CROSS SYSTEM TRANSPORT OF ORGANIC MATTER AND CONTAMINANTS IN SEMI-ARID AND ARID LOTIC ECOSYSTEMS

DISSERTATION

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Aquatics Resources

Doctor of Philosophy

by

Alisa A. Abuzeineh, M.S.

San Marcos, Texas
December 2011

CROSS SYSTEM TRANSPORT OF ORGANIC MATTER AND CONTAMINANTS

IN SEMI-ARID AND ARID LOTIC ECOSYSTEMS

Committee Members Approved:

_____
Weston H. Nowlin, Chair

_____
Dittmar Hahn

_____
Timothy H. Bonner

_____
Matthew M. Chumchal

_____
Blake Matthews

Approved:

_____
J. Michael Willoughby
Dean of the Graduate College

FAIR USE AND AUTHOR'S PERMISSION STATEMENT

Fair Use

Duplication Permission

ACKNOWLEDGEMENTS

I thank the members of my committee for their time and guidance through this entire process. I would also like to thank the members of Dr. Weston Nowlin's lab, past and present. Weston Nowlin, Pete Diaz, Alex Smith, Corey Pray, Jesse Becker, Kelly "Rodi" Rodibaugh, and Gabriel Timmins for their help in the field and in the lab, and for making being a member of the Nowlin lab feel like a family. I would also like to thank Pete Diaz for his help with identification and education of aquatic macroinvertebrates. I thank members of Dr. Timothy Bonner's lab, in particular Tom Heard, Casey Williams, Josh Perkin, Zach Shattuck, Megan Bean, and Becca Marfurt lab for their help in the field and laboratory. I also thank Susanna Scott and Kathryn Gilson for their help in the field and lab. I would like to thank my professors in the Department of Biology at Texas State University-San Marcos as well as my funding sources. Finally, I would like to thank my family for supporting me and encouraging me through this very long and rewarding journey.

This manuscript was submitted November 15, 2011

TABLE OF CONTENTS

Page

LIST OF TABLES

Table **Page**

LIST OF FIGURES

Figure **Page**

ABSTRACT

CROSS SYSTEM TRANSPORT OF ORGANIC MATTER AND CONTAMINANTS IN SEMI-ARID AND ARID LOTIC ECOSYSTEMS

by

Alisa A. Abuzeineh, M.S.

Texas State University-San Marcos

December 2011

SUPERVISING PROFESSOR: WESTON H. NOWLIN

Externally-derived resources are important for the dynamics and stability of the systems involved, especially for recipient systems. In addition, environmental scientists have expanded this concept of cross-ecosystem resource subsidies to include the transfer of bioaccumulating contaminants across ecosystem boundaries. The aim of my research was to examine the relative contribution of autochthonous and allochthonous OM sources to fish communities in the Rio Grande/Rio Bravo del Norte drainage in Texas. I

additionally assessed patterns in the potential movement of Hg from streams to riparian consumers. My research focused on three main areas: (1) the cycling of organic matter and contaminants within and across aquatic-terrestrial interfaces, (2) landscape- and regional-level parameters that influence macroinvertebrate assemblages at local and landscape spatial scales, and (3) the effect of environmental processes on aquatic communities using stable isotope-derived ecometrics. The information gathered from these studies provides greater understanding of the movements of OM and contaminants across local and landscape level environmental gradients.

CHAPTER I

INTRODUCTION

Nearly all ecosystems subsidize or receive subsidies of prey, nutrients, and organic matter from adjacent ecosystems. These externally-derived resources are important for the dynamics and stability of the systems involved, especially for recipient systems (Cummins et al. 1973, Polis 1997b, Huxel and McCann 1998, Sabo and Power 2002, Baxter et al. 2005). Although some communities can persist with limited or no subsidies, communities with low levels of autochthonous production are more likely to receive subsidies from more productive, adjacent ecosystems (Polis 1997b). Ecologists have long recognized that there is substantial exchange of resources across ecosystem boundaries; however, the magnitude and timing of allochthonous inputs are highly variable among ecosystems and it is still unclear for many of these systems how critical the subsidies are to community dynamics and stability of ecosystems.

Recently, ecologists have explored the role of allochthonous subsidies on community stability (Huxel and McCann 1998, Holt 2002, Huxel et al. 2002). These theoretical explorations indicate that several characteristics of recipient food webs and of the allochthonous subsidies (e.g. magnitude of resources, consumer preference, quality and timing) are critical for predicting the effects of allochthonous subsidies on recipient systems. Two of these characteristics importance are the magnitude of the subsidy and

the consumer preference for the subsidy (Huxel and McCann 1998, Huxel et al. 2002). Huxel and McCann (1998) found that low levels of allochthonous resource input or low consumer preference for the allochthonous resource tends to increase food web stability when compared to a community receiving no allochthonous resources. However, high levels of resource input or high preferences of consumers for the resource can make food chains unstable, leading to loss of consumers from food webs (Huxel and McCann 1998, Huxel et al. 2002). The quality of the resource subsidy can also play an important role in community stability; as quality of prey items increase so does stability; however in a single resource theoretical system, high levels of resource quality can destabilize food webs (Huxel 1999), reminiscent of the "paradox of enrichment" (e.g., Rosenzweig 1971). However, Huxel (1999) points out that natural systems which typically have multiple food sources available to consumers may be unlikely to exhibit destabilization when a food resource is of high quality. Finally, timing of subsidy inputs can also affect community stability. Takimoto et al. (2002) found that inputs of allochthonous subsidies during periods when autochthonous productivity is low increased consumer population stability. Given the potential effects of allochthonous subsidies in these theoretical frameworks, subsidies may be important for the maintenance and persistence of many communities and ecosystems.

In addition to theoretical predictions of the influence of allochthonous subsidies, there has been much recent empirical examination of the effects of the cross-ecosystem transport of resources. Examples of these transport mechanisms include the movement of organic matter via organism activities, and along ecological gradients such as climate, anthropogenic impact, and hydrology (Polis et al. 1997a, Polis et al. 1997b, Hein et al.

2003, Baxter et al. 2005, Ballinger and Lake 2006). In general, most of these studies have examined the movement of resources across the aquatic-terrestrial interface. Lotic ecosystems are appropriate systems to explore the community- and ecosystem-level influences of allochthonous subsidies because they can exhibit large exchanges of matter with adjacent terrestrial ecosystems due to their placement within landscapes (e.g., downhill positions receiving in watersheds and landscapes; Shurin et al. 2006, Leroux and Loreau 2008, Nowlin et al. 2008). Rivers and streams are also intriguing systems to examine the role of allochthonous subsidies because they (1) exhibit substantial variability in size or order, (2) variability in magnitude of longitudinal and lateral movements of water, and (3) often cross environmental gradients as they develop longitudinally (Vannote et al. 1980, Junk et al. 1989, Poff and Ward 1989, Thorp and Delong 1994).

Extensive studies have elucidated the intimate connectivity between lotic ecosystems and their adjoining watersheds by demonstrating how the flow of nutrients and organisms can have large influences on populations and communities in both aquatic and terrestrial ecosystems (Vannote et al. 1980, Baxter et al. 2005). The movement and fate of organic matter, nutrients, and contaminants from a terrestrial environment to a river is influenced by both biotic (i.e., consumption in the watershed and subsequent defecation in aquatic systems, deposition of terrestrial leaf litter) and abiotic vectors (i.e., sediment and terrestrial nutrient input via wind and recession of floodwaters; Cummins et al. 1973, Polis et al. 1997b, Wallace et al. 1997). Similarly, the transport of organic matter, nutrients, and contaminants from the river to its watershed is also influenced by both biotic (i.e., aquatic macroinvertebrate emergences and deposition of aquatic

organism carcasses on shorelines; Gray 1993, Sabo and Power 2002, Paetzold et al. 2005) and abiotic (flood transport of dissolved nutrients and sediments to riparian zones; Junk et al. 1989, Polis et al. 1997b) pathways. Indeed, riparian areas frequently exhibit higher productivity, environmental heterogeneity, and biodiversity than upland areas (Jackson and Fisher 1986, Gray 1993).

Organic Matter Sources in Riverine Ecosystems

Currently, ecologists recognize three main conceptual models that address the flow of nutrients and energy in riverine ecosystems: (1) the river continuum concept, (2) the flood pulse concept, and (3) the riverine productivity model (RCC, FPC, and RPM, respectively). Each model provides general predictions of how nutrients and energy move across river habitats (upstream to downstream) and across aquatic-terrestrial interfaces.

Vannote et al. (1980) introduced the widely-cited river continuum concept (RCC) in which the authors provide an explanation of food web structure as well as nutrient movement from the headwater streams (river orders 1-3), mid-sized rivers (4-6), and large river systems (>6) in temperate environments. Vannote et al. (1980) suggested that as rivers increase in order from headwaters to large river systems, turbidity, autotrophic- vs. heterotrophic-dominated food web bases, invertebrate and fish communities, and water temperatures change. For example, low-order headwater streams with extensive terrestrial shading have highly turbid water, reduced primary production, and greater allochthonous subsidy reliance. Additionally, headwater invertebrate and fish communities are typically dominated by shredders and small bodied insectivores, respectively. Mid-sized rivers with low turbidity and less direct interaction with the

riparian environment are more autotrophically-dominated and within river communities are thought to rely largely upon autochthonous carbon sources. Invertebrate and fish communities are much more diverse in mid-sized rivers and are dominated by scrapers and grazers as well as insectivores and piscivores, respectively. Finally, large order rivers with limited shading and larger flow volumes are dominated by invertebrate scrapers and piscivorous and benthivorous fish. While the RCC has increased our understanding of OM dynamics in riverine food webs, there are several major constraints with the original version of the RCC due to the fact that it (1) generally applies to constricted river channels with relatively steep gradient shores, (2) minimizes the effect of lateral exchange of organic matter between wetted channel and adjacent floodplain, and (3) was created after examination of north temperate, small order streams influenced by short duration, erratic flood events (Junk et al. 1989, Sedell et al. 1989, Thorp and Delong 1994, Junk and Wantzen 2004). Therefore, the lack of applicability of this model to a broad array of streams and rivers has lead to subsequent conceptual models of riverine OM dynamics.

Junk et al. (1989) proposed the flood pulse concept (FPC) to address some of the aforementioned constraints of the RCC. The main focus of the FPC is the description of the lateral exchange of water, nutrients, and organisms between the wetted river channel and its adjacent floodplain. Junk et al. (1989) defined the floodplain as "periodically inundated by the lateral overflow of rivers and lakes and/or by rainfall or groundwater" and suggest most river channels not constricted by steep gradient shores are subject to long- and short-duration flooding. Junk et al. (1989) suggest allochthonous inputs from the watershed due to flooding have a greater influence on nutrient and organic matter

transfer in the channel than downstream "leakage" or primary and secondary production within the channel. Additionally, they suggest that the terrestrial floodplain ecosystems can benefit greatly from the labile, dissolved nutrients from the river that are transported to terrestrial habitats during flood events. Overall, it is suggested that most of the primary and secondary production happens within the watershed-floodplain with the river functioning primarily as a transport of dissolved and suspended matter and water (Junk et al. 1989, Junk and Wantzen 2004). In general, this model describes high-order, lowland river systems with large, accessible floodplains that experience regular, predictable flooding; however, since not all streams and rivers fit these criteria, the FPC model is likely most applicable to only the above mentioned stream types (Sedell et al.1989, Thorp and Delong 1994).

Sedell et al. (1989) proposed that it is unlikely individual rivers will exhibit patterns described solely by the RCC or the FPC models. Thorp and Delong (1994) expanded this by the assertion that due to substantial spatial variation within a river channel the relative importance of alternate OM sources (autochthonous *versus* allochthonous) may vary. Thorp and Delong (1994) introduced the riverine productivity model (RPM), a hybrid of the RCC and FPC models. The main tenet of the RPM is the combination of local autochthonous production (i.e. micro- and macroalgae and macrophyte growth) and allochthonous inputs (OM from the adjacent floodplain) as important sources of C in large river systems. Therefore, in large rivers or reaches with constricted channels and firm substrate, a combination of autochthonous and within river allochthonous OM serve as C sources. However, in reaches with unconstricted channels, *in situ* primary production is likely the major contributor to riverine consumers and

dissolved inorganic nutrients from the watershed contribute to the growth of in stream primary producers. Furthermore, the RPM acknowledges that allochthonous C transported from upstream reaches, while abundant, is of low quality and receives limited use from consumers, leading to a dependence on autochthonous C sources. This conceptual model was developed by research on deep, large rivers found in the southern and midwestern regions of the United States and much more field research is necessary to substantiate this model in other lotic systems (Thorp and Delong 1994; Zeug and Winemiller 2008).

Ecological and Organic Matter Dynamics of Arid and Semi-arid Riverine Systems

The above models have been examined in mostly temperate riverine systems, thus there is limited research to address the applicability of riverine OM dynamic models to rivers in arid and semi-arid ecosystems. In addition, some of the riverine OM models examine ecological dynamics along a continuum of river size class/order (e.g., RCC), but there has been little examination of changes in ecological structure and function as riverine systems cross substantial abiotic gradients (i.e., precipitation gradients, soil characteristics, terrestrial biome types). In contrast to north temperate and southeastern U.S. river systems, arid rivers are more likely to have periods of drying or significant channel constriction for long periods associated with little or no precipitation (Thomas et al. 2006). In addition, unpredictable episodes of heavy precipitation and extreme flash flooding lead to the movement of substantial sediment loads and transport of organisms downstream (Thomas et al. 2006, Young and Kingsford 2006). Due to intermittent hydrological flows and tendency for short duration, unpredictable flooding, it is likely only macroinvertebrate and fish species populations that exhibit high resilience and

resistance under these conditions will persist in arid lotic systems (Meffe and Minckley 1987, Stanley et al. 1994). Although fish populations can resist flood disturbances better than macroinvertebrates, macroinvertebrates are able to recolonize and reproduce in the area very quickly after the event (Stanley et al. 1994). However, Stanley et al. (1994) found that drying of streambeds resulted in significant abundance declines in some macroinvertebrate species, particularly those species that were unable to utilize atmospheric oxygen. However, the same study found that if there was still a connection to upstream sites, there was very little population fluctuation during extended periods of desiccation.

In arid and semi-arid riverine systems, within-river primary production can be relatively high, leading to a ratio of *in situ* primary production to community respiration (P/R) that is frequently greater than 1 (Fisher et al. 1982, Fisher and Gray 1983). In addition, the high *in situ* primary production of these arid rivers may actually exceed that of the adjacent terrestrial environment. Thus, it is expected that autochthonous algal OM will be of greater importance for in-stream consumers than allochthonous terrestrial OM subsidies (Jones et al 1997, Schade and Fisher 1997, Forrester et al. 1999). Despite the fact that arid systems are subject to unpredictable, short duration flooding that wash terrestrial sediments into the channel, the relatively low rates of terrestrial production in watersheds and the small detrital pool in riparian habitats will likely contribute little OM to the riverine food web (Fisher and Gray 1983). This pattern is in contrast to temperate and semi-arid riverine systems, where the relatively higher productivity of riparian habitats supports the prediction that allochthonous terrestrial subsidization of OM (attributed to terrestrial leaf litter deposition, terrestrial OM runoff, and deposition of

terrestrial invertebrates; Polis et al. 1997b, Nakano and Murakami 2001, Allan et al. 2003, Baxter et al. 2005) into the riverine community can be just as or more important than autochthonous algal production (Cummins et al. 1973, Thorp and Delong 1994, Thorp 2002). Because most of the aforementioned riverine OM dynamic models (RCC, FPC, and RPM) were generated based upon observations of north temperate and subtropical systems in which OM dynamics are likely different from arid rivers, the applicability of these riverine models to arid river systems remains unknown.

It has been hypothesized that adjacent ecosystems that exchange OM and nutrients and vary in primary productivity will also vary in their contributions of allochthonous subsidies to one another. It has been predicted that the ecosystem with higher relative primary production will subsidize the less productive adjacent system (Polis et al. 1997b). Polis and Hurd (1996) found this relationship between the highly productive coastal waters and the adjacent terrestrial island environments with low primary productivity in the Gulf of California. Polis and Hurd (1996) also found that as island area increased, the effect of allochthonous C on terrestrial productivity, mediated by marine input, decreased. I hypothesize that in arid and semi-arid environments rivers will subsidize terrestrial ecosystems, and this the importance of this subsidy will decrease with distance from the river.

Low rates of terrestrial detrital production in arid and semi-arid terrestrial habitats will potentially increase the reliance of riparian consumers on allochthonous subsidization from the river channel. Riverine allochthonous inputs can lead to greater species abundance and diversity in riparian areas than in upland habitats (Sanzone et al. 2003). Further, it is likely a major source of energy and nutrients to arid and semi-arid

riparian secondary consumers comes from macroinvertebrate emergences from rivers and streams. Indeed, research has demonstrated that aquatic invertebrates are a substantial nutrient and energy source for terrestrial invertebrates, birds, mammals, and reptiles inhabiting riparian habitats (Jackson and Fisher 1986, Jackson 1988, Schade and Fisher 1997).

Methods for Determining Organic Matter Sources in Aquatic Ecosystems

Determination of the relative importance of supporting OM sources to food webs has been a central theme of community and ecosystem ecology for decades (Minshall 1967, Cummins et al. 1973, Polis et al. 1997b). Historically, ecologists have utilized several methods to assess food and energy sources in aquatic food webs. Four of the most commonly used methods are: (1) measurement of rates of production and inputs of OM to a system, (2) gut content analysis of members of the community, (3) analysis of fatty acid markers in OM sources and members of the community, and (4) stable isotope analysis of OM sources and members of the community. Each method has been used in combination with another and individually, in studies (Lancaster and Waldron 2001, Alfaro 2008, Budge et al. 2008) and has strengths and weaknesses in assessing trophic interactions in food webs.

Movement and production of OM and energy within and between ecosystems can be accomplished through measurement of production rates and quantification of OM inputs and outputs using observational and/or manipulative approaches (Polis and Hurd 1996, Nakano et al. 1999, Pace et al. 2004, Nowlin et al. 2007). While this approach provides information for mass balances and fluxes of OM for an ecosystem, these methods do not provide direct information on the pathways and degree of utilization of

these potential OM sources by the community. Therefore, if determination of actual uptake or utilization of C by consumers in a food web is of interest to a researcher, this method will not directly elucidate these relationships unless it is coupled with another method such as gut content analysis, fatty acid analysis, or stable isotopes.

In contrast to the mass balance/flux approach, analysis of gut content of consumers is a more direct and commonly-used method to examine OM sources for members of a food web. This analysis is temporally sensitive in that the examiner is typically unable to ascertain the organism's diet beyond the amount of time required for gut passage (Schooley et al. 2008). In addition, gut analysis of consumers that masticate or highly fragment food items before ingestion can present substantial logistical and identification issues. For example, Schooley et al. (2008) found that it was difficult to identify the prey items eaten by larval fish in the lab within a few hours of consumption. Also, differences in assimilation rate and nutrient content among prey items may lead researchers to conclude a dietary composition that does not reflect reality (Fry 2006). Additionally, items found in the gut can be difficult to identify due to cellular structure (e.g., live algal cells *versus* algal detritus). Although there are limitations, this method is still a highly useful tool when used in conjunction with some of the other methods mentioned here.

Another valuable approach to assess dietary composition is the use of fatty acid analysis. Typically, this analysis provides information on the consumption of organic matter in a time period from a few hours to days (Iverson et al. 2004). Unlike proteins, fatty acids are not extensively broken down during digestion and are deposited or stored in adipose tissue (with reduced modification in structure; Iverson et al. 2004). This

technique has been extremely useful in elucidating OM sources in terrestrial, marine, and freshwater ecosystems (Schwalme 1992, Budge et al. 2008, Thiemann 2008); however, there are a large number of fatty acids to choose from, each of which can yield varying results as well as their retention and transfer along body size and taxonomic groups, making the selection of a specific fatty acid maker critical for studies (e.g., Iverson et al. 2004, Kainz et al. 2004).

The use of stable isotopes has also been used to assess energy and nutrient sources to consumers and to infer trophic structure of communities (Post 2002, Fry 2006). This method has become widespread in environmental sciences over the past three decades and is used by anthropologists, oceanographers, hydrologists, and ecologists (Wolfsperger 1993, Krabbenhoft et al. 1994, Boutton et al. 1999, Sanzone et al. 2003, Voigt et al. 2003, Burman and Passe 2008). Due to the relatively low monetary cost of this type of analysis and our growing understanding of fractionation and mixing processes (see below), ecologists now employ stable isotopes in a variety of studies (Post 2002, Fry 2006).

*Use of Stable Isotopes to Study of Organic Matter Sources and Food Web Structur*e

Ecologists studying food web dynamics and OM flows are primarily concerned with the stable isotopes of five elements: carbon (C), nitrogen (N), sulfur (S), oxygen (O), and hydrogen [H or deuterium (D)]. The most common isotopes used by ecologists for understanding and following OM flows through food webs are ^{13}C and ^{15}N. For example, of the ratio of ^{13}C: ^{12}C ($\delta^{13}C$) in tissues can be used to distinguish between C_4 and C_3 plants in the diets of herbivores (Michener and Lajtha 2008). These plants utilize different photosynthetic pathways (C_4 plants tend to photosynthesize at a faster rate and

use water more efficiently than C_3 plants) which leads to different $\delta^{13}C$ values (Chisolm et al. 1982, Peterson and Fry 1987, Gannes et al. 1997).

Similar to the aforementioned methods used in food web studies, there are a number of critical considerations when using stable isotopes to elucidate OM sources and food web structure (Post 2002, Fry 2006). Carbon stable isotopes are useful to determine consumer C source(s); a consumer's $\delta^{13}C$ value can be used in conjunction with mixing models to ascertain the proportional contribution of different food sources to their diets (Post 2002, Fry 2006). As useful as the mixing models can be to elucidate the relative importance of different basal resources to consumers, it is important to keep the mixing models as simple as possible, therefore typically a two-source mixing model is employed (Phillips 2001). However, there are often occasions in which a slightly more evolved, multi-source model is necessary (Phillips 2001, Phillips and Gregg 2003, Moore and Semmens 2008, Jackson et al. 2009). One main consideration when using C stable isotopes is the temporal and spatial variability in baseline values of carbon sources (Post 2002, Anderson and Cabana 2007). In riverine systems, $\delta^{13}C$ value of periphyton can be strongly influenced by variables such as flow rate, concentration and $\delta^{13}C$ of inorganic carbon, and periphyton species composition (Findlay et al. 2001, Findlay et al. 2002, Singer et al. 2005). In addition, the temporal and spatial variability in $\delta^{13}C$ of periphyton can be reflected in herbivores (Findlay et al. 2001, Findlay et al. 2002, Findlay 2004). In contrast, Matthews and Mazumder (2003) did not find a significant difference in among-lake $\delta^{13}C$ signatures of the same zooplankton species among lakes, but found significant variance within lakes among taxonomic groups. However, further examination and increased sample size could show different results.

In addition to issues surrounding the use of C stable isotopes to examine basal C resources in food webs, the use of N stable isotopes to infer trophic positions of consumers in a food web also presents several substantial issues for consideration. Ecologists generally assume that there is a +2.5 - 4‰ fractionation of ^{15}N ($\delta^{15}N$) between a consumer and its food source (Post 2002, Fry 2006, Wolf et al. 2009). However, this fractionation factor is not a universal constant because a diversity of factors, such as the specific tissues being examined, starvation status of consumers, protein content of diets, and nitrogenous waste pathways (Hobson et al. 1993, Gannes et al. 1997, Wolf et al. 2009). Nevertheless, across a diversity of studies, recent reviews have found that mean $\delta^{15}N$ fractionation values are generally ~3-4‰ (Post 2002, McCutchan et al. 2003).

Cross-Ecosystem Movement of Contaminants

Ecotoxicologists and environmental scientists have recently focused on the movement of contaminants across boundaries (Blais et al. 2007, Cristol 2008). Similar to the movement of OM between ecosystems, there are a multitude of abiotic and biotic mechanisms associated with the transfer of contaminants between ecosystems (Whicker et al 2002, Tombul et al. 2005, Cristol 2008). Because many contaminants bioaccumulate in tissues (i.e., mercury, some organic pesticides), the transfer of many of these substances is intimately tied with the movement of organisms between ecosystems (Blais et al. 2007).

Mercury (Hg) is a toxic element with no known biological function found in environments around the world. Through anthropogenic activities, we have greatly altered the global Hg cycle and the subsequent release of large amounts of Hg to the environment (Munthe et al. 2007). Approximately two-thirds of current global Hg

release to the atmosphere is derived from human activity-emissions, such as peat, wood and coal-burning, chlor-alkali facilities, metal production, and waste incineration (Lindqvist 1991, Seigneur et al. 2004, Munthe et al. 2007). These emissions have led to Hg deposition into ecosystems up to four times higher than pre-industrial levels (Swain et al. 1992, Engstrom and Swain 1997, Schuster et al. 2002) and the transport of Hg has led to the contamination of ecosystems far from point sources (Schlager et al. 1997, Fitzgerald et al. 1998).

Mercury is emitted from sources largely as inorganic Hg (II) and is deposited into aquatic systems directly onto the surface of the water or as runoff from the watershed (Rada et al. 1989, Ullrich et al. 2001). Deposition of Hg (II) in aquatic ecosystems is a concern because it is transformed by microorganisms in oxic-anoxic boundary layers of rivers, lakes, and wetlands into highly toxic methylmercury (MeHg; Jensen and Jernelov 1969). The rate of MeHg production by microorganisms is influenced by numerous environmental parameters such as pH, salinity, availability of organic matter, and the composition of microbial communities (Ullrich et al. 2001). Although still relatively little is known about the mechanisms of inorganic-organic transformation, studies have pointed to sulfate-reducing bacteria (SRB) as the main microbial group of Hg methylators (Compeau and Bartha 1985, Gilmour et al. 1992, Macaladay et al. 2000). Regardless of factors affecting the rate of methylation and its sources, MeHg is neurotoxic and even at reasonably low concentrations can have severe developmental, endocrine, and reproductive inhibition effects on humans and wildlife (Drevnick and Sandheinrich 2003, Drevnick et al. 2006, Webb et al. 2006, Mergler et al. 2007).

Mercury and MeHg dynamics in lakes and wetlands have received much more attention (Fitgerald et al. 1998, Grigal 2003, Blais et al. 2007) than riverine systems (but see Weiner and Shields 2000, Paller et al. 2004, Paller and Littrell 2007, Peterson et al. 2007, Rypel et al. 2008). In particular, there has been little examination of Hg dynamics in riverine systems within arid landscapes (but see Gray et al. 2003, Gray et al. 2006). It is generally thought that Hg occurs in wetland areas in headwater and small-order streams that flow into larger river systems; these headwater and wetland sites are thought to be the source of MeHg to the main river channel and little MeHg is thought to be formed in the main river channel itself (Paller et al. 2004). This hypothesis may be true for larger river systems in more mesic, temperate environments; however, many river systems in the western United States drain largely arid and semi-arid landscapes with very little to no headwater wetland cover (Smith et al., 2010). Additionally, although there has been extensive study on Hg occurrence and transformation in temperate riverine systems, there is still limited information about the mechanisms of transformations and movement of mercury in arid ecosystems.

Despite the lack of widespread information on Hg in fishes in arid river systems, available data indicate that fish in arid systems can contain substantial amounts of Hg (Peterson et al. 2007, Smith et al. 2010). In a recent review of Hg levels in stream fishes across the western USA (which included many arid and semi-arid streams), Peterson et al. (2007) found that Hg in piscivorous fish were three times higher than in non-piscivorous fish and above minimum USEPA human consumption levels for whole fish (0.185 $\mu g\ Hg \cdot g^{-1}$). They also suggest that atmospheric deposition was the main factor for high mercury concentrations in aquatic systems in the western United States (Peterson et

al. 2007). An examination of fishes in the lower Rio Grande, Texas found that predatory fishes consistently exhibit Hg concentration levels above USEPA wildlife criterion (122 ±86.2 μg kg^{-1}) (Smith et al. 2010).

Although deposition of Hg (II) into aquatic systems occurs largely through abiotic pathways, the movement to the terrestrial environments is likely biologically mediated via organisms crossing ecosystems boundaries (e.g., aquatic to terrestrial). Burger (2002) measured metal contamination in the eggs and tissues of diamondback terrapins in coastal New Jersey and found Hg in their tissues was below interstate commerce levels (liver = 1139 ppb, muscle = 172 ppb); however, there was concern of bioaccumulation in larger marine and terrestrial predators of the terrapins (Burger 2002). More recently, Cristol et al. (2008) examined the movement of aquatically-derived mercury to terrestrial predators (birds and spiders). They found aquatically-derived mercury was a major contributor to MeHg in insectivorous spiders. They were, however, unsure if the MeHg concentrations found in spiders was a result of consumption of emerging aquatic invertebrates or from flood deposition (Cristol et al. 2008). Thus, there is still much more information needed to understand how Hg moves across ecosystem boundaries.

Scope of This Dissertation

The aim of my research was to examine the relative contribution of autochthonous and allochthonous OM sources to fish communities in the Rio Grande/Rio Bravo del Norte drainage in Texas. I additionally assessed patterns in the potential movement of Hg from streams to riparian consumers. My research focused on three main areas: (1) the cycling of organic matter and contaminants within and across aquatic-terrestrial interfaces, (2) landscape- and regional-level parameters that influence macroinvertebrate

assemblages at local and landscape spatial scales, and (3) the affect of environmental processes on aquatic communities using stable isotope-derived ecometrics. The information gathered from these studies provides greater understanding of the movements of OM and contaminants across local and landscape level environmental gradients.

Chapters 2 and 3 examined the basal C resources available to riverine communities and their affects on structure and function. The objective of Chapter 2 of this dissertation was to examine the relative contribution of OM sources to fish communities in the Rio Grande/Rio Bravo del Norte and several of its perennially-flowing tributaries. In this chapter, I assessed the relative importance of OM sources and food web structure of fish communities along lower Rio Grande drainage using N and C stable isotopes (e.g., $\delta^{13}C$ and $\delta^{15}N$). I then employed Bayesian mixing models to determine the proportional contribution of allochthonous C sources to fishes.

The focus of the third chapter of my dissertation was to explore the application of the stable isotope-derived community-wide metrics described by Layman et al. (2007; $\delta^{15}N$ range, $\delta^{13}C$ range, total niche area, mean distance to centroid, and standard deviation of nearest neighbor distances) throughout the range of the lower Rio Grande and its tributaries. These metrics allowed me to examine shifts in food web structure from small-to large-order streams and rivers as well as along an arid to semi-arid climatic gradient.

Chapter 4 of this dissertation was an examination of macroinvertebrate community structure and functional composition of a large complex drainage in the southwestern United States (i.e., the lower Rio Grande drainage in Texas; Fig. 1). I was

interested in broad scale differences of macroinvertebrate community composition at the family taxonomic level. The study objectives were three-fold.

1. Assess macroinvertebrate community composition and diversity along the Rio Grande drainage and across a substantial west-to-east/upstream-downstream physiographic gradient.
2. Examine whether differences in local site-specific environmental conditions or landscape-scale patterns would explain the variation in invertebrate community composition and diversity.
3. Assessed spatial patterns in the distribution and relative abundance of different invertebrate functional feeding groups in relation to predictions made by conceptual models of riverine communities, specifically, the RCC, FPC.

I collected aquatic macroinvertebrates from a variety of in-stream habitats and utilized multivariate ordination analyses to explore the above objectives.

The purpose of the final chapter (Chapter 5) of my dissertation was to assess patterns in the potential movement of Hg from streams to riparian consumers in an arid landscape. This study was conducted in three streams located along the lower Rio Grande drainage.

1. Examine Hg concentrations in portions of the aquatic food web in three tributaries in the Lower Rio Grande drainage in west Texas which potentially vary in Hg contamination.
2. Determine potential cross-ecosystem fluxes of Hg between streams and the adjacent terrestrial riparian systems.
3. Examine Hg contamination of several groups of terrestrial consumers (birds,

bats, and terrestrial arthropods) that inhabit or utilize riparian zones at the study stream reaches.

4. Compare patterns of Hg concentrations among aquatic and terrestrial consumers.

I assessed the total Hg concentrations of aquatic organisms (fish and macroinvertebrates) as well as terrestrial invertivores (arthropods, birds, and bats). I also estimated potential Hg export from riverine systems to terrestrial consumers via potential aquatic insect emergences. I was able to determine if terrestrial consumer Hg concentrations co-vary with those of aquatic consumers.

Literature Cited

Alfaro, A.C. 2008. Diet of *Littoraria scabra*, while vertically migrating on mangrove trees: Gut content, fatty acid, and stable isotope analyses. Estuarine Coastal and Shelf Science 79:718-726.

Allan, J.D., M.S. Wipfli, J.P. Caoette, A. Prussian, and J. Rogers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Science 60:309-320.

Anderson, C. and G. Cabana. 2007. Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. Journal of the North American Benthological Society 26:273-285.

Ballinger, A. and P.S. Lake. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. Marine and Freshwater Research 57:15-28.

Baxter, C.V., D.D. Fausch, and C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Blais, J.M., R.W. MacDonald, D. Mackey, E.Webster, C. Harvey, and J.P. Smol. 2007. Biologically mediated transport of contaminants to aquatic systems. Environmental Science and Technology 41:1075-1084.

Boutton, T.W., S.R. Archer, and A.J. Midwood. 1999. Stable isotopes in ecosystem science: Structure, function and dynamics of a subtropical Savanna. Rapid Communications in Mass Spectrometry 13:1263-1277.

Budge, S.M., M.J. Wooller, A.M. Springer, S.J. Iverson, C.P. McRoy, and G.J. Ivoky. 2008. Tracing carbon flow in an arctic marine environment using fatty acid-stable isotope analysis. Oecologia 157:117-129.

Burger, J. 2002. Metals in tissues of Diamondback Terrapin from New Jersey. Environmental Monitoring and Assessment 77:255-263.

Burman, J. and T. Passe. 2008. Oceanography in northwestern Europe during the last interglacial from intrashell delta O-18 ranges in *Littorina littorea* gastropods. Quaternary Research 70:121-128.

Chisholm, B.S., D.E. Nelson, and H.P. Schwarcz. 1982. Stable-isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science 216:1131-1132.

Compeau, G.C. and R. Bartha. 1985. Sulfate-reducing bacteria: principal methylators of mercury in anoxic estuarine sediment. Applied and Environmental Microbiology 50:498-502.

Cristol, D.A., R.L. Brasso, A.M. Condon, R.E. Fovargue, S.L. Friedman, K.K. Hallinger, A.P. Monroe, and A.E. White. 2008. The movement of aquatic mercury through terrestrial food webs. Science 320:335.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck, and V.I. Holt. 1973. Utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Drevnick, P.E. and M.B. Sanderheinrich. 2003. Effects of dietary methylmercury on reproductive endocrinology of fathead minnows. Environmental Science and Technology 37:4390-4396.

Drevnick, P.E., M.B. Sanderheinrich, and J.T. Oris. 2006. Increased ovarian follicular apoptosis in fathead minnows (*Pimphales promelas*) exposed to dietary methylmercury. Aquatic Toxicology 79:49-54.

Engstrom, D.R. and E.B. Swain. 1997. Recent declines in atmospheric mercury deposition in the upper Midwest. Environmental Science and Technology 31:960-967.

Finlay, J.C. 2004. Patterns and controls of lotic algal stable carbon isotope ratios. Limnology and Oceanography 49:850-861.

Finlay, J.C., S. Khandwala, and M.E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology 83:1845-1859.

Finlay, J.C., M.E. Power, and G. Cabana. 2001. Effects of water velocity on algal carbon isotope ratios: Implications for river food web studies. Limnology and Oceanography 44:1198-1203.

Fisher, S.G. and L.J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. Ecology 64:1217-1234.

Fisher, S.G., L.J. Gray, N.B. Grimm, and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. Ecological Monographs 52:93-110.

Fitzgerald, W.F., D.R. Engstrom, R.P. Mason, and E.A. Nater. 1998. The case for atmospheric mercury contamination in remote areas. Environmental Science and Technology 32:1-12.

Forrester, G.E., T.L. Dudley, and N.B. Grimm. 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. Limnology and Oceanography 44:1187-1197.

Fry, B. 2006. Stable Isotope Ecology. 308 pp. Springer Science Business Media LLC. New York, NY.

Gannes, L.Z., D.M O'Brien, and C. Martinez del Rio. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78:1271-1276.

Gilmour, C.G., E.A. Henry, and R. Mitchell. 1992. Sulfate stimulation of mercury methylation in freshwater sediments. Environmental Science and Technology 26:2281-2287.

Gray, J.E., M.E. Hines, and H. Biester. 2006. Mercury methylation influenced by areas of past mercury mining in Terlingua district, Southwest Texas, USA. Applied Geochemistry 21:1940-1954.

Gray, J.E., M.E. Hines, H. Biester, and B.K. Lasorsa. 2003. Mercury methylation in mine wastes collected from abandoned mercury mines in the USA. Journal de Physique IV 107:573-576.

Gray, L.J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. The American Midland Naturalist.

Grigal, D.F. 2003. Mercury sequestration in forests and peatlands: A review. Journal of Environmental Quality 32:393-405.

Hein, T., C. Baranyi, G.J. Herndl, W. Wanek, and F. Schiemer. 2003. Allochthonous and autochthonous particulate organic matter in floodplains of the River Danube: the importance of hydrological connectivity. Freshwater Biology 48:220-232.

Hobson, K.A., T. Alisauskas, and R.G. Clark. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analysis of diet. Condor 95:388-394.

Holt, R.D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. Ecological Reserch 17:261-273.

Huxel, G.R. 1999. On the influence of food quality in consumer-resource interactions. Ecology Letters 2:256-261.

Huxel, G.R. and K. McCann. 1998. Food web stability: influence of trophic flows across habitats. The American Naturalist 152:460-469.

Huxel, G.R., K. McCann, and G.A. Polis. 2002. Effects of partitioning allochthonous and autochthonous resources on food web stability. Ecological Research 17:419-432.

Iverson, S.J., C. Field, W.D. Bowen, and W. Blanchard. 2004. Quantitative fatty acid signature analysis: a new method of estimating predator diets. Ecological Monographs 74:211-235.

Jackson, A.L., R. Inger, S. Bearhop, and A. Parnell. 2009. Erroneous behavior of MixSIR, a recently published Bayesian isotope mixing model: a discussion of Moore and Semmens 2008. Ecology Letters 12:E1-E5.

Jackson, J.K. 1988. Diel emergence, swarming and longevity of selected adult aquatic insects from a Sonoran desert stream. The American Midland Naturalist 119:344-352.

Jackson, J.K. and S.G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. Ecology 67:629-638.

Jensen, S. and A. Jernelov. 1969. Biological methylation of mercury in aquatic organisms. Nature 223:753-754.

Jones, J.B., J.D. Schade, S.G. Fisher, and N.B. Grimm. 1997. Organic matter dynamics in Sycamore Creek, a desert stream in Arizona, USA. Journal of the North American Benthological Society 16:78-82.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publications of Fisheries and Aquatic Sciences 106:110-127.

Junk, W.J. and K.M. Wantzen. 2004. The flood pulse concept: new aspects, approaches and applications-an update. Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries, Vol. 2 R.L. Welcomme and T. Petr (eds). Food and Agriculture Organization & Mekong River Commission. FAO Regional Office for Asia and the Pacific, Bangkok. RAP Publication 16:117-149.

Kainz, M., M.T. Arts, and A. Muzumder. 2004. Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels. Limnology and Oceanography 79:1784-1793.

Krabbenhoft, D.P., C.J. Bowser, C. Kendall, and J.R. Gat. 1994. Use of O-18 and deuterium to assess the hydrology of groundwater-lake systems. Environmental Chemistry of Lakes and Reservoirs 237:67-90.

Lancaster, J. and S. Waldron. 2001. Stable isotope values of lotic invertebrates: Sources of variation, experimental design, and statistical interpretation. Limnology and Oceanography 46:723-730.

Lindqvist, O. 1991. Mercury in the Swedish environment. Water and Air Soil Pollution 55:23-30.

Leroux, S.J. and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147-1156.

Macalady, J.L., E.E. Mack, D.C. Nelson, and K.M. Scow. 2000. Sediment microbial community structure and mercury methylation in mercury-polluted Clear Lake, California. Applied and Environmental Microbiology 66:1479-1488.

Matthews, B. and A. Muzumder. 2003. Compositional and interlake variability of zooplankton affect baseline stable isotope signatures. Limnology and Oceanography 48:1977-1987.

Meffe, G.K. and W.L. Mincley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. The American Midland Naturalist 117:177-191.

McCutchen, J.H., W.M. Lewis, C. Kendall, C.C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378-390.

Mergler, D., H.A. Anderson, L.H.M. Chan, K.R. Mahaffrey, M. Murray, M. Sakamoto, and A.H. Stern. 2007. Methylmercury exposure and health effects in humans: a worldwide concern. Ambio 36:3-11.

Minshall, G.W. 1967. Role of allochthonous detritus in trophic structure of a woodland Springbrook community. Ecology 38:139-143.

Moore, J.W. and B.X. Simmons. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470-480.

Munthe, J., R.A. Bodaly, B.A. Branfireun, C.T. Driscoll, C.C. Gilmour, R. Harris, M. Horvat, M. Lucotte, and O. Malm. 2007. Recovery of mercury-contaminated fisheries. AMBIO 36:33-44.

Nakano, S., M. Hitoshi, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings from the National Academy of Science 98:166-170.

Nowlin, W.H., M.J. Gonzalez, M.J. Vanni, M.H.H. Stevens, M.W. Fields, and J.J. Valentei. 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of pond communities. Ecology 88:2174-2186.

Nowlin, W.H., M.J. Vanni, and L.H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89:647-659.

Pace, M.L., J.J. Cole, S.R. Carpenter, J.F. Kitchell, J.R. Hodgson, M.C. Van de Bogert, D.L. Bade, E.S. Kritzberg, and D. Bastviken. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature 427:240-243.

Paetzold, A., C.J. Schubert, and K.Tockner. 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8:748-759.

Paller, M.H., J.A. Bowers, J.W. Littrell, and A.V. Guanlao. 2004. Influences on mercury bioaccumulation factors for the Savannah River. Archives of Environmental Contamination and Toxicology 46:236-243.

Paller, M.H. and J.W. Littrell. 2007. Long-term changes in mercury concentrations in fish from the middle Savannah River. Science of the Total Environment 382:375-382.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystems studies. Annual Review of Ecological Systems 18:293-320.

Peterson, S.A., J. Van Sickle, A.T. Herlihy, and R.M. Hughes. 2007. Mercury concentration in fish from streams and rivers throughout the western United States. Environmental Science and Technology 41:58-65.

Phillips, D.L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127:166-170.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability of lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

Polis, G.A. and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396-423.

Polis, G.A., S.D. Hurd, C.T. Jackson, and F.S. Pinero. 1997a. El Nino effects on the dynamics and control of an island ecosystem in the Gulf of California. Ecology 78:1884-1897.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997b. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecological Systems 28:289-316.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Rada, R.G., J.G. Wiener, M.R. Winfrey, and D.E. Powell. 1989. Recent increases in atmospheric deposition of mercury in north-central Wisconsin lakes inferred from sediment analyses. Archives of Environmental Contamination Toxicology 18:175-181.

Rosenzweig, M.L. 1971. Paradox of enrichment – destabilization of exploitation ecosystems in ecological time. Science 171:385-387.

Rypel, A.L., D.A. Arrington, R.H. Findlay. 2008. Mercury in Southeastern U.S. Riverine Fish Populations Linked to Water Body Type. Environmental Science and Technology 42:5118-5124.

Sabo, J.L. and M.E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860-1869.

Sanzone, D.M., J.L. Meyer, E. Marti, E.P. Gardiner, J.L. Tank, N.B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134:238-250.

Schade, J.D. and S.G. Fisher. 1997. Leaf litter in a Sonoran desert stream ecosystem. Journal of the North American Benthological Society 16:612-626.

Schlager, R.J., K.G. Wilson, A.D. Sappey, G.L. Anderson, and D.W. Jackson. 1995. Continuous emissions monitor for total, elemental, and total speciated mercury. Abstracts of Papers of the American Chemical Society, Fuel Part 1 210:89.

Schuster, P.F., D.P. Krabbenhoft, D.L. Naftz, L.D. Cecil, M.L. Olson, J.F. DeWild, D.D. Susong, J.R. Green, and M.L. Abbott. 2002. Atmospheric mercury deposition during the last 270 years: A glacial ice core record of natural and anthropogenic sources. Environmental Science and Technology 36:2303-2310.

Seigneur C., K. Vijayaraghavan, K. Lohman, P. Karamchandani, and C. Scott. 2004. Modeling the atmospheric fate and transport of mercury over North America: power plant emission scenarios. Fuel Processing Technology 85:441-450.

Schooley, J.D., A.P. Karam, B.R. Kesner, P.C. Marsh, C.A. Pacey, and D.J. Hornbrugh. 2008. Detection of larval remains after consumption by fishes. Transactions of the American Fisheries Society 137:1044-1049.

Schwalme, K. 1992. A quantitative measure between diet and body fatty acid composition in wild northern pike (*Esox lucius*). Fish Physiology and Biochemistry 10:91-98.

Sedell, J.R., J.E. Richey, and F.J. Swanson. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? Canadian Journal of Fisheries and Aquatic Sciences 106:49-55.

Shurin, J.B., D.S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society B 273:1-9.

Singer, G.A., M. Panzenbock, G. Weigelhofer, C. Marchesani, J. Waringer, W. Wanek, and T.J. Battin. 2005. Flow history explains temporal and spatial variation of carbon fractionation in stream periphyton. Limnology and Oceanography 50:706-712.

Smith, A., A.A. Abuzeineh, M.M. Chumchal, T.H. Bonner, and W.H. Nowlin. 2010. Mercury Contamination of the Rio Grande Fish Community: Spatial Variation and Influence of Environmental Gradients. Environmental Toxicology and Chemistry 29:1762-1772.

Stanley, E.H., D.L. Buschman, A.J. Boulton, N.B. Grimm, and S.G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. The American Midland Naturalist 131:288-300.

Swain, E.B., D.R. Engstrom, M.E. Brigham, T.A. Henning, and P.L. Brezonik. 1992. Increasing rates of atmospheric mercury deposition in midcontinental North America. Science 257:784-787.

Thiemann, G.W. 2008. Using fatty acid signatures to study bear foraging: Technical considerations and future applications. Ursus 19:59-72.

Thomas, M.C., P. H. Beyer, and K.H. Rogers. 2006. Variability, complexity and diversity: the geomorphology of river ecosystems in dryland regions. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Thorp, J.H. 2002. Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. Oikos 96:543-550.

Thorp, J.H. and M.D. Delong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70:305-308.

Tombul, M., A.S. Koparal, and U.B. Ogutveren. 2005. Transport modelling of copper contamination in groundwater caused by a wood preservation plant. Water Quality Research Journal of Canada 40:469-475.

Ullrich, S.M., T.W. Tanton, and S.A. Abdrashitova. 2001. Mercury in the aquatic environment: a review of factors affecting methylation. Critical Review in Environmental Science and Technology 31:241-293.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130-137.

Voigt C.C., F. Matt, R. Michener, and T.H. Kunz. 2003. Low turnover rates of carbon isotopes in tissues of two nectar-feeding bat species. The Journal of Experimental Biology 206:1419-1427.

Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Webb, M.A.H., G.W. Feist, M.S. Fitzpatrick, E.P. Foster, C.B. Schreck, M. Plumlee, C. Wong, and D.T. Gundersen. 2006. Mercury concentrations in gonad, liver, and muscle of white sturgeon *Acipenser transmontanus* in the lower Columbia River. Archives of Environmental Contamination and Toxicology 50:443-451.

Whicker, J.J., D.D. Breshears, P.T. Wasiolek, T.B. Kirchner, R.A. Taviani, D.A. Schoep, and J.C. Rodgers. 2002. Temporal and spatial variation of episodic wind erosion in unburned and burned semiarid shrubland. Journal of Environmental Quality 31:599-612.

Wiener, J.G. and P.J. Shields. 2000. Mercury in the Sudbury River (Massachusetts, USA): pollution history and a synthesis of recent research. Canadian Journal of Fisheries and Aquatic Science 57:1053-1061.

Wolf, N., S.A. Carleton, and C.M. Del Rio. 2009. Ten years of experimental animal isotopic ecology. Functional Ecology 23:17-26.

Wolfsperger, M. 1993. Trace-element analysis of medieval and early-modern skeletal remains from Western Austria for reconstruction of diet. Homo 43:278-294.

Young, W.J. and R.T. Kingsford. 2006. Flow variability in large unregulated dryland rivers. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Zeug, S.C. and K.O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89:1733-1743.

CHAPTER II

SOURCES OF ORGANIC MATTER SUPPORTING FISH COMMUNITIES OF AN ARID AND SEMI-ARID RIVERINE SYSTEM

Introduction

The origin of resources supporting ecological communities has been a central focus of ecology for decades (Elton 1946, Polis et al. 1997b, Baxter et al. 2005). Ecologists have spent a great deal of effort identifying and characterizing the types, quality, and ultimate sources of resources that support a variety of food webs (Cummins et al. 1973, Vannote et al. 1980, Polis et al. 1997, Nakano and Murakami 2001, Nowlin et al. 2008). More recently, efforts have focused on examining the importance of organic matter (OM) and nutrients to communities which originate from outside the ecosystem in question (e.g., allochthonous subsidies; Polis and Hurd 1996, Polis et al. 1997, Ballinger and Lake 2006). Although allochthonously-derived OM and nutrients have been the subject of research for decades (e.g., Odum 1980), riverine ecosystems have been focal systems for examining allochthonous resources and their relative importance in supporting communities. Allochthonous resource inputs and utilization by riverine food webs is generally thought to be important because of the down slope position of rivers in landscapes, the fluvial transport of materials, and the often close connection of rivers with adjacent terrestrial systems (Vannote et al. 1980, Junk et al. 1989, Poff and Ward

1989, Thorp and Delong 1994, Baxter et al. 2005, Shurin et al. 2006). In riverine ecosystems, allochthonous resource subsidies from terrestrial ecosystems occur through inputs of terrestrial primary producer materials (e.g., leaf litter) and through the deposition of terrestrial arthropods (Cummins et al. 1973, Jackson and Fisher 1986, Gray et al. 1993). However, this flow of OM can occur reciprocally, through the emergence of aquatic invertebrates into riparian areas, providing OM resources for terrestrial consumers such as spiders, bats and birds (Baxter et al. 2005).

There is a need to determine the relative importance of allochthonous *versus* autochthonous C in lotic systems in arid regions in particular. Arid riverine ecosystems provide a unique opportunity for examining allochthonous subsidies due to the high variability in hydrology (e.g., flash flooding) as well as distinctive watersheds (e.g., reduced canopy cover and dominance of CAM plants). Arid rivers are more likely to have periods of drying or significant channel constriction for long periods associated with little or no precipitation inhibiting persistent algal growth (Thomas et al. 2006). In addition, unpredictable episodes of heavy precipitation and flash flooding lead to the transport of sediment and organisms laterally and downstream (Thomas et al. 2006, Young and Kingsford 2006). Additionally, relatively low canopy cover, high incident light on the water surface, and low terrestrial primary production in the adjacent landscape may lead to relatively high levels of autochthonous (in-stream) production potentially resulting in net autotrophy at the ecosystem level (Odum 1957, Vannote et al. 1980, Marcarelli et al. 2011). Data on whole stream gross primary production and community respiration from streams in the arid western United States and Australia generally support this prediction (Fisher 2006, Lake 2006); however, recent studies have

indicated that allochthonous OM subsidies can be important in open canopy systems (e.g., Menninger and Palmer 2007, Leberfinger et al. 2011). Indeed, recent meta-analysis of aquatic systems suggests that organisms select food items based upon food quality, irrespective of allochthonous or autochthonous origin (Marcarelli et al. 2011).

Stable isotopes are a useful tool in determining the origin of basal resources and trophic dynamics in aquatic food webs in general (Post 2002), and riverine ecosystems in particular (e.g. Findlay et al. 2002, Hoeinghaus et al. 2007). Carbon stable isotope ratios ($\delta^{13}C$) values can potentially be used to determine OM sources to consumers in food webs because $\delta^{13}C$ values are relatively conserved through food webs (Post 2002, Fry 2006). If various food resources exhibit reasonably distinct $\delta^{13}C$ values, then the proportional contribution of different food resources to consumers can be estimated (Fry 2006). For example, differences in allochthonous and autochthonous C sources have the potential to be distinguished from one another isotopically due to differences in the uptake in CO_2 during photosynthesis in terrestrial and aquatic systems (Fry 2006, Marshall et al. 2007). Multiple studies have employed stable isotopes to distinguish the proportional contributions of terrestrial *versus* aquatic OM sources to riverine communities (e.g., Findlay et al. 2002, Delong and Thorp 2006, Hoeinghaus et al. 2007, Zeug and Winemiller 2008). Although these studies have elucidated the relative importance of OM sources to riverine consumers, most studies have focused on spatially-limited (reach-scale) areas of riverine systems and do not assess larger regional patterns of the relative importance of OM sources in river systems that cross biogeophysical or environmental gradients (but see Hoeinghaus et al. 2007).

The aim of the study presented here was to examine the relative contribution of OM sources to fish communities in the Rio Grande/Rio Bravo del Norte and several of its perennially-flowing tributaries. The Rio Grande/Rio Bravo del Norte is a large, complex drainage that spans three US and four Mexican states, forming the United States - Mexico border along Texas (Fig. 1a). The river is of particular interest because it has been highly impacted by anthropogenic activities (e.g., urban development, agriculture, waste water discharge) for hundreds of years (Horgan 1984, Levings et al. 1998, Wong et al. 2007, Padilla 2008) and is home to roughly 30 state- and federally-listed aquatic species (Hubbs et al. 2008). I assessed the relative importance of OM sources and food web structure along lower Rio Grande drainage using N and C stable isotopes (e.g., $\delta^{13}C$ and $\delta^{15}N$; Fig. 1b). This portion of the Rio Grande drainage is distributed along a biogeoclimatic and precipitation gradient that ranges from the arid Chihuahuan Desert in the western portion of the drainage (mean annual rainfall < 400 mm/yr) to a semi-arid, subtropical grassland (~800mm/yr; Fig. 2.1 and Table 2.1). I sampled four sites along the mainstem of the river, spanning a distance of approximately 665 river km. Additionally, I sampled four of the first and second order perennially-flowing tributaries that contribute to the Rio Grande along this portion of the drainage (Fig. 2.1).

I hypothesized that the relative importance of allochthonous C (terrestrial plants) *versus* autochthonous (periphyton) C sources to fish communities would vary along the lower Rio Grande, indicating a large-scale spatial shift in supporting OM sources to the fish community in the drainage. Specifically, I predicted that the relative importance of terrestrial-derived C sources to fishes would be relatively lower in the more arid western portion of the drainage and become increasingly important in the more southeastern

portions of the drainage due to greater primary productivity in the arid streams than their watersheds. I also predicted that this trend would be more apparent among the smaller low-order tributary sites because they will be less affected by transport of allochthonous materials from upstream locations due to their much smaller drainage areas and higher connectivity with their watersheds.

Methods

Study sites

Fishes, periphyton, in-stream allochthonous detritus, aquatic invertebrates, and terrestrial plant material from the adjacent riparian area were sampled at all sites for a one-year period from October 2006 to October 2007. Sampling events were conducted during four periods, with a Fall sampling occurring in October 2006 and a Winter sampling conducted in February - March 2007. Summer sampling was conducted in April - May 2007, and a final Fall sampling was performed in September - October 2007. Four sites were sampled along the mainstem of the Rio Grande (Fig. 2.1, Table 2.1). Two of the sites are located along the Big Bend section of the river, which traverses a portion of the Chihuahuan Desert ecoregion: St. Elena Canyon and Hot Springs. Both of these sites lie within Big Bend National Park (BBNP). Due to high water levels and inability to access sites, I was only able to collect samples at the Summer and Fall 2007 sampling seasons at St. Elena and Hot Spring sites. The two downstream sites were at Quemado (~79 river km below Amistad Reservoir) and at Fronton (~32 river km below Falcon Reservoir; Fig. 2.1, Table 2.1). Additionally, due to inability to access sites due

to high flows the Rio Grande at Quemado site was sampled in Spring, Summer, and Fall 2007 and Frontera was sampled in Winter and Fall 2007.

In addition to the mainstem sites, I sampled four low-order, spring-fed perennially flowing sites tributary systems which contribute to the flows of the Rio Grande: Terlingua Creek, Tornillo Creek, Independence Creek, and Dolan Creek (Fig. 2.1, Table 2.1). Terlingua and Tornillo Creeks are located within BBNP and discharge directly into the Rio Grande. Sampling sites in both creeks were on average 200 – 300 m upstream from their confluence with the Rio Grande. Due to high water levels and inaccessibility we were unable to sample Terlingua and Tornillo Creeks during the Spring 2007 sampling period. Independence Creek is a tributary of the Pecos River and the sampling site was ~1 km upstream from the confluence with the Pecos River. Dolan Creek is a tributary of the Devil's River and the sampling site was ~150 m upstream of the confluence.

Fish and macroinvertebrate collection and processing

Fish were collected via kick and pull seining in the available meso-habitat types within each reach. Fish sampling at each site lasted ~1 h to ensure capture of a representative sample of the fish community. Fish were anesthetized with MS-222 and placed in 70% ethanol or on ice and transported to Texas State University-San Marcos (TXSTATE) for identification and processing. Once in the laboratory, all fish were identified to species (Thomas et al. 2007) and individual fish or a grouping of smaller, similar-sized fish of the same species had fillet or apaxial muscle removed. Tissues were dried at 60°C for 48 h. After drying, samples were homogenized using a clean mortar and pestle (rinsed with DI water and acetone and wiped clean between samples) until

they were a flour-like consistency and stored at room temperature in glass vials until packaging for stable isotope analysis.

Macroinvertebrates were collected at each site using a combination of kick nets, dip nets, and Hess samplers (Carter and Resh 2001). On each sampling occasion, kick nets were conducted in 1 -2 locations within each reach and lasted 1 min. Two riffle habitats within each reach were sampled with a Hess sampler, with each sampling duration lasting 1 min. Dip nets were used to sample shallow pools and edge habitats, with each reach having two individuals actively netting and sweeping areas for a total of 5 min. Upon collection, invertebrates were placed in stream water for 1-2 h to evacuate guts and then preserved in 70% ethanol. Invertebrates were identified to family (Merritt et al. 2008, Visual Taxonomy: www.visualtaxonomy.com) and dried using similar methods described for fish. Guts from larger macroinvertebrates and feet from gastropods and mollusks were removed prior to drying (Post 2002). If the dry mass of an invertebrate taxonomic group from a given site on a given sampling date was too small for analysis, then the sample was combined with individuals from within the same family/order and literature-defined functional feeding group (Merritt et al. 2008) from the same site and sampling date.

Periphyton, aquatic detritus, and terrestrial vegetation collection and processing

Terrestrial and aquatic primary producer and detritus samples were collected from sites. Periphyton was removed from rocks in pool and riffle habitats using a clean nylon bristled brush and Milli-Q water. Periphyton from pools, runs, and riffles was washed into separate pre-cleaned 50 ml screw-cap polypropylene tubes, and placed on ice. Samples of in-stream course particulate organic matter (CPOM; terrestrial leaves and

vegetation; 2-3 samples per site on each sampling date) were collected by hand. Vegetative ground detritus samples were collected by hand in the riparian zone at each site on each sampling date; samples were collected in an attempt to characterize the dominant vegetation and detritus at each site. Samples were placed in separate plastic bags and kept on ice until transported to the lab.

In the laboratory, terrestrial OM, and in-stream CPOM samples were cleaned of any sediment and debris with Milli-Q water and dried at 60°C for ~48 h. Terrestrial vegetation and in-stream CPOM samples were sorted according to the photosynthetic pathway of the vegetation type (i.e., C_3 and C_4 plants), homogenized using a cleaned mortar and pestle or an A11 basic analytical mill (IKA Works, Inc., Wilmington, NC), and stored in glass vials at room temperature. Periphyton slurry samples were well-mixed and filtered onto pre-combusted Whatman glass-fiber GF/F filters and dried at 60°C for ~48 h. Dried filters were placed in plastic boats in a fuming HCl chamber for 24 h to eliminate inorganic C, dried again at 60°C for ~24 h, and stored at -20°C until they were packaged and shipped for isotope analysis.

Stable isotope analysis

All stable isotope analyses were performed at the UC-Davis Stable Isotope Facility. Fish and macroinvertebrates samples were analyzed for ^{13}C and ^{15}N. Because we were interested in distinguishing the proportional contributions of allochthonous and autochthonous C sources to the fish community, we only used the reported $\delta^{13}C$ values for terrestrial vegetation and periphyton samples (Findlay et al. 2002, Leberfinger et al. 2011). The Stable Isotope Facility at UC Davis analyzes ^{13}C and ^{15}N isotope samples using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20

isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotope values are reported with δ notation, where values are equivalent to:

$$\delta R = ([R_{SAMPLE}/R_{STANDARD}]-1) \cdot 1000$$

where R is the $^{15}N:^{14}N$ or $^{13}C:^{12}C$ of the sample and an international standard (atmospheric N or Pee Dee Belemnite, respectively). Precision of analyses was determined through the duplicate analysis of internal standards (every ~12 samples). In addition, duplicates of unknown samples were run approximately every 15 samples with a mean standard error of $\leq$0.15‰.

Mixing Models and data analysis

For this study, I used the Bayesian mixing model, SIAR (Stable Isotope Analysis in R; cran.r-project.org/web/packages/siar/index) to assess the relative importance of allochthonous and autochthonous OM sources to fish communities of the lower Rio Grande. Traditional linear mixing models are limited to the number of sources that can be analyzed (i.e. number of isotopes + 1; Phillips 2001, Phillips and Gregg 2003). Although there has been an attempt to deal with greater number of sources (Phillips 2001, Phillips and Gregg 2003, Saito et al. 2007), it should be noted that even with these programs, as number of sources increase, there is an increase in uncertainty as to the contribution of each source. Further, these models do not incorporate sources of uncertainty, such as within an individual (i.e. due to measurement error, tissue variation, preservation and sampling techniques) or varying fractionation due to consumer diet or feeding rate (Moore and Semmens 2008, Jackson et al. 2009). Thus, I utilized a Bayesian approach, which determines the probability distribution of proportional source contributions and factors in uncertainty by defining the mean and variance parameters for

each source and isotope (Moore and Semmens 2008, Jackson et al. 2009). Bayesian models also allow for the inclusion of "user-specified" source isotope distributions and fractionations potentially obtained via gut content analysis or from the literature (Moore and Semmens 2008, Jackson et al. 2009, Parnell et al. 2010). These models are designed to lessen the influence of this *a priori* information as more data is provided (Jackson et al. 2009, Parnell et al. 2010).

Because I was interested in assessing the relative importance of basal C sources to fish communities of the lower Rio Grande drainage, allochthonous C sources were determined to be in-stream CPOM and terrestrial C_3 and C_4 plant detritus. Autochthonous C sources at each site (periphyton) were represented by aquatic macroinvertebrate grazer/scrapers (G/S) in place of periphyton due to the high temporal and spatial variability of periphyton associated with variation in discharge (Finlay et al. 1999, Singer et al. 2005, Rasmussen and Trudeau 2010). I was only able to collect taxonomic groups which are clearly classified as G/S (Psphenidae, Planorbidae, Thiaridae, and Physidae; Merritt et al. 2008) on every sampling event from Independence and Dolan Creek study sites. However, I was unable to capture G/S on every sampling event at the other study sites. At study sites in which I captured a G/S in at least two of the sampling events, I calculated the $\delta^{13}C$ and $\delta^{15}N$ values for G/S and used this value for the remaining sampling events at that site. For example, Psphenids were collected at Quemado on two of the three sampling dates (Spring and Summer 2007), thus I calculated the mean Psphenid $\delta^{13}C$ and $\delta^{15}N$ values and applied this value as the autochthonous C value for the Fall 2007 season. In addition, I did not capture an adequate number of invertebrate G/S at the Terlingua Creek study location for analysis;

however, I captured a known G/S fish species, the Mexican stoneroller (*Campostoma ornatum*), in Fall 2006 and Summer 2007 and used the mean $\delta^{13}C$ and $\delta^{15}N$ values for the remaining sampling events (Winter, Spring, and Fall 2007). For all other study locations (Tornillo Creek, and St. Elena, Hot Springs, and Fronton) in which I did not capture a known G/S, I employed a method similar to that of Anderson and Cabana (2007). I estimated G/S $\delta^{13}C$ and $\delta^{15}N$ values from periphyton values for each season, at each study location. I averaged the periphyton C and N values at each study location, each season then I enriched those values trophically (^{13}C: 0.4‰, ^{15}N: 3.4‰) to represent the G/S (Post 2002, Marty and Planas 2008). Prior to missing model analyses, all consumer C values were adjusted by 0.4‰ per trophic level, assuming N fractionation of 3.4±0.98‰ per trophic level (Post 2002). I did not correct $\delta^{13}C$ of consumers for lipid content because I was unsure of lipid content of study organisms, and thus unsure if lipid-normalizing corrections (Post et al. 2007).

Because of the large spatial area covered by this study, I elected to follow a two-step procedure in model analyses. For the first set of model analyses, I grouped all fishes in the community at each site on each sampling date and assessed the percent allochthonous C contribution to the fish community as a whole. This procedure allowed me to determine the relative importance of allochthonous C to the entire fish community, regardless of species composition. Mean proportion allochthonous C contribution proportions were compared among mainstem and tributary sites using a mixed model, one-way analysis of variance (ANOVA). Proportions were arcsine square root transformed to meet ANOVA assumptions of normality and homoscedasticity. For this analysis, mainstem Rio Grande sites were categorized as either “arid” (St. Elena and Hot

Springs) or "semi-arid" (Quemado and Frontera). Tributary sites were categorized as "arid" (Terlingua and Tornillo Creeks) or "semi-arid" (Dolan and Independence Creeks). Site type (mainstem arid, mainstem semi-arid, tributary arid, and tributary semi-arid) was set as the predictor variable, and the specific sites location was nested within site type as a random effect (Fig. 2.2). The allochthonous C proportion to the fish community $\delta^{13}C$ signature was the response variable. Significance was inferred at $p \leq 0.05$. If a significant effect was detected, post-hoc Tukey's honestly significant difference (HSD) tests were conducted to determine homogenous subsets. All statistical analyses were preformed in the Paleontological Statistics (PAST) version 2.02 and JMP statistical software version 9.

The second set of model analyses assessed the proportion allochthonous C contribution to two fish species which occurred at multiple sites (red shiner, *Cyprinella lutrensis*, and Mexican tetra, *Astyanax mexicanus*). I selected red shiner and Mexican tetra because of their broad distribution in Texas as well as their generally carnivorous opportunistic foraging (Thomas et al. 2007, Hubbs et al. 2008). For mixing model analyses, I used the same basal C sources in the mixing models that were used for fish community analyses and assessed the percent allochthonous C contribution to each fish species. Additionally in order to increase sample sizes, I combined individuals within each species captured across seasons per study site.

Results

Fish communities on the mainstem Rio Grande and tributaries utilized allochthonous basal C sources in greater proportion to autochthonous across most seasons. The exception was Terlingua Creek in Summer and Fall 2007 (42% and 39%,

respectively) and Tornillo Creek in Winter and Fall 2007 (47% and 25%, respectively; Fig. 2.3, Table 2.2). Additionally, I found that C derived from C_4 plants was typically a smaller contributor to allochthonous C in the fish community (Fig. 2.4, Table 2.2). Indeed, with the exception of Terlingua Creek and Tornillo Creek, C_4 plants composed typically ~10% of the contributions to fish community diets (Fig. 2.4, Table 2.2). In addition, the in-stream CPOM had $\delta^{13}C$ values that overlapped markedly with the terrestrial C_3 vegetation (Fig. 2.4). Finally, site type (mainstem arid and semi-arid, and tributary arid and semi-arid) differed significantly ($F_{3,26} = 12.133$, $P = 0.001$). Post-hoc Tukey's HSD tests indicated that fish communities at arid tributary sites utilized a significantly lower proportion of allochthonous C than at both arid (~19% less, $P = 0.04$) and semi-arid mainstem (~22% less, $P = 0.04$), as well as semi-arid tributary sites (~21% less, $P = 0.02$).

Mixing models indicated that both red shiner and Mexican tetra exhibited a higher proportional contribution of allochthonous C to $\delta^{13}C$ values than autochthonous C. Red shiner was captured at three out of the four mainstem sites (i.e., St. Elena, Hot Springs, and Quemado). At these sites, 76%, 68%, and 75% of the C in red shiner was from allochthonous sources (at St. Elena, Hot Springs, and Quemado, respectively; Fig. 2.5a). Mexican tetra occurred at all four tributary sites and three of the mainstem sites (Hot Springs, Quemado, and Fronton; Fig. 2.5b). At all sites, allochthonous C contributed the most to Mexican tetra diets (Fig. 2.5b).

Discussion

Utilization of C in the mainstem Rio Grande

The present study examined the relative contribution of basal C sources to fish communities in the Rio Grande/Rio Bravo del Norte and several low order tributaries. Contrary to my hypotheses, allochthonous C resources (C ultimately derived from terrestrial sources) were utilized in greater proportion by fish communities at both arid and semi-arid mainstem sites (mean: 67% and 71%, respectively). There are a variety of potential reasons why allochthonous C is relatively important in supporting fish communities of the Rio Grande. The Rio Grande is a large complex system and many mainstem sites likely integrate the downstream transport of upstream resources, including drifting invertebrates and coarse and fine particulate organic matter (Polis et al. 1997, Finlay et al. 2002). In addition, the mainstem sites of the Rio Grande are less turbid (mean NVSS: 21.95 mg/L; WH Nowlin, unpubl. data). Indeed the turbidity at the upper mainstem sites is more than a magnitude greater than at the lower mainstem sites (mean NVSS: 431.18 mg/L; WH Nowlin, unpubl. data). These high suspended sediment loads can inhibit in-situ photosynthesis and primary productivity of in-stream autotrophs. Lastly, much of the riparian area of the sites used in this study was occupied by dense stands of invasive vegetation, in particular giant reed (*Arundo donax*), a perennial C_3 grass, and saltcedar (*Tamarisk spp.*). Whitcraft et al. (2008) found saltcedar altered the trophic structure of a salt marsh food web by changing the detrital pool and thus the community composition of basal consumers which potentially affected higher trophic levels. Thus, it is likely the impact of the invasive plant species found along the Rio Grande may have the same impact on food web communities in the river.

Results of the current study also determined that mainstem Rio Grande fish communities received most of their allochthonous C from C_3 plant origin, and not from C_4 plants, such as grasses. According to model results, fish communities at the arid mainstem sites derived ~12% of their $\delta^{13}C$ signatures from C originating from C_4 vegetation, while semi-arid mainstem communities derived ~9% of their C from C_4 plants (Table 2.2). These results are in contrast to those of Onstad et al. (2000), who concluded there was an increase in C_4 particulate organic matter (POM) in the Rio Grande drainage as it transitioned from an arid region (New Mexico) to a more semi-arid region (confluence with the Pecos River, Texas). Further, the C:N analysis of suspended POM from a review of major drainages in the U.S. showed at least 50% of the C in the Rio Grande (in Texas) was derived from plankton; however, the authors note that given the temporal instability of $\delta^{13}C$ in POM, it was difficult to confirm these results (Kendall et al. 2001). Finally, these previous studies examine available POM suspended in the water column without regard to the consumer preference and utilization, our study shows that upper-level consumers reflect the importance of allochthonous inputs.

In contrast to the mainstem sites, results for smaller tributary sites indicated that fish communities in arid tributaries exploited autochthonous C resources (periphyton; 52%) in greater proportion than allochthonous C sources. It is possible that the primary production in the arid streams may be higher than that in their adjacent watershed. Further, given higher primary productivity and unpredictable episodes of flash flooding which leads to the later and downstream movement of OM, sediments, and organisms, it is possible these headwater arid streams conform to the "Outwelling Hypothesis" by providing subsidies of dissolved and particulate C to their watersheds as well as to rivers

they contribute to the flows of (e.g., the Rio Grande; Odum 1980, Ballinger and Lake 2006). Additionally, the results from the tributary mixing models in this study are somewhat contrary to recent research by Leberfinger et al. (2011) who found that allochthonous C was typically an important resource for invertebrate shredders in both closed (forested) and open (non-forested) canopy systems in Sweden. There were some exceptions, however, as autochthonous C was a more important resource to shredders at some open-canopied sites than in closed. Mean percent canopy cover at the semi-arid tributary sites in this study was slightly lower than at the arid sites (39% and 48%, respectively); however, fish diets were derived more from allochthonous C in semi-arid streams than in arid streams. A study of three headwater streams with riparian areas dominated by grasses and herbs in Maryland, USA, showed that even with the removal of shading from their streams and consequently increased autochthonous production, macroinvertebrates still preferred allochthonous C sources as they were higher in quality as indicated by higher N content (Menninger and Palmer 2007). These findings may explain the discrepancies I found in allochthonous C supply and its utilization by the fish community. Finally, when I examined the utilization of C sources by red shiner and Mexican tetra I found these species exploited the same types of C as the overall fish communities at the study sites. The exception was Mexican tetra at the arid tributary sites in which I found a greater proportion of allochthonous C in the species even though the fish community preferred autochthonous C. The Mexican tetras are typically invertivorous and carnivorous although there have been accounts of algivory and herbivory for species in the lower Rio Grande Valley in Texas (Estrada 1999, Thomas et al. 2007).

Concerns and caveats for the use of mixing model results

Although mixing model results in the present study indicated that there were relatively similar contributions of allochthonous and autochthonous C in many cases, distributions of $\delta^{13}C$ values for terrestrial C_3 plants, in-stream CPOM, and periphyton values inferred from invertebrate grazer/scrapers often substantially overlapped although sample sizes for most of these sources were typically robust for all sites ($n \geq 3$ for each source on each sampling data), it is still likely that mixing model estimations may be affected by this overlap in 3 of the 4 potential C sources to fishes. This overlap may mean that the mixing model would generate relatively equal proportions of allochthonous and autochthonous C. Despite these somewhat overlapping $\delta^{13}C$ values for some allochthonous and autochthonous C sources, mixing models indicated that C from C_4 plants were a relatively minor contributor to C signatures of fish communities. Thus, it appears that C_4 were not that important to fish diets and the models did a good job at elucidating this.

One of the advantages of Bayesian mixing models is the ability to include informative priors (*a priori* information) of consumer preference or utilization of sources (Jackson et al. 2009, Parnell et al. 2010). For example, information on gut content analysis or literature-based data on diets can be incorporated into models. In the present study, I did not include informative priors in analyses because gut content information from collected individuals was not available and literature-based information on diet preferences for many of the species in question in the Rio Grande drainage is sparse. However, by combining all fish from a community in the mixing model analyses, I was able to increase my sample sizes thus decreasing the need for informative priors. Ward et

al. (2010) suggested with small sample sizes, informative priors can lend to proper identification of source contributions to consumer diets; however, if sample sizes are large, informative priors have little effect on the estimates of proportional source contributions to consumers. I conclude that, in situations where there are overlapping distributions of several of the sources and thus lower confidence in estimates the fish community diets, effort should be made to collect gut content information from consumers whenever possible.

Many of the studies of which I compared my results used aquatic macroinvertebrates to examine consumer-source models. The assumption is that the source contributions will propagate through food webs to upper-level consumers such as fish, but there is some indication that this assumption may not always be correct. For example, Rasmussen et al. (2010) found that shifts in $\delta^{13}C$ values in periphyton associated with water velocity variation were transmitted to the invertebrate herbivores/scrapers and collector/gatherers; however, that signal did not cascade up to the mobile fishes likely because of "spatial averaging" of their food supply via movement between mesohabitats. Further, studies that have shown that fishes which exhibit relatively high habitat fidelity have $\delta^{13}C$ signal closely aligned with basal sources; however, these studies used much smaller scales than the present study (e.g., within a single reach; Finlay et al. 2002). In the lower Rio Grande drainage, fishes have the potential to move relatively large distances within and among tributaries and mainstem sites (Thomas et al. 2007, Hubbs et al. 2008). If this is the case for fishes within the Rio Grande drainage, many river fishes can traverse large distances and consume OM from

upstream and downstream sites, thus contributing to additional uncertainty in our mixing model estimations.

Conservation and management implications

Results of the present study clearly suggest that fish communities at locations throughout the lower Rio Grande derive a substantial (~64%) of their C from allochthonous sources. Given this important connection between the terrestrial landscape and the upper-level consumers in this drainage (i.e., the fish), it is important to consider the condition of the watersheds of the Rio Grande and its tributaries in Texas when establishing conservation and management practices. Additionally, land use practices (deforestation, urbanization, etc.) within the Rio Grande drainage cannot be ignored as they may have an impact on the already imperiled fish communities in the river and some of its tributaries and additional alteration has the potential for disastrous effects.

Literature Cited

Anderson, C. and G. Cabana. 2007. Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. Journal of the North American Benthological Society 26:273-285.

Ballinger, A. and P.S. Lake. 2006. Energy and nutrient fluxes from rivers and streams into terrestrial food webs. Marine and Freshwater Research 57:15-28.

Baxter, C.V., D.D. Fausch, and C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50:201-220.

Carter, J.L. and V.H. Resh. 2001. After site selection and before data analysis: sampling, sorting, and laboratory procedures used in stream benthic macroinvertebrates monitoring programs by USA state agencies. Journal of the North American Benthological Society 20:658-682.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck, and V.I. Holt. 1973. Utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Delong, M.D. and J.H. Thorp. 2006. Significance of instream autotrophs in trophic dynamics of the Upper Mississippi River. Oecologia 147:76-85.

Elton, C. 1946. Competition and the structure of ecological communities. Journal of Animal Ecology 15:54-68.

Estrada, M. 1999. The ecology and life history of the Mexican tetra, *Astyanax mexicanus*, (Teleostei: Characidae) in the lower Rio Grande Valley, Texas. Unpubl. M. S. thesis, The University of Texas-Pan American, Edinburg, TX, 53 pp.

Finlay, J.C., M.E. Power, and G. Cabana. 1999. Effects of water velocity on algal carbon isotope ratios: implications for river food web studies. Limnology and Oceanography 44:1198-1203.

Finlay, J.C., S. Khandwala, and M.E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology 83:1845-1859.

Fisher, S.G. 2006. Stream ecosystems of the western United States. *In*: River and Stream Ecosystems of the World. C.E. Cushing, K.W. Cummins, and G.W. Minshall (*eds*.). University of California Press, Berkley, California. Pp 61-88.

Fry, B. 2006. Stable Isotope Ecology. 308 pp. Springer Science Business Media LLC. New York, NY.

Hoeinghaus, D.J., K.O Winemiller, and A.A. Agostinho. 2007. Landscape-scale Hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10:1019-1033.

Horgan, P. 1984. Great River: The Rio Grande in North American History, 2 Vols. 4th ed. Holt Press, New York, NY.

Hubbs, C., R.J. Edwards, and G.P. Garrett. 2008. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. Texas Academy of Science, Second Edition.

Jackson, A.L., R. Inger, S. Bearhop, and A. Parnell. 2009. Erroneous behavior of MixSIR, a recently published Bayesian isotope mixing model: a discussion of Moore and Semmens 2008. Ecology Letters 12:E1-E5.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publications of Fisheries and Aquatic Sciences 106:110-127.

Lake, P.S. 2006. Of floods and droughts: river and stream ecosystems of Australia. *In*: River and Stream Ecosystems of the World. C.E. Cushing, K.W. Cummins, and G.W. Minshall (*eds*). University of California Press, Berkley, California. p. 659-694.

Leberfinger, K., I. Bohman, and J. Herrmann. 2011. The importance of terrestrial resource subsidies for shredders in open-canopy streams revealed by stable isotope analysis. Freshwater Biology 56:470-480.

Levings, G.W., D.F. Healy, S.F. Richey, and L.F. Carter. 1998. Water quality in the Rio Grande valley: Colorado, New Mexico, Texas, 1992-1995. U.S. Geological Survey.

Marcarelli, A.M., C.V. Baxter, M.M. Mineau, and R.O. Hall. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92:1215-1225.

Marshall, J.D., J.R. Brooks, and K. Lajtha. 2007. Sources of variation in the stable isotope composition of plants. *In* Stable Isotopes in Ecology and Environmental Science. R. Michener and K. Lajtha (*eds*) Blackwell Publishing Malden, Massachusetts, p.22-60.

Marty, J. and D. Planas. 2008. Comparison of methods to determine algal δ13C in freshwater. Limnology and Oceanography: Methods 6:51-63.

McCutchan, J.H, Jr. and W.M. Lewis, Jr. 2002. Relative importance carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742-752.

Menninger, H.L., and M.A. Palmer. 2007. Herbs and grasses as an allochthonous resource in open-canopy headwater streams. Freshwater Biology 52:1689-1699.

Merritt, R.W., K.W. Cummings, and M.B. Berg (*eds*). 2008. An introduction to aquatic insects of North America. 4th Edition. Kendall/Hunt Publishing Co., Dubuque, IA.

Moore, J.W. and B.X. Simmons. 2008. Incorporating uncertainty and prior information \ into stable isotope mixing models. Ecology Letters 11:470-480.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings from the National Academy of Science 98:166-170.

Nowlin, W.H., M.J. Vanni, and L.H. Yang. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. Ecology 89:647-659.

Odum, H.T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55–112.

Odum. E.P. 1980. The status of three ecosystem-level hypotheses 'regarding salt marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains. *In*: Estuarine perspectives. Kennedy, V. (*ed*.) Academic Press, New York, p. 485-495.

Onstad, G.D., D.E. Canfield, P.D. Quay, and J.I. Hedges. 2000. Sources of particulate organic matter in rivers from the continental USA: lignin phenol and stable carbon isotope compositions. Geochimica et Cosmochimica Acta 64:3539-3546.

Padilla, M. 2008. The thirsty Rio Grande: sustainable water planning along the Rio Grande in the age of global warming. Sustainable Development Law and Policy- Nbr. VIII-2.

Parnell, A.C., R. Inger, S. Bearhop, and A.L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672.

Phillips, D.L. 2001. Mixing models in analyses of diet using multiple stable isotopes: a critique. Oecologia 127:166-170.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability of lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805-1818.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecological Systems 28:289-316.

Polis, G.A. and S.D. Hurd. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. American Naturalist 147:396-423.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Post, D.M., C.A. Layman, D.A. Arrington, G. Takimoto, J. Quattrochi, and C.G. Montaña. 2007. Getting to the fat of the matter: models, methods, and assumptions for dealing with lipids in stable isotope analysis. Oecologia 152:179-189.

Rasmussen, J.B. and V. Trudeau. 2010. How well are velocity effects on $\delta^{13}C$ signatures transmitted up the food web from algae to fish? Freshwater Biology 55:1303-1314.

Saito, L., C. Redd, S. Chandra, L. Atwell, C.H. Fritsen, H. Christian, M.R. Rosen. 2007. Quantifying foodweb interactions with simultaneous linear equations: stable isotope models of the Truckee River, USA. Journal of the North American Benthological Society 26:642-662.

Shapiro, S.S. and M.B. Wilk. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.

Shurin, J.B., D.S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. Proceedings of the Royal Society B 273: 1-9.

Singer, G.A., M. Panzenböck, G. Weigelhofer, C. Marchesani, J. Waringer, W. Wanek, and T.J. Battin. 2005. Flow history explains temporal and spatial variation of carbon fractionation in stream periphyton. Limnology and Oceanography 50:706-712.

Thomas, C., T.H. Bonner, and B.G. Whiteside. 2007. Freshwater fishes of Texas. 202 pp. Texas A&M University Press, College Station, Texas.

Thomas, M.C., P. H. Beyer, and K.H. Rogers. 2006. Variability, complexity and diversity: the geomorphology of river ecosystems in dryland regions. *In* Ecology of Desert Rivers. R.T. Kingsford (*ed*). Cambridge University Press. Cambridge, New York. p. 47-75.

Thorp, J.H. and M.D. DeLong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70:305-308.

Young, W.J. and R.T. Kingsford. 2006. Flow variability in large unregulated dryland rivers. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130-137.

Whitcraft, C.R., L.A. Levin, D. Talley, and J.A. Crooks. 2008. Utilization of invasive tamarisk by salt marsh consumers. Oecologia 158:259-272.

Wong, C.M., C.E. Williams, J. Pittock, U. Collier, and P. Schelle. 2007. World's top ten rivers at risk. 53 pp. WWF International. Gland, Switzerland.

Zeug, S.C, and K.O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89:1733-1743.

Table 2.1. Names, type (mainstem or tributary), coordinates, gauging stations, and mean annual precipitation rates (mm) for each study site.

Site	Site Type	Coordinates	Gauging Station	Annual Precipitation
St. Elena	Mainstem	29°09'51.24" N, 103°36'35.34" W	Castolon	248.92
Hot Springs	Mainstem	29°10'38.90" N, 102°59'47.79" W	Castolon	248.92
Quemado	Mainstem	28°56'30.22" N, 100°38'38.81" W	Eagle's Pass	545.59
Fronton	Mainstem	26°24'49.00" N, 99°4'56.00" W	Falcon Reservoir	515.11
Terlingua	Tributary	29°10'02.43" N, 103°36'44.60" W	Castolon	248.92
Tornillo	Tributary	29°10'37.33" N, 103°00'02.95" W	Castolon	248.92
Independence	Tributary	30°27'52.68" N, 101°46'50.34" W	Carta Valley	577.85
Dolan	Tributary	29°53'05.16" N, 101°59'04.39" W	Sheffield	379.22

Table 2.2. Average percent contribution (95% CI) of allochthonous and autochthonous C sources for fish communities across study site and season for October 2006 to October 2007. Note allochthonous C sources are coded: CPOM (in-stream, well-conditioned detritus), C3 (terrestrial C3 plant detritus, and C4 (terrestrial C4 plant detritus). Autochthonous C sources are aquatic macroinvertebrate grazer/scrapers (G/S).

Site	Site Type	Source	Fall 2006	Winter 2007	Spring 2007	Summer 2007	Fall 2007
St. Elena	Mainstem	CPOM				25.52 (0.00-49.79)	23.75 (0.00-48.51)
		C3				24.63 (0.00-46.99)	24.84 (0.00-50.97)
		C4				20.67 (11.24-29.59)	10.60 (5.70-15.57)
		G/S				29.17 (3.32-51.12)	40.80 (7.78-76.45)
Hot Springs	Mainstem	CPOM				38.19 (3.69-70.85)	24.75 (0.00-49.68)
		C3				33.97 (0.06-63.14)	23.16 (0.00-47.56)
		C4				5.72 (0.00-13.37)	11.68 (0.47-22.62)
		G/S				22.11 (0.00-45.12)	40.40 (14.96-69.29)
Quemado	Mainstem	CPOM			41.75 (14.95-69.65)	26.57 (2.94-46.28)	30.71 (9.04-50.91)
		C3			32.46 (0.03-61.88)	25.77 (0.07-47.53)	27.46 (1.26-50.58)
		C4			6.01 (0-13.92)	13.67 (0.06-25.72)	8.13 (0.61-25.72)
		G/S			19.78 (0.15-37.61)	33.99 (5.40-61.86)	33.71 (5.40-61.86)
Fronton	Mainstem	CPOM		22.60 (0.00-48.08)			26.03 (0.00-54.55)
		C3		18.61 (0.00-41.42)			58.35 (0.00-41.42)
		C4		11.50 (1.91-20.89)			3.02 (1.92-20.89)
		G/S		47.29 (13.33-88.53)			12.60 (13.33-88.53)
Terlingua	Tributary	CPOM	15.39 (0.00-36.33)	15.66 (0.00-36.10)		3.72 (0.00-11.11)	2.33 (0.00-6.82)
		C3	16.88 (0.00-39.44)	17.22 (0.00-39.44)		4.52 (0.00-14.14)	2.81 (0.00-8.41)
		C4	24.63 (11.67-36.92)	27.10 (16.34-37.47)		33.36 (29.05-37.45)	33.81 (30.15-37.23)
		G/S	43.10 (12.70-76.02)	40.02 (13.58-68.10)		58.40 (47.13-67.13)	61.06 (53.88-67.13)
Tornillo	Tributary	CPOM	25.46 (0.00-51.06)	27.64 (0.00-57.49)		15.49 (0.00-38.22)	9.90 (0.00-28.92)
		C3	24.23 (0.00-48.53)	16.01 (0.00-41.17)		14.82 (0.00-38.01)	9.49 (0.00-26.75)
		C4	9.25 (0.00-20.88)	3.53 (0.00-11.52)		25.49 (14.91-35.41)	5.62 (0.00-13.73)
		G/S	41.06 (14.71-70.82)	52.83 (17.82-93.31)		44.20 (22.10-65.49)	74.99 (45.76-97.69)
Independence	Tributary	CPOM	57.25 (33.98-80.49)	33.83 (0.00-63.68)	46.26 (15.90-80.57)	39.83 (2.58-76.04)	42.71 (4.06-79.77)
		C3	23.16 (0.00-50.03)	14.93 (0.00-34.03)	21.46 (0.00-44.90)	26.97 (0.60-49.86)	10.43 (0.00-25.51)
		C4	2.65 (0.00-7.09)	2.50 (0.00-5.89)	2.79 (0.00-6.92)	4.81 (0.00-11.60)	1.84 (0.00-4.76)
		G/S	16.94 (0.00-36.45)	48.74 (14.56-88.18)	29.49 (0.02-56.13)	28.39 (4.17-50.23)	45.02 (12.08-77.43)
Dolan	Tributary	CPOM	36.41 (0.10-66.90)	34.26 (0.04-63.41)	36.47 (2.59-65.86)	37.51 (1.53-70.70)	79.68 (50.23-99.68)
		C3	23.20 (0.00-46.32)	24.99 (0.00-48.63)	31.68 (0.34-58.90)	23.93 (0.00-47.52)	9.50 (0.00-47.52)
		C4	3.58 (0.00-9.76)	4.27 (0.00-10.34)	6.64 (0.05-13.23)	3.81 (0.00-9.75)	1.05 (0.00-9.75)
		G/S	36.81 (3.48-65.94)	36.49 (2.84-65.60)	25.21 (0.00-49.82)	34.75 (2.33-62.23)	9.77 (0.00-30.07)

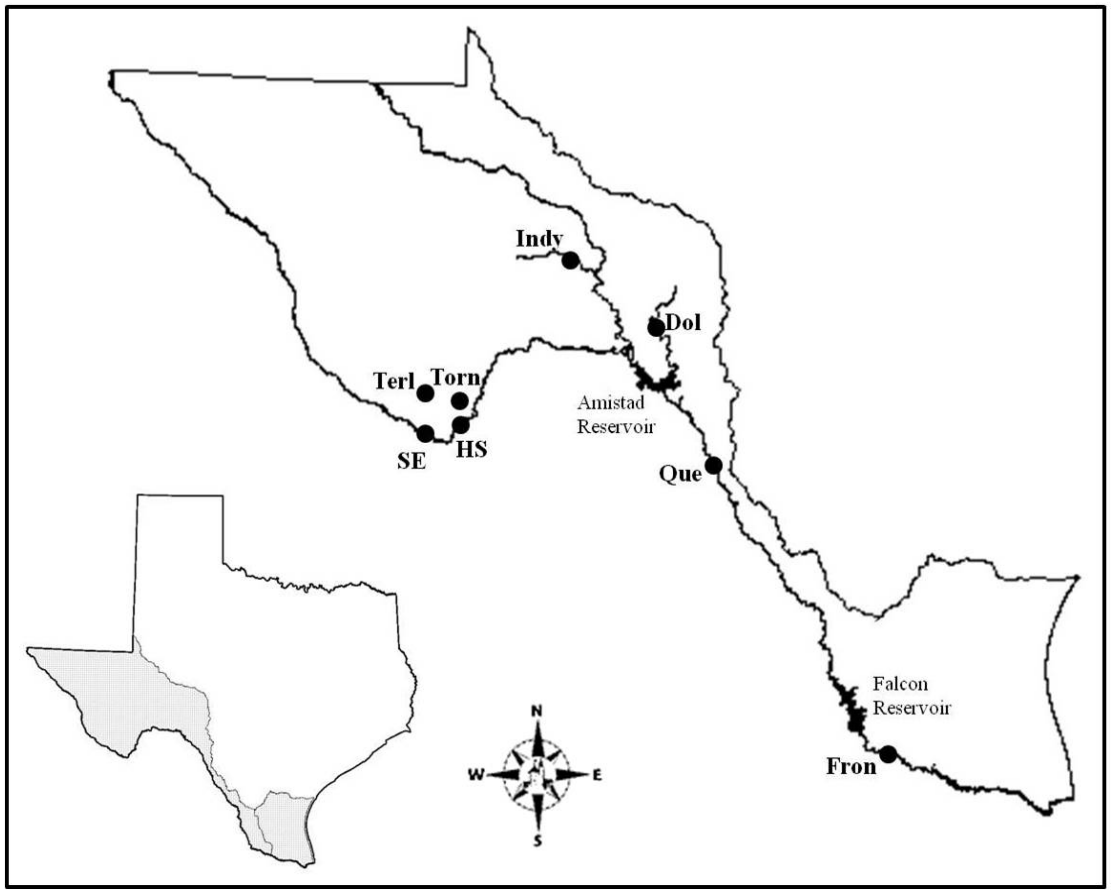

Figure 2.1. Map of Rio Grande and the various study sites. (a) illustrates the Rio Grande in the USA and Mexico with the section of the river associated with my study sites indicated in bold, and (b) an illustration of the study sites located within Texas. Note: site locations are abbreviated: SE = Rio Grande at St. Elena Canyon, HS = Rio Grande at Hot Springs, Terl = Terlingua Creek, Torn = Tornillo Creek, Indy = Independence Creek, Dol = Dolan Creek, Que = Rio Grande at Quemado, below Amistad Reservoir, and Fron = Rio Grande at Fronton, below Falcon Reservoir.

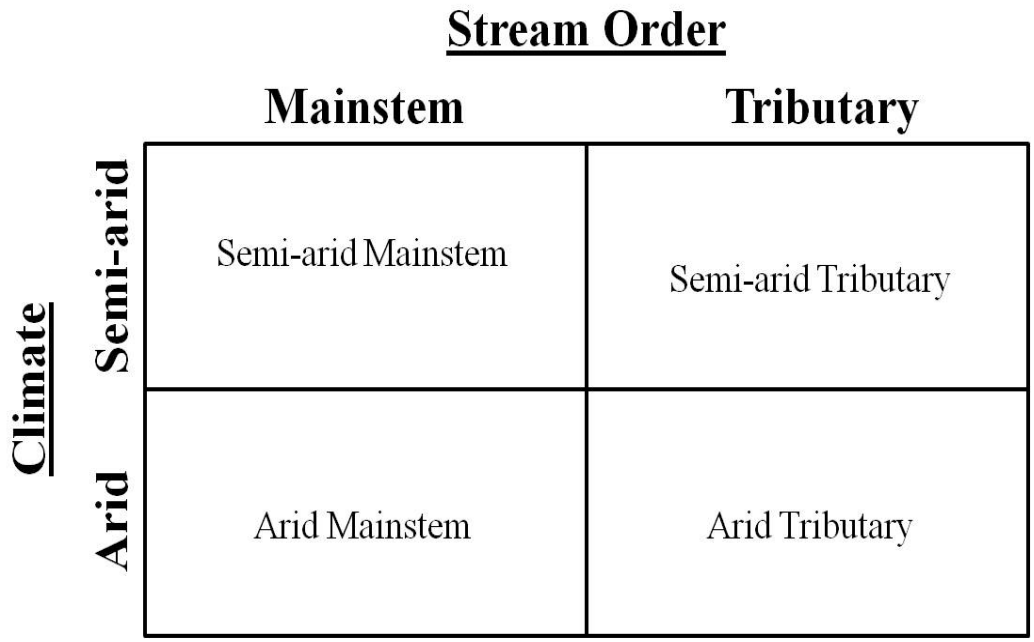

Figure 2.2. Conceptual model of analysis for mixed-model ANOVA design. There are four site types within two categories (stream order and climate). Each category was treated as a predictor variable with sites nested within.

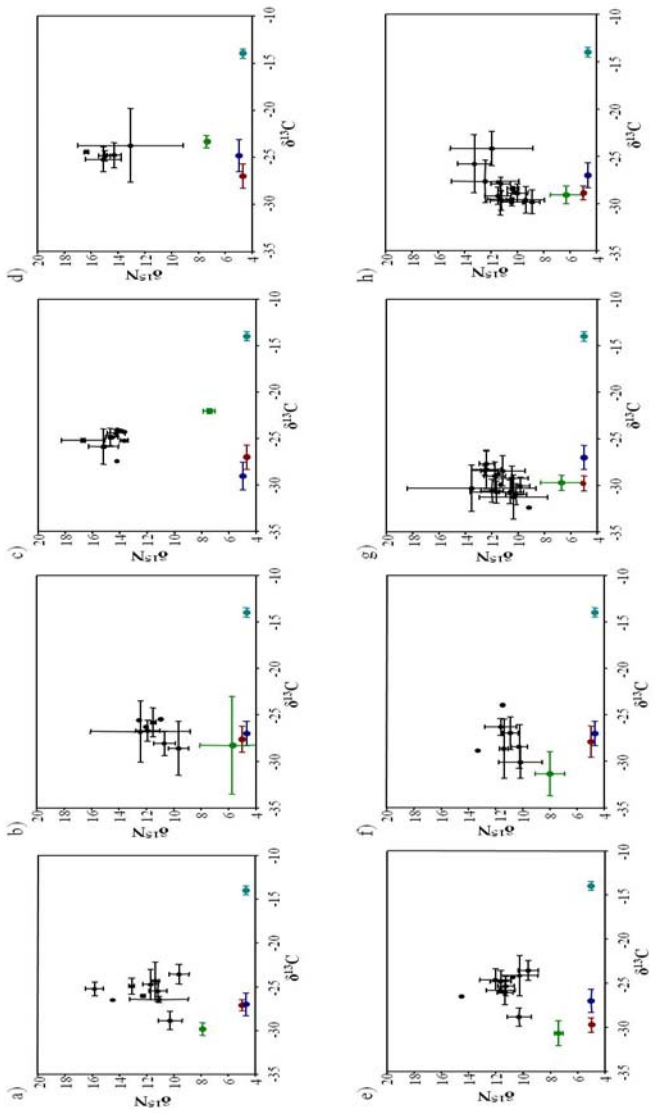

Figure 2.3. Bi-plots illustrate annual averages (±1SD) for C sources and fish consumers for each site. Bi-plots a-d are mainstem sites (a. St. Elena, b. Hot Springs, c. Quemado, and d. Fronton). Bi-plots e-h are tributary sites (e. Terlingua Creek, f. Tornillo Creek, g. Independence Creek, h. Dolan Creek). Green points represent grazer/scraper aquatic macroinvertebrates. Red points represent in-stream course particulate organic matter. Blue represents terrestrial C3 and teal represents terrestrial C4 plant detritus. Black points represent fishes. Note: Appendix A lists annual means (±1SD) for fish consumers per site.

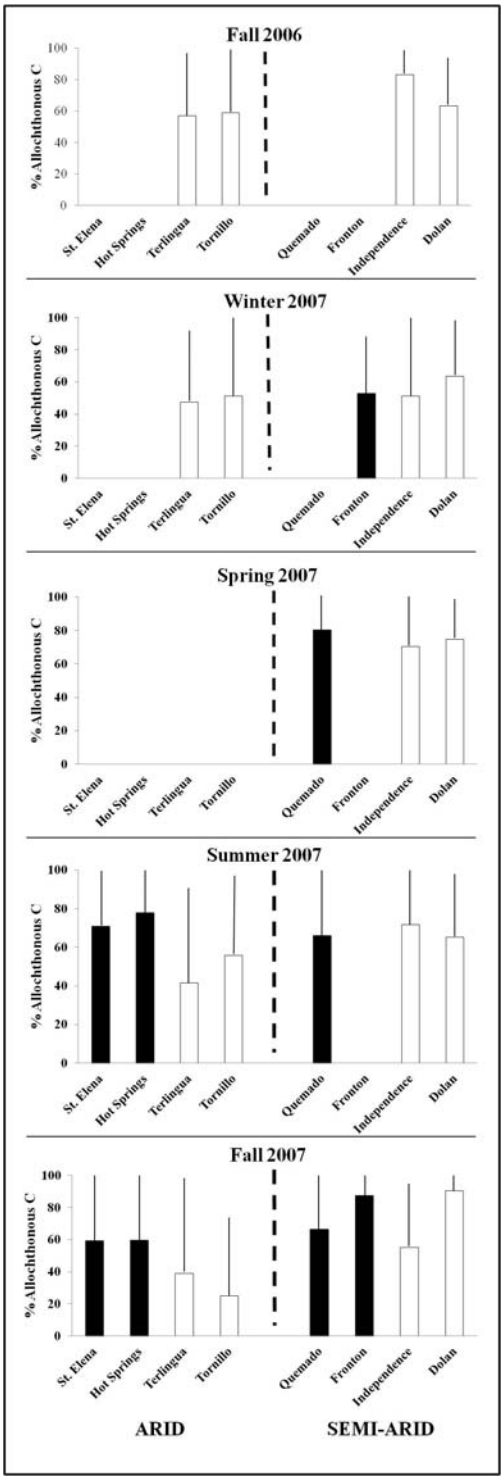

Figure 2.4. Percent allochthonous C source contributions to fish community diets (with 95% CIs) for each study season. Mainstem sites are denoted with black bars and tributary sites are denoted with white bars. Individual graphs are bisected with a dashed line separating arid (St. Elena, Hot Springs, Terlingua, and Tornillo) from semi-arid (Quemado, Fronton, Independence, and Dolan) sites.

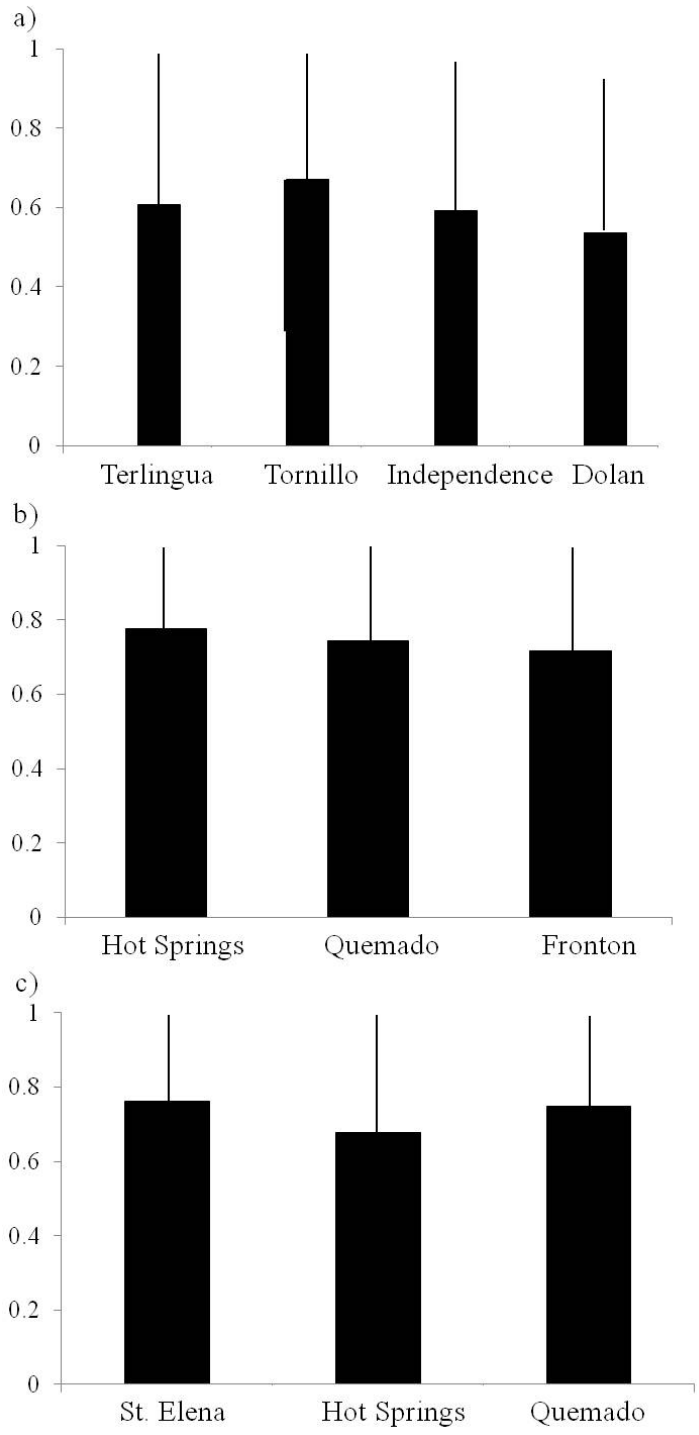

Figure 2.5. Illustrations of percent allochthonous C sources (with 95% CIs) for *Astyanax mexicanus* and *Cyprinella lutrensis* with seasons lumped. Figure 5a-b illustrate percent allochthonous C for *A. mexicanus* diets at tributary and mainstem sites (respectively). Figure 5c shows the percent allochthonous C to *C. lutrensis* diets from mainstem sites.

Appendix A

Annual mean and standard deviation (SD) for $\delta^{13}C$ and $\delta^{15}N$ in fish species captured at each study location site.

Site	Site Type	Species	Mean 13C	SD 13C	Mean15N	SD 15N
St. Elena	Mainstem	*A. mexicanus*	-26.43	0.34	11.10	2.15
		C. carpio	-25.48	1.15	11.17	0.67
		C. lutrensis	-24.73	1.73	11.71	0.57
		F. zebrinus	-24.32	2.13	11.36	0.29
		Gambusia sp.	-26.01	0.02	12.26	0.14
		I. punctatus	-23.54	1.13	9.62	0.73
		N. braytoni	-24.92	0.93	13.10	0.19
		P. vigilax	-26.49	0.00	14.50	0.00
		L. osseus	-25.23	0.79	15.83	0.66
Hot Springs	Mainstem	*A. mexicanus*	-26.71	1.14	11.91	0.88
		C. carpio	-28.60	2.89	9.65	0.74
		C. lutrensis	-26.80	3.30	12.44	3.64
		F. zebrinus	-28.07	1.30	10.68	0.79
		G. affinis	-26.28	0.00	12.04	0.00
		I. furcatus	-25.48	0.09	10.93	0.02
		I. punctatus	-25.57	0.00	12.53	0.00
		N. braytoni	-25.79	1.55	11.49	0.22
Quemado	Mainstem	*A. mexicanus*	-25.21	0.12	13.68	0.30
		C. cyanoguttatum	-25.85	0.00	15.14	0.00
		C. lutrensis	-25.86	1.90	15.19	1.09
		C. procerpina	-24.15	0.00	13.86	0.00
		C. venusta	-24.42	0.37	14.26	0.65
		G. affinis	-24.85	0.05	14.58	0.44
		L. megalotis	-24.03	0.00	14.18	0.00
		M. beryllina	-24.84	0.95	14.67	0.13
		M. congestum	-24.26	0.00	13.67	0.00
		M. salmoides	-27.44	0.00	14.20	0.00
		P. vigilax	-25.20	0.20	16.67	1.61
Fronton	Mainstem	*A. mexicanus*	-24.84	0.54	14.98	0.43
		C. cyanoguttatum	-24.77	1.33	14.27	0.53
		G. affinis	-23.74	3.93	13.07	3.93
		L. macrochirus	-25.20	1.33	15.09	1.33
		M. beryllina	-24.42	0.06	16.34	0.17
Terlingua	Tributary	*A. mexicanus*	-24.15	2.30	10.27	1.35
		C. carpio	-25.34	1.07	11.26	0.60
		C. lutrensis	-24.81	1.26	11.64	0.77
		F. zebrinus	-26.06	1.35	11.32	0.59
		Gambusia sp.	-25.83	0.32	11.66	1.04
		I. furcatus	-24.32	0.00	10.77	0.00
		I. punctatus	-23.54	1.13	9.62	0.73
		N. braytoni	-24.60	1.21	12.03	1.15
		P. vigilas	-26.49	0.00	14.50	0.00
Tornillo	Tributary	*A. mexicanus*	-26.30	0.91	11.62	1.17
		C. carpio	-28.42	2.34	10.25	0.58
		C. lutrensis	-26.96	1.75	10.91	0.58
		F. zebrinus	-30.10	1.70	10.15	1.60
		G. affinis	-23.94	0.00	11.47	0.00
		N. braytoni	-28.64	3.20	11.39	0.32
		P. vigilax	-28.84	0.00	13.29	0.00
Independence	Tributary	*A.mexicanus*	-30.57	1.23	11.98	0.86
		C.cyanoguttatum	-28.73	0.00	11.50	0.00
		C.procerpina	-28.97	1.50	11.78	0.80
		D.epistoma	-30.05	0.94	9.85	0.70
		E.grahami	-30.94	1.12	10.16	0.78
		G.affinis	-30.69	1.28	10.62	0.80
		I.lupus	-30.30	2.49	13.54	4.87
		I.punctatus	-31.26	2.37	10.37	2.57
		L.auritus	-28.28	2.08	12.42	1.11
		L.macrochirus	-28.44	1.65	11.16	1.67
		L.megalotis	-29.90	0.00	11.32	0.00
		M.congestum	-28.39	0.55	12.53	1.01
		M.salmoides	-30.70	1.19	11.64	2.02
		N.amabilis	-27.66	1.34	12.41	0.57
		P.olivaris	-32.34	0.00	9.16	0.00
		P.vigilax	-29.23	1.31	10.47	1.22
Dolan	Tributary	*A.mexicanus*	-29.18	0.90	11.49	1.02
		C.cyanoguttatum	-29.85	0.40	10.45	0.82
		C.procerpina	-29.54	1.67	11.30	0.98
		C.venusta	-28.39	0.23	10.35	0.46
		D.argentosa	-29.81	1.26	8.90	0.57
		D.epistoma	-29.61	1.41	9.39	1.44
		E.grahami	-28.81	0.00	10.25	0.00
		G.affinis	-25.79	3.06	13.28	1.26
		L.megalotis	-28.88	0.97	10.00	0.77
		Lepomis sp.	-27.64	2.24	12.45	2.56
		M.congestum	-24.15	1.81	11.97	3.13
		M.salmoides	-29.69	1.05	11.22	0.84
		N.amabilis	-27.90	0.70	11.28	0.74

CHAPTER III

COMMUNITY-WIDE $\delta^{13}C$ AND $\delta^{15}N$-BASED METRICS TO EXAMINE COMMUNITY STRUCTURE ACROSS A RIVERINE LANDSCAPE

Introduction

A long-term focus of community ecologists has been the examination of how community structure and function varies along biotic and abiotic gradients, such as ecosystem size, disturbance frequency, productivity, and the intensity of predation (Polis and Strong 1996, Mittelbach et al. 2001, Gotelli and Ellison 2006). In particular, riverine ecosystems have provided ecologists some of the clearer examples of how community structure and function respond to spatial and temporal variation in abiotic conditions, including landscape position, disturbance regimes, ecosystem size, and the intensity of across-ecosystem linkages (Fisher and Gray 1983, France 1995, Nakano et al. 1999, Miyake et al. 2003, Saito et al. 2007, Veraart et al. 2008).

Stable isotopes analysis is one method that ecologists have used to examine food web structure and function in a variety of riverine ecosystems (Findlay et al. 2002, Delong and Thorp 2006, Hoeinghaus et al. 2007, Zeug and Winemiller 2008). In particular, ecologists have utilized isotopic bi-plots (typically $\delta^{13}C$ - $\delta^{15}N$) to examine the

configuration of riverine food webs and multi-source mixing models have been increasingly employed to draw conclusions about resource. Although isotope bi-plots provide illustrative examples how members of a community relate trophically to each other and two- to multi-source mixing models provide quantitative measures of the degree of utilization of potential resources in a food web, these approaches are not without limitations (Phillips and Greg 2003, Schindler and Lubetkin 2004). Schindler and Lubetkin (2004) suggest there is need to move beyond 'standard' isotope bi-plots and to use alternate methods of using isotopic data to expand our understanding of the structure and function of communities. Recently, Layman et al. (2007) proposed an ecometric approach to quantify trophic structure on a community-wide scale by expanding on traditional $\delta^{13}C$ - $\delta^{15}N$ bi-plots. The use of stable isotope-defined metrics allows ecologists to quantitatively compare food web characteristics from a variety of communities, such as trophic diversity, the degree of functional redundancy, basal C resource diversity, and niche partitioning (Layman et al. 2007).

The focus of this study was to explore the application of the stable isotope-derived community-wide metrics described by Layman et al. (2007) along the lower Rio Grande drainage and a number of its tributaries (Fig. 3.1). Use of these metrics allowed me to accomplish two main goals: (1) examine how food web structure of small-order streams contrasts to a large-order river, and (2) make comparisons of arid to semi-arid systems. I used five stable-isotope defined community-wide metrics in this study (Layman et al. 2007):

(1) *$\delta^{15}N$ Range (NR)* - This metric measures the distance between taxa in a food web with the maximum and minimum $\delta^{15}N$ values, thus providing vertical range of possible trophic

levels within a food web. This metric allowed for comparison of trophic diversity among various sites on the Rio Grande.

(2) *$\delta^{13}C$ Range (CR)* – This metric measures the distance between taxa with maximum and minimum $\delta^{13}C$ values; it provides information on diversity of basal food web resources and niche diversification at the base of the food web.

(3) *Total Area (TA)* - Provided a quantitative representation of total niche space (e.g., total area of a polygon) and extent of total trophic diversity of the entire community. Thus, the larger the range in taxa $\delta^{13}C$ and $\delta^{15}N$ values in the food web, the larger the total area.

(4) *Mean Distance to Centroid (CD)* – This metric is the average Euclidean distance of each species in the food web from the mean $\delta^{13}C$ and $\delta^{15}N$ centroid value and provides information on the average degree of trophic diversity within the food web.

(5) *Standard Deviation of Nearest Neighbor Distance (SDNND)* – This metric is the standard deviation of distance for each taxon in the food web to its nearest neighbor in $\delta^{13}C$ - $\delta^{15}N$ bi-plot space. This community metric provides information about functional redundancy (Layman et al. 2007). High SDNND values indicate less evenness and more species packing.

The Rio Grande/Rio Bravo del Norte is a large, complex drainage that spans three US and four Mexican states, forming the United States - Mexico border along Texas (Fig. 3.1). The river has been highly impacted by anthropogenic activities (e.g., urban development, agriculture, waste water discharge) for hundreds of years (Horgan 1984, Levings et al. 1998, Wong et al. 2007, Padilla 2008). This portion of the Rio Grande drainage is distributed along a biogeoclimatic and precipitation gradient that ranges from

the arid Chihuahuan Desert in the western portion of the drainage (mean annual rainfall < 400 mm/yr) to a semi-arid, subtropical grassland (~800mm/yr; Fig. 3.1, Table 3.1). I sampled four sites along the mainstem of the river, spanning a distance of approximately 665 river km. Additionally, I sampled five of the first and second order perennially-flowing tributaries that contribute to the Rio Grande along this portion of the drainage (Fig. 3.1, Table 3.1).

I hypothesized that I would see variation in community-wide metric along the stream order and climatic gradients. I predicted an increase in trophic diversity (NR) as the Rio Grande and tributaries move from arid to more semi-arid environments (Fig. 3.2). Arid lotic systems are considered to be prone to perturbation associated with drying of the wetted channel and unpredictable, high-intensity flash flooding. These high frequency perturbations in more arid sites lead to a presence of species that are specifically adapted to these conditions (Meffe and Minckley 1987, Stanley et al. 1994). Further, although it is suggested that long food chains will be less resilient to disturbances (e.g., the dynamical constraints hypothesis; Pimm and Lawton 1977), Takimoto et al. (2008) found that food chain length was not affected by disturbance when the top predator(s) were trophic omnivores. Additionally, Sabo et al. (2010) found that river order and presence of reservoirs also play a role as larger drainage area had longer food chains because of less variability of flows and therefore fewer disturbances. This finding suggests that sites on the Rio Grande mainstem that are below impoundments (i.e., Quemado and Fronton) will exhibit longer food chains and potentially greater $\delta^{15}N$ range. Additionally, I predicted greater diversity of basal C resources in the semi-arid regions of the river because of higher autochthonous production associated with

increasing downstream river order (e.g., reduced shading from terrestrial vegetation and increased light availability), but also due to potentially higher subsidization from the more productive riparian areas and subsequent allochthonous OM inputs (see Chapter 1). I also expected to observe a more diverse food web base in the mainstem of the Rio Grande than in the smaller-sized tributaries due to an increased role of allochthonous subsidization from upstream habitats and adjacent terrestrial habitats (Fig. 3.2). I also expected greater basal C resource diversity in semi-arid tributaries due to increased terrestrial primary production in semi-arid riparian zones and increased subsidies of allochthonously derived C to semi-arid tributaries (Fig. 3.2). I expected to see a higher TA and CD in semi-arid Rio Grande habitats than in arid habitats because arid lotic environments are subject to greater frequency and magnitude of perturbation, which can lead to a dominance of taxa which are adapted to these conditions (Fig. 3.2). Additionally, C sources at the base of these arid riverine systems are likely derived mostly from autochthonous sources; whereas increasing terrestrial primary production diversifies and supplements aquatic basal C sources at Rio Grande semi-arid sites leading to a greater diversity in the patterns of resource use among consumers. I also expected the smaller tributaries to follow the same trends as the Rio Grande as it moves along the precipitation/terrestrial PPR gradient; however, exhibit lower resource diversity throughout their ranges than the Rio Grande sites due less habitat heterogeneity and size. Finally, I hypothesized that the Rio Grande sites in arid environments will show higher functional redundancy (SDNND) within trophic levels than the semi-arid ones (e.g., redundancy should decrease as precipitation and terrestrial PPR increase; Fig. 3.2). Additionally, as tributary sites are distributed along the precipitation gradient, they

should show a decrease in functional redundancy. However, SDNND values for tributaries will be consistently higher than mainstem Rio Grande sites. This research represented one of the first attempts to quantitatively assess conceptual models of riverine food web dynamics across river orders and physiochemical gradients.

Although these metrics present a great deal of promise in terms of moving isotopic measurements into more quantitative estimates of community trophic structure, there has been criticism that some of these metrics could lead to erroneous conclusions and are likely not appropriate in some situations (Hoeinghaus and Zeug 2008). However, it has been argued that these metrics can be utilized if researchers pay attention to sampling design (Turner et al. 2010). Additionally, Hoeinghaus and Zeug (2008) suggest data transformations are likely to resolve some of these issues.

Methods

Study sites

Mainstem Rio Grande samples were collected from study sites February to October 2007 (Fig. 3.1). Sites were *a priori* selected to represent an environmental gradient, from arid- to semi-arid, based primarily upon mean annual precipitation (NOAA 2004; Table 3.1). Sampling of the four Rio Grande mainstem locations were conducted during four periods: Winter (February – March), Spring (April – May), Summer (July), and a Fall (September – October) (Fig. 3.1, Table 3.1). Two of the sites are located along the Big Bend section of the river, which traverses a portion of the Chihuahuan Desert ecoregion: St. Elena Canyon and Hot Springs. Both of these sites lie within Big Bend National Park (BBNP). Due to high water levels and inability to access

sites, I was not able to collect samples at the St. Elena site in Spring 2007. The two downstream sites were at Quemado (~79 river km below Amistad Reservoir) and at Fronton (~32 river km below Falcon Reservoir; Fig. 3.1, Table 3.1). Additionally, due to inability to access sites due to high flows the Rio Grande at Quemado site was sampled in Winter, Spring, Summer, and Fall 2007 and Frontera was sampled in Winter and Fall 2007.

In addition to the four mainstem sites, I sampled five low-order (1st and 2nd order), spring-fed perennially flowing sites tributary systems which contribute to the flows of the Rio Grande. Sampling of the tributary sites began in Fall 2006 (October) but then followed the same sampling pattern as the mainstem sites for all subsequent sampling periods (i.e., Winter, Spring, Summer, and Fall 2007). The two arid tributaries, Terlingua and Tornillo Creeks, are located within BBNP and discharge directly into the Rio Grande. Sampling sites in both creeks were on average 200 – 300 m upstream from their confluence with the Rio Grande. Additionally, I sampled three semi-arid tributary sites (Fig. 3.1, Table 3.1). Independence Creek is a tributary of the Pecos River and the sampling site was ~1 km upstream from the confluence with the Pecos River. Dolan Creek is a tributary of the Devil's River and the sampling site as ~150 m upstream of the confluence. Pinto Creek was the final semi-arid tributary that is ~74 river kilometers long and drains directly into the Rio Grande.

Environmental and Physiochemical Data

Environmental and physiochemical variables were collected at each study site, each season. Temperature (^{o}C), dissolved oxygen (DO; mg/L), salinity (ppt), and specific conductance (μS/cm) data were collected with a YSI Model 85 or 650 MDS sonde when

possible, once at each site in Winter, Spring, Summer, and Fall 2007 from Rio Grande mainstem locations and once from each tributary in Fall 2006, and Winter, Spring, Summer, and Fall 2007. Additionally, I collected 1-4 L of surface water during all study seasons in brown or opaque Nalgene bottles which were kept on ice and transported to Texas State University-San Marcos (TXSTATE). I filtered water samples through ashed Pall A/E glass fiber filters (nominal pore size = 1 μm), and analyzed them for dissolved organic carbon (DOC), sulfate (SO_4^{2-}), phosphate (PO_4^{3-}) measured as soluble reactive phosphorous (SRP), and nitrate (NO_3^-) concentrations. Sulfate and DOC concentrations were ascertained on a Lachat FIA Quickchem Autoanalyzer (Hach) and Shimadzu TOC-V_{CSH} Analyzer, respectively. Finally, I determined NO_3^- concentrations by second derivative UV spectroscopy (Crumpton et al. 1992) and used the molybdenum blue method to ascertain SRP (Wetzel and Likens 2000).

Fish collection and processing

Fish from each site were collected via kick and pull seining. Collected individuals were anesthetized with MS-222, then placed in 70% ethanol or on ice and transported to TXSTATE for identification (Thomas et al. 2007, Hubbs et al. 2008). After identification, each fish (or grouping of small similar-sized fish within a species and from the same collection period and site) had fillet or apaxial muscle removed and dried at 60°C for 48 hours. After drying, the samples were homogenized using a mortar and pestle (cleaned with Milli-Q water and acetone after each sample) until they were of flour-like consistency and stored at room temperature in a clean glass vial until stable isotope analysis.

Macroinvertebrate collection and processing

Macroinvertebrates were collected at each site using kick nets and Hess samplers (2, 1 min. sessions riffle habitats each, for a total of four riffle habitats) and dip nets (2, 5 min. sessions in shallow pools and edge habitats) according to methods in Carter and Resh (2001). Invertebrates were sorted on site if time and conditions allowed; samples that were not sorted on-site were taken to the laboratory. Invertebrates were placed in stream water for 1-2 hours to evacuate guts and then preserved in 70% ethanol and transported to TXSTATE. Invertebrates were identified to family (Merritt et al. 2008, Visual Taxonomy: visualtaxonomy.com), dried, and processed using the same methods as described for fish. Large macroinvertebrates had guts removed and all gastropods and mollusks had feet removed prior to drying (Post 2002). Once dried, invertebrate samples were stored in clean glass vials at room temperature until analysis. If a sample of an invertebrate taxonomic group from a given site or collection period did not have enough mass for analysis, the sample was combined with individuals from the same site and collection period, as long as it was within the same family/order and literature-defined functional feeding group (Merritt et al. 2008).

Stable Isotope Analysis

All stable isotope analyses were conducted at the UC-Davis Stable Isotope Facility. All fish and macroinvertebrate samples were analyzed for both ^{13}C and ^{15}N isotopes. UC Davis analyzes ^{13}C and ^{15}N isotope samples using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) and solid samples are combusted at 1020°C. The UC Davis Stable Isotope Facility uses a variety of standards that are calibrated to the

National Institute of Standards and Technology (NIST) Standard Reference Materials (e.g. NIST 1547 peach leaves; NIST 1577b bovine liver, cellulose, and ammonium sulfate).

Data Analysis

I was interested in comparing community-wide metrics of trophic and food web structure using stable isotopes across arid and semi-arid mainstem and tributary sites. As I was interested in the spatial patterns in these metrics in relation to environmental factors and not the temporal dynamics, I compiled data across all sampling events for each site prior to analyses. In addition, to logistical constraints and site access, I was not able to sample each site the same number of times. Thus, I performed all analyses on the complete data across all dates. This prevented me from assessing temporal changes or trends in these community-wide metrics (i.e., Tuner et al. 2010), but allowed me to address community-wide food web and trophic structure across an entire year for all sites.

Community-wide metrics from Layman et al. (2007) were calculated with methods commonly-used in ecomorphometric studies (Ricklefs and Travis 1980, Winemiller 1991, Ricklefs and Miles 1994). Calculations were conducted in the R statistical or Microsoft Excel programs. The calculations were as follows:

(1) NR: The $\delta^{15}N$ value from the lowest consumer in the food web was subtracted from the highest consumer's $\delta^{15}N$.

(2) CR: The lowest $\delta^{13}C$ value in the food web subtracted from the highest $\delta^{13}C$.

(3) TA: Metric calculations were done using the total area of a polygon package in the R statistical program.

(4) CD: Euclidean distances to the centroid were calculated for each consumer in the food web using the equation below. I then averaged the distances to centroid for all consumers in the food web for the final value.

$$CD = ((\delta^{15}N_i - \text{mean } \delta^{15}N)^2 + (\delta^{13}C_i - \text{mean } \delta^{13}C)^2)^{0.5}$$

(5) SDNND: The Euclidean nearest neighbor distance (NND) was calculated for each consumer in the food web using the equation below. I then found the standard deviation for all NNDs in the food web. The standard deviation was used instead of the mean as it is less impacted by sample sizes.

$$NND = ((\delta^{15}N_i - \delta^{15}N_{i-1})^2 + (\delta^{13}C_i - \delta^{13}C_{i-1})^2)^{0.5}$$

Each community-wide metric was compared among mainstem and tributary sites using a mixed model, one-way analysis of variance (ANOVA). Ecometrics were log transformed to meet ANOVA assumptions of normality and homoscedasticity. Mainstem sites were categorized as "arid" (St. Elena and Hot Springs; n = 2) or "semi-arid" (Quemado and Frontera; n = 2). Tributary sites were categorized as "arid" (Terlingua and Tornillo Creeks; n = 2) or "semi-arid" (Pinto, Dolan and Independence Creeks; n = 3). Site type (mainstem arid and semi-arid, and tributary arid and semi-arid) was the predictor variable while the sites themselves were nested within site type as random effects and each community metric was used as the response variable. Further, Hoeinghaus and Zeug (2008) recommend using z-score transformations of $\delta^{13}C$ and $\delta^{15}N$ because isotope bi-plots are not appropriately scaled for some metrics. In essence, when NR and CR are on different scales, then those metrics based on Euclidean distances (e.g., TA, CD, and SDNND) will be affected by one isotope more than the other (Hoeinghaus and Zeug 2008). However, I found the $\delta^{13}C$ and $\delta^{15}N$ axes to be similarly scaled and

therefore did not transform my data (Table 2). Significance was inferred at $p \leq 0.05$. If the results from the ANOVA were significant, a post-hoc Tukey's honestly significant difference (HSD) test was conducted to determine homogeneous subsets. All statistical analyses were preformed in the Paleontological Statistics (PAST), version 2.02 and JMP statistical software, version 9.

Results

I found that community-wide metrics ranges of $\delta^{13}C$ (CR), $\delta^{15}N$ (NR), and standard deviation of nearest neighbor distances (SDNND) did not significantly differ among site types (Fig. 3.1, Table 3.2), indicating that these metrics were not significantly different across communities at all site types (arid mainstem, semi-arid mainstem, arid tributary, and semi-arid tributary). However, the ANOVA showed that mean centroid distance (CD), was smaller in semi-arid mainstem sites, indicating lower estimated trophic diversity at this type of system in the lower Rio Grande. In addition, TA (total niche area) was significantly smaller in the semi-arid mainstem site than arid and semi-arid tributaries (Fig. 3.3, Table 3.2).

Discussion

In general, the stable-isotope community-wide metrics explored in this study found little effect of site type (mainstem arid and semi-arid, and tributary arid and semi-arid) on community composition. Surprisingly, there was no significant variation in trophic diversity (NR) among site types; food chain length, as indicated by NR, in semi-arid tributaries and mainstem sites were not longer than in the arid sites. Additionally, food chain lengths were not affected by stream order. In contrast to these results, Sabo et

al. (2010) found that food chain lengths (calculated from $\delta^{15}N$ data) increased with drainage area and decreased with hydrological variability in 36 North American rivers. For the present study, I assumed that arid sites were subject to greater variability in flows than the semi-arid sites. It is critical to note that Sabo et al. (2010) obtained discharge records for each of their 36 rivers. Unfortunately, not all of my study sites have longer-term discharge measurements taken from them (i.e., a USGS gaging station is installed on-site), thus I was not able to directly examine the role of flow variability on NR. I also predicted that sites immediately downstream from reservoirs would exhibit greater trophic diversity (i.e., food chain length) due to the homogenization and stabilization of riverine discharge by impoundment. However, in the present study, this hypothesis was not supported. Certainly, future studies would greatly benefit from a greater range of sites with variable flow regimes and could thus treat river order and flow variability as continuous variables instead of a categorical variable in analyses.

Hoeinghaus and Zeug (2008) evaluated the community-wide metrics of Layman et al. (2007) and pointed out several major limitations for the application of these metrics to ecological communities. One of the major criticisms by Hoeinghaus and Zeug (2008) of these metrics is that the metrics do not accommodate shifting $\delta^{13}C$ and $\delta^{15}N$ values of food sources (e.g., shifting baselines; Hoeinghaus and Zeug 2008). A possible way to address a shifting $\delta^{15}N$ baseline value among sites or across time would be to use trophic position in lieu of actual $\delta^{15}N$ values (and thus the NR metric). Indeed, a consumer's trophic position is highly dependent upon the isotopic values of its food source (e.g., Matthews and Mazumder 2004), and the estimation of trophic position using a baseline consumer in the food web has been widely applied in the literature (Anderson and

Cabana 2007, Smith et al. 2010). Traditionally, the trophic position of a consumer in a food chain has been calculated with the equation:

$$\text{Trophic Position}_{consumer} = ([\delta^{15}N_{consumer} - \delta^{15}N_{baseline}]/f) + 2$$

where $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ value of the consumer in question, $\delta^{15}N_{baseline}$ is the $\delta^{15}N$ value of the baseline consumer in the food web (consumer with the lowest $\delta^{15}N$ value), and f is the $\delta^{15}N$ fractionation factor for the food web (typically assumed to be ~3.4‰). Using this kind of conversion on $\delta^{15}N$ values would correct for baselines of trophic position and would standardize a consumer's position in each food web across site. However, if trophic position is used, transformation of the axes will then be necessary. When I compared trophic position across site types (i.e. highest trophic position – lowest trophic position [2]) with the mixed model ANOVA used for other metrics, I found that they did not differ significantly ($p = 0.26$). Sabo et al. (2010) used a similar baseline correction approach to calculate food chain length across North American river sites, thus this alteration of the proposed NR metric may have a wider applicability.

Contrary to predictions, the diversity of basal C resources (CR) did not differ significantly among site types. I predicted greater CR in the semi-arid regions of the drainage than arid as well as in the mainstem of the Rio Grande than the smaller tributaries because higher terrestrial productivity in downstream sites would lead to greater allochthonous C subsidies and thus greater diversity in basal C sources available to consumers. The disagreement between my hypotheses and the study findings could be for several reasons. First, it is entirely possible that CR values were not significantly different across site types because there was little difference in diversity of C sources used by consumers. Chapter 1 of this dissertation found that, in general, fishes across

multiple sites in the lower Rio Grande used both autochthonous and allochthonous C sources in similar proportions. In addition, another reason for the observed patterns in CR may be due to substantial overlap in basal C sources available to the community (Hoeinghaus and Zeug 2008). As outlined in Chapter 1, I found substantial overlap in $\delta^{13}C$ values of C_3 terrestrial plants (the dominant source of allochthonous C inputs to the study reaches) and autochthonously-generated algal C sources. Thus, in the present study, a variety of potential C sources were *available* to consumers across sites, but patterns in *utilization* of these potential resources and/or overlapping or similar $\delta^{13}C$ values of C sources may have led to similar CR across sites.

A final reason for the observed lack of variation in CR across study site may be due to temporally or spatially shifting $\delta^{13}C$ baselines across sites. Although previous studies have successfully dealt with shifting $\delta^{15}N$ baselines, the issue of spatially or temporally shifting $\delta^{13}C$ baselines could lead to the limited applicability of the CR metric in community analyses. Indeed, correcting or adjusting for shifting $\delta^{13}C$ baselines prior to calculation of CR is a complicated issue, particularly for riverine ecosystems. In rivers and streams, $\delta^{13}C$ baseline values can be affected by a large number of factors including stream discharge, the diversity of available basal C sources, movement and dispersal of consumers across sites, and differences in consumer C assimilation (Finlay et al. 1999, Singer et al. 2005, Moore and Semmens 2008, Jackson et al. 2009, Rasmussen and Trudeau 2010). The CR metrics is calculated from the values of consumers in the community and does not include any values for sources; therefore there is essentially no way to incorporate baseline C values into the metric. The resource use mixing models,

such as in Chapter 1, are clearly a superior approach to estimating diversity of utilized resources and the CR metric is likely to have limited utility in many situations.

In their critique of the community-wide metrics of Layman et al. (200), Hoeinghaus and Zeug (2008) state that a lack of standardization and axis scaling when using $\delta^{15}N$ and $\delta^{13}C$ bi-plots is a major failing of the metrics. If one range is greater than the other, it will have a larger influence on some metrics, especially those which estimate area. For the study presented here, I did not standardize $\delta^{13}C$ and $\delta^{15}N$ values (such as with a z-score transformation) prior to analyses because the ranges of $\delta^{15}N$ and $\delta^{13}C$ values were similar. Thus, it is unlikely that the issue of scaling did not greatly affect the results of the current study; however, the application of transformations and standardization of data should be applied on a case-by-case basis and other studies that exhibit a much greater range in one isotope versus another will need to transform and standardize data (Turner et al. 2010).

Functional redundancy/species packing (SDNND) did not differ among site types as well. I hypothesized that the arid Rio Grande mainstem sites would exhibit higher trophic redundancy than semi-arid sites. I expected a decrease in functional redundancy as precipitation and terrestrial PPR increase; Table 3.1, Fig. 3.2). Further, I expected to see an effect of stream order size on SDNND; however, I found that tributary sites did not have greater species packing than the mainstem sites as I had expected.

The present study did determine that there were some differences among site type for two of the metrics - measures of niche area (TA) and the degree of trophic diversity (CD). Semi-arid mainstem communities had a significantly lower CD than all other sites, contrary to my predictions. I expected to see smaller trophic diversity at arid mainstem

and tributary sites than in semi-arid sites as arid rivers are subject to greater perturbation from variable hydrological regimes (channel constriction and flash flooding; Thomas et al. 2006, Young and Kingsford 2006). Additionally, arid rivers are likely to have relatively higher levels of in-stream primary production (autochthonous) as compared to their watersheds leading to decreased importance of allochthonous C subsidies (Odum 1957, Fisher 2006, Lake 2006, Marcarelli et al. 2011). With potentially less diverse C sources available to in-stream communities in arid riverine ecosystems, one would expect decreased trophic diversity in the community. However, as stated earlier, Bayesian isotopic mixing models showed overlap in C source $\delta^{13}C$ values at all sites (Chapter 2) which can affect measures of overall trophic diversity. Additionally, I expected the smaller tributaries would have smaller trophic diversity than the larger river since these communities are subject to more extreme hydrological changes than the larger system. Again, this is not what I found.

Finally, I predicted TA would follow the same trends as CD as it is also a measure of community trophic diversity. I found there was not a significant difference between the communities of arid and semi-arid mainstem sites. I did find that communities at semi-arid mainstem sites were significantly smaller than both arid and semi-arid tributary communities; however, there was not a significant difference between arid and semi-arid tributary communities. Essentially, I found that semi-arid mainstem sites had simpler food webs than the upstream sites. Again, both sites were positioned below a reservoir which suggests that river regulation may simplify food webs in terms of trophic diversity.

In conclusion, if performed and interpreted with caution, these metrics can be useful in quantitatively comparing communities among sites. Understanding the

composition of a community as well as how it may compare to a reference site, can be useful for river managers. Often management of rivers is focused on the identification and recovery of specific species (e.g., the Endangered Species Act). However, community- and ecosystem-level processes should also be of interest. This study contributes to the understanding of how riverine communities are composed and function across a large spatial and physiochemical gradient, and the role of organisms within a community.

Literature Cited

Carter, J.L. and V.H. Resh. 2001. After site selection and before data analysis: sampling, sorting, and laboratory procedures used in stream benthic macroinvertebrates monitoring programs by USA state agencies. Journal of the North American Benthological Society 20:658-682.

Cornwell, W.K., D.W. Schwilk, and D.D. Ackerly. 2006. A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465-1471.

Crumpton, W.G., T.M. Isenhart, and P.D. Mitchell. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. Limnology and Oceanography 37:907-913.

Finlay, J.C., S. Khandwala, and M.E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology 83:1845-1859.

Fisher, S.G. 2006. Stream ecosystems of the western United States. *In*: River and Stream Ecosystems of the World. C.E. Cushing, K.W. Cummins, and G.W. Minshall (*eds*.). University of California Press, Berkley, California. Pp 61-88.

Fisher, S.G. and L.J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. Ecology 64:1217-1234.

France, R.L. 1996. Scope for use of stable carbon isotopes in discerning the incorporation of forest detritus into aquatic foodwebs. Hydrobiologia 325:219-222.

Gotelli, N.J. and A.M. Ellison. 2006. Food-web models predict species abundances in response to habitat change. PLOS Biology 4:1869-1873.

Hoeinghaus, D.J. K.O. Winemiller, and A.A. Agostinho. 2007. Landscape-scale hydrologic characteristics differentiate patterns of carbon flow in large-river food webs. Ecosystems 10:1019-1033.

Hoeinghaus, D.J. and S.C. Zeug. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? Comment. Ecology 89:2353-2357.

Hubbs, C., R.J. Edwards, and G.P. Garrett. 2008. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. Texas Academy of Science, Second Edition.

Lake, P.S. 2006. Of floods and droughts: river and stream ecosystems of Australia. *In*: River and Stream Ecosystems of the World. C.E. Cushing, K.W. Cummins, and G.W. Minshall (*eds*). University of California Press, Berkley, California. p. 659-694.

Layman, C.A., A. Arrington, C.G. Montana, and D.M. Post. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? Ecology 88:1465-1471.

Layman, C.A. and D.M. Post. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? Reply. Ecology 89:2358-2359.

Marcarelli, A.M., C.V. Baxter, M.M. Mineau, and R.O. Hall. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology 92:1215-1225.

Meffe, G.K. and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. The American Midland Naturalist 117:177-191.

Merritt, R.W., K.W. Cummings, and M.B. Berg (*eds*). 2008. An introduction to aquatic insects of North America. 4th Edition. Kendall/Hunt Publishing Co., Dubuque, IA.

Mittelbach, G.G., C.F. Steiner, S.M. Schneiner, K.L. Gross, H.L. Reynolds, R.B. Waide, M.R. Willig, S.I. Dodson, and L. Gough. 2001. What is the observed relationship between species richness and productivity? Ecology 82:2381-2396.

Miyake, Y., T. Hiura, N. Kuhara, and S. Nakano. 2003. Succession in a stream invertebrate community: a transition in species dominance through colonization. Ecological Research 18:493-501.

Nakano, S., M. Hitoshi, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80:2435-2441.

Odum, H.T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55–112.

Phillips, D.L. and J.W. Gregg. 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261-269.

Pimm, S.L. and J.H. Lawton. 1977. Number of trophic levels in ecological communities. Nature 268:329-331.

Polis, G.A. and D.R. Strong. 1996. Food web complexity and community dynamics. American Naturalist 147:813-846.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Sabo, J.L., J.C. Finlay, T. Kennedy, and D.M. Post. 2010. The role of discharge variation in scaling of drainage area and food chain lengths in rivers. Science 330:965-967.

Saito, L., C. Redd, S. Chandra, L. Atwell, C.H. Fritsen, H. Christian, M.R. Rosen. 2007. Quantifying foodweb interactions with simultaneous linear equations: stable isotope models of the Truckee River, USA. Journal of the North American Benthological Society 26:642-662.

Schindler, D.E. and S.C. Lubetkin. 2004. Using stable isotopes to quantify material transport in food webs. *In* Food Webs at the Landscape Level. Eds. G.A. Polis, M.E. Power, G.R. Huxel. Pp 25-42. University of Chicago Press. Chicago, IL.

Stanley, E.H., D.L. Buschman, A.J. Boulton, N.B. Grimm, and S.G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. The American Midland Naturalist 131:288-300.

Takimoto, G., D.A. Spiller, and D.M. Post. 2008. Ecosystem size, but not disturbance, determines food-chain length on islands of the Bahamas. Ecology 89:3001-3007.

Thomas, C., T.H. Bonner, and B.G. Whiteside. 2007. Freshwater fishes of Texas. 202 pp. Texas A&M University Press, College Station, Texas.

Thomas, M.C., P. H. Beyer, and K.H. Rogers. 2006. Variability, complexity and diversity: the geomorphology of river ecosystems in dryland regions. *In* Ecology of Desert Rivers. R.T. Kingsford (*ed*). Cambridge University Press. Cambridge, New York. p. 47-75.

Veraart, A.J., A.M. Romani, E. Tornes, and S. Sabater. 2008. Algal response to nutrient enrichment in forested oligotrophic stream. Journal of Phycology 44:564-577.

Wetzel, R.G. and G.E. Likens. 2000. Limnological Analyses. 3rd Edition. Springer-Verlag, New York, NY USA.

Young, W.J. and R.T. Kingsford. 2006. Flow variability in large unregulated dryland rivers. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Zeug, S.C. and K.O. Winemiller. 2008. Evidence supporting the importance of terrestrial carbon in a large-river food web. Ecology 89:1733-1743.

Table 3.1. Site names, coordinates, site type (mainstem or tributary), gauging stations, mean annual precipitation rates, and mean environmental and physiochemical variables for each study site. Precipitation data is mean annual precipitation for 1971-2000 (NOAA 2004).

Site	Coordinates	Site Type	Gauge Station	Annual Precipitation	Dissolved Oxygen (mg/L)	Temperature (°C)	Specific Conductance (µS/cm)	Salinity (ppt)	DOC (mg/L)	SO_4^{3-} (µg/L)	PO_4^{3-} (µg/L)	NO_3^- (µg/L)
Santa Elena	29°09'51.24" N, 103°36'35.34W	Mainstem	Castolon	248.92	7.00	23.66	2201.00	3.27	3.34	494	46.50	261.36
Hot Springs	29°10'38.90" N, 102°59'47.79W	Mainstem	Castolon	248.92	8.60	24.71	1753.00	0.70	2.65	493	60.99	360.59
Quemado	28°56'30.22" N, 100°38'38.81" W	Mainstem	Eagle's Pass	545.59	6.69	25.05	782.00	0.30	1.08	57	32.36	231.00
Fronton	26°24'06.51" N, 99°00'08.94" W	Mainstem	Falcon Reservoir	515.11	3.87	27.70	925.00	0.50	0.38	16	4.91	79.15
Terlingua Creek	29°19'37.70" N, 103°33'12.31" W	Tributary	Castolon	248.92	8.57	24.39	1220.00	0.72	2.98	360	18.95	368.32
Tornillo Creek	29°10'37.33" N, 103°00'02.95" W	Tributary	Castolon	248.92	10.96	24.87	1057.00	0.60	0.49	386	4.49	378.04
Independence Creek	30°27'52.68" N, 101°46'50.34" W	Tributary	Sheffield	379.22	10.68	23.77	517.00	0.25	0.93	200	5.20	837.16
Dolan Creek	29°53'05.16" N, 101°59'04.39" W	Tributary	Carta Valley	577.85	10.32	20.42	1075.00	0.56	0.58	124	36.04	1406.88
Pinto Creek	29°24'10.80" N, 100°28'21.89" W	Tributary	Del Rio	477.52	9.31	21.27	3716.00	1.95	1.22	133	0.68	398.79

Table 3.2. Sites, site types (mainstem or tributary), and averages and ranges for ecometrics for each study site. NR = $\delta^{15}N$ range, CR = $\delta^{13}C$ range, CD = Euclidean distances to centroid, NND = average distances to nearest neighbors, SDNND = standard deviation of distances to nearest neighbors, and TA = total area.

Site	Site Type		NR	CR	CD	NND	SDNND	TA
St. Elena	Mainstem	mean	9.17	6.56	2.82	1.10	1.06	32.08
		range	8.21-10.23	4.69-9.08	2.72-2.97	0.98-1.22	0.90-1.26	23.06-40.63
Hot Springs	Mainstem	mean	8.64	7.59	2.90	1.09	1.14	33.62
		range	7.24-9.52	4.77-9.57	2.60-3.24	0.88-1.37	0.86-1.43	26.72-45.00
Quemado	Mainstem	mean	6.94	8.17	2.19	0.85	0.68	31.66
		range	1.77-14.32	2.25-13.39	0.70-3.29	0.60-1.34	0.36-1.19	2.34-59.01
Fronton	Mainstem	mean	5.32	3.50	1.72	0.51	0.39	11.64
		range	4.79-5.85	2.64-4.36	1.40-2.04	0.41-0.61	0.37-0.41	8.88-14.40
Terlingua	Tributary	mean	9.09	10.75	2.99	1.76	1.72	46.72
		range	6.18-12.28	9.42-16.35	2.73-3.50	1.02-3.15	0.86-3.73	24.32-83.23
Tornillo	Tributary	mean	8.71	8.07	3.28	1.38	0.97	39.42
		range	7.11-11.35	7.51-9.03	3.05-3.97	1.17-1.81	0.65-1.20	26.04-49.59
Independence	Tributary	mean	9.21	7.06	2.68	0.85	0.77	36.12
		range	3.95-16.02	2.06-10.03	1.07-3.63	0.54-1.31	0.33-1.90	4.03-61.36
Dolan	Tributary	mean	10.32	9.46	3.08	1.24	1.23	57.00
		range	8.29-12.58	4.09-19.93	2.41-3.75	0.66-1.93	0.45-2.76	25.41-116.59
Pinto	Tributary	mean	7.43	7.61	2.90	1.07	1.02	33.94
		range	5.44-10.78	3.10-10.68	2.20-3.60	0.63-1.56	0.43-1.32	21.21-51.45
One-way ANOVA			*p=0.08*	*p=0.24*	*p=0.002**	*p=0.08*	*p=0.18*	*p=0.04**

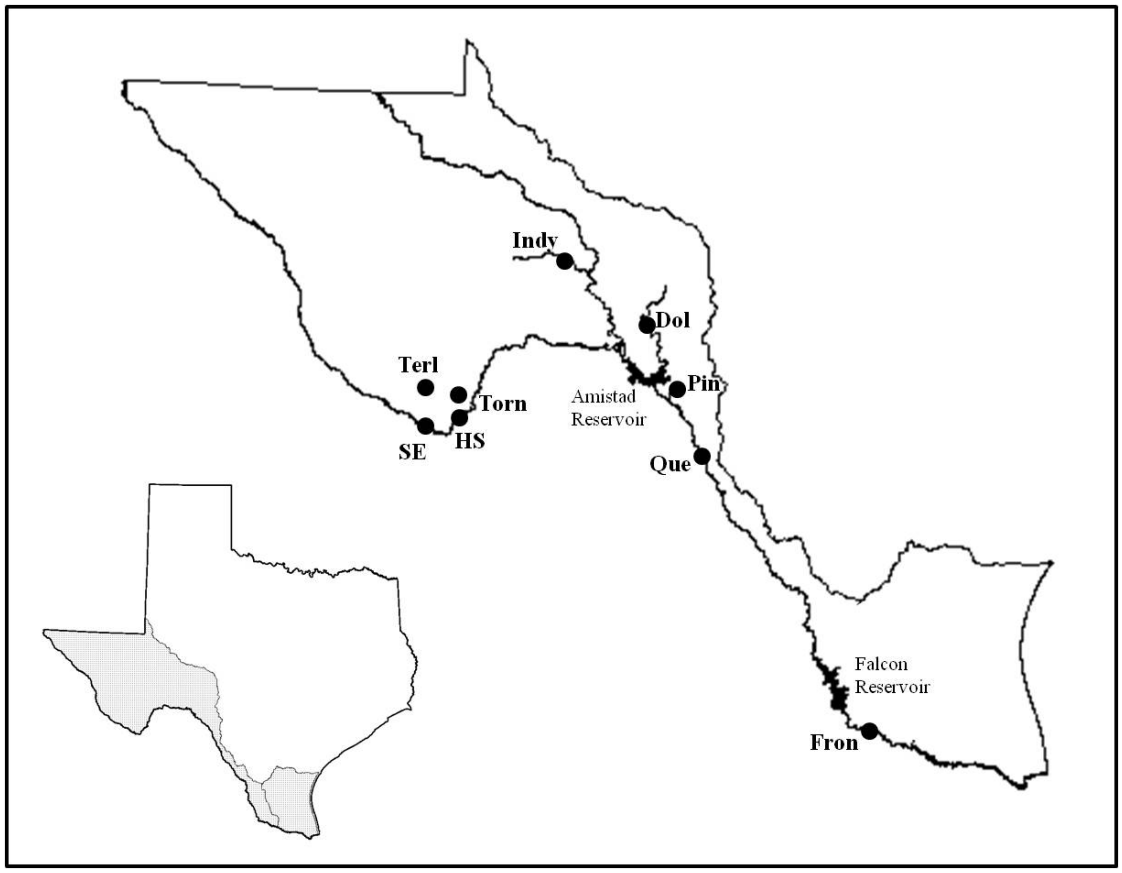

Figure 3.1. Map of Rio Grande and the various study sites. (a) illustrates the Rio Grande in the USA and Mexico with the section of the river associated with my study sites indicated in bold, and (b) an illustration of the study sites located within Texas. Note: site locations are abbreviated: SE = Rio Grande at St. Elena Canyon, Terl = Terlingua Creek, HS = Rio Grande at Hot Springs, Torn = Tornillo Creek, Indy = Independence Creek, Dol = Dolan Creek, Pin = Pinto Creek, Que = Rio Grande at Quemado, Fron = Rio Grande below Falcon Reservoir.

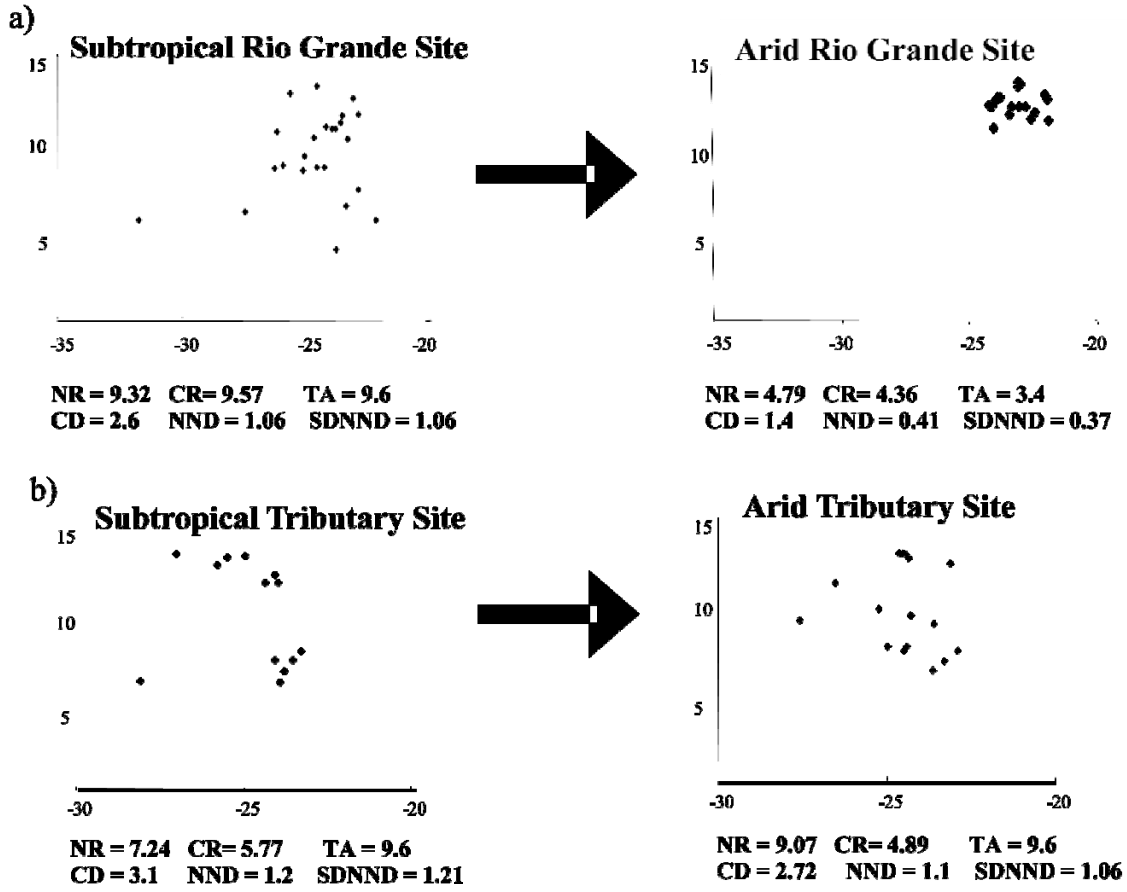

Figure 3.2. Predicted results of community-wide metric comparisons between semi-arid and arid sites of the Rio Grande and its tributaries. (a) The predicted configuration of communities at semi-arid and arid sites along the mainstem of the Rio Grande. The various ecometric values are presented. (b) The predicted configuration of communities and ecometrics of tributaries along the precipitation/terrestrial PPR gradient. NR = δ^{15}N range, CR = δ^{13}C range, TA = total area, CD = Euclidean distances to centroid, NND = average distances to nearest neighbors, and SDNND = standard deviation of distances to nearest neighbors.

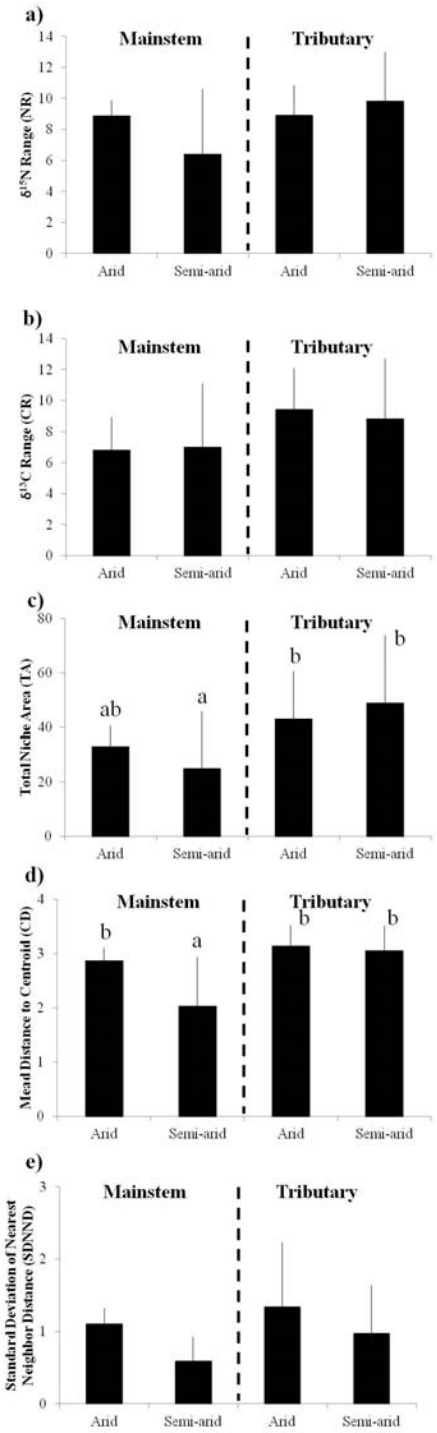

Figure 3.3. Results of community-wide metric analyses for all site types. Figures a and b show $\delta^{15}N$ (NR) and $\delta^{13}C$ (CR) ranges (respectively). Figures c, d and e show total niche area (TA), mean distance to centroid (CD), and standard deviation of nearest neighbor distance (SDNND), respectively. Comparisons among site types were non-significant for all metrics except TA and CD.

CHAPTER IV

BASIN- AND LOCAL-SCALE INFLUENCES ON PATTERNS OF MACROINVERTEBRATE COMMUNITY STRUCTURE IN THE LOWER RIO GRANDE DRAINAGE, TEXAS

Introduction

Multiple conceptual models have been developed to address the dynamics of organism distributions, nutrient dynamics, and energy fluxes in riverine ecosystems. These models include the river continuum concept, the flood pulse concept, and the riverine productivity model (RCC, FPC, and RPM, respectively). Each model provides general predictions on the flow of nutrients and organisms within and across riverine-terrestrial interface and their effects on community function and composition (Vannote et al., 1980; Junk et al., 1989; Thorp and Delong, 1994). Although these models are informative, they have largely been examined in north temperate and southeastern U.S. riverine systems. Thus, there is limited assessment of their applicability to rivers in arid and semi-arid ecosystems which are unique in their physiochemical characteristics and community structure and ecosystem functioning.

In contrast to north temperate and southeastern river systems, arid river systems are more likely to have periods of drying or significant channel constriction for long periods associated with little or no precipitation (Thomas et al. 2006). In addition,

episodes of heavy precipitation and associated high discharge lead to substantial downstream transport of sediments and organisms (Thomas et al. 2006, Young and Kingsford 2006). Due to intermittent hydrological flows and tendency for short duration, unpredictable flooding, it is predicted that macroinvertebrate and fish populations that exhibit high resilience and resistance under these variable conditions will dominate desert lotic systems (Meffe and Minckley 1987, Stanley et al. 1994). Although fish populations generally resist flood disturbances better than macroinvertebrates, macroinvertebrate taxa adapted to these conditions are able to recolonize and reproduce relatively quickly after disturbance events (Stanley et al. 1994). However, Stanley et al. (1994) found that drying of streambeds resulted in significant declines of some macroinvertebrate species, but if there was hydrological connectivity to upstream sites, there was very little population fluctuation during extended periods of low flow and channel restriction. Other studies have noted that macroinvertebrate communities in drought-prone, intermittent streams exhibit rapid recolonization of disturbed sites by desiccation-resistant and highly mobile taxa (Boulton 2003). Therefore, due to extreme environmental conditions in arid stream ecosystems and the high level of adaptation to these conditions by organisms associated with these systems, there is a need to understand the environmental factors that influence macroinvertebrate community dynamics in arid river systems.

There is a need for further examination of the distribution of aquatic macroinvertebrates in large and complex riverine networks. Models such as the RCC, FPC, and RPM predict shifts in macroinvertebrate taxa and the dominant functional feeding groups with stream order (Vannote et al. 1980). However, if a particular study covers a very large geographic area, in which study sites are located relatively far away

from one another, and the river system crosses strong geographical and physiochemical gradients, it is possible that there will be turnover in taxonomic and functional composition in macroinvertebrate communities due to changes in biogeographic distributions of taxa and not due to the changes in physiochemical conditions associated with changes in stream order. Under these circumstances, a researcher might conclude that there is high taxonomic "endemism" or "uniqueness" at each site, and those taxonomic shifts along the riverine gradients (i.e., physiochemical and stream order) may not be important. Thus, an examination of local and basin level physiochemical properties would provide insight as to patterns (if any) of macroinvertebrate community composition for a large riverine drainage.

The present study examined macroinvertebrate community structure and functional composition of a large complex drainage in the southwestern United States (i.e., the lower Rio Grande drainage in Texas; Fig. 4.1). I was interested in broad scale differences of macroinvertebrate community composition at the family taxonomic level. I chose to examine my study questions at the family level as many conceptual models base their predictions about trends in community composition at the higher taxonomic groups (e.g. family or order level). The study goals were three-fold. First, I assessed macroinvertebrate community composition and diversity along the main stem of a river as well as its tributaries across a substantial west-to-east/upstream-downstream physiographic gradient. Second, I examined whether differences in local site-specific environmental conditions could be used to explain a substantial portion of the variation in invertebrate community composition and diversity in this large and complex drainage. Third, I assessed spatial patterns in the distribution and relative abundance of different

invertebrate functional feeding groups in relation to predictions made by conceptual models of riverine communities, specifically, the RCC, FPC. Although previous studies have assessed macroinvertebrate community composition in of the lower Rio Grande and some of its tributaries (Gloyd 1958, Bane and Lind 1978, Davis 1980a, Davis 1980b, Baumgardner and Bowles 2005), most of these studies have either been conducted at very small spatial scales or have not specifically examined how large- (e.g., Davis 1980a and b) and small-scale (e.g., Bane and Lind 1978) environmental variation contribute to invertebrate community composition and diversity. Thus, it is unclear to what extent taxonomic and functional compositional shifts in macroinvertebrates are related to local and large scale spatial variation in lotic physiochemical characteristics and to what extent well-established conceptual models of riverine community composition are applicable to this drainage.

I hypothesized that that arid and semi-arid mainstem and tributary sites would vary along physiochemical gradients and predicted that arid mainstem and tributary sites would exhibit similar physiochemical characteristics due to the climatic and geological characteristics of the. I hypothesized that variation in invertebrate family composition and abundance would be strongly related to regionally-based climatic and physiochemical parameters. However, I predict that, in agreement with conceptual models of riverine community development (e.g., the RCC), invertebrate communities of the mainstem of the Rio Grande will be dominated by filter feeding invertebrates due to increased turbidity, high concentrations of suspended materials, and subsequent low levels of in-situ primary production. I also predict that, in contrast to the models, small-order arid region tributaries would have stream invertebrate communities dominated by

grazer/scrapers (rather than shredders and collector/gatherers) due to high levels of incident light (and therefore higher levels of in-situ periphyton production) and lesser inputs of terrestrial OM. Further invertebrate communities in the semi-arid regions (with accompanying increased shading and higher levels of terrestrially-derived OM) will have greater densities of invertebrate shredders and grazer/scrapers.

Methods

Study Area

The Rio Grande spans three US and four Mexican states, forming the U.S./Mexico border. It is ~3,000 km long, starting in the San Juan Mountains, Colorado, traveling south the Gulf of Mexico (Fig. 4.1). The total drainage area of the Rio Grande basin is ~300,000 km^2. The river has been highly impacted by anthropogenic activities (e.g., water extraction, urban development, agriculture, waste water discharge) for hundreds of years (Horgan 1984, Levings et al. 1998, Padilla 2008) and is thought to be an at-risk river system (Wong et al. 2007).

My study area consisted of sites located on the Rio Grande mainstem and multiple tributaries distributed throughout the drainage in Texas (Fig. 4.1). Two large reservoirs are located within the Texas region of the river; Amistad International Reservoir is located below the western Big Bend region and integrates the flows of the Rio Grande, the Devils River, and the Pecos River. Falcon Reservoir is located in the lower reaches of the drainage and its only major input is from the Rio Grande. In the current study, sampling sites in the mainstem of the Rio Grande were located from the Big Bend region to below Falcon Reservoir. The three sites located in the Big Bend region were

Contrabando Crossing, Santa Elena Canyon (in Big Bend National Park, BBNP), and Hot Springs (in BBNP). Additionally, two sites were located between Amistad International Reservoir and Falcon Reservoir (Quemado and San Ygnacio) and one site was located below Falcon Reservoir (Fronton). I additionally sampled six perennially flowing tributary sites along the drainage. Terlingua and Tornillo Creeks are located within BBNP and are currently subjected to little direct human impact. Independence Creek, the Pecos River (downstream of confluence with Independence Creek), and Dolan Creek, a major tributary of the Devil's River, were also sampled as tributary sites. The Independence Creek Preserve and Dolan Creek are located on Nature Conservancy-owned land in the Trans-Pecos region. Both creeks again have minimal direct anthropogenic impact and are considered relatively undisturbed. Pinto Creek is the final headwater stream sampled. It is located furthest east of all tributary sites, and lies downstream from Amistad International Reservoir. Pinto Creek has a predominantly clay substrate and the highest percent organic matter content and second highest dissolved organic carbon concentration (highest: Pecos River) of all tributary sites.

I gathered mean annual precipitation data for 1971-2000 (NOAA 2004) along the lower Rio Grande mainstem and tributary study sites. Sampling sites for this study were *a priori* selected to represent a precipitation gradient from arid to semi-arid. Mainstem and tributary sites located in Big Bend region received nearly half of the annual average precipitation than most of sites located further downstream of the Rio Grande drainage (NOAA 2004, Table 4.1). The San Ygnacio study site was the exception as its annual average precipitation was more similar to sites located within the Big Bend region (NOAA 2004; Table 4.1).

Environmental and Physiochemical Data

At each time of sampling, environmental and physiochemical variables were measured at each study site. I collected temperature (^{o}C), dissolved oxygen (DO; mg/L), salinity (ppt), and specific conductance (μS/cm) data with a YSI Model 85 or 650 MDS sonde once at each site in March, May, July, and October 2007 from Rio Grande mainstem locations and from each tributary site in October 2006, and March, May, July, and October 2007. On each sampling event, I collected 1 to 4 L of surface water in brown or opaque high density polyethylene bottles; water samples were kept on ice and transported to Texas State University within 48 h. In the lab, water samples were filtered through ashed Pall A/E glass fiber filters (nominal pore size = 1 μm), and analyzed for dissolved organic carbon (DOC), dissolved sulfate (SO_4^{2-}), dissolved phosphate (PO_4^{3-}), and nitrate (NO_3^-) concentrations. Sulfate and DOC concentrations were ascertained on a Lachat FIA Quickchem Autoanalyzer (Hach) and Shimadzu TOC-V_{CSH} Analyzer, respectively. Nitrate concentrations were determined with second derivative UV spectroscopy (Crumpton et al. 1992). Phosphate was measured as soluble reactive phosphorus (SRP) using the molybdenum blue method (Wetzel and Likens 2000).

Macroinvertebrate Collection and Preparation

I collected macroinvertebrates from Rio Grande mainstem locations in March, May, July, and October 2007, and from tributary sites in October 2006, and March, May, July, and October 2007. In order to estimate the abundance and distribution of the largest number of taxa within the macroinvertebrates, aquatic macroinvertebrates were sampled from a variety of mesohabitats at each site using several established methods (Carter and Resh 2001). Invertebrates were sampled with kick nets (500 μm mesh, 1 m^2 surface area;

1 min sampling time interval in each of 2 separate riffle habitats per site) and Hess samplers (500 μm mesh, 0.3 m in diameter; 1 min sampling time interval in each of 2 riffle habitats per site). Dip nets were additionally used at each site (1000 μm mesh; 2- 5 min. sampling periods per site) in runs and shallow pools and along stream edge habitats. At each site, samples collected using each method were kept separate and invertebrates were preserved in 70% ethanol for storage and transport to the lab. Preserved field samples were washed through a 5 mm mesh sieve and all invertebrates were sorted, identified to family and counted (Merritt et al. 2008). Again, I chose to examine my study questions at the family instead of species level, even though there is some loss of information of actual diversity in a community as previous conceptual models used higher taxonomic groups in discussing community composition trends and I was interested in making as direct a comparison as possible. Additionally, given the scope of the study (spatially and temporally), comparison at the family taxonomic level was more logistically feasible.

Data analysis

Each season at each Rio Grande mainstem and tributary site, I assessed taxa richness and community composition. In order to test the hypothesis that mainstem and tributary sites would vary along climatic and physiochemical gradients I utilized principal components analysis (PCA) to examine the correlation of study sites with twelve site-specific environmental variables (mean annual precipitation, terrestrial productivity, DO, temperature, specific conductance, salinity, SO_4^{2-}, PO_4^{3-}, NO_3^-, DOC, site latitude coordinates, and longitude coordinates). In order to examine the hypothesis that invertebrate family composition and abundance varied with environmental gradients, I

used the environmental variables with the highest loadings on principle components I and II and utilized canonical correspondence analysis (CCA) to examine how the abundance of the fifteen most abundant macroinvertebrate families varied with these environmental conditions. I also examined whether family richness (number of invertebrate families at a site over the year; denoted here as *S* varied along these environmental gradients. In order to test the hypothesis that small order arid and semi-arid streams as well as the larger Rio Grande macroinvertebrate communities will vary in dominant functional feeding groups depending on potential for instream primary productivity and upstream and terrestrial allochthonous inputs, we examined whether the different broadly-defined functional feeding groups (filter feeder, grazer/scraper, predator, decomposer, and shredder; Merritt et al. 2008) using CCA. All statistical analyses were preformed in Paleontological Statistics (PAST), version 2.02, and Canonical Community Ordination (CANOCO), version 3.1.

Results

Environmental Physiochemical Characteristics

Average annual water temperatures for the Rio Grande mainstem sites ranged from 22.3-27.7°C, with the lowest average temperatures in the western Big Bend region and temperatures increasing downstream to the southern study locations (Table 4.1). In contrast, I observed higher mean annual water temperatures in the streams in the Big Bend region. Annual mean DO varied greatly, with higher readings at mainstem sites located in the Big Bend region and lowest readings in the southern portion of the river. Additionally, mean annual DO concentrations were highest in Tornillo and Dolan Creeks

and lowest in Terlingua and the Pecos River (Table 4.1). Further, spatial patterns in salinity and specific conductance were found across mainstem and tributary sites, with higher salinities and specific conductance generally occurring in the western Rio Grande (Table 1, Fig. 2). Dissolved organic carbon, SO_4^{2-}, PO_4^{3-}, NO_3^- concentrations generally exhibited a similar trend of decreasing from western to southeastern Rio Grande mainstem sites (Table 4.1, Fig. 4.2). However, tributary sites did not exhibit this same spatial pattern in dissolved nutrients.

The first three PC axes explained 82% of the variance among study sites (Fig. 4.3). Principle component I explained 49% of the variation among sites along a gradient of sites with high mean annual precipitation and water temperature to sites with higher DOC, specific conductivity, and salinity; along this gradient, the more downstream mainstem and tributary sites (San Ygnacio, Dolan Creek, Frontera, Quemado, and Pinto Creek) were grouped together and the more upstream arid mainstem sites (Santa Elena Canyon, Contrabando, and Hot Springs) and tributaries (Independence Creek, Terlingua Creek, and Tornillo Creek) at the other end of the gradient. Principal component II explained 20% of the variation among sites and in general represented more site-specific environmental variables with tributary sites across the lower drainage (Dolan Creek, Independence Creek, Pinto Creek, Tornillo Creek and the Pecos River) having higher NO_3^- and DO concentrations and most of the mainstem sites (Quemado, Hot Springs, Contrabando, Santa Elena, San Ygnacio, and Frontera) exhibiting higher mean annual water temperatures, higher DOC, and higher salinity. Principal component III explained a remaining 13% of the variation among sites and also represented more site-specific environmental variables. There was little distinction among mainstem and tributary sites

along a gradient of sites with higher mean annual precipitation, specific conductance, and salinity to sites with higher mean annual water temperatures and DO concentrations.

Macroinvertebrate taxonomic assemblages

Macroinvertebrate families showed substantial variation along the environmental gradients depicted in the CCA (Fig. 4.3a). Canonical axis (CA) I explained 37% of the variation among invertebrate families with Hydropsychids (Tricoptera), dryopids (Coleoptera), heptageniids (Ephemeroptera), and simuliids (Diptera) were strongly associated with the more upstream sites which had higher DOC and specific conductance and lower mean annual precipitation (Fig. 4.3a). Additionally, CA II explained 24% of the variation, with chironomids (Diptera), coenagrionids (Odonata), other Tricoptera (philopotamids, limnephilids, and leptocerids), and tricorythidids (Ephemeroptera) associated with the downstream mainstem sites which had greater mean annual precipitation and lower DO concentrations. Baetid mayflies, naucorids (Hemiptera), and gomphids (Odonata) were associated with elevated DO and higher nitrate environments of the semi-arid, small-order streams (i.e., Dolan, Pinto, and Independence Creeks). Elmids (Coleoptera), corydalids (Megaloptera), and leptophlebids (Ephemeroptera) were more widespread across sites and their abundances were not substantially related to the environmental gradients in the CCA. In addition, family richness (*S*) exhibited little variation with environmental conditions.

Generally, variation in the abundance of invertebrates in most of the functional feeding groups exhibited relatively weaker associations along the environmental gradients (Fig. 4.3b). Canonical axis I only accounted for 19% of the variation among functional feeding groups and CA II accounted for 3%. Functional feeding groups such

as filter feeders, grazer/scrapers, decomposers, and predators were generalists typically found in similar abundances at all study sites. However, shredders were highly associated with small order semi-arid streams (i.e., Dolan and Independence Creeks).

Discussion

The results of the present study indicate that variation in physiochemical characteristics among study sites was related to both basin- and local-scale influences. Regional or basin scale influences appeared to have a primary influence (as indicated by the presence of these types of variables along PC1), with the upstream and western-most sites, within the Chihuahuan Desert ecoregion, having higher DOC, specific conductivity, and salinity. Additionally, the present study also found that local site-specific conditions (e.g., stream order [low-order versus high-order] and position in the landscape [arid versus semi-arid]) also had an important, but secondary influence (as indicated on PC2 and 3). These findings support my predictions that arid tributary and mainstem study locations had similar local physiochemical and climatic characteristics when compared to their semi-arid counterparts.

The present study also determined that macroinvertebrate community composition (at the family level) of the lower Rio Grande drainage varied along these basin- and local-scale characteristics. The western-most sites had higher densities of simuliids, hydropsychids, heptageniids, and dryopids; whereas the semi-arid and southeastern sites had more chironomids, coenagrionids, and other families of Tricoptera. These findings support my hypothesis that broad-scale family-level shifts along the drainage and that these differences were related to physiochemical gradients in the system.

When I compared my findings of Rio Grande mainstem sites to those of Davis (1980a), I found similar orders and families represented (Baetidae, Simulidae, Chironomidae, and Hydropsychidae). Additionally, when I compared the physiochemical properties measured in both my and Davis (1980a) studies, I found similar results. It should be noted that the sites in the Davis (1980a) study were different than mine; however, they encompassed a comparable area. Based on this information, it appears that community composition and structure has not changed much within the timeframe of the two studies. Similarly, a study by Haden et al. (2003) of the invertebrate community composition of two large order, turbid rivers in Utah, the Colorado and Green Rivers, showed an inhibition of primary production leading to the invertebrate communities being dominated by filter/collector species of mayflies (Ephemeroptera), caddisflies (Tricoptera), and Diptera (Hayden et al. 2003).

Further, I saw greater variation in relative abundances within and among tributary study locations than in the Rio Grande mainstem itself. Although, I didn't see as high a variability among arid and semi-arid sites for some families (e.g. baetids and chironomids), other families (e.g. elmids, gomphids, and heptageniids) were in greater abundance at semi-arid sites (Independence, Dolan, and Pinto Creeks, and Pecos River) than streams in the Big Bend region (Tornillo and Terlingua Creeks; Appendix B). It appeared that changes in average annual precipitation and physiochemical properties (DOC, specific conductance, salinity, PO_4^{3-} and NO_3^-) may play a role in community composition in these smaller streams. This variation in physiochemical properties and water clarity also likely accounted for the absence of certain families (i.e. bivalves and gastropods) in Big Bend streams and larger abundances in others.

Although the present study found observed variation in physiochemical characteristics and invertebrate community composition at the family level across Rio Grande drainage, few of the functional feeding groups exhibited a response to these gradients. Additionally, in contrast to the RCC, functional feeding groups varied to a much lesser degree than family composition along stream order and physiochemical gradients as many of the groups were found at all sites and in varying abundances. However, as I hypothesized there was a dominance of shredders and grazer/scrapers in the small order, semi-arid streams which have greater shading and *in situ* primary production. Further, there was also a slight filter feeder association with mainstem Rio Grande sites as hypothesized and conforming to RCC predictions. However, shredders were strongly associated with small-order, semi-arid streams and not the larger Rio Grande mainstem as predicted. Further, I predicted an increase of grazer/scrapers at mainstem Rio Grande sites that are downstream from reservoirs due to increased water clarity and potentially higher primary productivity. However, I did not see this association. Instead I found that grazer/scrapers were in very low abundances at downstream mainstem sites (Appendix A).

Aquatic macroinvertebrate communities can play an important role in lotic ecosystems, as a potential food source for instream and terrestrial consumers. This study shows both basin- and local-scale physiochemical conditions are important for structuring the invertebrate communities. Further, before applying metrics (e.g., EPT), influences of multiple scales need to be understood.

Literature Cited

Bane, C.A. and O.T. Lind. 1978. The benthic invertebrate standing crop and diversity of a small desert stream in the Big Bend National Park, Texas. The Southwestern Naturalist 23:215-226.

Baumgardner, D.E. and D.E. Bowles. 2005. Preliminary survey of the mayflies (Ephemeroptera) and caddisflies (Tricoptera) of Big Bend Ranch State Park and Big Bend National Park. Journal of Insect Science 5:1-13.

Boulton, A.J. 2003. Parallels and contrasts in the effects of droughts on stream macroinvertebrate assemblages. Freshwater Biology 48:1173-1185.

Carter, J.L. and V.H. Resh. 2001. After site selection and before data analysis: sampling, sorting, and laboratory procedures used in stream benthic macroinvertebrates monitoring programs by USA state agencies. Journal of the North American Benthological Society 20:658-682.

Crumpton, W.G., T.M. Isenhart, and P.D. Mitchell. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. Limnology and Oceanography 37:907-913.

Davis, J.R. 1980a. Species composition and diversity of benthic macroinvertebrates in the upper Rio Grande, Texas. The Southwestern Naturalist 25:137-150.

Davis, J.R. 1980b. Species composition and diversity of benthic macroinvertebrate populations of the Pecos River, Texas. The Southwestern Naturalist 25:241-256.

Davis, J.R. 1980c. Species composition and diversity of benthic macroinvertebrate populations of the lower Devil's River, Texas. The Southwestern Naturalist 25: 379-384.

Fore, L.S., J.R. Karr, and R.W. Wiseman. 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. Journal of the North American Benthological Society. 15(2):212-231.

Gloyd, L.K. 1958. The dragonfly fauna of the Big Bend region of Trans-Pecos Texas. Occasional Papers of the museum of Zoology, University of Michigan 593:1-23.

Hayden, G.A., J.P. Shannon, K.P. Wilson, and D.W. Blinn. 2003. Benthic community structure of the Green and Colorado Rivers through Canyonlands National Park, Utah, USA. The Southwestern Naturalist 48:23-35.

Hilsenhoff, W.L. 1981. Use of arthropods to evaluate water quality of streams. Tech. Bulletin No. 100. Department of Natural Resources. Madison, WI.

Horgan, P. 1984. Great River: The Rio Grande in North American History, 2 Vols. 4th ed. Holt Press, New York, New York.

Junk, W.J., P.B. Bayley, and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publications of Fisheries and Aquatic Sciences 106:110-127.

Lenat, D.R. 1988. Water quality assessment using a qualitative collection method for benthic macroinvertebrates. Journal of the North American Benthological Society 7:222-233.

Levings, G.W., D.F. Healy, S.F. Richey, and L.F. Carter. 1998. Water quality in the Rio Grande valley: Colorado, New Mexico, Texas, 1992-1995. U.S.Geological Survey.

Lieth, H. 1978. Primary productivity in ecosystems. Comparative analysis of global patterns. Pp 300-321 in H. Lieth (ed.). Patterns of primary production in the biosphere. Benchmark papers in ecology 8. Dowden, Hutchinson and Ross, Stroudsburg, PA.

Meffe, G.K. and W.L. Minckley. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran desert stream. The American Midland Naturalist 117:177-191.

Merritt, R.W., K.W. Cummings, and M.B. Berg (Eds). 2008. An introduction to aquatic insects of North America. 4th Edition. Kendall/Hunt Publishing Co., Dubuque, IA.

National Oceanic and Atmospheric Administration (NOAA). 2004. Monthly Station Climate Summaries, 1971-2000, Texas. Climatography of the United States No. 20. Ashville, NC.

Padilla, M. 2008. The thirsty Rio Grande: sustainable water planning along the Rio Grande in the age of global warming. Sustainable Development Law and Policy- Number VIII-2.

Smith, A., A.A. Abuzeineh, M.M. Chumchal, T.H. Bonner, and W.H. Nowlin. 2010. Mercury contamination of the Rio Grande fish community: spatial variation and influence of environmental gradients. Environmental Toxicology and Chemistry 29:1762-1772.

Stanley, E.H., D.L. Buschman, A.J. Boulton, N.B. Grimm, and S.G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. The American Midland Naturalist 131:288-300.

Thomas, M.C., P.H. Beyer, and K.H. Rogers. 2006. Variability, complexity and diversity: the geomorphology of river ecosystems in dryland regions. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Thorp, J.H. and M.D. Delong. 1994. The riverine productivity model: an heuristic view of carbon sources and organic processing in large river ecosystems. Oikos 70:305-308.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Science 37:130-137.

Wetzel, R.G. and G.E. Likens. 2000. Limnological Analyses. 3rd Edition. Springer-Verlag, New York, NY USA.

Wilson, M.V. and A. Shmida. 1984. Measuring beta diversity with presence-absence data. Journal of Ecology 72:1055-1064.

Wong, C.M., C.E. Williams, J. Pittock, U. Collier, and P. Schelle. 2007. World's top ten rivers at risk. 53 pp. World Wildlife Fund International. Gland, Switzerland.

Young, W.J. and R.T. Kingsford. 2006. Flow variability in large unregulated dryland rivers. *In* Ecology of Desert Rivers. Ed. R.T. Kingsford. Cambridge University Press. Cambridge, New York.

Table 4.1. Site names, coordinates, site type (mainstem or tributary), gauging stations, mean annual precipitation rates, and mean environmental and physiochemical variables for each study site.

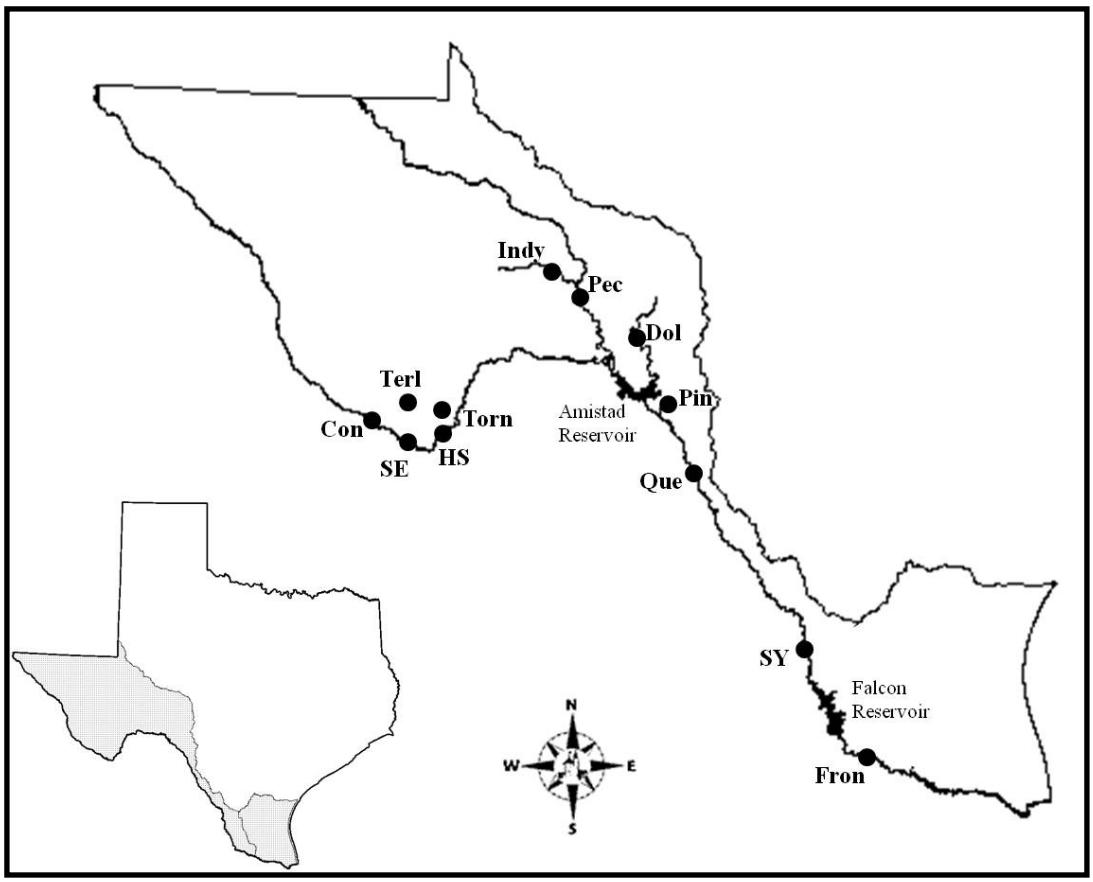

Figure 4.1. Map of Rio Grande mainstem and tributary study sites. (a) illustrates the Rio Grande along the USA and Mexico borders with the section of the river associated with our study in bold, and (b) an illustration of the study site locations. Note: site locations are abbreviated: Con = Rio Grande below confluence with Contrabando Creek, SE = Rio Grande at St. Elena Canyon, Terl = Terlingua Creek, HS = Rio Grande at Hot Springs, Torn = Tornillo Creek, Indy = Independence Creek, Pec = Pecos River, Dol = Dolan Creek, Pin = Pinto Creek, Que = Rio Grande at Quemado, SYg = Rio Grande at San Ygnacio, Fron = Rio Grande below Falcon Reservoir.

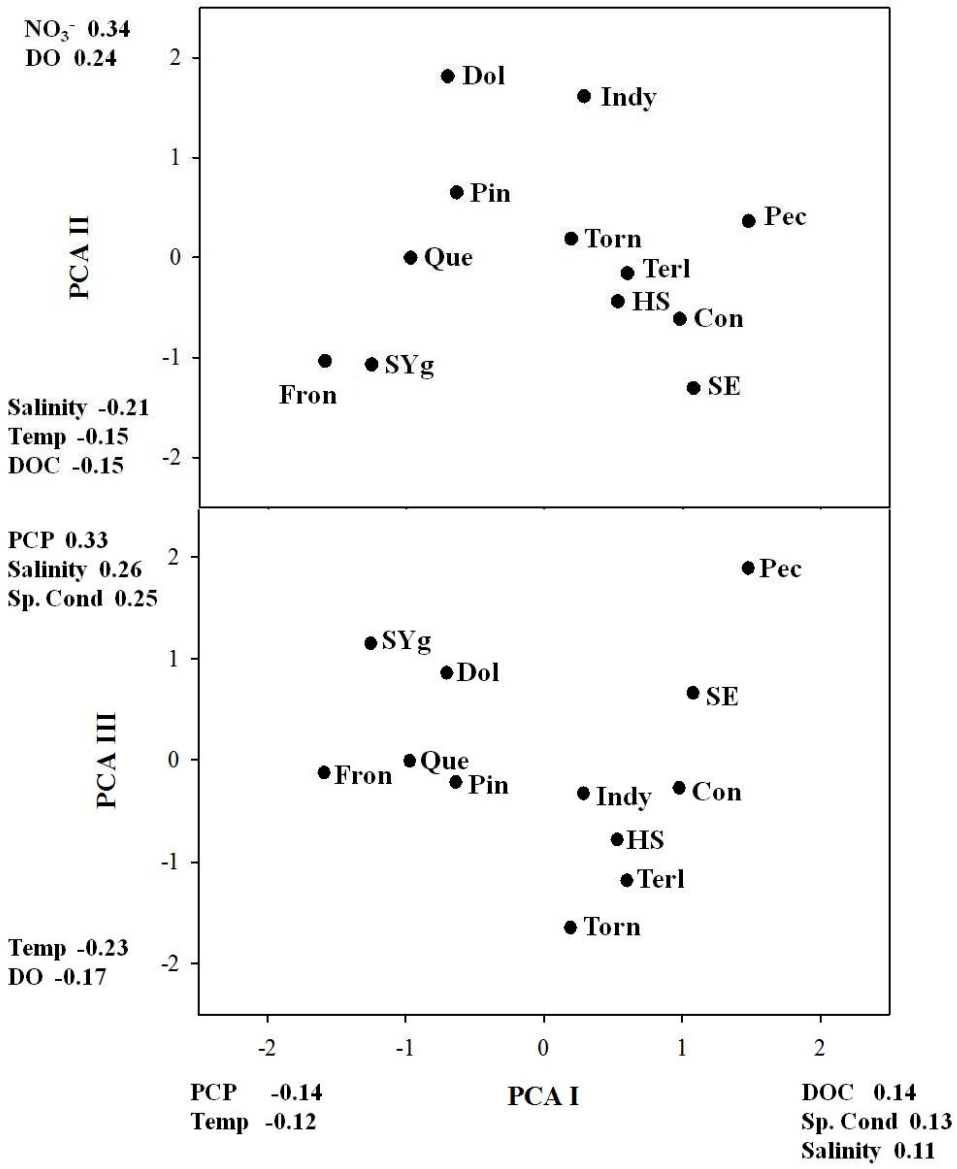

Figure 4.2. PCA results showing axes I, II, and III with each site denoted. The loadings for environmental variables are denoted. Site abbreviations are as follows: Con = Contrabando, SE = Santa Elena Canyon, HS = Hot Springs, Terl = Terlingua Creek, Torn = Tornillo Creek, Indy = Independence Creek, Pec = Pecos River, Dol = Dolan Creek, Pin = Pinto Creek, Que = Quemado, SYg = San Ygnacio, and Fron = below Falcon Reservoir.

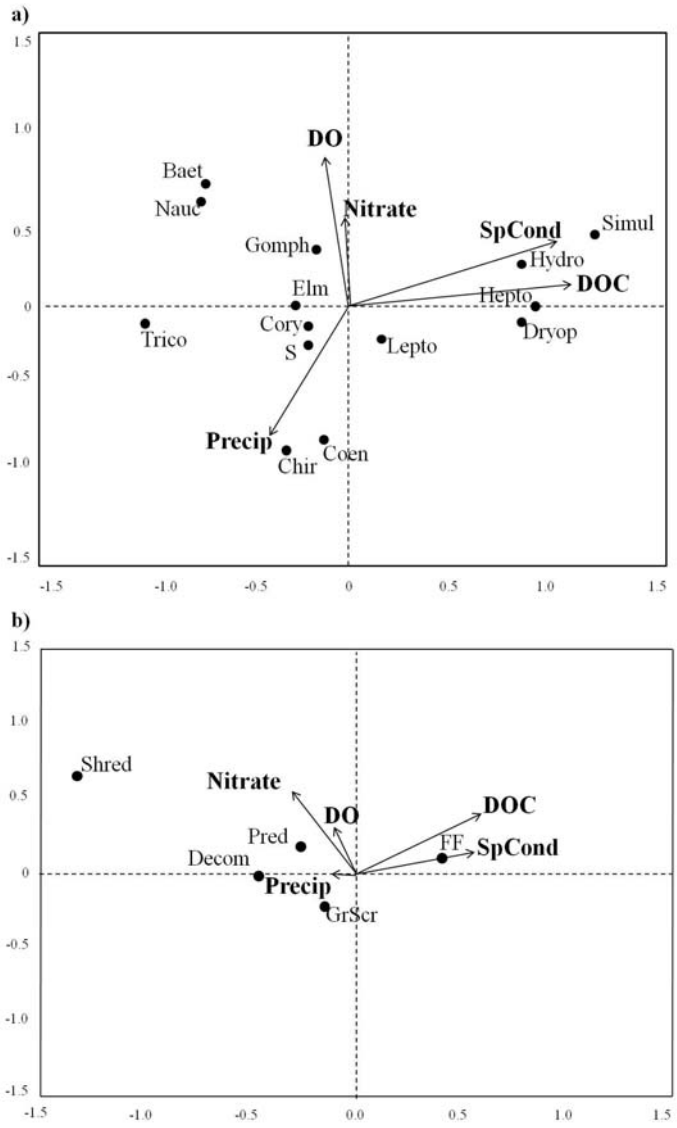

Figure 4.3. CCA results showing axes I and II for the 15 most abundant macroinvertebrate families and 5 functional feeding groups captured. Figure 3a shows the most abundant macroinvertebrate families associated with environmental variables. Environmental abbreviations are as follows: DO = dissolved oxygen, SpCond = specific conductance, DOC = dissolved organic carbon, and Precip = mean annual precipitation. Macroinvertebrate family abbreviations are as follows: Baet = Baetidae, Chir = Chironomidae, Coen = Coenagrionidae, Cory = Corydalide, Dryop = Dryopidae, Elm = Elmidae, Gomph = Gomphidae, Hepto = Heptogeniidae, Hydro = Hydropsychidae, Lepto = Leptophlebidae, Nauc = Naucoridae, Simul = Simulidae, and Tricor = Tricorythidae. Finally, taxa richness (S) is also illustrated. Figure 3b shows the most abundant functional feeding groups associated with the same environmental variables. Functional feeding group abbreviations are as follows: GrScr = grazer/scraper, Shred = shredders, Decom = decomposers, Pred = predators, and FF = filter feeders.

Appendix A

List of relative abundances (displayed as percentages) for macroinvertebrate families collected at Rio Grande mainstem sites from March 2007-October 2007. Numbers provided in parentheses are total captured individuals for the site during that study season. Note: Orders are coded: C=Coleoptera, D=Diptera, E=Ephemeroptera, H=Hemiptera, M=Megaloptera, O=Odonata, and T=Tricoptera. Classes are coded: B=Bivalvia and G=Gastropoda.

Contrabando

Winter 2007 *(31)*		Spring 2007 *(122)*		Summer 2007 *(307)*		Fall 2007 *(312)*	
Baetidae (E)	3.2	Baetidae (E)	0.8	Baetidae (E)	1.0	Baetidae (E)	5.4
Chironomidae (D)	9.7	Corixidae (H)	0.8	Chironomidae (D)	0.3	Chironomidae (D)	18.9
Corixidae (H)	3.2	Dytiscidae (C)	0.8	Coenagrionidae (O)	2.0	Coenagrionidae (O)	0.6
Corydalidae (M)	3.2	Elmidae (C)	0.8	Corydalidae (M)	2.0	Corduliidae (O)	0.3
Dryopidae (C)	6.5	Gomphidae (O)	16.3	Dryopidae (C)	8.1	Corydalidae (M)	4.5
Gerridae (H)	3.2	Hydropsychidae (T)	56.1	Gomphidae (O)	0.7	Dryopidae (C)	15.4
Heptageniidae (E)	3.2	Leptophlebidae (E)	9.8	Hydropsychidae (T)	18.9	Elmidae (C)	0.6
Hydropsychidae (T)	41.9	Naucoridae (H)	1.6	Leptophlebidae (E)	60.6	Gomphidae (O)	1.6
Leptoceridae (T)	6.5	Simulidae (D)	12.2	Limnephilidae (T)	0.3	Heptageniidae (E)	1.0
Naucoridae (H)	12.9			Naucoridae (H)	3.3	Hydropsychidae (T)	29.2
Simulidae (D)	6.5			Simulidae (D)	2.6	Leptoceridae (T)	0.3
				Tricorythidae (E)	0.3	Leptophlebidae (E)	16.3
						Naucoridae (H)	2.9
						Simulidae (D)	1.0
						Veliidae (H)	1.9

St. Elena

Winter 2007 *(133)*		Spring 2007		Summer 2007 *(62)*		Fall 2007 *(197)*	
Baetidae (E)	1.5	---		Coenagrionidae (O)	1.6	Baetidae (E)	3.0
Chironomidae (D)	14.3			Corydalidae (M)	4.8	Coenagrionidae (O)	0.5
Coenagrionidae (O)	1.5			Dryopidae (C)	8.1	Corydalidae (M)	1.5
Corydalidae (M)	3.0			Hydropsychidae (T)	58.1	Dryopidae (C)	4.6
Dryopidae (C)	21.1			Leptophlebidae (E)	21.0	Dytiscidae (C)	1.0
Heptageniidae (E)	6.0			Tabanidae (D)	1.6	Gomphidae (O)	2.5
Hydropsychidae (T)	15.0			Veliidae (H)	4.8	Hydropsychidae (T)	28.4
Leptophlebidae (E)	29.3					Leptophlebidae (E)	55.3
Naucoridae (H)	2.3					Naucoridae (H)	1.0
Simulidae (D)	5.3					Tabanidae (D)	0.5
Tabanidae (D)	0.8					Tricorythidae (E) (E)	1.5

Hot Springs

Winter 2007 *(299)*		Spring 2007 *(277)*		Summer 2007 *(85)*		Fall 2007 *(500)*	
Baetidae (E)	2.0	Baetidae (E)	3.2	Chironomidae (D)	5.9	Coenagrionidae (O)	0.6
Chironomidae (D)	11.7	Chironomidae (D)	1.1	Coenagrionidae (O)	12.9	Corydalidae (M)	1.2
Coenagrionidae (O)	0.3	Coenagrionidae (O)	1.8	Corydalidae (M)	2.4	Dryopidae (C)	2.4
Corixidae (H)	0.3	Corixidae (H)	0.4	Dryopidae (C)	52.9	Gomphidae (O)	1.0
Corydalidae (M)	0.7	Dytiscidae (C)	9.7	Gomphidae (O)	7.1	Hydropsychidae (T)	40.2
Dryopidae (C)	3.7	Elmidae (C)	0.4	Hydropsychidae (T)	8.2	Leptophlebidae (E)	52.6
Elmidae (C)	3.0	Gomphidae (O)	19.9	Leptophlebidae (E)	9.4	Simulidae (D)	2.0
Gomphidae (O)	0.7	Hydropsychidae (T)	16.2	Physidae (G)	1.2		
Heptageniidae (E)	18.7	Leptophlebidae (E)	45.5				
Hydropsychidae (T)	43.5	Naucoridae (H)	0.4				
Leptoceridae (T)	0.3	Simulidae (D)	1.4				
Leptophlebidae (E)	14.4						
Libellulidae (O)	0.7						

Quemado

Winter 2007 *(688)*		Spring 2007 *(75)*		Summer 2007		Fall 2007 *(569)*	
Baetidae (E)	7.2	Baetidae (E)	5.3	---		Baetidae (E)	23.9
Chironomidae (D)	44.1	Chironomidae (D)	21.3			Chironomidae (D)	1.2
Corydalidae (M)	0.9	Coenagrionidae (O)	2.7			Corydalidae (M)	3.3
Elmidae (C)	12.5	Corbiculidae (B) (B)	2.7			Elmidae (C)	5.6

Appendix A
Continued

Gomphidae (O)	0.1	Corydalidae (M)	1.3	Gomphidae (O)	0.4
Heptageniidae (E)	7.2	Elmidae (C)	16.0	Hydropsychidae (T)	6.5
Hydropsychidae (T)	3.7	Gomphidae (O)	1.3	Leptophlebidae (E)	41.7
Leptophlebidae (E)	1.2	Hydrophilidae (C)	2.7	Libellulidae (O)	0.4
Naucoridae (H)	3.1	Leptophlebidae (E)	26.7	Limnephillidae	0.4
Philopotamidae (T)	20.1	Libellulidae (O)	2.7	Naucoridae (H)	1.9
		Naucoridae (H)	2.7	Philopotamidae (T)	3.0
		Philopotamidae (T)	4.0	Psphenidae (C)	2.8
		Psphenidae (C)	4.0	Tabanidae (D)	0.4
		Tabanidae (D)	1.3	Tricorythidae (E) (E)	6.9
				Veliidae (H)	1.6

San Ygnacio

Winter 2007	Spring 2007	Summer 2007 *(11)*		Fall 2007	
		Baetidae (E)	27.3		
		Chironomidae (D)	18.2		
		Coenagrionidae (O)	9.1		
---	---	Elmidae (C)	9.1	---	
		Gomphidae (O)	18.2		
		Hydropsychidae (T)	9.1		
		Leptophlebidae (E)	9.1		

Below Falcon Reservoir

Winter 2007	Spring 2007	Summer 2007	Fall 2007 *(392)*	
			Baetidae (E)	8.44
			Chironomidae (D)	3.84
			Coenagrionidae (O)	12.28
			Corbiculidae (B)	1.79
			Decapoda[a]	0.26
---	---	---	Elmidae (C)	0.26
			Hydropsychidae (T)	2.30
			Leptophlebidae (E)	53.71
			Limnephilidae (T)	0.26
			Simulidae (D)	0.51
			Stratiomyidae (D)	0.26
			Tricorythidae (E)	15.86
			Veliidae (H)	0.26

[a]Crayfish are classified by their class, Decapoda, not identified to family

Appendix B

List of relative abundances (displayed as percentages) for macroinvertebrate families collected at tributary sites from October 2006-2007. Numbers provided in parentheses are total captured individuals for the site during that study season. Orders are coded: C=Coleoptera, D=Diptera, E=Ephemeroptera, H=Hemiptera, L=Lepidoptera, M=Megaloptera, O=Odonata, and T=Tricoptera. Classes are coded: B=Bivalvia and G=Gastropoda.

Terlingua Creek

Fall 2006 (*2*)		Winter 2007 (*73*)		Spring 2007 (*11*)		Summer 2007 (*129*)		Fall 2007 (*59*)	
Coenagrionidae (O)	50.0	Baetidae (E)	8.2	Baetidae (E)	18.2	Baetidae (E)	39.5	Baetidae (E)	49.2
Gomphidae (O)	50.0	Coenagrionidae (O)	54.8	Chironomidae (D)	9.1	Belastomatidae (H)	0.8	Chironomidae (D)	8.5
		Corydalidae (M)	1.4	Coenagrionidae (O)	9.1	Chironomidae (D)	11.6	Coenagrionidae (O)	8.5
		Dytiscidae (C)	11.0	Naucoridae (H)	63.6	Coenagrionidae (O)	5.4	Corduliidae (O)	1.7
		Leptophlebidae (E)	16.4			Corydalidae (M)	3.9	Corydalidae (M)	5.1
		Libellulidae (O)	1.4			Dryopidae (C)	19.4	Dryopidae (C)	3.4
		Naucoridae (H)	1.4			Dytiscidae (C)	4.7	Dytiscidae (C)	11.9
		Simulidae (D)	4.1			Gomphidae (O)	0.8	Elmidae (C)	1.7
		Tabanidae (D)	1.4			Leptophlebidae (E)	11.6	Hydropsychidae (T)	6.8
						Naucoridae (H)	0.8	Leptophlebidae (E)	1.7
						Tabanidae (D)	1.6	Tabanidae (D)	1.7

Tornillo Creek

Fall 2006		Winter 2007 (*541*)		Spring 2007 (*53*)		Summer 2007 (*40*)		Fall 2007 (*47*)	
---		Baetidae (E)	82.6	Baetidae (E)	1.9	Baetidae (E)	20.0	Baetidae (E)	68.1
		Chironomidae (D)	2.4	Chironomidae (D)	3.8	Belastomatidae (H)	5.0	Chironomidae (D)	19.1
		Coenagrionidae (O)	0.4	Dryopidae (C)	1.9	Chironomidae (D)	2.5	Dryopidae (C)	6.4
		Corixidae (H)	2.2	Dytiscidae (C)	3.8	Coenagrionidae (O)	5.0	Dytiscidae (C)	2.1
		Dryopidae (C)	0.2	Hydropsychidae (T)	1.9	Corydalidae (M)	2.5	Gomphidae (O)	4.3
		Dytiscidae (C)	0.2	Leptophlebidae (E)	1.9	Dryopidae (C)	20.0		
		Heptageniidae (E)	0.6	Naucoridae (H)	77.4	Dytiscidae (C)	32.5		
		Hydropsychidae (T)	0.4	Stratiomyidae (D)	1.9	Naucoridae (H)	5.0		
		Naucoridae (H)	7.2	Tabanidae (D)	3.8	Tabanidae (D)	5.0		
		Simulidae (D)	2.8	Veliidae (H)	1.9	Veliidae (H)	2.5		
		Stratiomyidae (D)	0.9						
		Tabanidae (D)	0.2						

Independence Creek

Fall 2006 (*239*)		Winter 2007 (*740*)		Spring 2007 (*249*)		Summer 2007 (*610*)		Fall 2007 (*908*)	
Baetidae (E)	12.1	Baetidae (E)	2.0	Baetidae (E)	8.0	Baetidae (E)	27.4	Baetidae (E)	17.3
Ceratopogonidae (D)	0.4	Chironomidae (D)	8.5	Decapoda	0.4	Belastomatidae (H)	0.8	Chironomidae (D)	2.4
Chironomidae (D)	2.1	Corbiculidae (B) (B)	0.5	Dytiscidae (C)	1.2	Chironomidae (D)	4.3	Coenagrionidae (O)	1.3
Coenagrionidae (O)	0.8	Corydalidae (M)	1.4	Elmidae (C)	5.6	Coenagrionidae (O)	1.0	Corduliidae (O)	0.1
Corbiculidae (B)	0.0	Elmidae (C)	12.0	Gammaridae (A)	14.9	Corbiculidae (B)	0.2	Corydalidae (M)	5.6
Corydalidae (M)	2.9	Gammaridae (A)	3.4	Gomphidae (O)	0.8	Corydalidae (M)	3.3	Decapoda[a]	0.1
Elmidae (C)	13.8	Gomphidae (O)	3.4	Heptageniidae (E)	1.2	Decapoda[a]	0.2	Elmidae (C)	10.1
Gammaridae (A)	1.7	Heptageniidae (E)	1.2	Hyalellidae (A)	2.0	Dytiscidae (C)	0.7	Gammaridae (A)	5.7
Gomphidae (O)	1.7	Hyalellidae (A)	1.2	Hydropsychidae (T)	12.9	Elmidae (C)	12.0	Gomphidae (O)	5.0
Hyalellidae (A)	3.3	Hydropsychidae (T)	15.9	Libellulidae (O)	0.8	Gammaridae (A)	6.4	Hydropsychidae (T)	4.4
Hydropsychidae (T)	8.4	Libellulidae (O)	1.1	Naucoridae (H)	16.1	Hydropsychidae (T)	5.1	Leptophlebidae (E)	21.0
Hydroptilidae (T)	0.8	Leptoceridae (T)	0.8	Physidae (G)	0.4	Leptophlebidae (E)	14.3	Libellulidae (O)	2.1
Leptophlebidae (E)	7.9	Leptophlebidae (E)	2.8	Psphenidae (C)	24.9	Libellulidae (O)	1.3	Limnephilidae (T)	0.2
Libellulidae (O)	2.9	Naucoridae (H)	14.6	Simulidae (D)	0.4	Limnephilidae (T)	0.5	Naucoridae (H)	4.5
Naucoridae (H)	14.2	Planorbidae (G)	2.7	Stratiomyidae (D)	1.6	MacroVeliidae (H)	3.0	Philopotamidae (T)	1.3
Physidae (G)	1.7	Psphenidae (C)	17.7	Thiaridae (G)	8.4	Naucoridae (H)	14.6	Psphenidae (C)	1.0
Planorbidae (G)	2.1	Simulidae (D)	1.4	Veliidae (H)	0.4	Nepidae (H)	0.2	Simulidae (D)	0.3
Pleuroceridae (G)	10.5	Stratiomyidae (D)	1.2			Philopotamidae (T)	0.3	Tabanidae (D)	5.5
Psephenidae (C)	1.7	Tabanidae (D)	1.8			Psphenidae (C)	0.7	Thiaridae (G)	0.8

Appendix B
Continued

Stratiomyidae (D)	1.7	Thiaridae (G)	2.4			Simulidae (D)	0.8	Tricorythidae (E)	11.0
Tabanidae (D)	2.1	Tipulidae (D)	0.3			Stratiomyidae (D)	0.5	Veliidae (H)	0.1
Tipulidae (D)	0.4	Tricorythidae (E)	3.6			Tabanidae (D)	2.6		
Tricorythidae (E)	6.7					Tricorythidae (E)	0.2		

Pecos River

Fall 2006 (*57*)		Winter 2007 (*1380*)		Spring 2007 (*650*)		Summer 2007 (*523*)		Fall 2007 (*583*)	
Baetidae (E)	1.8	Aeshnidae (O)	0.1	Baetidae (E)	11.2	Baetidae (E)	1.1	Baetidae (E)	0.3
Belastomatidae (H)	14.0	Baetidae (E)	1.9	Belastomatidae (H)	0.2	Chironomidae (D)	0.2	Chironomidae (D)	2.1
Coenagrionidae (O)	10.5	Chironomidae (D)	1.4	Chironomidae (D)	1.1	Coenagrionidae (O)	1.1	Coenagrionidae (O)	1.2
Corydalidae (M)	3.5	Coenagrionidae (O)	0.3	Coenagrionidae (O)	2.2	Corydalidae (M)	1.3	Corydalidae (M)	9.3
Gomphidae (O)	1.8	Corduliidae (O)	0.1	Elmidae (C)	7.5	Corbiculidae (B)	0.0	Elmidae (C)	7.2
Leptophlebidae (E)	59.6	Corydalidae (M)	0.7	Gammaridae (A)	0.3	Corduliidae (O)	0.0	Gomphidae (O)	0.7
Naucoridae (H)	1.8	Elmidae (C)	8.0	Hydropsychidae (T)	45.5	Dytiscidae (C)	0.2	Hydropsychidae (T)	49.7
Physidae (G)	5.3	Heptageniidae (E)	14.3	Leptophlebidae (E)	27.7	Elmidae (C)	3.3	Leptophlebidae (E)	25.2
Tabanidae (D)	1.8	Hydropsychidae (T)	25.7	Naucoridae (H)	2.6	Hydropsychidae (T)	28.9	Naucoridae (H)	2.6
		Leptophlebidae (E)	13.7	Psphenidae (C)	0.6	Leptophlebidae (E)	6.1	Psphenidae (C)	0.2
		Naucoridae (H)	1.4	Simulidae (D)	0.2	Naucoridae (H)	4.0	Tabanidae (D)	0.5
		Philopotamidae (T)	4.5	Tabanidae (D)	0.5	Psphenidae (C)	0.2	Tricorythidae (E)	0.5
		Physidae (G)	2.5	Veliidae (H)	0.5	Simulidae (D)	42.4	Veliidae (H)	0.5
		Polycentropodidae	0.2			Tabanidae (D)	0.8		
		Simulidae (D)	24.1			Veliidae (H)	10.3		
		Stratiomyidae (D)	0.9						
		Tabanidae (D)	0.2						
		Tricorythidae (E)	0.1						

Dolan Creek

Fall 2006 (*123*)		Winter 2007 (*74*)		Spring 2007 (*116*)		Summer 2007 (*106*)		Fall 2007 (*73*)	
Baetidae (E)	11.4	Aeshnidae	2.7	Baetidae (E)	5.2	Baetidae (E)	24.5	Baetidae (E)	4.1
Coenagrionidae (O)	3.3	Baetidae (E)	1.4	Chironomidae (D)	10.3	Chironomidae (D)	3.8	Chironomidae (D)	8.2
Corbiculidae (B)	0.8	Chironomidae (D)	20.3	Corbiculidae (B)	1.7	Coenagrionidae (O)	2.8	Coenagrionidae (O)	1.4
Corydalidae (M)	1.6	Corbiculidae (B)	2.7	Corydalidae (M)	46.6	Corduliidae (O)	1.9	Corydalidae (M)	1.4
Gomphidae (O)	4.9	Corydalidae (M)	5.4	Decapoda[a]	0.9	Elmidae (C)	11.3	Elmidae (C)	2.7
Heliocopsychidae (T)	0.8	Dytiscidae (C)	1.4	Elmidae (C)	1.7	Hydropsychidae (T)	11.3	Gomphidae (O)	1.4
Hyalellidae (A)	30.9	Elmidae (C)	13.5	Gerridae (H)	0.9	Leptophlebidae (E)	1.9	Heptageniidae (E)	2.7
Hydropsychidae (T)	0.8	Gomphidae (O)	2.7	Glossosomatidae	0.9	Libellulidae (O)	0.9	Hyalellidae (A)	8.2
Leptoceridae (T)	3.3	Heptageniidae (E)	2.7	Hydropsychidae (T)	2.6	Naucoridae (H)	3.8	Hydropsychidae (T)	1.4
Libelullidae (C)	1.6	Libellulidae (O)	4.1	Leptophlebidae (E)	5.2	Philopotamidae (T)	32.1	Leptophlebidae (E)	8.2
Physidae (G)	2.4	Melanoides	1.4	Naucoridae (H)	12.9	Psphenidae (C)	0.9	Naucoridae (H)	5.5
Planorbidae (G)	20.7	Naucoridae (H)	31.1	Psphenidae (C)	2.6	Tricorythidae (E)	4.7	Philopotamidae (T)	2.7
Polycentropodidae (T)	2.4	Polycentropodidae	6.8	Simulidae (D)	8.6	Baetidae (E)	24.5	Psphenidae (C)	1.4
Psephenidae (C)	8.9	Tabanidae (D)	4.1					Tricorythidae (E)	46.6
Pyralidae (L)	2.4							Veliidae (H)	4.1
Thiaridae (G)	1.6								

Pinto Creek

Fall 2006 (*41*)		Winter 2007 (*126*)		Spring 2007 (*57*)		Summer 2007 (*502*)		Fall 2007 (*346*)	
Baetidae (E)	7.3	Baetidae (E)	4.8	Chironomidae (D)	3.5	Baetidae (E)	2.6	Baetidae (E)	4.3
Caenidae	2.4	Chironomidae (D)	4.8	Coenagrionidae (O)	36.8	Chironomidae (D)	4.6	Chironomidae (D)	2.0
Chironomidae (D)	26.8	Coenagrionidae (O)	21.4	Decapoda	1.8	Coenagrionidae (O)	9.2	Coenagrionidae (O)	4.9
Coenagrionidae (O)	9.8	Corduliidae (O)	5.6	Gomphidae (O)	3.5	Corydalidae (M)	1.2	Corduliidae (O)	0.3
Corbiculidae (B) (B)	4.9	Philopotamidae (T)	49.2	Hydropsychidae (T)	5.3	Elmidae (C)	9.6	Corydalidae (M)	0.3
Heptageniidae (E)	2.4	Simulidae (D)	3.2	Leptoceridae (T)	1.8	Gomphidae (O)	0.2	Elmidae (C)	3.2
Hydrophilidae (C)	2.4	Stratiomyidae (D)	9.5	Libellulidae (O)	1.8	Hydropsychidae (T)	3.8	Hydropsychidae (T)	5.2
Leptophlebiidae	12.2	Tabanidae (D)	0.8	Naucoridae (H)	1.8	Leptophlebidae (E)	12.9	Leptophlebidae (E)	51.7
Philopotamidae (T)	12.2	Tricorythidae (E)	0.8	Philopotamidae (T)	36.8	Libellulidae (O)	0.8	Libellulidae (O)	1.2
Physidae (G)	14.6			Simulidae (D)	1.8	Naucoridae (H)	0.2	Naucoridae (H)	3.8
Tabanidae (D)	4.9			Stratiomyidae (D)	5.3	Philopotamidae (T)	53.8	Philopotamidae (T)	21.1
						Simulidae (D)	0.6	Simulidae (D)	1.7
						Tabanidae (D)	0.6	Veliidae (H)	0.3

[a]Crayfish are classified by their class, Decapoda, not identified to family

CHAPTER V

TRANSFER OF MERCURY ACROSS ECOSYSTEM BOUNDARIES IN ARID STREAMS

Introduction

Environmental mercury (Hg) contamination represents a substantial concern for both humans and wildlife. Humans have greatly altered the global Hg cycle by releasing Hg via coal-fired power plants, mining, and industrial activities; approximately two-thirds of current global Hg emissions are from human activities (Harris et al. 2007). Mercury released from anthropogenic sources is predominantly inorganic Hg (II) and a portion of these emissions is deposited into aquatic ecosystems where it is converted to highly toxic methylmercury (MeHg) by bacteria (Ullrich et al. 2001). Methylmercury, a potent teratogen and neurotoxin, is of great concern because even at reasonably low concentrations, it can affect neurological function, behavior, hormone production, morphological development, fecundity, immune responses, and cardiac function in humans and wildlife (Mergler et al. 2007, Schuehammer et al. 2007, Hawkley et al. 2009).

Mercury in aquatic ecosystems is a substantial issue because inorganic Hg is for the most part converted to MeHg within these systems. In contrast to inorganic Hg, MeHg is readily absorbed by algae and bacteria and is retained within cells (Hall et al.

1998, Morel et al. 1998). Consumption of MeHg contaminated food items is the main pathway for uptake by higher-level organisms and MeHg is typically ingested at a faster rate than eliminated, leading to bioaccumulation and biomagnification (Harris et al. 2007). Thus, upper trophic level aquatic and terrestrial consumers (e.g., piscivores and insectivores) that utilize aquatic food sources can have high tissue Hg concentrations in contaminated areas (Harris et al. 2007, Mergler et al. 2007, Scheuhammer et al. 2007).

Stream and river ecosystems are intimately connected to adjacent terrestrial habitats through the exchange of organic matter, nutrients, and organisms. Traditionally, it was thought that the dominant directionality of the movement of inorganic and organic matter (OM) was from terrestrial to stream habitats (e.g., Likens and Bormann 1974, Vannote et al. 1980); however, there has been a recent focus on the importance of aquatic-derived resources for adjacent riparian terrestrial habitats (Baxter et al. 2005). The reliance on aquatic-derived resources may be particularly relevant in arid landscapes because perennially-flowing rivers and streams can have relatively high *in situ* productivity; whereas, the productivity of the adjacent arid terrestrial environments is comparatively low (Fisher 2006, Sanzone et al. 2003). Thus, it can be predicted that terrestrial systems in arid environments will contribute little terrestrially-derived OM to streams, but the higher productivity of streams will lead to OM "spill out" to the surrounding terrestrial landscape, providing an allochthonously-derived resource subsidy to riparian consumers (i.e. insectivorous bats, birds, lizards, and spiders) in the form of emerging insects (Schade and Fisher 1997, Sabo and Power 2002, Sanzone et al. 2003, Baxter et al. 2005).

Ecotoxicologists and environmental scientists have recently expanded the concept of cross-ecosystem resource subsidies to include the transfer of bioaccumulating contaminants (Vander Zanden and Sanzone 2004). Indeed, emergent aquatic insects can play a key role in the transfer of aquatically-derived contaminants to terrestrial consumers in riparian zones (e.g., Cristol et al. 2008, Walters et al. 2010). Cristol et al. (2008) found several bird species which derive their diets primarily from aquatic sources, including emergent aquatic insects at an Hg-contaminated stream exhibited elevated levels of tissue Hg. Furthermore, studies by Cristol et al. (2008) and Walters et al. (2008 and 2010), which examined the movement of Hg and PCBs from aquatic habitats to riparian consumers, respectively, suggest that birds which derive a substantial portion of their diets from consuming riparian terrestrial spiders are at an elevated risk of contaminant exposure due to the bioaccumulation and biomagnification of these contaminants. Based upon results of these studies and the importance of aquatic-derived resources for riparian consumers in arid landscapes, I predicted that emergent aquatic organisms function as "biotransporters" of Hg, leading to contamination in terrestrial riparian consumers. However, most studies which have examined the transfer of contaminants from aquatic to terrestrial food webs have been largely conducted in more mesic environments, and this prediction remains unexamined for arid landscapes where aquatic resource subsidies to terrestrial consumers can be relatively important.

The purpose of this study was to assess patterns in the potential movement of Hg from streams to riparian consumers in an arid landscape. This study was conducted in three streams located in the arid landscape of the Big Bend and Trans-Pecos regions of west Texas. Two of the streams are located in Big Bend reach of the drainage and are

thought to experience relatively low atmospheric Hg deposition rates (Selin and Jacob 2008). However, some portions of the Big Bend area have substantial geological Hg sources and a history of Hg mining (Gray et al. 2006). Subsequently, streams and rivers in these locations have portions of the aquatic food web (sediments and fish) which exhibit elevated Hg concentrations when compared to other portions of the lower Rio Grande drainage in Texas (Schmitt et al. 2006, Smith et al. 2010). A third stream site lies within the Big Bend - Trans Pecos region, but does not have substantial geologic sources of Hg and no history of Hg mining in the area, and in general exhibits significantly lower Hg concentrations in sediments and fish than streams located within the Big Bend reach (Smith et al. 2010). Elevated Hg in portions of the aquatic food webs are of concern because the Rio Grande drainage contains multiple federally- and state-listed fish, bird, and mammal taxa and is considered one of the world's most at-risk rivers (Wong et al. 2007). Furthermore, understanding the potential exchange of Hg between riverine and terrestrial habitats along this river system is critical because several studies have also indicated that several terrestrial species may utilize the riparian areas (Powell 1983, Mora et al. 2006, Cristol 2008). The objectives of this study were (1) to examine Hg concentrations in portions of the aquatic food web (invertebrates and fish) in three tributaries in the Lower Rio Grande drainage in west Texas which potentially vary in Hg contamination, (2) to determine potential cross-ecosystem fluxes of Hg between streams and the adjacent terrestrial riparian systems, (3) to examine Hg contamination of several groups of terrestrial consumers (birds, bats, and terrestrial arthropods) that inhabit or utilize riparian zones at the study stream reaches, and (4) compare patterns of Hg concentrations among aquatic and terrestrial consumers . I hypothesize that Hg

concentrations in terrestrial consumers will mirror concentrations in fishes and aquatic macroinvertebrates at each given sites, resulting in higher Hg concentrations in fishes and aquatic macroinvertebrates will have terrestrial consumers with relatively higher Hg concentrations. However, I additionally hypothesize that Hg concentrations of terrestrial consumers will depend upon the feeding ecology, migratory behavior, and the degree to which the consumer group utilizes aquatic-derived resources.

Methods

Study sites

The present study was conducted in July and October - November, 2008. For this study, I consider one stream a "low Hg" location and two stream reaches in the Big Bend area as the "high Hg" sites. All sites are first order spring-flow dominated streams which exhibit perennial flows. The "low Hg" site is located at the Independence Creek Preserve (owned by the Nature Conservancy; 30°27'55.69" N, 101°49'33.06W). Independence Creek has minimal direct anthropogenic impact and is considered relatively undisturbed. The two "high Hg" sites are located within Big Bend National Park (BBNP; Terlingua Creek: 29°10'02.43" N, 103°36'44.60" W; Tornillo Creek: 29°10'37.33" N, 103°00'02.95" W). Both sites are currently subjected to minimal direct human impact; however, Terlingua and Tornillo Creeks are located within drainages that were historically mined for Hg. Cinnabar mining occurred in this region from the late 1800s until the mid-1900s accounting for ~25% of the United States Hg production (Blanton et al. 1975). Several inactive mines located within and in the vicinity of BBNP may serve as sources of Hg to surface- and groundwater (Gray et al. 2006).

Stream sample collection

Samples were collected from fish and macroinvertebrates for Hg and nitrogen (N) and carbon (C) stable isotope analyses in July and October 2008 at Independence Creek, and July and November 2008 at the two BBNP streams. For each stream, we sampled the same ~100 m reach section on both sampling dates. Within each read, fish were collected via kick or pull seining, anesthetized with MS-222, and placed in 70% ethanol (EtOH). Preservation of fish in EtOH has no effect on $\delta^{15}N$ values (Kelly et al. 2006) or Hg concentrations (Hill et al. 2010). Aquatic macroinvertebrates were collected from each stream reach using kick nets and Hess samplers from riffle habitats and dip nets from shallow pools and edge habitats (Carter and Resh 2001). Invertebrates were placed in stream water for 1-2 h to evacuate guts and then preserved in 70% EtOH. Fish and invertebrate samples were transported to the laboratory at Texas State University-San Marcos and organisms were taxonomically identified before processing for Hg and stable isotope analysis.

In the lab, fish were identified to species (Thomas et al. 2007, Hubbs et al. 2008) and individual fish (or a grouping of small similar-sized fish of the same species and from the same collection period and site) had apaxial muscle or fillets removed with a clean scalpel (ensuring no skin or scales were attached) and tissue was dried at 60°C for 48 h. Samples were homogenized using a clean mortar and pestle (rinsed thoroughly with DI water and acetone between samples) until they were a flour-like consistency. Macroinvertebrates were sorted and identified typically to family and processed in a similar fashion to fish; however, whole macroinvertebrate bodies were dried and homogenized, with the exception of larger macroinvertebrates, which had guts removed

prior to drying, and gastropods and bivalves, which only foot tissue was removed for analysis (Post 2002). If invertebrates within a taxonomic group were not numerous enough for Hg and isotopic analyses, individuals were combined with others from a closely related taxon within the family or order (Merritt and Cummins 2008).

Bird and bat sampling and THg analysis

Because we were interested in examining the potential movement of Hg from aquatic to terrestrial systems, we examined Hg concentrations of terrestrial consumers which may utilize aquatic-based resources. We focused on collecting samples from bats and birds within and adjacent to riparian areas. Bats were mist netted (38 mm mesh aperture, 2.6 x 6 m and 2.6 x 12 m nets; Avinet, Inc.) for 2-4 consecutive nights at two sites within riparian areas and directly over or near stream sites at BBNP (July and November 2008) and Independence Creek (July and October 2008, and March 2009). Mist nets were deployed prior to sunset and remained up until bat activity subsided. Captured bats were identified to species, sex and approximate age (juvenile or adult) was determined, and classified by functional feeding group (Schmidly 2004). I clipped a small amount of fur (Hickey et al. 2001) from the mid-ventral region of the body. This hair represents the Hg exposure of an individual bat since the time of the last molt. Migration and foraging behavior are variable among bat species and most typically molt annually (Schmidly and Davis 2004). These physiological and behavioral differences were taken into account for the bats captured for this study. All bats were immediately released after fur was removed. Individual fur samples were kept separate in clean plastic bags and at room temperature until Hg analysis.

Riparian zone-associated birds were captured using mist nets of the same size and dimensions as those used for bats during the same sampling periods. Nets were set in approximately the same locations as the bat nets around 1 hour prior to sunrise for 2-4 consecutive days. All captured birds were identified to species, sex, and age (i.e., juvenile or adult). The functional feeding group of each species was determined as was the migratory status of the species in the location (i.e., year-round resident versus migratory; Poole 2011). Breast feathers were collected from each captured individual according to Burger and Eichhorst (2007). Mercury concentrations in breast feathers represent uptake of Hg in diet prior to molting and is a result of long-term exposure (Burger 1993, Evers et al. 2008). Furthermore, the mercury in migrant bird feathers likely reflects uptake in areas other than our study locations. However, Hg levels in feathers of resident birds do represent dietary Hg ingested at those study sites. All birds were released immediately after feathers were removed. Individual feather samples were kept separate in clean plastic bags and at room temperature until Hg analysis.

We supplemented the samples we collected as a part of this project by obtaining additional breast and wing feathers from individual birds in the collections of Dr. Miguel Mora (Department of Wildlife and Fisheries Sciences, Texas A&M) and Raymond Skiles of BBNP. These additional samples were obtained in order to increase sample sizes used for analyses. Feathers from 8 *Sayornis nigricans* (Black Phoebe, resident species), 4 *Sayornis saya* (Say's Phoebe, resident species), 6 *Stelgidopteryx serripennis* (Rough-winged Swallow, resident species), and 9 *Petrochelidon pyrrhonota* (Cliff Swallow, migrant species), were collected by Miguel Mora from individuals at Mariscal Canyon in BBNP, approximately 27 km from the sites we sampled (Mora et al. 2002). Big Bend

National Park staff provided feathers of 3 *Bubo virginianus* (Great-horned Owl), 1 *Athene cunicularia* (Burrowing Owl), and 1*Buteo jamaicensis* (Red-tailed Hawk) all collected inside the park and kept frozen. After collection of feather samples from these birds, feathers were kept in plastic bags at room temperature until Hg analysis.

Riparian arthropod collection and THg analysis

Terrestrial arthropods were collected at each site using standard sampling techniques twice (months) at each site (Coddington et al. 1996, Sanzone 2001, Sanzone et al. 2003). We collected arthropods with plastic pitfall traps (~0.3 L total volume) filled to ~20 mL with a dilute soapy water solution. At each of the three study stream reaches, pitfall traps were established along 2 transects which ran perpendicular to the stream. Pitfall traps were placed, in triplicate at 10 m, 20 m, 30 m, 40, and 50 m from the wetted channel along a transects. A final set of pitfall traps were placed at 75 m at the end of each transect (exception: one transect in summer and fall 2008 at Tornillo Creek). Pitfall traps were left open for checked every 24 h over a 48 h period, and all arthropods were removed. Collected arthropods were separated by location on transect, site, and season and preserved in 70% EtOH. In the lab, arthropods were identified to family, and dried at 60°C for 48 hours. Dried samples were stored in glass vials at room temperature until Hg analysis.

Mercury analysis

Fish muscle and aquatic macroinvertebrate tissue samples were analyzed for total Hg (THg) concentration. Any fish and aquatic macroinvertebrates that were analyzed for Hg were also analyzed for stable isotopes (see below). Total Hg concentration of dried and homogenized tissue samples was measured with a Milestone DMA-80 Direct

Mercury Analyzer (Monroe, Connecticut), which uses thermal decomposition, gold amalgamation, and atomic absorption spectrometry (USEPA 1998). In fish, most of the THg (≥ 90%) in muscle is MeHg; therefore, THg in fish muscle is a reliable estimate of the amount of bioaccumulative Hg in an individual (Bloom 1992, Weiner et al. 2003, Paller and Littrell 2007). In contrast, in aquatic macroinvertebrates, tissue MeHg:THg in whole body tissue samples is considerably more variable, but MeHg accounts for a majority of the THg (56-100%) (Chumchal et al. 2011). Mercury concentration of terrestrial arthropods, bat hair, and bird feathers were also measured as THg with direct mercury analysis (Milestone DMA-80, Monroe, Connecticut; USEPA 1998).

For all analyses we included reference materials (marine sediment: MESS-3 or *Squalus spp*, dogfish liver: DOLT-4) every 10^{th} sample and duplicate samples every 20^{th} sample for quality assurance. The mean percent recovery for reference materials was 100 ± 5% (range = 92 - 108%, $n = 21$) and 102 ± 6% (range= 92 - 106%, $n = 6$) for MESS-3 and DOLT-4 reference materials, respectively. The mean percent difference in duplicate samples was 16.15% (range = 0.88 - 47.24, $n = 14$). Fish samples were analyzed dry, but THg concentrations were converted to THg concentration in wet tissues, by assuming 79% of mass is lost from fish tissues during drying (Chumchal 2007). Aquatic macroinvertebrate THg concentrations were kept as μg THg·kg^{-1} dry weight. All terrestrial arthropod, bat hair, and bird feather THg concentrations are reported in μg THg·kg^{-1} dry weight.

Stable isotope analysis

I wanted to examine whether Hg concentrations differed between trophically similar fishes at the High Hg and Low Hg sites. In addition, the fish community species

composition can differ substantially between the two study site areas (Big Bend versus Independence Creek) limiting our ability to compare Hg in the same fish species between the High and Low Hg sites. The use of stable isotopes permits comparison of Hg concentration in fishes from different sites that are within the same trophic level, regardless of species identity. Stable isotope analyses were conducted at the UC Davis Stable Isotope Facility. Fish and aquatic macroinvertebrate samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios of ^{13}C and ^{15}N in samples was determined with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Fish and aquatic macroinvertebrate trophic position was determined using $\delta^{15}N$ isotopic values. In order to estimate the trophic position of consumers in the aquatic food web, each season, I used a modification of the method similar to Anderson and Cabana (2007) by using a site-specific consumer with the lowest $\delta^{15}N$. The site-specific baseline consumer for each stream has its trophic position set at 2, and I then estimated upper consumer trophic positions in that food web using the equation

$$\text{Trophic position}_{\text{Consumer}} = ([\ \delta^{15}N_{\ \text{Consumer}} - \ \delta^{15}N_{\text{Baseline}}]/f) + 2$$

where $\delta^{15}N_{\ \text{Consumer}}$ is the value for the consumer in which the trophic position (TP) is being estimated and, $\delta^{15}N_{\text{Baseline}}$ is the value for the baseline organism in that food web, f is the $\delta^{15}N$ fractionation between a consumer and its food item (an assumed 3.4‰ enrichment per trophic level) (Post 2002), and 2 as the expected trophic position of the food web baseline consumer. Psphenidae had the lowest $\delta^{15}N$ at Independence Creek in both July and October 2008 and was set as the baseline consumer. At Terlingua and Tornillo Creeks, Dryopidae was the baseline consumer in July 2008. Gomphidae was the

baseline consumer at Terlingua Creek and Coenagrionidae was the baseline in November 2008. Trophic positions 2.0-2.99 were considered trophic level (TL) 2, while TP 3.0-3.99 were TL 3, and TP 4.0-4.99 were TL 4.

Data analysis

Mercury concentrations of fish in different trophic levels, aquatic macroinvertebrates, and terrestrial consumers (birds, bats and arthropods) were compared among the "low Hg" and "high Hg" sites. Because the design of the study was unequal (i.e,, one low Hg site and two high Hg sites) and I sometimes collected low numbers of some organisms from the "high Hg" sites, I combined fish data from Terlingua and Tornillo Creeks; THg concentrations in fishes at these sites were not significantly different (Students t-test: $t = -1.58$, $P = 0.14$). I additionally, combined data for aquatic macroinvertebrates at Terlingua and Tornillo Creeks. Thus, for these analyses, we compared Hg concentrations of in-stream organisms using the combined data sets from both "high Hg" sites to the "low Hg" site.

Two-way ANOVA was used to examine the main effect of location (two levels: high versus low Hg site) and sampling season (two levels: summer versus early fall sampling) and the interaction of these factors on fish and aquatic macroinvertebrate THg concentrations. Separate 2-way ANOVs were used to compare Hg concentration in fishes within different trophic levels (TL; determined from $\delta^{15}N$ analyses) between the high and low Hg sites. However, fish Hg within TL 2 was not compared between the sites because TL 2 fish were only captured at the low Hg site. Aquatic macroinvertebrates, within TL 2 were compared among study sites because

macroinvertebrates classified within TL 2 were the only trophic grouping found at both sites on all sampling dates.

Mercury concentrations of bats and birds were compared among and within high and low Hg sites with Student's t-tests. For bats, I compared Hg concentrations found within the hair of the various species across the two study locations using Student's t-tests. For birds, I used a combination of t-tests and one-way and two-way ANOVAs to compare functional feeding groups within and among "high" and "low" Hg sites and migratory status (resident or migrant). If the results from a one-way ANOVA were significant, subsets were compared using a post-hoc Tukey's honestly significant difference (HSD) test.

I combined results for terrestrial arthropods from Terlingua and Tornillo Creeks to represent the "high Hg" location. Additionally, because samples sizes in Fall 2008 from BBNP were relatively small, I compared distances from stream channel Hg concentrations in summer 2008 using a one-way ANOVA (i.e. 10 m, 20 m, 30 m, 40 m, 50 m, 75 m). However, I was able to compare distances from stream channel Hg concentrations in terrestrial arthropods in both seasons (summer and fall 2008) at the "low Hg" site using one-way ANOVAs. Further, I compared Hg concentrations between "high Hg" and "low Hg" sites. Prior to the between site comparison, I compared seasons (summer and fall 2008) at the "low Hg" site with a two sample t-test and found no significant difference ($t = 0.59$, $P = 0.56$), thus I combined families from both seasons. Finally, I compared the two most abundant invertivores captured, Lycosidae (wolf spiders) and Carabidae (ground beetles) between the "high" and "low" Hg sites using a two-way ANOVA. As with bat hair and bird feather comparisons, if results from the

one-way ANOVAs were significant, a post-hoc Tukey's honestly significant difference test was conducted on the subsets.

For all the above comparisons, I tested for normality (Shapiro and Wilk 1965) and homoscedasticity. If data was not normally distributed and homoscedastic, it was $\log_{10}$ transformed. Significance was inferred for all tests if p-values were less than α (set at $p \leq 0.05$). All statistical analyses were performed in PAST statistical software, version 2.02 (Hammer et al. 2001).

Results

Mercury of aquatic communities

There were several fish species which occurred at "high Hg" and "low Hg" sites that differed significantly in tissue Hg concentrations (Table 1, Fig. 1a). Across sites, fish TL ranged from 2.0 to 4.67 (Table 1, Fig. 1a). Fish captured at all study streams were small-bodied and predominantly herbivorous/invertivorous with total body lengths typically ≤ 70 mm. The three dominant species captured at the "low Hg" site were *Notropis amabilis* (Texas shiner), *Pimephales vigilax* (bullhead minnow), and *Gambusia affinis* (western mosquitofish). With study seasons combined, relative abundances of Texas shiner, bullhead minnow, and western mosquitofish were 35%, 28%, and 16%, respectively. Further, at the "high Hg" site, with seasons combined, the most dominant species captured were *Notropis braytoni* (Tamaulipas shiner), *Cyprinella lutrensis* (red shiner), and *Fundulus zebrinus* (plains killifish; relative abundances of 33%, 13%, and 12%, respectively). There was not a significant effect of season on THg concentrations ($F_{1,36} = 0.02$, $P = 0.90$); however, fishes at the "high Hg" site were significantly higher in

Hg concentrations than at the "low Hg" site ($F_{1,36} = 32.08$, $P < 0.0001$). Further, when I compared TL across sites, I found there was a significant difference between sites for TLs 3 and 4 (TL3: $t = 7.88$, $P < 0.0001$; TL4: $t = 6.27$, $P < 0.0001$; Fig. 1a); TL 3 fish captured at the "high Hg" site had Hg concentrations ~2X higher than those captured at Independence Creek (95.75 ± 5.53 μg Hg·kg^{-1} vs. 32.75 ± 15.13 μg Hg·kg^{-1}). Additionally, trophic level 4 fish at the "high Hg" site had Hg concentrations ~4X greater than those at "low Hg" site (166.44 ± 70.01 μg Hg·kg^{-1} vs. 37.37 ± 20.63 μg Hg·kg^{-1}).

Aquatic macroinvertebrate family abundances and THg concentrations varied across study stream sites as well (Table 1, Fig. 1b). Total captures of macroinvertebrates were more abundant at Independence Creek than BBNP (456 vs. 75 individuals, respectively). The most abundant orders captured at the "low Hg" site were Ephemeroptera (40%; Baetidae, Leptophlebidae and Tricorythidae), Coleoptera (17%; Elmidae and Psphenidae), and Diptera (13%; Chironomidae, Simulidae, and Tabanidae). Additionally, the most abundant orders captured the "high Hg" site were Coleoptera (43%; Dryopidae), Hemiptera (21%, Naucoridae, Corixidae, and Dytiscidae), and Odonata (17%; Coenagrionidae, Libelullidae, and Gomphidae). Mercury concentration of aquatic macroinvertebrate did not differ between the summer and fall seasons ($F_{1,11} = 0.02$, $P = 0.89$); however, concentrations were significantly higher at the "high Hg" site than the low ($F_{1,11} = 5.94$, $P = 0.04$; Fig. 1b).

Mercury concentrations of bats and birds

I captured two species of bats at the "high Hg" site: *Myotis yumanensis* (Yuma myotis) and *Antrozous pallidus* (pallid bat; Table 2). At the "low Hg" site, I only captured pallid bats. At the "high Hg" location, Yuma myotis exhibited average hair Hg

concentrations of 4332 μg $Hg \cdot kg^{-1}$ (range: 2959 - 7375 μg $Hg \cdot kg^{-1}$); whereas, the average pallid bat hair concentration at the "high Hg" site was roughly half as high (mean: 2397 μg $Hg \cdot kg^{-1}$, range: 1885 – 2916 μg $Hg \cdot kg^{-1}$; Table 2). However, Hg concentrations of the hair did not differ significantly between Yuma myotis, which feeds primarily on emergent insects, and pallid bats, which feed on terrestrial invertebrates, particularly scorpions and spiders ($t = -1.8183$, $P = 0.12$). Pallid bats at the low Hg site exhibited hair Hg concentrations of 1144 μg $Hg \cdot kg^{-1}$, and ranged from 263.69 - 1,908.32 μg $Hg \cdot kg^{-1}$. When the Hg concentrations of pallid bats were compared across "high" and "low" Hg sites, there was not a significant difference ($t = 2.2247$, $P = 0.08$).

Feathers from nine species of resident birds and six species of migrant birds were captured at the "high Hg" site and analyzed for THg (Table 2). Two of the resident species were carnivores, three were invertivores, and four were omnivores. Additionally, four migrant species were invertivores and two were omnivores. I also analyzed Hg content from three species of resident birds and 10 species of migrant birds from the "low Hg" location (Table 2). Two of the resident bird species were omnivores and the third was a piscivore. Further, seven of the migrant bird species were invertivores and three were omnivores.

Within each site, there was evidence of increasing Hg with resident functional feeding group (Fig. 2a). At the "high Hg" site, Hg concentrations significantly differed among resident carnivores, omnivores, and invertivores ($F_{2,27} = 23.52$, $P < 0.0001$). Carnivores had significantly higher Hg concentrations than omnivores and invertivores ($P = 0.03$ and $P = 0.02$, respectively) and omnivore feather Hg concentrations were higher than invertivores ($P < 0.0001$). Further, a t-test comparison of between resident

omnivores and piscivores at the "low Hg" location showed piscivores had significantly higher feather Hg concentrations than omnivores (t = -4.41, P = 0.005). Finally, I did not capture resident invertivores at the "low Hg" site so I was not able to compare that group across sites. However, I compared resident carnivores at the "high Hg" site to piscivores at the "low Hg" site and found there was not a significant difference in bird feather Hg concentrations (t = -2.19, P = 0.08; Table 2, Fig. 2a). Additionally, I compared resident omnivores across sites and found there was no significant difference (t = 1.95, P = 0.08; Table 2, Fig. 2a). Finally, it should be noted as resident birds, their feathers were grown on site and therefore are representative of Hg concentrations in their diets.

There were similar findings when migrant bird feathers were compared between "high Hg" and "low Hg" sites (Table 2, Fig. 2b). I did not capture any migrant carnivores or piscivores at either site. A two-way ANOVA comparison of Hg concentrations in omnivorous and insectivorous migrant bird feathers captured at the "high Hg" and "low Hg" sites found no significant difference between the two trophic guilds ($F_{1,31}$ = 1.84, P = 0.19, Table 2, Fig. 2b) or among sites ($F_{1,31}$ = 0.03, P = 0.86).

Terrestrial arthropod Hg concentrations

Terrestrial arthropod captures varied across site and season. At the "low Hg" site, we captured and identified to family 1275 individuals (1184 in summer 2008 and 91 in fall 2008) in 12 orders (Appendix A). At the "high Hg" sites, we captured 1483 individuals (1424 in summer 2008 and 59 in fall 2008) in 13 orders (Appendix A). Because collection effort did not differ between seasons, data indicates that activity declined markedly in the fall at both study sites. The most abundant families captured at the "low Hg" site were Formicidae (ants), Lycosidae (wolf spiders), and Armadillidiidae

(pill bugs; Appendix A). The most abundant families captured at the "high Hg" sites were Formicidae, Carabidae (ground beetles), and Entomobryidae (springtails; Appendix A).

Mean Hg concentration of arthropods, regardless of family, did not significantly differ along the transect distances from the stream channel during summer 2008 at the "high Hg" site ($F_{5,27} = 1.30$, $P = 0.30$) or summer and fall 2008 at the "low Hg" site ($F_{5,20} = 0.14$, $P = 0.96$; $F_{4,12} = 0.87$, $P = 0.45$; respectively). When I compared the mean Hg concentration of arthropods at compiled transect distances from the stream channel, near (≤30 m) and far (≥40 m), and across sites, I found there was not a significant difference in Hg concentrations among near and far distances within a site ($F_{1,64} = 2.36$, $P = 0.13$), but there was an effect of site on concentrations (i.e., near and far distances at the "high Hg" site had higher Hg concentrations than near and far distances at the "low Hg" site; $F_{1,64} = 7.32$, $P = 0.009$, Fig. 3). The mean Hg concentration for terrestrial arthropods at the "low Hg" site was 74.60 (range: 26.01 - 429.63) and the mean Hg in arthropods at the "high Hg" site was 130.66 (range: 30.05 - 348.49). When I further compared the Hg concentrations of the two most abundant invertivores that co-occurred at both study sites with a two-way ANOVA (ground beetles and wolf spiders) it showed that wolf spiders had significantly higher Hg concentrations than ground beetles within each study location ($F_{1,32} = 11.41$, $P = 0.002$); however, the Hg concentrations of these arthropods did not differ among the study sites ($F_{1,32} = 2.11$, $P = 0.16$).

Discussion

This study showed that the aquatic portions of the stream ecosystems differed in Hg concentrations. Smith et al. (2010) measured total- and MeHg concentrations in sediments in a number of stream and mainstem sites in the Rio Grande drainage. They found higher average total- and MeHg concentrations in BBNP (Tornillo and Terlingua Creeks) sediments (THg: 32.30±33.68 $\mu g \cdot kg^{-1}$ d.w.; MeHg: 0.23±0.30 $\mu g \cdot kg^{-1}$ d.w.) than Independence Creek sediments (THg: 1.90 $\mu g \cdot kg^{-1}$ d.w.; MeHg: 0.03 $\mu g \cdot kg^{-1}$ d.w.). I also measured MeHg in sediments at our stream sites in July 2008 and found sediments at the "high Hg" site had substantially higher MeHg concentrations than those at the "low Hg" site (0.31±0.26 $ug \cdot kg^{-1}$ d.w. and 0.03±0.03 $ug \cdot kg^{-1}$ d.w. respectively; unpubl. data). This difference in the sediment MeHg concentrations is reflected in the aquatic communities at the study locations. Historical mining activities (Gray et al. 2003, Gray et al. 2006), as well as low atmospheric Hg deposition (Selin and Jacob 2008) in the Big Bend region suggest that inputs of Hg in streams via groundwater and sediment pathways are important (Lee and Wilson 1997). These sediment results that geological sources and/or mining history may have played a role in the Hg of the aquatic community at the "high Hg" site.

Fish Hg concentrations significantly differed between "high Hg" and "low Hg" sites. The results from the current study are similar to those found by Smith et al. (2010) with fish captured in the Big Bend region having, on average, higher Hg concentrations than those at the Independence Creek Preserve. I additionally determined that predominantly invertivore and piscivore small-bodied fish were captured at both study sites. A study by Peterson et al. (2007) examining Hg in large fish in streams and rivers

in 12 western U.S. states found the mean Hg concentrations of invertivores and invertivore/piscivores were 167.4 and 257 μg $Hg \cdot kg^{-1}$ wet weight (w.w.), respectively. When I compare my invertivore and piscivorous fish Hg concentrations to those in the western U.S. (Peterson et al. 2007), I found Hg concentrations of fish at BBNP, the "high Hg" site, I found that invertivores average tissue Hg concentrations were ~96±5 μg $Hg \cdot kg^{-1}$ w.w. and invertivore/piscivore fish averaged ~166±70 μg $Hg \cdot kg^{-1}$ w.w. (Table 1). These concentrations are considerably lower than what was found, on average, throughout the rest of the western U.S. However, it should be emphasized the fish in my study were predominantly smaller-bodied fish (mean: 45.31mm, range: 25-110 mm) while the fish in the Peterson et al. (2007) study were all >120 mm in total length.

Results from this study confirm my assertions and categories of "high" and "low" Hg sites. If I additionally compare Hg concentrations in fish tissue from both study sites to the U.S. EPA wildlife criteria (163 μg $Hg \cdot kg^{-1}$; USEPA 1997), TL 3 and 4 fish at the "low Hg" site had average Hg concentrations below the benchmark (Table 1). Additionally, TL 3 fish at the "high Hg" site had Hg concentrations below the EPA wildlife benchmark, while TL 4 fish had Hg concentrations above it (Table 1).

I observed similar patterns in the aquatic macroinvertebrates as with the fish. The difference in the sediment MeHg concentrations is also reflected in the macroinvertebrate communities at the study locations. Studies have noted increases in aquatic invertebrate Hg downstream from sites which have Hg in sediments associated with anthropogenic mining activities (Agra et al. 2010). Further, a study by Tsui et al. (2009) showed that periphyton and filamentous algae are potential "hot spots" for Hg methylation which can bioaccumulate in the stream food webs. As the invertebrates sampled in this study were

predominantly benthic families, it is likely the Hg enters the food web via these organisms and is likely transferred to fish invertivores and higher trophic levels.

Emergent aquatic macroinvertebrates can be an important food source for terrestrial invertivores in riparian zones (i.e., bats, birds, and terrestrial arthropods; Baxter et al. 2005). Although emergent insects can represent a substantial organic matter (OM) source for riparian consumers, contaminants found within emergent insects including Hg will also become manifested in riparian consumers. In order to determine the rate of potential Hg export via emergent aquatic macroinvertebrates to terrestrial consumers in my study systems, I used a similar method as Walters et al. (2008). I assumed an average export of 5.71 g dry mass (DM)$\cdot m^{2} \cdot yr^{-1}$ of emergent aquatic insects using the mean macroinvertebrate community annual emergence reported in Jackson and Fisher (1986) (reported range: 2.05-23.10 g DM$\cdot m^{2} \cdot yr^{-1}$). Mercury export to the riparian zone associated with emergent insects was calculated by using the mean THg concentrations of aquatic macroinvertebrates at both "low" and "high" Hg sites (Table 1). Thus, I estimated the potential export of Hg from the "low Hg" site to be 0.25 µg THg DM$\cdot m^{2} \cdot yr^{-1}$ (range: 0.06 - 1.42 µg Hg DM$\cdot m^{2} \cdot yr^{-1}$; Amphipoda and Ephemeroptera, respectively). Alternatively, average potential export of THg from the "high Hg" site streams was nearly 2X higher, at 0.60 µg Hg DM$\cdot m^{2} \cdot yr^{-1}$ (range: 0.10-4.63 µg Hg DM$\cdot m^{2} \cdot yr^{-1}$; Coenagrionidae and Naucoridae, respectively). Therefore, if emergence densities were the same between sites, the overall higher THg concentrations in invertebrates at the "high Hg" site could lead to a substantially higher potential Hg flux to riparian consumers.

Thus, the substantial variability in potential Hg export between study sites may explain the significant differences we saw in Hg concentrations in some riparian consumers. In the present study, I did not find a significant difference in bat hair Hg concentrations. This likely because the only bats I captured at both sites were foragers of terrestrial arthropods. However, the concentrations were within the range of similar studies (Hickey et al. 2001, Mora et al. 2006, Wada et al. 2010). Previous studies have compared Hg in bats at contaminated and uncontaminated sites and have observed differences. Wada et al. (2010) compared Hg concentrations in Big Brown bats (*Eptesicus fuscus*) from a reference site and a highly contaminated site in Virginia and found higher Hg concentrations in at the contaminated site (mean hair: 10,940 μg $Hg \cdot kg^{-1}$ at reference site, and 28,010 μg $Hg \cdot kg^{-1}$ at contaminated site. It is critical to note that bat hair Hg for both the reference and contaminated sites in Wada et al. (2010) were considerably higher than what we found. However, it is difficult to determine if the concentrations from their study are very high and mine very low or if the difference is an artifact of my low samples sizes. Finally, bat hair mercury concentrations at BBNP and Independence Creek were well below the U.S. EPA wildlife toxicity benchmark for mammalian fur (11,000 $\mu g \cdot kg^{-1}$; USEPA 1997; Table 2).

Although, there is limited information on Hg concentrations in bat hair, there are studies that have examined Hg in guano, tissues (i.e. kidney, liver, etc.), and blood (O'Shea et al. 2001, Walker et al. 2007, Wada et al. 2010). Wada et al. (2010) noted that Hg concentrations in bat hair were 260X higher than in blood for bats in their study. Finally, Mora et al. (2006) collected a number of potential peregrine falcon prey including Western Pipistrelle and Mexican Free-tail bats (both insectivores) in 1994 and

1997 in the Big Bend Ranch State Park and BBNP, respectively. Mercury concentrations in tissue of the bats in their study ranged from 130 $\mu g \cdot kg^{-1}$ (Western Pipistrelle Bat) to 590 $\mu g \cdot kg^{-1}$ (Mexican Free-tail Bats; Mora et al. 2006).

My study also focused on the collection of breast feathers from resident and migrant birds at both "high" and "low" Hg sites. I did not see the same trends in resident or migrant birds as I saw in the aquatic organisms. In other words, there was not a significant difference among functional feeding groups at the "high" and "low" Hg sites. Further, although I measured breast feather Hg concentrations and not tissue, it should be noted that Lewis and Furness (1993) found feather Hg levels were positively correlated to tissue Hg levels. Additionally, it has been shown that pre-molt feathers represent up to 93% muscle MeHg with nearly all THg in feathers as MeHg (Braune and Gaskin 1987, Thompson and Furness 1989). Thus, feathers are a reasonable, non-lethal method for assessing Hg concentrations in birds. Finally, Brasso and Cristol (2008) found young female tree swallows with feather Hg levels ~13 ppm exhibited reproductive impairment. Most migrant birds captured at BBNP and Independence Creek had Hg levels that fell below 13 ppm. However, 28% of insectivorous resident birds captured at BBNP had feather Hg levels higher than 13 ppm (Table 2). Therefore, there is a concern about the health and management of resident birds located in the Big Bend region.

I found that Hg concentrations of terrestrial arthropods did not differ significantly at different distances from the stream channel within a site. However, I did find that Hg concentrations of terrestrial arthropods did differ among "high Hg" and "low Hg" sites. Additionally, I found that wolf spiders had higher Hg concentrations than ground beetles within each site; however, there was not a significant difference for these two families

across study site. There is little published information on Hg levels in riparian terrestrial arthropods along sites that exhibit elevated Hg in stream biota. However, Cristol et al. (2008) which compared spiders, lepidopterans, and orthopterans at a reference site to a highly contaminated site and found a significant difference in arthropods among sites, we did not find a significant difference. Additionally, spiders at the contaminated site in their study exhibited Hg levels ($1.24 \pm 1.47 \mu g \cdot g^{-1}$), whereas wolf spiders at our "high Hg" sites had considerably lower levels ($0.18 \pm 0.006\ \mu g \cdot g^{-1}$). It appears that terrestrial arthropods at my study sites are not as contaminated as what was seen in the Cristol et al. (2008) study. However, sample sizes for this study were quite small and Hg level ranges were large within some families and sites which may be a reason for inability to find significant differences so it is difficult to be sure that the differences documented for both studies are actual or due to lack of data.

Literature Cited

Anderson, C. and G. Cabana. 2007. Estimating the trophic position of aquatic consumers in river food webs using stable nitrogen isotopes. Journal of North American Benthological Studies 26:273-285.

Blais, J.M., R.W. MacDondald, D. Mackey, E. Webster, C. Harvey, J.P. Smol. 2007. Biologically mediated transport of contaminants to aquatic systems. Environmental Science and Technology 41:1075-1084.

Blanton, C.J., C.E. Desforges, L.W. Newland, and A.J. Ehlmann. 1975. A survey of mercury distributions in the Terlingua area of Texas. In: Trace substances in environmental health. Proceedings of University of Missouri's 9th Annual Conference on trace substances in environmental health. 495 pp.

Bloom, N.S. 1992. On the Chemical form of Mercury in Edible Fish and Marine Invertebrate Tissue. Canadian Journal of Fisheries and Aquatic Sciences 49(5): 1010-1017.

Brasso R.L. and D.A. Cristol. 2008. Effects of mercury exposure on the reproductive success of tree swallows (*Tachycineta bicolor*). Ecotoxicology 17:133–141.

Braune B.M. and D.E. Gaskin. 1987. Mercury levels in Bonaparte's gulls (*Larus philadelphia*) during autumn molt in the Quoddy region, New Brunswick, Canada. Archives of Environmental Contamination and Toxicology 16:539–549.

Burger, J. 1993. Metals in avian feathers: bioindicators of environmental pollution. Review of Environmental Toxicology 5:203-311.

Burger, J. and B. Eichhorst. 2007. Heavy metals and selenium in Grebe feathers from Agassiz National Wildlife Refuge in Northern Minnesota. Archives on Environmental Contamination and Toxicology 53:442-449.

Carter, J.L. and V.H. Resh. 2001. After site selection and before data analysis: sampling, sorting, and laboratory procedures used in stream benthic macroinvertebrates monitoring programs by USA state agencies. Journal of the North American Benthological Society 20:658-682.

Chumchal, M.M. 2007. Factors affecting mercury contamination in fish from Caddo Lake, Texas. PhD thesis. University of Oklahoma, Norman, OK, USA.

Coddington, J.A., L.H. Young, and F.A. Coyle. 1996. Estimating spider species richness in southern Appalachian cove hardwood forest. Journal of Arachnology 24:11–28.

Cristol, D.A., R.L. Brasso, A.M. Condon, R.E. Fovargue, S.L. Friedman, K.K. Hallinger, A.P. Monroe, and A.E. White. 2008. The movement of aquatic mercury through terrestrial food webs. Science 320:335.

Dewild, J.F., S.D. Olund, M.L. Olson, M.T. and Tate. 2004. Methods for the Preparation and Analysis of Solids and Suspended Solids for Methylmercury. United States Geological Survey. USGS Techniques and Methods 5 A-7.

Evers D., N. Burgess, L. Champoux, B. Hoskins, A. Major, W. Goodale, R. Taylor, R. Poppenga, and T. Daigle. 2005. Patterns and interpretation of mercury exposure in freshwater avian communities in northeastern North America. Ecotoxicology 14:193–221.

Fisher, S.G. 2006. Stream ecosystems of the western United States. In: River and Stream Ecosystems of the World (eds. C.E. Cushing, K.W. Cummins, and G.W. Minshall). University of California Press, Berkley, California. Pp 61-88.

Gray, J.E., M.E. Hines, H. Biester, and B.K. Lasorsa. 2003. Mercury methylation in mine wastes collected from abandoned mercury mines in the USA. Journal of Physiology IV 107:573-576.

Gray, J.E., M.E. Hines, and H. Biester. 2006. Mercury methylation influenced by areas of past mercury mining in Terlingua district, Southwest Texas, USA. Applied Geochemistry 21:1940-1954.

Hall, B.D., D.M. Rosenberg, and A.P. Wlens. 1998. Methylmercury in aquatic insects from an experimental reservoir. Canadian Journal of Fisheries and Aquatic Sciences 55: 2036–2047.

Hammer, O., D.A.T. Harper, and P.D. Ryan. 2001. PAST: Paleontological Statistics software package for education and data analysis. Palaeontologia Electronica 41: 9 pages.

Harris, R.C., D.P. Krabbenhoft, R. Mason, M.W. Murray, R. Reash, and T. Saltman (eds.). 2007. Ecosystem Responses to Mercury Contamination: Indicators of Change. 219 pages.

Hawkley, D.M., K.K. Hallinger, and D.A. Cristol. 2009. Compromised immune competence in free-living tree swallows exposed to mercury. Ecotoxicology 18:499-503.

Hickey, M.B.C., M.B. Fenton, K.C. MacDonald, and C. Soulliere. 2001. Trace elements in the fur of bats (Chiroptera: Vespertillionidae) from Ontario and Quebec, Canada. Bulletin of Environmental Contamination and Toxicology 66:699-706.

Hill, J.J., M.M. Chumchal, R.W. Drenner, J.E. Pinder III, and S.M. Drenner. 2010. Use of preserved museum fish to evaluate historical and current mercury contamination in fish from two rivers in Oklahoma, USA. Environmental Monitoring and Assessment 161:509-516.

Hubbs, C., R.J. Edwards, and G.P. Garrett. 2008. An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. Texas Academy of Science, Second Edition.

Kelly, B., J.B. Dempson, and M. Power. 2006. The effects of preservation on fish tissue Stable isotope signatures. Journal of Fish Biology 69:1595-1611.

Lee, R.W. and J.T. Wilson. 1997. Trace elements and organic compounds associated with riverbed sediment in the Rio Grande/Rio Bravo basin, Mexico and Texas. U.S. Geological Survey Fact Sheet FS-098-97. U.S. Geological Survey, Austin, TX.

Lewis, S.A. and R.W. Furness. 1993. The role of eggs in mercury excretion by Quail (*Coturnix coturnix*) and the implications for monitoring mercury pollution by analysis of feathers. Ecotoxicology 2:55–64.

Likens, G.E. and F.H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. Bioscience 24:447-456.

Mergler, D., H.A. Anderson, L.H.M Chan, K.R. Mahaffrey, M. Murray, M. Sakamoto, and A.H. Stern. 2007. Methylmercury exposure and health effects in humans: a worldwide concern. Ambio 36:3-11.

Merritt, R.W., K.W. Cummings, and M.B. Berg (eds). 2008. An introduction to aquatic insects of North America. 4th Edition. Kendall/Hunt Publishing Co., Dubuque, IA.

Mora, M., R. Skiles, B. McKinney, M. Paredes, D. Buckler, D. Papoulias, and D. Klein. 2002. Environmental contaminants in prey and tissues of peregrine falcon in the Big Bend region, Texas, USA. Environmental Pollution 116:169-176.

Mora, M.A., D. Musquiz, J.W. Bickham, D.S. Mackenzie, M.J. Hooper, J.K. Szabo, and C.W. Matson. 2006. Biomarkers of exposure and effects of environmental contaminants on swallow nesting along the Rio Grande, Texas, USA. Environmental Toxicology and Chemistry 25:1574-1584.

Mora, M.A., R.S. Skiles, and M. Paredes. 2007. Further assessment of environmental contaminants in avian prey of the peregrine falcon in Big Bend National Park, Texas. The Southwestern Naturalist 52:54-59.

Morel, F.M.M., A.M.L. Kraepiel, and M. Amyot. 1998. The chemical cycle and bioaccumulation of mercury. Annual Review of Ecology and Systematics 29: 543-566.

O'Shea, T.J., A.L. Everette, and L.E. Ellison. 2001. Cyclodiene insecticide, DDE, DDT, arsenic, and mercury contamination of big brown bats (*Eptesicus fuscus*) foraging at a Colorado superfund site. Archives of Environmental Contamination and Toxicology 40:112-120.

Paller, M.H. and J.W. Littrell. 2007. Long-term changes in mercury concentrations in fish from the middle Savannah River. Science of the Total Environment 382:375-382.

Poole, A. (Ed). 2011. The Birds of North America Online: http://bna.birds.cornell.edu/BNA/. Cornell Laboratory of Ornithology, Ithaca, NY.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718.

Powell, G.V.N. 1983. Industrial effluents as a source of mercury contamination in terrestrial riparian vertebrates. Environmental Pollution (Series B) 5:51-57.

Rimmer, C.C., E.K. Miller, K.P. McFarland, R.J. Taylor, and S.D. Faccio. 2010. Mercury bioaccumulation and trophic transfer in the terrestrial food web of a montane forest. Ecotoxicology 19:697-709.

Sabo, J.L. and M.E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology 83:1860-1869.

Saito, L., C. Redd, S. Chandra, L. Atwell, C.H. Fritsen, H. Christian, and M.R. Rosen. 2007. Quantifying foodweb interactions with simultaneous linear equations: stable isotope models of the Truckee River, USA. Journal of the North American Benthological Society 26:642-662.

Sanzone, D.M. 2001. Linking communities across ecosystem boundaries: the influence of aquatic subsidies on terrestrial predators. Doctoral Thesis. University of Georgia, Athens, Ga.

Sanzone, D.M., J.L. Meyer, E. Marti, E.P. Gardiner, J.L. Tank, and N.B. Grimm. 2003. Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134:238-250.

Schade, J.D. and S.G. Fisher. 1997. Leaf litter in a Sonoran desert stream ecosystem. Journal of the North American Benthological Society 16:612-626.

Scheuhammer, A.M., M.W. Meyer, M.B. Sandheinrich, and M.W. Murray. 2007. Effects of environmental methylmercury on the health of wild birds, mammals, and fish. Ambio 36:12-18.

Schmidly, D.J. and W.B. Davis. 2004. Mammals of Texas. University of Texas Press, Austin, Texas.

Schmitt, C.J., J.E. Hinck, V.S. Blazer, N.D. Denslow, G.M. Dethloff, T.M. Bartish, J.J. Coyle, and D.E. Tillitt. 2006. Environmental contaminants and biomarker responses in fish from the Rio Grande and its US tributaries: Spatial and temporal trends. Science of the Total Environment 350:161-193.

Selin, N.W. and D.J. Jacob. 2008. Season and spatial patterns of mercury wet deposition in the United States: constraints on the contribution from North American anthropogenic sources. Atmospheric Environment 42:5193-5204.

Shapiro, S.S. and M.B. Wilk. 1975. Analysis of variance test for normality (complete samples). Biometrika 52:591.

Smith, A., A.A. Abuzeineh, M.M. Chumchal, T.H. Bonner, and W.H. Nowlin. 2010 Mercury contamination of the fish community of a semi-arid and arid river system: spatial variation and the influence of environmental gradients. Environmental Toxicology and Chemistry 29:1762-1772.

Thomas, C., T.H. Bonner, and B.G. Whiteside. 2007. Freshwater fishes of Texas. 202 pp. Texas A&M University Press, College Station, Texas.

Thompson, D.R. and R.W. Furness. 1989. Comparison of total and organic mercury levels in seabird feathers. Marine Pollution Bulletin 20:577–79.

U.S. Environmental Protection Agency. 1998. Method 7473: Mercury in solids and solutions by thermal decomposition, amalgamation, and atomic absorption spectrophotometry. Washington D.C.

Ullrich, S.M., T.W. Tanton, and S.A. Abdrashitova. 2001. Mercury in the aquatic environment: a review of factors affecting methylation. Critical Review in Environmental Science and Technology 31:241-293.

Vander Zanden, M. J. and D. M. Sanzone. 2004. Food web subsidies at the land-water ecotone. In: Food Webs at the Landscape Level (eds. G.A. Polis, M.E. Power, G.R. Huxel). University of Chicago Press, Chicago, Illinois. Pp 185-188.

Wada, H., D.E. Yates, D.C. Evers, R.J. Taylor, and W.A. Hopkins. 2010. Tissue mercury concentrations and adrenocortical responses of female big brown bats (*Eptesicus fuscus*) near a contaminated river. Ecotoxicology 19:1277-1284.

Walker, L.A., V.R. Simpson, L. Rockett, C.L. Weinburg, and R.F. Shore. 2007. Heavy metal contamination in bats in Britain. Environmental Pollution 148:483-490.

Wiener, J.G., D.P. Krabbenhoft, G.H. Heinz, and A.M. Scheuhammer. 2003. Ecotoxicology of Mercury. In: Handbook of Ecotoxicology (eds. D.J. Hoffman, B.A. Rattner, G.A. Burton, Jr., J. Cairns, Jr.). Lewis Publishers, Boca Raton, Florida. Pp 409 – 443.

Wong, C.M., C.E. Williams, J. Pittock, U. Collier, and P. Schelle. 2007. World's top ten rivers at risk. 53 pp. WWF International. Gland, Switzerland.

Table 5.1. Total mercury concentrations and trophic levels (TL) for fish species and aquatic macroinvertebrate families captured at BBNP ("high Hg") and Independence Creek Preserve ("low Hg") study sites in summer and fall 2008. Fish values are in µg $Hg \cdot kg^{-1}$ (wet weight) and aquatic macroinvertebrate values are in µg $Hg \cdot kg^{-1}$ (dry weight).

			High Hg site		Low Hg site	
Group	Species/Family	Trophic Level	*n*	$\bar{x}$ (Min - Max)	*n*	$\bar{x}$ (Min - Max)
Fish	*Astyanax mexicanus*	2	2	90 (43 - 138)	0	n.d.
	Astyanax mexicanus	3	1	97	0	30
	Astyanax mexicanus	4	2	235 (234 - 237)	2	69 (62 - 75)
	Cichlasoma cyanoguttatum	3	0	n.d.	1	14
	Cichlasoma cyanoguttatum	4	0	n.d.	3	36 (19 - 65)
	Cyprinella lutrensis	2	2	100 (85 - 114)	0	n.d.
	Cyprinus carpio	3	2	97 (90 - 103)	0	n.d.
	Cyprinus carpio	4	3	110 (64 - 155)	0	n.d.
	Fundulus zebrinus	2	1	41	0	n.d.
	Fundulus zebrinus	3	1	93	0	n.d.
	Gambusia affinis	4	0	n.d.	1	19
	Ictalurus punctatus	2	1	48	0	n.d.
	Lepomis macrochirus	4	0	n.d.	2	37 (25 - 50)
	Lepomis spp.	4	0	n.d.	1	25
	Notropis amambilis	3	0	n.d.	1	57
	Notropis amambilis	4	0	n.d.	2	20 (22 - 34)
	Notropis braytoni	4	1	200	0	n.d.
	Pimephales vigilax	2	0	n.d.	1	34
	Pimephales vigilax	3	0	n.d.	4	37 (31 - 48)
	Pimephales vigilax	4	0	n.d.	1	29
Aq. Macroinvertebrates	Dryopidae	2	1	50	0	n.d.
	Gomphidae	2	1	123	0	n.d.
	Coenagrionidae	2	1	49	1	43
	Naucoridae	2	0	n.d.	2	34 (28 - 41)
	Naucoridae	3	1	200	0	n.d.
	Baetidae/Leptophlebidae	2	0	n.d.	1	62
	Gammeridae/Hyallelidae	2	0	n.d.	1	30
	Elmidae	2	0	n.d.	1	39
	Tabanidae	2	0	n.d.	1	52
	Tabanidae	3	0	n.d.	1	45

Table 5.2. Total mercury concentrations and functional feeding groups (FFG) for bat and bird species captured at BBNP ("high Hg") and Independence Creek Preserve ("low Hg") study sites for summer and fall 2008 combined. Values are in μg Hg·kg^{-1} (dry weight).

				High Hg site		Low Hg site	
Group	Species	FFG	Migration class	*n*	$\bar{x}$ (Min - Max)	*n*	$\bar{x}$ (Min - Max)
Bats	*Antrozous pallidus*	Insectivore	NA	3	2397 (1885 - 2916)	3	1144 (264 - 1259)
	Myotis yumanensis	Insectivore	NA	5	4332 (2959 - 7375)	0	n.d.
Birds	*Athene cunicularia*	Omnivore	Resident	1	563	0	n.d.
	Bubo virginianus	Carnivore	Resident	3	1083 (637 - 1375)	0	n.d.
	Buteo jamaicensis	Carnivore	Resident	1	743	0	n.d.
	Cardinalis cardinalis	Omnivore	Resident	2	238 (85 - 391)	4	80 (41 - 125)
	Cardinalis sinuatus	Omnivore	Resident	2	73 (38 - 108)	0	n.d.
	Chloroceryle americana	Piscivore	Resident	0	n.d.	3	2410 (999 - 3407)
	Molothrus ater	Omnivore	Resident	0	n.d.	1	57
	Peucaea cassinii	Omnivore	Resident	1	475	0	n.d.
	Sayornis nigricans	Invertivore	Resident	8	13803 (4118 - 19970)	0	n.d.
	Sayornis saya	Invertivore	Resident	4	2335 (744 - 5793)	0	n.d.
	Stelgidopteryx serripennis	Invertivore	Resident	6	2374 (1747 - 3438)	0	n.d.
	Chordeiles sp.	Invertivore	Migrant	0	n.d.	1	610
	Cistothorus palustris	Invertivore	Migrant	0	n.d.	1	12668
	Geothlypis trichas	Invertivore	Migrant	0	n.d.	3	550 (157 - 859)
	Hirundo rustica	Invertivore	Migrant	0	n.d.	2	478 (279 - 835)
	Icteria virens	Omnivore	Migrant	0	n.d.	4	234 (144 - 330)
	Melospiza lincolnii	Omnivore	Migrant	0	n.d.	2	495 (456 - 535)
	Molothrus ater	Invertivore	Migrant	1	666	0	n.d.
	Oreothlypis celata	Invertivore	Migrant	2	1931 (1060 - 2801)	1	480
	Passerculus sandwichensis	Omnivore	Migrant	0	n.d.	1	1395
	Petrochelidon pyrrhonota	Invertivore	Migrant	9	1674 (1135 - 2534)	0	n.d.
	Pipilo chlorurus	Invertivore	Migrant	1	86	0	n.d.
	Piranga rubra	Invertivore	Migrant	1	524	0	n.d.
	Sayornis phoebe	Invertivore	Migrant	0	n.d.	1	835
	Tyrannus forficatus	Invertivore	Migrant	0	n.d.	1	565
	Vireo bellii	Invertivore	Migrant	1	555	0	n.d.

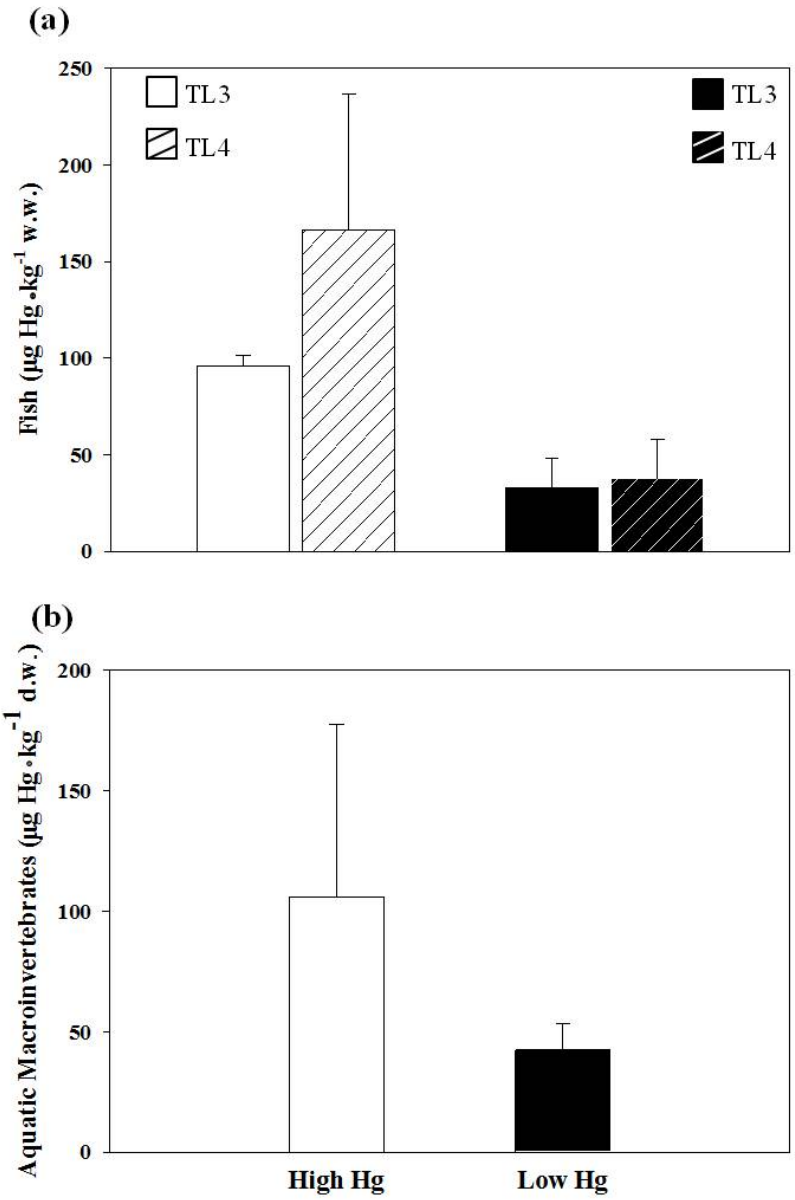

Figure 5.1. Mean (±1 SE) mercury concentrations in: (a) fish fillets (µg Hg kg^{-1} wet weight), and (b) aquatic macroinvertebrates (µg Hg·kg^{-1} wet weight) at the Independence Creek Preserve ("low Hg") and BBNP ("high Hg") study sites. Filled bars represent the "low Hg" site and non-filled bars represent the "high Hg" site. For figure 1a, solid bars represent TL3 and hashed bars represent TL4 fish.

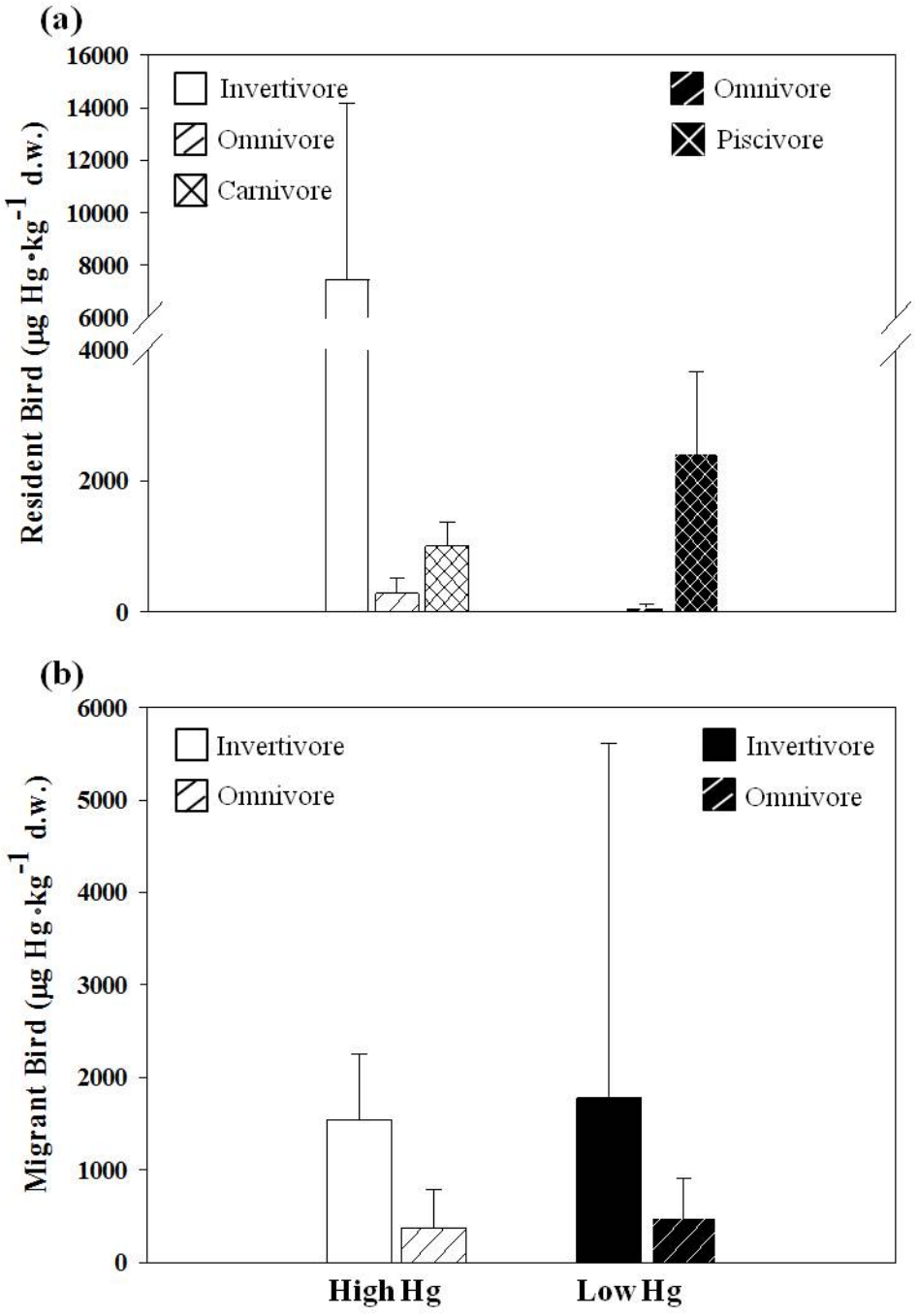

Figure 5.2. Mean (±1 SE) mercury concentrations in resident (a) and migrant (b) bird feathers (µg Hg kg^{-1} dry weight) at the Independence Creek Preserve ("low Hg") and BBNP ("high Hg") study sites. Solid bars represent invertivores, hashed bars represent omnivores, and cross-hatched bars represent piscivores/carnivores.

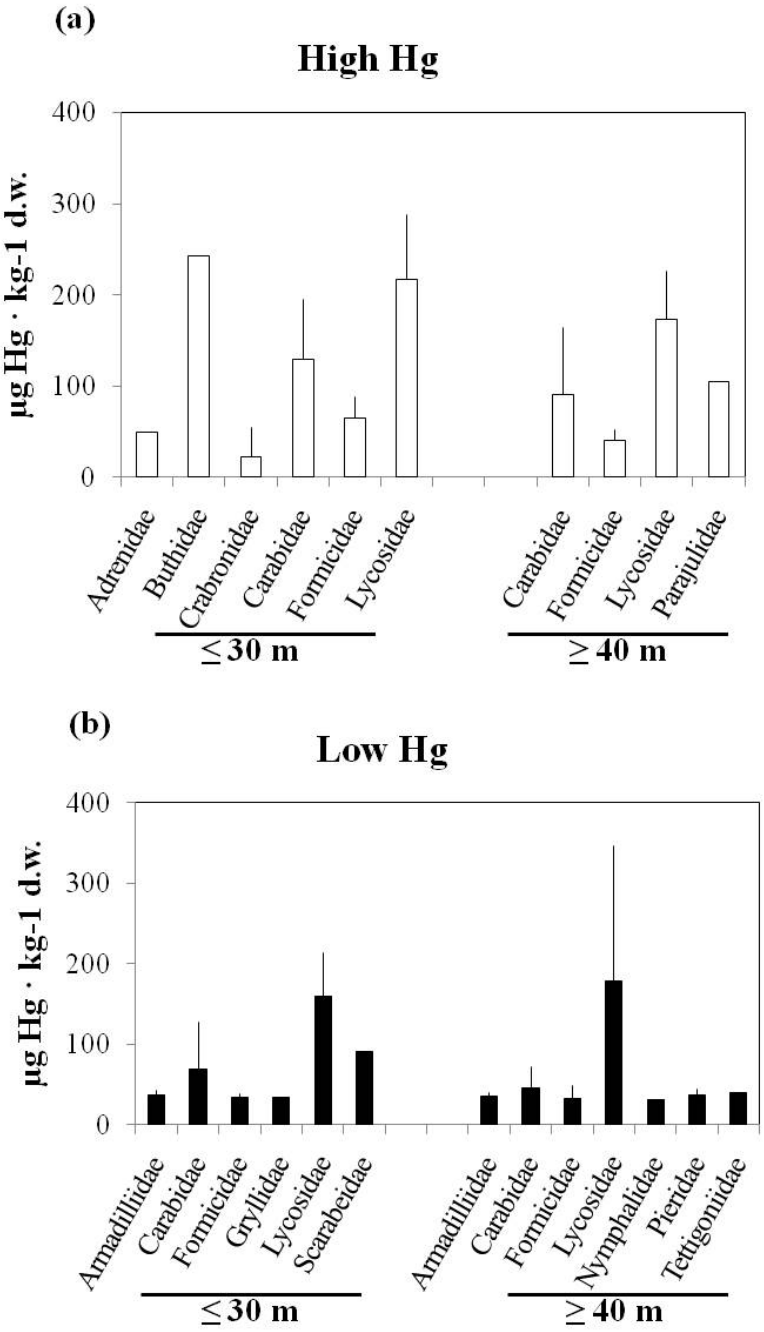

Figure 5.3. Terrestrial arthropod Hg concentrations at: (a) Independence Creek Preserve ("low Hg"), and (b) BBNP ("high Hg") study sites. Families captured and analyzed for THg are shown at distances from the stream channel (i.e. 10 m – 75 m). Values are µg $Hg \cdot kg^{-1}$ dry weight.

Appendix A

Terrestrial arthropod abundances across season and study site ("low" and "high" Hg). Total number (#) column shows number of individuals captured using all three methods of collection (kick and dip nets and Hess sampler).

Site	Season	Order	Family	Total #
"Low Hg" Site	Summer 2008	Araneae	Lycosidae	76
			Caponiidae	1
		Coleoptera	Carabidae	43
			Curculionidae	1
			Scarabeidae	2
			Staphylinidae	7
		Collembola	Entomobryidae	18
		Dermoptera	Labiduridae	11
		Dictyoptera	Blattellidae	2
			Polyphagidae	2
		Diptera	Simulidae	1
		Ephemeroptera	Baetidae	1
		Hemiptera	Miridae	1
			Acanthosomatidae	1
		Hymenoptera	Cabronidae	1
			Formicidae	933
			Halictidae	11
			Sphecidae	2
		Isopoda	Armadilliidae	58
		Lepidoptera	Pieridae	4
			Nymphalidae	1
		Orthoptera	Gryllidae	6
			Tettigoniidae	1
	Fall 2008	Araneae	Lycosidae	28
		Coleoptera	Carabidae	13
		Dermoptera	Labiduridae	1
		Diptera	Simulidae	10
		Ephemeroptera	Baetidae	2
		Hymenoptera	Andrenidae	3
			Formicidae	2
			Halictidae	1
		Isopoda	Armadilliidae	10
		Lepidoptera	Nymphalidae	11
			Pieridae	10
"High Hg" Sites	Summer 2008	Araneae	Caponiidae	3
			Lycosidae	49
		Coleoptera	Carabidae	245
			Entomobryidae	171
		Dermoptera	Labiduridae	1
		Diplopodia	Parajulidae	1
		Hemiptera	Blissidae	1
		Hymenoptera	Andrenidae	20
			Apidae	1
			Formicidae	913
			Halictidae	7
			sphecidae	3
		Lepidoptera	Pieridae	2
		Orthoptera	Gryllidae	5
		Scorpiones	Buthidae	2
	Fall 2008	Araneae	Lycosidae	11
		Coleoptera	Carabidae	14
			Staphylinidae	1
		Collembola	Entomobryidae	14
		Diptera	Simulidae	1
		Ephemeroptera	Baetidae	1
		Hymenoptera	Cabronidae	4
			Formicidae	3
			Halictidae	7
		Orthoptera	Gryllidae	3

CHAPTER VI

SUMMARY AND SYNTHESIS

Restatement of Research Objectives

The objective of Chapter 2 of this dissertation was to examine the relative contribution of OM sources to fish communities in the Rio Grande/Rio Bravo del Norte and several of its perennially-flowing tributaries. In this chapter, I assessed the relative importance of OM sources and food web structure along lower Rio Grande drainage using N and C stable isotopes (e.g., $\delta^{13}C$ and $\delta^{15}N$). I predicted that the relative importance of terrestrial-derived C sources to fishes would be relatively lower in the more arid region of the drainage than in the semi-arid due to greater primary productivity in the arid streams relative to their watersheds. I also predicted that this trend would be affected by stream order/size.

The focus of the third chapter of my dissertation was to explore the application of the stable isotope-derived community-wide metrics described by Layman et al. (2007; $\delta^{15}N$ range, $\delta^{13}C$ range, total niche area, mean distance to centroid, and standard deviation of nearest neighbor distances) throughout the range of the lower Rio Grande and its tributaries. I was interested in examining shifts in food web structure from small- to large-order streams and rivers as well as along an arid to semi-arid climatic gradient.

Chapter 4 of this dissertation was an examination of macroinvertebrate community structure and functional composition of a large complex drainage in the

southwestern United States (i.e., the lower Rio Grande drainage in Texas; Fig. 1). I was interested in broad scale differences of macroinvertebrate community composition at the family taxonomic level. The study objectives were three-fold.

1. Assess macroinvertebrate community composition and diversity along the Rio Grande drainage and across a substantial west-to-east/upstream-downstream physiographic gradient.

2. Examine whether differences in local site-specific environmental conditions or landscape-scale patterns would explain the variation in invertebrate community composition and diversity.

3. Assessed spatial patterns in the distribution and relative abundance of different invertebrate functional feeding groups in relation to predictions made by conceptual models of riverine communities, specifically, the RCC, FPC.

The purpose of the final chapter (Chapter 5) of my dissertation was to assess patterns in the potential movement of Hg from streams to riparian consumers in an arid landscape. This study was conducted in three streams located along the lower Rio Grande drainage.

1. Examine Hg concentrations in portions of the aquatic food web in three tributaries in the Lower Rio Grande drainage in west Texas which potentially vary in Hg contamination.

2. Determine potential cross-ecosystem fluxes of Hg between streams and the adjacent terrestrial riparian systems.

3. Examine Hg contamination of several groups of terrestrial consumers (birds, bats, and terrestrial arthropods) that inhabit or utilize riparian zones at the study

stream reaches.

4. Compare patterns of Hg concentrations among aquatic and terrestrial consumers.

Summary of Major Findings and Future Directions

Utilization of basal C sources by fish communities

Utilization of allochthonous C resources (those derived from terrestrial sources) varied among site types. Allochthonous C resources were utilized in greater proportion by fish communities at both arid and semi-arid mainstem sites (mean: 67% and 71%, respectively). I suggest one potential is the Rio Grande is a large complex system, and many mainstem sites likely integrate the downstream transport of upstream resources, including drifting invertebrates and course and fine particulate organic matter (Polis et al. 1997, Finlay et al. 2002). Additionally, greater turbidity at sites in the upstream region (mean NVSS: 431.18 mg/L; WH Nowlin, unpubl. data) than in the downstream (mean NVSS: 21.95 mg/L; WH Nowlin, unpubl. data) which can inhibit in-situ photosynthesis and thus long term productivity of in-stream autotrophs as well as high watershed productivity throughout its range potentially contributed to these results. In contrast to the mainstem sites, smaller tributary sites indicated that fish communities in arid tributaries exploited autochthonous C resources (periphyton; 52%) in greater proportion than allochthonous C sources. However, utilization of source type shifts to allochthonous as tributaries transition to semi-arid climates. When I examined two species found at multiple locations in this study, I found that red shiner and Mexican tetra typically the same types of C as the overall fish communities. The exception was Mexican tetra at the

arid tributary sites in which I found a greater proportion of allochthonous C in the species even though the fish community preferred autochthonous C. Finally the results of the this study determined that mainstem Rio Grande fish communities received most of their allochthonous C from C_3 plant origin, and not from C_4 plants, such as grasses (~12% and ~9% in arid and semi-arid communities, respectively).

Results from this study further illustrate the intimate connection riverine ecosystems and their watersheds. Additionally, it further elucidates the importance of land use (deforestation, urbanization, etc.) within the Rio Grande drainage as it can have an impact on fish communities in the river.

Examining community structure with community-wide $\delta^{13}C$ and $\delta^{15}N$-based metrics

In general, the stable-isotope community-wide metrics explored in this study found little effect of site type (mainstem arid and semi-arid, and tributary arid and semi-arid) on community composition. There was no significant variation in food chain length (NR), resource diversity (CR), and functional redundancy/species packing (SDNND) among site types. However, niche area (TA) and the degree of trophic diversity (CD) did differ significantly. Semi-arid mainstem communities had a significantly lower CD than all other sites, contrary to my predictions. I predicted TA to would follow the same trends as CD as it is also a measure of community trophic diversity. I found there was not a significant difference between the communities of arid and semi-arid mainstem sites. However, semi-arid mainstem sites were significantly smaller than both arid and semi-arid tributary communities. Essentially, I found that semi-arid mainstem sites had simpler food webs than the upstream sites.

These metrics can be useful in quantitatively comparing communities; however, they should be performed and interpreted with caution. Understanding the composition of a community as well as how it may compare to a reference site, can be useful for river managers. These metrics can potentially allow managers to explore the function and composition of entire communities and develop appropriate conservation protocols.

Basin- and local-scale influences on macroinvertebrate community structure

The present study showed that macroinvertebrate community composition (at the family level) of the lower Rio Grande drainage varied along basin- and local-scale characteristics. The western-most sites with higher DOC concentrations and specific conductance had higher densities of simuliids, hydropsychids, heptageniids, and dryopids; whereas the semi-arid and southeastern sites had more chironomids, coenagrionids, and other families of Tricoptera. Further, I saw greater variation in relative abundances within and among tributary study locations than in the Rio Grande mainstem itself. Although, I didn't see as high a variability among arid and semi-arid sites for some families (e.g. baetids and chironomids), other families (e.g. elmids, gomphids, and heptageniids) were in greater abundance at semi-arid sites (Independence, Dolan, and Pinto Creeks, and Pecos River) than streams in the Big Bend region (Tornillo and Terlingua Creeks; Appendix B). It appeared that changes in average annual precipitation and physiochemical properties (DOC, specific conductance, salinity, PO_4^{3-} and NO_3^-) may play a role in community composition in these smaller streams. Finally, although the present study found observed variation in physiochemical characteristics and invertebrate community composition at the family level across Rio Grande drainage, few of the functional feeding groups exhibited a response to these gradients.

Aquatic macroinvertebrate communities can play an important role in lotic ecosystems, as a potential food source for instream and terrestrial consumers. This study shows both basin- and local-scale physiochemical processes are important for structuring the invertebrate communities. Further, before applying metrics (e.g., EPT), influences of multiple scales need to be understood.

Transfer of mercury across ecosystem boundaries in arid streams

This study showed that Hg concentrations in aquatic consumers and potential movement of Hg to the terrestrial ecosystem differed among "high" and "low" Hg sites. However, the variability in potential Hg export between study sites only explained the difference in Hg concentrations in some riparian consumers. For instance, I did not see a significant difference in bat hair or resident and migrant bird feather Hg concentrations across sites. Additionally, I found that Hg concentrations in migrant and resident birds at my study sites were lower than levels found in other studies across the western U.S. I found that Hg concentrations of terrestrial arthropods did not differ significantly at different distances from the stream channel within a site.

Finally, I did find that Hg concentrations of the overall terrestrial arthropod community did differ among "high" and "low" Hg sites. Additionally, I found that wolf spiders had higher Hg concentrations than ground beetles within each site; however, there was not a significant difference for these two families across study site.

Literature Cited

Finlay, J.C., S. Khandwala, and M.E. Power. 2002. Spatial scales of carbon flow in a river food web. Ecology 83:1845-1859.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward and integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecological Systems 28:289-316.

VITA

Alisa A. Abuzeineh received a B.S. in Wildlife Biology from Kansas State University in May 2002. She then attended Texas Tech University earning an M.S. in Biology in May 2006. In fall 2006, Alisa entered the Aquatic Resources PhD program at Texas State University-San Marcos. While at Texas State, she was a NSF GK-12 fellow and received the Durenberger, Graduate College, ASG, and Fred and Yetta Richan Aquatic Biology Scholarships.

Permanent E-mail Address: wildbiol27@yahoo.com

This dissertation was typed by Alisa A. Abuzeineh.