Analysis of Food Web Effects of Non-native Fishes and Evaluation of Stream Restoration Potential for the San Rafael River, Utah

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ANALYSIS OF FOOD WEB EFFECTS OF NON-NATIVE FISHES AND EVALUATION OF RESTORATION POTENTIAL FOR THE SAN RAFAEL RIVER, UTAH

by

Timothy E. Walsworth

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE in

Ecology

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ABSTRACT

Analysis of Food Web Effects of Non-native Fishes and Evaluation of Stream Restoration Potential for the San Rafael River, Utah

by

Timothy E. Walsworth, Master of Science
Utah State University, 2011

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

The highly endemic native fish fauna has experienced dramatic reductions in abundance and range because of anthropogenic activity. In addition to a highly altered flow, temperature, and physical habitat template, many non-native fish species have established populations throughout the basin. The San Rafael River, a tributary of the Green River in southeastern Utah, is home to populations of flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), and roundtail chub (*Gila robusta*), and has experienced degradations representative of many rivers throughout the Colorado River Basin. Using the San Rafael River as a template, I examined (1) the effect of the non-native fishes on the food web structure of a Colorado River tributary and (2) whether any changes to the food web structure by non-native fishes impact fitness-related vital rates of native fishes in the river. Stable isotope analysis revealed that the non-native fishes present novel predator archetypes to the “three species,” but
size-at-age and body condition analyses did not reveal any reduction in fitness between native fishes captured in the presence of the non-native fishes.

Additionally, I used site-specific biotic and abiotic measurements to develop a model predicting “three species” relative abundance. Non-native fish abundance and spatially auto-correlated measures of physical habitat were found to be particularly important predictors of “three species” relative abundance. The model was used in combination with a longitudinal habitat survey to predict the current continuous distribution along the length of the lower San Rafael River, as well as to simulate population-level effects of relevant restoration actions. The eradication of non-native fishes resulted in significant population increases for each of the ‘three species,’ and physical habitat restoration resulted in significant population increases when executed in certain reaches, but significant population reductions if executed in other reaches. These results suggest that the restoration of physical habitat without addressing populations of non-native fishes will likely result in a limited response by the “three species,” and that the choice of restoration location is critical to its success.

(122 pages)
Native fishes of the Colorado River Basin have experienced dramatic reductions in range and abundance as a result of extensive human alterations to the basin’s waterways. Many of these native fishes are federally listed under the Endangered Species Act, while several others are subject to range-wide conservation agreements between state and federal management agencies. Three of the native species subject to range-wide conservation agreements are the flannelmouth sucker, bluehead sucker, and roundtail chub (hereafter, the “three species”). Each of the “three species” is still found in the San Rafael River of southeastern Utah, which has experienced habitat degradation and non-native species establishment representative of many desert streams.

In this study, I examined the effects of non-native species on the food web structure and relative growth rates of the “three species” (Chapter 2) in two sections of the river characterized by the presence and absence of non-native fish. I found that the presence of non-native species lengthens the food chain, presenting new predators and competitors to the ‘three species.’ However, I found no evidence of reduced growth in the presence of these non-native fishes, likely due to movement of individuals of the “three species” between the two sections of river. Secondly, I developed a model to identify and rank limiting factors to the “three species” along the continuum of the lower river. Finally, I used this model to simulate and predict the relative effect of different restoration actions at different locations along the river on the abundance of the ‘three species.’ These models predicted that removal of non-native fishes and the restoration of long stretches of suitable habitat would be most beneficial to the ‘three species.’ Models
such as those developed in this study can be useful for management agencies to prioritize restoration efforts to ensure the persistence of the “three species” both in the San Rafael River and throughout their historic range.
DEDICATION

I dedicate this thesis to my parents, Robert Walsworth and Mary-Margaret Lannon, who have always provided unwavering support for my academic and personal pursuits, and who introduced me to the wild places that sparked my fascination with the natural world.
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Timothy E. Walsworth
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CHAPTER 1
INTRODUCTION AND PROBLEM DEFINITION

As human populations continue to grow and press further into natural landscapes, the impacts of development increasingly threaten the native biodiversity of freshwater ecosystems (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). Anthropogenic alterations of these ecosystems often result in physical (e.g., dams, diversions, sedimentation, channelization, hydrograph alteration, land use changes), chemical (e.g., pollution, nutrient loading), and biological (e.g., invasive species, disease) degradation of natural habitats. This degradation can favor novel life-history strategies (Olden et al. 2006), decrease resource availability (Tyus and Karp 1990; Brouder 2001), increase predation pressure on native species (Tyus and Saunders 2000), and alter the flow of energy through ecosystems (Sousa et al. 2008; Nalepa et al. 2009). As such, anthropogenic alterations can result in new evolutionary and contemporary pressures on native biota that have evolved to succeed in their specific suite of environmental conditions.

Rivers and streams of the southwestern United States, home to a highly endemic fish fauna, have been particularly impacted by anthropogenic disturbances (Minckley and Deacon 1968). Native fisheries of the Colorado River Basin are a prime example of freshwater biota devastated by these changes, resulting from intensive damming and diversion of water for agricultural, industrial, and municipal purposes in the region’s arid climate. Anthropogenic developments throughout the basin have turned the historically dynamic Colorado River, with high seasonal variation in flow and temperature, into a
more temporally stable system, disrupting the natural flow regime (Van Steeter and Pitlick 1998).

Native fishes of the Colorado River Basin express life-history strategies adapted to the natural flow regime of the Colorado River, and alterations to this flow regime have resulted in a mismatch between many of these life-history strategies and the current environment (Olden et al. 2006). For example, the dampening of peak discharge by impoundments leads to a reduction in the availability of rearing habitat (Tyus and Karp 1990, Clarkson and Childs 2000; Brouder 2001; Thieme et al. 2001) and loss of cues for spawning activities (Tyus and Karp 1990; Brouder 2001). Further, barriers presented by dams and large diversions inhibit the ability of native fishes to migrate to spawning, wintering, or feeding grounds (Tyus and Karp 1990; Compton et al. 2008). Hypolimnetic releases from dams also lead to tailwater reaches that are colder than natural for the system, which can further decrease available habitat for native fishes and affect recruitment success (Vanicek et al. 1970; Clarkson and Childs 2000). As such, alterations to the natural flow regime create a multitude of issues for native fishes that have been accompanied by dramatic population declines.

In addition to being a cue for native life-history strategies, natural flow regimes are essential for maintaining the in-channel spawning and floodplain rearing and feeding habitats required by aquatic species (Poff et al. 1997). Tamarisk (Tamarix spp.) establishment in riparian zones has exacerbated the effects of water withdrawals and damming, as tamarisk roots stabilize banks and lower the water table (Di Tomaso 1998). The dampening of high flows reduces the ability of regulated rivers to move sediments, resulting in sedimentation and narrower, less complex channels (Van Steeter and Pitlick
The resulting channelization of streams and homogenization of riverine habitat has been suggested to lead to reductions in native species diversity (Gorman and Karr 1978). Additionally, the increase in sedimentation caused by water loss can inhibit benthic invertebrate populations (Kefford et al. 2010), an important prey item for many native fishes. Thus, not only do the alterations decrease the amount of quality habitat available, they can also decrease the resource base available to native fish populations.

With research documenting the negative effects of anthropogenic alterations on native biodiversity mounting, management agencies have used habitat restoration as a strategy to maintain and rebuild native species populations (Lake 2001), though these restorations have not always been well-targeted or successful (e.g., Klein et al. 2007; Palmer et al. 2010).

While physical habitat degradation is often argued to be the primary cause of population and range reductions of native fishes (Ross 1986), others have argued that non-native fishes are more important than habitat loss in the extinction of species (Tyus and Saunders 2000). The Colorado River Basin has experienced extensive invasion by non-native species (e.g., Tyus and Nikirk 1990; Tyus and Saunders 2000; Unmack and Fagan 2004). Non-native fishes often maintain a competitive edge over native fishes (Böhn and Amundsen 2001), as they escape their natural enemies (Shea and Chesson 2002) and represent novel predator or competitor archetypes to the native fishes (Cox and Lima 2006), thereby inhibiting the ability of natives to obtain resources necessary for growth and reproduction. Native fishes also experience negative indirect effects of invasive fish presence, such as altered prey growth and behavior (Going and Dudley 2008; McIntosh et al. 2010). As a result, the control of non-native species is increasingly
recognized as an important component of restoration, often in conjunction with physical habitat rehabilitation (e.g., Shepard et al. 2002).

Interactions between a degraded physical habitat and non-native species presence can have synergistic effects on native species’ populations, as physical habitat degradation can aid in the establishment and dispersal of invasive species (Brook et al. 2008). While change in flow regimes decouples many native fishes’ life histories from their current environmental template, many non-native fishes are pre-adapted to the new conditions (Olden et al. 2006; Johnson et al. 2008), providing the non-native species a competitive advantage over the native species. For example, large dams (e.g., Glen Canyon Dam) induce a change from a lotic to a lacustrine environment upstream of the dam, introducing a niche that was not previously found in the Colorado River system, and providing invasive fishes that have evolved in lakes with a niche for which they are much better adapted than the fluvial native fishes of the Colorado River. This combination of physical degradation and biotic invasions in the Colorado River Basin has led to the extirpation and the federal listing of many endemic fishes under the Endangered Species Act (Minckley and Deacon 1968), while conservation agreements between states of the Colorado River Basin are in place in an attempt to protect several additional species (e.g., UDWR 2004).

The flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), and roundtail chub (*Gila robusta*; hereafter, the “three species”) are three endemic Colorado River Basin fishes that have experienced dramatic reductions in range and abundance. These fishes typically co-occur and are managed as an ecological and management complex of species, subject to a range-wide conservation agreement with
the stated goal of ensuring the persistence of the “three species” populations throughout their range (UDWR 2004). Little is known about these fishes, and most research done to date has focused on the habitat requirements at different life stages (e.g., Bestgen and Propst 1989; Barrett and Maughan 1995; Bottcher 2009).

The San Rafael River, Utah, is home to populations of all ‘three species,’ and is representative of the degradation experienced by many tributaries of the Colorado River Basin (i.e., altered hydrograph, water loss, channelization, homogenization of habitat). The San Rafael River is one of the most over-allocated rivers in the state of Utah (Walker and Hudson 2004), and has also experienced extensive invasions by both fishes and riparian plants. Many of the non-native fishes present in the river have the potential to negatively impact populations of native fishes through competition or predation. Predation by channel catfish (*Ictalurus punctatus*) has been implicated in the decline of roundtail chub in the San Francisco River (Bestgen and Propst 1989), and red shiners (*Cyprinella lutrensis*) have been demonstrated to prey on native fishes in backwater rearing habitats (Tyus and Saunders 2000). In addition, channel catfish (Johnson et al. 2008) and virile crayfish (*Orconectes virilis*, Carpenter 2005) have been suggested of being significant competitors with native fishes for prey resources, thus inhibiting growth of the native fishes. Studies have suggested that non-native fishes have the greatest impact on juvenile fishes (e.g., Douglas and Marsh 1998; Pilger et al. 2010), demonstrating the need for caution when interpreting population assessments for these long-lived fishes. The presence of the non-native fishes, along with the degradation of the physical environment of the stream, may threaten the persistence of the “three species” in this river.
While much of the San Rafael River is highly degraded, physical and biotic alterations have not occurred uniformly along the river’s longitudinal gradient. The lower reaches of the river are more physically degraded than are the more upstream reaches, and non-native fishes are more densely populated and diverse in the lower reaches (McAda et al. 1980; Bottcher 2009). The San Rafael River is fragmented by natural and anthropogenic barriers to upstream fish passage, separating the “three species” into partially distinct populations. Populations of the “three species” appear to be controlled through source-sink dynamics (Bottcher 2009), with the populations in the upper San Rafael River acting as sources to the downstream sink populations. The main stem Green River likely acts as both a source of eggs for the lower San Rafael River, as large adult fish use it as a spawning tributary, but also as a sink for juvenile fishes washed out into the main stem. Juvenile drift is likely a primary mode of migration from the source to the sink habitats, as this has been implicated as a means for fragmented populations to sustain their residency in unsuitable areas (Compton et al. 2008).

Additionally, Bottcher (2009) found that “three species” density was limited by complex habitat availability, which is low throughout much of the lower San Rafael River (Budy et al. 2009; Bottcher 2009). This suggests that few reaches of the lower sections of the river are suitable for self-sustaining populations of these fishes. However, while most reaches in the lower San Rafael River are limited in respect to complex habitat availability, there are areas in which complex habitat is widely available (see Chapter 3). Yet, these reaches still contain low densities of native fishes, suggesting that factors other than habitat availability are contributing to source-sink dynamics, and resulting in consistently low densities of the “three species” supported in the lower San
Rafael River. The identification of factors most limiting populations of these imperiled fishes is critical to proper and effective management to ensure their persistence. Within this context, my thesis research investigates how the interactions between physical habitat degradation and non-native fish invasions affect the populations of the “three species” by asking the following questions:

1. How does the presence of non-native fishes affect food web structure in the San Rafael River (Chapter 2)?
   a. Does the presence of non-native fishes alter the trophic niche realized by the ‘three species’?
   b. Does the food web of the upper San Rafael River have an unoccupied niche available to non-native fishes?
   c. Does food availability to the “three species” differ in quantity or quality between the upper and lower San Rafael River?

2. Do any detected differences in resource availability or food web structure result in altered indicators of fitness (i.e., growth, size) of the “three species” (Chapter 2)?

3. Can biotic and abiotic conditions measured at discrete sampling sites be used to model relative abundance of the “three species” along the longitudinal gradient of the river, as well as predict effects of specific restoration actions (e.g., non-native fish eradication, reach-scale habitat restoration; Chapter 3)?

By answering these questions, my thesis provides managers with detailed information on the effects of non-native fish invasion on the ‘three species,’ as well as a spatially explicit model to aid decisions regarding the allocation of restoration efforts to most
benefit these imperiled fishes, both within the San Rafael River and across their extant range.

References


Carpenter J (2005) Competition for food between an introduced crayfish and two fishes endemic to the Colorado River basin. Environmental Biology of Fishes. 72: 335-342


CHAPTER 2
LONGER FOOD CHAINS AND CROWDED NICHE SPACE: EFFECTS OF MULTIPLE INVASIONS ON POPULATIONS OF IMPERILED DESERT FISHES

Abstract

The establishment of non-native species can negatively impact native species and the ecosystems they inhabit. The San Rafael River, Utah, is home to populations of the ‘three species;’ flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*Catostomus discobolus*), and roundtail chub (*Gila robusta*), each listed as state species of concern and subject to a range-wide conservation agreement. Alterations to flow and the physical habitat template have facilitated the establishment and exacerbated the impacts of non-native fishes in the river. In this study, I employ a suite of stable isotope techniques, size-at-age back calculation, and length-weight regression methods to compare food web structure and growth rates (as an indicator of fitness) of native fishes in river sections with and without established populations of non-native species. I found that non-native fishes lengthen the food chain in the river by 1.06 trophic positions. Further, the trophic niche spaces of several non-native species overlap almost entirely with each of the “three species” (bluehead sucker and flannelmouth sucker 100%, roundtail chub 96.86%). Though the established non-native species present novel predator and competitor archetypes, the “three species” demonstrated no evidence of reduced growth or condition in the presence of these non-native fishes. These results

Coauthored by Timothy Walsworth, Phaedra Budy, and Gary Theide.
suggest that the dispersal of fishes from areas without non-native fishes maintains the population structure where non-native fishes are present.

**Introduction**

As human populations continue to expand into natural landscapes, the impact of development increasingly threatens the native biodiversity of freshwater ecosystems (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). Anthropogenic alterations to rivers result in physical (e.g., dams, diversions, sedimentation, channelization, hydrograph alteration, land use changes), chemical (e.g., pollution, nutrient loading), and biological (e.g., invasive species, disease) degradation of natural habitats. These alterations can favor novel life-history strategies (Olden et al. 2006), decrease resource availability (Tyus and Karp 1990; Brouder 2001), alter the flow of energy through ecosystems (Sousa et al. 2008; Nalepa et al. 2009), and increase predation and competition pressure on native species (Tyus and Saunders 2000). As such, anthropogenic alterations can result in new evolutionary and contemporary pressures on native biota that evolved under a specific suite of environmental conditions, particularly in arid, desert environments.

Rivers and streams of the southwestern United States, home to a highly endemic fish fauna, have been particularly affected by anthropogenic disturbances (Minckley and Deacon 1968), due in part to the region’s arid climate and rapidly expanding human population. The Colorado River Basin is a prime example of a system highly altered by intensive damming and diversion of water for agricultural, industrial, and municipal purposes. Anthropogenic developments throughout the basin have disrupted the natural
flow and temperature regimes, changing the historically dynamic Colorado River into a
more static system (Van Steeter and Pitlick 1998). The altered flow regime has resulted
in native fish life-histories that are unsuited to their contemporary environment (Olden et
al. 2006). Spawning cues (Tyus and Karp 1990; Brouder 2001) have been lost, migration
pathways (Compton et al. 2008) are blocked, rearing habitat (Clarkson and Childs 2000;
Thieme et al. 2001) has been reduced, and in-stream conditions are no longer optimal for
spawning or rearing (e.g., Vanicek 1970; Poff et al. 1997; Van Steeter and Pitlick 1998).
Such changes to in-stream habitat conditions have been suggested to lead to a reduction
in native species diversity (Gorman and Karr 1978). Furthermore, greater sedimentation
has been demonstrated to lead to a reduction in benthic invertebrate populations (Kefford
et al. 2010), an important prey item to many fishes. Thus, not only do such alterations
decrease the amount of quality physical habitat available, they can also decrease the
resource base available to native fish populations.

While physical habitat degradation is often argued to be the primary cause of
population and range reductions of native fishes (Ross 1986), interactions with non-
native fishes may be equally or even more influential than habitat loss in the extinction of
species (Tyus and Saunders 2000; Woodford 2009). Invasion by non-native fishes has
the potential to alter the energetic pathways of the historic food web, resulting in
significant and negative ecosystem impacts (Eby et al. 2006; Britton et al. 2010; Pilger et
al. 2010). By altering these energy pathways, non-native fishes can modify habitat
coupling, nutrient cycling rates, and ecosystem resilience (reviewed in Eby et al. 2006),
and often maintain a competitive advantage over native fishes (Böhn and Amundsen
2001; Shea and Chesson 2002; Cox and Lima 2006). Native fishes are also sensitive to
negative indirect effects of invasive fish presence, such as altered prey growth and behavior (Going and Dudley 2008, McIntosh et al. 2010) and altered in-stream habitat conditions (Koehn 2004). Further, non-native fishes can have especially strong impacts on simple food webs (Carey and Wahl 2010), such as those of the historical Colorado River Basin (Tyus and Nikirk 1990; Tyus and Saunders 2000; Unmack and Fagan 2004).

The interaction between a degraded physical habitat and non-native species presence can have synergistic effects on native species and their habitat (Pimm et al. 2006; Brook et al. 2008). Physical habitat degradation, for example, can aid in the establishment and dispersal of non-native species (Marvier et al. 2004; O’Dell and Claassen 2006). While change in flow regimes may decouple the life-histories of native fishes from their current environmental template, many invasive fishes are pre-adapted to the new conditions (Olden et al. 2006, Johnson et al. 2008). For example, large hydropower dams induce a change from a lotic to a lacustrine environment upstream of the dam, introducing a niche to which invasive lentic fishes are much better adapted than the native lotic fishes of the Colorado River Basin. Additionally, the impact of non-native fishes has been suggested to be strongest at times of low flow (Pilger et al. 2010), a nearly perpetual state in degraded desert rivers. This combination of physical degradation and biotic invasions in the Colorado River Basin has led to the extirpation and the federal listing of many endemic fishes under the Endangered Species Act (Minckley and Deacon 1968; USDI 1994) and the protection of many others under conservation agreements between states of the Colorado River Basin (UDWR 2004).

The San Rafael River, Utah, is an ideal study stream, as it has experienced degradation representative of many tributaries of the Colorado River Basin (i.e., altered
hydrograph, water loss, channelization, homogenization of habitat, invasive species establishment; Walker and Hudson 2004; Bottcher 2009). The river is home to populations of flannelmouth sucker (Catostomus latipinnis), bluehead sucker (C. discobolus), and roundtail chub (Gila robusta; hereafter, collectively the “three species”), three endemic Colorado River Basin fishes listed as state species of concern and subject to a range-wide conservation agreement with the stated goal of ensuring their persistence throughout their range (UDWR 2004). Little is known about these fishes, and most research to date has focused on identifying their habitat requirements at different life stages (e.g., Bestgen and Propst 1989; Barrett and Maughan 1995; Bottcher 2009). Many of the non-native fishes present in the river have the potential to negatively impact populations of native fishes through competition or predation (e.g., Bestgen and Propst 1989; Tyus and Saunders 2000; Johnson et al. 2008). In fact, predation by non-native fish on early life-stages has been implicated in total recruitment failure for native fishes in the Colorado River Basin and other systems (Meffe 1985; Woodford 2009).

Populations of imperiled species may be able to persist in an area if recruitment cannot balance with mortality, provided there is a source habitat capable of supplying colonizers to the sink habitat (Pulliam 1988). Previous work has suggested that the populations of the “three species” in the lower San Rafael River occupy a sink habitat, and are maintained through colonization from sources in both the upper San Rafael River and the Green River (Bottcher 2009). Identification of the mechanisms by which the “three species” interact with non-native fishes in the lower San Rafael River may provide insight as to why the upper San Rafael River is an apparent source habitat and the lower San Rafael River is an apparent sink habitat to these species. In this paper, I use the San
Rafael River as a template to answer the following questions: (1) does the presence of non-native fish species alter the trophic position or niche width of native fishes, (2) do the reaches in tributaries above fish-barriers have an unoccupied trophic niche that could be exploited by an invading non-native fish, and (3) do changes in food web structure and resource availability in the presence of non-native fishes reduce the growth of native fishes? In addressing these questions, I explore an innovative combination of food web and growth analyses among different patches of a river to advance our understanding of how trophic interactions and dispersal ability impact community composition and population structure.

**Methods**

*San Rafael River*

The San Rafael River (hereafter, “SRR”) drains 4500 km$^2$ of southeastern Utah and is formed by the confluence of Ferron, Cottonwood, and Huntington Creeks (Figure 2-1). The SRR is a snowmelt driven system, draining the Wasatch Plateau, San Rafael Swell, and San Rafael Desert, and flows approximately 175 km from its headwaters in the Manti – La Sal National Forest to its confluence with the Green River near the town of Green River, UT. With over 300 dams and 800 surface points of diversion, the SRR is one of the most over-allocated rivers in Utah (Walker and Hudson 2004) and the lower 64 km are frequently dewatered during the summer (Bottcher 2009).

The SRR was historically home to all of the native “big-river” fishes of the Colorado River Basin. However, with flow alteration, habitat homogenization, and non-native fish establishment, native fish abundance has declined. Native fish species
currently inhabiting the SRR for at least a portion of their life-history include the flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), roundtail chub (*Gila robusta*), speckled dace (*Rhinichthyes osculus*), bonytail (*Gila elegans*), razorback sucker (*Xyrauchen texanus*), Colorado pikeminnow (*Ptychocheilus lucius*). Non-native species present include red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), fathead minnow (*Pimephales promelas*), channel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*), common carp (*Cyprinus carpio*), white sucker (*Catostomus commersoni*), green sunfish (*Lepomis cyanellus*), and northern virile crayfish (*Orconectes virilis*). Additionally, non-native tamarisk (*Tamarix* spp.) has invaded the riparian areas along much of the SRR (Fortney et al. 2011); tamarisk has been shown in other systems to stabilize stream banks and increase channelization, which disconnects the river from its floodplain and can inhibit the formation of complex habitat structures (Di Tomaso 1998).

Sampling sites in the lower SRR were chosen by a systematic sample design with a random seed start (Bottcher 2009). As much of the upper SRR is in extremely rugged terrain with little or no road access, sampling sites in the upper SRR were chosen opportunistically. All sampling sites were approximately 300 m in length. Twelve sample sites were chosen as food web sites, signifying where stable isotope samples, fin clips for ageing, and benthic invertebrate samples were collected. These food web sites were placed into three categories of degradation (Figure 2-1). The high quality category (all located in the upper SRR) had widely available complex habitat and very low densities of non-native fishes present. The medium quality category (all located in the lower SRR, with one reach upstream of the Hatt Ranch dam, but downstream of the San
Rafael Reef) had widely available complex habitat, but high densities of non-native fishes present. The poor quality category (all in the lower SRR) all had very limited complex habitat available and high densities of non-native fishes. A repeated measures analysis of variance, repeated on sampling site, was run to compare the catch per unit effort (CPUE) of native fishes and of non-native fishes between reaches in the different quality categories. For this analysis, only data from 2010 was used, as all sites were sampled in all seasons that year. For further information regarding the SRR, see Bottcher (2009).

Collection of biotic community data

Sampling events occurred during the spring (i.e., prior to spring snowmelt run-off), summer (i.e., immediately after recession of spring runoff), and autumn (i.e., October) of 2009 and 2010. Fish were sampled via barge electrofishing, using a Smith-Root GPP 2.5, powered by a canoe mounted generator (Honda GX 160). Electrofishing was carried out in a downstream to upstream direction with one anode and three collection nets. Additionally, backwaters were sampled with a seine pulled in a downstream to upstream direction. Occasionally, a trammel net spanning the entire channel was set for 2.5 hrs and checked every 15 min when water was too deep to electrofish safely. All native and non-native fishes were identified to species, weighed, measured, and clipped (lower caudal fin) for stable isotope analysis. Fin tissue has been shown to be comparable to dorsal muscle tissue for stable isotope analysis in other fish species (Shannon et al. 2001; Hanisch et al. 2010; Vinson and Budy 2011). These tissues have long turnover times, thus providing a measure of diet at a week to month time scale.
(McIntyre and Flecker 2006). Tissue samples were stored in ethanol until processed in
the lab, and native fishes were fin-clipped for age determination (see below). Storing
tissue samples in ethanol has been shown to enrich $\delta^{13}$C signatures in some studies
(Kaehler and Pakhomov 2001; Kelly et al. 2006), and to have no significant effect in
other studies (Sarakinos et al. 2002; Serrano et al. 2008). The biological significance of
enrichment caused by storage in ethanol has been debated, as shifts were found to be
small relative to ecological variation (Kelly et al. 2006). I am therefore comfortable
using these tissues, as long as carbon signatures are interpreted with caution. Following
sample collection, native fishes were held in a recovery tank until they showed no effects
of the anesthetic before being returned to the river. Non-native fishes were euthanized
via overdose with tricaine methanosulfate (MS-222).

Immediately following fish collection and measurement, benthic invertebrates
were sampled at each food web site from eight random locations within the fastest water
available in the reach. Eight 0.09 m$^2$ samples were taken from each reach and combined
in ethanol until returned to the lab, where they were sorted, identified to family (or lower)
and functional feeding group, and counted. These samples were used to determine
benthic invertebrate density and community composition, as well as to determine the
isotopic baseline of each sampling site.

*Stable isotope analysis of food web structure*

Once returned to the lab, caudal fin clips and benthic invertebrates of the
collector-filterer and predator functional feeding groups were prepared for stable isotope
analysis. Tissue samples were dried for 48 hours at 70°C, after which, samples were
crushed into a homogeneous powder with mortar and pestle. The powdered samples were then placed in tin capsules for shipment. To determine if two distinct food webs were present in the SRR, native and non-native fish tissue samples from reaches upstream of the San Rafael Reef (high quality reaches; hereafter “upper SRR”) and from those downstream of the reef (medium and poor quality reaches; hereafter “lower SRR”) were analyzed for stable isotopic signatures separately. When possible, I collected a minimum of ten samples from each species in both the upper and lower SRR were used to measure of the variability in isotopic signatures (Vinson and Budy 2011). The capsules were sent to the University of California – Davis Stable Isotope Facility (2009 samples; Davis, CA) or the Washington State University Stable Isotope Core Lab (2010 samples; Pullman, WA) for natural abundance analyses of $^{13}$C and $^{15}$N. Isotopic signatures are reported in δ-notation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\frac{R_{sample}}{R_{standard}} - 1\right] \times 1000,$$

where $R$ is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard for $\delta^{13}C$ is PeeDee belemnite and for $\delta^{15}N$ is atmospheric nitrogen. The stable isotopic signatures of the collector-filterer invertebrate group were used as a baseline to allow comparison between different sites along the longitudinal gradient of the SRR, as this was the functional group with the lowest trophic position consistently collected in Surber samples.

$\delta^{13}C$ and $\delta^{15}N$ values were corrected for basal resource variation before further analysis. Carbon signatures were corrected using the following equation:
\[ \delta^{13}C_{cor} = \frac{\delta^{13}C_i - \delta^{13}C_{mean cf}}{CRcf}, \]

where \( \delta^{13}C_i \) is the carbon isotope signal of organism \( i \), \( \delta^{13}C_{mean cf} \) is the mean collector filterer carbon isotopic signature from the site where organism \( i \) was collected, and \( CRcf \) is the carbon range of the same collector filterer invertebrates as above (Olsson et al. 2009). Nitrogen values were corrected for baseline variation by subtracting the difference in mean nitrogen value of collector filterer invertebrates between all sites and the site with the minimum mean collector filterer nitrogen value from all nitrogen signatures (Vander Zanden et al. 1999). Stable isotope data were pooled across seasons (spring, summer, and autumn) and years (2009-2010).

Species’ trophic niche space was analyzed using methods presented in Layman et al. (2007). For each species, the following measures were calculated: trophic position (TP), nitrogen range (NR), carbon range (CR), trophic niche width (NW), and trophic niche overlap (OV). Trophic position was calculated using the following equation:

\[ TP_i = \frac{\delta^{15}N_{cor i} - \delta^{15}N_{cor cf}}{3.4} + 2 \]

where \( TP_i \) is the trophic position of species \( i \), \( N_i \) is the nitrogen signature of species \( i \), and \( N_{cf} \) is the nitrogen signature of collector filterer invertebrates. Collector-filterer invertebrates are assumed to have a trophic position of 2, and I assume trophic fractionation of \( ^{15}N \) to be 3.4‰ as trophic level increases (Minagawa and Wada 1984). Trophic position and \( \delta^{13}C_{cor} \) signatures for each of the “three species” were compared.
between the upper and lower SRR with Student’s t-tests. Nitrogen range and carbon range were calculated from the following equations:

\[
NR = \delta^{15}Ncor_{max} - \delta^{15}Ncor_{min}, \\
CR = \delta^{13}Ccor_{max} - \delta^{13}Ccor_{min},
\]

for each species (Layman et al. 2007). Niche width was calculated as the convex hull area of isotopic signatures of each species plotted in C-N bivariate space (Layman et al. 2007). Overlap was calculated as the percent of a species niche width area that is overlapped by the niche width area of another species in the food web.

**Calculation of native fish growth rates**

The basal portion of the second dorsal fin ray was collected from each individual of the “three species” captured during sampling, and stored in vials until returned to the lab. The fin rays were placed in molds and heated at 70°C for 12 hours to allow the mold to harden. The molds were then mounted on metal chucks, and cut using a Buehler Isomet low-speed saw (Buehler Ltd., Lake Bluff, IL, USA). The fresh edge was sanded, polished, and a second cut was made to produce a thin (~1.5 mm) section. The section was placed on a microscope slide and polished if necessary. Fin ray sections were placed under a camera-mounted microscope and back-lit to reveal annuli. Digital images of each section were captured and analyzed for length at age using the Frasier-Lee back-calculation:

\[
L_t = c + (L_T - c) \left( \frac{S_T}{S_T} \right),
\]
where \( L_t \) is the length of the fish at time \( t \), \( L_T \) is the total length of the fish, \( c \) is the length of the fish at age 1, \( S_t \) is the length of the fin ray at time \( t \), and \( S_T \) is the total length of the fin ray (Francis 1990). The length of each species at age 1 (\( c \)) was determined from length-frequency plots. Length-at-age data for each species were then fit to a repeated measures non-linear Von Bertalanffy growth curve (VBGC; Jones 2000):

\[
L_t = L_\alpha(1 - e^{-k(t-t_0)}),
\]

where \( L_\alpha \) represents the maximum possible length achieved by the fish, \( L_t \) is the fish’s length at time \( t \), \( t_0 \) is the theoretical age of the fish when its length equals zero, and \( k \) is the Brody growth rate constant (Ricker 1975). The Brody growth constant (\( k \)), is a measure of the rate of approach to the growth asymptote (\( L_\alpha \)), and indicates how quickly the species approaches maximum length. Growth rates of fish in the upper and lower SRR were examined by comparing the standardized residuals from the VBGC of individual fish captured in each section. A Student’s t-test was used to compare the residuals between groups.

Body condition provides an additional means to explore potential differences in fitness-related performance between the upper and lower SRR. Length-weight regressions of the formula:

\[
\log W = \log(a) + b \times \log(L),
\]

where \( W \) is the weight (g) at capture, \( L \) is the length (mm) at capture, and \( a \) and \( b \) are constants, representing the intercept (\( \log a \)) and slope (\( b \)) of the regression. Individual
standardized residuals from the regression equation were compared between fish captured in the lower and upper SRR.

All statistical analyses were performed with R statistical software environment (R Foundation for Statistical Computing, R-project.org) and ArcGIS 9.3.1 (ESRI, 2009), and statistical significance was assessed at α=0.05.

**Results**

The downstream SRR fish community species composition was dominated by non-native fishes, while the fish collections in the upper SRR were almost entirely composed of native fishes (Table 2-1). The “three species” were captured in significantly greater numbers in the high quality reaches (CPUE = 26.22 ± 3.69 fish per hour) than in either the medium (CPUE = 3.93 ± 1.14 fish per hour) or low quality reaches (CPUE = 4.30 ± 1.04 fish per hour) repeated measures ANOVA, p = 0.001; Figure 2-2a), while non-native fishes were captured in significantly greater numbers in both the medium (CPUE = 61.01 ± 11.60 fish per hour) and low (CPUE = 53.09 ± 6.13 fish per hour) quality reaches than in the high quality reaches (CPUE = 0.79 ± 0.46 fish per hour; repeated measures ANOVA p < 0.001; Figure 2-2b). No significant seasonal or interaction effects were detected for CPUE of either native or non-native fishes (all repeated measures ANOVA p > 0.05). The only non-native fishes captured upstream of the San Rafael Reef were 3 green sunfish and 1 Utah chub (*Gila atraria*). Both native and non-native total fish catch was generally greater in 2010 than 2009, and 2010 was the first year that non-native white sucker (*Catostomus commersoni*) were captured in the SRR.
Stable isotope analysis

The upper SRR can be broadly characterized by a short food chain (FCL = 3.89; Figure 2-3a) and food web populated by few species. The bluehead sucker (“BHS”, TP = 2.91 ± 0.09), flannelmouth sucker (“FMS”, TP = 3.02 ± 0.11), and roundtail chub (“RTC”, TP = 3.00 ± 0.18) occupied similar trophic positions (ANOVA p = 0.32) that signify the assimilation primarily of secondary producers. In contrast, the “three species” displayed significantly different δ^{13}C_{cor} signatures (BHS δ^{13}C_{cor} = -0.45 ± 0.25; FMS δ^{13}C_{cor} = 1.46 ± 0.54; RTC δ^{13}C_{cor} = 1.15 ± 0.54; ANOVA p-value < 0.001). The bluehead sucker was more depleted in carbon than either the flannelmouth sucker (t-test p < 0.001) or the roundtail chub (T-test p < 0.001), but the flannelmouth and roundtail chub did not differentiate with regards to carbon signature (t-test p = 0.43). Speckled dace occupied the highest average trophic position in the upper SRR (TP = 3.42 ± 0.11) and were the most depleted with respect to ^{13}C among the fish community (δ^{13}C_{cor} = -0.65 ± 0.20).

While the food web of the upper SRR was structurally simple, the food web of the lower SRR was populated by more species distributed across a broader range of trophic positions (FCL = 4.96; Figure 2-3b). As in the upper SRR, the bluehead sucker (TP = 2.83 ± 0.07) and flannelmouth sucker (TP = 2.82 ± 0.06) occupied similar trophic positions (t-test p = 0.96); however, the two species did not differentiate with respect to carbon signature (BHS δ^{13}C_{cor} = 1.20 ± 0.19; FMS δ^{13}C_{cor} = 1.54 ± 0.33; t-test p-value = 0.09). The roundtail chub had a significantly elevated trophic position (TP = 3.26 ± 0.16) in the lower SRR compared to the two native suckers (ANOVA p < 0.001), and was significantly elevated, albeit marginally, from its trophic position in the upper SRR (t-test
The bluehead sucker carbon signature was significantly enriched in the lower SRR compared to the upper SRR (t-test p < 0.001), and the flannelmouth sucker trophic position was significantly lower in the lower SRR (t-test p = 0.005). All remaining stable isotope measures for the “three species” were similar between the upper and lower SRR (t-tests, all p > 0.05). Green sunfish held the highest trophic position in the lower SRR (TP = 3.64 ± 0.22), and five other non-native species occupied sufficiently high trophic positions to suggest the potential for piscivory on the “three species” (Figure 1b).

The food resources used by fishes and invertebrates in the upper SRR spanned a broad array of carbon sources and trophic positions (CR = 6.16, NR = 9.07, niche width = 24.17). Bluehead sucker occupied a narrow trophic niche (CR = 1.07, NR = 3.38, niche width = 7.42; Figure 2-4a), aligning closely with collector filterer insects with respect to carbon signature. The bluehead sucker niche space overlapped with other native species trophic niches by 28.93% (33.91% when non-native northern virile crayfish were included). Flannelmouth sucker had a wider, less distinct, trophic niche space than the bluehead sucker (FMS CR = 4.67, NR = 3.25, niche width = 12.21, overlap = 63.85%). The roundtail chub trophic niche space was similar in width and overlap to that of the flannelmouth sucker (CR = 3.66, NR = 4.32, niche width = 11.83, overlap = 64.92%).

The range of food resources used by fishes and invertebrates in the lower SRR was similar to that used in the upper SRR, though a slightly wider range of trophic positions are inhabited and there was greater variation in resource use at all given trophic positions (CR = 6.73, NR = 9.11, niche width = 26.04; Figure 2-4b). Bluehead sucker trophic niche space in the lower SRR was much narrower and less distinct than in the upper SRR (CR = 1.29, NR = 1.25, niche width = 3.30, overlap =100%). Flannelmouth
sucker trophic niche space was also considerably more narrow and less distinct than in the upper SRR (CR = 2.40, NR = 1.26, niche width = 6.16, overlap = 100%). Roundtail chub trophic niche space was slightly wider in the lower SRR (CR = 4.18, NR = 3.69, niche width = 12.19), but was overlapped with other species’ trophic niche spaces to a much greater degree (overlap = 96.86%) than in the upper SRR. Red shiners, sand shiners, channel catfish, common carp, and white suckers each occupied a trophic niche that overlapped significantly with those of the ‘three species.’

**Growth and condition**

While they are each long-lived species, the “three species” captured in the SRR demonstrated fairly limited ages relative to other studies (e.g., Sweet et al. 2008). The bluehead suckers captured and aged in the SRR had the most limited age range of the “three species” (Table 2-2). The oldest bluehead suckers (age = 6+) were captured in the upper SRR, while those captured in the lower SRR had a greater mean age than those captured in the upper SRR (lower SRR mean age = 4.27 years, upper SRR mean age = 4.00). Flannelmouth sucker and roundtail chub had the same maximum age measured in the SRR (maximum age =8+), though flannelmouth sucker demonstrated a wider range of ages. Flannelmouth sucker in the upper SRR exhibited an older maximum age (8+ yrs) measured, as well as an older mean age (5.07 yrs) than those aged in the lower SRR (max= 7+ yrs; mean = 4.39 yrs). The lower SRR held both the oldest individual (8+ years) and a greater mean roundtail chub age (4.59 yrs) than the upper SRR (4.20 yrs).

Flannelmouth sucker demonstrated the greatest maximum length ($L_\infty = 481.46$ mm; Figure 2-5), and roundtail chub the smallest predicted maximum length ($L_\infty = \ldots$).
267.00mm) of the ‘three species.’ Bluehead sucker exhibited the greatest Brody growth rate constant (K=0.21), and flannelmouth sucker the lowest predicted Brody growth rate coefficient (K = 0.19). No differences in length-at-age were detected between fish captured in the upper and lower SRR for either flannelmouth sucker (t-test p = 0.72) or roundtail chub (t-test p = 0.48). However, bluehead sucker captured in the lower SRR were significantly larger at age than those captured in the upper SRR (t-test p = 0.012).

Body condition provides an additional means to examine differences in growth and performance of the “three species” between the upper and lower SRR (Figure 2-6). Flannelmouth sucker captured in the lower SRR appeared to have greater condition (0.05 ± 0.18) than those captured in the upper SRR (-0.03 ± 0.14; Figure 2-7b), though the difference was not statistically significant (t-test p = 0.51). Bluehead sucker demonstrated greater condition in the lower SRR (0.45 ± 0.46) relative to the upper SRR (-0.04 ± 0.13; t-test p =0.05; Figure 2-7d). Roundtail chub captured in the lower SRR appeared to have greater condition (6.77 x 10^{-2} ± 0.15) than did those captured in the upper SRR (-4.96 x 10^{-2} ± 0.31; Figure 2-7f); however, the difference was statistically insignificant (t-test p =0.51).

Invertebrate composition

The composition of the benthic invertebrate community varied considerably between the upper and lower SRR (Figure 2-7). I captured 16 orders of invertebrates in the Surber samples, but the samples were numerically dominated by the orders Trichoptera in the upper SRR and Diptera in the lower SRR (Figure 2-7a), and by Trichoptera and Odonata in terms of biomass throughout the SRR (Figure 2-7b). Density
of trichopteran larvae was significantly greater in the upper SRR (t-test p < 0.001), but the density of dipteran larvae was similar between the two sections (t-test p = 0.22). A greater proportion of the invertebrate biomass in the lower SRR consisted of dipterans than in the upper SRR, while trichopterans contributed a greater proportion of the overall biomass in the upper SRR. The upper SRR appeared to contain greater overall biomass of benthic invertebrates (Figure 2-7c), though the difference was not significant (t-test p = 0.17). However, the biomass of trichopterans in the Surber samples was significantly greater in the upper SRR (t-test p = 0.02), while the biomass of dipterans was greater in the lower SRR, though the statistical significance was marginal (t-test p = 0.06). Based on the EPT index, the quality of the benthic invertebrate community as a food resource was not significantly different between the upper (EPT = 3.07 ± 0.73) and lower SRR (EPT = 2.28 ± 0.52; t-test p = 0.09).

**Discussion**

In this study, I analyzed stable isotope signatures and fitness-related measures to examine the effect of non-native species on populations of imperiled desert fishes. Results of the stable isotope analysis revealed that non-native fish species have significantly altered food web structure in the San Rafael River. After detecting these changes to the trophic structure of the river, I examined the relative growth and condition of the “three species” to determine whether the establishment of the non-native fish populations has had any effect on the relative fitness of these imperiled native fishes. While the data collected for this study cannot explicitly demonstrate predation, greater competition, or a change in fitness for the ‘three species,’ the weight of evidence from
my stable isotope analysis, abundance comparisons, and the results of previous studies throughout the Colorado River Basin suggest that the non-native fishes are having a strong negative impacts on the “three species.” These negative impacts appear to result from the establishment of novel predators and competitors in the ecosystem.

Non-native species can alter the flow of nutrients and energy through an ecosystem (Eby et al. 2006; Sousa et al. 2008; Britton et al. 2010) by altering the number and strength of trophic linkages in a food web. In the process, they may also facilitate the establishment of other non-native species (Simberloff and Von Holle 1999). The establishment of non-native fishes has increased the number of fish species in the food web from four in the upper San Rafael River (and assumed pre-invasion lower San Rafael River) to eleven (including seven non-native) species in the lower San Rafael River. Whereas the food web of the upper San Rafael River consists primarily of a crowded level of native, secondary consumers (the “three species” and speckled dace), the food web of the lower San Rafael River consists of a speciose level of secondary consumers, as well as a diverse level of tertiary consumers. While acknowledging that the potential ecological impact of an invading species is context dependent (i.e., on the abiotic conditions and biotic community of the invaded ecosystem; Ruesink 2003), the high diversity of invading species in the San Rafael River increases the likelihood that at least one of the established non-native species will be a high impact invader (Ricciardi and Kipp 2008). Additionally, ecosystems comprised of highly endemic faunas, such as streams in the Colorado River Basin, are more likely to be negatively impacted by invading species, as the invading species often represents a novel predator or competitor archetype (Ruesink 2003; Cox and Lima 2006).
Due to the inherent isolation and insularity of rivers and lakes, freshwater ecosystems often display high rates of endemism (Dudgeon et al. 2007). In isolation, prey species may not evolve defenses (e.g., behavioral or morphological) against predators not native to their range (Ruesink 2003), and often experience strong negative effects of introduced non-native predators (Kitchell et al. 1997). Three large-bodied non-native fishes in the lower San Rafael River (i.e., channel catfish, black bullhead, and green sunfish) have trophic positions indicative of piscivory. While previous studies suggest the large-bodied piscivore trophic niche was occupied seasonally by endangered Colorado pikeminnow in Colorado River tributaries (Tyus and Saunders 2001; Bottcher et al. *in review*), the established populations of channel catfish, black bullhead, and green sunfish present a novel, year-round source of mortality for all but the largest individuals of the ‘three species.’ Additionally, previous studies have shown red shiner to be significant predators on larval and juvenile stages of Colorado River fishes (Tyus and Nikirk 1990; Tyus and Saunders 2000). As such, the contemporary suite of novel predator archetypes in the river presents the potential for devastating impacts on the recruitment success and viability of the “three species” (Meffe 1985).

In addition to the negative effects of predation from exotic predators, these invaders may also compete with native species for resources. Competition for resources can be demonstrated by a numerical response (Pell and Tidemann 1997), a shift in resource usage (Werner and Hall 1979; Davey et al. 2006), change in morphology (Crowder 1984), and/or a change in vital rates in the presence of potential competitors (Kirk and Gosler 1994; Davey et al. 2006). While competition cannot be inferred from stable isotope signatures alone (Newsome et al. 2007), my convex hull analysis suggests
that the presence of the numerous non-native species in the lower San Rafael River has
the potential to significantly increase competition for food resources for the “three
species” (DeNiro and Epstein 1978; Hesslein et al. 1991; Zambrano et al. 2010). The
vast majority of the trophic niche space of each of the “three species” is overlapped by
multiple non-native fishes. Furthermore, the trophic niche of the bluehead sucker shifted
significantly in the presence of non-native fishes. In the lower San Rafael River, the
bluehead sucker demonstrated a more enriched $\delta^{13}$C signature than in the upper San
Rafael River, which can be indicative of a shift from riffle to pool derived resources
(Finlay et al. 2002). This shift in carbon signature, however, could result from
competitive exclusion by the non-native fishes, the scarcity of riffle habitats in the
degraded lower San Rafael River, or some combination of both.

As resources become concentrated into smaller areas, competition can intensify
over a progressively more limited resource pool (Mills et al. 2004). The lower San
Rafael River is characterized by extensive sandy run habitat and tamarisk dominated
banks, each of which has been demonstrated to result in reduced primary productivity and
abundance and diversity of benthic invertebrates (Death and Winterbourne 1995;
Kennedy and Hobbie 1995; Cardinale et al. 2002; Kennedy et al. 2005). Benthic
invertebrate samples indicate that diversity of resources in the San Rafael River is fairly
limited. In downstream reaches in particular, I observed low EPT scores, the near
complete dominance of the benthic invertebrate community by dipteran larvae, and
limited biomass of benthic invertebrates available to higher trophic levels in the lower
San Rafael River. The reduced abundance and biomass of high quality benthic resources
between the upper and lower San Rafael River may increase competition among the
“three species” and non-native fishes. Thus, the combination of the limited diversity of resources available and significant overlap of stable isotope signatures within the fish community increases the likelihood that competition over resources is occurring in the San Rafael River.

Changes to the energy intake of a fish (i.e., quantity or quality) can result in altered growth patterns, as they may not be able to obtain necessary resources, or may have to increase energy expenditure in order to feed (Mills et al. 2004; Davey et al. 2006). Decreased growth rates can negatively affect fish populations, as fecundity (Bagenal 1978), age at maturity (Alm 1959), and, often, survival (Campana 1996; Quinn and Peterson 1996) are strongly correlated with body size. For example, faster growth rates can enable fish to escape gape-limited predators and avoid starvation during extreme environmental conditions (Post and Evans 1989; Cargnelli and Gross 1996; Quinn and Peterson 1996). However, the “three species” do not demonstrate lower growth rates in the lower San Rafael River relative to the upper San Rafael River, even in the face of lesser resource abundance and greater potential for competition. These results suggest that processes other than those that reduce growth may be controlling the size structure of the “three species” in the San Rafael River (e.g., emigration, size-selective predation, etc.).

Many fish species make purposeful migrations to take advantage of different habitats during various life history stages (e.g., Schlosser 1991; Quinn 2005), and intraspecific growth differences are common between populations with different migration patterns (Meyer et al. 2003). The “three species” are all highly mobile species that make long distance movements in both downstream and upstream directions, either
through larval drift or directed adult movement (e.g., Chart and Bergersen 1992; Robinson et al. 1998; Compton et al. 2008). This mobility coupled with limited connectivity due to upstream movement barriers results in significant mixing of the populations of the “three species” in the upper and lower San Rafael River (Bottcher 2009), likely masking any relative differences in growth or condition. Access to different habitats may help the “three species” buffer against the negative effects of extreme environmental conditions (i.e., dewatering) and unfavorable biotic interactions (Fagan et al. 2002).

In addition to disrupting connectivity, dams and diversions alter flow regimes in rivers, often resulting in more stable conditions. In a static environment, Menge and Sutherland (1987) predicted that the effect of predation outweighs the effects of competition or physical factors on intermediate level consumers, such as the ‘three species,’ especially in systems with complex food webs and high levels of omnivory. The highly altered contemporary flow regime of the San Rafael River has led not only to habitat homogenization, but also to frequent low flow and dewatering events (Bottcher 2009). Predation should have a stronger impact on populations in homogeneous habitat (Caroffino et al. 2010) and at times of low flow (Pilger et al. 2010), as the fish are concentrated into smaller habitat areas with less refuge. The lack of significant growth differences in the San Rafael River, coupled with the greater abundances in the upper San Rafael River suggest that predation by the non-native fishes in the lower river has a stronger impact on the “three species” than does greater competition for resources, similar to findings of others (Pilger et al. 2010).
I recognize there are potential limitations to my inference of both the trophic structure and relative growth rates between the upper and lower San Rafael River. Previous research suggests using caution when estimating annual growth from more than the single most recent annuli, as this method inherits uncertainties due to size selective mortality (i.e., Lee’s phenomenon; Gutreuter 1987). However, by including all annuli in the analysis, I was able to estimate growth in years when the populations were not sampled, or when fin ray sections were not collected. In addition, isotopic signatures often vary with fish length and growth rate, as well as over time (Harvey et al. 2002; Vinson and Budy 2011). However, in this case ontogenetic diet shifts, if present, would result in more conservative estimates of non-native piscivore trophic positions, as smaller individuals would not yet be piscivorous. Further, my stable isotope signatures did not differ significantly within species between years or seasons.

The reduction, or loss, of native species in an ecosystem can lead to overwhelming ecosystem level effects, including, but not limited to, further species loss or reduced ecosystem resilience (Wootton and Downing 2003; Lockwood et al. 2007). My results demonstrate that non-native fish species significantly alter the food web structure of the San Rafael River, presenting novel predators and competitors to these endemic and imperiled species and threats to their persistence. In addition, the populations in the upper San Rafael River, isolated from the non-native predators, are supplying colonists and perhaps recruits to the sub-populations of the “three species” in the lower San Rafael River, likely facilitating their persistence in that inhospitable habitat (see Chapter 3; Bottcher 2009). Finally, it is important to note that given the high densities of exotic fishes in the lower river and the associated impacts suggested herein,
restoration of physical habitat in the lower river may have little effect on “three species” populations in the absence of efforts to minimize the effects of non-native fish species (see Chapter 3). Improving the physical habitat template could lead to increases in non-native performance and abundance as well. The eradication of non-native fishes, and restoration of the historical trophic linkages in the Colorado River Basin, may be a necessary step to ensure the persistence of the “three species” throughout their historical range.

References


Fortney ST, Schmidt JC, Dean DJ (2011) Establishing the geomorphic context for wetland and riverine restoration of the San Rafael River. Final Report. NRCS Cooperative Agreement #68-3A75-4-155


Werner EE, Hall DJ (1979) Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256-264


Table 2-1. Number of individuals captured in the San Rafael River in 2009 and 2010 by species and location in river.

<table>
<thead>
<tr>
<th>Species</th>
<th>2009</th>
<th></th>
<th>2010</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Upper San Rafael River</td>
<td>Lower San Rafael River</td>
<td>Upper San Rafael River</td>
<td>Lower San Rafael River</td>
</tr>
<tr>
<td>Age 0 Sucker</td>
<td>0</td>
<td>2</td>
<td>18</td>
<td>37</td>
</tr>
<tr>
<td>Black Bullhead</td>
<td>0</td>
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<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Bluehead Sucker</td>
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<td>4</td>
<td>155</td>
<td>16</td>
</tr>
<tr>
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<td>0</td>
</tr>
<tr>
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<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Common Carp</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Fathead Minnow</td>
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<td>0</td>
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</tr>
<tr>
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<td>17</td>
<td>110</td>
<td>25</td>
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<tr>
<td>Green Sunfish</td>
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<td>5</td>
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<td>15</td>
</tr>
<tr>
<td>Red Shiner</td>
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<td>0</td>
<td>453</td>
</tr>
<tr>
<td>Roundtail Chub</td>
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<td>14</td>
<td>40</td>
<td>21</td>
</tr>
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<td>Sand Shiner</td>
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<td>0</td>
<td>711</td>
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<tr>
<td>Shiner</td>
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<td>110</td>
<td>0</td>
<td>23</td>
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<tr>
<td>Speckled Dace</td>
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<td>321</td>
<td>15</td>
</tr>
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<td>Utah Chub</td>
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<td>0</td>
</tr>
<tr>
<td>White Sucker</td>
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<td>0</td>
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</tbody>
</table>
Table 2-2. Five number summaries of ages of the three species measured in the San Rafael River.

<table>
<thead>
<tr>
<th>Species</th>
<th>Section</th>
<th>Minimum</th>
<th>1st Quartile</th>
<th>Median</th>
<th>Mean</th>
<th>3rd Quartile</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Whole SRR</td>
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<td>3</td>
<td>3.4</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Upper SRR</td>
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<td>2</td>
<td>3</td>
<td>3.4</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Lower SRR</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>3.2</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
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<td>Whole SRR</td>
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<td>2</td>
<td>3</td>
<td>4.0</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Upper SRR</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>4.4</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Lower SRR</td>
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<td>2</td>
<td>3</td>
<td>3.6</td>
<td>4</td>
<td>7</td>
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<td>Whole SRR</td>
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<td>3</td>
<td>3.8</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Upper SRR</td>
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<td>2</td>
<td>3</td>
<td>3.2</td>
<td>4</td>
<td>5</td>
</tr>
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<td></td>
<td>Lower SRR</td>
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<td>2</td>
<td>3</td>
<td>3.8</td>
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</tr>
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</table>
Figure 2-1. Map of the San Rafael River watershed. Circles represent “high quality” sample sites, squares represent “medium quality” sampling reaches, and triangles represent “poor quality” sampling reaches. The dashed line represents the eastern edge of the San Rafael Reef, the geologic feature separating the upper and lower San Rafael River. The black bar represents the location of the Hatt Ranch diversion dam. Inset shows location of watershed in Utah.
Figure 2-2. Catch per unit effort (fish/hr) of native (a) and non-native (b) fish in the San Rafael River by reach quality. The high quality reaches have significantly greater CPUE of native fishes and significantly lower CPUE of non-native fishes than either the medium or poor quality reaches. Open circles represent outliers.
Figure 2-3. Trophic positions and food web structure of the upper (a) and lower (b) San Rafael River. The “three species” are marked in bold.
Figure 2-4. Trophic niche spaces occupied by fish species in the upper (a) and lower (b) San Rafael River. The “three species” are shown with solid lines. Solid lines: blue = bluehead sucker, green = flannelmouth sucker, and yellow = roundtail chub; Dashed lines: green = northern virile crayfish, blue = sand shiner, red = red shiner, gray = channel catfish, yellow = green sunfish, light blue = fathead minnow, black = collector-filterer insects, violet = predatory invertebrates; Dotted lines: yellow = common carp, red = white sucker, black = black bullhead; Dash-dotted lines; red = speckled dace.
Figure 2-5. Size at age with Von Bertalanffy growth function for flannelmouth sucker (a), bluehead sucker (b), and roundtail chub (c) in the San Rafael River. Open circles represent fish captured in the lower San Rafael River, closed circles represent fishes captured in the upper San Rafael River.
Figure 2-6. Weight at length and residuals for flannelmouth sucker (a-b), bluehead sucker (c-d), and roundtail chub (e-f) in the San Rafael River. Open circles represent fish captured in the lower San Rafael River, closed circles represent fishes captured in the upper San Rafael River.
Figure 2-7. Invertebrate composition by count (a) and biomass (b) in the upper and lower San Rafael River. Panel (c) shows the absolute density by mass in the upper and lower San Rafael River. Invertebrates were pooled by order. The ~84% of the dipterans collected were *Simulium* spp. and ~93% of the trichopterans collected were of the family Hydropsychidae (*Hydropsyche* spp. and *Cheumatopsyche* spp).
CHAPTER 3
LIMITING FACTORS AND RESTORATION POTENTIAL
FOR THREE IMPERILED DESERT FISHES

Abstract

The efficient allocation of resources for restoration is critical for the effective conservation and management of species. The San Rafael River is home to populations of three endemic and imperiled fishes (flannelmouth sucker *Catostomus latipinnis*, bluehead sucker *C. discobolus*, roundtail chub *Gila robusta*; the “three species”), yet has experienced extensive physical degradation and is now home to several non-native fishes. In this paper, I use site-specific biotic and abiotic parameters to develop a spatially explicit model of “three species” distributions in the lower San Rafael River, both under current conditions and following specific restoration actions. Biotic and abiotic parameters were measured at sampling sites throughout the river, and used to fit random forest models, in order to determine the factors most limiting to populations of the ‘three species.’ Non-native fishes were found to be important predictors of both flannelmouth sucker and bluehead sucker relative abundance, and spatially auto-correlated habitat variables were important predictors for all of the ‘three species.’ The random forest models were then used in combination with a longitudinal habitat survey to predict the continuous distribution of the “three species” in the lower San Rafael River. Each of the “three species” demonstrated a pattern of very low abundance over long stretches of river

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1Coauthored by Timothy Walsworth and Phaedra Budy.
punctuated by short stretches with much higher abundance. Each of the “three species” demonstrated a significant increase in abundance following the simulated eradication of non-native fishes. In contrast, simulation of reach-specific habitat restoration along the continuum of the lower San Rafael River resulted in disparate responses of “three species” populations for all reaches restored, demonstrating that the location of restoration is critical. Removal of non-native fishes and restoration of degraded reaches near already suitable habitat was predicted to be most beneficial to the ‘three species.’ In sum, my results and model developed in this paper will aid in prioritizing how and where to most effectively restore populations of the “three species,” not only in the San Rafael River, but throughout their historic range.

Introduction

Due to the concentration of biodiversity in freshwater ecosystems and the simultaneous concentration of human settlements along waterways, freshwater organisms are the most highly imperiled group of species (Ricciardi & Rasmussen 1998; Dudgeon et al. 2006). As the abundance and diversity of freshwater species and the habitats they require have rapidly declined, pressure to restore the degraded aquatic ecosystems has mounted (Bohn & Kershner 2002). In the face of such rapid population declines and limited funding resources, especially for non-game species, the prioritization of management actions to provide the greatest ecological benefit is essential (Hobbs & Harris 2001; Plummer 2005; Beechie et al. 2008). Models predicting species responses to multiple stressors can be an extremely valuable tool for managers when planning management or recovery strategies for certain species or biotic communities (Petersen et
al. 2008; Townsend et al. 2008), as they can provide a measure of which specific locations within the current or historical range of the species should be targeted first to benefit the imperiled species most.

Within the context of restoration, the identification of factors most limiting to species population persistence is critical to developing management plans to ensure their future viability (Donázar et al. 2002; Budy & Schaller 2007; Beechie et al. 2008). Efforts to determine limiting factors often rely on estimates of habitat suitability or environmental conditions at locations where the species does and does not occur (Brown et al. 2000; Vadas & Orth 2001). One popular approach to simulate habitat preferences and availability for fishes has been the “Physical habitat simulation model” (PHABSIM), which determines the amount of suitable habitat in a stream at a given discharge (Perrow et al. 2008). These models are inherently limited in that: (1) they are developed at a scale different from that experienced by in-stream biota (Heggenes 1994); (2) interactions within biological communities are discounted or ignored; and (3) there is often little concordance found between increased habitat and increased biomass (Gore & Nestler 1988; Perrow et al. 2008). Additionally, habitat suitability models often have limited applicability to other systems (Gore & Nestler 1988), as the combination of geology, hydrology, and biota all exert a strong influence on species habitat use and biomass, and are often unique between watersheds (Power et al. 1988). More recently, reach-scale multivariate habitat use models have been suggested as more effective and appropriate predictors of distribution and abundance than models incorporating only hydraulic statistics (Lamaroux et al. 1998; Parasiewicz 2001).
Ecological niche theory predicts that species have a range of ecological conditions within which they can maintain populations (Hutchinson 1957). Using this theory, ecologists have developed models to predict the geographical distribution of species based on environmental factors, where species distributions are fit to ecological space and evaluated based on known distributions, and then projected to areas outside of the known range (Peterson & Vieglas 2001). While ecological niche models do not necessarily characterize all abiotic and biotic variables important to a species niche, such models have demonstrated high predictability for birds (e.g., Godown & Peterson 2000; Peterson & Vieglas 2001), invertebrates (e.g., Hawkins et al. 2000; Peterson et al. 2005; Chinnayakanahalli et al. 2011), plants (e.g., Peterson 2003; Lentz et al. 2008), and fish (e.g., Chen et al. 2007; McNyset 2009). The ability to incorporate biotic community data to ecological niche models offers a significant advantage over simpler habitat suitability models. While ecological niche models are often implemented at a regional to continental scale, researchers have implemented them to predict species distributions at the watershed scale (Welsh et al. 2010), an approach that may have particular value for endemic species with limited home ranges.

The Colorado River Basin is part of a primarily desert ecosystem, characterized by a high level of anthropogenic impact and extremely limited freshwater resources (Booker & Young 1994; Christensen et al. 2004), which is home to a highly endemic, historically depauperate native fish fauna (Minckley & Deacon 1968). As the region’s human population has expanded, alteration of aquatic environments has increased in the form of dams, numerous water diversions, and extensive introductions of non-native species (Minckley & Deacon 1968; Olden et al. 2006). Dams and diversions disrupt the
natural flow regime of the river, decoupling the life history strategies of native plants and animals from the environment to which they are adapted (Olden et al. 2006; Stromberg et al. 2007). Non-native fish introductions have resulted in a highly altered fish fauna (Tyus & Saunders 2000; Yard et al. 2011), as many of these non-native fishes are pre-adapted to the contemporary conditions of the river caused by the alteration to the flow regime, and, thus, maintain a competitive advantage over native fishes (Olden et al. 2006).

This collection of impacts to sensitive desert rivers has led to dramatic declines in the range and abundances of many of the native Colorado River Basin fishes. Three such native species (flannelmouth sucker, *Catostomus latipinnis*; bluehead sucker, *Catostomus discobolus*; and roundtail chub, *Gila robusta*, hereafter the “three species”) are listed as state species of concern and subject to a range-wide conservation agreement (UDWR 2004). As these species are not valued for sport or food, little research has been conducted on their basic ecology until recently (e.g., Bestgen & Propst 1989; Barrett & Maughan 1995; Bottcher 2009).

The San Rafael River, in southeastern Utah, is home to populations of each of the ‘three species,’ and has experienced degradation representative of many desert rivers (i.e., altered flow regime, channelization, habitat homogenization, non-native species establishment; see Chapter 2; Walker & Hudson 2004). Previous research in the system suggests that the populations of the three species are controlled by source-sink dynamics (Bottcher 2009), with the upper San Rafael River home to a source population, the lower San Rafael River constituting a sink habitat, and the mainstem Green River acting as both a source and a sink (depending on the year, season, and life history stage of interest). Based on preliminary analyses, the factors limiting the presence of the three species in
the San Rafael River were fairly consistent across the species, suggesting that distance to a source population, complex habitat availability, and water depth were among the primary limiting factors for each of the three species (Bottcher 2009).

In more recent work (see Chapter 2), I showed that the presence of non-native fishes in the lower San Rafael River lengthens the food chain, and alters the trophic linkages in the system. Additionally, several of the non-native fishes currently occupy trophic niches that were previously unoccupied in the river, including that of the large-bodied piscivore. The presence of these fishes thus present novel predator archetypes to the “three species” and likely severely limit recruitment in the lower San Rafael River. Finally, the trophic niche spaces of many non-native fishes significantly overlap with those of the ‘three species,’ suggesting that competition over food resources may be another obstacle in the recovery of the imperiled fishes (see Chapter 2). These latter findings suggest non-native fishes may be a stronger limiting factor than has been previously detected (Bottcher 2009).

In this study, I aimed to quantify the relative contribution of the potential limiting factors to “three species” populations in the lower San Rafael River. I then used the limiting factors to develop a spatially explicit model predicting which reaches in the lower San Rafael River would be most beneficial for concentration of restoration efforts, as well as to evaluate which potential restoration actions would be most beneficial to populations of the ‘three species.’ This model will aid managers in focusing their efforts in the most effective parts of the San Rafael to have the greatest benefit for populations of the ‘three species.’ I adopt a multivariate approach to developing my predictive model of relative reach quality along the length of the river.
Methods

Study site

The San Rafael River (hereafter “SRR”) drains 4500 km$^2$ of southeastern Utah (Figure 3-1), and is formed by the joining of Ferron, Cottonwood, and Huntington Creeks. A snowmelt driven system draining the Wasatch Plateau, San Rafael Swell, and San Rafael Desert, the SRR flows approximately 175 km from its headwaters in the Manti – La Sal National Forest to its confluence with the Green River near the town of Green River, UT. With over 300 dams and 800 surface points of diversion, the SRR is one of the most over-allocated rivers in Utah (Walker & Hudson 2004), and the lower 64 km are frequently dewatered during the summer. The National Fish Habitat Action Plan identified the Green River Basin, including the SRR, as one of “10 Waters to Watch” in February, 2010. As such, the SRR was identified as a demonstration project by the Desert Fish Habitat Partnership.

The SRR was historically home to each of the native “big-river” fishes of the Colorado River Basin. However, native fish abundance has declined in the face of flow alteration, habitat homogenization, and non-native fish establishment (Bottcher & Budy in review). Native fish species currently inhabiting the SRR for at least a portion of their life-history include the flannelmouth sucker (*Catostomus latipinnis*), bluehead sucker (*C. discobolus*), roundtail chub (*Gila robusta*), speckled dace (*Rhinichthyes osculus*), bonytail (*Gila elegans*), razorback sucker (*Xyrauchen texanus*), Colorado pikeminnow (*Ptychocheilus lucius*). Non-native species inhabiting the SRR include red shiner (*Cyprinella lutrensis*), sand shiner (*Notropis stramineus*), fathead minnow (*Pimephales promelas*), channel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*),
common carp (*Cyprinus carpio*), white sucker (*Catostomus commersoni*), green sunfish (*Lepomis cyanellus*), and northern virile crayfish (*Orconectes virilis*). Additionally, non-native tamarisk (*Tamarix spp.*) has established in the riparian areas along much of the SRR, an exotic species which has been shown in other systems to stabilize stream banks and increase channelization, disconnect the river from its floodplain, and inhibit the formation of complex habitat structures (Di Tomaso 1998).

Sampling sites in the lower SRR were chosen by a systematic sample design with a random seed start (Bottcher 2009). As much of the upper SRR is in extremely rugged terrain with little or no road access, sampling sites in the upper SRR were chosen opportunistically. All sampling reaches were approximately 300 m in length. For further information regarding the SRR, see Bottcher (2009).

Ninety sampling events from 2008-2010 were used in the development and fitting of models (2008 N = 24; 2009 N = 28; and 2010 N = 38). These sampling events were chosen as they had independent measures of fish catch per unit effort (CPUE), habitat availability, substrate composition, and discharge available. However, as there are multiple samples taken from the same sites, the samples are not completely independent of one another. Due to the temporal distance between samples and the mobility of the ‘three species,’ I feel that relaxation of this assumption is valid with my data.

*Collection of fish community data*

Sampling events occurred during the spring (i.e., prior to spring snowmelt run-off), summer (i.e., immediately after recession of spring runoff), and autumn (i.e., October) of 2009 and 2010. Fish were sampled via barge electrofishing, using a Smith-
Root GPP 2.5, powered by a canoe mounted generator (Honda GX 160). Electrofishing was carried out in a downstream to upstream direction with one anode and three collection nets. All fish captured were anaesthetized with tricaine methanosulfate (MS-222), weighed, measured, identified to species, and held in a recovery tank before being released near the point of capture. Following measurement, non-native fishes were euthanized via overdose with MS-222, and removed from the system.

**Habitat measurements**

Various measures of the physical habitat were taken at each sampling site. Complex (i.e., riffle, pool, or backwater) habitat units were measured for width at the upstream end of the unit, length down the center line, and maximum depth. Five wetted widths were measured to estimate total reach area. These measurements were used to calculate the percent of each reach composed of each type of complex habitat unit. Mean and standard deviation of substrate particle size were measured for 100 pebbles within each reach, taken from 10 equally spaced transects, and measured using a gravelometer (AI-Sci Field Sieve/Gravelometer). All physical habitat measurements were taken once at each sampling site in 2008 and 2009, and at each sampling event in sites sampled for parallel food web analysis (see Chapter 2) during 2009-2010.

Additionally, as previous research has suggested that the populations of the “three species” are controlled through source sink dynamics in the SRR, I measured the distance (km) of each sampling reach from both the upper SRR (upstream of the San Rafael Reef) and the confluence with the Green River. The shorter of these two distances was used as the distance of the site to a source population.
In the summer of 2010, the entire lower SRR, from the diversion dam at Hatt’s Ranch downstream to the confluence with the Green River was surveyed for each of the physical habitat measures described above. This survey provided the physical habitat data required to predict densities of the “three species” continuously along the length of the lower SRR.

Model development

Complimentary approaches were employed to model the relative abundance of the “three species” in the SRR. These included random forest models (Cutler et al. 2001) and generalized linear models (glm's) with interactions between predictor variables (Vadas & Orth 2001). Catch per unit effort (CPUE) of the species of interest was used as the response variable. As CPUE for sampling events was dominated by zero values for each of the “three species”, a zero-inflated negative binomial distribution was used to fit the glm's (White & Bennets 1996; Hall 2000). Predictor variables collected for each sample were non-native fish CPUE, within reach riffle, pool, and backwater habitat, pebble size standard deviation, and distance to a source. Backwards selection by Akaike’s Information Criterion (AIC) was used to determine the most parsimonious model. Stream systems are often spatially auto-correlated, and the presence of fishes in a reach may be influenced by the habitat or biotic conditions in neighboring reaches (Diebel et al. 2010). Therefore, spatially auto-correlated models were developed from the most parsimonious model selected above. These models had additional predictor variables consisting of the weighted average of physical habitat variables found to be significant in the non-spatially auto-correlated glm's. Based on preliminary analyses, I
used a distance of 3 reaches (900m) both upstream and to include in the spatially auto-
correlated variables, as this distance takes into account the high mobility of the “three species,” without being so large as to average out spatial patterns in physical habitat availability. Models were first run without the spatial autocorrelation factors, and were then run with spatially weighted measures of the significant physical habitat predictor variables.

The random forest models were run with the same predictor variables as the glm, including the SAC riffle habitat, SAC pool habitat, SAC backwater habitat, and SAC pebble size standard deviation calculated above. Only sampling events which had independent measures of all habitat and biotic variables were used in this (and the glm) analysis (n=90). As glms explained little of the variation observed in the data, only random forest models were used for further predictions of native fish indices. Random forest models were fit for each of the “three species” individually (Figure 3-2A).

Current “three species” relative abundance model

In order to predict the density of the “three species” throughout the lower SRR, it was necessary to predict the density of non-native fishes in each reach. To model the non-native fish density, I again tested random forest and glms for their explanatory power. The glm explained more of the observed variance ($R^2=0.522$) in non-native fish CPUE than did the random forest model ($R^2=0.282$). A Poisson distribution was used for estimating non-native fish densities instead of the zero-inflated negative binomial distribution, as zero counts for non-native fish were rare in the lower SRR. For the generalized linear model, the full set of predictor variables included riffle habitat
availability (% reach area), pool habitat availability (% reach area), backwater habitat
availability (% reach area), pebble standard deviation (mm), distance to a source (m), and
discharge (cfs). Backwards selection by AIC was used to determine the most
parsimonious model. Non-native fish CPUE was then predicted for each reach in the
lower SRR with data from the longitudinal habitat survey.

Data from the longitudinal habitat survey and the predictions from the non-native
fish glm were entered into the random forest models developed for each of the “three
species” and used to predict the density of native fishes throughout the lower SRR
(Figure 3-2B). After predicting the density of the “three species” continuously along the
length of the lower SRR, the effects of different restoration actions at different locations
along the length of the river were examined by altering input parameters in the predictive
model.

*Non-native fish removal model*

The relative effect of removing non-native species from the SRR was evaluated
by setting the predicted non-native fish CPUE for each reach to zero (Figure 3-2C).
Random forest models (N = 1000 for each species) were then fit to bootstrapped subsets
of the observed data (the number of observations used to fit the random forest model
were maintained) and used to predict the relative abundance of each of the “three
species” in each reach. The mean and 95% confidence interval limits of relative
abundance in each reach were summed across the lower SRR to obtain an estimate of
relative abundance in the absence of non-native fishes. The summed mean and 95%
confidence interval predictions of relative abundance were then divided by the mean
predicted current relative abundance in the lower SRR to obtain an effect size of non-native fish eradication for each of the ‘three species.’

*Reach-scale habitat restoration model*

In addition to non-native fish removal, habitat restoration is commonly employed to benefit native fish species. I ran several models to simulate the effect of habitat augmentation in the lower SRR. To simulate the effect of increasing the amount of riffle habitat available to fish, I fit random forest models to bootstrapped subsets of the observed data, and used to predict the relative abundance in the lower SRR if each reach had its riffle habitat enhanced (Figure 3-2D). The predictions from these models were obtained as follows:

1. Select observations (with replacement) with which to fit random forest model.
2. If the within-reach riffle habitat of reach 1 is below 25%, increase to 25%.
3. Recalculate SAC riffle habitat and non-native fish parameters for all reaches.
4. Predict relative abundance of species in each reach of lower SRR.
5. Reset all adjusted parameters to original values, and repeat steps 2-4 for reaches 2-213.
6. Calculate relative abundance in lower SRR for each reach restoration scenario.
7. Calculate the effect size for each reach restoration scenario by dividing the results of step (6) by the result of step (2).
8. Repeat steps (1-7) 1000 times.
9. For each reach, order the predictions of effect size when it is restored, calculate the mean value, and select the 25th and 975th values for confidence intervals.
I repeated this process for pool habitat (increased to 15% if below this threshold), and again for both pool and riffle habitat under the conditions predicted following non-native fish removal (Figure 3-2E). I determined the threshold values for riffle and pool habitat by visually examining partial dependence plots of native fish CPUE dependent on riffle or pool habitat availability. I fit each of these models to each of the “three species” separately. All models were run in the R statistical software environment (R Foundation for Statistical Computing, R-project.org).

**Results**

*Model fitting*

Random Forest models fit the reach-specific data fairly well for each of the ‘three species.’ The random forest model predicting bluehead sucker CPUE explained 56.63% of the variation in the data. The three most important predictors of bluehead sucker abundance were SAC pebble size standard deviation, non-native fish CPUE, and within-reach pebble size standard deviation (Figure 3-3). Bluehead sucker abundance demonstrates a positive relationship with both SAC and within-reach pebble size standard deviation, and a negative relationship with non-native fish CPUE (Figure 3-3). The greater CPUE of bluehead suckers at the highest densities of non-native fishes is likely the effect of one sampling location (see discussion) and not biologically significant. The random forest model predicting flannelmouth sucker CPUE explained 52.02% of the variation. The three most important predictor variables of flannelmouth sucker abundance were SAC pool habitat, the distance to a source, and non-native fish CPUE (Figure 3-4). Flannelmouth sucker demonstrated a positive relationship with SAC pool
habitat, and a negative relationship with the distance to a source and non-native fish density (Figure 3-4). The random forest model predicting roundtail chub CPUE explained 55.78% of the variation. The three most important predictors of roundtail chub CPUE were SAC riffle habitat, SAC pool habitat, and within-reach pool habitat (Figure 3-5), all showing a positive relationship.

The non-native fish glm predicted relative abundance of non-native fish to range from 12.37 fish/hr in reach 200 to 4921.34 fish per hour in reach 14. The mean predicted CPUE of non-native fishes was 62.26 fish/hr ($s = 337.32$ fish/hr), with a median of 34.58 fish/h. The predicted non-native fish CPUE in reach 14 fell outside the range of two standard deviations, suggesting it was an outlier. The second highest predicted non-native fishes CPUE was 594.49 fish/hr in reach 131.

Current “three species” relative abundance model

My random forest model allowed me to predict CPUE for each of the three species continuously along the length of the lower San Rafael River, as well as a composite reach score that combined all three species’ predictions. The predictions of roundtail chub abundance are characterized by stretches of river with low predicted abundance broken up by short stretches predicted to have higher abundance, with relatively high abundance in the areas near the diversion dam at Hatt’s Ranch, near reaches 59-64, reaches 84-89, reaches 101-111, reaches 131-139, and again approaching the confluence with the Green River (Figure 3-6a). The stretch of the river between reaches 1 and 14 is predicted to be more suitable to the roundtail chub overall than the rest of the lower San Rafael River. Roundtail chub CPUE is predicted to range from
3.048 fish/hr (2.969 – 3.119 95% CI) in reach 7 to 0.025 fish/hr (0.019 – 0.031 95% CI) in reach 159 (Figure 3-6a), with a mean predicted CPUE of 0.531 fish/hr and a median of 0.310 fish/hr. The total predicted relative abundance of roundtail chub under current conditions in the lower San Rafael River is 113.17 (107.38 - 118.98 95% CI).

As with the roundtail chub, there are long stretches of river predicted to have very low abundance of bluehead sucker, punctuated with very short stretches predicted to hold greater abundances (Figure 3-6b). Predicted abundances of bluehead sucker are high near the dam at Hatt’s Ranch, near reach 68, near reach 131, and near the confluence with the Green River. Bluehead sucker CPUE is predicted to range from 0 in multiple reaches to 9.09 fish/hr (8.803, 9.372 95% CI) in reach 131, with a mean predicted CPUE of 0.538 fish/hr and a median of 0.138 fish/hr. The total predicted relative abundance of bluehead suckers under current conditions in the lower San Rafael River is 114.51 (105.36 - 123.92 95% CI).

The predicted abundance of flannelmouth suckers follows a trimodal pattern, with high abundance predicted near the dam at Hatt’s Ranch, near reach 131, and near the confluence with the Green River, with very low predicted abundances between these areas (Figure 3-6c). The flannelmouth sucker predicted CPUE ranged from 0.091 fish/hr (0.078 – 0.105 95% CI) in reach 153 to 8.696 fish/hr (8.457 – 8.934 95% CI) in reach 2, with a mean of 0.986 fish/hr and a median of 0.511 fish/hr. The total predicted relative abundance of flannelmouth suckers under current conditions in the lower San Rafael River is 210.11 (200.51 – 219.83 95% CI).

When the predictions for each of the three species were scaled to have a maximum of 1 and combined for the geometric mean, the overall reach scores followed a
similar pattern to that predicted for each of the individual species (Figure 3-7). The reaches near the dam at Hatt’s Ranch, near reach 68, near reach 131, and near the confluence with the Green River had higher overall scores than did the intervening reaches. Reach 131 had the highest overall score, suggesting the best current condition for the three species, and reach 202 had the lowest overall score, suggesting the worst current condition for the three species.

Restoration effects: non-native fish eradication

The simulated eradication of non-native fishes from the lower San Rafael River predicted substantial increases in relative abundance for each of the three species. Bluehead sucker relative abundance was predicted to increase by 171.5% (149.3 – 193.7 95% CI; Figure 3-6b), flannelmouth sucker by 43.2% (34.8 – 51.8 95% CI; Figure 3-6c), and roundtail chub by 22.4% (16.1 – 28.7 95% CI; Figure 3-6a). Bluehead sucker were predicted to increase in abundance in all reaches of the lower San Rafael, while flannelmouth sucker and roundtail chub were both predicted to decline in abundance slightly in at least two reaches. The reaches where this reduction in abundance is predicted to occur have very high predicted densities of non-native fishes. As the random forest models for the roundtail chub and flannelmouth sucker predict higher CPUE at very high densities of non-native fishes than at very low densities (see discussion), removing the non-native fishes actually reduces the predicted abundance of these native fish. However, this is likely a modeling artifact due to limited data, and these reaches are still predicted to hold relatively high densities of both the roundtail chub and flannelmouth sucker.
Restoration effects: riffle enhancement, no non-native eradication

Augmenting the riffle habitat in many reaches of the lower SRR is predicted to have little or even a negative impact on roundtail chub populations. Roundtail chub are predicted to get the greatest benefit from riffle enhancement if reach 196 is restored and the least benefit if reach 105 is restored (Figure 3-8a). Increasing the amount of riffle habitat in reach 196 is predicted to increase the abundance of roundtail chub in the lower San Rafael River by 3.98% (3.81–4.14%). Increasing the amount of riffle habitat in reach 105 is predicted to reduce the abundance of roundtail chub by 2.37% (2.24 – 2.49%). The reaches between 97 and 110 are all among the 25 least beneficial reaches to restore riffle habitat for roundtail chub, while 21 of the 25 most beneficial reaches to restore are between reaches 160 and 201.

In contrast to roundtail chub, augmenting riffle habitat in the lower SRR is predicted to have a generally positive effect on bluehead sucker populations (Figure 3-8b). Bluehead sucker are predicted to experience the greatest benefit from riffle enhancement in reach 196, and the least benefit if reach 6 is restored (Figure 3-8b). Increasing the amount of riffle habitat available in reach 196 is expected to increase bluehead sucker abundance in the lower San Rafael River by 2.28% (2.47 – 3.09%), while increasing the amount of riffle habitat in reach 6 is expected to decrease the abundance of bluehead sucker by 0.11% (0.03 – 0.18%). Only three reaches are predicted to result in reductions in abundance of bluehead sucker, and these are all located near the diversion dam at Hatt’s Ranch. As with the roundtail chub predictions,
the much of the river between reaches 160-200 is predicted to be especially beneficial to restore.

Similar to the bluehead sucker, flannelmouth sucker are generally predicted to increase with the augmentation of riffle habitat in the lower SRR. Flannelmouth sucker are predicted to experience the greatest benefit of riffle enhancement if reach 196 and the least benefit if reach 140 is restored (Figure 3-8c). Increasing the amount of riffle habitat available in reach 196 is predicted to result in a 1.78% (1.63 – 1.78%) increase in flannelmouth sucker abundance in the lower San Rafael River. Enhancing the riffle habitat in this reach is predicted to have a significantly greater impact on the population than restoration of any other reach. Increasing the amount of riffle habitat available in reach 104 is predicted to result in a reduction of flannelmouth sucker populations in the lower San Rafael River of 0.12% (0.07 – 0.16%). As with the roundtail chub and flannelmouth sucker, many of the most beneficial reaches to restore are between reaches 160-200.

*Restoration effects: pool enhancement, no non-native eradication*

While riffle enhancement was predicted to have little positive effect on roundtail chub populations, increasing pool habitat availability is predicted to have positive effects throughout most of the lower SRR (Figure 3-9a). Many of the reaches where pool enhancement is predicted to have the least benefit are located near the diversion dam at Hatt’s Ranch. Roundtail chub are predicted to gain the greatest benefit of pool enhancement if reach 134 is restored and the least benefit if reach 7 is restored. Increasing the amount of pool habitat available in reach 134 is predicted to increase
roundtail chub populations in the lower San Rafael River by 5.71% (5.51 – 5.91%), and enhancing pool habitat in this reach is predicted to have a significantly greater impact than restoring any other reach. Increasing the amount of pool habitat in reach 7 is predicted to result in a decrease in roundtail chub abundance by 0.06% (0.05 – 0.08%).

As predicted for roundtail chub, bluehead sucker populations are predicted to respond positively to increased pool habitat in the lower SRR, and are predicted to demonstrate a stronger response than to riffle enhancement (Figure 3-9b). Bluehead sucker are predicted to experience the greatest benefit from pool enhancement if reach 198 is restored and the least benefit if reaches 1, 2, 5 or 12 are restored. Increasing the amount of pool habitat available in reach 198 is predicted to increase bluehead sucker abundance in the lower San Rafael River by 2.94% (2.73 – 3.14%). Increasing the pool habitat available in reaches 1, 2, 5, or 12 is predicted to decrease the abundance of bluehead sucker in the lower San Rafael River by 0.08% (0.05 – 0.12%).

Flannelmouth sucker populations are predicted to respond similarly to bluehead suckers after enhancement of pool habitats (Figure 3-9c). Flannelmouth sucker are predicted to experience the greatest benefit from pool enhancement in reach 127 and the least benefit from restoring reaches 1, 2, 5, and 12. Increasing the amount of pool habitat available in reach 127 is predicted to increase flannelmouth sucker populations in the lower San Rafael River by 4.04% (3.93 – 4.16%), and enhancing the pool habitat in this reach is predicted to have a significantly greater impact on the population than would restoring any other reach. Increasing pool habitat in reaches 1, 2, 5, and 12 is predicted to lead to a decrease in flannelmouth sucker abundance in the lower San Rafael River of 0.03% (0.02 – 0.03%).
When riffle enhancement was coupled with non-native fish removal, a substantial increase in populations of each of the “three species” was predicted regardless of the reach restored (Figure 3-10), and no single reach was predicted to be significantly more beneficial to restore for any of the “three species” in the lower SRR. However, several reaches near the confluence with the Green River (reaches 165, 171, 174, 188, 196, and 197) are predicted to be generally more beneficial to restore than reaches 57-64, 80-88, and 96-112, though the confidence intervals for all reaches overlap. The majority of the restoration effect on the “three species” populations is a result of the removal of the non-native species throughout the lower San Rafael River, but the effect of the two restoration actions do not appear to be strictly additive. The reach with the predicted greatest benefit to roundtail chub was reach 196 with a mean predicted effect of restoration of 26.19% increase in relative abundance (23.52 – 28.87%, 95% CI), albeit statistically equal to the effect size of restoring other reaches. Bluehead sucker populations are predicted to benefit most from restoration of reach 165, with a predicted 174.66% increase in relative abundance (158.27 – 190.00%), though the effect size is not significantly larger than that for any other reach. The reach in the lower San Rafael River with the greatest mean predicted restoration effect on flannelmouth sucker abundance is reach 196, with a 45.35% (39.95 – 50.23%) predicted increase in relative abundance. However, as with the bluehead sucker and roundtail chub, this restoration effect is not significantly more beneficial than restoration in any other reach.
**Restoration effects: pool enhancement, with non-native eradication**

Similar to model predictions for coupled riffle enhancement and non-native fish removal, populations of each of the “three species” are predicted to increase substantially when pool enhancement was coupled with non-native fish removal (Figure 3-11), and no single reach was predicted to be most beneficial to restore for either the flannelmouth sucker or bluehead sucker in the lower SRR. However, the model predicted that, while most reaches would not be significantly more beneficial than any other reach to restore, pool enhancement in reach 137 following non-native fish removal would have a significantly greater impact on roundtail chub populations than restoration of many reaches near the diversion dam at Hatt’s Ranch (Figure 3-11a). The greatest effect of the combined restoration comes from the eradication of non-native fishes. Roundtail chub populations in the lower SRR are predicted to increase by 27.74% (25.11 – 30.33%). Restoration of reach 198 is predicted to have the greatest, albeit marginally, benefit to the populations of bluehead sucker in the lower San Rafael River, with a predicted increase in relative abundance of 174.42% (159.36 – 189.38%). Flannelmouth sucker are predicted to attain the greatest benefit from the restoration of reach 127, with a predicted increase in relative abundance of 46.79% (41.19 – 51.99%), though this effect is not significantly greater than the predicted effect of restoring any other reach.

**Discussion**

The native fishes of the upper Colorado River Basin are threatened by myriad factors, which must be addressed to ensure their persistence into the future. In this study, I predicted the relative benefit of particular restoration actions to three imperiled species
at discrete locations along the entire continuum of the lower San Rafael River. In the face of simultaneously altered biotic and abiotic conditions, multiple restoration actions have the potential to benefit the ‘three species.’ However, limited resources require that restoration actions be prioritized to achieve the greatest restoration benefit, and some actions may have unanticipated consequences if implemented in isolation.

As has been demonstrated for many fragmented populations (Dunham & Rieman 1999; Bottcher 2009), my results suggest that source-sink dynamics are controlling the populations of the “three species” in the San Rafael River. However, unlike in previous studies in this system (Bottcher 2009), non-native fishes were predicted to be an equally important driver of these dynamics as habitat limitation for the bluehead sucker and flannelmouth sucker. Our detection of the increased importance of non-native fishes likely resulted from the expansion of the study area to include the upper San Rafael River, which contains only very low densities of non-natives relative to the lower San Rafael River.

Control or eradication of exotic species is a commonly employed restoration strategy in many ecosystems, often with positive results (Myers et al. 2000; Zavaleta et al. 2001). The simulated eradication of non-native fishes from the lower San Rafael River led to predicted increases in abundance for each of the ‘three species,’ though the bluehead sucker was predicted to show the greatest response. The bluehead sucker may be more responsive to non-native fish levels due to a greater risk of predation from the non-native fish. For example, bluehead sucker have been shown to grow at slower rates than flannelmouth suckers in sympatric populations (Sweet et al. 2009), a difference which could subject the bluehead sucker to size-selective predation for longer periods of
time relative to the flannelmouth sucker. Additionally, of the ‘three species,’ only the trophic niche of bluehead sucker shifted in the presence of non-native fish in the San Rafael River (see Chapter 2), suggesting that non-native fishes impact their feeding behavior to a greater degree than the flannelmouth sucker or roundtail chub.

Habitat loss has been firmly and repeatedly implicated in population and range reductions of desert fishes (e.g., Minckley & Deacon 1968), as dams, diversions, and invasive riparian plants have dramatically altered in-stream and floodplain environments. Not surprisingly, my results suggest that, in addition to being limited by non-native fish populations, the “three species” are habitat limited in the San Rafael River. Complex habitat, important for spawning, rearing, and feeding for the “three species” (e.g., Brouder 2001; Thieme et al. 2001; Bower et al. 2008), in the is extremely limited in the lower San Rafael River, with long stretches of river devoid of any pools, riffles, backwaters, or non-sand substrate (Bottcher 2009). Based on partial dependence plots for each of the ‘three species,’ native fish abundance increases with increasing complex habitat. Further, although partial dependence plots should be interpreted with caution, some of these plots suggest a threshold value of complex habitat above which the species is much more abundant. This pattern makes sense biologically, as suitable habitat thresholds, below which species can no longer persist in a landscape, are predicted by theory (Fahrig 1997, 2002), and have been demonstrated in the field for birds (Andren 1994; Jansson & Angelstam 1999; Carlson 2000), mammals (Andren 1994; Fahrig 2002), and fish (Capra et al. 1995). Small populations are subject to demographic and environmental stochasticity, as well as inbreeding and Allee effects (Lande 1988).
Prediction of local patterns and responses of fishes to habitat availability at a large scale has proved a difficult undertaking for ecologists (Torgersen et al. 1999; Fausch et al. 2002). In this study, simulated restoration of physical habitat produced highly variable predictions depending on restoration location. Simulated restoration of certain reaches led to significant increases in the abundance of the “three species” in the lower San Rafael River, while restoring other reaches led to significant reductions in the abundance of the species. These results support the tenet of ecological restoration that the selection of restoration location is vital to the ultimate success of any restoration activity (Huxel & Hastings 1999; Budy & Schaller 2007). For example, pool habitat restoration simulations for most reaches for the “three species” led to a significant increase in total abundance, whereas other reaches that are already quite heterogeneous (e.g., near the Hatt Ranch dam) demonstrated minimal effects on the abundance of the ‘three species.’ Nonetheless, these models predicted that restoration of degraded reaches near already suitable habitat would be most beneficial to the “three species” (see discussion below).

Recently, ecologists have recognized the importance of examining stream systems in a landscape context and considering the effects of external forces on the stream (DeAngelis et al. 1998; Fausch et al. 2002). As spatially auto-correlated habitat measures had consistently higher variable importance values than their within-reach counterparts, my models suggest that the spatially auto-correlated habitat measures are better descriptors of the habitat available to these fish. Each of the “three species” is highly mobile, and can cover several kilometers in a day, moving between habitat units in search of food or refuge (Chart & Bergeson 1992; Bottcher 2009). The importance of the
spatially auto-correlated habitat variables suggests that larger patches of suitable habitat support larger populations of the ‘three species,’ reflecting general metapopulation theory (Hanski & Thomas 1994). Based on my model predictions, it would be most beneficial to create long stretches of suitable habitat in the river, as the sites that exhibited the greatest response were located near reaches where the “three species” are currently found in relatively high abundance. Thus, we expect a greater overall benefit if suitable habitats are enlarged, rather than if isolated habitats are enhanced, an idea also supported by island biogeography and metapopulation theory (MacArthur & Wilson 1967; Hanski & Thomas 1994).

Effective restoration of heavily degraded ecosystems often requires multiple complimentary approaches (Suding et al. 2004; Falk 2006). The combination of physical habitat rehabilitation and non-native fish removal is predicted to be most beneficial to populations of the “three species” in the San Rafael River. For example, restoration of riffle habitat in reach six was predicted to lead to a decrease in bluehead sucker abundance, likely caused by a predicted increase in non-native fish abundance following riffle enhancement. However, the predicted effect of riffle restoration on reach six following non-native fish eradication is a slight increase in abundance (over that predicted just due to non-native eradication). While synergistic effects are difficult to identify due to the large inherent prediction error of the effect of non-native fish removal relative to the effect size of any habitat restoration, the results are biologically intuitive. Restoration of physical habitat not only creates more favorable physical conditions for the native fishes, but also creates more suitable conditions for the non-native fishes. Thus, the more favorable physical habitat resulting from restoration is also predicted to
cause an increase in the negative effects of the non-native fishes. These results suggest that a combination biotic and abiotic restoration may be necessary to produce a significant increase in populations of the ‘three species.’

The effectiveness of stream restoration activities depends on the spatial extent of the actions undertaken (Minns et al. 1996; Bond & Lake 2003; Lake et al. 2007). My models predicted a much stronger response of the “three species” populations to eradication of non-native fish species than to the augmentation of different complex habitat units due to the scale at which they were implemented. Non-native fish eradication was modeled at the scale of the entire lower San Rafael River, whereas the habitat restorations only altered the conditions in short stretches of the river. These respective scales are appropriate, as these are the scales at which these restoration actions are typically executed in practice (e.g., Vanicek 1970; Bernhardt et al. 2005; Bay & Sher 2008).

Any effort to restore stream conditions must consider and address the processes that caused the degraded conditions originally (Rosenfeld 2003; Falk 2006). In the San Rafael River and many desert streams, dams and diversions have altered the flow regime to the point that habitat creating flows now occur only on extremely rare occasions (Patten et al. 2001; Schmidt et al. 2001; Fortney et al. 2011). To be effective in the long term, any efforts to improve habitat conditions (e.g., bank destabilization by riparian tamarisk removal; Fortney et al. 2011) must be coupled with restoration of in-stream flows and a more natural regime (Patten et al. 2001; Schmidt et al. 2001). Furthermore, in order for the eradication of non-native fishes to be effective, non-native fishes must be prevented from re-invading the lower San Rafael River. As the river is an important
corridor for fluvial spawners returning from the Green River (Bottcher et al, in review), an impassable barrier may present complications. Connectivity between the mainstem and tributaries maintains genetic variation and the representation of a viable, fluvial life history form (Petersen et al. 2008). Thus, management agencies are faced with the need to decide how to best prevent re-invasion, while still allowing for the movement of spawning and rearing native fishes between the San Rafael and Green Rivers.

Identification of limiting factors in degraded systems harbors many challenges (Kondolf et al. 2008). The San Rafael River was chosen a priori as an area of study as this system has experienced degradation (degree and source) representative of many desert rivers (Minckley & Deacon 1968; McAda et al. 1980; Bottcher 2009), which makes these results applicable to other systems. However, caution should be applied when making restoration or rehabilitation decision based on the relationships found in these models (Rosenfeld 2003). The San Rafael River is a highly degraded system, and even in relatively high quality reaches, it is far from pristine. The relationships detected in these models are based on the “three species” behavior in highly altered condition, such that the response of the “three species” in more or less degraded systems may be over- or underestimated. Additionally, the preferred habitat of the “three species” in the degraded San Rafael River may not be representative of truly beneficial habitat in a pristine system, as examinations of species-habitat relationships are inherently affected by fish density and rare species generally do not saturate the optimal habitat (Al-Chokhachy & Budy 2007).

As native fish populations continue to decline in the face of a highly altered environment, management agencies must decide how to most effectively allocate their
limited resources to provide the greatest benefit to native fish populations. Certain restoration actions may provide little benefit to species, the implementation of which would do little to slow population declines, let alone reverse the trends (e.g., Budy and Schaller 2007). Models identifying the most limiting factors for imperiled species are valuable tools in the decision-making process. Models such as those herein can provide spatially explicit information as to which management action will have the greatest positive effect on native fish populations. Proper use of such models can help develop a restoration approach to address both the individual and synergistic negative effects caused by concurrent physical and biotic degradation.

References


distribution and movements of the resident flannelmouth sucker (Catostomidae: 
*Catostomus latipinnis*) population in the White River, Colorado. Southwestern 

predictive tool: silver and bighead carps in North America. Biological Invasions 9:  
43-51.

regime, temperature and the composition and richness of invertebrate assemblages in 
streams of the western United States. Freshwater Biology. 56: 1248-1265.

effects of climate change on the hydrology and water resources of the Colorado 

Cutler, D.R., T.C. Edwards, Jr., K.H. Beard, A. Cutler, K.T. Hess, J. Gibson, and J.J. 

S.M. Sylvester. 1998. Landscape modeling for Everglades ecosystem 
restoration. Ecosystems 1: 64-75.


autocorrelative model for targeting stream restoration to benefit sensitive nongame 

2002. Conservation status and limiting factors in the endangered population of 
Egyptian vulture (*Neophron percnopterus*) in the Canary Islands. Biological 
Conservation 107: 89-97.

Dudgeon, D., A.H. Arthington, M.O. Gessner, Z.I. Kawabata, D.J. Knowler, C. Lévêque, 
2006. Freshwater biodiversity: importance, threats, status and conservation 

of physical, biotic, and geometrical landscape characteristics. Ecological 
Applications 9: 642-655.


Jansson, G., and P. Angelstam. 1999. Threshold levels of habitat composition for the
presence of the long-tailed tit (Aegithalos caudatus) in a boreal landscape.
Landscape Ecology 14: 283-290.

quality of spawning habitat. Pages 249-274 in D. Sear and P. DeVries, editors.
Salmonid spawning habitat in rivers: physical controls, biological responses, and
approaches to remediation. American Fisheries Society Symposium 65, Bethesda,
Maryland.

Lake, P.S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream

fish: linking statistical hydraulic models with multivariate habitat use models.

1455-1460.

Lentz, D.L., R. Bye, and V. Sanchez-Cordero. 2008. Ecological niche modeling and
distribution of wild sunflower (Helianthus annuus L.) in Mexico. International

University Press, Princeton, New Jersey.

Rafael River system of the upper Colorado River Basin. Southwestern Naturalist


Minckley, W.L., and J.E. Deacon. 1968. Southwestern fishes and the enigma of


Figure 3-1. Map of San Rafael River watershed. Inset shows location of watershed in Utah. The river downstream (southeast) of the Hatt Ranch Dam was modeled for current distribution of the “three species”, as well as for the predicted effects of restoration.
Figure 3-2. Flow chart for modeling strategy. (A) Fish community and habitat data from sampling sites are used to fit a random forest model to predict CPUE of the species of interest (i.e., one of the “three species”). (B) This model is then used to predict the relative abundance of the species of interest along the length of the San Rafael River below the Hatt Ranch diversion dam, using the longitudinal habitat survey data collected in 2010. Subsequently, three types of restoration strategies are modeled by altering one or more components of the longitudinal predictor variables; (C) set non-native fish CPUE to zero in all reaches to predict effect of non-native fish removal, (D) augment the riffle/pool habitat of one reach at a time and predict the effect of restoring each reach individually, and (E) combining non-native fish removal with habitat augmentation to examine the effect of augmenting the habitat in each reach after non-native fishes have been removed.
Figure 3-3. Variable importance for the random forest regression model predicting bluehead sucker CPUE in the San Rafael River (top left), and partial dependence plots for bluehead sucker CPUE on SAC pebble size standard deviation (top right), non-native species CPUE (bottom left), and within reach pebble size standard deviation (bottom right).
Figure 3-4. Variable importance for the random forest regression model predicting flannelmouth sucker CPUE in the San Rafael River (top left), and partial dependence plots for flannelmouth sucker CPUE on SAC pool habitat (top right), non-native species CPUE (bottom left), and SAC pebble size standard deviation (bottom right).
Figure 3-5. Variable importance for the random forest regression model predicting roundtail chub CPUE in the San Rafael River (top left), and partial dependence plots for roundtail chub CPUE on SAC riffle habitat (top right), SAC pool habitat (bottom left), and within reach pool habitat (bottom right).
Figure 3-6. Predicted catch per unit effort of the “three species” in the lower San Rafael River under current conditions (solid circles) and after non-native fish eradication (open circles). Reach 1 is located immediately downstream of the diversion dam at Hatt’s Ranch, and reach 213 is at the confluence with the Green River. Note the different y-axes.
Figure 3-7. Predicted relative reach quality under current conditions for the “three species.” Reach 1 is located immediately downstream of the diversion dam at Hatt’s Ranch, and reach 213 is at the confluence with the Green River.
Figure 3-8. “Three species” population effect size after restoring riffle habitat in different reaches of the San Rafael River. The solid line indicates no change from current abundance.
Figure 3-9. “Three species” population effect size after restoring pool habitat in different reaches of the San Rafael River. The solid line indicates no change from current abundance.
Figure 3-10. “Three species” population effect size after eradication of non-native fishes and restoring riffle habitat in different reaches of the San Rafael River. The dashed line indicates the 95% confidence interval. Note different y-axes for each species.
Figure 3-11. “Three species” population effect sizes after eradication of non-native fishes and restoring pool habitat in different reaches of the San Rafael River. The dashed line indicates the 95% confidence interval. Note the different y-axes for each species.
CHAPTER 4

SUMMARY

As native freshwater biodiversity continues to decline, the identification of factors and mechanisms contributing to these declines is critical to ensure future persistence and ecosystem health in general. A diverse array of factors have contributed to the decline on freshwater biodiversity, each of which present challenges to management and conservation agencies. In the Colorado River Basin, abiotic factors have long been implicated in the declines of native fish populations. However, recent research has begun to illustrate the impacts of non-native fishes (e.g., Johnson et al. 2008; Pilger et al. 2010). The San Rafael River, a tributary to the Green River, has experienced extensive degradation both in physical habitat and in biotic community structure, and provides a template for examining how non-native fishes and physical habitat degradation interact to impact populations of native Colorado River Basin fishes. My thesis research has advanced our understanding of (1) the effect of non-native fish establishment on food web structure, (2) the effects of food web restructuring on native fish growth and condition, and (3) factors limiting the abundance of the “three species” in the San Rafael River. Additionally, I developed a spatial model to predict the relative effect of restoration actions executed at different locations in the lower San Rafael River.

The first objective of my thesis was to examine the food web structure in areas of the San Rafael River where non-native fishes have and have not established. To address this objective, I compared the stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ for the fish community in the upper and lower San Rafael River. This analysis allowed me to
estimate both the trophic position and relative resource usage of both the native and non-native fishes. Additionally, the use of convex hulls to estimate trophic niche space allowed me to estimate the amount of overlap between the trophic niche space of different species, and therefore the potential for competition over resources to exist.

The results, covered in detail in Chapter 2, suggest that several non-native fishes occupy a higher trophic position than was historically occupied in the San Rafael River, and thus, present a novel source of predation to the ‘three species.’ Additionally, the trophic niche spaces of several non-native fishes overlap almost entirely with those of each of the ‘three species.’ Furthermore, the presence of the non-native fishes coincides with a shift in resource use for the bluehead sucker, suggesting that the non-native fishes may be competitively excluding this native species from its preferred trophic niche. The presence of the non-native fishes therefore increases the number and complexity of trophic linkages in the San Rafael River, altering the flow of nutrients and energy through the ecosystem.

The second objective of my thesis was to determine if the altered food web structure resulting from non-native species establishment was manifesting in altered growth rates of the ‘three species,’ an important vital rate and indicator of fitness. To address this objective, I used a combination of back-calculated size-at-age values to assess growth rate over the lifetime of individual fishes, and a comparison of the relative body condition of the fishes in the upper and lower San Rafael River. The results of this body of research, covered in detail in Chapter 2, demonstrate that the “three species” do not have reduced growth or condition in the presence of the non-native fishes. In fact, the bluehead sucker captured in the presence of non-native fish populations demonstrated
marginally higher growth and greater body condition than did those in the upper San Rafael River, free of non-native fishes. Source-sink dynamics and the unidirectional connectivity of the San Rafael River seemingly control this pattern. Fishes captured in the lower San Rafael River likely are colonists from populations in the upper San Rafael River and Green River, an aspect that could conceal growth differences caused by the increased competition and predation pressure from non-native fishes. Use of different habitats throughout the San Rafael and Green Rivers may represent diverse life-history strategies within the ‘three species,’ the advantages of which have seemingly been reduced by anthropogenic alterations to the ecosystem.

The third objective of my thesis research was to examine the limiting factors of the “three species” populations in the San Rafael River. I addressed this objective with random forest and generalized linear models of site-specific biotic and abiotic measurements used to predict native fish abundance. The results of this component of my research, described in detail in Chapter 3, suggest that the non-native fishes have a strong negative effect on each of the ‘three species,’ but are particularly limiting to populations of bluehead sucker and flannelmouth sucker. Additionally, spatially auto-correlated habitat measures were important predictors of the presence of each of the ‘three species,’ more so than within-reach habitat measurements. This latter result suggests that the highly mobile “three species” may choose locations based on habitat at a larger scale than the individual reaches used in this study. Finally, as previous studies have suggested (Bottcher 2009), the distance to a source population was an important predictor for each of the ‘three species,’ indicating that source sink dynamics are likely driving the “three species” population distribution and dynamics in this river.
Lastly, I was able to use the models I developed, in combination with continuous, longitudinal habitat measurements, to predict the current distribution of the ‘three species,’ as well as the likely effects of relevant restoration actions. The simulations suggested that the removal of non-native fishes would greatly increase the abundance of each of the “three species” in the lower San Rafael River, especially for the bluehead sucker. Simulations of habitat restoration at the reach-scale suggest that the reach chosen for restoration will have a significant impact on the success of the restoration. If restoration were executed near reaches that currently support large populations of the ‘three species,’ the restoration is predicted to have a greater positive effect on the populations than if executed distant from current populations. Thus, the models predict that larger areas of suitable habitat can support larger populations of the ‘three species,’ reflecting metapopulation and island biogeography theory (MacArthur and Wilson 1967; Hanski and Gilpin 1991).

As the “three species” sub-populations in the upper San Rafael River represent source populations sustaining the populations in the lower river, the protection of this habitat, particularly from non-native species invasion, is critical to their persistence. Additionally, if the lower San Rafael River is to be restored, habitat restoration without the removal of non-native fishes (or vice versa) will likely result in a limited response by populations of the ‘three species.’ The two restoration actions will have their greatest benefit if they are carried out in tandem. Additionally, any restoration action taken must address the underlying cause of the physical and biotic degradation. Non-native fishes are densely populated in the Green River, and any removal effort in the lower San Rafael River must also inhibit the ability of these fishes to re-colonize from the Green River.
Finally, and perhaps most importantly, the altered flow regime must be addressed, as the dampened spring snowmelt flood has reduced the occurrence of habitat-forming flows, and disconnected the river from its floodplain. If management agencies can address these issues, the outlook for the “three species” will be greatly improved in the San Rafael River. As the ecological niche of a species is conserved throughout its range (e.g., McNyset 2009), predictions from the model I developed for the San Rafael River should be applicable and useful for the prioritization of conservation and restoration actions throughout the historic range of the ‘three species.’

References


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