Fish community composition and movement in the Cache la Poudre River in Fort Collins, Colorado

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Executive Summary

The goal of this study was to better understand if the installation of fish passage over diversion dam structures benefits the distribution, abundance, and conservation of fishes in the Cache la Poudre (Poudre) River. This study provides important new insights into indicators of resilience of local fish populations, including measures of community richness and size structure, and movement rates of fishes over passage structures that increase longitudinal connectedness. Funded by our collaborators the City of Fort Collins and the Colorado Water Conservation Board this study, which spanned three years from autumn 2018 to summer 2021, focused on the transition zone of the Poudre River as it passes through the communities of Bellvue, Laporte, and Fort Collins, Colorado.

To accomplish project goals this study included three specific study tasks: 1) investigate fine-scale fish community composition; 2) monitor background fish movement rates in reaches with complex and simple habitat; and 3) measure passage rates of fish over existing diversion dams via fishways, and compare those to diversion dams without fishways. Because the relatively low numbers of fish recaptures in most river sections reduced our ability to understand movements described in Task 2, we integrated habitat information collected into Task 1 and our limited within-reach movement information was incorporated into Task 3. Thus, after subsuming the original Task 2 into other tasks, the final report has two main tasks.

The purpose of Task 1 was to investigate fine-scale fish community composition to better describe the distribution and abundance of fish species and life stages in specific reaches of the Poudre River, and relate this information to habitat characteristics of those reaches, which are often affected by proximity to diversion dams. This information will allow managers to assess which stream reaches are most impaired and, in turn, may benefit most from fish passage or

other river restoration efforts. Fragmented reaches were identified and several locations in each reach were chosen for sampling, based on a gradient of habitat features, ranging from simple to complex. This enabled us to separate effects on the fish community of: 1) diversions up and downstream from the site, from 2) effects of habitat characteristics within the reach. We expanded proposed sampling for Task 1 from just one year and two sample sessions to three years and six total sampling sessions. We did this because the data from Task 1 was valuable in helping describe seasonal changes in fish abundance. This also provided increased numbers of tagged fish for the movement portion of the study (original Task 3, now Task 2). Task 1 also now includes an additional analysis of 25 years of historical data spanning the period 1993-2017. This was not described in the original project proposal, but was added because those data gave longer-term context and relevance to fish species distribution and abundance information collected during this three-year study.

The purpose of Task 2, which now combines aspects of the original Tasks 2 with 3, was to monitor and estimate rates of fish passage over diversion dams with completed fishways, and compare to passage rates at diversions not fitted with fishways. This effort, originally proposed for just a single year (2020-2021) was also expanded to include all three years of study. This alteration allowed us to capitalize on the large numbers of fish tagged in the vicinity of fishways as well as near diversions without fishways. It also permitted examination of fish movement patterns over multiple seasons with differing flow patterns.

Thus, our two main tasks now include: 1) investigating fine-scale fish community composition and habitat correlates, including assessing changes to fish community distribution and abundance over the past several decades, and 2) monitoring fish movement rates over diversions fitted with fishways, and comparing to diversions that do not have associated fishways. This combination of effort provided the greatest amount of information about the fish community, habitat-related fish abundance, and fish movements.

Between autumn 2018 and spring 2021 we sampled fishes and habitat at 13 locations in the transition zone of the Poudre River and tagged and recaptured trout and suckers to assess fish passage over diversions with and without fishways. This was accomplished over a 24-km reach of river as it passes through the communities of Bellvue, Laporte, and Fort Collins, Colorado.

We highlight our main findings of the fish community study below with summary points and encourage the reader to investigate details of these findings in the body of the report.

- From autumn 2018 to spring 2021, we captured 27,024 fish that comprised 28 species, including 14 native and 14 nonnative kinds, including hybrids.
- Water temperatures were lowest upstream but increased in summer by as much as 7°C from up to downstream sites on a single day, over the relatively short study area distance.
- Native fishes were numerically abundant (77% of total) in the study area, with Longnose Dace *Rhinichthys cataractae*, White Sucker *Catostomus commersonii*, Longnose Sucker *Catostomus catostomus*, and Fathead Minnow *Pimephales promelas* the most abundant taxa.
- Native fishes were most abundant and diverse in downstream reaches of the study area where water was warmer, flow fluctuations were greater, and where relatively rare habitat features including large wood and backwaters were more abundant.
- Nonnative species, especially Brown Trout *Salmo trutta*, made up the majority of the total fish biomass (63%) in the study area, and were most abundant in

upstream reaches where water temperatures were cooler and coarse sediments dominated the substrate.

- Brown Trout and Rainbow Trout *Oncorhynchus mykiss* increased in size downstream, but juvenile trout were common only upstream of Site 6, located just downstream of Lincoln Avenue.
- The highest number of fish species (species richness) remaining in the study area was found in reaches downstream of the Timnath Reservoir Inlet Diversion (TRID, just upstream of Timberline Avenue) extending to Interstate-25.
- Rare fishes, recognized by the State of Colorado as taxa in need of conservation, were collected in the study area including Northern Redbelly Dace *Chrosomus eos*, Plains Topminnow *Fundulus sciadicus*, and Iowa Darter *Etheostoma exile.*
- Off-channel aquatic habitats that are intermittently connected to the Poudre River may act as source populations of naturally sustaining or stocked rare native fishes, but some may also harbor invasive nonnative fishes whose river access should be restricted.
- Species richness was similar just upstream and downstream of the Fossil Creek Reservoir Inlet Diversion (FCRID, located just upstream of the Environmental Learning Center), which is fitted with a fishway.
- Species richness was reduced upstream of two diversions where fish passage was not available, at the Lake Canal Diversion (LCD, just upstream of College Avenue) and the TRID.
- Differences in those species richness patterns indicated fishways may benefit upstream fish communities.

- Stream substrate shifted near the LCD from mainly cobble and gravel upstream to more sand and silt downstream.
- Bank stabilization to prevent channel meandering was present at most sites, except in reaches downstream of the FCRID.
- The diversity, distribution, and abundance of native species has declined since the early 1990s, with formerly rare taxa now apparently extirpated, some historically common forms now being rare, and present depleted populations more restricted to downstream portions of the study area.
- Diversions are partially responsible for native fish declines by reducing recolonization from downstream after species are eliminated upstream of them. For example, as many as 10 native species were documented from 1993-2015 upstream of the LCD near College Avenue, but no more than three have been found since.
- Historical data showed Brown Trout distribution expanded downstream, and abundance increased riverwide, concurrent with higher and perhaps cooler flows since around 2010.
- Predaceous Brown Trout, and lower water temperatures, may be responsible for the decline of native fishes, particularly in the lower half of the study area.

We used recaptures of tagged fish, and a variety of detection gears, including antennas installed in fishways, to track movements of large-bodied fishes, mainly Brown Trout, Rainbow Trout, White Sucker, and Longnose Sucker, in the study area. We highlight our main findings of the fish movement study below with summary points and encourage the reader to investigate details of these findings in the body of the report.

- A total of 6,573 individual fish were implanted with passive integrated transponder (PIT) tags from 2018-2021.
- Multiple years of tracking fish movement with physical recaptures and a variety of tag detection approaches confirmed tagged fish passed over diversions both with and without fishways in upstream and downstream directions, but at a substantially greater rate when fishways were available.
- Fish movement was also documented over or through less intensively studied locations including the low-head Kingfisher Point Natural Area sheet pile grade-control structure, and the Poudre River Whitewater Park, site of the formerly impassable Coy Diversion and boat chute, just downstream of College Avenue.
- Upstream movements were especially higher during spring and early summer, periods of greater flow due to snowmelt runoff, and patterns varied by species.
- Fish also moved in non-runoff periods, especially when short-term flow increases were noted, and movements were likely associated with reproduction.
- Downstream movements were also substantial and more prevalent in periods of lower flow.
- Fish movements in winter were low, especially in flow depleted reaches, which essentially precluded fish movements.
- Diversions without fishways blocked upstream movement of most fish, and species richness and abundance was reduced upstream of those diversions.
- Several species moved relatively long distances between the FCRID and TRID by using the bypass channel adjacent to the Boxelder diversion.

- Brown Trout and White Sucker movements during their respective reproductive seasons were linked with flow increases.

The findings of our two main tasks led us to several conclusions. The fish community of the Poudre River is in decline, including relatively recent reductions, due to several causes. Habitat fragmentation by diversion dams certainly has played a role, as evidenced by reduced species richness upstream of diversion dams that are impassable by most species compared to species richness downstream. Downstream range shifts and reductions in abundance through time support the notion that diversion dams in our study area are barriers to upstream movement for some species and may be part of the reason for the decline of native fishes in the study area. Counter to that point, fishways fitted to diversion dams may improve upstream recolonization, evidence for which is from the similar fish communities downstream and upstream of the FCRID.

Changes in longitudinal patterns of species richness and abundance throughout the study area may also be due to abiotic factors. For example, cooler water temperatures associated with higher flows in upstream reaches may have exceeded the thermal tolerance for some warmwater native fishes, and may be responsible for their reduced abundance.

Habitat shifts in the study area other than water temperatures, may also play a role, especially at local scales. For example, finer-grained sediments favor sucker species just upstream of diversion dams, but are also associated with increased abundance of those species at a broader scale because sand and silt are generally more abundant in downstream reaches of the study area. Longnose Dace and trout species generally favor reaches with larger substrate types, which, at a local scale, are more abundant just downstream of diversions, but also more abundant in upstream reaches of the study area.

In addition to physical habitat shifts, species interactions may also play a role in shaping fish distribution and abundance patterns. For example, habitat conditions favorable to Brown Trout may in turn negatively affect native species through competition for resources and predation. In support of this point, we commonly observed larger Brown Trout regurgitating native fish following electrofishing capture. Thus, the interplay between abiotic conditions, physical habitat, and species interactions likely influence fish assemblage structure at different scales in the Poudre River transition zone.

Whether changes in the fish assemblage over the past several decades are episodic or permanent in nature is difficult to determine. In the short, heterogeneous reach that comprises the transition zone of the Poudre River, it is reasonable to expect the fish assemblage structure to be in a state of shifting equilibrium influenced by stochastic events such as drought and flooding. The Poudre River is presently in a relatively wet period beginning around 2010, preceded by an extended period of drought beginning in 2000. Formerly common species in downstream reaches such as Sand Shiner were abundant during drought years, and have since been nearly eliminated from our study area following the onset of wetter years. It is possible their disappearance from the study area is a temporary range shift downstream into more thermally suitable habitat. However, this hypothesis does not explain Sand Shiner presence during wet years prior to the year 2000, and their near disappearance from downstream sites coincides closely with the first establishment of Brown Trout.

Our results also indicated that diversions with fishways facilitated passage of two native suckers and two nonnative trout more effectively than diversions without passage infrastructure, which doubtless improves conditions for those taxa and others that were not tagged but may have moved. Improved connectivity was illustrated both through the greater proportion of passage by tagged fish released in proximity to diversions with fishways than those without, as well as the higher modeled probability of transitioning over a low-head diversion (here < 1.2 m vertical drop) when a fishway was available. These findings complement studies of others, who demonstrated the capability of nine different species to ascend the FCRID fishway when fish were released in a downstream enclosure. Thus, we feel confident that installation of additional fish passages on other diversions would benefit the fish community of the Poudre River.

Our results showed that seasonal movements were greater during high flows, regardless if fish were moving over fishways, or were moving over short-time durations within reaches for presumptive spawning. What we cannot determine is if fish movements would be greater during other seasons if more flow was present in the river, say in winter. During our study, the reach immediately downstream of the FCRID in winter was typically desiccated except for isolated pools because what little water remained in the river upstream of FCRID was diverted, which obviated passage of any kind because fish could not access the fishway or diversion.

The effectiveness of fishways is directly dependent on the local reach having sufficient flows to physically enable movement to and from the diversion structure. So while its clear flows must be sufficient for fishways to function, more specifically it is important that spring and summer flows, when most fish move, are protected, and year-round flows are restored in river reaches that are presently desiccated. This will be especially important during periods of extended drought associated with a predicted hotter, drier climate, and proposed additional water development, which stands to further alter abiotic and physical habitat conditions in the Poudre River transition zone in the near future.

The extensive and destructive Cameron Peak fire in the upper Poudre River watershed in summer/autumn 2020 resulted in ash and sediment-laden flows in downstream reaches in summer 2021 following rain events. This caused high mortality of fish upstream and likely also reduced distribution and abundance of all fishes in our study reach. A smaller fish kill also occurred in summer 2018 in a downstream section of this study area (near Lemay Avenue) just prior to beginning sampling in this study. Thus, our study was temporally bounded by fish kills. Looking forward, improved understanding of such disturbances on fish community composition and structure would help practitioners identify the most effective management actions for recovery and conservation. This would be especially useful if the study area were expanded upstream to include reaches unaffected by ash flows, as well as reaches immediately downstream of them. Our results indicated additional reconnection of fragmented reaches may increase dispersal of fishes across the system and increase recolonization and conservation potential for native fishes. Reducing river fragmentation to enhance resilience of local fish populations may be especially important given numerous ongoing stresses to the system, including wildfires, land use changes in the floodplain, and potential further limitations to stream flows due to proposed future water development and climate change.

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Introduction

Fish require a mosaic of habitat types to complete their life cycles, which can vary in spatial scale from short reaches to entire river networks (Fausch et al. 2002). The capability of fish to move within and between habitats best suited for growth, refuge, spawning, and survival occurs seasonally and varies for different life stages (Schlosser 1998, Scheurer et al. 2003). For example, some fish require spawning gravel of a certain size or specific water temperatures for successful reproduction (Kondolf and Wolman 1993, Haworth and Bestgen 2017). In winter, fish may move to find suitable habitats for resting and surviving harsh, and typically, low flow conditions (Cunjak and Power 1986). Barriers to movement, which often occur in streams with regulated or diverted flows, may impede the ability of fish to move to these required habitats, and when needs are not met, reduced fish species richness, distribution, and abundance may result (Winston et al. 1991, Perkin et al. 2015). Barriers to movement may also result in imbalance in fish community structure. For example, if adults are unable to move to suitable spawning areas, stream reaches isolated by diversion dams may support only a single age group, leaving fish in those reaches more susceptible to local extinction in the face of disturbances (Alò and Turner 2005, Dudley and Platania 2007).

As the Cache la Poudre (Poudre) River flows through the City of Fort Collins and surrounding areas it transitions over an approximately 24-km reach from a confined high gradient mountain river with coarse substrate and cold water temperatures, to a lower gradient plains river, with mixed, small to large substrate composition, cool to warm thermal conditions, and mixed physical habitat, including limited access to floodplains (Shanahan et al. 2014, Bestgen et al. 2020). The abiotic intermediacy of streams in the transition zone provides a unique suite of conditions that historically supported a locally diverse native fish assemblage and species with a variety of life history and habitat requirements (Rahel and Hubert 1991, Fausch and Bestgen 1997, Bestgen et al. 2020; Haworth et al. 2020). The transition zone of the Poudre River has a long legacy of human alteration, and ecological conditions suitable for transition zone fishes have declined through time (City of Fort Collins 2017). In addition to depleted flows, human-caused channel change and other habitat alterations, and establishment of nonnative fishes, numerous in-channel water diversion structures contribute to habitat fragmentation and may prevent movements and passage of fish most months of the year, especially during low flows.

Construction of fish-passage structures (fishways) is an increasingly common means to mitigate negative effects of habitat fragmentation on Front Range stream fish communities. Passage structures are known to benefit large-bodied fishes, and if designed to pass a diverse suite of species including those with smaller body sizes (Bestgen et al. 2010; Ficke 2015, Swarr 2018, Richer et al. 2020), they may substantially benefit fish community structure and species composition. With significant investments into retrofitting numerous structures with fishways on the Poudre River and around the state, the City of Fort Collins and the Colorado Water Conservation Board sought to better understand effectiveness of these infrastructure additions to reduce effects of fragmentation and increase fish movements and potentially, improve fish community richness and size structure.

Study proposal and objectives— To accomplish the goal of better understanding effectiveness of these infrastructure additions to increase fish movements and subsequently improve fish community richness and size structure, our collaborators the City of Fort Collins and the Colorado Water Conservation Board funded our three-year research program, which began in September 2018. Our integrated objectives included three specific study tasks: 1) investigate fine-scale fish community composition; 2) monitor background fish movement rates in reaches with complex and simple habitat; and 3) measure passage rates of fish over existing diversion dams via fishways, and compare those to diversion dams without fishways. Because the relatively low numbers of fish recaptures in most river sections reduced our ability to understand movements described in Task 2, we integrated habitat information collected into Task 1 and our limited within-reach movement information was incorporated into Task 3. Thus, after subsuming the original Task 2 into other tasks, the final report has two main tasks.

In Task 1, investigate fine-scale fish community composition, the objective was to better describe the distribution and abundance of fish species and life stages in reaches of the Poudre River, and relate that to habitat characteristics of the reaches, which are affected by proximity to diversion dams. This information will allow managers to assess which stream reaches and habitat are most impaired and may benefit most from fish passage. Fragmented reaches were identified and several locations in each reach were chosen for sampling, based on a gradient of habitat, ranging from simple to complex. This enabled us to separate effects on the fish community of: 1) diversions up and downstream from the site, from 2) effects of habitat characteristics within the reach. We expanded proposed sampling for Task 1 from just one year and two sample sessions to three years and six total sampling sessions. We did this because the information was valuable to describe seasonal changes in fish abundance and also provided increased numbers of tagged fish for the movement portion of the study (original Task 3, now Task 2). Task 1 also now includes an additional analysis of 25 years of historical data spanning the period 1993-2017. This was not described in the original project proposal, but was added because those data gave longer-term context and relevance to fish species distribution and abundance information collected during this three-year study.

Task 2, which now combines aspects of the original tasks 2 with 3, describes monitoring and estimating passage rates of fish over diversion dams with completed fishways, and compares those movements to passage at diversions that were not fitted with fishways. This effort, originally proposed for just a single year (2020-2021) was also expanded to include all three years of study as well. This alteration allowed us to capitalize on the large numbers of fish tagged in the vicinity of fishways as well as near diversions without fishways, and permitted examination of fish movement patterns over multiple seasons with differing flow patterns.

Thus, our two main tasks now include: 1) investigate fine-scale fish community composition and habitat correlates, including assessing changes to fish community distribution and abundance over the past several decades, and 2) monitor fish movement rates over diversions fitted with fishways, compared to diversions that do not have associated fishways. This combination of effort provided the greatest amount of information about the fish community, habitat-related fish abundance, and fish movements, and aids in understanding the ecology, conservation, and restoration of the Poudre River fish community.

Study Area

The Poudre River originates at high elevation in the Southern Rocky Mountains at >4,000 m above sea level, and terminates on the eastern plains of northern Colorado where it is tributary to the South Platte River at approximately 1,500 m asl. It drains an area about 2,865 km^2 and hydrology is dominated by snowmelt (Bestgen et al. 2020). Peak annual flows occur in late spring and early summer, receding to relatively stable base flows during summer and early autumn, and are further reduced during late autumn and winter (Bestgen et al. 2020). Extensive water storage and diversion infrastructure has altered Poudre River hydrology in our study area, a 24-km-long transition-zone reach from Bellvue, CO, downstream to Interstate-25 (Figure 1). Additionally, structural hardening of riverbanks to prevent channel meandering and property damage is prevalent in our study area (Shanahan et al. 2014). There are 15 water diversion and grade control structures of varying size and configuration in this relatively short reach, although four have been recently removed or retrofitted with fishways. From upstream to downstream (Figure 2), these altered structures include: the Watson Lake Diversion (WLD, fishway completed 2019), the Josh Ames Diversion (removed 2013), the Poudre River Whitewater Park (Coy Diversion and boat chute removed 2019), and the Fossil Creek Reservoir Inlet Diversion (FCRID, fishway completed 2018).

The most upstream WLD fishway is approximately 50 m in length, which was needed to achieve desired lower slopes for this relatively high diversion, and is fitted with cobble-sized velocity breaks to aid fish movement. The fish community is dominated by trout but several native coolwater-tolerant species are also present. The Josh Ames Diversion, which had a vertical drop >2 m, was replaced by a boulder weir to provide grade control while also allowing recreational use and upstream fish passage. After reconstruction a large, deep pool was created on the downstream side of the boulder weir, and an additional 1 km of stream was reconnected on the upstream side for the fish assemblage that is comprised of species tolerant of cold and coolwater (not warmwater) regimes. Fish passage at this structure was not studied but was assumed to occur, based on lack of vertical drop and the subsequent connected habitat upstream and downstream. Located just downstream of College Avenue, the Whitewater Park was constructed to replace the Coy Diversion and boat chute and provide kayaking opportunities in the city. It consists of two grade control structures approximately 50 m apart with fish passage incorporated into the channel design in a reach with a mixed cold and coolwater fish assemblage.

The most-downstream FCRID is a low-head structure with a sluice gate and an ogee-shaped face with a vertical drop of 0.51 m, while the constructed fishway (0.46 m-high) on the north side of the diversion is 8.5-m long with a 5% slope, which is again fitted with flow velocity obstructions to benefit fishes as they pass. This fishway was designed with the intent of restoring upstream passage for resident fishes that include both small and large-bodied native taxa that are cool to warmwater tolerant, as well as introduced trout. During high flows the diversion face is inundated and creates a hydraulic wave downstream, with additional water sometimes passing through a radial gate on the south side of the diversion. Thus, fish have at least three potential routes to pass over the structure (Figure 3). Description of the FCRID fishway design and hydraulic performance are detailed by Richer et al. (2020).

Notable diversions and grade control structures in our study area without fish passage include, from upstream to downstream, the Larimer-Weld Canal, Lake Canal Diversion (LCD), Timnath Reservoir Inlet Diversion (TRID), and a sheet-pile grade-control structure that protects a buried natural gas pipeline at Kingfisher Point Natural Area (Figure 4). The Larimer-Weld Canal is upstream of our site 3 and 3.2 km upstream from the LCD, and is presumed impassable for fishes upstream due to diversion dam height (about 2 m) and a vertical concrete face. The LCD is located 4.8 km upstream from the TRID and just upstream of the Whitewater Park, and is a low-head diversion dam with a total vertical drop of 1.15 m that becomes inundated during peak annual flows and creates a hydraulic jump downstream of the structure. The most upstream drop of the diversion face is 0.75 m, with a 3.3 m long flat apron below it that leads into a 0.4 m drop at the downstream end of the diversion. Sheet flow over the apron was <0.1 m deep when measured during a discharge of 0.7 m^3/s. The TRID, located approximately 4 km upstream of the FCRID, has a 1.7 m high wall with concrete braces that disrupt flow as water passes over it, and often diverts all river flow during autumn and winter months (sweeps the river), greatly reducing flow downstream (Figure 5). The initial slope from a downstream direction consists of a smooth ogee-shaped face, which rises 0.98 m to a flat apron. The final section of the dam face rises vertically another 0.72 m to the crest of the diversion. Gates on the upper face leak small amounts of water but are insufficient to pass a large fish, so all passage we documented via tag detections was over the top of the structure. The sheet-pile grade-control structure at Kingfisher Point Natural Area is located 0.4 km upstream of Timberline Road, and 0.8 km downstream of the TRID. It has a minimum vertical drop of 0.28 m across the length of the structure, and during high flows is inundated without creating a downstream hydraulic wave. Due to close proximity to the river-sweeping TRID, little to no water spills over this structure during low flow periods, and remaining water passes as shallow (< 1 cm) sheet flow over the concrete surface upstream. Fish passage at this structure was not studied specifically, and we suspect it is a barrier during low flows which are prevalent at this location, but fish were documented moving past this structure upstream to near the TRID, likely during higher flows.

Methods – Fish Community Assessment

Fish community sampling– Thirteen sampling sites were selected to determine fish species composition, distribution, and relative abundance in the Poudre River transition zone. Several factors guided placement of sampling sites. The 2017 City of Fort Collins State of the Poudre Report (SOPR) guided establishment of sites in reaches identified as rural, urban, and plains zones based on land use, habitat characteristics, and prevailing biological communities (City of Fort Collins 2017; Figure 1). The SOPR identified 15 reaches (numbered 4-18) in these zones, and we established a sampling location in 13 of them (Table 1). We did not conduct sampling in reaches 4 (upstream of WLD) and 7 (up and downstream of Taft Hill Road) due to lack of access through private lands. The length of each sampling site encompassed two riffle-run-pool sequences, generally equal to about 10 wetted widths of river, and were placed to include unique habitat features such as backwaters. Placement of sites in SOPR reaches was also informed by identifying reaches fragmented by diversion dams and a gradient of habitat complexity, including the presence of existing or proposed fishways, to illustrate fish community differences between disconnected reaches and aid in evaluation and planning of future fish passage projects. Two fish passage projects were slated to begin construction during this study, one at the WLD, and one at the TRID, but only the former was completed. Discussions continue regarding the TRID fishway.

Fish sampling protocols were designed to obtain a robust assessment of fish community composition and size structure. Sampling occurred twice per year (spring and autumn) between autumn 2018 and spring 2021 when the river was wadeable before and after annual runoff. Fish were captured by backpack electrofishing and seining. Electrofishing used two units in a single-pass with a minimum of two netters per unit, and targeted all habitat present, particularly deep main channel areas and complex instream structure. Seining targeted open water and shallower habitat, which is less efficiently sampled by electrofishing. Sampling effort (time) for both gear types was recorded to estimate fish catch per unit of effort (CPUE; number of fish captured/hour of sampling) to facilitate comparisons between sites. The CPUE for electrofishing and seining were combined, and all samples were summed by site to account for seasonal variation in species presence and relative abundance. Captured fish were identified to species, counted, measured to the nearest mm total length (TL), weighed (g), and scanned for an existing passive integrated transponder (PIT) tag. Most adult Common Carp *Cyprinus carpio* were not netted and processed because of difficulty of handling and possible mortality of other fish in holding pens. However, total biomass of adult Common Carp was estimated with a mean individual adult weight (2,100 g) calculated from a sub-sample of weighed individuals (n = 15, range 1,350 - 2,900 g). All untagged fish greater than 120 mm TL received a half-duplex 12 mm PIT tag, inserted into the peritoneal cavity posterior to the left pectoral fin.

Habitat measurement— Habitat measurements were made concurrent with fish sampling at each site, and included both transect-based measurement of channel form and substrate characteristics, and site-wide habitat features. Velocity and depth measurements were taken at five equidistant points along 10 transects in each site, spaced apart by approximately one channel width between the up and downstream end of each site. The percent substrate composition was determined at each site by visually classifying dominant or co-dominant substrate particle size (diameter) in a circle in a 10-cm radius at each of these transect points using a modified Wentworth scale. Wetted and bankfull widths were measured at each transect, and a ratio of the two measures (wetted/bankfull) was calculated to obtain an estimate of the active floodplain at sites. Other habitat measurements included the amount of rip-rap, undercut bank, total submerged wood, and backwater area present. Rip-rap and undercut bank were linear measurements (m), submerged wood and backwaters were measured as area (m^2), and all were estimated by summing separate measurements of each feature at all locations in a site. All measurements were averaged across samples to account for seasonal differences. Additionally, 15 minute-interval water temperature measurements collected in a collaborative effort between the City of Fort Collins, Colorado State University, and In-Situ Inc. were summarized for four locations during 2020, a representative year, to describe seasonal longitudinal temperature patterns in the study area.

To describe broad patterns of habitat association for several species and guilds of fishes with the habitat variables listed above, we used the Pearson product-moment correlation with significance of $\alpha \leq 0.10$, a value that allowed exploration of potentially important effects. Only the most abundant species (> 500 individuals captured) were assessed to avoid bias created by small sample sizes. Groups or species examined included a native sucker guild (White Sucker *Catostomus commersonii* and Longnose Sucker *Catostomus catostomus*), a nonnative trout guild (Brown Trout *Salmo trutta* and Rainbow Trout *Oncorhynchus mykiss*), and small-bodied native fishes Longnose Dace *Rhinichthys cataractae*, Fathead Minnow *Pimephales promelas*, and Johnny Darter *Etheostoma nigrum*. Small-bodied species were assessed separately due to presumed differences in habitat preferences. Comparisons were made between the CPUE of these guilds or species at each site with each of the following habitat covariates; mean site depth (m), mean site velocity (m/s), wetted to bankfull ratio, length of linear rip-rap (m), length of undercut bank (m), total area of submerged wood (m^2), total backwater area (m^2), percent fine sediment (silt and sand), and percent coarse substrate (gravel, cobble, rubble). Correlations were calculated using CPUE and habitat measurements averaged across all samples to control for interannual and seasonal variation.

Historical fish community data– Records from previous fish community sampling completed by the Larval Fish Laboratory and Colorado Parks and Wildlife were used to compile a list of species occurrences and describe spatiotemporal changes in fish community composition and relative abundances from 1993 to present. We selected four historical sites to match the location of four contemporary sampling sites that are representative of a gradient of physical and biological conditions throughout the study area. The locations selected closely matched the location of our contemporary sites 2, 4, 8, and 12 (Table 1, see below). Because annual sampling records are more complete at some locations than others, sampling effort was not available for all samples, and completion of seasonal sampling was inconsistent, we used presence/absence and species relative abundance (% of each species among the total captured) metrics to examine fish community patterns at the site and study area scales throughout the period of interest.

Results – Fish Community Assessment

Fish community sampling– In the six sampling occasions completed between autumn 2018 and spring 2021, we captured 27,024 fish comprised of 28 species, 14 native and 14 nonnative, including hybrids (Table 2). Three native species (Longnose Dace, White Sucker, Longnose Sucker) and one nonnative species (Brown Trout) were distributed throughout the study area and captured at all 13 sampling sites. Sixteen species (7 native, 9 nonnative) were rare, represented by fewer than 50 individuals captured or were found at few locations, over the three-year study period. Native species were numerically dominant and accounted for 77% of all fish captured, with four species accounting for 95% of that total: Longnose Dace, White Sucker, Longnose Sucker, and Fathead Minnow. Brown and Rainbow Trout comprised 92% of all nonnative species captured.

Although native taxa were numerically dominant, nonnative species accounted for most of the total biomass (63%) among all fish captured. This was driven by Common Carp, Rainbow Trout, and especially abundant adult Brown Trout, which accounted for 39% of total fish biomass across all sites. White Sucker and Longnose Sucker accounted for nearly all (98%) native species biomass.

Species distribution and abundance patterns differed longitudinally, and were affected by the presence of diversion structures of varying size and function. Species richness was highest at sites downstream of the TRID (located between sites 7 and 8, Figure 6). In those reaches species richness was similar upstream of the FCRID fishway at sites 8-10 (range 12-20 species) and downstream at sites 11-13 (range 15-17 species). There was a progressive decrease in species richness moving upstream of the TRID (11-12 species) and the LCD (7-8 species), just upstream of College Avenue between sites 4 and 5. Native fish diversity was highest at the most downstream Site 13, and nonnative diversity was highest at Site 10 just upstream of the FCRID.

Nonnative fish abundance was higher at more upstream sites, specifically upstream of the TRID, due mainly to higher abundance of Rainbow, and especially, Brown Trout (Table 3, Figure 7). Alternatively, native species were more abundant at downstream locations, particularly downstream of the LCD, and peaked at sites 8-10.

Several rare and sensitive native taxa were captured during fish community sampling and they were also largely restricted to downstream of the TRID between sites 8-13 (Table 3). Most notable was Northern Redbelly Dace *Chrosomus eos*, which carries a statutory listing of endangered in Colorado (Colorado Parks and Wildlife 2015). A single juvenile specimen was captured at Site 13 in spring 2019, and was confirmed in the laboratory as the first record of this species from the Poudre River. Stocking of >20,000 adult Northern Redbelly Dace has occurred from 2016-2021 (excluding 2019) in adjacent off-channel wetland habitat in Topminnow Natural Area (B. Wright, Colorado Parks and Wildlife, Fort Collins, personal communication 2021), and our capture was likely the result of escapement from that population. However, the capture of this specimen is important because it indicates: 1) natural reproduction occurred among stocked and/or naturalized Northern Redbelly Dace; and 2) a connection to the main channel of the

Poudre River likely facilitated movement between these habitats. Other rare or sensitive taxa encountered included the Iowa Darter *Etheostoma exile* (State of Colorado Species of Special Concern) and Plains Topminnow *Fundulus sciadicus* (Tier I Species of Greatest Conservation Need). Iowa Darter were relatively rare and present in low numbers in downstream sites 10-13. Plains Topminnow were also found in low numbers, but were more widely distributed and found at six sites, including Sites 5 and 6 upstream of the TRID.

Along with differences in distribution and abundance between sites, size structure of the four most abundant large-bodied species, Brown Trout, Rainbow Trout, Longnose Sucker, and White Sucker, differed within and between sites. Brown Trout were present at all sampling sites, but both juveniles (< 200 mm TL) and adults (>200 mm TL) were only abundant from Site 6 upstream (Figure 8). In those six upstream sites, juveniles had a higher CPUE than adults (>200 mm TL) at all but Site 2, but were relatively balanced with adult abundance. Rainbow Trout were also present at all sites, but both juveniles and adults were largely restricted to sites upstream of the LCD, and juveniles were less abundant than adults at all locations other than Site 1. Linear regression of mean TL as a function of sampling site showed that both Brown (P=0.003) and Rainbow Trout (P=0.002) mean TL increased in a downstream direction supporting the idea of more large fish and fewer small fish present at more downstream sites, with site location explaining approximately 60% of the variation in abundance for each species (Figure 9).

Longnose Sucker were present at all sites, and more evenly distributed throughout the study area with highest abundance in middle reaches (sites 5-11, Figure 8). Abundance decreased upstream of the LCD and at the two most downstream sites, and juveniles were far more abundant than adults throughout the study area. White Sucker presence was largely restricted to downstream of the LCD, and juveniles were again more abundant than adults at all sites. However, abundance of adults was highest downstream of the TRID, where greater numbers of juveniles also existed. In contrast to both nonnative trout species, neither Longnose nor White Sucker exhibited a significant relationship between mean TL and site location ($P > 0.05$).

Habitat— Measurements and descriptions informed broad patterns of habitat conditions, as well as the location and relative abundance of specific habitat features throughout the study area. Mean depth was relatively comparable throughout the study area, but was slightly lower upstream, especially at sites 2 through 4 (Table 4). These generally shallower sites also had some of the highest mean water velocities, though this pattern was not uniformly present, and variation among measurements, reflecting presence of deep and shallow locations, was relatively high. Wetted to bankfull channel ratio, where values approaching 1 indicated an armored or perched riverbank, was variable throughout the study area, and showed no clear longitudinal pattern of change, but varied widely (range 0.33-0.84). A pronounced shift in substrate composition occurred near the LCD, with fines (silt, sand) averaging 15.8% (range 11.3-22.4%) of total substrate upstream of that point at Sites 1-4. Fines averaged 39.7% (range 30.8-51.6%) at sites downstream of the LCD. The highest proportion of fine sediment occurred at Sites 7 and 10 (51.2 and 51.6%, respectively), which are located immediately upstream the TRID and FCRID, respectively, where fines are deposited in low-velocity pools upstream of the diversion dams.

Presence and abundance of specific habitat features varied across sites. Rip-rap bank reinforcement was present at nearly all sites, but was absent at sites 11-13 downstream of the

FCRID (Table 4). Presence and size of backwaters was variable, but most large perennial backwaters were located downstream of the TRID, with the exception of Site 6. Instream wood increased in a downstream direction, especially downstream of the FCRID, where the amounts of wood at Sites 11 and 12 were an order of magnitude greater than sites 1-3 upstream of the LCD.

Analysis of CPUE data relative to habitat covariates showed different associations between species and guilds (Figure 10). Substrate types had the strongest correlations with native suckers, a positive relationship with fine substrate and negative with coarser sizes. Native sucker CPUE also had moderately positive correlations with higher mean water depth and increased backwater area, and moderately negative correlation with increased mean water velocity. Trout showed a strong negative correlation with higher percentage of fine substrate (also more common downstream) and higher mean water depth, and a strong positive correlation with higher amounts of coarse substrate. Trout also showed a moderately negative correlation with higher amounts of submerged wood. This relationship was unexpected because trout generally use cover, but may be an unrelated consequence that more wood is present in downstream locations where fewer trout reside. Fathead Minnow showed a strong positive correlation with increased backwater area. Longnose dace had a strong negative correlation with wetted to bankfull stream width ratio, those sites with less available active floodplain, and moderately positive correlation with higher amounts of undercut bank. Johnny Darter had moderately negative correlations with increased mean water velocity and coarse substrate, and a positive correlation with higher percentage of fine substrates.

Monitoring throughout 2020 showed mean monthly water temperature differed between sites during all months except October, and temperature increased in a downstream direction (Table 5). The months with the greatest amount of downstream warming were July, August, November, and December, all with differences greater than 4°C between the most upstream and downstream sites 1 and 12 (site 13 was not monitored). Annual temperature range, described as the difference between the warmest and coolest months at each site, also increased at more downstream sites (12.3°C and 14.8°C at sites 1 and 12, respectively). Maximum daily water temperature measured during August, typically the warmest month, increased between 2.1-2.8°C at each subsequent downstream measurement site (4 total), with a difference of 7.4°C between Site 1 and Site 12.

Historical fish community data– Changes in fish community composition at both the study area and site scale occurred in the transition zone since the early 1990's. Thirty-four different fishes were documented at the four selected sampling locations during 1993-2021, 17 native and 17 nonnative (Appendix II). Native species richness declined through time, ranging from 9-12 taxa during the 1990's and early 2000's, to 7-9 taxa from 2016-2020. This reduction in diversity is due to the apparent extirpation of several species, including Brassy Minnow *Hybognathus hankinsoni* (State Threatened), Northern Plains Killifish *Fundulus kansae*, and Orangespotted Sunfish *Lepomis humilis* (Tier 1 Species of Greatest Conservation Need) (Colorado Parks and Wildlife 2015). Nonnative species richness is generally lower than that of native species, and fluctuated more through time. This is due, in part, to sporadic single occurrences of some species including Walleye *Sander vitreus*, Gizzard Shad *Dorosoma cepedianum*, and Emerald Shiner *Notropis atherinoides*, all of which were captured at one location in only a single year. Fifteen species were present in approximately half or more of all years examined and comprised the more stable portion of the fish community, nine of them native and six nonnative.

The relative abundance of species in the transition zone has changed since the early 1990's. Five species, Longnose Dace, Fathead Minnow, Longnose Sucker, White Sucker, and Brown Trout, presently make up the majority of fish abundance at our representative sites (Table 3). All of these species have been at least moderately abundant throughout this comparative period except for Brown Trout, the only nonnative of the group, which has only recently become a dominant taxon throughout the transition zone in the past 10 years (Figure 11). Rainbow Trout, though less so than Brown Trout, has also increased in relative abundance in the past decade. Alternatively, two native minnows, Creek Chub *Semotilus atromaculatus* and Sand Shiner *Notropis stramineus*, which formerly comprised a sizable proportion of community relative abundance, are now limited to few individuals, and in fewer downstream locations (Figures 12 and 13)

Changes in species composition and abundance during this period have also been site-specific. The greatest decline in species richness occurred just upstream of the LCD at Site 4, where as many as 10 native taxa have been documented, but no more than four – White Sucker, Longnose Sucker, Longnose Dace, and Fathead Minnow – have been documented since 2011, with Fathead Minnow absent since 2015 (Appendix IV, Table 3). With the disappearance of five native warmwater taxa between 1994-2010 (Brassy Minnow, Plains Topminnow, Creek Chub, Green Sunfish *Lepomis cyanellus*, and Johnny Darter), the current fish assemblage was simplified and dominated by nonnative trout, which now make up >80% of relative abundance at that site. Trout have been present at this location since the early 1990's, but relative abundance was less than 10% before an abrupt increase in 1998 (Figure 11). Although fewer years of sampling data are available, there is evidence that similar patterns of decreased native fish abundance occurred upstream at Site 2, where White Sucker and Longnose Dace have experienced declines while Trout have increased to nearly 90% of relative abundance (Appendix III).

Native species remained dominant downstream of the TRID at Site 8 both in diversity and relative abundance, but one notable absence is that of Sand Shiner, which were last captured at this site in 2004 (Appendix V). Brown Trout were first captured at this site in 1999 and over the next decade were rare. Their abundance increased beginning in 2010, and though still relatively few in number, were recently > 20% of relative abundance in 2016 and 2017. Native species remained more diverse and abundant than nonnatives at Site 12, though nonnative species abundance has increased during some years since 2009 (Appendix VI). This was driven by increased Largemouth Bass *Micropterus salmoides* abundance from 2009-2012, and more recently, increased number of Brown Trout. This location is near the upstream extent of Western Mosquitofish *Gambusia affinis*, an invasive competitor thought to displace native Plains Topminnow, and they have remained sporadically present and in low abundance (Lynch and Roh 1996, Pasbrig et al. 2012). Sand Shiner formerly made up as much as half or more of the relative abundance prior to 2010, but are now nearly absent with only two individuals total captured since then, one each in 2015 and 2018.

Discussion – Fish Community Assessment

Recent sampling showed species composition in the Poudre River transition zone was dominated by a few species while most were relatively rare. Native species were numerically dominant, and most diverse and abundant in downstream reaches. Nonnative species, especially Brown Trout, made up the majority of the total fish biomass in the study area, and dominated upstream reaches. Species richness and abundance was more balanced in downstream reaches connected by fishways, and those metrics incrementally decreased upstream of two diversions without fishways over a relatively short distance. These observations paired with historical data revealed changes in the Poudre River fish assemblage have occurred over the past 30 years. Specifically, the diversity, distribution, and abundance of native species has declined since the early 1990s, where formerly rare taxa are now extirpated and some common forms are now rare, whereas predaceous nonnative Brown Trout increased in abundance and distribution throughout the study area, especially in the past decade. Below we discuss potential mechanisms for assemblage changes and challenges associated with native species conservation.

Habitat fragmentation from diversion dams directly influences fish assemblage structure in portions of our study area. Fish community data indicated reaches connected by fishways had more uniform species richness and abundance up and downstream of those structures, whereas those metrics decreased incrementally moving upstream of diversions without passage, namely the TRID and LCD (Figures 6 and 7). For example, sites 10 and 11, which are separated by the FCRID fishway, each had nine native taxa, compared to sites downstream and upstream of TRID which had nine vs six native taxa, respectively, and the LCD, which had five native fish downstream but only three upstream. The same patterns exist for native fish abundance, which was lower at sites just upstream of the TRID and LCD, but similar up and downstream of FCRID. Dams on plains streams can reduce species richness and abundance upstream, by acting as barriers to movement and removing the ability of some species to repopulate those areas (Winston et al. 1991, Walters et al. 2014, Perkin et al. 2015). Potential examples of species discontinuities in the Poudre River are Johnny Darter, Creek Chub, and Plains Topminnow, all of which were consistently present upstream of the LCD during the 1990s and early 2000s (Appendix IV). None of those species have been collected there recently, but each persist downstream of the LCD at one or more of sites 5-7 (Table 2). Similarly, Green Sunfish were only captured downstream of the TRID during our contemporary sampling but also occurred upstream of the LCD until 2002. Indeed, as many as 10 native species were documented upstream of the LCD from 1993-2015, but no more than three have been found since then. White Sucker are now present at all 13 sampling locations, but their abundance was greatly reduced upstream of the LCD from previous levels. For example, at Site 4 they formerly comprised as much at 30% of fish community abundance in 1997 but were less than 1% in our study. These downstream range shifts and reductions in abundance through time support the notion that diversion dams in our study area are barriers to upstream movement for some species and may be part of the reason for the decline of native fishes in the study area.

Longitudinal patterns of species richness and abundance in our study area may also be due to abiotic factors. Temperature differences are large between the upstream and downstream ends of our study area, and may be regulating the occupied range of both native and nonnative species. Cooler year-round temperatures at upstream sites favor the thermal requirements for trout reproduction and survival, evidenced by highest numbers of both adults and juveniles at sites 1-6 (Table 5, Figure 8). Alternatively, warmer temperatures, largely driven by more drastic flow reductions downstream of the river-sweeping TRID, may explain highest species richness and abundance of native species at more downstream sites given warmer water and the adaptation of native taxa to fluctuating conditions of plains rivers (Bestgen et al. 2017). Although thermal conditions downstream of the TRID appear to favor native species, large adult salmonids, particularly Brown Trout, have increased in recent years, a phenomena also documented in other Front Range streams (Haworth et al. 2020). The maximum August temperature during 2020 at Site 12 was below the critical thermal maxima of Brown Trout (Lee and Rinne 1980), and winter temperatures downstream of the TRID may in fact be more favorable to growth than upstream reaches during the coldest months of the year (Armstrong et al. 2021), a point supported by the increasing mean length of that taxon in downstream reaches.

Water delivery patterns and extraction may also dictate presence and abundance of some species. Water rights that call for water from Horsetooth Reservoir are delivered into the Poudre River via the Charles Hansen Canal less than 5 km upstream of our study area near Bellvue, CO. Depending on the seasonal timing, water released from the reservoir may be much colder than water in the river, which may extend cooler temperatures further downstream that are well suited to cold-tolerant trout and less suitable for warmwater native fishes (Olden et al. 2006). This appears to be true in our study area, where water releases during low, warm conditions in August and September homogenized temperatures throughout the 24-km study area, and rapidly cooled the most downstream reaches by up to 6°C (Figure 14). Such rapid cooling may also disproportionately affect native species that spawn during spring and summer and rely on warm temperatures to attain sizes that increase chances of overwinter survival (Post and Evans 1989, Shoup and Wahl 2011). Additionally, releases during early autumn are common when users call water prior to the end of the irrigation season, which can cool and homogenize river temperatures (e.g. October, Table 5), and provides additional water to inundate and clean spawning gravels during the Brown Trout reproductive season (Bestgen et al. 2020). During this study we commonly observed spawning redds throughout the study area during and immediately after autumn water releases; however, many are desiccated after flows are abruptly declined to winter baseflow levels, especially downstream of the TRID, which may explain low abundance of young trout there. Increased baseflows in the Poudre River may increase young brown trout survival and abundance.

Habitat conditions also influence patterns of species distribution and abundance. Throughout the study area, native sucker abundance was positively correlated with higher amounts of fine sediment. Substrate composition naturally becomes finer in a downstream direction through the transition zone, but may also be locally influenced by presence of diversions. Pooling of water on upstream side of diversions such as the TRID and FCRID (sites 7 and 10) increased depth, reduced velocity, and had finer substrate, where species adapted to lentic conditions like suckers can thrive. In contrast, Longnose Dace, a riffle-adapted species, are relatively rare upstream but more abundant at sites 8 and 11 immediately downstream from the TRID and FCRID that receive less fine sediment and have a greater amount of interstitial space needed for feeding and cover. Although analyses did not show positive correlations between Longnose Dace and coarse substrate or higher water velocity as expected, likely because water velocities are usually low at most sites and times due to depleted flows, it is an important consideration that diversion dams may have highly localized effects on species presence and abundance. Unique habitat features such as backwaters are also important for native species, as native suckers and Fathead Minnow were both positively correlated with backwater area. Though low overall abundance precluded analysis, backwaters are also important for rare Plains Topminnow, as their highest abundance at sites 6, 9, and 10 corresponded with presence of perennially available backwater habitat. Additionally, a large seasonally connected backwater created at Site 8 (Kingfisher Point Natural Area) following a channel realignment construction project was inhabited by several native species, including Fathead Minnow, Johnny Darter, and Plains Topminnow, but also large-bodied nonnative species including Largemouth Bass and Common Carp.

Increasing percentage of coarse substrate was the strongest correlate to increased nonnative trout abundance, which was more prevalent at sites upstream of the TRID. These were also locations where most spawning and recruitment occurred, and subsequently contained the highest numbers of age-0 trout, especially sites 3 and 4 (Figure 8). Therefore, the negative correlation of brown trout abundance and mean depth may explain the abundance of young trout near natal habitat, but miss the importance of local conditions for large adult Brown Trout present at downstream sites at lower abundances. For example, an historic flood in September 2013 may have facilitated the expansion of Brown Trout into downstream sites 11 - 13 by improving previously unsuitable habitat by scouring deep pools favored by large Brown Trout, and flushing or depositing spawning gravels (Cunjak and Power 1986, Larscheid and Hubert 1992, Ortlepp and Mürle 2003). Similarly, abundant submerged wood was not a strong correlate with higher abundance of the species or guilds we analyzed, but abundant wood was associated with some of the highest observed native species richness, and is known to benefit fish via increased habitat heterogeneity and invertebrate productivity (Angermeier and Karr 1984, Nagayama et al. 2012; Wohl et al. 2016). Therefore, although general habitat associations are useful to predict patterns of species distribution and abundance and inform how to benefit particular guilds or species of fish through habitat improvements, it is also important to consider how life history, stochastic events, and hydrologic variability may affect habitat availability and quality at both broad and local spatial scales.

In addition to physical habitat, species interactions may also play a role in shaping fish distribution and abundance patterns. Habitat conditions favorable to Brown Trout may in turn negatively affect native species through competition for resources and predation. Brown Trout are capable piscivores shown to reduce abundance of native species (Garman and Nielsen 1982, Townsend 1996), which they do so readily when present outside of their native range (Budy et al. 2013), and at relatively small sizes (Jonsson et al. 1999). For example, at Site 4, Longnose Dace commonly accounted for as much as half or more of the relative abundance of all fish in samples collected from 1993-2002, but have recently been reduced to approximately 15% (Appendix IV). Although habitat characteristics at Site 4, such as coarse substrate and high water velocity, are presumably favorable for Longnose Dace (Table 4), the increased abundance of Brown Trout coincides with the onset of reduced Dace abundance (Figure 11). Furthermore, species interactions may have affected habitat correlations of Longnose Dace, if Brown Trout predation has appreciably reduced their abundance in areas of their presumed preferred habitat. Additionally, though present at relatively low density, large Brown Trout may pose a particularly high predatory threat to native species in reaches downstream of the TRID, where extremely low winter flow crowds fish into isolated pools for many weeks at a time. In support of this point, we commonly observed larger Brown Trout regurgitating native fish following electrofishing capture. Thus, the interplay between abiotic conditions, physical habitat, and species interactions likely influence fish assemblage structure at different scales in the Poudre River transition zone (Jackson et al. 2001, Gibson-Reinemer and Rahel 2015).

Whether changes in the fish assemblage over the past several decades are episodic or permanent in nature is difficult to determine. In the short, heterogeneous reach that comprises the transition zone of the Poudre River, it is reasonable to expect the fish assemblage structure to be in a state of shifting equilibrium influenced by stochastic events such as drought and flooding (Grossman et al. 1982, Strange et al. 1993, Geheber and Piller 2012). The Poudre River is presently in a relatively wet period beginning around 2010, preceded by an extended period of drought beginning in 2000 (Figure 15). Formerly common species such as Sand Shiner were present in high abundances during drought years, and have since been nearly eliminated from our study area following the onset of wetter years (Figure 12). It is possible their disappearance from the study area is a temporary range shift downstream into more thermally suitable habitat. However, this hypothesis does not explain Sand Shiner presence during wet years prior to the year 2000, and their near disappearance from Site 12 coincides almost precisely with the first establishment of Brown Trout at that location in 2011 (Figure 11).

An extensive fish kill in the Poudre River occurred in summer 2021, a result of summer rain on upstream burn scars, and which removed many Brown Trout throughout the river (K. Battige, Colorado Parks and Wildlife, Fort Collins, personal communication 2021) including in our study area. Results of that event may offer an opportunity to evaluate if a reduction in predators causes a positive response by native fishes in some of these areas. Many species native to the Poudre River transition zone exist there at the extreme western periphery of their range or as isolated populations, and may be more prone to local extirpation and unable to recolonize upstream reaches in a fragmented riverscape (Bestgen 1989; Quist and Schultz 2014; Haworth et al. 2020). Therefore, changes to fish assemblage structure in response to stochastic events such as drought during the early 2000's, extreme flooding in 2013, or fish kills in 2018 and 2021 (Colorado Parks and Wildlife 2019), may be more permanent in some cases. Continued monitoring at the appropriate spatial and temporal scale is vital to improve understanding of drivers shaping the fish assemblage in the Poudre River transition zone, and to inform management actions aimed to enhance native fish populations.

Methods – Fish Movement

Fish tagging and detection– During fish community sampling at our 13 sampling sites, 12 mm PIT tags were implanted into the body cavity of all fish greater than 120 mm TL. PIT tags rely on radio-frequency identification (RFID) technology, and when a tagged fish encounters a PIT antenna, the energy emitted by the antenna causes the tag to transmit its unique identifying code, which is stored along with date and time of detection in the reader component of the antenna. PIT tags are dormant until activated, do not require an internal power source, and can have lifespans upwards of 20 years. Fish implanted with PIT tags were tracked both within and between the 13 sampling sites to understand movement patterns of fishes throughout the study area. Location of individual fish was achieved through a combination of repeated fish sampling and scanning specimens for implanted tags (physical captures), and several antenna detection techniques (detections) including a mobile PIT antenna, submersible PIT antennas, and PIT antenna arrays installed on fishways.

The mobile antenna consists of a single antenna reader (Oregon RFID) outfitted with a pole antenna with a flat looped wand end (29 cm radius) with a tag read range – the distance a tagged fish must be within to log a detection – of approximately 46 cm from any point on the wand (Figure 16). The mobile antenna is an active detection method, where the user walks the river sweeping the channel horizontally at various depths and probing the wand end of the antenna into all available habitat to detect fish. Mobile antenna passes were completed during base flow periods in late winter and early spring 2020 and 2021 to search the entire study area for tagged fish, both within and between sampling sites. A unique detection logs the date, time, PIT identification number, and location coordinates accurate to within 50 meters from a global navigation satellite system receiver integrated in the reader. These detections were used to inform movements that occurred during the winter period (November-March) between physical sampling events. Mobile passes were completed at this time of year because fish are limited in their dispersal capability by dry reaches or very shallow riffles and often seek cover such as instream wood or undercut banks or concentrate in isolated pools where they are more susceptible to active detection. Completing passes immediately prior to spring fish sampling enabled comparison of mobile detections and physical recaptures within sampling sites, which is important to understand the rate expelled or mortality-related tags are potentially being detected, which if not accounted for create bias in estimated vital rates (O'Donnell et al. 2010). If tags detected via mobile antenna never had a subsequent physical recapture or detection by passive antenna approaches (see below), that fish was not included in analyses to avoid a positive bias on parameter estimates. This approach was also valuable for establishing a last known location of tagged fish in early spring prior to high annual flows, which enabled tracking movement at greater temporal resolution.

Submersible antennas (Biomark, Inc.) are a passive detection method, meaning a tagged fish must pass within the read range of the antenna to log a detection. These portable antennas have a circular frame (46 cm radius), and read range of approximately 46 cm (Figure 16). Antennas are deployed on the streambed in a stationary position, tethered to a point on the shoreline, and store detection events that include date, time, and PIT identification number as tagged fish pass within the read range. These antennas were deployed in places of interest such as suspected travel corridors or congregation areas, including at the upstream and downstream sides of diversion dams and fishways. They were deployed more continuously over longer periods of time, and detections informed movement that occurred during the winter period (November-March), runoff (May-July), and post-runoff periods (August-October). Additionally, these antennas were used to complement mobile passes with shorter duration placement in deep areas not effectively searched with the mobile antenna.

Antenna arrays installed at fishways at the WLD (upstream of Site 1) and FCRID (between Sites 10 and 11) each consist of three antennas anchored to several points on the fishway (Figure 2). These arrays are also passive, so when a fish passes within read range of each antenna, the date, time, and PIT identification number is stored, making it possible to infer directionality of movement when multiple antennas in the array are encountered in succession. Antenna arrays are powered by solar-maintained battery banks allowing continuous operation, and detections informed movement during all intervals. Read range at the FCRID fishway was measured at 19-25 cm (Richer et al. 2020); the WLD range is presumed similar. We considered a fish to have successfully completed passage if they 1) encountered the most upstream antenna in the array with a release or previous detection downstream of the fishway, 2) encountered the most downstream antenna in the array with a release or previous detection upstream of the fishway, or 3) encountered multiple antennas on the array in succession, including either of the most upstream or downstream antenna.

Recaptures from physical sampling and detection data from the three antenna techniques were used to estimate movement rates over diversions in reaches with and without fish passage available. Descriptive summary detailed the number of each species that moved up or downstream over diversion structures with fishways (WLD, FCRID) and those without (LCD, TRID), the direction and distance moved to pass over structures, and movements through other areas of interest in the study area.

Statistical analysis— Analysis of mark-recapture data used program MARK (White and Burnham 1999) to estimate the probability of movement over select diversions. We used a multistate mark-recapture (MSMR) model (Lebreton et al. 2009) which contains three parameters: survival probability (*S*), capture probability (*p*) and transition probability (ψ). The ψ parameter is interpreted as the probability that a fish changes from one state to another, here either from downstream to upstream or upstream to downstream, in the time period of interest. For example, the upstream (ψ) for the FCRID analysis during the 2020 runoff period, indicates fish downstream of the diversion had a 0.21 probability that it would move upstream in that 3-month period, May-July (see below). We will not be reporting survival rates in this analysis because movement rate is our primary emphasis. If additional data are collected in the future, survival analyses will be explored further.

Based on numbers of tags released in proximity to diversions and the subsequent number of passages needed for identifiable estimates, analyses were limited to reaches up and downstream of the FCRID (fishway available) and the LCD (no fishway). We conducted a separate analysis for each of these reaches of river, grouping sites up and downstream of each diversion into single reaches (states) to increase sample sizes. The section of river divided by the LCD grouped Sites 3 and 4 into an upstream state, and Sites 5-7 into a downstream state. Sites 8-10 comprised the state upstream of the FCRID, and 11-13 the downstream state. The probability that fish would transition between states depending on the availability of a fishway was a question, making ψ our primary parameter of interest. We hypothesized the probability a fish would transition states would be higher when a fishway was present. We were also interested in the timing of those movements related to flow, the predominant direction of movements over fishways, and whether movements and directions differed among taxa.

Time intervals were defined relative to when physical sampling occurred (spring, fall) and antenna detection effort (discrete or continuous) and were established as: Winter 2018 (November 2018-April 2019, interval 1), Summer 2019 (May-October, interval 2), Winter 2019 (November 2019-March 2020, interval 3), early spring 2020 (March-April, interval 4), runoff 2020 (May-July, interval 5), post-runoff 2020 (August-October), Winter 2020 (November 2020-March 2021), early spring 2021 (March-April, interval 8) and runoff 2021 (May-July, interval 9); a timeline shows these intervals and their durations in more detail (Figure 17). The Winter 2018 interval was limited to only physical recapture data with no antenna data available. Summer 2019 was grouped as a longer time period due to lower numbers of movements early in the study, but increased detection numbers allowed for creating the runoff interval in 2020 and 2021 as flows increase and peak during late spring and early summer, and similarly, the post-runoff interval when peak flows subside during summer and early autumn. The early spring intervals in 2020 and 2021 described the time period between completion of mobile antenna passes and spring physical sampling in those years, were each 2-3 weeks in duration, and encompassed periods when river discharge remained near the low winter base flow level. Because of the short duration, we fixed survival during these intervals (S=1) so no mortality was assumed in time dependent model structures, but did generate estimates of ψ.

Model sets were constructed with the overall goal of fitting biologically realistic models that illuminate the ecology of these fishes. Each parameter (S, p, ψ) was held constant (.) or varied by combinations of species (Brown Trout, Rainbow Trout, Longnose Sucker, White Sucker), state (up or downstream of given diversion), and time dependent structures. Because the probability of transitioning over a diversion from one state into another was our central question, we fit the ψ parameter for state in all model structures. We first identified the best model for p by pairing it with the global models for S and ψ parameters (e.g., fit with species, state, and time variables). Of the evaluated models of p, results of model selection indicated that capture probability varied by species, state, and time in both analyses. Therefore, we used this structure for p in all subsequent models that examined factors influencing S and ψ. The fit of the data to the model was tested using the median c-hat ($\hat{c}$) procedure for the global model from each analysis with program MARK. Results indicated the data were moderately overdispersed ($\hat{c}$=2.31) for the analysis including fish passage, and more so for the analysis without passage ($\hat{c}$=4.89), likely due to sparse movement observations in that dataset. Therefore, we used delta quasi-Akaike information criterion values ($\Delta QAIC_c$) and Akaike weights (w) to determine which model, or models, were most supported by the data. The $QAIC_c$ is an adjustment of AIC that accounts for small sample size and overdispersion of data, and the QAIC weights can be interpreted as the probability that the model is the best among candidates in the set (Burnham and Anderson 2002).

Results – Fish Movement

Fish tagging and detection— Concurrent with fish sampling, 6,573 individual fish were implanted with PIT tags between 2018-2021. Four species, nonnative Brown Trout and Rainbow Trout and native White Sucker and Longnose Sucker, accounted for nearly all (98.6%) tagged fish released (Table 6). A large proportion of tagged fish were encountered at least once after release (1,718; 26%), but capture or detection rates varied by species and sampling gear. Recaptures of fish obtained via sampling with electrofishing gear (captures) averaged 12% for the four commonly tagged species during the study, but proportions were lower for Longnose Sucker, and higher for Brown Trout. Antenna detections (detections) were higher for all four commonly tagged species, especially White Sucker and Longnose Sucker, which had detection percentages of 35 and 23%, respectively. Antennas also detected five other species and a hybrid sucker that had lower numbers of tagged fish released.

Description of movements— Recapture and antenna detection data showed that fish moved over multiple diversion structures in upstream and downstream directions, including those both with and without fish passage infrastructure. This included the FCRID fishway, the Kingfisher Point grade-control structure, the TRID, the Poudre River Whitewater Park (between sites 4/5, former Coy Diversion location), the LCD, and the WLD fishway (Figure 1). There was no evidence, based on tag recaptures or detections, of fish moving past the Larimer-Weld Canal Diversion, or any other diversion between Sites 2 and 3, in either an up or a downstream direction.

Higher numbers of fish passed over diversions with fish passage available and at higher rates than those without. For example, 154 individuals in six species passed upstream and downstream over the FCRID and fishway, and 30 individuals in three species passed over the WLD and fishway (Tables 7 and 8). Based on numbers of tagged fish released upstream and downstream of each of these structures, that equated to 6.8% of all tagged fish in the defined reach moving over the FCRID, and 9.7% over the WLD. In contrast, only 0.8% of tagged fish released upstream and downstream of the LCD passed over that diversion, and 0.3% of those released upstream and downstream of the TRID passed; neither of those diversions has a fishway (Tables 9 and 10). Fish were also more likely to make multiple movements, in both directions, over diversions with a fishway. The mean number of passages per individual, expressed as the total number of passages over a diversion divided by the number of fish that passed it, over the WLD and FCRID were 2.1 and 1.8, respectively, versus 1.1 and 1.2 passages per individual at the LCD and TRID. Native species were also more likely to complete passage with a fishway available, as only two suckers moved over each of the LCD and TRID, compared to 113 White Sucker, Longnose Sucker, and Creek Chub that navigated the FCRID, which comprised 75% of all fish detected moving over that diversion during our study.

Though not directly studied, fish passage was noted at two other locations that were possible barriers to passage. Upstream fish passage at the Kingfisher Point Natural Area grade control structure was assumed, perhaps only at times of higher flow, based on recaptures of Brown Trout, Rainbow Trout, Longnose Sucker, White Sucker, Common Carp, and Green Sunfish tagged downstream (sites 9-13) that were detected upstream of there. Similarly, monitoring of fish passage over the LCD revealed successful passage of the Poudre River Whitewater Park in both upstream and downstream directions by Brown Trout, Rainbow Trout, Longnose Sucker, White Sucker, and Mountain Whitefish. For example, antennas placed just downstream of the LCD – which is located 0.5 km upstream of the Whitewater Park – detected 29 unique tagged fish from April-November 2020, all of which were released downstream of the Whitewater Park at sites 5 and 6 (Figure 18), movements which required Park passage. Numbers of unique fish detected per day was highest when flows rose above approximately 5 m^3/s, particularly during the onset of spring runoff, but also in response to flow augmentation in autumn. Additionally, among these fish were several large adult White Sucker that made upstream movements, presumably in response to increased flows during mid-May in consecutive years, which is in their reproductive season (Becker 1983).

The predominant direction of passage over a diversion, and the distance traveled to do so, also differed whether a fishway was available. The number of fish released downstream of the FCRID that passed over the diversion and fishway (n=75) was nearly identical to the number released upstream that went downstream (n=79), and of those, most (n=124, 80%) were released within 0.5 km of the structure (Figure 19). However, fish also made passages over the FCRID that were released more than 3 km away in both directions. No tagged fish were released upstream of the WLD, and all but one fish that completed passage were tagged within 0.8 km of the fishway. The remaining Brown Trout moved upstream approximately 4 km from Site 2 and passed over two other diversion structures without fish passage to reach and pass the WLD fishway; most distances moved are conservative because we do not know their maximum movement after last contact.

The predominant direction of travel over the LCD was downstream, where 24 of the 28 fish that passed over that diversion were released upstream at sites 3 and 4 (Figure 20). Very few fish passed over the TRID, but did so in both directions, and several traveled 3.5-6.9 km to do so (Figure 21). Three tagged Brown Trout made single passages upstream over the TRID from sites 8 and 12, and one made a single downstream passage from Site 5. One Brown Trout tagged at Site 8 in October 2019 made multiple passages, two upstream and one downstream between July 2020 and March 2021. Another large Brown Trout (467 mm TL) tagged at Site 8 in October 2019 was detected below the TRID early morning of 3 August 2020, and was subsequently detected 4.5 km upstream below the LCD early morning of 4 August 2020. Flows averaged 1.8 m^3/s in that reach during those two days, but briefly spiked > 5.0 m^3/s for one hour midday on 3 August. Two White Sucker were the only native species to pass over the TRID, both in a downstream direction from sites 5 and 7.

The size of fish (at tagging) that passed over diversions differed by species. Brown Trout and White Sucker had the greatest range of sizes pass over the FCRID, though approximately 75% were 300 mm TL or greater for both species (Table 11). Longnose Sucker had a higher proportion of fish smaller than 250 mm TL at tagging pass over the FCRID, however this species does not typically attain the adult sizes of White Sucker or Trout in our study area. Few Rainbow Trout passed over the FCRID, but all were greater than 250 mm TL at initial tagging. The three Brown Trout that successfully passed upstream over the TRID were 350 mm TL or greater at time of tagging. Patterns were not evident at the LCD, where only 28 fish were documented making passage. It is important to note that size at tagging does not necessarily equate to the capability or likelihood that a fish of a given size could pass over a diversion or fishway, since passage occurred months, or even years, after initial tagging, and smaller fish grow rapidly early in life. However, there was evidence of both substantial upstream movement and successful upstream passage of the FCRID fishway by small fish. A 122 mm TL White Sucker tagged on 28 April 2020 at Site 13 was detected moving over the fishway on 30 October 2020, and traveled 4 km upstream to do so. This same fish was subsequently recaptured just upstream of the fishway at Site 10 on 4 November 2020, and measured 216 mm TL. Given the comparatively weak swimming ability of White Sucker relative to other species present in this area of the river (see Richer et al. 2020 for summary), it is a reasonable assumption that young fish of other stronger-swimming species, and small-bodied species, can also ascend the fishway.

Antennas also showed that fish moved extensively in other areas of the river. Located 0.8 km upstream of the FCRID, the Boxelder Diversion on the main-channel directs water into a 0.8 km long side-channel constructed to deliver water into the Boxelder Ditch. This side-channel functions as the longitudinally connected river channel due to lack of fish passage on the Boxelder Diversion. Use of the side-channel by fish is of interest because during low-flow periods in the irrigation season (April-October), a channel-spanning earthen push-up dam has been sporadically constructed to divert water into the Boxelder Ditch. Antennas located at the up and downstream ends of the side-channel showed a total of 56 individuals comprised of native Creek Chub, Longnose Sucker, and White Sucker and nonnative Brown Trout and Rainbow Trout, used the side-channel either residentially in all seasons, or for bidirectional passage when the push-up dam was not present.

Statistical analysis of tag-recaptures and movements— A total of 32 separate model structures were assessed for each of the multistate mark-recapture analyses. The top model yielded from each was the same, where ψ varied by species and state (upstream or downstream reach change), and *S* varied only by time (Tables 12 and 13). This structure included 86 parameters for the FCRID analysis (72 estimates of *p*, 7 estimates of *S*, and 8 estimates of ψ over 9 intervals), and 72 parameters for the LCD analysis (64 estimates of *p,* 6 estimates of *S*, and 8 estimates of ψ over 8 intervals). The LCD analysis had one fewer interval due to no antenna monitoring during the runoff 2021 period, and the number of *S* estimates was reduced by two in each of the time dependent top models because survival was fixed (S=1) so no mortality occurred between mobile antenna passes and spring sampling intervals (Figure 17). The high $\Delta QAIC_c$ (>5.0) value and high Akaike weights (0.91) for the top model in the FCRID fishway analysis, and lower values ($\Delta QAIC_c$=1.39, w=0.61) but matching model structure in the LCD analysis led us to accept parameter estimates from both top models and forego model averaging (Burnham and Anderson 2002).

Estimates of ψ indicated that each of the four most-tagged species had a substantially higher probability to pass over a diversion when a fishway was available (Table 14). Among all species, probability of upstream passage over the FCRID and fishway for each interval was slightly higher (mean 0.226, range 0.097-0.358) than downstream (mean 0.143, range .054-

0.209), but patterns differed by species (Figure 22). For example, Longnose Sucker were much more likely to pass over the FCRID in an upstream direction (0.290) than downstream (0.054), whereas the opposite was true for White Sucker (0.097 and 0.194, respectively). Among nonnative trout, the probability of Brown Trout to pass in either an upstream (0.158) or downstream (0.209) direction was about equal, and Rainbow Trout were more likely to pass in an upstream direction (0.358), though precision of this estimate was low (SE 0.200; 95% confidence limit 0.091-0.754). Recall that these average estimates of passage are for *each* of nine intervals in the analysis, and not for the entire study period. Thus, the relatively high passage rates, over relatively short time durations, suggested that the average fish likely passed over the FCRID fishway during our study. In contrast, all four species were far less likely to pass over the LCD, which does not have a fishway. Results indicated that probability of downstream passage was greater than upstream passage, but passage rate for each was low. Among all species only Brown Trout had sufficient data for precise estimates of downstream (0.022, 95% confidence limit 0.007-0.061) and upstream (0.014, 95% confidence limit 0.003-0.065) transition.

Although ψ did not vary by time in top models because data were insufficient to measure those effects, we were interested in seasonal differences in passage at the FCRID, where larger sample sizes enabled relatively robust time-specific estimates of ψ. Therefore, we selected parameter estimates from the highest-ranking model that included the time variable for the ψ parameter (Table 12, model 3). This model considered state and time variables, but did not consider species-specific differences (i.e., species were grouped) in transition probability. On average, the probability of upstream movement was six times greater during summer intervals, including during and after runoff, (mean 0.239, range 0.108-0.368) than winter (mean 0.039, range 0.0-0.105, Figure 23). Seasonal differences in average probability of downstream movement were smaller, but movement in that direction were almost two times more likely to occur during summer (mean 0.185, range 0.097-0.287) than winter (mean 0.109, range 0.0-0.189) when flows were lower. Intervals used to calculate summer averages included summer 2019, runoff 2020, post-runoff 2020, and runoff 2021. Winter averages included the intervals winter 2018, winter 2019, mobile antenna to spring 2020 (early spring 2020), winter 2020, and mobile antenna to spring 2021 (early spring 2021) intervals. Examining the runoff and post-runoff periods from 2020 and 2021 separately showed that probability of upstream movement was higher during flows in the runoff period from May-July (mean 0.291, range 0.213-0.368) than during the post-runoff period from August - October (0.108, only 2020), and probability of downstream movement was higher post-runoff (0.286) than during runoff (mean 0.118, range 0.098-0.140).

Discussion – Fish Movement

Fish movements in streams are extensive and presumably benefit the life history of the species (Gowan et al. 1994; Fausch et al. 2002). Our results indicated that diversions in the Poudre River transition-zone with fishways facilitated passage of two native suckers and two nonnative trout more effectively than diversions without passage infrastructure, which doubtless improves conditions for those taxa and others that were not tagged but may have moved. Improved connectivity was illustrated both through the greater proportion of passage by tagged fish released in proximity to diversions with fishways than those without, as well as the higher modeled probability of transitioning over a low-head diversion when a fishway was available. These findings complement those of Richer et al. (2020), who demonstrated the capability of nine different species to ascend the FCRID fishway when fish were released in a downstream enclosure. By releasing and recapturing tagged fish at 13 locations over multiple years throughout a 24-km study area, we were able to observe how fish interacted with various diversions and fishways at different spatial and temporal scales. Below we discuss these observations and the implications of our findings related to fish movement and community structure in the Poudre River transition zone.

Total number of known passages over diversions with fishways were much higher than diversions without passage. The number of tagged fish that passed relative to the total number of tags released was relatively low (e.g. 6.8% of fish tagged in proximity to the FCRID, Table 7) but empirical tag recapture data presented for passages underestimates movement rates for several reasons. First, the conditions we set to count a fish as having transitioned over the fishway antenna array excluded 93 individuals from our analysis, which accounted for just over one-third of all fish that encountered the array. Second, we also excluded mobile antenna detections for fish that we could not confirm were alive at time of detection by subsequent physical recapture or passive antenna detection, which totaled approximately 25% of mobile detections in the reaches up and downstream of the FCRID. Finally, during higher flows there are opportunities for passage over the diversion without encountering the fishway as the FCRID becomes inundated, and the sluice gate is sometimes opened. Indeed, some individuals were tracked making multiple passages in only an up or downstream direction, indicating an undetected passage occurred between them.

We recognize that this underestimation rationale may also be true for passage at the LCD, which is similar in height to the FCRID. However, we don't believe this was the case for several reasons. Physical recapture rates upstream of the LCD at sites 3 and 4 were among the highest in the study (15.6 and 11.6%, respectively), but we never captured an individual that was first tagged downstream of the LCD at either of those locations. Alternatively, recapture of individuals that had moved up or downstream over the FCRID from their original release location was relatively common, especially later in the study when higher numbers of tagged fish were available. We believe this lack of recapture at LCD supports a lack of upstream passage, because mobile and submersible antenna sampling confirmed we were effective at recapturing tagged individuals upstream of the LCD. In antenna detection efforts completed in low flow conditions during early spring 2021 we detected 49 and 91 tagged fish within the bounds of sites 3 and 4, respectively. Less than 2 weeks later during physical sampling we recaptured 40 of the 49 fish detected at Site 3 (82%), and 76 of the 91 detected at Site 4 (84%). Finally, we tagged over 1,000 more fish at sites near the LCD than the FCRID (Tables 7 and 9), which inherently creates more opportunity for movements to occur. It is possible that fish made shorter duration passages over the LCD and returned undetected, especially during peak flows, but we do not believe undetected passage would have occurred at a rate that would alter our conclusions.

Although limited upstream passage over diversions without fishways did occur, antenna detections provided evidence that these diversions usually acted as barriers to upstream movement. Very few fish passed upstream over the TRID, however, higher numbers of fish (54 individuals, six species) were detected moving upstream from sites 8-13 to immediately below it where we had a submersible antenna that were never detected upstream of that diversion. Among those six species were the two trout and two sucker species, as well as nonnative Common Carp and native Green Sunfish, both released over 3 km away at Site 10. We also observed this phenomena at the LCD, where 41 individuals in four species (Brown Trout, Rainbow Trout, Longnose Sucker, and White Sucker) were detected moving upstream to immediately below that diversion (Figure 18) – which in the case of White Sucker appeared to be repeated annual spawning movements in response to increased spring flows – but were never captured or detected upstream. Taken together, blocked upstream movements during the reproductive period and the abrupt decrease in White Sucker abundance upstream of the LCD (see Fish Community section) show that this diversion has hindered dispersal to upstream reaches. Our observations of continued declines in native species richness and blocked upstream movement past the LCD suggests native species in our study area, especially those with weaker swimming abilities (Richer et al. 2020), may be disproportionately vulnerable to such effects. Furthermore, > 80% of all movements over the non-fishway equipped LCD and TRID were by Brown Trout, and an increased capability or willingness to pass over diversions without fishways may confer a dispersal advantage within our study area – especially in a downstream direction (Figure 11) – with implications for native species reductions via predation (see Fish Community section).

Model estimates indicated differences in directional and seasonal movement patterns over the FCRID. There was an overall higher probability of upstream passage, which could be due in part to the life histories of the focal species. White Sucker, Longnose Sucker, and Rainbow Trout all spawn in spring to early summer, whereas Brown Trout spawn in the autumn (Becker 1983; Bestgen et al. 2020). We released more tagged individuals of spring spawning species downstream of the FCRID (n=1,075) than upstream (n=735), which may have also influenced upstream movement during peak flows in late spring and early summer. Additionally, the timing and duration of annual peak flows varied greatly during our study period, which may have led to interannual differences in spawning movements. For example, 2021 runoff started early and flows remained higher for an extended period, which may explain the high upstream passage probability estimate for that period in our time explicit model (Figure 23). There was also evidence of probable spawning movements in response to increased flow by Brown Trout in autumn 2020. Flows increased from < 0.3 m^3/s during early October to > 5.5 m^3/s from October 23-31. During this short water pulse tag detections showed 12 Brown Trout >300 mm TL complete a full upstream passage through the Boxelder Ditch, perhaps as far upstream as the TRID, which was followed by a rapid return downstream of the Boxelder Ditch before flows fell to < 0.2 m^3/s by November 1. Indeed, our time explicit model provided some evidence that downstream movement by all species was more probable during late fall and winter, in support of those downstream movements. It may be that overwintering habitat downstream of the FCRID is preferable because it is warmer during winter months (possibly due to wastewater effluent inputs), is the longest stretch of connected river in and adjacent to our study area (~11 km), and it contains high amounts of cover in the form of submerged wood.

Our results showed that seasonal movements were greater during high flows, regardless if fish were moving over fishways, or were moving over short-time durations within reaches for presumptive spawning, per the Brown Trout example described above. What we cannot determine is if fish movements would be greater during other seasons if more flow was present in the river, say in winter. During our study, the reach immediately downstream of the FCRID in winter was typically desiccated except for isolated pools because what little water remained in the river upstream of FCRID was diverted, which obviated passage of any kind because fish could not access the fishway or diversion. Thus, a clear message is that river flows must be sufficient for fishways to function as passages in those seasons.

In that reach downstream of FCRID, and in other locations, we often observed several to many desiccated Brown Trout spawning redds each winter, which were likely constructed during short-term flow increases in late October. This was a likely reason why fish less than about 150 mm TL, the length of autumn spawned Brown Trout one year later (see Fish Community section above; Bestgen et al. 2020), were relatively rare in that reach.

Movement rates detected by simple tag recaptures provided information about passage rates over diversions such as FCRID. It is clear though, that tag recapture rates (physical captures and detections) of about 6.8% over the entire study underestimated movement rates of tagged fish over that diversion. This is because transition rates from one reach to the next estimated from tag-recapture models showed much higher movement rates, even during relatively short time periods, such as in higher flow runoff periods. Modeled movement rates are higher than empirical rates from tag recaptures because estimation accounts for the idea that not all fish that moved were detected (detection is < 100%); that difference is figured into the higher transition rate estimates via capture probabilities. Thus, modeling tag recaptures in a movement study such as this offers greater spatial perspective and more realistic insight into movement dynamics than is possible from simple tag recapture rates.

An implied conclusion from the above statements is that not all fish that moved over the FCRID used and were detected by fishway antennas. Several other possibilities exist. For example, fish could move through the fishway and not be detected, which could happen if the antenna was not functioning properly, if antenna batteries were depleted, or if effective detection distance was exceeded during high flows, which had documented high passage rates. Fish could also pass over the diversion face itself, which again, seems possible especially during high flow events. The reduced velocity boundary layer of even a relatively smooth surface like the dam face offers fish a substantial upstream swimming advantage (Bestgen et al. 2010), even for relatively small-bodied fish. Finally, passage around the FCRID may have been possible through an associated radial gate, although that gate was shut during most of our study. Further investigation and analyses may allow us to separate passage rates through the fishway relative to other means.

Conclusions

This study confirmed that fishways are effective in facilitating up and downstream passage and indicates they are a valuable tool for mitigating habitat fragmentation in the Poudre River and other Front Range streams. Our findings will further the goals of both the Colorado Water Conservation Board and the City of Fort Collins to promote healthy resilient rivers as described in the Colorado Water Plan and City Council priorities, respectively. Additionally, results of this study will inform planning in other basins in Colorado with similar priorities, including several in the Poudre River watershed. We highlight our main findings of the fish community study below with summary points below.

- From autumn 2018 to spring 2021, we captured 27,024 fish that comprised 28 species, including 14 native and 14 nonnative kinds, including hybrids.
- Water temperatures were lowest upstream but increased in summer by as much as 7°C from up to downstream sites on a single day, over the relatively short study area distance.
- Native fishes were numerically abundant (77% of total) in the study area, with Longnose Dace *Rhinichthys cataractae*, White Sucker *Catostomus commersonii*, Longnose Sucker *Catostomus catostomus*, and Fathead Minnow *Pimephales promelas* the most abundant taxa.

- Native fishes were most abundant and diverse in downstream reaches of the study area where water was warmer, flow fluctuations were greater, and where relatively rare habitat features including large wood and backwaters were more abundant.
- Nonnative species, especially Brown Trout *Salmo trutta*, made up the majority of the total fish biomass (63%) in the study area, and were most abundant in upstream reaches where water temperatures were cooler and coarse sediments dominated the substrate.
- Brown Trout and Rainbow Trout *Oncorhynchus mykiss* increased in size downstream, but juvenile trout were common only upstream of Site 6, located just downstream of Lincoln Avenue.
- The highest number of fish species (species richness) remaining in the study area was found in reaches downstream of the Timnath Reservoir Inlet Diversion (TRID, just upstream of Timberline Avenue) extending to Interstate-25.
- Rare fishes, recognized by the State of Colorado as taxa in need of conservation, were collected in the study area including Northern Redbelly Dace *Chrosomus eos*, Plains Topminnow *Fundulus sciadicus*, and Iowa Darter *Etheostoma exile.*
- Off-channel aquatic habitats that are intermittently connected to the Poudre River may act as source populations of naturally sustaining or stocked rare native fishes, but some may also harbor invasive nonnative fishes whose river access should be restricted.

- Species richness was similar just upstream and downstream of the Fossil Creek Reservoir Inlet Diversion (FCRID, located just upstream of the Environmental Learning Center), which is fitted with a fishway.
- Species richness was reduced upstream of two diversions where fish passage was not available, at the Lake Canal Diversion (LCD, just upstream of College Avenue) and the TRID.
- Differences in those species richness patterns indicated fishways may benefit upstream fish communities.
- Stream substrate shifted near the LCD from mainly cobble and gravel upstream to more sand and silt downstream.
- Bank stabilization to prevent channel meandering was present at most sites, except in reaches downstream of the FCRID.
- The diversity, distribution, and abundance of native species has declined since the early 1990s, with formerly rare taxa now apparently extirpated, some historically common forms now being rare, and present depleted populations more restricted to downstream portions of the study area.
- Diversions are partially responsible for native fish declines by reducing recolonization from downstream after species are eliminated upstream of them. For example, as many as 10 native species were documented from 1993-2015 upstream of the LCD near College Avenue, but no more than three have been found since.

- Historical data showed Brown Trout distribution expanded downstream, and abundance increased riverwide, concurrent with higher and perhaps cooler flows since around 2010.
- Predaceous Brown Trout, and lower water temperatures, may be responsible for the decline of native fishes, particularly in the lower half of the study area.

We used recaptures of tagged fish, and a variety of detection gears, including antennas installed in fishways, to track movements of large-bodied fishes, mainly Brown Trout, Rainbow Trout, White Sucker, and Longnose Sucker, in the study area. We highlight our main findings of the fish movement study below with summary points.

- A total of 6,573 individual fish were implanted with passive integrated transponder (PIT) tags from 2018-2021.
- Multiple years of tracking fish movement with physical recaptures and a variety of tag detection approaches confirmed tagged fish passed over diversions both with and without fishways in upstream and downstream directions, but at a substantially greater rate when fishways were available.
- Fish movement was also documented over or through less intensively studied locations including the low-head Kingfisher Point Natural Area sheet pile grade-control structure, and the Poudre River Whitewater Park, site of the formerly impassable Coy Diversion and boat chute, just downstream of College Avenue.
- Upstream movements were especially higher during spring and early summer, periods of greater flow due to snowmelt runoff, and patterns varied by species.
- Fish also moved in non-runoff periods, especially when short-term flow increases were noted, and movements were likely associated with reproduction.

- Downstream movements were also substantial and more prevalent in periods of lower flow.
- Fish movements in winter were low, especially in flow depleted reaches, which essentially precluded fish movements.
- Diversions without fishways blocked upstream movement of most fish, and species richness and abundance was reduced upstream of those diversions.
- Several species moved relatively long distances between the FCRID and TRID by using the bypass channel adjacent to the Boxelder diversion.
- Brown Trout and White Sucker movements during their respective reproductive seasons were linked with flow increases.

The findings of our two main tasks led us to several conclusions. The fish community of the Poudre River is in decline, including relatively recent reductions, due to several causes. Habitat fragmentation by diversion dams certainly has played a role, as evidenced by reduced species richness upstream of diversion dams that are impassable by most species compared to species richness downstream. Downstream range shifts and reductions in abundance through time support the notion that diversion dams in our study area are barriers to upstream movement for some species and may be part of the reason for the decline of native fishes in the study area. Counter to that point, fishways fitted to diversion dams may improve upstream recolonization, evidence for which is from the similar fish communities downstream and upstream of the FCRID.

Changes in longitudinal patterns of species richness and abundance throughout the study area may also be due to abiotic factors. For example, cooler water temperatures associated with higher flows in upstream reaches may have exceeded the thermal tolerance for some warmwater native fishes, and may be responsible for their reduced abundance.

Habitat shifts in the study area other than water temperatures, may also play a role, especially at local scales. For example, finer-grained sediments favor sucker species just upstream of diversion dams, but are also associated with increased abundance of those species at a broader scale because sand and silt are generally more abundant in downstream reaches of the study area. Longnose Dace and trout species generally favor reaches with larger substrate types, which, at a local scale, are more abundant just downstream of diversions, but also more abundant in upstream reaches of the study area.

In addition to physical habitat shifts, species interactions may also play a role in shaping fish distribution and abundance patterns. For example, habitat conditions favorable to Brown Trout may in turn negatively affect native species through competition for resources and predation. In support of this point, we commonly observed larger Brown Trout regurgitating native fish following electrofishing capture. Thus, the interplay between abiotic conditions, physical habitat, and species interactions likely influence fish assemblage structure at different scales in the Poudre River transition zone.

Whether changes in the fish assemblage over the past several decades are episodic or permanent in nature is difficult to determine. In the short, heterogeneous reach that comprises the transition zone of the Poudre River, it is reasonable to expect the fish assemblage structure to be in a state of shifting equilibrium influenced by stochastic events such as drought and flooding. The Poudre River is presently in a relatively wet period beginning around 2010, preceded by an extended period of drought beginning in 2000. Formerly common species in downstream reaches such as Sand Shiner were abundant during drought years, and have since been nearly eliminated from our study area following the onset of wetter years. It is possible their disappearance from the study area is a temporary range shift downstream into more thermally suitable habitat. However, this hypothesis does not explain Sand Shiner presence during wet years prior to the year 2000, and their near disappearance from downstream sites coincides closely with the first establishment of Brown Trout.

Our results also indicated that diversions with fishways facilitated passage of two native suckers and two nonnative trout more effectively than diversions without passage infrastructure, which doubtless improves conditions for those taxa and others that were not tagged but may have moved. Improved connectivity was illustrated both through the greater proportion of passage by tagged fish released in proximity to diversions with fishways than those without, as well as the higher modeled probability of transitioning over a low-head diversion when a fishway was available. These findings complement studies of others, who demonstrated the capability of nine different species to ascend the FCRID fishway when fish were released in a downstream enclosure. Thus, we feel confident that installation of additional fish passages on other diversions would benefit the fish community of the Poudre River.

The effectiveness of fishways is directly dependent on the local reach having sufficient flows to physically enable movement to and from the diversion structure. So while its clear flows must be sufficient for fishways to function, more specifically it is important that spring and summer flows, when most fish move, are protected, and year-round flows are restored in river reaches that are presently desiccated. Our results showed that seasonal movements were greater during high flows, regardless if fish were moving over fishways, or were moving over short-time durations within reaches for presumptive spawning. What we cannot determine is if fish movements would be greater during other seasons if more flow was present in the river, say in winter. During our study, the reach immediately downstream of the FCRID in winter was typically desiccated except for isolated pools because what little water remained in the river upstream of FCRID was diverted, which obviated passage of any kind because fish could not access the fishway or diversion. Thus, a clear message is that river flows must be sufficient for fishways to function as passages in those seasons. The effectiveness of fishways in facilitating up and downstream passage throughout the river would be especially great if spring and summer flows when most fish move are protected, and if year-round flows were restored in river reaches that are presently desiccated.

Significant future stressors will continue to affect the fish assemblage and overall river functioning and health including climactic shifts, extreme disturbances, and administrative changes in water and land use. However, efforts to support functional river flows, new installation of fishways, and restoration of floodplain connection have been prioritized by managers at the state and local level. While results of this study are a significant contribution to our understanding management complexities and ability to adaptively manage this resource amidst dynamic conditions, there are several reasons we believe continued study of how fishways affect fish movement and assemblage structure is necessary.

First, because this study took place during a decade of relatively high water, opportunities for upstream passage of a diversion like the FCRID were likely available before construction of the fishway, such as during peak flows or when the radial gate was opened. Therefore, it will be important to understand how individuals use the fishway, and how the local fish assemblage structure responds, during periods of extended drought resulting from a predicted hotter and drier climate (Udall and Overpeck 2017).

Second, proposed additional water development stands to alter abiotic and physical habitat conditions in the Poudre River transition zone in the near future (USACE 2018). This may have unforeseen effects on fish community dynamics and use of fishways.

Finally, it is becoming increasingly important to monitor the biological response to stochastic events such as ash and sediment laden flash floods in 2021, which were associated with the widespread and destructive 2020 Cameron Peak fire. Events such as this, and the more localized fish kill in summer 2018, just before this study began, may cause shifts in fish assemblage structure through behavioral effects or direct mortality. Thus, this is an opportunity to understand the role of fishways in the recolonization of depleted reaches of the Poudre River. Future studies to monitor movements and recolonization should continue to use tagged fish released across larger reach scales, to understand temporal dynamics and movement distances, especially related to flows, which offers greater and more realistic perspectives of fishway use. Continued monitoring of the fish community and use of fishways will provide critical insight to their long-term effectiveness to mitigate habitat fragmentation in the transition zone of the Poudre River amidst shifting environmental and biological conditions.

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Literature Cited

Alò, D., and T.F. Turner. 2005. Effects of habitat fragmentation on effective population size in the endangered Rio Grande Silvery Minnow. Conservation Biology 19(4):1138-1148.

Angermeier, P.L., and J.R. Karr. 1984. Relationships between woody debris and fish habitat in a small warmwater stream. Transactions of the American Fisheries Society 113(6):716-726.

Armstrong, J.B., A.H. Fullerton, C.E. Jordan, J.L. Ebersole, J.R. Bellmore, I. Arismendi, B.E. Penaluna, and G.H. Reeves. 2021. The importance of warm habitat to the growth regime of cold-water fishes. Nature Climate Change 11:354-361.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisonsin Press, Madison. 1052 pp.

Bestgen, K. R. 1989. Distribution and notes on the biology of the Northern Redbelly Dace, *Phoxinus eos*, in Colorado. Southwestern Naturalist 34(2):225-231.

Bestgen, K. R., B. Mefford, J. M. Bundy, C. D. Walford, and R. I. Compton. 2010. Swimming performance and fishway model passage success of Rio Grande Silvery Minnow. Transactions of the American Fisheries Society 139:433-448.

Bestgen, K.R., C.T. Wilcox, A.A. Hill, and K.D. Fausch. 2017. A dynamic flow regime supports an intact Great Plains stream fish assemblage. Transactions of the American Fisheries Society 146(5):903-916.

Bestgen, K.R., N.L. Poff, B.P. Bledsoe, D. Baker, D.M. Merritt, M. Lorie, G.T. Auble, J.S. Sanderson, and B.C. Kondratieff. 2020. Designing flows to enhance ecosystem functioning in heavily altered rivers. Ecological Applications 30(1):e02005.

Budy, P., G.P. Thiede, J. Lobón-Cervía, G. González Fernández, P. McHugh, A.R. McIntosh, L. Asbjørn Vøllestad, E. Bécares, and P.G. Jellyman. 2013. Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. Ecology 94:356-367.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

City of Fort Collins. 2017. State of the Poudre River Report. Fort Collins, Colorado, 111 pp. Available at: https://www.fcgov.com/poudrereportcard/pdf/sopr2016.pdf

Colorado Parks and Wildlife. 2015. State Wildlife Action Plan. Colorado Parks and Wildlife, Denver, Colorado.

Colorado Parks and Wildlife. 2019. CPW determines cumulation of factors resulted in the massive fish kill on the Cache la Poudre River in September 2018. Colorado Parks and Wildlife News Release, December 12, 2019. Available at: https://cpw.state.co.us/aboutus/Pages/News-Release-Details.aspx?NewsID=7172

Cunjak, R.A., and G. Power. 1986. Winter habitat utilization by stream resident Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 45:2156-2160.

Dudley, R.K., and S.P. Platania. 2007. Flow regulation and fragmentation imperil pelagic-spawning riverine fishes. Ecological Applications 17(7):2074-2086.

Fausch, K.D., and K.R. Bestgen. 1997. Ecology of fishes indigenous to the central and southwestern Great Plains. In: Knopf F.L. and F.B. Samson, editors. Ecology and conservation of Great Plains verterbrates. New York (NY): Springer-Verlag: 131-166.

Fausch, K.D., C.E. Torgerson, C.D. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. BioScience 52(6):483-498.

Ficke, A.D. 2015. Mitigation measures for barriers to Great Plains fish migration. Doctoral dissertation, Colorado State University, Fort Collins, Colorado. 194 pp.

Garman, G.C., and L.A. Nielsen. 1982. Piscivority by stocked Brown Trout (*Salmo trutta*) and its impact on the nongame fish community of Bottom Creek, Virginia. Canadian Journal of Fisheries and Aquatic Sciences 39:862-869.

Geheber, A.D., and K.R. Piller. 2012. Spatio-temporal patterns of fish assemblage structure in a coastal plain stream: appropriate scales reveal historic tales. Ecology of Freshwater Fish 21:627-639.

Gibson-Reinemer, D.K., and F.J. Rahel. 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. PLoS One 10:e1032103

Gowan, C., M.K. Young, K.D. Fausch, and S.C. Riley. 1994. The restricted movement of stream-resident salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626-2637.

Grossman, G.D., P.B. Moyle, and J.O. Whitaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. The American Naturalist 120(4):423-454.

Haworth, M.R., and K.R. Bestgen. 2017. Flow and water temperature affect reproduction and recruitment of a Great Plains cyprinid. Canadian Journal of Fisheries and Aquatic Sciences 74(6):853-863.

Haworth, M.R., K.R. Bestgen, E.R. Kluender, W.H. Keeley, D.R. D'Amico, and F.B. Wright. 2020. Native fish loss in a transition-zone stream following century-long habitat alterations and nonnative species introductions. Western North American Naturalist 80(4):462-475.

Jackson, D.A., P.R. Peres-Neto, J.D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58(1):157-170.

Jonsson, N., T.F. Næsje, B. Jonsson, R. Saksgård, and O.T. Sandlund. 1999. The influence of piscivory of life history traits of brown trout. Journal of Fish Biology 55:1129-1141.

Kondolf, G.M., and M.G. Wolman. 1993. The sizes of salmonid spawning gravels. Water Resources Research 29(7):2275-2285.

Larscheid, J.G., and W.A. Hubert. 1992. Factors influencing the size structure of Brook Trout and Brown Trout in southeastern Wyoming mountain streams. North American Journal of Fisheries Management 12:109-117.

Lebreton, J.D., J.D. Nichols, R.J. Barker, R. Pradel, and J.A. Spendelow. 2009. Modeling individual animal histories with multistate capture-recapture models. Advances in Ecological Research 41:87-173.

Lee, R.M., and J.N. Rinne. 1980. Critical thermal maxima of five trout species in the Southwestern United States. Transactions of the American Fisheries Society 109(6):632-635.

Lynch, J.D., and B.R. Roh. 1996. An ichthyological survey of the forks of the Platte River in western Nebraska. Transactions of the Nebraska Academy of Sciences 23:65-84.

Nagayama, S., F. Nakamura, Y. Kawaguchi, and D. Nakano. 2012. Effects of configuration of instream wood on autumn and winter habitat use by fish in a large meandering reach. Hydrobiologia 680:159-170.

O'Donnell, M.J., G.E. Horton, and B.H. Lechter. 2010. Use of portable antennas to estimate abundance of PIT-tagged fish in small streams: factors affecting detection probability. North American Journal of Fisheries Management 30(2): 323-336.

Olden, J.D., N.L. Poff, and K.R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. Ecological Monographs 76(1):25-40.

Ortlepp, J. and U. Mürle. 2003. Effects of experimental flooding on Brown Trout (*Salmo trutta fario* L.): The River Spöl, Swiss National Park. Aquatic Sciences 65:232-238.

Pasbrig, C.A., K.D. Koupal, S. Schainost, and W.W. Hoback. 2012. Changes in range-wide distribution of Plains Topminnow *Fundulus sciadicus*. Endangered Species Research 16:235-247.

Perkin, J.S., K.B. Gido, A.R. Cooper, T.F. Turner, M.J. Osborne, E.R. Johnson, and K.B. Mayes. 2015. Fragmentation and dewatering transform Great Plains stream fish communities. Ecological Monographs 85(1):73-92.

Post, J.R., and D.O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year Yellow Perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46:1958-1968.

Quist, M.C., and R.D. Schultz. 2014. Effects of land management legacies on stream fish and aquatic benthic macroinvertebrate assemblages. Environmental Management 54:449-464.

Rahel, F.J., and W.A. Hubert. 1991. Fish assemblages and habitat gradients in a Rocky Mountain – Great Plains stream: biotic zonation and additive patterns of community change. Transactions of the American Fisheries Society 120(3):319-332.

Richer, E.E., E.R. Featherman, E.A. Krone, F.B. Wright III, and M.C. Kondratieff. 2020. Multispecies fish passage evaluation at a rock-ramp fishway in a Colorado transition zone stream. North American Journal of Fisheries Management 40(6):1510-1522.

Scheurer, J.A., K.D. Fausch, and K.R. Bestgen. 2003. Multiscale processes regulate Brassy Minnow persistence in a Great Plains river. Transactions of the American Fisheries Society 132: 840-855.

Schlosser, I.J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogenous lotic environment. Oecologia 113(2):260-268.

Shanahan, J.O., D.W. Baker, B.P. Bledsoe, N.L. Poff, D.M. Merritt, K.R. Bestgen, G.T. Auble, B.C. Kondratieff, J.G. Stokes, M. Lorie, and J.S. Sanderson. 2014. An ecological response model for the Cache la Poudre River through Fort Collins, Colorado. 93 pp + appendices.

Shoup, D.E., and D.H. Wahl. 2011. Body size, food, and temperature affect overwinter survival of age-0 Bluegills. Transactions of the American Fisheries Society 140(5):1298-1304.

Strange, E.M., P.B. Moyle, and T.C. Foin. 1993. Interactions between stochastic and deterministic processes in stream fish community assembly. Environmental Biology of Fishes 36:1-15.

Swarr, T.R. 2018. Improving rock ramp fishways for small-bodied Great Plains fishes. Master's Thesis, Colorado State University, Fort Collins, Colorado. 78 pp.

Townsend, C.R. 1996. Invasion biology and ecological impacts of Brown Trout *Salmo trutta* in

New Zealand. Biological Conservation 78:13-22.

Udall, B., and J. Overpeck. 2017. The twenty-first century Colorado River hot drought and implications for the future. Water Resources Research 53:2404-2418.

[USACE] United States Army Corps of Engineers. 2018. Northern Integrated Supply Project: final environmental impact statement. Omaha District Area Office, Littleton, Colorado.

Walters, D.M., R.E. Zuellig, H.J. Crockett, J.F. Bruce, P.M. Lukacs, and R.M. Fitzpatrick. 2014. Barriers impede upstream spawning migration of Flathead Chub. Transactions of the American Fisheries Society 143:17-25.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl.):120-139.

Winston, M.R., C.M. Taylor, and J. Pigg. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society 120:98-105.

Wohl, E. E., B. P. Bledsoe, K. D. Fausch, N. Kramer, K. R. Bestgen, and M. N. Gooseff, 2016. Management of large wood in streams: an overview and proposed framework for hazard evaluation. Journal of the American Water Resources Association 52(2): 315-335.

Table 1. Sampling locations in the Cache la Poudre River including downstream (DS) and upstream (US) coordinates (Easting/Northing, NAD83 UTM Zone 13), corresponding State of the Poudre Report (SOPR) reach number, and site length in meters.

Site #	Site Name	SOPR #	DS, E	DS, N	US, E	US, N	Length (m)
1	Watson Lake	5	485777	4498098	485406	4498985	200
2	Lion's Park	6	488137	4496749	488020	4496994	315
3	Upstream of Shields St.	8	491812	4494769	491519	4494951	345
4	Salyer Natural Area	9	492901	4494214	492735	4494392	265
5	Gustav Swanson Natural Area	10	493921	4493488	493764	4493753	310
6	Udall Natural Area	11	494467	4492763	494270	4492919	305
7	Upstream of TRID	12	495993	4491723	495760	4491843	275
8	Downstream of TRID	13	496592	4491994	496374	4492008	355
9	Riverbend Ponds	14	497258	4491473	497047	4491684	310
10	Upstream of FCRID	15	498296	4489858	498127	4489974	215
11	Downstream of FCRID	16	498651	4489760	498472	4489692	280
12	Archery Range	17	499926	4488468	499802	4488724	320
13	Strauss Cabin	18	500022	4487462	500153	4487722	320

*TRID: Timnath Reservoir Inlet Diversion
*FCRID: Fossil Creek Reservoir Inlet Diversion

Table 2. Native and nonnative species captured, number and location of sites they were found at (13 possible), total number of each species captured, and total biomass (kg) for sampling completed in the Cache la Poudre River transition zone between autumn 2018 and spring 2021.

Species	# Sites	Sites present	*n*	kg
Native taxa				
White Sucker	13	1-13	6,418	614.4
Longnose Dace	13	1-13	6,307	9.3
Longnose Sucker	13	1-13	4,131	119.3
Fathead Minnow	9	5-13	2,864	3.6
Johnny Darter	8	6-13	619	0.8
Creek Chub	7	1, 7, 9-13	48	0.4
Green Sunfish	6	8-13	242	2.0
Plains Topminnow	6	5, 6, 8-10, 13	96	<0.1
Iowa Darter	4	10-13	38	<0.1
Sand Shiner	2	12, 13	3	<0.1
Black Bullhead	1	6	1	<0.1
Longnose x White Sucker	1	8	1	<0.1
Central Stoneroller	1	11	1	<0.1
Northern Redbelly Dace	1	13	1	<0.1
Subtotal			20,770	750.1
Nonnative taxa				
Brown Trout	13	1-13	5,095	795.5
Rainbow Trout	13	1-13	676	143.1
Largemouth Bass	10	4-13	109	1.9
Brook Stickleback	9	3-7, 9-13	158	0.2
Common Carp	6	5, 7, 8, 10, 12, 13	174	360.4
Bluegill	4	1, 8, 10, 11	12	0.6
Mountain Whitefish	4	2, 3, 5, 6	8	1.4
Bluegill x Green Sunfish	4	1, 8, 10, 11	5	0.3
Western Mosquitofish	3	11-13	6	<0.1
Black Crappie	2	7, 10	5	<0.1
Yellow Perch	2	10, 11	3	<0.1
Cutthroat Trout	1	2	1	0.4
Golden Shiner	1	10	1	<0.1
Smallmouth Bass	1	10	1	<0.1
Subtotal			6,254	1,303.8
Total			27,024	2,053.9

Table 3. Catch per unit effort (CPUE, number of fish captured per hour of sampling) of all native and nonnative species by sampling site (Figure 1) in the Cache la Poudre River, 2018-2021.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Native taxa													
White Sucker	2.5	0.5	2.3	1.7	17.4	119.0	155.7	53.4	75.0	179.5	83.8	152.6	124.2
Longnose Dace	2.8	6.2	27.4	35.9	25.9	37.2	33.9	163.7	370.4	8.3	145.9	47.1	60.9
Longnose Sucker	2.5	11.2	17.6	29.9	62.8	120.5	70.1	65.5	67.0	77.9	64.2	14.3	9.9
Fathead Minnow					1.6	2.5	1.1	200.8	1.1	191.0	10.4	6.1	10.4
Johnny Darter						0.1	1.4	1.6	0.4	51.9	3.7	29.8	7.0
Green Sunfish								0.7	0.4	17.9	1.0	1.8	12.8
Plains Topminnow					0.3	5.3		0.1	6.2	2.5			0.4
Creek Chub	0.6						0.2		1.4	3.8	0.8	0.8	0.2
Iowa Darter										2.2	1.1	0.2	1.8
Sand Shiner												0.2	0.2
Central Stoneroller											0.1		
Northern Redbelly Dace													0.1
Longnose x White Sucker								0.1					
Black Bullhead						0.1							
Total	8.4	17.9	47.3	67.5	108.0	284.7	262.4	486.0	521.8	535.1	311.1	252.7	228.0
Nonnative Taxa													
Brown Trout	71.3	112.3	158.6	151.4	58.6	121.0	5.8	16.2	9.4	5.9	22.7	13.9	11.6
Rainbow Trout	27.2	31.5	20.8	18.1	0.8	1.8	0.9	1.8	1.2	0.5	1.7	3.0	3.7
Common Carp					1.2		0.5	0.4		7.8		8.3	7.2
Brook Stickleback			3.2	0.4	0.1	9.4	3.2		1.4	1.9	0.6	0.3	2.1
Largemouth Bass				0.7	0.5	0.8	0.9	1.0	1.2	9.5	0.3	1.0	0.9
Bluegill	1.9							0.1		0.5	0.3		
Mountain Whitefish		0.2	0.4	0.0	0.1	0.4							
Western Mosquitofish											0.1	0.2	0.5
Black Crappie							0.2			0.6			
Bluegill x Green Sunfish	0.6							0.1		0.2	0.1		
Yellow Perch										0.3	0.1		
Golden Shiner										0.2			
Cutthroat Trout		0.2											
Smallmouth Bass										0.2			
Total	100.9	144.2	183.0	170.6	61.5	133.4	11.5	19.8	13.3	27.5	25.9	26.8	25.9

Table 4. Habitat characteristics at each sampling location including mean wetted channel depth (m), mean water velocity (m/s), wetted to bankfull channel width ratio (W/B), length of rip-rap present (m), length of undercut bank present (m), mean area of submerged wood (m^2), and mean backwater area (m^2). Coefficient of variation included parenthetically for mean depth and velocity values. Values are averaged across seasons to account for variability in discharge at time of sampling and differing amounts of wood present before and after annual peak discharge. Percent substrate composition at sampling sites determined by classifying dominant or co-dominant substrate particle size (diameter) in a circle within a 10 cm radius around each habitat transect point as follows; silt (Si)=0.004-0.064 mm, sand (Sa)=>0.064-2mm, gravel (G)=>2-64 mm, cobble (C)=>64-127 mm, rubble (R)=>127-256 mm, boulder (B)=>256 mm), and bedrock (Bd).

Site	Depth	Velocity	W/B	Rip-rap	Undercut	Wood	Backwater	Si	Sa	G	C	R	B	Bd
1	0.38 (50.4)	0.09 (52.2)	0.84	145.0	-	3.8	-	8.7	22.4	9.3	26.7	26.1	6.8	-
2	0.30 (77.1)	0.14 (79.2)	0.65	108.5	-	20.2	-	0.4	10.9	16.1	32.7	31.0	8.9	-
3	0.18 (58.5)	0.10 (76.9)	0.68	48.0	12.0	36.3	12.7	0.5	13.6	24.9	34.4	22.0	4.6	-
4	0.29 (69.4)	0.20 (48.4)	0.56	-	81.0	73.0	1.7	1.4	14.1	22.6	37.8	22.3	1.8	-
5	0.46 (64.2)	0.09 (80.6)	0.77	170.0	8.0	90.1	-	5.0	31.2	4.4	26.2	26.8	6.0	0.3
6	0.36 (71.8)	0.06 (69.1)	0.60	112.0	29.0	110.8	241.7	6.4	37.7	12.7	36.8	3.4	2.9	-
7	0.52 (53.3)	0.07 (46.1)	0.80	-	10.5	139.6	-	24.6	26.6	13.3	26.2	6.6	0.3	2.3
8	0.37 (67.8)	0.20 (78.2)	0.51	173.6	20.0	137.4	380.0	9.4	21.4	23.5	29.3	11.4	5.0	-
9	0.54 (81.1)	0.09 (70.1)	0.42	57.0	120.0	91.6	75.7	5.5	26.1	17.9	30.3	15.6	4.6	-
10	0.44 (48.1)	0.02 (40.1)	0.83	125.0	18.0	108.7	180.3	13.3	38.3	19.8	25.4	2.0	1.2	-
11	0.40 (72.2)	0.01 (73.1)	0.33	-	26.0	531.5	129.2	6.8	23.9	34.1	34.1	1.1	-	-
12	0.36 (64.2)	0.04 (72.2)	0.83	-	154.7	458.2	153.1	18.3	24.3	27.9	24.3	2.7	0.7	2.0
13	0.37 (61.7)	0.09 (68.5)	0.84	-	24.0	131.6	8.7	7.3	31.1	22.0	29.0	10.7	-	-

Table 5. Mean monthly water temperature, and maximum August water temperature (C) measured at 15-minute intervals during 2020. Differences presented are between the most upstream (1) and downstream (12) sites for each category.

Site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Max Aug
1	1.9	1.8	5.9	9.1	11.1	12.5	13.9	13.5	14.1	11.6	5.0	2.4	17.5
4	1.9	2.3	7.1	11.1	12.1	12.6	-	15.4	14.8	11.0	5.8	2.0	20.3
8	3.5	3.5	8.0	12.5	13.4	14.1	17.0	17.3	15.6	11.4	7.0	4.0	22.4
12	3.9	3.9	8.0	10.9	13.6	14.9	18.3	18.7	16.0	11.5	9.1	6.7	24.9
Difference	+2.0	+2.1	+2.1	+1.8	+2.5	+2.4	+4.5	+5.3	+2.0	-0.1	+4.1	+4.3	+7.4

Table 6. Number of passive integrated transponder (PIT) tags implanted by species across all sites, number and proportion of physical sampling recaptures (sampling), number and proportion of antenna detections (antennas), and total number and proportion of unique detections from all approaches (total). The total number of unique detections is not additive as some species were encountered both by physical recapture and antenna detection.

Species	Tags	Sampling	Prop.	Antennas	Prop.	Total	Prop.
Brown Trout	3,758	555	0.15	508	0.14	869	0.23
White Sucker	1,341	137	0.10	476	0.35	509	0.38
Longnose Sucker	881	27	0.03	206	0.23	216	0.24
Rainbow Trout	499	49	0.10	72	0.14	106	0.21
Green Sunfish	23	-	-	-	-	-	-
Largemouth Bass	20	-	-	3	0.15	3	0.15
Common Carp	17	-	-	5	0.29	5	0.29
Creek Chub	9	-	-	3	0.33	3	0.33
Bluegill	9	-	-	1	0.11	1	0.11
Mountain Whitefish	7	-	-	2	0.29	2	0.29
Hybrid Sunfish	5	-	-	-	-	-	-
Black Bullhead	1	-	-	-	-	-	-
Cutthroat Trout	1	-	-	-	-	-	-
Hybrid Sucker	1	-	-	1	1.00	1	1.00
Smallmouth Bass	1	-	-	-	-	-	-
Total	6,573	768	0.12	1,276	0.19	1,718	0.26

Table 7. Summary of fish passage by species over the Fossil Creek Reservoir Inlet Diversion (FCRID), which has a fish passage structure, including number of tagged fish released upstream of the FCRID at Sites 8-10 (US tags), and downstream of the FCRID at Sites 11-13 (DS tags) by species (Figure 1), number of each species that passed over the FCRID, and number of upstream (US), downstream (DS), and total passages by species. A subset of tagged fish were selected from release locations up and downstream of the FCRID as they were most likely to encounter that diversion and fishway.

Species	US tags	DS tags	Total	# passed	%	US	DS	Total
Native taxa								
White Sucker	366	769	1,135	82	7.2	77	70	147
Longnose Sucker	349	254	603	30	4.9	31	21	52
Creek Chub	7	2	9	1	11.1	1	1	2
Green Sunfish	17	6	23	-	-	-	-	-
Longnose x White Sucker	1	-	1	-	-	-	-	-
Subtotal	740	1,031	1,771	113	6.4	109	92	201
Nonnative taxa								
Brown Trout	156	231	387	34	8.8	34	26	60
Rainbow Trout	20	52	72	4	5.5	4	3	7
Common Carp	10	7	17	3	17.6	1	3	4
Largemouth Bass	13	3	16	-	-	-	-	-
Bluegill	2	2	4	-	-	-	-	-
Bluegill x Green Sunfish	2	1	3	-	-	-	-	-
Smallmouth Bass	1	-	1	-	-	-	-	-
Subtotal	204	296	500	41	8.2	39	32	71
Total	944	1,327	2,271	154	6.8	148	124	272

Table 8. Summary of fish passage by species over the Watson Lake Diversion (WLD), which has a fish passage structure, including number of tagged fish released downstream of the WLD at Site 1 (Figure 1) by species, number of each species that passed over the WLD, and number of upstream (US), downstream (DS), and total passages by species. A subset of tagged fish were selected from a release location downstream of the WLD as they were most likely to encounter that diversion and fishway.

Species	DS tags	# passed	%	US	DS	Total
Native taxa						
White Sucker	6	-	-	-	-	-
Longnose Sucker	4	1	25.0	2	1	3
Subtotal	10	1	10.0	2	1	3
Nonnative taxa						
Brown Trout[1]	162	22	13.6	24	6	30
Rainbow Trout	39	7	17.9	7	1	8
Bluegill	5	-	-	-	-	-
Bluegill x Green Sunfish	2	-	-	-	-	-
Subtotal	208	29	13.9	31	7	38
Total	308	30	9.7	33	8	41

[1]One individual tagged at Site 2 made single upstream passage

Table 9. Summary of fish passage by species over the Lake Canal Diversion (LCD), which does not have a fish passage structure, including number of tagged fish released upstream of the LCD at Sites 3 and 4 (US tags), and downstream of the LCD at Sites 5-7 (DS tags) by species (Figure 1), number of each species that passed over the LCD, and number of upstream (US), downstream (DS), and total passages by species. A subset of tagged fish were selected from release locations up and downstream of the LCD as they were most likely to encounter that diversion.

Species	US tags	DS tags	Total	# passed	%	US	DS	Total
Native taxa								
Longnose Sucker	18	211	229	2	0.9	2	1	3
White Sucker	2	194	196	-	-	-	-	-
Black Bullhead	-	1	1	-	-	-	-	-
Subtotal	20	406	426	2	0.5	2	1	3
Nonnative taxa								
Brown Trout	1,740	998	2,738	25	0.9	8	18	26
Rainbow Trout	233	23	256	1	0.4	0	1	1
Mountain Whitefish	3	4	7	-	-	-	-	-
Largemouth Bass	-	4	4	-	-	-	-	-
Subtotal	1,976	1,029	3,005	26	0.9	8	19	27
Total	1,996	1,435	3,431	28	0.8	10	20	30

Table 10. Summary of fish passage by species over the Timnath Reservoir Inlet Diversion (TRID), which does not have a fish passage structure, including number of tagged fish released upstream of the TRID at Sites 5-7 (US tags), and downstream of the TRID at Sites 8-10 (DS tags) by species (Figure 1), number of each species that passed over the TRID, and number of upstream (US), downstream (DS), and total passages by species. A subset of tagged fish were selected from release locations up and downstream of the TRID as they were most likely to encounter that diversion.

Species	US tags	DS tags	Total	# passed	%	US	DS	Total
Native taxa								
White Sucker	194	366	560	2	0.4	0	2	2
Longnose Sucker	211	349	560	1	0.2	1	0	1
Green Sunfish	-	17	17	-	-	-	-	-
Creek Chub	-	7	7	-	-	-	-	-
Longnose x White Sucker	-	1	1	-	-	-	-	-
Black Bullhead	1	-	1	-	-	-	-	-
Subtotal	406	740	1,146	2	0.2	0	2	3
Nonnative taxa								
Brown Trout	998	156	1,154	4	0.3	4	2	6
Rainbow Trout	23	20	43	-	-	-	-	-
Common Carp	-	10	10	-	-	-	-	-
Bluegill	-	2	2	-	-	-	-	-
Largemouth Bass	4	13	17	-	-	-	-	-
Mountain Whitefish	4		4	-	-	-	-	-
Bluegill x Green Sunfish	-	2	2	-	-	-	-	-
Smallmouth Bass	-	1	1	-	-	-	-	-
Subtotal	1,029	204	1,233	4	0.3	4	2	6
Total	1,435	944	2,379	6	0.3	5	4	9

Table 11. Total length at release (mm) of Brown Trout (BT), Rainbow Trout (RT), Longnose Sucker (LS), and White Sucker (WS), that passed over the Watson Lake Diversion and fishway, (W), Lake Canal Diversion (L), Timnath Reservoir Inlet Diversion (T), and Fossil Creek Reservoir Inlet Diversion and fishway (F) in either an up or downstream direction. Length at release does not indicate the fish was that size at time of passage as time between release and passage varied by individual.

	BT				RT				LS				WS			
TL	W	L	T	F	W	L	T	F	W	L	T	F	W	L	T	F
<200	10	7		6	1	-	-	-	-	1	-	13	-	-	-	12
201-250	2	-		-	1	-	-	-	-	1	-	8	-	-	-	3
251-300	2	9	1	3	-	1	-	1	-	-	-	5	-	-	-	10
301-350	6	6	1	6	5	-	-	2	-	-	1	3	-	-	-	7
351-400	2	3	1	13	-	-	-	-	1	-	-	1	-	-	2	24
401-450	-	-		4	-	-	-	-	-	-	-	-	-	-	-	22
451-500	-	-	1	1	-	-	-	1	-	-	-	-	-	-	-	4
501-550	-	-		1	-	-	-	-	-	-	-	-	-	-	-	-
Total	22	25	4	34	7	1	0	4	1	2	1	30	0	0	2	82

Table 12. Set of models (top 10 presented) used to estimate transition probability (ψ) of tagged fish released up and downstream of the Fossil Creek Reservoir Inlet Diversion and fishway (Figure 1) at 6 study sites (8-13) between autumn 2018 and summer 2021. Candidate variables for inclusion in model structures included effects of species (S), state or reach (R), time (T), and constant (.). The same structure on capture probability (*p*) was used for every model, and included S,R, and T. Survival (*S*) fit all combination of variables, and transition probability (ψ) fit the state variable (R) in all model structures.

Model Rank	Model Name	$QAIC_c$	$\Delta QAIC_c$	w	Model Liklihood	K	Qdeviance
1	*S* (T) ψ (S, R)	3602.96	0.00	0.91	1.00	86	1038.89
2	*S* (R, T) ψ (S, R)	3608.02	5.07	0.07	0.08	94	1027.06
3	*S* (T) ψ (R, T)	3612.45	9.50	0.01	0.01	96	1027.25
4	*S* (T) ψ (R)	3613.44	10.48	0.00	0.01	80	1062.00
5	*S* (S, T) ψ (S, R)	3615.86	12.90	0.00	0.00	104	1013.66
6	*S* (S, T) ψ (R, T)	3616.22	13.26	0.00	0.00	114	992.65
7	*S* (S, T) ψ (R)	3617.44	14.49	0.00	0.00	98	1028.00
8	*S* (R, T) ψ (R)	3619.23	16.28	0.00	0.00	88	1050.95
9	*S* (R, T) ψ (R, T)	3622.49	19.54	0.00	0.00	102	1024.55
10	*S* (S, R, T) ψ (R, T)	3651.36	48.40	0.00	0.00	139	973.78

Table 13. Set of models (top 10 presented) used to estimate transition probability (ψ) of tagged fish released up and downstream of the Lake Canal Diversion (Figure 1) at 5 study sites (3-7) between autumn 2018 and summer 2021. Candidate variables for inclusion in model structures included effects of species (S), state or reach (R), time (T), and constant (.). The same structure on capture probability (p) was used for every model, and included S,R, and T. Survival (*S*) fit all combinations of variables, and transition probability (ψ) fit the state variable (R) in all model structures.

Model Rank	Model Name	$QAIC_c$	$\Delta QAIC_c$	w	Model Liklihood	K	Qdeviance
1	*S* (T) ψ (S, R)	1351.22	0.00	0.61	1.00	72	120.76
2	*S* (T) ψ (R)	1352.61	1.39	0.31	0.50	72	122.15
3	*S* (.) ψ (S, R)	1357.17	5.95	0.03	0.05	67	137.10
4	*S* (.) ψ (R)	1357.91	6.69	0.02	0.04	67	137.84
5	*S* (R) ψ (S, R)	1359.44	8.22	0.01	0.02	68	137.29
6	*S* (R) ψ (R)	1359.88	8.66	0.01	0.01	68	137.73
7	*S* (S) ψ (S, R)	1361.65	10.43	0.00	0.01	70	135.34
8	*S* (R, T) ψ (S, R)	1362.27	11.04	0.00	0.00	78	119.30
9	*S* (S) ψ (R)	1362.78	11.55	0.00	0.00	70	136.47
10	*S* (R, T) ψ (R)	1363.68	12.46	0.00	0.00	78	120.72

Table 14. Transition probability (ψ) estimates for tagged fish released in reaches upstream and downstream of the Fossil Creek Reservoir Inlet Diversion (FCRID), which has a fishway, and for tagged fish released in reaches up and downstream of the Lake Canal Diversion (LCD), which does not have a fishway. Estimates are from top models (Tables 12 and 13), where the survival parameter varied by time, and ψ parameter varied by species and state.

		Upstream			Downstream		
Diversion	Species	Estimate (ψ)	SE	95% CI	Estimate (ψ)	SE	95% CI
FCRID	Brown Trout	0.158	0.044	(0.088-0.266)	0.209	0.060	(0.115-0.350)
	Rainbow Trout	0.358	0.200	(0.091-0.754)	0.118	0.115	(0.015-0.539)
	Longnose Sucker	0.290	0.069	(0.174-0.441)	0.054	0.019	(0.026-0.107)
	White Sucker	0.097	0.017	(0.067-0.138)	0.194	0.032	(0.138-0.267)
LCD	Brown Trout	0.014	0.011	(0.003-0.065)	0.022	0.011	(0.007-0.062)
	Rainbow Trout	0.000	0.000	(0.00-0.00)	0.143	0.175	(0.009-0.734)
	Longnose Sucker	0.065	0.111	(0.002-0.712)	0.091	0.220	(0.001-0.947)
	White Sucker	0.000	0.000	(0.00-0.00)	0.000	0.000	(0.00-0.00)

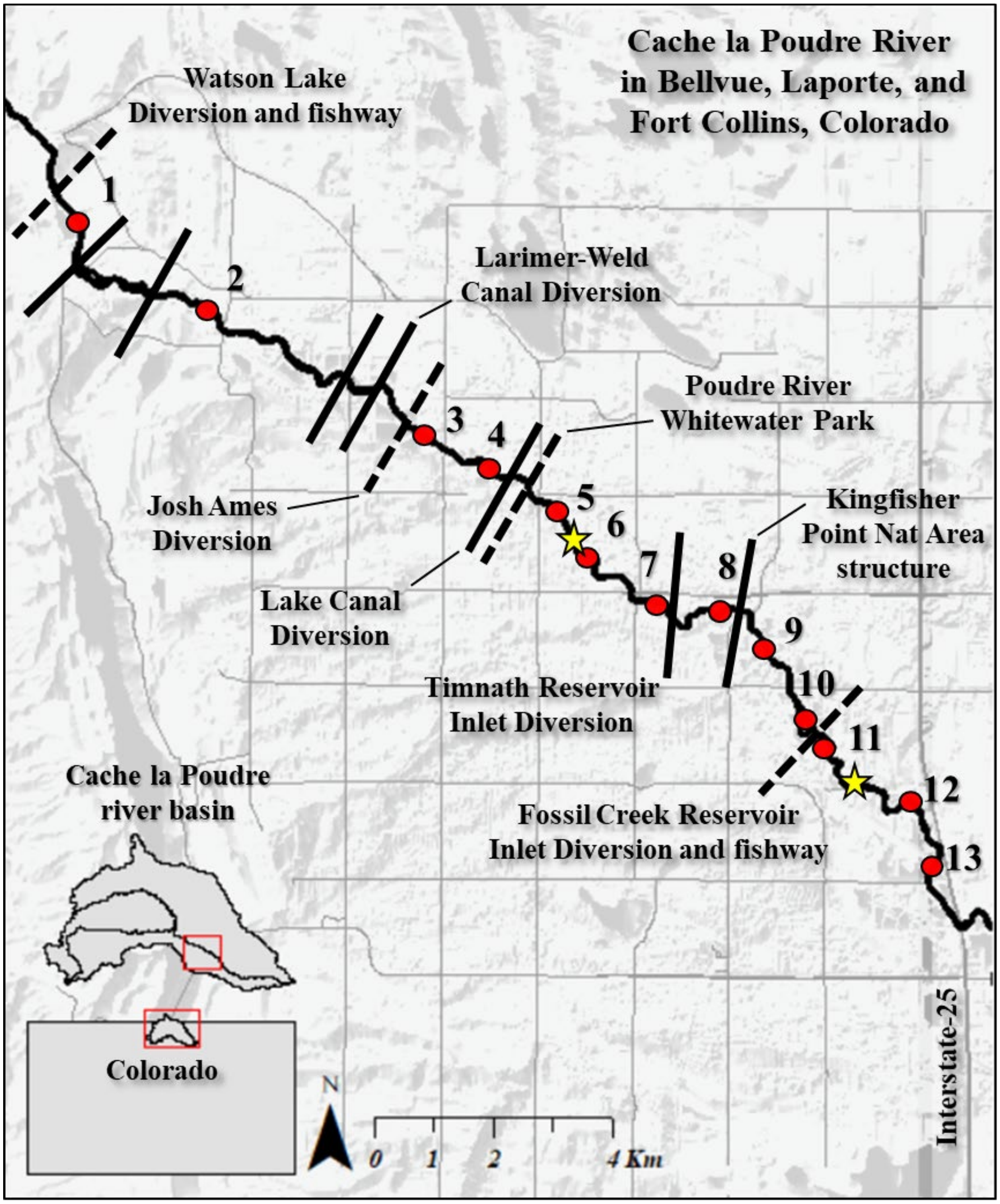

Figure 1. The Cache la Poudre River in Bellvue, Laporte, and Fort Collins, Colorado, including fish community and habitat sampling sites (red dots), and diversion structures that have been removed or retrofitted with fish passage (dashed lines) and those without (solid lines). Stars indicate location of USGS gauge 06752260 (Cache la Poudre at Fort Collins, CO; upstream) and USGS gauge 06752280 (Cache la Poudre above Boxelder Creek near Timnath, CO; downstream).

Figure 2. Diversion dams and grade control structures recently removed or retrofitted with fish passage in the Cache la Poudre River transition zone: The Watson Lake Diversion Fishway (top left), the Josh Ames Diversion (removed, top right), the Poudre River Whitewater Park (bottom left), and the Fossil Creek Inlet Diversion Fishway (bottom right). Red arrow points to channel designed for fish passage in the Poudre River Whitewater Park.

Figure 3. The Fossil Creek Reservoir Inlet Diversion and Fishway during high flows, highlighting the downstream hydraulic wave and radial gate that provide potential routes of passage over the diversion in addition to the fishway.

Figure 4. Notable diversion dams and grade control structures without fish passage during summer (left) and winter (right) baseflow conditions in the Cache la Poudre River transition zone: The Lake Canal Diversion (top), the Timnath Reservoir Inlet Diversion (TRID, middle), and the sheet-pile structure in Kingfisher Point Natural Area (bottom). The Larimer-Weld Canal, another large diversion comparable in size and scale to the TRID, is not pictured.

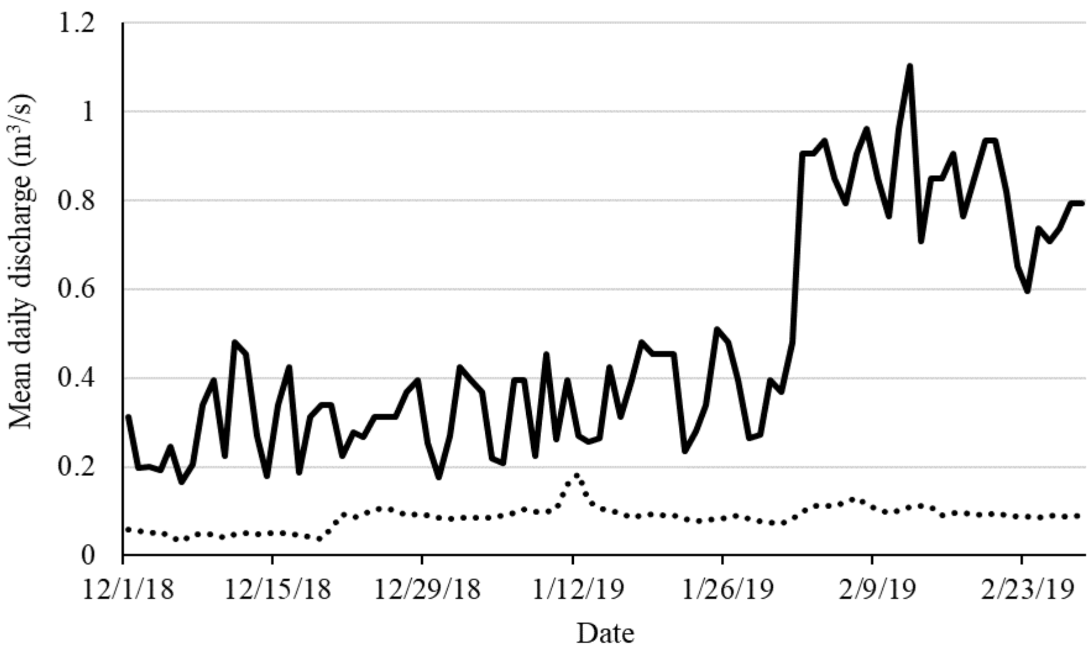

Figure 5. Winter discharge in the Cache la Poudre River upstream of the Timnath Reservoir Inlet Diversion (Figure 1) at USGS gauge 06752260 (Cache la Poudre at Fort Collins, CO; solid line), and downstream at USGS gauge 06752280 (Cache la Poudre above Boxelder Creek near Timnath, CO; dashed line). Discharge of 1 m^3/s equals approximately 35 ft^3/s.

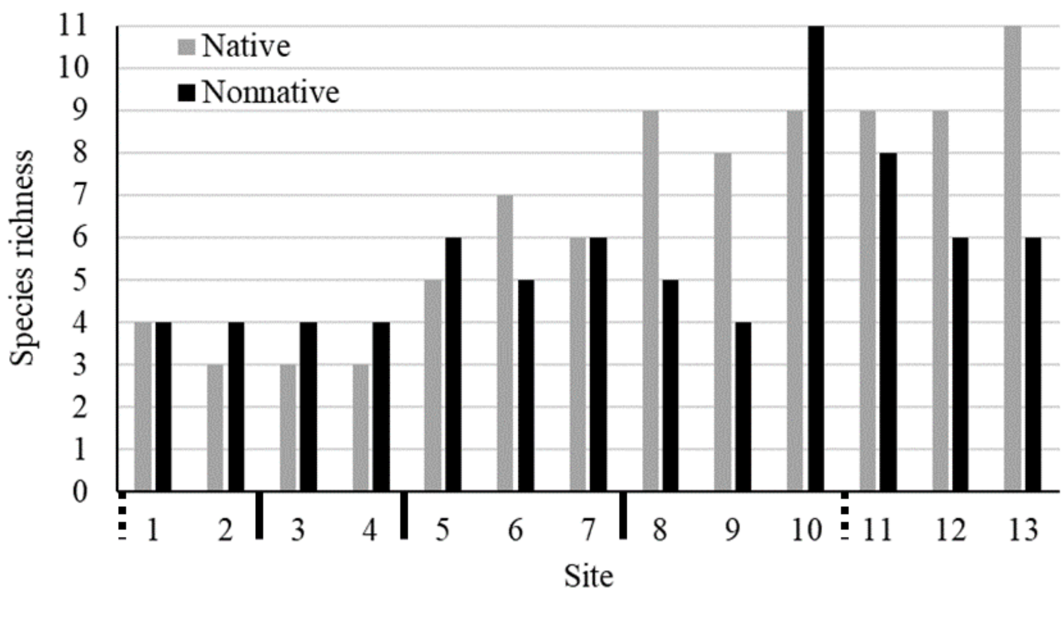

Figure 6. Native and nonnative species richness by sampling site in the Cache la Poudre River, 2018-2021. Solid bars on x-axis between site numbers indicates presence of a diversion without fish passage between those sampling sites, and dashed bars indicate presence of a fishway.

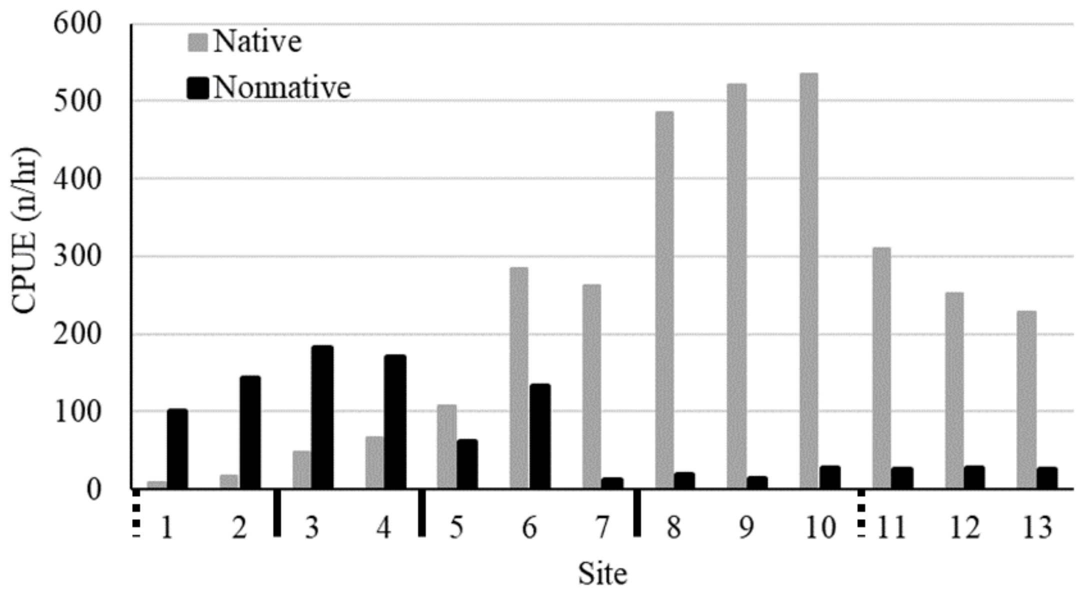

Figure 7. Catch per unit effort (CPUE, number of fish captured per hour of sampling) of all native and nonnative species by sampling site in the Cache la Poudre River, 2018-2021. Solid bars on x-axis between site numbers indicates presence of a diversion without fish passage between those sampling sites, and dashed bars indicate presence of a fishway

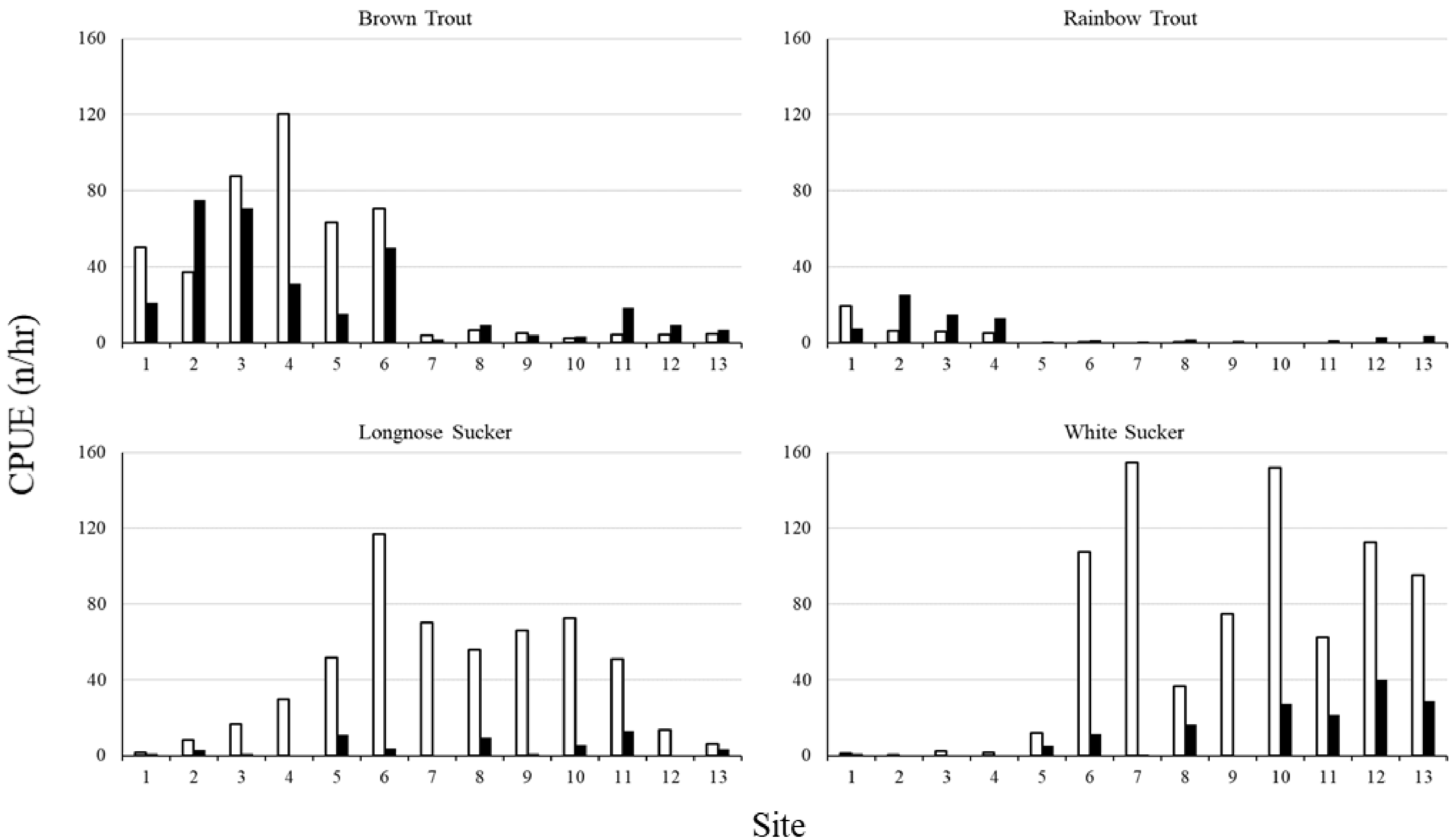

Figure 8. Catch per unit of effort (CPUE, number of fish captured per hour of sampling) of juvenile (< 200 mm TL; open bars) and adult (> 200 mm TL; filled bars) for the four most abundant large-bodied species captured during sampling completed in the Cache la Poudre River, 2018-2021.

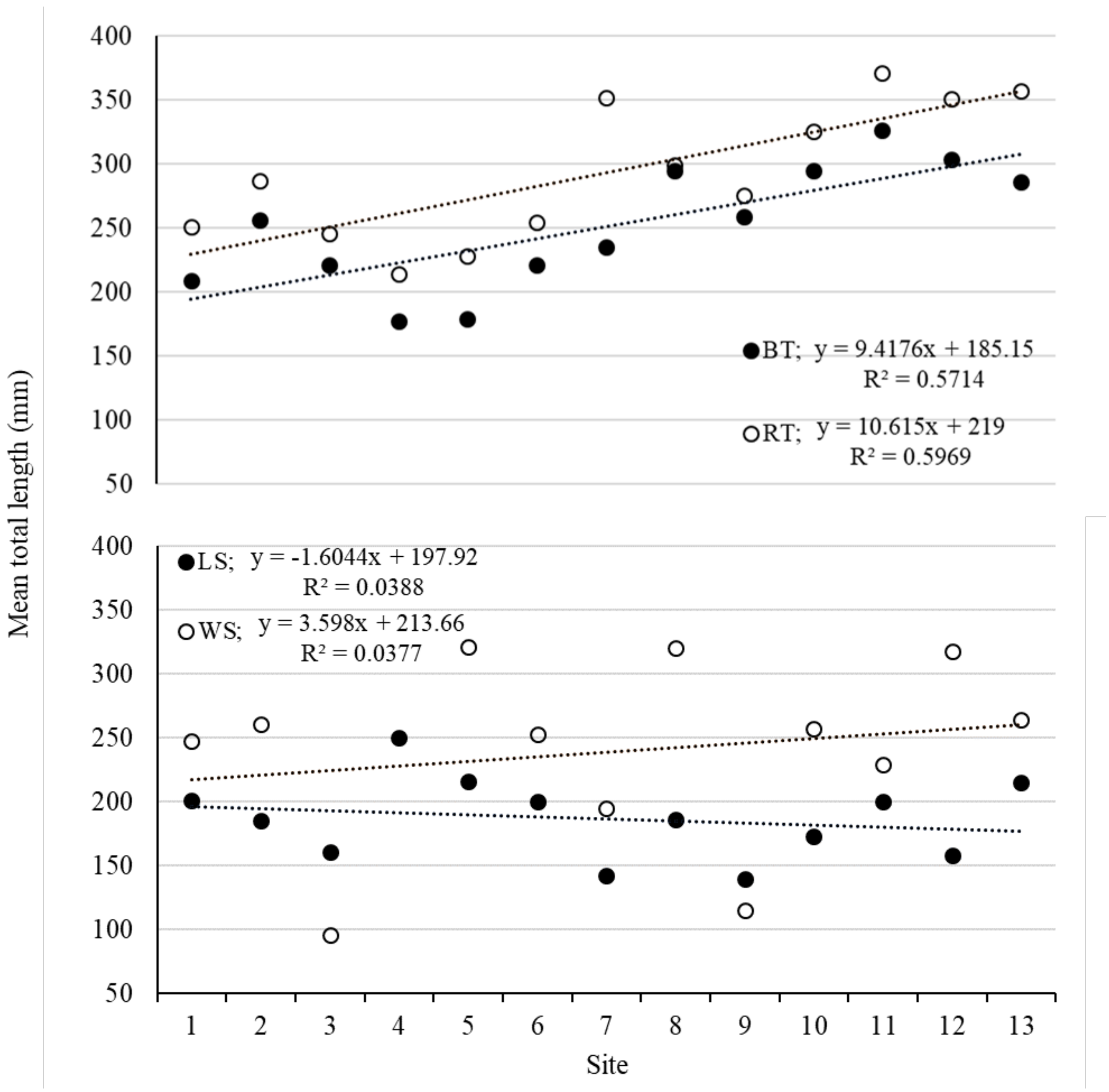

Figure 9. Linear regression of mean total length (mm) as a function of sampling site for the four most abundant large-bodied species captured in the Cache la Poudre River, 2018-2021; Brown Trout (BT;top panel), Rainbow Trout (RT; top panel), Longnose Sucker (LS; bottom panel), and White Sucker (WS; bottom panel).

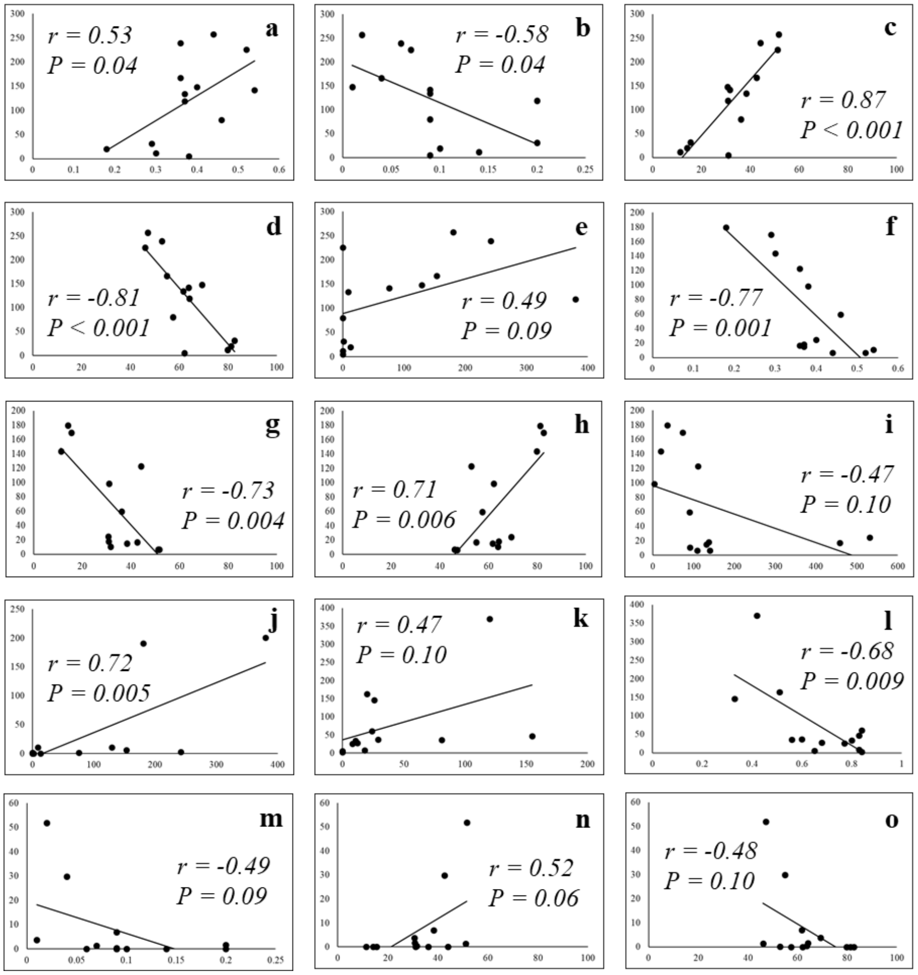

Figure 10. Pearson correlations of guild and species catch per unit effort (CPUE, y-axis) and habitat covariates (x-axis) for the six most abundant species at 13 sites in the Cache la Poudre River. Guilds include native suckers (White and Longnose Sucker) and nonnative trout (Brown and Rainbow Trout), and individual species include Fathead Minnow, Longnose Dace, and Johnny Darter. CPUE and habitat measurements were averaged across all samples to control for interannual and seasonal variability in both measures. Habitat covariates considered can be found in Table 4 and included; area of submerged wood (m^2), backwater area (m^2), linear amount of rip-rap (m), linear amount of undercut bank (m), mean depth (m), mean velocity (m/s), wetted to bankfull stream width ratio (W/B), % fine substrate (silt and sand), and % coarse substrate (gravel, cobble, rubble). Statistically significant correlations (*r*) for guilds and species where $\alpha = 0.10$ include: suckers and (a) mean depth, (b) mean velocity, (c) % fine substrate, (d) % coarse substrate, (e) and backwater area; trout and (f) mean depth, (g) % fine substrate, (h) % coarse substrate, and (i) submerged wood area; Fathead minnow and (j) backwater area; Longnose Dace and (k) undercut banks, and (l) W/B ratio; and Johnny Darter and (m) mean velocity, (n) % fine substrate, and (o) % coarse substrate.

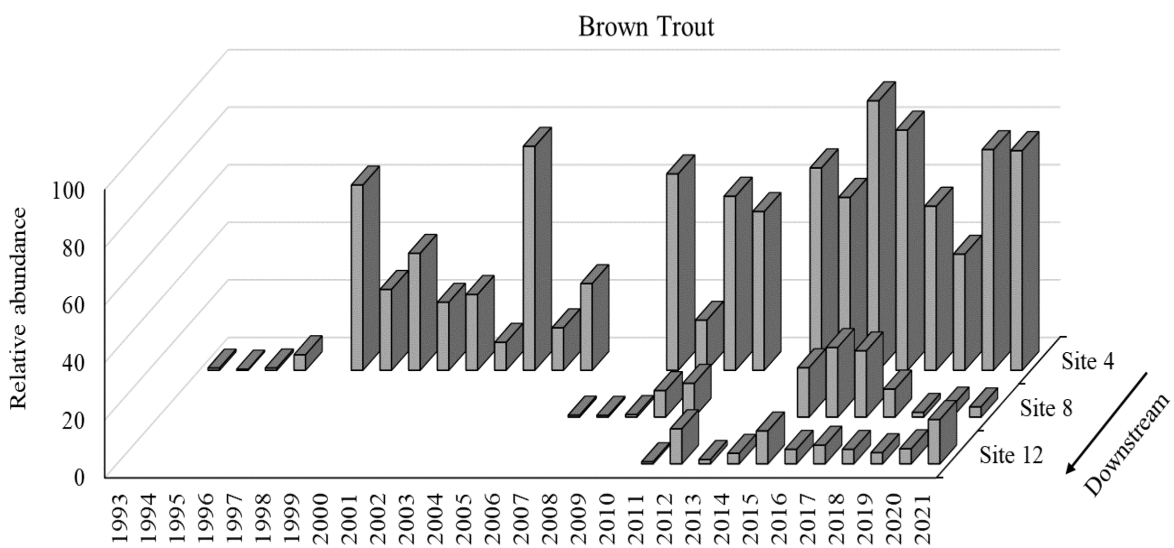

Figure 11. Relative abundance (% of each species among the total captured) of Brown Trout from fish community sampling completed at Sites 4, 8, and 12 (Figure 1) in our study area in the Cache la Poudre River transition zone, 1993-2021.

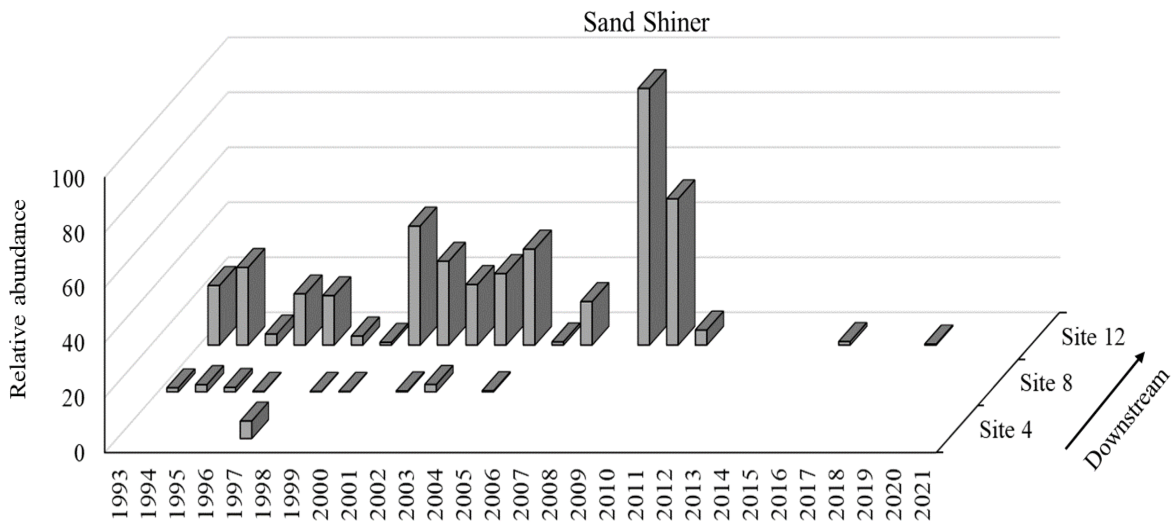

Figure 12. Relative abundance (% of each species among the total captured) of Sand Shiner from fish community sampling completed at Sites 4, 8, and 12 (Figure 1) in our study area in the Cache la Poudre River transition zone, 1993-2021.

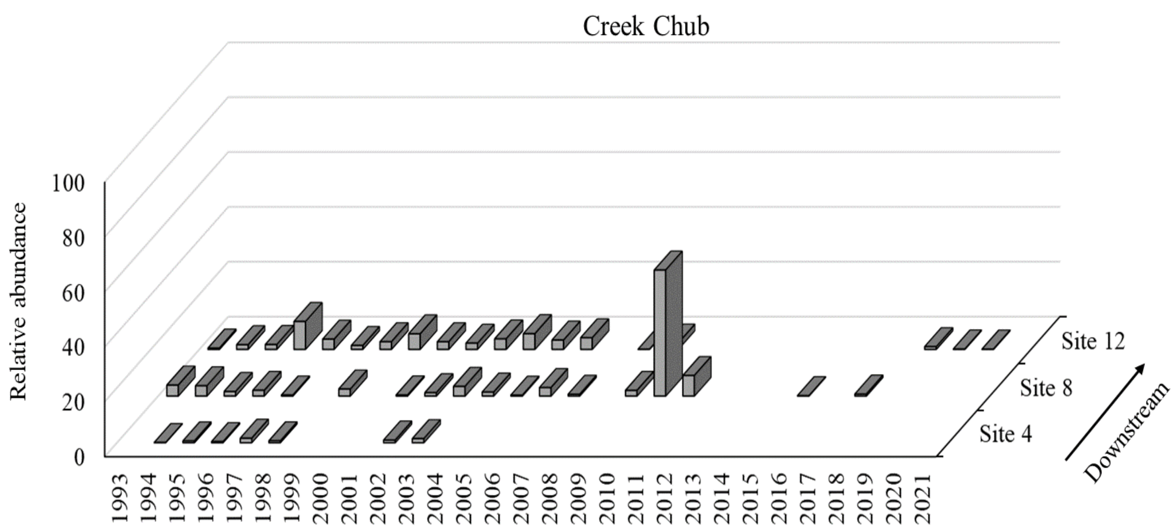

Figure 13. Relative abundance (% of each species among the total captured) of Creek Chub from fish community sampling completed at Sites 4, 8, and 11 (Figure 1) in our study area in the Cache la Poudre River transition zone, 1993-2021.

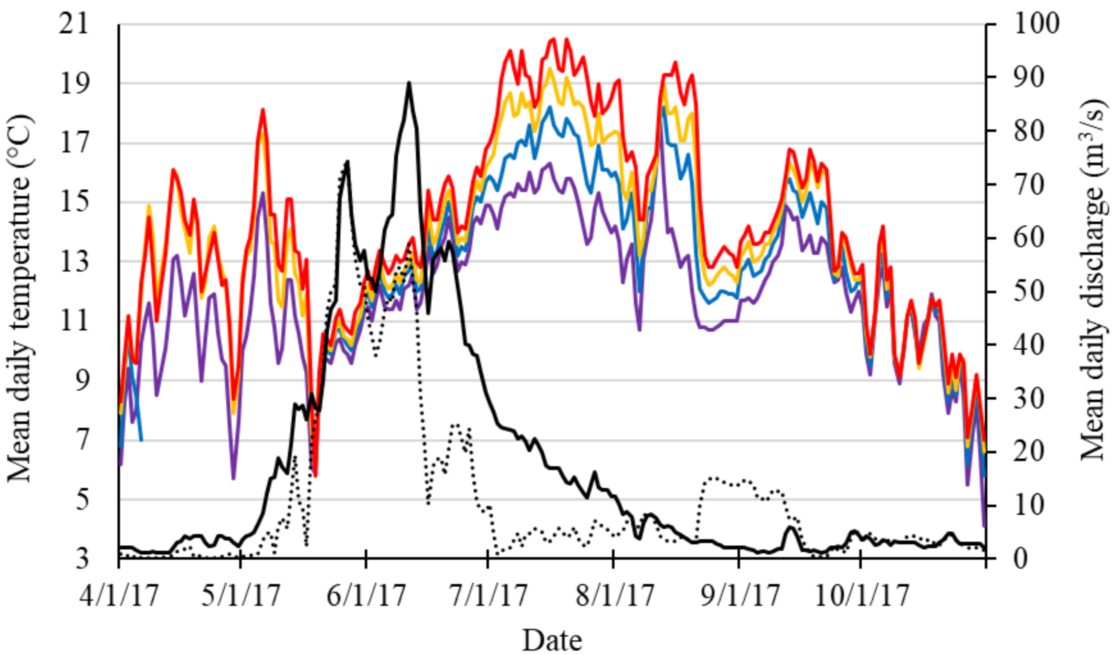

Figure 14. Mean daily water temperature measured near sites 1 (solid purple line), 3 (solid blue line), 8 (solid orange line), and 11 (solid red line), and mean daily discharges from the Colorado Division of Water Resources gauge at the mouth of Poudre Canyon (solid black line) and at USGS gauge 06752260 (Cache la Poudre at Fort Collins, CO; dashed black line) during the irrigation months of April-November 2017 in the Cache la Poudre River (Figure 1). Discharge of 1 m^3/s equals approximately 35 ft^3/s. Temperature data are publicly available from the Northern Water Conservancy District at: https://www.northernwater.org/.

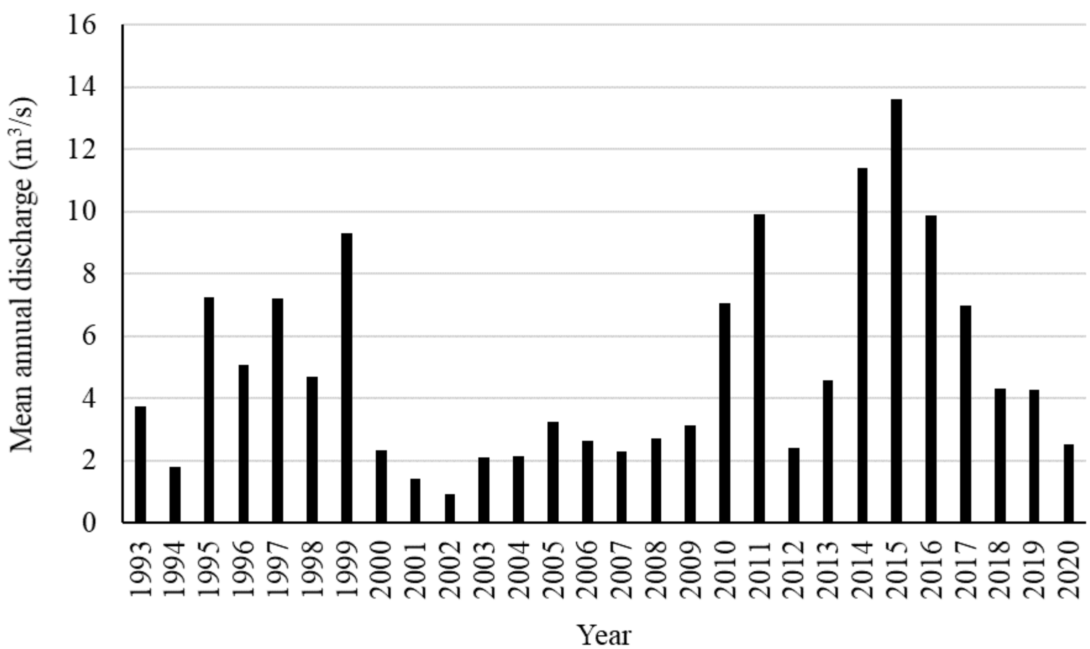

Figure 15. Mean annual discharge for the Cache la Poudre River measured at USGS gauge 06752260 (Cache la Poudre at Fort Collins, CO) from 1993-2020. Discharge of 1 m^3/s equals approximately 35 ft^3/s.

Figure 16. Submersible (top) and mobile (bottom) passive integrated transponder (PIT) tag detection antennas.

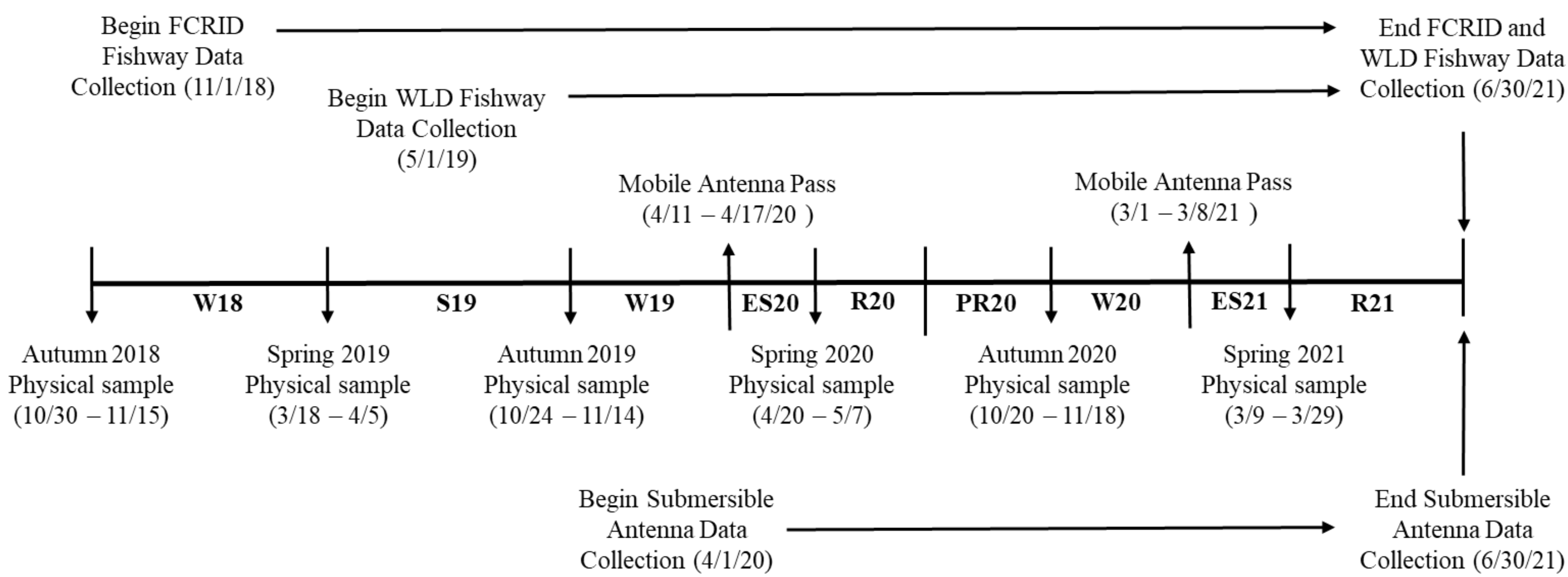

Figure 17: Timeline depicting the timing and duration of fish sampling and tagging events (physical sample), mobile antenna passes, submersible antenna monitoring, and fishway antenna monitoring in the Cache la Poudre River from October 2018-June 2021.

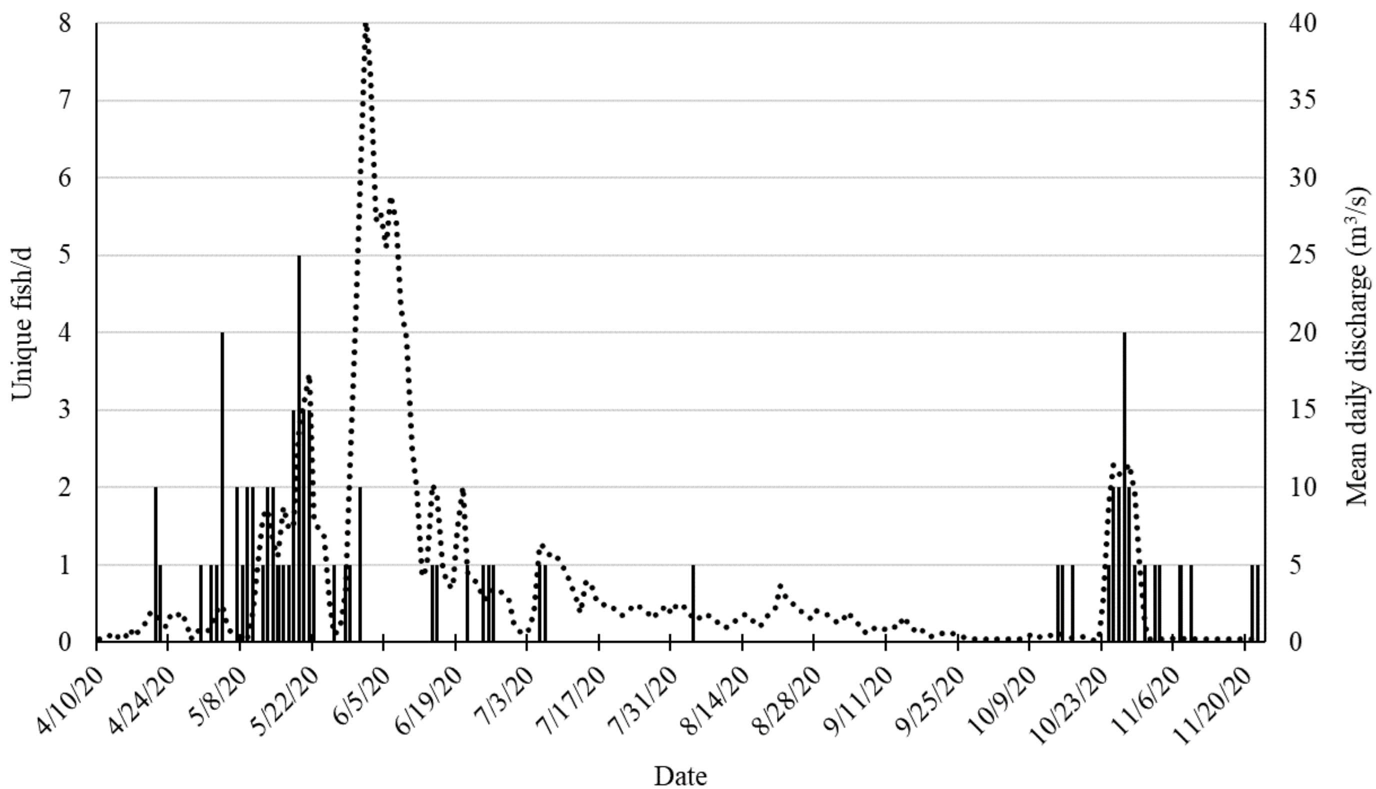

Figure 18: Number of unique tagged fish detected per day (n=29) relative to mean daily discharge at USGS gauge 06752260 (Cache la Poudre at Fort Collins, CO) at a submersible antenna placed on the downstream side of the Lake Canal Diversion in the Cache la Poudre River from April-November 2020. Discharge of 1 m^3/s equals approximately 35 ft^3/s.

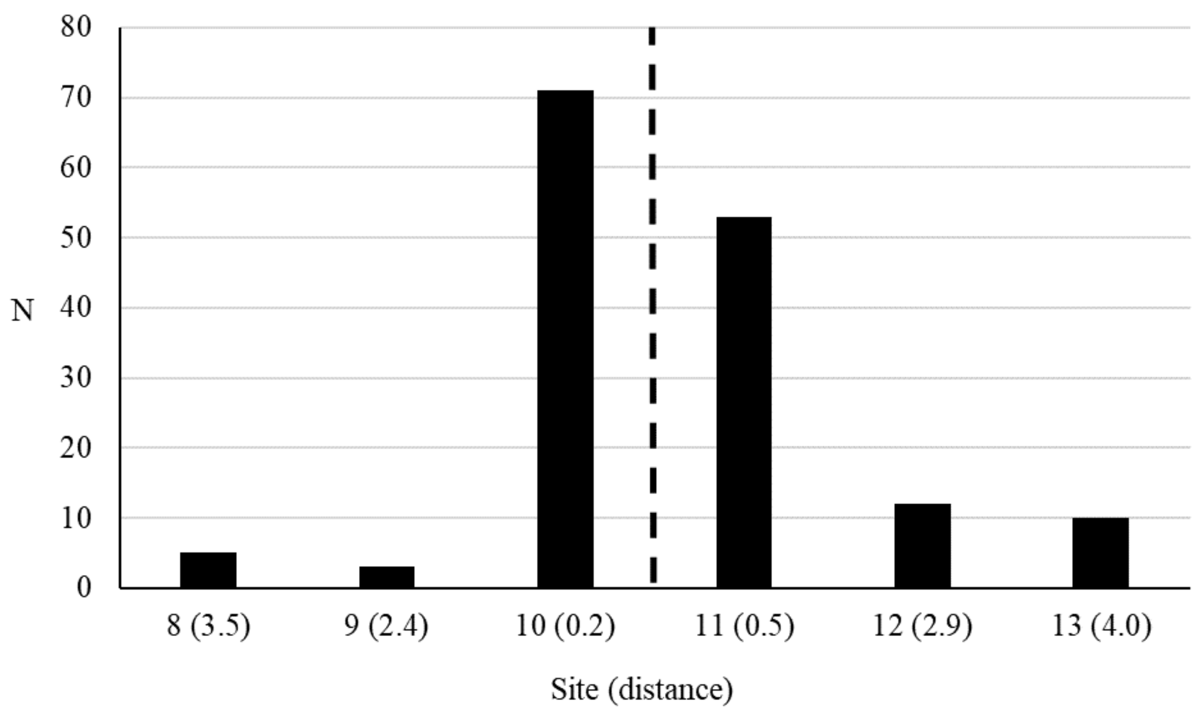

Figure 19. Number of tagged fish and their release location that passed over the Fossil Creek Reservoir Inlet Diversion (FCRID) and fishway. Sites and their distance from the FCRID (km) listed on the horizontal axis go in the upstream direction from left to right. The dashed vertical line between sites 10 and 11 represents the location of the FCRID.

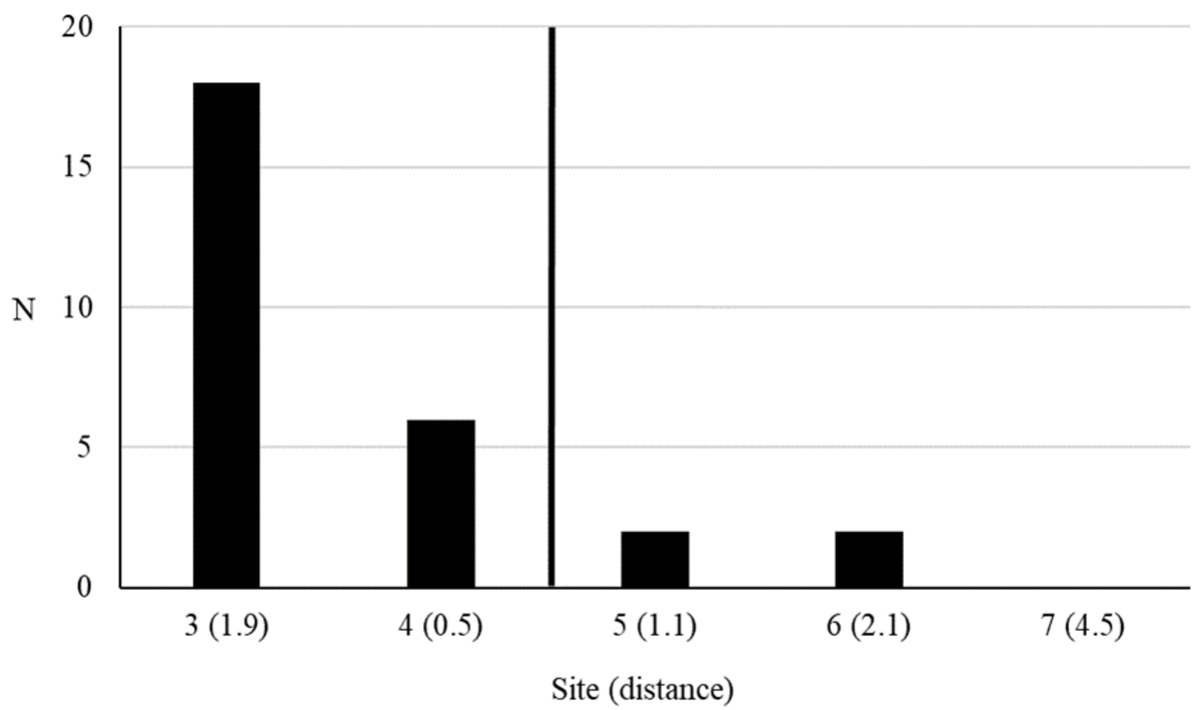

Figure 20. Number of tagged fish and their release location that passed over the Lake Canal Diversion (LCD). Sites and their distance from the LCD (km) listed on the horizontal axis go in the upstream direction from left to right. The solid vertical line between sites 4 and 5 represents the location of the LCD.

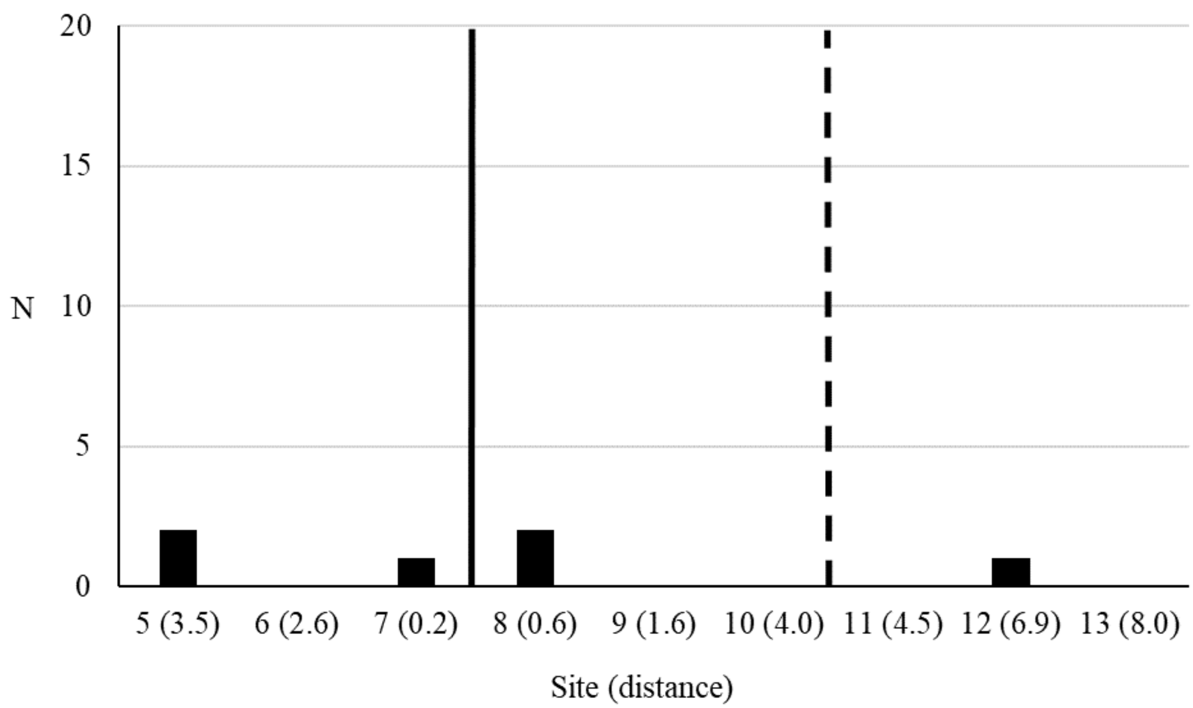

Figure 21. Number and release location of tagged fish that passed over the Timnath Reservoir Inlet Diversion (TRID). Sites and their distance from the TRID (km) listed on the horizontal axis go in the upstream direction from left to right. The solid vertical line between sites 7 and 8 represents the location of the TRID, and the dashed vertical line between sites 10 and 11 represents the Fossil Creek Reservoir Inlet Diversion (FCRID) and fishway.

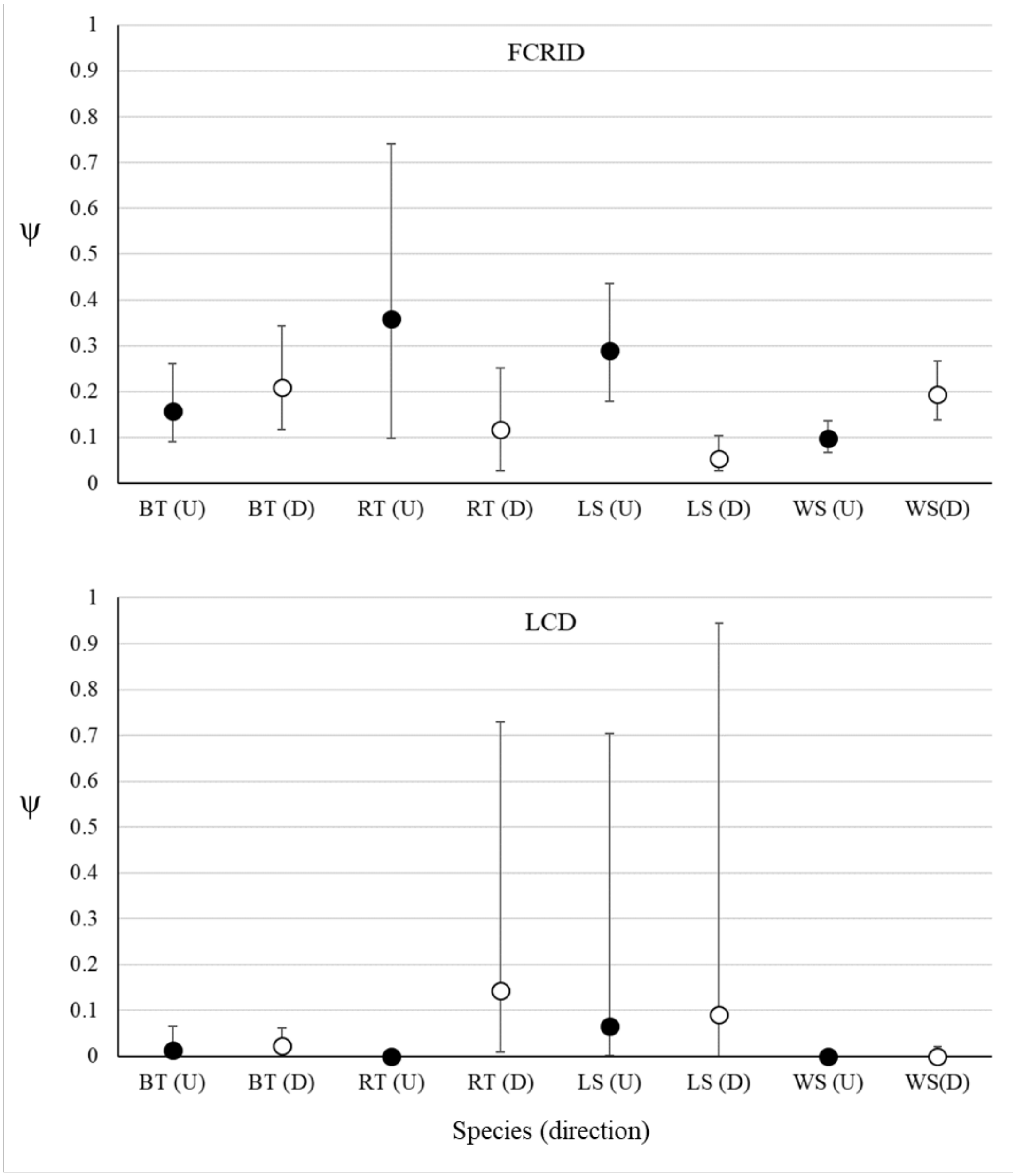

Figure 22. Transition probability estimates (ψ, 95% CI) for fish released in proximity to the Fossil Creek Reservoir Inlet Diversion (FCRID, top panel), which has fish passage (Table 7), and the Lake Canal (LCD, bottom panel) which does not have fish passage (Table 9). Filled circles represent probability of each species (BT-Brown Trout, RT-Rainbow Trout, LS-Longnose Sucker, WS-White Sucker) moving upstream (U) over a given diversion during each of the nine intervals defined by 10 sampling occasions (see Figure 17), and open circles are the probability of moving downstream (D) over a given diversion at any point between autumn 2018 and summer 2021 in the same intervals. Estimates presented are from the top models for both the FCRID (Table 12) and LCD (Table 13) MARK analyses.

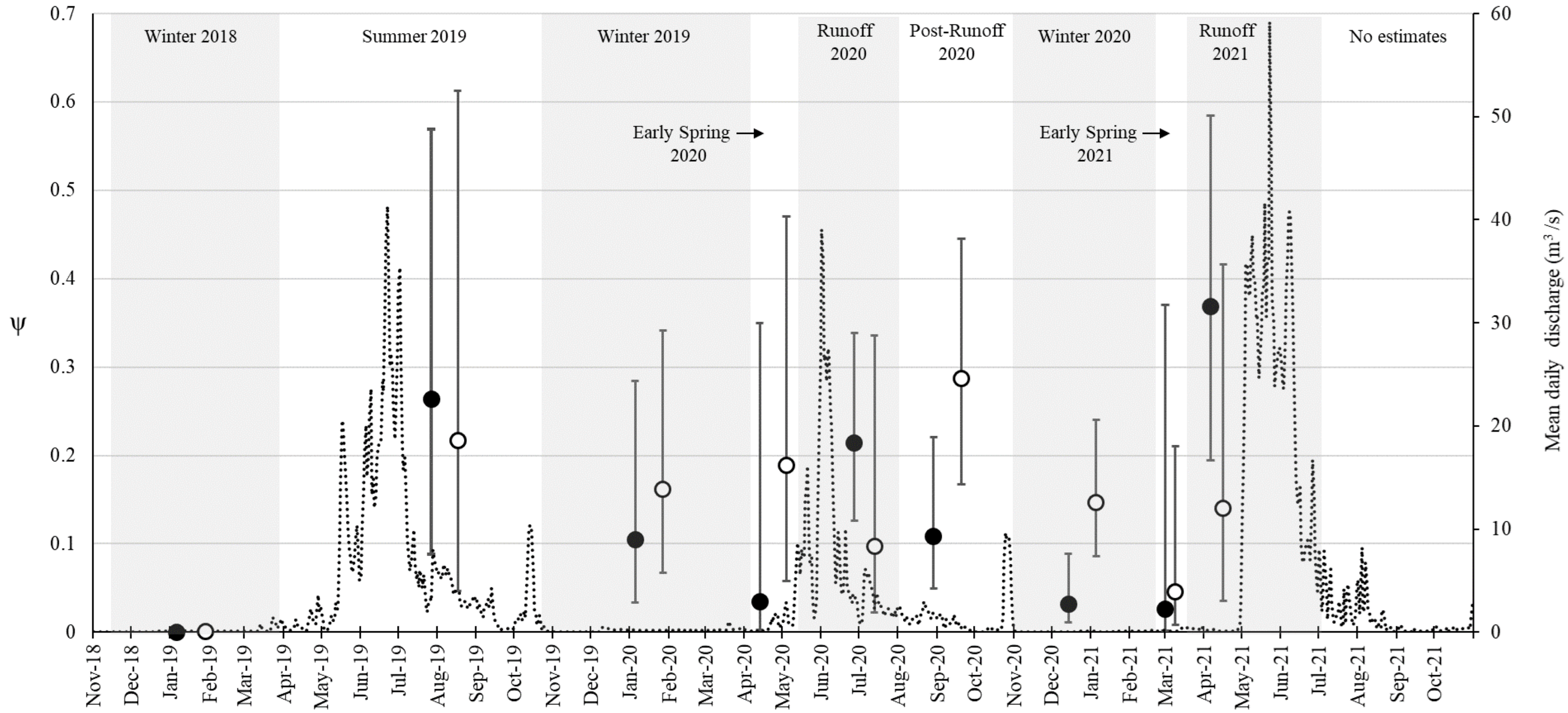

Figure 23. Seasonal transition probability (ψ, 95% CI) relative to mean daily discharge at USGS gauge 06752280 (Cache la Poudre above Boxelder Creek near Timnath, CO; dotted line) for any tagged fish (all species combined) released in proximity to the Fossil Creek Reservoir Inlet Diversion, which has fish passage (Table 7). Estimates are presented as upstream (filled circles) and downstream (open circles) transition probabilities for each interval. Intervals (see Figure 17) are separated by shading and have the corresponding seasonal period labeled above. Placement of estimates is intended to increase visibility, and their presence in a given interval means fish were exposed to the flow conditions described by the hydrograph during that period. Intervals cover time periods as follows: winter 2018 (November 2018-April 2019), summer 2019 (May-October), winter 2019 (November 2019-March 2020), early spring 2020 (March-April), runoff 2020 (May-July), post-runoff 2020 (August-October), winter 2020 (November 2020-March 2021), early spring 2021 (March-April), and runoff 2021 (May-July). Discharge of 1 m^3/s equals approximately 35 ft^3/s.

Appendix I. Species abbreviations used in appendices II-VI.

Native		*Nonnative*	
BB	Black Bullhead	BC	Black Crappie
BM	Brassy Minnow	BG	Bluegill
CS	Central Stoneroller	BG x GS	Bluegill x Green Sunfish
CR	Creek Chub	BS	Brook Stickleback
FM	Fathead Minnow	BT	Brown Trout
GS	Green Sunfish	CP	Common Carp
ID	Iowa Darter	CT	Cutthroat Trout
JD	Johnny Darter	ES	Emerald Shiner
LD	Longnose Dace	GZ	Gizzard Shad
LS	Longnose Sucker	LM	Largemouth Bass
LS x WS	Longnose x White Sucker	MW	Mountain Whitefish
OS	Orangespotted Sunfish	PM	Pumpkinseed
PK	Northern Plains Killifish	RT	Rainbow Trout
PT	Plains Topminnow	SB	Smallmouth Bass
RS	Red Shiner	WE	Walleye
SS	Sand Shiner	WM	Western Mosquitofish
WS	White Sucker	YP	Yellow Perch

Appendix II. Species presence combined from sampling completed at sites 2, 4, 8, and 12 (Figure 1) in the Cache la Poudre River between 1993-2021. Refer to Appendix I for species codes.

Species	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21
Native																													
BB				x		x			x	x																			
BM		x																											
CS			x																										
CR	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x		x	x	x	x	
FM	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
GS	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
ID		x				x			x	x									x		x							x	
JD	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x
LD	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
LS	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
LS x WS																								x			x		
OS				x	x	x	x				x																		
PK	x	x																											
PT	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x					x	x				x		
RS										x																			
SS	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x					x	x				x	
WS	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Subtotal	10	12	10	11	10	11	10	9	11	12	10	8	9	9	7	9	9		8	6	6	5	9	8	7	8	8	9	6
Nonnative																													
BC				x	x	x	x			x									x		x								
BG						x	x		x	x							x	x	x		x		x					x	
BG x GS				x					x										x				x				x		
BS								x	x	x		x	x			x	x	x	x	x			x	x	x			x	x
BT	x	x	x	x		x	x	x	X	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
CP	x	x	x	x	x	x	x		X	x	x	x				x		x	x	x	x		x			x	x	x	x
CT																										x			
ES																							x						
GZ									X																				
LM	x	x	x	x	x	x	x	x	X	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
MW								x					x						x	x	x						x		
PM												x																	
RT	x	x	x	x		x	x	x	X	x	x		x				x	x	x	x	x	x	x	x	x	x	x	x	x
SB													x				x			x		x							
WE										x																			
WM										x			x	x					x										
YP		x	x	x				x	X	x	x		x	x			x	x			x		x				x		
Subtotal	4	5	5	7	3	6	6	6	9	10	5	5	8	4	2	4	7	7	10	7	8	4	9	4	4	4	6	5	4
Total	14	17	15	18	13	17	16	15	20	22	15	13	17	13	9	13	16	15	18	13	14	9	18	12	11	12	14	14	10

Appendix III. Relative abundance (% of each species among the total captured) of species at Site 2 (Figure 1) in the Cache la Poudre River from sampling completed between 1993-2017. No sampling was completed in 1993-2000, 2002-2004, 2006-2010, and 2014-2017. Refer to Appendix I for species codes.

Species	01	05	11	12	13
Native					
GS			0.2		
LD		93.1	60.3	70.6	27.5
LS	3.7	4.1	10.4	2.5	15.8
WS	54.1		0.5		
Nonnative					
BT	28.4	2.5	19.4	24.2	42.9
LM	3.7				
MW		0.1	0.2		0.4
RT	10.1	0.2	9.0	2.7	13.6
SB		0.1		0.1	

Appendix IV. Relative abundance (% of each species among the total captured) of species at Site 4 (Figure 1) in the Cache la Poudre River from sampling completed between 1993-2017. No sampling was completed in 2007, 2008, and 2013. Refer to Appendix I for species codes.

Species	93	94	95	96	97	98	99	00	01	02	03	04	05	06	09	10	11	12	14	15	16	17
Native																						
BM		0.0																				
CR		0.1	0.7	0.4	1.7	0.7				1.0	1.5											
FM	1.8	1.1	24.0	1.1	15.8		1.0	0.5					1.1	4.4					2.7	3.4		
GS				0.1						0.3												
JD	3.8	1.5	1.0	0.1	0.7	0.7	0.3	1.8	6.0	9.4	11.2		1.1		7.2	2.2						
LD	88.8	75.2	48.6	73.9	26.9	15.4	44.2	14.8	43.4	48.4	63.4	7.4	32.6	32.7	15.4	46.7	8.2	18.6	2.7	8.3	0.8	7.7
LS	2.6	17.5	20.9	13.6	13.9	7.7	11.0	25.0	13.3	4.9	6.7	11.1	25.3	20.4	4.1	28.3	0.0	2.5	5.4	11.2	0.8	1.8
PT					0.2					0.6												
SS					6.4																	
WS	1.8	4.0	3.7	3.5	34.2	8.4	9.0	10.2	6.4	1.6	3.0	3.7	25.3	6.2	0.5		0.2			4.0	0.8	5.2
Nonnative																						
BG															0.5							
BS									0.3	1.9					1.5		0.3					
BT	0.8	0.4	0.8	5.4		64.3	28.1	40.6	23.6	26.3	9.7	77.8	14.7	30.1	68.2	17.4	60.4	55.1	70.3	60.1	93.6	83.4
CP					0.2																	
ES																				0.3		
LM			0.2	0.3		1.4	0.6	0.3	1.9	0.3				4.4	2.1	1.1	0.0			0.3		
MW								0.3														
RT	0.4	0.1	0.1	0.3	0.0	1.4	5.8	3.1	1.7	2.6	1.5					3.3	30.9	23.7	18.9	12.1	4.0	1.8
SB																		0.1				
WE										0.6												
YP		0.0	0.0	1.1				3.4	3.3	1.9	3.0			1.8	0.5	1.1				0.3		

Appendix V. Relative abundance (% of each species among the total captured) of species at Site 8 (Figure 1) in the Cache la Poudre River from sampling completed between 1993-2017. No sampling was completed in 1997 and 2012-2014. Refer to Appendix I for species codes.

Species	93	94	95	96	98	99	00	01	02	03	04	05	06	07	08	09	10	11	15	16	17
Native																					
CS			0.1																		
CR	4.0	3.8	1.7	2.1	0.4	2.6		0.4	1.2	3.5	1.5	0.3	3.1	0.7		2.1	45.9	7.5	0.2		0.7
FM	30.7	4.3	53.3	27.0	41.9	37.8	1.1	56.1	30.2	34.6	82.7	86.2	46.8	53.3	64.6	71.9	3.1	2.1	0.5	0.2	5.0
GS						0.1		0.2	1.2	3.2	0.4		1.3		0.6	0.1	2.0	0.3	1.1	0.1	0.3
ID																					
JD	1.0	1.3	0.9	4.1	1.5	1.5	0.7	1.0	10.7	12.2	9.9	0.4	2.1	0.7	2.4	5.3	2.0	0.6	1.1	0.7	0.9
LD	33.3	51.7	19.6	44.9	17.9	30.6	95.0	30.5	41.1	9.9	1.1	4.7	29.1	35.5	18.3	3.8	17.3	11.5	47.0	37.1	50.5
LS	12.7	15.9	12.0	5.7	7.2	6.0	0.4	3.1	1.6	1.0	1.1	0.9	2.6		3.9	2.5		8.0	17.1	6.9	10.6
PT	0.6	0.1	0.0			0.1	0.4	0.1		2.9		0.1	0.8		0.1	0.6			0.4	0.7	
SS	1.4	2.6	1.6	0.2	0.1	0.1		0.3	2.7		0.4										
WS	14.1	19.1	9.6	15.4	31.0	20.7	2.2	7.3	2.9	30.8	1.8	7.1	11.4	9.2	9.0	8.3	14.3	52.2	14.9	29.1	7.3
Nonnative																					
BC									0.2									0.6			
BG								0.1	1.2								2.0	0.2	0.0		
BS							0.1					0.1				3.5	3.1	1.6	0.3	0.7	1.2
BT						0.1	0.2	0.4					0.3	0.7	0.6	0.8	9.2	11.7	17.1	24.1	23.0
CP	2.3	1.3	1.3	0.6		0.3		0.5	6.2	0.3	0.4				0.2			3.0			
LM			0.0					0.1	0.8	0.3		0.1	2.6		0.2	0.9		0.3			0.3
PM											0.7										
RT								0.1		0.3								0.2	0.2	0.3	0.3
SB																0.1					
YP										1.0						0.2	1.0		0.1		

Appendix VI. Relative abundance (% of each species among the total captured) of species at Site 12 (Figure 1) in the Cache la Poudre River from sampling completed between 1993-2017. No sampling was completed in 2007. Refer to Appendix I for species codes.

Species	93	94	95	96	97	98	99	00	01	02	03	04	05	06	08	09	10	11	12	13	14	15	16	17
Native																								
BB				0.1		0.2			0.3	0.1														
CR	0.5	1.7	1.8	10.2	3.8	1.4	2.8	5.7	2.8	2.3	3.8	5.7	3.4	4.2	0.1	2.3								
FM	23.6	33.8	34.9	19.8	32.5	12.5	16.6	43.0	19.0	62.7	12.0	24.9	4.3	4.8	3.1	14.2	6.5	4.2	4.1	22.4	7.3	1.3	1.9	58.1
GS	1.0	0.2	0.8	1.1	1.5	4.3	4.4	0.4	1.2	0.1	2.0	1.1	1.1	0.6		0.7	12.0	40.1	24.3	7.5	36.4	16.5	14.3	13.7
ID		0.1				0.5			0.4	0.1								1.4		0.7				
JD	3.7	3.4	2.4	3.2	2.0	7.6	2.7	3.5	2.9	2.4	18.5	6.1	7.7	20.3	0.5	3.8	1.1	0.7	1.4	2.2		5.1	7.4	0.8
LD		0.3	13.0	4.1	0.4	0.9	2.5	2.6	8.8	1.4	15.8	0.8	5.7	10.7	0.0	0.2	1.1	2.8	14.9	1.5	3.6		1.2	4.8
LS	1.5	1.2	4.2	3.2	5.8	0.9	5.9	0.1	1.1	0.1					0.0	0.2	0.0	2.1	12.2	11.2	14.5	12.7	34.1	9.7
LS x WS																							0.4	
OS				0.6	2.7	0.4	0.1				2.0													
PK	3.4	0.1																						
PT	2.9	1.3	1.0	0.3	0.2					0.4	0.2					1.0							0.4	
RS										0.1														
SS	21.6	28.2	4.0	18.6	17.9	3.3	1.0	43.2	30.4	22.0	26.0	34.9	1.1	15.8	93.3	53.1	5.4					1.3		
WS	41.0	29.2	30.9	37.2	32.7	60.5	57.4	1.4	14.6	5.4	8.8	24.1	61.1	34.5	1.2	7.9	37.0	10.6	10.8	35.1	21.8	30.4	33.7	6.5
Nonnative																								
BC				0.1	0.4	0.2	0.3			0.1										5.2				
BG						0.5	1.0											8.5		6.0				
BG x GS				0.1					0.3									0.7				1.3		
BS												1.1			1.7	1.0		1.4	1.4					
BT																0.2		0.7	12.2	1.5	3.6	11.4	5.0	6.5
CP	0.7	0.5	2.4	1.2		0.5	1.5		2.1	0.9	6.5						10.9	8.5	2.7	1.5		11.4		
GZ									12.0															
LM		0.1	4.6	0.1		6.2	3.8	0.1	4.1	2.0	3.4	1.1	7.1	2.8	0.2	15.1	21.7	15.5	10.8	4.5	10.9	5.1	0.4	
RT																0.2	4.3	0.7	5.4			3.8	1.2	
SB																					1.8			
WM										0.1			8.0	6.2				2.1						
YP											0.9		0.3			0.2				0.7				

PROJECT TITLE:

Assessment of Cache la Poudre River fish community response to 2021 flooding

INVESTIGATORS:

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REPORTING PERIOD:

November 2021

SUMMARY:

In November 2021 we replicated fish community and habitat sampling completed at 13 locations (Table 1) in the Cache la Poudre River between autumn 2018 and spring 2021 (Haworth and Bestgen, draft report). This was completed, in part, in response to ash and sediment laden floods in July 2021 associated with the widespread and destructive 2020 Cameron Peak fire. This flood event caused "catastrophic" fish losses in canyon-bound upstream reaches of river (K. Battige, Colorado Parks and Wildlife, Fort Collins, personal communication 2021). Shortly after this event, we observed mortality of fish we previously tagged in our study area (Haworth and Bestgen, draft report), prompting repeated sampling as an

addendum to those efforts to provide insight to the extent of mortality and changes to fish community structure associated with extensive flooding.

Autumn 2021 Sampling

We captured 2,490 fish across sampling events and 13 sites, including 10 native and 9 nonnative species (Tables 1 and 2). Two native species (Longnose Dace, White Sucker) were distributed throughout the study area and captured at all 13 sampling sites. Eight species (five native, three nonnative) were uncommon, represented by fewer than fifteen individuals detected at only one or two sites. Plains Topminnow was the only sensitive native taxa captured during community sampling (Tier I State Species of Greatest Conservation Need), represented by 5 individuals captured at sampling sites just upstream and downstream of the Fossil Creek Reservoir Inlet Diversion (FCRID) and fishway. Species diversity increased in a downstream direction for both native and nonnative species (Figure 1).

Native species were numerically dominant and comprised 63% of all fish captured, with four species accounting for 96% of native taxa: Longnose Dace, White Sucker, Longnose Sucker, and Fathead Minnow (Table 2). Three species comprised 90% of all nonnative fish captured (Brown Trout, Gizzard Shad, and Largemouth Bass), with Brown Trout alone accounting for 67%. Brown Trout were only numerous at upstream sites 2-6, with only eight individuals captured at sites 7-13. Gizzard Shad were numerous just upstream of the FCRID, and presumably entered the river moving upstream through the canal into the river from Fossil Creek Reservoir.

Although native taxa were numerically dominant, nonnative species accounted for most of the total biomass among all fish captured (Table 2). This was primarily due to Brown Trout, which accounted for 45% of the total fish biomass across all sites. Taken together with large-bodied Common Carp, these two species accounted for 73% of the total fish biomass in the study area. Total biomass of Common Carp was estimated with a mean individual adult weight (2,100 g) calculated from a sub-sample of weighed individuals (range 1,350 - 2,900 g). Among native species, large-bodied Longnose Sucker and White Sucker accounted for 93% of all native fish biomass.

Qualitative comparisons between autumn 2021 sampling and that completed from autumn 2018 to spring 2021 (Haworth and Bestgen draft report) indicated reduced fish abundance in autumn 2021, especially for trout, following thunderstorm-produced summer ash flows, a reduction similar to that in autumn 2018 after a fish kill in the river downstream of Lemay Avenue (Figure 2). Qualitative comparison of habitat conditions in each period indicated lower velocity channel margins had higher amounts of fine sediment and ash in autumn 2021 (Figure 3), compared to observations from autumn 2018 to spring 2021.

References

Haworth, M. R., and K. R. Bestgen. Draft report. Fish community composition and movement in the Cache La Poudre River in Fort Collins, Colorado. Final report to the City of Fort Collins Natural Areas Department, Fort Collins, CO, and the Colorado Water Conservation Board, Denver, CO. Larval Fish Laboratory Contribution 226.

Table 1. Information for sampling sites in the Cache la Poudre River including downstream (DS) and upstream (US) coordinates (Easting/Northing, NAD83 UTM Zone 13), corresponding State of the Poudre Report (SOPR) reach number, and site length in meters.

Site #	Site Name	SOPR #	DS, E	DS, N	US, E	US, N	Length (m)
1	Watson Lake	5	485777	4498098	485406	4498985	200
2	Lions Park	6	488137	4496749	488020	4496994	315
3	Upstream of Shields St.	8	491812	4494769	491519	4494951	345
4	Salyer Natural Area	9	492901	4494214	492735	4494392	265
5	Gustav Swanson Natural Area	10	493921	4493488	493764	4493753	310
6	Udall Natural Area	11	494467	4492763	494270	4492919	305
7	Upstream of TRID	12	495993	4491723	495760	4491843	275
8	Downstream of TRID	13	496592	4491994	496374	4492008	355
9	Riverbend Ponds	14	497258	4491473	497047	4491684	310
10	Upstream of FCRID	15	498296	4489858	498127	4489974	215
11	Downstream of FCRID	16	498651	4489760	498472	4489692	280
12	Archery Range	17	499926	4488468	499802	4488724	320
13	Strauss Cabin	18	500022	4487462	500153	4487722	320

*TRID: Timnath Reservoir Inlet Diversion

*FCRID: Fossil Creek Reservoir Inlet Diversion

Table 2: Summary of all species captured at the 13 sites sampled during November 2021 in the Cache la Poudre River in Fort Collins, Colorado, including number of sites present, total number captured, and biomass (kg). Species are separated by native/nonnative status, and listed in descending order of numerical abundance.

Species	# Sites	Sites present	*n*	kg
Native taxa				
Longnose Dace	13	1-13	584	1.4
Longnose Sucker	12	2-13	354	10.2
White Sucker	13	1-13	317	24.8
Fathead Minnow	6	8-13	252	0.6
Green Sunfish	6	8-13	45	0.5
Johnny Darter	4	7,8,10,12	11	<0.1
Creek Chub	2	9,10	5	<0.1
Plains Topminnow	2	10,11	5	<0.1
Sand Shiner	2	12,13	3	<0.1
Black Bullhead	1	10	1	<0.1
Subtotal			1,577	37.6
Nonnative taxa				
Brown Trout	11	1-6,8,9,11-13	612	84.2
Gizzard Shad	1	10	120	2.7
Largemouth Bass	6	8-13	89	1.8
Common Carp	3	10-12	28	51.0
Bluegill	7	7-13	26	1.0
Rainbow Trout	5	1-5	21	7.4
Brook Stickleback	2	6,7	11	<0.1
Smallmouth Bass	1	1	4	<0.1
Black Crappie	2	12,13	2	<0.1
Subtotal			913	148.2
Total			2,490	185.8

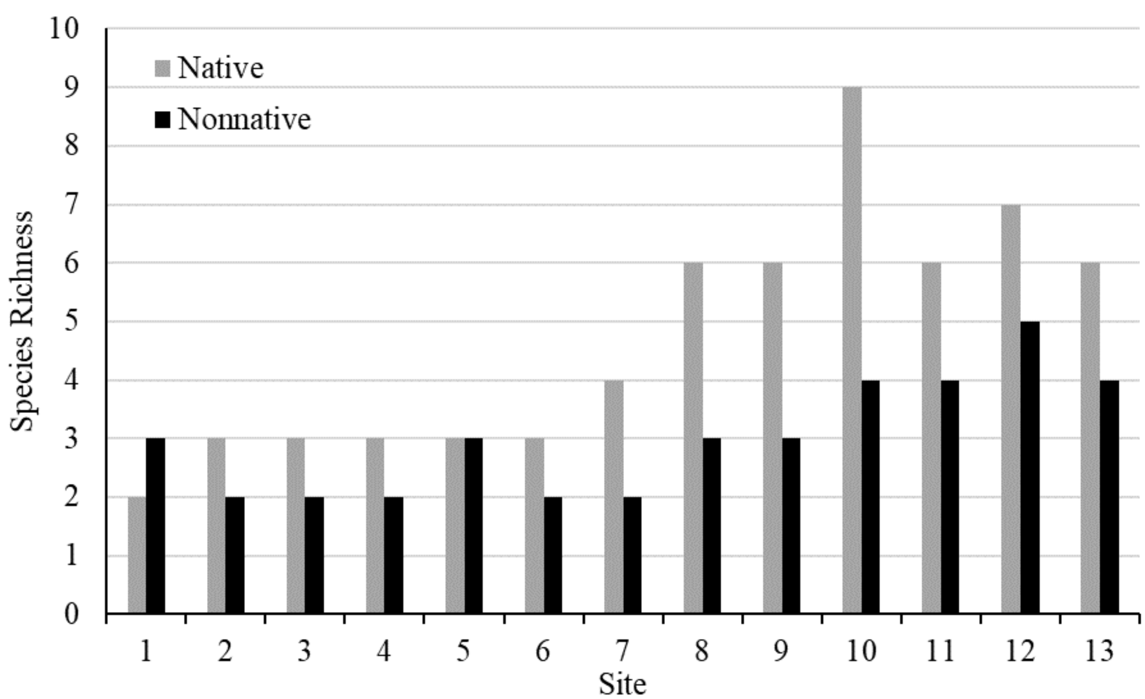

Figure 1. Native and nonnative species richness by sampling site in the Cache la Poudre River, November, 2021.

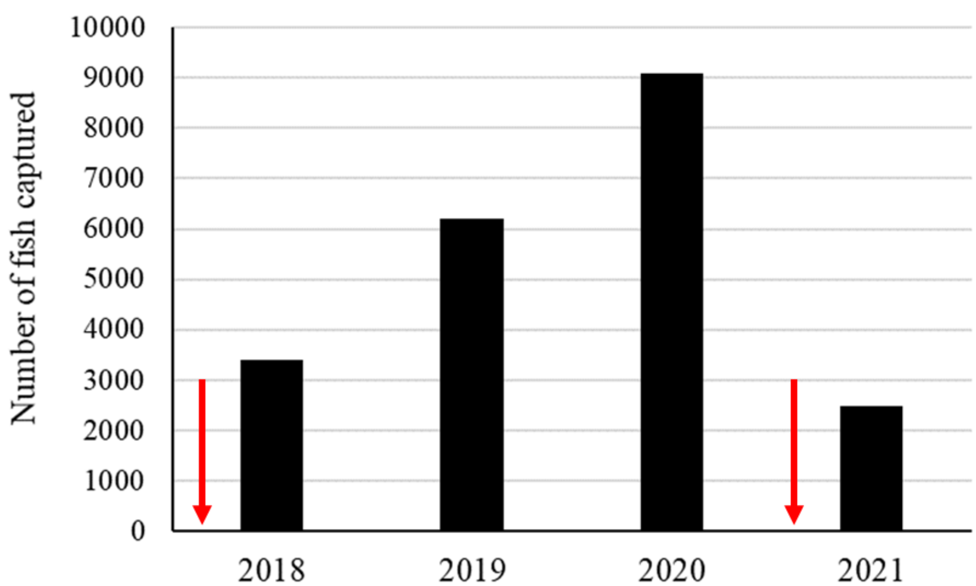

Figure 2. Total number of fish captured at sites 1-13 during autumn sampling in the Cache la Poudre River, 2018-2021. Red arrows indicate the September 2018 fish kill downstream of Lemay Avenue, and the July 2021 ash flows from heavy rains over the 2020 Cameron Peak Fire burn scar.

Figure 3. Fine sediment deposition along channel margins at Site 2 (Table 1) in the Cache la Poudre River, November, 2021.