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NATIVE FISHES IN THE SAN JUAN RIVER OF THE AMERICAN SOUTHWEST,
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A Thesis Submitted to the Graduate School in Partial Fulfillment of the Requirements for
the Degree of Master of Science

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Pittsburg State University

Pittsburg, Kansas

May 2023

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An Abstract of Thesis by
Blake Guy Hansen

The Razorback Sucker (*Xyrauchen texanus*) and Colorado Pikeminnow (*Ptychocheilus lucius*) are federally-endangered species occurring in the San Juan River of NM, CO, and UT, USA. These species have shown little natural recruitment in this system, with a lack of high-quality nursery habitats being one potential explanation for this phenomenon. The young-of-year of both species prefer backwaters, including those that form in secondary channels or in association with islands. However, it is unknown how factors that could limit imperiled fish recruitment, such as hydrologic stability, physicochemical features, resource availability, and nonnative fish densities, differ between secondary channel and island backwaters. Furthermore, how these environmental features vary during the critical post-spawning window of the July-September monsoon season within and across years is also poorly understood. As such, we compared hydrologic stability, shading, water temperature, dissolved oxygen (DO) concentrations, turbidity, percent substrate composition, mean backwater width and depth, large woody debris (LWD) area, chlorophyll-*a* concentrations, invertebrate biomass, and native and nonnative fish densities between the two backwater types across 20 sites (i.e., 10 of each type) sampled on five occasions each in 2021 and 2022. We found that values of several variables were similar between backwater types (e.g., hydrologic stability, turbidity, silt coverage, mean width and depth, zooplankton biomass), but several other variables differed. For instance, secondary channel

backwaters had greater shading, cooler water temperatures, higher DO concentrations, and more macroinvertebrates and fishes compared to island backwaters, although island backwaters had a greater coverage of coarse substrates. Many of these variables changed over time however in response to the monsoon season, which included increasing coverage of silt and decreasing widths, depths, LWD area, and abundances of macroinvertebrates and fishes. Our results suggested that secondary channel backwaters have more favorable physicochemical properties and are more productive compared to island backwaters, although both backwater types experienced degradation in quality throughout the monsoon season. Chronic and acute monsoonal-induced deteriorations in backwater habitat may explain the limited recruitment of imperiled native fishes in the San Juan River. Identifying strategies for improving backwater nursery quantity and quality (e.g., environmental flows management) will be paramount in helping to alleviate the recruitment bottleneck of imperiled Razorback Sucker and Colorado Pikeminnow in the San Juan River, thus aiding their recovery.

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CHAPTER I

INTRODUCTION

Restoration of imperiled native fishes in the deserts of the southwestern United States is of growing concern and, consequently, an increasing topic of research. Two species of concern are the federally endangered Razorback Sucker (*Xyrauchen texanus*) and Colorado Pikeminnow (*Ptychocheilus lucius*), which were listed in 1991 and 1974, respectively. Both species are large-bodied, long-lived, and highly mobile fishes that are endemic to the Colorado River Basin (CRB) of the American Southwest (Minckley and Deacon 1968). These fishes face a number of abiotic and biotic threats such as drought, in-stream barriers, altered flow and temperature regimes, and competition and predation from introduced species (Minckley et al. 2003; Williams et al. 2022). All these issues greatly impact their recruitment in the wild. Both populations have been augmented by stocking efforts throughout the CRB for some time, yet they are still struggling to maintain healthy and sustainable populations. For example, Schooley and Marsh (2007) reported that over 14 million Razorback Suckers have been stocked into the CRB since stocking began in 1980, yet population numbers continued to decline. It is clear that natural recruitment is of great concern for the future persistence of these fishes.

The San Juan River within the CRB is one river system where Razorback Sucker and Colorado Pikeminnow persist. The San Juan River is a large tributary (i.e., ~355

miles long) to the Colorado River that is located in the Four-Corners region of Colorado, Utah, Arizona, and New Mexico (Fig.1). The river originates in the San Juan Mountains of southern Colorado and now terminates in Lake Powell, Utah, which is the second largest reservoir in the United States, that when completed in 1964, inundated the San Juan's historical confluence with the Colorado River. Furthermore, the San Juan River is impounded near its headwaters on the Colorado-New Mexico border by Navajo Dam, which was completed in 1962 to create Navajo Lake. Since the installment of Navajo Dam, discharge of the San Juan has become much less natural because it is largely controlled by reservoir releases (Holden 1999). The completion of Navajo Dam coupled with other water withdrawals (e.g., irrigation diversions) has had significant impacts on the hydrology of the river by greatly decreasing high flow pulses that would have historically occurred during the spring snowmelt and summer monsoon seasons, in addition to contributing to lower summer base flows (Bliesner and Lamarra 2000). These hydrologic alterations negatively impact many of the natural processes within the river (e.g., sediment transport; scouring of riparian vegetation) that was crucial in creating spawning bars and backwater habitats on which Razorback Sucker and Colorado Pikeminnow rely (Holden 1999; Heins et al. 2004).

Low to zero-velocity backwaters and embayments are important rearing habitats for the early life stages of Razorback Sucker and Colorado Pikeminnow. For instance, a recent study by Farrington et al. (2016) on the San Juan River found that larval capture densities for both Razorback Sucker and Colorado Pikeminnow were greater in backwaters and embayments compared to other low velocity habitats (e.g., pool margins) or higher-velocity runs. Similarly, Minckley et al. (1991) and Mueller (2006) found that

backwaters were the preferred habitats for early life stage Razorback Suckers. Since backwater habitats are vital to the recruitment of imperiled fishes of the CRB, they have become an important management focus (USFWS 2002a, USFWS 2002b). Farrington et al. (2016) also found that although there was successful spawning occurring in late spring and early summer of both species in the San Juan River, young of year (YOY) fishes were no longer present in the river by August. Their evidence suggested that there is some factor or factors limiting recruitment from the larval stage to the juvenile stage (i.e., a recruitment bottleneck). Identifying the environmental factors responsible for the recruitment bottleneck is of great importance to the restoration and management of imperiled fishes.

Backwater habitat formation in the San Juan River has been reduced due to aridification, bank armoring by nonnative vegetation (i.e., Russian Olive *Elaeagnus angustifolia*), water withdrawals, and flow regulation (Holden 1999; Bliesner et al. 2010; Scott et al. 2018; Williams et al. 2022). Flow regulation in the spring has been particularly detrimental, as spring flows are important for triggering spawning events for Razorback Sucker and Colorado Pikeminnow, and are also a critical factor in scouring sediments and creating necessary backwater habitats (Mueller 2006). Holden (1999) found that larval Colorado Pikeminnow in the San Juan River may drift considerable distances in order to find suitable nursery habitat. If there is a lack of suitable nursery habitats, these larvae may spend substantial time drifting, and thus will be subject to higher mortality rates from starvation, predation, or injury.

Although backwaters are crucial to the early life stages of imperiled fishes within the CRB, there is a high degree of variability in habitat characteristics among backwaters.

For example, Bliesner and Lamarra (2000) revealed that geomorphological characteristics and resource availability of backwater habitats varied from upstream to downstream reaches within the San Juan River. Backwaters in the upstream reaches had higher resource availability (i.e., algal and invertebrate biomass), but also had higher mainstem river velocities that prevented most fish larvae from settling in the adjacent backwaters. Other studies have looked at the longitudinal and temporal changes occurring in these backwaters for several years; yet they have not investigated how the environmental conditions within the various types of backwaters, such as secondary channel versus island, may vary (Bliesner and Lamarra (2000; 2002; 2005); Lamarra and Lamarra (2013).

Lamarra and Lamarra (2020) categorized backwaters habitats into four types, including: 1) backwaters associated with secondary channels (typically at the tail of secondary channels), 2) island backwaters, 3) cobble and sand bar backwaters, and 4) bank and point bar backwaters. Secondary channels are smaller channels that branch off of the main channel and typically receive less flow than the main channel. When river flows diminish in the upstream end, they form a secondary channel backwater (hereafter secondary backwaters) that are connected to the main channel at the downstream end (Fig. 2A). Island and cobble/sand bar backwaters are the zero-velocity habitats that form in the scour-channel between an island or cobble/sandbar and the riverbank (Fig. 2B & 2C). Point bar backwaters form from the low-velocity habitats that occur downstream of alluvial deposits on the inside bend of a river. Island and cobble/sand bar (hereafter island backwaters) experience greater connectivity to the main river channel than do secondary backwaters based on their greater proximity to the mainstem (Lamarra et al. 2019).

Furthermore, the size of these low-velocity habitats can vary according to river base flow. As base flow increases, secondary backwater size will increase while island backwater size decreases as inundation transforms them into main channel habitats (Lamarra et al. 2019). Therefore, flow releases within the San Juan River will result in varying frequency, sizes, and stability of island and secondary backwaters (Lamarra and Lamarra 2019).

It is well-known that the early life stages of imperiled fishes select backwater habitats as nurseries and refugia (Minckley et al. 1991; Tyus and Haines 1991; Lentsch and Crowl 1996; Mueller 2006; Bliesner et al. 2010; Farrington et al. 2013). However, it is not currently understood whether early life stages prefer island backwaters or secondary backwaters. For instance, larval fish may prefer secondary backwaters due to greater overall stability. Secondary channels have lower connectivity to mainstem flow, and therefore, experience less scouring by monsoonal flows during late summer (Adams and Comrie 1997; Lamarra and Lamarra 2019). Larval fish inhabit backwater habitats during late summer, thus increased flow in backwaters from monsoonal storms could flush the larval fish into the mainstem where a number of factors (e.g., predation, injury, and exhaustion) could lead to increased mortality (Mueller et al. 2006; Gido and Propst 2012).

Shading from riparian canopy and canyon walls is another potential factor that may impact recruitment success within backwaters of the San Juan River, as shading may result in more favorable habitat conditions. Without shading, backwaters receive more direct sunlight which can cause increased water temperatures that exceed the thermal threshold of larval fish, causing hyperthermia, heat stress, and larval mortality

(Kappenman et al. 2010; Deslauriers et al. 2016). Increased water temperatures will also result in low dissolved oxygen (DO) concentrations and possibly lethal hypoxic conditions within backwaters (Fontenot et al. 2001; Rajwa-Kuligiewicz et al. 2015). Another impact of higher water temperature is an increase in metabolic rate since fish are ectothermic. Ectothermy means larval fish will need to increase their feeding rates to keep pace with their higher metabolism, which could result in high growth if food is available, or starvation if food is scarce (Houde 1989; Bestgen 1996; Bestgen 2008). Shilla and Shilla (2012) concluded that riparian habitats provided temperature control, allochthonous energy inputs to the streambed, and refugia during flooding, all of which resulted in good water quality and a healthy macroinvertebrate community. They also concluded that streams supporting the richest macroinvertebrate communities were characterized by having intact riparian zones, high DO concentrations, and low water temperatures (Shilla and Shilla 2012). Due to secondary backwaters being located closer to the river margins and riparian zone, they may experience greater shading than would island backwaters. The increased shading may minimize the above effects and result in a more favorable rearing habitat for imperiled larval fish of the San Juan River.

Turbidity and substrate composition may also differ between island and secondary backwaters. For instance, island backwaters may experience increased turbidity and silt deposition given their higher connectivity to the mainstem (Bliesner and Lamarra 2000; Lamarra and Lamarra 2019). Increased turbidity negatively impacts feeding ability for visual predators, and is harmful to respiration due to gill clogging or damage (Manning et al. 2014; Barkalow and Bonar 2015). Increased turbidity also elevates the risk of predation by giving an advantage to non-sight feeding nonnative predators, such as

Channel Catfish *Ictalurus punctatus* (Hedden et al. 2021). Lastly, backwater turbidity can influence the amount of primary production occurring in a habitat. With increased turbidity there is less light available for phytoplankton and periphyton, and therefore less energy available for fish larvae and the macroinvertebrate prey on which they rely. Negative effects of turbidity on basal productivity is exacerbated by silt deposition, which smothers coarser habitats (e.g., gravel and pebble) with a layer of unstable and anoxic mud that is generally avoided by most periphyton and macroinvertebrate species.

The high flow events in the mainstem associated with the monsoon season can also negatively impact resource availability for larval fish (Bestgen 1996). Theoretically, island backwaters should experience increased scouring of the substrate and pelagic zone due to the backwater's connection to the mainstem, which results in a greater reduction of macroinvertebrate and algal biomass in island backwaters compared to secondary backwaters (Speas 2000; Cross et al. 2011). With the main prey items for both Colorado Pikeminnow and Razorback Sucker larvae being chironomids, cladocerans, and copepods (Vanicek 1967; Muth et al. 1997; Pennock et al. 2019), higher starvation rates may be expected in island backwaters than secondary backwaters.

Predation pressure may also explain the lack of recruitment of imperiled fishes of the San Juan. Several nonnative species such as Red Shiner (*Cyprinella lutrensis*), Green Sunfish (*Lepomis cyanellus*), Fathead Minnow (*Pimephales promelas*), Western Mosquitofish (*Gambusia affinis*), and Channel Catfish have been linked to heavy predation rates on native larval fishes (Tyus and Haines 1991; Brandenburg and Gido 1999; Holden 1999; Ward 2020; Hedden et al. 2021). Bestgen (2008) found that predation by Red Shiner, along with environmental factors, limited Colorado

Pikeminnow recruitment. Furthermore, Loudermilk (1985) and Johnson et al. (1993) found that Razorback Sucker larvae showed very little defensive behavior around nonnative predators and were unlikely to survive in areas with high predator densities. Additionally, Hedden et al. (2021) found that native fish made up 54% of the fish biomass in Channel Catfish stomach samples. Thus, high numbers of predators and increased predation pressure are factors that may be limiting recruitment.

It is currently unknown whether hydrologic stability, physicochemical conditions, resource availability, or predation pressure differ between secondary and island backwaters. As such, the objective of this project was to assess whether these environmental factors differ between secondary and island backwaters within the San Juan River. This was done by testing four different hypotheses and their associated predictions.

Hypothesis and prediction #1: The overall hydrologic stability of secondary backwaters is greater than island backwaters. This is due to lower connectivity with the highly variable mainstem of the San Juan River, as well as lower frequency, magnitude, and duration of monsoonal flows.

Hypothesis and prediction #2 Physicochemical properties are more favorable in secondary backwaters than island backwaters due to greater stability and shading. Secondary backwaters have greater canopy cover, cooler water temperatures, increased DO concentrations, lower turbidity, larger substrate, greater wetted width and depth, as well as area of large woody debris (LWD) habitat than island backwaters.

Hypothesis and prediction #3: Secondary backwaters have greater resource availability than island backwaters because of more preferred physicochemical properties and

stability. Secondary backwaters have greater algal and macroinvertebrate biomass than island backwaters.

Hypothesis and prediction #4: The densities of small-bodied nonnative predators varies between secondary backwaters and island backwaters. Secondary backwaters have higher densities of small-bodied nonnative predators because of differences in stability, physicochemical properties, and resource availability.

Testing these hypotheses and predictions has important management implications since environmental flows management can be used to manipulate the prevalence of secondary channel versus island backwaters in the San Juan River. It would be unproductive to increase secondary backwater area by increased baseflow if there is not a significant difference between this backwater type and island backwaters (Lamarra in prep). If secondary backwaters have greater habitat quality and resource availability, using flow management (Tharme 2003; Propst and Gido 2004) to increase the number of secondary backwaters via greater baseflows could be a strategy to create more favorable habitat for imperiled larval fishes; thus, helping to alleviate the recruitment bottleneck (Lamarra in prep; Lamarra and Lamarra 2020). Lastly, since riverine desert ecosystems are temporally dynamic, we also sought to examine how response variables collected as part of our study varied during the critical post-spawning time period of the July-September monsoon season within and across years.

METHODS

Study Area

This study took place on the San Juan River between river mile (RM) 149 near Shiprock, NM, and RM 93 at Montezuma Creek, UT (Fig. 1). This stretch was selected

due to its high density of backwater habitats (Lamarra and Lamarra 2019). Within this reach, backwaters were categorized as secondary or island backwaters, with the island backwater category including both island and cobble/sand bar backwaters since they were so similar. We did not sample any bank/point bar backwaters because they were so ephemeral that they did not persist long enough to sample. Within the 56 river miles, we sampled 10 island backwaters and 10 secondary backwaters for a total of 20 sites. Potential sites were selected based on recent habitat maps and a scouting survey completed at the beginning of each study season. Our sampling occurred from July through September of 2021 and 2022, with sample trips occurring approximately every two weeks, resulting in five sampling trips per year and 10 trips in total. We chose this sampling time frame because it corresponds to the southwestern monsoon season and the critical post-spawning period when imperiled fish larvae disappear from the San Juan River. During sampling trips, we rafted down the river going from backwater to backwater collecting data as described below, with each sampling trip lasting 5-6 days. Our study design resulted in a potential total sample size of 200 unique sampling events, since there were twenty sites sampled per trip and five sample trips per year over two years. Finally, fourteen study site locations were repeated between study years.

Hypothesis #1: Hydrologic Stability

We used three data loggers in each study site to quantify hydrologic stability in backwaters. Loggers were deployed from July 16th – September 13th in 2021 and from July 17th – September 6th in 2022. An Onset HOBO U20L-01 water level logger enclosed in a PVC protective case was placed in the deepest point of each backwater and secured to a t-post with zip ties to minimize the chances of it being displaced during high flow

events. Each HOBO logger was set to record pressure in pounds per square inch every 30 minutes. Pressure measurements were then converted to water depth (m) using HOBOWare Pro software based on reference depth measurements taken at the time of logger deployment and retrieval, and also by correcting for atmospheric pressure recorded by a logger deployed in air near the middle of our study area. These HOBO depth loggers allowed us to quantify the magnitude and duration of both low and high flow events in backwaters, as well as overall hydrologic variability. Specifically, for each site and year, we calculated low flow magnitude and duration as the proportion of observations <1 inch of depth, high flow magnitude and duration as the proportions of observations >3 feet of depth, and hydrologic variability as the overall coefficient of variation (CV) of depth observations.

To further quantify hydrologic stability and connectivity in each backwater we deployed two electrical resistance sensors (Jaeger and Olden 2012) housed in protective casings, with one in the deepest point attached to the same t-post as the HOBO water level logger, and the other secured to a rebar in the lowest elevation point between a backwater and the mainstem. The electrical resistance sensors were Onset HOBO Pendant loggers that were modified to detect changes in relative conductivity (unitless) rather than light intensity. Every 30 minutes, these loggers recorded whether they were dry (low relative conductivity of $<2,000$) or submerged in water (high relative conductivity $\geq 2,000$; usually $>10,000$) (Goulsbra et al. 2009; Chapin et al. 2014). The resistance sensor deployed in the deepest point allowed us to measure how often a backwater dried (i.e., permanence), while the other resistance sensor afforded us the ability to quantify the frequency of connections between a backwater and the mainstem

(i.e., connectivity). We assessed permanence and connectivity by dividing the number of wet observations by the total observations for each site in each year using the deep sensor and lowest elevation sensor, respectively. We excluded any anomalous readings from our sensor data set prior to analysis.

Hypothesis #2: Physicochemical Variables

During each sample trip we mapped out a 50 m long sample reach within a study site, and then positioned three sampling transects at the downstream (0 m), middle (25 m), and upstream portions (50 m) of a sample habitat. Although, when backwaters were shorter than 50 m we sampled fewer transects. To mitigate mainstem influence on habitat variables, transects were not placed at the mouth of a backwater where it connected to the mainstem whenever possible. At each transect, backwater turbidity in nephelometric turbidity units (NTUs) was measured using an ExTech turbidity meter and DO concentrations in mg/l were taken using an ExTech DO600 waterproof ExStik II meter. Following water quality measurements one wetted width measurement was taken per transect using a 50 m measuring tape. Backwater shading was measured at each transect midpoint using a spherical concave densiometer. Each transect also had five cross-sectional sampling points, including river right (#1), then 25% (#2), 50% (i.e., transect midpoint; #3), and 75% (#4) of the distance from river right to river left, and then finally, at river left (#5) (Klemm and Lazorchak 1994; Lazorchak et al. 1998). At each sample location, a measurement for depth (measured with a telescoping fiberglass leveling rod) and substrate (e.g., clay, silt, sand, gravel, pebble, cobble, boulder, and bedrock) was taken. Substrate type at each transect was determined by visual and tactile examination. If the substrate at a measurement point was mixed, then it was categorized

by whichever substrate was dominant. Whenever large woody debris (LWD) was present within a backwater, the overall lengths and means widths of the LWD were measured. Together, these measurements were used to determine mean turbidity (NTU), mean DO (mg/l), mean wetted width (m), percent canopy cover, mean depth (m), percent coverage of silt and coarse substrates (gravel + pebble + cobble + boulder + bedrock), and LWD area (m²) for each backwater. Finally, backwater temperature was recorded every thirty minutes using the same HOBO U20L-01 data logger that recorded water level, with mean temperature calculated for each site during each year using temperature recordings from the logger deployment period.

Hypothesis #3: Resource Availability

Pelagic chlorophyll-*a* concentrations were used to estimate the algal biomass of backwaters. Chlorophyll *a* concentration (µg/L) was measured using a Turner Designs FluoroSense Handheld Fluorometer, with measurements taken along each transect at the same time as turbidity and DO measurements (Wetzel and Likens 2000; Rice et al. 2017). The availability of larval prey in backwaters was estimated from benthic, LWD, and pelagic macroinvertebrate samples. Benthic macroinvertebrate samples were collected using a benthic core sampler (0.018 m² sample area) at one random point along each of the three transects. When LWD was present within a transect, a subsection was enclosed in a bucket and scrubbed to remove macroinvertebrates. Afterwards, the LWD subsection was measured for total length and circumference to calculate area for the LWD sample (mean = 0.02 m²; range = 0.01-0.16 m²) (Gowns et al. 1999; Whitney et al. 2015). A maximum of two LWD samples were taken per site. Pelagic macroinvertebrates (e.g., Copepods and Cladocerans) were collected using a Wisconsin plankton net that was

towed through the water for 2 m at each transect (0.063 m³ sample volume; mesh = 250 μ m) (De Bernardi 1984). All macroinvertebrate samples collected were sieved (250 μ m) and stored in 10% formalin in a Whirl-Pak until they could be processed further.

In the laboratory some macroinvertebrate samples were subsampled by splitting them from 1 to 7 times using a Folsom plankton splitter, which helped reduce sample processing time. Under a dissecting microscope, insects were identified to family (Merritt et al. 2008), whereas non-insects were identified to class or phylum (Thorp and Covich 2009). Macroinvertebrates were then counted and measured for total length using 1 mm grid paper. Published length-mass relationships (Burgherr and Meyer 1997; Benke et al. 1999; Sabo et al. 2002) were used to estimate mg of dry mass (DM)/m² for each macroinvertebrate taxa, and biomass for each taxon was calculated separately for benthic, LWD, and pelagic samples. Biomass was then summed across taxa within a sample type and then averaged across replicates to generate an estimate for benthic, LWD, and pelagic macroinvertebrate resource availability.

Hypothesis #4: Small-bodied Nonnative Predators

The abundance of fishes was assessed by seining the 50 m backwaters sites in a downstream direction using a 4.6 m wide X 1.8 m tall seine that had 3.2 mm mesh. All fish species captured, native or nonnative, were identified to species, measured for total length (mm), and released alive back into the sample reach. The estimated densities for all species were calculated by dividing the number of individuals captured (#) by the total backwater area sampled (m²), then density values were summed across taxa to estimate overall nonnative and native fish densities. To make densities easier to interpret they were then multiplied by 100, producing estimates in units of #/100m².

Data Analysis

All data analyses were performed using program R (R Core Team 2020) and RStudio. We used two-way analysis of variance (ANOVA) to compare the main effects of backwater type (island versus secondary) and year (2021 and 2022) on response variables measured by our data loggers (i.e., stability, permanence, connectivity, and temperature). For all other response variables (e.g., physicochemical variables; resource availability; nonnative fish density) we used a two-way ANOVA that compared the main effects of backwater type and trip #. Trip # was a continuous metric that ranked trips chronologically beginning with trip #1 in July 2021 and ended with trip #10 in September 2022; trips 1-5 occurred in 2021 and trips 6-10 occurred in 2022. We also examined the interactive effects of backwater type and year or trip #, but since no interactive effects were significant, we focused on the main effects for simplicity. All data were tested for violations of normality and homoscedasticity assumptions using a Shapiro-Wilk's and Bartlett's test, respectively. If the data violated these assumptions, continuous data were $\log_{10}(x+1)$ transformed, while proportional data were empirical logit transformed (Warton and Hui 2011) prior to ANOVA. If a two-way ANOVA was significant ($\alpha = 0.05$), differences were identified using a Sidak's correction test (Abdi 2007). The mean and 95% confidence intervals of all transformed response variables were back-transformed to the original scale prior to displaying results.

Variation in discharge can exert strong control over mean wetted width and depth, which were two of our response variables. Since examining changes in width and depth over time (i.e., trip #) was one of our objectives, we wanted to remove the effect of discharge on these variables prior to doing analyses. We accomplished this by relating

mean daily discharge from the U.S. Geological Survey (USGS) discharge gages at Shiprock (gage # = 09368000) and Four-Corners (gage # = 09371010) to width and depth observations at our sites on particular sample dates using linear regression. If these linear relationships were significant, we then used the residuals from these relationships as response variables rather than the raw width and depth data to assess how width and depth changed over time in each backwater type independent of discharge.

RESULTS

Due to the highly variable hydrologic and geomorphic nature of the San Juan River and its backwaters, the number of sample sites per trip varied. Some backwaters were dry at the time we were planning to sample them or were fully inundated by high mainstem flows, with both scenarios making backwater sampling impossible. High flows were especially problematic on trip #7 (i.e., July 26-30, 2022) when we were only able to sample 2/20 sites. The high flows of trip #7 can be demonstrated using a discharge comparison from the USGS gage at Four-Corners (gage # 9371010), since during trip #6 (July 13-18, 2022) mean discharge was only 401 ft³/sec, but during trip #7 mean discharge rose by 683% to 3,138 ft³/sec. The two sites sampled during trip #7 were not included in data analyses. Because of these factors we completed data collection for 176/200 of our potential unique backwater sampling events.

Stability

Contrary to our predictions there were no major differences in hydrologic stability between secondary channel and island backwaters (Table 1), although there were some instances where stability varied between years. In terms of depth metrics describing hydrologic magnitude, duration, and variability, we did not detect effects of backwater

type or year on the proportion of observations < 1 inch (type $P = 0.17$; year $P = 0.32$), proportion of observations > 3 feet (type $P = 0.78$; year $P = 0.34$), or overall CV of depth (type $P = 0.20$; year $P = 0.79$). In general, the percentage of observations at extreme low (i.e., < 1 inch depth) or high (i.e., > 3 feet) depth values was small at 5% and 7%, respectively, averaged across backwater types and years. However, in 2021 there were two island sites that had from 32-38% of their observations < 1 inch, in addition to one island and one secondary channel site that had 16-20% of their values > 3 feet. Furthermore, backwater permanence ($P = 0.99$) and connectivity ($P = 0.14$) were similar between backwater types, although connectivity did vary between years ($P < 0.01$; Fig. 3). The mean proportion of observations that indicated mainstem connectivity was 0.99 in 2021, which was 11% greater than 2022 wherein proportional connectivity was 0.89. Lastly, permanence did not vary between years ($P = 0.92$).

Physicochemical Properties

In general, secondary channel backwaters had more benign conditions regarding shading, water temperature, and DO, with minimal changes occurring over time. In agreement with our predictions, the amount of shading was 81% greater in secondary channel backwaters compared to island backwaters ($P = 0.01$; Table 2; Fig. 4), with a mean percent canopy coverage of 8% in secondary channels compared to 3% in islands; this difference did not vary across trips ($P = 0.87$). Similarly, mean water temperatures were 3.5% cooler ($P = 0.01$; Table 1; Fig. 4) in secondary backwaters (mean = 22.3°C) than island backwaters (mean = 23.1°C). However, mean temperatures increased by 6.8% ($P < 0.01$) across both backwater types from 2021 to 2022 (Fig. 4). Lastly, as expected, we found that DO concentrations were 9% greater ($P < 0.01$) in secondary backwaters

(mean = 7.1 mg/l) compared to island backwaters (mean = 6.4 mg/l) (Table 2; Fig 4).

Dissolved oxygen also varied among trips ($P < 0.01$), tending to be lowest during trips #1, #2, and #5 in 2021 (Fig 4).

Surprisingly, water clarity and substrate composition showed few differences between backwater types. For example, turbidity did not differ between backwaters ($P = 0.81$) although it did vary among sample trips ($P < 0.01$; Table 2), as turbidity was at its lowest at the end of 2021 and the beginning of 2022 (Fig. 5). Similarly, substrate results were also contrary to our expectations since there was no significant difference among backwater types for proportion of silt coverage ($P = 0.17$), and island backwaters had greater ($P = 0.04$) prevalence of coarse substrate (mean = 10.8%) compared to secondary channels (mean = 6.5%). Both backwater types had high silt coverage (mean = 76% for island and 84% in secondary channel) that varied over time ($P = 0.02$), since silt coverage was lowest (57%) at the beginning of the study in 2021 and highest at the end of the study in 2022 (94%; Table 2; Fig. 5). Lastly, there were no significant differences in the coverage of coarse substrate among sample trips ($P = 0.11$).

Wetted width and depth were found to be correlated with discharge (width $F_{1,169} = 57.78$, $r^2 = 0.25$, $p < 0.001$; depth $F_{1,169} = 106.79$, $r^2 = 0.39$, $p < 0.001$). The residuals of discharge versus mean wetted width and depth exhibited no differences between backwater types ($P = 0.35$ and 0.65 , respectively; Table 2), although there was a decrease in both wetted width and depth residuals across sample trips ($P < 0.01$ for both variables) as the study proceeded (Fig. 6).

The area of LWD was 145% greater in secondary backwaters compared to islands ($P < 0.01$; Table 2; Fig. 7), with a mean area of 8.2 m² in secondary channels compared to

1.3 m² in islands. There was also significant variation in LWD area among sample trips ($P < 0.01$; Table 2; Fig. 7), with trip #1 having greater LWD area than all other trips except trip #2. Overall LWD area decreased by 97% over the two-year sample period.

Resource Availability

Counter to our expectations we did not detect differences in chlorophyll-*a* concentrations between backwater types ($P = 0.52$; Table 2). There were, however, significant differences in mean chlorophyll-*a* concentrations among sample trips ($P < 0.01$; Table 2; Fig. 8), with trips 4, 5, and 6 having greater chlorophyll-*a* concentrations than trips 2, 8, and 10.

In total we collected and processed 73,903 macroinvertebrates from 1,086 samples (54,956 individuals from 630 samples in 2021 and 18,947 individuals from 456 samples in 2022). This included 14,010 individuals from 462 plankton samples, 47,806 individuals from 462 core samples, and 12,087 individuals from 162 LWD samples. Oligochaeta (58.3%) and Chironomidae larvae (17.6%) were the dominant taxa found, comprising 75.9% of all invertebrates processed (Table 3). Furthermore, secondary backwaters may be more diverse in macroinvertebrates than islands since we found 75 taxa in secondary backwaters compared to 59 taxa in island backwaters.

Macroinvertebrate availability was greater in secondary channels compared to island backwaters, which agreed with our initial predictions. Benthic invertebrate core biomass was 77% greater ($P = 0.01$) in secondary backwaters compared to islands (Table 2; Fig. 9), with secondary backwaters having 180.9 mg DM/m² compared to 80.3 mg DM/m² in islands. Similarly, although substantially lower than core biomass, LWD invertebrate biomass was 120% greater ($P < 0.01$) in secondary backwaters (mean = 26.9

mg DM/m²) compared to islands (mean = 6.7 mg DM/m²; Table 2; Fig. 9). There were also significant decreases in core biomass ($P < 0.01$) and LWD biomass ($P < 0.01$) among sample trips (Table 2; Fig. 9). Finally, unlike the other macroinvertebrate biomass measurements, we found no significant difference for zooplankton biomass between backwater types ($P = 0.79$) or among sample trips ($P = 0.13$), as zooplankton biomass was consistently low in both backwaters (Tables 2 and 3).

Fish Densities

We collected 16,817 fish, across 9 nonnative and 5 native species, of which 13,713 (81.5%) were nonnative individuals (Table 4). Furthermore, many more individuals and species were captured in 2021 (15,601 individuals and 14 species) compared to 2022 (1,216 individuals from 9 species). The top three nonnative species represented 72% of the total fish caught, and included Western Mosquitofish (28%), Red Shiner (26.9%), and Fathead Minnow (17.1%). In contrast, the top three native species (i.e., Flannelmouth Sucker 14.7%, Speckled Dace 3.5%, and Bluehead Sucker 0.2%) represented 18.4% of total fish caught. We also caught five ~age-1 Colorado Pikeminnow (mean TL = 181 mm, range = 140-219 mm), and four unknown juvenile suckers believed to be either Razorback Suckers or Razorback-Flannelmouth Sucker hybrids (Fig. 10).

As expected, fish densities were greater in secondary channel compared to island backwaters for nonnative and native fishes alike. Mean densities of nonnative fish were 96.7% greater ($P < 0.01$) in secondary backwaters compared to islands, with secondary backwaters having a nonnative density of 9.2/100 m² compared to 3.2/100 m² in islands (Tables 2 and 4; Fig. 11). Although much lower compared to nonnative density, secondary backwaters (mean density = 2.2/100m²) also had a 78.2% greater native fish

density than islands (mean density = $0.9/100\text{m}^2$) (Tables 2 and 4; Fig. 11). We also found significant variation among sample trips for both nonnatives ($P < 0.01$) and natives ($P < 0.01$), with trip #1 tending to have much higher densities for both nonnatives and natives compared to all other sample trips (Tables 2 and 4; Fig. 11). There was a marked decrease in both nonnative and native fish density after trip #1 that coincided with a monsoonal flow pulse induced fish kill that we observed on July 24-25, 2021.

DISCUSSION

Our results indicated that secondary backwaters have more favorable physicochemical properties (i.e., more shading, lower water temperatures, higher DO concentrations, and greater LWD area) and were more productive (i.e., higher macroinvertebrate biomass and native fish densities) compared to island backwaters. All these factors contribute to secondary backwaters being potentially better nursery habitats for the early life stages of the imperiled fishes of the San Juan River. However, secondary backwaters also had less coarse substrate and higher nonnative fish densities compared to islands, which may lower their overall backwater quality and potential for imperiled fish recruitment. Nevertheless, these results have important implications for the potential use of environmental flow management as a conservation tool on the San Juan River.

We observed a chronic deterioration of both island and secondary channel backwaters during the summer monsoon season, which coincides with a crucial time for native fish development and recruitment. Chronic declines in habitat quality included increasing coverage of silt substrate and decreases in backwater width, depth, and LWD area. The monsoon season historically brought increased precipitation that ultimately elevated river discharge, increased suspended sediment loads, inundated the floodplain,

and contributed to habitat formation and complexity (Minckley et al. 1991; Holden 1999; Bliesner and Lamarra 2000; Propst and Gido 2004; Mueller 2006; Franssen et al. 2015). However, since the installment of Navajo Dam there has been substantial reductions to the magnitude and duration of peak flow events, which lower the river's ability to flush out sediments, reset substrates, and create and maintain vital habitats like backwater nurseries (Holden 1999; Heins et al. 2004). Dam-induced reductions in flow become especially problematic when the effects of the monsoon season (i.e., rapid increase in discharge and suspended sediments) are coupled with the recent impacts of drought and dewatering that contribute to lower base flows (<500 cfs) (Williams 2016; Williams et al. 2022) and backwater drying in between monsoonal flow pulses (Holden 1999; Franssen et al. 2015). Anthropogenic reductions in flow result in the descending limb of monsoonal high flow pulses being steeper than they would have been historically, which ultimately allows fine sediments to settle out and accumulate at a rapid rate (Yamada and Nakamura 2002; Izagirre et al. 2009; Jones et al. 2012). Resultantly, the declines in backwater width, depth, and LWD area that we observed were likely the consequence increasing silt coverage, since habitat aggradation resulting from silt deposition would cause backwaters to become narrower, shallower, and more disconnected from riparian LWD. (Holden 1999). This reduction in backwater habitat volume would also increase the likelihood of backwater drying in between monsoonal flow pulses, exacerbating drying from human water withdrawals and flow regulation. All of these factors may cause backwaters to function as ecological traps for the early life stages of native fishes (Vander Vorste et al. 2020), limiting their recruitment success and contributing to the recruitment bottleneck.

In addition to chronic deterioration in physical habitat, we also observed monsoonal-induced reductions in backwater resource availability. This likely occurred from two processes, including 1) the flushing of macroinvertebrates from backwaters during monsoonal high flow pulses and 2) silt deposition that occurred after and in between monsoonal spates. The depositional effect is evident in our results by the increase in silt substrate and reduction in macroinvertebrate biomass that occurred over time, since the smothering of coarser substrate by silt creates unfavorable habitat for invertebrates and periphyton, which in turn limits backwater resource availability (Holden 1999; Yamada and Nakamura 2002; Izagirre et al. 2009; Jones et al. 2012).

A monsoonal flood pulse also caused acute deterioration via the fish kill we observed during July 24-25, 2021. This event was characterized by a rapid discharge increase of 5,368 ft³/sec in ~2 hours. During this event we documented high mortality across all age classes, which was evident by the drastic decline in fish densities within backwater habitats after trip #1 (Fig. 11). This acute event seemed to have a negative impact that lingered into 2022, explaining the lack of recovery and low fish densities in our second study year. Monsoonal-induced fish kills appear to be rare on the San Juan River however, as this was the first one documented since the Trimble Expedition observed a fish kill on August 1, 1921 near Mexican Hat, UT (Aton and McPherson 2000). We do not know what aspect(s) of water quality during the monsoonal flow pulse that were responsible for the fish kill, but researching the causative factor behind this fish kill has important conservation implications given the high mortality it produced.

Environmental flow management is an effective strategy for mitigating habitat degradation and creating critical habitat, thus contributing to the recovery of imperiled

native fish species (Propst and Gido 2004; Kiernan et al. 2012). With the flows of the San Juan River being largely controlled by Navajo Dam operations, it should be possible to use releases from the dam to not only mimic historical environmental flows, but to also maintain discharge that would create and sustain additional secondary backwater habitat (Holden 1999; Lamarra and Lamarra 2020; Lamarra et al. In Prep). Lamarra et al. (In Prep) found that as baseflow increased within the San Juan River, the frequency of island backwaters increased, while secondary backwaters frequency remained constant. Furthermore, they also found that as baseflows increased the overall area of secondary backwaters increased while island backwater area was invariant. It appears that increased baseflows may have two separate benefits for imperiled native fishes of the San Juan River. First, elevating base flows creates more favorable nursery habitat for imperiled native fishes by increasing the area of secondary backwaters compared to islands. Secondly, increased baseflows could help maintain overall connectivity, permanence, and quality of all backwater habitats, thus limiting the seasonal deterioration that occurs during the summer monsoon season. For instance, although the proportion of depth observations <1 inch was generally low (i.e., $\leq 5\%$) for most backwaters, there were some backwaters that had a large percentage (i.e., 30-40%) of their observations at these extreme low depth values, which likely makes them unsuitable for fishes. Elevating summer base flows via greater releases from Navajo Dam could reduce this problem. Using environmental flows management to increase secondary channel backwater area and elevating base flows during July-September may increase the recruitment of native fishes and thus help ameliorate the recruitment bottleneck that is currently impacting the Colorado Pikeminnow and the Razorback Sucker.

Meeting environmental flow targets is increasingly challenging, as high-water demand, climate change, and drought conditions persist in the southwestern United States (Williams 2016; Williams et al. 2020; Williams et al. 2022). Williams et al. (2022) concluded that the last twenty-two years (2000-2022) have been the driest period in the last ~1,200 years, calling this time period the “megadrought”. They also indicated that the megadrought conditions are likely to persist into the foreseeable future. Going forward, it will be crucial for managers to find new and innovative ways to maintain adequate river flows in these arid environments (Chen and Olden 2017; Pennock et al. 2022a; 2022b), especially if the end goal is to promote self-sustaining populations, resulting in the recovery of the imperiled native fishes of the San Juan River (Gido et al. 2023).

Table 1. Results from two-way ANOVA examining the main effects of backwater type (secondary channel versus island) and year (2021 and 2022) on low (proportion of observations < 1 inch) and high (proportion of observations > 3 ft) flow magnitude and duration, overall coefficient of variation (CV) of depth, permanence, mainstem connectivity, and mean temperature in the San Juan River of New Mexico, Colorado, and Utah.

Variable Tested	Backwater Type			Year		
	F-Value	df	P-Value	F-Value	df	P-Value
Low Flow Magnitude and Duration	1.93	1, 33	0.17	1.02	1, 33	0.32
High Flow Magnitude and Duration	0.08	1, 33	0.78	0.95	1, 33	0.34
Overall CV	1.70	1, 33	0.20	0.07	1, 33	0.79
Permanence	<0.00	1, 29	0.99	0.01	1, 29	0.92
Connectivity	2.26	1, 30	0.14	19.02	1, 30	<0.01
Temperature (C°)	7.57	1, 33	0.01	26.29	1, 33	<0.01

Table 2. Two-way ANOVA results investigating the main effects of backwater type (secondary channel versus island) and sample trip # on response variables describing physicochemical characteristics (i.e., canopy cover, dissolved oxygen, turbidity, substrate coverages, wetted width, depth, LWD area), resource availability (chlorophyll-*a* and macroinvertebrate biomass values), and fish abundances (nonnative and native) in the San Juan River of NM, CO, and UT during July-September of 2021 and 2022.

Variable Tested	Backwater Type			Sample Trip		
	F-Value	df	P-Value	F-Value	df	P-Value
% Canopy Coverage	6.32	1, 143	0.01	0.47	8, 143	0.87
Dissolved Oxygen (mg/L)	7.51	1, 143	<0.01	9.53	8, 143	<0.01
Turbidity (NTU)	0.06	1, 143	0.81	13.89	8, 143	<0.01
% Silt Coverage	1.91	1, 143	0.17	2.39	8, 143	0.02
% Coarse Substrate Coverage	3.96	1, 143	0.04	1.66	8, 143	0.11
Mean Width Residuals (m)	0.88	1, 153	0.35	4.20	8, 153	<0.01
Mean Depth Residuals (m)	0.21	1, 153	0.65	3.66	8, 153	<0.01
LWD Area (m ²)	36.70	1, 143	<0.01	5.05	8, 143	<0.01
Chlorophyll- <i>a</i> (µg/L)	0.43	1, 143	0.52	8.04	8, 143	<0.01
Benthic Core Biomass (mg DM/m ²)	6.25	1, 153	0.01	4.26	8, 153	<0.01
LWD Biomass (mg DM/m ²)	10.28	1, 153	<0.01	3.08	8, 153	<0.01
Zooplankton Biomass (mg DM/m ³)	0.07	1, 153	0.79	1.58	8, 153	0.13
Nonnative Fish Density (#/100m ²)	15.97	1, 152	<0.01	7.28	8, 152	<0.01
Native Fish Density (#/100m ²)	8.06	1, 152	<0.01	3.24	8, 152	<0.01

Table 3. Macroinvertebrate taxa from backwater habitats on the San Juan River of NM, CO, and UT that represented $\geq 1\%$ of all individuals counted.

Taxon	Secondary Channel	Island	Overall Count	% of Total
Oligochaeta	34,003	9,074	43,077	58.3%
Chironomidae Larvae	4,937	8,071	13,008	17.6%
Ceratopogonidae Larvae	1,216	2,031	3,247	4.5%
Hydropsychidae Larvae	1,958	677	2,635	3.5%
Leptohyphidae Nymphs	1,843	291	2,134	2.9%
Copepoda	979	1,021	2,000	2.7%
Baetidae Nymphs	870	190	1,060	1.4%
Elmidae Larvae	568	161	729	1.0%
Leptophlebiidae Nymphs	745	33	778	1.0%
Total Individuals Counted	47,119	21,549	68,668	93%

Table 4. Fish species captured by backwater type and overall during July-September of 2021 and 2022 on the San Juan River of NM, CO, UT. * denotes four suckers that were suspected as Razorback Suckers or Razorback-Flannelmouth Sucker hybrids.

Common Name	Scientific Name	Status	Secondary Channel	Island	Total Count	% of Total
Western Mosquitofish	<i>Gambusia affinis</i>	Non-Native	3,732	973	4,705	27.97%
Red Shiner	<i>Cyprinella lutrensis</i>	Non-Native	2,916	1,606	4,522	26.89%
Fathead Minnow	<i>Pimephales promelas</i>	Non-Native	2,112	765	2,877	17.11%
Flannelmouth Sucker	<i>Catostomus latipinnis</i>	Native	1,654	813	2,467	14.67%
Black Bullhead	<i>Ameiurus melas</i>	Non-Native	920	342	1,262	7.50%
Speckled Dace	<i>Rhinichthys osculus</i>	Native	268	319	587	3.50%
Channel Catfish	<i>Ictalurus punctatus</i>	Non-Native	170	133	303	1.80%
Bluehead Sucker	<i>Pantosteus discobolus</i>	Native	26	15	41	0.24%
Common Carp	<i>Cyprinus carpio</i>	Non-Native	13	13	26	0.15%
Plains Killifish	<i>Fundulus zebrinus</i>	Non-Native	9	1	10	0.06%
Largemouth Bass	<i>Micropterus salmoides</i>	Non-Native	7	1	8	0.05%
Colorado Pikeminnow	<i>Ptychocheilus lucius</i>	Native	0	5	5	0.03%
*Unknown Sucker	<i>Catostomus</i> or <i>Xyrauchen</i> spp.	Native	2	2	4	0.02%
Green Sunfish	<i>Lepomis cyanellus</i>	Non-Native	1	0	1	0.01%
TOTAL			11,830	4,987	16,817	

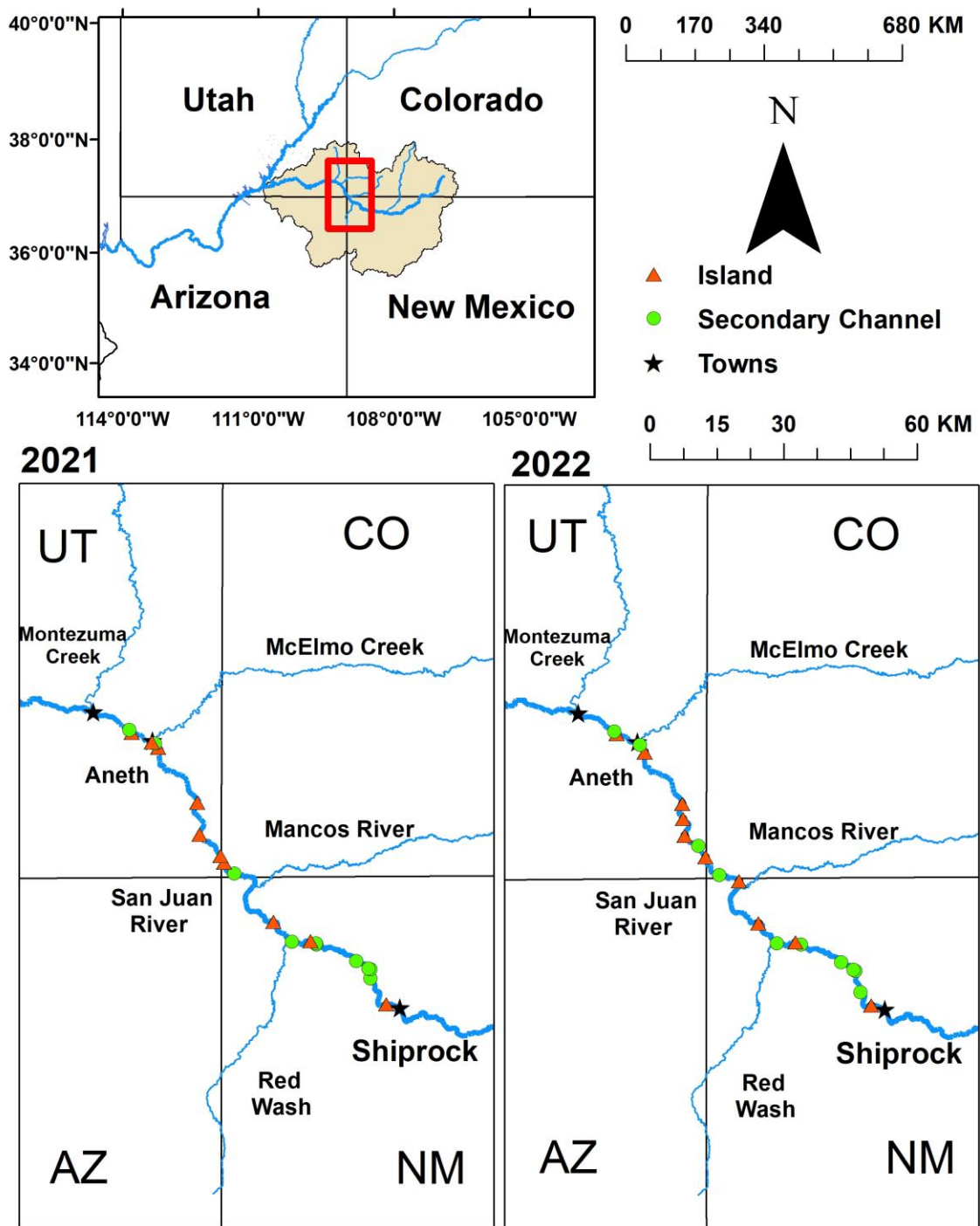


Figure 1. Map of the San Juan River indicating backwater sample sites in 2021 and 2022, with Shiprock marking the upstream end and Montezuma Creek marking the downstream end of the study reach.

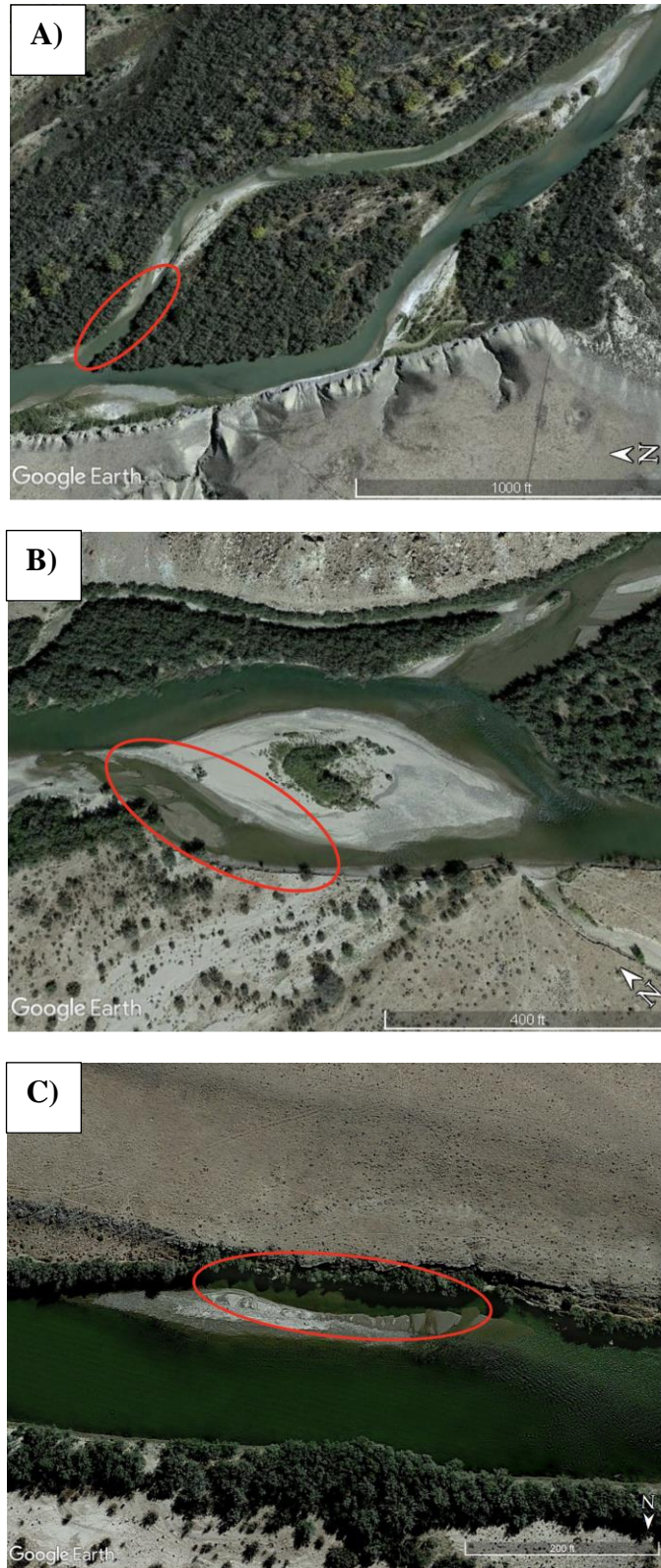


Figure 2. Examples of different backwater types within the San Juan River, (A) Secondary backwater, (B) Island backwater, (C) Cobble/Sand bar backwater.

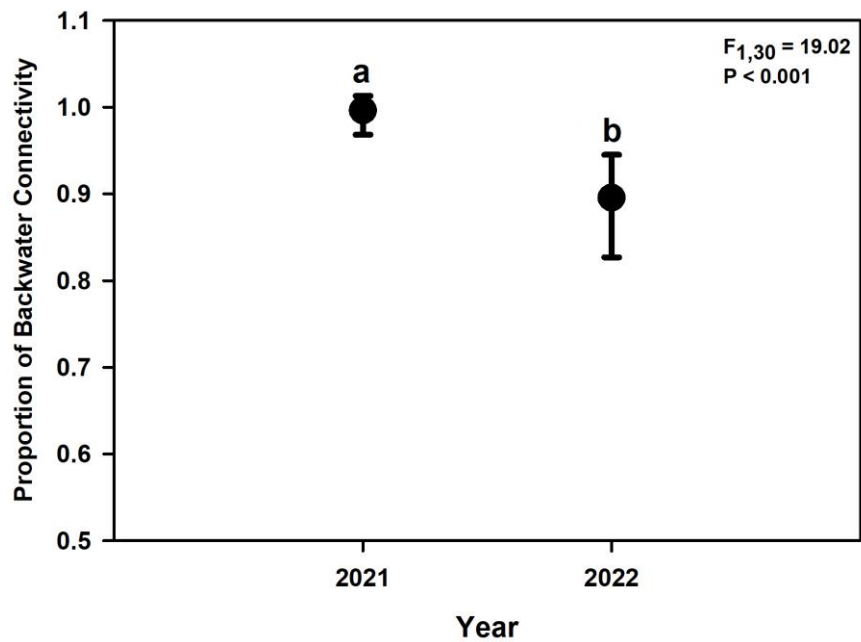


Figure 3. Two-way ANOVA results for differences in mean proportional (\pm 95% confidence intervals) backwater to mainstem connectivity compared between sample years within the San Juan River of NM, CO, UT.

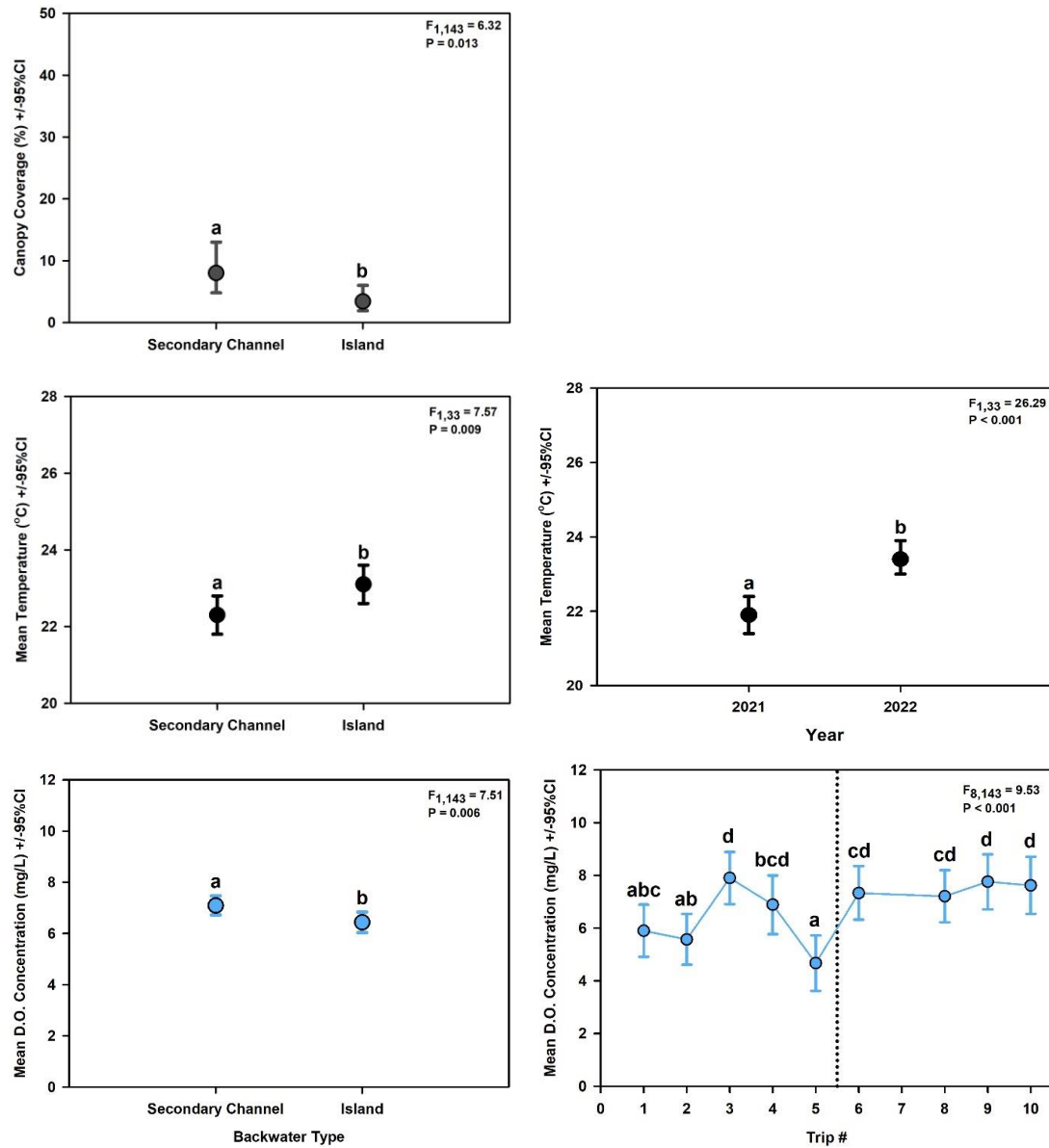


Figure 4. Two-way ANOVA results for canopy coverage, mean temperature (°C), and mean dissolved oxygen (DO) concentrations (mg/L) for comparisons between backwater types, among sample trips, and between sample years on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).

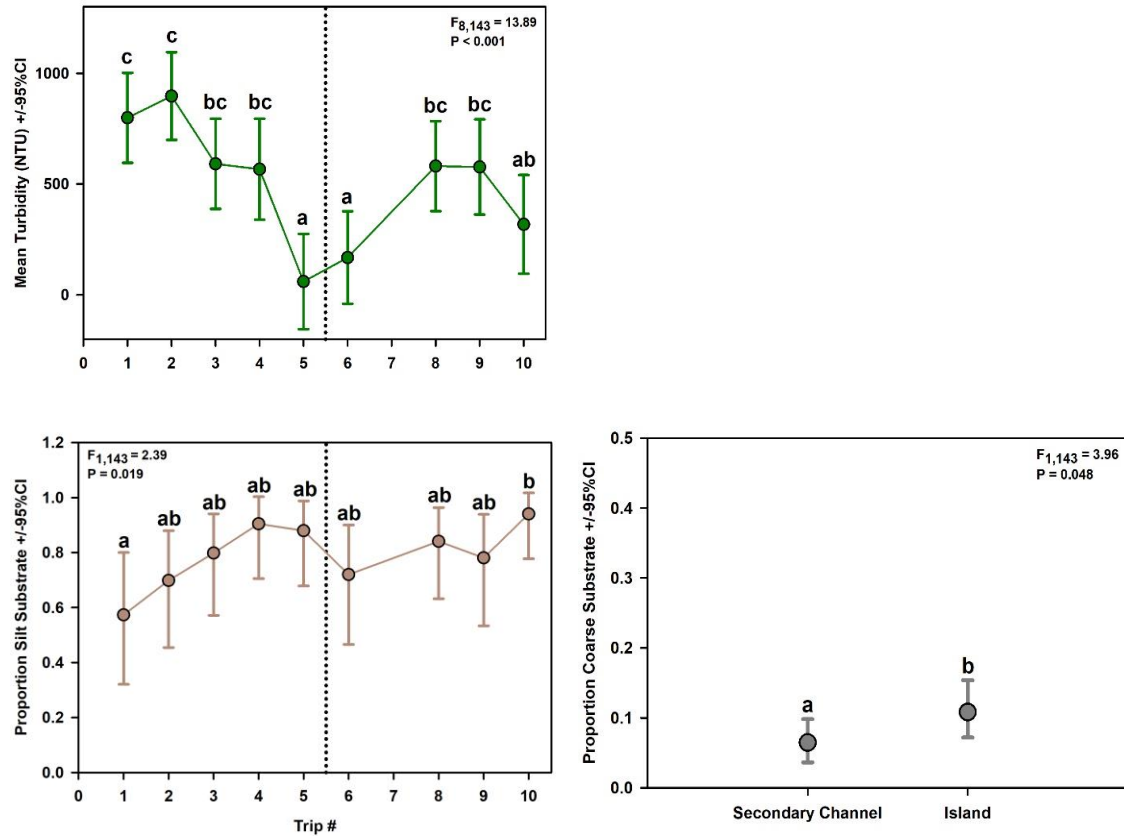


Figure 5. Two-way ANOVA results for mean turbidity (NTU), proportion of silt substrate, and proportion of coarse substrate for comparisons between backwater types and among sample trips during 2021-2022 on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).

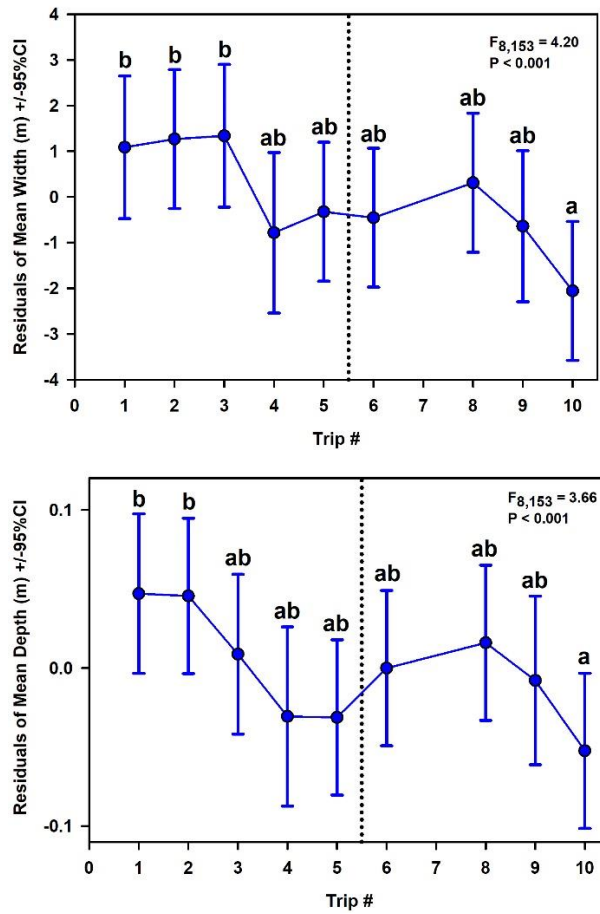


Figure 6. Two-way ANOVA results for residuals of discharge versus mean wetted width and depth for comparisons across sample trips during 2021-2022 on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).

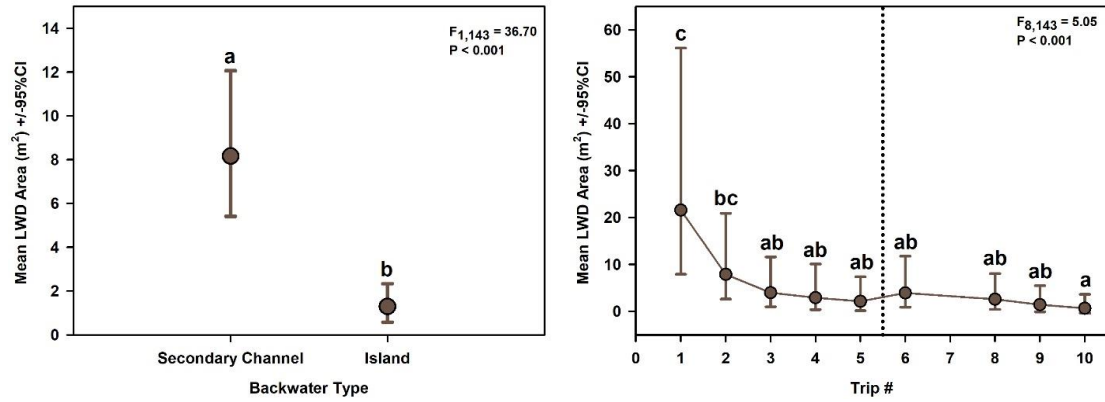


Figure 7. Two-way ANOVA results for mean large woody debris (LWD) area (m²) for comparisons between backwater types and among sample trips during 2021-2022 on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).

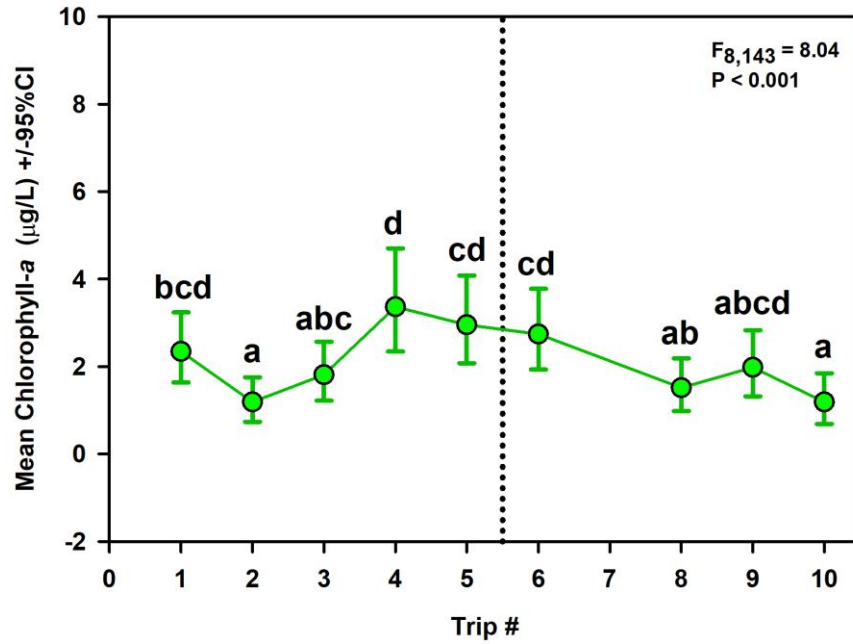


Figure 8. Two-way ANOVA results for mean chlorophyll-*a* ($\mu\text{g/L}$) differences among sample trips during 2021-2022 on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).

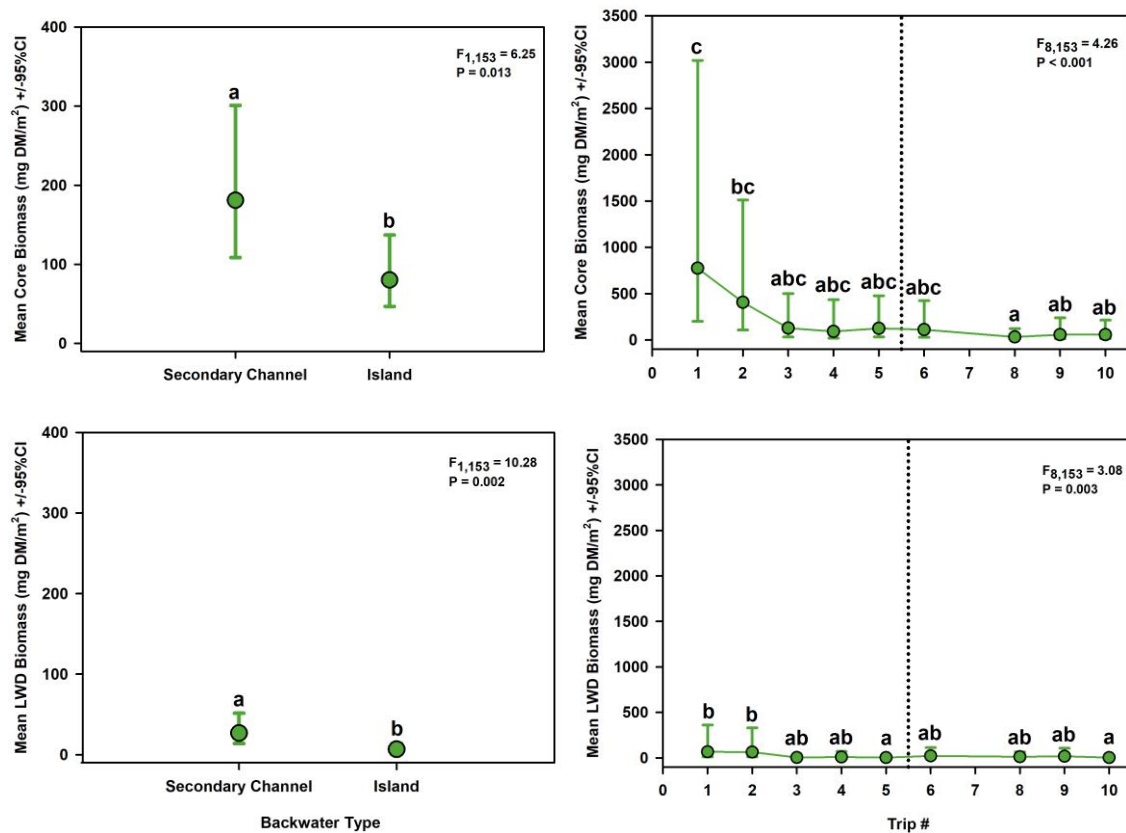


Figure 9. Two-way ANOVA results for mean benthic core biomass (mg DM/m²) and large woody debris (LWD) biomass (mg DM/m²) compared between backwater types and among sample trips during 2021-2022 on the San Juan River of NM, CO, UT. The vertical dotted line separates 2021 (left) from 2022 (right).



Figure 10. Examples of Colorado Pikeminnow (top; *Ptychocheilus lucius*) and comparison photo (bottom) of a suspected Razorback Sucker (upper; *Xyrauchen texanus*) and a Flannelmouth Sucker (lower; *Catostomus latipinnis*) collected from the San Juan River.

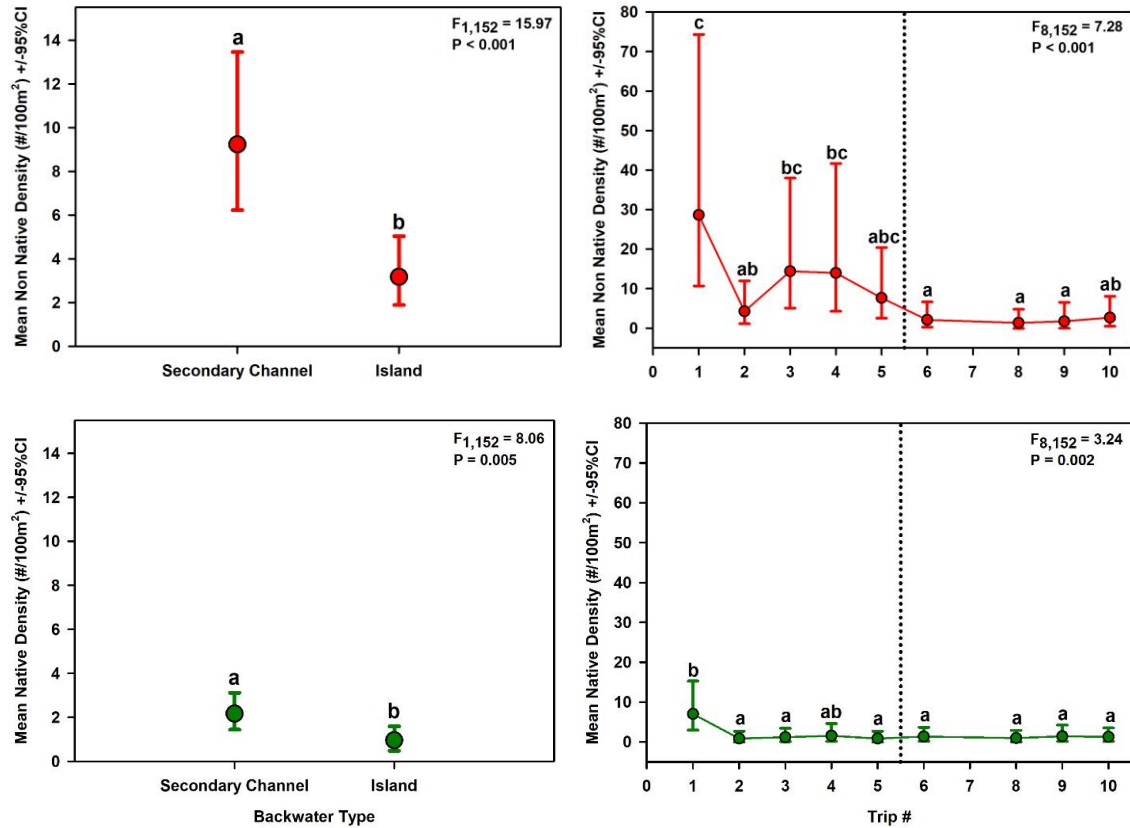


Figure 11. Two-way ANOVA results for differences in mean nonnative or native fish density (#/100m²) compared between backwater types and across sample trips within the San Juan River of NM, CO, UT during 2021-2022. The vertical dotted line separates 2021 (left) from 2022 (right).

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