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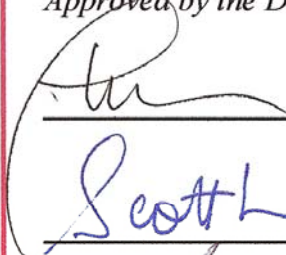
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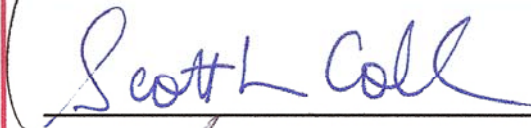
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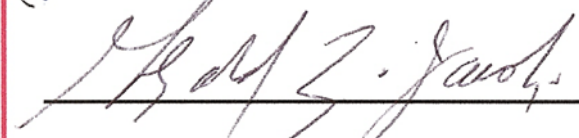
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This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

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**THE EFFECTS OF STREAM DISCHARGE AND CHANNELISATION
ON THE MACROINVERTEBRATE COMMUNITY
IN A SEMI-ARID LANDSCAPE**

BY

THOMAS L. KENNEDY

B.S., Biology, Florida State University, 1997
M.S., Environmental Science, University of Virginia, 2004

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

**Doctor of Philosophy
Biology**

The University of New Mexico
Albuquerque, New Mexico

May, 2009

DEDICATION

This dissertation is dedicated to my Brother, Mom, Dad, and grandfather, Roy “Papa” Kennedy. My Mom was a life-long science teacher and inspired me to go into the sciences. My grandfather was an excellent naturalist and taught me to identify my first birds and flowers. My Dad, who has a passion for hunting and fishing, which along with my grandfather inspired me to go into biology. And finally my brother, to all the friendly and productive competitions throughout the years, which constantly inspired me to do better whether at school or recreationally.

ACKNOWLEDGMENTS

First I would like to thank my dissertation committee Tom Turner, Jerry Jacobi, Scott Collins, and David Gutzler. Funding from NSF IGERT Program and the Cliff Crawford Fellowship. I would also like to thank many others who have helped along the way:, Wade Wilson, Craig McClain, Michelle Steinauer, Hagit Salamon, Nathan Daves-Brody, Eric Schaad, Eric Hulebak, Trevor Krabbenhoft, and (very importantly) Judy Calman.

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ABSTRACT

The Middle Rio Grande is the second largest watershed in the southwestern United States and is a vitally important component for the biodiversity in the region. Similar to many other rivers, the MRG is a temporally dynamic system that unfortunately, has been subjected to river regulation. As a result, the river has become channelised in many reaches disconnecting it from the surrounding floodplain. The effects of river regulation on the MRG and its surrounding riparian zone were largely unknown. I tested three main hypothesis with regards to the macroinvertebrates in the MRG: 1) Does flow variability structure the aquatic macroinvertebrate community; 2) Does flow variability affect lateral subsidies and food web dynamics of terrestrial and aquatic macroinvertebrates; and 3) Does channelisation affect the linkages between the aquatic and terrestrial systems with a focus on lateral subsidies and arthropod predators? Five years of survey data and stable isotope analyses of the common macroinvertebrates and arthropod predators was used to address these hypotheses. During the course of this study period there was a large amount

of variability in discharge having a significant impact on the macroinvertebrate community. Higher densities of macroinvertebrates were associated with lower discharge. Drought and flooding reduced the density of macroinvertebrate. Lateral inputs between the aquatic and terrestrial systems were also highest during times of low discharge and were reduced during higher discharge. The transition zone harbored higher rates of predators. Stable isotope analyses indicated that predators near the water's edge were heavily subsidized by lateral inputs from algae production. In channelised reaches, aquatic and terrestrial macroinvertebrate densities and richness were lower. The riparian zone and the wetted channel are intricately linked together and processes that occur in the river affect the surrounding riparian zone. Consequently, channelisation may be a threat to diversity by negatively impacting transition zone communities and adversely affecting predaceous arthropods.

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Introduction

The Rio Grande is the second largest watershed in the southwestern United States making it a vitally important component of the biodiversity in the region. As a result, there have been numerous biological and physical studies of the Rio Grande. For example, a quick search in Cambridge Abstracts with the term Rio Grande in the abstract returns over 1,000 articles. However, when the terms food web*, invertebrate*, or macroinvertebrate* are added, less than 10 peer-reviewed articles are listed. As a result, there is little known with regards to the macroinvertebrate community and food web dynamics and in the Rio Grande.

The goal of this dissertation was to gain a more detailed understanding of the macroinvertebrate community and the food web dynamics in the reach located in New Mexico, known as the Middle Rio Grande. Macroinvertebrates are a major component of diversity and a key component of food webs. Rivers are also intricately linked with their surrounding riparian areas. Therefore, this dissertation also included the surrounding riparian area. Additionally, the effects of seasonal variability and river regulation on aquatic and terrestrial macroinvertebrate communities are explored. To accomplish this, my dissertation is divided into three chapters that set out to: 1) determine the role of variability in stream discharge on the aquatic macroinvertebrate community; 2) determine the role of seasonal stream variability on lateral subsidies and food web dynamics of terrestrial and aquatic macroinvertebrates, with a focus on arthropod predators; and 3) determine the effects of channelisation on the interactions between the aquatic and terrestrial community with a focus on terrestrial arthropod predators.

Chapter 1: This chapter was an exploration of the aquatic macroinvertebrate community to set the stage for the next two chapters. The first goal was to explore the aquatic macroinvertebrate community, and therefore has a largely inductive approach. This chapter is based on almost 5 years of monthly invertebrate sampling beginning in 2004 and ending in August 2008. It set out to answer fundamental questions such as; how many species are present, what are the dominant and rare species, and what is the density of macroinvertebrates in the river? Abiotic factors, such as stream discharge, are known to be a key component in structuring aquatic communities. In addition to building a list of species, Chapter 1 also set out to explore the role of variability in stream discharge on the macroinvertebrate community.

Chapter 2: Previous studies have shown that adjacent systems are often linked together through the flow of nutrients and energy that can bolster secondary production and diversity in the recipient system. The directionality of the subsidy may be dependent on gradients in productivity. The goal of the second chapter was to explore seasonal changes in food web dynamics and whether changes in stream discharge affect the direction of lateral subsidies. Predaceous arthropods were the focus of this study.. A combination of survey data and stable isotope analyses from 2007 and 2008 were used for this chapter.

Chapter 3: The Rio Grande, similar to other rivers, is highly regulated. As a result several reaches in the Rio Grande have been channelised where the main channel is currently disconnected from the surrounding riparian areas. The transition zone between the aquatic and terrestrial system often harbors a unique species assemblage and is vitally important for overall diversity. Predator richness and abundances are known to be higher

at the transition zone between the aquatic and terrestrial system, as a result of lateral inputs. As a result, the purpose of this chapter was to investigate the effects of channelisation on lateral inputs to the terrestrial system and the macroinvertebrate community. This chapter used a combination of aquatic sampling, terrestrial pitfall trapping, and stable isotope analyses of predaceous arthropods to explore the differences in community structure and lateral subsidies between channelised and non-channelised reaches.

Chapter 1: The effects of a complex flow regime on the aquatic macroinvertebrate community in semi-arid land river ecosystems.

Abstract

Flow regime is a major driver of lotic community structure. The Rio Grande is a semi-arid land river that has a complex pattern of seasonal and annual variations in flow. Five years of survey data between 2004 and 2008 were used to determine the relationship of flow regime and the macroinvertebrate community. During this period of study there were significant variations in river discharge for spring flows and monsoonal rains that departed significantly from 30-year averages. Discharge was negatively correlated with total density and taxonomic richness. However, there were no major seasonal or annual shifts in species composition in relation to flow, with the exception of 2004 to 2005. The results of this study show that the Rio Grande has a complex pattern of temporal variability in discharge that reduced the density and taxonomic richness of macroinvertebrates. Changes in community structure were largely driven by turnover of a few dominant taxa.

Key Words: aquatic invertebrates, disturbance, drought, flooding, lotic, stream

1.0 Introduction

The role of environmental variability in structuring communities has received much interest (Connell 1978, Resh *et al.* 1988, Poff and Ward 1989, Dewson 2007). Lotic systems are often highly variable, with flow regime acting as a fundamental abiotic driver of community structure (Poff and Ward 1989, Junk *et al.* 1989, Thorp and Delong 1994, Puckridge *et al.* 1998). Flow rate can vary by several orders of magnitude in semi-arid streams in which high and low flow conditions often occur within the same year (Fisher *et al.* 1982, Stanley *et al.* 1997). Flooding and drying often create harsh conditions that exert intense pressures on the biota present and limit the community to organisms that are adapted to the intensity and frequency of disturbance (Lytle and Poff 2004, Dewson 2007).

Floods affect the physical characteristics of streams by altering and creating habitat heterogeneity at the landscape scale (Townsend *et al.* 1997, Lake 2000, Nelson and Lieberman 2002). The effects of floods on lotic communities have been well studied (Scrimgeour and Winterbourn 1989, Scarsbrook 2002, Collier and Quinn 2003, Robinson *et al.* 2003, Lepori and Hjerdt 2006, Suren and Jowett 2006) and generally indicate an immediate reduction in richness and density of macroinvertebrates after a flood. Additionally, the loss of diversity and density, as well as the recovery time of the community, are related to the magnitude and duration of flooding (Fisher *et al.* 1982).

In addition to floods, episodes of drought and low flows also serve as a source of disturbance in stream communities (Lake 2000, Humphries and Baldwin 2003, Suren and Jowett 2007). Similar to flooding, drought reduces the abundance and richness of organisms, and the impact on the invertebrate community is related to the duration of the

disturbance (Boulton 2003, Lake 2003). In some cases, macroinvertebrate communities have been shown to recover quickly within a few months after low flow and drought conditions (Cowx *et al.* 1984, Stanley *et al.* 1994, Stanley *et al.* 1997, Suren and Jowett 2007). Drought and flooding often have similar impacts on communities in terms of reducing richness and densities. However, the conditions in the environment and thus the pressures on organisms are quite different with drought and with flooding, leading to changes in the macroinvertebrate community (Townsend *et al.* 1997, Humphries and Baldwin 2003, Suren and Jowett 2007). Low flow conditions that are a normal part of the hydrograph can either reduce or increase densities and richness depending on the organisms present, and the biotic (predation or competition) and abiotic (changes in chemical and physical properties) processes that are occurring in the stream.

The response of macroinvertebrate communities to disturbance depends on several factors including the frequency, predictability, and severity of the disturbance (Lake 2000, Fritz and Dodds 2004, Dewson *et al.* 2007). To cope with disturbances, macroinvertebrates have evolved various responses such as short life-cycles, avoidance of stress, dormancy, or ability to recolonize quickly so that they can persist through the disturbance (Poff 1992, Townsend and Hildrew 1994). As a result, species turnover has been observed when streams experience seasonal high and low flows, where one set of organisms are present during wet times and a second set of organisms are present during dry times, creating temporal heterogeneity (Bogan and Lytle 2007). A similar pattern of 'dry year' and 'wet year' communities was also found in California streams that exhibited annual wet and dry fluctuations (Beche and Resh 2007).

Given enough time, many communities are resilient in that they return to a state similar to the community before the disturbance (Wallace 1990, Matthaei *et al.* 2000, Scarsbrook 2002, Suren and Jowett 2006). For example, Suren and Jowett (2006) demonstrated that community similarity increased with increasing stability in the community following a disturbance. Additionally, Lepori and Hjerdt (2006) demonstrated that diversity increased following periods of stability after a flood.

In unstable environments with unpredictable disturbances, richness is often reduced to a few taxa capable of surviving or quickly recolonizing a stream, which may add to long-term stability (Poff 1992). For example, Scarsbrook (2002) showed that where high interannual variation in the invertebrate community was observed, the community remained stable over a nine-year time period (Scarsbrook 2002).

Aquatic macroinvertebrates in arid-land rivers are subject to harsh conditions where streams are characterized by high coefficients of variation in stream flows that range between droughts with no flows to floods (Poff and Ward 1989). In the southwestern United States, the Rio Grande experiences wide variations in seasonal flow where the macroinvertebrate community can be subjected to both drought and flooding over a short period of time (Crawford *et al.* 1993, Vivoni *et al.* 2006). In New Mexico, the Rio Grande typically experiences peak discharge in the spring, lower flows in the summer, and monsoonal rains, creating a complex pattern of flows and disturbances. There are few studies that have focused on seasonal and annual changes in macroinvertebrate communities in streams with complex patterns of flow variability, especially the effects of severe drought.

The focus of this study is to analyze the effects of temporal variability in stream flow on the macroinvertebrate community in the Middle Rio Grande, New Mexico. The Middle Rio Grande is defined as the reach between Cochiti dam in the north and Elephant Butte Reservoir in the south. Specifically, I investigated whether there are shifts in the community (*i.e.* changes in species composition and community metrics) in response to the timing of different types of disturbance and seasons. To accomplish this, I used 5 years of continuous monthly survey data of aquatic macroinvertebrates, from 2004 to 2008, to test the relationship between seasonal and annual flow characteristics on the macroinvertebrate community structure. Additionally, the hydrograph of the middle Rio Grande was analyzed for the years between 1978 and 2008 by using US Geological Survey (USGS: <http://water.usgs.gov/>) gauge stations in the Rio Grande, to determine seasonal and annual patterns in flow regime since the development of Cochiti dam at the northern end of the Middle Rio Grande.

2.0 Materials and Methods

2.1 Site Description

The Rio Grande is the second largest watershed in the southwestern United States. Its headwaters are located in the San Juan Mountains of southern Colorado and it empties into the Gulf of Mexico in southern Texas. The Middle Rio Grande (MRG), for this study, is comprised of the stretch between the Cochiti Reservoir north of Albuquerque and Elephant Butte, encompassing 8% of the total length of the river (Fig 1-map of the MRG). In upstream reaches of the MRG, water temperature and flows are largely determined by hypolimnetic releases from Cochiti dam. Since the completion of the Cochiti dam in 1973,

high water flows have been capped at approximately 250 m³/s (USGS <http://water.usgs.gov/>).

Within the MRG, the river transitions from a restricted channel with clear, cold water and cobbly substrate to a more braided river with a historically wider floodplain and substrates that are primarily sand and silt. The stream hydrograph within the MRG can be variable due to monsoonal rains and draining for agricultural purposes. Therefore, flow data was obtained from three different locations within the MRG from the United States Geological Survey (USGS <http://water.usgs.gov/>) to coincide with the sampling locations (Fig. 1). Five sampling locations were selected to encompass the majority of the MRG (Fig. 1). Each location was sampled monthly for aquatic macroinvertebrates from May of 2004 to September of 2008. Each sample site was divided into one of three habitats; isolated pools, backwater, and the main channel. Flow and connectivity to the main channel were the major variables for habitat classification. An isolated pool (IP) was defined as being disconnected from the main channel and having no flow. Backwaters (BW) were defined as being connected to the main channel with flows less than 0.1m/s. The main channel was defined as the main stem of the river. The presence, longevity and relative proportions of each habitat type depended on the current and recent flow conditions, along with the physical characteristics of the river.

2.2 Macroinvertebrate sampling

Macroinvertebrates are an abundant and diverse component of aquatic ecosystems and are well suited for this study due to their abundance and often rapid population turnover. A 0.2 m² circular throw trap was used to quantify abundances and diversity of aquatic macroinvertebrates within habitats at each site. A total of three throws were used

for each habitat, with a maximum of nine throws at a sampling site. In the event that multiple isolated pools or backwater habitats were present, one throw per isolated pool or backwater habitat was performed. A pilot study was completed prior to the initiation of this study to determine spatial patterns in the density of aquatic macroinvertebrates in the MRG. Results from the pilot indicate that 99% of the macroinvertebrates were collected within 1 meter of the shoreline. Therefore for this study, each sample from the throw trap was haphazardly placed near the shoreline to ensure that the highest densities of macroinvertebrates were collected. Specimens were removed from the throw trap using a 500 μ m mesh net, sorted live in the field, placed in 95% ethanol and taken to the lab, where they were identified to the lowest practical taxonomic level (typically to family because of the presence of early instars; Bogan and Lytle 2007). Because the number of habitats sampled at each location and sampling period varied, abundance counts were converted to catch-per-unit densities. Jackknife analyses of the throw trap data at each site and habitat indicated that the collecting procedures captured over 95% of the diversity theoretically present (Krebs 1999). Jackknife estimates are based on the frequency of rare species in the community (Heltshel and Forrester 1983).

2.3 Data analyses

Flow data were obtained from the United States Geological Survey (USGS) website for Cochiti (USGS 08317400), Albuquerque (USGS 08330000), and San Acacia (USGS 08354900) monitoring stations (Website: <http://water.usgs.gov/waterwatch>). Monthly mean data between 1978 and 2008 at the three monitoring locations were used to determine the mean annual flows. Departures from average river discharge are determined by percentiles based on the discharge values recorded during all years that

measurements were made (USGS Website: <http://water.usgs.gov/waterwatch>). Values above 75% are considered “above normal” discharge and values below 25% are considered “below normal” discharge. For this study, 30 years of hydrograph data were used beginning in 1978, after the completion of Cochiti dam.

Due to the presence of rare taxa, only the 10 most abundant macroinvertebrates were used for statistical analyses of community-wide data. Differences in catch per unit effort (density), Simpson’s diversity (1-D), and taxonomic richness between sampling locations, season (with the exception of winter), and years were analyzed using a general linear model (GLM). Simpson’s diversity (1-D) is an index of diversity that takes into account the number of species present (species richness), the relative abundance of each species, and changes in abundant species. Values range from 0 to 1, with 1 being the highest diversity. Values for catch per unit effort were log+1 transformed to meet the assumptions of normality. The ten most abundant species were also tested for differences in catch per unit effort between sampling locations, seasons and years using a GLM. To meet the assumptions of normality, the density data for each species were log+1 transformed. Analyses were performed in SYSTAT 11.

A Spearman’s coefficient of rank correlation (r_s) was used to determine the correlations between catch per unit effort, Simpson’s diversity (1-D), and taxonomic richness on five characteristics of river discharge; average seasonal discharge (Q_{ave}), minimum seasonal average (Q_{min}), maximum seasonal average, (Q_{max}), the standard error (Q_{SE}), and the coefficient of variation (Q_{vc}). The ten most abundant taxonomic groups were also analyzed for individual responses to average seasonal and annual discharge.

Significance of each correlation was determined by using a two-tailed t-test. Data from all sites were pooled together for temporal analyses.

3.0 Results

3.1 Flow variability in the Rio Grande

Between 1978 and 2008, mean monthly discharge was highest in May as a result of snow-melt runoff (Fig. 2). April had the largest monthly variability in discharge which reflected the differences in amount of winter precipitation and the timing of snow melt (Fig. 2). Low discharge typically occurred between peak spring flows and before the onset of monsoonal rains that usually began in July and continued through August (Fig. 2). The lowest rate of stream discharge was typically in October (Fig. 2). Annual mean discharge was highly dependent on snow melt, meaning that lower snow pack in southern Colorado resulted in reduced spring and annual discharge. Annual discharge in the Rio Grande could be divided into wet and dry years determined by snow melt. When mean annual discharge was divided into one of two groups, above 30 m³/s (14 years) and below 30 m³/s (16 years), wet years had on average three times the annual discharge as dry years (Fig. 2).

Average monthly discharge between 2004 and 2008 ranged from a low of 0.067 m³/s in September 2004 at San Acacia to a high of 144 m³/s at Albuquerque in May 2005. The highest average daily discharge was 189 m³/s in June 2005 at Cochiti, and there were several days in 2004 and 2005 where daily flows reached zero m³/s at San Acacia (USGS Website: <http://water.usgs.gov/waterwatch>). The largest 24-hour fluctuation was in July 2006 at San Acacia when flows went from approximately 4.53 m³/s to peaking at nearly 255 m³/s and then returning to just under 17 m³/s in less than 24 hours due to monsoonal

precipitation (USGS Website: <http://water.usgs.gov/waterwatch>). It should also be noted that sections of the MRG between Albuquerque and San Marcial were dry during the summers of 2004 and 2003 (Pers. obs.)

The average annual discharge for the years within this study was considered normal with the exception of 2004 which was below normal (Table 1). However, there were several departures from normal for both spring and monsoonal discharge. The most notable departures from normal discharge occurred in 2005 and 2006. The snow pack in the winter of 2004/2005 was above normal resulting in above normal discharge for 54 days from April through June (USGS website: <http://waterdata.usgs.gov>). In contrast to the winter of 2005, the winter of 2006 was very dry, resulting in below normal spring discharge (Table 1). The monsoonal season also underwent extremes in 2005 and 2006. In 2005, the monsoon was below normal after above normal discharge in the spring (Table 1). The opposite situation occurred in 2006 where monsoonal discharge was above normal and spring discharge was below normal. Mean annual and seasonal discharge in 2007 and 2008 were near normal compared to the previous 30 years (Table 1). As a result of the seasonal variability in river discharge between 2004 and 2008, this study encompassed most of the variability that is typically observed in the Middle Rio Grande.

3.2 Invertebrate community results

Approximately 15,065 aquatic macroinvertebrates representing 42 families in 13 orders were collected between 2004 and 2008. The ten most abundant taxa accounted for 95.7% of all the organisms collected, and the 15 most abundant taxa accounted for 97.8% of all organisms collected (Table 2). Chironomids and corixids overwhelmingly dominated the community and accounted for 74.0% of all taxa collected (Table 2).

Average macroinvertebrate densities for the MRG ranged from a low of less than one organism/m² in November 2005 to a high of 806 organisms/m² in May 2004 representing an approximately 800% difference in densities between summer and winter months (Fig. 3).

Community differences: There were significant differences in the density, taxonomic richness, and Simpson's diversity of aquatic macroinvertebrates in the MRG ($F_{1,73}=9.05$, $P=0.005$ density; $F_{1,73}=5.65$, $P<0.02$ richness; and $F_{1,71}=6.75$, $P=0.011$ Simpson's diversity) (Fig 3). Based on the Spearman rank correlations, annual river discharge was negatively correlated with density ($r=-0.601$, $t_{1,23}=3.61$, $P=0.0014$), but was positively correlated with Simpson's diversity ($r=0.64$, $t_{1,23}=3.68$, $P=0.001$) (Table 4). Maximum and Standard Error of river discharge were both negatively correlated with density, however these correlations were not significant (Table 4). Excluding winter, there were no significant differences between seasons (*i.e.* between spring and summer, summer and fall) for the three community metrics during this study. However, the timing of peak macroinvertebrate densities was highly variable between years and occurred as early as April in 2006 or as late as September in 2005 (Fig 3). On average, spring had the highest densities with an average of 131 ± 67 organisms/m², and summer had the highest taxonomic richness with 20.2 ± 1.9 taxa for all years combined. The highest seasonal average for density for all sample sites combined was in 2004, and excluding winter, the lowest average seasonal density was in the spring of 2008 (Table 4).

Species differences: Changes in the densities of chironomids and corixids, the two most abundant taxa, were responsible for the major changes in the overall community structure (Table 3). Higher rates of river discharge significantly reduced the density of

chironomids and corixids ($F_{1,73}=7.33$, $P=0.008$ and $F_{1,73}=5.91$, $P=0.017$ respectively). There were also annual changes in the rank order of the 15 numerically dominant taxa (Table 3). For example, corixids underwent a hundred fold reduction from their highest recorded densities in 2004 and were ranked 4th in 2008 (Table 3). Chironomids, however, were the most abundant taxa in all subsequent years. Taxonomic richness also varied with a high of 26 taxa collected at HWY 60 in the summer of 2004 (Table 3). Heptageniids were the only taxa with significant differences in seasons ($F_{2,72}=3.57$, $P=0.033$).

Spatial differences: Based on the GLM, there were no significant differences in density, taxonomic richness or Simpson's diversity between the five sample sites in the Middle Rio Grande ($F_{4,70}=0.557$, $P=0.695$ density; $F_{4,70}=1.71$, $P=0.159$ richness; and $F_{4,70}=1.50$, $P=0.211$ Simpson's diversity). Of the 15 most abundant taxa, there were no individuals with significant responses to sample location. Only two families, both mayflies (Ephemeroptera) had significant population differences between sites ($F_{4,70}=6.43$, $P<0.01$ Baetidae, $F_{4,70}=8.91$, $P<0.01$), where they were more common in the northern reaches of the MRG.

4.0 Discussion

River discharge in the MRG during the course of this study included times that were above and below normal. Annual and seasonal patterns of discharge had major effects on the macroinvertebrate community. Analyses of the hydrograph indicated that there were three types of disturbance that occurred in the Middle Rio Grande; ramp disturbance from spring discharge, summer low or no discharge conditions, and pulse disturbance from monsoonal rains. Spring discharge from snow melt was the major factor determining annual discharge, which was augmented by monsoonal rains during the

summer in July and August. Floods have been typically been defined as ‘pulse disturbances’ because they are discrete events (Lake 2000). However, peaks in spring discharge were actually characteristic of a ‘ramp disturbance’ because they slowly increased and decreased in size, lasting over a month with few daily fluctuations. Stream discharge during the monsoon season tended to be ‘flashy’ in nature representing a ‘pulse disturbance’, where peak flows were a discrete event that lasted for several hours to a several days. Average daily discharge rates during the monsoon season varied dramatically with high coefficients of variation.

Higher river discharge reduced the densities and richness of macroinvertebrates regardless of whether they were spring or monsoonal discharges representing ramp or pulse disturbances. The loss of richness and densities during high stream discharge is consistent with other studies showing the negative relationship with high discharge (Dodds *et al.* 2004, Robinson *et al.* 2004, Lepori and Hjerd 2006, Liu and Wang 2008,). Peak density and richness occurred during low flow periods except when flow variability was higher during monsoonal rains. The highest densities and richness for this study were recorded in the springs of 2004 and 2006. Both of these peaks occurred in the spring of relatively dry years, after a dry monsoon season the previous summer. The density of macroinvertebrates remained much lower in 2007 through 2008. The reason for this may have been the very wet monsoon in 2006 that highly impacted the macroinvertebrate community. In 2005 and 2008 densities peaked in the late summer and early fall (the peak was in September), but densities remained an order of magnitude lower than the peak densities of 2004 and 2006.

One possible explanation for these large changes in densities is a time-lag effect where it takes the community longer to recover from above normal flows, which is similar to other streams (Lake 2004, Dewson *et al.* 2007). The lowest flow year for the decade was in 2003, an extremely dry year, which was followed by the highest density and richness found during the course of this study. The macroinvertebrate densities in 2004 were driven by corixids which overwhelmingly dominated the community. Despite high richness in 2004, Simpson's diversity was actually low because of the dominance of one species. However, the high taxonomic richness and presence of corixids indicates that the macroinvertebrate community may have the capacity to respond relatively quickly to low flow and drought conditions (Boulton 2003, Acuna *et al.* 2005, Dewson *et al.* 2007). In 2006, the dominant taxa were chironomids, and corixids were second. In 2005, 2007, and 2008, the wetter years, peak densities occurred several months after high discharge, but were much lower than peak densities in dry years. However, the duration of this study was too short to sufficiently test lag time effects for the community to recover after periods of high discharge.

Many of the differences in the MRG macroinvertebrate community were driven by seasonal and annual changes in the densities of corixids and chironomids in response to flow. Although richness and density were often positively correlated with low flow conditions, diversity was negatively correlated because of the overwhelming dominance of a few taxa. One of the major changes in community composition was the reduction of corixids during the study. The annual differences in the seasonal patterns of discharge were substantial and suggest a change in community between years (Boulton *et al.* 1992, Bogan and Lytle 2007). With the exception of two taxa, the 15 numerically dominant

taxa were present each year. Additionally, only heptageniids had a seasonal preference, indicating that there was no taxonomic turnover as seen in other systems (Beche and Resh 2007, Bogan and Lytle 2007, Robinson and Uehlinger 2008). However, since the dominant organisms were present year to year, persistence was high, which was similar to other streams in harsh conditions (Townsend *et al.* 1997). These findings were different than Scarsbrook's (2002) who found in that stability 26 streams was highest in frequently disturbed streams because relative abundance did not change, while persistence was highest in streams that were more stable.

Chironomids have very fast generation times, which would allow them to recover quickly after disturbance (Merritt and Cummins 1999). The rank order of the 15 most common taxa changed each year in the Rio Grande. Most notable was the constant decline of the Corixids from their highs in 2004. The reason for their unusually high numbers in 2004 was not known, but it could have been correlated with the extremely low stream discharge in the previous year. Corixids were also present in high numbers in the spring of 2006 after a dry monsoon season in 2005. They generally prefer lentic conditions that would prevail in years with extreme low flows (Merritt and Cummins 1996).

5.0 Conclusion

This study captured some of the highest seasonal variation in discharge the Rio Grande now experiences. Like many streams, invertebrate densities were negatively correlated with high discharge and high variability, which changed seasonally. It is unclear whether times of low discharge concentrated macroinvertebrates into a smaller area, or if their numbers became diluted as a result of increased surface area. The most likely explanation

is that the abundance of macroinvertebrates for a given reach is highest during times of lower discharge. The reasons for this include more stable habitats and increased food availability from in-stream primary production, which has been shown to be higher during times of reduced river discharge (Voelz and McArthur 2000, Dewson *et al.* 2003, Suren *et al.* 2003). Future studies should focus on quantifying the relationship of stream discharge and primary production to the abundance of aquatic macroinvertebrates in the MRG.

The Rio Grande was overwhelmingly dominated by a few taxonomic groups, which was most likely the result of the harsh environment acting as a filter limiting the community to taxa that are capable of surviving under harsh conditions. The dominance of corixids at the beginning of the study in a dry year, and their decline in abundance in years with higher seasonal discharge, may indicate species turnover between wet and dry years. However, this pattern did not remain consistent despite the fact that corixids did respond negatively to flow. These results highlight the necessity of long-term data sets to elucidate long-term trends. Without further temporal replication it is unclear whether the abundance in corixids in 2004 was anomalous, or driven by below normal discharge in the spring and summer of 2003. Additionally, without temporal replication and long-term data sets, lag-time effects which may play a very important role in the macroinvertebrate community cannot be resolved. As seen in this study, three extreme, different climatic events occurred in a five year time period, and only long term data sets can fully resolve the impact of these disturbances on the macroinvertebrate community.

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Figure 1: Sample locations in the middle Rio Grande, New Mexico. Cochiti is the northern boundary and Elephant Butte Reservoir forms the southern boundary. The five sample locations from north to south were Angostura, Rio Rancho, Highway 60, Escondida, and San Marcial

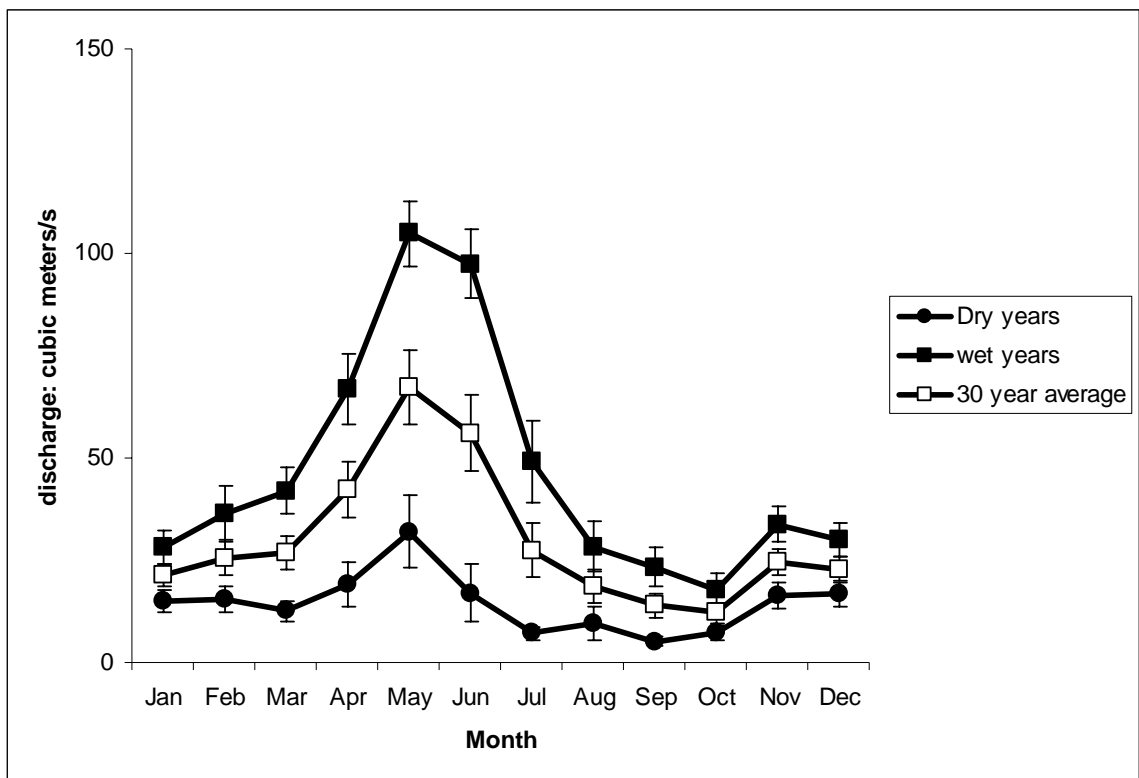


Figure 2: The average stream discharge by month for the Middle Rio Grande (MRG) for the 30 years after the construction of Cochiti dam (1978-2007). The average discharge was determined from daily discharge data from the US Geological Survey (USGS) stream gauges at Cochiti dam, Albuquerque, and San Acacia. The wet and dry years in the MRG were based on dividing the annual discharge into wet or dry based on a cutoff of $30\text{m}^3/\text{s}$. The error bars represent the Standard Error.

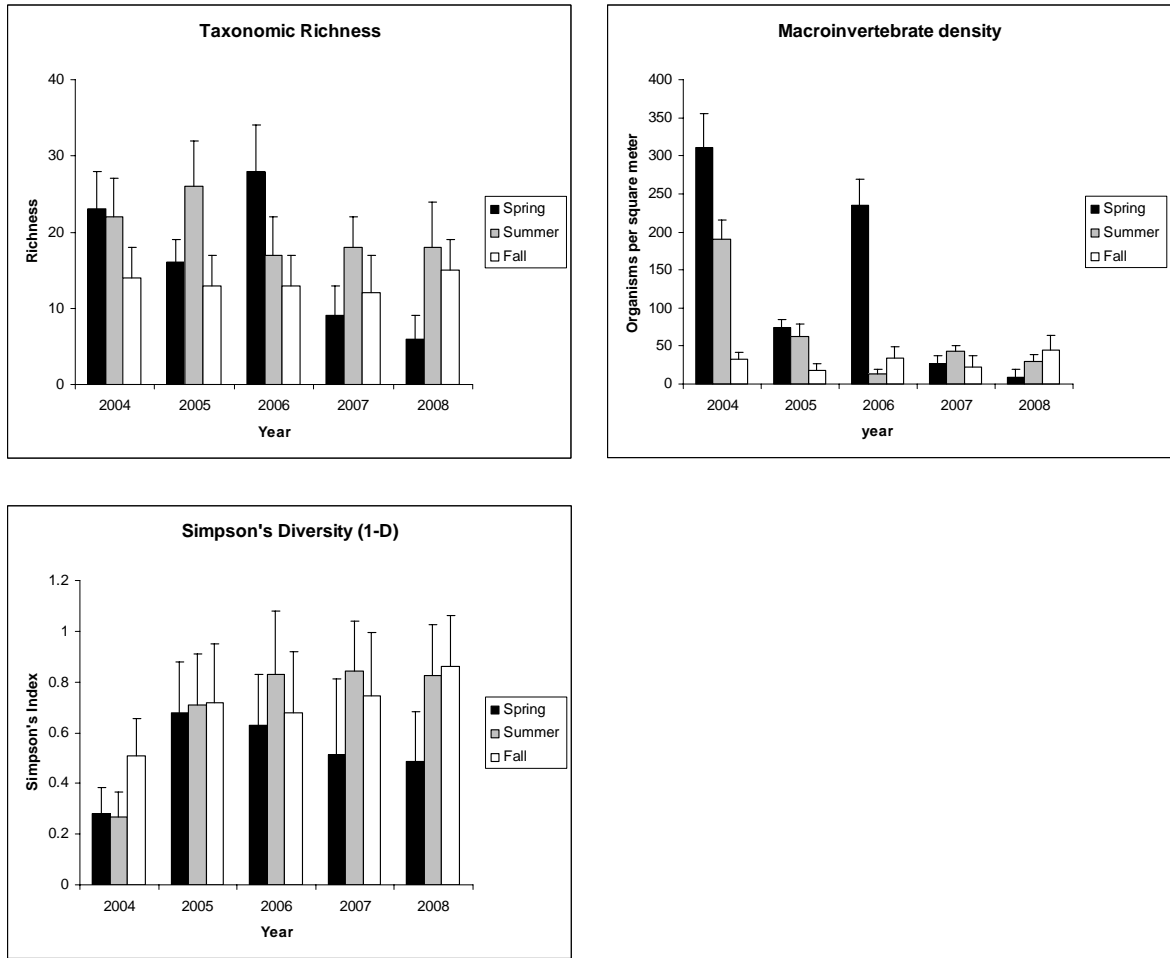


Figure 3: Time series data for the average macroinvertebrate density, taxonomic richness, and Simpson's Diversity (1-D) in the Rio Grande for each season. The location data for each season were pooled together. Error bars represent the standard Error (SE).

Table 1: *The mean annual and season (spring: May monsoon: August) discharge in cubic meters per second and percentiles in the Middle Rio Grande (MRG) between 2004 and 2008.* Percentiles were based on 30 years of hydrograph data. The mean discharge was an average from three USGS stream gauges in the MRG (Cochiti, Albuquerque, and San Acacia). An * denotes above or below normal river discharge for a given time period

| Year | Annual discharge | | Spring discharge | | Monsoonal discharge | |
|-------------|-------------------------|-------------------|-------------------------|-------------------|----------------------------|-------------------|
| | Mean | Percentile | Mean | Percentile | Mean | Percentile |
| 2004 | 21.4 ± 2.6 | 24* | 54.3 ± 8.5 | 30 | 8.0 ± 3.7 | 97* |
| 2005 | 34.6 ± 8.2 | 45 | 139.6 ± 4.6 | 85* | 10.8 ± 3.1 | 15* |
| 2006 | 21.1 ± 0.5 | 27 | 15.8 ± 5.9 | 9* | 41.1 ± 16.6 | 88* |
| 2007 | 25.2 ± 2.3 | 39 | 69.6 ± 5.0 | 42 | 13.2 ± 5.3 | 27 |
| 2008 | 46.2 ± 4.4 | 72 | 106.2 ± 6.0 | 64 | 17.3 ± 4.1 | 52 |

Table 2: The 15 most abundant macroinvertebrate taxa found in the middle Rio Grande from 2004 to 2008. An * denotes taxa that were not collected in all years.

Together, these taxa account for 98% of all the macroinvertebrates collected for this study.

| Order | Family | Total | Rank | Percentage |
|----------------|-----------------|--------------|-------------|-------------------|
| Diptera | Chironomidae | 5464 | 1 | 37.6 |
| Hemiptera | Corixidae | 5460 | 2 | 37.6 |
| Oligochaeta | | 1208 | 3 | 8.31 |
| Ephemeroptera | Baetidae | 815 | 4 | 5.61 |
| Ephemeroptera | Tricorythidae | 458 | 5 | 3.15 |
| Ephemeroptera | Heptageniidae | 321 | 6 | 2.21 |
| Diptera | Ceratopogonidae | 286 | 7 | 1.97 |
| Pulmonata | Lymnaeidae | 129 | 8 | 0.887 |
| Odonata | Gomphidae | 124 | 9 | 0.852 |
| Coleoptera | Dytiscidae | 117 | 10 | 0.802 |
| Pulmonata | Physidae | 100 | 11 | 0.688 |
| Ephemeroptera* | Siphonuridae | 95 | 12 | 0.653 |
| Hemiptera | Gerridae | 60 | 13 | 0.413 |
| Coleoptera | Hydrophilidae | 58 | 14 | 0.399 |
| Trichoptera* | Leptoceridae | 45 | 15 | 0.309 |

Table 3: The rank order by year of the 15 most abundant taxa in the middle Rio Grande.

An * indicates taxa that were absent in at least one year.

| Order | Family | 2004 | 2005 | 2006 | 2007 | 2008 |
|----------------|-----------------|-------------|-------------|-------------|-------------|-------------|
| Diptera | Chironomidae | 3 | 1 | 1 | 1 | 1 |
| Hemiptera | Corixidae | 1 | 2 | 2 | 4 | 4 |
| Oligochaeta | | 4 | 3 | 3 | 3 | 3 |
| Ephemeroptera | Baetidae | 2 | 4 | 4 | 2 | 2 |
| Ephemeroptera | Tricorythidae | 6 | 5 | 5 | 6 | 6 |
| Ephemeroptera | Heptageniidae | 9 | 6 | 8 | 5 | 5 |
| Diptera | Ceratopogonidae | 5 | 8 | 6 | 8 | 8 |
| *Pulmonata | Lymnaeidae | | | 7 | | |
| Odonata | Gomphidae | 11 | 10 | 11 | 7 | 7 |
| Coleoptera | Dytiscidae | 10 | 14 | 10 | 15 | 15 |
| Pulmonata | Physidae | | 9 | | | |
| *Ephemeroptera | Siphonuridae | | | 9 | 12 | 14 |
| Hemiptera | Gerridae | 4 | 12 | | | 9 |
| Coleoptera | Hydrophilidae | 12 | 15 | 14 | | |
| Trichoptera | Leptoceridae | | 7 | | 11 | |

Table 4: Spearman's rank correlation matrix between community metrics and annual discharge. An * indicates a significant correlation ($P \leq 0.05$).

| | <u>Density</u> | <u>Richness</u> | <u>Diversity</u> | <u>Ave Flow</u> | <u>SE</u> | <u>CV</u> | <u>Max</u> | <u>Min</u> |
|------------------------|----------------|-----------------|------------------|-----------------|-----------|-----------|------------|------------|
| Density | 1 | | | | | | | |
| Richness | 0.462* | 1 | | | | | | |
| Diversity (1-D) | -0.410* | -0.203 | 1 | | | | | |
| Ave. Discharge | -0.601* | -0.131 | 0.643* | 1 | | | | |
| SE | -0.440* | -0.254 | 0.393* | 0.532 | 1 | | | |
| CV | -0.357 | -0.337 | -0.052 | -0.048 | 0.514 | 1 | | |
| Max | -0.397* | -0.219 | 0.392* | 0.522 | 0.987 | 0.493 | 1 | |
| Min | -0.129 | -0.178 | 0.229 | 0.243 | 0.443 | 0.261 | 0.300 | 1 |

Chapter 2: Seasonal stream discharge variability, tangled food webs, and shifting resources of predaceous macroinvertebrates in a semi-arid river.

Abstract

Riverine systems and their surrounding terrestrial landscape are intimately linked together through the transfer of nutrients and energy. Flow variability can directly affect rates of aquatic primary productivity and macroinvertebrate communities. Survey data and stable isotope analyses of macroinvertebrates were used to gain a more detailed understanding of how variability in discharge affects lateral inputs between aquatic and terrestrial systems. Macroinvertebrates were surveyed during times of low and high discharge in 2007 and 2008. Survey results indicated that terrestrial and aquatic macroinvertebrates peaked in richness and abundance in late summer during low discharge. The synchronous peaking in macroinvertebrates abundance and diversity may be, in part, the result of peak production of aquatic and terrestrial systems coinciding during times of reduced discharge. As a result lateral subsidies in the form of insect prey were bidirectional. During times of higher discharge, the density of aquatic macroinvertebrates and terrestrial predators were lower with the exception of wolf spiders. Wolf spiders were the only predator that had significant changes in their reliance on aquatic production. Terrestrial arthropod predators at the water's edge may be strongly impacted by seasonal changes in discharge that affect the directionality of lateral subsidies. This study also highlights the need to quantify production at different stages of discharge to strengthen the conclusions.

Key Words: allochthonous, arthropod predators, lateral subsidies, riparian

1.0 Introduction

Streams and their surrounding riparian zones are intimately linked together through the exchange of nutrients and energy (Likens and Bormann 1974). Lateral inputs between aquatic and terrestrial systems are often reciprocal in nature (Nakano and Murakami 2001, Baxter *et al.* 2005). For example, leaves falling into aquatic systems can serve as major sources of carbon for detritivores and shredders that later emerge into the terrestrial system in the spring (Cummins 1974, Vannote *et al.* 1980). These lateral subsidies between aquatic and terrestrial systems have been shown to bolster secondary production above what the normal primary production of the system can maintain (Polis *et al.* 1997, Sanzone *et al.* 2003, Paetzold *et al.* 2005, Burdon and Harding 2008). As a result, these areas are home to some of the highest rates of diversity on the planet and are of critical importance to biodiversity (Junk *et al.* 1989, Bayley 1995, but see Sabo *et al.* 2005).

Terrestrial inputs into aquatic systems are of paramount importance for aquatic food webs (Vannote *et al.* 1980, Junk *et al.* 1989, Thorpe and Delong 1994, Thorp *et al.* 1997, Tockner *et al.* 2000, Reid *et al.* 2008). Allochthonous inputs include prey items mostly in the form of insects and plant material (Vannote *et al.* 1980, Junk *et al.* 1989, Kawaguchi *et al.* 2003). The importance of insects falling on the water's surface and providing a direct food source for stream fish such as salmonids has been well documented (Mason and MacDonald 1982, Baxter *et al.* 2005, Nakano and Murakami 2000, Kawaguchi *et al.* 2003). Additionally, leaf fall from the terrestrial environment provides a bottom-up effect, forming an indirect food source for predators (Wallace *et al.* 1997, Reid *et al.* 2008).

Aquatic primary production is known to be an important factor for higher rates of secondary production in terrestrial systems (Polis *et al.* 1997, Collier *et al.* 2002). Emerging adult insects from aquatic systems form a lateral subsidy to adjacent riparian areas that bolster the abundance and richness of riparian predators, including vertebrates and invertebrates (Herring and Plachter 1997, Sabo and Power 2002, Collier *et al.* 2002, Baxter *et al.* 2005, Paetzold *et al.* 2005). For arthropod predators, the increase in abundance and diversity is highest at the water's edge dropping off sharply within a few meters (Briers *et al.* 2005, Paetzold *et al.* 2005). Predaceous arthropods from diverse groups such as wolf spiders (Aranae: Lycosidae), predaceous ground beetles (Coleoptera: Carabidae), and toad bugs (Hemiptera: Gelastocoridae) congregate near the water's edge and rely on the emergence of adult insects (Herring and Plachter 1997, Brier's *et al.* 2005, Paetzold *et al.* 2005, Kennedy, Chapter 2).

The linkages between aquatic and terrestrial systems are also temporally dynamic (Vannote *et al.* 1980, Junk *et al.* 1989, Wallace *et al.* 1997, Nakano and Murakami 2000, Baxter *et al.* 2005, Paetzold *et al.* 2005). In a landscape where peaks in aquatic and terrestrial primary productivity are asynchronous, theory predicts that energy will flow from more to less productive systems (Huxel and McCann 1998). For example, Nakano and Murakami (2001) illustrated the importance of seasonal changes in allochthonous inputs between aquatic and terrestrial systems. The reciprocal nature of the food web was illustrated where aquatic insects emerged in the spring when terrestrial invertebrates were less common, providing a food source for forest birds. During the summer, terrestrial insects were an important subsidy to fish when in-stream production was lowest (Nakano and Murakami 2001).

Temporal variation in autochthonous and allochthonous inputs can strongly influence the resources an organism uses. For example, in temperate streams, salmonids feed on aquatic insects in the winter, which are primarily dependent on in-stream production (Kawaguchi and Nakano 2001). In contrast, during the summer, salmonids feed on terrestrial insects that fall on the water's surface. As a result, salmonids seasonally switch between allochthonous and autochthonous sources of production (Kawaguchi and Nakano 2001). Seasonal fluxes of emerging insects can also affect the distribution of web-building spiders (Kato *et al.* 2003). Through an experimental approach, Kato *et al.* (2003) demonstrated that a reduction in the flux of emerging insects reduced the density of horizontal orb-weaving spiders (Araneae: Tetragnathidae) along a stream. Additionally, ground-dwelling wolf spiders (Araneae: Lycosidae) have been shown to vary seasonally in the amount of aquatic prey they consume (Paetzold *et al.* 2005).

Seasonal variation in lateral inputs and subsidies has been shown to be a major influence on vertebrate and terrestrial invertebrate predators (Kawaguchi and Nakano 2001, Kato *et al.* 2003, Paetzold *et al.* 2005). However, the role of variability in stream discharge on lateral subsidies is less well known. Understanding the role of stream discharge on lateral inputs is crucial to our understanding of food web dynamics because discharge can have a large effect on in-stream primary productivity and density of macroinvertebrates (Scrimgeour and Winterbourn 1989, Lake 2000, Robinson *et al.* 2004). Arid-land rivers are temporally dynamic systems with large fluctuations in discharge which influence the density of aquatic macroinvertebrates (Kennedy, Chapter 1). The aim of this study was to gain a more detailed understanding of seasonal

variability in discharge on the directionality of lateral subsidies. Survey data and stable isotope analyses were used to simultaneously examine changes in terrestrial and aquatic macroinvertebrate populations between times of high and low discharge. Stable isotopes of carbon and a two stage mixing model were used to determine the reliance of arthropod predators on terrestrial or aquatic sources of carbon.

2.0 Materials and Methods

2.1 Study Location

The study was conducted in the Middle Rio Grande (MRG), a 363 km reach that is delimited by Cochiti dam upstream and Elephant Butte Reservoir downstream in New Mexico encompassing 8% of the total length of the river (Fig. 1). The Rio Grande originates in the San Juan Mountains of southern Colorado and empties into the Gulf of Mexico in southern Texas. The stream hydrograph within the MRG is seasonally variable with peak stream discharge in the spring. Stream discharge is typically lower in the summer, but is augmented from monsoonal precipitation in July and August. As a result, the MRG experiences seasonal episodes of high and low discharge that occur during the growing season. There is also annual variation in discharge that is driven by differences in the timing, magnitude, and duration of spring discharge and monsoonal rains.

Four sample locations were chosen in non-channelised reaches that were not as heavily impacted by channelisation. At the southern and northern most sample sites, the groundcover was dominated by either sand or gravel and was sparsely vegetated. The two middle sites had young vegetative cover that originated in 2005 after heavy spring flooding. The majority of the existing floodplain at each location was inundated during peak spring discharge in 2007 and 2008. Stream discharge data was obtained from the

United States Geological Survey (USGS) website for Cochiti (USGS 08317400), Albuquerque (USGS 08330000), and San Acacia (USGS 08354900) monitoring stations (Website: <http://water.usgs.gov/waterwatch>).

2.2 Macroinvertebrate Sampling

Pitfall Traps: Terrestrial and aquatic macroinvertebrates were collected to assess food web dynamics and differences in the community structure of predaceous arthropods during low and high discharge periods. Arthropods were collected in May and August of 2007 and 2008. Trapping times were scheduled to coincide with annual patterns of peak discharge in the spring and low discharge in the summer. Predaceous arthropods congregate near the water's edge to prey on emerging aquatic insects (Sanzone *et al.* 2003, Paetzold *et al.* 2005, Kennedy, Chapter 1). Therefore, at each location, a single row of 10 pitfall traps was placed approximately 5 meters apart, and approximately 1 meter from the water's edge. Each trap was a plastic cup with a 10 cm diameter and 250 ml volume containing 25 ml of 70% ethanol. Traps were checked 48 hours after they were set. Additional arthropod predators that reside at the water's edge, on the water's surface, and in the water were collected to supplement the sample size of predators for isotopic analyses. These included water striders (Hemiptera: Gerridae), damselflies (Odonata: Coenagrionidae), dragonflies (Odonata: Libulellidae), diving beetles (Coleoptera: Dytiscidae), and toad bugs (Hemiptera: Gelastocoridae). Macroinvertebrates were taken to the lab, identified to the lowest practical taxonomic level and preserved in 95% ethanol.

Aquatic Sampling: Aquatic macroinvertebrates were collected at the same locations and coincided with the pitfall trap sampling. At each site and sampling period,

the aquatic habitat was divided into three main habitat types; main channel (MC), backwater (BW), and isolated pools (IP). Flow and connectivity to the main channel were the major variables for habitat classification. The main channel was the main stem of the river. Backwaters were defined as being connected to the main channel but with conditions of zero or little flow (<0.1 m/s) relative to the main channel. Isolated pools were completely disconnected from the main channel with zero flow. The number and sizes of each type of habitat varied depending on the degree of channelisation and the current flow conditions of the river.

A circular throw trap (0.2 m²) was used to collect aquatic macroinvertebrates in each habitat. A total of three haphazard throws were made for each habitat with a maximum of nine throws at a sampling site. In the event that multiple isolated pools or backwater habitats were present, one throw per isolated pool or backwater habitat was performed. Based on preliminary data (Kennedy, Chapter 1), each throw trap was placed along the shoreline to ensure that the highest densities of macroinvertebrates were collected. All organisms within the area of the throw trap were collected, sorted live in the field, placed in 95% ethanol and taken to the lab where they were identified to the lowest practical taxonomic level, typically family.

2.3 Stable isotope analyses

Stable isotopes of carbon were used to discriminate between aquatic and terrestrial sources of primary production (Thorpe *et al.* 1998). Different than gut analyses, stable isotopes provide a picture of the overall feeding habits of organisms (Rounick and Winterbourn 1986). Arthropods often have fast turnover rates in their isotopic signatures making them well suited to study seasonal changes in diet (Ostrom *et al.* 1997). Primary

production in the Rio Grande is dominated by terrestrial plants using the C-3 photosynthetic pathway and benthic algae in the river. The dominant terrestrial plants along the Rio Grande typically have carbon isotope ratios of $\delta^{13}\text{C} = -26\text{‰}$ and algae is approximately $\delta^{13}\text{C} = -19\text{‰}$ (Edwards and Turner 2003, Tibbets and Molles 2005, Turner and Edwards in review). A total of eight predaceous macroinvertebrates were analyzed for their isotopic ratios of carbon and nitrogen. Three species resided in the transition zone, three species were primarily aquatic, and two species resided on the water's surface (Table 1). Five replicates of each species were analyzed during high and low discharge for 2007 and 2008 for a total of 20 replicates per species. A linear, two-stage mixing model was used to estimate the fraction of terrestrial versus aquatic source of carbon in the animals (Phillips and Gregg 2001). Typically there is roughly a 0.5‰ in $\delta^{13}\text{C}$ enrichment between trophic levels (Gannes *et al.* 1997). All samples were dried, weighed and transferred to tin capsules prior to analyses. Carbon isotopic composition was measured using a Finnigan Mat Delta Plus isotope ratio mass spectrometer. Data are reported in parts per thousand (‰ or per mil) in delta (δ) notation. Delta values were computed to commonly used standards, Pee-Dee Belemnite (PDB) limestone. Standards are accurate to 0.1‰ (Sharp 2006).

2.4 Community analyses

Terrestrial arthropod communities were characterized using taxonomic richness and catch/per unit effort for all arthropods and for arthropod predators collected in the pitfall traps. I used a general linear model (GLM) to test for differences in total terrestrial arthropod and predaceous arthropod abundances and richness between sample sites, sample times, and years. I also used a GLM to test for differences in the density and

richness of aquatic macroinvertebrates between sample sites, sample times and years. Terrestrial abundance and aquatic density data were log+1 transformed and met the assumptions of normality. No transformations were necessary for taxonomic richness. Ants were not included in the analyses of abundances because of uneven sampling for this group. However, they were included for taxonomic richness. All analyses were performed in SYSTAT 11.

3.0 Results

3.1 Seasonal variability in discharge

During the course of this study, the Rio Grande underwent the normal pattern of peak discharge in spring and low discharge in late summer (Fig 2). Collection of macroinvertebrates for this study coincided with times of low and high discharge. However, there were several departures from the 30 year average. Spring discharge in May 2008 was above the 30 year. Monsoonal discharge was below the 30-year average in August for both years (Fig 2).

3.2 Macroinvertebrate community

Pitfall trap data: A total of 451 macroinvertebrates and more than 52 taxa were identified in the pitfall traps during the course of this study. There were no significant differences annually in taxonomic richness and abundances or between sample locations. Total macroinvertebrate abundances and taxonomic richness at the water's edge were reduced by $70\pm 4\%$ and $54\pm 5\%$ respectively, during times of high discharge (Fig. 3, 4). Predaceous arthropods were 60% lower in abundance and 50% lower in richness during times of high discharge ($F_{1,33}=14.2$, $P=0.006$; $F_{1,33}=5.16$, $P=0.03$) (Fig. 3, 4). Wolf spiders (Araneae: Lycosidae) were the one arthropod predator that had similar

abundances during between times of low and high discharge (Fig. 5). In contrast, the abundance of toad bugs (Hemiptera: Gelastocoridae) were 90% lower during times of high discharge and exhibited the largest change of any terrestrial arthropod predator in the study (Fig. 5). During times of low discharge, terrestrial predators accounted for 50% of all arthropods collected (Fig. 6). Wolf spiders were the most numerically abundant species collected. However, during times of low discharge, they accounted for 17% of the arthropods collected but accounted for 54% of the arthropods collected during times of high discharge (Fig 5).

Aquatic sampling: Approximately 518 aquatic macroinvertebrates in 35 families were collected in 2007 and 2008. Between sample locations, there were no significant differences in density or in taxonomic richness. However, there were significant differences in density between years, which was driven primarily by changes in midges (Diptera: Chironomidae) ($F_{1,34} = 9.86$, $P=0.003$) (Fig. 7). The average density of aquatic macroinvertebrates and each taxon coincided with peaks in discharge (Fig. 7, Fig. 8). Chironomids were the dominant organism and accounted for 51% of all the taxa collected in the Rio Grande with peak densities coinciding with lower stream discharge (Fig. 8). Mayflies in the families Baetidae and Tricorythidae were the second largest group and accounted for almost 19% of the aquatic macroinvertebrate community (Fig 8). Freshwater annelids were the third most abundant taxa in the river and accounted for nearly 15% of the organisms collected (Fig 8).

3.3 Stable isotopes

Stable isotopes of carbon were measured for eight predaceous arthropod taxa during times of low and high discharge in 2007 and 2008. Three species were collected

near the water's edge (wolf spiders, toad bugs, and tiger beetles), two species of water striders resided on the water's surface (Hemiptera: Gerridae: *Gerris comatus* and *Metrobates trux*), and three species were primarily aquatic, dragonfly larvae (Odonata: Gomphidae), damselfly larvae (Odonata: Coenagrionidae), and adult diving beetles (Coleoptera: Dytiscidae). The three terrestrial predators found near the water's edge indicated varying degrees of reliance on algal production. In August, during times of lower discharge, wolf spider and toad bugs had a $\delta^{13}\text{C}$ that was similar to $\delta^{13}\text{C}$ values for algae production found in the Middle Rio Grande (*i. e.* -19‰) (Table 1). Results from the mixing model indicate that on average, toad bugs obtained 89% of their carbon from algal sources (Fig 9). Tiger beetles appeared to depend evenly on aquatic and terrestrial sources of carbon (Fig. 9). Wolf spiders were the only terrestrial predator to have significant changes in $\delta^{13}\text{C}$ based on seasonal differences ($F_{1,18} = 6.6$; $P = 0.019$) (Fig. 9, Table 1). During times of high discharge, wolf spiders had an approximate 47% reliance on aquatic production and increased to 75% reliance during times of low discharge (Fig. 9, Table 1). In contrast to wolf spiders, no other arthropod predator had significant temporal shifts in their $\delta^{13}\text{C}$. The two species of water striders that resided on the water's surface were quite different in their reliance on aquatic and terrestrial production. The larger species, *Gerris comatus*, obtained approximately 10% of its carbon from aquatic sources, relying mostly on terrestrial production (Fig. 9). In contrast, the smaller species, *Metrobates trux* obtained roughly 66% of its carbon from aquatic sources based on the mixing model results. Neither of these two species demonstrated any significant changes in their $\delta^{13}\text{C}$ between sample times or years.

Similar to the terrestrial predators, aquatic macroinvertebrate predators varied in their reliance on aquatic and terrestrial production. Diving beetles and dragonfly larvae had $\delta^{13}\text{C}$ values similar to terrestrial production (*i. e.* -26‰), indicating a strong reliance on terrestrial production (Fig 9, Table 1). Results from the mixing model indicate that diving beetles and dragonfly larvae obtained almost 100% to 90% respectively, of their carbon from terrestrial production. In contrast, damselfly larvae relied much more on algae production obtaining approximately 43-46% of their carbon from aquatic production (Fig 9).

4.0 Discussion

Lateral subsidies and trophic interactions are vital components to ecological landscapes. Temporal variations in productivity can have a large influence on the directionality of lateral subsidies where energy flows from areas of high to low productivity (Wallace *et al.* 1997, Nakano and Murakami 2001). In rivers where seasonal discharge can vary dramatically, primary production between aquatic and terrestrial systems can be asynchronous. In the Middle Rio Grande however, lower discharge rates occur in the late summer and would be associated with higher rates of aquatic primary production (Lake 2000). As a result, peaks in terrestrial and aquatic primary production may actually coincide, resulting in high rates of secondary production. This simultaneous timing of peak productivity in two systems may bolster diversity and abundance of macroinvertebrates, including predators. Community data from the aquatic and terrestrial systems provide support for this. The density and richness of aquatic macroinvertebrates was much higher during times of low discharge, which would be consistent with higher rates of primary productivity (Thorpe and DeLong 1994). The increase in lateral subsidies

would bolster secondary production in the terrestrial system, as seen with the higher rates of arthropod predators along the water's edge and a $\delta^{13}\text{C}$ value similar to aquatic production (Paetzold et al 2005, Kennedy Chapter 2). The overall increase in non-predaceous terrestrial arthropods also coincided with high rates of terrestrial primary production in the summer.

Nakano and Murakami (2001) showed that the temporal dynamics of reciprocal subsidies between aquatic and terrestrial systems is essential for subsidizing fish and terrestrial vertebrates on a seasonal basis. As predicted by Wallace *et al.* (1997), energy flowed from areas of high production to low production in this stream. In the Middle Rio Grande where peaks in terrestrial and aquatic production may be synchronous during the summer, predaceous arthropods depend on both terrestrial and aquatic sources of carbon. The values of $\delta^{13}\text{C}$ indicate that the arthropod predators vary in their reliance on aquatic and terrestrial sources of carbon. Individual species ranged from nearly 100% reliance on algal production as in toad bugs to nearly 100% reliance on terrestrial production for larger water striders, diving beetles and dragonfly larvae. Tiger beetles, smaller water striders, and wolf spiders relied about evenly on terrestrial and aquatic production during periods of lower discharge.

In May, higher discharge most likely coincided with lower rates of primary production (Lake 2000). Additionally, survey data showed that the density of aquatic macroinvertebrates was much lower during this time which would result in a reduction of lateral subsidies to the terrestrial system. During this time, predaceous arthropods had lower abundances with the exception of wolf spiders. Wolf spiders had no significant differences in their abundances between sample times, whereas toad bugs were 90%

lower in May compared to August. A reduction in lateral subsidies, which coincided with higher rates of discharge, is a possible explanation for the lower numbers of predaceous arthropods at the water's edge. Isotopic analyses of $\delta^{13}\text{C}$ for toad bugs indicated that they relied almost 100% on aquatic subsidies. Tiger Beetles were also lower in abundances in May, but only by approximately 40%. Their reduction is coincidentally similar to their reliance on aquatic production which is about 55%. Wolf spiders were consistently the dominant arthropod predator at the water's edge throughout the study. Unlike toad bugs and tiger beetles, wolf spiders can live for several years (Ubick *et al.* 2005). Wolf spiders have a higher reliance on terrestrial production and shift to a reliance on aquatic production as it increases later in the summer. In this study, wolf spiders went from a 53% to a 25% reliance on terrestrial production between times of high and low discharge.

Interestingly, adult diving beetles and dragonfly larvae in the aquatic environment relied heavily on terrestrial inputs as indicated by their $\delta^{13}\text{C}$ values (Fig. 9). The larger water strider species was also dependent on the lateral inputs from the terrestrial system. Unlike the aquatic system, terrestrial production was high in late May and could have served as a source of lateral subsidies in the form of insect prey to predaceous macroinvertebrates in the aquatic system. Nakano and Murakami (2001) and Kawaguchi *et al.* (2003) indicated the importance of insects falling on the water's surface as a source of lateral subsidy for fish in temperate streams. While the importance of insect prey falling on the water's surface has been shown to be an important lateral input for fish (Kawaguchi and Nakano 2001, Kawaguchi *et al.* 2003), it was also an important lateral subsidy for predaceous arthropods that resided in the water and on the water's surface.

While the density of aquatic arthropod predators was reduced during times of high discharge, it is difficult to determine if there was a dilution effect. For example, the number of macroinvertebrates in a given reach may be similar between high and low discharge, but the density was higher in times of low discharge because of a concentration effect resulting from reduced surface area. However, the majority of aquatic macroinvertebrates were most likely reduced in total abundance from the direct effects of flooding or a reduction in aquatic productivity (Resh *et al.* 1988, Poff and Ward 1998). As a result, the flux of aquatic macroinvertebrates would be reduced during high discharge, thus reducing lateral subsidies to the water's edge and negatively impacting arthropod predators. In contrast, aquatic macroinvertebrate predators such as dragonfly larvae and diving beetles may have the same abundance for a given reach because of their lack of reliance on algae production. Determining whether flooding or loss of aquatic productivity reduced the total abundances of aquatic predators was beyond the scope of this study. A future study could estimate the total abundance of water striders, diving beetles and adult dragonflies and damselflies along a given reach to determine if there are seasonal differences in populations. The next step would be to disentangle the effects of flooding versus loss of aquatic productivity on macroinvertebrate abundances. *A priori* expectations for reduced aquatic productivity would expect no change in the abundance of diving beetles, adult dragonflies and *Gerris comatus* along a given reach because of their reliance on terrestrial production. Lower abundances for damselflies and *Metrobates trux* would be expected during times of higher discharge due to their higher reliance on aquatic production.

Food web dynamics in the Middle Rio Grande landscape were temporally dynamic with the aquatic and terrestrial systems intricately connected through lateral subsidies. During times of low discharge when production was high, lateral subsidies were important for secondary production in both systems. At this time, lateral subsidies were reciprocal where aquatic predators relied on terrestrial inputs and terrestrial predators relied on aquatic inputs. Additionally, the abundances of terrestrial and aquatic predators were highest in times of lower discharge. Unlike previous studies, peak production in the aquatic and terrestrial system in the Rio Grande may be synchronous (Nakano *et al.* 2001). As a result, lateral subsidies were important for predators in both systems. Most predators in the Rio Grande may be dependent on one type of subsidy with limited ability to change their reliance on terrestrial or aquatic production with the exception of wolf spiders. When production may be asynchronous and macroinvertebrate communities were at lower densities as in the spring, lateral inputs to the aquatic system may be important for aquatic predators.

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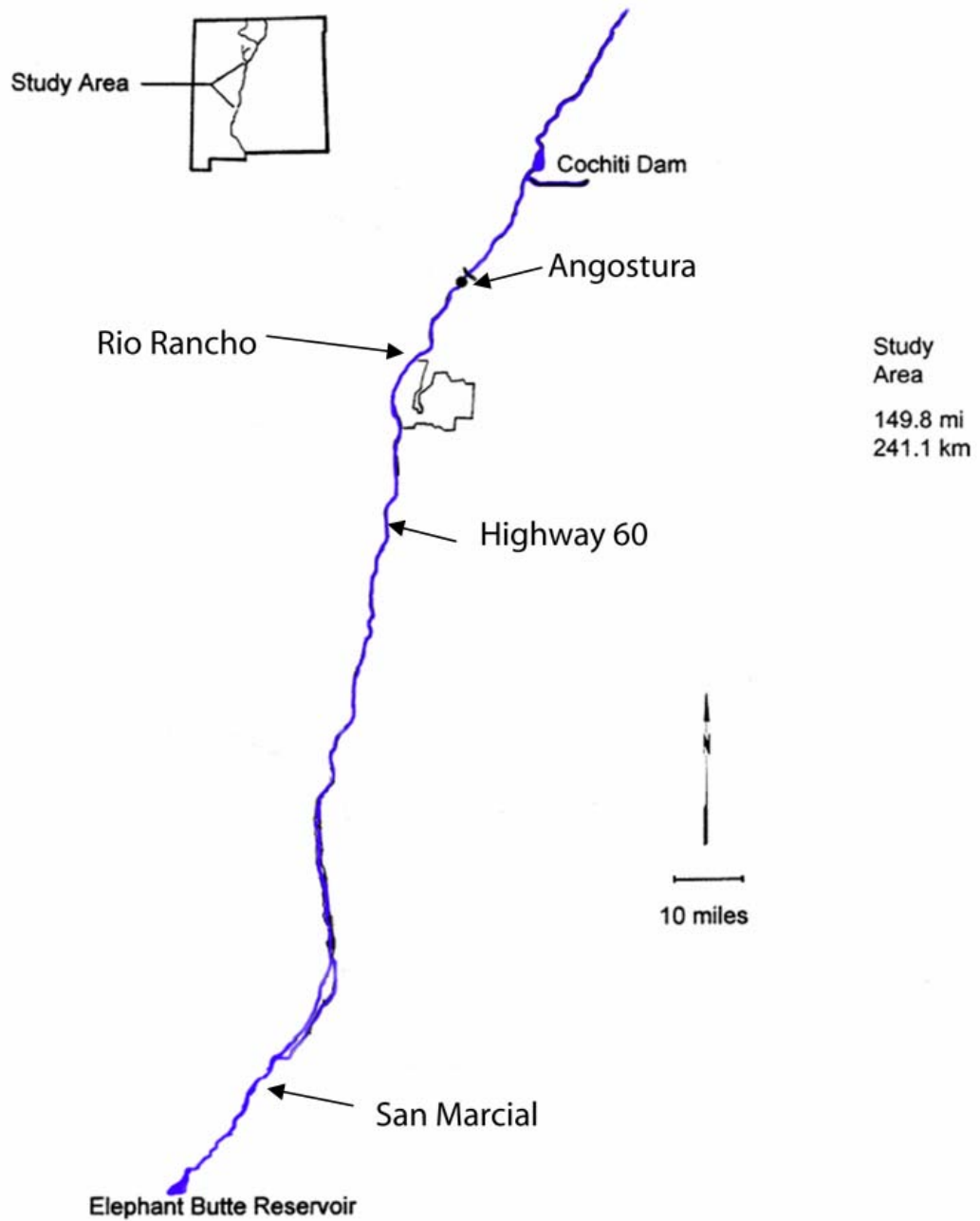


Figure 1: A map of the study locations in the Middle Rio Grande, New Mexico.

Cochiti is the northern boundary and Elephant Butte is the southern boundary. The four sample locations from north to south are Angostura, Rio Rancho, Highway 60 and San Marcial.

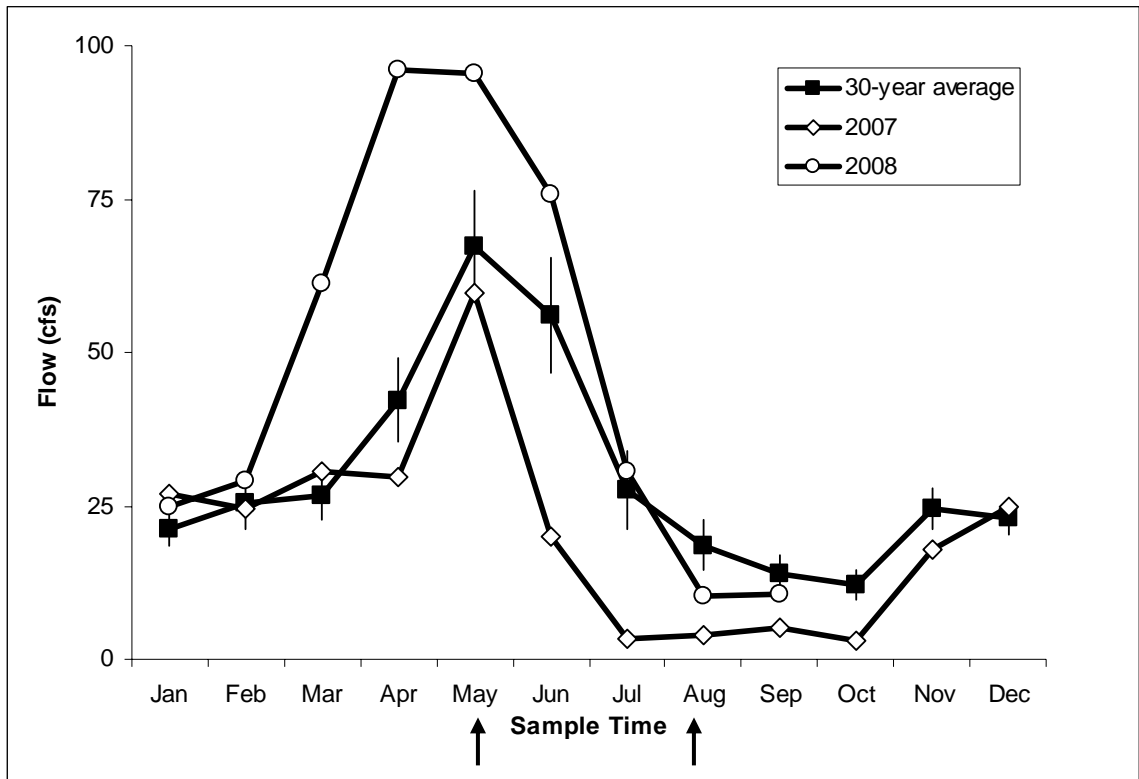


Figure 2: Mean discharge rates in the months of May and August for the Middle Rio Grande, NM during the collection times. The USGS gauging stations at Cochiti, Albuquerque, and San Acacia was the source of the data. Error bars represent the standard error (SE).

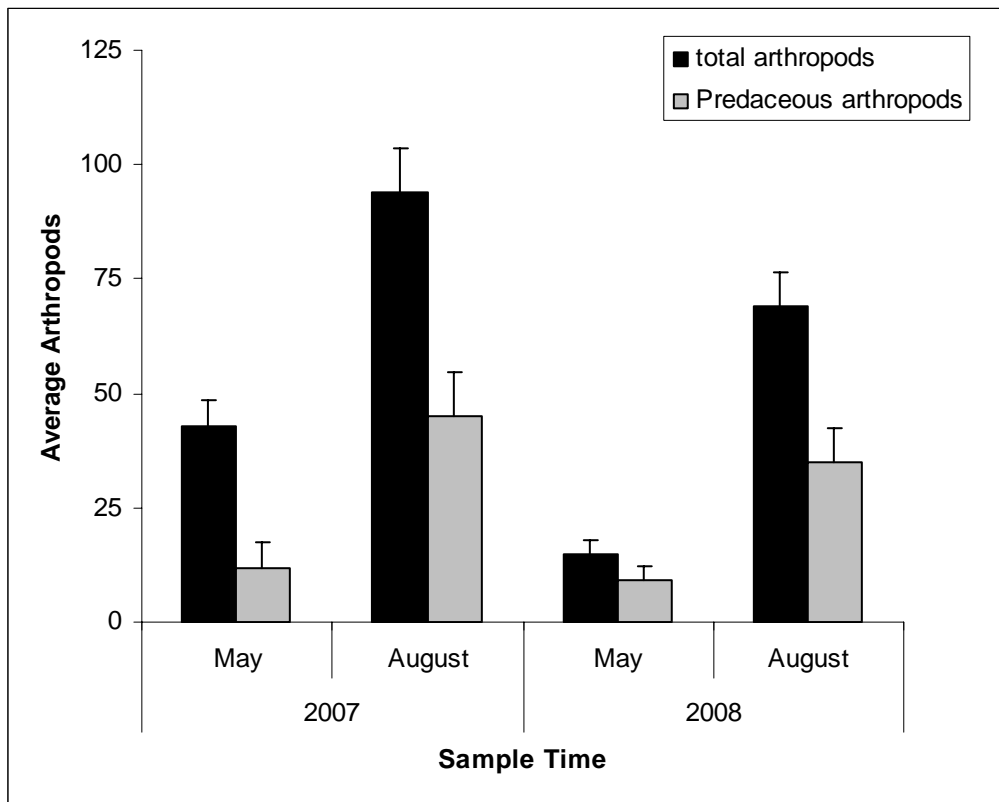


Figure 3: The average number of terrestrial and predaceous arthropods collected in 2007 and 2008. Ants (Hymenoptera: Formicidae) were excluded from the analyses for total arthropods. Four locations were sampled twice each year during historic high and low discharge times that coincide with peak discharge (May) and low discharge (August). There were no significant differences between sample locations. Error bar represents the standard error (SE).

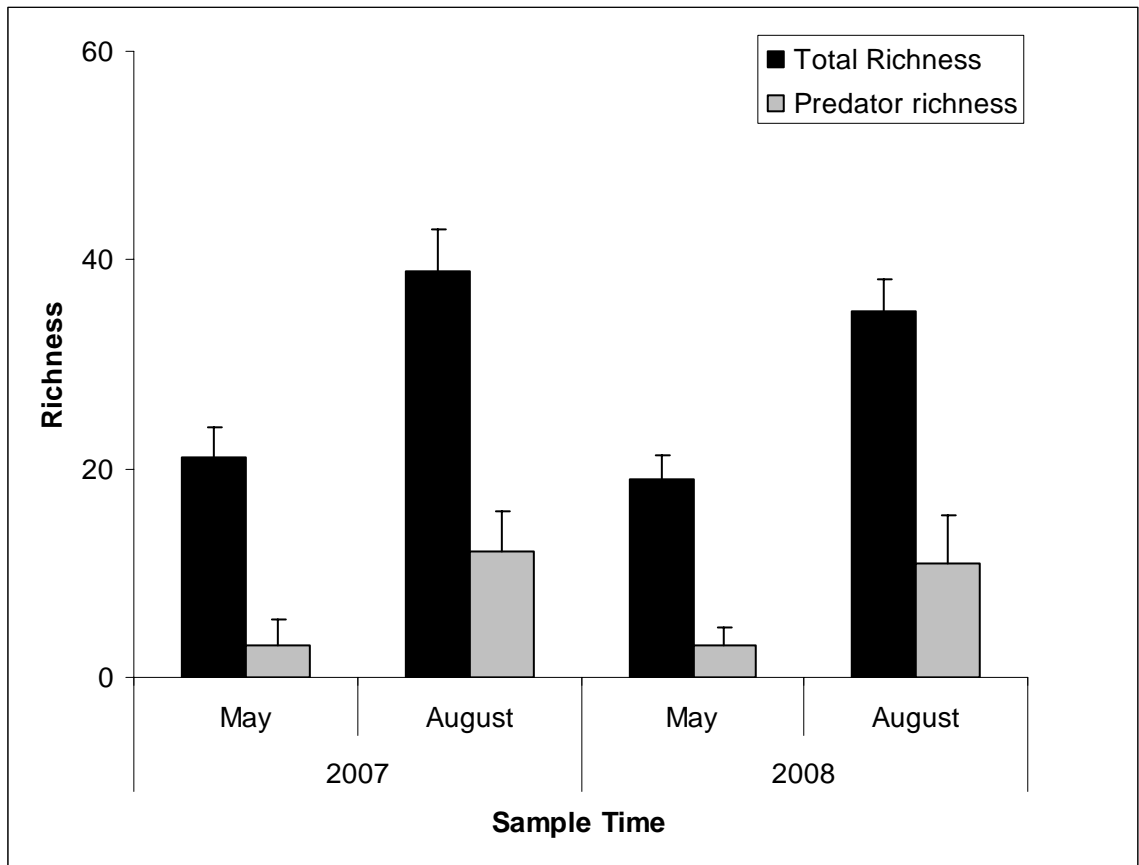


Figure 4: The average taxonomic richness for terrestrial and predaceous arthropods collected in the pitfall traps at each sample location in 2007 and 2008. Four locations were sampled twice each year during historic high and low discharge times that coincide with peak discharge (May) and low discharge (August). There were no significant differences between sample locations. Error bar represents the standard error (SE).

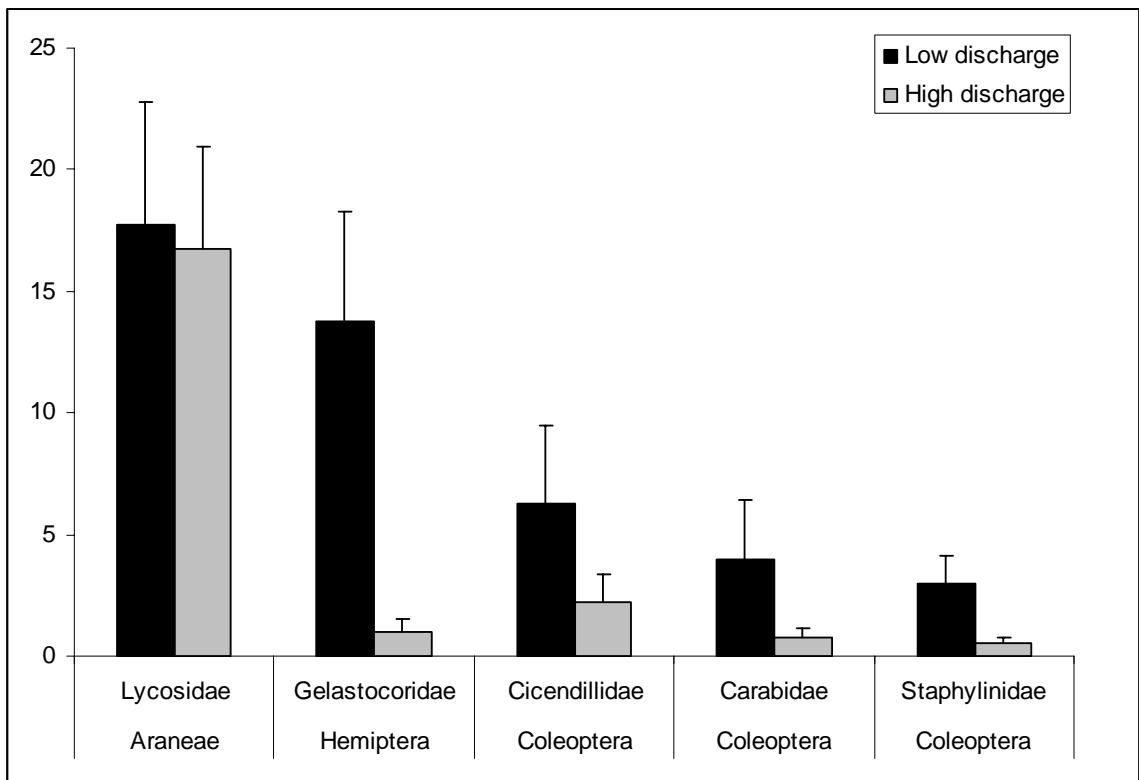


Figure 5: The average number of the five most abundant predators during low and high discharge time periods. There were no significant differences between sample locations or years. Error bars represent the standard error (SE).

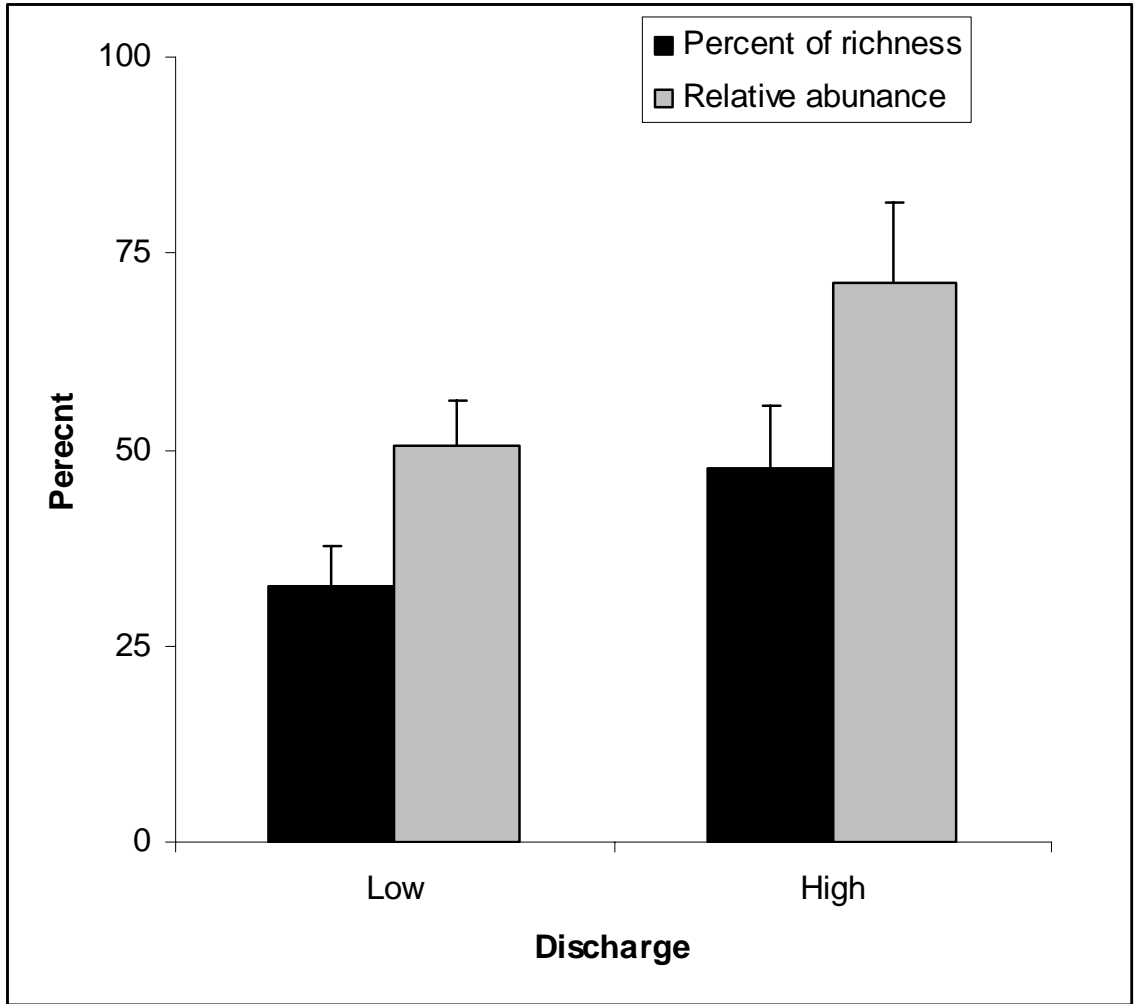


Figure 6: The relative abundance and the percent of taxonomic richness for arthropod predators during high and low discharge periods in the Middle Rio Grande. There were no significant differences between sample locations and years. Error bars represent the standard error (SE).

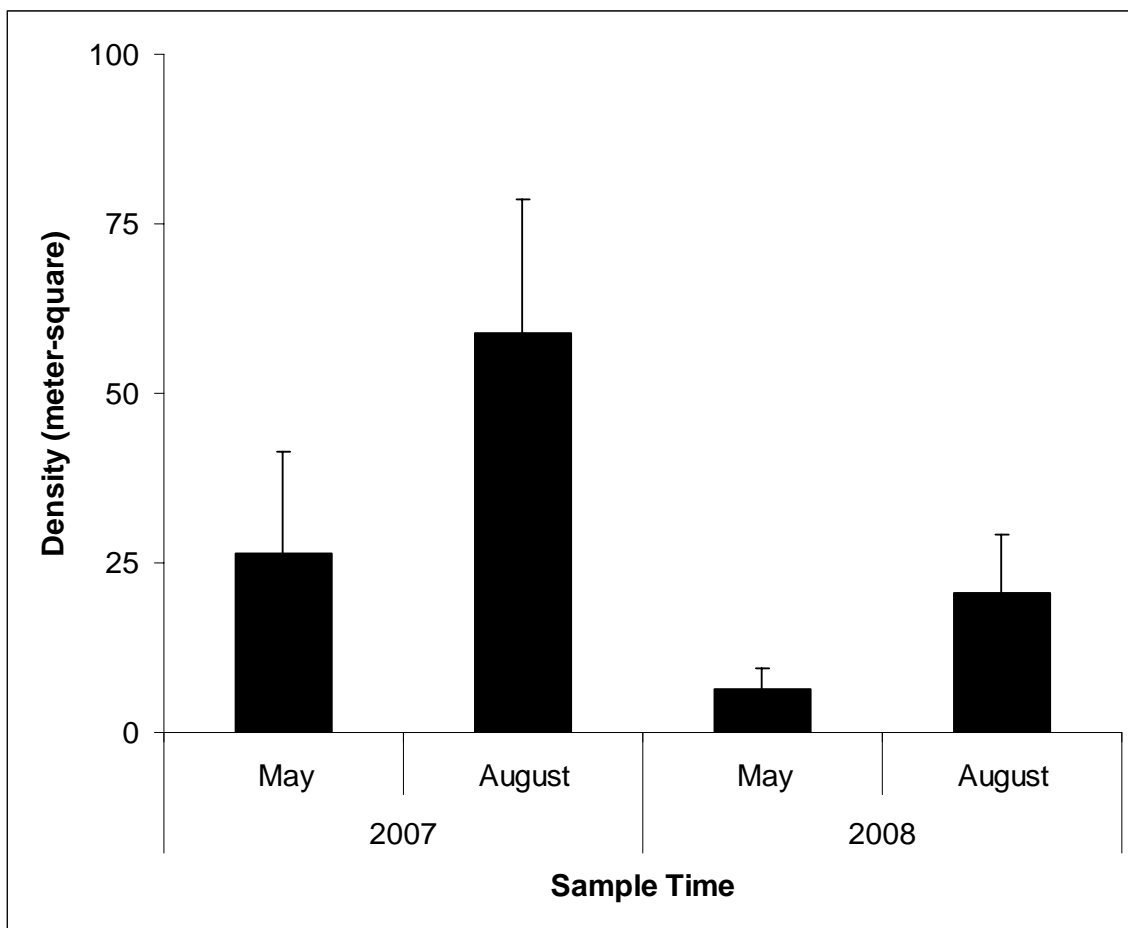


Figure 7: The average density of aquatic macroinvertebrates in the Middle Rio Grande. There were no significant differences between sample locations. Four locations were sampled twice each year to coincide with historical peak discharge (May) and low discharge times (August). Error bars represent the standard error (SE).

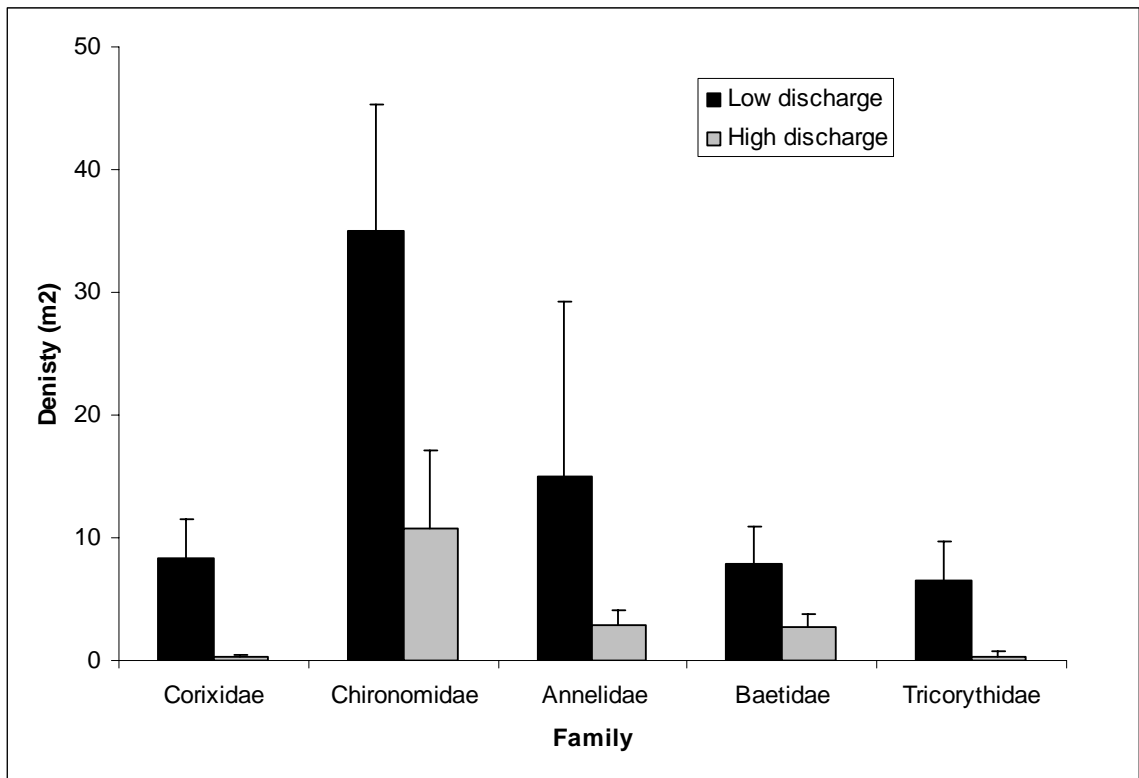


Figure 8: The average density of the five most abundant aquatic macroinvertebrates in the Middle Rio Grande. Collections were made at four sample locations to coincide with historical peaks (May) and lows (August) in discharge. Error bars represent the standard error (SE).

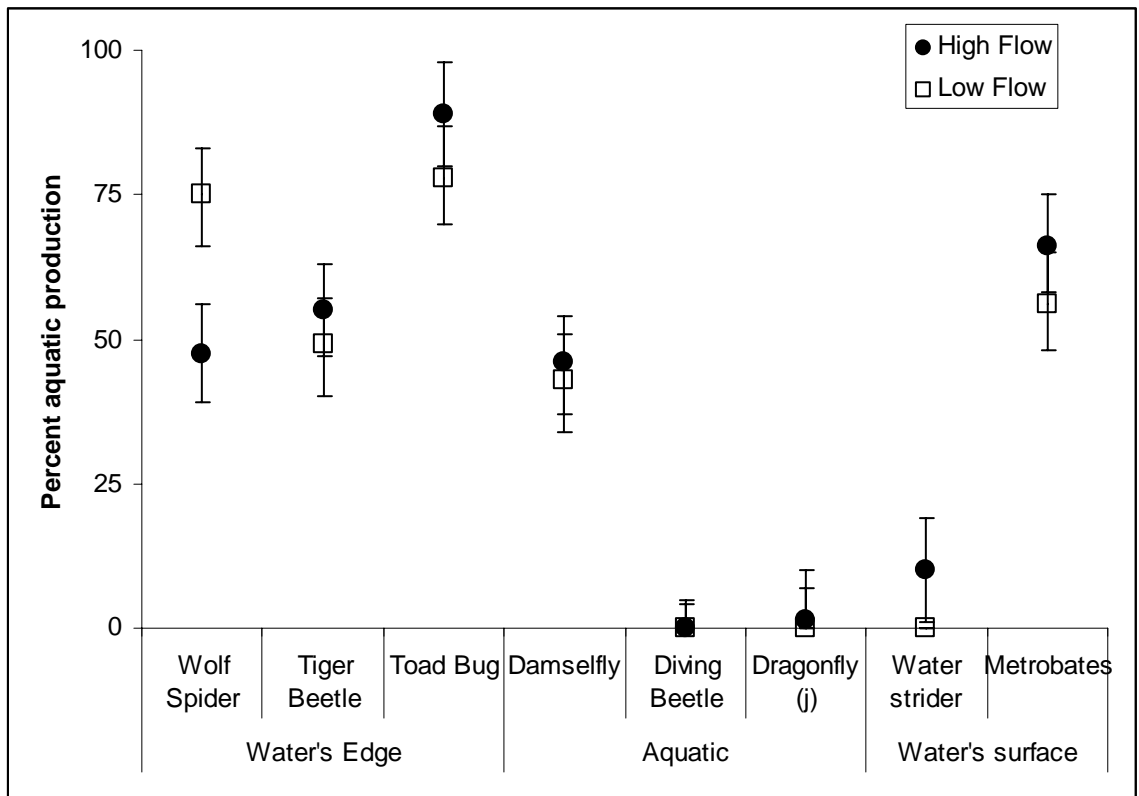


Figure 9: Results from a linear two-stage mixing model for predaceous arthropods (Phillips and Gregg 2001). The y-axis is the percent of aquatic production in each taxon for low and high discharge times. Samples were pooled for each year, high discharge was associated with samples in May and low discharge was associated with samples in August. A sample size of $n=10$ was used for data point for high or low discharge. Samples were pooled for each year. The error bars represent the upper and lower 95% confidence limits.

Table 1: *Arthropod predators in the Middle Rio Grande analyzed for their carbon isotopic ratios.* These include terrestrial arthropods, primarily aquatic, and aerial predators.

| Predator | Habitat | $\delta^{13}\text{C-High}$ | $\delta^{13}\text{C-Low}$ |
|------------------|-----------------|--|---|
| Wolf Spider* | Transition zone | $-22.7 \pm 0.6\text{‰}$ | $-20.8 \pm 0.4\text{‰}$ |
| Toad Bug | Transition zone | $-20.5 \pm 0.6\text{‰}$ | $-19.8 \pm 0.5\text{‰}$ |
| Tiger Beetle | Transition zone | $-22.6 \pm 0.6\text{‰}$ | $-22.2 \pm 0.5\text{‰}$ |
| Diving Beetle | Aquatic | $-26.3 \pm 0.03\text{‰}$ | $-26.5 \pm 0.07\text{‰}$ |
| Damselfly larvae | Aquatic | $-22.8 \pm 0.6\text{‰}$ | $-23.1 \pm 0.4\text{‰}$ |
| Dragonfly larvae | Aquatic | $-26.9 \pm 0.9\text{‰}$ | $-25.9 \pm 0.7\text{‰}$ |
| Gerridae | Water's Surface | $-25.3 \pm 0.7\text{‰}$ | $-26.9 \pm 1.2\text{‰}$ |
| Metrobates | Water's Surface | $-21.4 \pm 0.02\text{‰}$ | $-22.1 \pm 0.5 \text{‰}$ |

Chapter 3: The effects of channelization on the terrestrial-aquatic interface in an arid-land river.

Abstract

Lateral interactions and edge effects between the aquatic and terrestrial ecosystems have been shown to be a key component in maintaining higher rates of diversity. In many places, river regulation and channelization have isolated previously connected rivers from surrounding riparian areas. Survey data and stable isotope analyses of carbon and nitrogen for macroinvertebrates from the Rio Grande, New Mexico were used to determine whether channelisation affects the macroinvertebrate community. Aquatic and terrestrial macroinvertebrates were surveyed in the summer of 2008 at channelized and non-channelised reaches in the Middle Rio Grande. Results from the aquatic survey data indicate that average densities of aquatic macroinvertebrates were 50% lower in the channelized reaches. Taxonomic richness and the densities of macroinvertebrates in the transition zone were also lower in channelized reaches and this effect was especially pronounced for predator species. Isotopic analyses indicated that algae production served as the major source of carbon for predaceous arthropods in the transition zone between the river and forested floodplain. My results suggest that channelization can reduce diversity and macroinvertebrate densities at the landscape scale by severing linkages between the aquatic and riparian communities. These effects appear especially acute for macroinvertebrates in higher trophic levels, perhaps because preferred prey density is lowered.

Keywords: riparian, diversity, macroinvertebrates, predaceous arthropods

1.0 Introduction

Rivers and their surrounding riparian areas host some of the most productive ecosystems on the planet and harbor unique species, making them vitally important for global biodiversity (Sabo *et al.* 2005, Tockner and Stanford 2002, Ward *et al.* 1999, Naiman 1993). However, these areas are becoming increasingly altered and degraded as a result of anthropogenic activities. Dams, weirs, and other water control structures used for irrigation, transportation, or flood control have greatly altered and simplified the structure of rivers worldwide, resulting in loss of biotic diversity (Tockner and Stanford 2002, Poff and Hart 2002, Kingsford 2000, Power *et al.* 1996, Ward and Stanford 1995). In the northern hemisphere, approximately 70% of major rivers has been altered by river regulation (Dynesius and Nilson 1994).

River regulation is hypothesized to have a strong affect on the physical structure and presumably the functioning of rivers and the biota within these systems (Poff and Hart 2002, Kingsford 2000, Visnson 2001). The loss of natural flow variability often results in channelization. Channelization is defined here as a reach where a river is restricted to the main channel and is disconnected from the surrounding riparian zone. Natural variability in discharge, which affects the size of a stream, is a vital part of the heterogeneity within a riverine landscape and may be particularly susceptible to the effects of channelization (Stanley *et al.* 1997, Kingsford 2000, Postel 2002). Natural flow regimes are essential for creating and maintaining habitat heterogeneity that is required for a variety of organisms (Kingsford 2000, Power *et al.* 1996, Cowell and Stoudt 2002).

A transition zone occurs between the aquatic and terrestrial environment within the riparian zone and forms a hard but shifting boundary. They are a key component of

the habitat heterogeneity which is influenced by variability in river discharge (Amoros and Bornette 2002, Malmqvist 2002, Baattrup-Pederson *et al.* 2005, Humphries *et al.* 1999, Ballinger and Lake 2006). Globally, transition zones support a unique assemblage of species compared to upland areas (Sabo *et al.* 2005). Species richness and secondary production in transition zones have been shown to be bolstered by lateral subsidies from aquatic systems (Likens and Bormann 1974, Polis *et al.* 1997, Baxter *et al.* 2005). Lateral subsidies, also known as allochthonous inputs, can move from aquatic systems to terrestrial systems and *vice versa*. For example, aquatic subsidies have been shown to increase populations and species richness of riparian predators, including spiders (Williams *et al.* 1995, Collier *et al.* 2002, Kato *et al.* 2003, Sanzone *et al.* 2003, Briers *et al.* 2005, Burdon and Harding 2008), predaceous beetles (Hering and Plachter 1997), lizards (Sabo and Power 2002), and birds (Nakano and Murakami 2001). Likewise, terrestrial inputs to aquatic systems have been shown to be important subsidies that positively influence the populations of stream fishes (Kawaguchi *et al.* 2003).

Many arid-land rivers worldwide, including the Rio Grande, have been highly regulated and modified for human needs (Kingsford 2000). However, the effects of channelization on lateral subsidies on the macroinvertebrate community structure remain largely unknown. A priori expectations are that lateral subsidies (*i. e.* the emergence of adult aquatic insects) should allow a more diverse and abundant assemblage of predators within the transition zone (Polis *et al.* 1997, Paetzold *et al.* 2005). The goal of this study was to determine whether channelization affects the lateral movement of subsidies from the river to the riparian zone, and its effects on the macroinvertebrate community structure. For this study, I defined three habitat types: (1) the transition zone: the part of

the riparian zone that occurs at the water's edge and changes seasonally based on current stream discharge; (2) the Bosque: the wooded portion of the riparian zone (Molles *et al.* 1988); and (3) the aquatic environment. This study was conducted during the summer of 2008 in the Middle Rio Grande, NM (Fig 1). Terrestrial pitfall trap data and aquatic macroinvertebrate survey data were used to test for differences in species richness and abundances between channelised and semi-natural sample locations. An analysis of $\delta^{13}\text{C}$ was used to discriminate between terrestrial and aquatic sources of carbon in predaceous arthropods. Previous work has shown carbon signatures in aquatic and terrestrial sources to be distinct (Edwards and Turner 2003, and Turner and Edwards *in review*).

2.0 Materials and Methods

2.1 Study Location

The Rio Grande originates in the San Juan Mountains of southern Colorado and empties into the Gulf of Mexico in southern Texas. The drainage is semi-arid, and river flows are provided by snowmelt from southern Colorado and northern New Mexico (NM) and augmented in the summer by monsoonal precipitation. This study focuses on the Middle Rio Grande, a 363 km reach that is delimited by Cochiti dam upstream and Elephant Butte Reservoir downstream in New Mexico (Fig 1).

The Rio Grande has a long history of channelization and heavy usage for irrigation (Molles *et al.* 1998). Historical average peak flows prior to the closure of Cochiti dam were approximately 225 m³/s and sometimes were in excess of 700 m³/s (Follstad Shah and Dahm 2008). In an effort to control high flows, two river management actions were taken. First, metal structures ("Jetty Jacks") were placed along the edge of the river during the 1930s and 1940s to stabilize the banks of the Rio Grande and prevent

flooding. Second and most influential was Cochiti dam, constructed in 1973. After the completion of Cochiti, average peak river discharge within the study region has been reduced from 225 m³/s to 150 m³/s and peak river discharge has not been higher than 250 m³/s (Follstad Shah and Dahm 2008). These management efforts have reduced flow variability and isolated the aquatic environment from the historical riparian area in many reaches (Crawford *et al.* 1993).

Due to the changes brought about by channelization, the historical riparian floodplain forest (known colloquially as the “Bosque”) for this study was considered part of the surrounding upland habitat. It was rarely or never flooded, had larger trees and leaf litter. The transition zone was located at the water’s edge and was frequently flooded, lacked larger trees and leaf litter. Conversely, there were several locations in the MRG where channelization had progressed to incision (where the river cut into the channel shown in Fig. 1 and lowered the main channel several meters below the historical riparian zone). Because the entire the MRG has been altered, there are no longer any pristine reaches. However, the effects of river regulation were varied, and the least impacted reaches sampled were defined as “non-channelized.”

A total of ten sample sites were used. Five sites were classified as channelised and 5 sites were classified as non-channelised (Fig. 1). Three of the sampling sites were located in close proximity to each other (Fig 1). At the southernmost location at San Marcial, the Rio Grande made several sharp turns resulting in a wide sandy transition zone that was gently sloping and was approximately 50 meters in width. However, less than a hundred meters north of this location, the river was restricted to the main channel with a transition zone less than 2 meters wide and embankments approximately 4 meters

high (Fig 1). Angostura was the northernmost upstream location and had a wide floodplain that was sparsely vegetated on the eastern side, while the western side had a transition zone less than 2 meters wide (Fig. 1). San Acacia was located about 2.5 km south of the San Acacia diversion dam. At this location, the river was deeply incised on the western side and the river was 3 meters or more below the surrounding Bosque. A bend in the river, 50 meters upstream, created a similar site to San Marcial; a gently sloping sandy transition zone with sparse vegetation. Two sites, Rio Rancho and HWY 60 (Fig 1) were considered non-channelised sites, with transition zones that were nearly flat and had varying degrees of vegetation (Fig 1). Escondida and 5 km north of San Marcial were both channelised reaches.

2.2 Invertebrate collection

Terrestrial macroinvertebrates were collected to assess differences in the community structure between the transition zone and the Bosque in channelised and non-channelised reaches. In each habitat (transition zone and Bosque), fifteen pitfall traps were arrayed in three parallel rows of five traps with traps five meters apart (Fig. 2). In the transition zone, the first row was placed within one meter of the water's edge, the second row was in the middle of the transition zone and the third row was placed at the top of the transition zone near the Bosque's edge (Fig. 2). At San Acacia and 5 km above San Marcial, all pitfall traps in the transition zone were placed parallel to the Rio Grande because the transition zone was less than 1 meter in width. Pitfall traps in the Bosque were arrayed in a similar fashion. The first row of pitfall traps was placed at the Bosque's edge near the transition zone (Fig. 2). The following two rows in the Bosque were parallel and 5 meters apart from each other. Each trap was a 250 ml, 10-cm diameter,

plastic cup with 25ml of 70% ethanol. Each location was sampled a total of three times during low flow conditions in June, July and August of 2008. Traps were checked 48 hours after they were set. Macroinvertebrates were taken to the lab, identified to the lowest practical taxonomic level and preserved in 95% ethanol.

Aquatic macroinvertebrates were collected at the same locations coincident with the pitfall trap sampling. At each site and sampling period, the aquatic habitat was divided into three main habitat types; main channel (MC), backwater (BW), and isolated pools (IP). Flow and connectivity to the main channel were the major variables for habitat classification. The main channel was the major channel of the river. Backwaters were defined as being connected to the main channel but with conditions of zero or little flow (<0.1 m/s) relative to the main channel. Isolated pools were completely disconnected from the main channel with zero flow. The number and sizes of each type of habitat varied depending on the degree of channelisation and the current flow conditions of the river.

A circular throw trap (0.2 m²) was used to collect aquatic macroinvertebrates in each habitat. A total of three haphazard throws were made for each habitat with a maximum of nine throws at a sampling site. In the event that multiple isolated pools or backwater habitats were present, one throw per isolated pool or backwater habitat was performed. Based on preliminary data, each throw trap was placed along the shoreline to ensure that the highest densities of macroinvertebrates were collected. All organisms within the area of the throw trap were collected, sorted live in the field, placed in 95% ethanol and taken to the lab where they were identified to the lowest practical taxonomic level, typically family. Jackknife analyses of the throw trap data at each site and habitat

indicated that the collecting procedures captured over 95% of the diversity theoretically present (Krebs 1999). Jackknife estimates are based on the frequency of rare species in the community (Heltsh and Forrester 1983).

2.3 Stable isotope analyses

Stable isotopes of carbon and to a lesser extent, nitrogen can be used to discriminate differences between sources of primary production (Thorp *et al.* 1998). They also provide a picture of the overall feeding habits of organisms and what is actually integrated into tissues, rather than a single point observation obtained by gut-analyses (Rounick and Winterbourn 1986). In the Rio Grande landscape, primary production is dominated by terrestrial plants using the C-3 photosynthetic pathway and benthic algae in the river. The dominant terrestrial plants along the Rio Grande typically have carbon isotope ratios of $\delta^{13}\text{C} = -26\text{‰}$ and algae is approximately $\delta^{13}\text{C} = -19\text{‰}$ (Edwards and Turner 2003, Tibbets and Molles 2005, Turner and Edwards in review).

Terrestrial arthropod predators were analyzed for their isotopic ratios of carbon and nitrogen. A two-stage mixing model was used to estimate the fraction of terrestrial versus aquatic source of carbon in the animals (Phillips and Gregg 2001). Typically there is roughly a 0.5‰ in $\delta^{13}\text{C}$ enrichment between trophic levels (Gannes *et al.* 1997). All samples were dried, weighed and transferred to tin capsules. Carbon isotopic composition was measured using a Finnigan Mat Delta Plus isotope ratio mass spectrometer. Data are reported in parts per thousand (‰ or per mil) in delta (δ) notation. Delta values were computed to a commonly-used standard, Pee-Dee Belemnite (PDB) limestone. Standards are accurate to 0.1‰.

2.4 Community analyses

The macroinvertebrate community structure was characterized by taxonomic richness and the catch per unit effort which was reported as average density for aquatic samples and abundances for terrestrial samples. I used a general linear model (GLM) to test for differences in aquatic macroinvertebrate taxonomic richness and catch per unit effort (density) between channelised and non-channelised reaches in the MRG. I used a 2X2 factorial ANOVA to examine the combined effects of channelisation (channelised/non-channelised) and habitat (transition zone/Bosque) on the richness and abundance of terrestrial macroinvertebrates. The same analyses were also performed for terrestrial predator richness and abundances. Samples from June, July, and August were pooled together for each sample location. Terrestrial abundance data and aquatic density data were log transformed and met the assumptions of normality. No transformations were necessary for taxonomic richness. All analyses were performed in SYSTAT 11. Turnover between the transition zone and the Bosque was determined using the Jaccard index of similarity (Krebs 1999, Sabo *et al.* 2005): $J = c/(a+b+c)$ where a is the number of unique species in the transition zone, b is the number of unique species in the Bosque, and c is the number of species shared in both habitats. Values near zero indicate a high turnover between habitats.

3.0 Results

3.1 Aquatic community

In channelised reaches, the density of aquatic macroinvertebrates was 48% lower than in semi-natural reaches ($F_{1,28}=8.360$, $P=0.007$) (Table 1). The average taxonomic richness was also 47% lower in channelised reaches ($F_{1,28}=7.821$, $P=0.009$) (Table 1).

At all sample locations, chironomids were the dominant taxon. However, in channelised reaches they were more dominant, accounting for 42% of the organisms collected compared to 30% in natural reaches (Fig. 3). Mayflies (Ephemeroptera) were much less abundant in the channelised reaches where they accounted for only 5% of the organisms collected compared to 27.5% in natural reaches. Two families of mayflies, Siphonuridae and Tricorythidae were not collected in channelised reaches. There were fewer habitats (*i. e.* isolated pools, backwaters, and main channel) in channelised reaches compared to semi-natural reaches ($F_{1,28}=5.36$, $P=0.028$). Most notable was the loss of isolated pools in channelised reaches.

3.2 Terrestrial community

During the course of this study, 1,844 terrestrial macroinvertebrates were collected and 101 different taxa were identified. Ants (Hymenoptera: Formicidae) were not included in the analyses of abundance data due to highly uneven sample sizes; however they were included for analyses of richness. There were no significant differences in the abundance or richness of macroinvertebrates between sample times.

Differences between channelised and semi-natural reaches: There were no significant differences in the abundance and richness in the Bosque between channelised and non-channelised reaches. The same pattern was also similar for predaceous macroinvertebrates in the Bosque (Fig 4). However, there were large differences in the transition zone between channelised and non-channelised reaches (Fig. 4). For example, the average abundance of arthropods collected in the transition zone was 75% higher in non-channelised reaches ($F_{1,8}=8.39$, $P=0.02$) (Fig 4). Taxonomic richness in the transition zone was also 53% higher in non-channelised reaches compared to channelised reaches

($F_{1,8}=20.7$, $P=0.002$) (Fig 4). The presence of predaceous arthropods in the transition explained much of this trend. For example, 90% of the predaceous arthropods collected in the transition zone were in non-channelised reaches which was significantly different compared to channelised reaches ($F_{1,8}=123$, $P<0.001$) (Fig. 5). Predaceous arthropods accounted for 44.5% of all the arthropods collected in the transition zone for all sites. Predator richness was nearly three times higher in the non-channelised reaches ($F_{1,8}=32.3$, $P<0.001$) (Fig 5) and accounted for 35% of the total richness in this habitat. Wolf spiders in the genus *Pardosa* (Araneae: Lycosidae) and toad bugs (Hemiptera: Gelastocoridae) were the two most abundant predaceous arthropod collected in the transition zone (Fig. 6).

Differences between the transition zone and the Bosque: There was a significant interaction between channelised reaches and habitat for richness and abundance of macroinvertebrates and macroinvertebrate predators (richness: $F_{1,16}=15.9$, $P=0.001$; abundance: $F_{1,16}=5.07$, $P=0.039$). Therefore, examination of the average abundance of macroinvertebrates indicated that there were no major differences between the transition zone and the Bosque in non-channelised reaches (Fig 4). However, in channelised reaches, the abundance of macroinvertebrates was approximately 77% lower the transition zone compared to the Bosque. The same pattern was also true for the total richness which was 57% lower in the transition zone in channelised reaches but was similar to the Bosque in non-channelised reaches.

Although the transition zone and the Bosque were similar in patterns of richness and abundance of macroinvertebrates, the community composition between the habitats were different. Results from the Jaccard's coefficient indicate very high turnover between

the Bosque and the riparian zone in both channelised and non-channelised reaches ($J=0.108$, $SE=0.021$). Predaceous arthropods accounted for 20% of the taxonomic richness in the Bosque, and 32% of the taxonomic richness in the transition zone (Fig. 5). However, the average difference between the total percentage of predaceous arthropods collected in the two habitats was much larger. Predaceous arthropods accounted for only 4.2% of the organisms collected in the Bosque, while predators in the transition zone in non-channelised reaches accounted for 46% of arthropods collected (Fig 6).

For both habitat types, wolf spiders were the most abundant predators and were found at all locations (Fig. 6). However, in the Bosque wolf spiders were in the genus *Hogna*, while the genus *Pardosa* dominated the transition zone. Seventy-four wolf spiders were collected in the transition zone compared to only 13 wolf spiders in the Bosque. Nearly 90% of predators in the transition zone were collected within one meter of the water's edge. All of the toad bugs were collected within one meter of the water's edge and predaceous ground beetles and tiger beetles (Coleoptera: Carabidae) were found throughout the transition zone.

3.3 Isotope analyses

Isotopic analyses of $\delta^{13}\text{C}$ showed a separation between sources of carbon in the transition zone and Bosque predators (Fig 7). The dominant predaceous arthropods collected in the Bosque were wolf spiders and ground beetles (Fig 6). Jumping spiders (family: Salticidae) were the most depleted in $\delta^{13}\text{C}$, indicating they were obtaining their carbon entirely from terrestrial sources (Fig. 7, Table 2). Results from the mixing model indicate that wolf spiders in the Bosque (*Hogna* spp.), received approximately 91% of their carbon from terrestrial production (Table 2). Isotopic signatures of $\delta^{13}\text{C}$ for

predaceous arthropods at the water's edge in the transition zone indicate that their carbon was almost entirely from aquatic sources (Fig. 8). For example, results from the mixing model indicated that toad bugs and wolf spiders at the water's edge receive approximately 94% and 78.1% respectively, of their carbon from aquatic production. However, some of the ground beetles and other wolf spiders that were further than 1 meter from the water's edge in non-channelised reaches had isotopic signatures indicating carbon derived from both terrestrial and aquatic sources (Fig. 8).

The fractionation of $\delta^{15}\text{N}$ has often been used to determine the trophic position of organisms in a community. Typically a fractionation of +2 to 5‰ per trophic level has been reported in the literature (Gannes *et al.* 1997). In the Rio Grande, difference in fractionation of $\delta^{15}\text{N}$ was quite large, ranging between 3.2‰ in a toad bug to 15.6‰ in the ground beetle *Tetracha carolinenses*. Additionally, intraspecific and interspecific variation in fractionation was higher for nitrogen than for carbon. There were no apparent patterns between aquatic and terrestrial sources of nitrogen. However, while there was no overlap between the most abundant macroinvertebrate predators when plotted in two dimensions based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, there was overlap in trophic heights for organisms from the Bosque or in the riparian zone. Additionally, the riparian zone had the largest range in $\delta^{15}\text{N}$ between species, while predators in the Bosque were more closely clumped together (Fig 6).

4.0 Discussion

Channelised reaches in the Rio Grande were associated with reduced abundances and taxonomic richness of macroinvertebrates in both the aquatic system and in the transition zone. Considering both terrestrial and aquatic samples combined, the density of

aquatic organisms in channelised reaches was 50% lower, and coincided with a significant reduction in taxonomic richness and abundances of mainly predaceous arthropods in the transition zone. In contrast, the density and richness of macroinvertebrates in the Bosque were relatively unchanged between channelised and non-channelised reaches.

There are several potential explanations for the reduction of terrestrial predators in the transition zone in channelized reaches. The first could be the loss of area, resulting in a loss of taxonomic richness and abundance. However, the results presented here were similar to other studies showing that the majority of predators that specialize on emerging aquatic insects typically aggregate near the shoreline (Briers *et al.* 2005, Paetzold *et al.* 2005). Although the majority of predaceous arthropods were found near the water's edge, there were still major reductions in abundances of the predaceous arthropods in channelised reaches that coincided with lower aquatic macroinvertebrate density in these reaches. The reduction in transition zone predators may have been the result of a reduction of lateral subsidies to the transition zone. The $\delta^{13}\text{C}$ values indicated that predators near the water's edge were being heavily subsidized by instream production which is consistent with terrestrial predators adjacent to other streams (Sanzone *et al.* 2003, Paetzold *et al.* 2005).

The macroinvertebrate community in the Bosque was similar in abundances and taxonomic richness for all sample locations in the MRG. In non-channelised reaches, the abundance and diversity were similar between the Bosque and the transition zone, but there was high species turnover between the two habitats which was a similar pattern to other riverine systems (Sabo *et al.* 2005). A major difference was higher richness and

abundances of predaceous arthropods in the transition zone in non-channelised reaches. In the Bosque, the relative abundance of predaceous arthropods was only 4.2% compared to 46% in the transition zone for non-channelised reaches. Additionally, predaceous macroinvertebrates in the Bosque received less than 20% of their carbon from aquatic sources. Additionally, wolf spiders, the most abundant species, received more than 90% of their carbon from terrestrial sources. Two lines of evidence support the lack of any significant lateral subsidies to the Bosque. First, the proportion of predators in the Bosque was much lower compared to the transition zone, which was similar to other studies (Briers *et al.* 2005). Second, the $\delta^{13}\text{C}$ of Bosque predators indicated a heavy reliance on terrestrial production unlike the macroinvertebrate predators in the transition zone near the waters edge.

In non-channelised reaches where the width of the transition zone was larger, there were small differences in the fractionation of $\delta^{13}\text{C}$ between the water's edge and edge of the Bosque. For example, wolf spiders near the water's edge were more enriched with $\delta^{13}\text{C}$ than individuals near the top of the riparian zone. Tiger beetles and other ground beetles that were found throughout the transition zone relied about evenly on aquatic and terrestrial production. Also, toad bugs were the most enriched in $\delta^{13}\text{C}$, reflecting a nearly 100% reliance on aquatic production. They were located almost exclusively along the water's edge and were the most reduced in abundance in channelised reaches. The transition zone also had the widest range of $\delta^{15}\text{N}$ values for predaceous arthropods, with tiger beetles being the most enriched of all the predators. When plotted in niche space determined by carbon and nitrogen isotopes, there was no overlap between the 10 most abundant species (5 in the Bosque, 5 in the transition zone).

The large range in $\delta^{15}\text{N}$ may indicate higher trophic diversity in the transition zone which would also coincide with the higher rate of diversity in predaceous arthropods. Theory predicts that an increase in lateral subsidies would increase the secondary production in the transition zone (Polis *et al.* 1997). Results from this study strongly support this theory which may also explain the wider range in trophic variation in the transition zone.

The macroinvertebrate community in the transition zone in non-channelised reaches shares the community-wide properties with the Bosque in that they were similar in abundances and taxonomic richness. However, there was a large turnover in species between these two communities. The transition zone community had much higher relative abundances and richness of macroinvertebrate predators compared to the Bosque. When combined with isotope results for $\delta^{13}\text{C}$ indicating a reliance on aquatic production, it is evident that the higher rate of secondary production in the transition zone was supported by lateral subsidies from the aquatic environment as predicted by theory (Polis *et al.* 1997). Additionally, when aquatic macroinvertebrates were reduced in density, the arthropod predators in the adjacent transition zone were also greatly reduced in relative abundance. Predators accounted for 35% of the diversity and almost half the abundance in the riparian zone. Like other riparian zones, the transition zone community was different from adjacent upland areas and thus a vital component of the total diversity of the Middle Rio Grande. This study illustrates the importance of lateral subsidies to the transition zone for creating and maintaining diversity at the landscape scale. Channelisation may reduce lateral subsidies which subsidize the unique taxonomic richness of riparian areas, specifically predators, thus reducing the overall richness.

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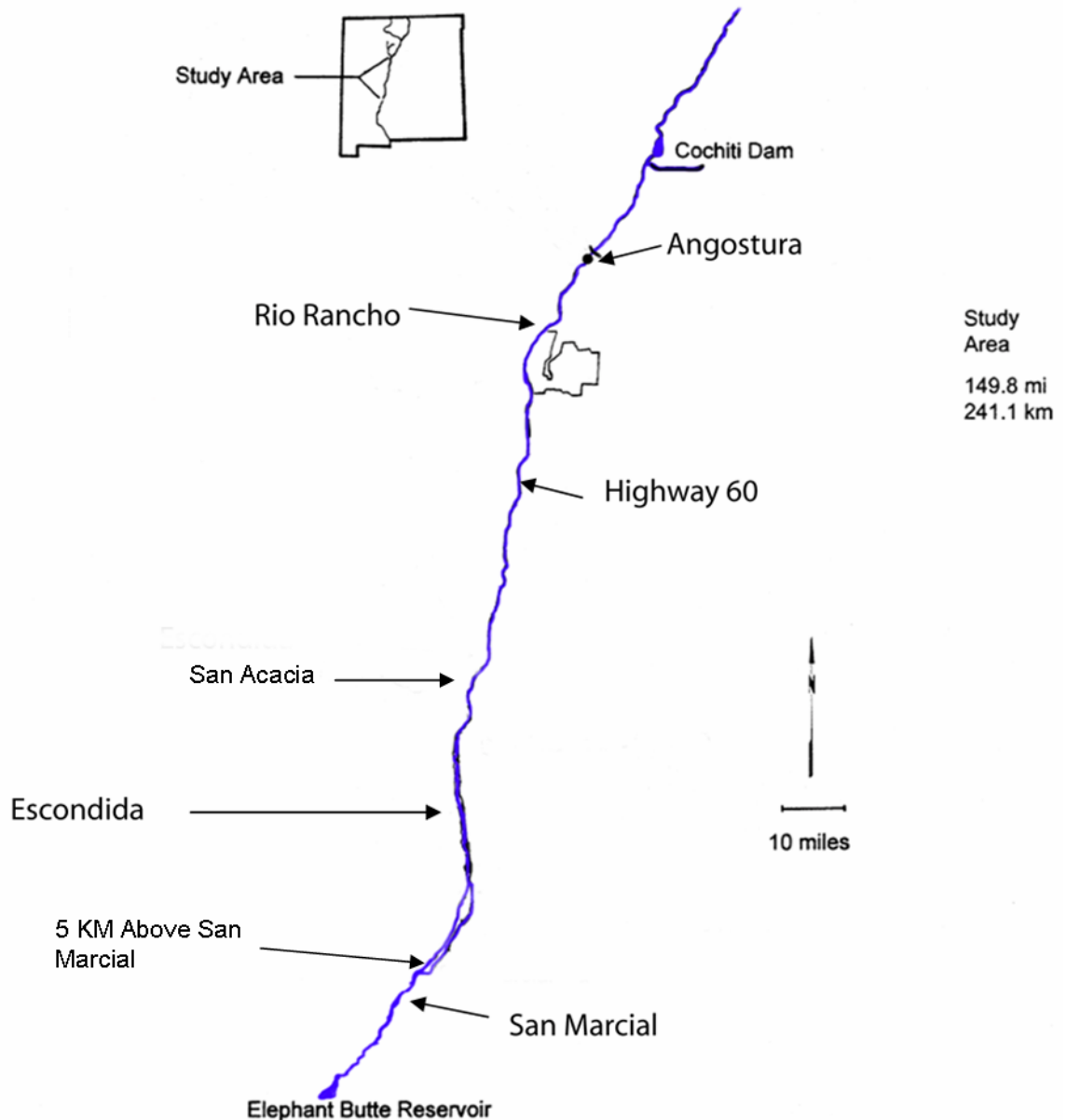


Figure 1: Sample locations in the Middle Rio Grande in New Mexico. Angostura, San Acacia and San Marcial were sampled as both channelised and non-channelised reaches. At these locations, bends in the river created incisions with very narrow transition zones on side. The opposite side of the river in contrast was gently sloping with wide transition zones. Rio Rancho and Highway 60 were non-channelised. Escondida and 5 km above San Marcial were channelised reaches.

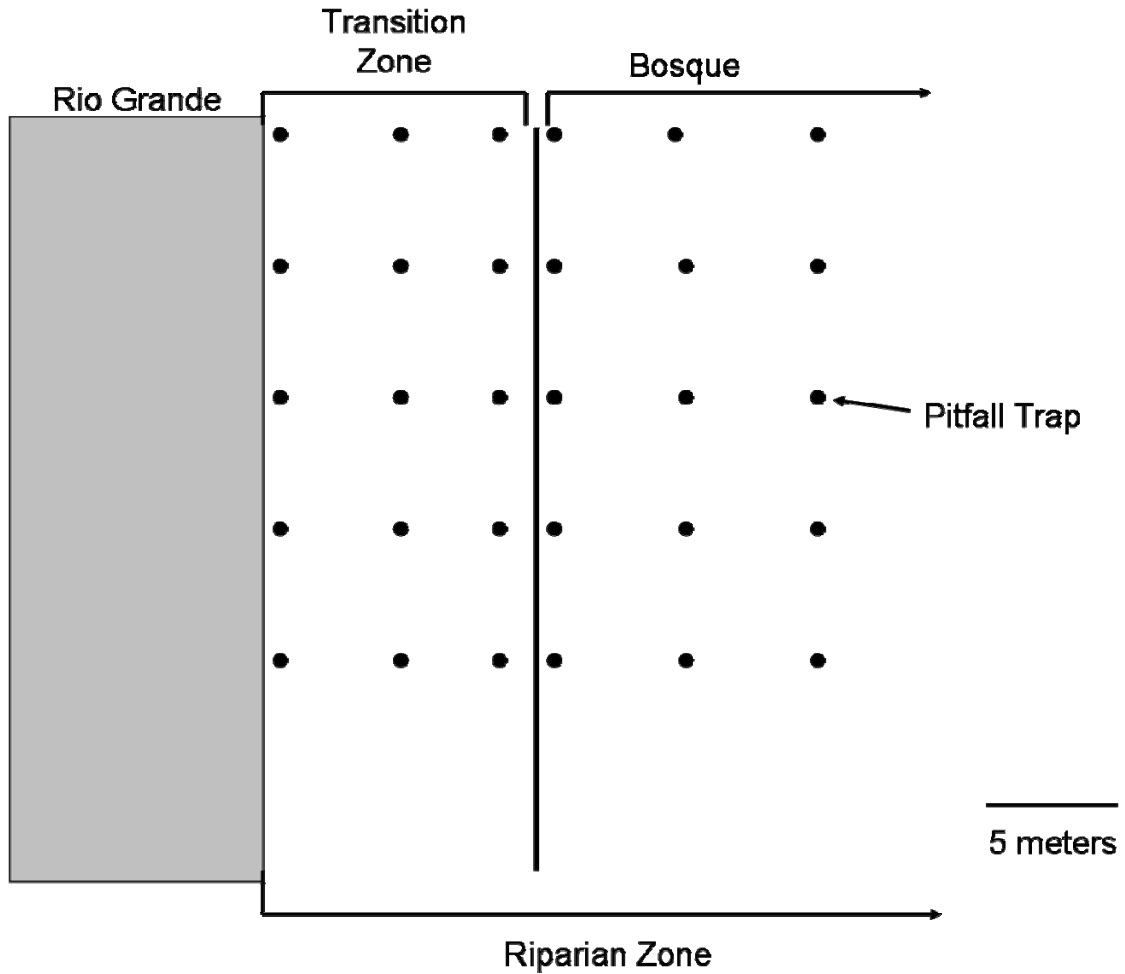


Figure 2: The typical array of pitfall traps at a sampling location. Pitfall traps were arrayed into three rows of five traps in each habitat parallel to the Rio Grande for a total of 30 pitfall traps at each location. Pitfall traps were typically placed 5 meters apart within a row. In the Bosque, each row was typically spaced 5 meters apart. In the transition zone, rows were placed approximately 1 meter from the water’s edge, in the middle of the transition zone at the edge of the transition zone where the Bosque begins. At San Acacia and 5 km above San Marcial, all pitfall traps in the transition zone were placed parallel to the Rio Grande because the transition zone was less than 1 meter in width.

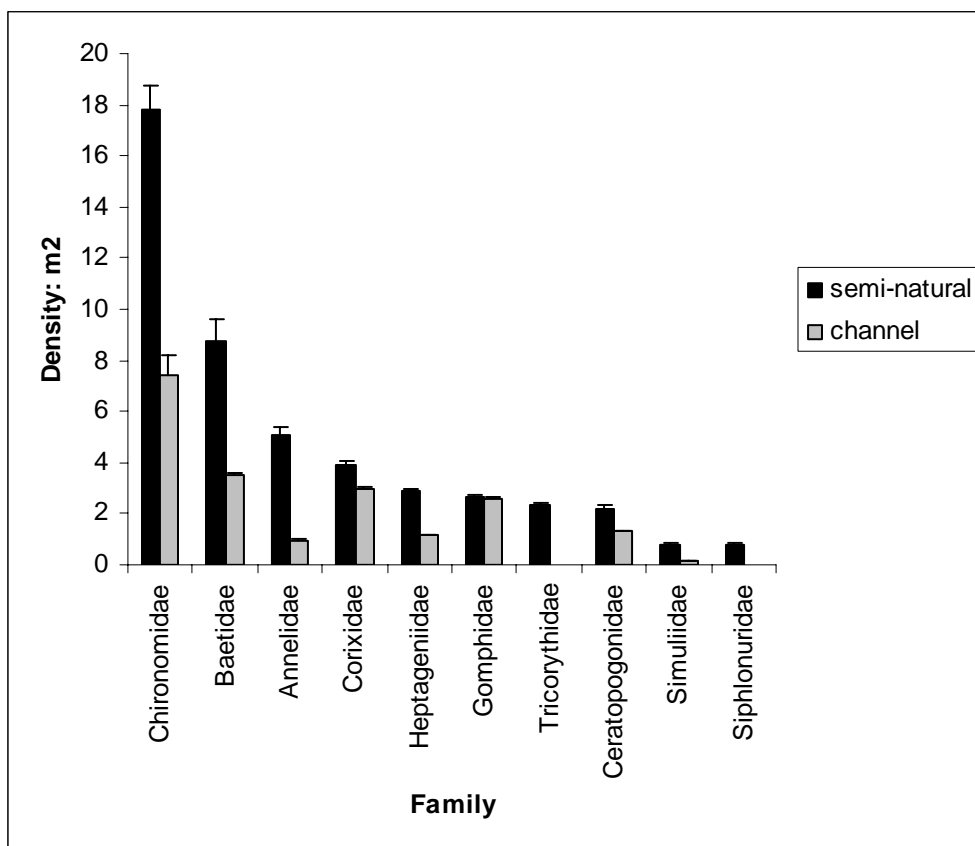


Figure 3: The difference in mean density of the ten most abundant aquatic macroinvertebrates taxa between channelised and non-channelised reaches in the Middle Rio Grande. The data for the five channelised and five semi-natural reaches were grouped together. Each taxonomic group had lower density in channelized reaches. Error bars represent the SE.

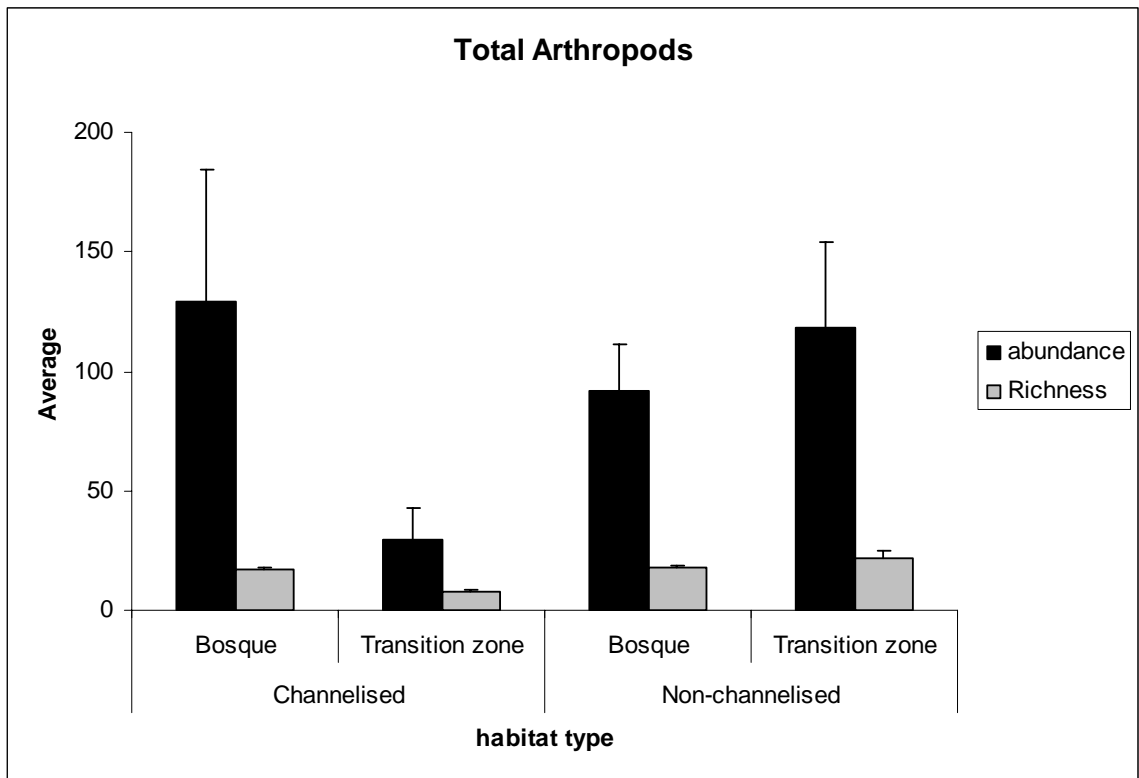


Figure 4: The differences in terrestrial macroinvertebrate taxonomic richness and relative abundances in the middle Rio Grande between the transition zone and the Bosque at channelised and non-channelised sample locations. Error bars represent the SE.

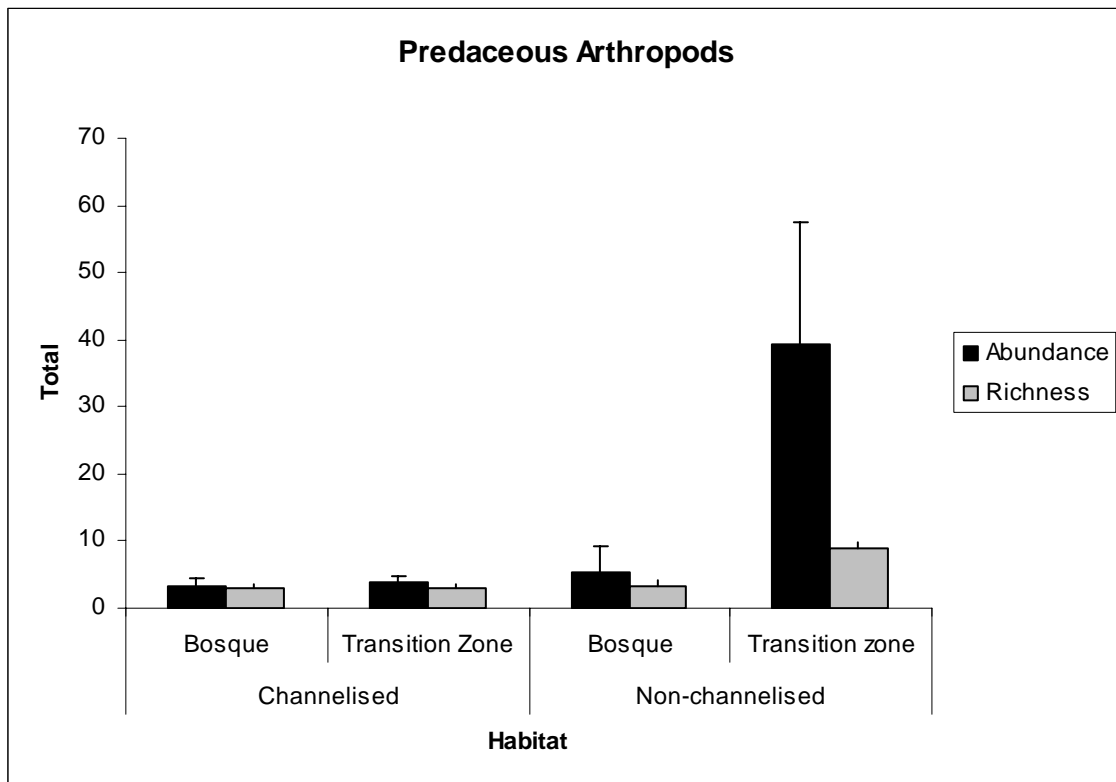


Figure 5: The relative abundance and taxonomic richness of arthropod predators in the Bosque and the transition zone between channelised and non-channelised reaches in the Middle Rio Grande. Error bars represent the standard error (SE).

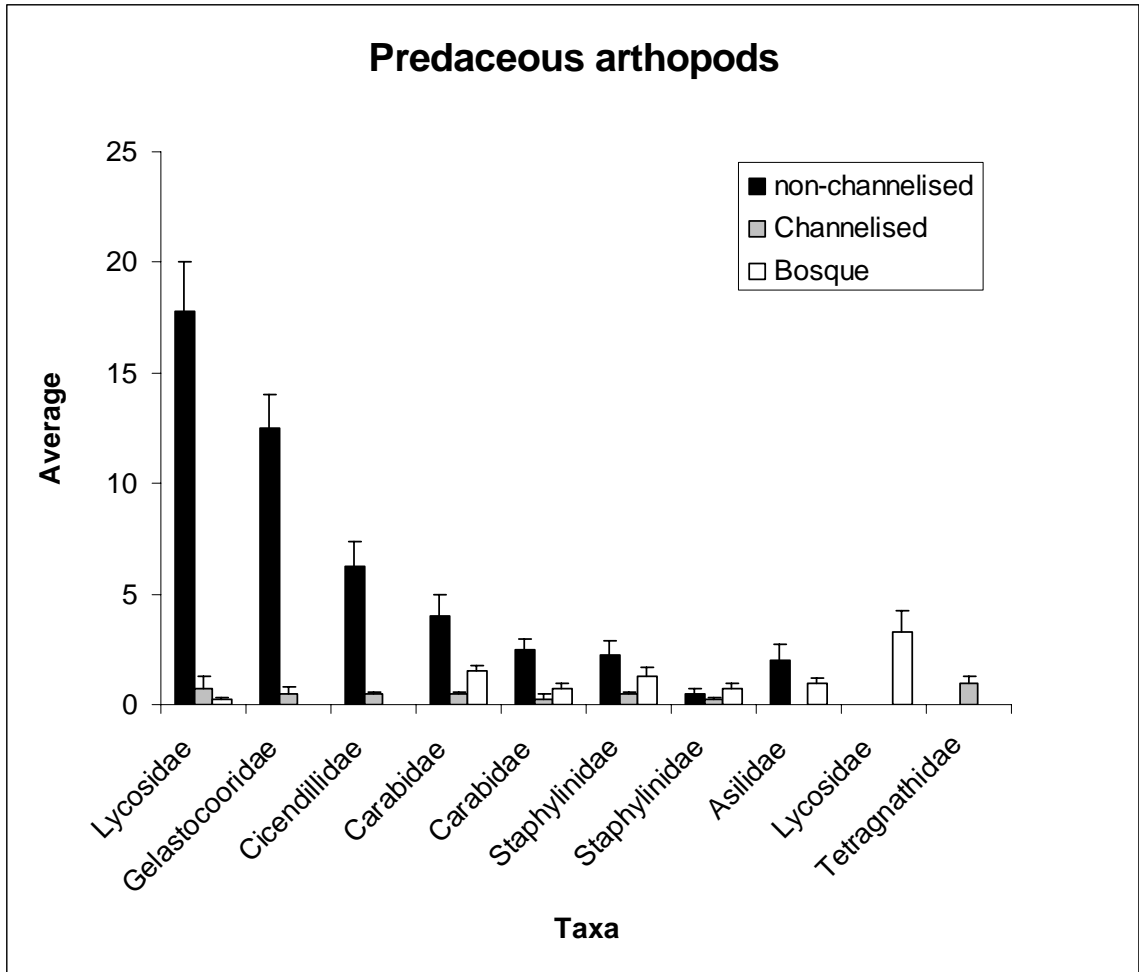


Figure 6: The average number of arthropod predators collected from pitfall traps in the Bosque for all sample locations and the transition zone for channelised and non-channelised reaches. Error bars represent the SE.

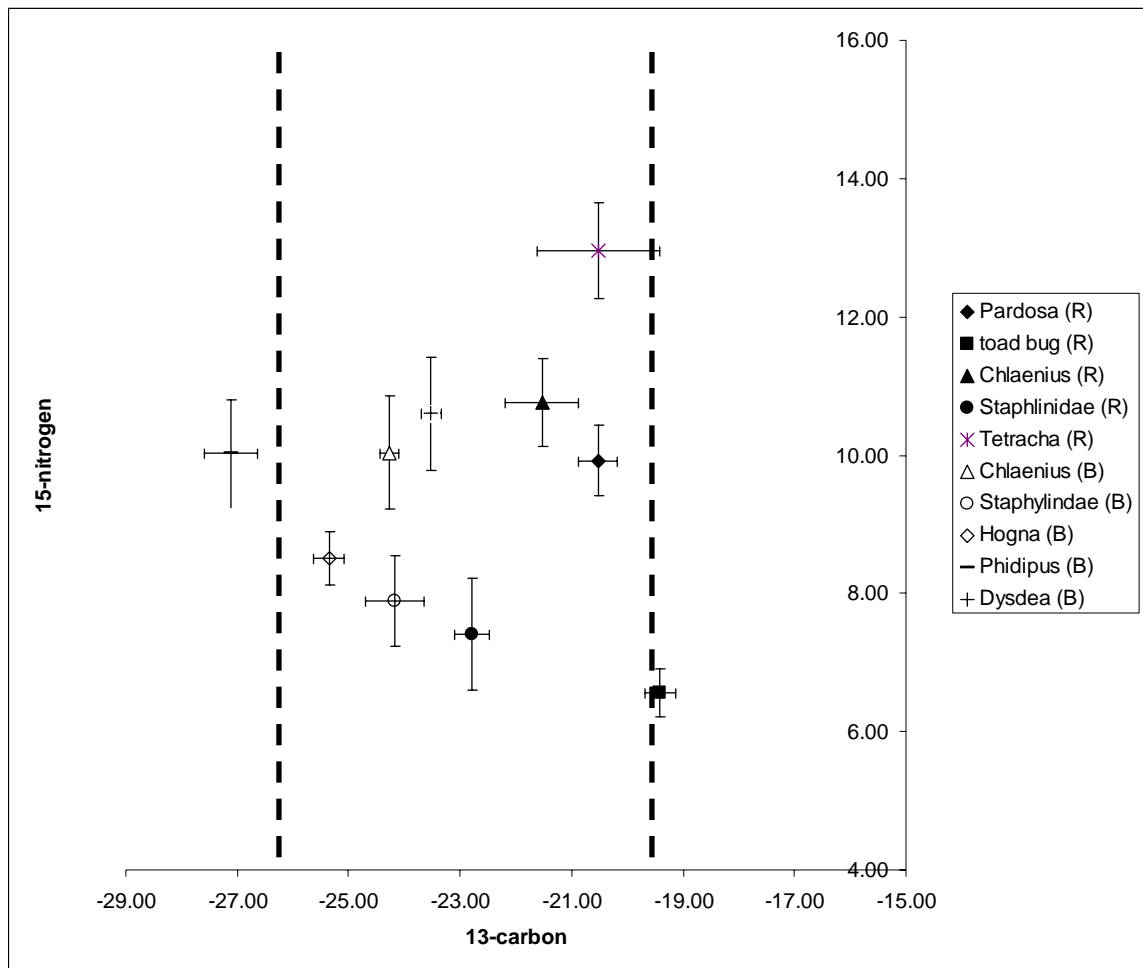


Figure 7: A bivariate plot of $\delta^{13}\text{C}$ by $\delta^{15}\text{N}$ for the five most abundant arthropod predators collected in the transition zone and the Bosque during the summer of 2008. The dashed lines represent the approximate $\delta^{13}\text{C}$ for terrestrial (-26‰) and aquatic (-19‰) production. Five replicates for each species was used for isotopic analyses. Error bars represent the SE.

Transition zone (R): Lycosidae (*Pardosa* spp.) = wolf spider, Carabidae (*Chlaenius* spp.) = ground beetle, Staphylinidae = rove beetle, Carabidae (*Cicindela* spp.) = tiger beetle, Gelastocoridae (*G. oculatus*) = toad bug.

Bosque (B): Carabidae (*Chleanius* spp.) = ground beetle, Lycosidae, (*Hogna* spp.) = wolf spider, Salticidae (*Phidippus* spp.) = jumping spider, Dysderidae (*Dysdera* spp.) = pill bug spider, Staphylinidae = rove beetle.

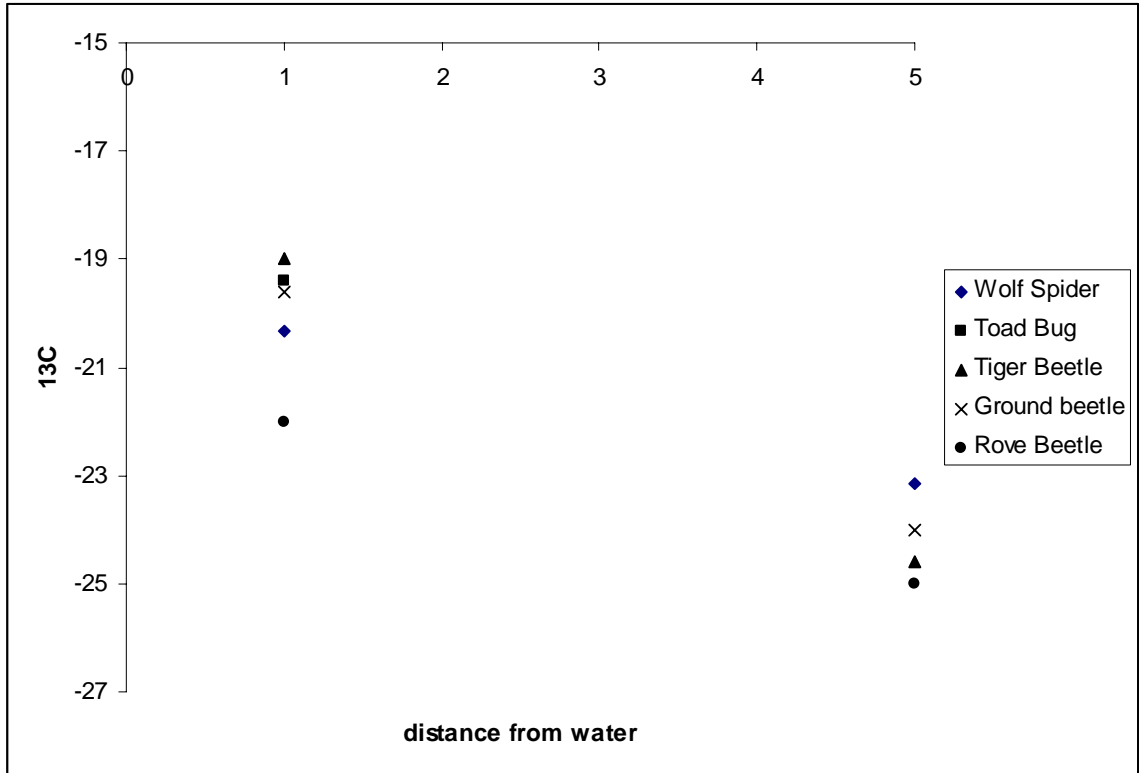


Figure 8: Differences in $\delta^{13}\text{C}$ in the predaceous arthropods in the transition zone in non-channelised reaches as a function of distance from the water's edge.

Table 1: *The average taxonomic richness and density of aquatic macroinvertebrates for each sample location in the Middle Rio Grande, New Mexico.* Each location was sampled 3 times during the summer of 2008.

| Reach | Location | Richness | Density (m²) |
|------------------------|-------------------|-----------------|--------------------------------|
| Channelised | Angostura | 5 | 42.3 |
| | San Acacia | 2 | 14.2 |
| | Escondida | 3 | 29.5 |
| | Above San Marcial | 1.3 | 18.1 |
| | San Marcial | 2.3 | 29.1 |
| Non-channelised | Angostura | 6.6 | 66.8 |
| | Rio Rancho | 3.7 | 31.2 |
| | Highway 60 | 8 | 59.8 |
| | San Acacia | 3.3 | 30.3 |
| | San Marcial | 4 | 42.2 |

Table 2: Results from a two stage linear mixing model for the most abundant predaceous arthropods in the Bosque and the transition zone (Phillips and Gregg 2001). The average is based on the percent reliance of aquatic carbon assuming a fractionation of $\delta^{13}\text{C} = -19\text{‰}$ and -26‰ for terrestrial production. The upper and lower limits represent the 95% confidence interval. Five replicates were used for each species.

| Habitat | Family | Genus | Average | 95% confidence | |
|-------------------|----------------|---------------------|----------------|-----------------------|--------------|
| | | | | Upper | Lower |
| Bosque | Carabidae | <i>Chlaenius</i> | 19% | 27% | 10% |
| | Staphylinidae | | 17% | 26% | 8% |
| | Lycosidae | <i>Hogna</i> | 9% | 18% | 0% |
| | Salticidae | <i>Phidippus</i> | 0% | 0% | 0% |
| | Dysderidae | <i>Dysdera</i> | 36% | 44% | 27% |
| Transition | Lycosidae | <i>Pardosa</i> | 78% | 87% | 70% |
| | Gelastocoridae | <i>Gelastocoris</i> | 94% | 100% | 85% |
| | Carabidae | <i>Chlaenius</i> | 64% | 72% | 55% |
| | Staphylinidae | | 46% | 54% | 37% |
| | Carabidae | <i>Cicindela</i> | 53% | 61% | 45% |

Conclusion

The Rio Grande is a highly dynamic ecosystem. Between 2004 and 2008, there was immense variability in stream discharge. As a result, a large amount of the range of variability that can occur in the Rio Grande took place during the course of this dissertation which provided unique insights into the macroinvertebrate community.

Chapter 1 focused on the role of variability in stream discharge on the aquatic macroinvertebrate community. Analyses of the hydrograph indicated that there were three types of disturbance that occurred in the Middle Rio Grande; a ramp disturbance from spring discharge, low or no discharge conditions (drought), and pulse disturbance from monsoonal rains. Any combination of these disturbances can occur within a year's time, thus exerting large abiotic pressures on the macroinvertebrate community. As expected, discharge was negatively correlated with total density and taxonomic richness. Peak densities were associated with lower discharge conditions, a more stable hydrograph, and after below normal monsoonal rains as seen in 2004 and 2006. There may be a lag-time effect, where it takes a season or two before macroinvertebrate communities are able to recover from unusually high discharges.

Chapter 2 expanded into the surrounding riparian area to determine the role of seasonal discharge on the linkages between the aquatic and terrestrial systems. The results of this study indicate that the food web in the Rio Grande is linked to the surrounding riparian area through reciprocal subsidies. For example, stable isotope analyses of aquatic predaceous arthropods indicated that they relied on terrestrial production and *vice versa*. Additionally, peak productivity in the aquatic and terrestrial system may be synchronous during low flows in the summer. However, during times of

peak discharge in the spring, terrestrial arthropod predators at the water's edge were lower in abundances. This may be due to the lack of prey subsidies from the aquatic system. Wolf spiders were the only terrestrial predaceous arthropod that had similar abundances during low and high discharge. It was also the only predator that indicated a shift from a reliance on terrestrial production in the spring to aquatic production in the summer that coincided with changes in discharge.

Chapter 3 focused on the effects of channelisation on the linkages between the aquatic and terrestrial system. Riparian zones are known to often have a unique species assemblage and are therefore a vital component of global diversity. In the Rio Grande, there was a very high species turnover between the transition zone and the Bosque indicating that the transition zone had a different community. A large portion of this difference was influenced by the abundances and richness of predators in the transition zone. Stable isotope analyses indicated that these predators were being heavily subsidized by aquatic production and may have a higher diversity. In channelised reaches, the arthropod predators were greatly reduced in abundance and in richness. Coinciding with that was a 50% reduction in the density of aquatic macroinvertebrates. This is an indication that the effects of channelisation are not confined to the aquatic environment but also extend into the surrounding riparian areas. Consequently, channelisation may be a threat to diversity by negatively impacting transition zone communities and adversely affecting predaceous arthropods.

In conclusion, the Rio Grande is a biologically complex ecosystem that is intricately linked to the surrounding riparian area. Seasonal and annual variability in

stream discharge and the effects of river regulation affect not confined to the aquatic systems but also influence the surrounding terrestrial system.