Assessing facilitated passage and spawning migration patterns of Razorback Suckers, *Xyrauchen texanus*, in the San Juan River

by

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B.S., Iowa State University, 2013

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Division of Biology

College of Arts and Sciences

KANSAS STATE UNIVERSITY

Manhattan, Kansas

2021

Approved by:

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Abstract

In the southwestern United States, decades of water diversions, construction of large impoundments, and loss of floodplain habitats have all contributed to a highly fragmented riverine landscape. River regulation, through damming, alters the magnitude and timing of discharge and temperature regimes and interrupts nutrient and sediment transport. Additionally, barriers negatively affect vital rates of riverine fish populations that rely on connected migratory routes to complete components of their life cycle, such as spawning migrations. A capture-translocation strategy has been implemented for Razorback Suckers, *Xyrauchen texanus*, in the San Juan River to mitigate negative effects of barriers, while precluding passage of nonnative species. We used active and passive radio telemetry to assess Razorback Sucker movements following translocation upstream of two barriers. Furthermore, we used seven years of Passive Integrated Transponder tag detection data at each barrier to test associations of Razorback Sucker occurrence and environmental parameters that may cue spawning migrations. While translocated individuals tended to return downstream of barriers within a year of passage, our results indicated that most individuals (>80%) remained upstream long enough to successfully spawn. Following translocation at each barrier, we observed upstream movements ranging from 2 to 262 km and detected distinct aggregations within the expected spawning season. Timing of putative spawning migrations had strong associations with water temperature, where the largest proportions of Razorback Suckers were first detected at barriers as mean weekly water temperature was increasing between 7.1 to 14.2 °C. Our research provided a model that managers can use to predict the timing of occurrence of migrating Razorback Suckers, serving as a tool to improve efficiency of selective passage facilities by prioritizing passage efforts during times of peak migration. While translocation provides an option of selective passage that may

seasonally reconnect migratory routes for a proportion of the population and increase spawning potential, it is not clear if this will be enough to mitigate other recruitment bottlenecks, (e.g., access to predator-free habitats) necessary to recover Razorback Sucker populations.

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Acknowledgments

I thank numerous individuals without who, this work would not have been possible. First, my advisor Dr. Keith Gido for providing direct and honest feedback, assistance in the field, and numerous discussions on the utility of models. Keith offered a tremendous amount of support and trust in uncertain times. I would also like to thank my committee members, Dr. David Haukos and Dr. Mark McKinstry for their advice while developing my research. Mark has been an excellent friend and mentor to me for more than six years, and I have always valued our campfire discussions. Additionally, I thank Dr. Casey Pennock for his mentorship and guidance in developing this research.

This work would not have been possible if not for the collaborative efforts of several state, tribal, federal, and non-government agencies. In no particular order, I thank the US Fish and Wildlife Service: B. J. Schleicher, D. Kaus, N. Franssen, S. Durst, E. Gilbert, M. Mata; Utah Division of Wildlife Resources: K. Creighton, B. Hines, K. Burke, S. Brockdorff; Navajo Nation Department of Fish and Wildlife: J. Bowman, T. K. Yazzie, A. Begay; New Mexico Department of Fish and Game: A. Barkalow, M. Ziegler; American Southwest Ichthyological Researchers LLC: S. Platania, M. Farrington, A. Wedemeyer; National Park Service: M. Trammel, J. Arnold; Bureau of Reclamation: Kerri Pedersen; Utah State University: P. MacKinnon; Jicarilla Apache Department of Fish and Wildlife: J. Mazzone; University of Arizona: C. Jenney, K. Gahl. Sophia Bonjour and Crosby Hedden deserve a special thanks for enduring numerous drives from Kansas to Utah, arduous field conditions, and countless philosophical debates. I thank all the members of the Gido Fish Ecology Lab for their support: Sky Hedden, Elizabeth Renner, Lindsey Bruckerhoff, Peter Pfaff, Eddy Wild, Trevor Jones, Andrew Hagemann, and Isabel Evelyn. I would also like to give a special mention to staff members of the Division of Biology for all their

support. Specifically, I thank Sarah Hacker, Tari Phillips, Melissa Bruce, and Becki Bohnenblust.

Lastly, I am extremely grateful to my friends and family for their encouragement throughout my career. My parents, Dennis and Linda Bogaard have provided tremendous support throughout my life. I am glad to know my field work always provides an excellent vacation destination for them.

Chapter 1 – Assessing translocation to restore spawning migration connectivity of Razorback Sucker, *Xyrauchen texanus*, in the San Juan River

Abstract

In the southwestern United States, decades of water diversions, construction of large impoundments, and loss of floodplain habitats have all contributed to a highly fragmented riverine landscape. Additionally, barriers negatively affect vital rates of riverine fish populations that rely on connected migratory routes to complete components of their life cycle, such as reproduction and recruitment. A capture-translocation strategy has been implemented for Razorback Suckers, *Xyrauchen texanus*, in the San Juan River to mitigate negative effects of barriers, while precluding passage of nonnative species. The goal of this study was to use radio telemetry to assess movement of Razorback Suckers following translocation above two barriers in the San Juan River. We deployed fixed remote radio receivers to determine residency time above each barrier and conducted mobile telemetry surveys to monitor upstream movements following translocation. Although individuals are likely to return downstream of barriers within a year of translocation, we provide evidence that most individuals remained upstream long enough to successfully spawn. After translocation above the Piute Farms Waterfall, 80% of individuals remained upstream for 26 days in 2020 and 23 days in 2021. Movement dynamics differed following translocation above the Public Service Company of New Mexico weir, where 80% of individuals remained upstream for 37 days in 2021. At each barrier, we observed upstream movements ranging from 2 to 262 km and detected distinct aggregations within the expected spawning season. While translocation efforts may seasonally reconnect migratory routes for a proportion of the population and increase spawning potential, it is not clear if this will be enough

to mitigate other recruitment bottlenecks, (e.g., predation by nonnative species) necessary to recover this species.

Introduction

Few aquatic ecosystems remain unaffected by human alterations and subsequent ecosystem fragmentation (Pringle 2001; Nilsson et al. 2005). The disruption of dynamic and natural flow regimes through impoundment, diversion, and channelization of rivers has profound consequences on ecological processes (Poff et al. 1997; Dudgeon et al. 2006). Such alterations disrupt temperature, frequency, magnitude, and timing of discharge events, negatively affecting the spatial and temporal heterogeneity of resources critical to native fish assemblages (Power et al. 1996; Marchetti and Moyle 2001; Armstrong et al. 2016). In addition to acting as physical barriers, large impoundments cause upstream lentification, resulting in a loss of habitat heterogeneity (Pringle 1997; Sabater 2008). Although large reservoirs provide one of the more dramatic examples of negative effects to native fish, even the presence of smaller physical barriers, such as low-head dams, diversions, and culverts, can reduce connectivity and be detrimental to species that depend on longitudinal migrations (Ward and Stanford 1983; Perkin and Gido 2012; Chappel et al. 2019).

Many riverine species rely on migrations between habitats to complete components of their life cycle, such as reproduction and recruitment (Cooke et al. 2011; Hicks et al. 2020). Barriers and fragmentation cause declines in fish populations by impeding dispersal and reducing gene flow among populations (Gido et al. 2016). Where barrier removal is difficult, bypass channels and active fish transportation above barriers are common methods to restore connectivity (Ovidio and Philippart 2002). When combined with restocking efforts, fish passages can increase fish production and improve gene flow among populations (Philippart 1994;

Catlano et al. 2007). Although efforts have been made to improve fish passage, there often exists a desire to prevent or reduce passage of undesirable species, such as nonnative or invasive fishes (Pratt et al. 2009). Thus, methods have been developed to allow selective passage based on physical, biological, and behavioral traits of species (Rahel and McLaughlin 2018). We focused on selective passage at two barriers in the San Juan River, which putatively disconnect critical habitats of endangered Razorback Sucker *Xyrauchen texanus* (Durst and Francis 2016; Pennock et al. 2020a, 2020b).

Although once abundant and widely distributed, Razorback Suckers are now rare and only persist because of extensive management efforts such as stocking, nonnative fish control and habitat manipulations (Bestgen et al. 2020). The former range of Razorback Suckers extended from the Colorado River delta at the Sea of Cortez to mainstem and tributary reaches in Arizona, Utah, New Mexico, Colorado, and Wyoming (Hubbs and Miller 1953; Marsh et al. 2015). Wild Razorback Suckers have been extirpated from most of their range, and there is virtually no documented natural recruitment to reproductive adults in river populations (Bestgen et al. 2020). Adult Razorback Suckers persist in large reservoirs within the Colorado River Basin, including Lake Powell, Lake Mead, and Lake Mohave, with recruitment detected only in Lake Mead (Albrecht et al. 2010, 2017). All other Razorback Sucker populations are supported through hatchery augmentation (USFWS 2018; Bestgen et al. 2020). Factors presumed to limit recruitment include predation by nonnative fish and access to predator-free habitats (Minckley et al. 2003). These long-lived, large-bodied fish occupy a variety of mainstem river habitat types as adults, including floodplains, backwaters, riffles, and deep eddies (Osmundson and Kaeding 1989). Although few studies focus on their spawning behaviors, Razorback Suckers have been observed spawning in aggregations over substrates including loose cobbles, gravel, and sand

(Tyus 1987; Tyus and Karp 1990). To help understand reproductive and recruitment limitations for this species, it is crucial to recognize the consequences of impeding movement of Razorback Suckers among potentially important habitats (Silva et al. 2018; Pennock et al. 2020a, 2020b).

In the San Juan River, a major tributary to the Colorado River in the southwestern United States, capture-translocate efforts to facilitate passage of Razorback Suckers, began in 2016 at a prominent waterfall barrier (Cathcart et al. 2018). Previous evaluations of these efforts determined that >80% of translocated Razorback Suckers returned below the barrier within a year; however, it was unclear how long after translocation downstream migration occurred (Pennock et al. 2020a). Likewise, it was not clear if translocated Razorback Suckers were using specific habitats during the spawning season. We used active and passive radio telemetry to quantify movement following capture-translocation efforts of Razorback Suckers at two barriers, including a waterfall and a water diversion structure. To assess the efficacy of translocation, we addressed three questions: (1) How long did translocated individuals remain upstream of a barrier? (2) Did fish continue upstream migration behavior following translocation? (3) Ded translocated Razorback Suckers aggregate at specific locations during the spawning season? Because we assumed these fish are moving upstream to spawn, we expected the majority of translocated individuals would remain upstream of the barrier for a period within the spawning season, and that aggregations of translocated Razorback Suckers would be identified upstream in putative spawning habitats.

Methods

Study Area

Originating in the San Juan Mountains in southern Colorado, the San Juan River and its tributaries drain 98,420 km², flowing 484 km to the Colorado River in an area currently

inundated by Lake Powell. The San Juan River was historically a highly variable stream with high spring runoff, followed by generally low baseflows, punctuated by periodic peaks from summer monsoon events (USFWS 2018). Following impoundment of the San Juan River by Navajo Dam in 1961, discharge was drastically altered, dampening flow and temperature variability by diminishing spring snowmelt and monsoonal flows while increasing summer baseflows. Beginning in 1993, experimental dam releases were used to mimic a natural flow regime, within the constraints of dam operations, with the goal of mitigating adverse dam effects on native fishes (Propst and Gido 2004). Lower reaches of the San Juan River, between the confluence of Chinle Creek and Lake Powell, are characterized as canyon-bound and having rapids between deep pools with intermixed cobble riffles (Bliesner and Lamarra 2000). Downstream of Slickhorn Canyon, the river was affected by the reservoir delta, thus is now generally shallow with shifting silt and sand. Upstream of Chinle Creek to Navajo Dam, the San Juan River has a relatively unconfined floodplain, with braided channels and cobble riffles.

Our study focused on two barriers to upstream fish movement within the San Juan River. First, the Piute Farms Waterfall (PFW) that was formed in the late 1980s, a result of sediment deposits left by the receding waters of Lake Powell (Ryden and Ahlm 1996). The sediment deposits in this delta caused the river channel to shift from its historic bed to a course that transected a bedrock outcrop, creating a complete barrier to upstream fish movement. The river shifted course again in 1995 following a subsequent rise and receding in lake levels. The river channel migration following this event replaced the old waterfall with a new waterfall, which formed approximately 3 km downstream in 2001 (Cathcart et al. 2018; Figure 1.1). The current waterfall is roughly 6 m tall and forms a complete barrier to upstream fish movement (Cathcart

et al. 2018). Since formation, the waterfall has only been inundated once for a two-week period in 2011 (Durst and Francis 2016).

The second barrier was a weir constructed by the Public Service Company of New Mexico (PNM) in 1971 to divert water to the San Juan Power Station near Fruitland, New Mexico (Figure 1.1). The current structure includes a river-wide concrete dam, approximately 1m tall, which obstructs upstream fish migrations (USBR 2001). To mitigate the effects of this barrier, a fish bypass channel was completed in 2003. The bypass channel includes a rock-ramp passage and a fish trap, built with the intention of providing selective passage to native fish, including Razorback Suckers, while removing nonnative fish from the river (Cheek 2014).

Fish Sampling and Tagging

Razorback Suckers were collected below each barrier using raft-mounted electrofishing for approximately two weeks in spring when high densities of migrating Razorback Suckers were present (Cathcart et al. 2018; Pennock et al. 2020b). Razorback Suckers were captured within 2 km downstream of PFW. Because the bed material was primarily sand and silt, we assumed individuals captured in this location were migrating upstream to spawn. We captured and transported Razorback Suckers in mid-March in 2020 (n = 156) and 2021 (n = 210). At the PNM weir, we captured Razorback Sucker in early April 2021 (n = 100). Because of potential spawning habitat (e.g., loose cobbles) in this area, we limited capture efforts to 0.5 km below the PNM weir, assuming individuals captured in this area were migrating upstream. All individuals were transported in a salted and aerated live-well and released approximately 2 km upstream of each barrier.

To investigate residency time and movement above each barrier, subsets of translocated Razorback Suckers were surgically implanted with a coded VHF radio transmitter with an

internal coil antenna (Advanced Telemetry Systems, Isanti, Minnesota, F1225C 150.234-151.172 MHz; estimated battery life of 300 days). In 2020, 41 Razorback Suckers (n = 23 female, n = 18 male) were released with radio transmitters upstream of the waterfall; 48 (n = 28 female, n = 20 male) individuals received radio transmitters at this location in 2021. In 2021, 11 individuals were recaptured and translocated at the waterfall with active radio transmitters that were implanted in 2020. Radio tagged individuals translocated in consecutive years were omitted from mean calculations in the second year, since we were unable to determine how long these transmitters remained active. In 2021, 40 individuals (n = 28 female, n = 12 male) were released with radio transmitters upstream of the PNM weir. All transmitters were less than 5% of individual fish body mass at the time of implantation to reduce effects on spawning or migration behavior (Brown et al. 1999). This model of transmitter produces a mortality signal when the internal microprocessor does not detect fish movement for >12h. Prior to surgical implantation, fish were anesthetized with tricaine methanesulfonate (MS-222; 100-200 mg/L). To implant each transmitter, an incision of about 10 mm was made into the peritoneal cavity, adjacent to the left pelvic fin. Incisions were closed with 2 to 3 external interrupted absorbable synthetic sutures (3-0, PDS 2; Ethicon, Inc., Sommerville, NJ). Fish were allowed to fully recover in an aerated tank with fresh river water. Individuals were not held more than one hour to minimize bias from long term post-operative care (Ovidio and Philippart 2002).

Data Collection

Passive tracking of fish through remote radio telemetry stations was used to detect the timing and movement of fish at each barrier and other critical locations within the river (Figure 1.3). Remote telemetry stations were equipped with two-directional four element yagi antennas and Advanced Telemetry Systems R4500C receiver and data logger (Advanced Telemetry

Systems Inc., Isanti, Minnesota) to record the time and signal strength of individuals returning to each barrier location following translocation. Six additional remote telemetry stations were deployed (7.5 km downstream of PFW to 294 km upstream) to detect individuals as they move throughout the river. Reference transmitters were placed near each fixed telemetry station to document the effective operation of each receiver.

Boat and aircraft mounted mobile telemetry surveys were conducted to identify distances moved above the barriers as well as potential spawning aggregations. Mobile telemetry surveys used 3- and 4-element yagi antennas with a radio receiver and data logger, equipped with a GPS antenna, to record associated frequency, individual code, signal strength, and coordinates. Aircraft-mounted surveys attempted to locate individuals throughout the San Juan River and San Juan arm of Lake Powell every 3 to 5 weeks from April through June in 2020 and 2021. Raft surveys occurred on 4 occasions, following the spawning season, from late May through early July in 2020. In 2021, river-wide boat surveys were conducted every 3 to 5 weeks from March through July.

Data Analyses

We used directional movement data at remote radio telemetry stations positioned at each barrier to quantify the duration each translocated fish remained above a barrier. These data allowed us to determine the individual's position (up or downstream) relative to the barrier. We calculated median and range residency time above a barrier for each site in each year.

Location of individuals identified during mobile telemetry surveys were used to quantify minimum linear ranges of Razorback Suckers. We acquired individual positions to the nearest 100 m for each survey using the maximum signal strength paired with the GPS location on a given day. We then used each known daily encounter, subtracting the furthest known

downstream location from the furthest known upstream location, to determine total linear range for individuals for one year following translocation.

In addition to total linear ranges, 50% core ranges were calculated within the spawning season to identify spawning aggregations. Core ranges were established for each fish by calculating the minimum distance containing 50% of the locations. We restricted spawning season ranges to mid-March through June, when mean water temperature ranged from 11 to 16.1°C (Clark-Barkalow et al. 2021). The spawning season core range represents the area individuals were likely to occupy in this time frame, which could exclude long distance movements to or from a spawning location (Crook 2004), while including the possibility that individuals may travel to other nearby spawning sites (Modde and Irving 1998). We classified Razorback Sucker spawning aggregations as areas where ≥2 individual spawning core ranges overlapped within seven days (Tornabene et al. 2020).

Results

How long did translocated fish remain above the barrier?

Remote telemetry data indicated 37 of 41 radio tagged Razorback Suckers (90.2%) returned downstream of PFW within a year of facilitated passage in 2020 (Figure 1.2). Median residency time was 56 days (range = one to 442 days; Table 1.1). Three fish returned to the capture location below the waterfall within two days of passage. Most individuals (>80%) remained upstream of PFW for at least 26 days. Although failed detections of reference transmitters indicated the remote radio receiver at the waterfall malfunctioned for 37 days (April 16 through May 22, 37 to 73 days following translocation), subsequent surveys indicated 36 (85%) of translocated individuals returned downstream of PFW by the end of the expected spawning season, 76 days after capture. A similar pattern was observed at PFW in 2021, where

we observed three individuals returning below the waterfall within the initial two days following translocation, and median residency was 36 days (range = 2 to 135 days; Table 1.1). In 2021, 80% of the translocated individuals remained upstream of the waterfall for 23 days (Figure 1.2). These fish moved downstream throughout the spawning season, with only 5 individuals remaining upstream of the barrier 73 days after capture and transport.

Following translocation above the PNM weir, 2 individuals returned downstream of the barrier within 2 days. Median residency was 100 days (range = 1 to 105) above the PNM weir (Table 1.1). Greater than 60% of the radio tagged individuals remained upstream of PNM weir throughout the expected spawning season.

Did translocated fish exhibit upstream migration behavior?

Mobile surveys and remote telemetry data demonstrated upstream movements among translocated Razorback Suckers were common above both PFW and PNM weir. In 2020, mobile survey effort was limited due to the pandemic; therefore, only seven individuals were detected above PFW (Table 1.2, 0.2 to 142 km). Remote telemetry data suggested Razorback Suckers were not likely to move upstream of canyon-bound reaches, between PFW and Chinle Creek (127 km upstream). Only one individual was detected upstream of the canyon reaches, at the Sand Island remote station, (142 km upstream) for a brief period (<24 hours). Razorback Suckers were detected within a mean range of 17.2 km (SD = 17.1) above PFW. In 2021, with greater mobile survey effort, 52 fish were detected (0.2 to 262.2 km) after being translocated above PFW (Figure 1.3), two of which moved upstream of the remote receiver at Sand Island. A third individual that was translocated in 2020 remained upstream of the waterfall and moved to a location 262.2 km upstream in 2021. On average, fish translocated in 2021 occupied a linear range of 44.6 km (SD = 32.8) before moving downstream of PFW to Lake Powell. Following

translocation above the PNM weir, 37 Razorback Suckers were detected upstream (0.5 to 34.9 km) of the barrier (Table 1.2). The average linear range of individuals was 19.4 km (SD = 9.2) before moving back downstream of the barrier.

Were aggregations detected within the spawning season?

Although Razorback Suckers occupied upstream habitats during the spawning season in 2020, limitations on mobile surveys impeded our ability to detect aggregations. The following year, in 2021, core spawning ranges were generally short (<10 km) with a mean core range of 3.3 km (SD = 6.5). These individuals formed four discrete aggregations, approximately 2.7, 31.4, 36.2, and 40.3 km above the waterfall (Figure 1.3). The lowest three aggregation sites were found at the first available riffle habitat types, containing mixed cobble, gravel, and sand, upstream of the waterfall. Forty radio-tagged individuals (83%) were detected at these riffles for up to 10 days within the spawning season. The fourth aggregation was approximately 4 km further upstream separated from other aggregations by Government Rapid.

Fish translocated above PNM weir occupied short core spawning ranges (<10 km); however, mean core spawning ranges were 2.1 km longer (mean = 5.4, SD = 6.4) than those translocated above the waterfall. We identified 5 distinct aggregations from individuals translocated above the PNM weir from 13.2 km downstream to 19.9 km upstream of the barrier. A small aggregation was detected 13.2 km downstream of the weir, where the core spawning ranges of 2 individuals overlapped (Figure 1.3). Twenty individuals (50%) used habitat within 2 km upstream of the PNM weir for >10 days after translocation (Figure 1.3). Remaining fish were distributed among upstream aggregations at 7.4, 12.7, and 19.9 km upstream of the PNM weir, with 6, 4, and 8 individuals detected at each location respectively.

Discussion

Results from remote radio telemetry stations supported our prediction that Razorback Suckers would remain upstream of barriers during the spawning season following translocation. Residency time and water temperatures above both barriers were likely adequate for individuals to spawn (Hink et al. 2011; Clark-Barkalow et al. 2021). Many individuals (>80%) remained upstream of PFW throughout late March, while mean water temperature was within previously observed spawning ranges (Bestgen et al. 2011; Clark-Barkalow et al. 2020; mean = 10.1°C, range = 8 to 12.4°C). As mean water temperature climbed above 15°C, individuals moved downstream, where >85% of Razorback Suckers returned below the waterfall within 77 days of translocation in 2020 and 73 days in 2021. We expect individuals moving downstream might be seeking warmer temperatures and greater food availability (Tyus and Karp 1990; Pennock et al. 2021). Downstream migration to Lake Powell, following spawning, provides evidence supporting the hypothesis that this population exhibits an adfluvial life history strategy, which is not addressed by species recovery goals (USFWS 2018; Pennock et al. 2020a).

Movement dynamics were different for fish translocated above the PNM weir. Fish translocated above PNM weir remained upstream for 19 days longer, on average, than those transplanted above PFW, with a greater percentage of individuals remaining upstream longer than 100 days (>47% at PNM weir, compared to 10% at PFW). While individuals at both barriers are likely to return downstream of the barrier within a year of translocation, we suspect the slower post-spawning movements of Razorback Suckers transplanted above the PNM weir was related to more complex and likely more productive habitat in this reach compared to low productivity in canyon reaches above PFW.

Most fish transplanted above PFW and PNM continued movements upstream following translocation, as predicted. While we observed long distance movements (>100 km) in some individuals, Razorback Suckers translocated above PFW generally remained within the canyon reaches of the San Juan River. Similarly, fish transplanted above PNM weir continued upstream migration, but traveled 28.5 km less and had smaller total linear ranges (25.3 km less), on average, than at PFW. This could be related to a higher density of riffle habitat and potentially suitable spawning substrate within proximity to PNM weir compared to PFW (Bliesner and Lamarra 2000). Upstream travel beyond those detected above PNM might be impeded by cold-water discharge from Navajo Dam (Miller and Swaim 2017), reducing the suitability of spawning conditions. Thus, distance moved upstream of barriers is likely determined by environmental conditions and the physical characteristics of the stream (i.e., occurrence of cobble and gravel substrates).

As predicted, Razorback Suckers were detected in aggregations during the spawning season, following facilitated passage. At each barrier location, several translocated individuals were detected using nearby riffles, with mixed sand, gravel, and cobble. We expect the presence of Razorback Sucker aggregations in habitat with loose cobble and gravel riffles within the spawning season is indicative of spawning behavior (Tyus and Karp 1990). Upstream of PFW, 14 Razorback Suckers aggregated in an area formerly inundated by Lake Powell, where tributaries discharged gravel and cobble that may serve as spawning substrate. Two aggregations comprising 50% of the translocated fish were detected near Slickhorn Canyon (34.6 km upstream of PFW; Figure 1.2). Aggregations encountered in this area were not surprising, since prior research suggested this was an important spawning location for Razorback Suckers (Elverud 2010). Similar behavior was observed above the PNM weir, where 50% of individuals were

detected in riffles within 3 km upstream of the barrier following spawning season. Other Razorback Suckers translocated upstream of PNM weir were detected in aggregations between 7 to 20 km upstream of the barrier. Because we observed a more uniform distribution of translocated individuals upstream of PNM weir compared to PFW, we hypothesize a greater availability of spawning substrates may exist in proximity to the PNM weir, whereas cobble and gravel riffles are likely patchy resources in downstream canyon reaches.

Endogenous and exogenous factors, not considered by this study, influence fish migrations and spawning site selection. For example, many salmonids rely on olfactory cues to return to natal streams (Bett et al. 2018); whereas hydrologic and morphologic factors predicted spawning site selection (Benjankar et al. 2016). Furthermore, presence of conspecifics may attract individuals to an aggregation (Anteneh et al. 2012) or increase competitive exclusion, driving individuals away from spawning sites (Grabowski and Isely 2006). It remains unclear how these factors affect hatchery stocks of Razorback Suckers in this regulated system. Prior research demonstrated movement of translocated fish may depend on source populations (Carpenter-Bundhoo et al. 2019). However, we believe the distinct movement observed at PFW compared to PNM weir were more likely driven by environmental conditions and resource availability, since these groups originated from the same hatchery (STReaMS 2021).

Although we do not provide evidence that translocated individuals successfully reproduced, we expect a possibility that larvae produced from aggregations detected in this study will drift below each barrier. Moreover, the location of putative spawning aggregations within the watershed might influence the growth and survival of subsequently produced larvae. For example, larvae produced near PFW could encounter warmer water conditions, leading to more rapid growth, but are more susceptible to predation once below PFW (Clark-Barkalow et al.

2021). Alternatively, drifting larvae produced near PNM weir might have a greater opportunity of entrainment in low-velocity habitat types with a longer river corridor available, with the consequence of colder water conditions decreasing growth rates (Clark-Barkalow et al. 2021). Because translocated fish and subsequently produced larvae were likely to move downstream of each barrier, annual passage efforts are needed to maintain connectivity to upstream habitats. Furthermore, recent evaluations of captured larvae indicated the number of effective breeders and repeat spawning adult Razorback Suckers were relatively low within the San Juan River (Diver et al. 2021). Reconnecting migratory routes of adult Razorback Suckers to spawning sites upstream of PFW and the PNM weir could be a valuable tool to increase reproductive output.

While the efficacy of selective fish passage is often variable by species and dependent on the availability of upstream resources (Harris and Hightower 2011; Rahel and McLaughlin 2018), our results indicated facilitated fish passage might be an effective strategy to reconnect migratory Razorback Suckers to spawning sites. Recent abundance estimates suggested approximately 755 adult Razorback Suckers migrate to the area below PFW each spawning season (Cathcart et al. 2018). Therefore, our translocation efforts facilitated passage to only ~20% of this population. Consequently, even with selective passage, these barriers restrict movements of Razorback Suckers and reduce reproductive potential. Barrier removal or more intensive mitigation measures should be considered to provide access to spawning habitats. For example, Knott et al. (2021) found engineered spawning grounds increased reproductive output and recruitment of rheophilic fishes. Although this does not decrease fragmentation, a similar strategy could be implemented to add course gravel and cobble substrates below PFW in effort to increase Razorback Sucker reproduction. In some cases, fish bypass channels restored habitat connectivity in migratory catostomids (Bunt et al 1999; Cooke et al. 2005). Because open

passage at either PFW or PNM weir has associated risk of increasing nonnative fish dispersal, managers will need to weigh the costs of hindering the reproduction output of an imperiled species against restricting the range and dispersal of nonnative species. While increasing reproductive output can potentially increase likelihood of recruitment, continued management and research are needed to address the bottleneck experienced in the early life stages of Razorback Suckers (Pennock et al. 2019).

Acknowledgments

We thank C. Hedden, S. Hedden, A. Hagemann, I. Evelyn, L. Bruckerhoff, C. Gido, P. Pfaff, L. Renner, D. Haukos (KSU); S. Platania, M. Farrington, A. Wedemeyer (ASIR); N. Franssen, S. Durst, E. Gilbert, M. Mata, D. Kaus, B. Schleicher (USFWS); P. MacKinnon, (USU); Utah Division of Wildlife Resources Moab Field Station, M. Trammel, J. Arnold (NPS); K. Pedersen (BOR); J. Mazzone (Jicarilla Apache Game and Fish); T. Pilger (Fish Bio Consultants) C. Jenney, and K. Gahl (University of Arizona) for advice, data collection, and field assistance. Fish sampling and tagging protocols were conducted under the approval of the Kansas State University Institutional Animal Care and Use Committee (Protocol Number: 4494). Fish sampling would not have been possible without permitting and access provided by the Navajo Nation (Permit Number: 1244, State of Utah, and US Fish and Wildlife Service (Permit Number: TE067729-6). This work was funded by the Bureau of Reclamation through the San Juan River Basin Recovery Implementation Program.

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Figures



Figure 1.1. Barriers to upstream fish movements in the San Juan River. Piute Farms Waterfall (PFW, top) formed in 2001 resulting from sediment deposits left from the receding waters of Lake Powell, Utah, causing the river to shift its course over a bedrock outcropping. The Public Service Company of New Mexico (PNM) weir (bottom) was constructed in 1971 to divert water to a nearby power plant in New Mexico.

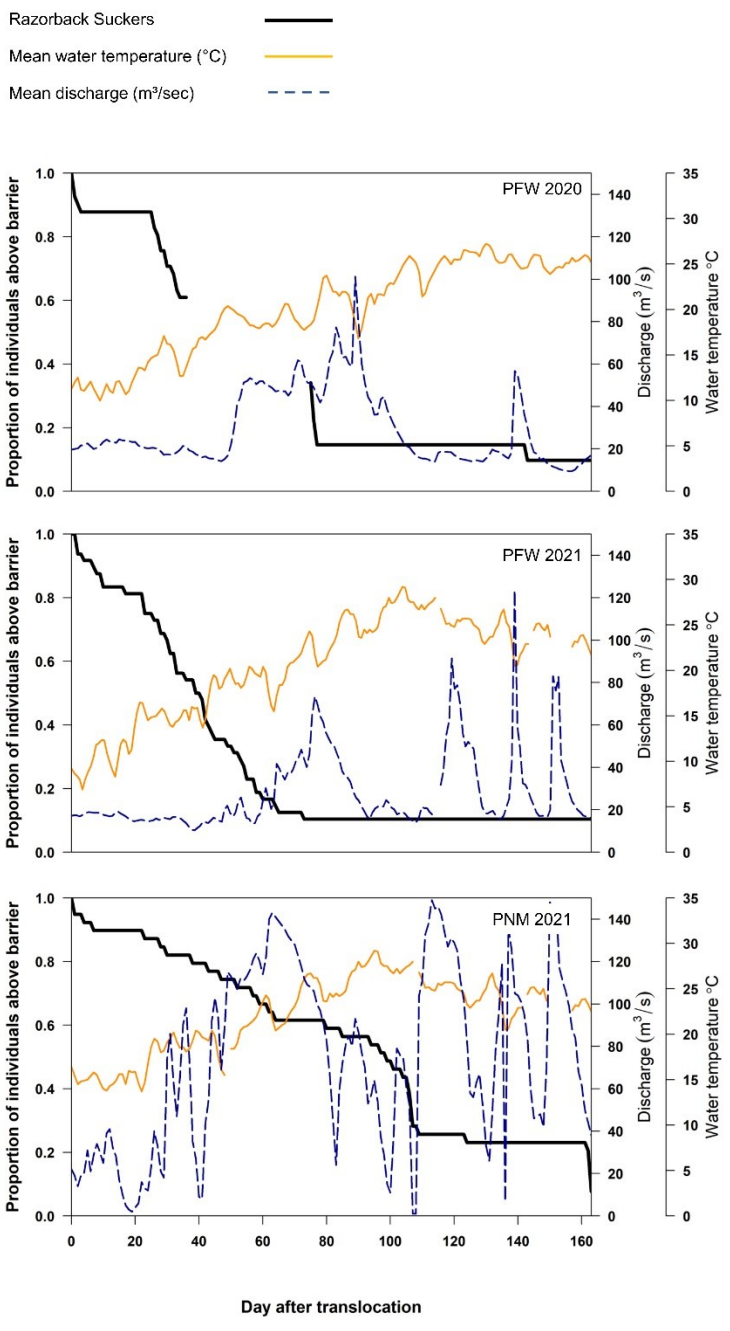


Figure 1.2. Proportion of Razorback Suckers remaining upstream of a barrier after being translocated above the Piute Farms Waterfall (PFW) and Public Service Company of New Mexico (PNM) weir, plotted with mean daily water temperature, and mean daily discharge at a USGS stream gage near Mexican Hat, UT #09379500. The remote radio receiver at PFW malfunctioned for 37 days in 2020 (37 to 73 days following translocation).

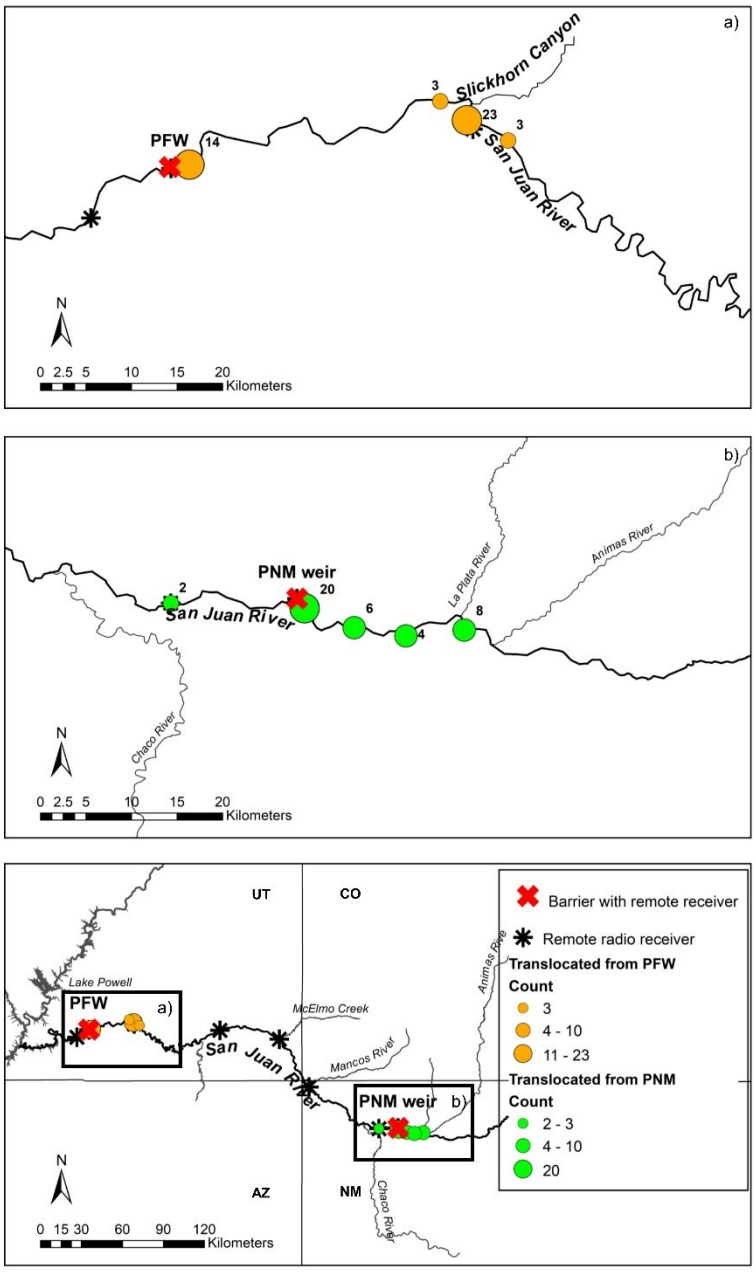


Figure 1.3. Distribution and counts of detected aggregations of Razorback Suckers within the spawning season in 2021, after facilitated passage beyond Piute Farms Waterfall (PFW, top panel) and the Public Service Company of New Mexico (PNM, center panel) weir. Reaches between PFW and Chinle Creek (127 km upstream of PFW) are generally canyon bound.

Tables

Table 1.1. Residency time (number of days) of Razorback Suckers upstream of a barrier following facilitated passage efforts at Piute Farms Waterfall (PFW) and the Public Service Company of New Mexico (PNM) weir in 2020 and 2021.

Site	Year	Number translocated	Number radio tagged	Residency time above barrier (Median, range days)
PFW	2020	156	41	56, 1 - >442
	2021	210	48	36, 2 - >135
PNM	2021	100	40	46.5, 1 - 435

Table 1.2 Maximum upstream distances traveled and mean linear ranges of Razorback Suckers release above the Piute Farms Waterfall (PFW) and the Public Service Company of New Mexico (PNM) weir. Distances refer to the distance traveled from the release location. Individuals with fewer than three detections were omitted from mean calculations.

Site	Year	Individuals detected upstream	Maximum upstream detection (Median, range km)	100% Range (Mean km ±SD)	Spawning season 100% range (Mean km ±SD)	Spawning season 50% range (Mean km ±SD)
PFW	2020	7	19, 2 - 141.9	17.2, 17.1		
	2021	52	36, 0.2 - 262.2	44.6, 32.8	20.7, 25.3	3.3, 6.49
PNM	2021	37	11.6, 0.6 - 34.9	19.4, 9.2	19.1, 28.4	5.4, 6.4

Chapter 2 – Environmental cues of Razorback Sucker, *Xyrauchen texanus*, spawning migrations in the San Juan River

Abstract

River regulation through reservoir management and habitat alterations have profound effects on aquatic and riverine communities by altering the magnitude and timing of discharge and temperature regimes and interrupt sediment and nutrient transport. Many riverine species have adapted life history traits related to spawning or reproduction that are suited to a natural and dynamic flow regime; thus, disturbances to a natural regime may limit reproductive success. Among several imperiled species endemic to the Colorado River Basin, Razorback Suckers (*Xyrauchen texanus*) have experienced drastic population declines attributed to an altered river landscape. Despite intensive management efforts, the species experiences reproductive and recruitment bottlenecks. Although previous studies suggested Razorback Suckers may spawn during increasing spring discharge, little is known about the abiotic cues that influence spawning movements. To test the association between timing of Razorback Sucker spawning migrations and environmental cues, we used Passive Integrated Transponder (PIT) tag detection data at two barriers to upstream movement. Because photoperiod, temperature, and discharge may affect spawning and movement behavior, we hypothesized that one or more of these variables could predict the timing of Razorback Sucker occurrence at each barrier within the spawning season. Our results indicated strong associations between putative Razorback Sucker spawning migrations and mean weekly water temperature, where the largest proportions of fish were detected below each barrier as water temperature was increasing between 7.1 to 14.2°C. We provide a model that may improve prioritization and efficiency at selective passage facilities,

increasing reproductive potential. However, we do not address other reproductive and recruitment limitations (e.g., access to predator-free habitats).

Introduction

Human activities through the construction of dams, river regulation, and habitat alterations have severe effects on ecological processes in riverine communities (Crook et al. 2015). Dams alter the magnitude and timing of discharge and temperature regimes and interrupt sediment and nutrient transport (Ligon et al. 1995; Bunn and Arthington 2002). These disruptions result in a decrease in habitat heterogeneity and increased fragmentation between habitats, adversely affecting native fish populations (Marchetti and Moyle 2001; Armstrong et al. 2016). Many riverine species have adapted life history traits related to spawning or reproduction that are suited to a natural and dynamic flow regime (Lytle and Poff 2004; Cooke et al. 2011). Damming of rivers causes declines in native fish populations by limiting dispersal, reducing gene flow between populations, and diminishing reproductive success (Dudgeon et al. 2006; Gido et al. 2016).

Among several imperiled species endemic to the Colorado River Basin, Razorback Suckers (*Xyrauchen texanus*) have experienced drastic population declines attributed to an altered river landscape (USFWS 2002; Bestgen et al. 2020). Although they were once widely distributed throughout the Colorado River Basin, Razorback Suckers have been extirpated from much of their historic range (Minckley et al. 2003). Since populations were dwindling and natural recruitment had not been detected, the species was listed as federally endangered in 1991, citing fragmentation from major dams and predation by introduced species as primary causes (USFWS 2002). Intensive hatchery augmentation of adult Razorback Suckers allows the species to persist in mainstem rivers and reservoirs (Zelasko et al. 2010; Albrecht et al. 2018; Bestgen et

al. 2020). Other management strategies include barrier mitigation, nonnative fish removal, floodplain restoration, and environmental flow releases from reservoirs (USFWS 2018). Razorback Suckers are long-lived and rely on connectivity among a variety of habitats, including mainstem rivers, tributaries, rivers, and floodplain wetlands (Osmundson and Kaeding 1989). Prior research demonstrated adult Razorback Suckers remain sedentary outside of the spawning season (Durst and Francis 2016) but exhibit long movements (>100 km) to reach spawning habitats (Tyus and Karp 1990; Pennock et al. 2020a). In the Upper Colorado River Basin, Razorback Suckers move into upstream habitats between March and May, where spawning aggregations have been observed in riffles with loose cobble and gravel substrates (Tyus 1987) when water temperatures were between 9 and 17°C (Tyus and Karp 1990; Clark-Barkalow et al. 2020, 2021). Previous studies in the Green River, Utah, suggested spawning migration cues for Razorback Suckers rely on increasing discharge within a temperature threshold, although they lacked a rigorous quantitative approach (Modde and Irving 2011) or focused on the act of spawning rather than migration behavior (Bestgen et al. 2011). Understanding the environmental components that influence the timing of Razorback Sucker spawning behavior might provide necessary information on environmental factors that influence reproduction and recruitment.

Knowledge of variables that affect movement and reproductive ecology of fishes can help identify habitat requirements and understand recruitment strategies (Dammerman et al. 2019). Prior studies demonstrated riverine fishes rely on environmental cues to initiate spawning behavior and migrations to spawning habitats (Northcote 1984; Serrat et al. 2019). For instance, some species move to spawning habitats at rising or peak discharge, which could increase dispersal into shallow habitats and clean spawning substrates (Tyus and Karp 1990; Keefer et al. 2008). Other fishes use a temperature threshold to determine timing of spawning to increase egg

survival and larvae growth (Clarkson and Childs 2000; Skov et al. 2010). Additionally, photoperiod may drive gonad development and melatonin regulation, which influence reproductive behavior in fishes (Migaud et al. 2010; McPherson and Kjesbu 2012). Furthermore, photoperiod may be a strong migration cue, because some fish species may have adapted to reproduce at a consistent time when other environmental conditions were historically optimal (Quinn and Adams 1996). While photoperiod is a fixed parameter, reservoir management decisions influence flow and temperature regimes, impacting fish communities (Marchetti and Moyle 2001; Propst and Gido 2004; Dibble et al. 2021).

To quantify inter-annual timing of Razorback Sucker spawning migrations, our study focused on occurrences of fish at two barriers to upstream movement, each with ongoing efforts to provide selective passage for Razorback Suckers (Figure 2.1). These barriers provide an opportunity to study spawning migration, since fish aggregate below these structures during the spawning season (Cathcart et al. 2018).

We first examined Razorback Sucker data collected below the Piute Farms waterfall (PFW), which formed as a result of sediment deposited by the receding waters of Lake Powell (Cathcart et al. 2018a). Through superimposition processes, the river cut through delta sediments, shifting from its historic channel to a course that flowed over a bedrock outcropping. Several waterfalls formed periodically in the San Juan River delta since the late 1980s due to changing lake levels (Ryden and Ahlm 1996). The current waterfall formed in the Piute Farms area in 2001, creating a 6m tall barrier. Since formation, PFW has only been inundated by Lake Powell for a single two-week period in 2011 (Durst and Francis 2016).

Secondly, we considered Razorback Sucker migrations at a weir 320 km upstream of PFW. The weir was constructed by the Public Service Company of New Mexico (PNM) in 1971

to divert water to the San Juan Power station, near Fruitland, New Mexico. The PNM weir includes a 1m tall river-wide concrete dam, impeding upstream fish movements (USBR 2001). To mitigate negative effects of this barrier, a fish bypass channel was constructed in 2003. The bypass channel includes a fish trap, designed to preclude nonnative fishes, while providing selective passage to Razorback Suckers (Cheek 2014).

Our goal was to test the association between the arrival of Razorback Sucker at PFW and PNM weir and environmental cues. Because photoperiod, temperature, and discharge can affect spawning and movement behavior, we hypothesized that one or more of these variables could predict the timing of Razorback Sucker occurrence at each barrier within the spawning season. Secondly, because the timing and magnitude of variable may not be the same at the two barriers, we predicted the relative importance of environmental covariates might vary between sites. Specifically, photoperiod will be virtually the same at both sites, therefore if this parameter is a cue for Razorback Sucker migrations, we expected patterns to be similar. Because PNM weir is higher in the watershed and water temperature is lower, we expected migrations to occur later than at PFW within the same temperature range, if temperature was a driver of migration. Lastly, we predicted discharge would have a stronger association with migration timing at PNM than PFW, because fish migrating to PFW originate in Lake Powell (Pennock et al. 2020b) and would not experience fluctuations in river discharge.

Methods

Study Area

The San Juan River drains the San Juan mountains in southern Colorado, flowing southwest through an arid landscape towards its confluence with the Colorado River. Historically, this was a highly variable river, fed by spring runoff from snowmelt and low

summer baseflows, punctuated by late summer monsoon runoff (USFWS 2018). The San Juan River was impounded by Navajo Dam in northern New Mexico in 1961, drastically altering natural discharge and temperature regimes. Since 1993, experimental dam releases were implemented to mimic a natural flow regime and reduce adverse effects on native fish (Propst and Gido 2004). Unfortunately, because of the constraints of dam operations and competing water interests, recommended releases were not always possible. Downstream, further fragmentation is caused by several smaller low-head weirs, constructed for industrial and agricultural purposes. Following its construction in 1966, Glen Canyon Dam impounded the Colorado River, inundating the lowest 100 km of the San Juan River at full pool.

Data Collection

Timing and duration of Razorback Sucker spawning migrations were determined using Passive Integrated Transponder (PIT) tag detection data from 2015 through 2021. Since the mid-1990s, annual stocking has augmented the Razorback Sucker population within the San Juan River. Razorback Suckers are generally stocked as adults (>300 mm) and implanted with a PIT tag (12 mm, full-duplex, 134.2 kHz; BioMark, Boise, Idaho) prior to release. Recruitment of naturally spawned adults has not been verified in the system; therefore, barring tag loss, migrating adults possessed PIT tags (Zelasko et al. 2010). The timing of individual detections was recorded using PIT antennas deployed at each barrier.

We obtained PIT tag detections using antennas deployed in the eddies below PFW from 2015 through 2021. A series of swim-through PIT tag antennas operated within the fish bypass channel at the PNM weir from summer 2014 through 2021. Within this period, 2 to 4 antennas were dispersed longitudinally through the channel, with each antenna spanning the width of the channel (approximately 5 m). Additional antennas were operated seasonally in the river channel,

below the concrete barrier. PIT tag detections from adult Razorback Suckers that have been in the river more than one year were queried from the Species Tagging Research and Monitoring System database (STReaMS 2021). STReaMS is a collaborative database that provides centralized sampling, stocking, and detection data from the Upper Colorado River and San Juan River endangered fishes recovery programs. Because this study focused on spawning migration behavior, we limited detection data to mid-February through June when temperatures typically range from 4 to 18°C and match the expected spawning and migration season at each barrier (Bestgen et al. 2011; Clark-Barkalow et al. 2021). When available, we used test-tag data to confirm the effective operation for each antenna array, removing weeks where antennas were not operational. Environmental covariate data, including photoperiod, discharge, and water temperature were obtained through NOAA and USGS stream gages located near Bluff, UT (#09379500) and Farmington, NM (#09365000).

Data Analysis

All analyses were performed in program R, version 3.6.3 (R Core Team 2020). We used generalized linear models (GLMs) in the R packages "AICcmodavg" and "MuMIN" (Barton 2010; Mazerolle 2020) to test association of environmental covariates with the timing of Razorback Sucker spawning migrations. We considered the date a fish was first detected below a barrier as the initiation of migration (Heim et al. 2015). Since small scale fluctuations in detections can be difficult to predict, we summarized counts of migrating Razorback Suckers on a weekly basis (Heim et al. 2015; Cathcart et al. 2017). We fit GLMs with a weighted binomial distribution, where the response variable equals a proportion of individuals detected for the first time in a given week compared to the total number of individuals detected in a season (Zuur et al. 2009; Warton and Hui 2011). Mean weekly water temperature, mean weekly discharge, and

mean weekly photoperiod, as well as 7-day lagged effects were included as continuous fixed effects. Lag effects were included since daily effects may not be indicative of fish behavior, which may take time to elicit a physiological response to an environmental cue (Forsythe et al. 2012; Vine et al. 2019). Quadratic terms for photoperiod, temperature, and discharge were also considered since these variables generally increase and decrease throughout the study period. Research has shown even slight fluctuations in temperature or discharge can affect migration behavior (Jones and Petreman 2014). Therefore, in addition to mean and lagged effects, we considered the change in mean temperature and discharge from the start of the period compared to the end of the period. In addition to continuous variables, we included temperature and discharge trends as categorical variables, depending if the means were increasing or decreasing based on the means from the previous week. All continuous predictor variables were scaled and centered to facilitate comparisons among coefficients (Barton 2010). To account for differences in timing and magnitude in environmental covariates between sites, we tested independent models for PFW and PNM weir.

We used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare additive global models and nested models for each site (Burnham and Anderson 2004). We used the "dredge" function with a Wald's Z-test to determine variable inclusion in global model functions, removing variables until all were significant ($P < 0.10$, Zuur et al. 2009; Barton 2010). We ensured all model assumptions were met, tested for correlation between covariates by calculating Person's correlation coefficients, and tested for multicollinearity among covariates in best-supported models by calculating variance inflation factors. We considered Pearson's coefficient $<|0.4|$ and variance inflation factors < 5 acceptable (Fox and Weisberg 2011; Daoud 2017). Support for top models included AIC weights and ΔAICc. We report model estimates

with 95% confidence limits for best-supported models, averaging estimates when ΔAICc < 2. We used McFadden's pseudo R^2 to test and report model performance, where values >0.20 were considered a good fit (Bennet 1999).

Results

Razorback Sucker detections

The seasonal number of Razorback Suckers detected below PFW from 2015 through 2021 ranged from 440 to 694 (mean = 549, SD = 97.4). The greatest proportion of detections typically occurred over a two to three week period in early to mid-March, with 40% of annual detections commonly occurring within a week. Seasonal detections were considerably more variable at PNM weir than PFW, ranging from 212 to 961 (mean = 544, SD = 249.2). We generally observed a longer duration of detections at PNM weir compared to PFW, with the greatest proportion of detections occurring over a three to four week period in late March throughout April. There was considerable inter-annual variation in both water temperatures and discharge at both sites throughout the study. Mean water temperature during the spawning season ranged from 10.8 to 16.2°C at PFW and 9.5 to 14.8°C at PNM and mean discharge ranged from 18.3 to 76.8 m^3/s at PFW and 23.2 to 114.9 m^3/s at PNM weir (Table 2.1).

Environmental factors and timing of migration

Photoperiod and temperature were strongly correlated (Pearson's $r > 0.71$), consequently, we constructed two sets of global models for each site to test these covariates independently, hereafter, referred to as photoperiod or temperature models. At both sites, models that included photoperiod as a quadratic term best predicted the occurrence of migrating Razorback Suckers. At PFW, the top-ranked model included photoperiod, discharge, minimum discharge, and discharge trend (AICc weight = 0.74; Table 2.2). Within this model, photoperiod as a quadratic

term best explained the variance (pseudo $R^2 = 0.36$), where the greatest proportion of Razorback Suckers peaked at a photoperiod near 676 minutes at PFW (β = -0.33, lower 95% confidence limit = -0.37, upper 95% confidence limit = -0.29; Figure 2.2, Table 2.3). Temperature models at PFW included temperature, discharge, change in magnitude of temperature, temperature trend, and discharge trend as the top-ranking model (AICc weight = 1.00; Table 2.2.). Here, temperature explained most of the variance (pseudo $R^2 = 0.29$), predicting peak Razorback Sucker migration would occur at mean weekly water temperatures near 9.6°C (β = -0.35, lower 95% confidence limit = -0.39, upper 95% confidence limit = -0.32; Figure 2.3, Table 2.3).

At the PNM weir, a model including photoperiod, change in magnitude of discharge, minimum discharge, and discharge trend was selected as the top-ranking model (AICc weight = 0.76, Table 2.2). Similar to PFW, photoperiod explained most of the variance in the model (pseudo $R^2 = 0.32$, Table 2.3). Unlike PFW, this model predicted Razorback Sucker migrations will occur at PNM weir in early April, when photoperiod reaches 773 minutes per day (β = -1.09, lower 95% confidence limit = -1.14, upper 95% confidence limit = -1.03, Figure 2.2, Table 2.3). Model selection determined temperature models at PNM weir included temperature, discharge, change in magnitude of temperature, temperature trend, minimum temperature, and discharge trend as a top-ranking model (AICc weight = 0.66). At PNM weir, Razorback Sucker migrations were correlated with temperature, which predicted most of the variance in the model (pseudo R^2 = 0.21, β = -0.69, lower 95% confidence limit = -0.74, upper 95% confidence limit = -0.64, Table 2.3). Although discharge parameters were included in top-ranking models, model selection indicated discharge was not a good fit as a univariate predictor of Razorback Sucker migrations at either barrier (pseudo $R^2 = 0.08$ at PFW, pseudo $R^2 = 0.05$ at PNM weir; Table 2.2, Table 2.3).

Discussion

Photoperiod

In contrast to previous research that demonstrated photoperiod may influence the timing of fish spawning behavior (Migaud et al. 2010; McPherson and Kjesbu 2012), our results did not support our prediction that photoperiod was an important cue for migration behavior because the timing of migration differed between sites. Razorback Suckers tended to migrate to PFW in early March when photoperiod was near 676 minutes per day (Figure 2.2), while the highest proportion of new detections at PNM weir were generally in early April, when daily photoperiod was near 773 minutes (Figure 2.2). PFW and PNM weir occur at a similar latitude and

Although photoperiod was a reliable predictor of Razorback Sucker detections at individual locations, we believe water temperature is a more plausible trigger of migration behavior.

Temperature

Our results indicated strong associations with water temperature and the timing of Razorback Sucker occurrence at PFW and PNM weir, as expected. At both barriers, Razorback Sucker detections were positively correlated with increasing water temperatures, where mean weekly water temperatures most precisely predicted Razorback Sucker occurrence. Below PFW, Razorback Suckers tended to migrate to this area as mean weekly water temperatures ranged from 7.1 to 12.7°C (Figure 2.3), which typically occurred in the first two weeks in March. At PNM weir, largest proportions of Razorback Sucker detections occurred while water temperature ranged between 10.8 and 14.2°C (Figure 2.3), which was observed between mid-March through early May. Although Razorback Suckers tended to migrate to PFW at cooler water temperatures, the predicted range of first detections overlapped between 10.8 and 12.7°C between the two

sites, providing support for our predictions. The timing of Razorback Sucker migrations within temperature ranges detected in this study coincides with the range of spawning temperatures (9-17°C) previously observed within the San Juan and Green River (Bestgen et al. 2011; Tyus and Karp 1990; Clark-Barkalow et al. 2021). Because mean water temperature was associated to the timing of Razorback Sucker spawning migrations, it was not surprising to us that migrations occurred later in the season at PNM weir compared to PFW. Because PNM weir is higher in the watershed, thus closer to snowmelt runoff and cold water hypolimnetic discharge from Navajo Dam, water temperatures warm later in the season (Miller and Swaim 2017).

Discharge

Compared to photoperiod and water temperature, discharge patterns were not strong predictors of Razorback Sucker detections at either barrier. We expected this result at PFW, because Razorback Suckers migrated from Lake Powell, where changes in river discharge were not likely to represent a migration cue (Pennock et al. 2020a). This was corroborated by other studies documenting Razorback Sucker reproduction within Lake Powell and Lake Mead in late winter to late spring, more likely responding to other environmental cues (Albrecht et al. 2018). At PNM weir, Razorback Sucker detections typically occurred prior to increases in discharge either from spring runoff from the Animas River or releases from Navajo Dam. Prior researchers observed Razorback Suckers spawning on the ascending limb of the hydrograph (Tyus and Karp 1990; Bestgen et al. 2011). While our research focused on spawning migration behavior, not the act of spawning, our results demonstrated movement behavior may not be dependent on discharge. Since flow regimes have been drastically altered within our study site, movement behavior from Razorback Suckers could differ from responses under a more natural flow regime.

Further Considerations

Exogenous and endogenous factors not tested here may influence spawning migrations. For example, prior research with other fishes demonstrated environmental parameters such as lunar phase, atmospheric pressure, precipitation, and turbidity dictated spawning behavior (Bizzotto et al. 2009; Carassou et al. 2011; Sudo et al. 2017), while other studies determined physical and chemical cues such as, age, body size, and hormone and lipid production affected timing of spawning behavior (Hink et al. 2011; Bett et al. 2016). In some fishes, demographic characteristics (i.e., operational sex ratio or proximity to conspecifics) affected the timing of reproduction (Dammerman et al. 2019). Further research is needed to understand the role of these factors in Razorback Sucker spawning ecology.

While we believe temperature cues migratory behavior in Razorback Suckers, hydrologic and geomorphologic conditions likely influence the timing of migration at PFW and PNM weir. For example, at PFW, fish migrate from Lake Powell through the dynamic San Juan River delta (Pennock et al. 2020b). It remains to be seen how declining reservoir levels might affect movement behavior (Graeb et al. 2009). In recent years, declining reservoir levels necessitate a longer migratory route for Razorback Suckers to reach PFW, requiring greater energy expenditure to reach available spawning substrate. Conversely, a longer lotic corridor could expose potential spawning substrate (i.e., cobble or gravel riffles), especially where tributary streams discharge loose cobbles. Furthermore, we acknowledge the timing of migrations to PNM weir could be delayed by two downstream barriers, which may be difficult for adult Razorback Suckers to navigate prior to early April, when irrigation operations are curtailed, and sluiceways are being operated to manage sediment in canals.

Conclusions

This study incorporated seven years of environmental data at two barrier locations in the San Juan River, testing associations of environmental cues and movement behavior of Razorback Suckers. By comparing two locations at similar latitudes but different thermal regimes, we were able to demonstrate water temperature was likely a better predictors of Razorback Sucker migrations than photoperiod. Putative spawning migrations were detected at barriers as mean weekly water temperatures were increasing between 7.1 to 14.2°C. This suggests individuals will spawn soon after detection at these barriers, since Razorback Suckers spawn within this temperature range (Clark-Barkalow et al. 2021). Given that spawning was imminent, passage delay would likely reduce reproductive potential of this imperiled species (Nyqvist et al. 2017).

Amid extended drought and increasing demand for water resources in the southwestern United States, it becomes increasingly important to understand factors linking Razorback Sucker movement and reproductive ecology. As water storage in Lake Powell and Lake Mead decline and greater demand calls for water resources from upstream impoundments, reservoir management will undoubtedly play a profound role in the future of this species. Moreover, both climate warming and lower reservoir levels result in increased river water temperatures as well as changes to timing and magnitude of flows, making understanding species responses an important step towards predicting future conservation challenges (Dibble et al. 2021).

Further research is needed to recognize the mechanisms that alter migration behavior, particularly behaviors that affect demographic vital rates, such as spawning success and recruitment. Our study provided a model that managers can use to predict the timing of occurrence of migrating Razorback Suckers. This model could serve as a tool to improve efficiency of selective passage facilities by prioritizing passage efforts during times of peak

migration. These strategies aimed to provide adult passage, which may lead to increased reproductive output, are imperative in meeting down listing and recovery criteria for Razorback Suckers (USFWS 2002). It remains unclear if increased reproductive output will overcome recruitment bottlenecks. Continued research to understand how, or if, management strategies such as floodplain connectivity and nonnative predator control can be used are critical to promoting recruitment and recovering wild Razorback Sucker populations.

Acknowledgements

This work was funded by the Bureau of Reclamation through the San Juan River Basin Recovery Implementation Program. We thank everyone involved in PIT antenna installation and tag management in the San Juan River, as well as facilitating discussion specifically, P. MacKinnon (USU), C. N. Cathcart C. Pennock, and S. Bonjour (KSU). Additionally, we thank the Upper Colorado River Endangered Fish Recovery Program, San Juan River Basin Recovery Implementation Program, and the Colorado Natural Heritage Program for managing and providing access to the STReaMS database.

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Figures

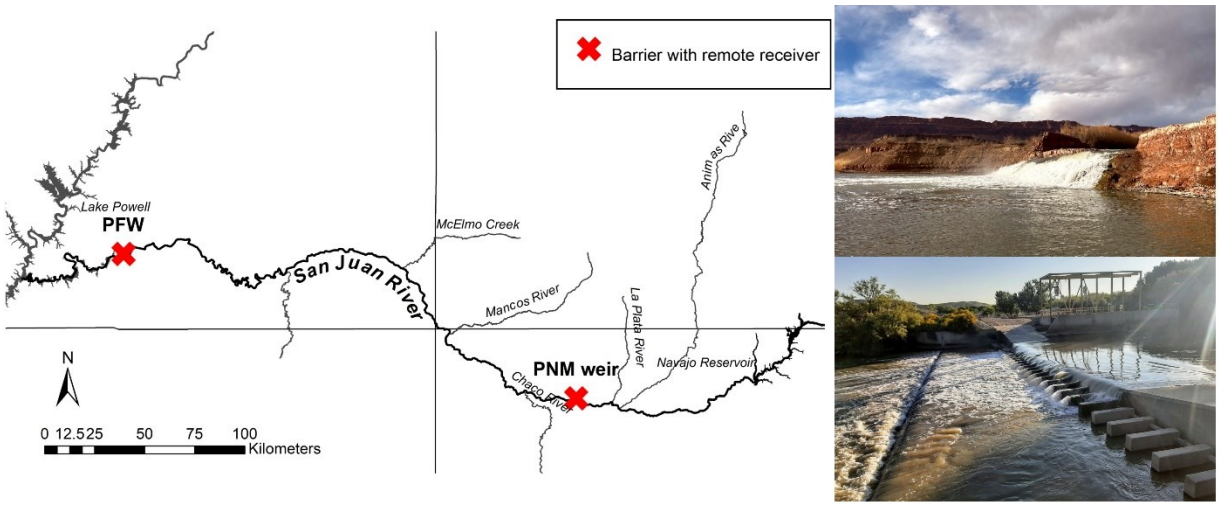


Figure 2.1. Map of the San Juan River between Navajo Dam and Lake Powell with locations of Piute Farms Waterfall (PFW, top right) and Public Service Company of New Mexico (PNM) weir (bottom right). Passive Integrated Transponder (PIT) tag antennas were deployed downstream of each barrier from 2015 through 2021.

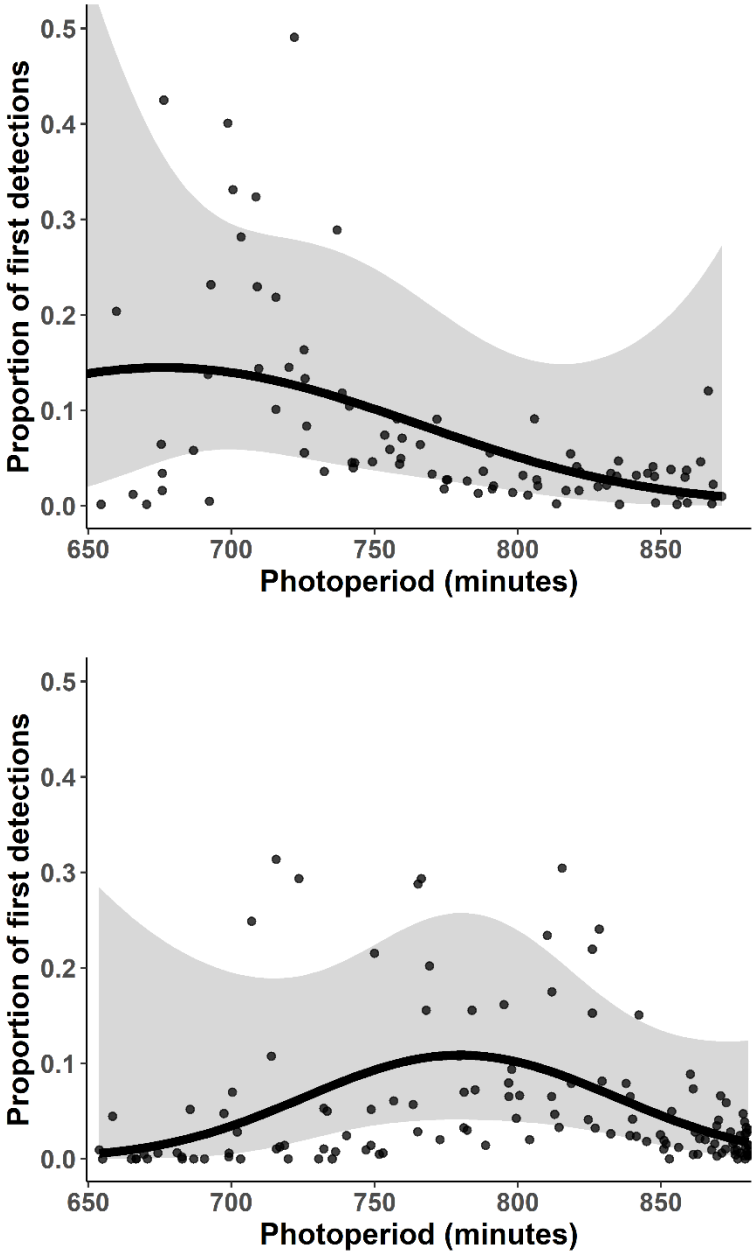


Figure 2.2. Model averaged probability of migration of Razorback Suckers (with 95% confidence bands) and increasing photoperiod at Piute Farms Waterfall (top) and PNM weir (bottom) from 2015 to 2021.

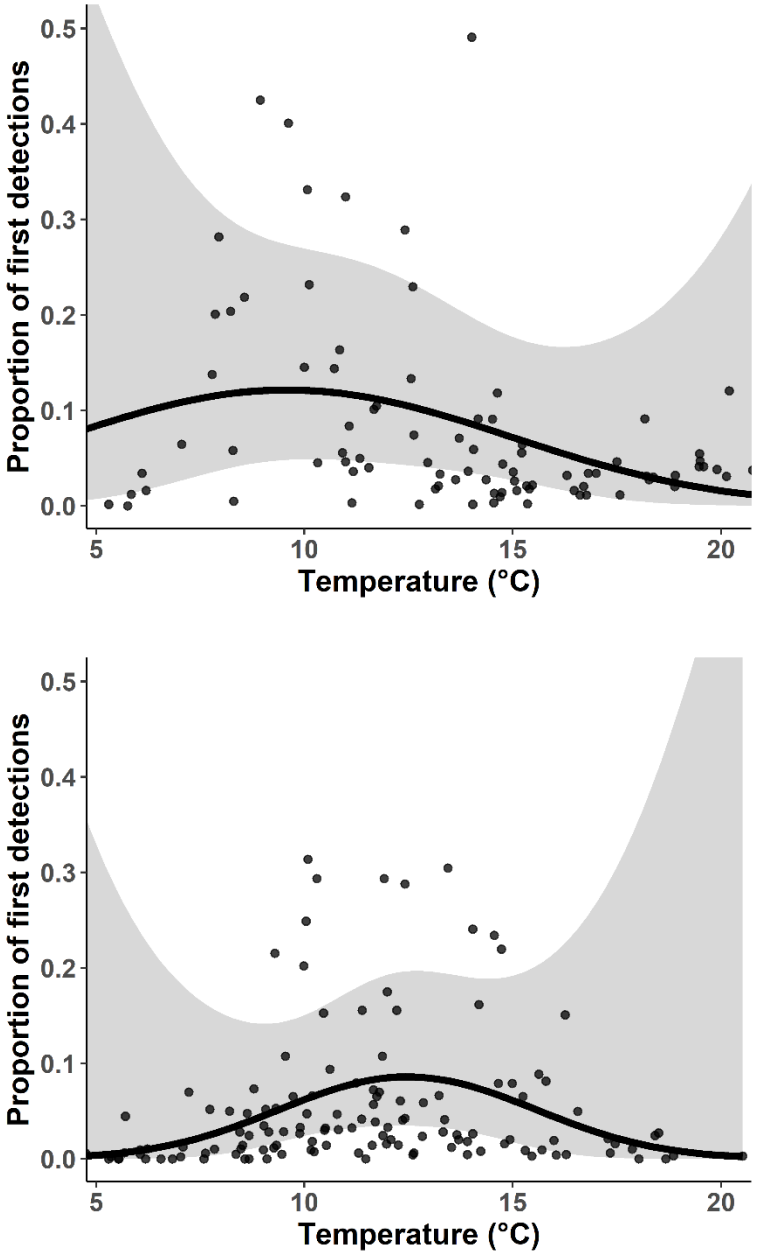


Figure 2.3. Model averaged probability of migration of Razorback Suckers (with 95% confidence bands) and increasing 7-day lagged temperature at Piute Farms Waterfall (top) and increasing mean weekly temperature at PNM weir (bottom) from 2015 to 2021.

Tables

Table 2.1. Summarized environmental data at Piute Farms Waterfall (PFW) and the Public Company of New Mexico (PNM) weir, during the spawning migration season (mid-February through mid-June) from 2015 to 2021. Water temperature and discharge data for PFW were obtained at a USGS gage near Bluff, UT, (#09379500) while a gage near Farmington, NM (#09365000) was used for the PNM weir.

Site	Year	Individuals detected	Mean seasonal water temperature (range °C)	Mean seasonal discharge (range m^3/s)
PFW	2015	440	16.2 (11.6-20.2)	29.3 (13.7-55.9)
	2016	446	10.8 (7.1-13.7)	27.4 (22.8-31.8)
	2017	623	11.9 (6.2-14.7)	76.8 (31.7-183.4)
	2018	618	14.9 (4.3-20.8)	18.3 (12.9-29.3)
	2019	694	12.1 (2.6 - 17.6)	55.7 (24.6-86.6)
	2020	515	15.8 (6.3-22.4)	30.1 (15.2-55.0)
	2021	504	13.9 (5.8-21.0)	19.5 (12.7-42.2)
PNM weir	2015	494	12.3 (5.7 - 18.4)	48.9 (14.8 - 155.5)
	2016	212	10.4 (6.1 - 15.7)	70.9 (19.3 -244.8)
	2017	491	9.5 (5.4 - 11.7)	114.9 (25.0 - 244.1)
	2018	663	14.8 (10.0 - 18.7)	23.2 (11.7 - 39.0)
	2019	961	10.2 (7.1 - 12.6)	80.2 (20.9 - 276.7)
	2020	316	12.6 (5.7 - 18.7)	35.5 (14.3 - 74.1)
	2021	674	13.0 (6.2 - 20.5)	25.9 (12.0 -74.6)

Table 2.2. Model selection statistics for general linear models relating environmental covariates to the timing of occurrence at Piute Farms Waterfall and Public Company of New Mexico weir in the San Juan River from 2015 to 2021. AICc = Akaike's Information Criterion corrected for small sample sizes, ΔAICc = difference in AIC compared to top-ranked model, AICcWt = Akaike weight, T = temperature °C, Photo = photoperiod minutes, Flow = discharge m^3/second.

Site	Model	K	AICc	ΔAICc	AICcWt	LL
PFW	**Photoperiod**					
	$Photo^2+Flow^2+Flow_{min}+Flow_{trend}$	7	3960.86	0.00	0.74	-1972.75
	$Photo^2+Flow^2+Flow_{trend}+Flow_{min}+\Delta Flow$	8	3962.96	2.10	0.26	-1972.60
	Temperature					
	$T^2+Flow^2+\Delta T+T_{trend}+Flow_{trend}$	8	3765.75	0.00	1.00	-1874.00
PNM	**Photoperiod**					
	$Photo^2+\Delta Flow+Flow_{min}+Flow_{trend}$	6	4228.77	0.00	0.76	-2108.05
	$Photo^2+Flow^2+\Delta Flow+Flow_{min}+Flow_{trend}$	8	4231.08	2.32	0.24	-2106.96
	Temperature					
	$T^2+Flow+\Delta T+T_{trend}+T_{min}+Flow_{trend}$	8	3691.41	0.00	0.66	-1837.12
	$T^2+Flow^2+\Delta T+T_{trend}+T_{min}+Flow_{trend}$	9	3692.73	1.32	0.34	-1836.63

Table 2.3. Model estimates from general linear models predicting the timing of Razorback Sucker occurrence at Piute Farms Waterfall and Public Company of New Mexico weir, with upper and lower 95% confidence limits. All univariate parameters were included using the "dredge" function (T = temperature °C, Photo = photoperiod minutes, Flow = discharge m^3/second). McFadden's pseudo R^2 represents the variance explained by each parameter, indicating model fit.

Site	Covariate	Pseudo R^2	Estimate	Lower 95% CL	Upper 95% CL
PFW	Photo²	0.36	-0.33	-0.37	-0.29
	Photo	0.31	-0.71	-0.74	-0.67
	T²	0.21	-0.35	-0.39	-0.32
	T	0.13	-0.43	-0.46	-0.4
	$Flow_{min}$	0.08	-0.49	-0.55	-0.44
	Flow²	0.08	-0.17	-0.23	-0.12
	Flow	0.07	-0.41	-0.46	-0.37
	T_{trend}	0.04	0.57	0.49	0.64
	Δ T	0.03	-0.22	-0.25	-0.19
	$Flow_{trend}$	0.01	0.22	0.16	0.29
PNM	Photo²	0.32	-1.09	-1.14	-1.03
	T²	0.21	-0.69	-0.74	-0.64
	T_{trend}	0.11	0.99	0.91	1.08
	$Flow_{trend}$	0.07	0.72	0.65	0.79
	$Flow_{min}$	0.06	-0.41	-0.46	-0.37
	Flow²	0.05	-0.09	-0.13	-0.05
	Flow	0.05	-0.35	-0.38	-0.31
	T_{min}	0.01	0.14	0.11	0.17
	Photo	0.01	-0.13	-0.17	-0.1
	T	<0.01	0.1	0.07	0.13
	Δ Flow	<0.01	-0.1	-0.13	-0.06
	Δ T	<0.01	-0.02	-0.04	-0.01