

**INVASION MELTDOWN: INVESTIGATING MUTUAL FACILITATION
ACROSS ECOSYSTEM BOUNDARIES**

by
Christopher Allen Cheek

A Dissertation

*Submitted to the Faculty of Purdue University
In Partial Fulfillment of the Requirements for the degree of*

Doctor of Philosophy



Department of Forestry and Natural Resources
West Lafayette, Indiana
December 2019

THE PURDUE UNIVERSITY GRADUATE SCHOOL
STATEMENT OF COMMITTEE APPROVAL

Dr. Reuben Goforth, Chair

Department of Forestry and Natural Resources

Dr. Paul Brown

Department of Forestry and Natural Resources

Dr. Keith Gido

Kansas State University, Department of Biology

Dr. Tomas Höök

Department of Forestry and Natural Resources

Dr. Brandon Peoples

Clemson University, Department of Forestry and Environmental Conservation

Approved by:

Dr. Robert G. Wagner

Dedicated to my wife and best friend, Dr. Jennifer Zavaleta Cheek

ACKNOWLEDGMENTS

The completion of this dissertation would not have been possible without the support of my loving wife, Dr. Jennifer Zavaleta Cheek. I will always be thankful for her encouragement during the tough times and for celebrating my progress and accomplishments. I would also like to acknowledge the support that I received from family and friends whose encouragement, love, and support was essential in my success. I also like to thank my mentors, Dr. Mark McKinstry and Dr. Tim Patton for teaching me how to do research, for always supporting me in my career, and for being the inspiration for my dissertation research.

Many undergraduate technicians and volunteers were critical for completing this research. Specifically, I would like to acknowledge the work of Josie Cline, Matthew Vorhees, Grace Walker, Rachel Brummet, Samantha Weiss, and Alexandra Perez for being the best lab technicians anyone could hope for. I would also like to thank all those who volunteered in my field research including Chad Smith, Casey Pennock, Sky Hedden, Ben Schlichter, Tevin Tomlinson, Scott Durst, Nathan Franssen, Byron Shorty, Megan Gunn, Andrew Fertig, Jake Mazzone, and Brian Hines. I am also grateful to Bob Rode for his help with experiments at the Purdue Aquaculture Research Laboratory.

I would like to acknowledge funding sources including The Intertribal Timber Council, The American Philosophical Society, the San Juan River Recovery Implementation Program, US Bureau of Reclamation, and Purdue Forestry and Natural Resources for financial support. I thank the National Science Foundation's Graduate Research Fellowship for supporting for my assistantship. In addition, I acknowledge the Sloan Foundation's Indigenous Fellowship Program for financial support, but I would also like to thank the program for fostering a supportive community of indigenous students and mentors. I would also like to acknowledge Navajo Nation and the employees of Navajo Nation Department of Fish and Wildlife for allowing me to conduct research on tribal lands and for providing logistical support for my fieldwork.

Finally, I would also like to acknowledge my committee members for their advice and mentorship that improved my research and helped me to develop professionally. I would to thank my advisor, Dr. Reuben Goforth, for allowing me the freedom to pursue this research project and always being supportive. I thank Dr. Brandon Peoples for his help in designing the research and

for being a great friend. Last, I would also like to thank Dr. Keith Gido, Dr. Tomas Höök, and Dr. Paul Brown for their assistance, advice, and for providing edits that improved the dissertation.

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ABSTRACT

Biotic interactions play key roles in determining invasive species' establishment success in receiving ecosystems (Tilman 2004). The invasional meltdown hypothesis suggests that initial invaders can facilitate subsequent invasions through direct (e.g., commensalism, mutualism) and indirect (e.g., changes in habitat and energy flow) pathways (Simberloff & Holle 1999; Simberloff 2006). Such positive interactions among invaders can alter community-level processes, but little research on this has been done in aquatic-terrestrial landscapes. My dissertation explores the links between reciprocal facilitation of invasive species and ecosystem change in a desert river system in the southwest USA.

Like most rivers in the southwestern United States, the San Juan River has been altered by hydrologic regulation and biological invasions that affect ecosystem function and act synergistically to induce substantial ecosystem change. Invasion of channel catfish (*Ictalurus punctatus*) has drastically altered the fish assemblage of the San Juan River, yet the impacts of riparian invasion by a fruit-bearing tree, Russian olive (*Elaeagnus agustifolia*) have largely been ignored. Channel catfish have been observed consuming Russian olive fruits, but the level of facilitation between species and corresponding impact on the ecosystem is unclear.

Channel catfish may benefit directly from Russian olive invasion by feeding on fallen fruits and/or indirectly from habitat alteration and invertebrate prey production from Russian olive detritus. Additionally, channel catfish may facilitate germination, growth, and seed dispersal of Russian olive. Mutualism between these invaders could increase the fitness of each species, thereby facilitating invasion success. Plant-animal mutualism is the most common form of facilitation among invaders, but no studies, to our knowledge, have evaluated facilitation between invasive riparian plants and aquatic invaders and their combined impact on ecosystem function. My goal preparing this dissertation is to determine whether mutual facilitation between riparian and aquatic invasive species influences ecosystem change through biotic interactions.

To test for mutual facilitation, I first determined the contribution of Russian olive fruits to channel catfish growth by evaluating seasonal diet composition across four sites and six time periods. I then used replicated growth experiments to determine assimilation rates of Russian olive fruits consumed by channel catfish. Using bioenergetics models, I then determined how Russian olive subsidies in San Juan River contribute to channel catfish biomass. To determine

whether channel catfish benefit Russian olive reproduction, I compared germination rates of seeds consumed by channel catfish to seeds consumed by terrestrial mammals and control seeds that had not been eaten.

Russian olive fruits were the most important diet item for channel catfish during the fall and spring, comprising up to 57 and 70% of stomach contents by mass, respectively, and were consumed throughout the year. Feeding trials revealed that Russian olive fruits contributed little to growth or lipid deposition, but they did provide metabolic energy allowing channel catfish fed exclusively Russian olive fruits to maintain weight. In addition, Russian olive trees received a reproductive benefit through increased germination success of seeds consumed by channel catfish over those transported by water. Using bioenergetic models, I showed that Russian olive fruits subsidized 46% of San Juan River channel catfish biomass, indicating that the subsidy from Russian olive fruits had a population-level impact. This dissertation thus establishes mutual facilitation by non-native species across ecosystem boundaries, a phenomenon that few studies heretofore have demonstrated in the ecology or invasion biology literature.

INTRODUCTION

Biotic invasions coupled with habitat loss and alteration are major threats to biodiversity, leading to homogenization of communities across the globe (Mooney and Hobbs 2000). Species invasion can disrupt ecosystem processes and impact native biodiversity through competition and predation. However, invasive species are often the beneficiaries of habitat alterations rather than the drivers of ecosystem and community change (McDougall and Turkington 2005). Changes in ecosystem properties that accompany altered habitats and disturbance regimes can facilitate invasions when the resulting conditions are more suitable for introduced species than for native species. As ecosystems shift in both physical and biotic properties, novel interactions can develop, wherein species that did not coevolve may interact in an ecosystem that differs from their historical context (Hobbs et al. 2009). In these novel ecosystems, interactions between species may be particularly important for structuring communities.

Facilitation, or a positive interaction between species that results in increased biomass or density for one or both species, may be as important as other drivers of community structure such as competition and predation (Hacker and Gaines 1997; Menge 2000; Stachowicz 2001; Rodriguez 2006; Goldberg et al. 1999; Arsenault and Owen-Smith 2002). Positive interactions may be particularly important under stressful scenarios that are likely to be encountered in altered ecosystems or for invaders outside of their native range (Bruno and Kennedy 2000; Stachowicz 2001). Although facilitation is well understood in uninvaded ecosystems, positive interactions are often ignored in the invasion literature compared to negative interactions that introduced species have on native communities (Rodriguez 2006). In fact, introduced species often have little or no impact on native communities and ecosystem function; yet, when this occurs, the invaders and their interaction with other species in the community is often ignored by researchers and managers (Larson 2007). In addition, non-native species may facilitate both introduced and native species through positive interactions (Rodriguez 2006). The preconceived notion that non-native species are inherently detrimental may be at least partially explained by the negative connotation of the terms used in invasion biology and our unconscious biases held by ecologists and conservationists (Larson 2007). As globalization continues to increase the rate of biotic invasion around the globe, interactions between non-native species are expected to increase (Hulme et al. 2009). Understanding how these interactions develop in novel ecosystems (i.e., ecosystems that have been

altered in terms of function and/or species composition compared to historical conditions) and the resulting impacts on ecosystem function and native communities is important for conserving biodiversity in the modern context. However, researchers and resource managers must resist the urge to assume all non-native interactions are negative.

Positive interactions between established invasive species and non-native propagules have the potential to facilitate subsequent invasions. Such positive interactions among non-native species may act synergistically to increase impacts on native communities and ecosystem function. This phenomenon was coined as “invasional meltdown” by Simberloff and Von Holle (1999). As with many invasion theories, the evidence to support invasion meltdown is mixed. For example, a recent meta-analysis by Jackson (2015) indicated that interactions between multiple invasive species are more likely to be negative or neutral. On the other hand, Braga et al. (2018) used a hierarchy of hypotheses approach and found that most studies evaluating invasional meltdown supported the phenomenon. Regardless, both studies noted that community and ecosystem level effects are notably rare in the literature. More research is thus needed to determine when and how positive interactions develop among invasive species and the corresponding impacts on populations, communities, and ecosystems.

The overwhelming majority of studies evaluating interactions between invasive species focus on interactions that occur within the same habitats. However, ecosystem “boundaries” are well known to be permeable. Movement of resources across these boundaries (i.e., resource subsidies) are important for maintaining consumers in recipient ecosystems (Polis et al. 1997). For example, fluxes of aquatic insects as they transition from aquatic larvae to terrestrial adults subsidize predators from spiders to bats in riparian communities and terrestrial insects reciprocally support predatory fishes in aquatic habitats (Nakano and Murakami 2001). Species introductions and habitat alteration have the potential to disrupt linkages and resource flows across these ecosystem boundaries. For example, in forested streams in Japan, invasive white spotted char (*Salvelinus leucomaenis*) were found to reduce aquatic insect subsidies to terrestrial environments, with cascading effects on riparian consumers (Baxter et al. 2004). In addition, reduction in flood pulses from water regulation can reduce subsidies between streams and riparian habitats in both directions (Schindler and Smits 2017). Invasion of riparian vegetation communities can also disrupt subsidies of allochthonous inputs of leaf litter that are important sources of nutrients in some aquatic systems. Mineau et al. 2012 found that Russian olive (*Elaeagnus angustifolia*)

invasion in spring-fed Idaho streams reduced ecosystem efficiency due to the slow decomposition rates and low-quality of litter inputs. Although it is clear that species invasion can impact resource flows between habitats, few studies have evaluated how invasive species interact across these permeable ecosystem boundaries.

The Upper Colorado River (USA) has been greatly altered in both physical and biotic properties. Flow regulation and water withdrawal have impacted both native community structure and physical habitat heterogeneity, facilitating the establishment and proliferation of non-native species (Tyus and Saunders 2000; Propst and Gido 2004; Gido and Propst 2012; Olden et al. 2016). Many of these non-native species have substantial impacts on native species and ecosystem function and are therefore considered invasive. The combined impacts of invasive species and hydrologic modification has led to declines in native fishes, ultimately resulting in four federally listed as endangered species: Colorado pikeminnow (*Ptychocheilus lucius*), razorback sucker (*Xyrauchen texanus*), humpback chub (*Gila cypha*), and bonytail chub (*Gila elegans*) (Tyus and Saunders 2000). In the San Juan River, a major tributary to the Upper Colorado River, non-native species richness is greater than native species (Sublette et al. 1990). In addition to aquatic invasions, riparian invaders, primarily Russian olive (*Elaeagnus agustifolia*; RO) and salt cedar (*Tamarix spp.*) have been facilitated reductions in flood magnitude and duration that scour banks and disturb riparian vegetation, leading to declines in native cottonwood (*Populus deltoides*) and willow (*Salix laevigata*). In addition, riparian invasion has greatly altered bank vegetation coverage. In the San Juan River, bank vegetation coverage increased from 10% in the 1930s to 90% in 2010s (Basset et al. 2015). Russian olive has succeeded salt cedar as the dominant invader in riparian communities of the San Juan River. This fruit-bearing riparian tree species produces large-quantities of carbohydrate-rich fruits in the fall and winter that are valuable food for some wildlife (Katz and Shafroth 2003).

Channel catfish (*Ictalurus punctatus*; CCF) invaded the San Juan River and the rest of the Upper Colorado River Basin as early as the late 1800s. In the San Juan River, which lacks other non-native, piscivorous predators found in other parts of the basin such as walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), and northern pike (*Esox lucius*), CCF are a primary concern for the San Juan River Recovery Implementation Program, a multiagency cooperative program tasked with the recovery of Colorado pikeminnow and razorback sucker in designated critical habitat. Mechanical removal programs have targeted CCF in an effort to reduce predation

pressure and competition thereby facilitating efforts to reestablish endangered species through augmentation programs (Franssen et al 2014; Pennock et al 2018). However, evidence of negative impacts of CCF on native fishes is sparse, and removal programs have shown little progress in reducing CCF abundance or increasing native fish populations (Franssen et al. 2014). Diet studies of CCF have shown low rates of piscivory, and direct predation of endangered species is rare (Patton et al 2012; Brooks et al. 2000). However, stomach content analyses of CCF in the San Juan River have shown that CCF consume RO fruits. Moreover, RO is a major seasonal component of CCF diet. Yet, little is known about how CCF may benefit from the interaction with RO trees.

The interaction between RO and CCF has the potential to be mutually beneficial. Subsidies of RO fruits may provide an abundant source of energy for CCF populations, and RO trees may benefit in reproductive success via increased germination probability and seed dispersal. The focus of my dissertation is to better understand the interactions between these two non-native species across the aquatic-terrestrial interface. In Chapter 1, I used traditional stomach content analysis to evaluate the seasonal use of RO fruits by San Juan River CCF. In addition, I measured prey and RO availability to determine the factors contributing to CCF use of this novel subsidy. In Chapter 2, I evaluated the mutual facilitation between these two non-native species using laboratory experiments. First, I conducted feed experiments to determine if CCF can utilize RO fruits for growth, lipid deposition, or metabolic energy. Second, I evaluated germination potential of RO seeds consumed by CCF, mammals, and seeds transported downstream by water flow. In Chapter 3, I determined the population-level effect of RO subsidies on CCF populations in the San Juan River. Using bioenergetic models coupled with abundance estimates, I determined the amount of CCF biomass that is facilitated by RO subsidies. My hypothesis and objectives were:

Hypothesis: Mutualism between RO and CCF positively affects the species' fitness (measured as reproduction and condition), thereby facilitating biological invasion and/or persistence.

Specific Objectives:

1. Determine seasonal diet composition of San Juan River CCF to determine the extent of RO fruit consumption
2. Determine the effect of prey availability, fish size, and temperature on use of RO subsidies by CCF

3. Using a laboratory feed experiment, evaluate CCF growth and lipid deposition when fed varying diets of RO fruit and insect meal
4. Evaluate the impact of CCF consumption on RO germination compared to mammals and water transported seeds
5. Formulate bioenergetic models to estimate the contribution of RO fruits to energetic consumption of San Juan River CCF
6. Use abundance estimates of CCF populations to determine the amount of CCF biomass that is facilitated by RO subsidies in the San Juan River

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CHAPTER 1: INVASIVE RIPARIAN TREES PROVIDE A NOVEL TROPHIC SUBSIDY TO A NON-NATIVE FISH IN A COLORADO RIVER TRIBUTARY

Abstract

Facilitation, or positive interactions between species, can determine the structure of biotic communities. Facilitation between non-native species has the potential to act synergistically to impact native species and ecosystem function. The San Juan River, a tributary to the Upper Colorado River, has been altered by water regulation benefiting establishment of non-native and invasive species in both aquatic and riparian ecosystems. Channel catfish invaded the San Juan River in the late 1800s and threaten native and endangered fishes via predation and competition. Russian olive, an invasive, fruit-bearing riparian tree, dominates bank vegetation in the San Juan River and has increased allochthonous inputs of litter and fruits from terrestrial habitats. Channel catfish have been observed to consume Russian olive fruits as a major component of their diet. However, little is known about this interaction. In this study I evaluate the importance of Russian olive fruits as a subsidy to channel catfish diets. I conducted stomach content analysis and collected food availability at four sites along a longitudinal gradient of the San Juan River every two months from September 2016 to September 2017. I used mixed-effects models to determine how prey availability and environmental conditions impact Russian olive fruit consumption by channel catfish. I found that channel catfish consumed Russian olive fruits throughout the year and the fruits comprised the majority of channel catfish stomach contents in the fall (56.7%) and spring (75%). Using a model selection approach, I determined that the best models of Russian olive fruit consumption were explained by temperature, total length, Russian olive availability, benthic macroinvertebrate availability, and season. There was also a significant interaction between Russian olive availability and season. Surprisingly, there was a positive correlation between Russian olive consumption and benthic availability, indicating the Russian olive consumption was not a result of low alternative prey availability. My results indicate that Russian olive fruits represent a significant subsidy to non-native channel catfish populations in the San Juan River.

Introduction

Aquatic habitats are becoming increasingly altered due to anthropogenic changes and increasing numbers of non-native and invasive species (Hobbs et al. 2009). Disturbed ecosystems now have more interactions between invasive and native species, as well as with other non-native species, that change the environmental context. These disturbed systems provide new opportunities to study interactions, and more information is required to guide management efforts. As biotic communities are affected by altered environmental conditions, mutually beneficial interactions may develop between invasive species that may improve the survival, reproduction, or growth of one or both species. Facilitation, or positive interactions between species that result in increased biomass or density of one or both species, is important in predicting community structure (Rodriguez 2006). The impact of facilitation on community structure plays an increasingly important role as environmental stress increases (Bruno and Kennedy 2000; Stachowicz 2001) and may be important for determining the success or failure of invasions.

Simberloff and Von Holle (1999) suggested that positive interactions among invasive species could increase the rate of invasion, leading to an “invasional meltdown”. Although some evidence suggests that this phenomenon does occur in some contexts, it is likely the exception as opposed to the rule. Instead, biotic resistance, or reduced invasion success with increasing number of invasive species, is more likely to occur due to negative interactions such as predation and competition Jackson (2015). Although positive interactions among invasive species may be rare they are nonetheless important, as multiple invasive species can act synergistically to increase impacts on native species and ecosystem function (Didham et al. 2007). Understanding these relationships in highly altered ecosystems that contain endangered animals is increasingly important as managers seek more information on if and how to manage invasive species.

Species invasion and habitat alteration are likely to change the magnitude, timing, distribution, and importance of resource subsidies compared to undisturbed or uninvaded habitats (Gergs et al. 2014; Larsen et al. 2016). For example, reduced flows and flood pulses from river regulation are associated with decreased emergence of aquatic insects into terrestrial ecosystems (Greenwood and McIntosh 2008; Schindler and Smits 2017). Such resource subsidies cross ecosystem boundaries and are important for maintaining consumers in recipient habitats (Polis et al. 1997). Invasive species can also disrupt linkages between aquatic and terrestrial ecosystems.

For example, Baxter et al. (2004) demonstrated that an invasive salmonid reduced the flux of insects from forest streams with cascading impacts on terrestrial consumers. As ecosystems become more disturbed, resource flows from outside the system may become increasingly important. For example, trout in streams contaminated by heavy metals rely more on terrestrial insect prey due to decreased aquatic insect prey availability (Kraus et al. 2016). A body of literature exists documenting the effects of aquatic invasions on aquatic-terrestrial subsidies, but few studies have assessed how terrestrial invasions, and in particular riparian invasive species, may influence aquatic communities.

Riparian habitats in arid regions are particularly susceptible to invasion (Hood and Naiman 2000). For example, invasions by Russian olive (RO; *Elaeagnus angustifolia*) and salt cedar (*Tamarix spp.*), combined with declines of native species such as plains cottonwood (*Populus deltoides*), have led to extensive assemblage shifts in riparian communities in many river basins in the southwestern United States (Brock 1994; Pearce and Smith 2007; Nagler et al. 2011). In addition, reduced disturbance from flood pulses has led to increased bank vegetation coverage. For example, in the San Juan River (New Mexico, USA), bank vegetation has increased from 10% in the 1930s to more than 90% in 2010s as indexed from historical aerial imagery (Basset et al. 2015). This increase was primarily driven by increases in RO trees that now dominate the riparian landscape. These invasions were at least partially facilitated by water withdrawal and reduced flood pulses that benefit native vegetation and maintain river channel morphology (Poff et al. 2011). The establishment of invasive bank vegetation combined with flow regulation has resulted in the loss of channel complexity, disconnection from the floodplain, and decreased channel width (Hultine and Bush 2011). Such changes can substantially alter both aquatic community composition and ecosystem function of affected rivers.

Russian olive, native to Central Asia, was introduced both as an ornamental plant and for erosion control via formation of wind breaks (Christensen 1963). Since introduction, the species spread across the Great Plains and Intermountain Western United States, primarily invading riparian and wetland areas (Katz and Shafroth 2003). The extent of the invasion is limited by cold temperatures required for seed germination, restricting RO invasion to elevation and latitudinal gradients (Guilbault et al. 2012). In the Colorado River Basin, RO invasion began as early as the early 1900s, was well established by the 1940's, and has continued to increase with the construction of large impoundments and increased water development (Katz and Shafroth

2003). In the San Juan River, RO was present as early as 1950. The construction of Navajo Reservoir in 1958 also likely benefited RO establishment and spread in the San Juan basin. Anthropogenic and natural processes have led to increased RO invasion that changes channel morphology and riparian ecosystems.

Although considerable research has demonstrated how riparian communities respond to RO invasion, less attention has been given to its effect on aquatic communities. Given the large increases in bank vegetation coverage, it follows that allochthonous inputs of RO leaf litter have greatly increased. Allochthonous inputs of leaf litter are well known to subsidize aquatic shredders (Leberfinger et al. 2011). However, RO litter is characterized by low decomposition rates and is, therefore, less efficient than native vegetation (Simons and Seastedt 1999). Mineau et al. (2012) found that although the invasion of RO increased litter inputs, there was not a resulting increase in stream respiration, suggesting that RO increased downstream transport of nitrogen and reduced ecosystem efficiency in a small spring fed creek in southern Idaho. In addition to impacts on ecosystem function, RO may provide direct subsidies to aquatic consumers. In the same study system as Mineau et al. (2012), Heinrich (2015, unpublished) found that common carp (*Cyprinus carpio*) utilized RO fruits in their diet. Using bioenergetic modeling, Heinrich proposed that RO provides a direct trophic subsidy that facilitates non-native common carp populations. However, the ability of RO to facilitate invasions by other invasive fishes has received little attention.

In addition to terrestrial invasions, the San Juan River has also been greatly impacted by aquatic invasions. The most common large-bodied aquatic invader in the system, channel catfish (*Ictalurus punctatus*; CCF), was introduced to the San Juan River in the late 1800s and is a primary conservation concern for native fishes as both a predator and competitor. The San Juan River is critical habitat for two endangered species, Colorado pikeminnow (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*). In addition to other management actions, the San Juan River Recovery Implementation Program has actively managed CCF through electrofishing and mechanical removal for the last two decades (Franssen et al. 2014). These management actions were implemented in response to the concern that invasive CCF preyed on Colorado pikeminnow and razorback sucker or directly competed with native fishes. However, this assumption was not well supported with empirical data. Even with intensive removal efforts, the program has been unable to show decreases in CCF abundance or corresponding responses in

native fish populations (Franssen et al. 2014). However, removal efforts are credited with reducing the number of fish in larger size-classes, ie.: those presumed to be the most piscivorous and thus posing the greatest risk to endangered fishes (Pennock et al. 2018). Managers are currently conducting a moratorium on removal efforts to determine the impact of management efforts and to determine the level of CCF predation on native fishes. Because CCF are the object of much management attention and funding, it is important to understand the trophic relationships between CCF and native species. In addition, it is important to understand the biotic interactions that facilitate the persistence of CCF in the San Juan River.

Fruits from RO trees may represent a significant subsidy to CCF populations in the San Juan River, but more research is needed to determine the extent of this interaction. Some of the first diet studies on CCF from the San Juan River in the early 1990s indicated that a high proportion of CCF consumed RO fruit (Brooks et al. 2000) and fruits comprised up to 40% of CCF diet for some size classes. More recent diet studies in 2010-2011 indicated that RO is still a primary component of CCF diet in the San Juan River (Patton et al. 2012). The use of RO fruits by CCF is not surprising given that they are known to exhibit frugivorous behavior in their native range by consuming primarily mulberry (*Morus rubra*) fruits (Chick et al. 2003). The San Juan River and most arid land rivers in the western USA lack native riparian vegetation that produces fruit. The invasion of RO in the riparian corridor may therefore provide a novel subsidy that CCF have the evolutionary experience to exploit, unlike native species. However, no studies have evaluated how large subsidies of RO fruits may facilitate invasive fish populations in the San Juan River.

In this study, I examined the spatial and seasonal patterns of RO consumption by CCF, illustrating the importance of RO fruits as a subsidy for San Juan River CCF. To do this, I estimated CCF diet, RO availability, and invertebrate prey availability in four river study sites along the longitudinal gradient of the San Juan River. I hypothesized that RO fruit provides a trophic subsidy to CCF populations and predicted that RO consumption would be greatest in the fall when the fruits are mature and most available to CCF. Further, I expected CCF fruit consumption to be greatest during periods when other prey items were the most limited. My specific objectives were to: 1) quantify seasonal diet consumption of CCF using stomach content analysis; 2) quantify seasonal benthic prey and RO fruit availability; and 3) use linear mixed models to develop a predictive model describing the consumption of RO fruits by CCF.

Methods

Field Methods

The study area included four 8 km river study sites along the longitudinal gradient of the San Juan River, with each study site separated from the others by at least 40 km (Figure 1.1). Within each study site, I randomly selected three 1.6 km reaches, each separated from the others by 1.6 km. I sampled fish diets and availability every other month from September 2016 to September 2017. Sampling efforts were grouped into the following seasonal categories: fall (September 24-30, 2016; November 15-20, 2016; and September 25-30, 2017), summer (July 21-26, 2017), and winter (January 24-30; February 1-2; and March 22-24, 2017).

CCF were captured using non-motorized, raft-based electrofishing (Smith Root GPP 9.0) operated as a single pass from upstream to downstream while focusing on shallow habitats near riverbanks. Shocking began along the left or right bank (randomly determined), and effort alternated between banks at the mid-point of the reach. CCF were netted, placed in a live well, and later euthanized using MS-222 (Tricane-S, Western Chemical). Total length (TL, mm), weight (g) and sex were determined for each fish and the complete gastrointestinal (GI) tract was removed. Care was taken to keep all contents in the stomach and lower GI. Excised GI tracts were placed in individually labeled Whirl-Pak® bags and stored on wet ice until they were later transferred to a freezer (-20 °C).

I quantified benthic macroinvertebrate biomass as a proxy for alternative prey availability. I quantified macroinvertebrate biomass based on six randomly selected transects within each study reach (18 transects per study site, 72 transects per season). I collected 10 kick samples along each transect in shallow, wadable habitats using a D-ring kick net (500 um mesh; Wildco®, Yulee, FL). Each kick encompassed $\approx 0.1 \text{ m}^2$ and the total sample along each transect was $\approx 1 \text{ m}^2$. When water depth or velocity prohibited sampling along a single transect, I sampled multiple transects, with each separated by $\geq 10 \text{ m}$. The combined 10 kicks along a transect were preserved as a single sample using 70% ethanol.

I measured RO fruit availability along the river reaches using litter traps. Traps consisted of a 25 cm diameter funnel attached to a 13 cm section of 6 cm diameter PVC pipe capped with wire screen on the bottom to catch the fruits. Traps were attached to a metal post 1 m from the base of a randomly selected RO tree to minimize predation by small mammals and to limit moisture pooling in the trap. Traps were placed under the canopy of three randomly selected RO

trees within each reach (nine per section; 36 total seed traps). Seed traps were emptied during each sampling event and the contents stored in a plastic bag and placed in the freezer (-20 °C). Litter and RO fruits were separated, counted, dried at 60 °C for 72 hr., and weighed (± 0.01 g). The measure of RO availability used in later models was dry weight of RO fruits per day ($\text{g/m}^2/\text{day}$).

Laboratory Methods

Frozen stomach content samples were thawed 1-2 hr. prior to processing. Once thawed, the stomach and intestines were separated at the pyloric sphincter. The stomach was dissected, and the contents rinsed into a 250- μm sieve. Coarse items such as RO seeds, fishes, and crayfish were removed and set aside. The remaining contents were placed in a Petri dish and sorted under a dissecting stereoscope (Nikon Model SMZ1275) or lighted bench magnifying glass. Insects were identified to order, and fishes were identified to species when possible. When identification was not possible, items were grouped into broader categories (e.g., aquatic insects, terrestrial insect, fishes, crayfish). Once the stomach contents were sorted and identified, individuals within each prey category were counted. Wet weight (± 0.01 g) was measured after removing surface water with a dry paper towel. Samples were placed in a drying oven at 60 °C for 72 hr. before measuring dry weight (± 0.01 g). After the samples were processed, prey items were grouped into broader categories for analysis. The categories were: RO, aquatic invertebrates, terrestrial arthropods, terrestrial vertebrates, fish, crayfish, plant debris, and unknown or other.

Benthic macroinvertebrate samples were sorted into two habitat categories: riffle and run. All samples of each habitat type were combined for each reach, typically three riffles and three runs, ending with one aggregate riffle sample and one aggregate run sample per reach. Aggregate samples were subsampled to estimate the biomass of invertebrates by first picking and rinsing coarse debris from the sample and then evenly spreading the remaining sample across a sorting tray with 15 7-cm cells. Three cells within the tray were randomly selected and the contents, both debris and invertebrates, were removed from the tray and placed in a Petri dish. The contents of the Petri dish were then sorted under a lighted bench magnifying glass and then checked for smaller invertebrates using the dissecting microscope. Sorted invertebrates were stored in 70% ethanol until later identified to order and counted. The sampling efforts primarily produced aquatic insect taxa in the orders Ephemeroptera, Tricoptera, Odonata, Plecoptera, and

Diptera. Insects were then combined and placed in a drying oven at 60 °C for 72 hr. before measuring dry weight (± 0.01 g). The total dry weight of all invertebrate samples was used as a proxy of over aquatic insect prey availability within a reach. Macroinvertebrate availability was calculated as dry biomass by square meter.

Analytical Methods

Mean daily water temperature (°C) data for the date of field sampling were obtained for the from United States Geological Survey (USGS) monitoring stations located at Shiprock (USGS 09368000), Four Corners (USGS 09371010), and Mexican Hat (USGS 09379500). Gages at Shiprock and Four Corners are within study segments, and the Mexican Hat gage is ≈ 1.6 km downstream of the last study segment. Study segment 3 has no gaging station close enough to provide direct temperature measures, and temperatures for this segment were averaged using data from the closest upstream and downstream stations. Finally, discharge (m^3/sec) and turbidity data were obtained from available USGS gaging stations.

Stomach content sample data were summarized as percent weight, percent count, and percent frequency of occurrence for each diet item category. Because each of these measures of diet composition may be biased by the digestibility of prey items with a higher proportion of indigestible material may be over represented in stomach contents compared to prey items composed primarily of soft tissue (ex: crayfish vs dipteran larvae). In order to account for this bias, I used the index of relative importance (IRI) to calculate overall importance of each diet item category. IRI is calculated as the percent frequency multiplied by the sum of percent number and percent weight. IRI is presented as percent IRI, as suggested by Cortes (1997), and is calculated as the IRI score divided by the sum of the IRI scores for all diet categories and multiplied by 100.

Understanding RO and prey fish consumption was a focus of this study; therefore, developing explanatory models was a critical component. I used generalized linear mixed models to predict the proportion of CCF diet composed of RO fruits. I selected five environmental and individual variables that I predicted to have an effect on RO consumption: CCF TL, RO availability, macroinvertebrate availability, water temperature, turbidity, and discharge. I checked for multicollinearity using the variance inflation factor (VIF), and all but one predictor was moderately correlated (VIF: 1-5), with a VIF = 5.6 for benthic

macroinvertebrate availability. Homogeneity of variance assumption was checked visually by plotting the residuals and examining box plots of the categorical variables.

I checked for collinearity, and the explanatory variables were not highly correlated (<0.5). Due to the varying scales of the continuous explanatory variables, I scaled and centered the data for all models. I also included season (as defined in sampling methods) as a fixed-effect and some models included interactions between season and temperature, RO availability, and invertebrate availability. The models were run with a random intercept for study sites with reaches nested within site because I was not interested in the effect of longitudinal distribution of the sampling sites. Proportion of stomach contents composed of RO fruit or seeds was used as the response variable. Proportional data were transformed using the arcsine square root transformation. Due to known issues with proportional data and the arcsine transformation (Warton and Hui 2011), I also used a logistic model with a binary response of RO in the stomach contents of CCF. The arcsine transformed proportion models were run using lmer function and the logistic models were implemented with the glmer function, both found within the lme4 package (Bates 2015) in RStudio version (v1.1.463).

To select the best model, I used a combination of model selection criteria including AIC, AICc, BIC, and log likelihood to evaluate models. I only compared models with the same random effects structure (reaches nested within sites) and the same response variable. Herein, I report the best models based on the model selection criteria and those with Δ AICc values <10 compared to the top-ranking model (Aho et al. 2014). I calculated the variance explained by the model as a pseudo r-squared (R^2) for mixed models following the methods of Nakagawa and Schielzeth (2013). This calculation provides a marginal R^2 , representing the variance explained by the fixed effects of the model, and the conditional R^2 , representing the combined variance explained by the fixed and random effects in the model. R^2 calculations were derived using the r.squaredGLMM function in the MuMin package in RStudio (Barton and Barton 2013).

Results

A total of 545 CCF stomachs were processed for dietary composition analysis. The number of CCF captured during each sampling period varied, with most stomachs collected during fall (Table 1.1). RO and aquatic invertebrates were the primary diet items across all

measures of diet composition (frequency of occurrence, number, weight, and IRI) and across all seasons sampled (Figure 1.2, Table 1.1). Surprisingly, RO was consumed across all time periods and was not limited to short pulses in the fall as originally hypothesized (Figure 1.3A). RO made up the greatest proportion of fall and spring diets. Aquatic invertebrate consumption was greatest in the summer and winter, when RO consumption was lower. Terrestrial invertebrates, primarily insects, spiders, and isopods, were secondary but common diet items that comprised a relatively low proportion of the diet by weight. Consumption of terrestrial vertebrates was documented but not common, including birds, lizards, and small mammals. Fish consumption was surprisingly low, with fish or fish parts detected in only 5.6% of stomachs. Non-native virile crayfish (*Orconectes virilis*) were detected in stomachs in all seasons, but they were more frequent during the winter and spring (Table 1.1); however, crayfish composed a small percent of the total stomach content by weight. Terrestrial vertebrates were most prevalent in the winter and spring time periods, and use of these prey items was more common in large size classes. Bycatch or debris, including plant material, filamentous algae, sand, and gravel, was common in CCF stomachs, but was likely not an important diet item. Diet composition was significantly different between seasons ($A=0.39$, $p=0.001$) and between sites ($A=0.48$, $p=0.001$), tested using multi-response permutation procedure. Pairwise comparisons showed that diet composition was significantly different between all seasons and all sites. RO fruits were available in all seasons but were spatially variable (Figure 1.3B). RO fruits were least available in the summer months when benthic invertebrate biomass was greatest (Figure 1.3C).

The highest-ranking model using both linear and logistic regressions included direct effects of TL, RO availability, benthic macroinvertebrate availability, mean daily water temperature, and season, as well as an interaction between RO availability and season. The coefficients, confidence intervals, and p-values of the explanatory variables are presented in Table 1.2 for the linear model and Table 1.3 for the logistic model. In both models, RO fruit availability in the environment was significantly and positively associated with the proportion of RO in the stomach contents, but the effect of RO availability depends on the time of year. Contrary to my hypothesis that RO consumption would be negatively associated with alternative prey availability, benthic invertebrate availability was positively associated with RO consumption. TL was positively associated with RO consumption, but the effect size was relatively small. Temperature, however, was strongly positively associated with RO

consumption. RO consumption was not different in fall and winter but was significantly lower in the summer and slightly lower in the spring. The interclass correlations for both models were low (0.01) indicating that the random effect of reaches nested in section was minimal.

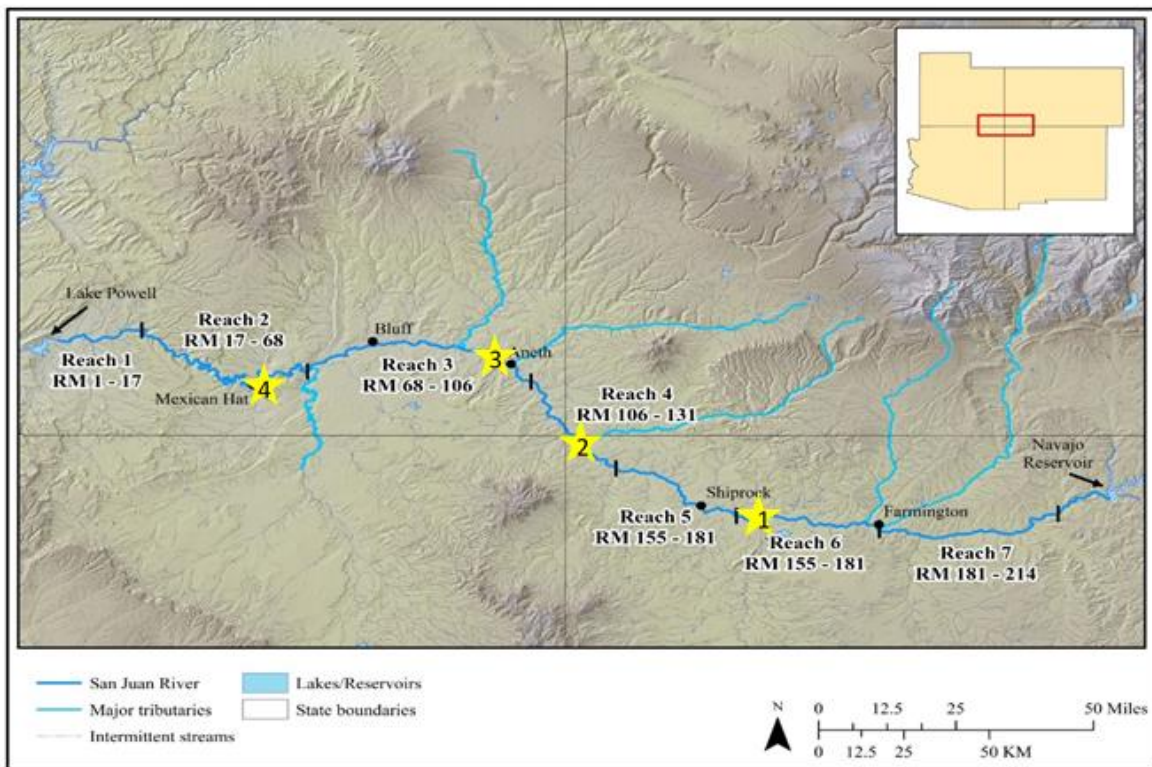


Figure 1.1. Map of study area on the San Juan River where channel catfish, *Ictalurus punctatus*, stomach content and prey availability data were collected. Yellow stars indicate study sites with site 1 most upstream. Reaches indicated on the map are designated by the San Juan River Recovery Program.



Figure 1.2 Proportion of channel catfish (*Ictalurus punctatus*) stomach contents by wet weight for nine prey categories by month collected in the San Juan River (NM/UT) from September 2016 to September 2017.

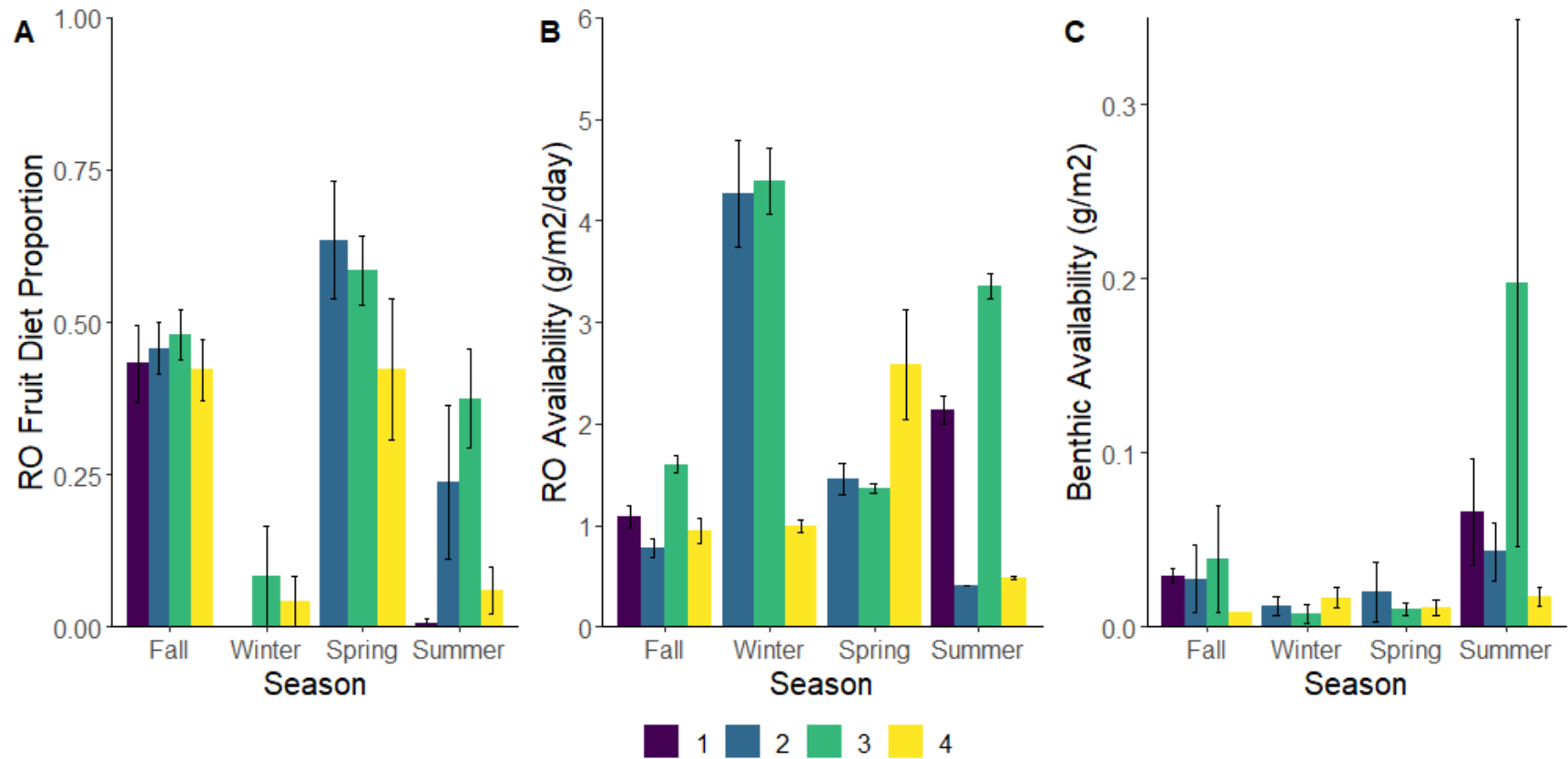


Figure 1.3. Mean (\pm SE) summarized by season and section for (A) proportion of channel catfish (*Ictalurus punctatus*) stomach contents composed of Russian olive fruit (*Elaeagnus angustifolia*), (B) Russian olive availability from seed traps (g/m²/day), and (C) benthic aquatic invertebrate availability from kick-net sampling (g dry weight/m²). All measurements are based on dry weights.

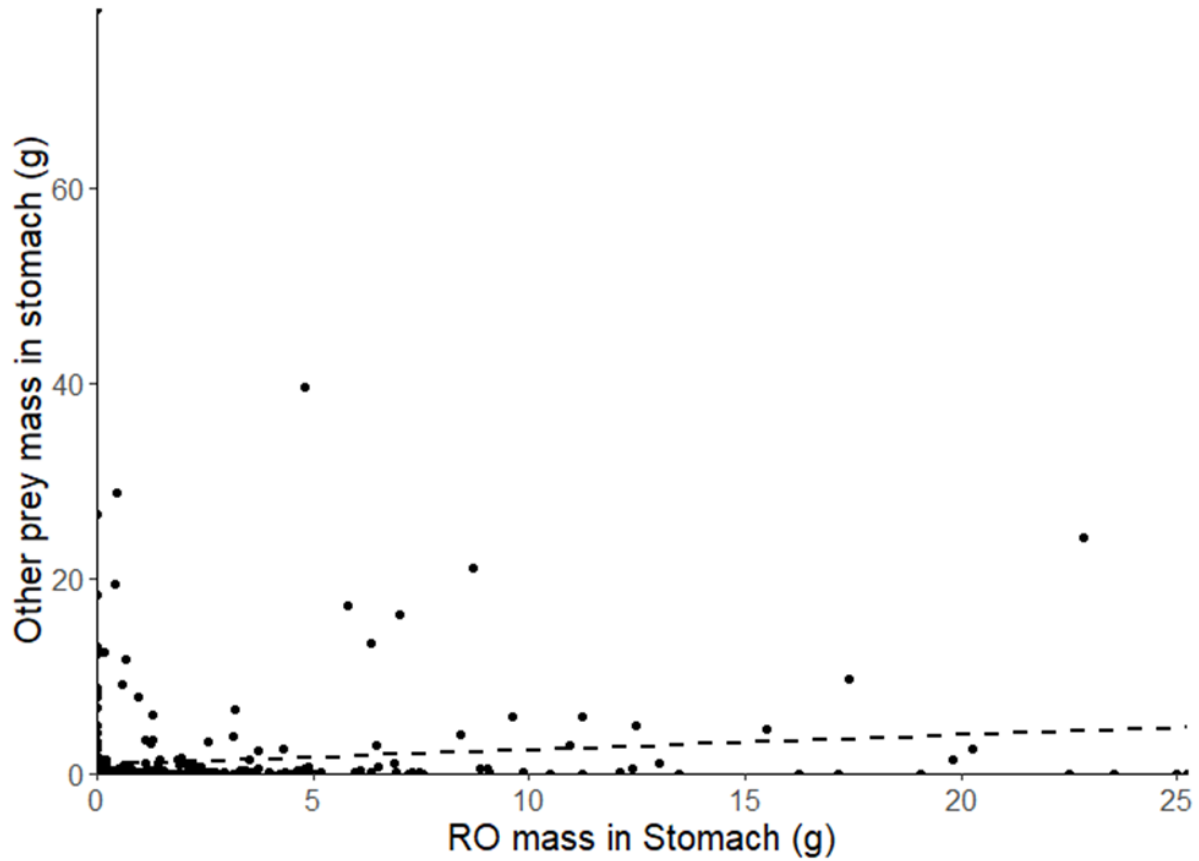


Figure 1.4. Mass of Russian olive fruits observed in channel catfish stomachs compared to other prey identified in the stomachs. Mass for other prey only includes item presumed to be important in the diet not including debris , algae, or other vascular plant material.

Table 1. 1. Percent occurrence (%O), number (%N)), weight (%W), and index or relative importance (%IRI) for diet categories for channel catfish (*Ictalurus punctatus*) each season from the San Juan River from September 2016 through September 2017

Diet Category	Fall (n=356)				Winter (n=45)				Spring (n=72)				Summer (n=72)			
	%O	%N	%W	%IR I	%O	%N	%W	%IR I	%O	%N	%W	%IR I	%O	%N	%W	%IR I
Russian																
Olive	56.7	42.6	45.5	53.1	4.4	30.9	4.1	1.4	75.0	52.1	56.0	72.9	31.9	34.4	17.5	21.7
Aquatic																
Insect	63.2	29.7	27.9	38.7	91.1	31.4	86.1	95.2	61.1	9.6	9.2	10.4	55.6	18.7	13.1	23.2
Isopods	11.2	2.5	3.3	0.7	0.0	0.0	0.0	0.0	40.3	7.6	9.8	6.3	22.2	2.2	6.3	2.5
Terr																
Arthropod	29.5	2.1	4.5	2.1	6.7	1.0	1.3	0.1	45.8	3.2	4.8	3.3	37.5	6.2	9.4	7.6
Terr																
Vertebrat																
e	0.8	1.3	0.8	0.0	6.7	2.0	5.0	0.4	6.9	8.2	2.3	0.7	2.8	0.5	1.3	0.1
Crayfish	5.9	16.2	3.3	1.2	8.9	33.0	2.5	2.8	20.8	14.9	4.8	3.7	5.6	22.9	3.1	1.9
Fish	6.2	1.2	2.8	0.3	4.4	0.4	1.0	0.1	6.9	0.7	1.9	0.2	4.2	0.3	2.3	0.1
Algae	5.3	0.5	2.5	0.2	0.0	0.0	0.0	0.0	1.4	0.2	1.0	0.0	56.9	6.9	42.3	36.6
Plants	28.1	3.7	8.6	3.7	2.2	0.7	0.0	0.0	30.6	2.7	3.9	1.8	40.3	7.9	3.9	6.2
Other	4.8	0.3	0.8	0.1	0.0	0.6	0.0	0.0	12.5	0.8	6.2	0.8	5.6	0.0	0.7	0.0

Table 1. 2. Coefficient estimates, confidence intervals, p-values, random effects, and R2 for the highest-ranking model of arcsine transformed proportion of channel catfish (*Ictalurus punctatus*) stomach contents that were identified as Russian olive fruits. Samples were collected from four sections from September 2016 to September 2017.

Interaction 1			
Predictors	<i>Estimates</i>	<i>CI</i>	<i>p</i>
Intercept	0.72	0.65 – 0.79	<0.001
TL	0.05	0.00 – 0.10	0.048
RO Availability	0.11	0.03 – 0.19	0.009
Benthic Availability	0.26	0.15 – 0.37	<0.001
Temperature	0.24	0.14 – 0.34	<0.001
Winter	-0.12	-0.40 – 0.16	0.408
Summer	-1.11	-1.33 – -0.89	<0.001
Spring	0.3	0.15 – 0.46	<0.001
RO x Winter	-0.08	-0.21 – 0.05	0.245
RO x Summer	-0.42	-0.65 – -0.19	<0.001
RO x Spring	-0.07	-0.24 – 0.09	0.361
Random Effects			
σ^2	0.3		
τ_{00}	0		
ICC	0.01		
N	4		
	3		
Variance Explained			
Observations	531		
Marginal R2	0.263		
Conditional R2	0.268		

Table 1. 3. Odds ratio, confidence intervals, and p-values, random effects, and R^2 for the highest ranking mixed-effect, logistic model of Russian olive (*Elaeagnus agustafolia*) presence in channel catfish (*Ictalurus punctatus*) diet based on AICc model selection. Samples were collected from four sections from September 2016 to September 2017.

Best Logistic Model			
Predictors	<i>Odds Ratios</i>	<i>CI</i>	<i>p</i>
Intercept	1.68	1.30 – 2.16	<0.001
TL	1.51	1.21 – 1.87	<0.001
RO Availability	1.28	0.92 – 1.77	0.136
Benthic Availability	2.88	1.83 – 4.54	<0.001
Temperature	1.78	1.21 – 2.62	0.003
Winter	0.09	0.01 – 0.71	0.023
Summer	0.03	0.01 – 0.09	<0.001
Spring	3.24	1.70 – 6.17	<0.001
RO x Winter	0.97	0.41 – 2.31	0.941
RO x Summer	0.21	0.08 – 0.54	0.001
RO x Spring	0.7	0.37 – 1.31	0.261
Random Effects			
σ^2	3.29		
τ_{00} section: reach	0.01		
ICC	0		
N section	4		
N reach	3		
Variance Explained			
Observations	531		
Marginal R^2	0.375		
Conditional R^2	0.376		

Discussion

RO fruit was a major diet item for San Juan River CCF in this study. RO fruits are plentiful in the system and available almost year-round. Consumption of RO fruit by CCF was most prevalent in the fall and spring, possibly related to a combination of RO fruit availability and temperature. I originally hypothesized that RO fruit consumption could be related to low availability of alternative prey available to CCF. However, my analyses indicated that RO fruit consumption was greatest during periods of high benthic prey availability. High prey availability during the fall, when RO fruits were abundant, temperatures were high, and stomach fullness was the greatest, likely drove this relationship. RO fruit consumption was lowest during the summer, which was related to low availability of RO fruit combined with high prey availability.

As far as I am aware, no other studies have documented the extent of frugivory by CCF in the San Juan River. I found only few mentions of CCF consuming RO fruits in the literature (Brooks et al. 2000), even though many river systems across the Southwest and Great Plains have considerable populations of RO and are native waters for CCF. Frugivory is a common trophic strategy in fishes from tropical regions, but it is relatively rare in temperate fishes. Many tropical catfish are known to be frugivorous and some act as dispersal agents (Correa et al. 2007). In North America, the first documented case of seed dispersal by a fish was CCF feeding on mulberry and swamp privet (*Forestiera acuminata*) fruits in the Middle Mississippi River in Illinois. Chick et al. (2003) found high occurrence of mulberry and swamp privet fruits in CCF diets and that CCF increased germination potential of seeds that were collected from the lower intestine. As the consumed seeds of RO fruits are passed whole, it is possible that CCF act as dispersal agents for RO. More research is needed to determine if the seeds are viable and increase germination probability after passing through digestive systems of CCF. I evaluated these questions using a common garden experiment in Chapter 2.

Although frugivory by CCF has been documented in their native habitats, little is known about how CCF benefit from consuming fruits, and no studies have individually evaluated this component of their diet. Other research often groups RO with other vascular plant material, which can comprise a relatively high proportion of stomach contents by weight and high percent occurrence (Tyus and Nikirk 1990; Michaletz 2006). I also observed relatively high

consumption of vascular plant material other than RO fruits that I categorized as debris. However, the quantity and consistency of RO fruit consumption led me to conclude that RO was more than ancillary bycatch of debris while feeding on other prey items. However, I did consider algae as likely bycatch during predation of aquatic invertebrates because the highest density of aquatic insects was observed where filamentous algae was abundant during summer sampling events.

RO fruits are not considered an ideal diet item for CCF. They are high in carbohydrates, low in protein, and low in fats, which has a far different nutrient profile than commercial catfish feed that is designed to optimize growth (See nutritional information in Chapter 2). CCF are inefficient at assimilating complex carbohydrates into growth in aquaculture settings (Wilson and Poe 1987). However, CCF are able to utilize carbohydrates for metabolic energy (Garling and Wilson 1977). With the availability of alternative prey such as aquatic insects or fish, which are higher quality diet items, it is not clear why RO fruits comprise such a high proportion of CCF diet. I have four hypotheses that I will explore further in this discussion: **1.** RO fruit is a viable diet item and CCF are able to assimilate it into growth and lipid deposition. **2.** RO fruit provides metabolic energy to CCF but does not provide dietary content required for lipid deposition or growth. **3.** RO fruit is a low-quality diet item but either availability or access to superior prey items is limited, forcing the use of sub-optimal energy sources. **4.** RO fruit is an ecological trap for CCF, providing no benefit to the fitness of CCF

It is unknown if CCF can assimilate RO fruits into growth, lipid deposition, or metabolic energy. It is unlikely that RO fruit is an optimal source of protein and lipids needed for growth, but it may provide a source of metabolic energy. If consumption of RO fruit can account for the energetic cost of metabolism, it may provide a benefit to growth of the fish and reduce the amount of insect or other prey required to achieve maximum possible growth. This may be particularly important during periods of high metabolic demand. In addition, there may be a difference in energetic cost between capturing other prey and RO fruit. Little energy is likely expended to capture RO fruits, which may not be true for capturing invertebrates or fish prey. In addition, if RO fruit consumption makes up for the metabolic cost, it could prevent the loss of weight during periods of low alternative prey availability. To really understand the interaction between RO and CCF, future research should address how CCF are able to utilize the energy

from RO fruits and how much CCF biomass is supported by RO in the system. I address this question with an experiment presented in Chapter 2 and bioenergetic modeling in Chapter 3.

Another possibility is that CCF consume large quantities of RO fruits because other prey is hard to access or limited in quantity. If other prey availability is limited, RO fruits may be the only dietary option for CCF. If RO fruits do provide metabolic energy, their benefit may be the greatest if other prey items are limited. Consuming RO fruit may allow for maintenance of weight during periods when the metabolic demands outpace the availability of other prey item.

It is also possible that RO fruits present an ecological trap for CCF. Having not co-evolved, the interaction may not be beneficial at all or even have negative consequences for CCF. Much of the literature on optimal foraging would suggest that this is not the case; however, it may occur in novel interactions between introduced species. RO fruits may represent a palatable but nutritionally valueless snack for CCF, rather than a main component of CCF diet.

Notably, piscivory rates in this study were low throughout seasons and between sites. Our observed piscivore rates were similar to other studies of CCF diet in the Colorado River Basin (Tyus and Nikirk 1990). However, large fish have a much higher occurrence and proportion of their diet that is material from other fish. By far the most common fish found in CCF stomach were young-of-year CCF. Cannibalism is well documented, especially in aquaculture settings, and some of what I observed could be related to filial cannibalism (Brown 1942; Manica 2002). Young-of-year fish were very prevalent in July when males were in spawning condition and possibly guarding nests. I observed both native and non-native fishes in the stomachs of CCF. Yet, I did not observe any predation on endangered razorback sucker or Colorado pikeminnow. This was surprising, especially considering I sampled 10 days following Colorado pikeminnow augmentation of 432,443 individuals ranging from 45-55 mm in November 2-3, 2016 (Furr 2017). Stocked fish are known to be naïve to predators, and I expected predation rates by CCF to be highest following stocking (Alvarez and Nicieza 2003). This observation does not negate that CCF may predate on the endangered species in the San Juan River. The likelihood of CCF eating large numbers of endangered species is low given the low densities of Colorado pikeminnow and razorback suckers and the rates of overall piscivory are low generally. With a larger sample size, it may be possible to detect the predation level on the endangered species, but that was not the objective of this study. A better understanding of predation demand of CCF is

needed to gain an understanding of how CCF impact Colorado pikeminnow and razorback sucker populations, which I will address in Chapter 3.

The San Juan River Recovery Implementation Program has a long-running non-native fish removal program focused on removing non-native predators and competitors in order to recover razorback sucker and Colorado pikeminnow populations. These removal efforts have not significantly reduced biomass of CCF in the system, but they have likely impacted the size distribution, increasing the frequency of smaller age classes (Franssen et al. 2014). These smaller age-class fish are less piscivorous. Critics of removal efforts have often cited a lack of progress toward lower stocks of CCF. However, removing the largest size classes that present the largest predation threat to native species may be an argument for maintaining removal efforts. The diet of small CCF is primarily aquatic insects. Higher biomass of CCF at smaller size classes could presumably increase competition with native species but has yet to be explored. The program is currently in the process of evaluating removal efforts in an ongoing experiment to determine how to move forward.

The relationship between RO availability and consumption of RO fruits in my logistic model was likely confounded by my sampling methods not accurately reflecting fruit availability to CCF. RO availability only accounted for fruits falling from the trees directly into the water. I was not able to account for fruits that dropped in terrestrial habitats and were carried by wind or water to the river, thus becoming available to CCF. The influx of fruits during rain events can be substantial (C. Cheek, pers. obs.). The largest influx of fruits occurred in November and March. The fruits ripen in late summer and early fall, but some fruits remain on the trees through the winter. The dry fruits that remain on the tree are released the following spring when the trees begin to bud, which was in late March in this study system. The arid environment allows for the preservation of the fruits nearly year-round, even on the ground. Major rain events and high water allows for buoyant fruits to be carried over long distances (Brock 1998; Pearce and Smith 2001). Given these observations from the field, my measure of RO fruit availability may not have accurately reflected the true availability to CCF.

More research is needed to determine whether inputs of RO fruits are facilitating CCF populations, but it is also important to understand if the interaction positively benefits both species. Determining the benefit of RO fruit consumption by CCF will allow understanding of whether RO fruits facilitate CCF populations in the San Juan River by providing a trophic

subsidy. In addition, it is important to understand whether RO receive a reproductive advantage from CCF through increased germination and seed dispersal. If these two species are exhibiting mutual facilitation, it may be an example of invasion meltdown, where positive interactions among invaders facilitate one another, thereby increasing their biomass, establishment success, or persistence on the landscape (Simberloff and Von Holle 1999; Simberloff 2006). More research is needed to determine if this is indeed an example of mutual facilitation among invaders that crosses the aquatic-terrestrial interface.

Ecological researchers need to focus more on the impact of RO because it threatens rivers in grasslands and arid environments that are already imperiled by river regulation, fragmentation, water withdrawals, and aquatic non-native species. Because these ecosystems did not evolve with large abundance of fruit-bearing trees in the riparian corridor, RO can completely alter food webs. RO fruits are known to be important food resources for many birds and mammals (Borell 1951), and I observed many terrestrial vertebrates utilizing RO fruits in their diet including bears, raccoons, squirrels, mice, coyotes, horses, and turkeys and many other bird species. However, few native aquatic species are likely to be able to take advantage of this resource directly because they did not evolve with fruit bearing riparian trees, and in the San Juan River this provides a disproportionate advantage to non-native species. Given the prevalence of RO and its potential to continue to alter channel geomorphology and biochemical processes, it is important to determine whether non-native species like CCF are facilitating its spread and how that may affect native species and the ecosystems they live in.

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CHAPTER 2: FACILITATION ACROSS ECOSYSTEM BOUNDARIES: ARE INTERACTIONS BETWEEN TWO INVADERS, RUSSIAN OLIVE (*ELAEAGNUS ANGUSTIFOLIA*) AND CHANNEL CATFISH (*ICTALURUS PUNCTATUS*), MUTUALLY BENEFICIAL?

Abstract

In highly invaded ecosystems, positive interactions between invasive species may increase the extent and magnitude of impacts on native communities and ecosystem processes, yet few studies have evaluated facilitation between invasive species. I investigated an interaction between invasive riparian vegetation and non-native channel catfish in the San Juan River (NM/UT, USA), an Upper Colorado River tributary. Russian olive tree fruits are known to comprise a large proportion of San Juan River channel catfish diets, although the benefits of this interaction are unknown. I hypothesized that channel catfish receive a trophic subsidy from Russian olive fruits, providing for growth and energetic benefits. In addition, I hypothesized that Russian olive trees benefit from increased germination potential and seed dispersal. I determined the benefit that each species receives from this interaction separately by designing two experiments. First, I determined whether Russian olive fruits provided a growth or energetic benefit to channel catfish using a laboratory feeding trial. Second, I evaluated the impact of channel catfish seed consumption on reproductive potential of Russian olive trees by conducting a common garden experiment with fruits and seeds collected from the field. I found that Russian olive fruit is a low-quality diet item for channel catfish growth; however, channel catfish fed only Russian olive fruits-maintained weight and lipid content. Given the low protein, high carbohydrate nutritional content of Russian olive fruits, I concluded that Russian olive provides an energetic subsidy to channel catfish populations. In addition, I found that seeds consumed by channel catfish were four times more likely to germinate than seeds left intact, suggesting that channel catfish are a viable seed disperser. My experiments indicated that the interaction between Russian olive and channel catfish in the San Juan River is mutually beneficial. This interaction represents the first example of mutual facilitation that spans ecosystem boundaries across the aquatic-terrestrial interface. More research is needed to determine the degree to which facilitation between Russian olive and channel catfish impacts populations of both native and non-native species in the system. In addition, more

information is needed to determine how positive interactions between non-native species impact community-level processes and ecosystem function.

Introduction

Biological invasions, along with habitat loss and alteration, contribute greatly to global biodiversity loss (Mooney and Hobbs 2000). Rates of invasion are expected to continue increasing as human populations grow and habitat disturbances increase (McKee et al. 2003; Hulme 2009). Currently, many ecosystems host multiple invasive species, and in highly altered ecosystems, invasive species often outnumber native species (Johnson et al. 2009). As ecosystems become increasingly pressured by new invasions, interactions among native and invasive species become more common. These interactions may decrease, increase, or have no effect on invasion success.

While positive interactions between invasive species are relatively rare, they are nonetheless critical to study because they may increase the likelihood of establishment and spread of invasive species. Simberloff and Holle (1999) suggested an “invasional meltdown” could occur when invaders facilitate subsequent invasions through direct (e.g., commensalism and mutualism) and indirect (e.g., changes in habitat and energy flow) positive interactions (Simberloff & Holle 1999; Simberloff 2006). Although evidence for invasion meltdown is sparse, it is most likely to occur in highly disturbed areas that have multiple invaders and have incurred anthropogenic alterations (Simberloff and Von Holle 1999). Mutual facilitation among invasive species may enhance the extent or magnitude of invasions and increase community-level and ecosystem impacts (Braga et al. 2018). It is therefore important to understand positive interactions between invasive species and determine how these interactions impact native species and other ecosystem attributes.

Understanding the relationship among non-native species in the Colorado River Basin is needed because it presents a clear case where non-native species interact with native species in a novel ecosystem context that differs from historical conditions (Hobbs et al. 2009) and managers have spent a lot of effort and money to remove non-native species. The Colorado River, like most rivers in the arid Southwestern United States, has been altered by hydrologic regulation and biological invasions that affect ecosystem function (Tyus and Saunders 2000). As often occurs, the altered habitats and disturbance regimes have facilitated the invasion and establishment of invasive fishes in the Colorado River Basin (Olden et al. 2006; Gido and Propst 2012). Ultimately,

the combination of habitat degradation and species invasion has resulted in native species declines, including four fishes that are now federally listed as endangered. In the San Juan River, a tributary to the Upper Colorado River, the fish assemblage is characterized by greater non-native species richness than native species richness (Sublette et al. 1990). Along with habitat change, non-native species are considered a major impediment to the recovery of native species, including endangered Colorado pikeminnow (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*) (Tyus and Saunders 2000; Olden et al. 2006).

Even though non-native channel catfish (*Ictalurus punctatus*; CCF) are considered the most deleterious non-native species and the most likely predation threat for native and endangered species in the San Juan River, the evidence to support this threat is anecdotal (Patton et al. 2012). Native to eastern North America, CCF do not naturally occur west of the Rocky Mountains. CCF were first documented in the San Juan River in the late 1800s and were likely introduced as a sport fish (Dill 1944). Currently, the San Juan River Recovery Implementation program is removing CCF because of their potential predation threat and potential for interspecific competition with endangered fishes (Tyus and Saunders 2000; USFWS 2002). Although it is recognized that eradication is likely impossible, the goal of the program is to reduce predation on the endangered species and reduce competition for native species recovery. Reduction efforts have decreased the abundance of larger size (>500 mm) classes of CCF, but overall estimates of biomass have not decreased with removal efforts (Pennock et al. 2018), and there has not been any evidence that removal efforts improve native fish abundance (Franssen et al. 2014).

In addition to changes in hydraulic regulation and fish invasion, the San Juan River Basin has been shaped by invasive plants. Throughout the western US, riverbanks have been altered by the introduction of invasive riparian vegetation (Nagler et al. 2011). Reductions in floodplain inundation have caused declines in native species such as plains cottonwood (*Populus deltoides*) (Williams and Cooper 2005), opening niche space for other riparian species. Both Russian olive (*Elaeagnus angustifolia*; RO) and salt cedar (*Tamarix* spp.) have successfully invaded riparian habitats along the Colorado River. RO is particularly pervasive in San Juan River riparian zones, composing up to 90% of floodplain vegetation coverage in some reaches (unpublished data). In the late 1800s, US conservation agencies introduced RO for erosion control, wind breaks, and wildlife habitat (Van Dersal 1939, Wilson 1944). The horticulture and ornamental use of RO have also contributed to its spread across the landscape (Katz and Shafroth 2003). RO success is

attributed to reductions in river flows (via regulation and water withdrawal), seed size, and longevity (Christansen 1963; Knop and Olson 1984). Combined impacts of flow alteration and riparian invasion create a feedback loop that accelerates river-channel complexity loss through bank armoring and incision (Tickner et al. 2001). In addition to altering San Juan River riparian communities, RO provides a novel resource in the form of carbohydrate-rich fruit known to be consumed by many different animals, including birds, mammals, and fishes (personal observations, Knop and Olson 1984). Large pulses of RO fruits fall from the trees from fall to spring, many of which are transferred to aquatic habitats either directly or carried by surface runoff (see Chapter 1). Stomach content analysis has documented that RO fruits comprise a large proportion of CCF diets in the fall and spring (see Chapter 1). However, the nutritional benefits of autochthonous inputs of RO fruits for CCF remains unknown.

Plant-animal mutualisms are the most common form of facilitation among invasive species, although no studies, that we know of, have evaluated facilitation between invasive riparian plants and aquatic invaders and their combined impacts on ecosystem function (Simberloff and Von Holle 1999). Animals provide a vector for long distance dispersal of seeds and in some cases provide reproductive benefits via germination potential (Traveset 1998). In return, fruiting plants provide predictable forage with high nutritional content. These interactions are common and well-studied in terrestrial ecosystems, although fruit-fish mutualisms have received less attention.

Only recently have researchers begun to investigate seed dispersal and germination potential of fishes (Horn et al. 2011; Pollux 2011). Most studies about fish frugivory assume that fishes benefit from consuming fruits. However, it is unclear just how beneficial frugivory is to fish fitness. In cases where fruiting trees and fish co-evolved (e.g., the Amazon River), fishes have become adapted for digesting and assimilating fruits in their diet to take advantage of the available resource (Waldhoff and Maia 2000). These fishes can utilize the fruits and convert sugars into growth. Frugivory is therefore a common interaction between fishes and riparian vegetation in tropical floodplain rivers, with some species adapted to primarily feed on seeds and fruits. Frugivory in fishes is far less common in temperate regions.

Carbohydrate-rich food sources are rarer in temperate aquatic ecosystems, and fishes native to temperate regions are less efficient at processing these resources (Hemre et al. 2002). For example, the vast literature evaluating CCF nutritional needs for commercial aquaculture indicates that they are inefficient at processing complex sugars present in fruit, and fruits lack the fat and protein

required for growth (Page and Andrews 1973; Winfree and Stickney 1984; Cho and Lovell 2002). However, CCF can utilize carbohydrates and sugars for energetic needs (Garling and Wilson 1977; Wilson and Poe 1987). Alone, RO is not an ideal CCF diet item, although consumption of RO fruit may still provide some nutritional benefit when combined with other diet items.

Frugivory can also benefit riparian trees. In the Amazon River basin, fishes are valuable seed dispersers for native plants and may be primary agents of seed dispersal for some plants (Anderson et al. 2009). RO is primarily thought to be dispersed by birds and mammals, but dispersal by fish has not been evaluated (Katz and Shafroth 2003; Kindschy 1998). For example, European Starlings (*Sturnus vulgaris*) have been shown to disperse viable RO seeds in field observations, although no increased germination success was documented (Kindschy 1998). It is possible that CCF act as a dispersal agent for RO in the San Juan River. Although studies of seed dispersal by fishes are sparse in temperate regions of the world, CCF is one of few documented cases in North America. In their native habitat, CCF consume seeds of swamp privet (*Forestiera acuminata*) and red mulberry (*Morus rubra*), and Chick et al. (2003) found increased germination rates of seeds consumed and passed by CCF. If mutual facilitation exists between RO and CCF, RO likely benefits from seed germination potential and seed dispersal.

In this study I investigated mutual facilitation between CCF and RO in the San Juan River. I sought to untangle this complex interaction by exploring the benefits received by each invasive species individually. For CCF, I explored the impact of RO fruit consumption on growth, lipid deposition, and assimilation efficiency. In addition, I sought to determine whether CCF facilitate RO by acting as a dispersal agent and by increasing germination probability. My specific objectives were to: (1) determine whether RO fruit diets yielded growth in CCF and (2) measure germination probability of RO seeds consumed by CCF and compare it to unconsumed seeds and seeds consumed by small mammals, another potential dispersal agent. I hypothesized that: (1) RO fruit would provide energetic benefits to CCF but would not provide sufficient nutrition for growth and lipid deposition, and (2) RO seeds consumed and passed by CCF would have a higher germination probability than seeds not consumed by CCF.

Methods

Catfish Feeding Trial Experiment

To determine the nutritional benefit CCF receive from consuming RO fruits, I designed a common feeding experiment with diets of varying nutritional compositions. Given that San Juan River CCF do not exclusively consume RO fruits, I designed five treatment diets that consisted of varying proportions of RO fruit and soldier fly meal. I also used commercial aquaculture (Purina Aquamax 500) feed as a positive control to ensure that culture conditions for growth were sufficient (six total treatments). I used 30, 113.6 L aquariums as experimental units, with five replicates (n=5) per treatment. The aquariums were on a recirculating water supply, and there was little variation in temperature throughout the system. The experimental array was constructed inside an experimental chamber where I could control both air temperature and photoperiod (discussed later).

The fish were sourced from an aquaculture supplier (Andry's Fish Farm LLC, Birdseye IN) as fingerlings and transported to the Purdue Aquaculture Research Laboratory in West Lafayette, IN, in August 2017. CCF were held in 3 m circular tanks with a flow through system that maintained temperatures between 26 and 28 °C. Fish were fed to satiation on commercial feed from August to December 2018 and grown until fish reached a size where they were observed consuming RO fruits in the field (mean TL = 254 mm). Fish were starved for seven days prior to transfer from communal tanks to the experimental units. Three fish were randomly selected from the communal tanks and placed in each experimental unit. Fish were all fed the same commercial diet for two weeks while acclimating to the experimental aquaria. Fish that appeared to stress or that refused to feed were removed and replaced. After two weeks of acclimation, fish were transitioned to the treatment diets for an additional week.

To formulate the feed, I first collected RO fruits from the San Juan River floodplain in New Mexico and Utah, USA. Fruits were collected from the trees in late September and early October 2016 and 2017 during periods of high fruit drop (see Chapter 1). Fruits were collected from four sites along the longitudinal gradient covering 160.9 km of river. Fruits were placed in plastic bags and frozen (-20 °C) for later processing. The seeds and fruit were thawed and separated in the lab by pushing the seeds through wire mesh and then sifting out the seeds. The remaining pulp included the leathery exterior of the fruit and the fleshy part of the fruit that had a mealy

consistency. After removing the seeds, the fruits were dried in a drying oven at 60 °C for 48 hours. The dried RO fruit material was then run through a mill, creating a fine meal with consistently-sized granules. I used commercially available black soldier fly (family: *Stratiomyidae*) larvae meal (FM; Repashy Superfoods Inc.) as the best nutritional approximation to aquatic and terrestrial insect prey items common in San Juan River CCF diets. These two diet items were combined into five mixes proportionately by weight: 100% RO, 75% RO/ 25% FM, 50% RO/ 50% FM, 25% RO/75% FM, and 100% FM. In addition, I added a non-nutritious binder (carboxymethyl cellulose) to all feed mixes to enhance formation of cohesive food pellets. Ingredients were mixed dry using a v-blender (Patterson-Kelly Lab 8 qt V-blender) for 5 min. The ingredients were then mixed with water and extruded into 8 mm diameter strands. Extruded feed was then dried for 24 hr. and broken into pellet-sized pieces by hand. Feed was stored in the freezer (-20 °C) until used.

After the acclimation period, I measured the total length (TL, mm), standard length (mm) and weight (g) of the three CCF in each tank. One fish from each tank was removed and euthanized using MS-222 (Tricane-S, Western Chemical). Sacrificed fish were weighed (\pm 0.01 g) measured for total and standard length (mm). Fish were placed in plastic bags, sealed, labeled, and immediately frozen at -80 °C. These fish were removed to provide baseline information on lipid content and energy density. In addition, removing fish from the tank prevented crowding later in the experiment. Fish were fed once daily at simulated sunrise until satiated. Any feed remaining in the tanks 30 min after initial feeding was removed, dried, and weighed. I recorded the amount of feed consumed in each tank once per week throughout the experiment.

I controlled environmental conditions for the CCF feed experiment using an environmental chamber. Decreasing photoperiod and temperature are both physiological triggers that determine how nutrients are utilized and assimilated by many fishes. I simulated a summer-to-fall transition in temperatures and photoperiod to match the environmental conditions that would be experienced by CCF in the San Juan River from September through December. These conditions were selected because they coincide when RO fruits are ripe and dropping from the trees and when RO fruit consumption by CCF is high (Chapter 1). Specifically, I incrementally (0.18 °C/day) decreased water temperatures from 22 °C to a final temperature of 14 °C and daylength period from 14 hours to 10 hours (decrease of 5.4 min/day). The temperature control in the environmental chamber malfunctioned at the beginning of the experiment and there was fluctuation in temperature for the first 10 d with steadily declining temperatures for the rest of the experiment (Figure 2.1A). Water

temperature values were taken from average mean daily temperatures across three USGS gages along the San Juan River. Daylength hours were collected from sunrise-sunset tables. The rate of change was accelerated to the 6-week feeding period of this study. Water temperature was measured daily to ensure that all tanks remained within $\pm 0.5^{\circ}\text{C}$ throughout the study period. Dissolved oxygen (mg/L), pH, and conductivity were checked daily and remained at acceptable levels throughout the study (i.e., $> 5\text{mg/L}$, 7.2-7.3, and $320\ \mu\text{S}$, respectively). Nitrate, nitrite, and ammonia were checked weekly and remained at acceptable levels (i.e., $<0.25\ \text{ppm}$, $<0.50\ \text{ppm}$, and $<0.25\ \text{ppm}$, respectively).

The feed experiment lasted 44 d, and all remaining fish were euthanized and frozen as previously described above at the end of the experiment. The fish were later thawed in a refrigerator, sampled for muscle and fin clips for stable isotope analysis, and homogenized (whole fish) using a blender (Nutribullet HD). Homogenized fish tissue was stored (-80°C) for later lipid content and fatty acid profile analysis. Moisture content was measured by placing a 10 g sample of homogenized tissue in a drying oven, drying the sample at 60°C for 72 hr, and weighing before and after. Moisture content was used to calculate energy density based on Hartman and Brandt (1992). Lipid content was determined by extracting the lipids from homogenized tissue in methanol following the methods of Folch et al. (1987).

Ideally, this study would have included a negative control (i.e., a treatment with CCF fasted for the duration of the experiment). However, the guidelines of animal husbandry and responsible research with animals prevented that approach. To determine the difference in observed growth on a diet of exclusively RO fruit and zero consumption, I estimated the metabolic demand and weight loss for each experimental unit using bioenergetic modeling. I used the Wisconsin bioenergetic model developed by Kitchell et al. (1977) implemented using Fish Bioenergetics 4.0 (v1.1.2) (Deslauriers et al. 2017). The parameters for the bioenergetic models were not provided within the FB 4.0 base code. I followed the parameters used in a similar model of CCF bioenergetics developed by Blanc and Margraf (2002). To estimate a model for negative growth, I incorporated the same environmental conditions (measured daily temperature data) and initial weight of each fish and set consumption to zero. Because fish were fed to satiation, it was necessary to consider the amount of feed consumed. I used feed efficiency to account for differences in consumption, calculated as growth (g) divided by weight of feed consumed (g). Percent lipid was calculated as the percent by weight of lipids to other tissue in a homogenized

sample. I used analysis of variance (ANOVA) tests to determine the effect of the diet treatments on growth, feed efficiency, percent lipid, and energy density for each tank. I used Tukey Highly Significant Difference (HSD) test to determine pairwise differences between treatments.

Russian Olive Germination Experiment

To determine whether CCF facilitate RO germination and seed dispersal, I designed a germination trial with RO seeds that consisted of four treatments: whole seeds with fruit intact, whole seeds with the fruit manually removed, seeds consumed and passed by mammals, and seeds collected from the lower intestine of San Juan River CCF. All seeds or fruits were collected in October 2018. Whole seeds were collected directly from the San Juan River or picked up where they washed ashore. Whole fruits were divided into two treatments after the fact, one with the fruits and seeds intact (Figure 2.4: bank intact) and the other with the fruit manually removed from the seeds (Figure 2.4: bank removed). Seeds consumed and passed by mammals were collected from scat collected on sand bars near the river shore. I collected seeds from a variety of mammal scats, primarily raccoon (*Procyon lotor*) and coyote (*Canis latrans*). Scat samples were collected whole and placed in paper bags with silicon desiccant packets to prevent molding. Seeds were later removed from the scats in the lab. Seeds for CCF were collected from the lower half of the lower intestine. Specifically, CCF were collected using a raft-based electrofishing (see Chapter 1 Methods). Total length (mm) and location (river km as designated by San Juan River Recovery Program) were recorded for each fish. Fish were then euthanized using MS-222 and dissected to remove seeds. Twenty-two CCF were collected, providing 466 total seeds for the CCF treatment. I was not interested in individual variation for this experiment and combined all samples from CCF stomachs. All collected seeds were placed in plastic bags with a moist paper towel and transported in a cooler on wet ice.

RO seeds require a period of cold stratification to germinate, which limits the distribution of RO on the landscape (Nagler et al. 2011). Therefore, I placed treatment seeds singly into plastic containers filled with wet sand. Containers were placed in a refrigerator at 5 °C for 12 weeks until I was ready to plant. Seeds were shipped with ice packs to Fort Lewis College (FLC), Durango, CO, for planting, and the remaining experiment was conducted at the FLC campus. Seeds were separated and placed in plastic bags with wet paper towels and kept at room temperature. Seeds were checked multiple times for germination, and germinated seeds were removed for the second part of the experiment. Seeds that had not germinated after 34 d were considered to be nonviable.

I used a Chi-square test to evaluate the probability of germination probability across different treatments.

Germinated seeds were moved to seedling pots and grown to determine whether there was an advantage for plant growth after being consumed and passed by CCF. Plants were grown for 28 d and kept sufficiently watered. Low germination rates of the whole fruit treatment seeds precluded inclusion of seedling growth from that treatment in the analysis. At the end of the growing period, plants were removed from pots and soil was cleaned from the roots. Plants were dried in a drying oven for 48 h at 60°C. Stems were cut at ground level and roots and stems were separated. Weight (g) of the above and below ground biomass were recorded. I determined differences between treatments in plant biomass using ANOVA with Tukey HSD tests to determine pairwise differences between treatments. All analyses were performed in RStudio (v1.1.463). Significance was determined using an alpha of 0.05.

Results

Channel Catfish Growth and Lipid Deposition

CCF were significantly larger at the end of the trial in all treatments except those fed 100% RO (F: 78.6, df: 2, $p < 0.001$; Figure 2.2A). Both growth (F: 26.6, df = 2, $p < 0.001$) and feed efficiency (F: 98.8, df: 2, $p < 0.001$; Figure 2.2B) were significantly different between treatments. Growth was the highest for CCF provided with the commercial aquaculture feed. CCF fed a diet of 100% RO fruit lost weight (1 ± 1.03 SE)g, although they increased in standard length by 2.1 ($1.11 \pm$ SE) mm. However, the 95% confidence intervals for growth by mass overlap zero, indicating that CCF maintained weight during the trial. Growth in all other treatments was positive, with growth increasing with decreasing amounts of RO fruit in the diet. However, growth as measured by both weight and feed efficiency were not different between the 100% RO and the 75% RO diets ($p = 0.26$) or between the 25% RO and 0% RO ($p = 0.70$).

Using the measured water temperature data and the size of fish at the beginning of the experiment, I estimated the weight loss that would be observed if RO consumption by CCF was zero. The mean weight loss estimated from the bioenergetic models during the period of the experiment was 32.6 ± 1.5 g (Figure 2.2A). This was significantly lower (F: 8.23, df = 6, $p < 0.001$) than the 100% RO diet, indicating that consuming RO fruits was nutritionally beneficial for CCF.

I found no difference in percent lipids among feed treatments ($F: 1.39$, $df: 6$, $p = 0.23$; Figure 2.3A). However, energy density ($F: 7.0$, $df: 6$, $p < 0.001$; Figure 2.3B) as measured by percent dry weight of homogenized samples was significantly different among treatments. Energy density was lowest in the 100% RO treatment. In the 100% RO and 75% RO treatments, energy density decreased during the experiment. All other treatments with RO and FM exhibited no difference in energy density before and after the experiment except the commercial aquaculture feed, which showed significantly higher energy density at the end of the experiment. This indicates that CCF fed a diet of 50% RO were able to sufficiently maintain lipid storage.

Russian Olive Germination

Germination probability was significantly different between treatments ($X^2 = 694.7$, $df = 3$, $p < 0.001$). Seeds consumed by CCF were 4.2 times (SE: 0.42) more likely to germinate than fruits that were left intact. However, germination probability for seeds consumed by CCF was significantly lower than mammal and manually removed fruit treatments ($p < 0.001$). Significantly higher germination probability occurred in seeds consumed by mammals (90.7%) and those with manually removed fruits (92.7%). However, these two treatments were not significantly different from one another ($p = 0.74$). The seeds consumed by CCF were 61.6% more likely to germinate, which was significantly greater than the germination probability for intact fruits (2.4%). RO seedling above and below ground biomasses were not significantly different among seed treatments ($F: 0.24$, $df = 2$, $p = 0.75$).

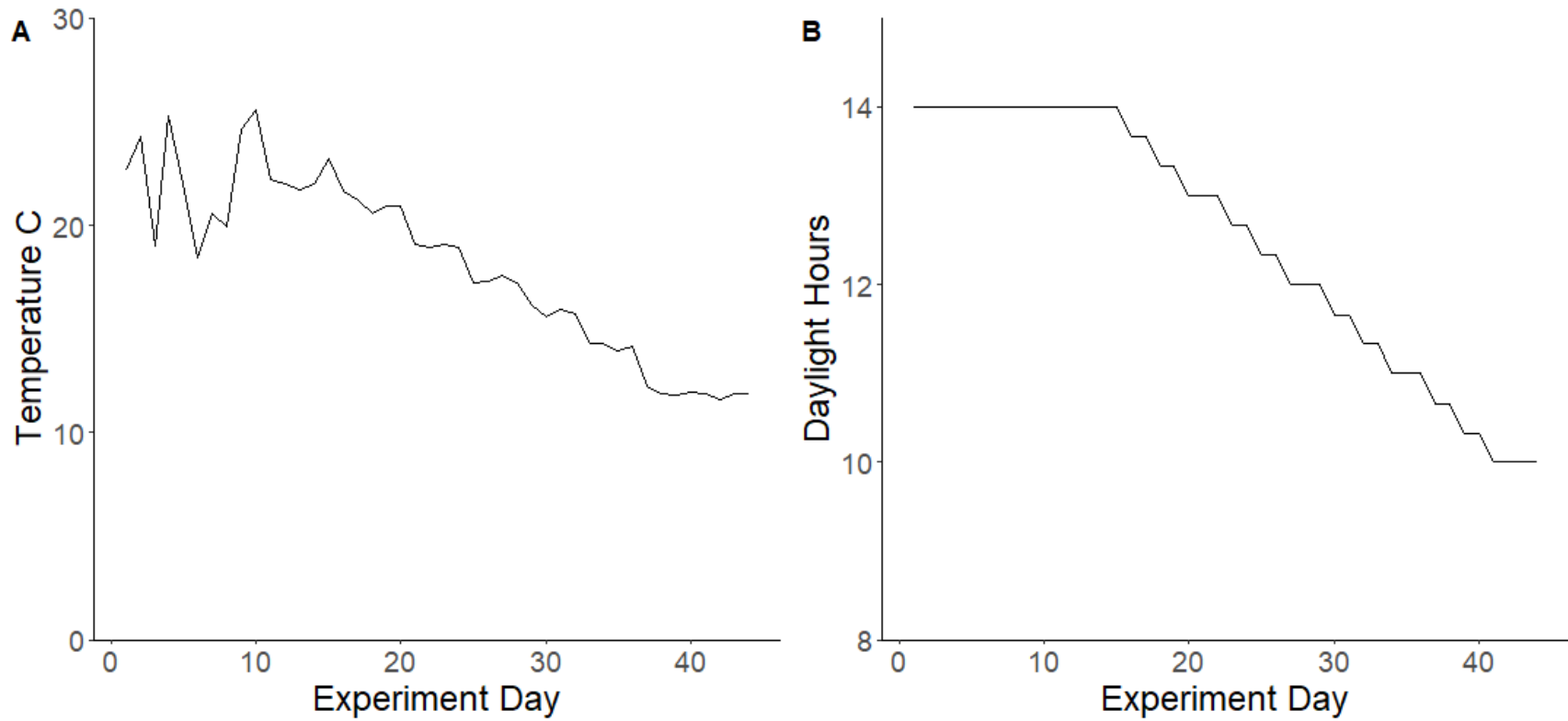


Figure 2. 1. Water temperature (A) and daylight hour (B) regimes for all channel catfish (*Ictalurus punctatus*) experimental feed treatments. Temperature and daylength were manipulated to reflect decreasing temperatures and daylength that fish experience during fall time period in the San Juan River at Four Corners, UT, USA.

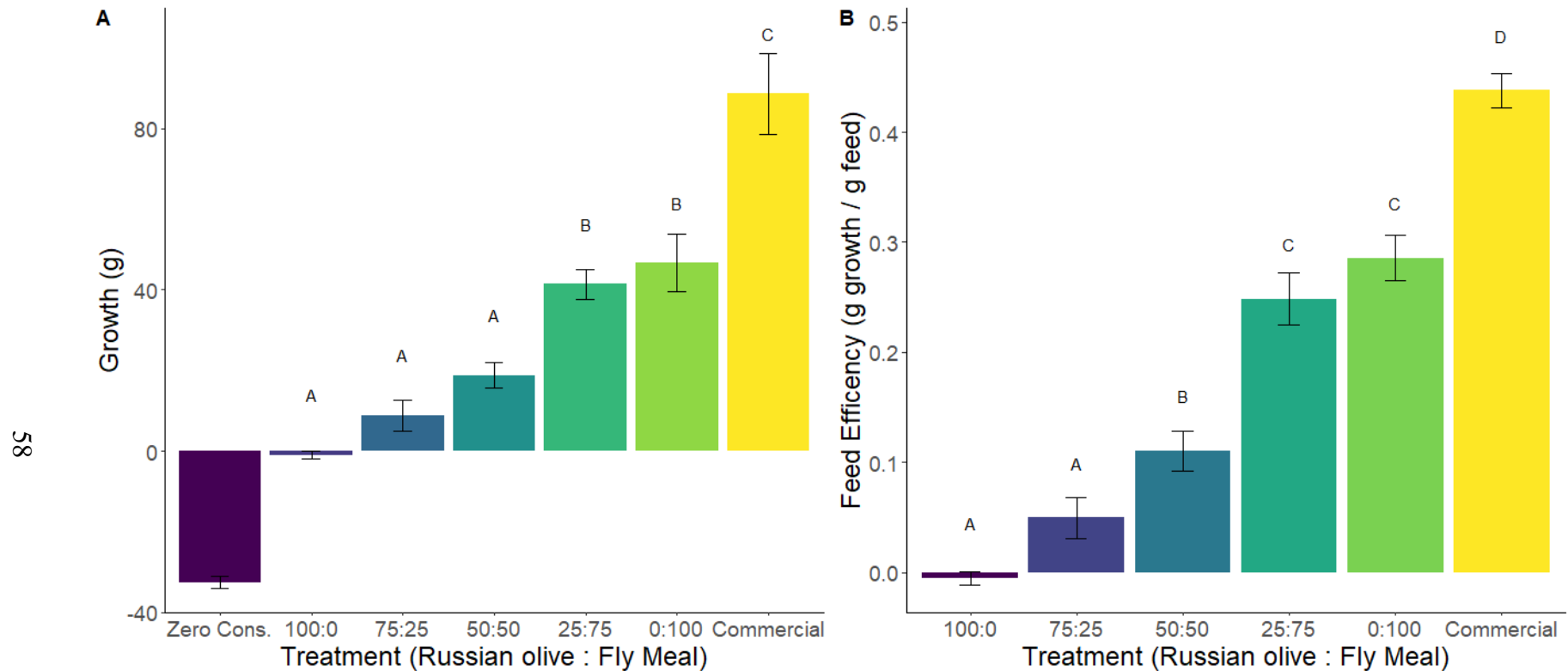


Figure 2. 2. Growth of channel catfish (*Ictalurus punctatus*) fed six treatment diets (A). Weight loss given zero consumption was estimated using Wisconsin bioenergetic models and implemented using Fish Bioenergetics 4.0 with species specific parameters and known water temperatures. (B) Feed efficiency (growth [g]/ feed consumed [g]) for each of the treatment diets. Treatment diets were mixes of Russian olive (*Elaeagnus angustifolia*) fruits and soldier fly (*Stratiomyidae*) larvae meal. Commercial aquaculture feed (Repashy Superfoods Inc) was used a positive control.

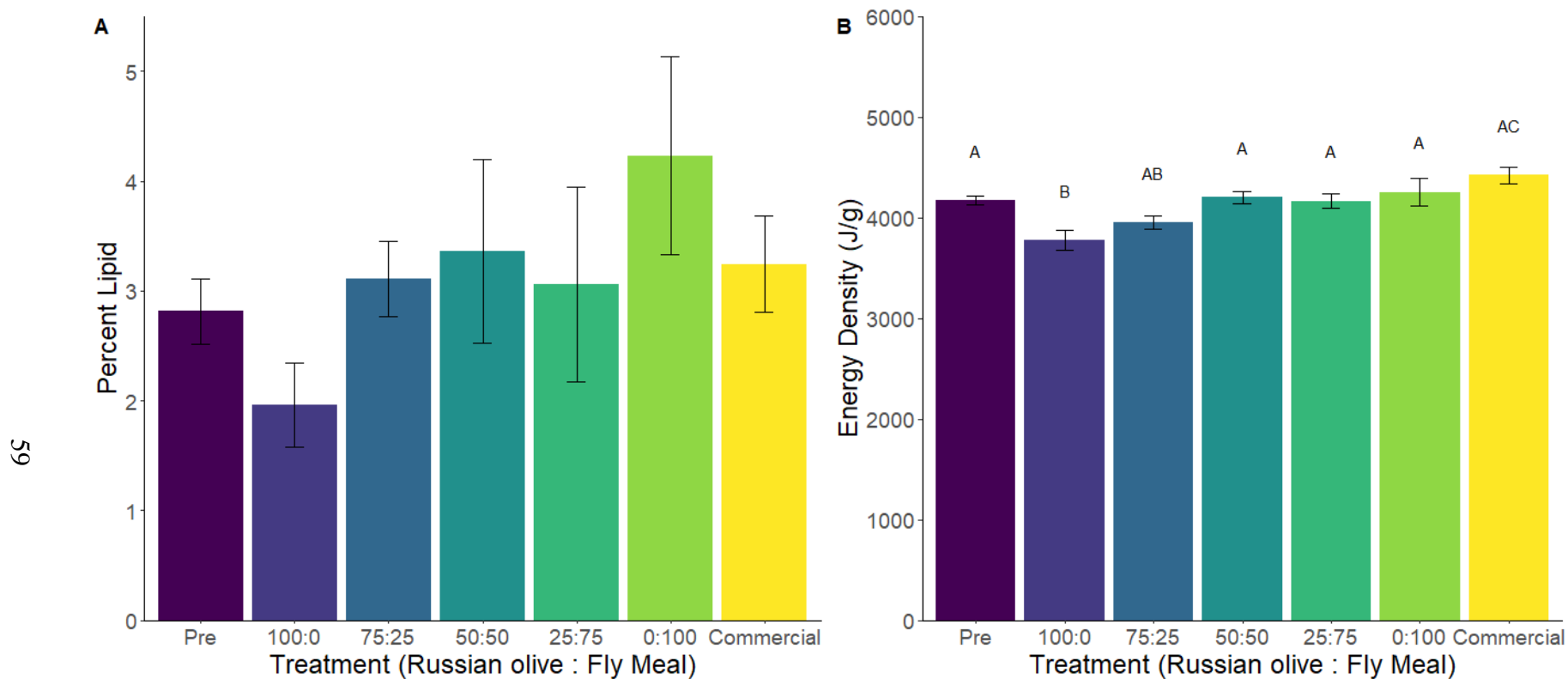


Figure 2. 3. Lipid content and energy density of channel catfish (*Ictalurus punctatus*) before (Pre) and after being given the six treatment diets. Five of the treatment diets were a mix of Russian olive (*Elaeagnus angustifolia*) and commercial soldier fly (*Stratiomyidae*) larvae meal. Commercial aquaculture feed was used as a positive control. Significant pairwise differences (at alpha < 0.05 level) between treatments are indicated with different letters.

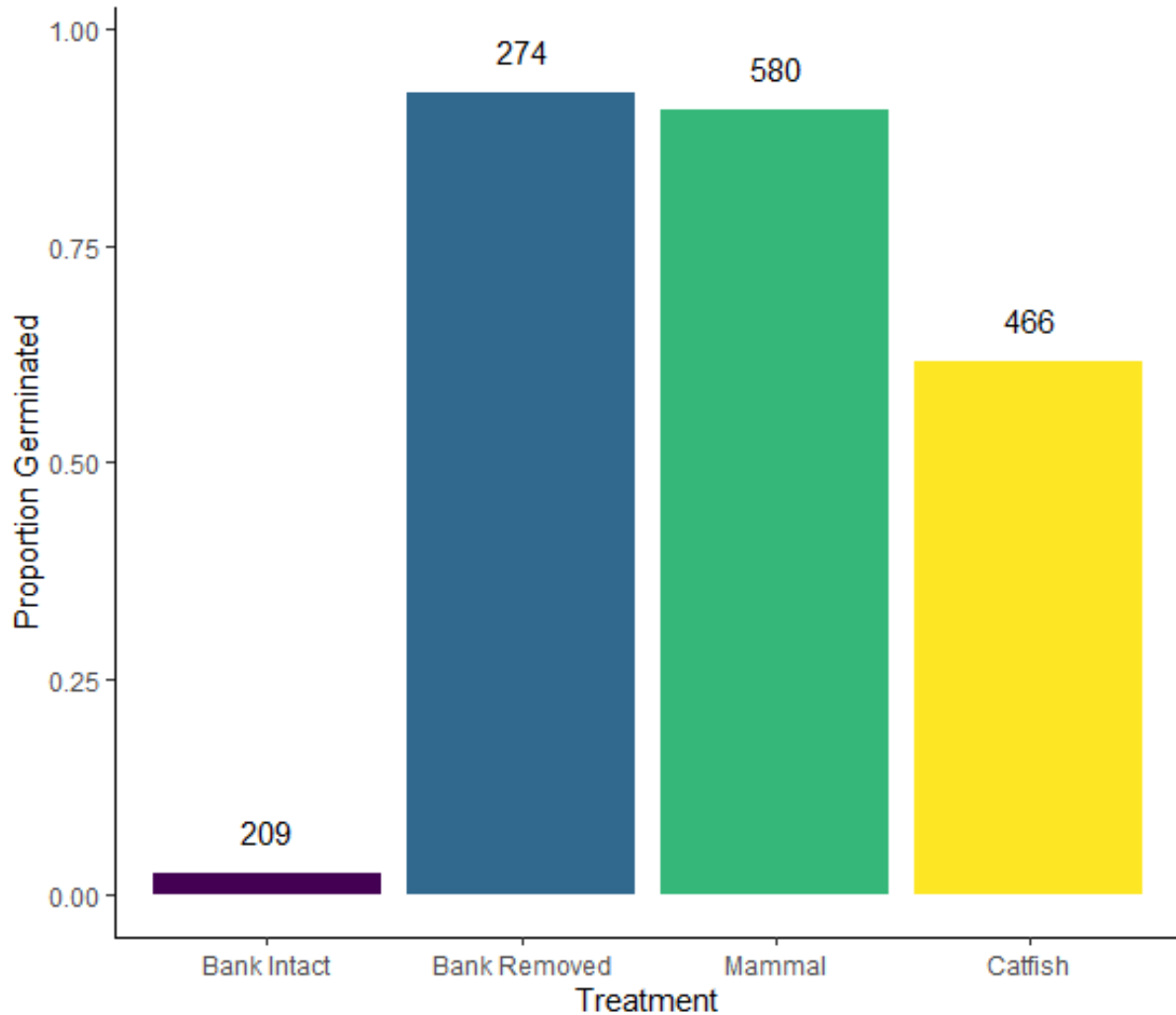


Figure 2. 4. Germination probability of Russian olive (*Elaeagnus angustifolia*) seeds given experimental treatments. Seeds were collected from the San Juan River, NM/UT. Bank intact were planted as whole fruits with the fruit and seed intact. Treatments where the fruit was removed by hand prior to planting are labeled as “Bank Removed”. Mammal seeds were collected from mammal scat along the riverbank and channel catfish (*Ictalurus punctatus*, Catfish) seeds were consumed and removed from the lower intestine in the field. Number of observations is listed above the bar for each treatment.

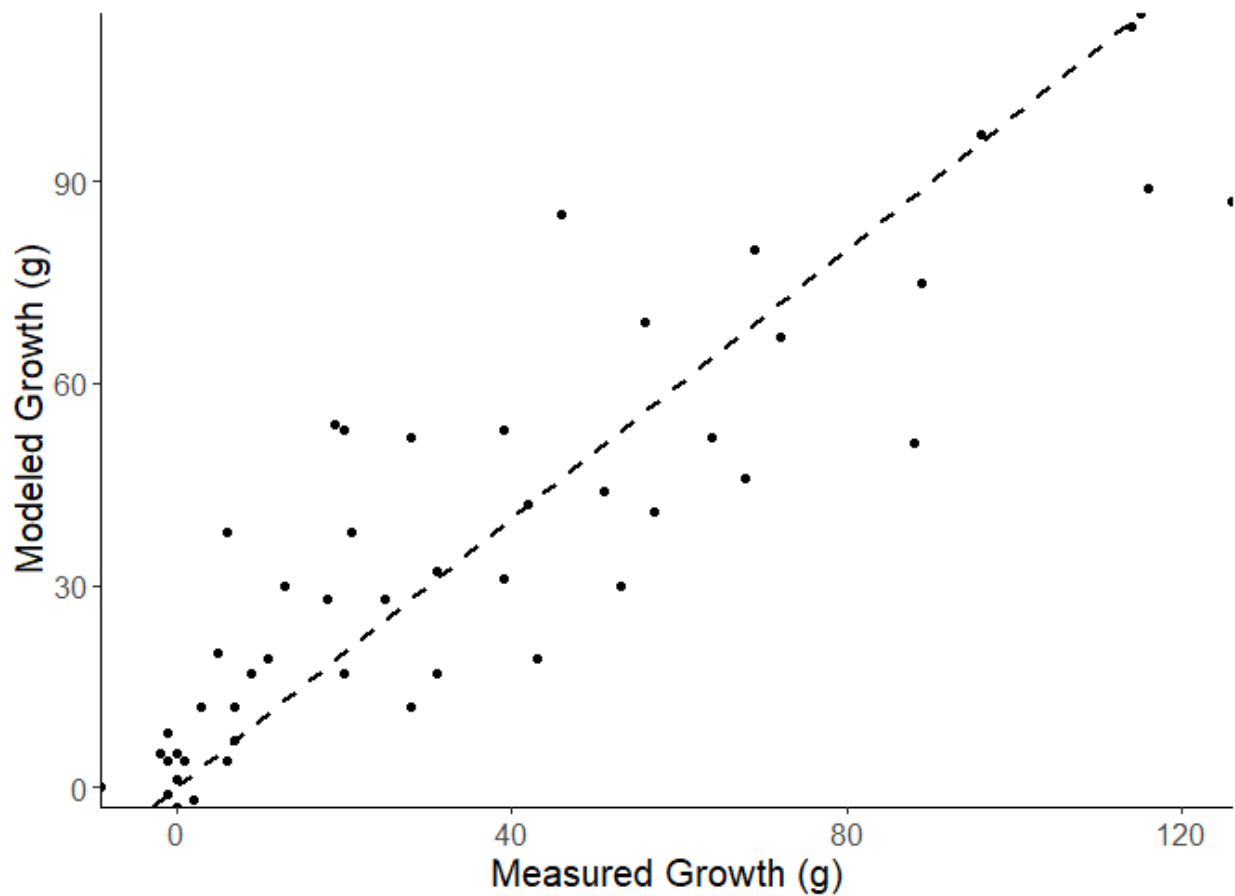


Figure 2. 5. Measured growth (g) of channel catfish after 44 day feeding period. Fish were fed six treatment diets consisting of Russian olive fruit, soldier fly larvae meal and commercial aquaculture feed. Weights were measured at the beginning and end of the trial. We use Fish Bioenergetics 4.0 to estimate growth given known consumption rates during the feeding trial. The estimated growth is plotted against the modeled growth and the dashed line represents perfect fit between the measured and modeled data.

Table 2. 1. Nutritional components of the three diet components used in the feed trial. Fly meal and commercial nutrition provided by manufacturer. Russian olive nutrition was provided by the University of Missouri Nutrition Laboratory

Nutrient	Russian olive	Fly Meal	Commercial
Crude protein	5.55	50	41
Crude Fat	1.7	10	12
Crude Fiber	5.76	6	4
Ash	3.31	12	11
Carbohydrate	83.68	22	32

Discussion

The experimental results of this study suggest that the interaction between RO and CCF is mutually beneficial in the San Juan River. RO fruits provided a readily-available subsidy for CCF and CCF facilitated the germination of RO seeds. Not only are the two invasive species potentially mutually beneficial, their exchange may create a positive feedback where increased germination from CCF on seed dispersal may expand the spread of RO and RO has the potential to subsidize diets of invasive species. However, given that RO did not contribute to growth, it is possible that RO represent an ecological trap.

RO can facilitate CCF

Results indicate that CCF were able to utilize RO fruit in the form of metabolic energy, but they were not able to assimilate fruits into depositions of muscle or fats. Therefore, RO fruit is beneficial as an energy source but sub-optimal from a nutritional standpoint. CCF are known to utilize carbohydrates as well as dietary lipids within ranges of energy to lipid ratios (Wilson and Poe 1985). In fact, most commercial CCF feeds contain 25% digestible carbohydrates. CCF are able to utilize polysaccharides found in RO fruits better than di- and monosaccharides. Given that CCF can utilize carbohydrates better than other fishes such as salmonids, they are uniquely able to benefit from RO fruits as a subsidy.

Even though RO fruit provides readily available carbohydrates, it is not as optimal as other diet items like aquatic invertebrates or other prey items that have more fat and protein content. RO fruits alone are not sufficient for sustaining CCF growth or reproduction. According to optimal foraging theory (Werner et al. 1974), CCF select prey items that maximized their energetic intake while minimizing search and handling time. If CCF were optimally foraging in the San Juan River, their consumption of RO fruits should have increased at low densities of alternative prey (e.g., aquatic macroinvertebrates). However, my findings in Chapter 1 suggested a positive relationship between invertebrate biomass (i.e., alternative prey availability) and consumption of RO fruits. Yet, periods of high benthic availability also coincided with periods of high consumption. Unfortunately, I was not able to estimate true prey availability because I could not account for all types of prey in the availability measurements, especially given the wide variety of taxa (e.g., fish, terrestrial vertebrates, terrestrial insects) that CCF consumed. Given that aquatic invertebrates comprised a major component of CCF diet from my field studies, they were an important prey item for small and mid-sized CCF. If CCF are feeding on RO during periods of high prey

availability, this may indicate that fish are selecting RO fruits over other types of prey available. Even though CCF should select prey that will maximize growth, prey densities may not be sufficient to maximize growth, so CCF subsidize their diet with RO fruits.

A growing body of literature suggests that many animals do not seek to maximize consumption and instead regulate intake of multiple nutrients to minimize dietary imbalance (Simpson et al. 2004; Simpson and Raubenheimer 2001; Berthoud et al. 2012). Many studies, mostly based on locusts, have shown that consumption rates change in response to nutritional deficiencies and that they behaviorally select foods that address the imbalance (Simpson et al. 2004). RO may provide nutrients that are deficient in San Juan CCF diet. In this case, CCF would likely select RO fruits to address a deficiency and increase their fitness. RO fruits contain polysaccharides, flavonoids, coumarins, phenolcarboxylic acids, amino acids, saponins, carotenoids, vitamins, and tannins (Abizov et al. 2008). In addition, RO fruits are considered to have anti-inflammatory properties and are often consumed as a homeopathic treatment for joint pain and arthritis (Panahi et al. 2016). Micronutrient deficiencies are understudied in ecology, but there is a wealth of information from the aquaculture literature. Deficiencies of vitamins A, B1, C, and E have been shown to decrease growth in laboratory trials of CCF (Robinson and Li 2002). Other fishes, including Atlantic salmon (*Salmo salar*) have been shown to develop thiamine (B1) deficiencies due to food web alteration by invasive species, leading to declines in reproductive success (Harder et al. 2018). Because CCF are not native in the San Juan River, it is possible they are limited by vitamins, minerals, or amino acids necessary for growth and reproduction. If RO fruits provide required nutrients that are otherwise not part of the system, RO may provide more than energy and may contribute to growth, survival, or reproduction. Future research should consider the nutrient contribution of RO for CCF diets.

Alternatively, RO could represent an ecological trap for San Juan River CCF, where fruits are perceived to be a high-quality diet item even though they may not be compared to alternative diet items. RO fruits, or “oleaster” in commercial settings, are sweet carbohydrates that are eaten during celebrations in Central Asia where they are native (Abizov et al. 2008). The “trap” may exist because even if RO provides energy, it has comparably low digestibility and, when consumed, may reduce the space available to consume more nutrient-dense foods. Future research should evaluate how trophic interactions between species, especially non-coevolved species, could present an ecological trap. It is possible that wild CCF may be able to digest RO fruits more easily

than commercial fish. Fish are known to undergo shifts in stomach enzyme production and gut microbiota in response to changes in diet (Ray et al. 2012). Given that CCF have been interacting with RO in the San Juan River for the last 120 years, it is possible that they have become adapted to better utilize resources available from RO fruits. My experiment was limited to commercial fish because of the difficulty of wild-caught fish to transition to aquaculture settings. Therefore, estimates of benefits provided to CCF from consuming RO fruits are conservative because fish from the San Juan river may be better able to digest and assimilate nutrients from RO fruits.

CCF can facilitate RO

CCF can benefit RO by acting as a seed dispersal agent, but CCF are not the only seed dispersers in the San Juan River Basin. In experiments, seeds that had passed through mammals had higher probability of germination than those that had passed through CCF. Even though birds also consume RO fruits in large numbers, I did not include them as a treatment. Previous literature has demonstrated that birds have lower rates of germination than mammals, and insufficient data exist from fish to find an effect within a meta-analysis framework (Travest 1998). Previous work with European starlings indicated that they did not increase germination probability of RO fruits, although seeds remained viable seeds after passing (Kindschy 1998). Birds and mammals may be better dispersers of RO given that they can travel long distances over land, but they may deposit seeds too far from sufficient water. Seeds dispersed by CCF most likely end up in the river or on sandbars and cobble bars, increasing vegetation encroachment on the river channel.

The impact of mutual facilitation between RO and CCF on native species is not yet understood. RO fruits were not documented in the stomachs of native flannelmouth sucker (*Catostomus latapinnis*) and Bluehead sucker (*Catostomus discobolus*) (Chapter 1) in the San Juan River and appear to disproportionately benefit CCF (Chapter 1) and common carp (*Cyprinus carpio*), a less common non-native species in the San Juan River (personal observation in the San Juan River; Heinrich 2015 in spring-fed Idaho streams). If RO subsidizes CCF populations, increased carrying capacity could result in increased impacts on native species like increased predation pressure on native fishes or increased competition for invertebrate prey that are important for species such as endangered Colorado pikeminnow (*Ptychocheilus lucius*). Conversely, CCF receiving energetic subsidies from RO may reduce competition for aquatic insect prey or predation pressure on small-bodied fishes by providing an additional food source. Future

studies should consider both the positive and negative benefits of mutual facilitation of invasive species on native populations and ecosystem function.

Additional research should also describe the ecosystem effects of the CCF-RO interaction not explored in this study. For example, CCF may increase the recycling rates of nutrients from RO fruits, leading to indirect benefits of the interaction for other species. Heinrich (2015) found that common carp consuming RO fruits excreted 2-3 times more nitrogen than carp that did not consume RO fruits. RO trees have high nitrogen content in leaves and fruit due to their microbial associations, but RO litter and fruits have low rates of decomposition (Mineau 2012). If CCF recycle nitrogen and/or phosphorus contained RO fruits, they may increase nutrient availability for aquatic primary producers. More research is needed to determine how RO fruits in CCF diet affect excretion rates and how increased nitrogen availability impacts ecosystem function.

Eradication of both CCF and RO from the San Juan River Basin is unlikely with current removal techniques and would be cost prohibitive even if it were possible. Rather than seeking to remove invasive species from the system, efforts to understand how multiple invasive and non-native species interact and how those interactions impact native species may be more fruitful for successful management. Understanding how invasive species interactions affect ecosystem function will allow managers to take a more holistic approach to the recovery of native and endangered species. Unfortunately, managers may be constrained to managing within the current ecosystem context, rather than seeking historic assemblages or habitat conditions.

My results show that mutual facilitation between invasive species can occur across ecosystem boundaries. Specifically, CCF receive an energetic subsidy from RO fruits, but fruits alone are not sufficient for growth or lipid deposition. Additionally, CCF increase the germination potential of RO seeds and may act as a seed dispersal agent. To my knowledge, this is the first example of mutual facilitation that occurs across ecosystem boundaries and is mediated by terrestrial to aquatic resource subsidies.

As human activities continue to alter ecosystems, interactions among invasive species are likely to increase. Therefore, understanding the potential mutualism and potential tradeoffs is important to understand as managers seek to better manage these disturbed systems. In this study, I showed that interactions between RO and CCF can be mutually beneficial in experimental settings. However, the real measure of facilitation between invasive species is at the population-level, which was not captured within this study. Future research into the RO-CCF interaction

should examine whether benefits for each species result in population-level effects such as increases biomass or density for one or both species. Quantifying the impact of RO subsidies on CCF biomass is the main objective of Chapter 3.

Future studies research should focus, not just on the impact of invasive species on native populations, but how invasive and non-native species interact with each other. As more positive interactions are documented, it will be possible to determine functional traits of species that are likely to facilitate subsequent invasions and allow for managers to mitigate future invasions.

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CHAPTER 3: INVASIVE TREE FRUIT AS A NOVEL ENERGETIC SUBSIDY FOR NON-NATIVE FISH IN A COLORADO RIVER TRIBUTARY

Abstract

Positive interactions among invasive species can act synergistically to alter ecosystem functions and community processes. Understanding how such invasive species interactions affect receiving ecosystems is important for preserving native biodiversity and managing invasive species. The Upper Colorado River (USA) has undergone drastic changes in both physical and biotic properties, primarily caused by construction of hydropower dams and water withdrawals. The resulting altered flow regimes and associated physical changes have benefited invasive species in both riparian and aquatic habitats, creating novel interactions between species in an ecosystem where they did not co-evolve. Previous research has shown that invasive channel catfish (*Ictalurus punctatus*) and Russian olive (*Elaeagnus angustifolia*) an invasive, fruit bearing riparian trees interact across the aquatic-terrestrial habitat boundaries. Channel catfish consume allochthonous inputs of Russian olive fruits, making up to 50% of their diet in the fall and spring time periods, and laboratory trials have indicated that channel catfish are able to utilize these subsidies for metabolic energy, but not growth. In addition, laboratory trials evaluating germination of Russian olive fruits passed by channel catfish show that Russian olive trees may receive a reciprocal benefit from the interaction with channel catfish in the form of seed dispersal and germination. Although laboratory experiments show that channel catfish benefit from Russian olive subsidies, there must be a population level effect to determine if Russian olive tree facilitate channel catfish. I used a bioenergetic models to estimate the amount of energy that Russian olive fruits provide channel catfish in the San Juan River (NM/UT, USA), a major tributary to the Upper Colorado River. After estimating channel catfish Russian olive consumption, I used abundance estimates to determine the amount of channel catfish biomass subsidized by allochthonous inputs of Russian olive fruits. I found that Russian olive fruits provided a subsidy that accounted for 36% of the per-capita energetic demand of channel catfish. Based on channel catfish abundance estimates, I calculated that allochthonous inputs of Russian olive fruits subsidized 24.7% of total energy consumed by channel catfish populations >300mm in the San Juan River. I concluded that novel resource

subsidies support channel catfish populations, but the impact of this interaction on native species and ecosystem function requires additional research. My study provides evidence that positive interactions between invasive species can occur across ecosystem boundaries, including the terrestrial-aquatic interface.

Introduction

Species introductions and habitat alterations have caused global declines in biodiversity (Mooney and Hobbs 2000). Species introductions can have large impacts on invaded ecosystems, disrupting community and ecosystem properties. However, invasive species are often not the drivers of ecosystem change; rather, they are passengers of habitat and ecosystem changes, compounding negative impacts on stressed populations of native species (McDougall and Turkington 2005). Habitat and disturbance regime changes caused by human activities alter ecosystem function and provide habitat conditions that facilitate invasion and novel interactions among species, both native and invasive (Hobbs et al. 2009). Such interactions can play a large role in determining invasion success and could have impacts on native community food web and structure (Simberloff et al. 1999, Simberloff 2006).

Invasion success is largely a product of species' functional traits and interactions with other species (Hayes and Barry 2008, Peoples and Goforth 2017). Although ecologists often portray invasive species as having only negative effects on native species, they are just as likely to have little to no effect on community structure or ecosystem function (Larson 2007). In some cases, invasive species may even benefit native species through direct or indirect positive interactions (Rodriguez 2006). To better understand how invasive species impact native ecosystems, it is important to determine how they interact with resident species in the community, including both native and other invasive species. Facilitation, or a positive interaction that results in increased biomass or density of at least one species (Rodriguez 2006), is a well known factor in determining community assembly (Hacker and Gaines 1997; Menge 2000; Stachowicz 2001), positive interactions are likely to be most important under stressful conditions (Bruno and Kennedy 2000; Stachowicz 2001). Facilitation can have as much impact on community structure as other biological interactions such as competition and predation (Goldberg et al. 1999; Arsenault and

Owen-Smith 2002). Although facilitation is well-studied in uninvaded ecosystems, positive interactions have received less attention in the invasion literature.

Facilitation between established invaders and invasive propagules has also been proposed to increase the probability of invasion success for both species. The idea was first proposed by Simberloff and Von Holle (1999), who suggested that positive interactions between invasive species may facilitate subsequent invasion, leading to increased rates of successful invasions over time, known as “invasional meltdown”. However, recent meta-analysis by Jackson (2015) suggested that, although facilitation among invasive species occurs, it is the exception and not the rule, with most study results showing neutral or negative interactions as more common outcomes. However, when facilitation among invasive species does occur, it has the potential to act synergistically to increase impacts on native species or ecosystem function (Simberloff and Von Holle 1999; Ricciardi 2001; Grosholz 2005). Therefore, understanding when and how facilitation occurs among co-existing invasive species in an ecosystem is essential for mitigating the effects of invasive species in receiving ecosystems. However, existing studies are overwhelmingly focused on interactions between native and invasive species (Rodriguez 2006). More research is needed to determine the conditions that promote positive interactions among invasive species and how mutualistic facilitation among invasive species affects native species. In an effort to address these research gaps, I evaluated the impact of a facilitative interaction between two invasive species and estimated the effect on invader biomass.

Literature on species interactions primarily focuses on interactions that occur within a shared habitat; yet, species interactions often occur across ecosystem boundaries. Resource fluxes between habitats (i.e., resource subsidies) are important for sustaining consumer communities in many ecosystems (Polis et al. 1997, Richardson et al. 2008). At the aquatic-terrestrial interface, the reciprocal movement of invertebrate prey supports diverse communities of consumers in riparian and aquatic ecosystems (Nakano and Murakami 2001). Allochthonous inputs of leaf litter are also well known to subsidize aquatic invertebrate communities in shaded streams (e.g., Burdon and Harding 2008). However, interactions between species that cross the aquatic-terrestrial boundary can be disrupted by invasive species. For example, invasive char (*Salvelinus alpinus*) in forested streams in Japan were shown to decrease flux of invertebrate prey into the riparian ecosystems, with cascading impacts on terrestrial consumers (Baxter et al. 2004). The introduction of riparian vegetation can also alter allochthonous inputs to aquatic ecosystems. In many cases,

litter from invasive plants is of lower nutritional quality for aquatic consumers than native plant litter (Moline and Poff 2008; Mineau et al. 2011; Mineau et al. 2012). Although it has been demonstrated that invasive species, whether terrestrial or aquatic, can alter habitat linkages, few studies have evaluated how invasive species may interact across ecosystem boundaries. To address this knowledge gap, I evaluated how invasive fruit-bearing, riparian trees, Russian olive (*Elaeagnus agustafolia*, RO), facilitate introduced, channel catfish (*Ictalurus punctatus*, CCF) in the San Juan River as an example of an inter-ecosystem interaction between invasive species.

The San Juan River can be considered a novel ecosystem because it has been subjected to multiple environmental alterations and its fish communities and their food webs have changed drastically in the last 100 years. Altered flow regimes and water withdrawal in the San Juan Basin have resulted in habitat complexity loss and facilitated non-native species (Propst and Gido 2004; Gido and Propst 2012, Lamarra 2016). Corresponding changes in environmental conditions, combined with fragmentation and species introductions, have caused large-scale declines of fishes throughout the Colorado River Basin, resulting in the listing of four fish species as federally endangered (Tyus and Saunders 2000; Olden et al. 2016). Currently, non-native fish species richness is greater than native species richness in the San Juan River (Sublette et al. 1990). CCF are the most abundant predatory non-native species in the San Juan River and are of great concern as potential competitors with and predators of native and endangered fishes (Gido and Propst 2012, Franssen et al. 2014, Pennock et al. 2018). In addition to aquatic invasions, riparian communities have also been invaded throughout the Colorado River Basin, primarily by RO and salt cedar (*Tamarix spp.*). In the San Juan River, bank vegetation substantially increased from 1930 to 2010, and RO currently dominates the riparian community (Basset et al. 2012). RO is a fruit-bearing tree that produces large quantities of carbohydrate-rich fruit in the fall and winter (Katz and Shafroth 2003) and has likely altered the quantity and composition of allochthonous inputs to the San Juan River. Mineau et al. (2012) showed that RO invasion increased allochthonous inputs into spring fed streams in Idaho, but the RO litter decomposed more slowly than native willow (*Salix laevigata*), resulting in a decreased ecosystem efficiency after the invasion. This study showed that species invasion can alter resource subsidies and have impacts that span ecosystem boundaries. In addition to the impact of changes in allochthonous inputs, RO also directly interacts with CCF in the San Juan River. RO and CCF may be mutually beneficial because CCF readily consume RO fruits throughout the year and CCF disperse RO seeds by passing them whole. Previous chapters

have described the interaction between RO and CCF and the benefit of the interaction for both species.

The goal of this chapter is to determine the degree to which RO subsidies facilitate CCF populations in the San Juan River. I used a bioenergetic modeling approach to estimate daily and annual energetic consumption of CCF. I combined data collected in the field, data from laboratory experiments, and parameter values from the literature to predict energetic consumption given annual CCF growth in the San Juan River. In addition, I used population and mortality estimates to model population-level consumption of channel catfish > 300 mm in the San Juan River.

My specific objectives in this study were to:

1. Formulate bioenergetic models to estimate CCF energy consumption for each age cohort in the San Juan River
2. Determine the proportion of per capita annual energy consumption that RO fruit subsidies provide to CCF
3. Use daily per capita consumption estimates and population estimates to determine the proportion of annual energy consumed by channel catfish that is subsidized by RO fruits

I hypothesized that energetic subsidies provided by RO fruits satisfy metabolic energy demand throughout the year but support little growth for individual CCF. I also hypothesized that RO fruits provide an energetic subsidy to CCF populations that facilitates San Juan River CCF populations.

Methods

Study Site

This study focused on a portion of the San Juan River from Waterflow, NM, to Mexican Hat, UT. Within this segment, I modeled consumption using temperature data from Four Corners (UT). Daily mean temperature data were downloaded from US Geological Survey monitoring Four Corners, UT (09371010) and rounded to a whole number in °C (Figure 3.1). Temperatures were downloaded from September 21, 2016 to August 31, 2017.

Field and Lab Methods

Here I provide a summary of field methods, and detailed field methods are presented in Chapter 1. I determined diet proportion based on wild-caught CCF using traditional stomach

content analysis. CCF were sampled in each of the study reaches every other month from September 2016 to August 2017 for a total of seven sampling events. I sampled four 8 km segments along the longitudinal gradient separated by 39 river km. Each site was 8.05 km long based on designated river miles set by US Fish and Wildlife Service, and fish were sampled from shallow habitats using single-pass raft-based electrofishing (Smith Root GPP 9.0) while drifting with the current. Fish were euthanized with MS-222 (Tricane-S, Western Chemical) and dissected in the field. Excised gastrointestinal tracts were placed in individually labeled Whirl-Pak® bags and stored on wet ice until transferred to a freezer (-20 °C). I measured total length (TL; mm), weight (g), and sex for each fish. Stomachs were thawed and the contents were separated into categories (i.e., RO, aquatic insects, crayfish, fish, terrestrial invertebrates, terrestrial vertebrates, algae, vascular plants, and other) in the laboratory and weighed for both wet (± 0.01 g) and dry weight (± 0.01 g).

I used bioenergetic mass balance models to predict consumption to determine the proportion of energy intake RO fruits provide to CCF in the San Juan River. Specifically, I used the equation presented by Kitchell et al. (1977) in the Hewett and Johnson (1992) model of fish growth to predict consumption. The model as originally presented (Eq. 1) includes G (somatic growth), C (energetic consumption), R (energy lost to respiration), and U and F (energy lost to excretion and feces). The equation can be easily balanced to solve for energetic consumption when fit to known growth rates following Equation 2.

$$\text{Eq. 1: } G = C - (R + U + F)$$

$$\text{Eq. 2: } C = G + (R + U + F)$$

Model Inputs

To predict CCF energetic consumption for each prey category, I used inputs of temperature, prey energy density, predator energy density, diet proportion, a set of physiological parameters, and the indigestible proportion of prey items. The model inputs used included a combination of field data (Chapters 1 and 2) and values from the literature (Table 3.1).

Growth

All models presented in this paper were fit to CCF growth in the San Juan River. I did not measure CCF growth at the field study sites, so I modeled fish growth, varying growth by age class but assuming that growth is constant throughout sites. I estimated daily growth for each age using the von Bertalanffy growth equation and length-weight relationships presented in Pennock et al.

(2018). I estimated annual growth in total length for each age class. We only estimated consumption for catfish >300 mm because electrofishing is ineffective for fish below this size and therefore, abundance estimates only included fish with acceptable detection probabilities. The length-at-age values from the Von Bertalanffy growth curve and were converted to mass-at-age using the length-weight formula from Pennock et al. (2018). I modeled consumption fit to growth for each age cohort from Age 3 to Age 10.

Diet Proportion

Proportion of each prey category by wet weight of CCF stomach contents was summarized across all sample sites at each sampling period for each age cohort. Because we did know age of fish in the diet study we used length at age estimates to place fish that were assessed for diet into age classes. I calculated the proportion of diet for each of the seven bimonthly field sampling events. I allowed the model to interpolate diet proportions between sampling events, meaning the diet proportions incrementally changed by the day to transition to the next diet sampling event. I interpolated the diet data to more realistically represent daily diet shifts rather than maintain a constant diet throughout sampling events.

Bioenergetic Parameters

Since CCF were not included as a pre-set physiological parameter, in the model, I used the same physiological parameters that Blanc and Margraf (2002) used to estimate CCF consumption in West Virginia lakes (Table 3.1). I modified that model to adjust for varying digestibility of each prey category. Constant egestion is reasonable when all prey items are similar in the indigestible proportion. CCF diets are diverse, so I chose to use a temperature and consumption dependent model where I could correct for the proportion of indigestible material for each prey category (Stewart et al. 1983). Indigestible proportion estimates were primarily taken from the literature (Table 3.1). I determined the indigestible proportion of RO fruits by first estimating the mean ratio of fruit to seed. The indigestible proportion of the fruit was calculated from nutrition information in Chapter 3. Using these combined calculations, I determined that RO fruits were 48% indigestible material for CCF. The indigestible proportion of RO was based on a whole fruit (with seed) wet weight. This yielded a considerably higher proportion of indigestible material compared to other prey items of the diet (Table 3.1). Prey energy values were also taken from the literature (Table 3.1) except for RO, which was measured from nutritional analysis (Chapter 3). The energy density used for RO fruit was the digestible portion of the fruit. Since seeds are not digested, I did

not include them in the nutritional analysis. I included plant (mostly RO leaves) and other (e.g., sand, woody debris, rocks) in the diet proportions because they were often found in fish stomachs at considerable volume. I assumed that these categories provided little to no energy intake, so I used 1 as the indigestible proportion. The model would not run if given a prey energy of zero, so I set energy density at 1 J/g to be functionally equivalent to zero. I used seasonal predator energy densities from Blanc and Margraf (2002) to interpolate predator energy density between seasonal estimates.

I used the Wisconsin bioenergetic model that is openly available as Fish Bioenergetics 4.0 (version v1.1.2) (Deslauriers et al. 2017). The model is implemented through a shiny application (v1.4.0) (Chang et al. 2015) in RStudio version (R-Studio Inc, v3.5.3). Model runs encompassed 365 d, from September 1, 2016 to August 31, 2017. Each run represented the annual consumption of an individual CCF of the same age cohort.

In order to determine the total consumption for channel catfish populations in the San Juan River, I used Lincoln-Peterson mark-recapture abundance estimates of CCF and the 95% confidence intervals around those estimates. These estimates were part of a separate study of CCF populations conducted by the San Juan River Recovery Implementation Program. Abundance estimates only included CCF >300 mm total length due to inefficient sampling of smaller size classes and associated low recapture rates (Pennock et al. 2017). Therefore, I did not estimate the consumption for fish <300 mm or those age 0 to age 2. Length-frequency estimates from Pennock et al. 2018 were used to determine the proportion of the population within each age class > 2 years old. Multiplying the proportion in each age class by the abundance estimate was used to determine the number of channel catfish in each age class. Because diet sampling was conducted in 2016, we used channel catfish abundance estimates from 2015, the closest estimate to our sampling time period.

Fish Bioenergetics 4.0 model allows the user to specify population size and annual mortality. Mortality for channel catfish in this system is not known, so we used an annual mortality of 10% of the population and was kept constant for all age classes. The model interpolates annual mortality to daily mortality to reflect the loss of individuals from the population and the resulting reduction in consumption. The estimated per-capita daily consumption (Joules) for each prey item was multiplied by the cohort abundance at each time step (1 day). The sum of daily consumption for each cohort was used to determine the total annual consumption for each age class. The sum

of age classes 3-10 was used to calculate the total population consumption for channel catfish in the San Juan River.

Table 3. 1 Parameters for channel catfish bioenergetic model implemented with Fish Bioenergetics 4.0.

Definition	Parameter	Value	Reference
Consumption			
Intercept Cmax	CA	0.33	Cuenco <i>et al.</i> (1985), Andrews <i>et al.</i> (1973)
Slope	CB	-0.33	Cuenco <i>et al.</i> (1985)
Temperature coefficient	CQ	2.3	Andrews and Matsuda (1975)
Optimum temperature	CTO	31	Blanc and Margraf (2002)
Maximum temperature	CTM	37	Blanc and Margraf (2002)
Respiration			
Intercept	RA	0.00833	Andrews and Matsuda (1975)
Slope	RB	-0.2	Andrews and Matsuda (1975)
Temperature coefficient	RQ	2	Andrews and Matsuda (1975)
Optimum temperature	RTO	35	Larimore et al. (1979)
Maximum temperature	RTM	38	Jobling (1981)
Activity	ACT	1	Blanc and Margraf (2002)
Waste			
Specific Dynamic Action	SDA	0.15	Brett and Groves (1979)
Excretion constant	FU	0.05	Brett and Groves (1979)
Egestion Intercept	FA	0.212	Dieterman and Anderson 2004
Egestion slope	FB	-0.222	Dieterman and Anderson 2004
Indigestible Proportion			
RO		0.48	
Aq Invert		0.1	Stewart et al (1983)
Fish		0.033	Stewart et al (1983)
Crayfish		0.25	Stein and Murphy (1976)
Terr Invert		0.1	Stewart et al (1983)
Terr Vert		0.5	Wallick and Barret (1976)
Prey Energy Density (J)			
RO		1600	
Aq Invert		4300	Cummins and Wuycheck (1971)
Fish		4200	Hansen et al. (1997)
Crayfish		3800	Roell and Orth (1993)
Terr Invert		3100	Hewitt and Johnson (1992)
Terr Vert		5160	Wallick and Barret (1976)
Predator Energy Density (J)			
September 2016		3289	Blanc and Margraf (2002)
January		3044	Blanc and Margraf (2002)
April		2835	Blanc and Margraf (2002)
July		2764	Blanc and Margraf (2002)
September 2017		3289	Blanc and Margraf (2002)

Results

All model runs were balanced and predicted p-values, or the proportion of maximum consumption ranged from 0.71 -0.76. Total per-capita consumption was greatest in summer months when temperature was highest. Total energetic consumption from RO fruits was also greatest in the fall and spring time periods. Aquatic insect consumption comprised the majority of consumption across all seasons and size classes; however, they made up a lower proportion in the largest CCF size classes. Terrestrial invertebrates (primarily insects, but also arachnids and isopods) were important sources of energy for CCF during the winter and spring. Non-native virile crayfish (*Orconectes virilis*) provided up to 30% of energetic demand for CCF >500 mm and were also an important energy source for 400-500 mm fish.

Annual cohort consumption was greatest for fish ages 3 and 4 because they were the most abundant in the length-frequency estimates. These age classes also consumed the greatest proportion of their diet from Russian olive fruit. After summing annual consumption across all cohorts, we calculated that energy consumed from RO fruits made up 24.7% of annual consumption for channel catfish populations > 300mm in the San Juan River.

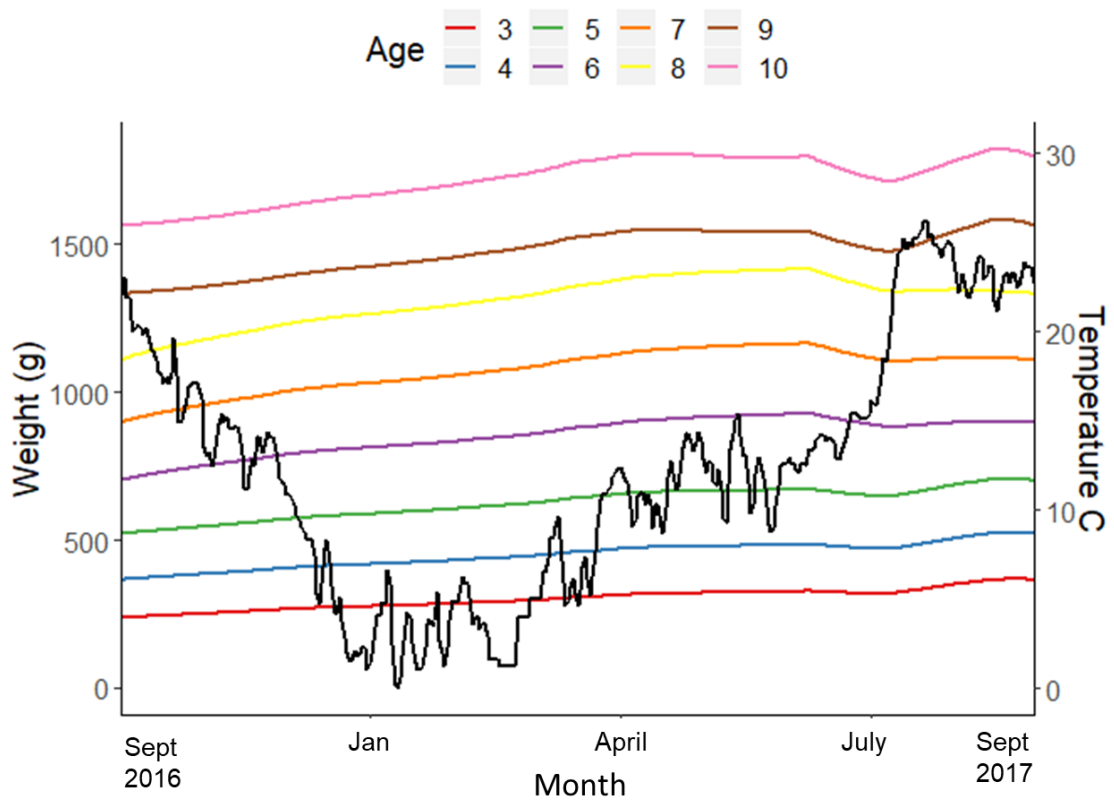


Figure 3. 1. Daily body weight for channel catfish in each age cohort (colored lines) and average daily temperature (C°) (black lines) from the San Juan River at Four Corners, UT used to estimate consumption using Fish Bioenergetics 4.0 model

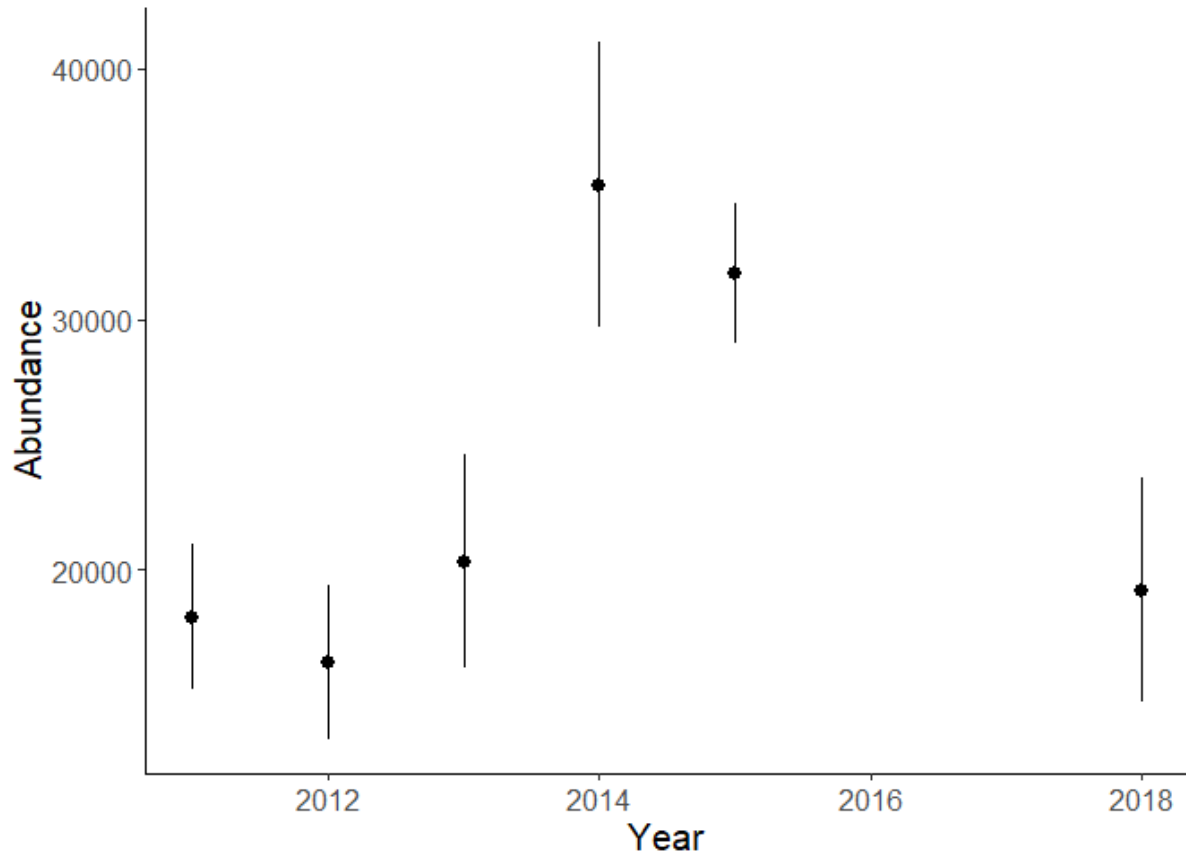


Figure 3. 2. Abundance and 95% confidence intervals for channel catfish (*Ictalurus punctatus*) >300 mm between Shiprock, NM and Mexican Hat, UT in the San Juan River. Estimates from Lincoln-Peterson mark-recapture models across from 2005 to 2018.

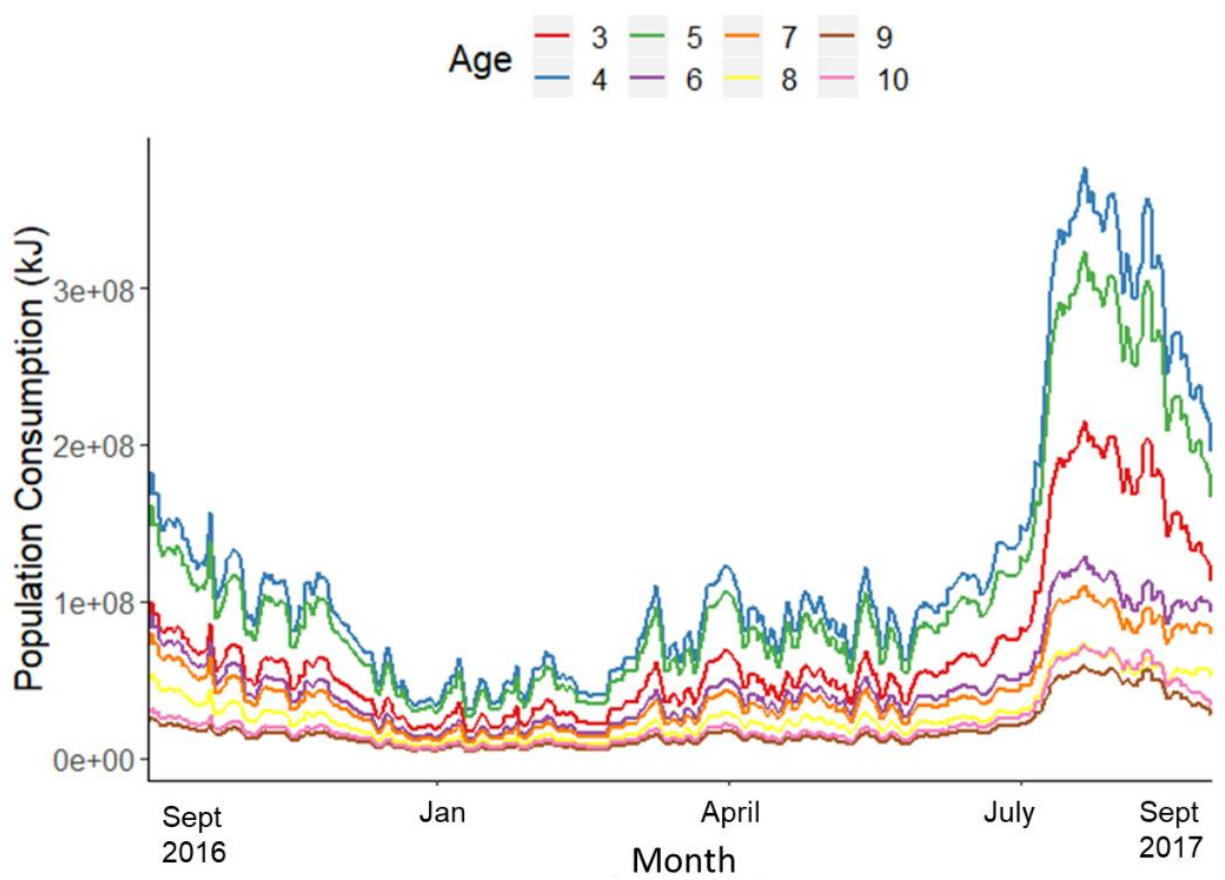


Figure 3. 3. Population consumption (KJ) per day for channel catfish in the San Juan River from September 2016 to September 2017. Per-capita consumption for each cohort was estimated using Fish Bioenergetics 4.0.

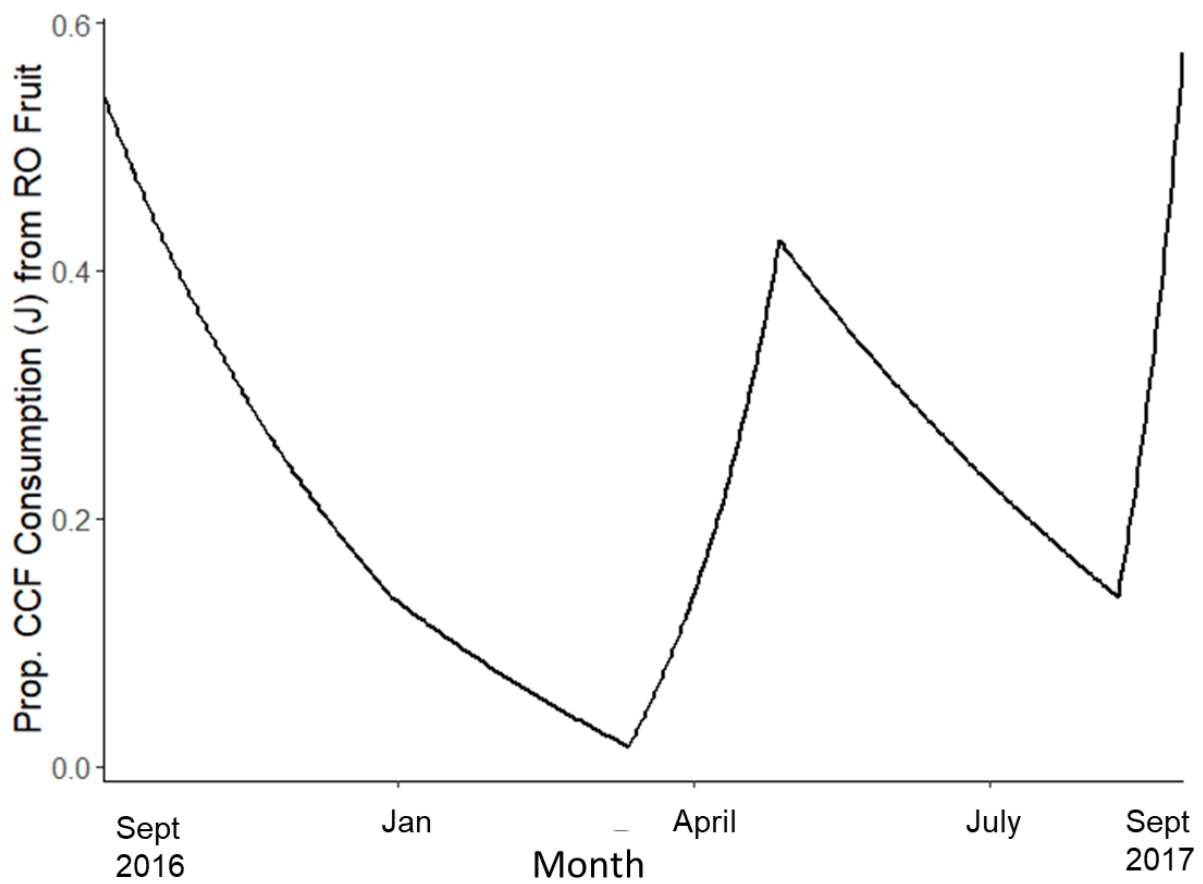


Figure 3. 4. Estimated daily proportion of total energy (J) consumption that is provided by Russian olive fruits to channel catfish populations in the San Juan River from September 2016 to September 2017.

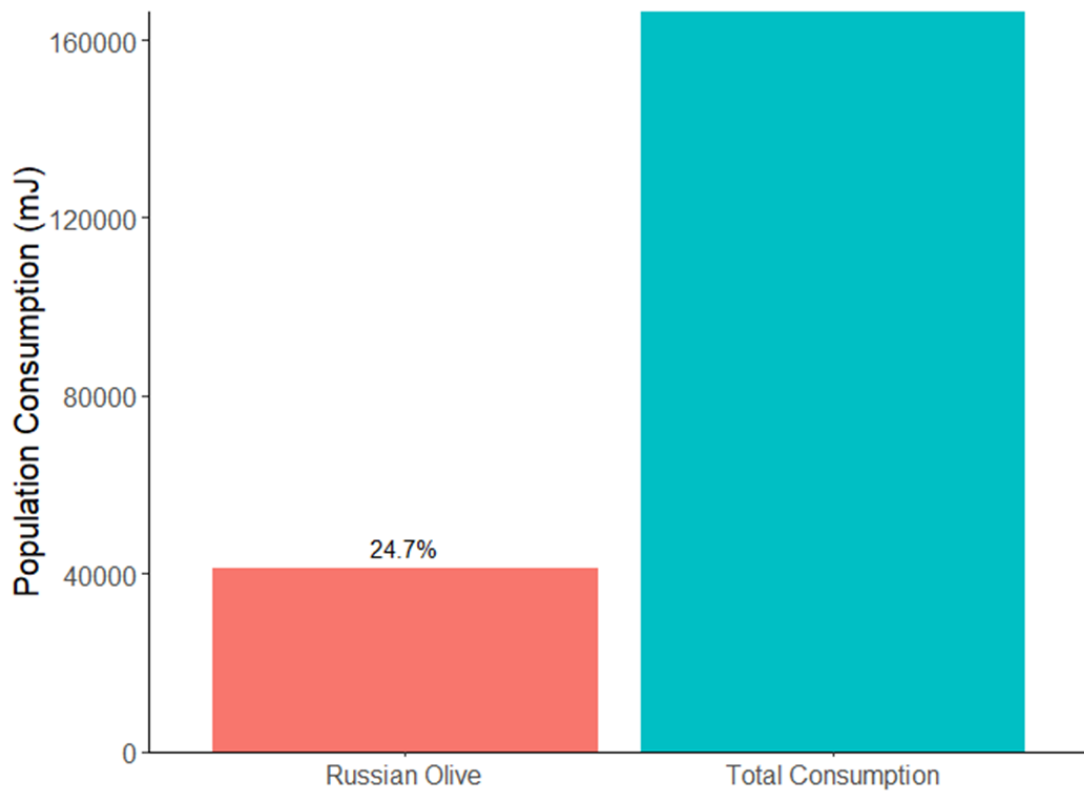


Figure 3. 5. Estimated annual consumption (J) for channel catfish populations in the San Juan River (NM/UT) from September 2016 to September 2017 and the annual energy consumed from Russian olive fruits. Consumption was estimated using Fish Bioenergetics 4.0.

Discussion

The model estimates indicated that RO fruits provide an energetically valuable resource subsidy to non-native CCF populations in the San Juan River. RO fruits subsidized all size classes and across the entire year but were most valuable to catfish in age 3 and 4 cohorts. Although RO fruits did not provide fitness benefits by contributing to growth, the subsidy provided enough energy to satisfy more than half of the metabolic demand for CCF for the year modeled. My consumption estimates indicated that RO subsidies facilitated CCF populations, providing an energetic subsidy that supported increased biomass of CCF. This is especially notable because it serves as an example of an invasive species facilitating another invasive species across an ecosystem boundary.

In addition to RO fruit subsidies, terrestrial prey subsidies were important for CCF in the San Juan River. Terrestrial prey was common in all size classes and accounted for 24.5% of total energetic consumption across all size classes. Terrestrial prey items were diverse, but terrestrial insects and isopods were particularly common. Terrestrial vertebrates, including rabbits, lizards, snakes, and birds, provided a small amount of energetic consumption and were more important for fish >500 mm TL. Many studies have shown the importance of terrestrial subsidies for supporting consumer populations in rivers and streams (e.g., Wipfli 1997, Menher 2005). My study further demonstrates the importance of terrestrial resource subsidies in freshwater ecosystems and expands understanding to include roles played by both native and invasive terrestrial species in supporting invasive aquatic consumers.

RO fruit was not the only non-native diet item that supported San Juan River CCF in this study. Virile crayfish made up 34.1% of total consumption for CCF > 500 mm TL. Crayfish are a major prey item in CCF diet studies from native habitats (Bailey and Harison 1948; Gerald and Brown 1971). However, there are no native crayfish in the San Juan River or the Upper Colorado River Basin. In addition to being an important prey item for CCF, virile crayfish are also important prey items for other invasive species found in the Yampa River (Upper Colorado River Basin), including smallmouth bass (*Micropterus dolomieu*) and Northern pike (*Esox lucius*) (Johnson et al. 2008). These piscivorous species are a serious threat to native fishes in the Upper Colorado River, yet little is known about how non-native crayfish may facilitate invasive predators. Non-native crayfish in the Upper Colorado River have received little attention from researchers or managers despite of their abundance and potential for impacts on native species.

More research is needed to understand how interactions between crayfish and non-native fish impact native fishes and ecosystem function in the San Juan River and beyond.

CCF are opportunistic omnivores and have wide ranging diets allowing them to colonize diverse habitats throughout their native and invasive ranges. The use of RO fruits by CCF is not surprising given their use of tree fruits in their native range such as mulberry (*Morus rubra*) (Chick and Cosgrif 2003). However, no other studies have evaluated how much CCF benefit from fruit subsidies regardless of whether they are derived from native or non-native species. I showed that CCF can utilize fruits for metabolic energy, and CCF feeding on native mulberry fruits within their native distribution are likely benefiting in the same way.

RO fruits provided a predictable and highly abundant resource that may provide CCF with a competitive advantage over native species. Native San Juan River catostomids, bluehead sucker (*Catostomus discobolus*) and fannelmouth sucker (*Catostomus latipinnis*), do not utilize RO fruits based on limited diet sampling (C. Cheek, pers obs.; Chapter 1). Lack of competition for RO fruits may make them a valuable resource for sustaining San Juan River CCF. In addition, the high availability of this subsidy likely requires CCF to expend little energy searching for RO fruit. Fruits primarily float on the water surface and are often found in large quantities in slack water and eddies. A highly abundant, low cost resource provides the greatest energetic return to the consumer, making RO a valuable diet item despite the nutritional deficiencies for growth.

CCF in the San Juan River have been heavily managed to reduce predation on and competition with endangered Colorado pikeminnow. Based on my diet data and modeled estimates of consumption, the level of fish predation was low and limited to fish >400 mm TL. These fish comprised a small proportion of the total biomass, yet they had a higher per capita consumption of fish prey. The limited number of diet samples on fish >500 mm TL may bias my estimates of large CCF diet. However, my estimates were similar to other CCF diet studies from the San Juan River (Patton et al. 2012; Brooks et al. 2000). Using the model estimates of per-capita annual consumption of fish and abundance estimates, I calculated that total consumption of prey fish in 2016 as 2835 kg. This reflects the predation of all fish prey in the diet of CCF in a given year. I did not document the predation of Colorado pikeminnow or razorback sucker in my field estimates of diet. Therefore, I could not estimate consumption at a species-specific level. In addition, I observed a high level of cannibalism, with the majority (74%) of fish in stomach

contents identified as young-of-year CCF. However, CCF spines make them easily identifiable and may have biased this estimate.

Removal efforts that have been a major management action for recovering endangered fishes in the San Juan River are currently under review due to insufficient evidence for CCF predation and increasing evidence that removal efforts are not effective at reducing CCF abundance. However, Pennock et al. (2018) showed that removal efforts affect size structure of the population. Removal efforts have reduced the number of large catfish in the system that exhibit the highest predation rates on prey fishes. This finding supports that removal efforts that target large-bodied fish are potentially useful, even if total CCF biomass does not decline. Future model scenarios should evaluate how changes in size structure of the population may impact predation rates on native fishes. Increased numbers of stomach content samples will improve estimates of CCF predation rates and research is currently in progress to address this. My bioenergetic model of consumption for the San Juan River will be valuable for evaluating fish predation under future scenarios of CCF population and size structure as the San Juan River Recovery and Implementation Program decide whether and how non-native removal programs will continue.

The impact of the interaction between RO fruits and CCF on native fishes is unknown. Presumably, it could affect native species in two ways. First, RO subsidies could indirectly benefit native fishes by reducing both predation pressure and competition for aquatic insect prey. Alternatively, RO subsidies may facilitate increased abundance of CCF, resulting in increased predation risk and competition. More research is needed to determine the impact of this interaction on native species. In addition, more research is needed to determine if native species that do not directly benefit from RO fruit subsidies benefit from indirect facilitation from RO allochthonous inputs. This could happen through allochthonous inputs of RO fruits or litter that support invertebrate or detrital food webs.

The bioenergetic models of CCF consumption I present only represent one year of data (September 2016 – September 2017), and more years of diet data would provide better understanding of interannual variation. Another potential limitation of the models is that I did not incorporate natural individual variation in diet or growth into the model since it assumes that all fish within a size class-season combination have the same growth and diet composition. Future models should incorporate individual variation in diet that was observed in the field. In addition,

better estimates and variability of seasonal growth would greatly improve model estimates of consumption. Bioenergetic models are sensitive to energy density estimates for both the prey and predator, and all prey energy density values, except RO, were collected from the literature. Better estimates of energy density for both predators and prey would increase model accuracy.

In this chapter I evaluated the impact of RO subsidies on CCF populations and showed that RO contribute to CCF biomass in the San Juan River. The results from Chapter 2, indicated that CCF benefit RO through increased germination probability and possibly seed dispersal. Future research should determine the effect of channel catfish on the biomass, density, or spread of Russian olive populations.

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CONCLUSION

In Chapter 1, I demonstrated that channel catfish (*Ictalurus punctatus*; CCF) utilize Russian olive (*Elaeagnus angustifolia*; RO) fruits as a main component of their diet based using traditional stomach content analysis. CCF utilized RO fruit throughout the year, but consumption was most prevalent in the fall and spring diet samples. RO fruits composed 50-70% of the stomach contents by weight during these time periods. Stomach contents were diverse, but aquatic macroinvertebrates were the second most prevalent diet item across all time periods, after RO. Although RO comprised a large proportion of the diet by weight, these data do not clearly show that RO are nutritionally beneficial to CCF. Stomach content analysis has been criticized for biases for prey items with high proportions of indigestible biomass. Because it has a large, indigestible seed, RO is an example of a diet item that is likely to be over-represented in stomach contents. In addition, weight alone does not completely reflect the importance of a prey item when prey varies greatly in energy density and micro-nutrients. Thus, there is need to estimate the energy intake from RO fruits and the difference in nutritional value and digestibility of RO fruit to estimate the degree to which RO subsidies facilitate CCF populations.

In Chapter 2, I showed that RO fruit is a poor-quality diet item for growth and lipid deposition; however, when fed a diet of 100% RO fruit for six weeks, CCF maintained weight. The results of the feed trial indicated that CCF can utilize RO fruit as a source of metabolic energy, but this food source alone was not nutritionally sufficient for assimilating muscle or fat tissue. In addition, I illustrate that CCF facilitate RO germination, provided a 4-fold increase in germination probability over seeds that were not consumed. Given that CCF are not the only animals that provide this service to RO, their relative importance for the spread of RO is limited. CCF in our trials, RO seeds germinated the best when consumed by mammals and seed dispersal by birds has been documented in the literature (Kindschy 1998). In both the feeding trial and the germination experiment I showed that there is potential for a mutualistic interaction to occur between two invasive species that cross ecosystem boundaries. However, facilitation between two invasive species requires a resulting effect of the interaction on biomass or density in the environment. Understanding the impact of facilitation among invasive species on community and ecosystem properties is difficult, and many studies focus on individual fitness and presume population or ecosystem-level effects (Simberloff 2006). To understand the interaction between RO and CCF,

it is important to understand how CCF biomass responds to RO subsidies. Ideally, this question would be answered using before and after invasion data or through an *in situ* experimental approach. In my study system both approaches were unrealistic given the remoteness of field sites and dynamic nature of flows in the San Juan River. Instead I use a bioenergetic modeling approach to address the population level impact of RO subsidies on CCF populations.

In Chapter 3, I present the results of a bioenergetic model of annual CCF consumption to determine how RO subsidies facilitate CCF biomass in the San Juan River. Bioenergetic models are a mass balance approach that allow the user to estimate energy consumption and assimilation, such as growth and consumption, given known parameters including energy lost to respiration and waste. The bioenergetic approach also allowed me to account for difference in digestible material for each prey item, a major issue with interpreting Chapter 1 results given the large disparity in digestibility (52% - 97%). I fit my bioenergetic models to CCF growth using a model of seasonal growth estimated from length-at-age data collected in the San Juan River, converted to growth in weight (g) by season. I used the stomach content data, summarized by season and size class to model annual per-capita energy consumption for each size class of fish at three sites (Shiprock, Four Corners, and Mexican Hat) along the San Juan River. Several parameters in the model (maximum consumption, egestion, and respiration) are temperature dependent, so I used temperature data from adjacent USGS monitoring stations. Other parameters including the indigestible proportion of diet items, the energy density of prey items, predator energy density, and physiological parameters were taken from the literature, except RO indigestible proportion which I estimated from nutritional information and seed to fruit ratios. After fitting the models of per-capita growth for each season, size class, site combination, I used CCF abundance estimates from the San Juan River Recovery Implementation Program to estimate annual energy consumption for the population across all sites. I then use the proportion of energy consumed in the form of RO fruits to estimate the biomass of CCF that is facilitated by subsidies of RO fruit in the San Juan River. I illustrate that RO subsidies provide enough energy to satisfy an average of 36% of annual energy demand for CCF respiration. I also estimate that RO subsidies facilitate up to 46% of the total biomass of CCF (>300 mm) in the San Juan River. As far as I know, this is first attempt to show the population-level effect of a positive interaction between two invasive species that cross an ecosystem boundary. The model would be better able to predict the population response to RO if it incorporated individual variation in diet and growth.

The results of this dissertation indicate that mutual facilitation between RO and CCF is likely to occur, with CCF receiving an energetic subsidy from RO fruits and RO receiving a benefit in reproductive potential. However, I was not able to demonstrate increases in biomass or density of RO trees from the interaction with CCF. Future research, possibly using an individual based population modeling approach, could untangle if CCF increase RO composition in the San Juan River.

In addition, future research should utilize the bioenergetic modeling framework to estimate CCF predation pressure on native fishes. In Chapter 3, I estimated the annual consumption of fish prey by CCF populations in the San Juan River. However, our estimates were based on a relatively small number of large fish (500+ mm), which have the highest rates of piscivory. Greater resolution and increased number of samples of large CCF would improve the estimates of fish predation and allow for species-specific estimates of predation rate and ultimately to estimate mortality from CCF. Gaining a better understanding of CCF predation on endangered fishes is the primary objective of an ongoing research project being conducted by the San Juan River Recovery Implementation Program and the Gido Lab at Kansas State University. Diet sampling from this project will provide better sample sizes and estimates of fish predation, especially in the large size classes of CCF. Given that the current estimates of fish predation are low, and I did not detect any endangered fish in stomach contents, predation may not alone justify removal efforts for CCF in the San Juan River. However, the importance of macroinvertebrate prey in CCF diets and for all native fishes, and especially early life stages of Colorado pikeminnow, competition between CCF and native fishes may justify removal efforts alone.

More research is needed to understand how allochthonous inputs from RO fruits impact ecosystem function. Given the large increases in bank vegetation following the invasion of RO, allochthonous inputs of low-quality leaf litter has likely greatly increased compared to historic inputs of native cottonwood and willow. Understanding how these subsidies impact invertebrate production and indirectly impact both native and non-native fishes is important for understanding how RO have altered energy flows and ecosystem function. In addition, CCF also rely on subsidies of terrestrial prey (terrestrial invertebrates and vertebrates). RO may indirectly subsidize CCF populations by facilitating terrestrial production and more research is needed to determine these relationships. Stable isotope and fatty acid analysis approaches could help illustrate how energy flows from terrestrial and aquatic pathways, allowing us to determine how RO may indirectly

facilitate CCF. I am currently working on sample processing and analysis to address these questions.

The interaction between RO and CCF may also alter the flow of nutrients through the food web. RO being a nitrogen-fixing plant, has high levels of nitrogen in the fruit and leaf material. However, both include tannins that are slow to decompose and are lower quality forage for shredding guild insects. The consumption of RO fruit by CCF may recycle nutrients held in fruits making them more available to other consumers and primary producers. Future research should evaluate how CCF nutrient recycling from RO fruits impacts primary production, consumer growth, and ecosystem function.

The long-established populations of RO and CCF in the San Juan River are unlikely to be eradicated. Decades long CCF removal programs have made little impact in reducing non-native populations in the San Juan River and have shown some benefits for native species. RO is likely to remain in the system since seeds have long dormancy periods and seed banks are extensive and viable. In fact, small scale riparian restoration projects, with the goal of reconnecting historic secondary channels have struggled to maintain restoration sites due to re-sprouting of RO following mechanical clearing and require years of herbicide application to ensure the establishment of native vegetation. It is unknown how the eradication of these species would impact the other facilitator. Given the low probability of complete eradication more attention should be given to understanding how this interaction between RO and CCF impacts native species.

In the management of invasive species, a gram of prevention is worth a kilogram of cure. Although eradication of RO and CCF, where they are established in large connected systems like the Upper Colorado River, is very unlikely, managers can prevent invasions from occurring in other ecosystems. The facilitation that I document in this dissertation may, in fact, allow for higher probability of successful invasion when one of the species is already established. For example, many desert spring complexes have been invaded by RO, but have not been invaded by CCF. In these systems, with high levels of endemism, the invasion of CCF would be particularly damaging for native biodiversity and RO facilitation may provide niche space needed for CCF establishment. Managers should understand these risks to prevent future invasion in these systems.

In conclusion, this dissertation illustrates the potential for invasive species to interact across ecosystem boundaries and for those interactions to be mutually beneficial. I show that invasive species can alter resource subsidies, which can have implications for community structure in

neighboring habitats. More research should evaluate how the impacts of invasive interactions impact native fishes, in order to have comprehensive understanding of ecosystem function and to better manage native biodiversity.