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Movement Patterns of a Federally Endangered Minnow in a Fragmented Desert River

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MOVEMENT PATTERNS OF A FEDERALLY ENDANGERED MINNOW IN A FRAGMENTED DESERT RIVER

by

Martinique J. Chavez

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

MASTER OF SCIENCE

in

Ecology

Approved:

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Movement Patterns of a Federally Endangered Minnow in a Fragmented Desert River

by

Martinique J. Chavez, Master of Science

Utah State University, 2023

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Department: Watershed Sciences

Fishes are unified in their innate need to move within the systems they occupy, and their movement patterns can be fundamental to their ecology and survival. Many large rivers in North America are fragmented by dams that modify natural flow regimes, compromise longitudinal connectivity of freshwater ecosystems, and imperil freshwater fishes dependent on unrestricted movement in order to complete their life history. Coincident with widespread river fragmentation are the declines of numerous endemic desert fishes in the American Southwest. The Rio Grande Silvery Minnow (*Hybognathus amarus*, RGSM), has experienced a dramatic 95% reduction in its historical range and is now restricted to a highly modified and fragmented stretch of the Rio Grande. Despite the important ecological role of space use in riverine fishes, there is a lack of evidence extensively quantifying the movement patterns of RGSM. The overall goal of this study is to document and better understand the movement ecology and patterns of RGSM. We used passive integrated transponder (PIT) tags in hatchery-reared RGSM with stationary and mobile PIT tag antenna systems to detect and track movement patterns across time and space. We released a total of 37,215 PIT-tagged RGSM between 2018 and 2022. Of those released, we detected 13,706 RGSM making at least one movement (e.g., detected at two different locations). We found RGSM to be highly mobile and documented individuals moving farther distances than ever previously recorded. Individuals moved a mean total distance of 12.2 river kilometers (rkm) over the course of one year, with a maximum total distance of 103.0 rkm. Overall, total distances moved by individuals was larger than linear home range sizes, suggesting RGSM were moving at finer scales within the extent of the river they occupied. Although individuals moved large distances, movement patterns were leptokurtic, with a larger portion of RGSM remaining near their initial release location. Notably, we documented a total of 198 unique upstream passages through a diversion dam that is not equipped with a formal fish passage structure. The documentation of these passages is particularly meaningful as passage through this diversion by RGSM has not been previously documented. As indicated by the high number of repeated detections over the study period, as well as our high redetection rate (36.8%), the efficacy of our study design to detect an imperiled small-bodied fish species has crucial conservation applications and can serve as an important model to guide future recovery efforts in fragmented systems.

(111 pages)

PUBLIC ABSTRACT

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Martinique J. Chavez

Fishes are unified in their need to move within the systems they occupy, and their movement patterns can be fundamental to their ecology and survival. Many large rivers in North America are fragmented by dams that modify natural flow regimes, compromise connectivity, and imperil freshwater fishes dependent on unrestricted movement in order to complete their life history. Coincident with widespread river fragmentation, are the declines of numerous endemic desert fishes in the American southwest. The Rio Grande Silvery Minnow (*Hybognathus amarus*, RGSM), has experienced a 95% reduction in its historical range and is now restricted to a highly fragmented stretch of river. Despite the important role of movement in riverine fishes, there are few studies describing the movement patterns of RGSM. The overall goal of this study is to document and better understand the movement ecology and patterns of RGSM. We used Passive Integrated Transponder (PIT) tags in hatchery-reared RGSM with stationary and mobile PIT-tag antenna systems to detect and track movement patterns across time and space. We released a total of 37,215 PIT-tagged RGSM between 2018 and 2022. Of those released, we detected 13,706 RGSM making at least one movement (e.g., detected at two different locations). We found RGSM to be highly mobile and documented individuals moving farther distances than ever previously recorded. Individuals moved a mean total distance of 12.2 river kilometers (rkm) over the course of one year, with a maximum total distance of 103.0 rkm. Overall, total distances moved by individuals was larger than linear home range sizes within one year of release, suggesting RGSM were moving at finer scales within the extent of the river they occupied. Although individuals moved large distances, movement patterns were leptokurtic, with a larger portion of RGSM remaining near their initial release location. We documented a total 198 unique upstream passages through a diversion dam. The documentation of these passages is particularly meaningful as passage through this diversion by RGSM has not been previously documented and the diversion is not equipped with a formal fish passage. As indicated by the high number of repeated detections over the study period, as well as our high redetection rate (36.8%), the efficacy of our study design to detect an imperiled small-bodied fish species has crucial conservation applications. Our study elucidates the movement patterns of RGSM and can be an important model for other fish species in fragmented desert systems.

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CONTENTS

Page

Abstract ... iii

Public Abstract ... v

Acknowledgments ... vii

List Of Tables ... x

List Of Figures ... xi

Chapter 1 Introduction ... 1

    References ... 8

Chapter 2 Big Moves by a Little Fish: Characterizing Movement Patterns of a Small-Bodied Minnow in a Fragmented Desert River ... 12

    Abstract ... 12
    Introduction ... 13
    Materials and Methods ... 18

        Study Area ... 18
        Fish Tagging and Release ... 19
        Fish Detection ... 20
        Movement Metrics and Potential Correlates ... 21
        Restricted Movement Paradigm ... 23
        Colonization Cycle Hypothesis ... 24

    Results ... 24

        Movement Metrics and Potential Correlates ... 25
        Restricted Movement Paradigm ... 26
        Colonization Cycle Hypothesis ... 27

    Discussion ... 27

    References ... 35
    Tables and Figures ... 42

Chapter 3 Quantifying Transition Probabilities Among Fragmented Reaches for an Endangered Desert Minnow ... 55

Abstract 55
Introduction 56
Materials and Methods 60

Study Area 60
Materials 61
Data Analysis 62
Bayesian Hierarchical Estimates 67

Results 68

Discussion 71

References 77

Tables and Figures 83

Chapter 4 Conclusions 91

References 95

Appendix 96

LIST OF TABLES

Page

Table 2-1. Rio Grande Silvery Minnow released between 2018 and 2022 in the Middle Rio Grande of New Mexico, USA showing the year and month released, release location (rkm), and the number of PIT-tagged individuals released....................42

Table 2-2. Float trips conducted in the Middle Rio Grande of New Mexico, USA by year, showing the dates and extent (rkm) of each float trip. Active float trips spanned 170.5 km of the Middle Rio Grande...43

Table 2-3. Expected and observed distances of stationary and mobile components of the Rio Grande Silvery Minnow population by year produced under the Restricted Movement Paradigm using the R program 'fishmove'...44

Table 2-4. Summary statistics of annual net movement detections of Rio Grande Silvery Minnow between 2019 and 2021 by direction...45

Table 2-5. Results of two-way ANOVA for net distance moved upstream and downstream by Rio Grande Silvery Minnow by year and season (n = 11,775)...............46

Table 3-1. Rio Grande Silvery Minnow released between 2019 and 2021 in the Middle Rio Grande of New Mexico, USA showing the number of tagged individuals released, release state (location), and year/season released..83

Table 3-2. Number Rio Grande Silvery Minnow detected at least once in two distinct 4–month time intervals (i.e., used in the multistate analysis) for fish released between 2019 and 2021 in the Middle Rio Grande of New Mexico, USA showing group cohorts by release season...84

Table 3-3. Model selection output of multistate movement analysis for Rio Grande Silvery Minnow detected at least once (n = 1,469) in the Middle Rio Grande of New Mexico, USA, 2019-2022. The top 20 models are presented...85

LIST OF FIGURES

Page

Figure 2-1. Map of study area within Middle Rio Grande, showing locations of fish releases and locations of submersible antennas by year, with San Acacia Diversion Dam zoomed within the left center box..........47

Figure 2-2. Total distance moved (absolute value), both upstream and downstream, by PIT-tagged Rio Grande Silvery Minnow in the Middle Rio Grande from 2018 to 2022 (panel a) 48

Figure 2-3. Total distance moved (km, log-10 scale) by PIT-tagged Rio Grande Silvery Minnow in the Middle Rio Grande on the y-axis by season (Irrigation = March–October; Off = November–February) on the x-axis, with the black diamonds representing the mean total distance moved (km) by season..........49

Figure 2-4. Total distance moved (km) by 100% linear home range size (km) of Rio Grande Silvery Minnow between 2018 and 2022 in the middle Rio Grande, with shades of grey representing release location in relation to San Acacia Diversion Dam..........50

Figure 2-5. Covariates included in the binomial logistic regression and zero-truncated lognormal model assessing variation in Rio Grande Silvery Minnow movement patterns by season on the y-axis and standardized regression coefficients on the x-axis, with shade representing model and horizontal bars showing the 95% confidence interval..........51

Figure 2-6. Significant interaction between season and release location (above or below San Acacia Diversion Dam) produced by binomial logistic regression with probability of movement (0 = no movement; 1 = movement) on the y-axis and season on the x-axis, with shaded shapes corresponding to release location and error bars representing the 95% confidence interval..........52

Figure 2-7. Significant interaction between season and release location (above or below San Acacia Diversion Dam) produced by zero-truncated lognormal model assessing the positive total distances moved by season, with log-transformed total distances by season on the y-axis and season on the x-axis, with shaded shapes corresponding to release location and error bars representing the 95% confidence interval..........53

Figure 2-8. Violin plots of net distance moved downstream or upstream (km; absolute values) by PIT-tagged Rio Grande Silvery Minnow by year and season (Irrigation = March– October; Off = November– February)..........54

Figure 3-1. Map of Middle Rio Grande with spatial states represented by color and inset zoomed into San Acacia Diversion Dam..86

Figure 3-2. Hydrograph of Middle Rio Grande below San Acacia Diversion Dam (United States Geological Survey Gage 08354900) between 2019 and 2022. Black points represent corresponding dates of PIT-tagged Rio Grande Silvery Minnow releases, with fill color representing the season of release...87

Figure 3-3. Transition probabilities for PIT-tagged Rio Grande Silvery Minnow released in winter between 2019 and 2021 in the Middle Rio Grande (n = 1,031), with the width of the arrows corresponding with the probability of each state transition..88

Figure 3-4. Transition probabilities for PIT-tagged Rio Grande Silvery Minnow released in spring between 2019 and 2021 in the Middle Rio Grande (n = 438), with the width of the arrows corresponding with the transition probability between each state...89

Figure 3-5. Frequency of state transitions by direction, with color representing the release season cohort (spring: March–June, winter: November–February) for RGSM released between 2019 and 2021 in the MRG...90

Figure A-1. Percent frequency of Rio Grande Silvery Minnow detections on the y-axis by habitat type on the x-axis, with shade representing antenna type......................97

Figure A-2. Upstream passages through San Acacia Diversion Dam by Rio Grande Silvery Minnow, with number of unique passages on the y-axis and season on the x-axis, with shade representing season on a finer scale..98

Figure A-3. Mean daily discharge (cubic feet per second) for the Middle Rio Grande below San Acacia Diversion Dam, New Mexico USA (USGS Gage 08354900) by year. Gradient represents magnitude of daily mean discharge..99

CHAPTER I

INTRODUCTION

The distribution and remarkable diversity of fishes reflects, in part, the harsh environmental variability prevalent throughout Earth's history. Despite having survived mass extinction events, severe climate variation, volcanism, and continental shifts (while simultaneously colonizing virtually every aquatic ecological niche), it is unknown whether this successful lineage will survive the deleterious actions of mankind. Freshwater ecosystems support about 40% of global fish diversity, yet the alarming rate of biodiversity decline in fresh waters far exceeds those in other biomes (Sala et al. 2000; Dudgeon et al. 2006). The freshwater ecosystems of North America support the highest degree of non-tropical aquatic biodiversity on Earth (Abell et al. 2002), but 39% of described fish species inhabiting these ecosystems are imperiled (Jelks et al. 2008). The vulnerable status of these fragile aquatic ecosystems is largely due to human activities that extensively alter natural landscapes and exploit aquatic resources (Poff et al. 1997).

Humans have long been appropriating free-flowing fresh water, compromising the ecological integrity of rivers to meet societal demands (e.g., water supply, irrigation, hydroelectric power, and recreation). Demands on the world's freshwater supply are increasing exponentially with rapid global population growth (Glieck 2003). Competition between humans and aquatic organisms for increasingly limited water resources is likely to incur a grave ecological cost. Long-term efforts to alleviate the severity of water scarcity have had catastrophic global impacts on freshwater fishes and ecological processes (Jelks et al. 2008). Most notably, the impoundment of river systems is among the most widespread and detrimental anthropogenic modifications to riverscapes around the world (Nilsson et al. 2005). In North America, nearly every river is regulated and fragmented by dams that modify natural flow regimes, degrade habitats, and contribute to the imperilment of native freshwater fishes (Collier et al. 1996; Poff et al. 1997; Dudgeon et al. 2006). Habitat degradation through flow modification is one of the principal causes of aquatic ecosystem imperilment and poses a persistent threat to freshwater fishes (Richter et al. 1997; Gido et al. 2015; Pennock et al. 2021). Given the prevalence of fragmentation and degradation, understanding how native fish species use and move within these altered riverscapes should help assess the ecological integrity of an ecosystem.

Animals are ecologically unified by their innate need to move within the systems they occupy. An individual's decision to move is a fundamental life history strategy decision faced by almost all species and can act as a driver of ecological processes (e.g., dispersal, migration, distribution, colonization, extinction, metapopulation dynamics, gene flow, species interactions, and individual fitness). Movement has the capacity to facilitate reproduction, survival, and even connect populations (Jeltsch et al. 2013). However, insight into how, why, when, and where animals move is often insufficient (Morales et al. 2010). As such, there is a need to better understand movement patterns and the factors that influence them. In particular, there is a need to acquire baseline information on imperiled species' patterns of movement, distribution, habitat use, and both the drivers and consequences of movement (Avgar et al. 2013). The quantification of species' movement patterns can be used to determine its intent and ability to colonize or recolonize areas, and in part, its potential for population recovery. The field of movement ecology is expanding rapidly, and advances in tracking technology have enabled researchers to track movements with greater accuracy and precision.

Movement is a fundamental ecological process that greatly influences the survival and population dynamics of riverine fishes (Davis et al. 2018). Defined as a one-way movement by an organism away from their existing home range or natal habitat to a subsequent location (Lowe and Likens 2006; Coates et al. 2019), fish dispersal occurs at the individual level at different life stages and various temporal and spatial scales. The propensity for dispersal varies greatly among individuals, based on body condition or personality (Rasmussen and Belk 2017; Coates et al. 2019). As it occurs along the linear and branched dimensions of rivers, fish dispersal plays a pivotal role in shaping population dynamics, species distribution, and long-term persistence. The impetus to move away from their current location could be for increased resource availability, decreased competition, improved reproduction, or better habitat quality at the next destination. There are also risks associated with movement, such as energetic expenditures, reduced habitat quality and resources, and the risk of predation (Tonkin et al. 2022). The spatial and temporal patterns of fish movement in riverine ecosystems represent a complex and largely understudied paradigm (Fausch et al. 2002; Radinger and Wolter 2014). Despite their important role in riverine fish communities, there is little information characterizing the dispersal patterns of small non-migratory species (Comte and Olden 2018). Only about 1% of riverine fish species have been considered in movement studies worldwide (Comte and Olden 2018). Additionally, many fish movement studies focus on large-bodied and long-lived species in large rivers. A better understanding of how and at what scale imperiled riverine fishes complete their life histories can be used to determine long-term population dynamics and inform conservation and water management strategies.

Fragmentation, coupled with increased channel drying, is a major disturbance and threat to endemic fishes (Hoagstrom 2015; Ruppel et al. 2020). The suite of stressors placed on desert fish species in modified southwestern rivers, such as the Colorado River Basin, is well documented (Olden et al. 2008; Propst et al. 2008; Hoagstrom 2015; Perkin et al. 2019). Most native fishes in this region have experienced alarming declines in their distribution and abundance (Budy et al. 2015). These desert fishes likely evolved in flow regimes with little resemblance to present-day regimes, and therefore may be poorly adapted to these degraded conditions. Specialized life histories (i.e., delayed maturity, low parental care, and small geographic distribution) have been correlated with a heightened degree of endemism and extinction risk (Olden et al. 2008). Additionally, the life histories of many endemic desert fishes are poorly understood due to their lack of commercial/recreational importance coupled with a perceived lack of charisma (Abell 2002).

Coincident with widespread river fragmentation are declines of numerous endemic desert fishes, suggesting fragmentation may be particularly detrimental to endemic desert fish species with specialized life histories. A guild of pelagic-broadcast spawning minnows, known as pelagophils, has declined rapidly over the past 60 years (Perkin and Gido 2011). The dam-induced extirpation of four Great Plains minnows (Winston et al. 1991; Platania and Altenbach 1998) provides direct evidence of fragmentation disrupting the early life history of pelagophils (i.e., propagules drift downstream over dams) and acting as an important driver of their population declines (Perkin et al. 2015). The shared life history of these extirpated species highlights the importance of unrestricted movement between habitat types to help displaced individuals recolonize upstream populations (Perkin and Gido 2011; Platania et al. 2020).

In addition to widespread fragmentation, other pervasive anthropogenic disturbances (i.e., non-native species, reservoirs, flow modifications) have resulted in novel ecosystems with characteristics outside the evolutionary history of native and often endemic fishes (sensu Hobbs et al. 2006). Anthropogenic disturbances have been particularly devastating for rivers in the American Southwest, due in part to their arid nature, naturally variable flow regime, and increasing competition with humans for limited water. The flow regimes of perennial and intermittent rivers are more vulnerable to impacts of climate change than any other aquatic biomes (Dhungel et al. 2016). Many of these once-perennial rivers have become intermittent (Leigh et al. 2016; Archdeacon and Reale 2020), or are predicted to experience an increase in intermittency, because of intensifying water demands and climate change (Döll and Schmied, 2012). Increasing human populations and declines in precipitation supply in these arid regions have increased human reliance on water diversions for storage, irrigation, and flood control. The proliferation of infrastructure results in heavily modified flow regimes and a reduction in lateral and longitudinal connectivity (Gido et al. 2015). As flow regimes continue to fluctuate and demands continue to rise, southwestern regions are likely to experience increased water stress, driving the need for management strategies to balance the risks between societal and ecological needs (Palmer et al. 2008).

Although the Rio Grande in New Mexico historically supported five pelagophils, Rio Grande Silvery Minnow *Hybognathus amarus* is the only remaining extant species. Given its shared life history with the four extirpated species, it is reasonable to presume that Rio Grande Silvery Minnow (hereafter "RGSM") is at risk of sharing their fate. Listed as federally endangered in 1994 (United States Office of the Federal Register, 1994), RGSM has experienced a 95% reduction in its historical range. Once widely distributed across the Rio Grande, the only remaining wild population of RGSM occurs solely within the Middle Rio Grande (Bestgen and Platania 1991). Restricted to about 250 rkm of an extensively modified river reach, the current distribution of RGSM is fragmented by multiple diversion dams that act as either partial or complete barriers to fish movement.

In Chapter 2, our goals were to characterize and quantify movement patterns of RGSM within the Middle Rio Grande, identify potential drivers of those patterns, and assess how well two riverine movement theories explained RGSM movement patterns. The first theory we assessed is known as the restricted movement paradigm (RMP), where fish movement is expected to be heterogeneous and limited in range. Although we hypothesized that RGSM movement potential would be greater than expected under the RMP, we did expect to see a heterogeneous movement distribution. The second theory we assessed is the colonization cycle hypothesis (CCH), where individuals are expected to display biased upstream movements to prevent upstream extirpation. We hypothesized that at least a small portion of RGSM would display an upstream bias, and that movement patterns would be best described by the CCH. In the event that RGSM displayed a larger capacity for movement than expected by the RMP but did not display the upstream movement bias required under the CCH, we would conclude support for the drift paradox (DP). We also found a significant relationship between movement and season, flow magnitude, and whether an individual was released above or below a barrier.

In Chapter 3, we utilized PIT tag data to quantify the movement probabilities and reach-specific dynamics of RGSM. We parameterized a Bayesian multistate model using Markov chain Monte Carlo (MCMC) simulation. Our results revealed transition probabilities among fragmented reaches of river and identified the potential consequences of release locations and conditions. We found a very low probability of moving upstream between reaches fragmented by a diversion dam, with the majority of individuals remaining within their initial release reach. The results of our model provide further support for a heterogeneous movement distribution within

RGSM, as well as highlight the extent to which the diversion dam acts as a barrier to fish movement.

In Chapter 4, we integrate the findings of the two research chapters to summarize the movement patterns of RGSM in the current fragmented system and how a greater integration of movement ecology into conservation biology may be critical for endemic fish species. As fragmentation of habitats within riverine systems becomes increasingly pervasive (Fahrig 2003), there is a growing need to better understand the impacts of barriers to adaptive responses in movement patterns. Our research fills a gap in knowledge of riverine fish movement patterns and provides a framework to gain insight into movement ecology of small-bodied fishes in turbid fragmented systems.

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CHAPTER 2

BIG MOVES BY A LITTLE FISH:

CHARACTERIZING MOVEMENT PATTERNS OF A SMALL BODIED MINNOW IN A FRAGMENTED DESERT RIVER

ABSTRACT

Unfettered movement among habitats is crucial for fish to access patchily distributed resources and complete their life history, but many riverscapes in the American Southwest are highly fragmented by dams. The federally endangered Rio Grande Silvery Minnow (*Hybognathus amarus,* RGSM) persists in a fragmented remnant of its former range (ca. 95% range reduction), and its movement has not been extensively quantified. We tracked movements of hatchery-reared RGSM, tagged with passive integrated transponder tags, using multiple antenna types. We also related variation in RGSM movement patterns to potentially correlated covariates. We then assessed how well two prevailing riverine movement theories (i.e., restricted movement paradigm [RMP] and colonization cycle hypothesis [CCH]) explained RGSM movement patterns. We detected 36.8% of released RGSM (n = 37,215) making at least one movement. Movements were greater than expected based on the RMP and were highly leptokurtic with most fish moving shorter distances and a few fish moving longer distances. On average, RGSM moved a total of 12.2 km within a year, and the maximum total distance moved was 103.0 km. Similarly, we observed a multimodal distribution of linear home range sizes with a mean 100% home range of 2.4 km and a maximum linear home range of 78.2 km. We found little support for an upstream movement bias, as expected under the CCH, and most movements (74%) were directed downstream. Our data suggest RGSM are highly mobile, with the ability and predilection to make long-distance movements. The movement patterns of RGSM were not best described by either prevailing movement theory; instead, our findings support nomadic movements and an apparent drift paradox matching recent studies of other pelagic-broadcast spawning minnows with drifting eggs. Resolution of the drift paradox may be achieved through further, targeted studies. Quantification of RGSM movement provides crucial insights that could help target recovery efforts and highlights the need to restore connectivity.

INTRODUCTION

Many riverscapes are fragmented by dams and water diversions that modify natural flow regimes, degrade habitats, and contribute to the imperilment of native freshwater fishes. Adverse environmental conditions, such as drought, also drive habitat fragmentation. Dam construction and water extraction have compromised habitat quality, riverine connectivity, and restricted fish movement (Hoagstrom 2015), contributing to widespread range reductions and local population declines (Winston et al. 1991; Jelks et al. 2008). Quantifying movement patterns can provide important information to guide management actions, such as restoring longitudinal and lateral connectivity among habitats during critical life-stages or guiding design of fish passage (Cooke et al. 2022). Despite the potential for movement data to inform management of riverine fishes, there is a paucity of quantitative information on movement ecology for many species (Comte and Olden 2018). A recent study classifying the migratory tendency of 1,250 North American fishes suggested 44% lack sufficient movement data (Dean et al. 2022). Quantifying movement patterns of more species and framing results within broader movement theories will contribute to a better understanding of riverine fish ecology and help guide appropriate restoration efforts on the appropriate scale of actions (Wolter et al. 2015).

Several movement theories are used to describe movement within populations of riverine fishes. For over three decades, the prevailing thought was that fish generally displayed restricted movement, whereby individuals remain in relatively small home ranges for the entirety of their lifespan (Gerking 1959). Gowan et al. (1994) formalized this idea as the restricted movement paradigm (RMP), but Rodríguez (2002) pointed out that most studies of fish movement searched for tagged fish mostly within or very near habitats where fish were released, underestimating the mobility of stream fishes. Now, movement within fish populations is thought to be more heterogeneous with most individuals having a 'stationary' tendency and a smaller component of 'mobile' individuals (Skalski and Gilliam 2000; Rodríguez 2002; Radinger and Wolter 2014). In a metanalysis of the movement of 40 riverine fishes, Radinger and Wolter (2014) presented a model of the RMP but included heterogenous movement tendencies to predict the expected movement of stationary and mobile components of populations based on a suite of characteristics. This model has been validated for a few species (e.g., Wells et al. 2017; Santee et al. 2022); however, as movement studies are being conducted on a broader range of species, more tests are required to assess the generality of the RMP (e.g., Steffensmeier et al. 2022). A second theoretical framework to describe riverine fish movements is the colonization cycle hypothesis (CCH), which assumes organisms experience some degree of downstream drift and must make net upstream movements to offset this displacement (Müller 1982; Pachepsky et al. 2005). For the CCH to be true, some adults must undertake upstream movements to prevent local extirpation from upstream habitats. Situations where upstream persistence occurs in the absence of mass upstream movement has led to development of the drift paradox (DP; Hershey et al.

1993; Humphries and Ruxton 2002). For aquatic invertebrates, simulations suggested density-dependent small-scale movements can resolve the drift paradox (Anholt 1995; Humphries and Ruxton 2002). The DP has been used to describe the apparent lack of directed upstream movement of juveniles and adults among a unique reproductive guild of freshwater pelagic-broadcast spawning (PBS) minnows (Archdeacon et al. 2018; Platania et al. 2020; Steffensmeier et al. 2022). Currently, there is no resolution of the drift paradox for freshwater PBS minnows. Chase et al. (2015) used otolith microchemistry to infer both upstream dispersal and retention of propagules near spawning locations in Pecos Bluntnose Shiner *Notropis simus pecosensis*, either of which could partially explain the apparent paradox.

Pelagic-broadcast spawning is a unique reproductive strategy for freshwater fishes (Hoagstrom and Turner 2015), and likely promoted survival in the historically dynamic and harsh conditions of large, arid riverscapes (Fausch and Bestgen 1997; Hoagstrom and Turner 2015). Species in the PBS guild release nearly-neutrally buoyant, nonadhesive eggs into the water column, that drift passively into a variety of downstream habitats (Moore 1944; Platania and Altenbach 1998). Drifting is likely more efficient for delivering propagules to appropriate nursery habitats rather than a fish visiting each habitat to spawn, particularly in rapidly changing environments (Hoagstrom and Turner 2015). The CCH predicts upstream movements by juvenile and adult PBS fishes are important for the persistence of upstream populations, allowing them to recolonize and offset the net downstream displacement of ichthyoplankton (Archdeacon et al. 2018; Platania et al. 2020). These upstream movements are often blocked by fragmentation in contemporary riverscapes (Archdeacon and Remshardt 2012; Walters et al. 2014). There are a few studies that present evidence for upstream movement by PBS fishes (e.g., Chase et al. 2015; Ruppel et al. 2020; Steffensmeier et al. 2022), but evidence of synchronized mass upstream movement by juveniles or adults is limited to a few observations (Archdeacon et al. 2018). Movement information for small-bodied fishes in larger rivers is lacking generally due to marking and recapture limitations of small fishes in larger rivers (Archdeacon et al. 2022). More research is needed, across spatiotemporal scales relevant to management (e.g., Fausch et al. 2002), to understand the importance of upstream movements for the long–term persistence of PBS fishes.

Species of PBS fish were formally widespread and numerically dominant in rivers across the Great Plains and the Rio Grande Basin in the Southwest USA. The Rio Grande in New Mexico, USA, historically supported five PBS fishes, and all except the Rio Grande Silvery Minnow (*Hybognathus amarus,* RGSM) are extirpated. Fluctuations in the occurrence and density of RGSM over the past three decades are closely related to variation in spring and summer flows (Walsworth and Budy 2021; Yackulic et al. 2022). Extensive geomorphic and hydrological modifications along the Middle Rio Grande have compromised habitat quality, complexity, and connectivity (Dudley and Platania 2007). Bank modifications, for flood control have increased river incision and further reduced habitat complexity (Cowley 2006; Swanson et al. 2011), contributing to diminished refuge during periods of drought (Archdeacon and Reale 2020). The active channel width of the Rio Grande has been decreasing since the 1930s, and the river has almost completely lost connection to the historical floodplain (Swanson et al. 2011; Makar and Aubuchon 2012), coinciding with a decrease in flood frequency, amplitude, and total water volume in the river (Blythe and Schmidt 2018; Budy and Schmidt 2018). Frequent river drying, due to seasonal drought and irrigation withdrawals to meet agricultural demands, exacerbates adverse impacts on seasonal recruitment and population persistence (Archdeacon and Reale 2020; Archdeacon et al. 2020; Walsworth and Budy 2021). Consequently, there is a low effective population size of wild RGSM in the Middle Rio Grande (Alo and Turner 2005; Osborne et al. 2012), and the species is maintained by nearly annual stocking (Archdeacon et al. 2023).

Since being listed as federally endangered, RGSM has been the subject of numerous recovery efforts which include: (1) augmenting wild populations with hatchery-reared fish, (2) attempting to transport stranded RGSM upstream during periods of river drying, and (3) restoring aquatic habitats in the Middle Rio Grande (USFWS 2010). In addition to these recovery actions, long-term demographic and genetic population monitoring occurs across the species' remaining range (Osborne et al. 2012; Dudley et al. 2022). However, long-term recovery of this species will not be achieved without addressing and ameliorating the adverse effects of the extensive anthropogenic modifications to the river, including extensive river drying and fragmentation (Dudley and Platania 2007; Walsworth and Budy 2021).

The specialized life history of RGSM, coupled with fragmentation-induced declines of other broadcast spawning minnows (Dudley and Platania 2007; Perkin and Gido 2011; Pennock et al. 2017), suggests upstream dispersal may be important for long-term population persistence; however, data on RGSM movement patterns are limited. Laboratory research suggests RGSM have the physiological capability to make long distance movements upstream (Bestgen et al. 2010). In the wild, long-distance movements (>25 km) by a few individuals have been documented in mark–recapture studies using visible implant elastomer (VIE) tagged-RGSM (Platania et al. 2020). Additionally, Archdeacon et al. (2018) visually observed the upstream dispersal of juvenile PBS species on multiple occasions. However, these observations were not part of systematic research, were not replicated over time, occurred over limited spatiotemporal scales, and do not appreciably inform our understanding of population-wide movement dynamics. Insight into how the unique life history and reproductive mode of RGSM relates to movement ecology can help scale future recovery efforts and increase our understanding of the space-use of small-bodied fishes in modified riverscapes.

In this study, we capitalized on the ability to use large numbers of tagged, hatchery-reared RGSM coupled with redetection efforts across broad spatiotemporal scales (days-years; 10^2-10^5 m; Fausch et al. 2002) to explore and better understand RGSM movement patterns. Our goal was to quantify movement of RGSM and identify relationships between these patterns and environmental variables. Additionally, we assessed how well prevailing movement theories explained RGSM movement patterns (RMP, CCH, DP). We hypothesized that RGSM movement would be greater than expected under the RMP because of previously observed long distance movements (Platania et al. 2020). If the CCH explains RGSM movement patterns, movement should be biased in an upstream direction to counteract the downstream drift of propagules. Given the unique reproductive mode of RGSM, we further hypothesized there would be a strong positive relationship between its movement distances and increased spring runoff flows that preceded spawning.

MATERIALS AND METHODS

Study Area

The Rio Grande originates in the San Juan Mountains of southern Colorado, draining over 550,000 km^2 in the United States and Mexico (Patiño-Gomez et al. 2007). The fourth longest river in the United States, the Rio Grande runs ~3040 km from southern Colorado, southward through New Mexico, before reaching its confluence with the Pecos River and forming the international border between Texas and Mexico. We conducted our study along two reaches of the Rio Grande located within the Rio Grande Valley in central New Mexico (Figure 2-1). The Middle Rio Grande (hereafter referred to as “MRG”) flows about 330 river km between the upstream impoundment of Cochiti Dam and downstream into Elephant Butte Reservoir (Richard and Julien 2003). Historically, the MRG was a wide, braided, aggrading system with sandy substrate and expansive floodplains and wetlands during periods of high flow (Scurlock 1998; Mortensen et al. 2019). The contemporary MRG has a highly modified flow regime and dries frequently, with current annual water volume of northern reaches estimated to be 95% lower than historical volume (Blythe and Schmidt 2018). Diversion dams along the MRG divert water into a complex system of ditches, drains, and conveyance canals, facilitating extensive irrigation throughout the MRG valley.

Diversion dams delineate the MRG into four reaches (*upstream to downstream*): Cochiti (36.2 river km), Angostura (65.6 river km), Isleta (85.5 river km), and San Acacia (102.3 river km). Our study area was limited to the three lowermost reaches, spanning about 300 river km from Cochiti Dam to Elephant Butte Reservoir. The length of the San Acacia reach varies based on the water level of the reservoir. The MRG in the Angostura, Isleta, and San Acacia reaches is primarily shallow with sand substrates. An inflatable-bladder dam (Alameda Diversion) within the Angostura reach incorporates a fish bypass structure. Long-term population monitoring occurs across these three reaches within the MRG, and the highest abundance of RGSM is often within the San Acacia reach (Dudley et al. 2022). A large portion (~90%) of the San Acacia reach is designated as critical habitat for RGSM (U.S. Department of Interior 2003).

Fish tagging and release

The U.S. Fish and Wildlife Service’s Southwestern Native Aquatic Resources Recovery Center, Dexter, New Mexico and Albuquerque BioPark Aquatic Conservation Facility provided hatchery-reared RGSM used in this study. Fish from the Aquatic Conservation Facility were age-5 brood-stock originally collected as eggs and tagged at the New Mexico Interstate Stream Commission Los Lunas Silvery Minnow Refugium (n = 1,701). Fish provided by the U.S. Fish & Wildlife Service were age–1 and tagged at the Southwestern Native Aquatic Resources and Recovery Center (n = 36,649). We surgically implanted fish with a Passive Integrated Transponder (PIT) tag (Biomark Model TX1411SST; 134.2 kHz, 12.50 x 2.07 mm, 0.102 g) following methods outlined in Archdeacon et al. (2009). We tagged hatchery-reared RGSM greater than ~50 mm standard length (SL). In addition to PIT tag identification codes, we recorded age-class and SL of each fish during tagging. Then, we placed tagged RGSM into recovery tanks immediately after tag implantation and held them for a minimum of two weeks prior to release to remove fish that died or lost their tag. We excluded individuals in poor condition from release. Between 2018 and 2022, we released eight batches of PIT-tagged RGSM (Table 2-1). Release locations were selected based on truck access as well as proximity to diversion dams.

Fish detection

We used semi-permanent submersible, floating raft-mounted, and mobile wand antennas to detect tagged RGSM. We installed multiple semi-permanent submersible PIT tag antennas (Biomark; Boise, Idaho, USA, two sizes: 0.91 m and 1.8 m diameter) in the river channel that detect tags as fish swim or drift over an antenna. The 0.91 m antennas had a read range of 31–45 cm and the 1.8 m antennas had a read range of 45–94 cm. We maintained antennas in the river throughout the study period. Occasionally, we removed and relocated antennas due to placement and maintenance logistics. On average, there were 11–20 antennas deployed at any given time (submersibles were deployed in 2019 [n = 20], 2020 [n = 20], 2021 [n = 11], and 2022 [n = 11]).

We also searched for tagged RGSM using floating Passive Integrated Transponder Portable Antenna SystemS (PITPASS) with raft-mounted antennas (Stout et al. 2020). The PITPASS system consists of floating antenna modules, a multiplexer, battery power supply, an integrated Global Positioning System (GPS), and a data recorder. The PITPASS system had a read range of 76–101 cm which is ideally suited for shallow river channels like that of the MRG. We simultaneously launched three PITPASS equipped rafts (each with 6 m of antenna coverage) at the same location, making multiple passes during each sampling trip (n = 2–5 passes of each stretch per float). We considered active detection within a river section, typically in one day, to be one pass. Each raft covered a distinct section of the river channel: river right, center channel, or river left. The duration of trips and river extent sampled varied based on flow and river access, ranging 2–12 days. We conducted multiple active detection trips in 2019, 2021, and 2022, including initial trips within 5 days following fish releases, (Table 2-2). We did not conduct active detection in 2018, and our efforts in 2020 were limited to one active detection trip by the COVID-19 pandemic. Given summer low flows and intermittency in the MRG, low-velocity habitats (e.g., backwaters) were not always accessible by raft. In those habitats, we used portable PIT tag antennas (wands), to actively sample for RGSM. We also used wands to search for PIT-tagged fish during periods of river drying during summer 2021.

Movement metrics and potential correlates

We calculated movement metrics for individuals with at least one movement (i.e., two detections after release). To account for the typical life span of hatchery-reared RGSM (generally < 12 months after release; Yackulic et al. 2022) and reduce the effects of ‘ghost tags’ (e.g., Stout et al. 2019), we limited analyses to detections that occurred within 365 days of a fish being released. We used ArcGIS Pro to round detection locations (within 0.1 km) of the sampled river network to allow calculation of movement distances between detections and facilitate calculation of movement metrics (Figure 2-1). To describe RGSM movements, we calculated several metrics including: total distance moved, net distance moved, and home range size. We calculated total distance moved as the sum of the distances between all successive detection locations regardless of direction (upstream or downstream), treating the first detection after release as the starting point. We also tested the distribution of the total distance moved metric for skewness and kurtosis. We calculated net distance moved as the net displacement between the first detection location after release and last detection location for each individual both across seasons and for each season separately. We also classified net distance moved as being in either the upstream or downstream direction. Finally, for linear home range size, we calculated the distance between the most downstream and most upstream detection (100% home range; Crook 2004), which represents the total linear extent of the riverscape used over the course of one year. We also calculated total distance moved by season. We defined season as either "off" or "irrigation", based on the operational months of the MRG irrigation system. The irrigation system is operational from March to October and off from November to February. The early irrigation season coincides with peak spring runoff from March to June, and the late irrigation season coincides with increased irrigation demands and subsequent river drying from July to October. All data manipulation and analyses were performed using R version 4.1.2 (R Core Team 2022).

We related spatiotemporal variation in movement patterns to biological and environmental covariates. We calculated the total distances moved by season, which includes zeros for individuals detected multiple (>2) times at the same location within a season (i.e., not moving) and positive values for all other individuals within a season (i.e., moving). Because seasonal movement data were positive-only, continuous, and contained many zeros, we first modeled the probability of movement (δ) and the probability of no movement ($1-\delta$), and then modeled the positive total distances moved. We used a binomial logistic regression with zeros and nonzeros as the response variable (i.e., did fish move?) and a zero-truncated lognormal model with the log-transformed positive total distances moved as the response variable (i.e., how far did fish move?). We included year detected (categorical), cumulative days at large (continuous), mean daily cfs (continuous), body length at release (SL mm; continuous), and the interaction between season (categorical) and release location (above or below San Acacia Diversion Dam; categorical) as fixed effects in the model, with individual PIT tag ID included as a random effect. We calculated cumulative days at large as the number of days between the first and last detection occasion for each individual within a season. We calculated the mean daily cfs for the corresponding days an individual was at large within each season. We used USGS gage data from San Acacia (USGS 08354900) to calculate cfs metrics (USGS 2023). We screened all covariates for multicollinearity and found minimal correlations between covariates included in the models (all VIF < 5). Finally, we ensured model assumptions were reasonably met by inspecting residual plots.

Restricted Movement Paradigm

We used the total distance moved metric in the R package ‘fishmove’ to test the hypothesis that RGSM would move farther distances than expected under the RMP (Radinger and Wolter 2014; R Core Team 2022). This function predicts the average distance moved for the stationary and mobile component of a population using a multiple regression with body length, caudal fin aspect ratio ($A = \text{height}^2/\text{surface area}$), stream order, and time as predictor variables. We parameterized the expected movement model with the mean body length (TL mm; estimated from SL mm using a formula developed by Horwitz et al. 2018) of tagged individuals, the stream order of the Middle Rio Grande (7th order), caudal fin aspect ratio reported in the literature (Bestgen and Propst 1996), and the mean number of days between release date and date of last detection for individuals in our study. We fit a double normal distribution to our observed total distances moved by individual RGSM by year to estimate the distances moved by the stationary and mobile components. We then assessed whether our observed movement distances fell within the 95% confidence intervals of the expected movements from the RMP model.

Colonization Cycle Hypothesis

To test if RGSM exhibited upstream movement bias expected by the CCH, we used a two-way analysis of variance (ANOVA). We used net distance moved as the response variable and included the additive effects of season and year and their interactive effect. We also calculated effect sizes (η^2) for each term in the model. We excluded fish released in 2018 due to the limited sample size and fish released in 2022 because we did not conduct sampling after May 2022.

RESULTS

We successfully encompassed a large portion (70%) of the MRG in our detection locations, spanning 176 km of river fragmented by two diversion dams. The majority of detections were made by submersible antennas (n = 79,505), which were operated nearly continuously throughout the study, followed by floating antennas (n = 12,771). Based on the number of detections by habitat type, adults occupied habitats with moderate velocity and occurred predominantly in shoreline and main channel runs; however, submersible antennas predominately sampled shoreline runs due to placement and maintenance logistics (Figure A-1). Of the 37,215 PIT-tagged RGSM released between 2018 and 2022, 13,706 unique PIT tags were detected at least twice after release; a 36% resight rate. Forty-eight percent of detections occurred within the first two months following a release. Fish were at large in the study system for an average of 25 days (with a range of 15–365 days). Throughout the study period, 57% of all detections occurred within 15 km below San Acacia Diversion Dam (54% of all fish released were released within 15 km below San Acacia Diversion Dam).

Movement metrics and potential correlates

The distribution of total distances moved was leptokurtic and highly skewed (kurtosis = 8.8, $z = 85.9$, $P < 0.001$). A total of 64 individuals moved over 100 km within one year of release, and a total of 30% of individuals in the study moved farther than the mean total distance of 10.4 km. The maximum total distance moved was 103.0 km (Figure 2-2). The mean total distance moved was 19.8 km for individuals moving upstream and 15.2 km for individuals moving downstream. The mean total distance moved was 1.8 km during the off season and 1.5 km during irrigation season. The highest maximum total distance moved by season occurred in the off season; however, the distributions of the metric greatly overlapped between both the irrigation and off seasons (Figure 2-3).

The mean linear home range size of individuals in our study was 2.4 km, and the maximum was 78.2 km (Figure 2-4). On average, tagged RGSM utilized 21% of the study area, and individuals with the largest linear home ranges utilized 44% of the study area. The individual with the largest linear home range also had the largest total distance moved. Individuals in our study had larger total distances moved than their 100% linear home ranges, suggesting RGSM are moving at much finer scales within their 100% linear home range.

Statistically significant covariates (all $P < 0.001$) in the binomial logistic regression model assessing biological and environmental factors that may prompt changes in whether an individual had a zero or nonzero total distance moved by season included mean daily cfs, cumulative days at large, year detected, and the interaction between release location and season (Figure 2-5). Cumulative days at large ($\beta = 3.49$, SE = 0.18) and mean daily cfs ($\beta = 2.54$, SE = 0.19) had a positive relationship with probability of an individual having a nonzero total distance move by season. Individuals released below the dam had a higher probability than those released above the dam of having a nonzero total distance move in both irrigation and off seasons (Figure 2-6).

Statistically significant covariates (all $P < 0.001$) in the zero-truncated lognormal model assessing the positive total distances moved by season included mean daily cfs, cumulative days at large, body length at release, year detected, and the interaction between release location and season (Figure 2-5). Individuals released below the dam had a higher total distance moved in the off season, while individuals released above the dam had a higher total distance moved in the irrigation season (Figure 2-7).

Restricted Movement Paradigm

Individuals in our study moved at least an order of magnitude greater than expected under the RMP across all years (Table 2-3). The fitted mean (95% confidence interval) expected movement distances of the stationary and mobile component of the population were 0.005 km (0.002–0.011) and 0.073 km (0.067–0.794), respectively. The double normal distribution fitted to the observed data across all years produced movement distance estimates of 0.2 and 21.2 km for the stationary and mobile components, respectively.

Colonization Cycle Hypothesis

Movement patterns of RGSM were not explained by the CCH. We found no evidence of upstream bias in RGSM movement (Figure 2-8). The maximum distance moved downstream was 72.5 km, and the maximum distance moved upstream was 48.8 km. Tag movements were generally directed downstream, with 74% of all detected movements directed downstream (67,205 downstream directed movements and 19,198 upstream directed movements; Table 2-4). There was a statistically significant interaction between season and year ($F = 12.69$, $df = 4$, $P < 0.001$); although, our power to detect differences was large ($n = 11,775$) and effect sizes for all terms in the model were small (all $\eta^2 < 0.001$; Table 2-5). Net distances moved were generally farther in the downstream direction, and the frequency of downstream movements were consistently larger across years and seasons.

DISCUSSION

We used a combination of passive and active PIT tag antennas, along with the ability to tag and release large numbers of hatchery-reared fish, to robustly quantify movement of adult RGSM. Quantifying movement patterns of small-bodied fishes in medium to large riverscapes is logistically challenging for several reasons, including limitations on the ability to tag small fishes, acquiring re-encounter rates to adequately describe movement patterns, and the dynamic nature of lotic ecosystems, among others. Our approach was effective as indicated by our relatively high redetection rate, and could prove effective for other studies in larger, open systems. Additionally, the data presented build upon emerging narratives regarding the movement ecology of PBS fishes and advance our ability to test movement theories in poorly understood species. The observed patterns of RGSM movement in this study do not follow the expectations under the RMP or the CCH, and suggest a drift paradox, like patterns observed in other studies on PBS fishes (e.g., Platania et al. 2020; Steffensmeier et al. 2022).

Our results support the ability and predilection of some RGSM to make long-distance movements, matching results documented in other PBS fishes (Walters et al. 2014; Ruppel et al. 2020; Steffensmeier et al. 2022). For example, a mark-recapture study of Flathead Chub (*Platygobio gracilis*) documented upstream movements up to 33 km, with farther upstream movement blocked by a dam (Walters et al. 2014). Previous studies reported movement of considerable distances upstream by RGSM (25.2 km; Platania et al. 2020), and our results substantiate these observations of a few individuals. We documented RGSM moving farther upstream than previously recorded (48 km), and this was not limited to a few individuals.

Rio Grande Silvery Minnow demonstrated a leptokurtic movement distribution, with most individuals remaining near their initial release site (< 10 km), and a smaller portion of individuals making longer distance movements (> 100 km). This heterogeneous movement distribution is well documented in many other fish species (Radinger and Wolter 2014). Pelagic-broadcast spawning minnows move substantially more than predicted by the RMP (Steffensmeier et al. 2022, this study). The model developed by Radinger and Wolter (2014) has been used in other studies to predict expected dispersal of stream fishes (e.g., Troia et al. 2019; De Fries et al. 2022), and efforts to incorporate data from recent fish movement studies from more species into the 'fishmove' package model are warranted to ensure dispersal capabilities are not underestimated, particularly for smaller bodied fishes.

The CCH suggests organisms that experience downstream drift must compensate with upstream dispersal to maintain upstream populations. Early work suggested movements should be biased in an upstream direction (Müller 1982), but later work built on simulations suggested any upstream dispersal component may be sufficient for population persistence (Anholt 1995; Humphries and Ruxton 2002). Movements by RGSM were not as expected under the CCH, with biased upstream dispersal to maintain persistence, as movement patterns were generally skewed downstream. Observations of this behavior in hatchery-reared RGSM are common (Archdeacon and Remshardt 2012; Platania et al. 2020; Archdeacon et al. 2023). When we excluded detections within the first week of release to account for this immediate downstream tendency, movement patterns were largely unchanged, and movements were consistently more often in the downstream direction. This result, along with a reproductive biology involving downstream transport of eggs and larvae, invokes the drift paradox for RGSM persistence.

Resolution of the apparent drift paradox has important management consequences. There are several potential resolutions to the drift paradox in the absence of biased upstream dispersal of adults: (1) random diffusive dispersal with an upstream component by adults sufficient to maintain persistence (Naman et al. 2016), (2) upstream dispersal of younger life-stages (Chase et al. 2015; Archdeacon et al. 2018), (3) drifting eggs and larvae exceed the carry-capacity (e.g., habitat features retain eggs within the natal reach, or (4) a combination of these. Indeed, Chase et al. (2015) determined both retention and upstream movement of juveniles played a role in upstream population persistence of Pecos Bluntnose Shiner. Historically, drift distances of eggs and larvae were likely much lower (Dudley and Platania 2007). Under contemporary, degraded conditions, appropriate nursery habitats no longer occur except at high flows, resulting in loss of eggs downstream and high variance in reproductive success among individuals (Alò and Turner 2005). Recruitment is minimal during low-flow years (Perkin et al. 2019; Archdeacon et al. 2020), likely leading to negligible density-dependent dispersal. Further, upstream dispersers are blocked by diversion dams, resulting in ecological ratchet mechanisms (Perkin et al. 2015), where upstream population segments are extirpated, and downstream segments can no longer supply colonizers.

Each of these resolutions carries distinct management actions. Removal of longitudinal barriers should improve persistence by allowing upstream dispersal, regardless of life stage. If dispersal of juvenile fish is the primary driver of upstream population persistence, maintaining surface flows post-spawning in addition to fish passage will be necessary. Conversely, if persistence is primarily maintained through retention of eggs and larval near natal areas, conservation efforts should focus on restoring floodplain connectivity to improve retention and increase the carrying capacity. Persistence of PBS via upstream dispersal of adults or retention of eggs and larvae has spurred significant debate (Zymonas and Propst 2009; Medley and Shirey 2013); we find it unlikely one occurs to the exclusion of the other given significant collections of larvae in upstream reaches in high-flow years (Valdez et al. 2021) and empirical evidence both occur in the same species at the same point in time (Chase et al. 2015). However, persistence under contemporary flow and channel conditions may now rely more on the extreme upstream dispersers because displacement distances have increased.

Our results indicate RGSM exhibit generally nomadic movement patterns as adults, common among animals in systems with high inter-annual environmental variability (Teitelbaum and Mueller 2019). Historically, PBS minnows persisted through extreme environmental variation and were often subjected to extended periods of intense drought (Hoagstrom 2015; Worthington et al. 2018). This historical persistence likely required access to refugia during periods of drying and subsequent connectivity to allow recolonization of extirpated reaches. In contemporary riverscapes, many PBS fishes have suffered expansive range reductions because of the ratcheting effect of fragmentation and stream drying (Perkin et al. 2015). The nomadic movement patterns and ability to move long-distances documented in our study, combined with high reproductive effort and relatively short generation times suggest RGSM would be able to recolonize habitats over relatively short temporal scales.

The individuals with the largest home ranges were not those with the farthest total distance moved, indicating individuals who tend to actively move among locations (i.e., antennae) are not necessarily regularly travelling across large distances over time. Instream barriers artificially restrict movement for fishes and might even increase residency within populations over time (e.g., Branco et al. 2017). The upstream- or downstream-most detection point used to calculate linear home range sizes was frequently located within +/- 5 km of San Acacia Diversion Dam. Additionally, the significant interaction ($P < 0.001$) between season and whether an individual was released above or below the dam in both movement correlates models suggests the presence of barriers certainly reduces the extent of movement for many individual RGSM. We were surprised to document 198 unique upstream passages through the slightly open gates at the San Acacia Diversion Dam, with most upstream passages (n = 129) occurring during irrigation season (Figure A-2). Prior to our study, upstream passage through San Acacia Diversion Dam by RGSM had not been documented. Although these upstream dam passages are impressive, and reflect the predilection of RGSM to move upstream, they account for < 0.5% of the total number of individuals released in the study. Increasing connectivity by providing more efficient passage around barriers and ensuring adequate river flows during irrigation season would likely allow for fish to expand their home ranges and recolonize upstream habitats.

We acknowledge several limitations of the study. First, the behavior of hatchery-reared fish might not fully reflect that of wild RGSM; however, hatchery-reared fish are first generation offspring of brood-stock wild-caught eggs. After initial stocking mortality, hatchery-reared

RGSM survival is similar to wild fish (Yackulic et al. 2022). Further, hatchery-reared fish are often found in the same isolated pools as wild fish (Archdeacon 2023), suggesting similar behaviors. Second, our detection efforts were limited to tracking the movements of adult fish >45 mm SL. Future research including a broader range of fish ages and sizes may elucidate movement patterns undocumented in our study. It is possible that juvenile fish may be more likely to disperse upstream than adults, as documented in Pecos Bluntnose Shiner (*Notropis simus pecosensis*) in the Pecos River (Chase et al. 2015). Increased body size has been associated with the ability to maintain swimming position in the river channel and move upstream (Ward et al. 2003). As our study included RGSM in the upper ranges of the species' size potential, and body size was not a strong indicator of movement potential, we argue that body size is unlikely to be a strong driving factor in movement patterns for this species.

Flow conditions were also extremely variable throughout our study period, with record high discharge in 2019 contrasted by extended low discharge the following year (USGS 08354900). Mean daily discharge was positively related to the probability of movement in the binary logistic regression, suggesting increased flows are a strong indicator of movement patterns. Although we did observe a weakly negative relationship between mean daily cfs and the total distances moved by season in the zero-truncated lognormal model, movement distances calculated from detections on days with the highest mean discharge (> 3,000 cfs) occurred in the lowest reaches of the study area. As such, it is likely these individuals were flushed downstream, outside of the detection area. Individual behavioral responses, rather than swimming ability, have been ascribed to the persistence of fishes under extreme variations in flow (Leavy and Bonner 2009). Future detection efforts across a longer period, and under a larger variation in flow conditions, may provide additional insight into the relationship between individual movement patterns and variations in flow magnitude.

Prior to this study, most information available on hatchery-reared RGSM was based on Visual Implant Elastomer (VIE) marked individuals, and recapture rates in VIE marked hatchery-reared RGSM were extremely low (< 0.5%) in recent years (Archdeacon et al. 2023). The use of PIT tags in RGSM alleviates the shortcomings of VIE marking, as it does not require physical recapture, and provides unique individual IDs. The relatively short life span of RGSM (i.e., known fate tag status) allowed for less complicated analyses, and eliminated one of the common hurdles in mark-recapture studies (Stout et al. 2020). Given the short life span of RGSM, we were able to simply censor detections out of our analyses at the time the fish should be deceased, minimizing the complications of accounting for ‘ghost’ tags (Stout et al. 2019). Notably, the amount of time a PIT tag stays in a system may be highly dependent on the flow and velocity of the release location (Stout et al. 2019). Interestingly, we detected a total of 14 unique PIT tags on the May 2022 float trip that had been released in 2009 and 2010 in RGSM. Two tags were detected in a backwater with very little flow, raising the question of how quickly shed and deceased PIT tags are buried by sediment or carried downstream by flow events (Stout et al. 2019). Unlike GPS collars frequently used in mammal movement studies, PIT tags do not emit locations on regular time intervals and are dependent upon the locations and quantity of antennas.

Incorporating knowledge of movement patterns in the management of imperiled species may be crucial for their recovery in highly modified and degraded river systems. Occupying just 5% of its historical range, knowledge that RGSM make long distance movements and have the predilection to move upstream, a movement pattern blocked by diversion dams in many cases, highlights the importance of connectivity and unfragmented river stretches in the persistence of PBS fishes (Perkin and Gido 2011; Walters et al. 2014; Pennock et al. 2017). Given the widespread fragmentation of rivers, this research could serve as an important model that can be applied to imperiled small-bodied fishes in other fragmented systems. A greater understanding of how fishes are using fragmented rivers and their abilities to recolonize habitats can help guide future recovery efforts of riverscapes to ultimately achieve self-sustaining populations of native fishes.

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TABLES AND FIGURES

Table 2-1. Rio Grande Silvery Minnow released between 2018 and 2022 in the Middle Rio Grande of New Mexico, USA showing the year and month released, release location (rkm), and the number of PIT-tagged individuals released.

Year	Month	Release location (rkm)	Number released
2018	May	186.0	196
2018	Jul	186.0	540
2019	Mar	180.9, 182.9, 186.0, 191.5	1,701
2019	Nov	180.9, 182.9, 186.0, 191.5	9,875
2020	Mar	180.9, 182.9, 186.0, 191.5	7,916
2021	Mar	139.4, 166.2, 183.0, 191.5, 211.1	4,865
2021	Dec	183.1, 191.5, 227.4, 250.9	9,131
2022	Mar	191.5, 227.4, 248.6	2,991
Total			37,215

Table 2-2. Float trips conducted in the Middle Rio Grande of New Mexico, USA by year, showing the dates and extent (rkm) of each float trip. Active float trips spanned 170.5 km of the Middle Rio Grande.

Year	Date	Range (rkm)
2019	Mar 20–31	123.9–192.6
2019	Jul 16–22	153.2–183.8
2019	Nov 20–25	154.0–191.5
2019	Dec 3–7	134.4–193.1
2020	Dec 8–11	168.0–186.0
2021	Mar 25–27	169.6–257.7
2021	May 16–23	169.3–257.7
2021	Jul 16–17	180.7–186.1
2021	Dec 8–14	170.4–294.4
2022	Mar 14–17	180.9–294.4
2022	May 9–13	180.9–294.4

Table 2-3. Expected and observed distances of stationary and mobile components of the Rio Grande Silvery Minnow population by year produced under the Restricted Movement Paradigm using the R program 'fishmove'.

	Stationary		Mobile	
Year	Expected distance (km)	Observed distance (km)	Expected distance (km)	Observed distance (km)
2019	0.003 (0.001-0.005)	3.0	0.38 (0.24-0.59)	20.5
2020	0.005 (0.003–0.009)	2.3	0.082 (0.055–0.123)	21.8
2021	0.003 (0.001–0.005)	1.1	0.038 (0.024–0.059)	9.8
2022	0.005 (0.003–0.009)	1.3	0.083 (0.055–0.125)	9.8

We parametized the model with the median length (mm TL) and median number of days at large for individuals by year: (83.7 mm TL and 20 days in 2019; 79.9 mm TL and 92 days in 2020; 76.9 mm TL and 25 days in 2021; 77.6 mm TL and 102 days in 2022)

Table 2-4. Summary statistics of annual net movement detections of Rio Grande Silvery Minnow between 2019 and 2021 by direction.

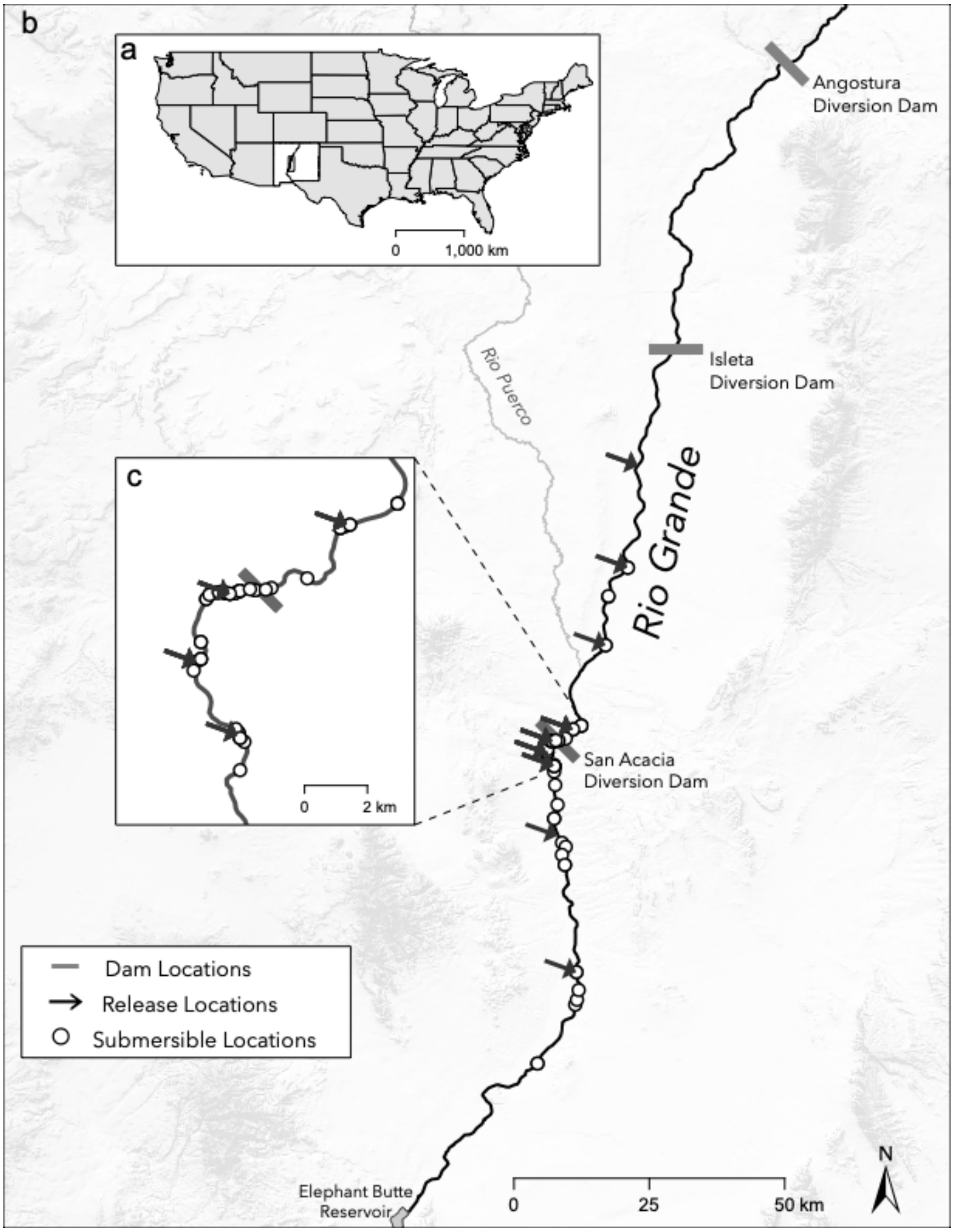
Year	Direction	Count	Mean	SD	Median
2019	Downstream	4,045	4.81	6.92	2.90
	Upstream	1,278	2.24	4.25	1.04
2020	Downstream	3,438	9.15	13.70	4.27
	Upstream	2,017	4.59	7.85	1.69
2021	Downstream	560	4.71	7.30	2.89
	Upstream	437	2.80	6.75	0.08

Table 2-5. Results of two-way ANOVA for net distance moved upstream and downstream by Rio Grande Silvery Minnow by year and season (n = 11,775).

	F-statistic	*P*-value	*df*	η^2
Season	0.37	0.6889	2	<0.001
Year	29.93	<0.001	2	<0.001
Season:Year	12.68	<0.001	4	<0.001

Figure 2-1.

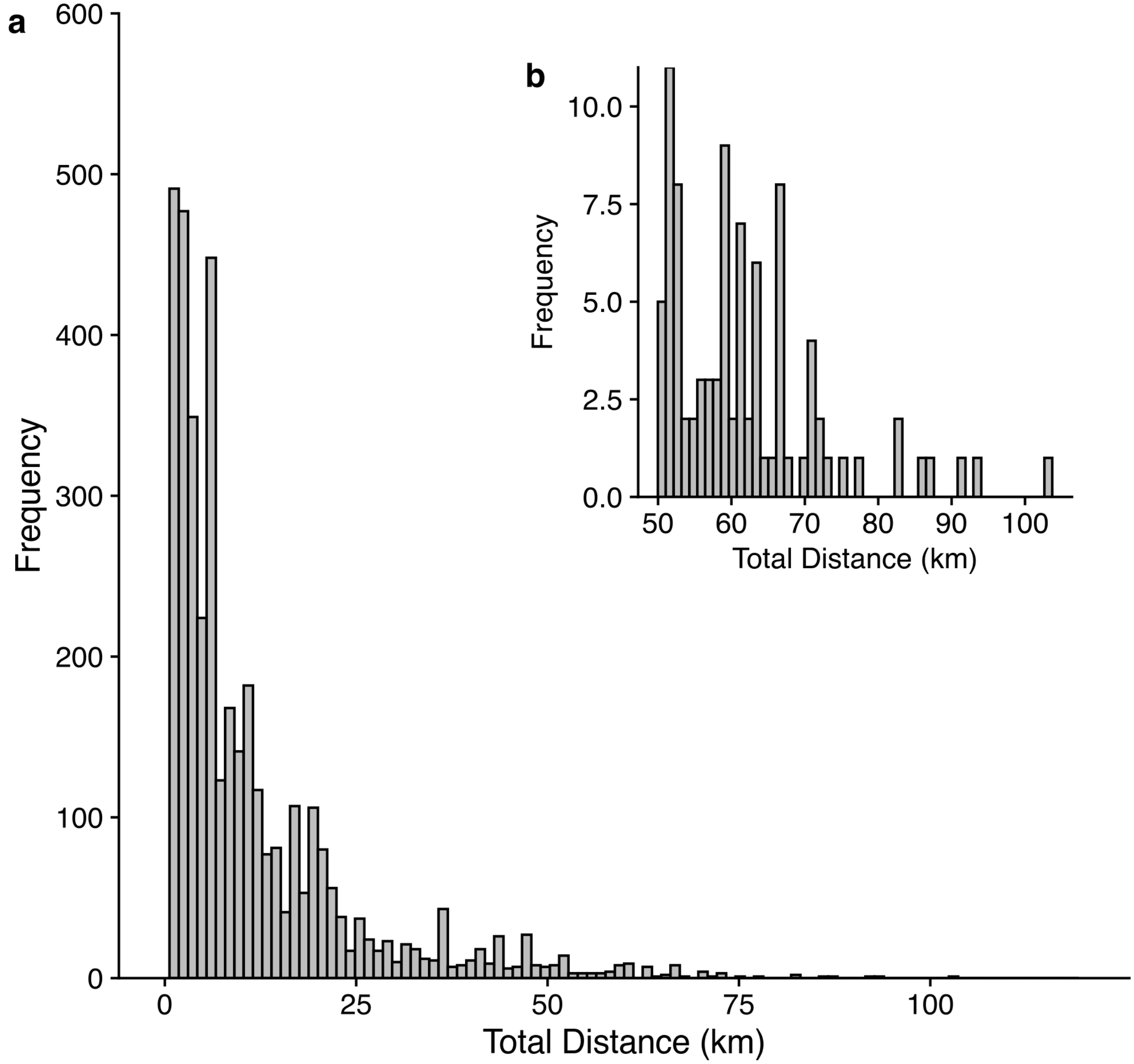
Map of Study Area Within Middle Rio Grande



Note. Map of study area within Middle Rio Grande, showing locations of fish releases and locations of submersible antennas (b), with San Acacia Diversion Dam zoomed within the left center box (c).

Figure 2-2.

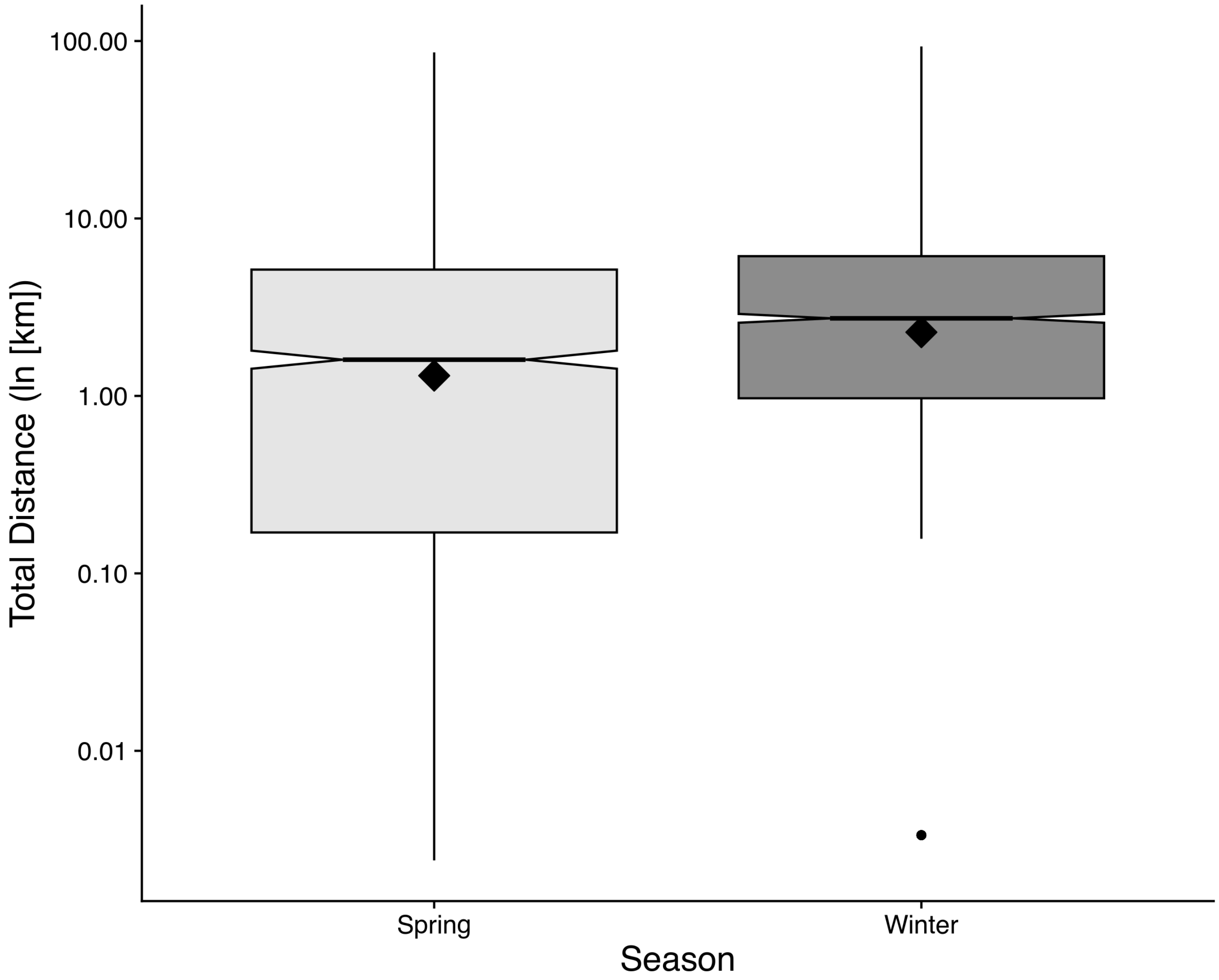
Total Distance Moved by PIT-Tagged Rio Grande Silvery Minnow



Note. Total distance moved (absolute value), both upstream and downstream, by PIT-tagged Rio Grande Silvery Minnow in the Middle Rio Grande from 2018 to 2022 (panel **a**). To show the few individuals making longer distance movements, panel **b** is zoomed in, including individuals with a total distance moved >50 km. The distribution of total distances moved was leptokurtic (kurtosis = 8.78, z = 85.99, *P* <0.01), with a smaller number of individuals moving farther distances.

Figure 2-3.

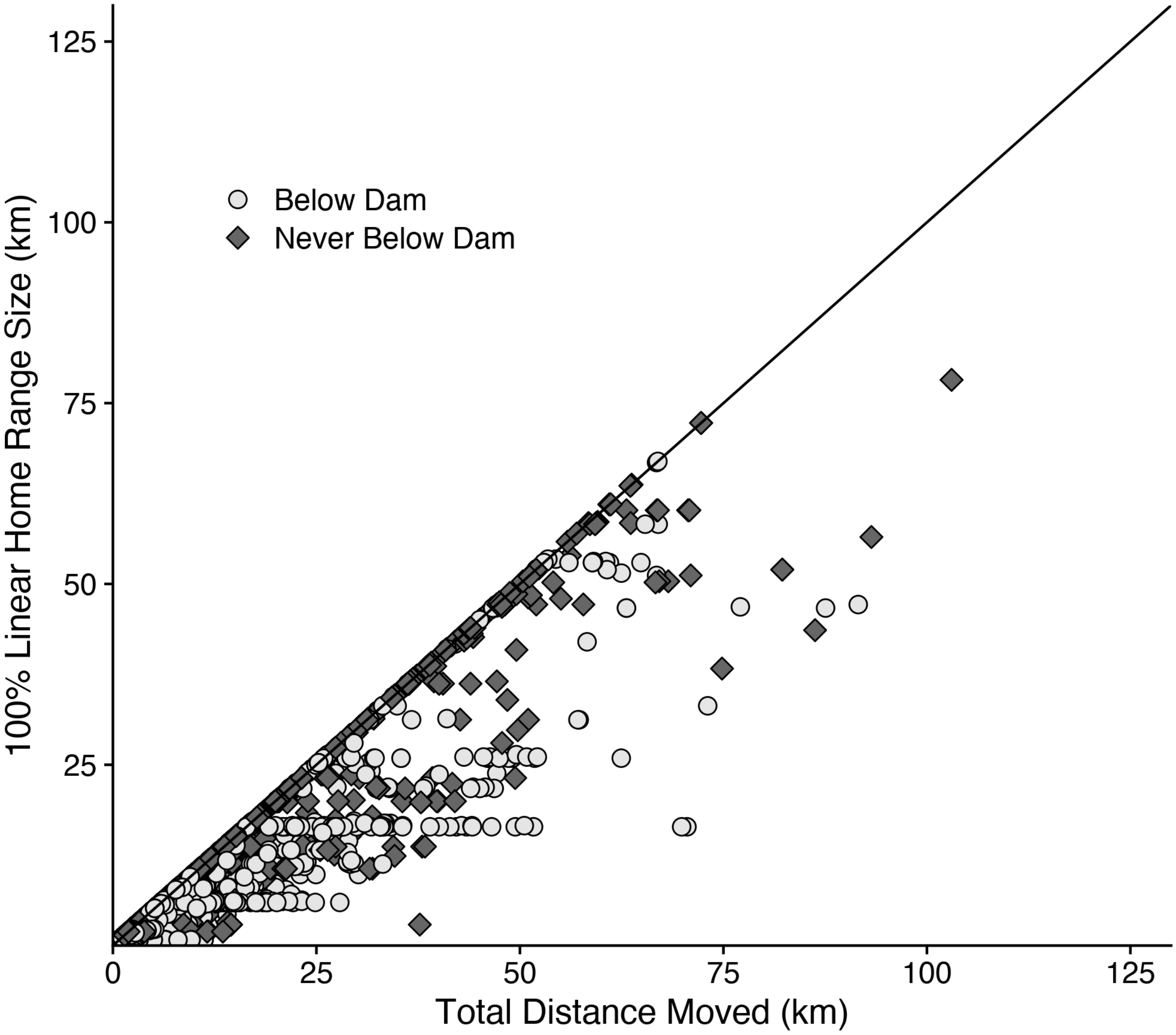
Total Distance Moved by PIT-Tagged Rio Grande Silvery Minnow by Season



Note. Total distance moved (km, log-10 scale) by PIT-tagged Rio Grande Silvery Minnow in the Middle Rio Grande on the y-axis by season (Irrigation = March–October; Off = November–February) on the x-axis, with the black diamonds representing the mean total distance moved (km) by season. Each box displays the interquartile range with the bold line representing the median total distance moved (km), and error bars representing the minimum and maximum total distance moved (km). The mean total distance moved was 1.5 km in the irrigation season and 1.8 km in the off season. The greatest maximum total distance moved by season occurred in the off season; however, the distributions of distances in both seasons greatly overlap.

Figure 2-4.

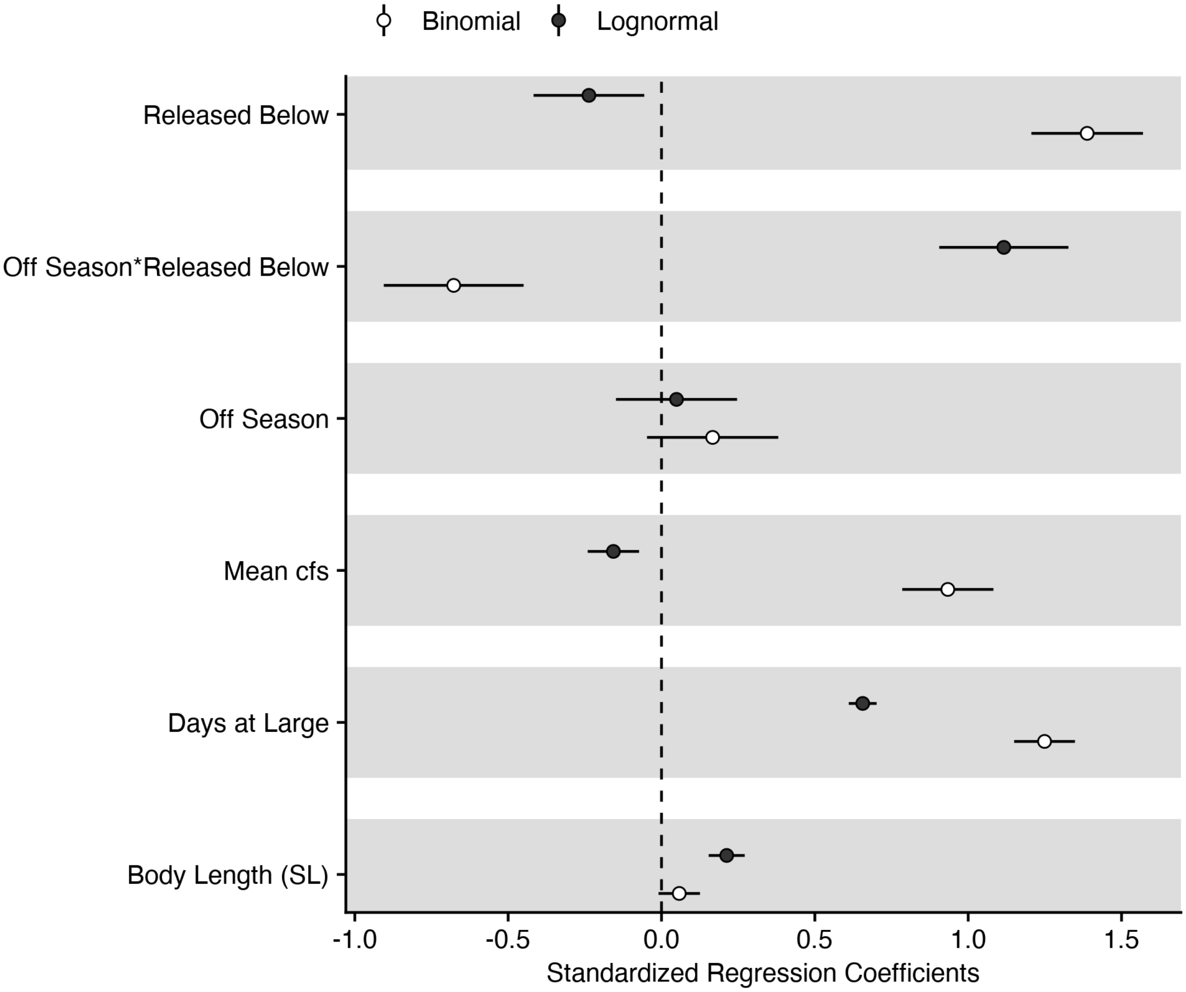
Total Distance Moved by 100% Linear Home Range of Rio Grande Silvery Minnow



Note. Total distance moved (km) by 100% linear home range size (km) of Rio Grande Silvery Minnow between 2018 and 2022 in the middle Rio Grande, with shades of grey representing release location in relation to San Acacia Diversion Dam. The individual with the largest 100% linear home range of 78.2 km moved a total distance of 103.0 km. The line represents 1:1, suggesting the total distance moved is sometimes notably larger than home range size.

Figure 2-5.

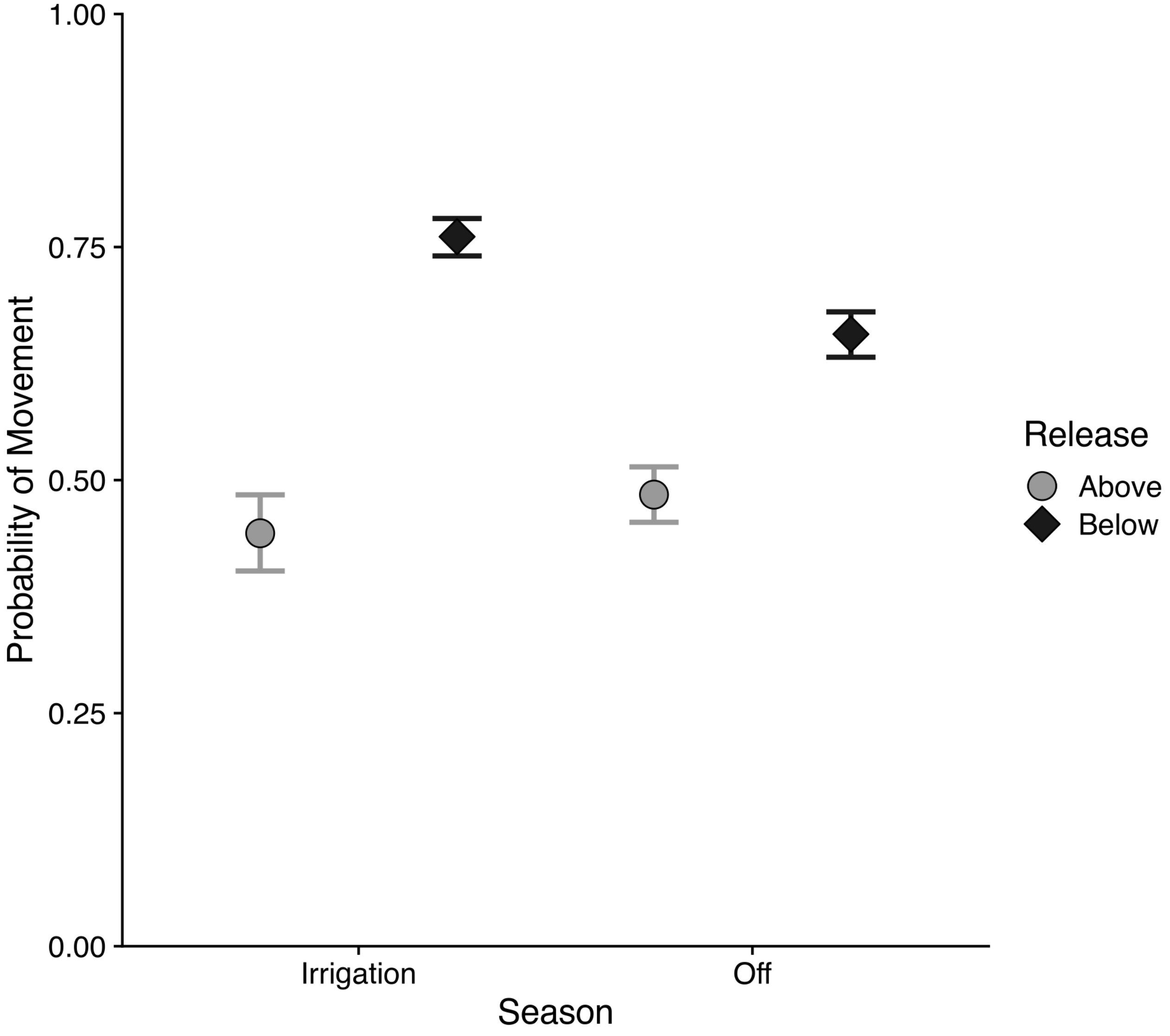
Covariates Included in Binomial Logistic Regression and Zero-Truncated Model



Note. Covariates included in the binomial logistic regression and zero-truncated lognormal model assessing variation in Rio Grande Silvery Minnow movement patterns by season on the y-axis and standardized regression coefficients on the x-axis, with shade representing model and horizontal bars showing the 95% confidence interval. The number of cumulative days at large and the interaction between season and release location (above or below San Acacia Diversion Dam) were significant effects ($P < 0.001$) in both models.

Figure 2-6.

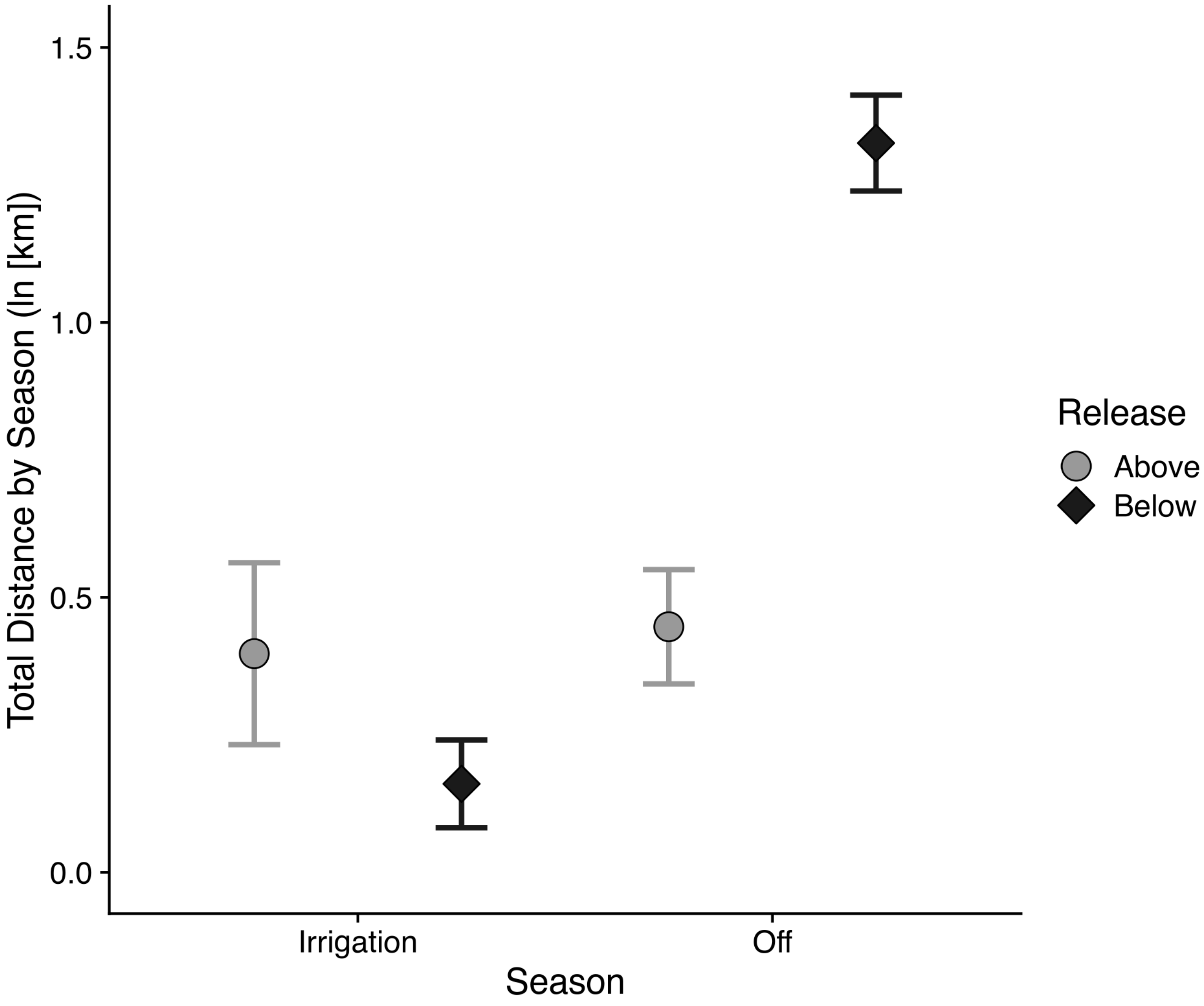
Significant Interaction Produced by Binomial Logistic Regression



Note. Significant interaction between season and release location (above or below San Acacia Diversion Dam) produced by binomial logistic regression with probability of movement (0 = no movement; 1 = movement) on the y-axis and season on the x-axis, with shaded shapes corresponding to release location and error bars representing the 95% confidence interval. The interaction between season and release location ($\beta = 0.51$, SE = 0.06) was a significant indicator of movement ($P < 0.001$), with individuals released below the dam having higher probabilities of movement in both irrigation and off season.

Figure 2-7.

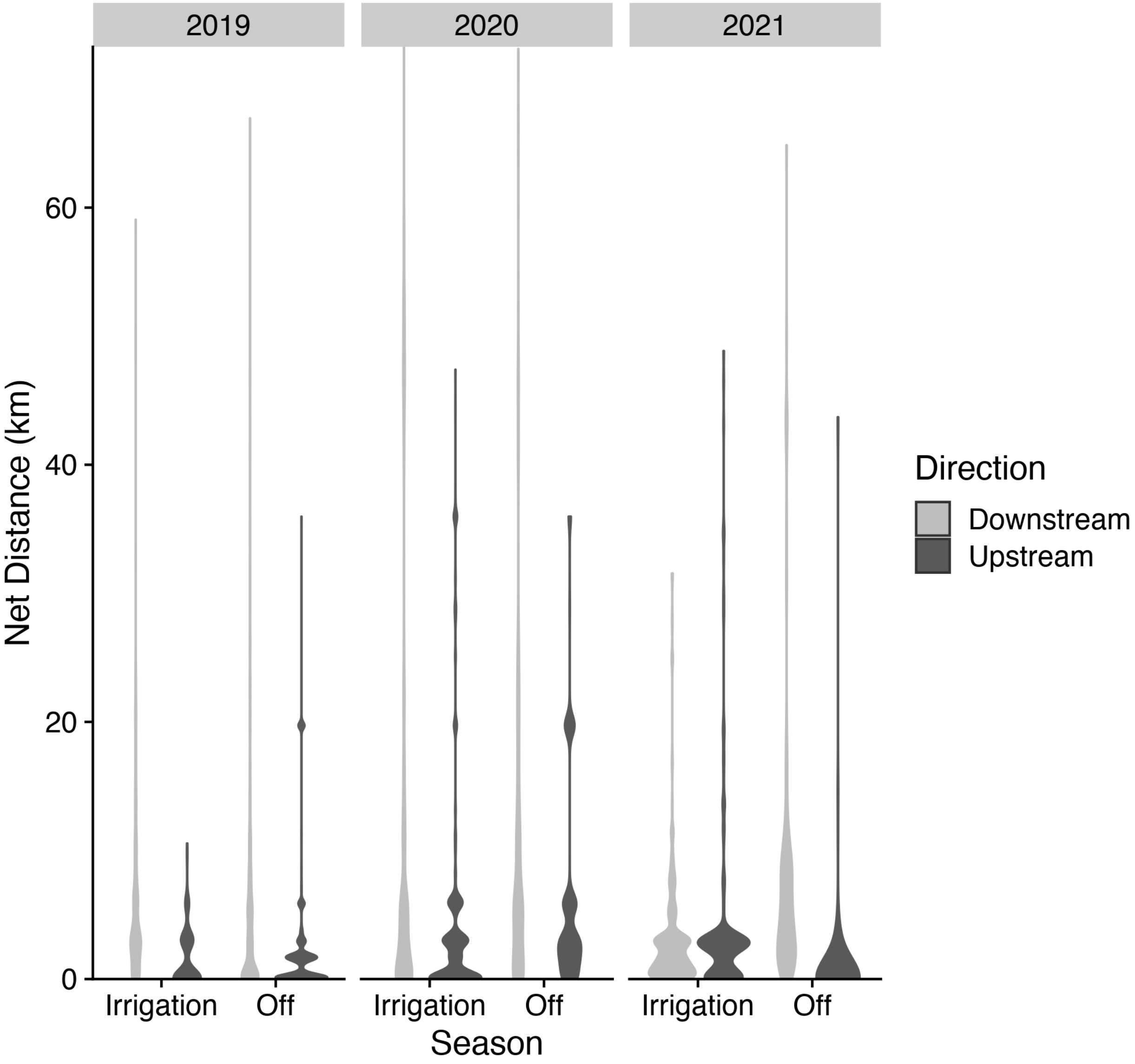
Significant Interaction Produced by Zero-Truncated Model



Note. Significant interaction between season and release location (above or below San Acacia Diversion Dam) produced by zero-truncated lognormal model assessing the positive total distances moved by season, with log-transformed total distances by season on the y-axis and season on the x-axis, with shaded shapes corresponding to release location and error bars representing the 95% confidence interval. The interaction between season and release location (β = 0.68, SE = 0.07) was a significant indicator of total distances moved (P < 0.001), with individuals released below the dam having larger total distances moved in the off season, and individuals released above the dam having larger total distances moved in the irrigation season.

Figure 2-8.

Net Distance Moved by PIT-Tagged Rio Grande Silvery Minnow



Note. Violin plots of net distance moved downstream or upstream (km; absolute values) by PIT-tagged Rio Grande Silvery Minnow by year and season (Irrigation = March– October; Off = November– February). The width of each violin plot corresponds with data density and frequency of net directional movements. Net distances moved were generally farther in the downstream direction across years and seasons.

CHAPTER 3

QUANTIFYING TRANSITION PROBABILITIES AMONG FRAGMENTED REACHES FOR AN ENDANGERED DESERT MINNOW

ABSTRACT

Insight into the spatial distribution of imperiled small-bodied fish species can be a valuable conservation status assessment tool; however, few studies formerly estimate movement (i.e., transition) probabilities of riverine fish species in fragmented systems in order to guide management. To address this gap, we used Passive Integrated Transponder (PIT) tag data to estimate transition probabilities and characterize reach-specific, movement potential of a federally endangered minnow in the American Southwest. The Rio Grande Silvery Minnow (*Hybognathus amarus*, RGSM) occurs in a highly modified stretch of the Middle Rio Grande running through central New Mexico and has declined following widespread fragmentation. We parameterized a Bayesian multistate model using Markov chain Monte Carlo simulation in Program MARK. Overall, RGSM demonstrated higher downstream transition probabilities than upstream; however, individuals released in the winter season had higher upstream transition probabilities than those released in the spring season. Surprisingly, approximately 1.5% of the RGSM in this study transitioned from below to above the San Acacia Diversion Dam, which is not equipped with fish passage. With our results, we revealed reach-specific transition probabilities, characterized spatial dynamics between reaches using estimated movement probabilities, and identified the potential

consequences of transition between reaches depending on release locations and seasonally and irrigation-influenced abiotic conditions. The approach used in this study may have important applications for the management and conservation of riverine fishes in fragmented systems, including evaluating the impact of barriers and fish passage efficiency for other small-bodied fishes.

INTRODUCTION

Riverine systems are some of the most highly modified ecosystems in the world (Poff and Zimmerman 2010). Pervasive anthropogenic alterations of rivers to meet water demands have resulted in extensive habitat degradation, widespread fragmentation, and alarming declines in biodiversity (e.g., Dudgeon et al. 2006, Tickner et al. 2020, Pennock et al. 2022). The freshwater systems in North America contain the highest degree of non-tropical biodiversity on earth, yet 39% of the fish species in these systems were imperiled as of 2008 (Jelks et al. 2008). Furthermore, extinction rates within freshwater ecosystems are projected to accelerate amidst climate change and increasing drought (Poff et al. 1997; Palmer and Ruhi 2019). Understanding the implications of climate and habitat disturbances is crucial to the conservation of biodiversity in fragile aquatic ecosystems.

Riverine ecosystems are connected via physical and biological pathways which facilitate a range of ecological processes. Anthropogenic modifications coupled with an increasingly arid climate have fragmented the linear frameworks of riverine systems in which fish movement occurs (Karatayev et al. 2020). Disturbing the ecological connectivity in an aquatic ecosystem not only limits the extent of individual movement between habitats, but also has the capacity to fundamentally alter meta-population dynamics and change the evolutionary trajectories of species by restricting genetic input and immigration (Allendorf et al. 2013; Rasmussen and Belk 2017). Freshwater fishes require access to a range of habitats in order to complete their life cycle, and the impacts of flow modification and habitat fragmentation on fish species with connectivity-dependent life histories can be particularly devastating (e.g., Yackulic et al. 2022). Despite the important role of fish movement in shaping population and community composition in linear frameworks, few studies explicitly quantify the probability of successfully transitioning between fragmentated reaches and the associated consequences of that movement (Comte and Olden 2018). As such, understanding the individual movements of riverine fish species, particularly those occurring in altered and fragmented systems, may help establish the scales at which future recovery efforts will be most effective.

There are several challenges associated with studying riverine fish movement over ecologically-relevant space and time scales (Ogburn et al. 2017). The propensity for movement within a species can vary among individual fishes, in part, based on body condition and individual behavior (Peterson and Fausch 2003; Villegas-Ríos et al. 2017; Coates et al. 2019). Additionally, the common disparate distribution in movement distances among fishes within a population necessitates a large sample size in order to characterize movement patterns (Comte and Olden 2018, e.g., leptokurtic). The use of Passive Integrated Transponder (PIT) tag and receiver antenna technology alleviates many of the challenges associated with movement studies in riverine fishes (Stout et al. 2020; Zenter et al. 2021). This remote detection methodology is relatively inexpensive and less invasive compared to other tag types (e.g., telemetry), which makes tracking a larger number of individuals in a study more feasible (Stout et al. 2019; Pennock et al. 2020). Furthermore, this technology allows researchers to detect smaller-scale movements with greater accuracy, with floating PIT tag antennas detecting tags at depths up to 1.0 m (Biomark). As movement over relatively small spatial scales is crucial for many fish species, the capacity to detect these movements may yield new insights into fish movement ecology with respect to individual responses within altered habitats (Kanno et al. 2020; Cooke et al. 2022).

Remote detection data can also provide robust individual encounter histories and can be used to obtain mark-recapture estimates of abundance and movement probabilities (e.g., space use, survival, and passage; Rogers and White 2007). However, this method of tracking technology requires tagged individuals to swim within the read range of an antenna in order to be redetected (the location of an individual between antenna detections is unknown, only the locations of the antenna are known), and continuous redetection at set time intervals is not always possible, potentially challenging analyses (Kelly et al. 2017; Saboret et al. 2020). Therefore, the number and locations of antennas must be relative to the movement of an individual. Achieving this level of lateral and longitudinal spatial coverage is rarely possible in aquatic systems, resulting in situations where a fish can go undetected within a stretch of river (Raabe et al. 2014). The use of Bayesian inference in concordance with mark-recapture models can be a useful tool when dealing with inevitable gaps from these empirical data (Lebreton and Cefe 2002; Hostetter et al. 2022). A transition probability estimated with Passive Integrated Antenna (PIA) technology and an appropriate mark-recapture multistate model is a mathematical formalization of an observed movement attempt that incorporates both the probability of resight/recapture and the success of that movement attempt (Calvert et al. 2009).

In this study, we used a mark-recapture approach and multistate models to evaluate the effect of fragmentation on the movement of RGSM. The Rio Grande Silvery Minnow (*Hybognathus amarus*, RGSM) is the only remaining extant pelagic broadcast spawning minnow in the Rio Grande. Listed as federally endangered in 1994, RGSM is now restricted to an estimated 5% of its historical range and occurs in a highly modified and fragmented stretch of river in central New Mexico (Bestgen and Platania 1991; USFWS 1994). The decline of RGSM has largely been attributed to increased fragmentation and a highly regulated flow regime (Dudley and Platania 2007), anthropogenically-exacerbated drought and decreasing spring runoff (Walsworth and Budy 2021), and channel narrowing and desiccation (Swanson et al. 2011; Archdeacon 2016). A suite of management and conservation efforts focusing on the recovery of RGSM, including population monitoring (Dudley et al. 2022), translocations post-river drying (Archdeacon et al. 2022), and regular supplementation of the existing wild population using hatchery-reared fish (Osborne et al. 2020; Archdeacon et al. 2023) have succeeded in staving off RGSM extinction but have not led to a self-sustaining population in the wild. The species is now largely dependent on hatchery supplementation and assisted translocation to mitigate the impacts of advection and increased river drying. Pelagic broadcast spawning minnows, like RGSM, are presumed to require some degree of compensatory upstream movement to offset the downstream displacement of eggs and larvae; however, the current system in which RGSM occurs is highly fragmented by diversion dams, especially in the upstream direction. Until recently, the ecological aspects of RGSM movement patterns between reaches in the Middle Rio Grande had not been widely described (Chapter 2).

Our goals were to 1) quantify reach-specific transition probabilities of RGSM, 2) better understand the role of abiotic conditions controlled by season and irrigation on those transition probabilities and 3) more qualitatively, identify potential consequences of transitions between reaches on the likely persistence of RGSM. To meet these goals, we used RGSM detections from PIT tag data to parameterize a Bayesian multistate model using Markov chain Monte Carlo simulation. In previous work, we quantified the movement ecology and metrics of PIT-tagged RGSM using detection data from 2019 to 2022 and assessed the applicability of existing movement theories to RGSM movement patterns (Chapter 2). The movement metrics quantified in Chapter 2 work in concordance with and fortify the transition estimates of the model developed herein. Due to the vast amount of instream structures affecting the movement potential of small-bodied fishes in riverine systems, as well as the connection between fish movement and population dynamics, this research has the potential to better predict population responses to environmental changes. Such responses define the spatiotemporal scale of conservation efforts, therefore increased accuracy of estimates can guide proper strategic planning for the recovery of a suite of small bodied native fishes.

MATERIALS AND METHODS

Study Area

The Rio Grande flows approximately 3,040 river kilometers (rkm) from the San Juan Mountains of southern Colorado, southward through central New Mexico, before forming the international border between Texas and Mexico. Data in this study was collected in the Middle Rio Grande (MRG), a stretch of the river occurring within the Rio Grande Valley in central New Mexico through Albuquerque (Figure 3-1). The MRG begins below Cochiti Dam and flows approximately 300 rkm until reaching Elephant Butte Reservoir. Characterized by a wide and shallow channel, the MRG has a highly modified flow regime and is fragmented by four diversion dams that delineate the river into four reaches. These diversion structures heavily influence reach-scale geomorphology and hydrology, resulting in varying habitat quality between reaches. The uppermost Cochiti reach spans 36.2 rkm from Cochiti Dam to Angostura Diversion Dam. The Angostura reach is highly urbanized and flows 65.6 rkm from below Angostura Diversion Dam, through Albuquerque, New Mexico, to the Isleta Diversion Dam. The Alameda Diversion dam (inflatable-bladder dam) occurs within the Angostura reach and incorporates a fish bypass structure. The Isleta reach spans 85.5 rkm from Isleta Diversion Dam to San Acacia Diversion Dam. The San Acacia Diversion Dam, located approximately 116 km south of Albuquerque, New Mexico, is the upstream boundary of the longest and lowermost San Acacia Reach. The San Acacia reach flows 102.3 rkm from the San Acacia Diversion Dam to Elephant Butte Reservoir and contains the highest abundance of RGSM (Dudley et al. 2022). The majority (~90%) of the San Acacia reach is designated as critical habitat for the species (U.S. Department of Interior 2003). Detection data included in this study was collected in the three lowermost reaches (Angostura, Isleta, and San Acacia), as RGSM are largely extirpated from the Cochiti reach of MRG (Bestgen and Platania 1991).

Materials

We worked with the U.S. Fish and Wildlife Service’s Southwestern Native Aquatic Resources Recovery Center (SNARRC), Dexter, New Mexico to implant hatchery-reared RGSM with PIT tags (Biomark Model TX1411SST; 134.2 kHz, 12.50 x 2.07 mm, 0.102 g).

Hatchery-reared RGSM selected for tagging were 41–110 in body length (SL, mm). Eight batches of PIT-tagged RGSM were released between 2018 and 2022 across spring and winter, with release locations spanning >110 rkm of the MRG, above and below the San Acacia Diversion Dam (Table 3-1). Out of the 37,215 PIT-tagged RGSM released, ~40% (n = 15,049) were released above San Acacia Diversion Dam and ~60% (n = 22,166) were released below.

We used detection data from PIT tag antennas to estimate transition probabilities of PIT-tagged RGSM released in the three lowermost MRG reaches. Data was taken from a network of 11–20 submersible antennas deployed in the river throughout the study period. The number of submersible antennas varied temporally based on availability and river access (2019 [n = 20], 2020 [n = 20], 2021 [n = 11], and 2022 [n = 11]). Submersible antennas were focused upstream and downstream of San Acacia Diversion Dam, as well as stretches of river where raft access was limited. Submersible antennas were biased toward shoreline habitats, due to deployment and maintenance limitations (i.e., river drying). We also used detection data from floating Passive Integrated Transponder Portable Antenna SystemsS (PITPASS) with raft-mounted antennas (Stout et al. 2020). A total of 11 float trips were conducted between 2019 and 2022, spanning ~170 rkm of the study area, with initial floats occurring within 5 days following fish releases. More detail descripting field methods is available in Chapter 2.

Data Analysis

We constructed encounter (i.e., capture) histories for hatchery-reared RGSM that were released, marked (i.e., PIT-tagged), and redetected at least once after release in the study area by submersible or floating antennas. As individuals were not physically recaptured, the term redetection is used herein. Using these data, we estimated movement (transition) probability between states (ψ) and detection probability (p) using a multistate model for live recaptures in Program MARK (Pollock, Kendall, White and Burnham 1999). An extension of Cormack–Jolly–Seber mark–recapture models (Cormack 1964; Jolly 1965; Seber 1965), multistate models are open models that also estimate apparent survival (φ), which is the probability of staying within a state and surviving in that state.

Submersible antennas collect data continuously, therefore we had to choose an appropriate time period to bin the data. Although we aimed to estimate movement probabilities at a relatively fine temporal scale (e.g., weeks or months), when the data were parsed into short intervals, the multistate model either did not converge or converged poorly. As such, we used 4–month intervals, which provided a high enough redetection probability to avoid convergence issues with the multistate model. These 4–month intervals correspond with the operation of the irrigation system in the MRG, which largely dictates the hydrograph of the study area (Figure 3-2). The irrigation system is off in the winter from November to February and operational from March to October, with the early irrigation season occurring in the spring from March to June and corresponding with increased spring peak runoff. The late irrigation season coincides with increased water demands and river drying in the summer from July to October.

We separated RGSM into cohorts by release season, and within that cohort we assigned a group covariate indicating whether they were released above or below San Acacia Diversion Dam. As we only constructed encounter histories for RGSM that were redetected at least once after their release in a subsequent time step, this excluded individuals released in 2018 and 2022. For each individual RSGM, we created an encounter history for one-year following release, as the number of redetections declined following the one-year post-release period and the typical life span of hatchery-reared RGSM is <12 months after release (Yackulic et al. 2022). Thus, each encounter history had four occasions (release and three subsequent encounters), consisting of release at timestep 1, detection at timestep 2, detection at timestep 3, and detection at timestep 4.

We defined states based on geomorphic and physical attributes of the study area. Delineation of these spatial states provided a basis to evaluate how the distinct geomorphic characteristics within these reaches influence movement patterns. State A was the entirety of the study area above San Acacia Diversion Dam, state B was 0–1 rkm below the dam, and state C was >1 rkm below the dam (Figure 3-1). We defined state B as the 1 rkm stretch below the dam in order to assess whether individuals who were detected immediately below San Acacia Diversion Dam had a higher probability of successfully moving upstream through the barrier into state A. Multiple individuals in our data set were detected in two different states within the same time step, therefore we assigned each encounter to the state the RSGM was last detected in to maintain consistency. An encounter history for each individual RSGM included its state (e.g., AA0B) and individual covariates. To account for differences among years within release cohorts, we included individual covariates for each year of release. We did not include a size covariate because there is very little variation in body size in the species and released individuals were within a narrow size range (46–100 mm SL). We modeled the data using two groups based on their release location in relation with San Acacia Diversion Dam; released above the dam (state A) and released below the dam (state B or C). Because we hypothesized detection probability may increase with the number of submersible antennas, and the number of submersible antennas deployed varied by group (i.e., release location above or below of the dam) and by 4–month interval, we also included individual covariates for the number of submersible antennas active during each 4–month encounter interval.

Model construction focused on accurately estimating upstream and downstream movement probabilities across the San Acacia Diversion Dam (i.e., transition probabilities among states). As a secondary goal, we also wanted to evaluate whether flow was related to movement probability across the dam. To evaluate the effect of flow on movement and account for the variation in flow across years within each cohort, we included covariates for minimum, maximum, and mean cubic feet per second (cfs) during each 4-month interval following release.

Our primary analysis goal was to select a model with the appropriate group and temporal structure to use in a hierarchal Bayesian approach to estimate movement probabilities. We were not interested in model averaging, so we did not attempt to construct all possible combinations of models. In addition, during preliminary analysis, we found many models did not converge well (i.e., no estimate of standard error and/or all confidence intervals were 0–1, even using simulated annealing). Consequently, we focused on models that performed well in preliminary analysis, which still resulted in a considerable number of possible models. To reduce the total number of models considered, we used a sequential model development process. First, we constructed models with different temporal effects and then increased model complexity by adding covariates (although the covariates release season and year were also temporal). However, as our primary objective was to investigate movement among states and because we restricted our analysis to RSGM detected at least once post-release (resulting in a positive bias in estimates of φ), φ was set as constant by state (φ(state)) for all models and is not reported. For the first set of models, we modeled ψ and p with a categorical time effect (t), with these temporal structures being the same and different by group (g) additively and multiplicatively. We also tried a structure for p in which p was the same for states B and C (below the dam). We used Akaike's Information Criterion adjusted for small sample sizes (AICc) and normalized AICc weights (w_i) to rank models (Burnham & Anderson, 2002), and carried through the structure of the top models (models within 2 ΔAICc units from the top model) from the first phase of modeling as the base model for all subsequent analyses.

The best structure from this phase was ψ(state×g×t) p(state×g×t) (it was 187.5 ΔAICc from next best model, ψ(state×t) p(state×g×t)). Using this structure, we then included additional temporal effects of release season and release year (yr), which we modeled using additive and multiplicative interactions with state, group, and time for ψ and p. We aimed to evaluate model fit using the most global model that converged well from this phase of modeling (Cooch and White 2019), which was ψ((state×g×season)+(g×t)+yr) p((state×g×season)+(g×t) +yr). However, because Program MARK does not allow individual covariates (i.e., season and year) in its procedures to evaluate fit (Cooch and White 2020), we separated the data set by season to remove the seasonal variables from the model. We tried separating the data set by year and year and season, but only 2019 and winter 2019 had enough data (n = 1,122 and 1,022 respectively) for models to converge. The years 2020 and 2021 had 317 and 30 individuals (n), while the season year combinations had 9,317 individuals. After we separated the dataset by season, we used the model ψ(state×g×t)

p(state×g×t) to evaluate model fit. We tested the goodness of fit of this model structure by using the median c-hat ($\hat{c}$) procedure (Cooch and White 2020). We corrected and reweighted the final model set (quasi-AICc [QAICc]) based on the resultant $\hat{c}$ to account for a lack of fit due to overdispersion.

For the final phase of modeling, we constructed models for p in which g×t was replaced by number of submersible antennas because number of submersible antennas were unique by g and t. We also included models with additive intercepts on ψ for fish that stay (AA, BB, or CC), fish that move downstream (AB, AC, or BC), and fish that move upstream (BA, CA, CB). We included these intercepts because preliminary analysis showed movement probabilities were generally very low for upstream movement, moderate for staying in the same state, and variable for downstream movement. Then, to evaluate the relationship between flow and ψ, we replaced t with flow covariates in the top model(s). Finally, because flow has been found to be related to p (citations), we also constructed models where we replaced t with flow covariates for p.

Bayesian hierarchical estimates

From the top model with temporal effects, ψ((state×g×season)+(g×t)+yr) p((state×g×season)+(g×t) +yr), we used a Bayesian hierarchical model to estimate movement probabilities among states for each release season. That is, we reran the model with the individual covariate for season set for spring and then winter. We did not run the Bayesian procedure by year because sample sizes were too small for 2020 and 2021; the movement probabilities are across years. We used Markov chain Monte Carlo (MCMC) sampling implemented in Program MARK. Because this was the first time we analyzed movement data for this system, we used uninformative flat priors. Because all model parameters were logit transformed to constrain the real estimates to be between 0–1, we used a normal prior on the logit scale: logit(θ) N(0,1.75). This provided a relatively flat prior when back transformed to the real 0–1 scale (2.5th and 97.5th percentiles of approximately 0.02 and 0.98, with a uniform distribution between those percentiles when back transformed). We assessed convergence of the Markov chains by visual inspection of the trace of MCMC chains of the posterior samples of the parameters and by using the Gelman-Rubin statistic, $\hat{R}$ (Gelman 2004). For each parameter, we used 10 chains of 1,000 each and used a threshold of $\hat{R} < 1.1$ to indicate adequate sampling of the posterior distribution. Based on diagnostics in Program MARK's MCMC routine (Cooch and White 2020), we determined posterior distributions needed to be thinned and accordingly saved every tenth sample to achieve first-order Markovian independence. We used 1,000 burn in samples and kept 10,000 samples after thinning.

RESULTS

A total of 1,469 unique RSGM were detected on ≥1 occasion in a subsequent time step following release and were therefore included in the multistate analysis (Table 3-2). We documented a total of 1,944 unique transitions between spatial states. The sample size varied by year, with 76% of samples from 2019, and only 2% from 2021. Sample sizes were higher for winter releases (70%) compared to spring releases, and 63% of RSGM included in the analysis were released below and 37% were released above the dam (Table 3-2).

Goodness-of-fit testing indicated moderate overdispersion of the data for spring releases ($\hat{c}$ = 2.83, SE = 0.03; 1,000 simulations) and winter releases ($\hat{c}$ = 2.10, SE = 0.05;

1,000 simulations). We suspect some of the overdispersion came from differences in movement and detection probabilities among years. We used a sample-size weighted averages of what from the 2 seasons ($\hat{c} = 2.34$). The final candidate model set was adjusted with $\hat{c}$ prior to interpretation.

Top base models resulted in an interaction between state, group, and sampling period, but these models performed poorly compared to models that included release season and release year (Table 3-3). Release season and year were important for transition probabilities; the best model structure including release season and year had a similar structure for ψ and p; $\psi((\text{state}\times g\times\text{season})+(g\times t)+\text{yr})$ $p((\text{state}\times g\times\text{season})+(g\times t)+\text{yr})$. This model indicates movement and detection probabilities were different by state, group, and season, and varied by sampling occasion for groups with additive differences among years. Models allowing different movement probabilities for different state changes (stay in same state, move upstream or move downstream; $\psi((\text{state}\times\text{updownstay}\times\text{season})+(g\times t)+\text{yr})$ performed better than the same model using a group effect (Table 3-3), although estimates of movement probabilities were very similar.

While release cohort was in important covariate for movement and detection, flow variables were not. Models with flow variables replacing t in the structure of ψ in the top model were >153 ΔQAICc lower (Table 3-3). Models with flow variables replacing t in the structure of p in the top model were >810 ΔQAICc lower. From the Bayesian hierarchical model (i.e., $\psi((\text{state}\times g\times\text{season})+(g\times t)+\text{yr})$ $p((\text{state}\times g\times\text{season})+(g\times t)+\text{yr})$), we provide estimates of movement probabilities for the first sampling period (t1) because only this period, between release (first encounter) and second encounter had an adequate sample size.

That is, 78% (1,146) of the 1,469 RGSM were detected during this period. While the number of encounters during second sampling period was relatively high (303), the number of RGSM detected during both the second and third was low (22), which resulted in unreliable and asymmetric? estimates. Movement probabilities for the third sampling period were confounded with *p*.

For RGSM released above San Acacia Diversion Dam movement was variable, with approximately a third remaining above the dam (state A) and two thirds moving across the dam downstream (Figure 3-3). For fish released below the dam (state B or C) most movement was either downstream or no movement (staying within the state). Movement probabilities upstream across the dam were very low (≤0.02) and similar for fish close to the dam (state B) and fish farther downstream (state C). There appeared to be somewhat more upstream movement in the winter than spring (Figure 3-4). The probability of a fish staying in the same state was high for C (0.76–0.98) and lower for A (0.32–0.42) and B (0.23–0.33).

Although sample sizes were not sufficient to estimate probability of transition for the second sampling period (t2) and confounded for the third, the raw data suggest that after the first sampling period fish tended to say in the same state. Repeat detections on distinct occasions were highest in state C (n = 16,340), followed by state A (n = 8,643) and state B (n = 8,425). Across all time steps, 61–67% of RSGM remained in the same state (i.e., were AA, BB, or CC). Similar to transition probabilities estimated from our model, a very small percentage (1.5%) of individuals included in our analyses moved from below to above San Acacia Diversion Dam (Figure 3-5). Of the individuals released below the dam who successfully moved upstream through the dam into state A, n = 99 remained above the dam (i.e., with two additional distinct redetections in state A).

DISCUSSION

We utilized RGSM PIT tag detection data to develop a multistate model estimating movement (i.e., transition) probabilities between reaches for adult hatchery-reared RGSM in the MRG. Our results from the multistate model provided insight into the space-use surrounding the San Acacia Diversion Dam and allowed us to compare transition probabilities between fragmented and unfragmented reaches as well as potential passage above a large diversion dam. We observed transitions between each of the three spatial states and documented 198 unique upstream passages through the San Acacia Diversion Dam. However, estimated transition probabilities varied substantially among reaches and release cohorts. Given the dynamic nature of the MRG, it is likely these differences in transition probabilities among reaches are a result of differences in reach-scale conditions and season. Overall, these results correspond with related work (Chapter 2), where we documented RGSM exhibiting nomadic movement patterns, which are uninformed and driven by the conditions immediately surrounding an individual (Teitelbaum and Mueller 2019).

As spatial states in our model were delineated by San Acacia Diversion Dam, our results highlight the ecological impact of the barrier. While we documented 198 unique upstream passages through the San Acacia Diversion Dam, transition probabilities were consistently higher downstream (44%) and between unfragmented states (41%, states B and C), suggesting the existing dam impedes the upstream movement potential of RGSM. Further, the upstream transition probability between states B and C was higher for individuals released in the winter (22%) than for those released in the spring (2%). The San Acacia Diversion Dam has largely altered the hydrologic and geomorphic characteristics of the river, resulting in contrasting conditions between reaches, and thus partially explaining differing transition probabilities among reaches (Massong et al. 2010). The channel morphology of the spatial state above the dam (state A) is characterized by increased channel incision, reduced floodplain connectivity, and reduced habitat availability (Blythe and Schmidt 2018). The spatial state immediately below the dam (state B) is highly aggraded, with similar levels of habitat availability to state A (Doidge et al. 2020). In contrast, habitat complexity and availability are higher in state C (below state B). Variable hydrologic conditions impact the extent of these reach-scale characteristics, as well as the efficacy of antenna read range and coverage. As a result, the population responses and detection efficiency within each distinct reach likely varied across the different flow magnitudes throughout our study period. Despite the decreased access to suitable habitat in states A and B, we documented individuals leaving state C (with the greatest habitat quality) and remaining in states A and B, highlighting the innate predilection of some RGSM to exhibit higher levels of mobility and subsequently expand their range upstream.

Our model results support the heterogeneous movement distribution documented in many other riverine fish species, including RGSM (Radinger and Wolter 2014; Chavez 2023). In small-bodied fish species in fragmented systems, relatively short distance movements by a small portion of individuals may achieve a level of diffusive dispersal sufficient to maintain population persistence in upstream reaches (Skalski and Gilliam 2000). Further, Branco et al. (2017) found instream barriers not only restrict fish movement but may lead to adjustments in life-history strategy within populations over time. Increasing passage efficiency from below to above a dam may allow access to spawning areas with greater habitat for larval retention and offset downstream displacement (Perkin et al. 2015). Therefore, even a slight increase in transition probabilities between fragmented river reaches may have population-level implications for RGSM.

The tendency of certain individuals to be more mobile than others in our study highlights the importance of intraspecific variability as well as the role of individual behavior responses in population dynamics (Leavy and Bonner 2009; Coates et al. 2019). Our results demonstrated the highest probability of transition between states within the first time-step after release. The majority of individuals (61–67%) were redetected in the same state as their initial release, and these individuals were more likely to remain stationary in subsequent time-steps, representing a larger stationary component of the population than mobile. Additionally, individuals who displayed increased mobility initially were generally more mobile in subsequent time-steps, representing the smaller mobile component of the population. There has been increasing emphasis placed on the role of intraspecific variability and individual personality as it relates to movement predilection in fish species (Coates et al. 2019). When assessing fish dispersal in a nonmigratory fish species, Hirsch et al. (2016) found that the probability of fish crossing a barrier was largely dependent on personality traits. As such, the presence of variable transition probabilities among individual RGSM in our study suggest individual personality may act as a mechanism for population persistence. Successful transition between reaches, especially those fragmented by dams, may be more selective to passages of a smaller group of mobile individuals with distinct personality traits within the population. Therefore, the ability to identify and better predict behavior responses and personality traits which promote successful transition through movement barriers may help advance conservation efforts of imperiled fish species in highly fragmented systems.

The extant population of RGSM in the MRG are reliant upon the release of hatchery-reared conspecifics for persistence (Archdeacon et al. 2023). Population supplementation is an increasingly important conservation tool for endangered fish species (Archdeacon et al. 2023); however; there are limited examples of population recovery in the wild based solely on supplementation (Seddon et al. 2007; Tickner et al. 2020). Given the costs and risks associated with implementing population augmentation or supplementation, it is necessary to evaluate the efficacy of existing programs in meeting their recovery goals, and if goals are not being met, there is a need to identify the most limiting factors for recovery (e.g., Budy and Schaller 2007, Pennock et al. 2022). Our study results provide crucial insights regarding the fate of hatchery-reared RGSM following release. We found release location and season impacted transition probabilities of RGSM. In both release cohorts (spring and winter releases), individuals released above the dam in state A largely moved downstream to occupy state C. Additionally, individuals in the spring release cohort had higher probabilities of remaining within their initial release state than those in the winter release cohort. Overall, individuals released in the winter had higher transition probabilities than individuals released in the spring. An increase in upstream transitions in the winter and spring could indicate an attempt to achieve an optimal position prior to and during spawning (early-late spring). As such, the ability to predict responses of hatchery-reared RGSM can inform the magnitude, timing, and location of releases to maximize the efficiency of supplementation efforts and meet reach-specific goals.

Although the probability of transition from below to above the dam was low in our model, any rate of exchange could be considered surprising given the lack of formal fish passage structure and the narrow hydrological circumstances under which individuals have the opportunity to attempt upstream passage, or even in some years downstream movement (e.g., intermittent drying). Based on our model, we estimated low probabilities of upstream transitions in both release cohorts released below the dam. However, the relatively higher probability of upstream transitions in the winter release cohort occurred during a 4–month interval associated with lower magnitudes of flow, indicating that upstream movements are often opportunistic and associated with minimized energy expense for the individual (Burbank et al. 2022). While discharge as a covariate did not improve our multistate model, elsewhere we have shown it is a significant driver of movement distances for RGSM (Chavez 2023). The ability to include group covariates (such as discharge) strengthens this modeling approach, but the power to detect large scale patterns can be quickly masked by the desire to maintain parsimony.

Like most large scale, uncontrolled field studies, our study had inherent limitations. Given our model structure, states A and C encompassed a large stretch of river (79.7 and 67.1 rkm respectively); therefore, a redetection in the same state over multiple time steps could still represent substantial movement distances but within the same ‘reach’. Further, individuals who remained near their initial release location likely had higher chances of redetection based on proximity to antennas, versus individuals who may have moved downstream outside of the study area. While the detection efficiency of our approach was high, it is inevitable that many movements were undetected as antenna coverage across the entirety of each state was obviously not possible. As we required included encounter histories to have an individual redetected at least once in a subsequent time step after release, many initial transitions between states within the same 4-month interval were not included in analyses (64 %). A larger sample size of tagged individuals within a narrower time period and fine-scale river reaches to allow additional and sustained antenna coverage may elucidate finer scale transition probabilities (Kanno et al. 2020). Nonetheless, our multistate model provides a flexible base model that embraces emerging tracking technology and advances our ability to understand space use patterns in fragmented rivers (Raabe et al 2014).

As fragmentation becomes increasingly pervasive in desert rivers, research that provides insights into the potential factors that constrain or promote fish movement and the consequences of fragmentation should be prioritized. Multistate models provide useful quantification of space-use patterns and can ultimately help resource managers identify where efforts should be best allocated to meet recovery goals. Our results suggest that RGSM are not only physically capable of, but also display the determination to pass through barriers to movement in order to expand upstream, highlighting the need to restore connectivity in fragmented reaches of the MRG. Understanding the magnitude of fragmentation and resulting reach-scale differences may also inform future habitat restoration efforts, such as the removal or redesign of dams to include fish passage. In addition, insight into the spatial structure of a population and fate of hatchery-reared RGSM following release can help define an appropriate spatiotemporal scale at which recovery efforts occur, resulting in a more efficient use of resources. Further, given the pervasiveness of fragmentation by diversion dams in riverine systems, our approach can be replicated and expanded upon to assess future fish passage efficiency in small-bodied fish species after dam modification.

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TABLES AND FIGURES

Table 3-1. Rio Grande Silvery Minnow released between 2019 and 2021 in the Middle Rio Grande of New Mexico, USA showing the number of tagged individuals released, release state (location), and year/season released.

Spring Release			Winter Release		
Year	State	Number	Year	State	Number
2019	A	0	2019	A	2,604
	B	550		B	2,428
	C	1,151		C	4,846
2020	A	1,746	2020	A	0
	B	2,192		B	0
	C	3,979		C	0
2021	A	1,980	2021	A	5,730
	B	0		B	0
	C	2,885		C	3,422

Table 3-2. Number Rio Grande Silvery Minnow detected at least once in two distinct 4–month time intervals (i.e., used in the multistate analysis) for fish released between 2019 and 2021 in the Middle Rio Grande of New Mexico, USA showing group cohorts by release season.

	Released Above				Released Below		
Year	Spring	Winter	Total	Year	Spring	Winter	Total
2019	0	469	469	2019	100	553	653
2020	64	0	64	2020	253	0	253
2021	4	4	8	2021	17	5	22
Total	68	473	541	Total	370	558	928

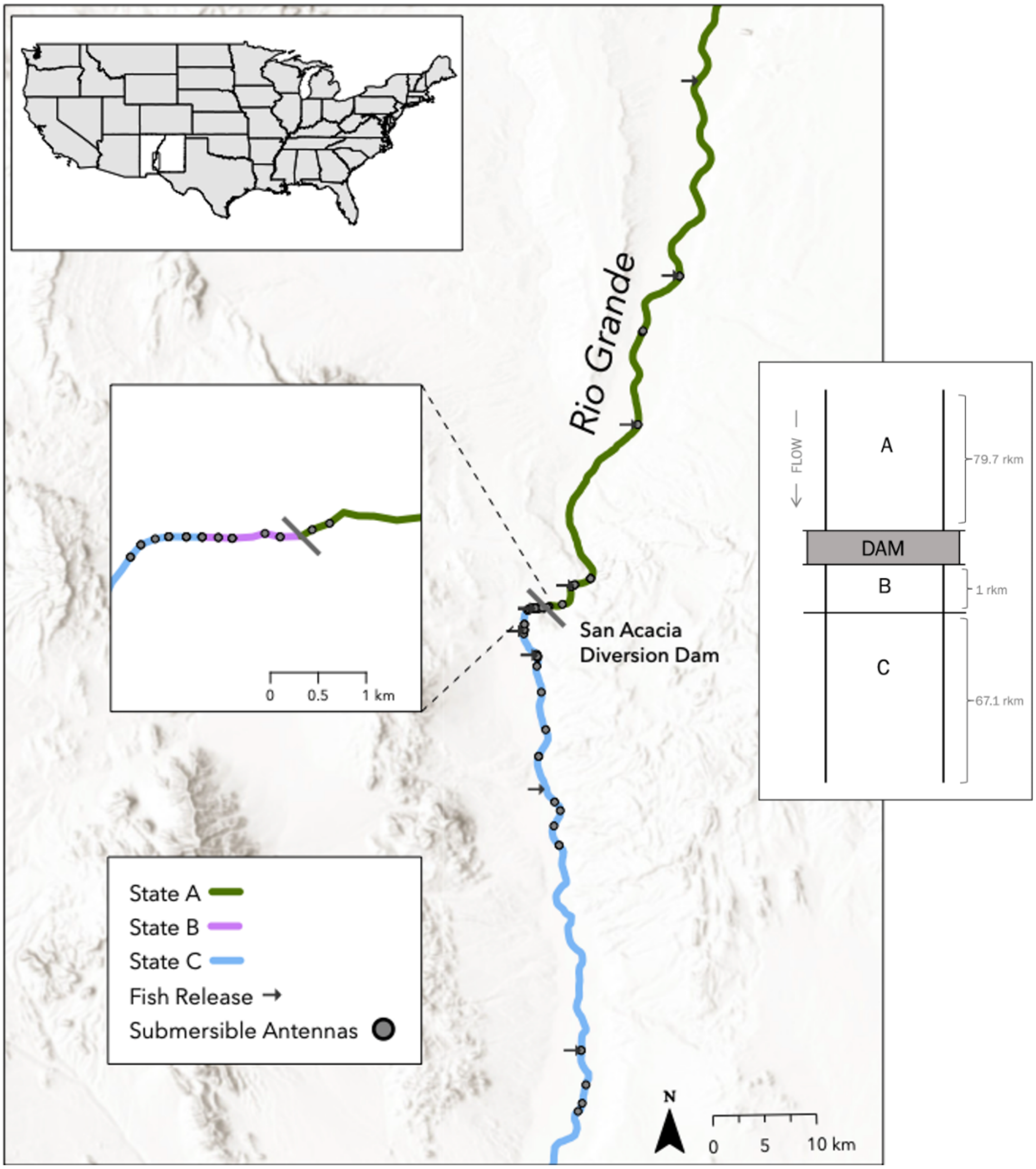
Table 3-3. Model selection output of multistate movement analysis for Rio Grande Silvery Minnow detected at least once (n = 1,469) in the Middle Rio Grande of New Mexico, USA, 2019-2022. The top 20 models are presented.

Model[a]	*K*	$\Delta QAIC_c$	w_i	QAICc	*QDeviance*
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×updownstay×season)+(g×t)+yr)	72	0.00	0.85	2413.98	2266.29
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×g×season)+(g×t)+yr)	73	4.45	0.09	2418.43	2268.63
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×g×updownstay×season)+(g×t)+yr)	79	6.53	0.03	2420.52	2258.06
φ(state) p((state×g×season)+(g×t)+yr) ψ((updownstay×season)+(g×t)+yr)	70	7.92	0.02	2421.90	2278.41
φ(state) p((state×g×season)+(g×t)+yr) ψ((updownstay×g×season)+(g×t)+yr)	73	9.66	0.01	2423.65	2273.85
φ(state) p((state×season)+(g×t)+yr) ψ((updownstay×season)+(g×t)+yr)	67	16.87	0.00	2430.85	2293.66
φ(state) p((state×g×season)+(g×t)) ψ((state×g×season)+(g×t)	69	119.46	0.00	2533.44	2392.05
φ(state) p((state×g×season)+(g×t)) ψ((updownstay×season)+(g×t)	66	120.07	0.00	2534.05	2398.95
φ(state) p((state×g×season)+(g×t)+yr) ψ((updownstay×season)+(g×season×mincfs)+yr)	43	153.35	0.00	2567.34	2480.02
φ(state) p((state×g×season)+(g×t)+yr) ψ((updownstay×season)+(g×season×meancfs)+yr)	43	172.26	0.00	2586.24	2498.92
φ(state)p((state×g×season)+(g×t)+yr)ψ((state×updownstay×season)+(g×season×maxcfs)+yr)	43	249.92	0.00	2663.91	2576.59
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×updownstay×season)+(g×mincfs)+yr)	37	384.74	0.00	2798.72	2723.75
φ(state) p(state×g×t+season) ψ(state×g×t+season)	59	506.87	0.00	2920.85	2800.38
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×updownstay×season)+(g×meancfs)+yr)	37	515.75	0.00	2929.74	2854.76
φ(state) p(state×g×t) ψ(state×g×t+season)	58	518.30	0.00	2932.28	2813.89
φ(state) p((state×season×nosubs)+(yr×nosubs)) ψ((state×updownstay×season)+(g×t)+yr)	55	553.99	0.00	2967.97	2855.82
φ(state) p(state×g×t) ψ(state×g×t)	57	588.07	0.00	3002.05	2885.74
φ(state) p((state×g×season)+yr)+(g×nosubs)) ψ((state×updownstay×season)+(g×t)+yr)	54	588.92	0.00	3002.90	2892.83
φ(state) p((state×g×season)+(g×t)+yr) ψ((state×updownstay×season)+(g×maxcfs)+yr)	37	601.76	0.00	3015.74	2940.76
φ(state) p((state×season×nosubs)+yr) ψ((state×updownstay×season)+(g×t)+yr)	53	636.78	0.00	3050.76	2942.77

[a] Key to model notation: *K* = no. of parameters (increased by one for $\hat{c}$); $QAIC_c$ = quasi Akaike Information Criteria corrected for small sample size and lack of model fit; $\Delta QAIC_c$ = difference between the model listed and the $QAIC_c$ of the best model; w_i = model weight based on model $QAIC_c$ compared to all other model $QAIC_c$ values; φ = apparent survival; *p* = probability of detection; *ψ* = probability of transition (moving) from one state to another; *t* = sampling interval as a categorical variable; . = no trend (constant); g = release group (released above or below San Acacia Diversion Dam; season = release season; yr = release year; updownstay = movement category of whether thee movement was upstream, downstream, or stayed in same state; meancfs, mincfs, maxcfs = flow variables described in text.

Figure 3-1.

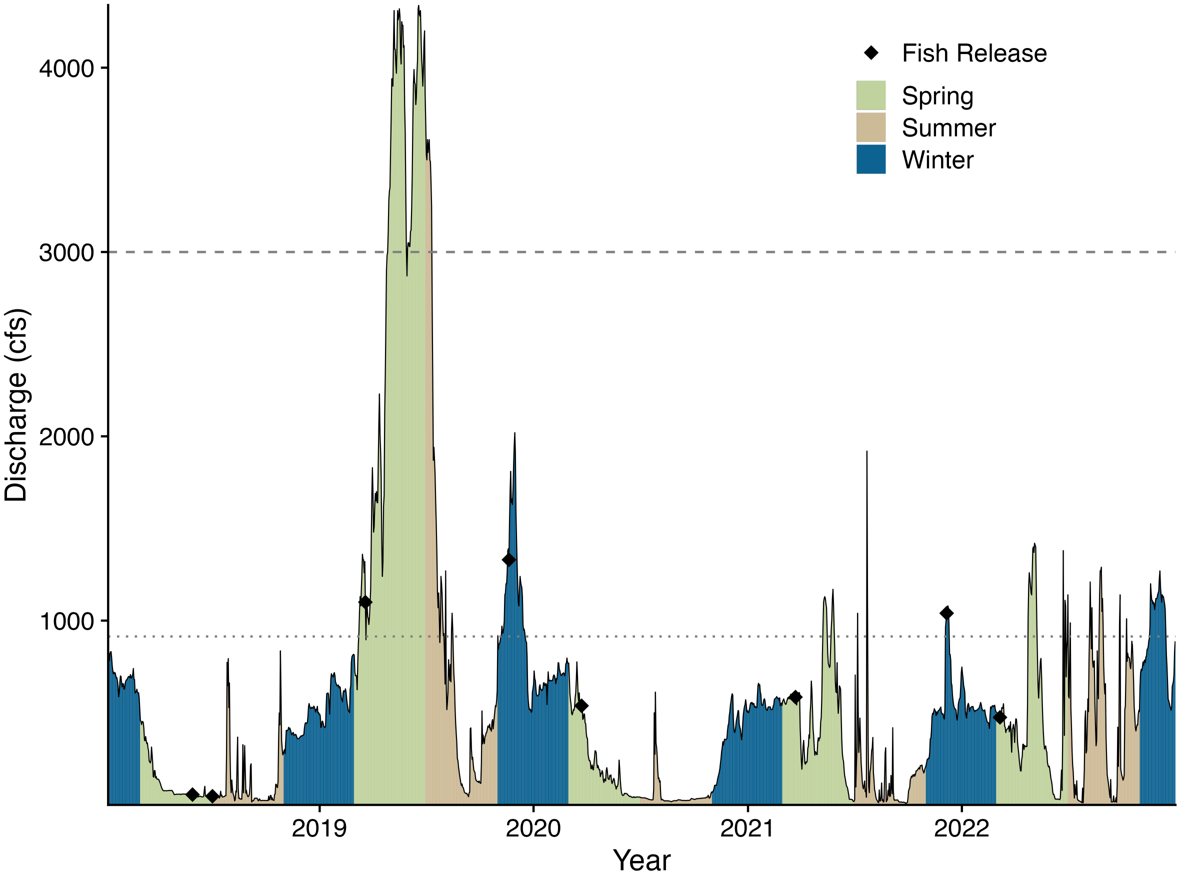
Map of Middle Rio Grande Spatial States



Note. Map of Middle Rio Grande with spatial states represented by color and inset zoomed into San Acacia Diversion Dam. Locations of submersible antennas are represented by grey points and fish release locations are represented by black arrows.

Figure 3-2.

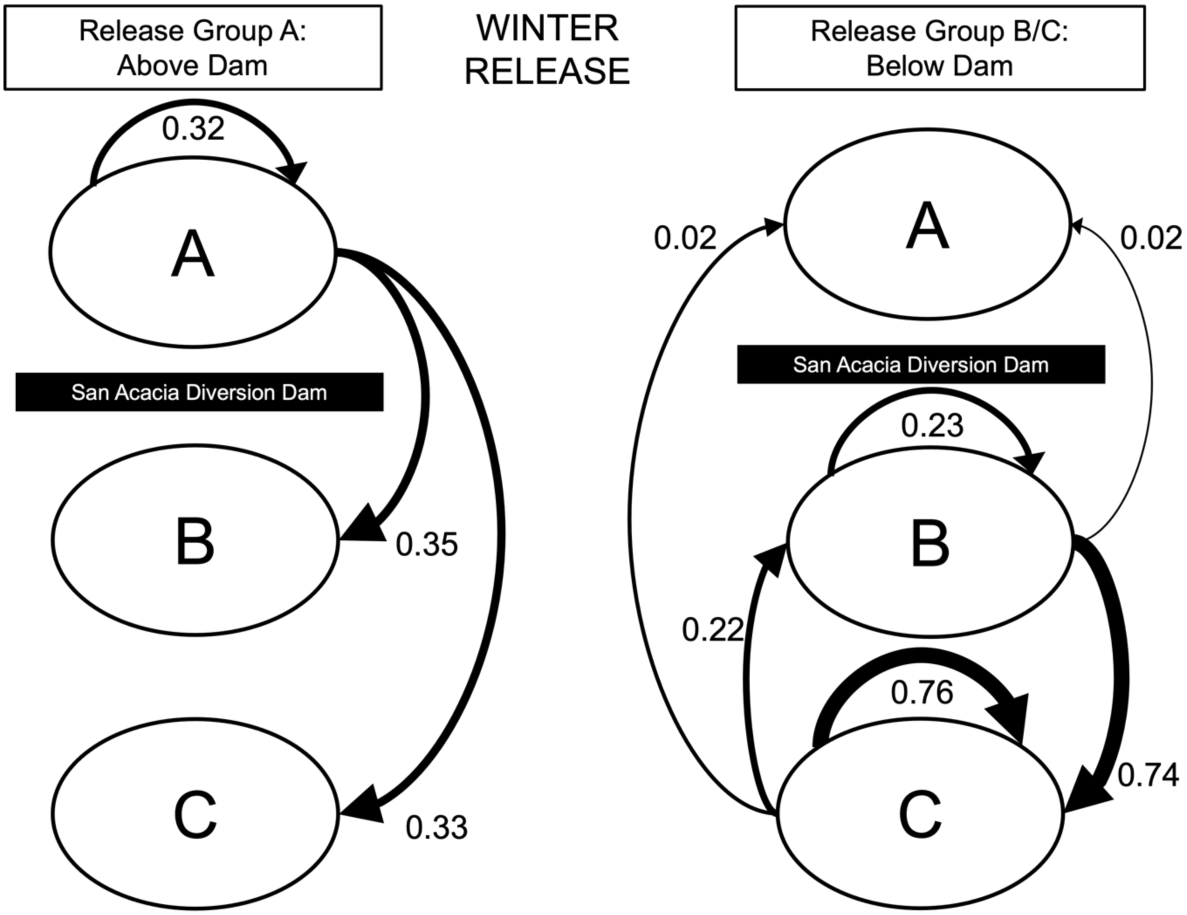
Hydrograph of Middle Rio Grande Below San Acacia Diversion Dam



Note. Hydrograph of Middle Rio Grande below San Acacia Diversion Dam (United States Geological Survey Gage 08354900) between 2019 and 2022. Black points represent corresponding dates of PIT-tagged Rio Grande Silvery Minnow releases, with fill color representing the season of release. The horizontal grey dashed line represents the threshold for floodplain inundation (at 3,000 cfs), with the horizontal dotted line representing the long-term historical mean flow since 1974 (at 914 cfs) in the study area.

Figure 3-3.

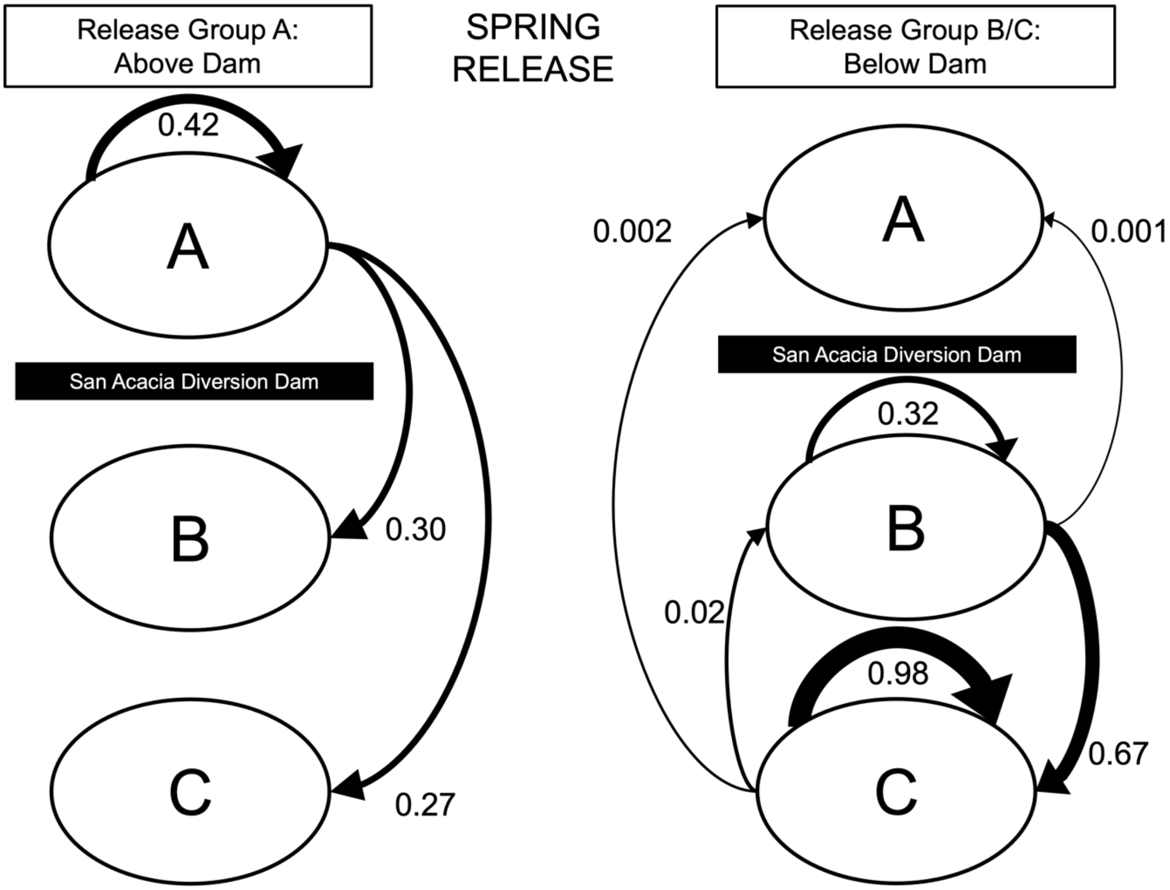
Transition Probabilities for Winter Release Cohort



Note. Transition probabilities for PIT-tagged Rio Grande Silvery Minnow released in winter between 2019 and 2021 in the Middle Rio Grande (n = 1,031), with the width of the arrows corresponding with the probability of each state transition.

Figure 3-4.

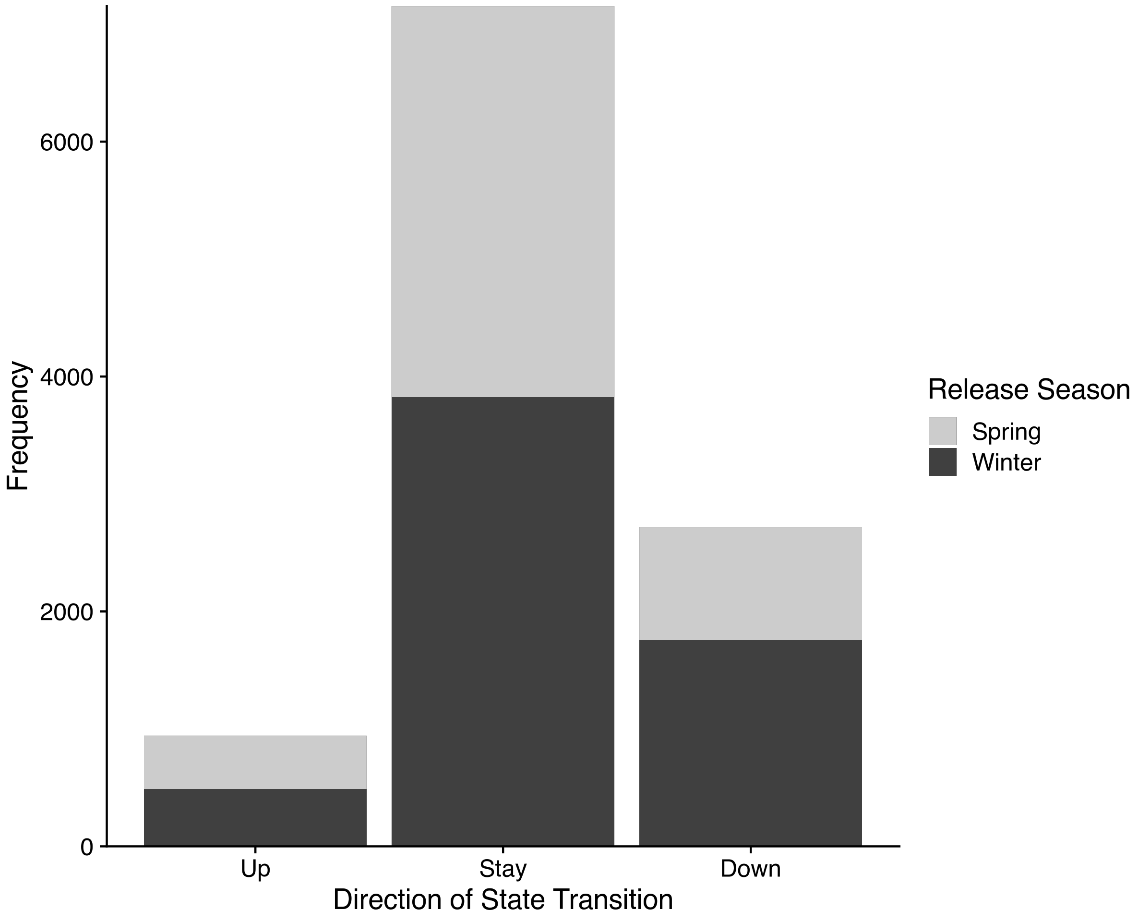
Transition Probabilities for Spring Release Cohort



Note. Transition probabilities for PIT-tagged Rio Grande Silvery Minnow released in spring between 2019 and 2021 in the Middle Rio Grande (n = 438), with the width of the arrows corresponding with the transition probability between each state.

Figure 3-5.

Frequency of State Transitions



Note. Frequency of state transitions by direction, with color representing the release season cohort (spring: March–June, winter: November–February) for RGSM released between 2019 and 2021 in the MRG. The frequency of upstream transitions was much lower than downstream transitions in both release cohorts; however, upstream transitions were higher in the winter release cohort.

CHAPTER 4

CONCLUSIONS

This study elucidates the movement ecology and space use of Rio Grande Silvery Minnow (*Hybognathus amarus*, RGSM) in a highly modified and fragmented desert river. We utilized floating raft-mounted PIT tag antennas, in concordance with stationary antennas, to quantify movement metrics, estimate movement probabilities, and characterize the range potential of RGSM. The use of mobile PIT tag tracking technology in this study allowed us to overcome many of the challenges associated with traditional monitoring approaches or use of stationary antennas alone, thus contributing to a larger base of knowledge regarding movement dynamics of small-bodied desert fishes (Stout et al. 2020). Further, our floating raft-mounted antenna system was repeated in short successions, which allowed us to build individual encounter histories and acquire fine-scale movement metrics across a broader geographic extent. We implanted 37,215 hatchery-reared RGSM with passive integrated transponder (PIT) tags and released the individuals at multiple locations in the Middle Rio Grande, New Mexico between 2019 and 2022. Given their relatively small body size, we were pleased to document a combined retention and survival-to-release rate of 83% in PIT-tagged RGSM. We successfully documented RGSM movement across 42% of their current range in the Middle Rio Grande, with detections spanning nearly 140 river kilometers (RKM).

In Chapter 2, we quantified spatial and temporal movement metrics of RGSM, complementing and building upon previous evidence of the species' movement potential (Bestgen et al. 2010; Platania et al. 2019). We assessed the applicability of two existing movement theories to the movement patterns documented in RGSM, and identified potential correlates with movement patterns. We detected RGSM making longer distance movements than ever previously documented, highlighting the value of quantitative movement data in imperiled small-bodied fish species (Comte and Olden 2018; Steffensmeier et al. 2022). The movement patterns we documented in Chapter 2 indicate that individual RGSM are in fact highly mobile, and like many other fish species, utilize their home ranges at varying scales (Burbank et al. 2023). Notably, we documented successful upstream passages by RGSM through a diversion dam that is not equipped with a formal fish passage structure. Although the strong physiological swimming capabilities are well documented in this species, upstream passage through this barrier was never previously documented (Bestgen et al. 2010; Archdeacon and Remshardt 2012). Additionally, RGSM movement was not accurately described by the two prevailing movement theories; rather, we found RGSM movement to be generally nomadic. Nomadic movement patterns are commonly exhibited in animals that exist within highly variable environments (Teitelbaum and Mueller 2019). The movement patterns observed in this study, combined with the unique life history of RGSM, provide insight into their historical persistence through extreme environmental stressors (i.e., drought and river drying). The long-distance movements and upstream passages through barriers demonstrate the determination and ability of individual RGSM to expand their range and recolonize upstream, given sufficient connectivity. The current system is fragmented, not only by increasing periods of intermittency, but also by multiple diversion dams.

Our detection approach, and large sample size of RGSM in this study, created a robust data set that allowed us to quantify fundamental metrics with crucial conservation applications. In Chapter 3, we utilized the detection data collected between 2019 and 2021 to develop a reach-specific multistate model which provides transition estimates between reaches for RGSM in the Middle Rio Grande. Our model estimated a very low probability of transition from below to above the San Acacia Diversion Dam. Conversely, we detected high movement rates both up and downstream within unfragmented river reaches. In tandem, these results demonstrate the extent to which diversion dams act as a barrier to movement to many RGSM individuals. Although the probability of upstream movement was low, this does not demonstrate the small number of individuals making upstream movements are inconsequential to the persistence RGSM in upstream reaches.

Future research across years may provide additional insight into the behaviors and responses to variable abiotic conditions in RGSM. Our study occurred across years with highly fluctuating conditions and across intermittent reaches of river. In 2019, there were above average stream flow the Middle Rio Grande, with discharge exceeding 4,000 cfs near San Acacia (USGS 08354900), subsequently followed by three below average discharge years, with increased drying (Archdeacon and Reale 2020). As RGSM are relatively short-lived, the conditions of the previous year often dictate the individual's success in the following year. Variable abiotic conditions can also dictate whether RGSM will have a high reproductive output, and therefore have multi-generational impacts (Archdeacon et al. 2022).

Our study was conducted in a heavily modified desert riverscape, and amidst an increasingly arid climate. As such, our results confer several potential conservation applications for desert fish species. Knowledge of how different detection approaches can be applied in altered ecosystems may help guide restoration and conservation approaches. Improving our understanding of these dynamics and patterns may increase the efficacy of recovery efforts and ultimately achieve ecosystem level change. Given the unique life history of RGSM, as well as their federally endangered status, better estimates of range potential can help increase the precision and scale of monitoring and recovery efforts. Further, the demonstrated efficacy of our approach to detect RGSM in the Middle Rio Grande serves as an important model that can be applied to other fish species in similarly fragmented systems.

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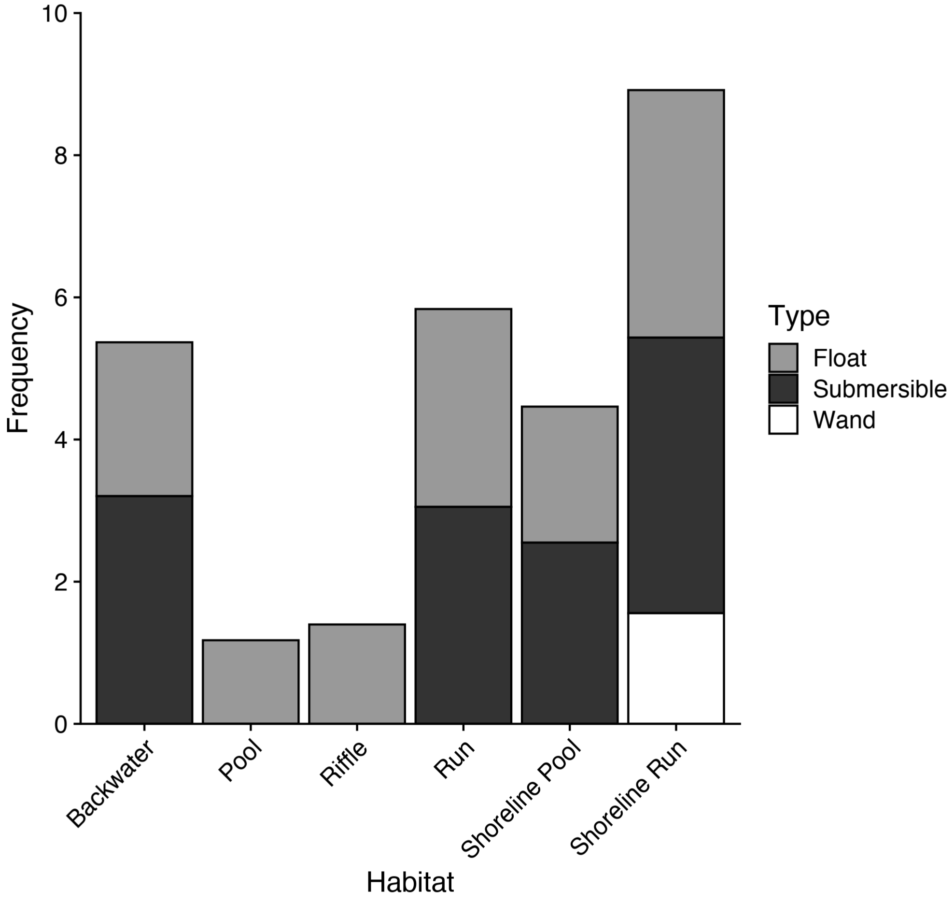
APPENDIX

SUPPLEMENTARY FIGURES

Figure A-1.

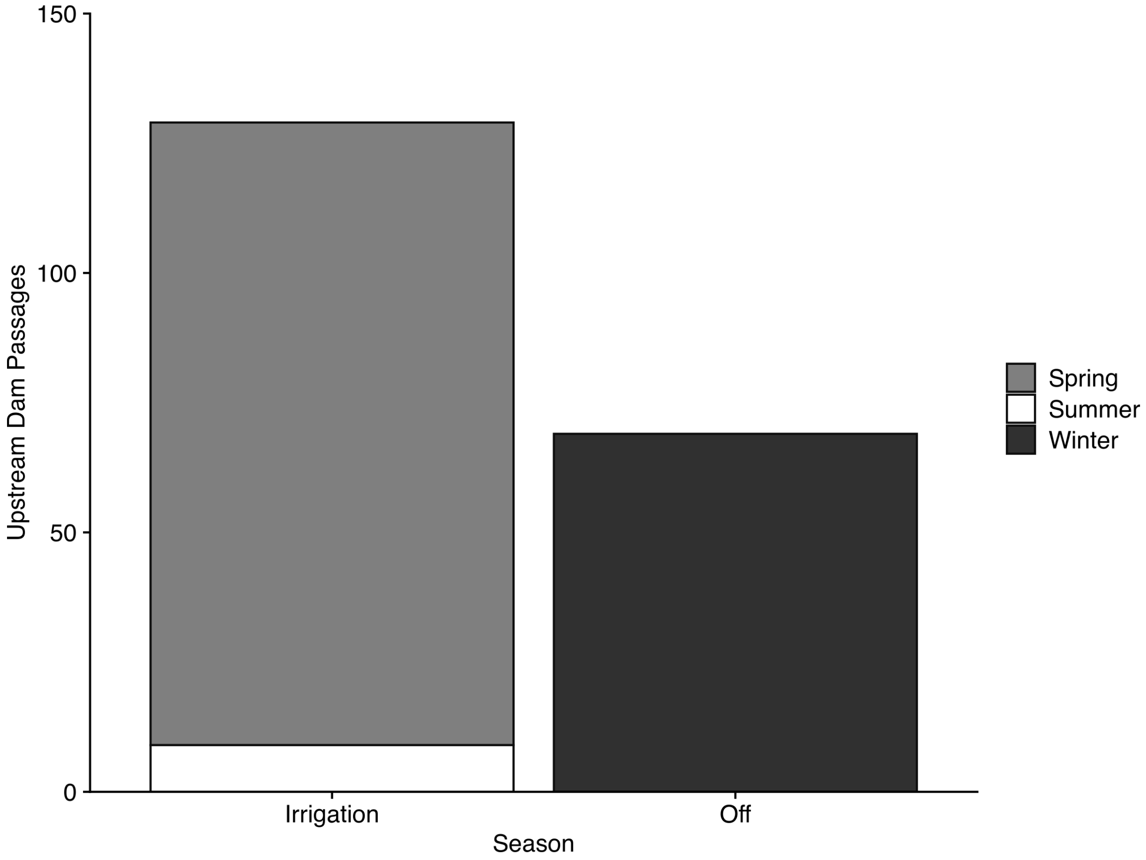
Percent Frequency of Detections by Habitat Type



Note. Percent frequency of Rio Grande Silvery Minnow detections on the y-axis by habitat type on the x-axis, with shade representing antenna type. The habitat types sampled by submersible antennas were primarily shoreline runs due to placement and maintenance logistics. Based on the number of detections by habitat type, however, adults occupied habitats with moderate velocity (defined as > 20 cm/s) and occurred predominantly in shoreline and main channel runs.

Figure A-2.

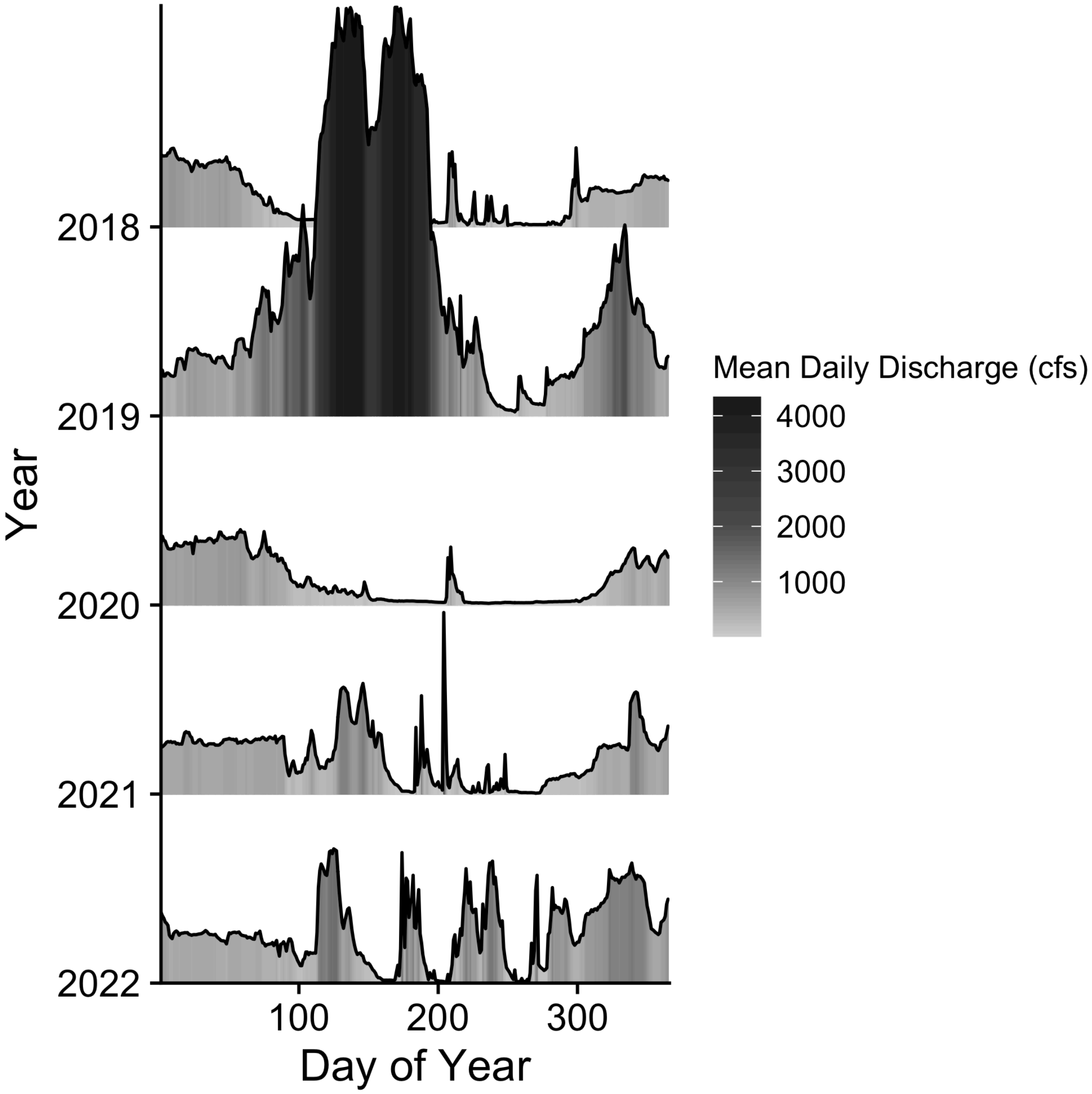
Upstream Passages Through San Acacia Diversion Dam



Note. Upstream passages through San Acacia Diversion Dam by Rio Grande Silvery Minnow, with number of unique passages on the y-axis and season on the x-axis, with shade representing season on a finer scale. Most upstream passages through San Acacia Diversion Dam occurred in the irrigation season, with 122 unique passages between March and June.

Figure A-3.

Mean Daily Discharge for Middle Rio Grande



Note. Mean daily discharge (cubic feet per second) for the Middle Rio Grande below San Acacia Diversion Dam, New Mexico USA (USGS Gage 08354900) by year. Gradient represents magnitude of daily mean discharge.