LARGE RIVER FOOD WEBS: INFLUENCE OF NUTRIENTS, TURBIDITY, AND FLOW, AND IMPLICATIONS FOR MANAGEMENT

A Dissertation

by

KATHERINE ANNE ROACH

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2012

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Large River Food Webs: Influence of Nutrients, Turbidity, and Flow, and Implications for Management. (August 2012)

Katherine Anne Roach, B.Sc., Buena Vista University; M.A., University of Kansas
Chair of Advisory Committee: Dr. Kirk O. Winemiller

Humans impact rivers in many ways that modify ecological processes yielding ecosystem services. In order to mitigate anthropogenic impacts, scientists are challenged to understand interactions among physicochemical factors affecting large river food webs. An understanding of socioeconomic factors also is critical for ecosystem management. In this dissertation, I explore spatiotemporal patterns in floodplain river food webs and political barriers to management of environmental flows, an important factor influencing river ecology.

In Chapter II, I reviewed the scientific literature to test conceptual models of river food webs and predictions of environmental factors that might produce variation in basal production sources supporting consumer biomass. My review indicates that algae are the predominant production source for large rivers worldwide, but consumers assimilate C_3 plants in rivers 1) with high sediment loads and low transparency during high flow pulses, 2) with high dissolved organic matter concentrations, and 3) following periods of high discharge or leaf litter fall that increase the amount of terrestrial material in the particulate organic matter pool.

In Chapter III, I descrobe field research conducted to examine relationships among hydrology, nutrient concentrations, turbidity, and algal primary production and biomass in the littoral zone of five rivers in Texas, Peru, and Venezuela differing in physicochemical conditions. I used stable isotope signatures to estimate contributions of algal- versus terrestrial-based production sources to consumers during different hydrologic periods. My research indicates that during flow pulses in floodplain rivers, a decrease in algal biomass and productivity, combined with increased inputs of terrestrial organic matter, can result in increased terrestrial support of metazoan consumers in the aquatic food web.

In 2007, Texas Senate Bill 3 directed that environmental flow recommendations be developed for river basins. Despite emphasis on use of the “best available science” to develop environmental flow regimes and “stakeholder involvement” to address needs of all water users, for the first two basins to complete the SB3 process, final environmental flow rules did not mimic a natural flow regime. In Chapter IV, I reviewed this process, concluding that incentives for river authorities to increase compromise with diverse stakeholders should result in more sustainable management of freshwater.

To Mama and Daddy, who limited
TV watching to one hour a day

ACKNOWLEDGEMENTS

I am extremely grateful to the many mentors and colleagues who have assisted me during my pursuit of a PhD. My advisor, Kirk Winemiller, is the reason I chose to move to College Station, Texas. I couldn’t have made a better decision – Kirk taught me more about food web ecology, fisheries biology, and the scientific process than I ever could have imagined. He also is an excellent editor, and I appreciate his rapid feedback on manuscripts. In addition to his support as a mentor, Kirk provided me with a great deal of funding for my own research.

I am also grateful to other mentors who influenced my intellectual development. Steve Davis has consistently provided me with detailed, insightful feedback on manuscripts and research proposals. Furthermore, he allowed me to not only use his five internally logging Hydrolab minisondes, but also to travel with them to Benin, Peru, and Venezuela. The Peruvian field school led by Lee Fitzgerald, Amanda Stronza, and Don Brightsmith was instrumental in teaching me how to get around Peru before conducting my own field research. Micky Eubanks also provided support and instruction during my time at Texas A&M University.

I also thank all of the graduate and post-doctoral students in Kirk Winemiller’s lab: Liz Carrera, Bibiana Correa, Dan Fitzgerald, Andrew Jackson, Nathan Lujan, Chevaun McCray, Carmen Montaña, JV Montoya, Chouly Ou, Allison Pease, Becca Pizano, Michi Tobler, and Crystal Watkins. The opportunity to routinely interact with students from all over the world, including Brazil, Cambodia, Colombia, Peru, and

Venezuela, in addition to the US, has been extremely fulfilling. I was fortunate to have been able to take classes, conduct research, and travel with such an enjoyable, intelligent group of people.

Also, thank you to the many colleagues who assisted me in the field, particularly those who helped me with field work in the Tambopata River in Peru. It would not have been possible without the help of Crissel Vargas Laura, who cheerfully assisted me with purchasing equipment in Peru months before the field season began so that I could begin conducting research as soon as I arrived. Thank you to Gaby and Don Brightsmith, who let me use their boat, the Pionus menstruus. I am grateful to the Ese Eja community of Infierno for granting me access to their land, and to local field assistants David Flores and Roberto Amosins for their invaluable assistance in catching fish. Kurt Holle, manager of the ecotourism company Rainforest Expeditions, allowed Andrew Jackson, Carmen Montaña and me to stay at the ecotourism lodge Posada Amazonas. Hernan Ortega Torres, curator of fishes from the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, helped me to obtain a permit so that I could take samples from Peru into the United States. I am also grateful to the Applied Biodiversity Science field school participants who took chlorophyll a and nutrient samples. At the Cinaruco River in Venezuela, Wilson and Yarisma Garcia collected stable isotope samples, Carmen Montaña and JV Montoya assisted with handing off of sampling supplies, and JV Montoya allowed me to use his nutrient, primary production, and chlorophyll *a* data. A large group of undergraduate students, graduate students, and visiting researchers assisted with sampling in the Brazos, Guadalupe, and Neches Rivers:

Anthony Braden, Andrew Jackson, Adam Landon, Nathan Lujan, Zach Peterson, Nicole Smolensky, Ursulla and Fabio Souza, Crystal Watkins, Chevaun McCray, and many others. Finally, I am grateful to those who took the time to explain their perspective of the Texas Environmental Flow program to me: Kathy Alexander, Kip Averitt, Dave Buzan, Ken Kramer, Kevin Mayes, David Roemer, Mark Wentzel, and Kirk Winemiller.

I was fortunate to receive the Merit Fellowship from Texas A&M University which funded my first year of PhD study. The Applied Biodiversity Science IGERT at Texas A&M University program provided me with funding for two years, in addition to encouraging me to collaborate with graduate students outside of my discipline. I was fortunate to spend many hours attending Applied Biodiversity Science – sponsored events, including journal club, seminars, and the Peruvian field school. I value the time I spent with fellow ABS students and coordinators, Elizabeth Shapiro and Leslie Ruyle. I also wish to extend my gratitude for receiving the Tom Slick Graduate Research Fellowship, which funded me while I wrote this dissertation.

I owe thanks to my parents, Mike and Sara Roach, who have provided endless encouragement throughout my long-term graduate student status. They were not only cheerleaders, but also assisted me financially by paying for clothing, plane tickets home for Christmas, and student fees. Finally, I thank my husband Andrew Jackson. He not only endured bowel problems, extreme humidity, and sand fly bites during four months of field work in Peru and several months of field work in Texas, but also has provided me with emotional support while finishing his own thesis.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

GENERAL INTRODUCTION

Humans have historically constructed civilizations along the banks of rivers. In addition to providing vital supplies of water and easy access to nutrient-rich, alluvial soils, rivers filter and remove nutrients, provide cultural and recreational opportunities that increase quality of life, and produce harvestable fish biomass, particularly for low-income people in rural areas of developing countries (Allan et al. 2005). Ecologists have sought to understand spatial and temporal patterns in instream primary production that influence river food webs, and thereby production of fishery biomass. Conceptual models such as the Riverine Continuum Concept (RCC) by Vannote et al. (1980), the Flood Pulse Concept (FPC) by Junk et al. (1989), and the Riverine Productivity Model (RPM) by Thorp and Delong (1994, 2002) have been influential and continue to be widely cited. In the RCC, Vannote et al. (1980) hypothesized that longitudinal, downstream trends in turbidity and landscape characteristics, such as the degree of shading by riparian trees, affect the relative amount of detritus versus algae in the particulate organic matter pool and the structure of macroinvertebrate communities. In lowland rivers, the RCC predicted that depth and turbidity limit instream primary production, and the great width of large rivers limits inputs of leaves from riparian plants, thus secondary consumers derive their energy from fine particulate organic matter (FPOM) from upstream. In the FPC, Junk et al. (1989) proposed that seasonal

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This dissertation follows the style of Ecology.

overbank flooding connecting the river channel and the floodplain has a major influence on primary and secondary production, and in unaltered large rivers with intact floodplains, secondary consumers derive the majority of their energy from terrestrial plants from within the floodplain. In the RPM, Thorp and Delong (1994) predicted that, because algae and terrestrial plants from the riparian zone are more labile than material from upstream or the floodplain, they are more likely to be assimilated by secondary consumers. However, in the Revised RPM, Thorp and Delong (2002) modified their original hypothesis and predicted that the primary energy source supporting secondary consumers in large rivers is algae, and not terrestrial plants.

Research using stable isotope analysis to trace the movement of material through river food webs has indicated the importance of algae (Jepsen and Winemiller 2002, Clapcott and Bunn 2003, Herwig et al. 2004, Delong and Thorp 2006) and the low importance of C_4 macrophytes for supporting biomass of metazoan consumers (Thorp and Delong 1998, Clapcott and Bunn 2003, Herwig et al. 2004, Zeug and Winemiller 2008a). However, terrestrial C_3 macrophytes also have been documented to support consumers, particularly during periods of high flows (Huryn et al. 2001, Zeug and Winemiller 2008a). Clearly, our understanding of the processes that affect primary and secondary production in large rivers needs refinement. Variation in the basal production sources that support secondary consumer biomass has been hypothesized to be caused by hydrologic regime, turbidity, concentrations of dissolved organic matter, lateral connectivity between the river channel and floodplain, floodplain vegetation, presence of upstream impoundment, and other environmental factors (e.g., Johnson et al. 1995). In

Chapter II of my dissertation, I review the scientific literature in a rigorous manner to identify environmental factors producing spatio-temporal variation in basal production sources supporting consumer biomass in floodplain rivers. In Chapter III, I describe field research conducted to examine potential relationships among hydrology, nutrient concentrations, turbidity, and algal primary production and biomass in the littoral zone of five rivers differing in physicochemical conditions. I also use stable isotope signatures of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and deuterium (δD) to estimate contributions of algal- versus terrestrial-based production sources to consumers during different hydrologic periods.

Because humans are rapidly changing river flow regimes (i.e., natural variability in the magnitude, timing, frequency, duration, and rate of change of flow), the necessity of determining the factors that maintain secondary consumers in large rivers now has a sense of urgency. The construction of one dam per 28 km of large (3-8 order) river channel across the United States has significantly dampened seasonal and annual variation in river streamflow, contributing to the loss of biodiversity (Poff et al. 2007). Hydropower projects are now rapidly being constructed in developing countries. Across all the Andean tributaries of the Amazon River, 151 new dams with > 2 MW capacity are planned over the next 20 years (Finer and Jenkins 2012). Furthermore, because of rapid growth of the human population and increasing demand by industry, diversions of fresh surface water are increasing, some across watershed boundaries. It is well accepted that the structure and function of Earth’s ecosystems can no longer be understood without accounting for the influence of humans (Vitousek et al. 1997). Thus, a conceptual framework has emerged indicating that because humans now are an integral part of ecosystems, an understanding of socioeconomic factors such as politics, institutions, and incentives of multiple actors is critical for effective ecosystem management (Fitzgerald and Stronza 2009). In 2007, the Texas legislature passed Senate Bill 3 mandating formation of science and stakeholder committees to make recommendations on the environmental flows needed to maintain the ecological integrity of river basins. The Texas Commission on Environmental Quality, the state agency that issues water rights permits, was to promulgate these recommendations and develop environmental flow rules. For the first two basins to have completed environmental flow recommendations, the Sabine and Neches Basins and Sabine Lake Bay and the Trinity and San Jacinto Basins and Galveston Bay, final environmental flow rules were only subsistence flows, one level of base flows, and low flow pulses at a limited number of sites – flow that does not approximate the historical flow regime. In Chapter IV of my dissertation, I discuss why the Senate Bill 3 process was derailed for these basins.

Below I provide a brief summary of the background and main results of each of my chapters.

CHAPTER II THE INFLUENCE OF NUTRIENTS AND TURBIDITY ON RIVER FOOD WEBS: A LITERATURE REVIEW

I review the scientific literature on the use of tracers (stable isotope analysis and fatty acid biomarkers) to estimate the basal production sources that support metazoans in floodplain rivers. I use a weight-of-evidence approach to test hypotheses regarding factors that might contribute to variation in basal production sources over space and time, including hydrologic regime, turbidity, concentration of dissolved organic matter, floodplain vegetation, lateral connectivity between river channel and floodplain, and upstream impoundment. Based on my results, I develop a conceptual model of physicochemical factors influencing entrance of terrestrial material into river food webs. My review indicates that C_4 grasses rarely support riverine metazoans and algae are the predominant production source for large rivers worldwide, but that consumers assimilate C_3 plants in rivers with high sediment loads and low transparency during high flow pulses. Exceptions to this pattern occur when river reaches are located downstream from an impoundment, in which case algae assume greater importance. Terrestrial C_3 plants also subsidize consumers in rivers with high dissolved organic matter concentrations and in other rivers following periods of high discharge or leaf litter fall that increase the amount of terrestrial material in the particulate organic matter pool. I highlight the natural causes of differences in turbidity and dissolved organic matter among large rivers, the consequences of human alterations of turbidity and nutrient concentrations for aquatic organisms, and the importance of transported materials as a source of nutrients for ecologically and economically important fish species.

CHAPTER III HYDROLOGIC REGIME, NUTRIENTS, AND TURBIDITY INFLUENCE ENTRANCE OF TERRESTRIAL MATERIAL INTO RIVER FOOD WEBS

In order to investigate how the basal production sources supporting metazoans in floodplain rivers might change seasonally because of varying environmental conditions, I measured seasonal changes in percent bankfull discharge, nutrient concentrations (soluble reactive phosphorus, dissolved inorganic nitrogen, silica), turbidity, and algal net primary production (NPP) and biomass (chlorophyll *a*) in the littoral zone of five floodplain rivers varying in hydrologic regime, turbidity, and nutrient concentrations. I also used stable isotope signatures of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and deuterium (δD) and MixSIR, a Bayesian stable isotope mixing model, to estimate contributions of algal- versus terrestrial-based production sources to consumers during different hydrologic periods. The Brazos River (Texas) and Tambopata River (Peru) carry high loads of suspended sediments of fine grain size. The Neches River (Texas) and Cinaruco River (Venezuela) carry low levels of suspended sediments and relatively high concentrations of dissolved organic matter (DOM). The Guadalupe River (Texas) carries moderate suspended sediment load and low concentrations of dissolved organic matter. Inorganic nutrient concentrations are lower and flooding patterns more seasonal in the tropical rivers compared to the Texas rivers.

I based my predictions for this chapter on the conceptual model I developed in Chapter II indicating that discharge, light, and nutrients might interact to limit the availability of algal-based production sources to the food web in floodplain rivers. In the Brazos river, I hypothesized that high turbidity and low transparency would limit algal production during high flow pulses, and terrestrial-based production sources would support metazoan consumers during high-flow periods. However, as a result of high inorganic nutrient concentrations and the settling of sediments during low-flow periods, I predicted that algae in littoral zones would become highly productive and algal-based production sources would support metazoans during low-flow periods. In the Tambopata River, because of high turbidity and low inorganic nutrient concentrations, I predicted that algal productivity and biomass would be low and terrestrial-based production sources would support consumer biomass throughout the annual hydrologic cycle. Soils are less erodible in the Neches, Cinaruco, and Guadalupe watersheds compared to the Brazos and Tambopata watersheds, thus because of high transparency at all flow levels, I expected consumers to be supported by algal-based production sources throughout the annual hydrologic cycle.

I found that in some of the temperate rivers, nutrients were higher during relatively short duration high-flow pulses. In the tropical rivers, nutrients tended to be higher during the annual low-water period. Turbidity was higher following periods of high flows in the Brazos, Tambopata, and Guadalupe rivers compared to the Neches and Cinaruco rivers. Whereas littoral zones in the Neches, Cinaruco, and Guadalupe rivers were consistently autotrophic (positive water-column + benthic NPP), littoral zones in the sediment-laden rivers (Brazos and Tambopata) became heterotrophic (negative water-column + benthic NPP) during periods of high discharge. Algae and C_3

macrophytes both made major contributions to consumer biomass, with contributions varying temporally in all rivers that were sampled during different hydrologic periods. Algae made a greater contribution to the biomass of consumer species following extended low-flow periods, and C_3 macrophytes made a greater contribution following high flow pulses. A primary conclusion from Chapters II and III is that during high-flow pulses in floodplain rivers, when a decrease in algal biomass and productivity is combined with increased inputs of terrestrial organic matter, terrestrial C_3 plants can be important basal production sources supporting metazoan consumers.

CHAPTER IV TEXAS WATER WARS: HOW POLITICS AND SCIENTIFIC UNCERTAINTY INFLUENCE ENVIRONMENTAL FLOW DECISION-MAKING IN THE LONE STAR STATE

Diversions of freshwater from Texas streams and rivers are increasing due to growth of the human population, increasing demand by industry, and depletion and mandatory reductions in pumping of groundwater. Withdrawals and the construction of large reservoirs have altered the flow regime of many rivers in Texas, contributing to the degradation of river and estuarine ecosystems. In 2007, Texas passed Senate Bill (SB) 3 directing that environmental flow recommendations be developed using a regional approach with stakeholder involvement. Science committees were formed and instructed to develop environmental flow regimes without regard to the needs of water for other uses. Stakeholder committees were to review the environmental flow regime and develop their own recommendations considering present and future human needs for water. Both committees were to use the best available science to develop a recommended environmental flow regime through a collaborative process designed to achieve consensus. The Texas Commission on Environmental Quality (TCEQ), the state agency that issues water rights permits, was to promulgate these recommendations and develop environmental flow rules.

For the first two basins to complete the SB3 process, the Sabine and Neches Basins and Sabine Lake Bay and the Trinity and San Jacinto Basins and Galveston Bay, final e-flow rules did not mimic a natural flow regime, rather, only subsistence flows, one level of base flows, and low flow pulses at a limited number of sites were adopted. The SB3 process was derailed as a result of several factors. Both science and stakeholder committees were skewed with more members representing short-term economic than ecological and recreational interests for freshwater. Many individuals on the science and stakeholder committees worked for river authorities, semiautonomous state agencies that receive the majority of their funding from surface water sales and other activities that require diversions of large amounts of surface water, and consulting firms that regularly contract with the river authorities. Water rights holders, and particularly personnel of river authorities, were from the outset distrustful of the SB3 process. There was a high degree of uncertainty associated with e-flow science, and adaptive management was used as justification for making low e-flow recommendations. Although SB3 emphasized the science of e-flows and stakeholder involvement, in the end, TCEQ set environmental flow rules at levels much lower than those recommended for protection of environmental benefits by the science committees.

CONCLUSIONS

Scientists face a pressing need to make better predictions about how anthropogenic modifications to rivers will alter ecological processes that yield ecosystem services, and also to understand how policies and institutions should be structured to ensure that freshwater is allocated equitably and used sustainably. My hope is that this dissertation demonstrates that 1) anthropogenic impacts to rivers are likely to affect the relative importance of algal versus macrophyte detritus pathways, with concomitant changes in secondary biomass and community structure, and 2) incentives for river authorities to increase dialogue and compromise with diverse stakeholders should result in more sustainable management of freshwater.

CHAPTER II

THE INFLUENCE OF NUTRIENTS AND TURBIDITY ON RIVER FOOD WEBS: A LITERATURE REVIEW

INTRODUCTION

Investigations of the basal production sources that support large river food webs are important because understanding movement of material from primary producers to metazoans carries implications for the biomass and diversity produced at higher trophic levels. Ecosystems in which a high proportion of organic matter passes through microbes before being assimilated by consumers may support less secondary production because of the increased number of trophic transfers (Legendre and Rassooulzadegan 1995, Cotner and Biddanda 2002), but because of their lower productivity, detrital-based food chains may allow for higher species diversity (Rooney and McCann 2011). Three widely cited conceptual models have made predictions regarding production sources supporting consumers in floodplain river ecosystems: the River Continuum Concept (RCC, Vannote et al. 1980), Flood Pulse Concept (FPC, Junk et al. 1989), and Riverine Productivity Model (RPM, Thorp and Delong 1994, Thorp and Delong 2002).

The first conceptual model to link the physical condition of stream reaches with changes in primary producer and consumer composition, the RCC, stimulated much discussion about the factors that determine the structure of river ecosystems. Vannote et al. (1980) proposed that, because the great width of large rivers minimizes input of coarse particulate organic matter (CPOM) from the riparian zone, food webs in large rivers are primarily derived from fine particulate organic matter (FPOM) from upstream processing of dead leaves and woody debris. Instream (autochthonous) primary production is proposed to be limited by depth and turbidity causing large rivers to be heterotrophic (net primary production/respiration < 1), thus autochthonous primary production is not predicted to be an important source of nutrients for consumers.

In the FPC, Junk et al. (1989) proposed that the pulsing of river discharge into the floodplain has a major influence on primary and secondary production in large, lowland rivers. Junk et al. (1989) made the case that in unaltered large rivers with intact floodplains, the majority of animal biomass is derived from production within the floodplain and not from downstream transport of organic matter as predicted in the RCC. Consumption of living plant tissue, such as leaves, pollen, fruits and seeds, as well as consumption of plant detritus, including FPOM and CPOM, are major pathways in river-floodplain food webs according to the FPC. Because highest fish yields in large rivers are associated with extensive floodplains, Junk et al. (1989) argued that the main channel serves primarily as a route for organisms to gain access to the floodplain for feeding and reproduction, as well as refuge during low-flow periods or winter.

The RPM was originally developed for large rivers with relatively constricted channels and limited floodplain and lateral connectivity. In the RPM, Thorp and Delong (1994) proposed that the RCC and FPC underestimate the role of local autochthonous production (phytoplankton, benthic algae, aquatic vascular plants, and mosses) and inputs of organic matter from the riparian zone (leaves, particulate organic carbon, dissolved organic carbon) during low flow periods. They felt that these models produce results that tend to overemphasize the importance of recalcitrant organic material passively transported from headwaters and floodplains. Thus, Thorp and Delong (1994) emphasized that, because autochthonous organic material and allochthonous material from the riparian zone are more labile, they are more easily assimilated by metazoan heterotrophs, including microcrustaceans, aquatic insects, mollusks and fishes. Additionally, Thorp and Delong (1994) contended that, because in some large rivers benthic algae and aquatic macrophytes are substantial sources of organic matter, and because low-velocity areas such as nearshore and side channels allow for retention of riparian-derived organic matter, these sources are frequently available for consumers. Thus, Thorp and Delong (1994) suggested that in floodplain rivers instream primary production, and phytoplankton in particular, is a significant contributor to secondary productivity, but that material from riparian plants also is important. In their Revised RPM, Thorp and Delong (2002) modified their original hypothesis and concluded that C_3 and C_4 plants from the riparian zone are less important than they originally thought, and that “the primary, annual energy source supporting overall metazoan production and species diversity in mid- to higher-trophic levels of most rivers ($\geq 4^{th}$ order) is autochthonous primary production entering food webs via algal-grazer and decomposer pathways." Thorp and Delong (2002) proposed that the Revised RPM is predicted to be true even in heterotrophic rivers, because ecosystem respiration is mostly derived from bacteria that are supported by allochthonous carbon (the aquatic decomposer food pathway), and not by autotrophic carbon (the algal-grazer food pathway). In their Riverine Ecosystem Synthesis, Thorp et al. (2005) stated that "algal production is the primary source of organic energy fueling aquatic metazoan food webs in the floodplains of most riverine landscapes during supra-bankfull floods, especially in rivers with seasonal, warm-weather floods."

The use of tracers, such as stable isotope and fatty acid analysis, has enabled ecologists to test these models by estimating relative contributions of production sources assimilated by consumers (e.g., Phillips and Gregg 2003). Many such studies of large rivers have found that algal carbon is the predominant production source and that C_4 grasses (C_4-dicarboxylic acid pathway of carbon fixation) are unimportant (Delong and Thorp 2006, Roach et al. 2009). However, it is increasingly apparent that terrestrial C_3 plants (those using the Calvin cycle pathway of carbon fixation during photosynthesis) also can support consumers in some rivers (Hoeinghaus et al. 2007, Zeug and Winemiller 2008a) and that production sources supporting consumers can change seasonally (Huryn et al. 2001, Hladyz et al. 2010). Differences in hydrology, water clarity, nutrient concentrations, floodplain vegetation type, lateral connectivity between the river channel and floodplain, and the upstream presence of dams have been suggested as contributors to variation in primary producers supporting large river food webs, but these predictions have yet to be tested (Meyer 1990, Sedell et al. 1989, Johnson et al. 1995, Winemiller 2004).

Metazoan consumers in turbid rivers may have greater proportional contributions of terrestrial-based organic matter because suspended particles can substantially reduce the productivity of water bodies (Kirk 1985, Søballe and Kimmel 1987). Generally, turbidity is high because of the presence of inorganic, suspended particles that are < 0.22 μm in size (Kirk 1985). In sediment-laden rivers, frequently referred to as "whitewater" rivers in the tropics, sediments are often resuspended during high or rising discharges and deposited on the river bed at low or falling discharges, resulting in a positive correlation between suspended sediment load and discharge (Meade 1988). During periods of high discharge, shear stress and abrasion by inorganic sediment can limit growth of periphyton and the combination of low light and scour can limit phytoplankton production (e.g., Wissmar et al. 1981, Steinman and McIntire 1990). However, shallow, turbid, slow-moving water can be highly productive (Kirk 1985).

Relative differences in concentrations of dissolved organic matter (DOM) in the water column can have consequences for the transfer of terrestrial plants to higher trophic levels. Water bodies with low concentrations of inorganic nutrients and high concentrations of organic nutrients are frequently associated with greater rates of respiration than instream primary production (Cotner and Biddanda 2002). The small size and high surface-to-volume ratio of microbes may allow them to be competitively superior to phytoplankton in absorption of dissolved organic nutrients (Azam et al. 1983). Thus, rivers with high DOM concentrations as a result of humic compounds leached from surrounding wetlands and forests (i.e. blackwater rivers) frequently have high bacterial biomass present on decomposing terrestrial vegetation, fueling an active microbial loop (Meyer 1990). Protozoa and fungi may provide organic matter to metazoans by both conditioning terrestrial detritus and acting as a trophic link from bacteria to higher consumers (Goulding et al. 1988, Meyer 1990, Waichman 1996).

Among-river differences in predictability of hydrology also might explain variation in the amount and palatability of production sources. For example, Lewis et al. (2000) explored deterministic, seasonal linkages between water transparency, nutrient concentrations, algal production, and energy flow to consumers in the strongly seasonal Orinoco River. In contrast, consumers in rivers with unpredictable flow regimes may derive more of their organic carbon from terrestrial production sources because flow regimes with rapid, unpredictable flood pulses create conditions unsuitable for production of benthic algae, provide limited time for decomposition of submerged floodplain vegetation, and flush terrestrial invertebrates from the riparian zone into the river channel where they can be consumed by aquatic consumers (e.g., Zeug and Winemiller 2008a).

Johnson et al. (1995) suggested that lateral connectivity between the river channel and floodplain and the type of vegetation on the floodplain might influence the basal production sources assimilated by consumers by affecting the quantity and quality of floodplain-derived terrestrial material. Indeed, this occurs in some upper stream reaches. In Ichawaynochaway Creek, a tributary of the Flint River in Georgia, USA, seston quality (measured as C:N ratio, $\delta^{13}C$, and $\delta^{15}N$) is greater in upper reaches during high-flow conditions as a result of transport of higher-quality materials from the floodplain, but in lower-reaches, high-quality seston is also present during low-flow conditions because lack of shading allows for autochthonous primary production (Atkinson et al. 2009).

Finally, some authors have perceived dams as disruptors of physical parameters and biological processes normally present in rivers (e.g., Ward and Stanford 1983). Impoundments can retain nutrients, in particular phosphorus and silica, resulting in lower concentrations downstream (Wahby and Bishara 1980, Conley et al. 2000). In high-sediment rivers, impoundments lower current velocity, causing sediment to settle resulting in greater water clarity. Clearly, impoundments have the potential to modify resources at the base of the food web.

Here, I present a comprehensive review of the scientific literature on the use of tracers (stable isotope analysis and fatty acid biomarkers) to estimate the basal production sources that support metazoans in floodplain rivers. I focus on studies that were conducted in main-channel habitats, but also include some studies where samples were collected from major aquatic habitats of the floodplain (e.g., Hamilton et al. 1992, Jepsen and Winemiller 2007). For each study, I report taxonomic classification of the consumer and its dominant production source as well as turbidity, hydrologic regime, concentrations of DOM, floodplain vegetation cover, and lateral connectivity between the river channel and floodplain at the study site. I also indicate if the river reach studied was located below a dam. Finally, based on review results, I develop a conceptual model of physicochemical factors influencing entrance of terrestrial material into river food webs.

METHODS

I used a weight-of-evidence approach to evaluate the generalities of current food web hypotheses by compiling published data from 26 rivers from Australia, Brazil, New Zealand, the United States, and Venezuela. For each study, predictability of hydrology was considered to be high if flooding occurs at the same time every year in response to seasonal rainfall patterns (i.e., tropical rivers), intermediate if flooding occurs at approximately the same time every year (e.g., because of winter snow melt) and the river tends to be permanent with regular flows, and low if high-flow periods do not exhibit a seasonal pattern because the river tends to have high flow variability (e.g., because of unpredictable spates and prolonged periods of low flow). Magnitude of discharge was considered to be high if flooding was reported during the study period, average if no flood or drought was reported, and low if a drought or low-flow period was reported. Turbidity was classified as high if the river was described as turbid and low if the river was described as clear. A river reach was classified as constrained if, during the time of the study, there was little to no hydrologic connections with the floodplain via side channels, and floodplain if such hydrologic connections were present.

Thirteen of the study rivers (Gwydir River in Australia; Amazon River, Paraná River, Paranapanema River, Iguatemi River, and Ivinheima River in Brazil; Colorado River, Hudson River, Mississippi River, Missouri River, Ohio River, and Rio Grande in the United States; and Orinoco River in Venezuela) can be characterized as part of a large river system, defined by Nilsson et al. (2005) as a system having in its catchment a river channel section with a mean annual discharge before human manipulation of ≥ 350 m^3/s. The Gwydir River, a tributary in the Murray-Darling drainage, has a mean annual discharge recorded by the Australian Natural Resources Atlas of 29 m^3/s. The Cooper River, located in central Australia, has an extremely variable hydrologic regime, with an average annual discharge of 97 m^3/s (Hamilton et al. 2005). The Flinder, Gregory, and Logan Rivers are smaller catchments draining south-eastern Australia. The Iguatemi, Ivinheima, and Paranapanema Rivers (Brazil) are tributaries of the Paraná River. The average annual streamflow from historical USGS gage data of the Brazos, Mattaponi, and Paria Rivers (USA) are 142 m^3/s, 16 m^3/s, and 1 m^3/s, respectively. The Paria River is an intermittent river, and seasonal flooding can cause discharge to increase to 191 m^3/s. The Aguaro, Apure, and Cinaruco Rivers (Venezuela) are tributaries of the Orinoco River, and the Pasimoni River (Venezuela) is a tributary of the Rio Negro. The Taieri River, the only river in the dataset located in New Zealand, has an average annual discharge of 37 m^3/s (Young and Huryn 1996).

RESULTS

At least 24 publications (11 qualitative and 13 quantitative) have used stable isotope analysis and/or fatty acid biomarkers to trace the production sources supporting river consumers (Table 1.1 and 1.2). One study, Caraco et al. (2010), used radioisotopes ($\Delta^{14}C$) to trace the age of carbon sources assimilated by zooplankton in the Hudson River. Rivers varied in hydrologic regime and floodplain land cover (Table 1.3). Furthermore, variable degrees of turbidity, ambient DOM concentrations, magnitude of discharge, and degree of interaction with the floodplain were documented in these studies (Table 1.3).

Table 1.1. Qualitative estimates using stable isotope analysis and fatty acid analysis of production sources supporting metazoans in rivers. “Qualitative” means that the author provided a stable isotope bi-plot and/or written assessment of the production sources, but did not use a stable isotope mixing model. The system (river name, whether the study was conducted in the floodplain or the main channel, and if the study reach was located below a dam), consumer type, its dominant production source, and the analytical approach that was used are indicated. “Phytoplankton” indicates that an analysis was conducted (i.e., chlorophyll *a*, colloidal silica centrifugation, microscopic analysis) to ensure that particulate organic matter (POM) was mostly algal, and “seston” indicates that no such analysis was done.

System	**Consumer type**	**Dominant production source**	**Approach**	**Reference**
1. Aguaro River floodplain and main channel, central Venezuela	Fishes (Auchenipteridae, Characidae, Cichlidae, Cynodontidae, Erythrinidae, Loricariidae, Prochilodontidae)	Benthic algae and C_3 plants or C_4 grasses	$\delta^{13}C$, $\delta^{15}N$	Jepsen and Winemiller 2008
2. Amazon River floodplain near Manaus, Brazil	Detritivorous fishes (Characiformes) Omnivorous fishes (Siluriformes)	Phytoplankton C_3 plants	$\delta^{13}C$	Araujo-Lima et al. 1986; Forsberg et al. 1993
3. Apure River floodplain and main channel, central Venezuela	Fishes (Anostomidae, Characidae, Cichlidae, Cynodontidae, Erythrinidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae)	Seston or benthic algae	$\delta^{13}C$, $\delta^{15}N$	Jepsen and Winemiller 2007
4. Cinaruco River floodplain and main channel, south-western Venezuela	Fishes (Acestrorhynchidae, Anostomidae, Auchenipteridae, Characidae, Chilodontidae, Cichlidae, Ctenoluciidae, Curimatidae, Cynodontidae, Doradidae, Loricariidae, Sciaenidae	Benthic algae or seston	$\delta^{13}C$, $\delta^{15}N$	Jepsen and Winemiller 2007

Table 1.1 continued

System	Consumer type	Dominant production source	Approach	Reference
5. Colorado River main channel downstream from Glen Canyon Dam, USA	Macroinvertebrates (Chironomidae, Gammarus lacustris, Oligochaeta)	Benthic algae or seston	δ^{13}C, δ^{15}N, δ^{34}S	Angradi 1994
	Fishes (*Catostomus latipinnis*, *Cyprinis carpio*, *Oncorhynchus mykiss, Rhinichthys osculus*)	Benthic algae or seston		
6. Mississippi River main channel near Louisiana, Missouri, USA	Zooplankton	Seston or dissolved nutrients	δ^{13}C, δ^{15}N	Delong et al. 2001
	Macroinvertebrates (Odonata, Oligochaeta, Plecoptera, Trichoptera)	Seston or dissolved nutrients		
	Snails, mussels (*Dreissena polymorpha*, Pleurocera)	Seston or dissolved nutrients		
	Fishes (Centrarchidae, Clupeidae, Ictaluridae, Moronidae, Sciaenidae)	Seston or dissolved nutrients		
7. Missouri River main channel near New Haven, Missouri, USA	Macroinvertebrates (Ephemeroptera, Odonata, Plecoptera, Trichoptera)	Benthic algae	δ^{13}C, δ^{15}N	Delong et al. 2001
	Fishes (Centrarchidae, Clupeidae, Ictaluridae, Moronidae, Sciaenidae)	Benthic algae		
8. Ohio River main channel ~32 km upstream from confluence of Ohio and Mississippi Rivers, USA	Zooplankton	Seston or dissolved nutrients	δ^{13}C, δ^{15}N	Thorp et al. 1998; Delong et al. 2001
	Macroinvertebrates (Ephemeroptera, Odonata)	Seston or dissolved nutrients		
	Clams, mussels, snails (*Corbicula fliminea*, *Dreissena polymorpha*, *Lithasia* sp.)	Seston or dissolved nutrients		
	Fishes (Centrarchidae, Clupeidae, Cyprinidae)	Seston or dissolved nutrients		

Table 1.1 continued

System	Consumer type	Dominant production source	Approach	Reference
9. Orinoco River floodplain near Ciudad Bolívar, Venezuela	Zooplankton (Cladocera, Copepoda, Rotifera)	Phytoplankton	$\delta^{13}C$, $\delta^{15}N$	Hamilton et al. 1992, Lewis et al. 2001
	Macroinvertebrates (Conchostraca, Decapoda, Diptera, Hemiptera, Hydracarina, Ephemeroptera, Hydrophilidae, Odonata)	Phytoplankton		
	Snails, sponges (Basommatophora, Gastropoda, Mesogastropoda, Porifera, Unionoida)	Detritus derived from C_3 plants		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Clupeidae, Cynodontidae, Doradidae, Engraulidae, Loricariidae, Pimelodidae, Prochilodontidae)	Benthic algae or phytoplankton		
10. Paraná River main channel near Paraná City, Brazil	Detritivorous fish (adult *Prochilodus lineatus*)	Detritus derived from phytoplankton or benthic algae	fatty acid analysis	Bayo and Cordiviola de Yuan 1996
11. Paria River main channel near the Utah-Arizona border, USA	Macroinvertebrates (Chironomidae, Gammarus lacustris, Oligochaeta)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$	Angradi 1994
	Fishes (*Catostomus latipinnis*, *Cyprinis carpio*, *Oncorhynchus mykiss*, *Rhinichthys osculus*)	C_3 plants		
12. Pasimoni River floodplain and main channel, southern Venezuela	Fishes (Acestrorhynchidae, Anostomidae, Characidae, Cichlidae, Curimatidae, Cynodontidae, Erythrinidae, Loricariidae, Pimelodidae)	Seston or benthic algae	$\delta^{13}C$, $\delta^{15}N$	Jepsen and Winemiller 2008

Table 1.1 continued

System	Consumer type	Dominant production source	Approach	Reference
13. Rio Grande main channel in the Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico, USA	Larvae and juvenile fishes (Catostomidae, Cyprinidae, Poeciliidae)	Benthic algae	$\delta^{13}C$, $\delta^{15}N$	Pease et al. 2006

Table 1.2. Quantitative estimates using stable and radio isotope analysis of production sources supporting metazoans in rivers. “Quantitative” means that the author used a stable isotope mixing model to estimate % contributions of production sources. The system (river name, whether the study was conducted in the floodplain or the main channel, and if the study reach was located below a dam), consumer type, its dominant production source, and the analytical approach that was used are indicated. “Phytoplankton” indicates that an analysis was conducted (i.e., chlorophyll *a*, colloidal silica centrifugation, microscopic analysis) to ensure that particulate organic matter (POM) was mostly algal, and “seston” indicates that no such analysis was done.

System	**Consumer type**	**Dominant production source**	**Approach**	**Reference**
14. Brazos River main channel near Bryan, Texas, USA	Macroinvertebrates (Cambaridae, Palaemonidae)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Zeug and Winemiller 2008a
	Fishes (Centrarchidae, Clupeiformes, Cypriniformes, Lepisosteidae, Poeciliidae)	C_3 plants		
15. Cinaruco River main channel and floodplain, south-western Venezuela	Fishes (Characiformes, Clupeiformes, Myliobatiformes, Perciformes, Siluriformes, Symbranchiformes)	Seston	$\delta^{13}C$, $\delta^{15}N$	Roach et al. 2009

Table 1.2 continued

System	Consumer type	Dominant production source	Approach	Reference
16. Cooper River main channel near Lake Eyre, Australia	Clams, mussels, snails (*Corbiculina* spp., *Notopala sublineata*, *Velesunio* spp.)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Bunn et al. 2003
	Macroinvertebrates (Chironomidae, Dysticidae, Odonata, Palaemonidae, Viviparidae)	Benthic algae		
	Fishes (Ambassidae, Clupeidae, Eleotridae, Melanotaeniidae, Osmeridae, Percichthyidae, Plotosidae, Poeciliidae, Terapontidae	Benthic algae		
17. Flinders River main channel near the Gulf of Capentaria, Northern Australia	Zooplankton	Seston or benthic algae	$\delta^{13}C$	Leigh et al. 2010
	Mussels (*Velesunio* sp.)	Seston or benthic algae		
	Macroinvertebrates (Decapoda, Hydracarina, Insecta)	Seston or benthic algae		
18. Gregory River main channel near the Gulf of Capentaria, Northern Australia	Macroinvertebrates (Decapoda, Hydracarina, Insecta)	Seston or benthic algae	$\delta^{13}C$	Leigh et al. 2010
	Zooplankton	Seston or benthic algae		
	Mussels (*Velesunio* sp.)			
	Macroinvertebrates (Decapoda, Insecta)	Seston or benthic algae		
19. Gwydir River main channel in New South Wales, Australia	Clams, snails (Bivalvia, Gastropoda)	Benthic algae	$\delta^{13}C$, $\delta^{15}N$	Hadwen et al. 2010
	Macroinvertebrates (*Cherax* sp., *Macrobrachium* sp.)	Benthic algae		
	Fishes (*Gambusia holbrooki*, *Hypseleotris galii*)	Benthic algae		
20. Hudson River main channel near Albany, New York, USA	Zooplankton (Cladocera, Copepoda)	Phytoplankton or aged allochthonous organic matter	$\Delta^{14}C$, $\delta^{13}C$, δD	Caraco et al. 2010

Table 1.2 continued

System	Consumer type	Dominant production source	Approach	Reference
21. Iguatemi River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	Zooplankton (Cladocera, Copepoda)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Hoeinghaus et al. 2007
	Clams, snails (*Corbicula fluminea*, *Pomacea canaliculata*)	C_3 plants		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae, Serrasalmidae)	C_3 plants		
22. Ivinheima River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	Zooplankton (Cladocera, Copepoda)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Hoeinghaus et al. 2007
	Clams, snails (*Corbicula fluminea*, *Pomacea canaliculata*)	C_3 plants		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae, Serrasalmidae)	C_3 plants		
23. Logan River main channel in Queensland, Australia	Clams, snails (Bivalvia, Gastropoda)	Benthic algae	$\delta^{13}C$, $\delta^{15}N$	Hadwen et al. 2010
	Macroinvertebrates (*Cherax* sp., *Macrobrachium* sp.)	Benthic algae		
	Fishes (*Gambusia holbrooki*, *Hypseleotris galii*)	Benthic algae		
24. Mattaponi River main channel near Beaulahville, Virginia, USA	Zooplankton (Cladocera, Copepoda)	Phytoplankton	$\delta^{13}C$, $\delta^{15}N$	Hoffman et al. 2007; Hoffman et al. 2008
	Macroinvertebrates (Malacostraca, Ostrocoda, Insecta)	Phytoplankton		
	Fishes (*Alosa sapidissima*)	Phytoplankton		
25. Mattaponi River main channel near Beaulahville, Virginia, USA	Zooplankton (Cladocera, Copepoda)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Hoffman et al. 2007; Hoffman et al. 2008
	Macroinvertebrates (Malacostraca, Ostrocoda, Insecta)	C_3 plants		
	Fishes (*Alosa sapidissima*)	C_3 plants		

Table 1.2 continued

System	Consumer type	Dominant production source	Approach	Reference
26. Mississippi River main channel near Savanna and Grafton, Illinois, USA	Zooplankton (Copepoda)	C_3 plants or seston	$\delta^{13}C$, $\delta^{15}N$	Herwig et al. 2007
	Macroinvertebrates (Chironomidae, Heptageniidae, Hydropsychidae)	C_3 plants or seston		
	Snails, mussels (*Dreissena polymorpha*)	C_3 plants or seston		
	Fishes (Catostomidae, Centrarchidae, Clupeidae, Cyprinidae, Hiodontidae, Ictaluridae, Lepisosteidae, Sciaenidae)	C_3 plants or seston		
27. Mississippi River main channel near Winona, Minnesota, USA	Macroinvertebrates (Amphipida, Coleoptera, Diptera, Ephemeroptera, Erpobdella, Isopoda, Odonata, Oligochaeta, Plecoptera, Trichoptera)	Phytoplankton	$\delta^{13}C$, $\delta^{15}N$	Delong and Thorp 2006
	Snails, mussels	Benthic algae or phytoplankton		
28. Ovens River main channel in Victoria, Australia	Clams, snails (Bivalvia, Gastropoda)	Benthic algae	$\delta^{13}C$, $\delta^{15}N$	Hadwen et al. 2010
	Macroinvertebrates (*Cherax* sp., *Macrobrachium* sp.)	Benthic algae		
	Fishes (*Gambusia holbrooki*, *Hypseleotris galii*)	Benthic algae		
29. Ovens River main channel in Victoria, Australia	Macroinvertebrates (Decapoda, Diptera, Ephemeroptera, Hemiptera, Trichoptera, Odonata)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Hladyz et al. 2010
	Fishes (Cyprinodontiformes, Perciformes)	C_3 plants		
30. Ovens River main channel in Victoria, Australia	Macroinvertebrates (Decapoda, Diptera, Ephemeroptera, Hemiptera, Trichoptera, Odonata)	Seston or benthic algae	$\delta^{13}C$, $\delta^{15}N$	Hladyz et al. 2010
	Fishes (Cyprinodontiformes, Perciformes)	Seston or benthic algae		

Table 1.2 continued

System	Consumer type	Dominant production source	Approach	Reference
31. Paraná River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	Zooplankton (Cladocera, Copepoda)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Hoeinghaus et al. 2007
	Clams, snails (*Corbicula fluminea*, *Pomacea canaliculata*)	C_3 plants		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae, Serrasalmidae)	C_3 plants		
32. Paraná River main channel downstream from Porto Primavera Reservoir, Brazil	Zooplankton (Cladocera, Copepoda)	Seston	$\delta^{13}C$, $\delta^{15}N$	Hoeinghaus et al. 2007
	Clams, snails (*Corbicula fluminea*, *Pomacea canaliculata*)	Seston		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae, Serrasalmidae)	Seston		
33. Paranapanema River main channel downstream from Rosana Reservoir, Brazil	Zooplankton (Cladocera, Copepoda)	Seston	$\delta^{13}C$, $\delta^{15}N$	Hoeinghaus et al. 2007
	Clams, snails (*Corbicula fluminea*, *Pomacea canaliculata*)	Seston		
	Fishes (Anostomidae, Characidae, Cichlidae, Curimatidae, Loricariidae, Pimelodidae, Prochilodontidae, Sciaenidae, Serrasalmidae)	Seston		
34. Taieri River main channel in the southeast of the South Island, New Zealand	Macroinvertebrates (Diptera, Ephemeroptera, Orthoptera, Plecoptera, Trichoptera)	Benthic algae	$\delta^{13}C$, $\delta^{15}N$	Huryn et al. 2001
	Fishes (*Galaxias depressiceps*)	Benthic algae		
35. Taieri River main channel in the southeast of the South Island, New Zealand	Macroinvertebrates (Diptera, Ephemeroptera, Orthoptera, Plecoptera, Trichoptera)	C_3 plants	$\delta^{13}C$, $\delta^{15}N$	Huryn et al. 2001
	Fishes (*Galaxias depressiceps*)	C_3 plants		

Table 1.3. Turbidity (high vs. low), concentrations of dissolved organic matter (DOM, high or low), predictability of hydrology (high, intermediate, or low), magnitude of discharge (high-water, average, low-water, or throughout low- and high-water), floodplain land cover (agriculture, desert scrub, forest, grassland, or urban), and degree of interaction with floodplain (constrained reach vs. floodplain reach) for each river system during the time that production sources were estimated.

System	**Turbidity**	**Concentrations of DOM**	**Predictibility of hydrology**	**Magnitude of discharge**	**Dominant floodplain cover**	**Degree of interaction with floodplain**	**Reference**
1. Aguaro River floodplain and main channel, central Venezuela	Low	Low	High	Low-water	Grassland	Floodplain reach	Jepsen and Winemiller 2007
2. Amazon River floodplain near Manaus, Brazil	High	Low	High	Throughout low- and high-water	Forest	Floodplain reach	Araujo-Lima et al. 1986; Forsberg et al. 1993
3. Apure River floodplain and main channel, central Venezuela	High	Low	High	Low-water	Grassland	Floodplain reach	Jepsen and Winemiller 2007
14. Brazos River main channel near Bryan, Texas, USA	High	Low	Low	High-water	Agriculture	Floodplain reach	Zeug and Winemiller 2008a
4. Cinaruco River floodplain and main channel, south-western Venezuela	Low	High	High	Low-water	Grassland	Floodplain reach	Jepsen and Winemiller 2007

Table 1.3 continued

System	**Turbidity**	**Concentrations of DOM**	**Predictibility of hydrology**	**Magnitude of discharge**	**Dominant floodplain cover**	**Degree of interaction with floodplain**	**Reference**
15. Cinaruco River main channel and floodplain, south-western Venezuela	Low	High	High	Throughout low- and high-water	Grassland	Floodplain reach	Roach et al. 2009
5. Colorado River main channel downstream from Glen Canyon Dam, USA	High	Low	Intermediate	Average	Desert scrub	Constrained reach	Angradi 1994
16. Cooper River main channel near Lake Eyre, Australia	High	Low	Low	Low-water	Grassland	Constrained reach	Bunn et al. 2003
17. Flinders River main channel near the Gulf of Capentaria, Northern Australia	High	Low	Intermediate	Low-water	Agriculture	Floodplain reach	Leigh et al. 2010
18. Gregory River main channel near the Gulf of Capentaria, Northern Australia	Low	Low	Intermediate	Low-water	Agriculture	Floodplain reach	Leigh et al. 2010
19. Gwydir River main channel in New South Wales, Australia	High	Low	Low	Low-water	Agriculture	Constrained reach	Hadwen et al. 2010

Table 1.3 continued

System	Turbidity	Concentrations of DOM	Predictibility of hydrology	Magnitude of discharge	Dominant floodplain cover	Degree of interaction with floodplain	Reference
21. Iguatemi River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	High	Low	High	Low-water	Forest	Constrained reach	Hoeinghaus et al. 2007
22. Ivinheima River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	High	Low	High	Low-water	Forest	Constrained reach	Hoeinghaus et al. 2007
23. Logan River main channel in Queensland, Australia	High	Low	Low	Low-water	Agriculture	Constrained reach	Hadwen et al. 2010
24. Mattaponi River main channel near Beaulahville, Virginia, USA	High	Low	Low	Low-water	Forest	Constrained reach	Hoffman et al. 2007; Hoffman et al. 2008
25. Mattaponi River main channel near Beaulahville, Virginia, USA	High	Low	Low	High-water	Forest	Constrained reach	Hoffman et al. 2007; Hoffman et al. 2008
6. Mississippi River main channel near Louisiana, Missouri, USA	Low	Low	Intermediate	Average and high-water	Forest	Floodplain reach	Delong et al. 2001

Table 1.3 continued

System	Turbidity	Concentrations of DOM	Predictibility of hydrology	Magnitude of discharge	Dominant floodplain cover	Degree of interaction with floodplain	Reference
26. Mississippi River main channel near Savanna and Grafton, Illinois, USA	Low	Low	Intermediate	Throughout low- and high-water	Agriculture	Constrained and floodplain reach	Herwig et al. 2007
27. Mississippi River main channel near Winona, Minnesota, USA	Low	Low	Intermediate	Low-water	Forest	Floodplain reach	Delong and Thorp 2006
7. Missouri River main channel near New Haven, Missouri, USA	Low	Low	Intermediate	Average and high-water	Forest	Constrained reach	Delong et al. 2001
8. Ohio River main channel ~32 km upstream from confluence of Ohio and Mississippi Rivers, USA	Low	Low	Intermediate	Average	Forest	Constrained and floodplain reach	Thorp et al. 1998; Delong et al. 2001
9. Orinoco River floodplain near Ciudad Bolívar, Venezuela	Low	Low	High	High-water	Forest	Floodplain reach	Hamilton et al. 1992, Lewis et al. 2001
28. Ovens River main channel in Victoria, Australia	High	Low	Low	Low-water	Agriculture	Constrained reach	Hadwen et al. 2010
29. Ovens River main channel in Victoria, Australia	High	Low	Low	Low-water	Agriculture	Constrained and floodplain reach	Hladyz et al. 2010

Table 1.3 continued

System	Turbidity	Concentrations of DOM	Predictibility of hydrology	Magnitude of discharge	Dominant floodplain cover	Degree of interaction with floodplain	Reference
30. Ovens River main channel in Victoria, Australia	High	Low	Low	High-water	Agriculture	Constrained and floodplain reach	Hladyz et al. 2010
31. Paraná River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil	Low	Low	High	Low-water	Forest	Floodplain reach	Hoeinghaus et al. 2007
10. Paraná River main channel near Paraná City, Brazil	Low	Low	High	Throughout low- and high-water	Urban	Floodplain reach	Bayo and Cordiviola de Yuan 1996
32. Paraná River main channel below Porto Primavera Reservoir, Brazil	Low	Low	High	Low-water	Forest	Floodplain reach	Hoeinghaus et al. 2007
33. Paranapanema River main channel below Rosana Reservoir, Brazil	High	Low	High	Low-water	Forest	Constrained reach	Hoeinghaus et al. 2007
11. Paria River main channel near the Utah-Arizona border, USA	High	Low	Intermediate	Average	Desert scrub	Constrained reach	Angradi 1994
12. Pasimoni River floodplain and main channel, southern Venezuela	Low	High	High	Low-water	Grassland	Floodplain reach	Jepsen and Winemiller 2007

Table 1.3 continued

System	Turbidity	Concentrations of DOM	Predictibility of hydrology	Magnitude of discharge	Dominant floodplain cover	Degree of interaction with floodplain	Reference
13. Rio Grande main channel in the Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico, USA	High	Low	Low	Low-water	Desert scrub	Floodplain reach	Pease et al. 2006
34. Taieri River main channel in the southeast of the South Island, New Zealand	Low	Low	Low	Low-water	Grassland	Constrained reach	Huryn et al. 2001
35. Taieri River main channel in the southeast of the South Island, New Zealand	Low	Low	Low	High-water	Grassland	Constrained reach	Huryn et al. 2001

C_4 grasses do not support floodplain river food webs

Riverine metazoans may have been partially supported by C_4 grasses in only one study in the Aguaro River (Venezuela). In the Aguaro River, benthic algae and either C_3 plants or C_4 grasses were the dominant production sources supporting fishes. Consumers were supported by algal-based production sources at 19 of the study sites (16 rivers) and by C_3 plants in five of the study rivers. In the Amazon River, characiform fishes were supported by phytoplankton and siluriform fishes were supported by C_3 plants. In the Hudson River, either phytoplankton or aged allochthonous organic matter provided the foundation for zooplankton biomass, and at one study site in the Mississippi River, consumers were supported by either seston or C_3 plants. In three rivers, the Mattaponi, Ovens, and Taieri, the dominant production source shifted from algae to C_3 plants with seasonal changes in river discharge.

Factors affecting the relative importance of algae vs. C_3 plants

Turbidity. Among all of the rivers studied, 10 had relatively low turbidity and 16 had relatively high turbidity. Consumers that were supported by C_3 plants were almost entirely from rivers that were described as turbid, including the Amazon River (Brazil), the Brazos River (USA), the Iguatemi River (Brazil), the Ivinheima River (Brazil), the Mattaponi River (Virginia), the Ovens River (Australia), and the Paria River (Arizona). Brazil’s Paraná River, in contrast, has low turbidity, but Hoeinghaus et al. (2007) found that the food web in this river had a higher relative contribution of seston compared to the Iguatemi and Ivinheima Rivers and, unlike the latter, in the Paraná River the standard deviation bars for 99th percentile contribution estimates of C_3 plants and seston overlapped.

During high flows in sediment-laden rivers, consumers appear to assimilate either C_3 plants or detritus derived from it because there is less algal biomass available, but during lower flows algae frequently become more productive and can rapidly enter food chains. I found that all of the studies in rivers with high suspended-sediment concentrations that concluded autochthonous production sources supported the food web were conducted during the low-water period (7 rivers) or during “average” flow (1 river). For example, in the Mattaponi River, Hoffman et al. (2008) found that phytoplankton comprised $< 5\%$ of the POM pool and supported only 14-25% of zooplankton production during high discharge, but comprised $> 10\%$ of the POM pool and supported 61-74% of zooplankton production during low discharge, indicating that zooplankton disproportionately assimilate phytoplankton relative to other production sources, but only when it is abundant. Bunn et al. (2003) found that, in the Cooper River (Australia) during a low-flow period, despite high turbidity, filamentous algae that grew along shallow, littoral zones supported consumers in disconnected pools within the river bed.

DOM concentrations. Two rivers in Venezuela had high DOM concentrations, the Cinaruco and Pasimoni. Metazoan consumers in these rivers were estimated to be mostly supported by seston or benthic algae, however 94% of consumers in the Cinaruco River and 97% of consumers in the Pasimoni River were within the range of $\delta^{13}C$ for C_3 plants. In contrast, in two rivers with lower DOM concentrations, the Apure and Aguaro

Rivers, 54% and 41% of consumers were within the $\delta^{13}C$ range for plants. Jepsen and Winemiller (2007) concluded that seston or benthic algae must have been important because most of the detritivores and algivores surveyed were more depleted in ^{13}C than C_3 plants, but all detritivores in the Pasimoni River also were enriched in ^{15}N, suggesting that material from microbes colonizing plant detritus was assimilated by these consumers.

Predictability of hydrology. In total, predictability of hydrology was high for 11 rivers, intermediate for eight rivers, and low for nine rivers. C_3 plants were the dominant source of basal production supporting consumers from rivers with high (3 rivers), intermediate (1 river), and low (1 river) hydrologic predictability. One study indicated that consumers in rivers with unpredictable flow regimes can be supported by C_3 plants following high-flow events even when suspended sediment concentrations are low, because high-flow periods increase the amount of terrestrial-based organic material comprising POM in the water column. In New Zealand's Taeiri River, an autotrophic river with low turbidity, consumers were supported by benthic biofilm following a low-flow period and C_3 plants following a high-flow period (Huryn et al. 2001). Seston $\delta^{13}C$ values were more depleted and closer to the values measured for terrestrial vegetation following the high-flow period compared to the low-flow period, and it was suggested that this was because high-flow pulses enhanced terrestrial carbon inputs while scouring algae from the channel, and the low-flow period reduced terrestrial carbon inputs while allowing algae to accumulate.

Lateral connectivity between the river channel and floodplain / floodplain vegetation type. In total, 16 of the river reaches were classified as floodplain, 15 were classified as constrained, and in four studies consumers were pooled from floodplain and constrained reaches. The dominant floodplain cover was agriculture for nine reaches, desert scrub for three reaches, forest for 14 reaches, grassland for eight reaches, and urban for one reach. I did not find any evidence that floodplain interaction or vegetation type affects basal production sources in lowland rivers; 13 of the study sites where consumers were supported by autochthonous sources were floodplain reaches and seven were constrained reaches. Two of the study sites where consumers were supported by allochthonous sources were floodplain reaches and three were constrained reaches. Furthermore, both constrained and floodplain reaches shifted from autochthonous to allochthonous production sources with increasing river discharge. Both autochthonous and allochthonous production sources also supported consumers in river reaches with diverse floodplain vegetation types; consumers derived their nutrients from algae in reaches with all floodplain vegetation types (agriculture, desert scrub, forest, grassland, and urban), and consumers derived nutrients from terrestrial plants in river reaches where agriculture, desert scrub, and forest were the dominant floodplain vegetation types.

Presence of upstream impoundment. Three study reaches were located ≤100 km downstream from an impoundment: the Colorado River main channel below Glen Canyon Dam, USA; the Paraná River main channel below Porto Primavera Reservoir, Brazil; and the Paranapanema River main channel below Rosana Reservoir, Brazil.

These studies also analyzed production sources in neighboring main channel habitats that were not located below a dam (the Paria River main channel near the Utah-Arizona border, USA; the Paraná River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil; the Iguatemi River main channel between Itaipi Reservoir and Porto Primavera Reservoir, Brazil; and the Ivinheima River main channel between Itaipu Reservoir and Porto Primavera Reservoir, Brazil.) Each of these studies found that autochthonous production sources became more significant when the river reach was located downstream from a reservoir.

Climate / phenology. Finally, one study indicates that riverine consumers can be supported by C_3 plants following events related to the phenology of deciduous plants and their influence on POM in the water-column. Contradicting other studies, Hladyz et al. (2010) found that in the Ovens River in Australia, seston was the primary production source supporting consumers following a high flow event, and terrestrial plants were the primary production source following a low flow event. In this study, assimilation of terrestrial material by the aquatic food web corresponded with annual peak litterfall, which was apparently rapidly incorporated into the aquatic food web.

DISCUSSION

The results of my literature survey indicate that C_4 grasses rarely support riverine metazoans and that algae are the dominant basal production source for large river food webs worldwide. However, I also found that in rivers carrying high sediment loads, consumers are frequently supported by C_3 plants, unless the river reach is located below an impoundment. Apparently, during high-flow periods, shear stress and resuspension of sediment cause abrasion and light limitation of instream (autochthonous) production. Terrestrial C_3 plants also subsidize consumers in rivers with high DOM concentrations and low inorganic nutrient concentrations because of increased activity of the microbial loop, and following periods of high discharge or leaf litter fall that increase the amount of terrestrial material in the particulate organic matter pool (Figure 1.1).

Ecologists have long acknowledged differences in nutritional value between C_3 and C_4 plants. Caswell et al. (1973) argued that herbivores should avoid feeding on C_4 species because they are a poorer food source compared to C_3 plants. Compared to C_3 plants, C_4 grasses are higher in hemicellulose, cellulose, and lignin which make them tough and difficult to digest (Minson 1971). There are also biochemical differences between the plant groups; the nitrogen, phosphorus, and protein content of C_4 grasses tends to be lower (Wilson and Haydock 1971, Caswell et al. 1973). Despite their lower nutritional value, a few aquatic consumers are able to assimilate C_4 grasses; Forsberg et al. (1993) found that the anostomid *Schizodon fasciatus* from the Amazon River, Brazil assimilated material from C_4 grasses, and Jepsen and Winemiller (2007) estimated that *Schizodon isognatus* in a floodplain lake on the Apure River floodplain, Venezuela, obtained the majority of its carbon from C_4 plants. Despite assimilation by a few species, it is apparent that because of their poor nutritional quality, C_4 grasses are unimportant in the majority of large river food webs.

In contrast, microalgae typically have high nutritional value and lack structural proteins that inhibit digestibility (Sarkanen and Ludwig 1971, Renaud et al. 1999). Because C_3 plants frequently contain structural and secondary chemical compounds that inhibit herbivory, in most circumstances consumers prefer to consume algae over C_3 leaves. However, secondary metabolites such as phenol, tannin, and lignin, as well as nutrient concentrations present in C_3 leaves varies with exposure to herbivory and resource availability. For example, C_3 plants grown under low light and high nutrient conditions have leaves with low concentrations of secondary defense compounds and high concentrations of soluble nitrogen (Chapin et al. 1987). Furthermore, the process of decomposition can further increase the nutritional value of C_3 plants through the leaching of plant-defense compounds, deposition of nitrogen-rich exopolymers by microorganisms and fungi (Bowen 1987, Caraco et al. 1998), and accumulation of epiphytic bacteria (Davis et al. 2006, Davis and Childers 2007). Despite the secondary chemicals that C_3 plants can use as defense against herbivores, particularly in tropical regions, C_3 leaves are apparently more palatable to aquatic consumers than C_4 grasses.

Bacteria and fungi, frequently more abundant in DOM-rich watersheds (Meyer 1990), are high-quality food for many consumers. Bacteria have a lower C:P ratio compared to phytoplankton because they have larger amounts of RNA (Neidhardt et al. 1990) and can store phosphorus (Kornberg et al. 1999), thus bacteria are considered one of the most nutritious components of plankton (Makino and Cotner 2004). However, because metazoans are many orders of magnitude larger than microbes, fungi, which are similar in nutritional value to algae, may concentrate the nutrients provided by bacteria at a scale that consumers can more efficiently use (Sadler 2003). In lowland streams that are rich in DOM, terrestrial-based detritus and DOM have been shown to enter the metazoan food web following processing by bacteria and fungi (Walker 1985, Wallace et al. 1987).

My review indicates that algae are the dominant production source for large rivers worldwide, but organic matter derived from C_3 plants can subsidize aquatic food webs in watersheds with highly erodible sediments during the high-water period, inorganic nutrient-poor blackwater rivers, and less frequently, following events that increase the amount of terrestrial material in the POM pool (Figure 1.1). In nutrient-rich watersheds with fine clays and highly erodible sediments, during the high-water period, sediment deposition, scour, and low light penetrance can limit the production of algae, and consumers from the main channel may be more frequently supported by terrestrial C_3 plants. During the low-water period, plankton and benthic algae often become more prevalent and support metazoan consumers (Welcomme 1979, Lundberg et al. 1987). However, all “sediment-laden” rivers are not alike. Some rivers with very high suspended sediment concentrations have sufficient energetic capacity to transport suspended materials and remain “white” year-round regardless of seasonal changes in hydrology (Townsend-Small et al. 2008). Organic material originating from C_3 plants may consistently support consumer biomass in these rivers. Furthermore, because more solar radiation is scattered at the short-wavelength end of the light spectrum, the degree to which suspended particles limit algal production also depends on their reflectance properties (Kirk 1985).

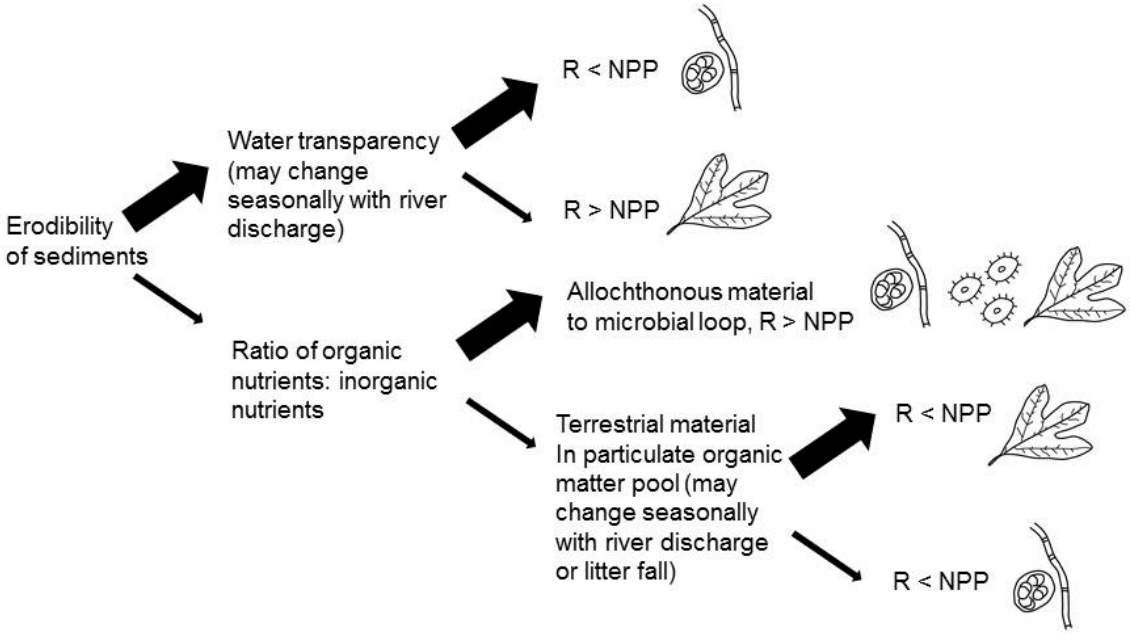

Figure 1.1. Schematic diagram of the basal production sources supporting consumers in rivers with different physicochemical characteristics, and hypotheses of how these factors affect instream productivity (R = respiration, NPP = net primary production). The assimilation of allochthonous production by metazoan consumers is indicated by a leaf, assimilation of autochthonous production is indicated by algal cells, and increased carbon flux through the microbial loop is indicated by microbes.

In watersheds that are rich in DOM, poor in inorganic nutrients, and have coarse, inorganic sediments, autochthonous primary production tends to be low and the microbial loop seems to have a larger impact on energy flow to metazoans, resulting in assimilation of allochthonous material. However, because these watersheds still have relatively high light penetrance, although their biomass is low, phytoplankton and periphyton can also be found throughout the hydrologic cycle and are likely to support higher trophic levels to some extent (Goulding et al. 1988). Assimilation of nutrients from microbes can be observed when trophic linkages between bacteria, protozoa, and fungi result in herbivores or detritivores with elevated $\delta^{15}N$ values relative to plants (e.g., Jepsen and Winemiller 2007). Evidence also indicates that nutrients derived from microbes can be assimilated by detritivores in some nutrient-poor, whitewater rivers. Lujan et al. (2011) found that five species of wood-eating catfishes (Loricariidae) from the Marañon River, Peru, were enriched in ^{15}N relative to wood, consistent with assimilation of microbial decomposers. Some metazoans even have physical adaptations to aid in digestion of the microbial component of detritus. The detritivorous cichlid fish *Sarotherodon mossambicus* has highly acidic gastric secretions (pH < 2) for lysis of heterotrophic microorganisms (Bowen 1976).

A few studies indicated that, even in watersheds with high instream primary production, terrestrial material can be incorporated into the pool of POM and subsequently assimilated by consumers following periods of high-flow or seasonal litterfall. Studies investigating C:N ratio of riverine organic matter have also revealed this pattern. At several sites on the Columbia River there is a strong correlation between C:N of seston and flow, with C:N > 15 indicating terrestrial inputs during periods of high flow and high turbidity (Kendall et al. 2001). This isn’t always the case, however. There was no relationship between C:N and flow of POM collected over a range of flows at sites in the Ohio, Missouri, and Rio Grande Rivers. At many sites on the relatively clear Ohio and Missouri Rivers, POM consistently is dominated by plankton, and at many sites on the sediment-laden Rio Grande, POM consistently is a mixture of plankton, macrophytes, and soil (Kendall et al. 2001).

All the studies on reaches located below dams were conducted in high-sediment rivers. Metazoan consumers in these ecosystems likely assimilated material from phytoplankton because its abundance was greater in reservoirs as a function of higher water residence time and water clarity. A comparison of the factors affecting phytoplankton abundance in rivers, impoundments, and natural lakes across the United States found that water residence time explained more variation than dam presence, suggesting there may be a residence-time threshold value above which there is a significant change in algal abundance (Søballe and Kimmel 1987). In rivers with little transported material in the water-column or impoundments with low residence time, the pattern observed by Angradi (1994) and Hoeinghaus et al. (2007) may be less likely to occur.

Although no stable isotope studies indicated that lateral interaction between the river channel and floodplain affects basal production sources, floodplains are clearly vital to the health of riverine ecosystems. Restoration of historical flooding of off-channel habitats in the Missouri River resulted in twice as many fish species in restored reaches compared to reaches that were still isolated from the floodplain (Galat et al. 1998). However, in response to the FPC's proposal that the main channel serves primarily as a route for organisms to gain access to the floodplain, Galat and Zweimüller (2001) conducted an assessment of the proportion of fish communities that complete their life cycles exclusively in the river channel in eight rivers of North American and Europe. Their evidence indicated that > 25% of fish species primarily used the main channel, indicating that the main channel and the floodplain provide essential habitat for organisms. My review indicates that, although floodplains are vital nursery habitats for fish species with equilibrium life history strategies (i.e., low fecundity, parental care, Winemiller and Rose 1992) which can be exported to the main channel during inundation (e.g., Zeug and Winemiller 2008b), they are seldom a source of organic matter for biota in the main channel.

Metazoans in many sediment- and DOM-rich rivers assimilate material originating from C_3 plants. Placing these results in a larger context reveals that these types of rivers are distributed throughout the world. Differences in sediment yield among rivers are related to drainage basin size and topography. As drainage basin size becomes larger, there is a greater chance that a sediment particle from upstream will be eroded and transported downstream, and high topographic relief is associated with fractured and brecciated rock, steep slope, and seismic and volcanic activity (Milliman and Syvitski 1992; Walling and Webb 1996). Most of the rivers draining the eastern United States, Europe (except for rivers that drain the Alps and drain south into the Mediterranean), Russia, Africa (except for rivers draining the rift mountains and mountains in Morocco, Algeria, and Tunisia), and Australia (except for rivers draining mountainous areas in the north and east) have low sediment yields (Milliman and Syvitski 1991). The rivers that naturally have the greatest sediment yield drain western Canada and Alaska, the Andes Mountains, the Caucasus, Anatolian and Taurus Mountains in Turkey, the Himalayan

Mountains, and the high-standing islands between Australia and Asia (Milliman and Syvitski 1991). However, sediment erodability, which is related to river discharge and the stability of the river channel and banks, also can also affect the turbidity of surface waters (Wood and Armitage 1997). In Australia and southern Africa, sediment yield is low but the sparse vegetation cover, aridity of the climate, irregular but heavy rains, and high concentrations of fine clay in the soils cause many of the surface waters to be turbid (Kirk 1985).

Blackwater rivers drain ancient geological formations that, because of eons of weathering, are poor in nutrients. Most are low-gradient with broad floodplains and course, inorganic substrates (Meyer 1990). Blackwater rivers frequently arise in swamps that leach humic acids derived from terrestrial vegetation, resulting in high concentrations of DOM and low pH (Adis et al. 1979, St John and Anderson 1982). There is no weathering of ancient marine deposits to contribute inorganic carbon to these ecosystems, thus the source of CO_2 for aquatic photosynthesis may largely be carbon respired from plankton or soil (e.g., Medina et al. 1986). Blackwater rivers are present throughout the world, draining Precambrian rock formations such as the Canadian Shield in North America, the Brazilian, Guiana, and Atlantic Shields in South America, exposed shields of the African Craton in Africa, and the Baltic Shield in Scandanavia (Goodwin 1996). When comparing surface waters of the world, rivers of Africa and South America have the lowest overall dissolved materials, with inputs dominated by precipitation as a result of drainage of highly leached areas, compared to temperate rivers where geology and evaporation have a greater influence on the chemical composition of water (Allan 1995). Because of overall lower inorganic nutrient concentrations in tropical blackwater rivers, the microbial loop may play a larger role in providing energy for metazoans. Furthermore, in South America, several abundant fish species have morphological and physiological adaptations to feed on allochthonous materials such as fruits and seeds (Goulding 1980, Correa et al. 2007).

Human activities have strong and differing impacts on turbidity and nutrient concentrations in aquatic ecosystems. Dams have likely had the largest influence on sediment fluxes by decreasing the sediment yield of many rivers (Walling and Fang 2003). For example, before 1930, the Colorado River discharged 100,000 tons of sediment to the Gulf of California each year, > three orders of magnitude more sediment compared to current levels (Meade and Parker 1985). In addition, the construction of five dams on the Missouri River has reduced the sediment load entering the Mississippi River by approximately 25%, and the sediment load of the Mississippi River recorded in 1984 was less than half what it was in 1953 (Meade and Parker 1985). Terrestrial-based detritus may have been more important to consumers in these rivers before the construction of impoundments and concomitant declines in suspended sediment load. In contrast, other human activities such as agriculture, mining, logging, and construction have caused inorganic nutrient concentrations and turbidity to increase in rivers (Wood and Armitage 1997, O'Donnell et al. 2008).

Differences in suspended sediment and nutrient concentrations among rivers have strong effects on aquatic organisms. In rivers of northern Australia, herbivorous fish from the family Tetrapontidae exhibit intraspecific trophic polymorphisms where intestinal length differs in response to natural variation in water transparency (Davis and Pusey 2010). Anthropogenic increases in turbidity, for example resulting from eutrophication, can alter the courtship activity of fishes, resulting in hybridization of separate species in some instances (e.g., Seehausen et al. 1997). Several studies have documented declines in the abundance of aquatic organisms as a result of human-induced increases in turbidity (Berkman and Rabeni 1987, Henley et al. 2000). Suspended sediments have two major effects in lotic ecosystems. Sediment particles scatter and absorb light, limiting visibility and the production of algae, and they also provide substantial surface area upon which sorption of nutrients can occur (Kirk 1985). Thus, when rivers are naturally high in transported materials, for example as a result of erosion of mountains, this material can be a vital source of organic matter and nutrients. For example, in watersheds draining the Andes Mountains, economically important characiform fishes (e.g., species from the genera *Anodus*, *Brycon*, *Colossoma*, *Mylossoma*, *Prochilodus*, *Semaprochilodus*, and *Triportheus*) make yearly migrations from sediment- and nutrient-poor blackwater and clearwater rivers into nutrient-rich Andean headwaters to feed and spawn (Lowe-McConnell 1975, Carvalho de Lima and Araujo-Lima 2004, McClain and Naiman 2008). Upon their return migration, these fish act as resource subsidies of whitewater-derived nutrients for resident piscivorous species (Hoeinghaus et al. 2006).

Natural abundance radiocarbon (^{14}C) has begun to be used as a tracer of highly aged organic material. These studies indicate that in rivers, weathering of sedimentary rock can provide inputs of ancient terrestrial organic matter (Leithold and Blair 2001, Masiello and Druffel 2001, Raymond et al. 2004). In the Amazon River (Brazil) and Hudson River (USA), the average age of organic material decreases downstream from its entry in headwaters (Cole and Caraco 2001, Mayorga et al. 2005). Apparently, even when organic material is highly aged, it can still be a significant source of energy for higher consumers. Caraco et al. (2010) found that, in the Hudson River, highly aged organic material that had been stored in sediments for thousands of years significantly contributed to zooplankton biomass. In Alaska, peat contains highly aged organic matter that enters rivers (Guo et al. 2007) where it subsidizes freshwater organisms including fishes and birds (Schell 1983).

Thorp and Delong (1994) argued that the RCC and FPC underestimated inputs of nutritious autochthonous production and terrestrial material from the riparian zone to riverine food webs, and also overemphasized contributions of refractory organic matter from headwaters or the floodplain. My review is consistent with their assessment. Furthermore, the assumption by Thorp and Delong (1994) that consumers tend to assimilate more nutritious material explains why, in reaches of sediment-laden rivers that are located below an impoundment, metazoan biomass is largely derived from algae. However, the Revised RPM (Thorp and Delong 2002) assumed that large rivers tend to be heterotrophic, not accounting for among-river differences in light and nutrient concentrations that have large effects on instream productivity. In nutrient-rich watersheds with fine clays and highly erodible sediments, low water clarity during the high-water period can limit algal primary production, which then results in greater assimilation of allochthonous material by metazoan consumers. In watersheds rich in dissolved organic nutrients, poor in inorganic nutrients, and having coarse, inorganic sediments, carbon flux through the microbial loop increases, and both autochthonous and allochthonous production sources are assimilated. Furthermore, in rivers high in suspended sediments, particularly in the tropics where inorganic nutrient concentrations are low, ecologically and economically important fish species may assimilate highly aged, recalcitrant organic matter originating from the erosion of mountains because nutrients have sorbed to this material. Sediment- and DOM-rich watersheds are present throughout the world, and recognition that terrestrial C_3 plants are important basal production sources supporting metazoan consumers in many of these rivers is an important step in understanding food web dynamics.

CHAPTER III

HYDROLOGIC REGIME, NUTRIENTS, AND TURBIDITY INFLUENCE ENTRANCE OF TERRESTRIAL MATERIAL INTO RIVER FOOD WEBS

INTRODUCTION

Around the world, the construction of large dams has altered river hydrology, suspended sediment yields, and nutrient dynamics (Ligon et al. 1995, Petts and Gurnell 2005, Graf 2006, Poff et al. 2007). Additional human impacts on rivers include water diversions (Dynesius and Nilsson 1994, Postel et al. 1996, Kingsford 2000) and increases in nutrient runoff from urban areas and agricultural fields located in watersheds and floodplains (Meybeck 1982, Bouwman et al. 2005). There is a pressing need to better understand how these modifications to rivers alter ecological process in rivers that yield ecosystem services. The structure and dynamics of river food webs determine the production of harvestable fish biomass, an important ecosystem service of large rivers (Chapin et al. 1997, Dugan et al. 2010). Recent research has focused on potential impacts of climate change on energy and material transfers in food webs (e.g., Harrington et al. 1999, Petchey et al. 1999, Urabe et al. 2003). Identification of production sources that support the metazoan consumers inhabiting large rivers with different physicochemical characteristics is essential for predicting how environmental change will alter material fluxes affecting biomass and diversity at higher trophic levels. For example, ecosystems in which plant detritus supports metazoan consumers have been hypothesized to support less secondary production but higher species diversity because of lower efficiency and weaker interaction strength associated with a greater number of trophic transfers between microbes and higher consumers (Legendre and Rassooulzadegan 1995, Cotner and Biddanda 2002, Rooney and McCann 2011).

Several conceptual models predict the most important production sources supporting river food webs, but none of these specifically address how production sources shift seasonally or spatially. In the River Continuum Concept, Vannote et al. (1980) proposed that consumers in floodplain rivers are dependent on terrestrial material transported from upstream. In the Flood Pulse Concept, Junk et al. (1989) proposed that terrestrial production sources enter the river food web from the floodplain during overbank flooding. Thorp and Delong (1994) proposed in the Riverine Productivity Model that, because most of the organic matter that is passively transported from headwaters or the floodplain is recalcitrant, the former models underestimated the importance of riparian plants and instream productivity to secondary production. However, in the Revised Riverine Productivity Model, Thorp and Delong (2002) proposed that most aquatic consumers are supported by autochthonous (algal) organic matter because it is more nutritious and labile than allochthonous (terrestrial) organic matter. Thorp and Delong (2002) believed this was the case even in net heterotrophic rivers (gross primary production, GPP, < respiration, R); they predicted that, whereas overall system metabolism is based on allochthonous carbon, consumer biomass should be supported by an algal-grazer pathway that is of minor importance to system metabolism. However, other authors have proposed that resource subsidies should occur more frequently in systems where net primary productivity is relatively low in the recipient ecosystem (Polis and Hurd 1996, Stapp and Polis 2003, Winemiller and Jepsen 2004).

In the last 20 years, research using stable isotope analysis has emphasized the importance of autochthonous production sources to river food webs (Jepsen and Winemiller 2002, Clapcott and Bunn 2003, Herwig et al. 2004, Delong and Thorp 2006) and indicated the low importance of C_4 macrophytes for supporting biomass of metazoan consumers (Thorp and Delong 1998, Clapcott and Bunn 2003, Herwig et al. 2004, Zeug and Winemiller 2008a). However, most of these studies were conducted during the low-water period in temperate rivers with naturally low levels of suspended sediments, or with low sediment yield as a result of entrapment by impoundments. In the Brazos River, Texas, average annual sediment yield is higher than any other river in Texas (Curtis et al. 1973), and the steep banks contribute to high current velocity during flood pulses. Analysis of stable isotopes indicated that during a period of frequent flooding, terrestrial C_3 macrophytes were the most important basal production source supporting fishes in the main channel (Zeug and Winemiller 2008a), presumably as a result of low light penetrance and scour that limited the growth of algae. Furthermore, high flows in some tropical floodplain rivers are associated with lower nutrient concentrations as a result of dilution and thus lower algal primary production (Cotner et al. 2006). These findings suggest that environmental factors such as discharge, light, and nutrients may interact to limit the availability of algal-based production sources to the food web in floodplain rivers.

I conducted field research to examine potential relationships between hydrology, watershed and sediment characteristics, climatic region, and sources of primary production supporting consumers in river channels. I measured seasonal changes in % bankfull discharge, nutrient concentrations, turbidity, and water-column and benthic net primary production (NPP) and biomass (chlorophyll *a*) in five floodplain rivers with diverse physicochemical characteristics. I used stable isotope signatures of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and deuterium (δD) to estimate the relative proportions of autochthonous- versus allochthonous-based production sources supporting aquatic consumers during different hydrologic periods. The study rivers are different in terms of hydrology, nutrient concentrations, turbidity, and autochthonous productivity, and I therefore predicted that these differences in physical characteristics would reveal relationships among the key factors influencing energy transfers from primary producers to consumers. The Brazos River (eastern Texas) and Tambopata River (south-eastern Peru) carry high loads of suspended sediments of fine grain size that limit light penetrance and algal primary production. The Neches River (eastern Texas) and Cinaruco River (south-western Venezuela) have sandy substrates, low levels of suspended sediments and relatively high concentrations of dissolved organic matter (DOM) as a result of humic substances leached from surrounding watersheds. The Guadalupe River (Texas) carries moderate suspended sediment load and has low concentrations of DOM. The Texas rivers have higher inorganic nutrient concentrations compared to the tropical rivers. Compared to the Neotropical rivers, the Texas rivers have relatively unpredictable hydrology and relatively short duration high flow pulses;

flooding patterns in the tropical rivers are strongly seasonal.

Traditionally, $\delta^{13}C$ has been useful for revealing production sources supporting consumers because this ratio has a low level of trophic fractionation (i.e., generally < 0.5‰ versus approximately 2.5‰ for nitrogen, Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003). However, $\delta^{13}C$ values do not always differ sufficiently between alternative production sources to be an effective tracer (e.g., Doucett et al. 1996). Recent advances in stable isotope technology have shown that deuterium (δD) can be a useful natural tracer. Because algae is consistently more depleted in deuterium compared to terrestrial plants, δD can effectively partition autochthonous versus allochthonous production sources (Doucett et al. 2007, Cole et al. 2011). Experimental studies indicate that trophic fractionation of deuterium is negligible (Smith and Ziegler 1990, Hobson et al. 1999), and recent methodological advances have addressed uncertainties regarding contributions of water to consumer tissue δD (Solomon et al. 2009).

I hypothesized that the relative importance of algae versus terrestrial-based production sources supporting the food web would vary with discharge and turbidity in the Brazos River, terrestrial-based production sources would consistently support consumers in the Tambopata River, and algal-based production sources would consistently support consumers in the Neches, Cinaruco, and Guadalupe Rivers. Soils in the Brazos and Tambopata watersheds are highly erodible, but the Brazos River has higher inorganic nutrient concentrations than the Tambopata River. In the Brazos River, I expected a shift in production sources to occur as a result of the resuspension of inorganic sediment during high or rising discharge that scours algae through shear stress and abrasion and causes high turbidity and light limitation. During falling or low discharge, the deposition of inorganic sediment lowers turbidity and water velocities and can cause shallow waters to become highly productive (Kirk 1985, Meade 1988). Thus, at high river discharge, I expected littoral zones to be heterotrophic (negative water-column + benthic NPP), algal biomass to be negligible, and the food web to be supported by terrestrial-based production sources. At low river discharge, I expected littoral zones to be autotrophic (positive water-column + benthic NPP), algal biomass to be high, and the food web to be largely supported by algae. In the Tambopata River at high river discharge, I anticipated little algal biomass in littoral zones because of scour and light limitation, but I also predicted relatively little algal production during low water when, despite the fact that transparency is higher, inorganic nutrient concentrations remain low. Therefore, I hypothesized that terrestrial production sources would account for a large portion of consumer biomass throughout the annual hydrological cycle. Soils are less erodible in watersheds of the Neches, Cinaruco, and Guadalupe rivers, and previous studies have indicated that when suspended sediments are low during periods of high flows, river littoral zones are consistently autotrophic (Lewis 1988, Cotner et al. 2006, Montoya et al. 2006), thus I expected consumers in these rivers to be supported by algal-based production sources throughout the annual hydrologic cycle.

METHODS

Study Sites

This study examined rivers from five watersheds with divergent characteristics (Figure 2.1): the Brazos River in Texas (30º37′N, 96º30′W), the Tambopata River in Peru (12º47′S, 69º17′W), the Neches River in Texas (30º22′N, 94º06′W), the Cinaruco River in Venezuela (6º32′N, 67º24′W), and the Guadalupe River in Texas (28º49′N, 97º01′W). The Brazos River is a lowland river flowing from Blackwater Draw, New Mexico, to the Gulf of Mexico. Although high flow periods do not exhibit a predictable seasonal pattern (Zeug and Winemiller 2008a), median flows tend to be higher in the winter and spring. Large-scale flooding has been reduced due to flow regulation in upstream reaches, but high flows periodically inundate floodplains of the lower reaches. The Tambopata River originates in the Andean piedmont and flows unregulated to the lowland Madre de Dios River, which becomes the Beni River in Bolivia and the Madeira River in Brazil before joining the Amazon River. The hydrologic regime shows a distinct seasonal pattern, but rapid fluctuations in stage height of two to three meters per day occur throughout the year (Hamilton et al. 2007). The Neches River originates in eastern Van Zandt County, Texas, and flows through the coastal plains to Sabine Lake, a shallow bay connected by a narrow outlet to the Gulf of Mexico. Though the hydrologic regime is partially regulated by dams in the upper basin, higher flows that generally occur during spring months can result in overbanking into riparian wetlands along the lower reaches. The Cinaruco River, located in the Venezuelan llanos, is an unregulated tributary of the Orinoco River. The hydrologic regime is strongly seasonal with a prolonged annual flood pulse (Montoya et al. 2006). Among the five study rivers, the Guadalupe River is under the greatest regulation, with 10 impoundments located along the mainstem in its upper reaches. The Guadalupe River flows from Kerr County, Texas, to the Gulf of Mexico. Much of the base flow in the lower Guadalupe River is provided by springs located in headwaters (e.g., Comal and San Marcos springs). Flow in the lower, floodplain reaches is partially regulated by the U.S. Army Corps of Engineers at the Canyon Lake dam, however overbanking flows frequently occur in the lower reaches during the spring. Geomorphology of all rivers is single-channel meandering, with broad sandbanks (point bars) located on alternating sides of channel meanders.

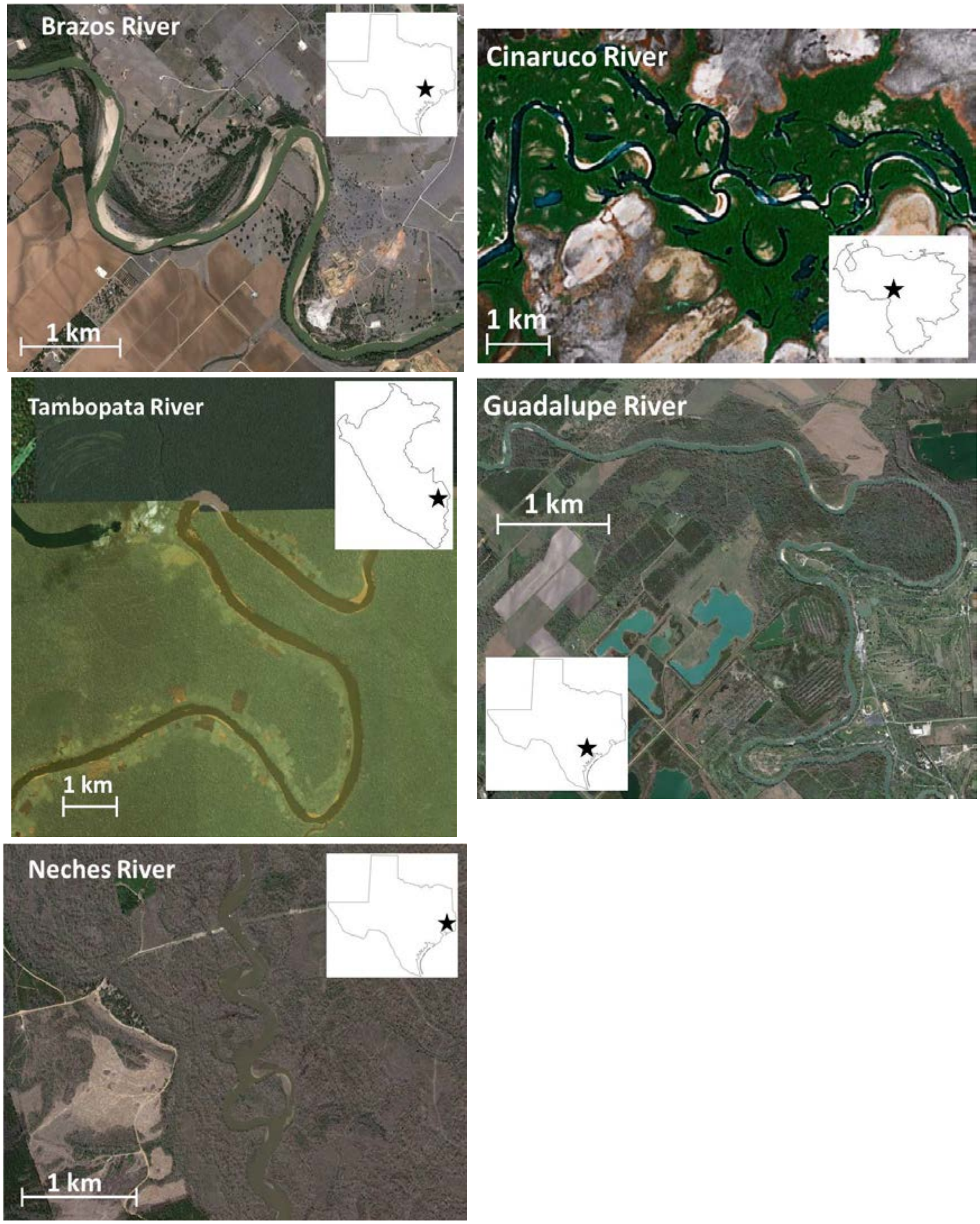

Figure 2.1. Satellite photographs of the five study reaches.

Physicochemical estimates and algal primary production

Repeated measurements of % bankfull discharge, nutrient concentrations (mg/L) including soluble reactive phosphorus (SRP), NH_4, NO_2, and NO_3, and silica (SiO_3 in the Cinaruco River, SiO_2 in all other rivers), turbidity (FTU), water-column and benthic respiration and algal net primary production, and water-column and benthic chlorophyll *a* were made at point sandbars located on the low-velocity side of river meanders. I focused on point sandbars because current velocity tends to slow in these shallow areas, thus they have the highest light penetrance and algal primary production of any riverine habitat (Cotner et al. 2006). Furthermore, they are important feeding areas for many common and diverse macroinvertebrates and fishes (Arrington and Winemiller 2003, Roach and Winemiller 2011). A total of 112 nutrient, turbidity, and instream productivity measurements were taken from the rivers. For the Cinaruco River, data were available from a previous study (Cotner et al. 2006). Specific conductivity (μS/cm), pH, and water temperature (°C) also were measured in littoral zones with a Hydrolab MiniSonde.

For the Texas rivers, % bankfull discharge was estimated using mean daily stage height from the United States Geological Survey (USGS, station 081087800 for the Brazos river, 08041000 for the Neches River, 08176500 for the Guadalupe River) and bankfull stage condition from the National Weather Service. In the Tambopata River, % bankfull discharge was determined by measuring daily water level using a meter stick and by visually estimating periods when the river exceeded bankfull stage from the floodplain levee height. In the Cinaruco River, % bankfull discharge was estimated using measurements from Montoya et al. (2006). To measure nutrient concentrations, water samples were collected in acid-rinsed polyethylene bottles, filtered through a Whatman GF/F filter, and analyzed immediately using colorimetric assays and a Technicon II Autoanalyzer for the Cinaruco River and a Hach DR 2800 mass spectrophotometer for all other rivers. Detection limits achieved with the Technicon II Autoanalyzer were 0.006 mg/L NO_3^-, 0.001 mg/L NO_2^-, 0.001 mg/L NH_4^+, 0.002 mg/L PO_4^-, and 0.005 mg/L SiO_3. Detection limits achieved with the Hach DR 2800 mass spectrophotometer were 0.004 mg/L NO_3^-, 0.001 mg/L NO_2^-, 0.010 mg/L NH_4^+, 0.002 mg/L PO_4^-, and 0.004 mg/L $SiO_{2.}$ A Hanna microprocessor turbidity meter was used to measure turbidity.

Light and dark chambers were used to estimate R, NPP, and gross primary production (GPP) of the water-column and benthos. Water-column measurements followed Wetzel and Likens (1991). Six 300-mL light and six dark biological oxygen demand (BOD) bottles were filled with water from the study site and incubated at approximately 0.5 m depth. Changes in DO concentrations were measured with a YSI Model 85 DO probe. For benthic measurements, four circular Plexiglass benthic chambers, each with a propeller to gently mix water, were pressed into the sediment to enclose the substrate and approximately 8 L of river water. Dissolved oxygen concentrations were measured every 5 min with an internally logging Hydrolab MiniSonde. All light measurements were taken for 3-4 h during sunny or partly sunny weather conditions, and all dark chamber measurements were taken for 1.5 h so that DO concentrations did not decrease below ambient levels. Water-column fluxes in DO were subtracted from the total benthic chamber flux, resulting in sediment-only fluxes (Cotner et al. 2006). A respiratory quotient of 0.8 and photosynthetic quotient of 1.2 was used when converting data from O_2 to C based on the fairly low organic matter content in sediments where I performed the incubations (Brazos River = 0.98%, Tambopata River = 0.53%, Neches River = 0.38%, Cinaruco River = 0.17%, Guadalupe River = 1.25%, sediment organic matter content measurements used the % ash-free dry method from APHA 1992). A respiratory and photosynthetic quotient of 1.0 can underestimate benthic primary production if anoxic metabolism occurs in the benthos (Cotner et al. 2004). Benthic flux was calculated using the methods in Dollar et al. (1991). Daily measurements were averaged and multiplied by 24 h (for R) or 12 h (for NPP and GPP).

For chlorophyll *a*, triplicate samples of water were collected in acid-rinsed polyethylene bottles and filtered through Whatman GF/C filters. Triplicate samples of sediment were taken using a small plastic Petri dish (5-cm diameter and 1.3-cm height) and a spatula. Filter and sediment samples were immediately placed into individual dark vials for extraction for 24 h using 90% ethanol. Chlorophyll *a* was measured spectrophotometrically and corrected for phaeophytin by subtracting absorbances after addition of 0.1N HCl (Wetzel and Likens 1991).

To explore the effect that hydrology has on nutrient concentrations and autochthonous production, I used student's t-tests to compare nutrients and algal production parameters (water-column and benthic NPP and chlorophyll *a*) between the samples taken at the low-water period versus the high-water period. I used historical stage height data from the study rivers to plot % frequency versus mean bimonthly % bankfull discharge, and the greatest difference in subsequent bin was used to distinguish between the low-water period and the high-water period. Historical stage height data were not available for the Tambopata River, so I used stage height data taken by Los Amigos Biological Station staff from the Madre de Dios River at a location ca. 43 km from its confluence with the Tambopata River. Pearson correlations were used to examine the relationship between % bankfull discharge, turbidity, and physicochemical characteristics (specific conductivity, pH, and water temperature) in each of the rivers.

Sample collections for stable isotope analysis

Samples of water, primary producers, and consumers for stable isotope analysis were collected in each river during three hydrologic periods for the Brazos and Neches Rivers, two hydrologic periods for the Tambopata River and Guadalupe Rivers, and one hydrologic period for the Cinaruco River. In the Brazos River, samples were collected following a prolonged low-flow period (average daily % bankfull discharge 30 days prior to sample collection = 18, st dev = 1), a low-flow period followed by a flow pulse event (average daily % bankfull discharge 30 days prior to sample collection = 23, st dev = 6), and a period of high discharge (average daily % bankfull discharge 30 days prior to sample collection = 39, st dev = 9). In the Tambopata River, samples were collected during the seasonal low-flow period (average daily % bankfull discharge of 16-d sample collection period = 4, st dev = 2) and high-flow period (average daily % bankfull discharge of 69-d sample collection period = 42, st dev = 1). Collection periods in the Neches River followed a period of prolonged low-flows (average daily % bankfull discharge for 30 days prior to sample collection = 20, st dev = 2), a period of low-flow followed by a pulse event (average daily % bankfull discharge for 30 d prior to sample collection = 31, st dev = 8), and a period of moderate river discharge that approached bankfull followed by falling water level (average daily % bankfull discharge for 30 d prior to sample collection = 38, st dev = 2). In the Cinaruco River, samples were collected during the annual falling-water period (average daily % bankfull discharge for 30 d prior to sample collection = 84, st dev = 16). Collection periods in the Guadalupe River followed a prolonged low-flow period (average daily % bankfull discharge for 30 d prior to sample collection = 31, st dev = 1) and a period of higher river discharge (average daily % bankfull discharge for 30 d prior to sample collection = 52, st dev = 18).

Water samples for analysis of deuterium stable isotope ratios were collected from the littoral zone of three different sandbanks of each river, filtered through Whatman GF/F filters and collected in acid-rinsed polyethylene bottles. Replicate leaves from the dominant species of C_3 macrophytes (Brazos n = 21, species included *Ambrosia trifida*, *Populus deltoides*, *Salix nigra*, *Ulmus americanus*; Tambopata n = 39, species included *Cecropia* sp., *Ficus incipida*, *Gynerium sagittatum*, *Ochroma* sp.; Neches n = 21, species included *Salix nigra*, *Sapium sebiferum*, *Polygonum* sp.; Cinaruco n = 10, species included *Bactris* sp., *Campsiandra angustifolia*; Guadalupe n = 14, species included *Ambrosia trifida*, *Salix nigra*, *Sapium sebiferum*) and C_4 grasses (Brazos n = 14, species included *Cynodon dactylon*, *Cyperus* sp., *Leptochloa fusca*; Tambopata n = 10, species included *Paspalum* sp.; Neches n = 17, species included *Cynodon dactylon*, *Cyperus erythrorhizos*, *Muhlenbergia lindheimeri*; Cinaruco n = 5, species included *Trachypogon plumosis*; Guadalupe n = 12, species included *Cynodon dactylon*, *Cyperus* sp., *Digiteria sanguinalis*, *Paspalum urvillei*, *Sorghum halepense*) were collected from the riparian zone. Benthic algae (Brazos n = 5, Tambopata n = 3, Neches n = 9, Cinaruco n = 4, Guadalupe n = 5) were scraped using a spatula from substrates including rock and woody debris, taking care not to contaminate the sample with substrate particles. Seston samples (Brazos n = 8, Tambopata n = 11, Neches n = 7, Guadalupe n = 4) were collected by filtering water through a 64-mm sieve to remove zooplankton and large debris onto a pre-combusted (450ºC for four hours) GF/F filter. Consumers including fishes and shrimps (Brazos n = 58, Tambopata n = 36, Neches n = 83, Cinaruco n = 25, Guadalupe n = 33) were collected using seines, gill nets, cast nets, hook and line, and/or electroshocking. In each river, an attempt was made to collect adult size classes of the same species during different hydrologic periods. Representatives of different feeding guilds, including herbivores, detritivores, omnivores, invertivores and predators, were collected (Table 2.1). All individuals were identified, measured to the nearest 1.0 mm standard length, and a sample of muscle from the dorso-lateral region of fishes and shrimps was removed with a scalpel after euthanasia by emersion in a 1% solution of tricaine methanesulfonate. All primary producer and consumer samples were frozen for the Texas rivers or preserved in salt for the tropical rivers until processing in the laboratory at Texas A&M University. Salt preservation causes negligible isotopic shifts of tissues (Arrington and Winemiller 2002). In the laboratory, samples preserved in salt were soaked in deionized water for 4 h. Seston samples were backwashed from GF/F filters onto glass plates using deionized water. All samples were then dried at 60ºC for 48 h in a drying oven.

Table 2.1. Consumer species representing feeding guilds, with family and common name when applicable in parentheses. NC indicates that I was unable to collect consumers from that feeding guild during all hydrologic periods or that individuals representing that feeding guild were not present (e.g., herbivores in the Brazos, Neches, and Guadalupe rivers).

River	**Herbivore**	**Detritivore**	**Omnivore**	**Invertivore**	**Piscivore**
Brazos	NC	*Dorosoma cepedianum* (Clupeidae, gizzard shad)	*Carpiodes carpio* (Catostomidae, river carpsucker) *Cyprinella lutrensis* (Cyprinidae, red shiner) *Notropis buchanani* (Cyprinidae, ghost shiner) *Pimephales vigilax* (Cyprinidae, bullhead minnow) *Macrobrachium ohione* (Palaemonidae, Ohio River shrimp)	*Macrhybopsis hyostoma* (Cyprinidae, shoal chub)	*Ictalurus punctatus* (Ictaluridae, channel catfish) *Lepisosteus osseus* (Lepisosteidae, longnose gar)
Tambopata	NC	*Prochilodus nigricans* (Prochilodontidae)	*Astyanax abramoides* (Characidae) *Leporinus* sp. (Anostomidae) *Pimelodella* sp. (Pimelodidae)	*Anchoviella* sp. (Engraulidae)	*Cetopsis coecutiens* (Cetopsidae) *Pimelodus blochii* (Pimelodidae) *Pinirampus pirinampu* (Pimelodidae)

Table 2.1 continued

River	**Herbivore**	**Detritivore**	**Omnivore**	**Invertivore**	**Piscivore**
Neches	NC	*Dorosoma cepedianum* (Clupeidae, gizzard shad)	*Ictiobus bubalus* (Catostomidae, smallmouth bufalo) *Cyprinella venusta* (Cyprinidae, blacktail shiner) *Fundulus notatus* (Fundulidae, blackstripe topminnow) *Pimephales vigilax* (Cyprinidae, bullhead minnow) *Notropis volucellus* (Cyprinidae, mimic shiner) *Macrobrachium acanthurus* (Palaemonidae, cinnamon river shrimp)	*Lepomis macrochirus* (Centrarchidae, bluegill) *Lepomis megalotis* (Centrarchidae, longear sunfish) *Aplodinotus grunniens* (Sciaenidae, freshwater drum)	*Micropterus punctulatus* (Centrarchidae, spotted bass) *Lepisosteus oculatus* (Lepisosteidae, spotted gar) *Lepisosteus osseus* (Lepisosteidae, longnose gar)
Cinaruco	*Metynnis hypsauchen* (Characidae) *Myleus schombergki* (Characidae)	*Hemiodus unimaculatus* (Hemiodontidae) *Semaprochilodus kneri* (Prochilodontidae)	*Aphyoxharax alburnus* (Characidae) *Hemigrammus analis* (Characidae) *Moenkhausia lepidura* (Characidae)	*Geophagus dichrozoster* (Cichlidae) *Mesonauta festivus* (Cichlidae)	*Cichla temensis* (Cichlidae) *Boulengerella lucius* (Ctenoluciidae)
Guadalupe	NC	*Dorosoma cepedianum* (Clupeidae, gizzard shad) *Mugil cephalus* (Mugilidae, striped mullet)	*Cyprinella lutrensis* (Cyprinidae, red shiner) *Pimephales vigilax* (Cyprinidae, bullhead minnow)	*Lepomis megalotis* (Centrarchidae, longear sunfish)	*Micropterus punctulatus* (Centrarchidae, spotted bass) *Lepisosteus oculatus* (Lepisosteidae, spotted gar)

Stable isotope analysis

Primary producer and consumer samples were ground to a fine powder using a mortar and pestle. For carbon and nitrogen stable isotope ratios, subsamples were weighed into tin capsules and sent to the W.M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory, University of Kansas, Lawrence, Kansas for analysis using a Thermo Finnigan MAT 253 mass spectrometer (Thermo Fisher Scientific, Bremen, Germany). Standards were Pee Dee Belemnite limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. For deuterium stable isotope ratios, subsamples were weighed into silver capsules and sent to the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University, Flagstaff, Arizona, where they were equilibrated with local water vapor to account for H isotope exchange (Wassenaar and Hobson 2000) before isotopic analysis using a Thermo Finnigan TC/EA mass spectrometer (Thermo Fisher Scientific). The standards were chicken feather, cow hoof, and bowhead whale baleen calibrated against Vienna Standard mean ocean water and standard light Antarctic precipitation. Water samples were analyzed for δD by headspace equilibrium with H_2 gas and a Pt catalyst using a Thermo Finnigan Gas-Bench II mass spectrometer (Thermo Fisher Scientific).

Production sources supporting aquatic consumers

Proportional contributions of production sources to aquatic consumers were estimated using the MixSIR stable isotope mixing model (Moore and Semmens 2008). This Bayesian model uses the stable isotope values of sources and consumers and fractionation estimates to calculate feasible ranges of source contributions from 0% to 100%. Consumer samples were not corrected for lipids because C:N ratios were relatively low (mean C:N for Brazos fishes = 3.8, macroinvertebrates = 3.2; Tambopata fishes = 4.6; Neches fishes = 3.5, macroinvertebrates = 3.5; Cinaruco fishes = 3.6; Guadalupe fishes = 3.5). Before running the models, I corrected consumer tissue H for contributions of dietary water using the equation:

$$\delta D_{food} = \delta D_{consumer} - 0.124 * \delta D_{water} / (1 - \omega),$$

where ω was 0.124, the mean proportion of tissue H derived from dietary water for fishes reported by Solomon et al. (2009). I also investigated the possibility of trophic compounding of deuterium water (i.e., that the accumulation of dietary water increases up the food chain) hypothesized by Solomon et al. (2009) using the equation:

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

where τ is the difference in trophic position between the resource and the consumer. I calculated trophic position of consumers using the equation:

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

where $\delta^{15}N_{reference}$ was the mean $\delta^{15}N$ of the basal production sources (C_3 macrophytes, C_4 grasses, benthic algae, and seston) collected from each river, and 2.54‰ was the mean value from a meta-analysis of trophic fractionation studies (Vanderklift and Ponsard 2003). In all of the rivers except for the Cinaruco, this calculation resulted in δD_{food} values that were more depleted than the most D-depleted basal production source collected from all of the rivers (approximately – 220, benthic algae from the Tambopata River) indicating that little trophic compounding of dietary water had occurred, therefore

I ran all MixSIR models based on a ω of 0.124.

MixSIR models were run separately for species collected from each river and season using terrestrial plant samples collected during that period (Table 2.2). In the Tambopata River during the high-water period, all of the grass samples collected had $\delta^{13}C$ signatures indicative of C_3 macrophytes (grass $\delta^{13}C$ range -24.1 to -24.9), but during the low-water period, grass $\delta^{13}C$ ranged from -12.9 to -14.1. Because all grass and macrophyte $\delta^{13}C$ signatures were similar during the high-water period, they were pooled to yield one average value for terrestrial plants. Benthic algae collected during both low- and high-water periods were used for Neches, Cinaruco, and Guadalupe models, but for the Brazos and Tambopata rivers benthic algae were scarce during the high-water period due to scour and light limitation; therefore values for benthic algae collected during the low-water period were used for all models. Cole et al. (2011) suggested that, because of the high contrast of δD between terrestrial and algal photosynthesis, δD can be used as a tool for estimating the isotopic signature of pure algae. In the Brazos, Tambopata, Cinaruco, and Guadalupe rivers, samples of benthic algae had depleted δD signatures similar to those reported in the scientific literature, indicating samples were mostly pure algae with little contamination from fine particulate organic matter. Seston samples collected from every river were not as depleted as the phytoplankton deuterium signatures reported in the literature (i.e., algae tend to have a δD signature ≤ approximately -200, Doucett et al. 2007, Cole et al. 2011). However, after accounting for dietary water contributions, gizzard shad, filter feeders that ingest material from the water-column, collected during the low-water period in the Neches and

Guadalupe Rivers had strongly depleted deuterium signatures close to the values frequently reported for phytoplankton (gizzard shad mean δD Neches = -206.4, Guadalupe = -208.3), thus I assumed that my seston samples consisted of a large fraction of terrestrial-based fine particulate organic matter. Gizzard shad collected during the low-water period in the Brazos River had slightly more enriched deuterium values (mean δD = -157.8), but were still more depleted than C_3 macrophytes or C_4 grasses. Therefore, for the Texas rivers, after accounting for dietary water contributions and trophic fractionation of $\delta^{15}N$ (Vanderklift and Ponsard 2003, Solomon et al. 2009), I used the mean $\delta^{13}C$, $\delta^{15}N$, and δD signatures of gizzard shad collected during the low-water period as standards for estimating the stable isotope signature of phytoplankton. In the Cinaruco River, the pelagic fish *Hemiodus unimaculatus*, which consumes algae and detritus, was depleted in δD (mean δD after accounting for dietary water contributions = -178.1), and therefore I used the corrected mean stable isotope signature of this species as the stable isotope signature of phytoplankton. In the Tambopata River, I did not collect any consumers that primarily feed on plankton, and because our measurements indicated that autochthonous production in the water column of this river is consistently very low (see results section), I did not include phytoplankton as a potential production source. Because I could not be certain that these fishes were ingesting phytoplankton and not benthic algae (e.g., Mundahl and Wissing 1987), estimates of benthic algae and phytoplankton contributions were pooled to yield an estimate of the feasible contribution of algae. To account for fractionation of $\delta^{15}N$ in MixSIR models, I calculated trophic fractionation based on the number of trophic links leading to a consumer species using the equation:

$$\text{Trophic fractionation} = 2.5‰ * (\text{mean TP} - 1),$$

where 2.5‰ was $\delta^{15}N$ fractionation per trophic level from a synthesis of field studies (Vander Zanden and Rasmussen 2001) and mean TP was the mean trophic position calculated for each species. I used the standard deviation of trophic fractionation value of 2.5 from Vander Zanden and Rasmussen (2001) in MixSIR models. I assumed no trophic fractionation for $\delta^{13}C$ and δD (Vander Zanden and Rasmussen 2001, Vanderklift and Ponsard 2003, Smith and Ziegler 1990, Hobson et al. 1999). For each model, I performed sufficient iterations (range 1,000,000 to 1,000,000,000) to ensure that there were > 1,000 posterior draws, there were no duplicate draws in the posterior chain, and the ratio between the posterior at the best draw and the total posterior density was < 0.01.

Table 2.2. Carbon, nitrogen, and hydrogen stable isotope values (mean ± st dev) of basal production sources used in MixSIR models.

River	**Hydrologic period**	**Sample type**	**$\delta^{13}C$**	**$\delta^{15}N$**	**δD**
Brazos	Low water	C_3 plant	-29.8 (0.8)	6.3 (1.5)	-111.3 (19.9)
		C_4 grass	-14.1 (0.0)	8.0 (1.6)	-102.2 (10.3)
		Benthic algae	-28.3 (6.0)	13.2 (3.0)	-215.0 (53.3)
		Phytoplankton	-21.1 (0.2)	9.3 (0.1)	-157.8 (3.4)
	Flow pulse following low water	C_3 plant	-28.6 (0.7)	5.5 (1.5)	-87.7 (7.4)
		C_4 grass	-14.3 (0.1)	6.0 (2.2)	-79.5 (4.1)
		Benthic algae	-28.3 (6.0)	13.2 (3.0)	-215.0 (53.3)
		Phytoplankton	-21.1 (0.2)	9.3 (0.1)	-157.8 (3.4)
	High water	C_3 plant	-30.2 (0.6)	7.7 (2.8)	-127.9 (18.2)
		C_4 grass	-11.8 (0.5)	8.4 (0.9)	-96.7 (34.6)
		Benthic algae	-28.3 (6.0)	13.2 (3.0)	-215.0 (53.3)
		Phytoplankton	-21.1 (0.2)	9.3 (0.1)	-157.8 (3.4)
Tambopata	Low water	C_3 plant	-29.8 (4.4)	1.4 (2.4)	-96.5 (23.2)
		C_4 grass	-13.7 (0.9)	3.6 (1.5)	-83.2 (19.9)
		Benthic algae	-35.4 (3.4)	4.1 (7.2)	-219.4 (12.8)
	High water	Terrestrial plant	-31.3 (2.9)	0.9 (1.4)	-155.0 (23.1)
		Benthic algae	-35.4 (3.4)	4.1 (7.2)	-219.4 (12.8)
Neches	Low water	C_3 plant	-27.4 (1.5)	2.4 (1.6)	-60.7 (37.8)
		C_4 grass	-13.8 (0.2)	7.4 (2.1)	-63.9 (2.0)
		Benthic algae	-28.6 (0.7)	4.8 (0.8)	-111.1 (1.5)
		Phytoplankton	-22.1 (3.1)	7.3 (0.1)	-206.4 (43.8)
	Flow pulse following low water	C_3 plant	-30.8 (0.5)	4.2 (2.4)	-113.7 (5.5)
		C_4 grass	-13.2 (1.0)	5.1 (2.0)	-78.1 (12.5)
		Benthic algae	-29.3 (5.4)	1.5 (0.0)	-120.6 (13.8)
		Phytoplankton	-22.1 (3.1)	7.3 (0.1)	-206.4 (43.8)
	Falling water	C_3 plant	-29.2 (1.3)	3.4 (2.7)	-102.4 (11.1)
		C_4 grass	-13.6 (0.9)	6.9 (3.7)	-97.9 (17.3)
		Benthic algae	-26.5 (1.6)	4.9 (0.6)	-102.5 (3.7)
		Phytoplankton	-22.1 (3.1)	7.3 (0.1)	-206.4 (43.8)

Table 2.2 continued

River	Hydrologic period	Sample type	$\delta^{13}C$	$\delta^{15}N$	δD
Cinaruco	Falling water	C_3 plant	-30.1 (1.7)	0.7 (2.6)	-114.3 (15.8)
		C_4 grass	-13.4 (0.7)	3.9 (3.5)	-100.7 (27.4)
		Benthic algae	-25.1	2.1	-182.8
		Phytoplankton	-32.8 (2.3)	2.3 (0.1)	-178.1 (11.7)
Guadalupe	Low water	C_3 plant	-28.7 (1.4)	5.7 (1.0)	-87.7 (23.0)
		C_4 grass	-13.4 (0.9)	4.3 (0.7)	-82.4 (13.7)
		Benthic algae	-19.3 (3.7)	7.1 (1.9)	-177.8 (28.2)
		Phytoplankton	-23.9 (1.9)	6.3 (0.1)	-208.3 (2.4)
	Flow pulse following moderate flow	C_3 plant	-30.1 (1.4)	6.0 (3.2)	-123.1 (20.2)
		C_4 grass	-13.3 (1.0)	5.8 (0.9)	-100.9 (7.1)
		Benthic algae	-22.3 (3.5)	7.9 (0.0)	-206.1 (37.4)
		Phytoplankton	-23.9 (1.9)	6.3 (0.1)	-208.3 (2.4)

RESULTS

Frequency histograms of mean bimonthly % bankfull discharge

Frequency histograms of % bankfull discharge were right-skewed for the Brazos and Guadalupe rivers, an indication of the flashiness of these rivers; flooding is associated with a high volume of water that remains in the channel for a short period of time (Figure 2.2). Frequency histograms for the Neches and Madre de Dios rivers (representing hydrology of the Tambopata River) approached a normal distribution. In the Cinaruco River, a bimodal distribution was present, associated with the monomodal hydrological regime of this river characterized by annual low-flow and high-flow periods separated by gradual transitions.

Specific conductivity, pH, and water temperature

There was no relationship between specific conductivity and discharge in the Brazos River, but in the Tambopata, Neches, Cinaruco and Guadalupe rivers, specific conductivity decreased as discharge increased (Tambopata PCC = -0.925, $\mathrm{p} < 0.01$; Neches PCC = -0.748, $p < 0.001$; Cinaruco PCC = -0.779, $p < 0.001$; Guadalupe PCC = -0.774, $p < 0.001$, Table 2.3). In all of the rivers but the Cinaruco, pH tended to decrease as % bankfull discharge increased (Brazos PCC = -0.691, $p < 0.01$; Tambopata PCC = -0.634, $p < 0.05$; Neches PCC = -0.714, $p < 0.001$; Guadalupe PCC = -0.776, $p < 0.001$). Water temperature tended to decrease with greater river discharge in all the rivers, but the relationship was significant only for the Tambopata, Cinaruco, and Guadalupe rivers (Tambopata PCC = -0.742, $p < 0.001$; Cinaruco PCC = -0.496, p < 0.001; Guadalupe PCC = -0.596, $p < 0.05$).

Nutrients, turbidity, and algal primary production

Hydrology had an effect on nutrient concentrations in several of the rivers. In some of the temperate rivers, SRP and DIN concentrations tended to be higher during relatively short duration high-flow pulses (Table 2.4, Brazos SRP t = -4.96, df = 5, $p < 0.01$; Brazos DIN t = -3.50, df = 4, $p < 0.05$; Neches DIN t = -8.38, df = 8, $p < 0.001$). However, in the tropical rivers, the opposite pattern was observed; concentrations of some nutrients tended to be higher during the low-water period (Tambopata SRP t = 2.61, df = 9, $p < 0.05$; Cinaruco DIN t = 3.56, df = 41, $p < 0.001$). Silica concentrations were significantly higher during the low-water period in the Brazos River (t = 6.37, df = 15, $p < 0.001$) and Cinaruco River (t = 2.40, df = 41, $p < 0.001$).

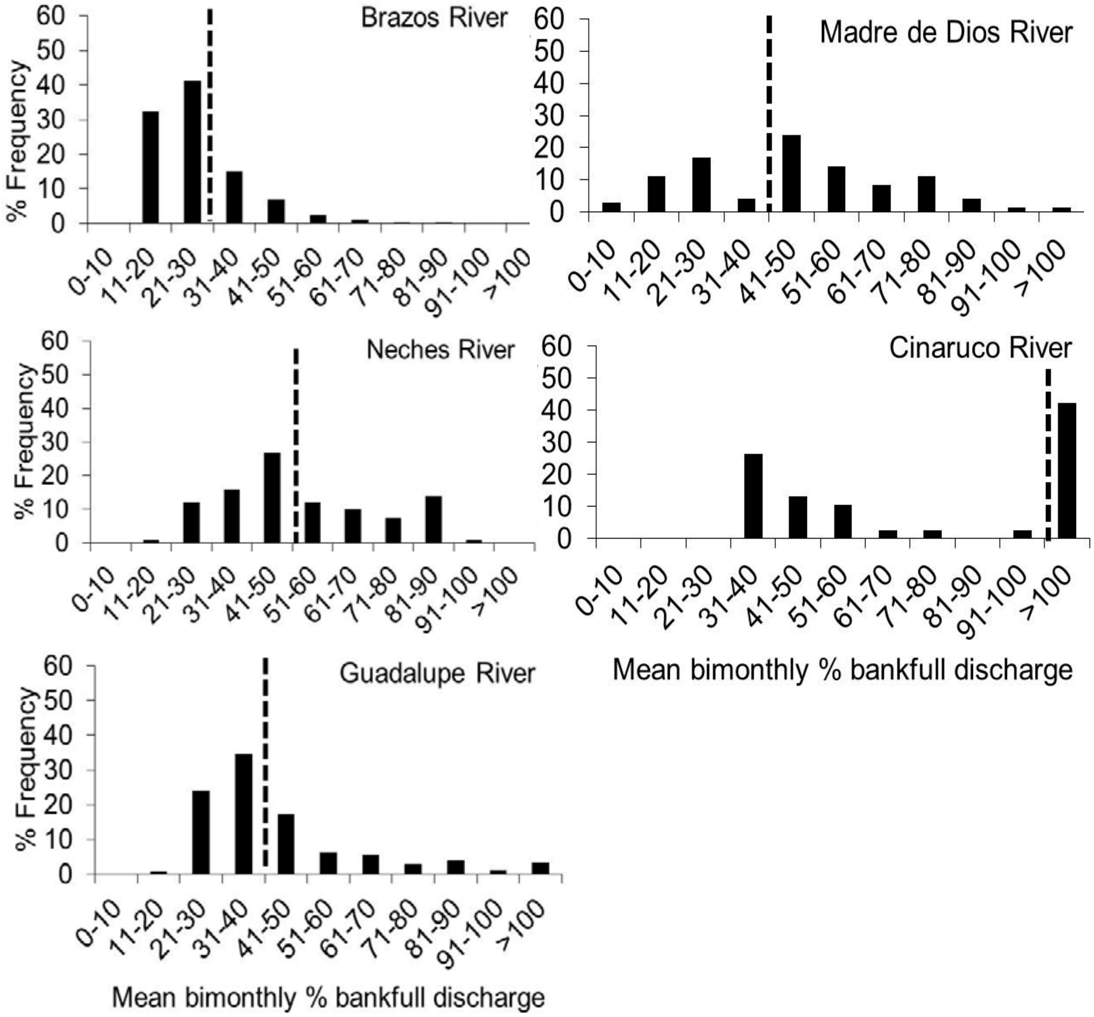

Figure 2.2. Historical stage height data plotted as % frequency versus mean bimonthly % bankfull discharge for the study rivers. Historical stage height data were not available for the Tambopata River, therefore data from the Madre de Dios River, of which the Tambopata River is a tributary, were used as a surrogate. Dotted line indicates river stage used to distinguish low-water period from high-water period.

Table 2.3. Physicochemical variables (mean ± st dev) measured in each of the study rivers.

River	pH	Conductivity (µS/cm)	Water temperature (°C)
Brazos	8.3 (0.3)	894 (318)	22 (5)
Tambopata	7.0 (0.1)	71 (1)	26 (2)
Neches	7.2 (0.4)	168 (19)	25 (7)
Cinaruco	5.7 (0.5)	5 (2)	30 (1)
Guadalupe	8.2 (0.3)	489 (90)	25 (4)

Table 2.4. Nutrient concentrations (mean ± st dev in mg/L) measured during low- and high-water periods in each of the study rivers analyzed using colorimetric assays and a Technicon II Autoanalyzer for the Cinaruco River and a Hach DR 2800 mass spectrophotometer for all other rivers. SRP = soluble reactive phosphorus, DIN = dissolved inorganic nitrogen (the sum of NO_3, NO_2, and NH_4), and silica = SiO_3 in the Cinaruco River and SiO_2 in other rivers. Brazos n = 18, Tambopata n = 12, Neches n = 22, Cinaruco n = 53, Guadalupe n = 17.

River	SRP		DIN		Silica	
	Low-water	High-water	Low-water	High-water	Low-water	High-water
Brazos	0.28 (0.29)	1.42 (0.49)	0.40 (0.16)	1.17 (0.48)	6.34 (2.66)	1.10 (0.82)
Tambopata	0.41 (0.31)	0.16 (0.01)	0.12 (0.06)	0.08 (0.03)	0.44 (0.25)	0.62 (0.13)
Neches	0.41 (0.34)	0.59 (0.71)	0.30 (0.16)	0.63 (0.03)	8.74 (2.83)	11.05 (1.06)
Cinaruco	0.01 (0.00)	0.01 (0.01)	0.01 (0.01)	0.01 (0.00)	1.92 (2.88)	0.38 (0.22)
Guadalupe	0.65 (0.95)	3.22 (2.14)	0.51 (0.29)	0.93 (0.50)	8.39 (4.04)	6.87 (1.27)

Turbidity was higher following periods of high flows in the sediment-laden rivers (i.e., Brazos and Tambopata) compared to the Neches, Cinaruco, or Guadalupe rivers; in the Brazos and Tambopata rivers, flow pulses frequently produced turbidity levels in excess of 150 FTU (Brazos maximum = 1474, Tambopata maximum = 399), compared to a maximum of 109 FTU for the Neches River, 7.9 FTU for the Cinaruco River, and 367 FTU for the Guadalupe River (Figure 2.3). Turbidity was positively correlated with % bankfull discharge in both of the sediment-laden rivers (Brazos PCC = 0.642, $p < 0.01$; Tambopata PCC = 0.837, $p < 0.001$) and the Guadalupe (PCC = 0.734, $p < 0.001$). In the Neches and Cinaruco Rivers, turbidity was highest during periods of low flow as a result of increased concentrations of humic substances and phytoplankton. In the Neches River, turbidity increased slightly following flow pulses, thus turbidity was not correlated with discharge (PCC = 0.148, $p = 0.491$). In the Cinaruco River, turbidity was negatively correlated with discharge (PCC = -0.836, $p < 0.001$).

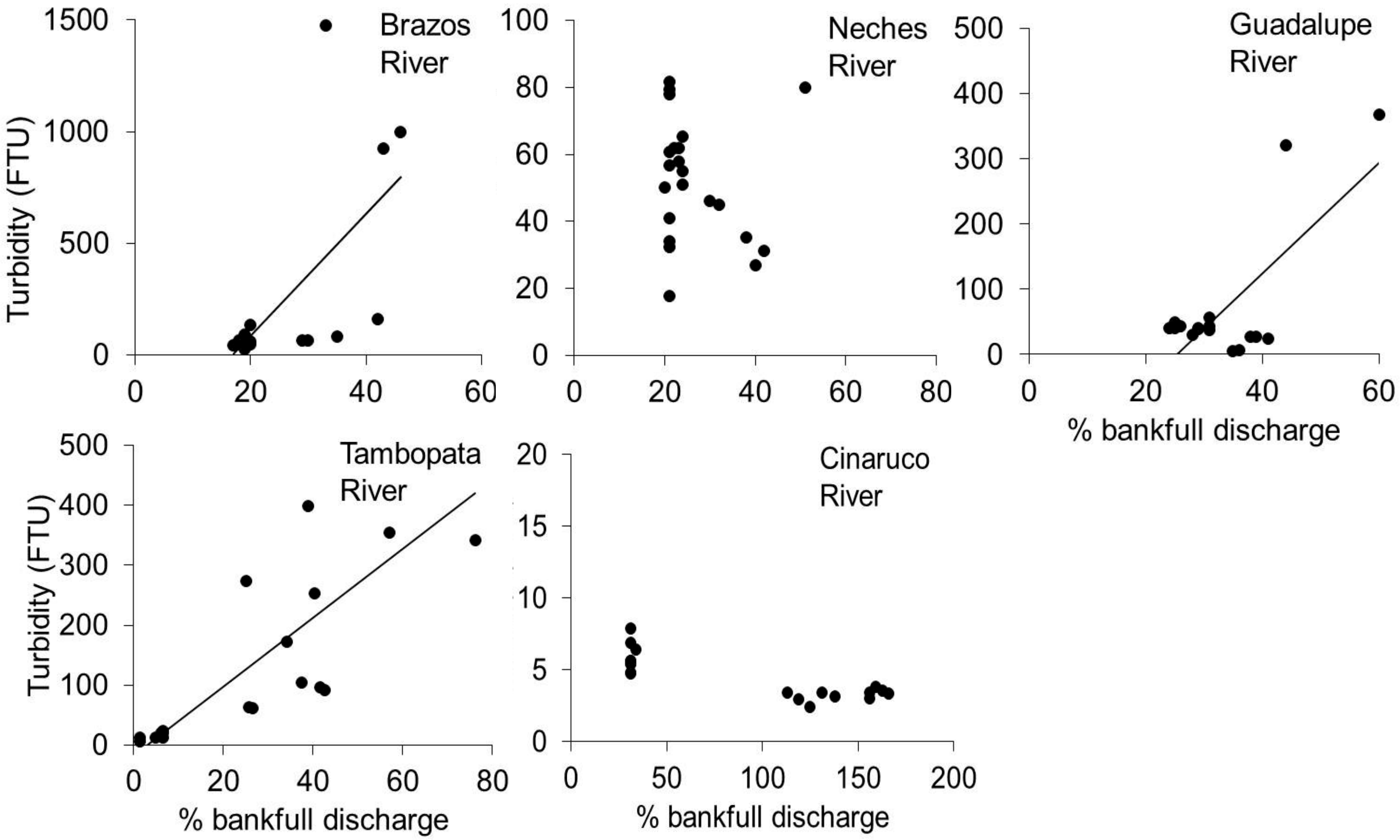

Figure 2.3. Relationship between % bankfull discharge and turbidity in the Brazos, Tambopata, Neches, Cinaruco, and Guadalupe rivers.

Water-column NPP was significantly greater during the low-water period compared to the high-water period for the Tambopata River (t = 2.64, df = 5, $p < 0.05$), Neches River (t = 6.19, df = 16, $p < 0.001$), and Cinaruco River (t = 3.72, df = 16, $p < 0.01$). Benthic NPP values were more variable than water-column NPP values; there were significant differences in benthic NPP with hydrologic season only for the Cinaruco River (t = -2.87, df = 13, $p < 0.05$). In all of the rivers but the Guadalupe, the overall magnitude of NPP tended to be higher for the water column than for the benthos. Littoral zones in both of the sediment-laden rivers were heterotrophic, indicated by negative total (water-column + benthic) NPP values, following periods of high discharge (Figure 2.4). I sampled two periods when total NPP in Brazos River littoral zones was negative. For the first period (occurring in May of 2009), flooding of similar magnitude (25% bankfull discharge) had not occurred for > 8 mo. For the second period (occurring in January/February of 2012), flooding of similar magnitude (53% bankfull discharge) had not occurred for > 16 mo. Positive total NPP measurements occurred at higher magnitudes of discharge compared to negative total NPP measurements, but when littoral zones were autotrophic, flooding of similar magnitude had occurred relatively recently. For example, in May of 2010, the littoral zone was autotrophic at 42% bankfull discharge, but flooding of similar magnitude had occurred < 1 month prior. In the Tambopata River, total NPP was consistently positive only after the water level fell below approximately 10% bankfull discharge. In contrast, in the other study rivers, total NPP was almost always positive during both low- and high-water periods.

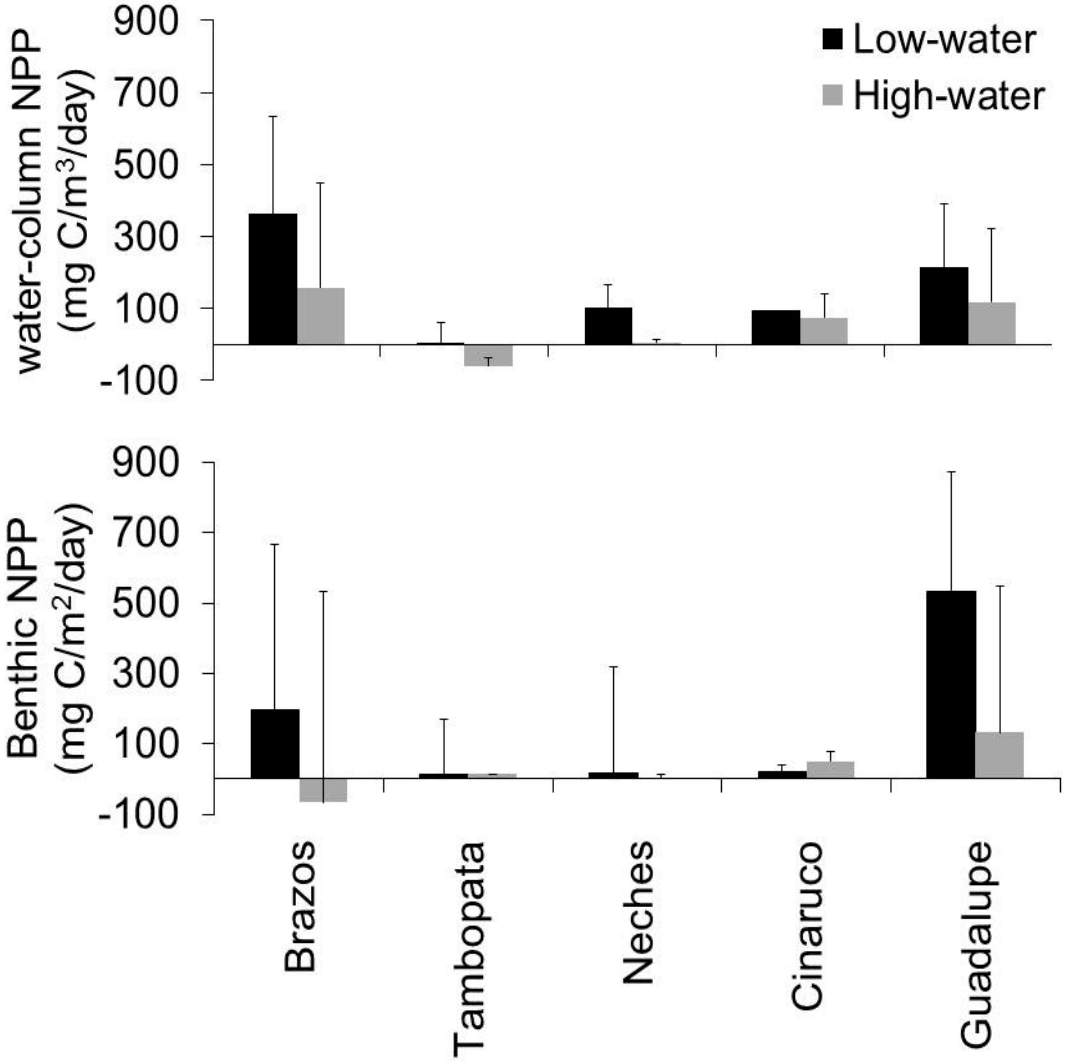

Figure 2.4. Water-column and benthic net primary production during the low- and high-water periods in each of the study rivers. Positive values indicate production (release into the water-column) and negative values indicate consumption or uptake into sediment. Brazos n = 20, Tambopata n = 12, Neches n = 22, Cinaruco n = 41, Guadalupe n = 17.

Among all the study rivers, the Brazos had highest average water-column and benthic chlorophyll *a* measurements (Figure 2.5). However, chlorophyll *a* in the Brazos River greatly decreased following high-flow periods (i.e., 1.8 mg/m^3 for the water column and 0.0 mg/m^2 for the benthos at 43% bankfull discharge). Tambopata River water-column chlorophyll *a* measurements were low during both hydrologic periods, but benthic measurements were slightly higher during the low-water period for a maximum measurement of 2.4 mg/m^2. Chlorophyll *a* followed the same seasonal pattern as NPP measurements, in which average values were higher during the low-water period compared to the high-water period. Water-column chlorophyll *a* was significantly higher during the low-water period for the Brazos River ($t = 4349$, $df = 13$, $p < 0.01$) and Neches River ($t = 5.37$, $df = 6$, $p < 0.01$), and benthic chlorophyll *a* was significantly higher during the low-water period for the Brazos ($t = 4.96$, $df = 13$, $p < 0.001$), Tambopata ($t = 4.75$, $df = 4$, $p < 0.01$), Neches ($t = 2.55$, $df = 9$, $p < 0.05$), and Cinaruco ($t = 4.21$, $df = 25$, $p < 0.001$) rivers. Similar to NPP measurements, average water-column chlorophyll *a* was higher than benthic chlorophyll *a* for the Brazos and Neches rivers, but benthic measurements were higher for the Guadalupe River.

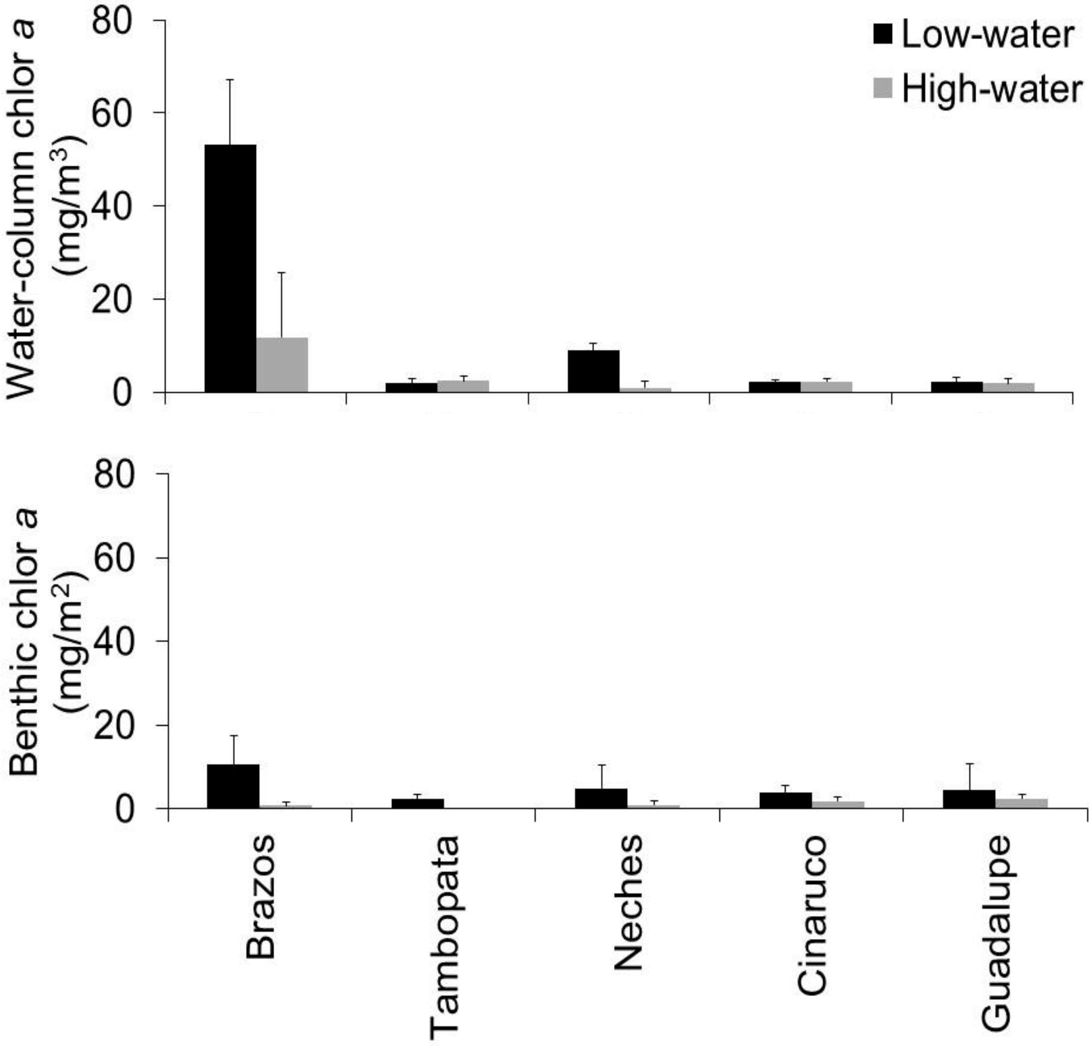

Figure 2.5. Water-column and benthic chlorophyll *a* (chlor *a*) during the low- and high-water periods in each of the study periods. Brazos n = 18, Tambopata n = 8, Neches n = 21, Cinaruco n = 28, Guadalupe n = 16.

Stable isotope signatures of water, primary producers, and consumers

In all five rivers, water samples collected from different reaches during the same survey period had similar δD values. There was more temporal variation in water δD values; the Brazos River revealing the greatest seasonal difference (Table 2.5). Terrestrial plants also exhibited seasonal shifts in δD; C_3 macrophytes and C_4 grasses tended to be enriched in ^2H (high δD values) during periods of low discharge (Table 2.5). Generally, benthic algae and tissues of consumers that are known to feed primarily on algae were more ^2H-depleted than terrestrial plants, providing good discrimination between autochthonous and allochthonous production sources.

Consumer tissue $\delta^{13}C$ was intermediate between the $\delta^{13}C$ of algae and macrophytes for all species from the temperate rivers (Table 2.6, Brazos range = -29.0 to -20.9, Neches range = -32.1 to -19.8, Guadalupe range = -31.6 to -20.0). However, two species from the tropical rivers, *Prochilodus nigricans* from the Tambopata River and *Myleus schombergki* from the Cinaruco River, were more depleted in ^{13}C than any sources that were collected (Tambopata River $\delta^{13}C$ range = -43.1 to -2.4, Cinaruco River range = -36.6 to -21.8). After correcting for dietary water contributions, consumer tissue δD_{food} was intermediate relative to the range of sources measured either directly from primary producer or indirectly from consumer tissue (Brazos δD_{food} range = -205.7 to -108.6, Tambopata range = -216.9 to -103.9, Neches range = -251.1 to -64.1, Cinaruco range = -191.1 to -81.2, Guadalupe range = -220.5 to -96.2).

Table 2.5. Hydrogen stable isotope values (mean ± st dev) and sample sizes for river water samples from the Brazos, Tambopata, Neches, Cinaruco, and Guadalupe rivers during different hydrologic periods.

River	**Hydrologic period**	**n**	**δD**
Brazos	Low water	3	-17.1 (1.3)
	Flow pulse following low water	2	-8.4 (2.5)
	High water	1	-45.9
Tambopata	Low water	3	-37.6 (0.7)
	High water	1	-57.0
Neches	Low water	2	-17.0 (0.1)
	Flow pulse following low water	1	1.1
	Falling water	1	-9.5
Cinaruco	Falling water	3	-36.7 (0.5)
Guadalupe	Low water	3	-17.7 (0.5)
	Flow pulse following moderate flow	1	-21.5

Table 2.6. Carbon, nitrogen, and hydrogen stable isotope values, trophic position, and hydrogen stable isotope values corrected for dietary water (δD_{food}) of consumer species collected from the Brazos, Tambopata, Neches, Cinaruco, and Guadalupe rivers (mean ± st dev).

River	Hydrologic period	Consumer	n	$\delta^{13}C$	$\delta^{15}N$	Trophic position	δD	δD_{food}
Brazos	Low water	River carpsucker	2	-26.1 (0.4)	13.8 (3.7)	2.8 (1.5)	-140.4 (6.3)	-157.9 (7.2)
		Gizzard shad	3	-21.1 (0.2)	14.9 (0.3)	3.2 (0.1)	-140.4 (3.0)	-157.8 (3.4)
		Red shiner	3	-28.5 (0.5)	15.6 (0.3)	3.5 (0.1)	-165.5 (20.7)	-186.5 (23.6)
		Bullhead minnow	3	-27.9 (0.4)	16.0 (0.2)	3.7 (0.1)	-146.8 (1.7)	-165.2 (2.0)
		Ohio River shrimp	3	-26.1 (0.2)	15.9 (0.2)	3.6 (0.1)	-119.7 (5.4)	-134.2 (6.2)
		Channel catfish	3	-25.8 (1.5)	15.5 (0.1)	3.4 (0.0)	-115.3 (8.0)	-129.2 (9.2)
		Longnose gar	3	-25.3 (0.9)	18.8 (0.5)	4.7 (0.2)	-136.4 (6.9)	-153.3 (7.9)
Brazos	Flow pulse following low water	River carpsucker	2	-22.9 (0.9)	15.7 (0.1)	3.5 (0.1)	-135.1 (4.9)	-153.0 (5.6)
		Red shiner	3	-26.2 (0.4)	17.7 (1.0)	4.3 (0.4)	-152.4 (8.6)	-172.8 (9.9)
		Shoal chub	3	-25.9 (0.5)	18.2 (0.2)	4.5 (0.1)	-127.4 (5.8)	-144.3 (6.7)
		Ghost shiner	3	-26.8 (0.7)	17.4 (0.2)	4.2 (0.1)	-150.9 (27.6)	-171.1 (31.5)
		Bullhead minnow	3	-25.7 (0.4)	17.3 (0.4)	4.1 (0.1)	-130.9 (3.9)	-148.2 (4.5)
		Ohio River shrimp	3	-24.8 (0.1)	16.5 (0.3)	3.8 (0.1)	-115.6 (2.9)	-130.7 (3.3)
		Channel catfish	1	-24.4	17.8	4.3	-120.6	-136.5
		Longnose gar	3	-27.8 (1.1)	19.1 (0.8)	4.9 (0.3)	-163.9 (13.6)	-185.9 (15.5)
Brazos	High water	River carpsucker	3	-24.7 (0.3)	17.5 (0.4)	4.2 (0.1)	-110.1 (7.0)	-119.2 (8.0)
		Gizzard shad	2	-23.4 (0.9)	14.5 (0.6)	3.0 (0.3)	-131.2 (1.0)	-143.3 (1.1)
		Red shiner	3	-25.9 (1.4)	12.7 (0.5)	2.3 (0.2)	-113.4 (10.9)	-123.0 (12.4)
		Shoal chub	2	-25.0 (0.4)	16.5 (0.1)	3.8 (0.0)	-101.1 (0.3)	-108.9 (0.4)
		Ghost shiner	1	-26.0	17.1	4.1	-116.9	-127.0
		Bullhead minnow	3	-25.3 (0.4)	14.0 (0.9)	2.9 (0.3)	-112.0 (11.7)	-121.4 (13.3)
		Longnose gar	3	-25.1 (1.3)	18.9 (0.8)	4.8 (0.3)	-125.8 (14.7)	-137.1 (16.8)

Table 2.6 continued

River	Hydrologic period	Consumer	n	δ^{13}C	δ^{15}N	Trophic position	δD	δD_{food}
Tambopata	Low water	*Prochilodus nigricans*	1	-33.8	7.0	2.5	-167.8	-186.2
		Anchoviella sp.	3	-36.0 (3.0)	9.4 (0.3)	3.4 (0.1)	-153.2 (21.9)	-169.6 (25.0)
		Astyanax abramoides	1	-26.6	8.2	2.9	-115.7	-126.8
		Leporinus sp.	1	-30.7	9.0	3.2	-143.9	-159.0
		Pimelodella sp.	2	-26.2 (0.5)	8.1 (0.6)	2.9 (0.2)	-111.3 (2.6)	-121.7 (2.9)
Neches	Flow pulse following low water	Bluegill	3	-29.4 (1.6)	10.1 (0.9)	3.1 (0.3)	-90.3 (9.1)	-103.2 (10.4)
		Longear sunfish	3	-29.6 (0.6)	11.4 (0.5)	3.7 (0.2)	-103.8 (8.4)	-118.6 (9.6)
		Freshwater drum	1	-27.9	9.2	2.8	-96.9	-110.8
		Spotted bass	3	-27.3 (2.1)	11.8 (1.8)	3.8 (0.7)	-90.4 (11.8)	-103.4 (13.5)
		Spotted gar	3	-27.5 (1.6)	12.3 (0.8)	4.0 (0.3)	-104.6 (33.5)	-119.6 (38.2)
Neches	Falling water	Smallmouth buffalo	1	-29.3	11.6	3.7	-104.0	-117.4
		Gizzard shad	4	-27.3 (1.9)	8.7 (0.2)	2.6 (0.1)	-138.5 (13.1)	-156.7 (15.0)
		Blacktail shiner	3	-28.1 (0.9)	10.6 (1.1)	3.3 (0.4)	-112.4 (9.7)	-127.0 (11.1)
		Blackstripe topminnow	3	-25.0 (1.0)	10.1 (0.2)	3.1 (0.1)	-100.7 (10.7)	-113.6 (12.2)
		Bullhead minnow	5	-27.3 (0.7)	11.1 (0.3)	3.5 (0.1)	-112.9 (14.4)	-127.5 (16.4)
		Bluegill	1	-30.5	11.0	3.5	-87.4	-98.5
		Longear sunfish	3	-26.3 (0.2)	10.9 (0.6)	3.5 (0.3)	-73.3 (6.0)	-82.3 (6.8)
		Freshwater drum	3	-27.2 (1.6)	10.7 (0.9)	3.4 (0.4)	-93.0 (3.3)	-104.8 (3.7)
		Spotted bass	1	-28.4	12.7	4.1	-97.1	-109.5
		Spotted gar	2	-28.4 (0.5)	13.2 (0.3)	4.3 (0.1)	-92.2 (11.4)	-103.9 (13.1)
		Longnose gar	1	-29.2	13.6	4.5	-110.9	-125.2

Table 2.6 continued

River	**Hydrologic period**	**Consumer**	**n**	**δ^{13}C**	**δ^{15}N**	**Trophic position**	**δD**	**δD_{food}**
Cinaruco	Falling water	*Metynnis hypsauchen*	3	-26.5 (4.1)	7.0 (0.3)	2.9 (0.1)	-126.6 (34.4)	-139.4 (39.3)
		Myleus schombergki	3	-34.4 (2.0)	5.4 (0.9)	2.2 (0.4)	-139.4 (10.3)	-154.0 (11.7)
		Semaprochilodus kneri	3	-31.8 (2.3)	5.1 (0.3)	2.1 (0.1)	-133.0 (12.1)	-146.7 (13.8)
		Aphyocharax alburnus	1	-33.4	9.9	4.0	-75.7	-81.2
		Hemigrammus analis	2	-32.2(0.7)	10.3 (0.3)	4.1 (0.1)	-112.8 (0.4)	-123.6 (0.4)
		Moenkhausia lepidura	3	-29.1 (1.1)	8.0 (0.3)	3.2 (0.1)	-117.0 (8.4)	-128.4 (9.6)
		Hemiodus unimaculatus	3	-32.8 (2.3)	5.9 (0.2)	2.4 (0.1)	-160.5 (10.2)	-178.1 (11.7)
		Geophagus dichrozoster	1	-32.5	7.2	2.9	-98.7	-107.5
		Mesonauta festivus	1	-27.1	7.7	3.1	-117.8	-129.3
		Cichla temensis	3	-30.2 (1.0)	9.1 (0.3)	3.6 (0.1)	-116.4 (15.0)	-127.7 (17.1)
		Boulengerella lucius	2	-30.2 (0.2)	8.9 (0.1)	3.6 (0.0)	-97.5 (3.4)	-106.2 (3.9)
Guadalupe	Low water	Gizzard shad	3	-23.9 (1.9)	14.8 (1.7)	4.4 (0.7)	-184.7 (2.1)	-208.3 (2.4)
		Red shiner	3	-27.1 (0.4)	14.5 (0.1)	4.2 (0.0)	-152.5 (5.8)	-171.6 (6.6)
		Bullhead minnow	3	-27.5 (1.0)	14.5 (0.2)	4.2 (0.1)	-142.7 (8.0)	-160.9 (9.1)
		Longear sunfish	4	-26.8 (0.3)	14.5 (0.4)	4.2 (0.2)	-120.0 (13.0)	-134.5 (14.9)
		Striped mullet	3	-24.8 (2.7)	12.5 (1.1)	3.4 (0.5)	-157.7 (13.8)	-177.6 (15.8)
		Spotted bass	1	-25.0	15.8	4.7	-131.7	-147.9
		Spotted gar	1	-24.7	17.8	5.5	-111.0	-124.2
Guadalupe	Flow pulse following moderate flow	Gizzard shad	3	-24.8 (6.1)	12.4 (3.8)	3.4 (1.5)	-146.6 (42.7)	-164.3 (48.8)
		Red shiner	3	-26.8 (0.6)	13.3 (1.1)	3.8 (0.4)	-129.0 (8.3)	-144.2 (9.5)
		Bullhead minnow	3	-25.7 (0.6)	13.6 (0.5)	3.9 (0.2)	-117.0 (5.8)	-130.5 (6.6)
		Longear sunfish	1	-24.3	12.2	3.3	-87.0	-96.2
		Striped mullet	3	-26.5 (2.3)	15.3 (1.0)	4.5 (0.4)	-146.8 (12.5)	-164.6 (14.3)
		Spotted bass	1	-24.2	15.0	4.4	-102.3	-113.8
		Spotted gar	1	-24.3	15.5	4.6	-124.4	-138.9

Production sources supporting Brazos River consumers

Low-water. MixSIR models indicated that the seven species examined assimilated a mixture of algae and C_3 macrophytes. Gizzard shad and red shiner had high 5% confidence percentiles of algae (> 35, Table 2.7) and 95% confidence percentiles equaled 100. Bullhead minnow, longnose gar, and river carpsucker likely assimilated a mixture of algae and C_3 macrophytes, with relatively low 5% confidence percentiles (range 13 to 15 for algae, 11 to 21 for C_3 macrophytes) and high 95% confidence percentiles (range 85 to 100 for algae, 46 to 59 for C_3 macrophytes) for both production sources. Channel catfish and Ohio River shrimp assimilated a large fraction of C_3 macrophytes (5% contribution percentiles > 30, 95% confidence percentiles ≥ 60).

Flow pulse following low-water. Similar to the low-water period, algae were the most important production source supporting secondary consumer biomass, with a few species supported mainly by C_3 macrophytes. Ghost shiner, longnose gar, and red shiner had high 5% confidence percentiles of algae (range 29 to 40), and 95% confidence percentiles equaled 100. River carpsucker had lower 5% confidence percentiles of algae (< 20), but 95% confidence percentiles equaled 100, indicating that a large contribution from algae was possible. Bullhead minnow, channel catfish, and Ohio River shrimp probably assimilated a mixture of algae and C_3 macrophytes, with relatively low 95% confidence percentiles (< 35 for algae and C_3 macrophytes) and high 95% confidence percentiles (> 75 for algae, ≥ 45 for C_3 macrophytes) for both sources.

High-water. Contributions of C_3 macrophytes to consumer tissues increased during extended high flows compared to the low-water period and a short-duration flow pulse following an extended low-water period for five of the eight species examined. Three of these five species, bullhead minnow, red shiner, and shoal chub, assimilated a large fraction of material derived from C_3 macrophytes (5% confidence percentiles > 30). Longnose gar and river carpsucker may have assimilated material from C_3 macrophytes or algae; 5% confidence percentiles were relatively low for all three basal production sources for these species. Gizzard shad seemed to assimilate a large fraction of algae, with 95% confidence percentiles for C_3 macrophytes equaling 34 and 95% confidence percentiles for algae equaling 100.

Table 2.7. Median and 5 – 95% confidence percentiles (in parentheses) of basal production source contributions to consumers in the Brazos River. Consumers with 5% confidence percentiles ≥ 25 are in bold.

Hydrologic period	**Consumer**	**C_3 macrophytes**	**C_4 grasses**	**Algae**
Low water	River carpsucker	36 (11-55)	8 (<1-26)	54 (15-100)
	Gizzard shad	2 (<1-8)	7 (1-24)	**91 (52-100)**
	Red shiner	29 (7-48)	5 (<1-19)	**63 (37-100)**
	Bullhead minnow	41 (21-59)	5 (<1-17)	52 (23-85)
	Ohio River shrimp	**54 (42-64)**	7 (<1-20)	39 (7-68)
	Channel catfish	**48 (32-60)**	16 (4-28)	35 (12-67)
	Longnose gar	33 (18-46)	8 (<1-24)	60 (13-90)
Flow pulse following low water	River carpsucker	14 (3-26)	10 (1-31)	75 (16-100)
	Red shiner	21 (4-38)	6 (<1-22)	**71 (29-100)**
	Shoal chub	36 (21-49)	5 (<1-20)	58 (17-88)
	Ghost shiner	22 (5-40)	7 (<1-23)	**67 (35-100)**
	Bullhead minnow	32 (17-45)	5 (<1-20)	62 (17-94)
	Ohio River shrimp	**42 (33-48)**	3 (<1-15)	54 (22-77)
	Channel catfish	30 (6-48)	12 (1-35)	55 (8-100)
	Longnose gar	20 (3-38)	6 (<1-20)	**71 (40-100)**
High water	River carpsucker	34 (7-54)	18 (3-37)	46 (5-100)
	Gizzard shad	23 (9-34)	9 (1-31)	64 (13-100)
	Red shiner	**49 (31-61)**	11 (2-25)	39 (15-70)
	Shoal chub	**58 (41-65)**	14 (6-26)	28 (3-59)
	Ghost shiner	44 (11-63)	10 (<1-30)	44 (9-91)
	Bullhead minnow	**48 (33-58)**	13 (3-27)	39 (10-69)
	Longnose gar	34 (17-48)	12 (2-28)	54 (18-86)

Production sources supporting Tambopata River consumers

Low-water. Algae made a large contribution to three of the eight species examined, *Anchoviella* sp., *Leporinus* sp., and *Prochilodus nigricans* (Table 2.8). For these three species, algae had 5% confidence percentiles > 30, and 95% confidence percentiles ≥ 65. Ranges of source contributions were broader for *Astyanax abramoides*, *Pimelodella* sp., and *Pimelodus blochii*, but these species probably assimilated material from algae and C_3 macrophytes. Two piscivorous species, *Cetopsis coecutiens* and *Pinirampus pirinampu*, likely assimilated a large fraction of C_3 macrophytes, with 5% confidence percentiles > 30 and 95% confidence percentiles > 80.

High-water. All eight of the species examined assimilated large fractions of C_3 macrophytes, with 5% confidence percentiles > 45 and 95% confidence percentiles > 90. Two species, *Anchoviella* sp. and *Pinirampus pirinampu*, seemed to assimilate a small fraction of algae, with 95% confidence percentiles > 40.

Table 2.8. Median and 5 – 95% confidence percentiles (in parentheses) of basal production source contributions to consumers in the Tambopata River. Consumers with 5% confidence percentiles ≥ 25 are in bold.

Hydrologic period	**Consumer**	**Terrestrial plants**		**Algae**
		(C_3 macrophytes)	**(C_4 grasses)**	
Low water	*Prochilodus nigricans*	17 (3-38)	9 (1-22)	**75 (58-85)**
	Anchoviella sp.	**39 (28-51)**	2 (<1-7)	**59 (48-68)**
	Astyanax abramoides	44 (18-76)	30 (7-46)	27 (9-42)
	Leporinus sp.	33 (8-59)	16 (2-32)	**52 (33-65)**
	Pimelodella sp.	**43 (25-68)**	33 (15-44)	25 (11-35)
	Cetopsis coecutiens	**61 (38-85)**	25 (5-43)	14 (2-28)
	Pimelodus blochii	42 (16-74)	31 (7-47)	28 (10-43)
	Pinirampus pirinampu	**76 (57-93)**	2 (<1-6)	23 (4-41)
High water	*Prochilodus nigricans*	**96 (86-100)**		4 (<1-15)
	Anchoviella sp.	**73 (58-92)**		27 (8-42)
	Astyanax abramoides	**91 (76-99)**		9 (1-24)
	Leporinus sp.	**95 (85-100)**		5 (<1-15)
	Pimelodella sp.	**98 (93-100)**		2 (<1-7)
	Cetopsis coecutiens	**97 (90-100)**		3 (<1-10)
	Pimelodus blochii	**96 (88-100)**		4 (<1-12)
	Pinirampus pirinampu	**70 (48-93)**		30 (7-52)

Production sources supporting Neches River consumers

Low-water. Algae and C_3 macrophytes made large contributions to the 11 species examined. Three of the 11 species, freshwater drum, gizzard shad, and mimic shiner, assimilated a large fraction of algae (Table 2.9, 5% confidence percentiles > 50, 95% confidence percentiles = 100). Six of the 11 species could have assimilated either algae or C_3 macrophytes. The range of contributions of both algae and C_3 macrophytes was large (5% confidence percentiles < 20 for both algae and C_3 macrophytes, 95% confidence percentiles = 100 for algae and > 60 for C_3 macrophytes) for these six species. Two species, bluegill and spotted gar, assimilated a large amount of material from C_3 macrophytes, with 5% confidence percentiles ≥ 60 and 95% confidence percentiles > 75.

Flow pulse following low-water. Similar to the low water period, both algae and C_3 macrophytes supported secondary consumer biomass. Four species, blackstripe topminnow, gizzard shad, spotted bass, and spotted gar, assimilated large fractions of algae, with 5% confidence percentiles > 30 and 95% confidence percentiles > 70. The range of contributions of both algae and C_3 macrophytes was large for five species, with both sources having low 5% confidence percentiles (≤ 20 for algae, < 25 for C_3 macrophytes) and high 95% confidence percentiles (> 75 for algae and C_3 macrophytes). C_3 macrophytes accounted for a large fraction of consumer biomass for bluegill and longear sunfish, with 5% confidence percentiles > 25 and 95% confidence percentiles > 75.

Falling-water. Compared to the low-water and flow pulse following low-water periods, contributions of C_3 macrophytes seemed to increase and contributions of algae seemed to decrease for several species. Blackstripe topminnow, gizzard shad, and spotted gar had increased 5% and 95% confidence percentiles for C_3 macrophytes. C_3 macrophytes made major contributions to five of the 11 species examined, blacktail shiner, bluegill, bullhead minnow, longear sunfish, and spotted gar, with 5% confidence percentiles > 25 and 95% confidence percentiles > 70. Either algae or C_3 macrophytes could have accounted for a large fraction of five of the 11 species examined: blackstripe topminnow, freshwater drum, longnose gar, smallmouth buffalo, and spotted bass. Ranges of both algae and C_3 macrophytes were broad for these species (5% confidence percentiles > 20, 95% confidence percentiles > 60). Algae contributed a large fraction to gizzard shad, with 5% confidence percentiles equaling 34 and 95% confidence percentiles equaling 89.

Table 2.9. Median and 5 – 95% confidence percentiles (in parentheses) of basal production source contributions to consumers in the Neches River. Consumers with 5% confidence percentiles ≥ 25 are in bold.

Hydrologic period	**Consumer**	**C_3 macrophytes**	**C_4 grasses**	**Algae**
Low water	Smallmouth buffalo	15 (2-63)	2 (<1-7)	81 (15-100)
	Gizzard shad	6 (1-18)	4 (<1-14)	**86 (69-100)**
	Blacktail shiner	25 (1-84)	<1 (0-3)	64 (3-100)
	Bullhead minnow	20 (2-76)	1 (<1-3)	74 (10-100)
	Mimic shiner	3 (<1-22)	1 (0-2)	**81 (55-100)**
	Cinnamon river shrimp	38 (5-95)	1 (0-3)	56 (1-100)
	Bluegill	**83 (60-95)**	1 (0-3)	14 (1-47)
	Freshwater drum	12 (6-37)	1 (<1-3)	**86 (55-100)**
	Spotted bass	50 (13-87)	1 (0-2)	47 (5-100)
	Spotted gar	**57 (40-78)**	6 (1-12)	36 (7-66)
	Longnose gar	41 (17-80)	2 (<1-7)	55 (6-100)
Flow pulse following low water	Smallmouth buffalo	51 (7-91)	6 (1-23)	39 (4-91)
	Gizzard shad	23 (3-48)	2 (<1-8)	**73 (38-100)**
	Blacktail shiner	61 (20-81)	8 (2-18)	31 (2-77)
	Blackstripe topminnow	23 (3-48)	3 (<1-11)	**72 (37-100)**
	Mimic shiner	57 (21-78)	2 (<1-9)	41 (14-77)
	Cinnamon river shrimp	52 (17-76)	3 (<1-11)	44 (20-81)
	Bluegill	**65 (41-82)**	2 (<1-7)	32 (14-58)
	Longear sunfish	**72 (29-89)**	4 (<1-11)	17 (2-67)
	Freshwater drum	52 (8-79)	14 (3-29)	32 (2-89)
	Spotted bass	19 (2-44)	25 (12-37)	**52 (32-73)**
	Spotted gar	39 (7-58)	3 (<1-9)	**56 (33-99)**
Falling water	Smallmouth buffalo	70 (16-89)	2 (<1-8)	25 (1-93)
	Gizzard shad	44 (22-59)	1 (<1-5)	**53 (34-89)**
	Blacktail shiner	**65 (38-79**)	2 (<1-6)	31 (12-69)
	Blackstripe topminnow	36 (7-62)	14 (4-22)	49 (8-94)
	Bullhead minnow	**56 (29-72)**	2 (<1-6)	41 (18-76)
	Bluegill	**82 (30-94)**	2 (<1-7)	14 (1-75)
	Longear sunfish	**76 (65-85)**	17 (10-24)	6 (<1-22)
	Freshwater drum	34 (6-73)	4 (<1-11)	62 (14-96)
	Spotted bass	58 (10-85)	3 (<1-11)	37 (3-99)
	Spotted gar	**72 (46-89)**	3 (<1-10)	23 (2-61)
	Longnose gar	66 (14-86)	2 (<1-8)	29 (4-98)

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Production sources supporting Cincaruco River consumers

Falling-water. Both algae and C_3 macrophytes made large contributions to consumers in the Cinaruco River (Table 2.10). Algae accounted for a large portion of *Hemiodus unimaculatus*, *Myleus schombergki*, and *Semaprochilodus kneri* biomass (5% confidence percentiles > 35, 95% confidence percentiles > 75). Six of the 11 species examined assimilated a large fraction of C_3 macrophytes (5% confidence percentiles > 45, 95% confidence percentiles > 75). Two species, *Metynnis hypsauchen* and *Mesonauta festivus*, could have assimilated C_3 macrophytes, C_4 grasses, and algae. For these two species, feasible ranges of algae and C_3 macrophyte contributions were broad (5% confidence percentiles > 25, 95% confidence percentiles > 70) and at least some fraction of C_4 grass was assimilated, with 95% confidence percentiles > 25.

Production sources supporting Guadalupe River consumers

Low-water. Algae were the most important production source supporting biomass of three of the seven species examined, gizzard shad, red shiner, and striped mullet (Table 2.11), with 5% confidence percentiles > 25 and 95% confidence percentiles > 75. Two of the seven species, longear sunfish and spotted gar, primarily assimilated C_3 macrophytes, with 5% confidence percentiles > 30 and 95% confidence percentiles > 65. One species, bullhead minnow, assimilated a fraction of both algae and C_3 macrophytes; 95% confidence percentiles were > 50 for both production sources.

Flow pulse following moderate-water. Contributions of algae decreased compared to the low-water period, and C_3 macrophytes supported a large fraction of secondary consumer biomass for five of the seven species examined. For these five species, 5% confidence percentiles were ≥ 30 and 95% confidence percentiles > 55. Algae accounted for a large fraction of one of the seven species, gizzard shad, with 5% confidence percentiles equaling 63 and 95% confidence percentiles equaling 100. Both algae and C_3 macrophytes likely made a large contribution to spotted gar, with 95% confidence percentiles > 50 for both production sources.

Table 2.10. Median and 5 – 95% confidence percentiles (in parentheses) of basal production source contributions to consumers in the Cinaruco River. Consumers with 5% confidence percentiles ≥ 25 are in bold.

Hydrologic period	**Consumer**	**C_3 macrophytes**	**C_4 grasses**	**Algae**
Falling water	*Metynnis hypsauchen*	3 (<1-76)	34 (15-39)	62 (5-73)
	Myleus schombergki	23 (7-36)	2 (<1-6)	**75 (61-94)**
	Semaprochilodus kneri	40 (24-56)	2 (<1-9)	**56 (38-78)**
	Aphyocharax alburnus	**91 (81-97)**	2 (<1-7)	6 (<1-21)
	Hemigrammus analis	**72 (56-90)**	2 (<1-6)	25 (4-50)
	Moenkhausia lepidura	**64 (48-79)**	7 (1-15)	27 (3-58)
	Hemiodus unimaculatus	5 (<1-13)	2 (<1-7)	**91 (72-100)**
	Geophagus dichrozoster	**82 (65-94)**	3 (<1-8)	13 (1-41)
	Mesonauta festivus	50 (22-71)	17 (5-29)	31 (2-78)
	Cichla temensis	**70 (56-85)**	4 (<1-10)	24 (4-52)
	Boulengerella lucius	**83 (70-93)**	4 (<1-12)	11 (1-32)

Table 2.11. Median and 5 – 95% confidence percentiles (in parentheses) of basal production source contributions to consumers in the Guadalupe River. Consumers with 5% confidence percentiles ≥ 25 are in bold.

Hydrologic period	**Consumer**	**C_3 macrophytes**	**C_4 grasses**	**Algae**
Low water	Gizzard shad	1 (0-2)	<1 (0-2)	**99 (73-100)**
	Red shiner	30 (24-38)	1 (<1-4)	**68 (54-84)**
	Bullhead minnow	**41 (33-52)**	1 (<1-4)	**56 (38-76)**
	Longear sunfish	**64 (52-70)**	2 (<1-7)	37 (16-61)
	Striped mullet	17 (5-28)	2 (<1-7)	**82 (28-100)**
	Spotted bass	40 (21-58)	7 (1-17)	50 (6-100)
	Spotted gar	**51 (34-68)**	12 (2-23)	34 (2-81)
Flow pulse following moderate flow	Gizzard shad	10 (1-29)	3 (<1-12)	**83 (63-100)**
	Red shiner	**61 (51-71)**	9 (2-16)	29 (3-63)
	Bullhead minnow	**61 (52-70)**	19 (11-26)	18 (1-45)
	Longear sunfish	**60 (34-71)**	30 (13-39)	7 (<1-58)
	Striped mullet	**45 (30-58)**	4 (<1-10)	50 (5-99)
	Spotted bass	**55 (34-67)**	29 (12-39)	14 (1-59)
	Spotted gar	46 (24-61)	22 (7-33)	30 (2-82)

DISCUSSION

I originally predicted that, due to resuspension of sediment during periods of high or rising discharge that causes light limitation and abrasion of attached algae and the settling of sediments and increased light penetrance during low-flow periods (Kirk 1985, Meade 1988), the relative importance of algae versus terrestrial-based production sources supporting the food web would vary seasonally in the sediment-laden, nutrient-rich Brazos River. However, because of low inorganic nutrient concentrations, I predicted that algal productivity and biomass would be low and terrestrial-based production sources would support consumer biomass throughout the annual hydrologic cycle in the sediment-laden Tambopata River. In watersheds where pedological conditions result in soils that are less susceptible to erosion, studies have documented that river littoral zones are consistently autotrophic because of high transparency at all flow levels (Lewis 1988, Cotner et al. 2006, Montoya et al. 2006). Soils are less erodible in the Neches, Cinaruco, and Guadalupe watersheds compared to the Brazos and Tambopata watersheds, thus I expected consumers to be supported by algal-based production sources throughout the annual hydrologic cycle. I observed temporal changes in physicochemical parameters and algal productivity and biomass in all five rivers. Additionally, I observed a temporal shift in production sources assimilated by consumers in all rivers that were sampled during different hydrologic periods.

Temporal changes in nutrients, turbidity, and algal production and biomass

In some of the temperate rivers, nutrients were higher during relatively short duration high-flow pulses (i.e., SRP and DIN in the Brazos River and DIN in the Neches River). In contrast, in the tropical rivers, dissolved inorganic nutrient concentrations tended to be higher during the annual low-water period (i.e., SRP in the Tambopata River and DIN in the Cinaruco River). Many studies have found that in temperate rivers, nutrient concentrations are highest following periods of high flows, particularly if flooding is preceded by a prolonged low-flow period (Fisher and Minckley 1978, Mitsch et al. 2001, Doyle et al. 2005). However, in tropical rivers, nutrient concentrations are frequently highest during the annual low-water period (Forsberg et al. 1988, Lewis 1988, Castillo 2000, Cotner et al. 2006). Riverine solutes arise from atmospheric, weathering, or anthropogenic sources. Increased nutrient concentrations that follow flooding in temperate rivers may be a result of greater weathering in temperate compared to tropical watersheds that frequently drain highly leached areas (Allan 1995). Additionally, intensive agriculture and cattle grazing is practiced in all of our temperate study river basins. Extended periods without precipitation allow nutrients from fertilizer and livestock to accumulate along river banks and other areas of watersheds; subsequent rainfall results in high concentrations in runoff. In the Tambopata Basin, farmers typically practice shifting cultivation and small-scale cattle production solely for local subsistence markets (Foster et al. 1994). In the Cinaruco Basin, soils are poor in nutrients and high in quartzite, a mineral with high silica content (Sarmiento and Pinillos 2001), thus very little agriculture is practiced. Presumably, because anthropogenic nutrient sources are minor in our tropical study river basins, dilution reduces dissolved nutrient concentrations during extended high-water periods. Despite the different patterns in seasonal nutrient concentrations, our instream production and chlorophyll *a* measurements indicated that, in all the rivers, algal production tended to be higher during the low-water period compared to the high-water period, likely because of reduced flow that scours algal cells, higher nutrient concentrations in the tropical rivers, and lower turbidity in the Brazos, Tambopata, and Guadalupe rivers.

Whereas NPP in littoral zones of the Neches, Cinaruco, and Guadalupe rivers was almost always positive, indicating that littoral zones were autotrophic, NPP of littoral zones in the sediment-laden rivers was negative (heterotrophic) during periods of high discharge. In the Brazos River, in addition to magnitude of discharge, frequency and duration of hydrology also explained NPP. Littoral zones were heterotrophic during turbid, high-flow events that followed prolonged periods of low flow. In temperate rivers and streams, it is well established that the concentration of particles in the water-column is dependent not only on magnitude of discharge, but also on the length of time since a similar water level has occurred (Cummins et al. 1983, Meyer 1990, Doyle et al. 2005). In the Tambopata River, dissolved nutrient concentrations were much lower and flooding patterns more seasonal compared to the Brazos River, and consequently littoral zones were consistently heterotrophic above approximately 10% bankfull discharge.

Potential assimilation of methanotrophic bacteria

Although most consumers were intermediate in $\delta^{13}C$ and δD relative to the range of source signatures, two fish specimens, *Prochilodus nigricans* from the Tambopata River and *Myleus schombergki* from the Cinaruco River, were more depleted in ^{13}C than any of the basal sources collected. These fishes could have assimilated methanotrophic bacteria, which can be extremely depleted in ^{13}C; Kankaala et al. (2006) estimated the $\delta^{13}C$ of methane-oxidizing bacteria at -60‰. Methane-oxidizing bacteria require anoxic conditions, and such conditions frequently occur in benthic habitats that are high in organic matter. *Prochilodus nigricans* is morphologically specialized for feeding on fine benthic detritus (Bowen 1983). *Myleus scholbergki* is an herbivore, but in addition to vegetation, species from the same genera have been documented to feed on aquatic invertebrates (de Mérona and Vigouroux 2006), some of which can assimilate methane-oxidizing bacteria (Bunn and Boon 1993, Kohzu et al. 2004, Deines et al. 2009).

Production sources supporting consumer biomass

MixSir model estimates indicated that C_4 grasses were the least important contributor to consumer biomass; 5 and 95% confidence percentiles were low for almost all species collected. Algae and C_3 macrophytes both made major contributions to consumer biomass, with contributions varying temporally in the Brazos, Tambopata, Guadalupe, and Neches rivers. Algae made greater contributions to species biomass following extended low-flow periods, and C_3 macrophytes made a greater contribution following flow pulses.

In the Brazos River, algae and C_3 macrophytes accounted for the largest portion of consumer biomass during an extended low-water period, when littoral zones were consistently autotrophic, and during a flow pulse following low-water period. Ghost shiner, red shiner, and shoal chub assimilated a large fraction of algae during the low-water and flow pulse following low-water periods, and channel catfish and Ohio River shrimp were supported by C_3 macrophytes. Following a period of high flows, ghost shiner, red shiner, and shoal chub assimilated a large fraction of material derived from C_3 macrophytes. Furthermore, 5% confidence percentiles of C_3 macrophytes increased for all species but river carpsucker and longnose gar following the high-water period. The apex predator longnose gar derived its organic carbon and nutrients from algae and C_3 macrophytes regardless of hydrologic period. Analysis of longnose gar gut contents has revealed a broad diet, supported by catfish and minnows (Robertson et al. 2008), thus during low-flow periods, longnose gar assimilate material from prey supported by aquatic and terrestrial sources. Mobile consumers at the highest trophic levels such as longnose gar have been regarded as couplers of spatially isolated resources (McCann and Rooney 2009).

The stable isotope half-life of muscle tissue of adult freshwater fishes has been estimated at 18 to 173 days (Hesslein et al. 1993, MacAvoy et al. 2001, Harvey et al. 2002, McIntyre and Flecker 2006). Thus, C_3 macrophytes likely accounted for a greater fraction of consumer biomass following the high-water period but not the flow pulse following low-water hydrologic period because, since the latter collection period was less than two weeks after the beginning of the flow pulse, consumer tissue turnover did not yet reflect greater assimilation of C_3 macrophytes. Furthermore, there is an inverse relationship between body size and stable isotope turnover rate in fishes. Because small fishes have faster metabolic rates and mass-specific growth (Gillooly et al. 2001), stable isotopes in the diet are assimilated more rapidly by smaller fish (Vander Zanden et al. 1998, Harvey et al. 2002, McIntyre and Flecker 2006). C_3 macrophytes likely did not account for a larger fraction of longnose gar biomass following the high-flow period because there was insufficient time for the material assimilated by herbivores to be assimilated by these apex predators.

During the low-water period in the Tambopata River, detritivorous and omnivorous species mostly assimilated algae, however C_3 macrophytes were a major contributor to piscivorous fishes. Piscivores in the Tambopata River were supported by terrestrial carbon because our sampling during the low-water period followed a prolonged period of high flows. Additionally, littoral zones are much less productive in the Tambopata River compared to the Brazos River (Figure 2.6), and the Tambopata is autotrophic for only a relatively short period of time each year. In the Tambopata, allochthonous material also accounted for the largest fraction of consumer biomass during the high-water period, when littoral zones were consistently heterotrophic.

Figure 2.6. Two sediment-laden rivers are compared in photos taken during extended low-flow periods. The Brazos River shows an obvious green coloration from phytoplankton biomass stimulated by high nutrients and high transparency.

Several other stable isotope studies have indicated that consumers derive a large portion of their carbon and nitrogen from C_3 macrophytes in rivers carrying high sediment loads, particularly during periods of high flows. For example, C_3 macrophytes were the most important basal production source supporting consumer biomass in several high-turbidity rivers, including the Iguatemi, Ivinheima, and Paraná rivers in Brazil (Hoeinghaus et al. 2007), and the Brazos (Zeug et al. 2008a), Mattaponi (Hoffman et al. 2007, Hoffman et al. 2008), and Paria (Angradi 1994) rivers in North America. Many studies have shown that suspended, inorganic particles significantly decrease algal biomass in river channels (Kirk 1985, Søballe and Kimmel 1987, Henley et al. 2000). For example, during a synoptic cruise of the Amazon River mainsteam from Iquitos, Peru, to Belém, Brazil, during the high-water period, Wissmar et al. (1981) found very little phytoplankton production because of high concentrations of suspended material.

In the Neches River, production sources also revealed temporal shifts in their contributions to consumer biomass following a period of high flows. Two consumer species assimilated a large fraction of material from C_3 macrophytes (i.e., 5% confidence percentiles > 25) following the low water and flow pulse following low water periods, and five consumer species assimilated a large fraction of terrestrial material derived from C_3 macrophytes following the falling water period. In the Cinaruco River during the falling-water period, six out of 11 species assimilated a large fraction of material from C_3 macrophytes. In contrast to the whitewater rivers, in which no species likely assimilated a large fraction of algae during the high-water period, algae was the primary source of energy and nutrients for several species during the falling water periods in the

Neches and Cinaruco Rivers. In the Neches River, gizzard shad predominantly assimilated algae regardless of hydrologic period, and in the Cinaruco River during the falling water period, *Hemiodus unimaculatus*, *Myleus schombergki*, and *Semaprochilodus kneri* assimilated a large fraction of algae. Compared to the other study rivers, the Neches and Cinaruco have higher concentrations of dissolved organic matter (DOM) derived from degradation of macrophyte tissues (Roelke et al. 2006). Watersheds that are rich in DOM frequently have high biomass of heterotrophic microbes and fungi, which, during the process of decomposition, can increase the nutritional value of detritus derived from terrestrial plants and thus have been hypothesized to increase contributions of terrestrial-based production sources to aquatic food webs (Goulding et al. 1988, Meyer 1990, Waichman 1996). Accordingly, terrestrial material has been documented to support metazoan consumer biomass in DOM-rich streams (Wallace et al. 1987, Hall and Meyer 1998, Wallace et al. 1999, Hall et al. 2000) and floodplain rivers (Jepsen and Winemiller 2007). However, because suspended sediment concentrations are low in these rivers, and turbidity does not increase following periods of high flow, littoral zones are autotrophic throughout the annual hydrologic cycle, and algae also have been documented to support many species at higher trophic levels (Jepsen and Winemiller 2007, Roach et al. 2009).

The relative importance of autochthonous versus allochthonous production sources also shifted seasonally for many consumers in the Guadalupe River. During the low-water period, algae likely were the dominant source supporting bullhead minnow and red shiner. C_3 macrophytes made major contributions to these species following the period of higher flows. In the Guadalupe River, similar to the sediment-laden rivers, there was a significant correlation between turbidity and discharge, presumably indicating increased inputs of allochthonous organic material to the standing stock of instream organic matter following a period of high flows. Other studies have found that terrestrial material can support river food webs following flow pulse events, even when the river is net autotrophic. Following a high-flow event in the Taieri River, a river with low suspended sediment concentrations in New Zealand, consumers assimilated terrestrial-based production sources because the relative amount of terrestrial- versus algal-material comprising seston (i.e., particulate organic matter) increased (Huryn et al. 2001). Three fish species in the Guadalupe River revealed little change in source materials assimilated during variable flow conditions. Algae consistently made major contributions to gizzard shad, and C_3 macrophytes were a consistent contributor to bullhead minnow and longear sunfish regardless of hydrologic conditions.

In the Riverine Productivity Model, Thorp and Delong (2002) predicted that terrestrial material makes little contribution to secondary production in large rivers because of its poor nutritional value. Our MixSIR model results revealed that algal carbon, nitrogen, and hydrogen were assimilated by consumers in all of the study rivers, particularly during low-flow periods. Algae were not available to consumers in rivers with high loads of suspended sediment during periods of high flow. C_3 macrophytes made major contributions to consumer biomass in the Brazos and Tambopata rivers when flow was high and littoral zones were heterotrophic, providing support for the hypothesis that resource subsidies should occur in ecosystems where net primary productivity is low (Polis and Hurd 1996, Strapp and Polis 2003, Winemiller and Jepsen 2004). However, C_3 macrophytes also contributed to the biomass of consumer species in the Neches and Cinaruco rivers following periods of higher flows, probably because biomass and productivity of algae was lower in the high-water period compared to the low-water period and high concentrations of DOM in these rivers contributed to an abundance of heterotrophic microbes and fungi that increased nutritional quality of macrophyte detritus. Finally, in the Guadalupe River, C_3 macrophytes were a source of organic matter for most consumer species during the high-water period despite autotrophic littoral zones, indicating that, even in rivers with low DOM concentrations, secondary consumers can assimilate production sources derived from C_3 plants following flow pulses that increase its relative abundance in the particulate organic matter pool. Recent studies have advocated for the consideration of basal production source quality and quantity when making predictions about the importance of food web subsidies (Marcarelli et al. 2011). Our study highlights that during flow pulses in floodplain rivers, a decrease in algal biomass and productivity, combined with increased inputs of terrestrial organic matter, can result in increased terrestrial support of metazoan consumers in the aquatic food web.

Predicting anthropogenic impacts on energy flow in large rivers

Humans are having a dramatic influence on the physicochemical conditions of rivers through land transformations such as deforestation, livestock grazing, cropping systems and urbanization, and the construction of dams and other water diversion infrastructure (e.g., Petts and Gurnell 2005, Poff et al. 2007). These alterations are increasing river nutrient loads, decreasing suspended sediment loads, and altering flow regimes (e.g., Postel et al. 1996, Bouwman et al. 2005). Anthropogenic impacts to rivers are likely to affect the relative importance of algal versus macrophyte detritus pathways, with concomitant changes in secondary biomass and community structure. Algae, because of their higher nutritional value, have been hypothesized to support greater secondary production than terrestrial plants or detritus derived from them (Legendre and Rassooulzadegan 1995, Cotner and Biddanda 2002). Because algal-based pathways may be associated with consumers having rapid growth and reproduction, and detritus-based pathways associated with lower efficiency, weaker interaction strength, and the introduction of time lags that stabilize complex networks, a decrease in the importance of detritus as a basal production source is expected to reduce species diversity (DeAngelis 1992, Rooney and McCann 2012).

In rivers that normally carry high loads of suspended sediments, a reduction in flow pulses and suspended sediment concentrations caused by impoundments or water diversions would cause a shift toward consumer reliance on algal-based trophic pathways. Increased importance of algae as a production source sometimes has been associated with an increase in the abundance of non-native, generalist species at the expense of native species that were associated with the detrital food web. For example, in a survey of food webs from ten sites differing in landscape-scale hydrologic characteristics in the sediment-laden Paraná River, Brazil, Hoeinghaus et al. (2007) found that C_3 plants were the principal carbon source supporting metazoan consumers in turbid, low-gradient rivers, and algae were the principal source supporting secondary consumers in relatively clear impoundments and river stretches downstream from impoundments. In one of these impoundment food webs, the Itaipu Reservoir, the pre-impoundment fishery was dominated by native, piscivorous species of high commercial value, whereas during post-impoundment, native species declined in abundance and non-native, omnivorous species of lower commercial value thrived (Hoeinghaus et al. 2009). Furthermore, in addition to altering basal production sources supporting consumer biomass, the impoundment impeded fish migrations and reduced the duration of the flood pulse, thus total fishery yield declined two-fold (Hoeinghaus et al. 2009). The decrease in turbidity associated with entrapment of sediment by impoundments also has been documented to alter fish community structure in the lower Sabine River, Texas (Bart 2008) and the Sacramento-San Jaquin Delta, California (Feyrer and Healey 2003).

Human-induced nutrient loading should alter energy flow through food webs irrespective of watershed characteristics. In sediment-laden, tropical rivers that have been affected by dams or water diversions, the additional human impact of nutrient loading is likely to amplify shifts from terrestrial to algal support of food webs because low ambient nutrient concentrations ordinarily limit instream primary production. In undammed, sediment-laden rivers, algal production should respond less to anthropogenic nutrient loading due to light limitation, but energy flow patterns are still likely to be altered. In a study examining the influence of landscape-scale differences in SRP concentrations on forested, headwater streams at La Selva Biological Station, Costa Rica, Rosemond et al. (2002) found that streams with greater SRP concentrations were associated with increased organic matter decay rate and biomass of macroinvertebrate detritivores. Nutrient loading also may be associated with increased reliance on algal-based trophic pathways in rivers with coarse, inorganic sediments, low turbidity, and high DOM concentrations. For example, nutrient enrichment of Peter Lake in Indiana resulted in increased algal support of secondary consumers, suggesting that terrestrial support may be more important in oligotrophic ecosystems (Cole et al. 2006). At high levels, increased nutrient inputs to high-transparency water-bodies can cause eutrophication, toxic algal blooms, and anoxic conditions that lead to fish kills (Carpenter et al. 1998, Hilton et al. 2006).

Whereas bottom-up effects (i.e. control by nutrients) clearly can influence community structure, other factors also regulate river communities, including top-down effects (i.e. control by consumers, Power 1992, Winemiller et al. 2006, Cross et al. 2008) and physicochemical factors (e.g., DO, Winemiller 2005). Furthermore, because rivers are pulsing ecosystems with high habitat heterogeneity, many consumers have responded adaptively by migrating in response to spatiotemporal variation in habitat and resources. Thus, anthropogenic impacts, such as dams and surface water withdrawals that cause reduced lateral connectivity between the channel and floodplain lakes, can affect local consumer biomass by limiting dispersal (e.g., Zeug and Winemiller 2008b). Many human impacts to rivers likely shift food webs toward domination of pathways originating from algae, which can result in increased productivity of generalist species but an overall decrease in species diversity. The recognition that there is spatiotemporal variation in contributions of basal production sources supporting river consumers, related to production source quality and quantity, will allow for better predictions of how environmental change affects biomass and diversity at higher trophic levels.

CHAPTER IV

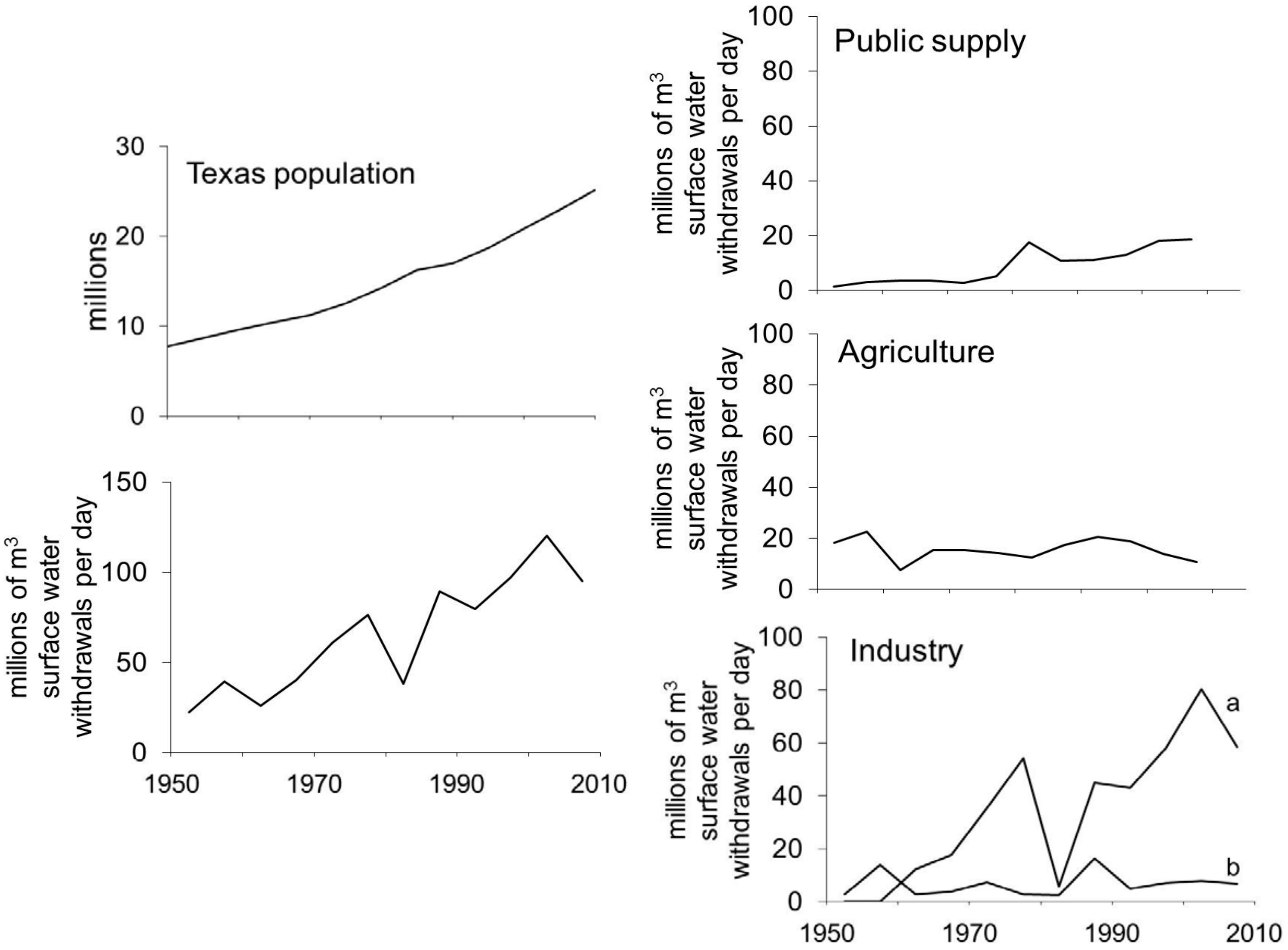
TEXAS WATER WARS: HOW POLITICS AND SCIENTIFIC UNCERTAINTY INFLUENCE ENVIRONMENTAL FLOW DECISION-MAKING IN THE LONE STAR STATE

INTRODUCTION

In Texas, rising human population size, increasing demand by industry, and depletion and mandatory reductions in pumping of groundwater have contributed to an overall increase in freshwater withdrawals from streams and rivers (Figure 3.1; TWDB 2012). Water demands of growing urban populations have overtaken the collective demand for water by agriculture, historically the biggest user in Texas (Figure 3.1, Rosegrant and Cai 2002). Thermoelectric power generation plants currently withdraw approximately 40 percent of the state’s water supply, require impoundments that can dramatically affect the flow regimes of rivers, and are predicted to increase demand for freshwater in coming years (TWDB 2012). The plants return a portion of the withdrawn water to the reservoir, but there is discrepancy as to how much. The electric industry estimates that it consumes approximately three percent of Texas’ water supply, but independent studies indicate that plants may consume ten times that much (Copelin *public communications*, Ross 2012). Furthermore, the number of hydraulic fracturing operations, which use approximately 18,900 m^3 of water to drill and fracture a typical deep-shale gas well (Considine et al. 2009, NYSDEC 2009, ALL Consulting 2010), also is expected to increase significantly in Texas (TWDB 2012).

A recent assessment of water availability that took into account human population growth and migration, economic development, and global climate change projections which, in Texas, predict a hotter and drier climate in the coming years, found that parts of Texas could experience water stress in the future (Vörösmarty et al. 2000). Because of this concern, even though few reservoirs are being constructed and many are being decommissioned in the rest of the United States (Doyle et al. 2003a and b), reservoirs continue to be built in Texas. The 2012 Texas Water Plan recommended the construction of 26 new reservoirs in addition to the state’s 188 major reservoirs (i.e., those with a storage capacity of 0.62 hm^3) already used for water supplies (TWDB 2012).

Figure 3.1. On left, changes in the human population size of Texas and the total millions of m^3 of fresh surface water withdrawn per day from Texas streams and reservoirs from 1950 to 2010. Data on human population size is from the U.S. Bureau of the Census and data on water withdrawals is from the U.S. Geological Survey reports on estimated use of water in the United States. On right, trends in millions of m^3 of fresh surface water withdrawn per day in Texas for the purpose of public supply, agriculture, and industry (a indicates withdrawals for steam-electric power generation and b indicates withdrawals for other types of industry including mining and manufacturing. Fresh water withdrawn for the purpose of hydrofracking is not included). Public supply includes water withdrawals for domestic use, public services such as pools, parks, and wastewater treatment, commercial use, and industry that obtains its water from public supply. Agriculture indicates surface water withdrawn for crop irrigation, livestock, and fish hatcheries. Industry indicates surface water withdrawn for mining and manufacturing facilities.


Texas population
millions
30
20
10
0
millions of m³ surface water withdrawals per day
150
100
50
0
1950
1970
1990
2010
Public supply
millions of m³ surface water withdrawals per day
100
80
60
40
20
0
Agriculture
millions of m³ surface water withdrawals per day
100
80
60
40
20
0
Industry
millions of m³ surface water withdrawals per day
100
80
60
40
20
0
a
b
1950
1970
1990
2010

Large reservoirs have already altered the flow regime of many of Texas' rivers (Magilligan and Nislow 2005, Wellmeyer et al. 2005, Perkin and Bonner 2011). The importance of the natural variability of flow, in particular the magnitude, frequency, duration, timing, and rate of change in flow, to the ecological integrity of river ecosystems is well known (Richter et al. 1996, Poff et al. 1997, Anderson et al. 2006, Arthington et al. 2006, Mathews and Richter 2007). Because many organisms have life history, behavioral, and morphological adaptations that are associated with long-term flow patterns, when the natural flow regime is modified, native species can experience a reduction in fitness, facilitating invasion by non-native organisms (Lytle and Poff 2004). Throughout the USA and Canada, changes to the natural flow regime have been documented to cause declines in native species of fish, riparian and floodplain vegetation, and birds that are dependent on floodplain forests (Marchetti and Moyle 2001, Pettit et al. 2001, Rood et al. 2003, Rood et al. 2005, Hoover 2009, Poff and Zimmerman 2010). Changes in hydrology associated with dams also have altered the grain size of the river bed and disrupted the dynamic equilibrium between depositional and erosional processes that maintain river geomorphology, resulting in channel incision, accentuated bank erosion, removal of bank vegetation, and reduction in the lateral channel migration that forms oxbow lakes (Stevens et al. 1995, Hupp et al. 2009, Osterkamp and Hupp 2010). In Texas, disruption of the natural flow regime has been associated with extinction and extirpation of freshwater fishes in several rivers (Bolin 1993, Anderson et al. 1995, Hubbs et al. 2008) and a reduction in channel migration rates of the Brazos River (Gillespie and Giardino 1997).

Withdrawals and impoundments of Texas rivers also have decreased the magnitude and altered the timing of freshwater inflow to estuaries in the Gulf of Mexico (Copeland 1966, Rozengurt and Haydock 1991, Sklar and Browder 1998). Freshwater inflow affects environmental conditions in estuaries by influencing factors such as circulation patterns, haloclines, and dissolved oxygen. Because many native species have adaptations that are associated with long-term inflow patterns, and because alterations to freshwater inflow can result in estuarine conditions that are no longer physiologically tolerable to organisms, its alteration has been associated with a decrease in the abundance of commercially and recreationally important fish, shellfish, and waterbird species in estuaries throughout the world (Zedler and Onuf 1984, Whitfield and Bruton 1989, Hallim 1991, Drinkwater and Frank 1994, Ravenscroft and Beardall 2003). In addition, reductions in freshwater inflow have been linked to reduced delivery of nutrients and sediments to coastal bays, estuarine eutrophication (Alber 2002), the disappearance of native grasses and trees that have low salinity tolerance (Shaffer et al. 2009), and the submergence or disappearance of deltas (Baumann et al. 1984, Kensel 1989). Alterations of the freshwater inflow regime to Texas estuaries have contributed to the increased prevalence of hypersaline conditions in estuaries in the south-east part of the state (Browder and Moore 1981), a decrease in the abundance and diversity of benthic fauna in the Rincon Bayou, part of the Nueces River Estuary (Montagna et al. 2002), declines in river sediment yield of the Colorado River (Blum and Price 1994), and erosion of estuaries and wetlands (White and Calnan 1990). In the Gulf of Mexico, there is a positive association between the fishery yield of estuaries and river discharge

(Deegan et al. 1986); accordingly, droughts have caused drastic reductions in annual shellfish harvest (Copeland 1966).

Inspired by devastating flooding in 1913 and 1914, Texas passed legislation in 1917 to create the river authorities, semiautonomous agencies responsible for managing and developing the surface water of distinct segments of watersheds. Because the 13 river authorities have no budgetary support from the state, they are required to sell products and services in order to survive, and since their creation they have operated upon a philosophy of acquisition, use, and reallocation of goods to higher paying customers (Hendrickson 1985, Harper and Griffin 1988). The majority of river authority funding is from the wholesale selling of surface water. River authorities own the rights to a significant amount of the state’s surface water, having already controlled 25 percent of surface water deliveries by the 1980s (Harper and Griffin 1988). Some river authorities also receive monetary support from sales of electricity from thermoelectric power plants and hydropower from dams. Various authors and environmental non-government organizations, such as the Sierra Club, have been critical of the consumptive philosophy of river authorities, arguing that river authorities have become prominent organizations with excessive control over Texas water resources, are driven to construct reservoirs with capacity in excess of projected needs, lack public accountability, and have a tendency to neglect nonconsumptive water uses that benefit the public because they do not result in river authority funding (Hendrickson 1985, Harper and Griffin 1988).

Texas historically based its water law on riparian doctrine, meaning those who owned land bordering a water body had the right to use the water. In an important first step to managing its water resources, in 1967 Texas converted to a prior appropriation system through the Water Rights Adjudication Act, which required all water users to file a claim with the Texas Water Development Board (i.e., state water supply planning agency). This law provided all users with a transferable permit and established a beneficial use provision which included a priority list. By 1968 the state water supply planning agency had already recognized the adverse consequences of impoundments and water diversions on the state's rivers and estuaries, but its annual water management plans continually recommended additional study on how to manage the negative impacts of impoundments while advocating their construction (Kaiser and Binion 1998).

Starting in the 1970s, Texas began passing legislation addressing freshwater inflow into major bays. In 1985, instream protection of marine life, bays and estuaries, water quality, and fish and wildlife habitat were added as beneficial uses of water rights; reservoirs within 200 river miles of the coast were required to appropriate five percent of their annual firm yield to be dedicated to the Texas Parks and Wildlife Department (TPWD), the state's natural resource agency, to make releases for instream flows; and the state environmental regulatory agency, the Texas Commission of Environmental Quality (TCEQ) began to include instream flow provisions on some new water rights using the Lyon's Method, which determines the minimum level of flow needed to remain instream based on a percentage of monthly median flows (Kaiser and Binion 1998). However, by this time most of Texas' rivers were already overallocated, particularly in the western part of the state where rainfall is much lower (U.S. Water Resources Council 1978).

In 1997, Senate Bill (SB) 1 was passed, putting freshwater-related decision making into the hands of regional water planning groups rather than the Texas Water Development Board (TWDB), the state water supply planning agency. As part of this process, regional water planning groups could designate stream reaches as “ecologically unique stream segments,” prohibiting the state from constructing a reservoir on that reach. However, to date, only five bayous or lakes, eight stream reaches, and one river reach on the Rio Grande have been designated as ecologically unique stream segments. Also in 1997, the state water supply planning agency established the Texas Water Trust to hold water rights that have been donated for the purpose of environmental flows (e-flows), but because of lack of state funding (Kaiser and Binion 1998), lack of a financial incentive to put water rights in the trust, and because there is no guarantee that water rights that were donated would remain instream and not be withdrawn by downstream water users, there are currently only two water rights in the trust: one on the Rio Grande and one on the San Marcos River, a tributary of the Guadalupe River.

In 2001, the Texas Legislature passed SB2, establishing the Texas Instream Flow Program directing the TCEQ, TWDB, and TPWD to conduct studies to determine the flow conditions necessary to support a sound environment in the state’s rivers and streams. Following guidance by the National Research Council, a non-governmental agency composed of independent scientists whose mission is to improve the science involved in government decision making and public policy, the Texas Instream Flow

Program deemed four components of a flow regime necessary to support a sound environment: subsistence flows, base flows, flow pulses, and overbank flows (NRC 2005). The objectives in identifying subsistence flows are to ensure maintenance of water quality and aquatic habitat for focal species and/or guilds during infrequent drought periods. Base flows represent normal flow conditions, and provide a range of conditions suitable for supporting the native biological community. Flow pulses represent short-duration, in-channel events following rainfall; their functions include providing spawning cues for aquatic species as well as riparian functions. Overbank flows are infrequent flow events that provide lateral connectivity between the river channel and floodplain, maintain native riparian vegetation, and aid in maintaining a stable channel geomorphology. A state Science Advisory Committee that was assembled to assist SB2 research proposed that a sound environment should sustain the full complement of native species in perpetuity, sustain key habitat and natural flow regime features required by these species to complete their life cycles, and sustain key ecosystem processes and services, such as elemental cycling and productivity of important plant and animal populations (SAC 2006). The National Research Council expert science panel criticized the lack of stakeholder involvement in the SB2 process, concluding that because of the potential for conflict among competing uses of water, early and frequent public participation would increase support for the program and be critical to the Texas Instream Flow Program’s success (NRC 2005).

In response to concern about the lack of inflow from the Guadalupe River into San Antonio Bay, in 2000 the non-profit San Marcos River Foundation and over 15 other organizations filed a water rights application to pledge the unallocated Guadalupe Rivers surface water rights to the Texas Water Trust so that it would remain instream. The application was opposed by water suppliers, and in 2003 TCEQ denied the application and enacted a moratorium on new water rights permits for instream flow protection. The San Marcos River Foundation filed a lawsuit against TCEQ, and between 2003 and 2005 an interim study group began to negotiate a proposal so the issue could be addressed by the legislature rather than the courts. Compromises among different interest groups resulted in more representation on the stakeholder committees for agricultural and industry groups than had originally been envisioned. In return, any water right permits that were issued after September 1, 2007 were subject to changes in environmental conditions up to 12.5% as a result of e-flow provisions. The proposed legislation did not pass in 2005, but in a similar form, SB3 was passed in 2007 mandating use of a stakeholder-based process to implement e-flow provisions for new water rights in Texas rivers that were not already overallocated.

THE TEXAS ENVIRONMENTAL FLOW PROGRAM

SB3 established a process whereby e-flows necessary to support a sound environment for the state’s major river basins and bays would be determined using the best available science. The legislature determined that “in the river basins where water is available for appropriation, an environmental set aside below which water should not be available for appropriation should be determined” and “in those basins in which the unappropriated water…is not sufficient to satisfy the e-flow standards, a variety of market approaches, both public and private, for filling the gap must be explored and pursued" (Texas Water Code §11.0235). Additionally, the legislature warranted that instream flow recommendations be developed using a consensus-based, regional approach involving stakeholders, and that the final recommendations be adaptively managed, or evaluated on a regular basis to reflect improvements in science and future changes in human needs for water.

For this purpose, the legislature created the Environmental Flows Advisory Group consisting of three members appointed by the governor (one from the TCEQ, one from TWDB, and one from TPWD; Figure 3.2), three members of the senate appointed by the lieutenant governor, and three members of the house of representatives appointed by the speaker of the house of representatives. The e-flows advisory group, in turn, appointed a Science Advisory Committee consisting of nine people with expertise in hydrology, hydraulics, water resources, biology, geomorphology, geology, water quality, or modeling (Texas Water Code §11.0236 and §11.02361). The Environmental Flows Advisory Group defined the geographic extent for each basin and appointed a stakeholder committee for each river basin, and each stakeholder committee established its own science committee.

SB3 intended to establish stakeholder committees that would "reflect a fair and equitable balance of interest groups concerned with the particular river basin and bay system, and be representative of appropriate stakeholders, including agricultural water users (agricultural irrigation, free-range livestock, and concentrated animal feeding), recreational water users (coastal recreational anglers and businesses supporting water recreation), municipalities, soil and water conservation districts, industrial water users (refining, chemical manufacturing, electricity generation, and production of paper products or timber), commercial fishermen, public interest groups, regional water planning groups, groundwater conservation districts, environmental interests, and river authorities" (Texas Water Code §11.02362).

Science committees were "composed of technical experts with special expertise regarding the river basin and bay system" and "developed e-flow analyses and a recommended e-flow regime through a collaborative process designed to achieve consensus, based solely on the best science available, without regard to the need for the water for other uses (paraphrased, Texas Water Code §11.02362). Each science committee submitted its e-flow analyses and e-flow regime recommendation to the pertinent stakeholder committee, advisory group, and TCEQ.

Stakeholder committees were required to review and consider their respective science team's recommendations in conjunction with the present and future needs of water for other uses. The stakeholder committees then developed their e-flow standards and strategies to meet the standards and submitted their recommendations to the advisory group and TCEQ. Additionally, each stakeholder committee developed a work plan establishing monitoring studies for adaptive management and review of e-flow standards at least once every 10 years. Using recommendations from the science committee, recommendations from the stakeholder committee, and input from other interested parties, TCEQ promulgated instream flow standards at a public hearing and formulated initial permit restrictions for future water rights to ensure that environmental set asides were satisfied. Following publication of the initial e-flow rules, the public was provided 30 days to comment. TCEQ was required to respond to all comments before adopting final e-flow rules.

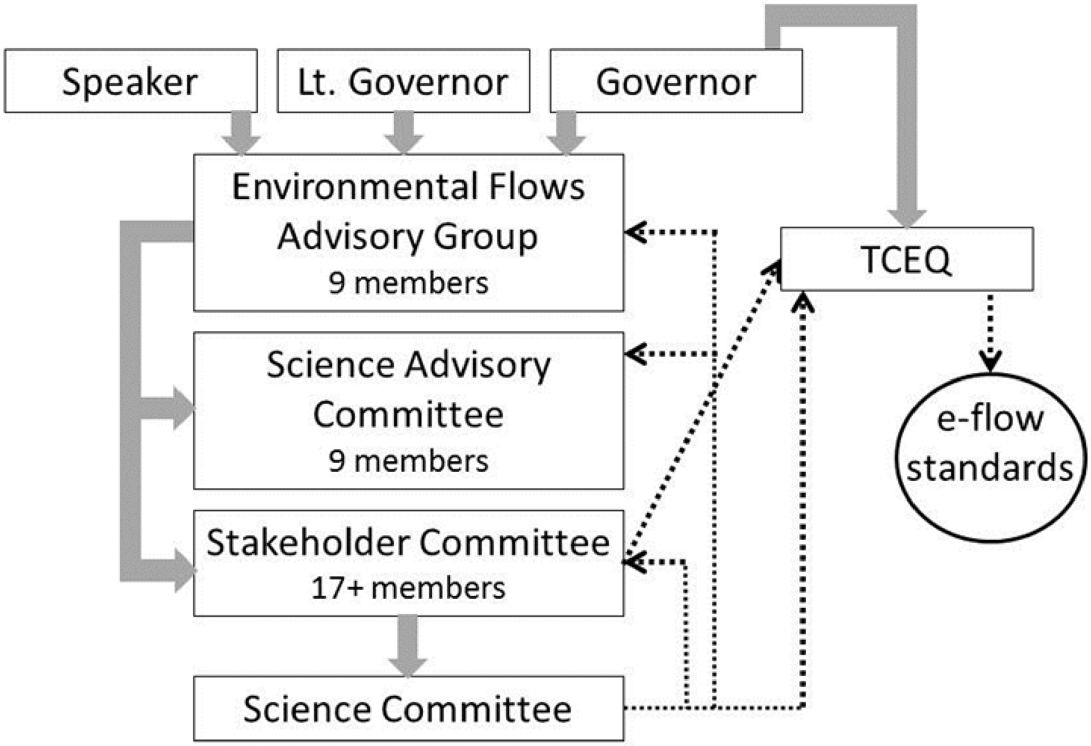


Figure 3.2. Texas Senate Bill 3 process for establishing environmental flows (e-flows). Grey arrows indicate appointment of agency or committee members, and black dotted arrows indicate submittal of e-flow recommendations or standards. TCEQ = Texas Commission on Environmental Quality, the state agency that issues water rights permits.

In the following sections, I give a brief overview of the SB3 process for establishing e-flow standards in Texas and summarize how the science and stakeholder committees justified their recommendations and the main critiques of science committee e-flow recommendations by the science advisory committee and TPWD. I further summarize the e-flow rules proposed by TCEQ, public comments on initial rules, responses by TCEQ, and final streamflow rules. For the first two river basins to have completed the process (Sabine and Neches Basins and Sabine Lake Bay [SNB], Trinity and San Jacinto Basins and Galveston Bay [TSJB]), I describe the shortcomings of this process due to the dominant roles of river authorities, engineering consulting firms, and TCEQ. The river authorities face a conflict of interest in that they are legally delegated to manage the surface water under their jurisdiction, but also obtain the majority of their funding from water sales and other activities that result in diversions of large amounts of surface water. Furthermore, many of the individuals on the expert science teams worked for consulting firms that regularly contract with the river authorities, representing a similar conflict of interest. Although SB3 emphasized the science of e-flows and stakeholder involvement, TCEQ had ultimate authority to set the e-flow rules that influence new water rights permits. Because the river authorities apply for permits from and are regulated by TCEQ, the agency also had a conflict of interest in its SB3 role.

THE SABINE AND NECHES BASINS (SNB) AND SABINE LAKE BAY

The Sabine River originates northeast of Dallas and flows 820 km to Sabine Lake, a shallow brackish estuary on the Gulf coast near the Texas-Louisiana border. In its lower course, the river forms the boundary between Texas and Louisiana. The Sabine River Basin has 14 major reservoirs, 11 of which are in Texas. The headwaters of the approximately 670-km long Neches River are located in Van Zandt County, and this river also empties into Sabine Lake. The Neches River Basin has 10 major reservoirs including Sam Rayburn Reservoir, the largest in Texas. From Lake B.A. Steinhagen to the city of Beaumont, the Neches River flows through the Big Thicket National Preserve, which was designated a Biosphere Reserve by the United Nations Educational, Scientific and Cultural Organization (UNESCO) because of its diversity of herbaceous plant, reptile, and bird species.

Major changes in minnow communities in the lower Sabine River are believed to be due to upstream impoundments; entrapment of floodwaters by the dams has caused an overall decrease in suspended sediment load in the channel reach below the dam, and during extended dry periods, dam releases artificially stabilize flow. These changes favor minnows that prefer clear-water conditions (e.g., *Cyprinella venusta*) over minnows that prefer turbid-water conditions (e.g., *C. lutrensis* and *Notropis buchanani*; Bonner and Runyan 2007, Bart 2008). In the lower Neches River, a saltwater barrier operated by the Lower Neches Valley Authority prevents saltwater intrusion upstream from the Gulf of Mexico. Prior to the 1970s, inflow of toxic chemicals (e.g., heavy metals and organochlorinated dioxins and furans) from paper mills and petrochemical plants below the saltwater barrier polluted the Neches River Estuary and Sabine Lake (Harrel and Hall 1991, Harrel and McConnell 1995, Long 2000, Harrel and Smith 2002).

Science committee recommendations

The SNB science committee consisted of a total of 11 voting members employed by the Sabine River Authority (1), the Lower Neches Valley Authority (1), engineering consulting firms (6), and universities (4). The chair of the committee was employed by the Sabine River Authority, and the co-chair was employed by the Lower Neches Valley Authority. The science committee adopted the definition of sound environment from the SB2 Science Advisory Committee (SAC 2006) and concluded that current conditions of the Sabine and Neches Rivers and the Sabine-Neches estuary were “sound,” noting also that changes had occurred, including extirpation of a self-sustaining population of paddlefish (*Polyodon spathula*). None of the river segments had been listed as impaired based on water quality, and Sabine Lake has good overall water quality and diverse fish and wildlife despite major modifications, including a major ship channel to facilitate shipping for the region’s petrochemical industry. The science committee recognized that the ship channel has increased salinity and allowed the salt wedge to penetrate further inland compared to historical conditions, thus inflows alone cannot maintain the historic wetland communities surrounding the bay. Hydrology was different between the pre- and post-reservoir period of record for three sites located downstream of reservoirs, however the science committee decided to use the full period of record when using

Hydrology-based Environmental Flow Regime (HEFR) software created by TPWD hydrologists to facilitate the SB3 process. This software defines important e-flow components including subsistence, base low, base medium, base high, flow pulse and overbank flows based on user-defined parameters and historical streamflow data. The science committee used USGS average daily streamflow to develop instream flow recommendations for four seasons based on differences in hydrology for a total of 12 freshwater sites and one bay. Instream flow components included subsistence flows, base flows, flow pulses, overbank flows, and bay freshwater inflows (Table 3.1). The science committee also performed an analysis of the flows needed for channel maintenance, but did not recommend that these flows occur. In addition, the science committee included an extensive discussion of state water planning activities in its report.

For its subsistence flow recommendations, the science committee examined water quality data and historical records of fishes (Bonner and Runyan 2007, Bart 2008), freshwater mussels (Howells 2002), and wetland/floodplain plants. Although little water quality data were available at low streamflow values for the SNB study sites, comparisons of the relationship between water quality data parameters and flow indicated that water quality generally was not a problem during drought periods. The science committee proposed, on the grounds that no species of fishes (other than paddlefish), mussels, or wetland/floodplain plants appear to have been extirpated from the basins during previous drought periods, that subsistence flows above recorded minimum flows should be sufficient to protect species. HEFR subsistence flows based on the 5th percentile of all flows, a value substantially lower than the subsistence flows recommended by US Fish and Wildlife Service studies for the lower Sabine and lower Neches (Werner 1982a and b), were recommended by most members of the science committee biology subcommittee. However, the full membership of the science committee later proposed lower subsistence flows based on 1st to 3rd percentile ranges (Table 3.1). If the seasonal subsistence value was less than the summer subsistence value, the science committee adopted the summer value. Additionally, HEFR failed to calculate a winter value for some sites, and therefore the lowest recorded winter flow value at those sites was adopted. The science committee recommended that issuance of future surface water appropriations or amendments should not result in more frequent occurrence of flows less than the recommended seasonal subsistence values, but did not provide information on the historical frequency of subsistence flow levels.

Table 3.1. The Sabine and Neches Basins and Sabine Lake Bay science committee environmental flow recommendations and the Texas Commission on Environmental Quality (TCEQ) draft environmental flow rules for the Neches River at Evadale. Winter = January – March, Spring = April – June, Summer = July – September, and Fall = October – December. Adopted from Sabine and Neches Rivers and Sabine Lake BBEST Environmental Flows Recommendation Report (2009).

	Winter	**Spring**	**Summer**	**Fall**
Subsistence	6.46 m^3/s	7.53 m^3/s	6.46 m^3/s	6.46 m^3/s
Base low	49.55 m^3/s	46.44 m^3/s	14.92 m^3/s	13.17 m^3/s
Base medium	74.61 m^3/s	90.90 m^3/s	63.71 m^3/s	44.46 m^3/s
Base high	141.24 m^3/s	112.13 m^3/s	91.46 m^3/s	77.30 m^3/s
2 flow pulses per season	Trigger: 57.20 m^3/s Volume: 2.58 hm^3 Duration: 6 days	Trigger: 108.45 m^3/s Volume: 8.48 hm^3 Duration: 12 days	Trigger: 43.61 m^3/s Volume: 2.66 hm^3 Duration: 9 days	Trigger: 44.46 m^3/s Volume: 2.20 hm^3 Duration: 7 days
1 flow pulse per season	Trigger: 246.36 m^3/s Volume: 30.36 hm^3 Duration: 22 days	Trigger: 246.36 m^3/s Volume: 30.36 hm^3 Duration: 22 days	Trigger: 104.21 m^3/s Volume: 8.58 hm^3 Duration: 13 days	Trigger: 117.80 m^3/s Volume: 8.82 hm^3 Duration: 13 days
1 overbank pulse per year	Trigger: 563.51 m^3/s; Volume: 100.27 hm^3; Duration: 37 days			

The science committee used information derived from the scientific literature about how focal fish and mussel species respond to flow variation (e.g., Strayer 2008), site-specific studies (e.g., Werner 1982a and b, Moriarty and Winemiller 1997), and because many of the fish species in the Sabine and Neches Rivers also are present in the Colorado River, a PHABSIM model of fish guilds in the lower Colorado River (BIO-WEST, Inc. 2008) as justification for its base flow recommendations. The PHABSIM modeling component of the Instream Flow Incremental Methodology (Stalnaker et al. 1995) combines a hydraulic model with a biological habitat model (i.e., the habitat suitability criteria) in order to make predictions about how changes in discharge will affect the availability of that species' or guild's habitat (i.e., weighted usable area of habitat categories). Three levels of base flows were generated for each season for 11 of the 12 sites using the HEFR software. For one site, one seasonal base flow HEFR estimate was raised to the 5th percentile of all flows because the HEFR base flow estimate equaled the subsistence flow estimate. However, the science committee did not provide information on the historic frequencies of the three base flow estimates. Additionally, it recommended that the combined water supply storage in all upstream major reservoirs be used to define hydrologic condition in order to determine the climatic condition (dry, average, wet) that determines flow rules for the base flow component.

For its flow pulse recommendations, the science committee conducted a literature review of how high flow components maintain populations of fishes from the region. The science committee also estimated the amount of forested wetlands in several study reaches that would be inundated by flow pulses of various magnitudes based on analyses conducted by the National Wildlife Federation and Greater Edwards Aquifer Alliance. Estimates revealed that the recommended flow pulses would provide good levels of riparian zone inundation for upper basin sites, but overbank flows would be necessary to inundate wetlands and riparian zones at lower basin sites. Based on this information, the science committee recommended two levels of seasonal flow pulses and one level of overbank flow for each study site derived from HEFR analyses. For the seasonal flow pulses, HEFR results were reduced so that peak flow rates were associated with the approximate bankfull stage condition as defined by the National Weather Service (NWS).

The science committee recommended one overbank flow pulse every year for three sites and one overbank pulse every two years for nine sites based on the NWS flood stage. However, science committee members affiliated with the river authorities expressed concern for legal liability for dam operators. The science committee stated that “overbank flows may cause extensive damage to private property and endanger the public. The science committee recognizes the ecological benefits of these events, but cannot recommend such events be produced."

For its channel maintenance flows, the science committee evaluated the long-term stage discharge curve at seven of the 12 sites. These analyses indicated that there has been a decrease in the volume of water and sediment that passes through each of these sites, and that the channel may become unstable and incise or the meander wavelength could decrease, leading to bank caving and losses in channel width and depth. However, the science committee concluded that “the assumption of (channel) equilibrium is not always valid and is increasingly criticized as a reasonable assumption for models and assessments” and that “equilibria are arguably used as reference conditions, but should not be assumed to necessarily be any more common, important, or natural than disequilibrium or nonequilibrium states. Managers cannot assume that there is any single normal, natural, or otherwise normative condition for alluvial rivers of the study area, and should recognize the possibility – indeed, the likelihood – of multiple modes of adjustment and potential responses to disturbance.” The science committee also calculated effective discharge for the recommended e-flow regime, and concluded that flow pulses and overbank flows would provide sufficient flow to maintain the existing dynamic equilibrium of the streams and rivers in the two basins. The science committee concluded that “it is assumed that future permitting activities will protect the high flow pulses and overbank flows prescribed.”

The science committee addressed freshwater inflow into Sabine Lake by performing a literature review establishing ten species of wetland plants, bivalve mollusks, crustaceans, and fishes as focal species. Next, the science committee analyzed the potential response of the focal species to the salinity regimes resulting from the flow recommendation for the three river sites located nearest the estuary. They did this with models developed by the National Wildlife Federation that used salinity to develop habitat suitability curves for the estuary. The science committee also examined the relationship between the HEFR-derived freshwater inflows for the three river sites with the inflow requirements for the bay recommended by TPWD (Kuhn and Chen 2005).

Both analyses indicated that the flow recommendations for the three river sites should also provide sufficient freshwater inflow to maintain a sound environment within Sabine Lake.

Critiques of science committee recommendations

In its critique of the science committee recommendations, the state Science Advisory Committee determined that reasonably available science was used for the e-flow recommendations, including information on hydrology, biology/ecology, geomorphology (sediment transport), and water quality. However, the committee was concerned that the report did not make a recommendation for overbank flows because of potential property damage, concluding that this was beyond the charge of the science committee as mandated by SB3 and therefore should have been an issue for consideration by the stakeholder committee. Furthermore, the state committee concluded that the discussion of state water planning activities was unnecessary; that a comparison of numerical values between the science committee flow recommendation and other reports such as Werner (1982a and b) and Kuhn and Chen (2005) would have been helpful; and that without information about historical subsistence and base flow frequencies, there is uncertainty about whether the reservoir storage approach used by the science committee for defining climatic conditions for base flows will be sufficient to maintain a sound environment.

The TPWD, in its assessment, concluded that with some exceptions, the science committee met the mandates of SB3. It found the definition of e-flow regime and sound environment by the science committee reasonably consistent, but was concerned that the science committee did not sufficiently address decreases in native species, significant loss of important wetlands due to salt water intrusion, and changes in historical streamflow. Other criticisms included 1) the lack of recommended attainment frequencies for subsistence and base flows, 2) failure to modify HEFR to accurately calculate subsistence flow (i.e., the failure of HEFR to calculate a value is a result of user input of subsistence parameters that do not occur historically), 3) the implementation rules for base flows being embedded in the flow regime recommendations, 4) the use of the entire period of record for HEFR analyses, despite substantial alterations of streamflow by impoundments at some locations, 5) tuning of the hydrographic separation algorithm in HEFR in a manner that resulted in extremely low subsistence flow recommendations and all runoff being placed into the flow pulse category, when these events should appropriately be classified as base flow, 6) lack of rationale for flow pulse implementation rules, 7) the lack of a recommendation for overbank flows, and 8) because the estimate of inflows provided to the bay were made with an initial e-flow recommendation that was later reduced by the science committee, there were inconsistencies in the bay inflow recommendations. TPWD concluded that e-flow and inflow recommendations proposed by the science committee were too low and could result in bay inflows substantially lower than those experienced historically.

Stakeholder committee recommendations

The SNB stakeholder committee had 23 voting members representing agricultural water users (3), recreational water users (2), municipalities (2), soil and water conservation districts (1), industrial water users (4), commercial fishermen (1), public interest groups (2), regional water planning groups (1), groundwater conservation districts (2), river authorities (3), and environmental interests (2). Again, the stakeholder committee chair and co-chair both were employees of river authorities. The stakeholder committee used Water Availability Modeling (WAM) to assess the impacts of applying the science committee e-flow recommendations on the water yield and level of Toledo Bend Reservoir and on the water yield of two proposed reservoir projects. WAM simulations, developed by TCEQ, predict the amount of surface water available in a river after taking into account historic streamflow; geospatial data such as drainage area, evaporation, and reservoir area; and the location of water users and self-reported information on the amount of water each user diverts (e.g., Trungale et al. 2003). The analysis indicated that the water level of Toledo Bend Reservoir would be reduced by 0.61 to 1.22 m under current water usage conditions and by 3.05 m under water usage conditions predicted for the future. The stakeholder committee concluded that the impacts were unreasonably excessive and suggested that use of HEFR-derived flow values for e-flow recommendations was inappropriate. The group concluded that the e-flow regime would cause significant and potentially unacceptable reduction to the economic viability of proposed reservoir projects. In addition, the committee proposed that reservoir fisheries and recreational values were just as important to consider as river, stream, and estuarine values. The stakeholder committee recommended that the science committee’s flow regimes not be used to develop e-flow standards, and that there is no urgency to develop e-flow standards prior to having the information needed. The committee proposed that since current water-use practices in the basins have maintained a sound environment, no requirement to produce flow pulses or overbank flows should be imposed on a reservoir owner until a liability shield is in place.

TCEQ draft environmental flow rules

Because TCEQ did not receive stakeholder committee recommendations, its draft e-flow rules simply followed the science committee’s e-flow recommendations (Table 3.2). However, following submission of draft streamflow rules, the stakeholder committee requested that TCEQ allow it to submit new recommendations. The stakeholder committee requested several members from the basin’s science committee to create an alternative e-flow regime that did not include as many high flow pulses. Subcommittee members were employed by the Sabine River Authority, the Lower Neches Valley Authority, and consulting agencies; none of the science committee members who were employed by universities were given the option of participating in this activity (KO Winemiller, *personal communications*). The subcommittee recommended one seasonal base flow level instead of three, one small flow pulse twice per year instead of two seasonal pulses, and eliminated the higher flow pulse recommended by the science committee for eleven sites within the basins (Table 3.2).

The SNB stakeholder committee accepted the flow components proposed by this subset of the science committee as its e-flow recommendations to TCEQ.

Public comments on draft rules

In their public comments on the proposed streamflow rules, state and federal agencies dedicated to the management of natural resources including the U.S. Fish and Wildlife Service and TPWD, and environmental organizations including the Big Thicket National Preserve, Friends of the Neches River, National Wildlife Federation Action Fund, and Texas Conservation Alliance were concerned that the Sabine and Neches rivers were not in fact sound environments, and that the proposed e-flows were too low to maintain ecological integrity in the SNB. For example, Big Thicket National Preserve and the U.S. Fish and Wildlife Service commented that TCEQ's finding that the Sabine and Neches rivers and their associated tributaries and estuaries are sound environments is not supported by present water quality or ecological criteria; impairments include elevated mercury levels in fish, elevated bacteria, low dissolved oxygen, low pH, significant declines of wetlands, and decline of fisheries and wetland-dependent birds, and altered flow regimes have been identified as one contributor to these declines. The

Big Thicket National Preserve, Texas Conservation Alliance, state natural resource agency, and over 1,600 individuals were concerned that subsistence flows were too low and may lead to water quality problems. The state natural resource agency commented that the schedule of high flow pulses in the proposed rules does not provide adequate flow variability needed to maintain a sound environment. The Big Thicket National Preserve was concerned that the proposed rules did not adequately provide for fluvial sediment transport and geomorphic processes. National Wildlife Federation Action Fund, TPWD, the U.S. Fish and Wildlife Service, and more than 1,600 individuals commented that the standards did not provide for the protection of freshwater inflow into Sabine Lake. The environmental organizations Friends of the Neches River, Texas Conservation Alliance, and several individuals commented that the recommendation of the stakeholder committee to reduce flows was solely based on a desire to sell water in the future.

Table 3.2. The Sabine and Neches Basins and Sabine Lake Bay stakeholder committee revised environmental flow recommendations and Texas Commission on Environmental Quality (TCEQ) draft and final environmental flow rules for the Neches River at Evadale. Winter = January – March, Spring = April – June, Summer = July – September, and Fall = October – December. Adopted from Sabine and Neches Rivers and Sabine Lake BBASC Technical Memorandum (2010).

		Winter	**Spring**	**Summer**	**Fall**
BBASC Revised Recommendations & Draft Rules	Subsistence	6.46 m^3/s	7.53 m^3/s	8.16 m^3/s	6.46 m^3/s
	Base low	49.55 m^3/s	46.44 m^3/s	14.92 m^3/s	13.17 m^3/s
	Base medium	None	None	None	None
	Base high	None	None	None	None
	1 flow pulse per season	None	Trigger: 108.45 m^3/s Volume: 8.48 hm^3 Duration: 12 days	None	Trigger: 44.46 m^3/s Volume: 2.20 hm^3 Duration: 7 days
	1 flow pulse per season	None	None	None	None
	1 overbank pulse per year	None			
Final Rules	Subsistence	6.46 m^3/s	7.53 m^3/s	6.46 m^3/s	6.46 m^3/s
	Base low	54.51 m^3/s	51.08 m^3/s	16.42 m^3/s	14.50 m^3/s
	Base medium	None	None	None	None
	Base high	None	None	None	None
	1 – 2 flow pulses per season	Trigger: 57.20 m^3/s Volume: 2.58 hm^3 Duration: 6 days	Trigger: 108.45 m^3/s Volume: 8.48 hm^3 Duration: 12 days	Trigger: 43.61 m^3/s Volume: 2.66 hm^3 Duration: 9 days	Trigger: 44.46 m^3/s Volume: 2.20 hm^3 Duration: 7 days
	1 flow pulse per season	None	None	None	None
	1 overbank pulse per year	None			

In contrast, many river authorities, oil and gas companies, and utility companies were concerned about the potential loss of water rights and suggested lowering the proposed e-flow rules. For example, the Angelina and Neches River Authority commented that it supported a decision by TCEQ not to establish e-flow set asides, to apply flow pulse standards only to large-scale projects, and not to require overbank flows. The Lower Neches Valley Authority, Texas Oil and Gas Association, and Upper Neches River Municipal Water Authority recommended that no requirement to pass high flow pulses in excess of the stakeholder committee recommended flow regime be imposed on a water supply reservoir operator until a liability shield is in place. The Brazos River Authority recommended that diversions not be curtailed but regulated during a high flow pulse. The Angeline and Neches River Authority, Dallas Water Utilities, Lower Neches Valley Authority, Texas Oil and Gas Association, and Upper Neches River Municipal Water Authority supported adopting the revised flow regime recommended by the stakeholder committee. The Sabine River Authority supported TCEQ's decision to avoid establishing freshwater inflow requirements for the estuary.

TCEQ responses and final streamflow rules

In response to concerns that subsistence flow values were too low, TCEQ reviewed the relationship between water quality parameters and streamflow conducted by the science committee. The agency's analysis did not identify any areas of concern, so it did not modify the proposed subsistence flow values. TCEQ indicated that, in response to consideration of all relevant factors, including human needs for water and comments, it was including only subsistence flows, one level of base flows and one to two seasonal flow pulses for four seasons and ten freshwater sites in the adopted standards (Table 3.2). TCEQ's subsistence flows and its single level of base flows were similar to the stakeholder committee's revised recommendations (65% of base flow rules were slightly higher than and 35% slightly lower than stakeholder committee revised recommendations). Flow pulses were similar in magnitude and duration to the lowest level of flow pulses recommended by the science committee, but for winter and summer, only one flow pulse per season was recommended instead of two. The agency stated that neither the science committee nor the stakeholder committee recommended freshwater inflow requirements for the estuary, so it did not include freshwater inflow requirements in its adopted standards.

THE TRINITY AND SAN JACINTO BASINS (TSJB) AND GALVESTON BAY

The Trinity River flows from its headwaters in Archer County 1,140 km to Galveston Bay. The Trinity River basin has a greater density of reservoirs than any other basin in Texas (Chin et al. 2008); its main stem has one major impoundment, Lake Livingston, and impoundments on its major tributaries include Lake Bridgeport, Eagle Mountain Lake, and Lake Worth (West Fork); Lake Weatherford and Benbrook Lake (Clear Fork); Ray Roberts Lake, Lake Dallas, and Lake Lewisville (Elm Fork); and Lake Lavon and Lake Ray Hubbard (East Fork). The two forks of the San Jacinto River originate near the city of Huntsville and meet at Lake Houston, flowing 115 additional km until reaching Galveston Bay. The upper West Fork of the San Jacinto River is impounded, forming Lake Conroe. Galveston Bay contains the largest estuary on the Texas coast. The coastal prairies of the basin support the federally endangered Attwater's prairie chicken, *Tympanuchus cupido attwateri* (Lockwood et al. 2005), provide nesting habitat for 22 species of colonial-nesting waterbirds (King and Krynitsky 1986, Gawlik et al. 1998), contain important wintering areas for ducks and geese (Hobaugh et al. 1989), and surround productive fish and shellfish nurseries (Stunz et al. 2002). Furthermore, Galveston Bay supplies an estimated 2/3 of Texas' oyster harvest, accounts for 40% of all seafood harvested from Texas' bay systems (Haby et al. 1989), and supports a recreational fishing industry. Approximately 50% of the United States' chemical production and 30% of its petroleum industry are in the Galveston Bay area (Ditton et al. 1989).

Science committee recommendations

The TSJB science committee consisted of a total of 15 voting members employed by engineering consulting firms (7), the Houston Advanced Research Center (1), the Tarrant Regional Water District (1), the Trinity River Authority (1), the U.S. Fish and Wildlife Service Texas Coastal Program (1), the USGS Texas Water Sciences Center (1) and universities (3). The science committee chair was employed by a consulting firm, and the co-chair was employed by Houston Advanced Research Center. The science committee was unable to reach consensus on a recommended e-flow regime. Therefore, two flow regimes were presented to the stakeholder committee, one recommended by seven of the members (the “Science Based Conditional Phased Approach,” hereafter called “Conditional Group”), and one recommended by eight of the members (the “Science Based Environmental Flow Regime,” hereafter called “Regime Group”).

The Conditional Group, made up of members employed by consulting firms (4), the Tarrant Regional Water District (1), the Trinity River Authority (1), and the USGS Texas Water Science Center (1) concluded that (paraphrased) “there is a preponderance of hydrological data available…but there is an insufficient amount of information regarding the geomorphology of the system, as well as the behavior of flows within the Trinity River related to habitat at varying flow levels, to establish biological-flow relationships.” Therefore, the Conditional Group recommended that (paraphrased) “until further supporting science can be developed in the future to specifically identify flows necessary for a sound environment…recommended flow amounts for a limited number of flow conditions at a limited number of stations are offered.” The Conditional Group used USGS average daily streamflow from the pre-reservoir period of record to made recommendations for four seasons based on differences in historical streamflow at a total of four freshwater sites, reaching a consensus that each of these sites is a sound environment. The instream flow components that were recommended included subsistence flows and base flows (Table 3.3). The Conditional Group did not offer recommendations for flow pulses, overbank flows, or bay freshwater inflows in their report.

The Regime Group, made up of members employed by consulting firms (3), Houston Advanced Research Center (1), universities (3), and U.S. Fish and Wildlife Service Texas Coastal Program (1) concluded that “Fish have been collected from the Trinity and San Jacinto Rivers since the nineteenth century. Flows have been measured for extended time periods at 45 sites including some locations for over 100 years. Water quality also has been measured intensively for over 40 years. In addition to long-term monitoring of flow and water quality, numerous intensive studies of river biology, water quality, and flow have been conducted. Over 520 studies were reviewed and over 33,000 unique records were generated in preparation for the biological overlay analysis.” The Regime Group used USGS average daily streamflow from the pre-reservoir period of record to make recommendations for four seasons at a total of 11 freshwater sites and three bay sites located throughout the basin, concluding that all of these locations currently have acceptably sound environments. Instream flow components that were recommended included subsistence flows, base flows, flow pulses, overbank flows, and bay freshwater inflows (Table 3.3).

Table 3.3. The Trinity and San Jacinto Basins and Galveston Bay “Conditional Group” and “Regime Group” science committee environmental flow recommendations for the Trinity River near Oakwood. Winter = December – February, Spring = March – May, Summer = June – August, and Fall = September – November. Recommendations adapted from Trinity and San Jacinto and Galveston Bay BBEST Environmental Flows Recommendations Report (2009).

		Winter	**Spring**	**Summer**	**Fall**
Conditional Group	Subsistence	$2.78\ m^3/s$ Frequency: 100%	$2.27\ m^3/s$ Frequency: 100%	$2.12\ m^3/s$ Frequency: 97%	$2.41\ m^3/s$ Frequency: 96%
	Base flow	$7.50\ m^3/s$ Frequency: 91%	$9.12\ m^3/s$ Frequency: 95%	$5.27\ m^3/s$ Frequency: 85%	$4.59\ m^3/s$ Frequency: 82%
	Flow pulses	The BBEST recognizes that high flow pulses provide an important ecological function to riverine habitat. Lacking specific ecological data, the conditional flow magnitudes identified are an arbitrary representation of high flow pulses, and are not a representation of the flow necessary to support a sound ecological environment until such supporting specific ecological data are developed.			
	Overbank pulses	Peak discharge: $696.59\ m^3/s$ Variation in duration: 18 – 61 days Average duration: 33 days BBEST does not recommend action be taken to produce such flows.			

Table 3.3 continued

		Winter	Spring	Summer	Fall
Regime Group	Subsistence	5.55 m^3/s Frequency: 95%	7.93 m^3/s Frequency: 95%	1.98 m^3/s Frequency: 95%	2.86 m^3/s Frequency: 95%
	Base low	9.63 m^3/s Frequency: 85%	12.97 m^3/s Frequency: 89%	7.28 m^3/s Frequency: 69%	7.50 m^3/s Frequency: 73%
	Base medium	17.64 m^3/s Frequency: 72%	23.22 m^3/s Frequency: 79%	11.64 m^3/s Frequency: 53%	12.43 m^3/s Frequency: 57%
	Base high	31.43 m^3/s Frequency: 58%	39.59 m^3/s Frequency: 66%	19.31 m^3/s Frequency: 36%	23.19 m^3/s Frequency: 41%
	2 flow pulses per season	Trigger: 90.61 m^3/s Volume: 2.34 hm^3 Duration: 5 days	Trigger: 222.00 m^3/s Volume: 17.48 hm^3 Duration: 11 days	Trigger: 33.41 m^3/s Volume: 0.60 hm^3 Duration: 2 days	None
	1 flow pulse per season	Trigger: 317.15 m^3/s Volume: 31.74 hm^3 Duration: 14 days	Trigger: 444.57 m^3/s Volume: 44.76 hm^3 Duration: 11 days	Trigger: 82.97 m^3/s Volume: 3.26 hm^3 Duration: 5 days	Trigger: 86.65 m^3/s Volume: 4.84 hm^3 Duration: 5 days
	2 flow pulses per year	Trigger: 424.75 m^3/s; Volume: 40.23 hm^3; Duration: 18 days			
	1 overbank pulse per 2 years	Trigger: 696.59 m^3/s; Volume: 77.27 hm^3; Duration: 26 days			

The Conditional Group initially calculated subsistence flows using HEFR based on the 10th percentile of historic streamflow, but then lowered these values, concluding that the results from the HEFR analysis were arbitrary. The Conditional Group justified that low flows from wastewater discharges, dissolved oxygen, and fish species diversity have increased since the 1970s. The Regime Group based subsistence flows on the 5th percentile of all daily average flows. The Regime Group justified that water quality modeling indicated that water quality criteria for dissolved oxygen would be met at subsistence flows, but did not provide information about the type of modeling used or modeling results. Both the Conditional Group and Regime Group provided information on the historical frequency of subsistence flow levels.

The Conditional Group used HEFR to generate base flows for the 6 sites and recommended the 25th percentile base flow magnitude as the single base flow level. The Regime Group used HEFR to generate three levels of base flows for each of the 11 sites. Because the Trinity and San Jacinto Rivers have many of the same fish species as the Colorado River, the Regime Group used habitat suitability curves developed for seven fish habitat guilds in the lower Colorado River by BIO-WEST, Inc. (2008) to make predictions about which fish species may become more abundant in the TSJB at each of the three base flow levels. Both groups provided information on the historical frequencies of base flow levels.

The Conditional Group recognized that high flow pulses provide an important ecological function, but concluded that “lacking specific ecological data, conditional flow magnitudes identified are an arbitrary representation of high flow pulses, and not a representation of the flow necessary to support a sound environment until such supporting specific ecological data are developed.” The Regime Group conducted a literature review on how flow maintains fish species in the Trinity and San Jacinto Rivers. Based on this information, four levels of seasonal and annual flow pulse events generated from the HEFR analysis were recommended at each study site.

The Conditional Group advised that “the science committee does not recommend action be taken to produce overbank flows.” Of the four levels of flow pulse events recommended by the Regime Group, the events in which the flow rate equaled or exceeded the flood stage as indicated by NWS were labeled as overbank flows. The Regime Group advised that, instead of action being taken to create overbank flows, permit restrictions be considered for future projects that alter overbank flows.

The Conditional Group endorsed simulated inflow required to the Trinity-San Jacinto estuary for a minimum and maximum fishery harvest in Galveston Bay as developed cooperatively by TWDB and TPWD using the TxEMP and TxBLEND models (Longley et al. 1994, TPWD 2001). The TxEMP model evaluates the freshwater inflows necessary to generate a fishery harvest based on salinity-inflow and fishery harvest abundance regression equations. The TxBLEND model produces simulations of long-term circulation and salinity conditions within a bay using information on tides, river inflows, winds, evaporation, and salinity concentrations (e.g., Schoenbaechler et al. 2011). The agencies also used the models to generate the minimum inflow needed to maintain salinity requirements to sustain fishery harvest. The Region H Water Planning

Group, a stakeholder group created under SB1 to develop strategies to maintain adequate freshwater inflow to Galveston Bay, also recommended these flows. The Conditional Group included the annual inflow values for minimum and maximum fishery harvest, minimum inflow needed to maintain salinity, and minimum annual inflow to Galveston Bay over the period of record (1941-1990). However, whereas the TWDB and TPWD computed the monthly inflow distribution to maintain the ecological health of the bay, the Conditional Group recommended only annual inflow values. The Regime Group provided recommendations for freshwater inflow from three sources to Galveston Bay: the Trinity River, the San Jacinto River, and coastal streams (e.g., Clear Creek, Dickinson Bayou, Cedar Bayou) for spring, summer, and fall seasons. The Regime Group used the TxBLEND model to estimate the area of suitable habitat for wild celery *Vallisneria americana*, the estuarine bivalve *Rangia cuneata*, and the Atlantic oyster *Crassostrea virginica* for a range of inflow volumes. Recommendations for inflow volumes were those that provided more than zero acres of suitable habitat for the indicator species. The Regime Group recommendations for each location included a trigger discharge and target frequency and timing of freshwater inflow. Furthermore, the Regime Group recommended that every five to ten years, a two week period of salinity < 5 ppt should occur in Galveston Bay to reduce oyster infection by the dermo-causing protozoan parasite *Perkinsus marinus*. An analysis of historical hydrology in the Trinity River indicated that an increase in return flows has resulted in an approximately 6% increase in daily streamflow in the most recent 30 years compared to 1940 – 1970. Thus, the Regime Group lowered their Trinity River inflow volume recommendations by 6%

so that inflows generated by the TxBLEND model would more closely approximately natural inflow patterns.

Critiques of science committee recommendations

According to the state Science Advisory Committee, the Conditional Group recommendations failed to meet the minimum requirements of an e-flow regime. The committee concluded that the best available science was not used in the report to any extent, and instead the recommendations stemmed from the opinion that because there were no established relationships between flow and ecosystem response, the available science was wholly insufficient to allow for a defensible e-flow analysis. The Science Advisory Committee did not agree with the Conditional Group’s argument that there must be site-specific, species/flow relationship data in order to develop a flow regime recommendation. Furthermore, it believed that it was disconcerting that the Conditional Group made only subsistence and base flow recommendations for a limited number of sites, given their strong position on the uncertainty of the science. Furthermore, it concluded that the Conditional Group’s bay inflow targets were based on both science and stakeholder negotiations, and hence not based solely on science.

The Science Advisory Committee determined that the Regime Group did a better job of using the best available science, including information on hydrology and water quality. The committee concluded that, because the Regime Group concluded that the system currently is sound, the large dependence on historical hydrological analysis was an appropriate starting point for the flow regime analysis. It also approved of their science-driven process of using a salinity zonation/focal species approach for bay inflow recommendations. The Science Advisory Committee concluded that in all aspects – quantities, seasonality, and geographic scope – the Regime Group recommendations constitute an e-flow regime. However, it was concerned that the Regime Group's inflow recommendations were based on only a few indicator species and did not embody a comprehensive range of inflow conditions, including high flows and inflow minima.

TPWD also did not support the methodology or recommendations of the Conditional Group. The agency was concerned that the geographic scope was too limited, the recommended flows were lower than flows that have occurred in the last several decades, and the recommendations were based only on a small part of the entire flow spectrum. Furthermore, it expressed confusion about many aspects of the Conditional Group's report, including why hydrology alone was deemed sufficient to make flow recommendations at a few sites but not others, and were concerned about the lack of documentation supporting many of the Conditional Group's conclusions. Additionally, TPWD did not endorse the Conditional Group bay inflow recommendations because they were not developed through a strictly science-based process and did not explicitly include monthly or seasonal freshwater inflow quantities. It concluded that the Conditional Group recommendations were inconsistent with the e-flow regime as defined by the National Research Council, the Science Advisory Committee, and the Texas Instream Flow Program.

TPWD supported the Regime Group instream flow recommendations, but with some reservations. The agency was concerned that the report 1) did not provide flow recommendations for tributaries, 2) did not document water quality modeling that was used to justify its subsistence flow recommendations, 3) recommended subsistence flows that increased the frequency of zero flows at some sites where intermittence naturally occurred, 4) overbank flow events were not included, 5) regression equations used for the TxBLEND model provided a poor fit, 6) bay inflows were not recommended for all months and seasons, 7) the 6% adjustment to freshwater inflow recommendations was not appropriate, and 8) because oysters take three years to grow (Kraueter et al. 2007), a two week period of salinity < 5 ppt every five years is insufficient to maintain healthy populations. The state natural resource agency concluded that, in cases in which there are inconsistencies between flow recommendations, the appropriate procedure is to apply the more protective recommendation.

Stakeholder committee recommendations

The TSJB stakeholder committee consisted of a total of 24 voting members representing agricultural water users (2), recreational water users (2), municipalities (2), soil and water conservation districts (1), industrial water users (4), commercial fishermen (1), public interest groups (1), regional water planning groups (2), groundwater conservation districts (3), river authorities (3), and environmental interests (3). The stakeholder committee chair represented the river authorities, and the co-chair represented environmental water interests. Stakeholder committee members also were unable to reach consensus on a recommended e-flow regime. Thus, two separate recommendations were submitted, one recommended by 15 of the members (Group 1, endorsed by members representing agricultural water users, municipalities, industrial water users, regional water planning groups, groundwater conservation districts, and river authorities), and one recommended by eight of the members (Group 2, endorsed by members representing recreational water users, soil and water conservation districts, commercial fishermen, public interest groups, and environmental interests). One member representing an industrial water user did not endorse either of the reports. Group 1 recommended subsistence flows, base flows, and bay freshwater inflows as e-flow components at the four sites chosen by the Conditional Group, and Group 2 recommended subsistence flows, base flows, flow pulses, and bay freshwater inflows as e-flow components at ten of the 11 sites chosen by the Regime Group (Table 3.4). Group 2 did not develop flow recommendations for the Elm Fork of the Trinity River near Carrollton because of the belief that conditions in the area did not merit the development of flow standards. Group 2 also did not develop flow pulse recommendations for Brays Bayou in the Houston metropolitan area.

Both Groups 1 and 2 recommended subsistence flows developed by the Conditional Group. However, Group 2 also recommended that flows remain above subsistence levels > 95% of the time and not extend longer than the maximum duration values they calculated using historic USGS streamflow.

Group 1 recommended the single base flow level developed by the Conditional Group. In contrast, Group 2 recommended three base flow levels corresponding with the Regime Group base flows, and WAM was used to develop frequency recommendations for each base flow level. If water availability models indicated that human water appropriation already resulted in river flow that was less than the Regime Group recommendations, the frequencies recommended by the Regime Group were reduced. No flow pulses were recommended by Group 1, corresponding with the Conditional Group recommendations. Group 2 reduced the Regime Group flow pulse recommendations by eliminating one annual flow pulse and moving a seasonal pulse to the spring when most flow pulses typically occur, reducing the number of flow pulse recommendations during the summer and fall, and combining separate summer and fall flow pulse requirements into one summer/fall requirement. Overall, the levels of flow pulse and overbank flow recommendations were reduced from four (10 – 14 flow and overbank pulses in total) to three (nine flow and overbank pulses in total).

Both stakeholder committee groups recommended that no action be taken to produce overbank flows because of the possibility of property damage and loss of life. However, Group 2 suggested that as part of adaptive management, future change in the frequency, magnitude, and volume of overbank flows should be monitored and compared to the Regime Group overbank flow recommendations.

Group 1 recommended the annual quantity of freshwater inflow required for a minimum and maximum fishery harvest simulated by TWDB and TPWD using the TxEMP and TxBLEND models (Longley et al. 1994, TPWD 2001). Group 2 recommended three levels of inflow conditions (drought, low, and medium) based on the Regime Group recommendations. Each level included recommendations on the magnitude, frequency, and timing of inflow per season.

Table 3.4. The Trinity and San Jacinto Basins and Galveston Bay “Group 1” and “Group 2” stakeholder committee environmental flow recommendations for the Trinity River near Oakwood. Winter = December – February, Spring = March – May, Summer = June – August, and Fall = September – November. Group 1 recommendations adapted from Report of the Trinity – San Jacinto – Trinity Bay and Stakeholder committee (2010). Group 2 recommendations adapted from Recommended Environmental Flow Standards and Strategies for the Trinity and San Jacinto Basins and Galveston Bay (2010).

		Winter	**Spring**	**Summer**	**Fall**
Group 1	Subsistence	2.78 m^3/s Frequency: 100%	2.27 m^3/s Frequency: 100%	2.12 m^3/s Frequency: 97%	2.41 m^3/s Frequency: 96%
	Base	7.50 m^3/s Frequency: 91%	9.12 m^3/s Frequency: 95%	5.27 m^3/s Frequency: 85%	4.59 m^3/s Frequency: 82%
	Flow pulses	None			
	Overbank pulses	None			

Table 3.4 continued

		Winter	**Spring**	**Summer**	**Fall**
Group 2	Subsistence	$3.40\ m^3/s$ Frequency: 95% Maximum duration: 8 weeks	$4.53\ m^3/s$ Frequency: 95% Maximum duration: 3 weeks	$1.98\ m^3/s$ Frequency: 95% Maximum duration: 8 weeks	$2.83\ m^3/s$ Frequency: 95% Maximum duration: 8 weeks
	Base low	$9.63\ m^3/s$ Frequency: 75%	$12.74\ m^3/s$ Frequency: 80%	$7.10\ m^3/s$ Frequency: 55%	$7.36\ m^3/s$ Frequency: 60%
	Base medium	$17.56\ m^3/s$ Frequency: 60%	$23.22\ m^3/s$ Frequency: 65%	$11.33\ m^3/s$ Frequency: 40%	$12.03\ m^3/s$ Frequency: 45%
	Base high	$31.15\ m^3/s$ Frequency: 45%	$38.94\ m^3/s$ Frequency: 55%	$19.11\ m^3/s$ Frequency: 25%	$22.94\ m^3/s$ Frequency: 35%
	2 flow pulses per season	Trigger: $84.95\ m^3/s$ Percent of years in which met or exceeded: 66 and 33	Trigger: $198.22\ m^3/s$ Percent of years in which met or exceeded: 66 and 33	Trigger: $70.79\ m^3/s$ Percent of years in which met or exceeded: 50 and 40	
	1 – 2 flow pulses per season	Trigger: $283.17\ m^3/s$ Percent of years in which met or exceeded: 40	Trigger: $424.75\ m^3/s$ Percent of years in which met or exceeded: 45 and 22	None	
	Overbank pulses	None, but changes in the frequency, magnitude, and volume of overbank pulses should be monitored and compared to those recommended by the Regime Group BBEST.			

TCEQ draft environmental flow rules

TCEQ proposed e-flow rules including subsistence flows, one level of base flows, one seasonal flow pulse, and bay freshwater inflows for four seasons and six freshwater sites (Table 3.5). The agency did not include seasonal flow pulses or overbank flows in its proposed streamflow rules. It adopted all of the subsistence and base flow recommendations proposed by the Group 1 stakeholder committee at its four study sites. For the other two sites, the proposed subsistence and base flow rules were lower than the subsistence and base low flows recommended by the Group 2 stakeholder committee. The one seasonal flow pulse proposed as a streamflow rule approximated the lowest pulse recommended by the Group 2 stakeholder committee, but with a lower magnitude for the summer and fall seasons. The agency also proposed three levels of annual inflow magnitude and target frequency from the Trinity and San Jacinto Rivers to Galveston Bay.

Table 3.5. The Trinity and San Jacinto Basins and Galveston Bay Texas Commission on Environmental Quality (TCEQ) draft and final environmental flow rules for the Trinity River near Oakwood. Winter = December – February, Spring = March – May, Summer = June – August, and Fall = September – November.

		Winter	**Spring**	**Summer**	**Fall**
Draft Rules	Subsistence	2.78 m^3/s	2.27 m^3/s	2.12 m^3/s	2.41 m^3/s
	Base	7.50 m^3/s	9.12 m^3/s	5.27 m^3/s	4.59 m^3/s
	1 flow pulse per season	Trigger: 90.61 m^3/s Volume: 2.34 hm^3 Duration: 5 days	Trigger: 222.00 m^3/s Volume: 17.48 hm^3 Duration: 11 days	Trigger: 33.41 m^3/s Volume: 0.60 hm^3 Duration: 2 days	
	1 - 2 flow pulses per season	None			
	1 overbank pulse per year	None			
Final Rules	Subsistence	3.40 m^3/s	4.53 m^3/s	2.12 m^3/s	2.83 m^3/s
	Base	9.63 m^3/s	12.74 m^3/s	7.08 m^3/s	7.36 m^3/s
	2 flow pulses per season	Trigger: 84.95 m^3/s Volume: 2.22 hm^3 Duration: 5 days	Trigger: 198.22 m^3/s Volume: 16.04 hm^3 Duration: 11 days		Trigger: 70.79 m^3/s Volume: 2.84 hm^3 Duration: 5 days
	1 - 2 flow pulses per season	None			
	1 overbank pulse per year	None			

Public comments on draft rules

State and federal agencies dedicated to the management of natural resources and environmental and social organizations were concerned that the proposed environmental streamflow rules were too low and not sufficiently distributed throughout the watershed to be protective of the Trinity and San Jacinto rivers. For example, Bayou Land Conservancy, Environmental Stewardship, Galveston Baykeeper, Galveston Bay Foundation, Houston Audubon, Junior Anglers and Hunters of America, Lone Star Chapter of the Sierra Club, National Wildlife Federation, National Wildlife Federation Action Fund, the U.S. Fish and Wildlife Service, and over 2,300 individuals commented that the proposed e-flow rules were too low to be protective. Environmental Stewardship and Houston Audubon commented that the proposed e-flow standards did not meet statutory requirements because they did not include all of the flow components deemed necessary by the Texas Instream Flow Program to support a sound environment. Bay Area Houston Economic Partnership, Bayou Land Conservancy, Coastal Conservation Association Texas, Galveston Bay Foundation, Houston Regional Group of the Sierra Club, and more than ten individuals were concerned that the proposed streamflow rules did not provide the high flow pulses necessary for completion of many riverine species' life cycles, channel maintenance, and sediment transport. Bay Area Houston Economic Partnership, Bayou Land Conservancy, Coastal Conservation Association Texas, Houston Sierra Club, National Wildlife Federation, Lone Star Sierra Club, TPWD, and ten individuals commented that six measurement locations were not sufficient to adequately protect e-flow standards.

State and federal agencies dedicated to the management of natural resources, environmental organizations, social organizations, and seafood companies were also concerned that the proposed environmental streamflow rules would not protect Galveston Bay. The non-governmental environmental organizations Houston Audubon and Galveston Baykeeper; the recreation company Junior Anglers and Hunters of America; restaurants and companies selling seafood including Café Express, Evangeline Café, Fish City Grill, Foodways Texas, and Louisiana Foods Global Seafood Source; the non-profit organization Consumer Energy Alliance; and more than 700 individuals requested that TCEQ strengthen inflow standards to Galveston Bay. Bay Area Houston Economic Partnership Bayou Land Conservancy, Coastal Conservation Association Texas, Galveston Baykeeper, Galveston Bay Foundation, Houston Sierra Club, National Wildlife Federation, TPWD, U.S. Fish and Wildlife Service, and more than 20 individuals were concerned about the lack of rules concerning seasonal distribution of inflow to Galveston Bay. Bay Area Houston Economic Partnership, Bayou Land Conservancy, Coastal Conservation Association Texas, Galveston Baykeeper, Houston Sierra Club, and more than 15 individuals were concerned about the absence of drought-period inflow criteria for Galveston Bay.

Because of these concerns, many organizations, including the Bay Area Houston Economic Partnership, Bayou Land Conservancy, Big Thicket National Preserve, Environmental Stewardship, Galveston Baykeeper, Galveston Bay Foundation, Houston Audubon, Junior Anglers and Hunters of America, Lone Star Sierra Club, National Wildlife Federation Action Fund, TPWD, and over 1,700 individuals, requested that alternative e-flow recommendations submitted by the National Wildlife Federation and Sierra Club-Lone Star be adopted by TCEQ. These e-flow recommendations included more flow components, were generally of higher magnitude, and protected more sites throughout the watershed.

In contrast, river authorities including the Angelina and Neches River Authority, Brazos River Authority, and San Jacinto River Authority; the engineering consulting firm Freese and Nichols, Inc., and North Texas Municipal Water District were concerned about the implementation of flow pulses and whether or not the new e-flow rules would apply to existing water rights. Tarrant Regional Water District recommended removal of any language relating to high flow pulses in streamflow rules. NRG Energy and WW Chambers-Liberty Counties Navigation District supported the e-flow standards proposed by TCEQ. Tarrant Regional Water District recommended adoption of e-flows proposed by the Group 1 stakeholder committee.

TCEQ responses and final streamflow rules

In response to these concerns, TCEQ stated that there is not sufficient existing scientific evidence to support the need for multiple levels of base flow, so it adopted a simplified flow regime. TCEQ acknowledged that overbank flows are considered to be a necessary component of a flow regime for a sound environment, but justified that overbank flows result from naturally occurring large rainfall events and are likely to continue to occur and thus did not include them as a component of the adopted standards (Texas Water Code §298.1). However, TCEQ increased some of the base flow levels in the San Jacinto Basin and included a seasonal component for inflow to Galveston Bay. In response to many of the comments, TCEQ indicated that it had considered all of the recommendations provided by the science team, stakeholder groups, other relevant factors, alternate recommendations, and comments to the proposed rules when drafting the adopted standards.

TCEQ made its final e-flow rules for four seasons and six freshwater sites. E-flow components included subsistence flows, one level of base flows, two seasonal flow pulses, and bay freshwater inflows (Table 3.5). Recommendations for overbank flows were not included. At many sites, the higher of the subsistence flows recommended by the Group 1 or Group 2 stakeholder committee were adopted; 8% of its final subsistence flow rules were the same as Group 1 stakeholder committee recommended subsistence flows, 50% of its subsistence flow recommendations were the same as Group 2 stakeholder committee subsistence flow recommendations, and 33% of subsistence flow rules were higher and 8% lower than either of the stakeholder committee groups' recommendations. The agency adopted or slightly adjusted the seasonal base flow recommendation from the Group 2 stakeholder committee for the majority of its final base flow rules. The agency made 33% of its base flow rules higher and 13% of its base flow rules lower than either of the stakeholder committee groups' recommendations. For flow pulse rules, the agency adopted an additional seasonal flow pulse, accepting or slightly modifying the two lowest seasonal flow pulses recommended by the Group 2 stakeholder committee. However, the agency also made the modification that for the two-per-season flow pulse requirement, summer and fall seasons can be considered together (Texas Water Code §298.220). Finally, bay freshwater inflow rules for the Trinity and San Jacinto Rivers, including three levels of seasonal inflow, each with a magnitude and target frequency, were adopted from the Group 2 stakeholder committee inflow recommendations.

WHAT HAPPENED, WHY, AND WHAT DOES IT MEAN FOR THE FUTURE?

The original purpose of Texas' SB3 Environmental Flows Program was to allow diverse interest groups to discuss the gains and losses incurred by various e-flow scenarios and make decisions based on compromise (e.g., McShane et al. 2011). Ultimately, in the case of the SNB and TSJB, these decisions were dominated by individuals representing politically powerful groups that view water primarily as a commodity. Conflicts over the management of natural resources are fundamentally about differences in values, yet rather than make value-based arguments, policy disagreements almost always discuss issues using highly technical scientific, economic, and engineering terminology (Layzer 2006). A survey of Texas voters conducted for the National Wildlife Federation in 2002 found that 93% of people surveyed believe it is important for the state to provide protection to rivers, bays and wildlife as it plans for the state's future water needs (Tringali et al. 2002). In addition, 54% of those surveyed prefer that a city adopt water conservation measures rather than build new dams and pipelines (Tringali et al. 2002). Because most Texans seem to support many goals of the environmental movement, rather than proclaim anti-environmental values, adversaries of natural resource conservation often choose to couch their arguments in indirect ways.

In the case of the SNB science committee, the number of members representing river authorities and affiliated consulting firms was much greater than the number of members from academia, and none specifically represented environmental interests. Decisions were made via consensus rule, in which members negotiated until e-flow recommendations were developed upon which all members could agree. Because the group was dominated by members representing water development interests (i.e., river authorities and consulting firms), several members of the biology sub-committee of the SNB science committee had to make incremental reductions to initial e-flow recommendations in order to gain acceptance by the group majority (Appendix H, SNB BBEST Environmental Flows Recommendation Report 2009). For example, the biology subcommittee originally supported use of 5th percentile of historical flow values as subsistence flow criteria, citing growing support for its use in the scientific literature (e.g., Acreman et al. 2006, Hardy et al. 2006). However, as a result of deliberations by the full science committee membership, subsistence flow recommendations were lowered to the 1-3 percentile. Given that stakeholder committee decisions were made via 2/3 majority vote, they similarly were dominated by employees of river authorities and engineering consulting firms. The SNB stakeholder committee cited potential economic risk as justification for recommending additional study and delaying implementation of a management plan. Because the general public often has a limited attention span for environmental issues, proponents of the status quo frequently use a delay tactic

(Kingdon 1989). However, after realizing that this tactic might result in several levels of base flows and flow pulses being accepted by TCEQ as e-flow rules, the stakeholder committee, which was dominated by water development interests and strongly influenced by the river authorities, made new recommendations that were, for the most part, adopted by TCEQ.

In the case of TSJB science committee, the number of scientists affiliated with water developers and academia was approximately equal, and as a result, both committees were unable to reach a consensus. The TSJB science committee "conditional group," composed of the river authorities and their professional consultants, cited scientific uncertainty as being a major impediment to the development of flow recommendations. Because the science committee did not reach a consensus, it was perhaps inevitable that the stakeholder committee majority, representing short-term, economic interests, would vote for the lower e-flow recommendations (the recommendations from the "Conditional Group" science committee).

SB3 emphasized use of "best available science" to develop environmental flow regimes and "stakeholder involvement" to address the needs of all water users, but the process was derailed for the SNB and TSJB as a result of several factors. Both science and stakeholder committees were skewed with more members representing short-term economic than ecological and recreational needs for freshwater. Many individuals on the science and stakeholder committees worked for river authorities and consulting firms that regularly contract with the river authorities. Water rights holders, and particularly personnel of river authorities, were from the outset distrustful of the SB3 process. There was a high degree of uncertainty associated with e-flow science, and adaptive management was used as justification for making low e-flow recommendations.

As a result of compromises among different interest groups during the legislative process, the stakeholder committees were skewed resulting in nine stakeholders specifically advocating for short-term, economic values for freshwater (i.e., agricultural irrigation, free-range livestock, concentrated animal feeding, municipalities, refining, chemical manufacturing, electricity generation, production of paper products or timber, and river authorities) versus only four stakeholders specifically advocating for ecological, recreational, and related societal values for freshwater (i.e., coastal recreational anglers, businesses supporting water recreation, commercial fishermen, and environmental interests). Because the stakeholder committee appoints members of the science committee, the SNB and TSJB science committees represented the interests of water suppliers over the interests of environmental and recreational groups.

Although the SB3 legislation specified that existing water right permits would not be affected by the new e-flow standards, TCEQ did not provide information about how it would implement e-flow rules prior to the development of e-flow recommendations by the science and stakeholder committees. This unknown led to suspicion that the SB3 process would affect the exercise of river authorities' water rights. The stakeholder committee for one of the next basins to complete the SB3 process, the Colorado and Lavaca Rivers and Matagorda and Lavaca Bays, made consensus e-flow recommendations that were more representative of a flow regime than either the SNB or TSJB "Group 1" stakeholder committee recommendations. In addition to having access to site-specific studies from the lower Colorado River (i.e., BIO-WEST, Inc. 2008), this group had the opportunity to learn from mistakes during the SNB and TSJB efforts. Furthermore, the Lower Colorado River Authority's water management plan, as required by a 1989 court settlement, must include recommendations from a stakeholder committee consisting of 16 members representing groups dependent on water from Lake Travis and Lake Buchanan (i.e., cities, industry, agriculture, environmental groups, and lake-side residents and businesses) before it is approved by TCEQ. None of the other river authorities are obligated to negotiate with stakeholders and apply to TCEQ for approval of their water management plans (Scott Swanson, *personal communications*). Colorado River Basin stakeholders from both sides of the issue thus have had more experience with negotiation and compromise than stakeholders from the SNB or TSJB.

The high degree of uncertainty associated with the science used to derive e-flow recommendations for the SNB and TSJB also likely led to low flow standards because it resulted in degrees of ambiguity in decision-making. E-flow decisions are inherently based on incomplete scientific understanding, because in fluvial ecosystems, the growth of macroinvertebrate and fish populations is not only affected by flow, but also by other abiotic factors, including temperature and nutrients, and biotic factors, such as predation and competition, that may be exceedingly difficult to tease apart. Furthermore, the science committees did not always have site-specific information available to link e-flows with environmental responses and thus to specifically discuss the environmental versus economic trade-offs of alternative e-flow regimes. Some members used adaptive management as an excuse to recommend an e-flow regime with a limited number of flow components under the premise that e-flows can be changed later when more information becomes available. Adaptive management can be defined as evaluating biotic responses to implementation of e-flows so that adjustments can then be made to meet ecological goals. If these steps are repeated iteratively, uncertainty is reduced, improving e-flow recommendations. For example, if biotic response to a flow regime is deemed insufficient (e.g., a flow pulse is too low to cause recruitment of floodplain tree species), levels can be adjusted before the ecosystem degrades. Alternatively, if biotic integrity is clearly maintained, more water may be available for human uses. Adaptive management is “learning by doing,” not an excuse to recommend low flows that lack components of an environmental flow regime (Lee 1999, Richter et al. 2006).

In the end, TCEQ set environmental flow rules at levels much lower than those recommended for protection of environmental benefits by the science committees. The TCEQ commissioners are appointed by the governor, and the commissioners can influence priorities for the regulatory agency. News media, political and environmental groups have complained that TCEQ commissioners have close connections to both the governor and the corporations that the agency regulates (e.g., Hamby and Lucas *public communications*, Wilder *public communications*). For example, in 2010, the Environmental Protection Agency invalidated all “flexible air quality permits” issued by TCEQ to oil and chemical refineries, including BP, Chevron Phillips, Exxon Mobil, Shell Oil and Valero, on the grounds that they allowed polluters to emit levels of chemicals known to cause cancer, asthma, and other health problems. Also in 2010, TCEQ was found guilty by the State Office of Administrative Hearings of violating the law by aiding a petroleum power plant near the city of Corpus Christi to complete its particulate matter air pollution modeling. TCEQ apparently had intended to aid the plant in obtaining a permit before new EPA greenhouse gas regulations went into effect. The plant had been criticized by environmental organizations, medical groups, and citizens for contributing to the city's high asthma rates. Based on a survey of stage agencies, water rights holders, river interest and citizen groups, Kaiser and Binion (1998) predicted that TCEQ would be a major impediment to the success of the Texas Environmental Flow Program. Their survey found that instream flow protection suffers from "agency recalcitrance," and that this institutional culture may be difficult to change.

Sustainability is frequently discouraged when distinct government agencies have responsibility for natural resource exploitation as well as natural resource protection. As agencies performing natural resource exploitation prosper economically, their goal shifts from ecosystem management to maximization of economic efficiency, which ultimately results in a decline in quantity or quality of the natural resource (i.e., "command and control" management, Holling and Meffe 1996, Rogers et al. 2000, Rogers 2006). As goals shift to maximize profit, agency personnel may focus more on short-term gain and become insensitive to concerns about environmental sustainability (Holling and Meffe 1996). Agencies with overlapping jurisdictions but differing mandates thus work against each other, hindering ecosystem management (Cortner et al. 1998). The science and stakeholder committees' e-flow decisions for the SNB and TSJB were strongly influenced by the river authorities and affiliated consulting firms, and the end result of the process was successively lower e-flows leading to rules ultimately adopted by TCEQ (Figures 3.3 and 3.4). Low flows that do not mimic a natural flow regime will contribute to continuing degradation of fluvial ecosystems (Poff et al. 1997, Arthington et al. 2006). For management of sustainable ecosystems, government agencies should be structured so that they do not become self-serving bureaucracies (Rogers et al. 2000).

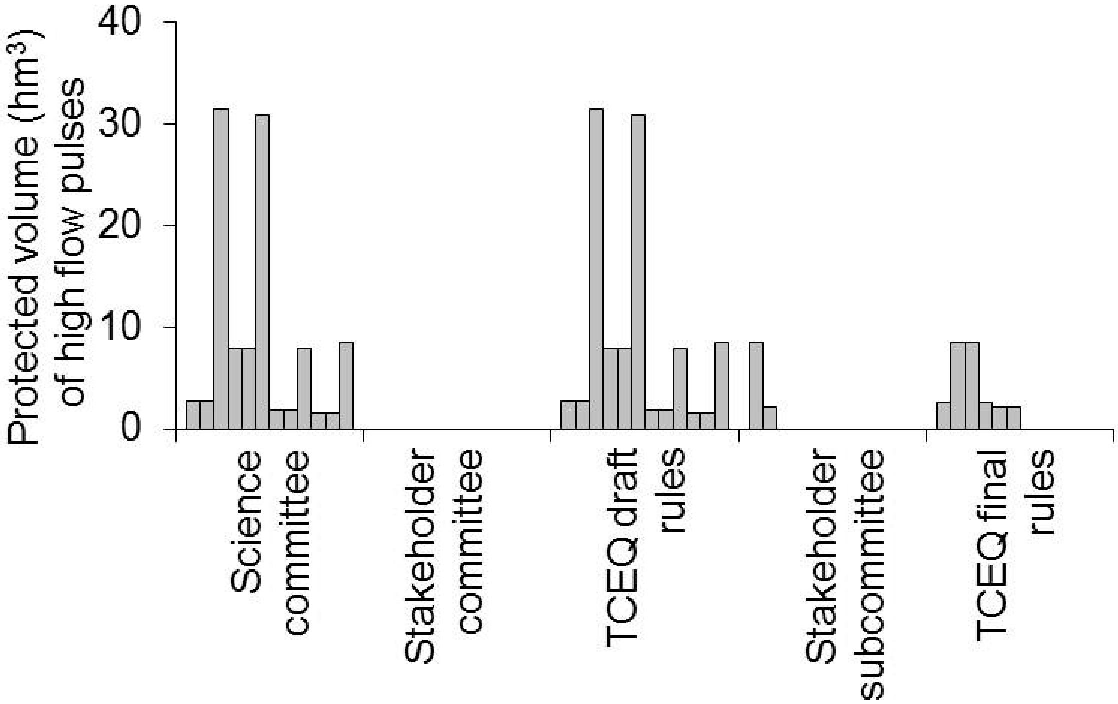


Figure 3.3. Annual volume (hm^3) and number of instream flow pulses recommended by the Sabine and Neches Basins and Sabine Lake Bay science and stakeholder committees, stakeholder subcommittee, and adopted as standards by the Texas Commission on Environmental Quality (TCEQ), the state agency that issues water rights permits, for the Neches River at Evadale. 1 hm^3 = 1,000,000 m^3.

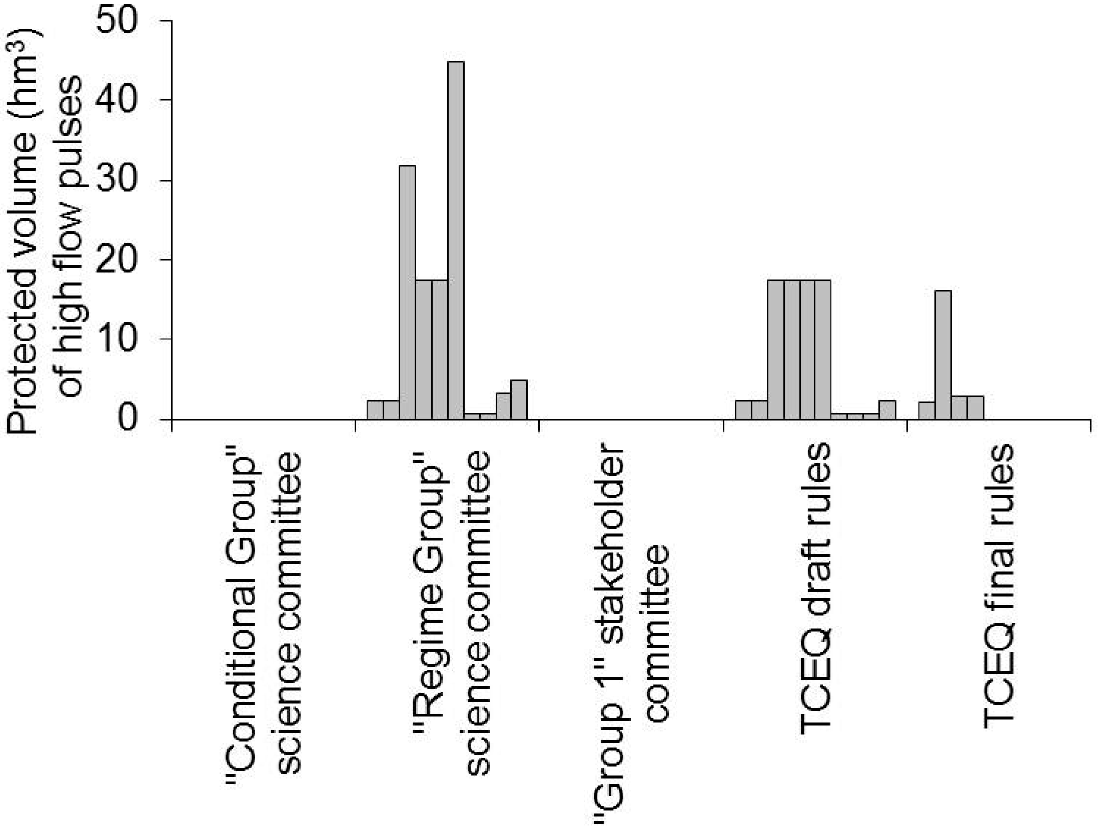


Figure 3.4. Annual volume (hm^3) and number of instream flow pulses recommended by the Trinity and San Jacinto Basins and Galveston Bay science committees and "Group 1" stakeholder committee, and adopted as standards by the Texas Commission on Environmental Quality (TCEQ), the state agency that issues water rights permits, for the Trinity River near Oakwood. Volume of flow pulses are not shown for the "Group 2" stakeholder committee because it only recommended flow pulse trigger discharges and not flow pulse volume. 1 hm^3 = 1,000,000 m^3.

One option to decrease scientific uncertainty in e-flows recommendations is to use a methodology called ELOHA (Ecological Limits of Hydrologic Alteration) to compare environmental conditions along a flow-impairment gradient for classes of streams with similar flow regimes (Arthington et al. 2006, Poff et al. 2009). This methodology was recently proposed for formulating scientifically defensible flow recommendations for rivers lacking site-specific ecological data, and has been used in e-flow management throughout the United States and Australia (e.g., Kendy et al. 2009, Kennard et al. 2010). The adaptive management component of SB3 allows for re-evaluation of e-flow rules with an interval not to exceed ten years, and ELOHA could provide more reliable e-flow standards. Unfortunately, by the time e-flow rules are re-evaluated, additional major water rights will have been allocated. For example, the Brazos River Authority recently re-applied for a water right permit for all unappropriated surface water in the Brazos River. If differences in personal values are the main factor dividing participants in policy disputes, no amount of technical information is likely to change the positions of adversaries (Layzer 2006). Incentives to change the “command and control” structure of river authorities may be as important to achieving consensus on e-flow recommendations as addressing data deficiencies and sources of uncertainty in e-flow science.

E-flows sustain the ecosystem services that rivers provide for humans, including retention of fresh water, removal of nutrients, support for fishery production, maintenance of aquatic riparian vegetation communities, and provision of cultural and recreational opportunities (de Groot et al. 2002). The “natural capital” provided by rivers has been estimated at hundreds of billions of dollars per year (Costanza et al. 1997, Postel and Carpenter 1997). However, water is highly valued in the marketplace (i.e., “blue gold,” Barlow and Clarke 2002), and it is difficult for natural capital to compete against immediate monetary gains from the sale of water rights. Governing authorities have an obligation to protect natural assets for future generations, and only by adopting the public trust doctrine – the idea that essential services and benefits people receive from healthy ecosystems should be assured before water is treated as a commodity – will water be allocated equitably among competing uses (Postel 2003).

CHAPTER V

GENERAL CONCLUSIONS

This dissertation explored physicochemical factors causing spatiotemporal patterns in floodplain river food webs and barriers to management of environmental flows, an important factor influencing food web dynamics. In Chapter II, I reviewed the scientific literature to examine the influence of several key environmental factors, including hydrologic regime, turbidity, concentrations of dissolved organic matter, lateral connectivity between the river channel and floodplain, floodplain vegetation, and presence of upstream impoundment, that might cause basal production sources supporting consumer biomass in floodplain rivers to vary over space and time. In Chapter III, I report findings from field research that examined potential relationships among hydrology, nutrient concentrations, turbidity, and algal primary production and biomass in the littoral zone of five rivers differing in physicochemical conditions. I also use stable isotope signatures of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and deuterium (δD) to estimate contributions of algal- versus terrestrial-based production sources to consumers during different hydrologic periods. In Chapter IV, I conducted interviews of people involved in the Senate Bill 3 (SB3) process to understand why, despite its emphasis on use of the “best available science” to develop environmental flow (e-flow) regimes and “stakeholder involvement” to address the needs of all water users, e-flow recommendations were sequentially reduced until they did not reflect the natural flow regimes for the first two basins to complete the SB3 process. Ultimately, only subsistence flows, one level of base flows, and low flow pulses, the latter for a limited number of sites, were adopted as e-flow rules by the state agency responsible for water rights permitting.

In Chapter II, my review indicated that floodplain vegetation and lateral connectivity between the river channel and floodplain have little influence on the basal production sources supporting secondary consumer biomass. In lowland rivers, organic material that is passively transported from floodplains may play relatively little role in subsidizing aquatic consumers in the river channel. Hydrology, turbidity, dissolved organic matter concentrations, and presence of upstream impoundment explained variation in assimilation of terrestrial material by secondary consumers. Although algae are the dominant production source for large rivers worldwide, organic matter derived from C_3 macrophytes can subsidize aquatic food webs in watersheds with highly erodible sediments during the high-water period (except when river reaches are located downstream from an impoundment), oligotrophic blackwater rivers, and less frequently, following high-flow pulses that increase the amount of terrestrial material in the particulate organic matter pool. Based on these results, I developed a conceptual model of physicochemical factors influencing entrance of terrestrial material into river food webs.

In Chapter III, I found that, despite differences in physicochemical factors including nutrient concentrations, turbidity, and hydrologic regime among my study rivers, algal production and biomass tended to be higher during the low-water period compared to the high-water period. Algae and C_3 macrophytes both made major contributions to consumer biomass, with algae making a greater contribution following extended low-flow periods, and C_3 macrophytes made a greater contribution following high-flow pulses. My research indicates that during flow pulses in floodplain rivers, a decrease in algal biomass and productivity, combined with increased inputs of terrestrial organic matter, can result in increased terrestrial support of metazoan consumers in the aquatic food web.

In Chapter IV, my interviews and review of public records indicated that the Texas SB3 process to set environmental flow rules was derailed as a result of several factors. Both science and stakeholder committees were skewed with more members representing short-term economic needs for freshwater than ecological and recreational needs for freshwater. Many individuals on the science and stakeholder committees worked for river authorities, semiautonomous state agencies that receive the majority of their funding from surface water sales and other activities that require diversions of large amounts of surface water, and consulting firms that regularly contract with the river authorities. These groups appeared to be from the outset distrustful of the SB3 process. Many aspects of e-flow science have high and unavoidable uncertainty. Adaptive management, which often is proposed as a means to reduce uncertainty, was used as justification for making low e-flow recommendations. In the end, the Texas Commission on Environmental Quality, the state agency that regulates and issues water rights permits to river authorities, and other water users set environmental flow rules at levels much lower than those recommended for protection of environmental benefits by the science committees.

Several important points emerge from my dissertation research. First, conceptual lotic food web models including the River Continuum Concept (RCC, Vannote et al. 1980), the Flood Pulse Concept (Junk et al. 1989), and the Revised Riverine Productivity Model (Thorp and Delong 2002) all identify dominant basal production sources. All three models may at times be able to predict the basal production sources supporting riverine consumers, but depending on circumstances. For instance, in sediment-laden river reach located below an impoundment, metazoans seem to be frequently supported by organic matter transported from upstream, as suggested by the RCC. My review (Chapter II) indicates that in order to more accurately predict basal production sources for riverine metazoans, it will be necessary to address spatiotemporal changes in nutrients, turbidity, and hydrology.

Second, humans are having a dramatic influence on the physicochemical conditions of rivers through land transformations such as deforestation, livestock grazing, cropping systems and urbanization, and the construction of dams and other water diversion infrastructure. These alterations are increasing river nutrient loads, decreasing suspended sediment loads, and altering flow regimes. Because I conducted field research on river systems varying in suspended materials, ambient inorganic and organic nutrients, and hydrologic regime, my research provides a foundation upon which predictions can be made about how these changes will influence energy transfers to higher trophic levels. For example, in tropical rivers with high suspended sediment loads, dams or water diversions that lower current velocity and increase water clarity are likely to amplify shifts from terrestrial to algal support of food webs (Chapter III).

Increased importance of algae as a production source sometimes has been associated with an increase in the abundance of non-native, generalist species (e.g., Hoeinghaus et al. 2009).

Third, my research highlights the importance of C_3 macrophytes from riparian zones as sources of energy and nutrients for secondary consumers in large rivers. In all of my study rivers, C_3 macrophytes were an important basal production source supporting the biomass of secondary consumers, particularly following periods of high flow. This suggests that deforestation of riparian zones might result in the unexpected consequence of reduced fish biomass. Lower yields from river fisheries would have particularly devastating effects on the rural poor of developing countries in the tropics.

Finally, my research indicates that, although legislation intended to promote sustainability of freshwater resources and ecosystems may be well-intentioned, unless there is strong incentive to compromise with diverse stakeholders, individuals representing politically powerful groups that view freshwater as a commodity have incentive to undermine conservation policies. In the case of Texas SB3, environmental flow decisions were dominated by individuals employed by river authorities and associated environmental consulting firms advocating for short-term, economic values for freshwater. Repeated negotiations between these stakeholders and stakeholders advocating for ecological, recreational, and related societal values for freshwater ultimately resulted in environmental flow regimes with very limited flow components and that were much reduced from those recommended by ecologists. To maintain the ecological integrity of river basins in Texas, incentives for river authorities to increase dialogue and compromise may be just as important as addressing data deficiencies and sources of uncertainty in environmental flow science.

As human populations and economies continue to expand, human impacts on rivers are increasing and compounding in a synergistic matter. For example, a river is rarely impacted by only a single factor, such as a dam; there are virtually always additional factors, such as watershed changes that affect nutrient and sediment dynamics. My hope is that this foundation provides a framework for future predictions about how anthropogenic impacts to rivers will produce variation in the relative importance of algal versus macrophyte sources supporting consumer biomass, affecting biomass and diversity at higher trophic levels. Furthermore, my dissertation highlights how political obstacles and entrenched water utility interests in Texas pose a daunting challenge to maintaining a semblance of the natural flow regime that sustains native biodiversity.

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