

Spatial and temporal variation in aquatic food-web structure in the Pecos River in New Mexico and Texas, USA

by

Jessica L. East

A Thesis

In

Wildlife, Aquatic, and Wildlands Science and Management

Submitted to the Graduate Faculty
of Texas Tech University in
Partial Fulfillment of the
Requirements for the Degree of

MASTER OF SCIENCES

Approved

Dr. Allison Pease
Chair of Committee

Dr. Timothy Grabowski

Dr. Scott Longing

Mark Sheridan
Dean of the Graduate School

May, 2015

Copyright 2015, Jessica L. East

Acknowledgments

This project was made possible by many moving parts. First and foremost, I would like to thank my major advisor, Dr. Allison Pease, who has become my professional and personal mentor. I appreciate the incredible investment she placed in my project and professional development. My committee members have been exceptional sources of knowledge, Dr. Tim Grabowski provided invaluable edits, and Dr. Scott Longing spent time and energy on invertebrate identification and study design. I would like to thank Dr. Chris Hoagstrom, Steve Davenport, Natascha Israel, and Matthew Vanlandeghem for their expertise on the Pecos River and allowing me to tag along on their Pecos projects. Thank you to Dr. Tom Turner, Dr. Jake Vander Zanden, Dr. Juske Horita, and Ushio Kawai for their knowledge of the art of stable isotope sample preparation and analyses. I would also like to thank the Clark Hubbs Scholarship Foundation through the Texas Chapter of the American Fisheries Society for additional funding. I appreciate the help trudging in the Orla sludge and the long days at Independence Creek from Matthew Acre, Jared Breaux, Jordan Calvert, Andrew East, Ashton Howe, Grant Kilcrease, Wade Massure, Jessica Pease, Allison Pease, Cassie Vaughan, and Chris Wilcut. For what probably felt like endless hours, Chris Wilcut, Jared Breaux, and Cassie Vaughan assisted in sample preparation in the lab; I could not thank you enough. The staff at Bitter Lake National Wildlife Refuge and The Nature Conservancy Preserve at Independence Creek, especially Jeff Sanchez, Floyd Truetken, Jason and Lisa Wrinkle, and Corbin Neil were gracious enough to allow us access to the Pecos and on-site lodging. Lastly, but quite possibly the most important, I need to thank my husband Andrew East for becoming incredibly skilled at solving existential crises. I could not have completed this thesis without you.

Table of Contents

Acknowledgments ii

Abstract..... iv

List of Tables vi

List of Figures..... ii

 I. Introduction..... 1

 II. Methods 8

 III. Results 16

 IV. Discussion..... 40

Literature Cited..... 51

Abstract

Understanding how aquatic communities change with natural variation along longitudinal gradients and how they respond to anthropogenic impacts is critical for effective riverine management. In addition to natural shifts along its continuum, the Pecos River is impacted by a variety of anthropogenic influences that affect discharge, salinity, and riparian and instream habitat structure. I assessed variation in main-stem river food webs by estimating carbon sources, trophic positions, niche breadth and resource use by consumers at twelve sites using stable isotope analysis (carbon and nitrogen). Across physiographic regions, fish species richness, food chain length, and assemblage-wide niche breadth were inversely related to specific conductivity. IsoError mixing models revealed differences in sources of dietary carbon supporting fish production along the longitudinal fluvial gradient, with a shift toward reliance on algal production in the middle reaches of the river. Trophic niche breadth was greatest for assemblages in less degraded sites with higher fish species richness. My analyses also suggest that anthropogenic inputs may be enriching baseline nitrogen isotope ratios at one study site. Across seasons, isotope signatures remained fairly constant in five common fish species. In general, my results suggest that anthropogenic influences in portions of the Pecos River have negative impacts on the diversity of consumers and trophic resources in local food webs. Characterizing changes in food-web structure in relation to natural and anthropogenic factors is important for habitat assessment, stream restoration, and management and conservation strategies.

List of Tables

| | |
|--|----|
| 1. A subset of environmental variables measured during field surveys in summer 2013 representing local habitat variation across physiographic regions. Three-month average discharge was estimated using data from nearest USGS flow gages..... | 17 |
| 2. Percent land use categories of sub-watersheds of sample sites across physiographic regions..... | 18 |
| 3. . Presence of fish species at each site across physiographic regions..... | 20 |
| 4. Presence of macroinvertebrate families at each site across physiographic regions. Data is not available for site 5 due to sampling error..... | 22 |
| 5. Mean isotopic ratios \pm SE for fish species across physiographic regions. Sample size (n) refers to number of specimens used for stable isotope analysis..... | 28 |
| 6. Mean isotopic ratios \pm SE for macroinvertebrate families across physiographic regions. Sample size (n) refers to number of specimens used for stable isotope analysis. Families may have been present at a site (see Table 4) but not analyzed due to cost limitations..... | 30 |
| 7. Community-wide metrics: nitrogen range (NR), carbon range (CR), total convex hull area (TA), nearest neighbor distance (NND), standard deviation of NND (NNDsd), and food-chain length (FCL) across physiographic regions..... | 36 |

List of Figures

1. Map of study area. Study sites are designated by shaded circles. Shades represent the physiographic regions within the Pecos Basin..... 10

2. Longitudinal trends for fish species richness and specific conductivity. Sites are placed in longitudinal order (upstream-downstream) from left to right. The black line indicates specific conductivity ($\mu\text{S}/\text{cm}$) and the color of species richness bars indicate physiographic region..... 24

3. Total Pecos River food-web structure. Small shapes represent individual samples and large shapes represent averages of each taxa. Squares denote fish, triangles denote macroinvertebrates, diamonds represent riparian vegetation, and circles represent instream sources..... 26

4. Mean isotopic ratios with standard error bars of fishes across the Pecos River. Species codes are the same as listed in Table 3. 31

5. Proportions of carbon sources derived from ISOError two-source mixing model. Plot A is the basal carbon sources of fishes and Plot B is macroinvertebrate carbon sources. The sources are listed in a longitudinal gradient, with dotted lines delineating change in physiographic region.....33

6. Isotope biplots of sample sites in longitudinal order, site 1 is in the Pecos Plains physiographic region, sites 2-3 are in the Roswell Basin, sites 4-9 are in the Permian Basin, and sites 10-12 are in the Edwards Plateau. Dark symbols represent consumers and white symbols represent producers. The squares represent all fishes at a site, triangles represent invertebrates, diamonds indicate riparian trees, and circles represent instream producers..... 35

7. Simple linear regression of specific conductivity for each site against food chain length ($R^2=0.391$, $p\text{-value}=0.02$). 37

8. Total convex hulls of each physiographic region calculated from consumer ratios from each site..... 38

9. Seasonal variation found in fish species at site 3 near Artesia, NM. Different color squares indicate species, general trends across species appear to have enriched nitrogen ratios in the spring and summer compared to fall and spring. 39

10. Seasonal variation found in fish species at site 11 downstream of the confluence of Independence Creek. Difference color squares indicate different species, general trend is a broadening of carbon signatures in summer and fall compared to tighter clustering in the winter and spring..... 39

Chapter I

Introduction

Understanding and predicting how aquatic communities change with natural variation along longitudinal gradients, and how they respond to anthropogenic impacts, is critical for effective riverine management. As such, elucidating the complex interactions influencing stream ecosystem food-web structure, including linkages between landscape features, local abiotic conditions, and biotic assemblages, remains one of the main challenges confronting stream ecologists (Richards, Johnson & Host, 1996). Natural variation in river ecosystems is influenced by climate, basin geology, topography, and vegetation, which interact at multiple spatial and temporal scales (Poff & Ward, 1990; Bunn & Arthington, 2002; Olden, 2010).

Variation in food-webs along natural longitudinal gradients

Stream systems are organized as nested hierarchies whereby larger-scale abiotic factors (e.g, surficial geology, climate, land use) constrain the structural and dynamic organization of local-scale physical habitat elements (e.g, geomorphology, physicochemistry), which may in turn regulate biological communities (Frissell et al. 1986, Poff 1997). Fish and macroinvertebrate communities are expected to shift along the longitudinal gradient as the presence and distribution of riffles, runs, and pools changes (Schlosser, 1987) and substrate composition shifts (Berkman & Rabeni, 1987; Pease *et al.*, 2011) along with changes in temperature, conductivity, turbidity, and instream cover (Montgomery, 1999; Fischer & Paukert, 2008).

Traditional models have described the spatial and temporal shifts in basal carbon sources of riverine food webs as a function of stream canopy cover, stream width, connectivity, productivity, and the magnitude and timing of flooding of energy rich

riparian areas (Vannote *et al.*, 1980; Ward & Stanford, 1983; Junk, Bayley & Sparks, 1989; Thorp & DeLong, 1994). According to the river continuum concept (Vannote *et al.*, 1980), allochthonous inputs contribute more energy to the upper reaches of streams and as the river widens, a shift to autochthonous inputs occurs with decreases in canopy cover. However, lower reaches can have similar contributions of autochthonous and allochthonous carbon as the depth of the photic zone decreases. In floodplain rivers, the flood pulse concept (Junk, Bayley & Sparks, 1989) describes how regular, high-magnitude flooding allows carbon from the energy-rich floodplain to be available to the aquatic food web, making the shift from allochthonous to autochthonous less distinct. Previous studies of fish communities along longitudinal gradients have shown that addition of species and functional feeding groups should be expected from upstream to downstream and should correlate with an increase in ecosystem size (e.g., Schlosser, 1987; Rahel & Hubert, 1991; Pease *et al.*, 2012).

Natural seasonal variation in riverine systems

Seasonal variation in habitat characteristics, resource availability, and fish and invertebrate communities also influences food-web structure in rivers (Winemiller, 1990; Closs & Lake, 1994; Zeug & Winemiller, 2008). Rivers of the US Great Plains have pronounced variation in habitat characteristics associated with natural flood-drought cycles (Poff *et al.*, 1997; Dodds *et al.*, 2004). The contribution of autochthonous and allochthonous sources also varies with flooding and seasonal drying (Pease *et al.*, 2006; Zeug & Winemiller, 2008). Seasonality can restructure food webs as consumers are able to capitalize on shifting availability of food sources. In seasons with greater availability

and diversity of prey items, some consumers may move up a trophic level (Hoeninghaus *et al.*, 2003; Deus & Petrere-Junior, 2003).

Anthropogenic influences on Southwestern rivers

In lotic systems, anthropogenic disturbances influence local and landscape-scale abiotic factors by disrupting the hierarchy of natural variables which drive stream ecosystems (Poff *et al.*, 1997; Allan, 2004). Studies of altered rivers and streams have shown that anthropogenic factors disrupt the natural longitudinal patterns of food-web structure in relation to consumer diversity (Wang, Lyons & Kanehl, 2001; Allan, 2004), alter basal resource use and availability (Power, Dietrich & Finlay, 1996; Bunn, Davies & Winning, 2003; Burford *et al.*, 2008), and enrich nitrogen isotopic ratios (DeBruyn, Marcogliese & Rasmussen, 2003; Anderson & Cabana, 2005; Winemiller *et al.*, 2011).

The Pecos River lies at the southwestern edge of the Great Plains in New Mexico and Texas and is an example of a highly altered freshwater system. The Pecos River is affected by threats common to rivers in semi-arid regions including altered flow regime and watershed land use (e.g., agricultural, urban, potash mining, and oil and gas drilling), which also can increase the salinity of the system (Hoagstrom, 2009; Linam & Kleinsasser, 1996; Williams, 2001).

Stream ecosystems in the North American Great Plains and arid Southwestern U.S. regions display natural “boom and bust” flow variability (Thoms & Sheldon, 2002) which is sensitive to flood-pulse alterations. Inhibition of these floods via dams has led to surface-flow intermittence and homogenization of habitat via channel incision (Hoagstrom, 2009). For example, when the storage capacities of reservoirs are greater than the runoff rates, as in the arid Southwest, downstream flows can be reduced up to 100% (Graf, 1999) which reduces connectivity. Reduced habitat availability with

diminished flow can decrease local consumer diversity and prevent access to riparian resources by aquatic species (Bunn, Davies & Winning, 2003; Dekar & Magoulick, 2007; Bogan, Boersma & Lytle, 2013). These impacts, coupled with increased sedimentation and altered temperature regimes, can lead to shifts in species richness and local assemblage structure (Ward & Stanford, 1983; Allan & Castillo, 2007). For example, an increase in sediment can cause a shift in invertebrates assemblages towards burrowing taxa, making them less accessible to predators (Suttle *et al.*, 2004). Downstream of dams, a decrease in the flux of nutrients can shift the sources of primary production (Winemiller *et al.*, 2011), and a decrease in total suspended solids can lead to loss of species that are adapted to a sediment-rich and turbid conditions, triggering a decline in biodiversity (Ward & Stanford, 1983; Kumm & Varis, 2007). According to the Serial Discontinuity Concept (Ward & Stanford, 1983), position of impoundments along the longitudinal gradient can influence multiple abiotic and biotic parameters. The presence of seven major dams and other flow alterations (abstractions, diversions) along the Pecos River likely has affected aquatic food-web structure via the mechanisms described above.

Agricultural and urban land-use practices may influence aquatic food-web structure by increasing nutrient and sediment loads to streams, decreasing aquatic consumer diversity, reducing availability of riparian vegetation and woody debris, and alteration of flows (Wang *et al.*, 1997; Quinn, 2000; Wang, Lyons & Kanehl, 2001; Stepenuck, Crunkilton & Wang, 2002; Allan, 2004; Yuan & Miyamoto, 2005; Hoagstrom, 2009; Marzin, Verdonschot & Pont, 2013). Additional nutrient loads increase autotrophic biomass and production, and have been shown to shift consumer assemblages, reduce biodiversity, and disrupt natural ecosystem functions (Allan, 2004;

Anderson & Cabana, 2005). An increase of sedimentation to a stream has been shown to cause a decrease in primary production by causing bottom-up effects through food webs as it fills interstices of benthic substrate. Filling of interstitial habitat influences fish and invertebrate community structure as it coats gills and respiratory surfaces, increases turbidity, scouring, and abrasion (Allan, 2004). Portions of the Pecos watershed have been converted for water-intensive row crops (National Land Cover Database, 2011), using the river as a source for irrigation. Large dairy farms are present in parts of the watershed in New Mexico, possibly contributing increased nutrients to the system (J.L. East, observation, April 2013). While urban land cover is not extremely high in the region, studies have shown that a relatively low amount of impervious surfaces can have large impacts on riverine ecosystems (Wang *et al.*, 1997; Wang, Lyons & Kanehl, 2001). The dominant source of impervious surfaces in the Pecos watershed comes from the infrastructure associated with mining, oil, and gas production in the region including, roads and pump-jack platforms (J.L. East, observation, April 2013).

Increased salinity associated with anthropogenic change is a concern in many river ecosystems (Cañedo-Argüelles *et al.*, 2013; Williams, 2001). Naturally occurring salinity in rivers is the result of climate, catchment geology, distance from the ocean, topography, and vegetation (Cañedo-Argüelles *et al.*, 2013). Agriculture increases salinity by replacing natural, deep-rooted vegetation with shallow-rooted species, thus increasing saline wastewater discharge to the rivers (Williams, 2001). Irrigation for agriculture also affects salinity of nearby rivers as crops tend to absorb only a small portion of the salt in water while the rest returns to the river channel via runoff. Diversion of inflows for irrigation also increases evapotranspiration leading to a higher salinity (Cañedo-Argüelles *et al.*, 2013; Hoagstrom, 2009). Increased salinity can have dramatic

impacts on the diversity and function of a system (Brock, Nielsen & Crossle, 2005). One such impact is a shift to a more simplified euryhaline food web (Cañedo-Argüelles *et al.*, 2013; Dickman & Gochnauer, 1978). It can also increase growth of bacteria (Dickman & Gochnauer, 1978), decrease invertebrate abundance (Carver *et al.*, 2009), and reduce fish diversity (Ostrand & Wilde, 2002). The natural salinity in the Pecos River is attributed to saline strata which underlie much of the watershed and saline springs which feed into the main channel (Hoagstrom, 2009). Frequent floods, historically part of the Pecos flow regime, would have diluted streamflows and facilitated salt export from the area. Anthropogenic salinization in the Pecos River has been associated with flow alteration from dams and water extraction, agricultural practices, and mining, oil, and gas wastewater (Hoagstrom, 2009).

Assessing changes in food-web structure with stable isotope analysis

Characterizing spatial and temporal changes in food-web structure in relation to environmental gradients altered by anthropogenic factors is important for habitat assessment, stream restoration, and conservation strategies. Stable isotope analysis has been widely adopted as a useful tool to characterize changes in trophic positions in food webs, resource acquisition, and amount of niche space occupied by assemblages (Boecklen *et al.*, 2011). Ratios of stable carbon ($\delta^{13}\text{C}$) can be used to infer basal production sources, while nitrogen ($\delta^{15}\text{N}$) isotopes indicate trophic position of consumers within a food-web (Fry, 2006). Isotope ratios have been used extensively to examine individual and population-level responses to physiochemical variation and biotic interactions that influence community structure across complex ecotones, such as

longitudinal fluvial gradients, freshwater-marine transitions in estuaries, and shifts in anthropogenic influences within the watershed (Anderson & Cabana, 2005; Gido, Franssen & Propst, 2006; Winemiller *et al.*, 2011).

The objectives of this study were to (1) examine differences in taxonomic and functional structure of fish and invertebrate assemblages across multiple environmental gradients along the Pecos River (2) estimate changes in aquatic food-web structure related to natural physiography and anthropogenic impacts across the basin and (3) examine seasonal variation in aquatic food-web structure at a subset of reaches. In accordance with the RCC and studies relating aquatic diversity with habitat size, I expected to see an increase in consumer diversity from upstream to downstream sites, but previous studies have shown that anthropogenic factors can lead to deviations from this expected pattern (DeLong & Brusven, 1998; Cheek & Taylor, 2015). Additionally, I expected sources of carbon to shift from greater relative importance of allochthonous carbon in upstream sites with gradually increasing contribution of autochthonous carbon downstream (Vannote *et al.*, 1980). Similar to other North American Great Plains rivers, I expected to see temporal shifts in food-web structure with changes in availability of carbon sources and prey items (Pease *et al.*, 2006; Zeug & Winemiller, 2008).

Chapter II

Methods

Study region

The Pecos River flows for 1480 km through Texas and New Mexico. The river begins in the mid-elevation conifer forests of the Sangre de Cristo Mountains in northcentral New Mexico and flows south-southeast approximately 672 km before its confluence with the Rio Grande in Texas. It is the largest tributary of the Rio Grande, with a drainage area of approximately 115,000 km², and contributes high levels of salinity when entering Lake Amistad near Langtry, Texas (Jensen *et al.*, 2006; Gregory & Hatler, 2008). Below the Sangre de Cristo Mountains, the Pecos River enters the Great Plains where it flows through four main geographic regions: the Pecos Plains, Roswell Basin, Permian Basin, and the Edwards Plateau (Fiedler & Nye, 1933; Head & Orcutt, 2002; Hoagstrom, 2009) (Figure 1). The river is impounded by seven large dams on the main stem and many smaller low-head irrigation dams (Yuan & Miyamoto, 2008). Salinity of the Pecos River in some segments is far higher than historical levels mainly because of irrigation, increased evapotranspiration, and flood suppression (Hoagstrom, 2009). Much of the natural stream flow in the upper portion of the river is derived from springs and spring snow melt which is then captured in the Santa Rosa Reservoir in New Mexico (Hatch, Baltosser & Schmitt, 1985; Yuan & Miyamoto, 2008). The river perennially meanders through a broad, sandy valley in the Roswell Basin, with low discharge controlled by Fort Sumner Dam releases, groundwater inflows and treated wastewater returns (Hoagstrom, Brooks & Davenport, 2008). Natural salinity in this region is derived from brine aquifer discharge near New Mexico-Texas border. In the Permian Basin the channel is wide, discharge is low, and the salinity is high as flows are

derived from irrigation returns, minimal releases from dams, and a small amount is contributed by seeps and springs between Red Bluff Dam and Girvin, TX (Hoagstrom, 2009). The river then flows through the limestone canyons of the Edwards Plateau, where the influence of freshwater springs and tributaries, the largest of which, Independence Creek (watershed area of $\sim 1976 \text{ km}^2$), greatly increases discharge while decreasing salinity levels (Linam & Kleinsasser, 1996; Hoagstrom, 2009).

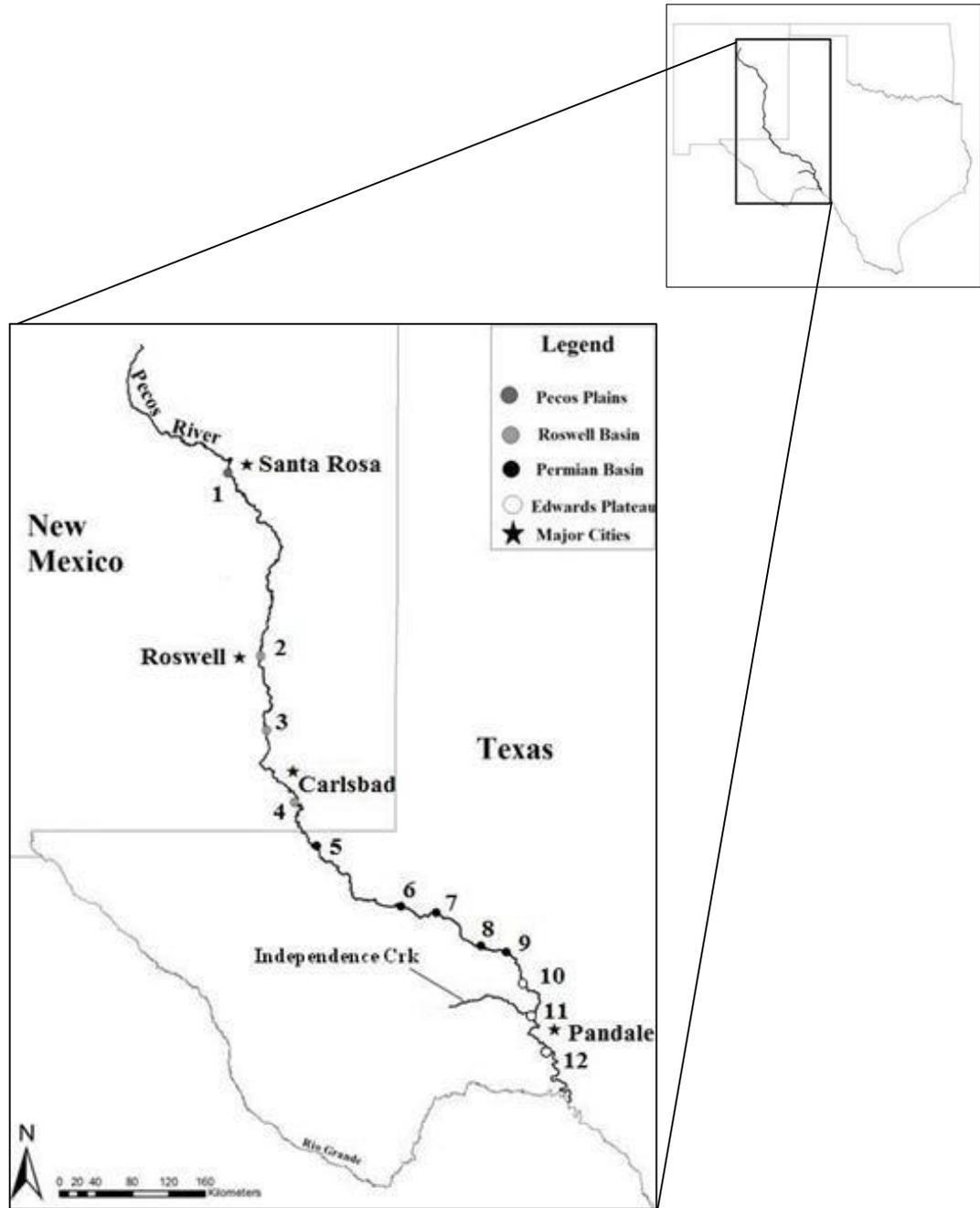


Figure 1. Map of study area. Study sites are designated by shaded circles. Shades represent the physiographic regions within the Pecos Basin.

Field data collection

In June and July 2013, twelve sites were sampled in the main stem of the Pecos River: one site in the Pecos Plains region, two in the Roswell basin, six in the Permian Basin and three in the Edwards Plateau (Figure 1.1). Five sites were resampled seasonally, two in the Roswell Basin, two in the Permian Basin, and one in the Edwards Plateau region. Each sample reach was approximately 150 m in length.

Temperature, pH, dissolved oxygen, and specific conductance were measured at each site using an EXO1 multi-probe sonde (Yellow Springs Instruments, Yellow Springs, Ohio). Reach-wide characteristics of number of riffles and maximum pool depth were taken at each study site. Additional environmental variables were assessed using one to four habitat transects, 50 m apart, at each site. Transects spanned the width of the river and were chosen to represent the variety of mesohabitats across the reach. Variables measured at each transect included in-stream cover, wetted width, depth and flow velocity profile, canopy cover, bank slope, substrate composition, riparian buffer width, and composition of riparian vegetation. Percent land cover was calculated using ArcGIS 10.1 for USGS cataloging hydrologic unit (subwatershed scale). Land-cover types were classified under five categories: cropland, developed and other human use, open shrubland-grassland, forested land, or semi-arid desert using the publicly available National Land Cover Database (NLCD) for 2011 (<http://www.mrlc.gov/nlcd2011.php3>).

Macroinvertebrates were collected using a 500 μm mesh kick net and a 500 μm mesh Surber sampler. Riparian vegetation, aquatic macrophytes, and multicellular benthic algae were grab sampled to obtain a representative sample of the most abundant taxa in each reach. In sites where rocks were present (in the Pecos Plains and Edwards Plateau), a representative sample of periphyton was scraped from the rocks. Fishes were collected

using a 1.8 m by 6.1 m, 4.8 mm braided cotton mesh seine. Number of seine hauls was determined by species composition of hauls, with a minimum of five 5-m seine hauls per reach until no new species were captured. In reaches where deep pools were present, experimental gill nets, trotlines, and angling were used for supplemental sampling of large-bodied fishes. Fishes were identified, counted, and either released or euthanized in MS-222. White muscle tissue free of bone, scales, or exoskeletal fragments was used for stable isotope analysis of consumers. Macroinvertebrates were placed in a cooler with water for 10-12h to clear gut contents and then placed on ice for transport to lab where they were identified to the taxonomic level of family. Three replicate grab samples of algae, aquatic macrophytes (where present), and riparian vegetation from each site were preserved on ice for transport to the lab and identified to lowest taxonomic level possible. All tissue samples were placed on dry-heat sterilized Petri dishes and desiccated in a drying oven at 60°C for 48h and then ground into fine powder with a mortar and pestle. Composite samples of similar sized small fish and macroinvertebrate specimens per family were used to ensure adequate sample mass.

To assess temporal variation, five common fish species, *Cyprinella lutrensis* (Red Shiner), *Cyprinodon variagatus* X *Cyprinodon pecosensis* hybrid (Sheepshead Minnow X Pecos Pupfish), *Fundulus grandis* (Gulf Killifish), *Lucania parva* (Rainwater Killifish), and *Gambusia affinis* (Western Mosquitofish), were also sampled seasonally in October 2013, February 2014, and April 2014 at a subset of sites (Sites 2, 3, 5, 9, 11) and prepared for stable isotope analysis as described above.

Stable isotope analyses

Fish, macroinvertebrate, riparian and instream vegetation samples were weighed in tin capsules (Costech Analytical Technologies Inc., Valencia, CA) prior to analysis of carbon and nitrogen isotope ratios at the Laboratory for Stable Isotope Geochemistry, Department of Geosciences, Texas Tech University (TTU), or University of Wyoming Stable Isotope Facility (UWYOSIF), depending on Delta V (TTU) or ThermoFinnigan Delta Plus (UWYOSIF) mass spectrometer instrument availability. Ratios of stable isotopes were reported in parts per thousand (‰ or per mil) in standard delta (δ) notation. The δ -values were computed as:

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

where R is equal to $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Fry, 2006; Sharp, 2007). Pee Dee Belemnite limestone was used as the standard for the carbon isotopes, and atmospheric nitrogen for the nitrogen standard.

Bi-plots of mean $\delta^{13}\text{C}/\delta^{15}\text{N}$ signatures of consumers were used to identify general patterns of variation according to site, consumer species or family, season, and physiographic region. Trophic position of consumers was calculated using the formula from Vander Zanden and Rasmussen (2001), with primary consumers as baseline trophic position ($\lambda=2$).

$$\text{Trophic Position}_{\text{consumers}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4 + \lambda$$

Sources of carbon used by consumers were divided into instream (autochthonous) and riparian (allochthonous) sources to determine the percent contribution of each production source. Mean $\delta^{13}\text{C}$ values for common instream autotrophs (*Chara* algae and submerged macrophytes) made up the autochthonous sources, and mean $\delta^{13}\text{C}$ values for common riparian trees and shrubs (*Salix nigra*, *Prosopis spp.* and *Tamarix spp.*) were

used for allochthonous carbon sources. Along with the $\delta^{13}\text{C}$ ratios for the instream and riparian carbon sources, $\delta^{13}\text{C}$ signatures for fishes and macroinvertebrates were pooled and averaged per site and analyzed using a two-source single isotope mixing model, ISOERROR 1.04 (Phillips & Gregg, 2001). The model uses consumer isotopic values to estimate proportions of allochthonous and autochthonous basal resources supporting secondary production.

I calculated site-specific, stable-isotope-based community metrics to quantify variation in trophic structure among sites (Layman *et al.*, 2007). I calculated the following four metrics to describe trophic diversity based on the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plots, with metrics serving as a proxy for niche space: range in $\delta^{13}\text{C}$ (CR), range in $\delta^{15}\text{N}$ (NR), total area (TA), and mean distance to centroid (CD). These metrics were calculated using the mean ^{13}C and ^{15}N ratios of fish species at each site. CR is a measure of basal $\delta^{13}\text{C}$ variation; theoretically, a larger range indicates greater basal resource availability. NR represents the magnitude of vertical structure within a food web in relation to the $\delta^{15}\text{N}$ values of a baseline specific to each sample site. In this study I used macroinvertebrates classified as either shredders (Coleoptera Elmidae larvae, Coleoptera Hydrophilidae larvae, and Ephemeroptera Tricorythidae) or scrapers (Gastropoda Physidae) as the baseline at each site depending on availability. To measure the extent of trophic diversity across both axes (carbon and nitrogen), total area of the convex hull in Euclidean space (TA) was compared across sites. Trophic redundancy was measured using nearest neighbor distance (NND) and standard deviation of nearest neighbor distance (SDNND). Food chain length (FCL) was calculated for each site using a trophic position (λ) of 2.0 as a baseline for primary consumers (Vander Zanden & Rasmussen, 1999):

$$FCL = (\delta^{15}N_{\text{top predator}} - \delta^{15}N_{\text{baseline}})/3.4 + \lambda$$

As with NR calculation above, I used shredders and scrapers as a baseline across sites, with the exception of site 5, where no shredders were collected where we substituted a filterer-collector taxon, Hydropsychidae (Trichoptera). In this case $\delta^{15}N$ values were deemed appropriate for baseline values as they were between producers and secondary consumers. Simple linear regression was used to determine relationships between community-wide metrics and environmental variables.

Results

Abiotic factors at the watershed and local reach scale varied along the longitudinal gradient. Specific conductivity was lowest in the Pecos Plains and Edwards Plateau regions, while peaking in the Permian Basin (Table 1). Discharge was lowest in the Roswell Basin, and highest in the Edwards Plateau. Dominant substrate was sand in Pecos Plains and Roswell Basin, mud/silt in the Permian Basin, and cobble/bedrock in the Edwards Plateau. Land-cover analysis revealed semi-arid desert as the dominant land cover type across all sub-watersheds except for the Pecos Plains where shrub and grassland was dominant (Table 2). The Roswell Basin had the most agriculture vegetation cover of the four regions, the Permian Basin had the most developed or anthropogenically disturbed land cover. The Edwards Plateau had the greatest variety of land-cover types.

Table 1. A subset of environmental variables measured during field surveys in summer 2013 representing local habitat variation across physiographic regions. Three-month average discharge was estimated using data from nearest USGS flow gages.

| Site Name | Site No. | Specific Conductivity ($\mu\text{S}/\text{cm}$) | 3-month Average Discharge (m^3/s) | Instantaneous Discharge (m^3/s) | Dominant Substrate | <i>Tamarix</i> spp. Abundant | Max Depth (cm) | No. Riffles in Reach | Presence of Aquatic Macrophytes |
|------------------------------------|----------|---|---|---|--------------------|------------------------------|----------------|----------------------|---------------------------------|
| Pecos Plains | | | | | | | | | |
| <i>Santa Rosa, NM</i> | 1 | 149 | 0.207 | 0.68 | Sand | N | 45.9 | 1 | Common |
| Roswell Basin | | | | | | | | | |
| <i>BLNWR, NM</i> | 2 | 31575 | 1.070 | 0.056 | Sand | Y | 54.4 | 0 | Absent |
| <i>Artesia, NM</i> | 3 | 15835 | 1.383 | 1.051 | Sand | Y | 150 | 0 | Absent |
| Permian Basin | | | | | | | | | |
| <i>Loving, NM</i> | 4 | 9352 | 0.575 | 1.362 | Cobble | N | 46.5 | 2 | Common |
| <i>Orla, TX</i> | 5 | 34499 | 0.001 | 0.000 | Mud/Silt | Y | 67 | 0 | Common |
| <i>Coyanosa, TX</i> | 6 | 29690 | 0.066 | 0.374 | Mud/Silt | Y | 60.8 | 1 | Common |
| <i>FM1053, TX</i> | 7 | 32373 | | 0.344 | Mud/Silt | Y | 45.4 | 1 | Common |
| <i>Girvin, TX</i> | 8 | 39370 | 0.266 | 3.112 | Mud/Silt | Y | 80.1 | 1 | Common |
| <i>Iraan, TX</i> | 9 | 13769 | | 0.288 | Cobble | Y | 72.1 | 3 | Abundant |
| Edwards Plateau | | | | | | | | | |
| <i>I-10 Bridge, TX</i> | 10 | 13568 | | 0.430 | Cobble | Y | 91.5 | 0 | Common |
| <i>Independence Crk Confl., TX</i> | 11 | 5221 | 0.298 | 6.594 | Cobble | N | >200 | 2 | Rare |
| <i>Pandale, TX</i> | 12 | 3805 | 1.597 | 18.449 | Bedrock | N | 48.8 | 4 | Rare |

Table 2. Percent land use categories of sub-watersheds of sample sites across physiographic regions.

| Land-Use Categories (km²) | Pecos Plains (n=1) | Roswell Basin (n=2) | Permian Basin (n=6) | Edwards Plateau (n=3) |
|---|-----------------------------------|------------------------------------|------------------------------------|--------------------------------------|
| Semi-arid Desert | 3.5% | 91.3% | 92.9% | 90.1% |
| Cropland (km ²) | 0.0% | 1.5% | 0.9% | 0.1% |
| Developed and Other Human Use | 0.7% | 0.0% | 4.2% | 0.6% |
| Open Shrubland or Grassland | 79.5% | 5.0% | 1.3% | 4.3% |
| Forested Land | 16.3% | 2.1% | 0.7% | 4.9% |

A total of thirty fish species were collected from the 12 sample reaches; of these species, six were non-native: *Fundulus grandis*, *Hybognathus placitus*, *Cyprinella venusta*, *Cyprinus carpio*, *Lepomis auritus*, and *Cyprinodon* hybrids. No species was present at all sites, but *Menidia beryllinia* and *Cyprinodon* hybrids were found at eight sites, all downstream of Brantley Dam, NM. *Hybognathus placitus* was collected exclusively in the Roswell Basin, at Bitter Lake National Wildlife Refuge. *Cyprinella proserpina* was observed only in the Edwards Plateau at sites downstream of the Independence Creek confluence. Larger-bodied fishes like *Polydictis olivaris*,

Micropterus salmoides and *Lepisosteus osseus* were collected only in the Edwards Plateau (Table 3). The most abundant fish species in the Permian Basin was the *Cyprinodon* hybrid which comprised 48.6% of total catch. *Cyprinella proserpina*, a vulnerable species in Texas, was the most abundant species collected in the Edwards Plateau. *Fundulus grandis*, *C. lutrensis*, and *Gambusia affinis* were the most abundant species in the Roswell Basin. Fish species richness at sites ranged from four to 15 and was negatively associated with specific conductivity (Figure 2). Thirty-two invertebrate families were collected from 11 sample reaches. One site (Site 5) was excluded from analysis of invertebrate diversity due to inadequate sampling. Order Ephemeroptera was collected exclusively in the Edwards's Plateau, the non-native gastropod (Physidae) was present at seven sites, and the most common macroinvertebrate families were Elmidae (Coleoptera) and Coenagrionidae (Odonata). Macroinvertebrate family diversity was highest in the Edwards Plateau and lowest in the Roswell Basin (Table 4.) Invasive, nonnative saltcedar (*Tamarix* spp.) was abundant in the riparian zones at eight of the 12 reaches.

Table 3. . Presence of fish species at each site across physiographic regions.

| Family | Species | Species Code | Physiographic Regions and Site Numbers | | | | | | | | | | | |
|----------------|---------------------------------|--------------|--|---------------|---|---------------|---|---|---|---|---|-----------------|----|----|
| | | | Pecos Plains | Roswell Basin | | Permian Basin | | | | | | Edwards Plateau | | |
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Atherinopsidae | <i>Menidia beryllina</i> | MENBER | | | | X | X | X | X | | X | | | X |
| Catostomidae | <i>Carpoides carpio</i> | CARCAR | X | | | | | | | | | | | |
| | <i>Catostomus commersoni</i> | CATCOM | X | | | | | | | | | | | |
| | <i>Moxostoma congestum</i> | MOXCON | | | | | | | | | | | X | X |
| Centrarchidae | <i>Lepomis auritus</i> | LEPAUR | | | | | | | | | | | X | X |
| | <i>L. cyanellus</i> | LEPCYA | X | | | | | | | | | | | |
| | <i>Micropterus salmoides</i> | MICSAL | | | | X | | | | | | | X | X |
| Characidae | <i>Astyanax mexicanus</i> | ASTMEX | | | | X | | | | | | X | X | X |
| Cichlidae | <i>Herichthys cyanoguttatus</i> | HERCYA | | | | | | | | | | X | | |
| Clupeidae | <i>Dorosoma cepedianum</i> | DORSEP | | | | | | | | | | X | | |
| Cyprinidae | <i>Cyprinus carpio</i> | CYPCAR | | | X | X | | | | | | | | |
| | <i>Cyprinella lutrensis</i> | CYPLUT | X | | X | X | | | | | X | X | X | |
| | <i>Cyprinella proserpina</i> | CYPPRO | | | | | | | | | | X | X | |
| | <i>Cyprinella venusta</i> | CYPVEN | | | | | | | | | | | X | |
| | <i>Dionda episcopa</i> | DIOEPI | | | | | | | | | | X | | |
| | <i>Hybognathus placitus</i> | HYBPLA | | X | | | | | | | | | | |
| | <i>Notropis amabilis</i> | NOTAMA | | | | | | | | | | | X | X |
| | <i>N. stramineus</i> | NOTSTR | X | | | | | | | | | | X | |

| Table 3 Continued. | | | | | | | | | | | | | | |
|--------------------|----------------------------|--------------|--|---------------|---|---|---------------|---|---|---|---|-----------------|----|----|
| | | | Physiographic Regions and Site Numbers | | | | | | | | | | | |
| | | | Pecos Plains | Roswell Basin | | | Permian Basin | | | | | Edwards Plateau | | |
| Family | Species | Species Code | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | <i>Pimephales promelas</i> | PIMPRO | X | | X | | | | | | | | | |
| | <i>P. vigilax</i> | PIMVIG | | | | X | | | | | | | | X |
| Cyprinodontidae | <i>Cyprinodon hybrid</i> | CYPSPP | | | | | X | X | X | X | X | X | X | X |
| Fundulidae | <i>Fundulus grandis</i> | FUNGRA | | | | X | X | X | X | X | X | X | | |
| | <i>F.zebrinus</i> | FUNZEB | | X | X | | X | X | X | X | X | X | X | |
| | <i>Lucania parva</i> | LUCPAR | | | | | X | X | | X | X | X | X | |
| Ictaluridae | <i>Ictalurus punctatus</i> | ICTPUN | X | | | | | | | | | | | X |
| | <i>Pylodictis olivaris</i> | PYLOLI | | | | | | | | | | | | X |
| Lepisosteidae | <i>Lepisosteus osseus</i> | LEPOSS | | | | | | | | | | | | X |
| Poeciliidae | <i>Gambusia affinis</i> | GAMAFF | | X | X | X | | | | | | | | X |

Table 4 Presence of macroinvertebrate families at each site across physiographic regions. Data is not available for site 5 due to sampling error.

| Order | Family | Feeding Group | Physiographic Regions and Site Numbers | | | | | | | | | | | |
|---------------|------------------|----------------------|--|---------------|---|---------------|---|---|---|---|-----------------|----|----|---|
| | | | Pecos Plains | Roswell Basin | | Permian Basin | | | | | Edwards Plateau | | | |
| | | | 1 | 2 | 3 | 4 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | |
| Amphipoda | | Omnivore | | | | X | X | | | | | X | X | X |
| Annelida | Oligochaeta | Gathering Collectors | | | | | X | | | | | | | |
| Coleoptera | Dytiscidae | Predator | | | | | | | | X | | X | | X |
| | Elmidae (larvae) | Scraper | | | | | X | | X | X | | X | X | |
| | Gyrinnidae | Predator | | X | X | | X | | | X | | X | X | X |
| | Hydrophilidae | Shredder | | X | | | | | X | | X | | | |
| | Psephenidae | Scraper | | | | | | | | | | | | X |
| Diptera | Chironomidae | Omnivore | X | X | X | | X | | X | X | | X | | |
| | Culicidae | Filtering collector | | | | | | | X | | | | | |
| | Ephydriidae | Shredders, scrapers | | | | | X | | | | | | | |
| | Stratiomyidae | Collector, gatherer | | | | | X | | | | | | | |
| | Tabanidae | Predator | | | | | | | | | | X | X | |
| Ephemeroptera | Baetidae | Scraper | X | | | | | | | | | | | |
| | Caenidae | Collector, Gatherer | X | | | | | | | | | | | X |
| | Ephemerellidae | Collector, Gatherer | | | | | | | | | | X | X | |

| Table 4. Continued. | | | Physiographic Regions and Site Numbers | | | | | | | | | | |
|---------------------|--------------------------|---------------------|--|---------------|---|---------------|---|---|---|---|-----------------|----|----|
| Order | Family | Feeding Group | Pecos Plains | Roswell Basin | | Permian Basin | | | | | Edwards Plateau | | |
| | | | 1 | 2 | 3 | 4 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Gastropoda | Leptophlebiidae | Shredder | X | | | | | | | | | | |
| | Tricorythidae | Collector, Gatherer | X | | | | | | | | | | |
| Hemiptera | Physidae | Scraper | X | | X | X | X | | | | X | X | X |
| | Belostomatidae | Predator | | X | | X | X | | | | | X | |
| | Corixidae | Predator | X | | X | | X | X | | | | | |
| | Gerridae | Predator | | | | | | | | | X | | |
| | Mesoveliidae | Predator | | | | | X | | | | | | |
| | Vellidae | Predator, Scraper | X | | | | | | | | | X | X |
| | Naucoridae | Predator | X | | | X | | | | | | X | X |
| | Notonectidae | Predator | X | X | | | | | | | | X | |
| Lepidoptera | Crambidae | Shredder | | | | | | | | | | X | |
| Odonata | Anisoptera Aeshinidae | Predator | | | | | | | | | | X | X |
| | Anisoptera Gomphidae | Predator | X | | X | X | | | | | | | X |
| | Anisoptera Libellulidae | Predator | X | | | | | | | X | | X | |
| | Zygoptera Coenagrionidae | Predator | X | X | X | X | X | X | X | | | X | X |
| Trichoptera | Hydropsychidae | Filtering Collector | | | | X | | | | | | X | |
| | Molannidae | Predator, Scraper | X | | | | | | | | | | |

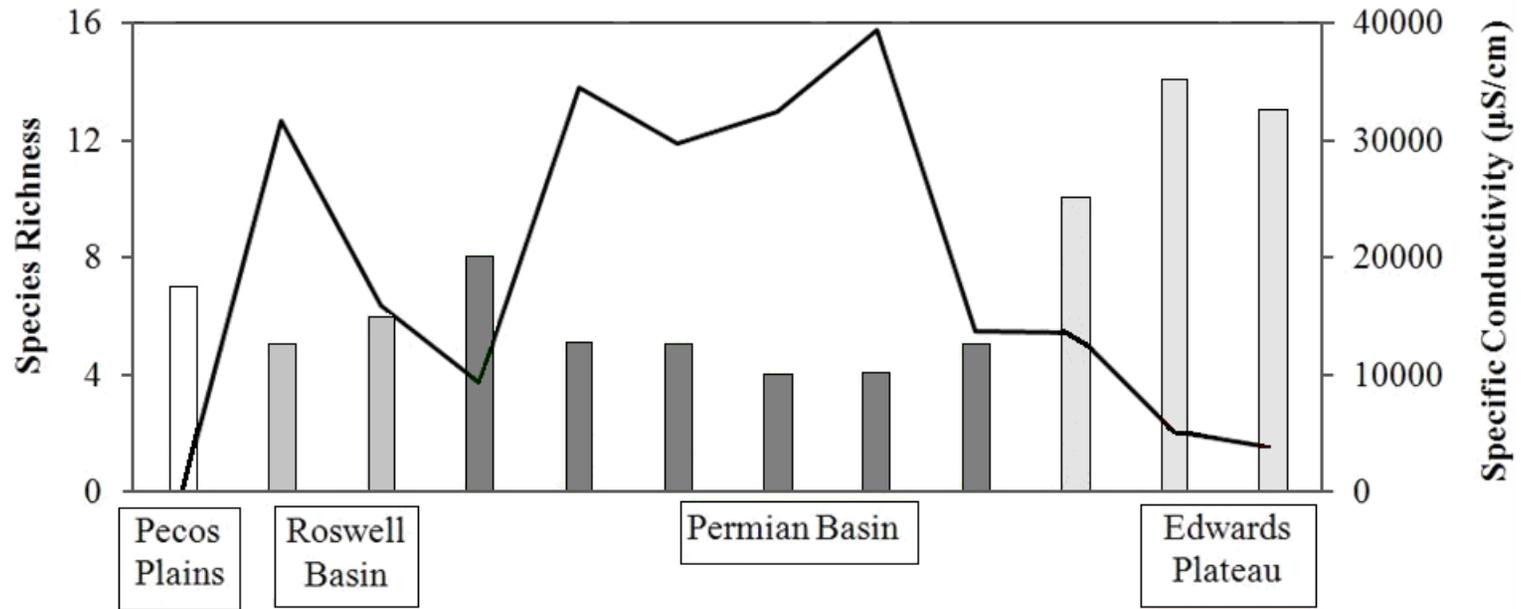


Figure 2. Longitudinal trends for fish species richness and specific conductivity. Sites are placed in longitudinal order (upstream-downstream) from left to right. The black line indicates specific conductivity ($\mu\text{S}/\text{cm}$) and the color of species richness bars indicate physiographic region.

Isotopic signatures of consumers across the longitudinal gradient

Across sites, fishes occupied a large space on the $\delta^{13}\text{C}$ axis (-25.5 to -8.68‰, $n = 224$; Figure 3). Similarly, macroinvertebrates occupied a large range on $\delta^{13}\text{C}$ axis (-28.6 to -13.7‰, $n = 70$) across the Pecos River. Instream (algal)carbon signatures were enriched (-14.9‰ \pm 2.9 SD, $n = 54$) compared to the average riparian carbon signature (-22.6‰ \pm 6.3 SD, $n = 73$; Figure 3).

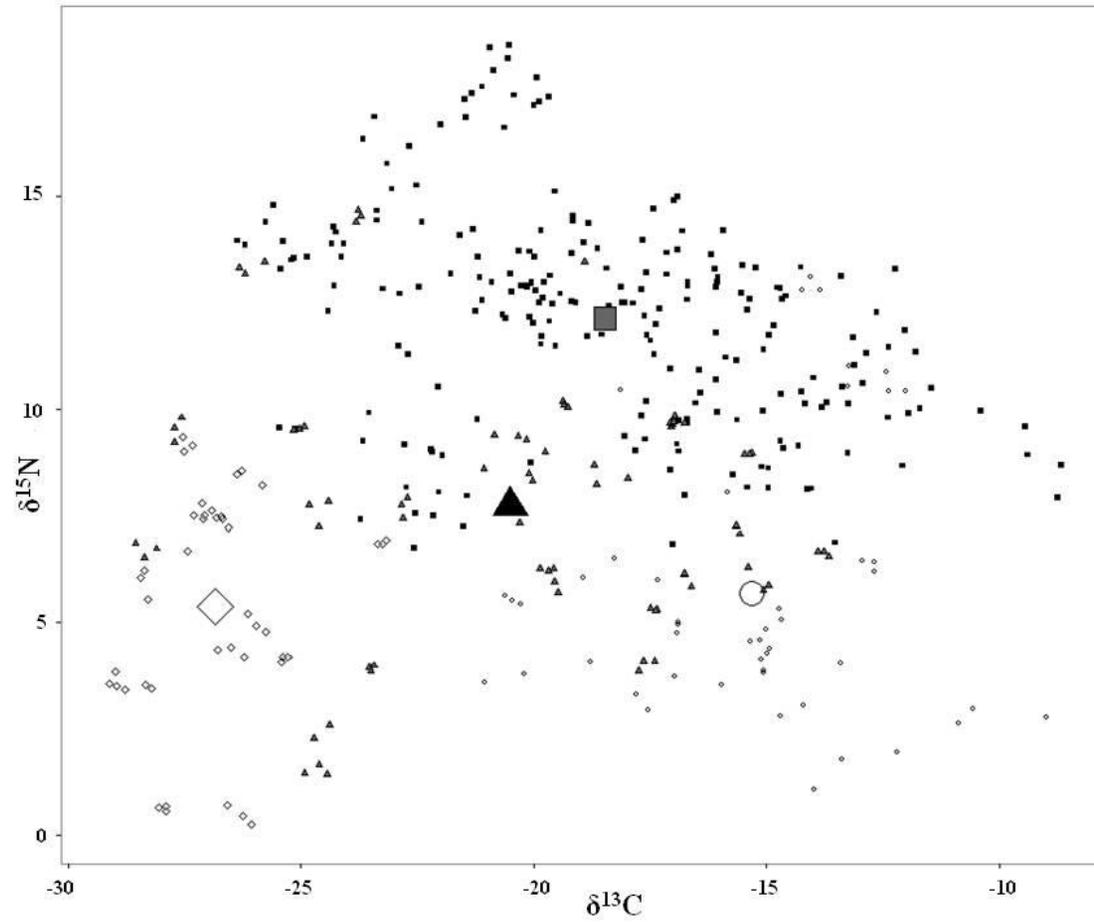


Figure 3. Total Pecos River food-web structure. Small shapes represent individual samples and large shapes represent averages of each taxa. Squares denote fish, triangles denote macroinvertebrates, diamonds represent riparian vegetation, and circles represent instream sources.

Fish isotopic ratios varied considerably across physiographic regions (Table 5). The Pecos Plains and Edwards Plateau fish assemblages were depleted in $\delta^{13}\text{C}$ compared to assemblages in the Roswell and Permian Basin. On average, $\delta^{13}\text{C}$ of macroinvertebrates from the Pecos Plains and the Edwards Plateau were also depleted compared to the Roswell and Permian Basins (Table 6). Four species found at multiple sites had high variation in $\delta^{15}\text{N}$: *Fundulus grandis* (9.27-17.97‰, n=25), *Gambusia affinis* (9.77-17.60‰, n=16), *Menidia beryllina* (8.71-18.57‰, n=23), and *Cyprinella lutrensis* (8.76-17.3‰, n=22; Figure 4). *Lepisosteus osseus* occupied the highest trophic position (4.79) across all sites based on site-specific $\delta^{15}\text{N}$ baselines, whereas *Cyprinodon* hybrids occupied the lowest (2.86). Non-native *F. grandis* occupied a higher trophic position than the native *F. zebrinus*.

Table 5. Mean isotopic ratios \pm SE for fish species across physiographic regions. Sample size (n) refers to number of specimens used for stable isotope analysis

| Species | Pecos Plains | | | Roswell Basin | | | Permian Basin | | | Edwards Plateau | | |
|---------------|-------------------------------|-------------------------------|---|-------------------------------|-------------------------------|---|-------------------------------|-------------------------------|----|-------------------------------|-------------------------------|----|
| | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | n | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | n | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | n | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | n |
| <i>ASTMEX</i> | | | | | | | | | | -22.9 \pm 0.6 | 12.9 \pm 0.5 | 6 |
| <i>CARCAR</i> | -22.6 \pm 0.0 | 7.6 \pm 0.0 | 1 | | | | | | | | | |
| <i>CATCOM</i> | -22.6 \pm 0.0 | 6.8 \pm 0.0 | 1 | | | | | | | | | |
| <i>HERCYA</i> | | | | | | | | | | -19.7 \pm 0.0 | 12.1 \pm 0.0 | 1 |
| <i>CYPCAR</i> | | | | -17.4 \pm 0.0 | 11.9 \pm 0.3 | 3 | | | | | | |
| <i>CYPLUT</i> | -22.9 \pm 1.1 | 9.2 \pm 0.2 | 4 | -16.8 \pm 0.4 | 14.2 \pm 0.3 | 3 | -20.8 \pm 0.4 | 16.6 \pm 0.6 | 5 | -19.3 \pm 0.7 | 13.3 \pm 0.6 | 10 |
| <i>CYPPRO</i> | | | | | | | | | | -25.3 \pm 1.0 | 13.6 \pm 0.4 | 3 |
| <i>CYPSPP</i> | | | | | | | -14.1 \pm 0.8 | 8.5 \pm 0.2 | 16 | -16.8 \pm 1.1 | 11.4 \pm 0.8 | 4 |
| <i>CYPVEN</i> | | | | | | | | | | -21.8 \pm 0.9 | 12.5 \pm 0.6 | 6 |
| <i>DORCEP</i> | | | | | | | | | | -21.2 \pm 0.0 | 9.8 \pm 0.0 | 1 |
| <i>DIOEPI</i> | | | | | | | | | | -25.3 \pm 0.1 | 13.4 \pm 0.1 | 2 |
| <i>FUNGRA</i> | | | | | | | -16.5 \pm 0.5 | 12.5 \pm 0.5 | 22 | -18.7 \pm 0.5 | 13.4 \pm 0.4 | 3 |
| <i>FUNZEB</i> | | | | -14.8 \pm 0.06 | 11.0 \pm 0.2 | 8 | -14.5 \pm 0.6 | 10.0 \pm 0.2 | 11 | -18.7 \pm 0.9 | 12.6 \pm 0.5 | 6 |
| <i>GAMAFF</i> | | | | -14.6 \pm 0.26 | 12.0 \pm 0.3 | 7 | -18.3 \pm 1.2 | 15.4 \pm 0.9 | 6 | -20.3 \pm 0.9 | 13.2 \pm 0.1 | 5 |
| <i>HYBPLA</i> | | | | -17.7 \pm 1.4 | 10.3 \pm 1.7 | 3 | | | | | | |
| <i>ICTPUN</i> | -22.5 \pm 1.1 | 9.0 \pm 1.0 | 2 | | | | | | | -20.67 \pm 0.5 | 13.0 \pm 0.1 | 2 |
| <i>LEPAUR</i> | | | | | | | | | | -25.2 \pm 0.5 | 14.5 \pm 0.2 | 3 |

Table 5. Continued

| Species | Pecos Plains | | | Roswell Basin | | | Permian Basin | | | Edwards Plateau | | |
|---------------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|
| | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | <i>n</i> |
| <i>LEPCYA</i> | -22.2±0.0 | 9.1±0.0 | 1 | | | | | | | | | |
| <i>LEPOSS</i> | | | | | | | | | | -22.6±0.3 | 16.2±0.3 | 3 |
| <i>LUCPAR</i> | | | | -16.9±0.0 | 9.2±0.0 | 1 | -15.7±0.7 | 11.4±0.3 | 12 | -17.2±0.8 | 13.0±0.2 | 4 |
| <i>MENBER</i> | | | | | | | -16.9±1.0 | 12.9±0.7 | 17 | -18.7±0.4 | 12.5±0.3 | 6 |
| <i>MICSAL</i> | | | | | | | | | | -21.5±1.1 | 15.5±0.5 | 5 |
| <i>MOXCON</i> | | | | | | | | | | -22.2±2.2 | 12.2±0.1 | 2 |
| <i>NOTAMA</i> | | | | | | | | | | -21.7±1.3 | 13.3±0.5 | 3 |
| <i>NOTSTR</i> | -23.2±1.1 | 9.2±0.2 | 3 | | | | | | | -19.4±0.0 | 12.7±0.0 | 1 |
| <i>PIMPRO</i> | -21.9±0.2 | 7.6±0.2 | 3 | -17.5±1.0 | 12.8±0.7 | 3 | | | | | | |
| <i>PIMVIG</i> | | | | | | | -17.0±0.0 | 15.0±0.1 | 2 | | | |
| <i>PYLOLI</i> | | | | | | | | | | -19.6±0.0 | 15.1±0.0 | 1 |

Table 6. Mean isotopic ratios \pm SE for macroinvertebrate families across physiographic regions. Sample size (n) refers to number of specimens used for stable isotope analysis. Families may have been present at a site (see Table 4) but not analyzed due to cost limitations.

| Family | Feeding Group | Pecos Plains | | | Roswell Basin | | | Permian Basin | | | Edwards Plateau | | |
|----------------------------------|-------------------------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|-------------------------------|-------------------------------|----------|
| | | Average $\delta^{13}\text{C}$ | Average $\delta^{15}\text{N}$ | <i>n</i> |
| Ephemeroptera Leptophlebiidae | Shredder | -24.6 \pm 0.2 | 2.4 \pm 0.2 | 2 | | | | | | | | | |
| Ephemeroptera Tricorythidae | Collector , gatherer | -24.7 \pm 0.1 | 1.5 \pm 0.1 | 3 | | | | | | | | | |
| Odonata Libellulidae | Predator | -23.5 \pm 0.0 | 3.9 \pm 0.0 | 3 | | | | -19.7 \pm 0.1 | 6.3 \pm 0.0 | 3 | -27.7 \pm 0.1 | 9.6 \pm 0.2 | 3 |
| Gastropoda Physidae | Scraper | -20.0 \pm 0.1 | 8.6 \pm 0.2 | 3 | -18.5 \pm 0.2 | 8.5 \pm 0.1 | 3 | -18.9 \pm 0.0 | 13.5 \pm 0.0 | 1 | -21.8 \pm 1.0 | 9.4 \pm 0.3 | 8 |
| Coleoptera Elmidae larvae | Shredder | | | | -16.9 \pm 0.1 | 9.7 \pm 0.1 | 3 | -17.1 \pm 0.7 | 5.7 \pm 0.1 | 8 | -25.3 \pm 0.8 | 7.4 \pm 0.2 | 9 |
| Odonata Coenagrionidae | Predator | | | | -16.9 \pm 0.1 | 7.9 \pm 0.8 | 6 | -17.6 \pm 1.6 | 10.1 \pm 1.2 | 9 | -20.5 \pm 0.2 | 9.4 \pm 0.0 | 3 |
| Tricoptera Hydropsychidae | Filtering Collector | | | | | | | -26.1 \pm 0.2 | 13.3 \pm 0.1 | 3 | | | |

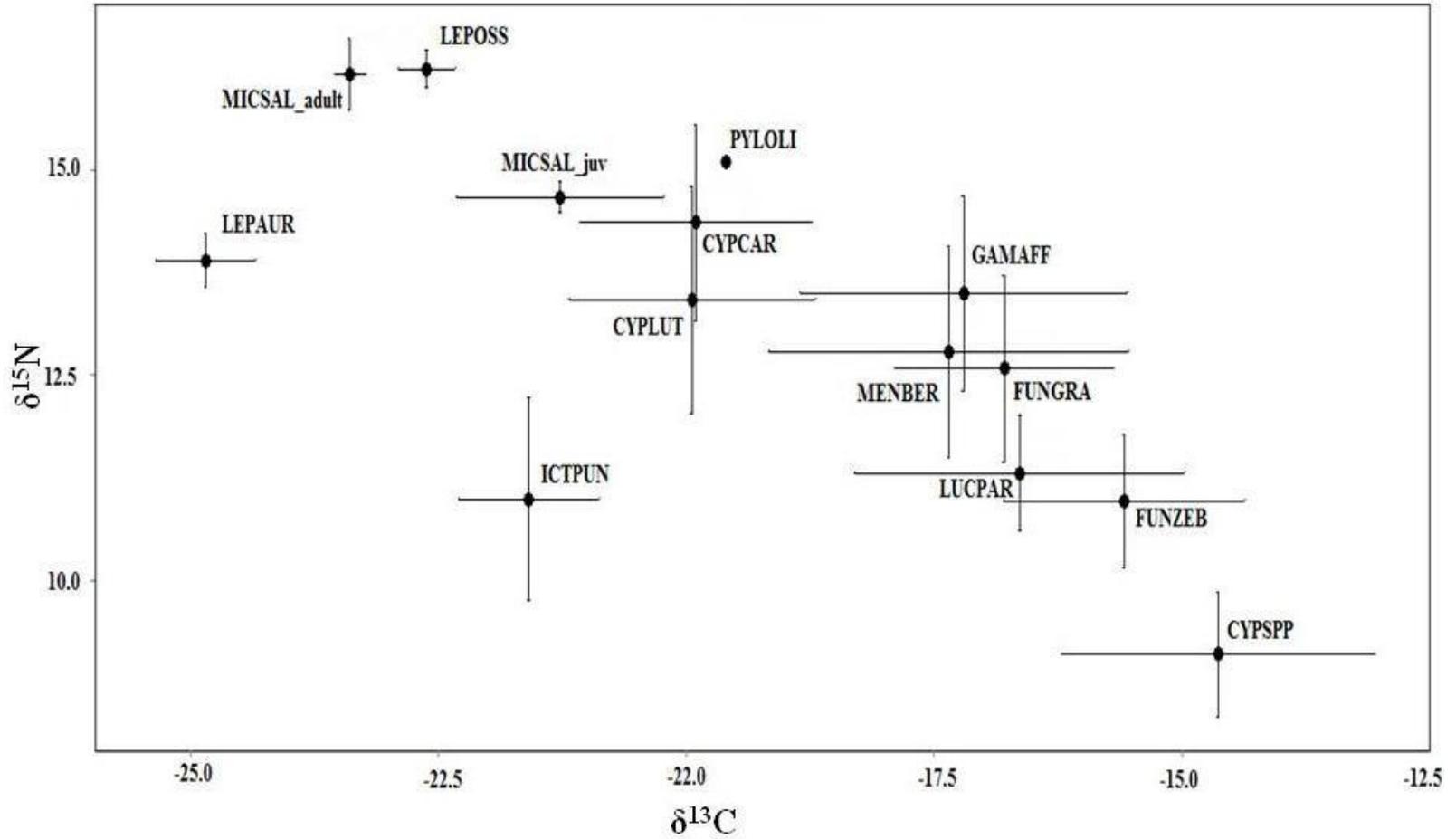


Figure 4. Mean isotopic ratios with standard error bars of fishes across the Pecos River. Species codes are the same as listed in Table 3.

The two-source mixing model revealed that the proportion of dietary carbon supporting fishes shifted from riparian sources to instream sources along the longitudinal gradient. The Pecos Plains had a higher riparian carbon influence, then shifted to more instream contribution in the Permian Basin, and in the Edwards Plateau the model showed an increase of riparian input, with autochthonous carbon still the dominant source (Figure 5a). Invertebrates showed a similar pattern of a shift from riparian in the Pecos Plains to predominately instream production in the Permian, then riparian carbon increasing in importance in the Edwards Plateau (Figure 5b).

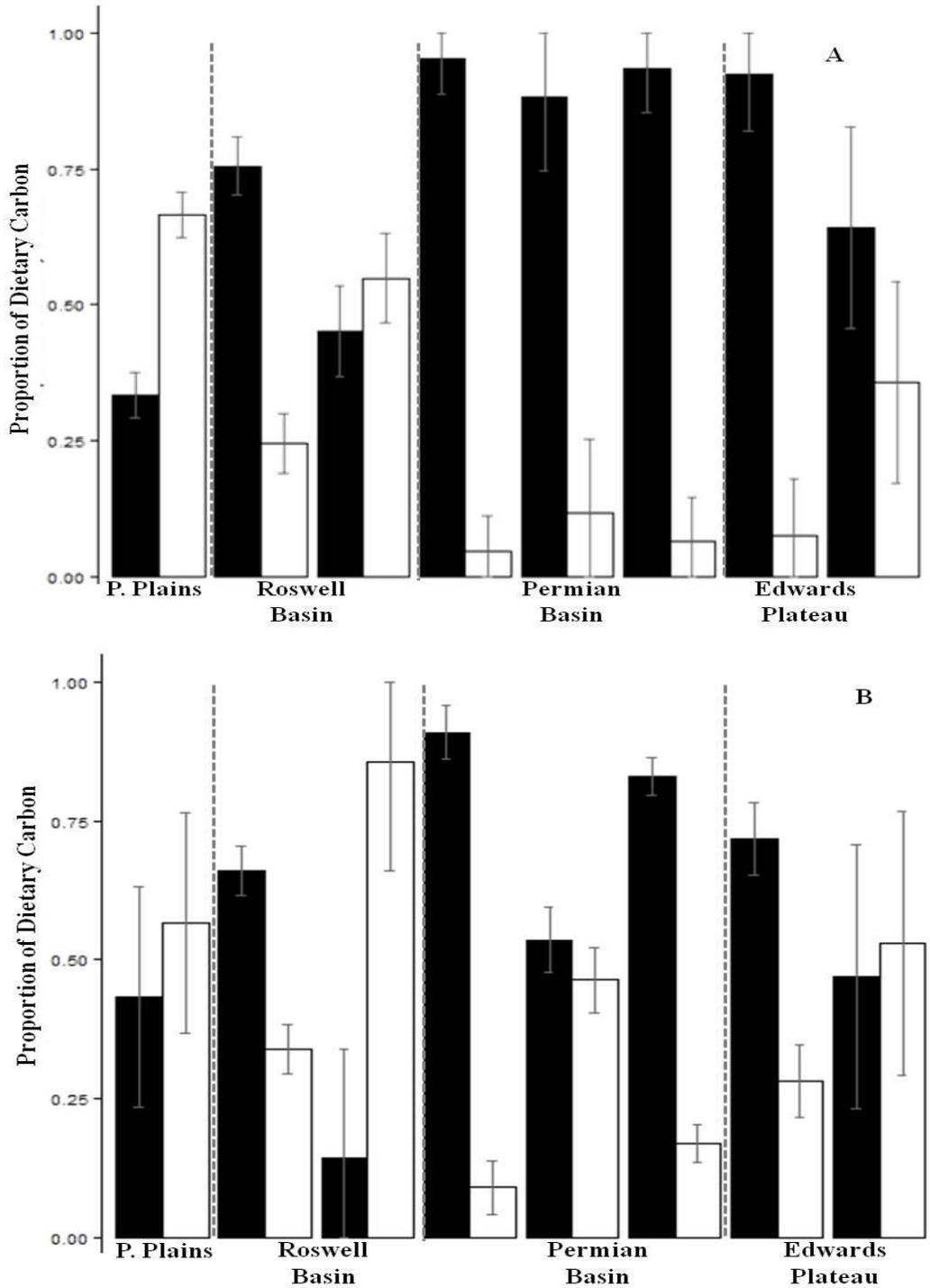


Figure 5. Proportions of carbon sources derived from ISOError two-source mixing model. Plot A is the basal carbon sources of fishes and Plot B is macroinvertebrate carbon sources. The sources are listed in a longitudinal gradient, with dotted lines delineating change in physiographic region

Spatial variation in food-web structure

Consumers in the northernmost site in the Pecos Plains were depleted on both the $\delta^{13}\text{C}$ ($-22.70\text{‰} \pm 1.3\text{SD}$) and $\delta^{15}\text{N}$ ($8.48\text{‰} \pm 0.94\text{SD}$) axes (Figure 6). Roswell Basin sites were enriched in carbon and nitrogen compared to the Pecos Plains (Figure 6). The northernmost Permian Basin site had elevated mean $\delta^{15}\text{N}$ signatures for instream producers and consumers, the highest of all sites (Figure 6). Further downstream in the Permian Basin, sites were $\delta^{13}\text{C}$ enriched compared to upstream sites ($-15.31\text{‰} \pm 2.81\text{SD}$) (Figure 6). The largest ranges in nitrogen (NR) were in the Pecos Plains and Edwards Plateau. The largest ranges of carbon (CR), highest total convex hull area (TA), and longest food chain length (FCL) were found in the Edwards Plateau (Table 7). CR and NR were positively associated with environmental variables including river kilometer and discharge. TA had a positive relationship with instantaneous discharge at the study reach ($p\text{-value}=0.02$, $r^2=0.37$). FCL and NR had an inverse relationship with specific conductivity (Figure 7, $p\text{-value}=0.06$, $R^2=0.24$, $p\text{-value}=0.005$, $R^2=0.31$, respectively)

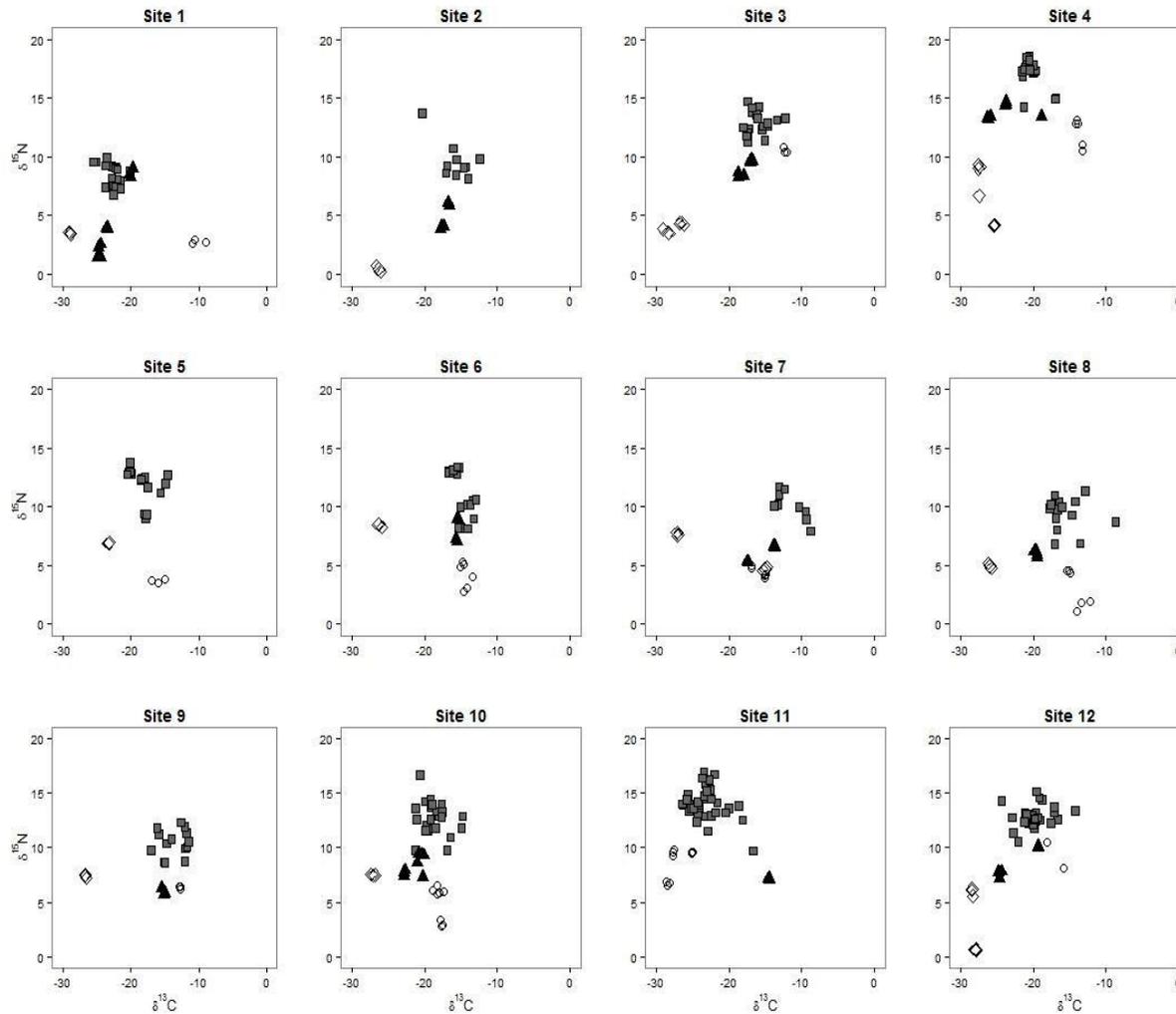


Figure 6. Isotope biplots of sample sites in longitudinal order, site 1 is in the Pecos Plains physiographic region, sites 2-3 are in the Roswell Basin, sites 4-9 are in the Permian Basin, and sites 10-12 are in the Edwards Plateau. Dark symbols represent consumers and white symbols represent producers. The squares represent all fishes at a site, triangles represent invertebrates, diamonds indicate riparian trees, and circles represent instream producers.

Table 7. Community-wide metrics: nitrogen range (NR), carbon range (CR), total convex hull area (TA), nearest neighbor distance (NND), standard deviation of NND (NNDsd), and food-chain length (FCL) across physiographic regions

| Physiographic Region | NR | CR | TA | NND | NND sd | FCL |
|-----------------------------|-----------|-----------|-----------|------------|---------------|------------|
| Pecos Plains | 7.68 | 2.75 | 7.35 | 0.81 | 0.51 | 4.26 |
| Roswell Basin | 6.55 | 5.37 | 18.90 | 1.86 | 0.40 | 3.84 |
| | 5.78 | 3.96 | 9.64 | 0.97 | 0.63 | 3.7 |
| Permian Basin | 5.11 | 9.16 | 24.23 | 1.62 | 0.88 | 3.5 |
| | 3.77 | 3.22 | 5.14 | 1.79 | 1.06 | - |
| | 6.07 | 2.88 | 8.97 | 0.98 | 0.20 | 3.79 |
| | 5.65 | 7.92 | 15.99 | 2.42 | 2.03 | 3.66 |
| | 4.42 | 6.66 | 12.51 | 1.13 | 1.01 | 3.3 |
| | 3.22 | 3.22 | 9.96 | 1.72 | 0.72 | 3.8 |
| Edwards Plateau | 7.37 | 5.86 | 20.69 | 1.55 | 0.71 | 4.17 |
| | 9.68 | 10.23 | 42.36 | 1.27 | 0.87 | 4.8 |
| | 7.51 | 10.35 | 33.01 | 1.29 | 1.10 | 4.21 |

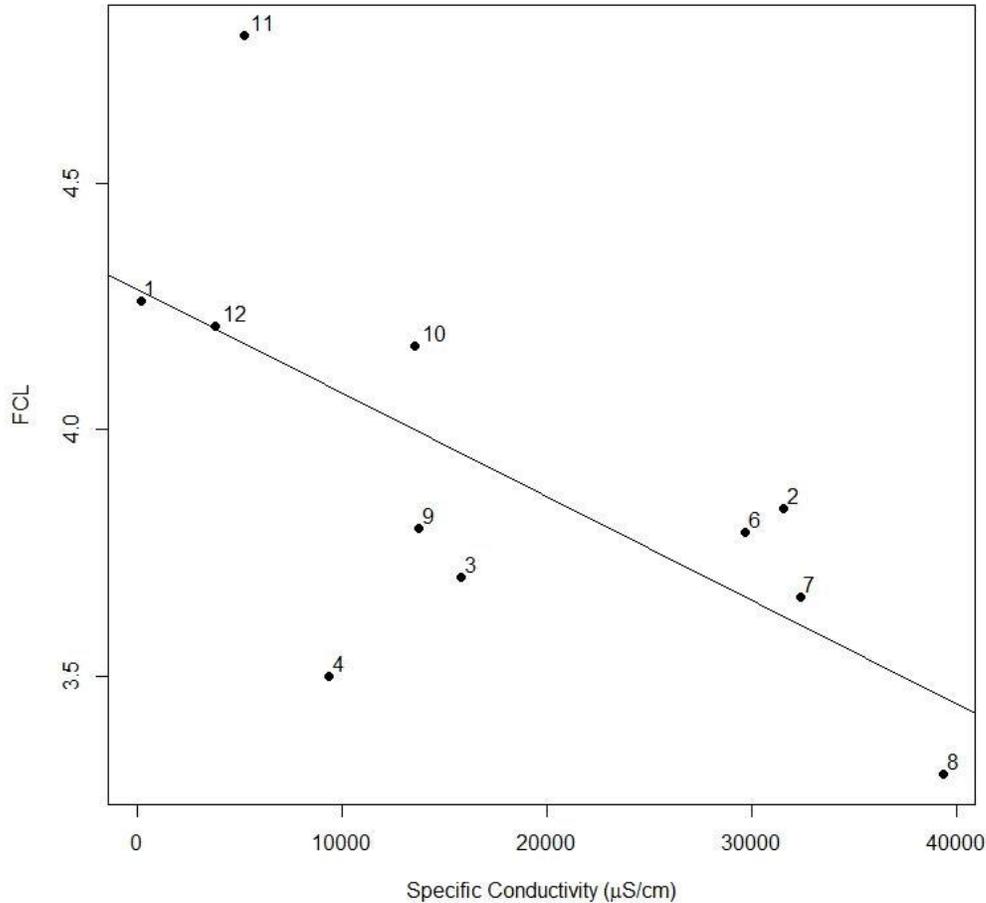


Figure 7. Simple linear regression of specific conductivity for each site against food chain length ($R^2=0.391$, $p\text{-value}=0.02$).

The TA of sample sites aggregated according to ecoregion, with an exception of one Permian basin site with enriched N values (Figure 8). The Edwards Plateau sites occupied a generally larger space on the left side of the $\delta^{13}\text{C}$ axis and along a wider range on the $\delta^{15}\text{N}$ axis, indicating more diverse resource use. The Permian basin sites occupied a space higher on the $\delta^{13}\text{C}$ axis, indicating greater instream input and a tighter range on the $\delta^{15}\text{N}$ axis, indicating smaller niche space occupied by fishes at those sites (Figure 8). The Pecos Plains orientation on the $\delta^{13}\text{C}$ axis indicates a greater influence from riparian sources and its lower nitrogen ratios indicate lower trophic diversity. The Roswell Basin TA was intermediate in size, similar to Permian Basin sites, and occupied the region in between instream and riparian carbon sources.

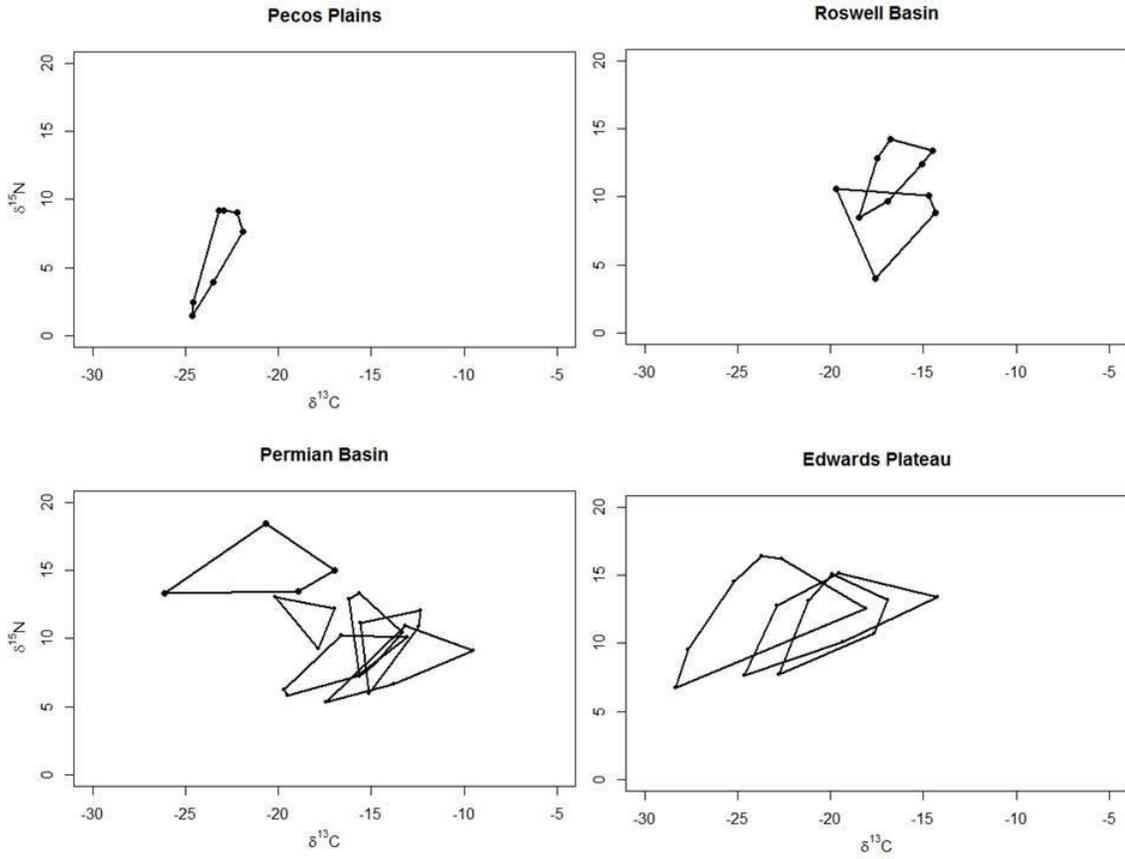


Figure 8. Total convex hulls of each physiographic region calculated from consumer ratios from each site.

Temporal variation in food-web structure

Overall, carbon and nitrogen signatures of fish consumers did not show substantial temporal variation. Stable carbon and nitrogen isotope ratios of *C. lutrensis* varied seasonally at one Roswell Basin site; mean $\delta^{15}\text{N}$ was higher in the spring and summer than the fall and winter (Figure 9). Breadth of carbon supporting fish production downstream of the confluence of Independence Creek increased in the summer and fall (Figure 10).

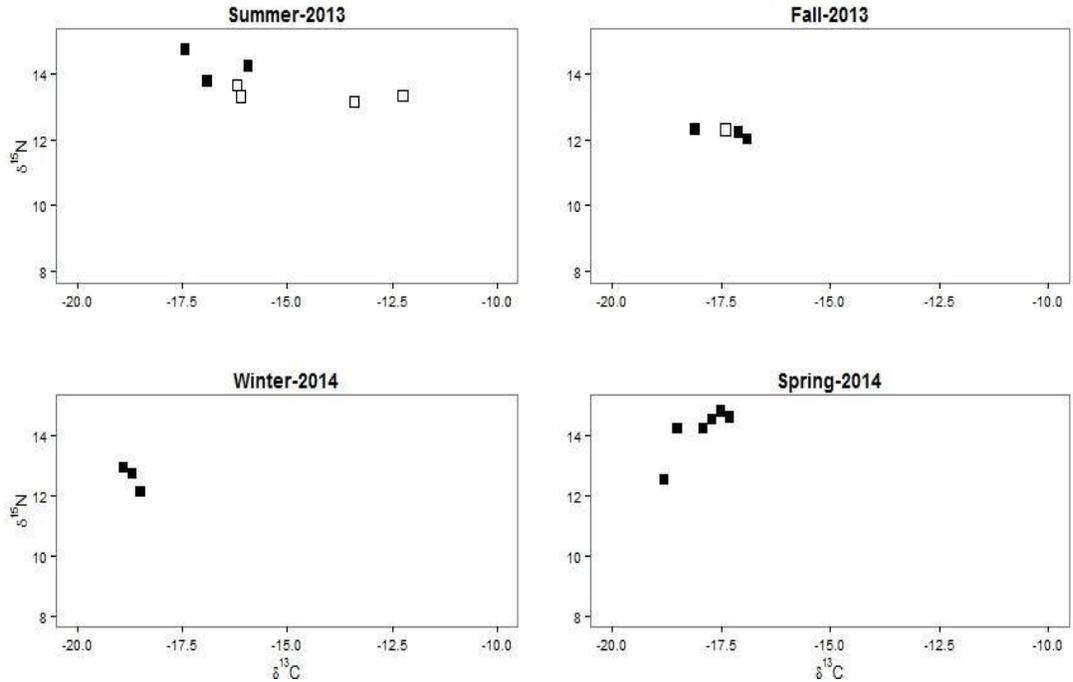


Figure 9. Seasonal variation found in fish species at site 3 near Artesia, NM. Different color squares indicate species, general trends across species appear to have enriched nitrogen ratios in the spring and summer compared to fall and spring.

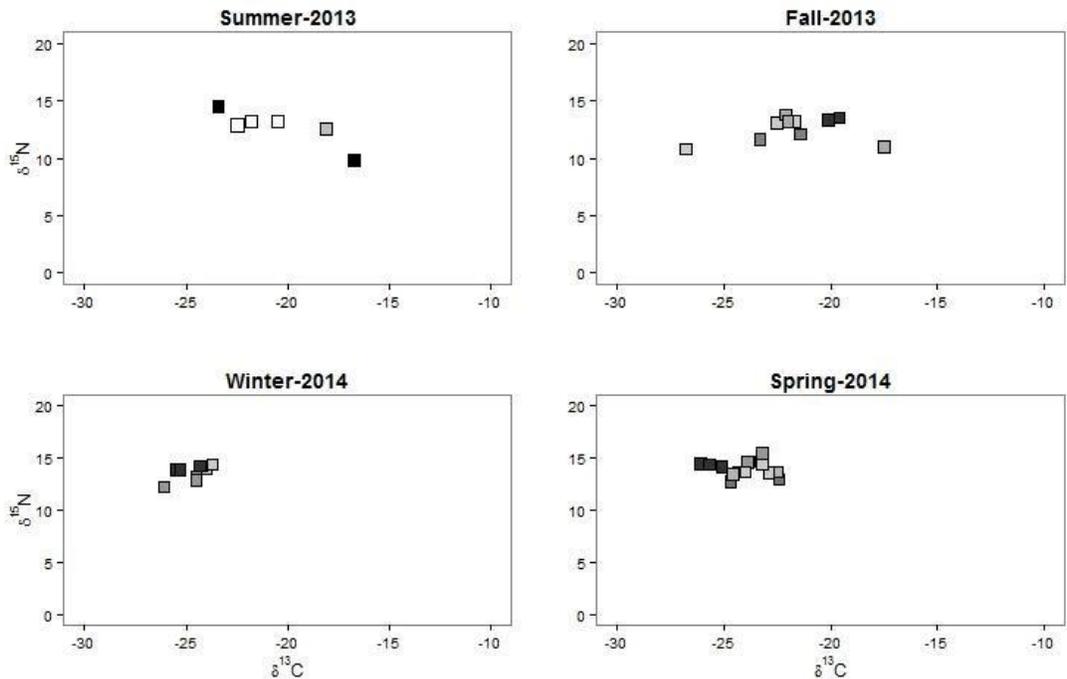


Figure 10. Seasonal variation found in fish species at site 11 downstream of the confluence of Independence Creek. Different color squares indicate different species, general trend is a broadening of carbon signatures in summer and fall compared to tighter clustering in the winter and spring

Chapter IV

Discussion

The above results indicate that food-web structure and biotic diversity in the Pecos River follow some theoretical expectations for longitudinal patterns, while deviations due to anthropogenic impacts were also apparent. Results also suggested that resources used by aquatic consumers shifted seasonally in some cases. These findings provide additional evidence for the potential detrimental impacts of secondary salinization and diminished flow in river ecosystems of the semi-arid southwest.

Shifts in production sources and consumer signatures across the longitudinal gradient

Consumer diversity varied along the longitudinal gradient as would be expected according to the river continuum concept (Vannote *et al.*, 1980) and previous studies describing an increase in fish diversity from upstream to downstream in river systems (Angermeier & Karr, 1984; Schlosser, 1987; Beecher, Dott & Fernau, 1988). However, the relationship was nonlinear as a decline in diversity was observed in the Permian Basin, the region impacted most by anthropogenic salinization. Anthropogenic impacts such as agricultural runoff, irrigation, impoundments, and oil and gas mining are the main sources of secondary salinization in the Pecos River (Hoagstrom, 2009; Cheek & Taylor, 2015). Other factors that could have confounded longitudinal patterns of consumer diversity include regional shifts in geomorphology and lack of a pronounced relationship between longitudinal position and depth or temperature (Evans & Noble, 1979; Schlosser, 1987; Rahel & Hubert, 1991). However, a recent study on the lower Pecos River in Texas determined salinity was the factor with greatest influence on fish diversity (Cheek & Taylor, 2015). As the river entered the Edwards Plateau I observed a sharp decrease in

salinity and an increase in consumer diversity in both fish and macroinvertebrate communities.

Riparian sources were generally more depleted in carbon isotope ratios compared to instream sources. Filamentous algae samples were collected at a few sites but were not included in dietary carbon analyses as they were generally more depleted ($\sim -21\text{‰}$) than other instream sources. This could be due to several factors: (1) samples were not properly filtered of terrestrial detritus leading to an allochthonous signature; (2) the samples taken were actually contaminated with *Prymnesium parvum* (golden algae), an invasive marine algae found in the Pecos River (Rhodes & Hubbs, 1992; Israël *et al.*, 2014) that has been shown to vary widely in carbon signature (-22 to -10‰) (Lindehoff, Granéli & Granéli, 2009); (3) the samples were comprised of other salt-tolerant estuarine macroalgae which tend to be depleted ($\sim -20\text{‰}$) compared to freshwater algae (Kwak & Zedler, 1997); or (4) high variation in algal $\delta^{13}\text{C}$ is associated with the amount of dissolved inorganic carbon sources available to algae in the system (Finlay, 2001; Michener & Lajtha, 2008). More robust filtration methods, more precise identification of algal species present, and investigation of *P. parvum* carbon signatures and presence in the Pecos River could elucidate this relationship.

Across the Pecos River, basal carbon sources supporting the fish and invertebrate communities generally followed expectations from the River Continuum Concept (RCC) (Vannote *et al.* 1980), with an increasing influence of production from instream carbon in the downstream sites, and greater contributions from riparian carbon in the upstream sites. However, the steep drop-off in allochthonous production supporting food webs in Permian Basin sites was unexpected based on river continuum position. This could be

explained by the absence of palatable riparian litter, by expectations from the Riverine Productivity Model (RPM) (Thorp & Delong, 1994; 2002), or by a breakdown of the Flood-Pulse Concept (FPC) (Junk, Bayley & Sparks, 1989). As seen in similar arid or semi-arid systems with riparian litter of low nutritional value, terrestrial carbon may not be as important as instream sources due to the structure and composition of riparian habitats (Grimm, 1987; Francis & Sheldon, 2002; Bunn, Davies & Winning, 2003; Dodds *et al.*, 2004; Turner & Edwards, 2012). Saltcedar, although found to be palatable in some systems (Whitcraft *et al.*, 2008), may influence the terrestrial carbon input as it has a faster decomposition rate than native willows and cottonwoods (Bailey, Schweitzer & Whitham, 2001), and a faster decomposition rate than native grasses that previously dominated the riparian zone (Gregory & Hatler, 2008; Hultine *et al.*, 2009). Alternatively, Pomeroy (2000) found that an absence of shredding macroinvertebrates likely reduced accessibility of saltcedar and other native riparian tree sources of carbon. Degraded habitat conditions in Permian Basin sites may have limited abundance of shredder taxa such as Trichoptera and Plecoptera.

A breakdown of the FPC due to the altered flow regime along with drought conditions (Tinker, 2015) could have made the riparian carbon inaccessible to consumers. A study by Turner & Edwards (2012) was also carried out in a relatively dry year in the Rio Grande, and they posited that some aquatic habitats may have been inaccessible to fishes, thus limiting energy transfer from some riparian macroinvertebrates to fishes. However, I saw similar $\delta^{13}\text{C}$ ratios in macroinvertebrate signatures at Permian Basin sites, suggesting that riparian carbon is relatively inaccessible to all aquatic consumer groups in some parts of the Pecos River. Lastly, the RPM predicts a high relative

importance of algae compared to riparian inputs to large river food webs with constricted channel habitats due to inaccessibility of the resources (Thorp & Delong, 1994; 2002), which may explain the high relative importance of instream carbon I observed in a majority of the sample sites.

As expected, nitrogen isotope signatures revealed that fishes generally occupied higher trophic levels than macroinvertebrates. Looking specifically at five common fish species, the observed high variance in nitrogen ratios could indicate a wide niche breadth for these species across the longitudinal gradient. However, it is important to note that a source of variation is driven, in part, by the inclusion of ratios from an N-enriched site in the Permian Basin. The enrichment at the Loving site accounted for most of the variation in *F. grandis*, *G. affinis*, and *M. beryllina*; however it only explains ~4% of the variation among *C. lutrensis*. This large variation in *C. lutrensis* indicates a wide diet variety. *C. lutrensis* have been generally regarded as generalists (Hale, 1962; Goldstein & Simon, 1999; Hendrickson & Cohen, 2012). In the Pecos River *C. lutrensis* have been found to feed mostly on aquatic insects based on gut contents analysis (A.A. Pease, *unpubl. data*). Diet variation in *M. beryllina* may be explained by their feeding ecology; generally they are planktivorous and size-selective invertebrate pickers (Goldstein & Simon, 1999; Hendrickson & Cohen, 2012), and a diet study in the Pecos revealed that they fed consistently across sites on terrestrial and benthic macroinvertebrates in the Pecos River (A.A. Pease, *unpubl. data*). *Fundulus grandis* and *G.affinis* had narrower niche breadths, as their diets remained consistent across sites. These results enforce the importance of using $\delta^{15}\text{N}$ baselines and complimentary diet studies to accurately interpret differences across communities.

In terms of expectations for nitrogen signatures across the longitudinal gradient, the Permian basin consumer assemblages were more depleted in nitrogen than expected according to the functional structure of riverine systems (Poff & Allan, 1995), with a divergence from a predicted increase in functional feeding groups with stream order. The anthropogenically increased salinity and habitat degradation present in the Permian Basin have caused declines in local diversity (Cheek & Taylor, 2015) and this has likely constrained the food-web structure. In the Edwards Plateau $\delta^{15}\text{N}$ ratios were relatively enriched due to the presence of Largemouth Bass, Longnose Gar, and Flathead Catfish as top predators. These species are rare in the Pecos Plains and Roswell Basin regions, and they have not been recorded in recent surveys of the Permian Basin (Cheek & Taylor, 2015; Linam & Kleinsasser, 1996).

Differences in food-web structure across physiographic regions

Variation in isotopic signatures among regions may have been driven by a combination of natural and anthropogenic environmental variables. As mentioned above, carbon ratios did not exhibit a linear longitudinal relationship, which could be explained by the differences among the physiographic regions. In the Pecos Plains site, the river is a lower order, higher elevation, has low natural salinity, and diverse riparian habitat. The average ratios at this site were depleted in carbon and nitrogen, suggesting use of the riparian carbon sources and presence of fewer large piscivores as expected in lower order, higher elevation streams (Schlosser, 1987; Beecher, Dott & Fernau, 1988). Downstream in the Roswell Basin, the sites were more enriched in carbon and nitrogen compared to the Pecos Plains, but lower than the Edwards Plateau, which could be due to the historically high flow variability (Hoagstrom, 2009) which generally supports smaller

bodied fish communities (Poff, 1997). The dominance of generalist, small-bodied cyprinids and cyprinodontiforms in Roswell Basin assemblages prevented signatures from reaching those expected for assemblages with large piscivores. In addition to flow variability, the dominant shifting sand substrate may have also constrained macroinvertebrate (Anderson & Day, 1986) and macrophyte diversity (Nuttall, 1972). The Pecos River enters the Chihuahan desert landscape in the Roswell basin, which may account for the enrichment in carbon as there are fewer litter depositing trees.

The Permian Basin sites had a high variation across the carbon scale, but this variation tracked a broad range of carbon signatures within the instream producers. The reason for the broad range of signatures among instream producers is unknown, but it could be due to a slight variation in flow across the seven sites; water velocity has been shown to influence $\delta^{13}\text{C}$ ratios in periphyton (Singer *et al.*, 2005), or due to variation in the taxonomic composition, as identification was quite broad in this study (Finlay, 2001). The riparian zone in the Permian Basin has been dominated by saltcedar in recent decades, and has likely impacted availability of allochthonous carbon sources as mentioned above. High salinity and low habitat diversity with substrate dominated by mud and silt are generally not conducive to supporting high trophic diversity, including top predators like Largemouth Bass and Longnose Gar. These species historically occurred in the Permian Basin, but were only found in the Edwards Plateau in surveys of the Pecos in Texas (Linam & Kleinsasser, 1996). The local extirpation of piscivorous species may explain the low nitrogen signatures in the Permian Basin. The enriched nitrogen levels found in consumers from one Permian Basin site are associated with enriched nitrogen signatures at the base of the food web. This enrichment is most likely

due to a combination of agricultural runoff in the watershed and effluent water from a wastewater treatment plant in the city of Carlsbad. Other studies have shown that urban wastewater input or agricultural runoff can enrich baseline nitrogen signatures in aquatic food webs (Anderson & Cabana, 2005).

Introduction of non-native *F. grandis* via baitbucket releases has also likely changed Pecos river food-web structure in the Permian Basin. In the Pecos River, *F. grandis* have been found to consume mostly detritivorous *Cyprinodon* hybrids (A.A. Pease, *unpubl. data*), but are omnivorous elsewhere in their range (Simpson & Gunter, 1956; Hendrickson & Cohen, 2012). Non-native species with dietary flexibility are often successful invaders (Ricciardi & Rasmussen, 1998). The native *F. zebrinus* primarily feed on aquatic insects (A.A. Pease, *unpubl. data*; (Echelle, Mosier & Hill, 1972) indicating that there may not be direct niche overlap and competition between the two *Fundulus* killifish species as previously suggested (Cheek & Taylor, 2015), but predatory interactions may be impacting local fish assemblages. Previous studies have shown that when predacious non-native species occupy a higher trophic position than that of the equivalent native species, they are more successful invaders and are likely to have a significant impact on native food-web structure (Vander Zanden, Casselman & Rasmussen, 1999; Simon & Townsend, 2003; Cucherousset *et al.*, 2007).

Once the river enters the Edwards Plateau, the increase in discharge due to the influx of spring-fed Independence Creek, the largest tributary to the Pecos, creates deep pools and dilutes high salinity levels. The river has heterogeneous macrohabitats in the Edwards Plateau region, with many run-riffle-pool sequences, allowing for gravel and cobble deposits creating multiple mesohabitats that support a higher diversity of species.

The carbon ratios are more widely dispersed and I observed the highest trophic positions in the Pecos at the lowest three sites. Higher $\delta^{15}\text{N}$ signatures in fish consumers in the Edwards plateau were due to presence of large predators in the lower reaches of the river. This is in concordance with the increase in stream order, discharge, and rocky substrate, and with the decrease in salinity.

Spatial variation in assemblage-wide measures of food-web structure

Nitrogen ranges are an index of total distance from bottom to top of a food chain measured in relation to the $\delta^{15}\text{N}$ values of a standardized baseline (Post, 2002). The largest NR was found in the Edwards Plateau which suggests that this region supports a larger number of trophic levels and trophic diversity within fish assemblages (Layman *et al.*, 2007). The shortest NR was found in the Permian Basin indicating that these highly impacted sites had fewer trophic levels and were less diverse in terms of trophic resource use. The Edwards Plateau, the most downstream physiographic region sampled with the highest discharge and least amount of anthropogenic impact, had the highest carbon ranges and total convex hull area which are both aspects of diversity in trophic resource use (Layman *et al.*, 2007). Degraded habitats are likely to contain simple food-webs as fewer food resources and consumer taxa are supported. The Permian Basin had some of the smallest convex hull areas and narrow carbon ranges, further suggesting that foodweb structure in this region was constrained due to poor habitat conditions.

The food-chain lengths of sites on the Pecos River were on average 3.9 which is in line with the global average for streams (Vander Zanden & Fetzer, 2007). As expected, in the Edwards Plateau region I observed longer FCLs along with an increase in fish

diversity, higher discharge, and less anthropogenic disturbance compared to the rest of the river. These conditions are expected to support longer food-chain lengths (Pimm, 1977; Pimm, 1982; Cohen & Newman, 1991; Power, Dietrich & Finlay, 1996). Food-chain lengths generally increase along longitudinal gradients of rivers (Post, 2002), however, similar to research carried out by Turner and Edwards (2012) on the Rio Grande, I found a nonlinear pattern with food-chain length. This was caused by the dropoff in FCL for the Permian Basin sites. Food-chain lengths were negatively correlated with salinity, indicating that the salinity gradient may have more of an influence on foodweb structure than the longitudinal gradient.

Temporal variation in food-web structure

Winemiller (1990) found that major causes for temporal variation in aquatic foodwebs were changes in the amount and availability of habitat and prey resources. Seasonal and ontogenetic shifts are common in freshwater fishes (Werner & Gilliam, 1984), and the variation in nitrogen ratios of *C. lutrensis* in the Roswell Basin sites potentially provides an example of this. An increase in nitrogen ratios in the summer and spring could be attributed to prey availability following the resource pulse concept which states that rare, concentrated, short periods of increased resource availability can have impacts on diet and food-web structure in regards to invertebrate aggregations and flow variability (Vanni *et al.*, 2001; Gratton & Denno, 2003; Yang *et al.*, 2008). In this feast-or-famine type of seasonality, consumers may shift their foraging efforts to less nutritional prey items depending on availability (Yang *et al.*, 2008). The shifts in breadth of carbon signatures in the Edwards Plateau reveals how the relative importance of autochthonous and allochthonous food sources varied temporally. In other arid-land rivers, seasonal

changes in the contribution of algal resources have been attributed to increasing water temperatures and decreasing flow in summer (Pease *et al.*, 2006). Seasonal changes in algal resources are commonly observed in aquatic ecosystems (Fabbro & Duivenvoorden, 2000). The lack of seasonal shifts in carbon and nitrogen shifts in the Permian Basin may be influenced by the suppression of the natural flow regime (Bunn & Arthington, 2002), salinization, degradation of the riparian buffer, or any combination of the three. Stable isotope ratios are a useful measure of energy flow through a system; however rate of carbon assimilation or turnover rate has a large influence on interpretation (Fry, 2006). The coarse scale at which we sampled temporal variation, and sampling over only one year, may not have allowed me to observe the timing of variation across all sites. Further investigation of the seasonality of the invertebrate community and a detailed seasonal diet study could reveal the factors influencing the carbon and nitrogen shifts in this system.

Conservation implications

The implications of altered flow regimes in concert with anthropogenic salinization on sensitive arid aquatic food web systems is extremely important because of the fragility of the systems and the extreme endemism of the species in these regions (Minckley & Meffre, 1987). Specific impacts of river salinization on organisms has been studied, however the ecosystem impacts of secondary salinization has not been extensively researched. Along with increasing water demand, climate change is expected to increase river salinization globally through an increase in evaporation rates with increase in water temperatures, and a decrease in precipitation lowering dilution rates (Cañedo-Argüelles *et al.*, 2013). Alleviation of anthropogenic impacts, such as flow restoration in the Permian Basin, would lessen current and future impacts of climate

change on the salinity of the river. What I found in the Edwards Plateau suggests that where there is a more natural flow regime, natural salinity levels, intact riparian and instream habitats, and diverse resource availability the Pecos River can support fairly diverse fish assemblages and aquatic food-webs. With the mechanistic understanding that links salinity and altered flow regime, one could better implement management strategies of controlled flood pulses to mimic the natural flow regime, aiding in mitigation of the salinity inputs from natural and anthropogenic sources.

Literature Cited

- Allan J.D. (2004) Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology Evolution and Systematics*, **35**, 257-284.
- Allan J.D. & Castillo M.M. (2007) *Stream Ecology: Structure and Function of Running Waters.*, Springer, Dordrecht, the Netherlands.
- Anderson C. & Cabana G. (2005) Delta N-15 in riverine food webs: effects of N inputs from agricultural watersheds. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 333-340.
- Anderson R.V. & Day D.M. (1986) Predictive quality of macroinvertebrate—habitat associations in lower navigation pools of the Mississippi River. *Hydrobiologia*, **136**, 101-112.
- Angermeier P.L. & Karr J.R. (1984) Fish communities along environmental gradients in a system of tropical streams. In: *Evolutionary ecology of neotropical freshwater fishes* pp. 39-58. Springer.
- Bailey J.K., Schweitzer J.A. & Whitham T.G. (2001) Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. *Wetlands*, **21**, 442-447.
- Beecher H.A., Dott E.R. & Fernau R.F. (1988) Fish species richness and stream order in Washington State streams. *Environmental Biology of Fishes*, **22**, 193-209.
- Berkman H.E. & Rabeni C.F. (1987) Effect of siltation on stream fish communities. *Environmental Biology of Fishes*, **18**, 285-294.
- Boecklen W.J., Yarnes C.T., Cook B.A. & James A.C. (2011) On the Use of Stable Isotopes in Trophic Ecology. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 411-440.
- Bogan M.T., Boersma K.S. & Lytle D.A. (2013) Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. *Freshwater Biology*, **58**, 1016-1028.
- Brock M.A., Nielsen D.L. & Crossle K. (2005) Changes in biotic communities developing from freshwater wetland sediments under experimental salinity and water regimes. *Freshwater Biology*, **50**, 1376-1390.
- Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492-507.
- Bunn S.E., Davies P.M. & Winning M. (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology*, **48**, 619-635.
- Burford M.A., Cook A.J., Fellows C.S., Balcombe S.R. & Bunn S.E. (2008) Sources of carbon fuelling production in an arid floodplain river. *Marine and Freshwater Research*, **59**, 224-234.

- Carver S., Storey A., Spafford H., Lynas J., Chandler L. & Weinstein P. (2009) Salinity as a driver of aquatic invertebrate colonisation behaviour and distribution in the wheatbelt of Western Australia. *Hydrobiologia*, **617**, 75-90.
- Cañedo-Argüelles M., Kefford B.J., Piscart C., Prat N., Schäfer R.B. & Schulz C.-J. (2013) Salinisation of rivers: An urgent ecological issue. *Environmental Pollution*, **173**, 157-167.
- Cheek C.A. & Taylor C.M. (2015) Salinity and geomorphology drive long-term changes to local and regional fish assemblage attributes in the lower Pecos River, Texas. *Ecology of Freshwater Fish*, **In Press**.
- Closs G. & Lake P. (1994) Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecological Monographs*, 2-21.
- Cohen J.E. & Newman C.M. (1991) Community area and food-chain length: theoretical predictions. *American Naturalist*, 1542-1554.
- Cucherousset J., Aymes J., Santoul F. & Céréghino R. (2007) Stable isotope evidence of trophic interactions between introduced brook trout *Salvelinus fontinalis* and native brown trout *Salmo trutta* in a mountain stream of south-west France. *Journal of Fish Biology*, **71**, 210-223.
- Debruyne A.M., Marcogliese D.J. & Rasmussen J.B. (2003) The role of sewage in a large river food web. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1332-1344.
- Dekar M. & Magoulick D. (2007) Factors affecting fish assemblage structure during seasonal stream drying. *Ecology of Freshwater Fish*, **16**, 335-342.
- Delong M.D. & Brusven M.A. (1998) Macroinvertebrate community structure along the longitudinal gradient of an agriculturally impacted stream. *Environmental Management*, **22**, 445-457.
- Deus C.D. & Petrere-Junior M. (2003) Seasonal diet shifts of seven fish species in an Atlantic rainforest stream in southeastern Brazil. *Brazilian Journal of Biology*, **63**, 579-588.
- Dickman M. & Gochnauer M. (1978) Impact of sodium chloride on the microbiota of a small stream. *Environmental Pollution (1970)*, **17**, 109-126.
- Dodds W.K., Gido K., Whiles M.R., Fritz K.M. & Matthews W.J. (2004) Life on the edge: the ecology of Great Plains prairie streams. *BioScience*, **54**, 205-216.
- Echelle A.A., Mosier D. & Hill L.G. (1971) Aspects of the feeding ecology of *Fundulus zebrinus kansae*. In: *Proceedings of the Oklahoma Academy of Sciences*, pp. 6-9.
- Evans J.W. & Noble R.L. (1979) The longitudinal distribution of fishes in an east Texas stream. *American Midland Naturalist*, 333-343.
- Fabbro L.D. & Duivenvoorden L.J. (2000) A two-part model linking multidimensional environmental gradients and seasonal succession of phytoplankton assemblages. *Hydrobiologia*, **438**, 13-24.

- Fiedler A.G. & Nye S.S. (1933) Geology and ground water resources of the Roswell artesian basin, New Mexico. U.S. Geol. Surv., Water Supply Paper 639, 372 p.
- Finlay J.C. (2001) Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology*, **82**, 1052-1064.
- Fischer J. & Paukert C. (2008) Habitat relationships with fish assemblages in minimally disturbed Great Plains regions. *Ecology of Freshwater Fish*, **17**, 597-609.
- Francis C. & Sheldon F. (2002) River Red Gum (*Eucalyptus camaldulensis* Dehnh.) organic matter as a carbon source in the lower Darling River, Australia. *Hydrobiologia*, **481**, 113-124.
- Fry B. (2006) *Stable isotope ecology*, Springer-Verlang, New York, NY.
- Gido K.B., Franssen N.R. & Propst D.L. (2006) Spatial variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes in the San Juan River, New Mexico and Utah: implications for the conservation of native fishes. *Environmental Biology of Fishes*, **75**, 197-207.
- Goldstein R.M. & Simon T.P. (1999) Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. *Assessing the sustainability and biological integrity of water resources using fish communities*. CRC Press, Boca Raton, Florida, 123-202.
- Graf W.L. (1999) Dam nation: A geographic census of American dams and their largescale hydrologic impacts. *Water Resources Research*, **35**, 1305-1311.
- Gratton C. & Denno R.F. (2003) Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology*, **84**, 2692-2707.
- Gregory L. & Hatler W. (2008) A watershed protection plan for the Pecos River in Texas. Texas Water Resources Institute: College Station, Texas.
- Grimm N.B. (1987) Nitrogen dynamics during succession in a desert stream. *Ecology*, 1157-1170.
- Hale M. A comparative study of the food of the shiners *Notropis lutrensis* and *Notropis venustus*. In: *Proceedings of the Oklahoma Academy of Science*, pp. 125-129.
- Hatch M.D., Baltosser W.H. & Schmitt C.G. (1985) Life-history and ecology of the bluntnose shiner (*Notropis simus pecosensis*) in the Pecos River of New Mexico. *Southwestern Naturalist*, **30**, 555-562.
- Head G.N. & Orcutt J.D. (2002) *From Folsom to Fogelson: The Cultural Resources Inventory Survey of Pecos National Historical Park*, Anthropology Projects, Cultural Resources Management, Intermountain Region, National Park Service, Department of the Interior.
- Hendrickson D.A. & Cohen A.E. (2012) Fishes of Texas Project and Online Database. Vol. December 30. Texas Natural History Collection, a division of Texas Natural Science Center, University of Texas at Austin.
- Hoagstrom C.W. (2009) Causes and impacts of salinization in the lower Pecos River. *Great Plains Research*, **19**, 27-44.

- Hoagstrom C.W., Brooks J.E. & Davenport S.R. (2008) Recent habitat association and the historical decline of *Notropis simus pecosensis*. *River Research and Applications*, **24**, 789-803.
- Hoeninghaus D., Layman C., Arrington D. & Winemiller K. (2003) Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes*, **67**, 379-387.
- Hultine K.R., Belnap J., Van Riper III C., Ehleringer J.R., Dennison P.E., Lee M.E., Nagler P.L., Snyder K.A., Uselman S.M. & West J.B. (2009) Tamarisk biocontrol in the western United States: ecological and societal implications. *Frontiers in Ecology and the Environment*, **8**, 467-474.
- Israël N.M., Vanlandeghem M.M., Denny S., Ingle J. & Patiño R. (2014) Golden alga presence and abundance are inversely related to salinity in a high-salinity river ecosystem, Pecos River, USA. *Harmful Algae*, **39**, 81-91.
- Jensen R., Hatler W., Mecke M. & Hart C. (2006) The Influences of Human Activities on the Waters of the Pecos Basin of Texas: A Brief Overview. Texas Water Resources Institute.
- Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian special publication of fisheries and aquatic sciences*, **106**, 110-127.
- Kummu M. & Varis O. (2007) Sediment-related impacts due to upstream reservoir trapping, the Lower Mekong River. *Geomorphology*, **85**, 275-293.
- Kwak T.J. & Zedler J.B. (1997) Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia*, **110**, 262-277.
- Layman C.A., Arrington D.A., Montaña C.G. & Post D.M. (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, **88**, 42-48.
- Linam G.W. & Kleinsasser L.J. (1996) Relationship between fishes and water quality in the Pecos River, Texas. *Texas Parks and Wildlife Dept., Resource Protection Division River Studies Report*.
- Lindehoff E., Granéli E. & Granéli W. (2009) Effect of tertiary sewage effluent additions on *Prymnesium parvum* cell toxicity and stable isotope ratios. *Harmful Algae*, **8**, 247-253.
- Marzin A., Verdonschot P.F.M. & Pont D. (2013) The relative influence of catchment, riparian corridor, and reach-scale anthropogenic pressures on fish and macroinvertebrate assemblages in French rivers. *Hydrobiologia*, **704**, 375-388.
- Michener R. & Lajtha K. (2008) *Stable isotopes in ecology and environmental science*, Blackwell Publishers, Boston, MA.
- Minckley W. & Meffre G.K. (1987) Differential selection by flooding in stream-fish communities of the arid American Southwest. *Community and Evolutionary Ecology of North American Fishes* (eds W.J. Matthews and D.C. Heins), pp. 93-104. University of Oklahoma Press, Oklahoma.

- Montgomery D.R. (1999) Process domains and the river continuum. *Journal of the American Water Resources Association*, **35**, pp. 397-410.
- Nuttall P. (1972) The effects of sand deposition upon the macroinvertebrate fauna of the River Camel, Cornwall. *Freshwater Biology*, **2**, 181-186.
- Olden J.D., and Mark J. Kennard. (2010) Intercontinental comparison of fish life history strategies along a gradient of hydrologic variability. pp. 83-107. *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*.
- Ostrand K. & Wilde G. (2002) Seasonal and spatial variation in a prairie stream-fish assemblage. *Ecology of Freshwater Fish*, **11**, 137-149.
- Pease A.A., Justine Davis J., Edwards M.S. & Turner T.F. (2006) Habitat and resource use by larval and juvenile fishes in an arid-land river (Rio Grande, New Mexico). *Freshwater Biology*, **51**, 475-486.
- Pease A.A., Taylor J.M., Winemiller K.O. & King R.S. (2011) Multiscale Environmental Influences on Fish Assemblage Structure in Central Texas Streams. *Transactions of the American Fisheries Society*, **140**, 1409-1427.
- Phillips D.L. & Gregg J.W. (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia*, **127**, 171-179.
- Pimm S.L. (1982) *Food webs*, Chapman & Hall, New York, NY.
- Pimm S.L., J.H. Lawton. (1977) The numbers of trophic levels in ecological communities. *Nature*, **268**, 329-331.
- Poff N.L. (1997) Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391-409.
- Poff N.L. & Allan J.D. (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, **76**, 606-627.
- Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime. *BioScience*, 769-784.
- Poff N.L. & Ward J.V. (1990) Physical habitat template of lotic systems- recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management*, **14**, 629-645.
- Pomeroy K.E., Shannon J.P. & Blinn D.W. (2000) Leaf breakdown in a regulated desert river: Colorado River, Arizona, USA. *Hydrobiologia*, **434**, 193-199.
- Post D.M. (2002) The long and short of food-chain length. *Trends in Ecology & Evolution*, **17**, 269-277.
- Power M.E., Dietrich W.E. & Finlay J.C. (1996) Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental management*, **20**, 887-895.

- Quinn J. (2000) Effects of pastoral development. *New Zealand stream invertebrates: ecology and implications for management*, 208-229.
- Rahel F.J. & Hubert W.A. (1991) Fish assemblages and habitat gradients in a Rocky Mountain–Great Plains stream: biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society*, **120**, 3193-322.
- Rhodes K. & Hubbs C. (1992) Recovery of Pecos River fishes from a red tide fish kill. *The Southwestern Naturalist*, 178-187.
- Ricciardi A. & Rasmussen J.B. (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1759-1765.
- Richards C., Johnson L.B. & Host G.E. (1996) Landscape-scale influences on stream habitats and biota. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 295-311.
- Schlosser I. (1987) A conceptual framework for fish communities in small warmwater streams. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman, **17**, 24.
- Sharp Z. (2007) *Principles of stable isotope geochemistry*, Pearson Education Upper Saddle River, NJ, USA.
- Simon K.S. & Townsend C.R. (2003) Impacts of freshwater invaders at different levels of ecological organisation, with emphasis on salmonids and ecosystem consequences. *Freshwater Biology*, **48**, 982-994.
- Simpson D.G. & Gunter G. (1956) Notes on habitats, systematic characters and life histories of Texas salt water cyprinodonts.
- Singer G.A., Panzenböck M., Weigelhofer G., Marchesani C., Waringer J., Wanek W. & Battin T.J. (2005) Flow history explains temporal and spatial variation of carbon fractionation in stream periphyton. *Limnology and Oceanography*, **50**, 706-712.
- Stepenuck K.F., Crunkilton R.L. & Wang L. (2002) Impacts of urban land-use on macroinvertebrate communities in southeastern Wisconsin streams. *Journal of the American Water Resources Association*, **38**, 1041-1051.
- Suttle K.B., Power M.E., Levine J.M. & Mcneely C. (2004) How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications*, **14**, 969-974.
- Thoms M.C. & Sheldon F. (2002) An ecosystem approach for determining environmental water allocations in Australian dryland river systems: the role of geomorphology. *Geomorphology*, **47**, 153-168.
- Thorp J.H. & DeLong M.D. (1994) The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. *Oikos*, 305-308.
- Thorp J.H. & DeLong M.D. (2002) Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos*, **96**, 543-550.

- Tinker R. (2015) United States Drought Monitor. Vol. January 22. National Drought Mitigation Center.
- Turner T.F. & Edwards M.S. (2012) Aquatic foodweb structure of the Rio Grande assessed with stable isotopes. *Freshwater Science*, **31**, 825-834.
- Vander Zanden M. & Fetzer W.W. (2007) Global patterns of aquatic food chain length. *Oikos*, **116**, 1378-1388.
- Vander Zanden M. & Rasmussen J.B. (1999) Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology*, **80**, 1395-1404.
- Vander Zanden M. & Rasmussen J.B. (2001) Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and oceanography*, **46**, 2061-2066.
- Vander Zanden M.J., Casselman J.M. & Rasmussen J.B. (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, **401**, 464-467.
- Vanni M.J., Renwick W.H., Headworth J.L., Auch J.D. & Schaus M.H. (2001) Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: A fiveyear study. *Biogeochemistry*, **54**, 85-114.
- Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian journal of fisheries and aquatic sciences*, **37**, 130-137.
- Wang L., Lyons J., Kanehl P. & Gatti R. (1997) Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. *Fisheries*, **22**, 6-12.
- Wang L.Z., Lyons J. & Kanehl P. (2001) Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environmental Management*, **28**, 255-266.
- Ward J.V. & Stanford J. (1983) The serial discontinuity concept of lotic ecosystems. *Dynamics of lotic ecosystems*, 29-42.
- Werner E.E. & Gilliam J.F. (1984) The ontogenetic niche and species interactions in size structured populations. *Annual review of ecology and systematics*, 393-425.
- Whitcraft C.R., Levin L.A., Talley D. & Crooks J.A. (2008) Utilization of invasive tamarisk by salt marsh consumers. *Oecologia*, **158**, 259-272.
- Williams W. (2001) Anthropogenic salinisation of inland waters. *Hydrobiologia*, **466**, 329-337.
- Winemiller K.O. (1990) Spatial and temporal variation in tropical fish trophic networks. *Ecological monographs*, **60**, 331-367.
- Winemiller K.O., Hoinghaus D.J., Pease A.A., Esselman P.C., Honeycutt R.L., Gbanaador D., Carrera E. & Payne J. (2011) Stable isotope analysis reveals food web structure and watershed impacts along the fluvial gradient of a mesoamerican coastal river. *River Research and Applications*, **27**, 791-803.
- Yang L.H., Bastow J.L., Spence K.O. & Wright A.N. (2008) What can we learn from resource pulses. *Ecology*, **89**, 621-634.

- Yuan F. & Miyamoto S. (2008) Characteristics of oxygen-18 and deuterium composition in waters from the Pecos River in American Southwest. *Chemical Geology*, **255**, 220-230.
- Yuan F.S. & Miyamoto S. (2005) Dominant processes controlling water chemistry of the Pecos River in American southwest. *Geophysical Research Letters*, **32**, 1-4.
- Zeug S.C. & Winemiller K.O. (2008) Evidence supporting the importance of terrestrial carbon in a large-river food web. *Ecology*, **89**, 1733-1743.