'intégration des interactions entre l'hydrologie et la turbidité dans les modèles d'écosystèmes fluviaux devrait faciliter des prévisions plus exactes de la dynamique des chaînes trophiques. [Traduit par la Rédaction]

Introduction

Current food web theory compartmentalizes material and energy originating from living primary producers as the “green” or “grazer” pathway and material and energy originating from dead organic matter as the “brown” or “detrital-microbial” pathway. Most food web studies focus on the grazer pathway (Vadeboncoeur et al. 2003; Moline et al. 2004); however, it is well known that much terrestrial vegetation enters terrestrial and aquatic food webs as detritus and is processed by microbes. This pathway of entrance (recycling of material) has implications for system dynamics and stability. For example, ecosystems in which plant detritus supports metazoan consumers have been hypothesized to support less secondary production but higher species diversity because of lower efficiency and weaker interaction strength associated with a greater number of trophic transfers between microbes and higher consumers (Legendre and Rassoulzadegan 1995; Cotner and Biddanda 2002; Rooney and McCann 2012). The flow of energy from detrital

food web pathways also can affect food chain length, the distribution of biomass among trophic levels, and the strength of trophic cascades (Halaj and Wise 2002; Moore et al. 2004).

In river ecosystems, several alternative models have predicted the most important autochthonous and allochthonous sources supporting higher consumers. In the River Continuum Concept, Vannote et al. (1980) proposed that contributions of algal versus terrestrial basal production sources to consumer biomass would vary as a function of position along the river continuum, from headwaters to lower reaches. They expected that relative to middle reaches, consumers in lower reaches would be more dependent upon particulate organic material transported from upstream reaches and less dependent on autochthonous production. In the Flood Pulse Concept, Junk et al. (1989) proposed that most aquatic consumers in large rivers with intact floodplains assimilate organic matter from production originating from submerged floodplains and associated backwater habitats. They assumed that

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detritus from terrestrial plants and, to a lesser extent, live plant tissues were the main sources of organic matter supporting aquatic invertebrates and fishes during floodplain inundation. In the Riverine Productivity Model, [Thorp and Delong \(1994\)](#) proposed that most of the allochthonous organic matter originating from headwaters or floodplains tends to be recalcitrant, and therefore the two earlier models underestimate the importance of in-channel productivity to secondary production. They suggested that aquatic invertebrates and fishes mostly assimilate autochthonous (algal) production even in net heterotrophic rivers (gross primary production is less than respiration). [Thorp and Delong \(2002\)](#) hypothesized that since algae are generally more nutritious and labile than material derived from terrestrial plants, an algae-grazer pathway that is of lesser importance to system metabolism may support considerable metazoan biomass, even when overall system metabolism is based on allochthonous carbon. However, other authors have proposed that resource subsidies should assume greater importance for food webs when net primary productivity is lower within the recipient ecosystem ([Polis and Hurd 1996](#); [Stapp and Polis 2003](#)). In the first ecosystem model to address how temporal variation of abiotic environmental factors influences entrance of production sources into river food webs, the River Wave Concept, [Humphries et al. \(2014\)](#) conceptualized flow as a wave, with the position of the wave influencing the relative proportions of autochthonous and allochthonous basal production sources transferred to higher trophic levels. [Humphries et al. \(2014\)](#) hypothesized that local autochthonous and allochthonous sources should support the food web of rivers at low flow, and allochthonous sources should become more important following high flow pulses as a result of transport of organic matter from the floodplain and upstream.

In the last 20 years, research using stable isotope analysis has revealed the dominance of autochthonous production sources in support of metazoan consumers in river food webs ([Jepsen and Winemiller 2002](#); [Herwig et al. 2007](#); [Marcarelli et al. 2011](#)) and indicated relatively low assimilation of material from terrestrial plants ([Thorp et al. 1998](#); [Clapcott and Bunn 2003](#); [Herwig et al. 2007](#); [Marcarelli et al. 2011](#)). Most of these studies were conducted during low-flow periods in rivers with naturally low levels of suspended sediments or with low sediment yield as a result of entrapment by impoundments. A recent review of stable isotope studies by [Roach \(2013\)](#) concluded that algae were the predominant basal production source supporting upper trophic levels of large rivers worldwide. However, terrestrial C_3 plants were the most important basal production source supporting consumer biomass in many turbid rivers, including the Iguatemi, Ivinheima, and Paraná rivers in Brazil ([Hoeinghaus et al. 2007](#)), the Brazos ([Zeug and Winemiller 2008](#)) and Paria ([Angradi 1994](#)) rivers in North America, and the Burdekin River in Australia ([Davis et al. 2012](#)). These findings suggest that environmental factors, such as discharge and light, interact to limit the availability of algal-based production sources to food webs of lowland rivers. Because watersheds and rivers vary in geomorphology, nutrient concentrations, hydrology, and other environmental factors, it is challenging to make general predictions.

We conducted field research in three lowland rivers in Texas (USA) spanning a gradient of turbidity and light penetration to examine potential relationships among hydrology, watershed and sediment characteristics, and sources of primary production supporting consumers. The Brazos River carries high loads of suspended clay and silt (sediments of fine grain size) that limit light penetration and algal primary production. The Guadalupe River carries moderate suspended sediment loads and has low concentrations of dissolved organic matter (DOM). The Neches River has sandy substrate, low levels of suspended sediments, and relatively high concentrations of DOM in the form of humic substances leached from surrounding watersheds. In a previous study, we measured net ecosystem production (NEP) within the water column and benthos of littoral zones in the study rivers and found

that in the sediment-laden river, resuspension of inorganic sediment causes littoral zones to become heterotrophic (negative NEP) during periods of high flow that follow prolonged periods of low flow ([Roach et al. 2014](#)). In the two study rivers with less erodible soils, total (water-column + benthic) NEP in littoral zones was almost always positive during periods of high flow as well as periods with low flow.

In this study, we used stable isotope signatures of deuterium (δD) to estimate the relative proportions of autochthonous- versus allochthonous-based production sources supporting aquatic consumers, including fishes and macroinvertebrates, in the three study rivers during different hydrologic periods. Traditionally, $\delta^{13}C$ has been useful for revealing production sources supporting consumers because this ratio has a low level of trophic fractionation (i.e., generally <0.5‰ versus approximately 2.5‰ for nitrogen; [Vander Zanden and Rasmussen 2001](#); [Vanderklift and Ponsard 2003](#)). However, $\delta^{13}C$ values do not always differ sufficiently between alternative production sources to be an effective tracer (e.g., [Doucett et al. 1996](#)). Studies indicate that algae consistently have lower δD signatures compared with terrestrial plants, suggesting that δD can more effectively differentiate autochthonous versus allochthonous production sources ([Doucett et al. 2007](#); [Jardine et al. 2009](#); [Finlay et al. 2010](#); [Cole et al. 2011](#)). Furthermore, water velocity, which affects the $\delta^{13}C$ signature of algae in streams, has been shown to have little influence on algae δD ([Finlay et al. 2010](#)). Correction of consumer δD for environmental (dietary) water, the assimilation of H directly from ingested and absorbed water ([Solomon et al. 2009](#); [Soto et al. 2011](#); [Peters et al. 2012](#)), required estimation of consumer vertical trophic positions to account for trophic compounding of δD . Trophic positions were estimated based on assumptions for trophic fractionation of stable isotope signatures of nitrogen ($\delta^{15}N$; [Vanderklift and Ponsard 2003](#)). We hypothesized that in the river dominated by clays and silts, terrestrial-based production sources would support the food web during high-flow periods when littoral zones became heterotrophic, and during low-flow periods we expected the food web to be largely supported by algae. In the rivers dominated by less-erodible, sandy soils, we expected consumers to be supported mostly by algal-based production sources during all hydrologic phases.

Methods

Study sites

We studied three meandering lowland rivers that differ considerably in turbidity, inorganic nutrient concentrations, aquatic primary production, chlorophyll *a* concentration, and other characteristics: the Brazos River (30°37'N, 96°30'W), Guadalupe River (28°49'N, 97°01'W), and Neches River (30°22'N, 94°06'W; [Appendix A, Table A1](#)). In the Brazos River, flow pulses produce high turbidity compared with moderate levels in the Guadalupe River and lower levels in the Neches River ([Roach et al. 2014](#)). The hydrologic regimes of these rivers are under the influence of dams built for water storage and hydroelectric power generation. Although the hydrologic regime of upper reaches of these rivers is regulated, overbank flooding into floodplains and riparian wetlands still occurs in response to regional rainfall. Winter and spring tend to have greater rainfall; however, high flow pulses can occur during any month. All the rivers are located at low altitudes (Brazos = 58 m above sea level (asl), Guadalupe = 12 m asl, Neches = 5 m asl) and have relatively low channel gradients. At our study sites, channel width at bankfull is approximately 0.10 km for the Brazos River, 0.05 km for the Guadalupe River, and 0.08 km for the Neches River. Mean annual discharge is 138 m³·s⁻¹ in the Brazos River, 55 m³·s⁻¹ in the Guadalupe River, and 163 m³·s⁻¹ in the Neches River.

Sample collections for stable isotope analysis

Samples of water, primary producers, and consumers for stable isotope analysis were collected from the Brazos and Neches rivers during three periods with contrasting hydrologic conditions and from the Guadalupe River during two periods with contrasting hydrologic conditions. Our goal was to examine the impact of varying discharge on basal production sources within a river, rather than to examine the effect of absolute discharge. Hydrology during each survey period was characterized as daily discharge ($\text{m}^3\cdot\text{s}^{-1}$) over the 3 months preceding sample collection using data from the United States Geological Survey (USGS, station 081087800 for the Brazos River, 08176500 for the Guadalupe River, 08041000 for the Neches River). Water samples for analysis of δD were collected from the littoral zone of three different sandbanks of each river, filtered through Whatman GF/F filters, and collected in acid-rinsed polyethylene bottles. Replicate leaves from the dominant species of terrestrial C_3 plants (Brazos: $n = 21$; Guadalupe: $n = 14$; Neches: $n = 21$) and C_4 grasses (Brazos: $n = 14$; Guadalupe: $n = 12$; Neches: $n = 17$) were collected from the riparian zone. Seston samples (Brazos: $n = 45$; Guadalupe: $n = 33$; Neches: $n = 48$) were collected by filtering water through a 64 mm sieve to remove zooplankton and large debris onto a precombusted (450°C for 4 h) GF/F filter. Seston samples consist of a heterogeneous mixture of autochthonous and allochthonous material. To determine which seston samples consisted mostly of planktonic algae, we also measured chlorophyll *a* of seston. Water samples were collected in acid-rinsed polyethylene bottles and filtered through Whatman GF/C filters. Each filter was placed into a dark vial for extraction for 24 h with 90% ethanol. We used a Hach DR 2800 mass spectrophotometer to measure chlorophyll *a*. Phaeophytin was corrected by subtracting absorbances after the addition of $0.1\text{ mol}\cdot\text{L}^{-1}$ HCl (Wetzel and Likens 1991). Benthic algae (Brazos: $n = 27$; Guadalupe: $n = 45$; Neches: $n = 36$) were scraped using a spatula from substrates including rock and woody debris, taking care not to contaminate the sample with substrate particles. Adult size classes of shrimps and fishes were collected using seines, gill nets, cast nets, hook and line, and (or) electroshocking. Representatives of different feeding guilds, including algivores–detritivores, omnivores, invertivores, and piscivores, were collected (Appendix A, Table A2). In our study rivers, fishes do not have morphological adaptations for direct consumption of leaves and seeds; thus, material from terrestrial plants is largely incorporated into aquatic food chains through consumption of terrestrially derived fine particulate organic matter (FPOM) as well as invertebrates that feed upon it. All individuals were identified, measured to the nearest 1.0 mm standard length, and a sample of muscle from the dorso-lateral region of fishes and shrimps was removed with a scalpel after euthanasia by immersion in a 1% solution of tricaine methanesulfonate. Primary producer and consumer samples were placed on ice until processing in the laboratory at Texas A&M University. In the laboratory, seston samples were backwashed from GF/F filters onto glass plates using deionized water. All samples were then dried at 60°C for 48 h in a drying oven.

Stable isotope analysis

Primary producer and consumer samples were ground to a fine powder using a mortar and pestle. To analyze sufficient mass of organic material, it was necessary to consolidate algae samples. We consolidated samples of seston and benthic algae that were collected over a period of 1–3 days. This reduced the sample size of our samples of seston (Brazos: $n = 8$; Guadalupe: $n = 4$; Neches: $n = 7$) and benthic algae (Brazos: $n = 5$; Guadalupe: $n = 5$; Neches: $n = 6$). When comparing water-column chlorophyll *a* concentrations with seston δD , we averaged chlorophyll *a* over the same time period. We analyzed macroinvertebrate and fish species that were collected during at least two survey periods in each river (Brazos: $n = 58$; Guadalupe: $n = 33$; Neches: $n = 83$).

For δD , subsamples were weighed into silver capsules and sent to the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University, Flagstaff, Arizona, where they were equilibrated with local water vapor to account for H isotope exchange (Wassenaar and Hobson 2000) before isotopic analysis using a Thermo Finnigan TC/EA mass spectrometer (Thermo Fisher Scientific). The standards were chicken feather, cow hoof, and bowhead whale baleen calibrated against Vienna Standard mean ocean water and standard light Antarctic precipitation. Water samples were analyzed for δD by headspace equilibrium with H_2 gas and a Pt catalyst using a Thermo Finnigan Gas-Bench II mass spectrometer (Thermo Fisher Scientific). For $\delta^{15}\text{N}$, subsamples were weighed into tin capsules and sent to the W.M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory, University of Kansas, Lawrence, Kansas, for analysis using a Thermo Finnigan MAT 253 mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). The standard for $\delta^{15}\text{N}$ was atmospheric nitrogen.

Basal production sources

δD discriminated between benthic algae and terrestrial plants in the Brazos and Guadalupe rivers (Brazos River mean benthic algae $\delta\text{D} = -214.9$, mean terrestrial plant $\delta\text{D} = -107.1$; Guadalupe River mean benthic algae $\delta\text{D} = -189.1$, mean terrestrial plant $\delta\text{D} = -96.3$). Cole et al. (2011) suggested that because of the high contrast of δD between terrestrial and algal photosynthesis, δD can be used as a tool for estimating the isotopic signature of pure algae. In the Brazos and Guadalupe rivers, samples of benthic algae had low δD signatures similar to those reported in the scientific literature (Appendix A, Table A3; Brazos low flow mean = -215.0 ; Guadalupe low flow mean = -177.8 , moderate flow mean = -206.1), indicating samples were mostly pure algae with little contamination from FPOM. However, benthic algae samples from the Neches River had higher δD values (mean = -114.8).

Seston had similar δD values as C_3 plants in the Guadalupe and Neches rivers. Seston had higher δD values than many published values of phytoplankton δD in the scientific literature, ranging from -145.2 to -79.8 in the Brazos River, from -109.3 to -77.2 in the Guadalupe River, and from -125.1 to -105.0 in the Neches River. Chlorophyll *a* of seston ranged from 3.1 to $91.8\text{ mg}\cdot\text{m}^{-3}$ in the Brazos River, from 1.8 to $8.6\text{ mg}\cdot\text{m}^{-3}$ in the Guadalupe River, and from 3.7 to $14.2\text{ mg}\cdot\text{m}^{-3}$ in the Neches River. Correlations revealed no significant relationship between chlorophyll *a* and δD of seston in the three rivers. Because benthic algae in some of the study rivers had very low δD values and seston δD signatures were so similar to δD of C_3 plants, we assume that our seston samples were dominated by terrestrial-based organic matter, which is consistent with previous inferences from research on the Brazos River (Zeug and Winemiller 2008).

Production sources supporting aquatic consumers

To correct consumer δD signatures for trophic compounding of dietary water, we first determined the total contribution of dietary water to tissue H using the following equation:

$$\omega_{\text{compound}} = 1 - (1 - \omega)^\tau$$

where ω was 0.124, the mean proportion of tissue H derived from dietary water for fishes reported by Solomon et al. (2009), and τ was the difference in trophic position between the resource and the consumer. We calculated trophic position of consumers using the following equation:

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

where $\delta^{15}\text{N}_{\text{reference}}$ was the average of the mean $\delta^{15}\text{N}$ value of each basal production source collected during each hydrologic period, and 2.54‰ was the mean value from a meta-analysis of trophic fractionation studies (Vanderklift and Ponsard 2003). We then calculated $\delta\text{D}_{\text{corrected}}$, the consumer δD signature corrected for dietary water contributions, using the following equation:

$$\delta\text{D}_{\text{corrected}} = (\delta\text{D}_{\text{consumer}} - \omega_{\text{compound}} \times \delta\text{D}_{\text{water}}) / (1 - \omega_{\text{compound}})$$

where $\delta\text{D}_{\text{consumer}}$ was the δD value of each consumer, and $\delta\text{D}_{\text{water}}$ was the δD value of water collected from each river. In all three rivers, water samples collected from different reaches during the same survey period had similar δD values (Appendix A, Table A4); therefore, for $\delta\text{D}_{\text{water}}$, we used the mean δD value of water collected during each hydrologic period.

Proportional contributions of production sources to aquatic consumers were estimated using the Stable Isotope Analysis in R (SIAR) mixing model (Parnell et al. 2010). This Bayesian model uses the stable isotope values of sources and consumers and fractionation estimates to calculate feasible ranges of source contributions with lower and upper credibility intervals showing the probability that the true value will lie within that interval. Mixing models were run separately for consumer species collected from each river and survey period. Two-way analysis of variance (ANOVA) with hydrologic period as the first factor and plant type as the second factor revealed no difference in δD between C_3 plants and C_4 grasses in the Brazos River ($F_{[1,29]} = 1.17, P = 0.29$), the Guadalupe River ($F_{[1,22]} = 3.15, P = 0.09$), or the Neches River ($F_{[1,32]} = 0.02, P = 0.89$). However, C_3 plants and C_4 grasses were significantly different in δD depending on hydrologic period in the Brazos River ($F_{[2,29]} = 7.92, P < 0.01$), Guadalupe River ($F_{[1,22]} = 12.65, P < 0.01$), and Neches River ($F_{[2,32]} = 7.76, P < 0.01$). Therefore, C_3 plants and C_4 grasses collected during each hydrologic period were averaged to yield the “terrestrial plant” end member. Because food web studies have reported that benthic and planktonic algae are similar in δD (Appendix A, Table A3), we used benthic algae δD as the signature for the “algae” end member in SIAR models. In the Brazos River, benthic algae were scarce during the high-flow period because of substrate scouring and light limitation; thus, values for benthic algae collected during the low-flow period were used for all models. Because benthic algae δD was similar between hydrologic periods in the Guadalupe River (Welch two sample t test, $t = 2.55, P = 0.16$), we pooled benthic algae samples collected during different periods for Guadalupe models. Benthic algae δD also was similar among hydrologic periods in the Neches River (one-way ANOVA, $F_{[2,3]} = 6.62, P = 0.08$); however, in many instances, all basal production sources had higher δD values than $\delta\text{D}_{\text{corrected}}$ of consumers, indicating that samples contained FPOM or that we had under-sampled benthic algae. During the low-flow period, gizzard shad (*Dorosoma cepedianum*, Clupeidae) from the Neches River had low δD values (mean $\delta\text{D} = -182.9$), similar to gizzard shad from the Brazos River (mean $\delta\text{D} = -140.4$) and Guadalupe River (mean $\delta\text{D} = -184.7$). Mixing model results revealed that benthic algae were the most important basal production source for gizzard shad in the Brazos and Guadalupe rivers during the low-flow survey periods (Brazos River lower and upper credibility intervals = 37–86; Guadalupe River lower and upper credibility intervals = 95–100). Therefore, in the Neches River, after accounting for dietary water contributions, we used δD signatures of gizzard shad collected during the low-flow period as a standard to estimate the signature of benthic algae.

For each model, we performed 500 000 iterations, discarded 50 000 initial iterations, and retained one of every 15 remaining iterations. During some hydrologic periods we only collected one individual per macroinvertebrate and fish species; thus, we did not include the residual error term in SIAR models (Parnell et al. 2010). We report lower and upper 95% credibility intervals of basal

production sources, with narrower lower and upper credibility intervals indicating more conclusive discrimination between alternative sources. To characterize the average basal production source dependence of all sampled taxa at a site, we used two-way ANOVA to model the relationship between the mean lower and upper 95% credibility intervals of terrestrial plants, rivers, and hydrologic periods. We treated 95% terrestrial contributions for the various species in each river as independent observations and the mean of those values as an index of overall community dependence. Independent variables were river, hydrologic period, and the interaction between river and hydrologic period. When a variable was significant, we used post hoc pairwise t tests to determine which pairs of levels were significantly different. We used the software program R (R Core Team 2013) for all statistical analyses and considered results with $P < 0.05$ to be statistically significant.

Results

Hydrology

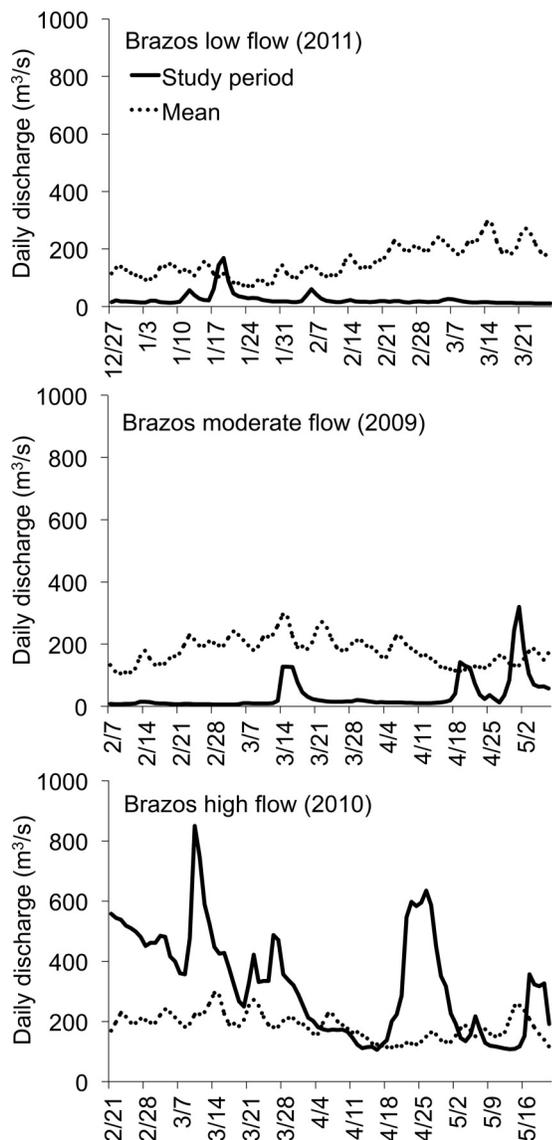
In the Brazos River, samples were collected after an extended period of low flow when daily discharge was consistently $\leq 169 \text{ m}^3 \cdot \text{s}^{-1}$ (low-flow period), an extended low-flow period followed by a short-duration flow pulse (maximum daily discharge = $320 \text{ m}^3 \cdot \text{s}^{-1}$, moderate-flow period), and a period of high flows that did not produce overbank flooding onto the floodplain (maximum daily discharge = $850 \text{ m}^3 \cdot \text{s}^{-1}$, high-flow period; Fig. 1). In the Guadalupe River, samples were collected after an extended period of low flow when daily discharge was consistently $\leq 44 \text{ m}^3 \cdot \text{s}^{-1}$ (low-flow period) and an extended period of moderate flow followed by a high-flow pulse that approached bankfull stage condition (maximum daily discharge = $240 \text{ m}^3 \cdot \text{s}^{-1}$, moderate-flow period; Fig. 2). In the Neches River, samples were collected after an extended period of low discharge when daily discharge was consistently $\leq 94 \text{ m}^3 \cdot \text{s}^{-1}$ (low-flow period), an extended period of low discharge followed by a flow pulse (maximum daily discharge = $159 \text{ m}^3 \cdot \text{s}^{-1}$, moderate-flow period), and a period when discharge gradually declined (maximum daily discharge = $270 \text{ m}^3 \cdot \text{s}^{-1}$, high-flow period; Fig. 3).

Stable isotope signatures of secondary consumers

Some shrimps and fishes had $\delta\text{D}_{\text{corrected}}$ signatures that were lower than δD of algae. In the Brazos River, consumers had more negative $\delta\text{D}_{\text{corrected}}$ values than algae during the low-flow period (one out of seven consumers) and the moderate-flow period (three out of eight consumers; Fig. 4). These consumers had $\delta\text{D}_{\text{corrected}}$ values that were slightly more negative than δD values of algae (25.9‰, on average). In the Guadalupe River, consumers had negative $\delta\text{D}_{\text{corrected}}$ relative to algae during the low-flow period (six out of seven consumers) and the moderate-flow period (one out of seven sources; Fig. 5). In the low-flow period, gizzard shad $\delta\text{D}_{\text{corrected}}$ was 93.6‰ more negative than δD of algae, and the other six of these consumers had $\delta\text{D}_{\text{corrected}}$ more similar to algae δD (26.1‰ more negative, on average). In the Neches River, after estimating δD of benthic algae from gizzard shad δD , $\delta\text{D}_{\text{corrected}}$ values of consumers were consistently greater than or equal to the δD signature of benthic algae (Fig. 6).

In the Brazos River, shifts in consumer $\delta\text{D}_{\text{corrected}}$ values were not entirely consistent with predictions. As expected, consumers revealed highest $\delta\text{D}_{\text{corrected}}$ values following the high-flow hydrologic period (Fig. 4). This shift in $\delta\text{D}_{\text{corrected}}$ occurred for algivores–detritivores, omnivores, invertivores, and piscivores. The only exception was bullhead minnow (*Pimephales vigilax*), which had similar $\delta\text{D}_{\text{corrected}}$ values following the low- and moderate-flow periods (low flow = -199.3 , moderate flow = 199.2) and lowest $\delta\text{D}_{\text{corrected}}$ values following the high-flow period (-129.1). However, contrary to expectation, consumer $\delta\text{D}_{\text{corrected}}$ signatures shifted towards a more terrestrial signature following the low-flow hydrologic period compared with the moderate-flow hydrologic

Fig. 1. Daily discharge (solid line) and mean daily discharge over the period of record (dashed line) for the 3 months preceding sample collection in the Brazos River.



period. Again, this was true for all consumers except bullhead minnow.

Somewhat unexpected shifts in consumer $\delta D_{corrected}$ values with hydrologic phase also occurred in the Guadalupe River. Consumers had lower $\delta D_{corrected}$ signatures during the low-flow period than the moderate-flow period (Fig. 5). All consumers had lower $\delta D_{corrected}$ during the low-flow period, including algivores-detritivores, omnivores, invertivores, and piscivores.

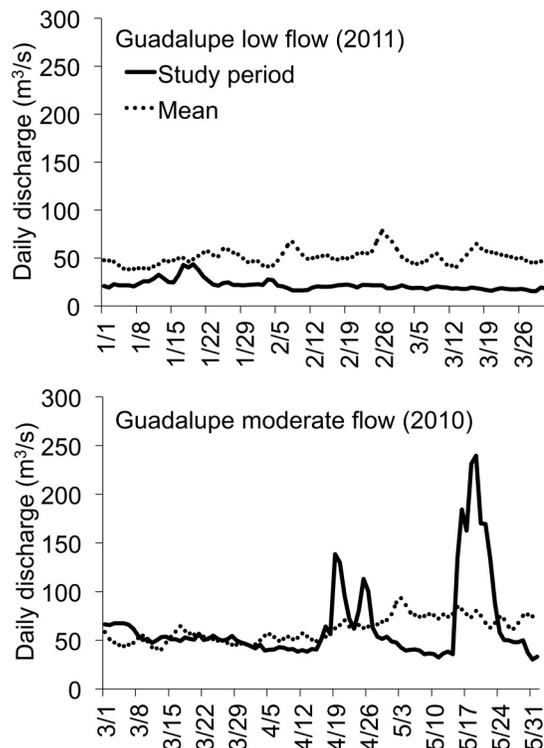
A predictable pattern of change in consumer $\delta D_{corrected}$ with hydrologic period was not as apparent in the Neches River. Most species revealed lowest $\delta D_{corrected}$ values during the low-flow and moderate-flow periods, but for two species (smallmouth buffalo (*Ictiobus bubalus*) and longnose gar (*Lepisosteus osseus*)), $\delta D_{corrected}$ values were lowest during the high-flow period (Fig. 6).

SIAR models

Brazos River low flow

The SIAR model estimated that all seven of the species that were examined had assimilated algae and a lesser fraction of material from terrestrial plants (Fig. 7). Algae had relatively large lower

Fig. 2. Daily discharge (solid line) and mean daily discharge over the period of record (dashed line) for the 3 months preceding sample collection in the Guadalupe River.



credibility intervals (≥ 19) and large upper credibility intervals (≥ 66). For most species, lower and upper credibility intervals were low for terrestrial plants, indicating relatively little assimilation of this material. Channel catfish (*Ictalurus punctatus*) probably assimilated some material from terrestrial plants, with lower credibility intervals = 34 and upper credibility intervals = 81.

Brazos River moderate flow

Similar to the low-flow period, algae were the most important production source supporting consumer biomass, with all eight species having large lower credibility intervals (≥ 40) and large upper credibility intervals (≥ 83). Material from terrestrial plants contributed little to consumer biomass, with all species having relatively small lower and upper credibility intervals for this basal production source.

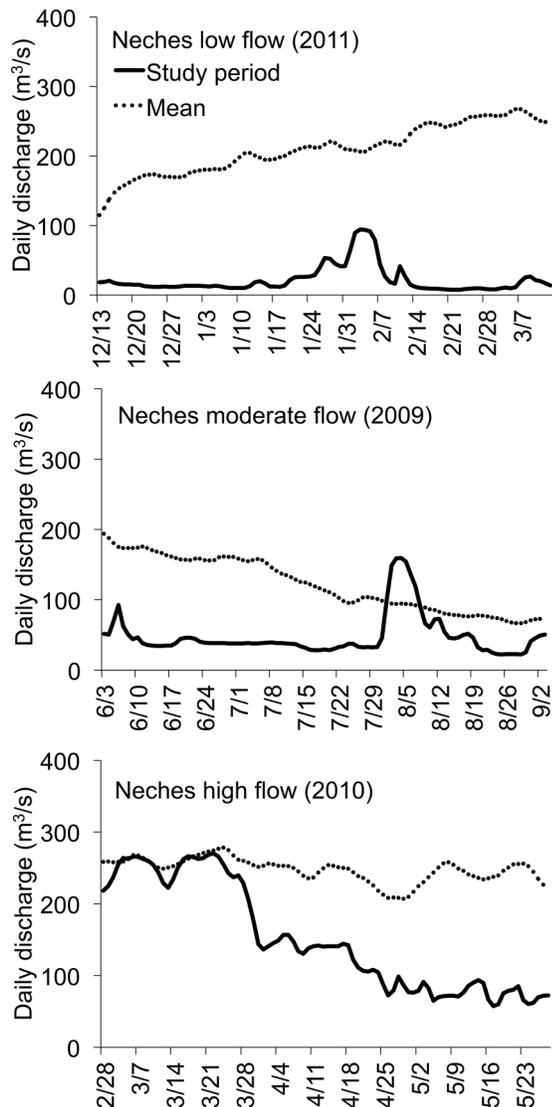
Brazos River high flow

For six of the seven species examined, contributions of terrestrial plants to consumer tissue increased during periods of extended high flows compared with a period of sustained low flow and an interval that experienced a short-duration flow pulse after an extended low-flow period (Fig. 7). For these species, lower and upper credibility intervals of terrestrial plants were greater than lower and upper credibility intervals of algae. Longnose gar apparently had assimilated large fractions of material derived from algae, with lower credibility intervals = 17 and upper credibility intervals = 74.

Guadalupe River low flow

Algae were the most important production source supporting each of the seven consumer species examined, with lower credibility intervals ≥ 58 (Fig. 8). All of the species had assimilated material mostly derived from algae.

Fig. 3. Daily discharge (solid line) and mean daily discharge over the period of record (dashed line) for the 3 months preceding sample collection in the Neches River.



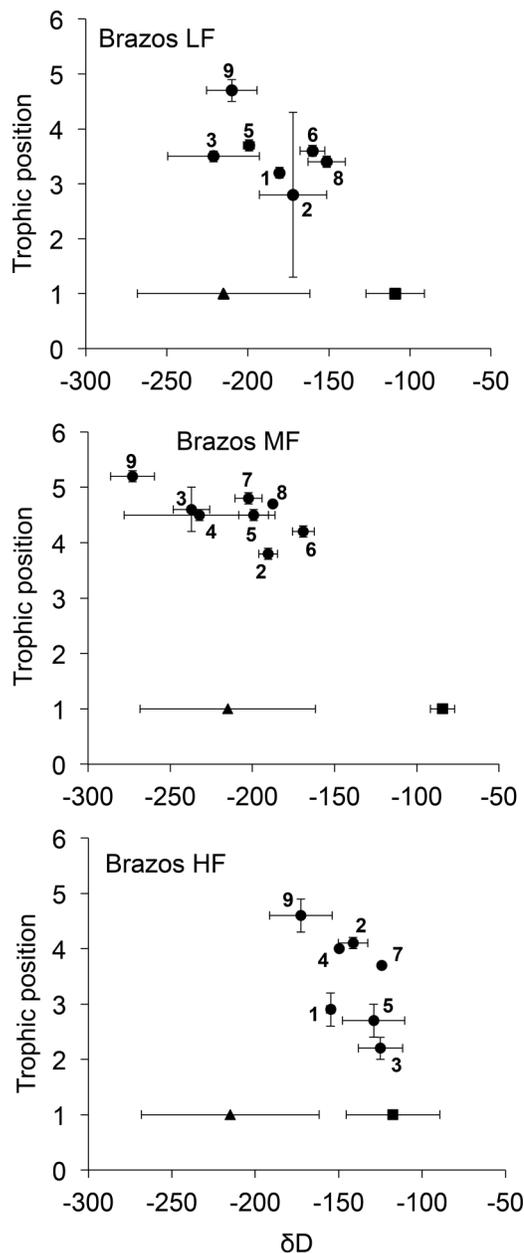
Guadalupe River moderate flow

After a high-flow pulse that followed an extended period of moderate flow, algae contributed a large fraction of material to five of the seven consumer species. During this period, contributions of material from terrestrial plants increased for many consumer species, with lower credibility intervals increasing for all species but gizzard shad, spotted gar (*Lepisosteus oculatus*), and striped mullet (*Mugil cephalus*). Material from terrestrial plants apparently supported longear sunfish (*Lepomis megalotis*) and spotted bass (*Micropterus punctulatus*); lower credibility intervals were ≥ 15 , and upper credibility intervals were ≥ 91 .

Neches River low flow

Ranges of source contributions for algae and terrestrial plants were large for many consumer species (Fig. 9). Six of the eleven species examined apparently had assimilated fractions of material from terrestrial plants, with lower credibility intervals ≥ 30 and upper credibility intervals ≥ 75 . Spotted gar probably assimilated a large fraction of material from terrestrial plants, with lower credibility intervals = 65 and upper credibility intervals = 100.

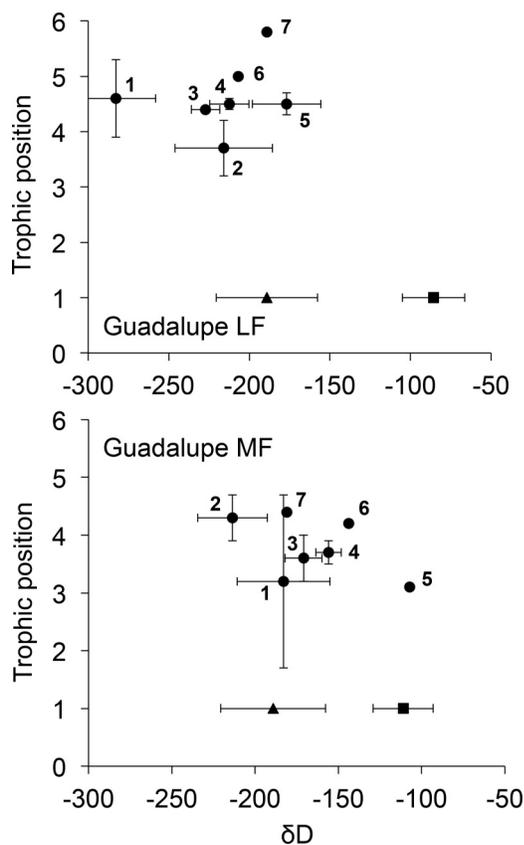
Fig. 4. Deuterium stable isotope (δD) signatures and trophic positions (mean \pm standard deviation) of consumer taxa and basal production sources following low-flow (LF), moderate-flow (MF), and high-flow (HF) hydrologic periods in the Brazos River. Triangles = algae, squares = terrestrial plants, and circles = consumer taxa. For consumers, δD was corrected for dietary water contributions. Consumer taxa codes are as follows: 1 = gizzard shad, 2 = river carpsucker, 3 = red shiner, 4 = ghost shiner, 5 = bullhead minnow, 6 = Ohio River shrimp, 7 = shoal chub, 8 = channel catfish, and 9 = longnose gar.



Neches River moderate flow

Compared with the low-flow period, lower credibility intervals for terrestrial plants increased for all species except blacktail shiner (*Cyprinella venusta*), freshwater drum (*Aplodinotus grunniens*), and spotted gar after a flow pulse that followed an extended period of low discharge. Ranges of source contributions were large for many consumer species. Several species, including smallmouth buffalo, blackstripe topminnow (*Fundulus notatus*), cinnamon river shrimp (*Macrobrachium acanthurus*), and freshwater drum, could

Fig. 5. Deuterium stable isotope (δD) signatures and trophic positions (mean \pm standard deviation) of consumer taxa and basal production sources following low-flow (LF) and moderate-flow (MF) hydrologic periods in the Guadalupe River. Triangles = algae, squares = terrestrial plants, and circles = consumer taxa. For consumers, δD was corrected for dietary water contributions. Consumer taxa codes are as follows: 1 = gizzard shad, 2 = striped mullet, 3 = red shiner, 4 = bullhead minnow, 5 = longear sunfish, 6 = spotted bass, and 7 = spotted gar.



have assimilated a large fraction of material from either terrestrial plants or algae.

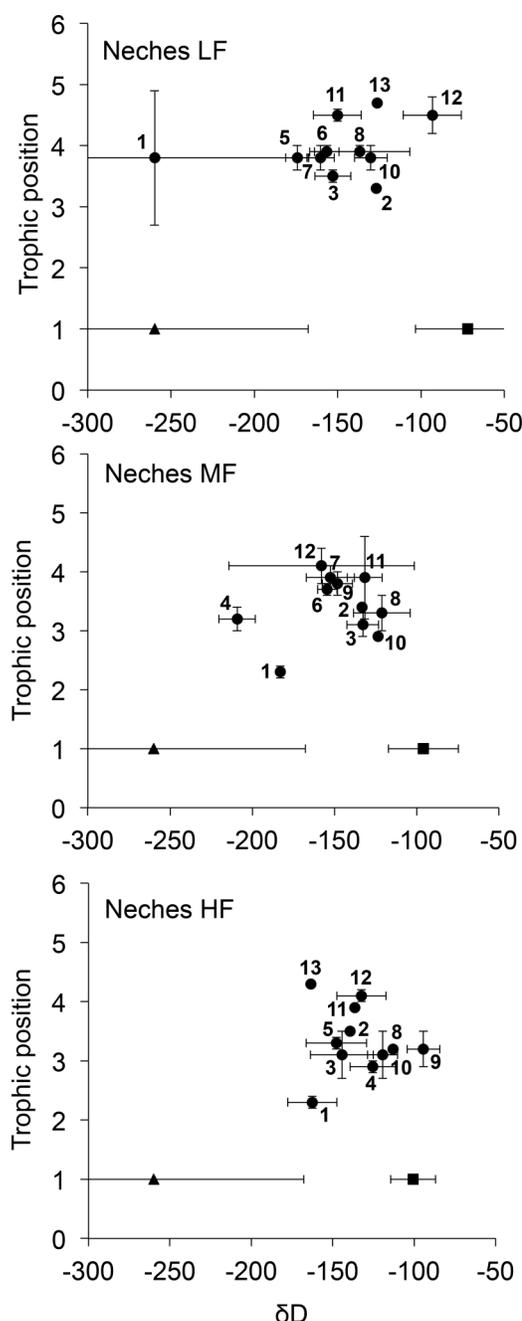
Neches River high flow

Ranges of source contributions for algae and terrestrial plants were large for almost all consumer species during the period when discharge gradually declined. Material from terrestrial plants probably contributed a large fraction to longear sunfish and freshwater drum, with relatively high lower credibility intervals (≥ 70) and high upper credibility intervals (≥ 100). Algae apparently contributed to the biomass of gizzard shad, with lower credibility intervals = 21 and upper credibility intervals = 58.

ANOVA of basal production sources

ANOVA revealed that mean terrestrial contributions were significantly different among the study rivers ($F_{[2,60]} = 36.83, P < 0.001$) and among hydrologic periods ($F_{[2,60]} = 29.41, P < 0.001$). The interaction between study river and hydrologic period also was significant ($F_{[3,60]} = 11.08, P < 0.001$), indicating that differences in terrestrial contributions among hydrologic periods depended on the river. Pairwise *t* tests showed that mean terrestrial contributions were different between all three pairs of rivers ($P < 0.001$). Because seasonal differences in terrestrial contributions depended on the river, we also used one-way ANOVA to investigate whether mean terrestrial contributions were significantly different among hydrologic periods in each study river. This analysis revealed that

Fig. 6. Deuterium stable isotope (δD) signatures and trophic positions (mean \pm standard deviation) of consumer taxa and basal production sources following low-flow (LF), moderate-flow (MF), and high-flow (HF) hydrologic periods in the Neches River. Triangles = algae, squares = terrestrial plants, and circles = consumer taxa. For consumers, δD was corrected for dietary water contributions. Consumer taxa codes are as follows: 1 = gizzard shad, 2 = smallmouth buffalo, 3 = blacktail shiner, 4 = blackstripe topminnow, 5 = bullhead minnow, 6 = mimic shiner, 7 = cinnamon river shrimp, 8 = bluegill, 9 = longear sunfish, 10 = freshwater drum, 11 = spotted bass, 12 = spotted gar, and 13 = longnose gar. The benthic algae stable isotope signature is the mean of benthic algae from the Neches and Brazos rivers.



terrestrial contributions to consumer biomass varied with hydrology in the Brazos River ($F_{[2,19]} = 24.41, P < 0.001$) and the Guadalupe River ($F_{[1,12]} = 8.95, P < 0.05$) but not in the Neches River ($F_{[2,29]} = 1.83, P = 0.18$). In the Brazos River, pairwise *t* tests indicated

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Fig. 7. Plots indicate percent contributions of terrestrial material (C_3 plants and C_4 grasses) and algae to consumer species biomass in the Brazos River. The box boundaries represent lower and upper 95% credibility intervals. LF = low-flow period, MF = moderate-flow period, and HF = high-flow period. A/D = algivore–detritivore, O = omnivore, I = invertivore, and P = piscivore. The dashed line shows the 50% contribution mark.

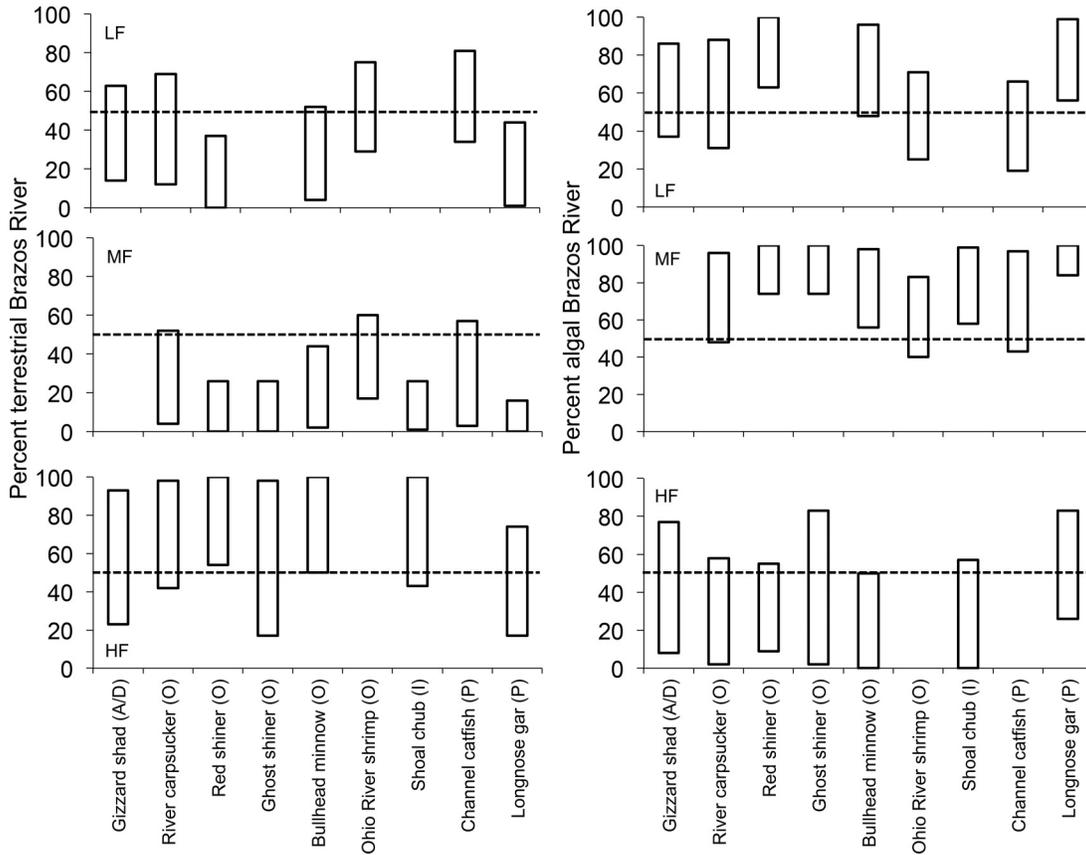


Fig. 8. Plots indicate percent contributions of terrestrial material (C_3 plants and C_4 grasses) and algae to consumer species biomass in the Guadalupe River. The box boundaries represent lower and upper 95% credibility intervals. LF = low-flow period and MF = moderate-flow period. A/D = algivore–detritivore, O = omnivore, I = invertivore, and P = piscivore. The dashed line shows the 50% contribution mark.

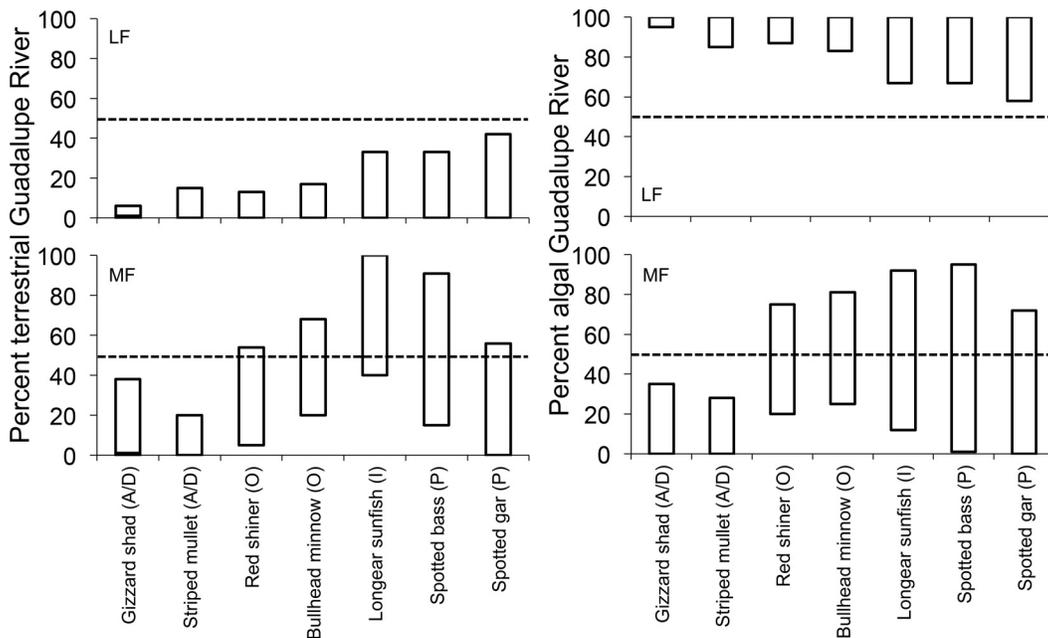
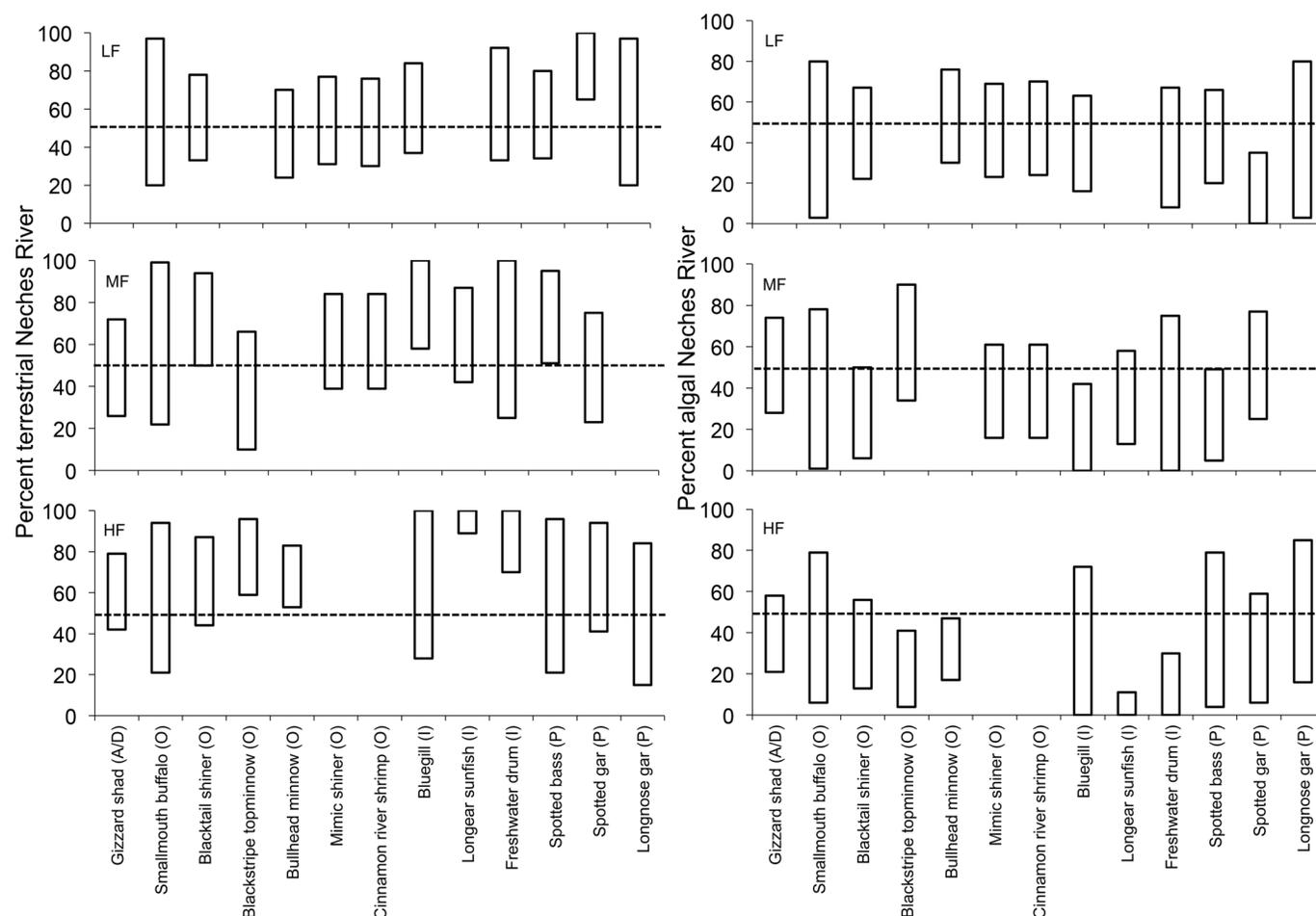


Fig. 9. Plots indicate percent contributions of terrestrial material (C_3 plants and C_4 grasses) and algae to consumer species biomass in the Neches River. The box boundaries represent lower and upper 95% credibility intervals. LF = low-flow period, MF = moderate-flow period, and HF = high-flow period. A/D = algivore–detritivore, O = omnivore, I = invertivore, and P = piscivore. The dashed line shows the 50% contribution mark.



that terrestrial contributions were different among all three hydrologic periods ($P < 0.001$ for low flow – high flow and moderate flow – high flow comparisons, $P < 0.05$ for low flow – moderate flow), with lowest mean terrestrial contributions occurring during the moderate-flow period and highest mean terrestrial contributions occurring during the high-flow period. In the Guadalupe River, mean terrestrial contributions were significantly lower during the low-flow period compared with the moderate-flow period.

Discussion

Based on temporal patterns in algal primary production and biomass in river littoral zones (Roach et al. 2014), we originally hypothesized that the relative importance of algal- versus terrestrial-based production sources supporting the food web would vary seasonally in the sediment-laden Brazos River, and consumers would be supported mostly by algal-based production sources throughout the annual hydrologic cycle in the Guadalupe and Neches rivers. In the Brazos River, fishes and macroinvertebrates revealed predictable temporal variation in $\delta D_{corrected}$. Consumers assimilated more negative $\delta D_{corrected}$ signatures during periods of moderate flow and more positive $\delta D_{corrected}$ signatures during periods of high flow. SIAR model estimates indicated that in the Brazos River, material from terrestrial plants accounted for the largest portion of consumer biomass following an extended high-flow period, when scouring and high turbidity yielded hetero-

trophic littoral zones and reduced algal biomass (Roach et al. 2014). Contrary to our hypothesis, the fraction of material from terrestrial plants supporting the upper food web increased following an extended period of low flows compared with a moderate-flow period. In the Guadalupe River, many consumers had more negative $\delta D_{corrected}$ signatures during the period of low flow than the moderate-flow period. Also contrary to expectation, the relative importance of autochthonous versus allochthonous production sources shifted temporally in the Guadalupe River, with consumers assimilating a greater fraction of material from terrestrial plants following a high-flow pulse that followed an extended period of moderate flow compared with an extended low-flow period. We did not observe predictable variation in $\delta D_{corrected}$ in relation to flow in the Neches River, where contributions of material from terrestrial plants to consumer biomass were similar during all hydrologic periods.

Implicit in our sampling design is the assumption that isotope ratios of consumer tissue reflect production source availability near the time of sampling. However, the degree that tissue stable isotope signatures reflect basal production source signatures at the time of sampling is dependent on tissue equilibration rate, which varies according to metabolism and biomass turnover. Larger ectothermic animals generally have slower growth and tissue turnover (Gillooly et al. 2001) and assimilate food more slowly (Vander Zanden et al. 1998; Harvey et al. 2002). Consequently, variation in the rate of isotopic change in muscle tissue is nega-

tively associated with consumer body size (McIntyre and Flecker 2006; Weidel et al. 2011). Warmer temperatures cause faster turnover rates in ectotherms; thus, in addition to body size, differences in water temperature among the hydrologic periods could have influenced our source estimates to some extent. For example, McIntyre and Flecker (2006) found that in a tropical river in Venezuela, rates of $\delta^{15}\text{N}$ turnover for muscle tissue of snails, tadpoles, and armored catfish (*Ancistrus triradiatus*) were rapid, with a half-life of N ranging from 18 to 50 days. Their experiment was conducted during the dry season when water temperatures ranged from 20 to 27 °C. Studies conducted in colder regions have found lower $\delta^{15}\text{N}$ turnover rates, such as 102 days for whitefish (*Coregonus nasus*) (10 °C; Hesslein et al. 1993) and 69 days for lake trout (*Salvelinus namaycush*) (11 °C; Harvey et al. 2002). In the three study rivers, water temperature during the period of sample collection ranged from 17 to 22 °C during the low-flow periods and from 25 to 30 °C during the moderate- and high-flow periods. Most consumers sampled during low-flow conditions likely reflected assimilation of resources over the previous few months, and most consumers sampled during moderate- and high-flow conditions likely reflected assimilation of resources over the previous few weeks or months depending on body size.

In the Brazos River, estimated contributions of terrestrial plants to consumer tissue were greater for all species for samples collected after high-flow periods compared with those collected after low- and moderate-flow periods, with the exception of longnose gar. The longnose gar is a large top predator in this system. The interval required for longnose gar to reach isotopic equilibrium with a new diet probably was longer than the intervals between hydrologic phases of the Brazos River examined during our study. The isotopic signature of this species, therefore, probably was not in equilibrium with its recent feeding history. Contributions of terrestrial plants to consumer biomass may have increased following the low-flow period compared with the moderate-flow period because during the low-flow period, Texas experienced a record drought that reduced mean annual discharge in the Brazos River. Agriculture and cattle grazing on the floodplain of our study area contribute to eutrophication of the river water column, stimulating blooms of cyanobacteria. Many cyanobacteria have toxins and can interfere with filter feeding by zooplankton and therefore are avoided or consumed in low amounts (Lampert 1987). The dominance of cyanobacteria during the low-flow period could have caused aquatic invertebrates to consume more detritus, resulting in a shift in basal resources supporting the upper food web. Regardless, the increase in contributions of material from terrestrial plants following the low-flow compared with moderate-flow period was minor relative to the increase in importance of terrestrial-based production sources following the high-water period.

In the Guadalupe River, contributions of terrestrial plants to consumer tissue increased following a high-flow pulse. Other studies have found that terrestrial material can support river food webs following flow pulse events, even when the river is autotrophic. Following a high-flow event in the Taieri River, a New Zealand river with low suspended sediment concentrations, consumers assimilated terrestrial-based production sources because the relative amount of terrestrial-derived material versus algae within seston (i.e., suspended FPOM) had increased (Huryn et al. 2001). Apparently, during flow pulses, lower algal biomass and production, combined with increased inputs of terrestrial organic matter from watersheds and riparian habitats, can result in greater inputs of material derived from terrestrial production sources into aquatic food chains. Because littoral zones in the Guadalupe River were autotrophic when material from terrestrial plants made greater contributions to consumers in the aquatic food web (Roach et al. 2014), our findings provide only limited support for the hypothesis that allochthonous resource subsidies

should be most important in ecosystems where net primary productivity is low (Polis and Hurd 1996; Stapp and Polis 2003).

The use of δD rather than $\delta^{13}\text{C}$ allowed us to more effectively distinguish the basal production sources supporting the upper food web, and this was because algae and terrestrial plants in the Brazos and Guadalupe rivers had distinctive δD signatures. Furthermore, the use of δD allowed us to infer the fraction of particles derived from terrestrial plants versus algae in our seston samples. Consumer $\delta\text{D}_{\text{corrected}}$ values that were more negative than values of local basal production sources suggest that consumers had assimilated material at another location that had different isotopic ratios than the same material at the survey site or that one or more influential production sources were not sampled at the survey site. Most consumers had $\delta\text{D}_{\text{corrected}}$ values that were slightly more negative than δD of algae. However, in the Guadalupe River, $\delta\text{D}_{\text{corrected}}$ of gizzard shad, an algivore–detritivore, was considerably more negative than algae δD . We may have failed to sample algae taxa important in the shad diet. In any event, it seems unlikely that this source of error would greatly affect our inferences regarding shad assimilation of basal production sources. Tissue lipid and water content also can confound interpretations of consumer assimilation of production sources based on δD (Jardine et al. 2009). C:N ratios were relatively low for our consumer samples, and therefore lipids were unlikely to have been a significant source of error. Differences in contributions of water to consumer tissue δD among species or size classes could account for some variation in consumer δD . Laboratory extraction of lipids from benthic algae samples (Logan et al. 2008) and methods that effectively separate algae and FPOM (Hamilton et al. 2005) could improve resolution of estimates of algal contribution to consumer tissues.

Results from SIAR models indicated that in the Brazos and Guadalupe rivers, algae made greater contributions to consumer biomass following low-flow periods and terrestrial plants made greater contributions following high-flow pulses. These results indicate that hydrologic phase has a strong influence on basal production sources. Other studies also have linked hydrologic and temporal context to the structure of riverine food webs. For example, Power et al. (1996) found that in a northern California river, year-to-year variation in the magnitude and variability of floods controlled the length of food chains. In that river, hydrologic regime during the preceding winter also was shown to be a strong determinant of fish impacts on algal biomass and invertebrate density (Power et al. 2008). In our study, turbidity also must have played a role in influencing source contributions, because shifts in $\delta\text{D}_{\text{corrected}}$ of basal production sources with hydrology was most apparent in the Brazos River, the river with highest turbidity levels, and this shift did not occur in the Neches River, the one with lowest turbidity levels. These results are most consistent with predictions of the River Wave Concept (Humphries et al. 2014). This ecosystem model predicts that local autochthonous and allochthonous basal production sources should support the food web when discharge is low and there is little lateral or longitudinal transport of organic matter. Humphries et al. (2014) hypothesized that if discharge is increasing or decreasing, allochthonous organic matter originating from upstream should dominate, and at peak flow following floodplain inundation, allochthonous organic matter originating from the floodplain should dominate. Because none of our sampling periods followed floodplain inundation, the material derived from terrestrial plants that entered the food web following flow pulses must have originated from upstream reaches and (or) runoff from local watersheds. The River Wave Concept was intended to unify other river ecosystem concepts, including the River Continuum Concept, Flood Pulse Concept, and Riverine Productivity Model. Although incorporation of interactions between hydrology and physicochemical factors, such as turbidity, adds complexity to fluvial ecosystem models,

this should facilitate more accurate predictions of food web dynamics.

Estimation of production sources that support aquatic consumers of large rivers with different physicochemical characteristics is necessary for predicting how environmental change alters material fluxes affecting biomass and diversity at higher trophic levels. Dams, water diversion, and watershed impacts have altered hydrology, sediment and nutrient dynamics, and ecological processes of rivers throughout the world (Dynesius and Nilsson 1994; Ligon et al. 1995; Bouwman et al. 2005; Graf 2006; Poff et al. 2007). Some of these impacts have been shown to reduce flux through detritus-based pathways relative to primary producer–grazer pathways characterized by more rapid exchange of material between basal production sources and consumers (Tewfik et al. 2005; Layman et al. 2007). Algae, because of their higher nutritional value, have been hypothesized to support greater secondary production than terrestrial plants or detritus derived from plants (Legendre and Rassoulzadegan 1995; Cotner and Biddanda 2002). In fluvial ecosystems, algae–grazer pathways tend to be associated with small invertebrates and fishes that have relatively rapid growth and high population turnover that tend to enhance demographic resilience in response to frequent disturbances (Townsend et al. 1997). However, detrital pathways also are important, as the present study has shown, and these have been hypothesized to be associated with lower trophic efficiency, weaker interaction strength, and time lags that can stabilize food webs (DeAngelis 1992; Rooney and McCann 2012). Consequently, human-induced changes to river ecosystems, such as impoundments, that cause shifts in basal production sources are associated with food webs that are less stable, with fewer dominant energy pathways (Cross et al. 2013). Greater recognition of spatial and temporal variation in the importance of detritus as a basal production source will improve predictions of how human impacts to watersheds and rivers affect secondary production and consumer–resource interactions.

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References

- Angradi, T.R. 1994. Trophic linkages in the lower Colorado River: multiple stable isotope evidence. *J. N. Am. Benthol. Soc.* **13**: 479–495. doi:10.2307/1467845.
- Bouwman, A.F., Van Drecht, G., Knoop, J.M., Beusen, A.H.W., and Meinardi, C.R. 2005. Exploring changes in river nitrogen export to the world's oceans. *Global Biogeochem. Cycles*, **19**: GB1002. doi:10.1029/2004GB002314.
- Clapcott, J.E., and Bunn, S.E. 2003. Can C_4 plants contribute to aquatic food webs of subtropical streams? *Freshw. Biol.* **48**: 1105–1116. doi:10.1046/j.1365-2427.2003.01077.x.
- Cole, J.J., Carpenter, S.R., Kitchell, J., Pace, M.L., Solomon, C.T., and Weidel, B. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. *Proc. Natl. Acad. Sci. U.S.A.* **108**: 1975–1980. doi:10.1073/pnas.1012807108. PMID:21245299.
- Cotner, J.B., and Biddanda, B.A. 2002. Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems. *Ecosystems*, **5**: 105–121. doi:10.1007/s10021-001-0059-3.
- Cross, W.F., Baxter, C.V., Rosi-Marshall, E.J., Hall, R.O., Jr., Kennedy, T.A., Donner, K.C., Wellard Kelly, H.A., Seegert, S.E.Z., Behn, K.E., and Yard, M.D. 2013. Food-web dynamics in a large river discontinuum. *Ecol. Monogr.* **83**: 311–337. doi:10.1890/12-1727.1.
- Davis, A.M., Blanchette, M.L., Pusey, B.J., Jardine, T.D., and Pearson, R.G. 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshw. Biol.* **57**: 2156–2172. doi:10.1111/j.1365-2427.2012.02858.x.

- DeAngelis, D.L. 1992. Dynamics of nutrient cycling and food webs. Chapman & Hall, New York.
- Doucett, R.R., Barton, D.R., Guiguer, K.R.A., Power, G., and Drimmie, R.J. 1996. Comment: Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. *Can. J. Fish. Aquat. Sci.* **53**(8): 1913–1915. doi:10.1139/f96-114.
- Doucett, R.R., Marks, J.C., Blinn, D.W., Caron, M., and Hungate, B.A. 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. *Ecology*, **88**: 1587–1592. doi:10.1890/06-1184. PMID:17601150.
- Dynesius, M., and Nilsson, C. 1994. Fragmentation and flow regulation of river systems in the northern third of the world. *Science*, **266**: 753–762. doi:10.1126/science.266.5186.753. PMID:17730396.
- Finlay, J.C., Doucett, R.R., and McNeely, C. 2010. Tracing energy flow in stream food webs using stable isotopes of hydrogen. *Freshw. Biol.* **55**: 941–951. doi:10.1111/j.1365-2427.2009.02327.x.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., and Charnov, E.L. 2001. Effects of size and temperature on metabolic rate. *Science*, **293**: 2248–2251. doi:10.1126/science.1061967. PMID:11567137.
- Graf, W.L. 2006. Downstream hydrologic and geomorphic effects of large dams on American rivers. *Geomorphology*, **79**: 336–360. doi:10.1016/j.geomorph.2006.06.022.
- Halaj, J., and Wise, D.H. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology*, **83**: 3141–3151. doi:10.1890/0012-9658(2002)083[3141:IOADSO]2.0.CO;2.
- Hamilton, S.K., Sippel, S.J., and Bunn, S.E. 2005. Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. *Limnol. Oceanogr. Methods*, **3**: 149–157. doi:10.4319/lom.2005.3.149.
- Harvey, C.J., Hanson, P.C., Essington, T.E., Brown, P.B., and Kitchell, J.F. 2002. Using bioenergetics models to predict stable isotope ratios in fishes. *Can. J. Fish. Aquat. Sci.* **59**(1): 115–124. doi:10.1139/f01-203.
- Herwig, B.R., Wahl, D.H., Dettmers, J.M., and Soluk, D.A. 2007. Spatial and temporal patterns in the food web structure of a large floodplain river assessed using stable isotopes. *Can. J. Fish. Aquat. Sci.* **64**(3): 495–508. doi:10.1139/f07-023.
- Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing brood whitefish (*Coregonus nasus*) in response to change in diet traced by $\delta^{34}\text{S}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$. *Can. J. Fish. Aquat. Sci.* **50**(10): 2071–2076. doi:10.1139/f93-230.
- Hoeinghaus, D.J., Winemiller, K.O., and Agostinho, A.A. 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. *Ecosystems*, **10**: 1019–1033. doi:10.1007/s10021-007-9075-2.
- Humphries, P., Keckeis, H., and Finlayson, B. 2014. The river wave concept: integrating river ecosystem models. *BioScience*, **64**: 870–882. doi:10.1093/biosci/biu130.
- Huryn, A.D., Riley, R.H., Young, R.G., Arbuckle, C.J., Peacock, K., and Lyon, G. 2001. Temporal shift in the contribution of terrestrial organic matter to consumer production in a grassland river. *Freshw. Biol.* **46**: 213–226. doi:10.1046/j.1365-2427.2001.00648.x.
- Jardine, T.D., Kidd, K.A., and Cunjak, R.A. 2009. An evaluation of deuterium as a food source tracer in temperate streams of eastern Canada. *J. N. Am. Benthol. Soc.* **28**: 885–893. doi:10.1899/09-046.1.
- Jepsen, D.B., and Winemiller, K.O. 2002. Structure of tropical river food webs revealed by stable isotope ratios. *Oikos*, **96**: 46–55. doi:10.1034/j.1600-0706.2002.960105.x.
- Junk, W.J., Bayley, P.B., and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. *In Proceedings of the International Large River Symposium*. Edited by D.P. Dodge. *Can. Spec. Publ. Fish. Aquat. Sci.* **106**: 110–127.
- Lampert, W. 1987. Laboratory studies on zooplankton–cyanobacteria interactions. *N.Z. J. Mar. Freshw. Res.* **21**: 483–490. doi:10.1080/00288330.1987.9516244.
- Layman, C.A., Quattrochi, J.P., Peyer, C.M., and Allgeier, J.E. 2007. Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol. Lett.* **10**: 937–944. doi:10.1111/j.1461-0248.2007.01087.x. PMID:17845294.
- Legendre, L., and Rassoulzadegan, F. 1995. Plankton and nutrient dynamics in marine waters. *Ophelia*, **41**: 153–172. doi:10.1080/00785236.1995.10422042.
- Ligon, F.K., Dietrich, W.E., and Trush, W.J. 1995. Downstream ecological effects of dams: a geomorphic perspective. *BioScience*, **45**: 183–192. doi:10.2307/1312557.
- Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A., and Luttcavage, M.E. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modeling methods. *J. Anim. Ecol.* **77**: 838–846. doi:10.1111/j.1365-2656.2008.01394.x. PMID:18489570.
- Marcarelli, A.M., Baxter, C.V., Mineau, M.M., and Hall, R.O., Jr. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology*, **92**: 1215–1225. doi:10.1890/10-2240.1. PMID:21797150.
- McIntyre, P.B., and Flecker, A.S. 2006. Rapid turnover of tissue nitrogen of primary consumers in tropical freshwaters. *Oecologia*, **148**: 12–21. doi:10.1007/s00442-005-0354-3. PMID:16456686.
- Moline, M.A., Claustre, H., Frazer, T.K., Schofield, O., and Vernet, M. 2004. Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob. Change Biol.* **10**: 1973–1980. doi:10.1111/j.1365-2486.2004.00825.x.

- Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., and Wall, D.H. 2004. Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* **7**: 584–600. doi:10.1111/j.1461-0248.2004.00606.x.
- Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, **5**: e9672. doi:10.1371/journal.pone.0009672. PMID:20300637.
- Peters, J.M., Wolf, N., Stricker, C.A., Collier, T., and del Rio, C.M. 2012. Effects of trophic level and metamorphosis on discrimination of hydrogen isotopes in a plant-herbivore system. *Plos ONE*, **7**: e32744. doi:10.1371/journal.pone.0032744. PMID:22470423.
- Poff, N.L., Olden, J.D., Merritt, D.M., and Pepin, D.M. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *Proc. Natl. Acad. Sci. U.S.A.* **104**: 5732–5737. doi:10.1073/pnas.0609812104. PMID:17360379.
- Polis, G.A., and Hurd, S.D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *Am. Nat.* **147**: 396–423. doi:10.1086/285858.
- Power, M.E., Parker, M.S., and Wooten, J.T. 1996. Disturbance and food chain length in rivers. In *Food webs: integration of pattern and dynamics*. Edited by G.A. Polis and K.O. Winemiller. Chapman and Hall, New York. pp. 286–297.
- Power, M.E., Parker, M.S., and Dietrich, W.E. 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecol. Monogr.* **78**: 263–282. doi:10.1890/06-0902.1.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roach, K.A. 2013. Environmental factors affecting incorporation of terrestrial material into large river food webs. *Freshw. Sci.* **32**: 283–298. doi:10.1899/12-063.1.
- Roach, K.A., Winemiller, K.O., and Davis, S.E., III. 2014. Autochthonous production in shallow littoral zones of five floodplain rivers: effects of flow, turbidity, and nutrients. *Freshw. Biol.* **59**: 1278–1294. doi:10.1111/fwb.12347.
- Rooney, N., and McCann, K.S. 2012. Integrating food web diversity, structure and stability. *Trends Ecol. Evol.* **27**: 40–46. doi:10.1016/j.tree.2011.09.001. PMID:21944861.
- Solomon, C.T., Cole, J.J., Doucett, R.R., Pace, M.L., Preston, N.D., Smith, L.E., and Weidel, B.C. 2009. The influence of environmental water on the hydrogen stable isotope ratio in aquatic consumers. *Oecologia*, **161**: 313–324. doi:10.1007/s00442-009-1370-5. PMID:19471971.
- Soto, D.X., Wassenaar, L.L., Hobson, K.A., and Catalan, J. 2011. Effects of size and diet on stable hydrogen isotope values (δD) in fish: implications for tracing origins of individuals and their food sources. *Can. J. Fish. Aquat. Sci.* **68**(11): 2011–2019. doi:10.1139/f2011-112.
- Stapp, P., and Polis, G.A. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia*, **134**: 496–504. doi:10.1007/s00442-002-1146-7. PMID:12647121.
- Tewfik, A., Rasmussen, J.B., and McCann, K.S. 2005. Anthropogenic enrichment alters a marine benthic food web. *Ecology*, **86**: 2726–2736. doi:10.1890/04-1537.
- Thorp, J.H., and Delong, M.D. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, **70**: 305–308. doi:10.2307/3545642.
- Thorp, J.H., and Delong, M.D. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, **96**: 543–550. doi:10.1034/j.1600-0706.2002.960315.x.
- Thorp, J.H., Delong, M.D., Greenwood, K.S., and Casper, A.F. 1998. Isotopic analysis of three food web theories in constricted and floodplain regions of a large river. *Oecologia*, **117**: 551–563. doi:10.1007/s004420050692.
- Townsend, C.R., Scarsbrook, M.R., and Dolédec, S. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *J. N. Am. Benthol. Soc.* **16**: 531–544. doi:10.2307/1468142.
- Vadeboncoeur, Y., Jeppesen, E., Vander Zanden, M.J., Schierup, H.-H., Christoffersen, K., and Lodge, D.M. 2003. From Greenland to green lakes: cultural eutrophication and the loss of benthic pathways in lakes. *Limnol. Oceanogr.* **48**: 1408–1418. doi:10.4319/lo.2003.48.4.1408.
- Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.* **46**: 2061–2066. doi:10.4319/lo.2001.46.8.2061.
- Vander Zanden, M.J., Hulshof, M., Ridgway, M.S., and Rasmussen, J.B. 1998. Application of stable isotope techniques to trophic studies of age-0 small-mouth bass. *Trans. Am. Fish. Soc.* **127**: 729–739. doi:10.1577/1548-8659(1998)127<0729:AOSITT>2.0.CO;2.
- Vanderklift, M.A., and Ponsard, S. 2003. Sources of variation in consumer-diet $\delta^{15}N$ enrichment: a meta-analysis. *Oecologia*, **136**: 169–182. doi:10.1007/s00442-003-1270-z. PMID:12802678.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**(1): 130–137. doi:10.1139/f80-017.
- Wassenaar, L.L., and Hobson, K.A. 2000. Improved method for determining the stable-hydrogen isotopic composition (δD) of complex organic materials of environmental interest. *Environ. Sci. Technol.* **34**: 2354–2360. doi:10.1021/es990804i.
- Weidel, B.C., Carpenter, S.R., Kitchell, J.F., and Vander Zanden, M.J. 2011. Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake ^{13}C addition. *Can. J. Fish. Aquat. Sci.* **68**(3): 387–399. doi:10.1139/F10-158.
- Wetzel, R.G., and Likens, G.E. 1991. *Limnological analyses*. 2nd ed. Springer, New York.
- Zeug, S.C., and Winemiller, K.O. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. *Ecology*, **89**: 1733–1743. doi:10.1890/07-1064.1. PMID:18589537.

Appendix A

Table A1. Average physicochemical characteristics and algal primary production and biomass (chlorophyll *a*) in littoral zones of the study rivers during low-flow (LF) and high-flow periods (HF).

Characteristic	Brazos		Guadalupe		Neches	
	LF	HF	LF	HF	LF	HF
Turbidity (FTU)*	64	618	35	238	54	91
Soluble reactive P (mg·L ⁻¹)	0.3	1.4	0.6	3.2	0.4	0.6
Dissolved inorganic N (mg·L ⁻¹)	1.6	4.5	2.0	3.8	1.2	2.8
Silica (mg·L ⁻¹)	6.3	1.1	8.4	6.9	8.7	11.1
Water-column net ecosystem production (mg C·m ⁻³ ·day ⁻¹)	363	157	215	117	101	5
Benthic net ecosystem production (mg C·m ⁻² ·day ⁻¹)	197	-66	533	133	17	<1
Water-column chlorophyll <i>a</i> (mg·m ⁻³)	48.2	11.8	5.4	2.1	9.1	0.9
Benthic chlorophyll <i>a</i> (mg·m ⁻²)	11.3	0.7	12.0	4.5	4.8	0.8

Note: Measurements were made on point sandbanks. Methods are available in Roach et al. (2014).

*FTU, formazin turbidity unit.

Table A2. Consumer species representing feeding guilds, with family and common name when applicable in parentheses.

River	Order	Family	Species	Common name	Feeding guild
B, G, N	Clupeiformes	Clupeidae	<i>Dorosoma cepedianum</i>	Gizzard shad	Algivore–detritivore
N	Cyprinodontiformes	Fundulidae	<i>Fundulus notatus</i>	Blackstripe topminnow	Omnivore
B	Cypriniformes	Catostomidae	<i>Carpionodes carpio</i>	River carpsucker	Omnivore
G			<i>Ictiobus bubalus</i>	Smallmouth buffalo	Omnivore
B, G		Cyprinidae	<i>Cyprinella lutrensis</i>	Red shiner	Omnivore
N			<i>Cyprinella venusta</i>	Blacktail shiner	Omnivore
B			<i>Macrhybopsis hyostoma</i>	Shoal chub	Invertivore
B			<i>Notropis buechanani</i>	Ghost shiner	Omnivore
N			<i>Notropis volucellus</i>	Mimic shiner	Omnivore
B, G, N			<i>Pimephales vigilax</i>	Bullhead minnow	Omnivore
N	Decapoda	Palaemonidae	<i>Macrobrachium acanthurus</i>	Cinnamon river shrimp	Omnivore
B			<i>Macrobrachium ohione</i>	Ohio River shrimp	Omnivore
G, N	Lepisosteiformes	Lepisosteidae	<i>Lepisosteus oculatus</i>	Spotted gar	Piscivore
B, N			<i>Lepisosteus osseus</i>	Longnose gar	Piscivore
G	Mugiliformes	Mugilidae	<i>Mugil cephalus</i>	Striped mullet	Algivore–detritivore
N	Perciformes	Centrarchidae	<i>Lepomis macrochirus</i>	Bluegill	Invertivore
G, N			<i>Lepomis megalotis</i>	Longear sunfish	Invertivore
G, N			<i>Micropterus punctulatus</i>	Spotted bass	Piscivore
N		Sciaenidae	<i>Aplodinotus grunniens</i>	Freshwater drum	Invertivore
B	Siluriformes	Ictaluridae	<i>Ictalurus punctatus</i>	Channel catfish	Piscivore

Note: B, Brazos River; G, Guadalupe River; N, Neches River.

Table A3. Hydrogen stable isotope values ($\delta D \pm$ standard error, SE) of algae in streams, rivers, and lakes from the scientific literature.

System	Location	Algae classification	δD	Reference
Ash Fork	Nevada, USA	Cyanobacteria	-245.5 ± 3	Doucett et al. 2007
		Diatoms	-231.2 ± 6	
		Filamentous algae	-240.0 ± 3	
Colorado River	Arizona, USA	Filamentous algae	-291.6 ± 5	Doucett et al. 2007
	Nevada, USA	Cyanobacteria	-244.6 ± 4	Doucett et al. 2007
Fossil Creek	Arizona, USA	Diatoms	-214.3 ± 10	Doucett et al. 2007
		Diatoms	-251.4 ± 4	
		Filamentous algae	-277.3 ± 8	
Boston Brook	New Brunswick, Canada	Biofilm	-212.1 ± 59	Jardine et al. 2009
Blue Rock Brook	New Brunswick, Canada	Biofilm	-180.7 ± 36	Jardine et al. 2009
Cains River	New Brunswick, Canada	Biofilm	-213.1 ± 10	Jardine et al. 2009
Middle Branch Catamaran Brook	New Brunswick, Canada	Biofilm	-173.5 ± 12	Jardine et al. 2009
Culvert crossing	New Brunswick, Canada	Biofilm	-141.3 ± 6	Jardine et al. 2009
Cedar Brook	New Brunswick, Canada	Biofilm	-253.9 ± 31	Jardine et al. 2009
Cochrane Brook	New Brunswick, Canada	Biofilm	-139.7 ± 9	Jardine et al. 2009
Cains River, downstream	New Brunswick, Canada	Biofilm	-208.4 ± 1	Jardine et al. 2009
Dungarvon River	New Brunswick, Canada	Biofilm	-208.7 ± 2	Jardine et al. 2009
Flewellling Brook	New Brunswick, Canada	Biofilm	-135.3 ± 10	Jardine et al. 2009
Gaspereau River	New Brunswick, Canada	Biofilm	-169.2 ± 11	Jardine et al. 2009
Gounamitz River washout	New Brunswick, Canada	Biofilm	-247.2 ± 29	Jardine et al. 2009
Little Southwest Miramichi	New Brunswick, Canada	Biofilm	-215.5 ± 2	Jardine et al. 2009
Muzroll Brook tributary	New Brunswick, Canada	Biofilm	-193.1 ± 2	Jardine et al. 2009
Newcastle Creek	New Brunswick, Canada	Biofilm	-158.9 ± 2	Jardine et al. 2009
Newcastle Creek tributary	New Brunswick, Canada	Biofilm	-188.8 ± 30	Jardine et al. 2009
Newcastle Creek, upstream	New Brunswick, Canada	Biofilm	-188.7 ± 2	Jardine et al. 2009
North Renous headwaters	New Brunswick, Canada	Biofilm	-182.3 ± 11	Jardine et al. 2009
North Renous Lake	New Brunswick, Canada	Biofilm	-196.5 ± 2	Jardine et al. 2009
North Renous 108	New Brunswick, Canada	Biofilm	-177.5 ± 4	Jardine et al. 2009
North Renous washout	New Brunswick, Canada	Biofilm	-206.3 ± 12	Jardine et al. 2009
Otter Brook	New Brunswick, Canada	Biofilm	-193.1 ± 16	Jardine et al. 2009
Restigouche at Boston Brook	New Brunswick, Canada	Biofilm	-265.4 ± 47	Jardine et al. 2009
Renous River at Red Bridge Road	New Brunswick, Canada	Biofilm	-192.7 ± 11	Jardine et al. 2009
Restigouche straight reach	New Brunswick, Canada	Biofilm	-236.1 ± 44	Jardine et al. 2009
Smith Forks	New Brunswick, Canada	Biofilm	-239.5 ± 29	Jardine et al. 2009
Salmon River, downstream	New Brunswick, Canada	Biofilm	-172.1 ± 5	Jardine et al. 2009
Salmon River, upstream	New Brunswick, Canada	Biofilm	-183.6 ± 12	Jardine et al. 2009
Upper Libbie's Brook	New Brunswick, Canada	Biofilm	-161.7 ± 6	Jardine et al. 2009
Unnamed stream	New Brunswick, Canada	Biofilm	-126.3 ± 3	Jardine et al. 2009
Wasson Creek	New Brunswick, Canada	Biofilm	-173.8 ± 12	Jardine et al. 2009
McKinley	California, USA	<i>Cladophora</i>	-204.9 ± 5	Finlay et al. 2010
Barnwell	California, USA	<i>Nostoc</i>	-196.2	Finlay et al. 2010

Table A3 (concluded).

System	Location	Algae classification	δD	Reference
Fox	California, USA	Diatoms	-145.8 \pm 4	Finlay et al. 2010
		<i>Cladophora</i>	-194.7 \pm 15	
Jack Hearts	California, USA	<i>Nostoc</i>	-218.0 \pm 1	Finlay et al. 2010
		Diatoms	-185.2 \pm 3	
Elder	California, USA	<i>Cladophora</i>	-228.8 \pm 5	Finlay et al. 2010
		Diatoms	-189.6 \pm 4	
South Fork Eel	California, USA	<i>Cladophora</i>	-213.9 \pm 4	Finlay et al. 2010
		<i>Lemanea</i>	-136.0	
		<i>Nostoc</i>	-183.5 \pm 15	
		<i>Cladophora</i>	-241.6 \pm 5	
Ten Mile	California, USA	<i>Lemanea</i>	-138.1	Finlay et al. 2010
		<i>Nostoc</i>	-225.8 \pm 5	
		<i>Cladophora</i>	-264.2 \pm 9	
Paul Lake	Wisconsin, USA	<i>Lemanea</i>	-149.1 \pm 3	Cole et al. 2011
		<i>Nostoc</i>	-213.6 \pm 6	
Paul Lake	Wisconsin, USA	Benthic algae	-180 \pm 6	Cole et al. 2011
		Phytoplankton	-198 \pm 12	
Crampton Lake	Wisconsin, USA	Deep phytoplankton	-212 \pm 4	Cole et al. 2011
		Benthic algae	-186 \pm 15.2	
		Phytoplankton	-195 \pm 8.2	
		Deep phytoplankton	-200 \pm 8.3	

Table A4. Hydrogen stable isotope values (δD , mean and range in parentheses) and sample sizes for water samples from the Brazos, Guadalupe, and Neches rivers during different hydrologic periods.

River	Hydrologic period	<i>n</i>	δD
Brazos	Low flow	3	-17.1 (-18.5 to -15.9)
	Moderate flow	2	-8.4 (-10.2 to -6.6)
	High flow	1	-45.9
Guadalupe	Low flow	3	-17.7 (-18.3 to -17.4)
	Moderate flow	1	-21.5
Neches	Low flow	2	-17.0 (-17.1 to -16.9)
	Moderate flow	1	1.1
	High flow	1	-9.5