FISH ASSEMBLAGE RESPONSE TO HABITAT RESTORATION IN ELK SPRINGS CREEK, MONTANA: IMPLICATIONS FOR ARCTIC GRAYLING (*Thymallus arcticus*) RESTORATION

by

Jason William Marsh

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DEDICATION

I dedicate this thesis to my family. To my parents, John and Barb, who raised me to never give up on my dreams; you taught by example, and with love and encouragement. To my brother, Ryan, who inspires me to strive for greatness every day. Words cannot express how grateful I am to not only be your brother, but have you as a best friend.

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ABSTRACT

The abundance and distribution of Arctic Grayling *Thymallus arcticus* in Montana have declined substantially during the past century as a result of habitat degradation and loss. Biologists tasked with conserving Arctic Grayling populations in the Centennial Valley of southwestern Montana implemented two habitat restoration projects to reclaim historical Arctic Grayling migration corridors and spawning habitats in Elk Springs Creek. I used before-after and before-after control-impact (BACI) study designs to evaluate the effects of these habitat restoration projects on physical habitat, water quality, and Arctic Grayling in Elk Springs and Picnic creeks. Because Arctic Grayling were rare in Elk Springs and Picnic creeks, I also examined the effects of restoration on two additional species (Brook Trout *Salvelinus fontinalis* and White Suckers *Catostomus commersonii*) with habitat requirements and life history characteristics similar to those of Arctic Grayling. I used electrofishing to monitor the abundance, biomass, and size distribution of each species before the restoration in 2016, and after the restoration during 2017 and 2018. A PIT-tag detection network monitored the seasonal movements of Arctic Grayling, Brook Trout, and White Suckers from spring 2016 through autumn 2018. In situ data loggers measured summer stream temperatures and dissolved oxygen concentration in expected fish migration corridors both before and after restoration. The abundances and biomasses of Arctic Grayling and White Suckers were similar before and after restoration. However, Brook Trout abundance and biomass increased significantly in the restored (impacted) reaches relative to the unrestored (control) reaches two years after habitat restoration. The size-class distributions of Arctic Grayling and Brook Trout broadened after restoration. Movements of Arctic Grayling, Brook Trout, and White Suckers among unique habitat segments in Elk Springs and Picnic creeks increased after restoration, but pre-restoration movement data was sparse and limited inference. Following channel restoration, summer stream temperatures decreased, and dissolved oxygen concentration increased and equilibrated. Physical habitat improved (i.e., fine sediments decreased, and depth, percentage of pools, and gravels increased) in restored historical Arctic Grayling spawning areas. I thereby showed that channel reconnection and spawning habitat restoration can substantially improve water quality and physical habitat. However, the restoration measures implemented in Elk Springs Creek affected my target species disproportionately.

INTRODUCTION

Humans have altered the form and function of many aquatic ecosystems. Anthropogenic manipulations of riverine systems have altered stream morphology, flow dynamics, and water quality (Holden 1979). Dams constructed for flood control, irrigation, and recreation have fragmented stream habitats, thereby reducing or eliminating longitudinal connectivity and disrupting fish migrations among feeding, spawning, and wintering habitats (Lucas and Baras 2001; Calles and Greenberg 2009), especially of migratory salmonids (Reeves et al. 1995; Morita et al. 2009; Junge et al. 2014). Moreover, fragmentation of stream habitats has isolated salmonid populations, thereby increasing their risk of local extinction (Caughley 1994; Fausch et al. 2009). Dams, channelization of rivers, and water losses from irrigational withdrawals can increase stream temperature and reduce dissolved oxygen concentration by reducing peak flows and preventing rejuvenation of the aquifer structure (Lucas and Baras 2001; Poole and Berman 2001). Stream temperature increases and reductions in dissolved oxygen concentration can reduce access to previously suitable stream habitats, and therefore result in habitat loss (Isaak et al. 2010; Hallock et al. 1970). These habitat losses are exacerbated by fragmentation of large habitat patches and decreases in connectivity among remaining stream habitats, and ultimately threaten the persistence of salmonid populations (Rieman et al. 2007; Isaak et al. 2010).

Stream and river restoration can ameliorate the effects of human disturbance if habitats are reclaimed and connectivity and water quality and quantity are restored

(Bernhardt et al. 2005; Shirey et al. 2016). Methods for reconnecting fragmented habitat for salmonids include removal of fish barriers, installation of fish ladders, and stream rerouting. For example, the removal of the Elwha and Glines Canyon dams on the Elwha River allowed several species of salmon to expand into and reoccupy fluvial habitat above the two dams (Hansen et al. 2016). Salmon reoccupied upstream habitats by ascending a fish ladder on Pitlochry Dam on the Tummel River in Perthshire, Scotland (Gowans et al. 1999). Several salmonid species reoccupied freshwater habitats after hydrologic connectivity was restored in the Grays River tidal freshwater system of Washington (Roegner et al. 2010). Excavation of a 3.4-km artificial stream in the Barrenlands region of the Northwest Territories, Canada, which was constructed to increase habitat connectivity, allowed adult adfluvial Arctic Grayling to establish spawning runs in the newly created channel (Jones et al. 2003).

Methods for reclaiming stream habitats and water quality and quantity for salmonids include channel reconfiguration, spawning gravel additions, and reestablishment of native vegetation along stream banks. Channel reconnection and remeandering increased water depths, improved riparian vegetation, and increased the abundance of salmonids in two reaches of the Kushiro River in Japan (Nakamura et al. 2014). Chinook Salmon (*Oncorhynchus tshawytscha*) used restored spawning habitats in the Mokelumne River of California after habitat enhancements added gravels and reduced the amount of fine (diameter $\leq$ 8 mm) stream substrates, increased average water velocities and dissolved oxygen concentrations, and equilibrated ambient stream temperatures (Merz and Setka 2004). Channel remeandering and restoration of habitat increased the biomass of trout and broadened the size distribution of trout in a restored reach of Juday Creek, a 3rd-order tributary of the St. Joseph River in Indiana (Moerke and Lamberti 2003). Additionally, channel remeandering and restoration of habitat increased abundance and distribution of native bass species in Juday Creek (Shirey et al. 2016). Trout abundance and biomass increased after log drop structures were installed in six northern Colorado streams, which increased pool volume, decreased current velocity, and increased depth and cover (Riley and Fausch 1995).

In all restorations, the persistence and productivity of colonizing populations are dependent on alignment of the physical and ecological characteristics of the new habitats with the life history and habitat requirements of the target species. Therefore, identifying these requirements before implementing any habitat restoration is imperative (Hansen et al. 2016).

The Arctic Grayling (*Thymallus arcticus*) is a salmonid that was historically abundant in the Upper Missouri River and its tributaries upstream from the Great Falls of the Missouri River (Henshall 1907; Nelson 1954; Vincent 1962; Kaya 1990). However, the only remaining indigenous populations in Montana reside in the upper Big Hole and Red Rock (Centennial Valley) drainages of southwestern Montana (Nelson 1954; Liknes and Gould 1987; Kaya 1992; Mogen 1996). Arctic Grayling inhabiting the Big Hole watershed represent the only remaining native fluvial (i.e., using riverine habitats exclusively) population in Montana (Kaya 1991). Arctic Grayling in the Centennial Valley are the only remaining native adfluvial population in Montana, generally occupying lentic environments in Upper Red Rock Lake, but spawning in cold, clear tributaries to the lake (Nelson 1954; Kaya 1992; Mogen 1996; Davis 2016). Historically, Arctic Grayling spawned in 12 streams in the Centennial Valley (Henshall 1907; Mogen 1996; Nelson 1954), but their abundance and distribution declined over the past 100 years (Nelson 1954; Kaya 1990; Mogen 1996; Peterson and Ardren 2009). Presently, Red Rock Creek is the only Upper Red Rock Lake tributary supporting a substantial run of spawning Arctic Grayling, with spawner abundance estimates ranging from 122 individuals in 1995 to 214 individuals in 2016 (Paterson 2013; Warren et al. 2016). The cumulative effects of dam installation, stream rerouting, irrigation and associated entrainment, elevated stream temperatures resulting from water withdrawals, livestock grazing, beaver dams, and interactions with nonnative trout species appear to be associated with decreased Arctic Grayling abundance in the Centennial Valley (Vincent 1962; Unthank 1989; Kaya 1992; Peterson and Ardren 2009). Additionally, livestock grazing along Upper Red Rock Lake tributaries is thought to have increased sediment transport to Upper Red Rock Lake thereby reducing water depths and available habitat in Upper Red Rock Lake; however, this hypothesis remains controversial (Gangloff 1996). Reduction of livestock grazing and reintroduction of native vegetation along stream banks in the Centennial Valley was implemented to bolster Arctic Grayling numbers in the Centennial Valley. However, these management actions have not led to an increase in numbers of spawning Arctic Grayling in Upper Red Rock Lake tributaries.

Elk Springs Creek, a tributary to Upper Red Rock Lake, supported a substantial Arctic Grayling spawning run until 1909 (Henshall 1907; Dean 1910), when the number of Arctic Grayling spawning therein decreased significantly (Dean 1910; Nelson 1954;

Kaeding and Boltz 2004). Elk Springs Creek was reportedly diverted into Swan Lake by duck hunters in 1907 (Figure 1), potentially creating a physical or chemical fish barrier or both (Henshall 1909). Swan Lake is shallow (< 1 m) and is probably inhospitable to Arctic Grayling, at least seasonally, because of elevated water temperatures or anoxia or both in summer.

Fishery managers tasked with preserving Arctic Grayling populations in the Centennial Valley made several attempts to restore Arctic Grayling in Elk Springs Creek. Remote site incubators were used to reestablish a population of Arctic Grayling (RSIs; Kaeding and Boltz 2004), and McDonald Pond, an impoundment located downstream of historical spawning sites, was removed in 2010 (Figure 1) (G. D. Boltz [retired], USFWS, personal communication). McDonald Pond inundated historical Arctic Grayling spawning habitat and blocked their movement (G. D. Boltz, personal communication). Sub-adult Arctic Grayling were occasionally detected in Elk Springs and Picnic creeks after RSI use began in 1999 (Figure 1) (B. West [retired], USFWS, personal communication; my unpublished data). However, no adults returned to Elk Springs Creek to spawn and the fate of the RSI-produced Arctic Grayling is unknown.

Red Rock Lakes National Wildlife Refuge managers implemented two additional habitat restoration projects in autumn 2016 to improve water quality and increase access to Arctic Grayling spawning habitat in Elk Springs Creek (Figure 1). Elk Springs Creek was rerouted into its historical channel to bypass Swan Lake, and efforts aimed at restoring historical spawning habitats near the head of Elk Springs Creek were completed in autumn 2016 (M. Jaeger, Montana Fish, Wildlife and Parks, personal communication).

Fireline explosives were used to excavate deposited materials and vegetation along the historical stream channel. Fireline explosives were deposited in a 40-cm-deep by 60-cm-wide trench prior to detonation to create stream channel dimensions suitable for containing anticipated stream flows (B. West, personal communication). Additionally, spawning habitat restoration measures implemented near the head of Elk Springs Creek in autumn 2016 consisted of mechanically removing sediment deposited by McDonald Pond, importing spawning gravels where needed (because trout spawn in riffle habitats where fine sediments are minimal and gravel substrates are abundant; Hunter 1991), restoring natural channel dimensions and sinuosity by mechanically configuring a pool-riffle sequence and adding an additional 103 m of stream, and increasing cross-sectional stream velocities to prevent deposition of fine sediment. Sinuous channels are important for spawning trout because cross-sectional velocities are greater in riffles and slower in pools, thus allowing sediment to be transported from riffle habitats to deeper pool habitats to clean the gravel for trout attempting to build redds (Hunter 1991). The restored stream reach was mechanically constructed by narrowing channels to ultimately reduce width-to-depth ratios and increase depth and cross-sectional stream velocities, and by fortifying stream banks using salvaged wetland sod mats and backfilling existing soils behind banks (M. Jaeger, personal communication). Wetland sod mats incorporate riparian vegetation that can stabilize stream banks and create additional overhead cover for trout (Hunter 1991).

My goal was to evaluate the effects of these habitat reconnection and restoration projects on Arctic Grayling in Elk Springs Creek using both before-after and before-after control-impact (BACI) study designs. Because Arctic Grayling were rare in Elk Springs Creek, I also examined the responses of Brook Trout (*Salvelinus fontinalis*) and White Suckers (*Catostomus commersonii*) to the habitat and connectivity restoration in the creek. Brook Trout and White Suckers also migrate between Upper Red Rock Lake and its tributaries to spawn (Nelson 1954; Mogen 1996; Boltz 2000; A. T. Gilham, USFWS, unpublished data). Because these fishes are probably also affected by the factors perceived to be limiting Arctic Grayling movement, abundance, and distribution in Elk Springs Creek, I posited that they may serve as effective surrogates for Arctic Grayling and supplement my evaluation of the responses of Arctic Grayling to the habitat restoration measures implemented in Elk Springs Creek.

My specific objectives were to determine the effects of restoration on (1) habitat conditions in Elk Springs Creek; (2) seasonal movements of the three fish species in Elk Springs and Picnic creeks; and (3) density, biomass density, and size of each species in Elk Springs and Picnic creeks. I hypothesized that restoration would (1) improve stream habitat conditions in Elk Springs Creek for these species; (2) increase access of each species to spawning and foraging habitats; and (3) increase the density, biomass density, and size of individuals of each species. Meeting these objectives allowed me to assess the consequences of spawning habitat restoration and channel reclamation on Arctic Grayling and other fishes in Elk Springs and Picnic creeks.

STUDY AREA

Upper Red Rock Lake and its tributaries are located in the Centennial Valley of southwestern Montana about 64 km west of Yellowstone National Park (Figure 2). The valley is 80 km long and 13 km wide. The south side of the valley is bordered by the Centennial Mountains, which form the Continental Divide (Nelson 1954). The north side of the valley is bordered by the Gravelly and Snowcrest mountains (Nelson 1954). Red Rock Lakes National Wildlife Refuge (RRLNWR) was established in 1935 and protects more than 33,000 ha of the Centennial Valley (Figure 2). The minimally developed valley floor within RRLNWR lies at an elevation of 2,010 m and is dominated by sagebrush grasslands (*Artemisia* spp. and *Festuca* spp.) and wetlands with an abundance of willows (*Salix* spp.) (Nelson 1954).

Elk Springs Creek is the second largest tributary to Upper Red Rock Lake (in terms of discharge) and lies within the boundaries of RRLNWR (Figures 2 and 3). Elk Springs Creek begins as two springwater upwellings below Elk Lake on the northeast side of RRLNWR. Picnic Creek drains Widgeon Pond and meanders about 0.5 km before joining Elk Springs Creek about 1 km below the headwaters of Elk Springs Creek. Prior to restoration, Elk Springs creek flowed 9.5 km from the confluence of upper Elk Springs Creek and Picnic Creek to Swan Lake, and then flowed 0.7 km from the outlet of Swan Lake to Upper Red Rock Lake. Presently, Elk Springs Creek flows 10.5 km from the confluence of upper Elk Springs and Picnic creeks to Upper Red Rock Lake. Upper Red Rock Lake has an area of 893 ha and a maximum depth of about 2 m. The primary substrate in Swan and Upper Red Rock lakes is peat. Aquatic vegetation is abundant throughout both lakes (Nelson 1954). Upper Red Rock Lake and Lower Red Rock Lake are connected by 11 km of river marsh. Lower Red Rock Lake has an area of 456 ha and a maximum depth of about 0.5 m (Mogen 1996; Nelson 1954). The Red Rock River drains Lower Red Rock Lake and flows west for 19 km before emptying into Lima Reservoir.

Study Reaches

I sampled physical habitat conditions in 11 reaches and fish in 9 of those reaches in Elk Springs Creek and its tributaries. These study reaches varied in length (113–952 m; Table 1) and were located in the West and East forks of Elk Springs Creek, the mainstem of Elk Springs Creek, and Picnic Creek (Figure 3). The remoteness and topography of the middle 7.2-km section of Elk Springs Creek precluded sampling there. The East and West fork, Mainstem 1, and Picnic Creek reaches were selected because of the historical spawning sites of Arctic Grayling there, the presence of suitable spawning gravels, or both. I assigned a unique number to all possible 200-m stream reaches in the 3-km section of Elk Springs Creek below Mainstem reach 1 and randomly selected Mainstem reaches 2, 3, 4, and 5 before I knew when and where the upper Elk Springs Creek habitat restoration would occur. Three reaches (Historical Channel, Former Diversion, and Mainstem 6) in the lower section of Elk Springs Creek were selected to determine if reclamation of the Historical Channel improved physical habitat conditions and increased fish density. However, I was unable to sample fish in the Former Diversion and Mainstem 6 reaches because excessive fine sediment in these reaches precluded safe wading. Additionally, the remoteness of the Historical Channel, Former Diversion, and Mainstem 6 reaches prevented me from attempting or completing all planned fish surveys.

Two restored reaches (Mainstem 1 and 2) located below the confluence of the West and East forks were characterized by straight runs, sand and silt substrates, minimal overhanging vegetation, and shallow stream depths (< 0.5 m) prior to restoration. The Mainstem 1 and 2 reaches were restored to recreate historical Arctic Grayling spawning habitats that were degraded after the creation and subsequent removal of McDonald Pond. Restoration applied to Mainstem reaches 1 and 2 in autumn 2016 created a pool-riffle sequence, reduced stream widths, increased stream depths, and added gravels to the streambed. Moreover, native grasses were planted to stabilize the streambanks of these restored reaches. The third restored reach (Historical Channel) was located 10 km downstream of Mainstem reach 2. Elk Springs Creek was redirected into the Historical Channel in autumn 2016 to reclaim historical stream habitats and bypass Swan Lake and a 0.6-km-long section of Elk Springs Creek (Former Diversion) located upstream of Swan Lake. Moreover, Elk Springs Creek was redirected into the Historical Channel to improve connectivity for Arctic Grayling attempting to migrate between spawning habitats in upper Elk Springs Creek and foraging habitats in Upper Red Rock Lake. Stream habitats in the Historical Channel were characterized by a pool-run sequence, sand and silt substrates, abundant overhanging vegetation, and stream depths ranging from 0.2 to 1.3 m. Two unrestored reaches (West Fork and East Fork) upstream of the restored Mainstem 1 and 2 reaches were characterized by straight runs, gravel and cobble substrates, shallow stream depths (< 0.5 m), and moderate amounts of overhanging vegetation. Picnic Creek, an unrestored tributary to Elk Springs Creek, was characterized by a pool-run sequence with moderate amounts of overhanging vegetation, stream depths ranging from 0.1 to 1.2 m, and sand, silt, and gravel substrates. Five unrestored reaches (Mainstem 3, 4, 5, and 6, and Former Diversion) were located downstream of the restored Mainstem 1 and 2 reaches. Mainstem reach 3 was a straight run with sand and silt substrates, minimal overhanging vegetation, and shallow stream depths (< 0.5 m). Mainstem reaches 4 and 5 were pool-run sequences with sand and silt substrates, minimal overhanging vegetation, and stream depths ranging from 0.1 to 1.1 m. The Former Diversion was characterized by a straight channel with stream depths ranging from 0.1 to 1.0 m, minimal overhanging vegetation, and sand and silt substrates. Mainstem reach 6 was located downstream of Swan Lake, and was characterized by a pool-run sequence, stream widths of about 10 m, sand and silt substrates, minimal overhanging vegetation, and shallow stream depths (< 1 m).

Fish Movement and Water Quality Monitoring Sites

I selected four sites in Elk Springs Creek and one in Picnic Creek to monitor fish movements (Figure 3). Additionally, I selected two sites in Elk Springs Creek and one in Picnic Creek to monitor water quality (Figure 3). Fish movement and water quality monitoring sites were purposely installed in habitats I expected my target species to move through when migrating between foraging habitats in Upper Red Rock Lake and spawning habitats in upper Elk Springs Creek and Picnic Creek.

Ecology of the Study Species in the Study Area

Arctic Grayling migrate among a variety of habitat types to complete their life cycles in the Centennial Valley (Henshall 1907; Nelson 1954; Mogen 1996). Arctic Grayling mature at age two or three in the Centennial Valley. Adults move upstream to spawn in early to late May when stream discharges and temperatures increase (Mogen 1996), and spawn primarily 7 to 15 km upstream of Upper Red Rock Lake in Red Rock Creek (Mogen 1996; A. T. Gilham, USFWS, personal communication). Downstream movements of spawners to Upper Red Rock Lake occur in late May through early June (Mogen 1996). Stream residency averages 17.7 days (SD = 11.2) by females and 34.8 days (SD = 10.2) by males; however, some adult Arctic Grayling occupy Red Rock Creek throughout the summer (Mogen 1996). Juveniles emerge from gravels in early to mid-June in Red Rock Creek, and outmigrate to Upper Red Rock Lake in mid-July to late-August (Mogen 1996). Arctic Grayling exhibit a physiological and behavioral stress response to dissolved oxygen concentrations < 4 mg/L (Davis 2016). The upper incipient lethal temperature (UILT) for Arctic Grayling is 23 °C for fish acclimated from 8.4 °C to 16 °C, and 25 °C for fish acclimated to 20 °C (Lohr et al. 1996).

White Suckers are spring spawners that can undergo extensive migrations between foraging and spawning habitats (Mogen 1996; Doherty et al. 2010; Jones and Mackereth 2016), which are located in fast-flowing tributary streams (Geen et al. 1966;

Scott and Crossman 1973; Doherty et al. 2010). White Suckers migrate from Upper Red Rock Lake into its tributaries to spawn in late May (Mogen 1996; Boltz 2000; A. T. Gilham, unpublished data), but no additional information describing the movements and spawning habitats of White Suckers, or environmental conditions during their spawning migration in the Centennial Valley exists. Elsewhere, White Suckers moved from Big Beaver Lake, Michigan, into its tributaries to spawn from early May to early June, and peak spawning activity occurred in mid-May when stream temperatures ranged from 8 to 12 °C (Armichardy 2008). White Suckers traveled up to 40 km to spawn (mean = 9.2 km, SD = 11.0 km) in the Saint John River, New Brunswick (Doherty et al. 2010). White Suckers typically spawn in riffles where depths range from 20 to 25 cm (Twomey et al. 1984). White Suckers avoided areas where dissolved oxygen concentration was ≤ 2.4 mg/L (Dence 1948); however, specific information on adult and juvenile dissolved oxygen requirements is generally lacking (Twomey et al. 1984). White Suckers can tolerate warm water; the critical thermal maximum for White Suckers is about 31 °C (Reutter and Herdendorf 1976).

Stream-resident, lacustrine (i.e., complete their life cycle within a lake), and lacustrine-adfluvial life histories are present among Brook Trout (Northcote 1997; Huckins et al. 2008). Both stream resident and lacustrine-adfluvial life histories are present in the Upper Red Rock Lake system (Boltz 2000). Adfluvial Brook Trout migrate from Upper Red Rock Lake into its tributaries to spawn in autumn, and peak spawning activity typically occurs from early to mid-October (Boltz 2000). No additional information describing the movements and spawning habitats of Brook Trout, or environmental conditions during their spawning migration in the Centennial Valley exists. Elsewhere, large (≥ 300 mm) adfluvial Brook Trout moved upstream from Lake Superior into the Salmon Trout River, Michigan, from the end of July through early November to spawn, and peak spawning activity occurred from September through October (Huckins and Baker 2008). Brook Trout can move long distances to reach suitable foraging and spawning habitats (Rodriguez 2002; Petty et al. 2012). For example, Brook Trout moved as much as 2,000 m in two, high-elevation (> 2,700 m) Colorado streams, and movements to foraging habitats were most common in late spring near the end of snowmelt runoff and again during mid-September to spawning habitats (Gowan and Fausch 1996). Brook Trout prefer to spawn in upwelling areas where gravels are abundant and fine substrates are minimal (Smith 1947; Raleigh 1982). Additionally, optimum dissolved oxygen levels for Brook Trout are not well documented, but appear to be ≥ 7 mg/L at temperatures < 15 °C and ≥ 9 mg/L at temperatures ≥ 15 °C (Raleigh 1982). The UILT for Brook Trout is 24.5 °C (McCormick et al. 1972).

METHODS

Stream Habitat

I used a transect method to characterize physical habitat conditions in seven reaches (East Fork, West Fork, and Mainstem 1, 2, 3, 4, and 5) during the summer of 2016 (before restoration), two reaches (Mainstem 1 and 2) during the summer of 2017 (after restoration), one reach (Picnic Creek) during the summer of 2018, and three reaches (Historical Channel, Former Diversion, and Mainstem 6) during the autumn of 2018 (Figure 3; Table 2). I wanted to determine physical habitat in the Picnic Creek, Former Diversion, and Mainstem 6 reaches before restoration, and physical habitat in East Fork, West Fork, and Mainstem 3, 4, and 5 reaches after restoration, but was unable to because of time constraints (Table 2). Bank-full widths were measured at transects located perpendicular to stream flow at 10-m intervals if reach lengths were less than or equal to 500 m, at 30-m intervals if reach lengths were between 500 m and 900 m, and at 80-m intervals if reach lengths were greater than or equal to 900 m. Stream depth and substrate size were measured along each transect at 0.2-m intervals if stream widths were less than 5 m and at 0.5-m intervals if stream widths were greater than 5 m. Substrate was categorized into 4 size classes ranging from 2 to 180 mm using a gravelometer (Wildco Supply, Buffalo, New York), and with a meter stick to measure particles greater than 180 mm. Additionally, substrate particles less than 2 mm were visually assessed if they could easily pass through the 2-mm slot on the gravelometer. One person wading in the stream picked up the first substrate particle touched with the tip of their finger in front of their boot at each interval along a transect, with eyes averted to reduce sampling bias. The number of transects and distances between intervals along each transect at which substrate particles were collected were modified from the Wolman pebble count method (Wolman 1954) to acquire a random sample of particles throughout each reach while reducing sampling time; at least 100 substrate particles were measured at each reach. Substrate size categories (Sestrich et al. 2011) were fines (< 2 mm), gravel (2-64 mm), cobble (64-256 mm), and boulder (> 256 mm). I also measured the dimensions of all large (≥ 1 m long × ≥ 15 cm in diameter) woody debris in each reach. I identified and recorded the habitat type that was bisected by each cross-stream transect to determine the proportions of pool, riffle, and run habitats at each reach.

Two temperature loggers were deployed in Elk Springs Creek and one temperature logger was deployed in Picnic Creek to monitor stream temperatures hourly in expected fish migration corridors (Figure 3). Temperature loggers (Onset Computer Corporation, Bourne, Massachusetts; HOBO U22-001) were installed at the Upper Elk Springs Creek (Upper ESC) and Picnic Creek stations in June 2015 and at the Mainstem 6 station in July 2015 (Figures 3 and 4). The temperature logger installed at the Mainstem 6 station was replaced with a temperature and DO logger (Onset; HOBO U26-001) in June 2016. The temperature and DO logger installed at the Mainstem 6 station was periodically removed for membrane replacement and calibration, which resulted in data gaps (Figure 4).

A dissolved oxygen concentration (DO) logger (Onset; HOBO U26-001) was installed to monitor DO hourly in an expected fish migration corridor in Elk Springs

Creek downstream from Swan Lake (Figure 3). Dissolved oxygen concentration was measured at the Mainstem 6 station from June 1, 2016, to October 4, 2018 (Figures 3 and 4). The DO logger installed at the Mainstem 6 station was periodically removed for membrane replacement and calibration, which resulted in data gaps (Figure 4).

Fixed PIT (Passive Integrated Transponder) Interrogation Stations

A network of fixed PIT interrogation stations was placed throughout Elk Springs and Picnic creeks to determine the seasonal movements of PIT-tagged Arctic Grayling, White Suckers, and Brook Trout (Figure 3). Passive integrated transponder telemetry is popular for monitoring fish movements and habitat use in small streams (Prentice et al. 1990; Ritter 2015; Roussel et al. 2000; Teixeira and Cortes 2007). I installed three PIT interrogation stations throughout Elk Springs Creek and one in Picnic Creek in spring 2016 (Figures 3 and 5). Additionally, one PIT interrogation station was installed in the Historical Channel after Swan Lake and the Former Diversion were bypassed in autumn 2016 (Figures 3 and 5). Passive integrated transponder tag interrogation stations were purposely installed in locations I expected my target species to move through when migrating between foraging habitats in Upper Red Rock Lake and spawning habitats in upper Elk Springs Creek and Picnic Creek.

Passive integrated transponder tag interrogation stations consisted of a PIT-tag reader (Oregon RFID, Portland, Oregon; multi-antenna HDX reader), two stream-width antennas, and a tuning capacitor that accompanied each antenna (Oregon RFID, standard remote tuner board). Each station was powered by two 12-V marine deep-cycle batteries connected in a parallel circuit. Batteries were charged by two 80-W solar panels connected in a series circuit. Solar controllers (Morningstar, Newtown, Pennsylvania; Sunsaver MPPT 15-L) were used to maximize energy harvest from the solar panels and provide load control to prevent excessive battery discharge. I installed vertically oriented, swim-through PIT-antennas at most stations to maximize the probability of detecting PIT-tagged fish (Connolly et al. 2008; Zydlewski et al. 2006). Swim-through antennas could be used in my study area because of infrequent spring run-off events and relatively stable flow conditions in Elk Springs and Picnic creeks; however, I used a pass-over antenna design at the Mainstem 6 station because this section of stream would occasionally freeze over during winter months; ice can dislodge antennas. Paired antennas at each site were spaced about 3 m apart to determine the direction of fish movement and prevent antenna interference (Armstrong et al. 1996; Lucas et al. 1999; Ritter 2015). Antennas were made of fine-stranded power cable or speaker wire (Absolute USA, Los Angeles, California; 4 to 12 AWG). Antennas were tuned until the maximum read range (i.e., the maximum distance from the antenna at which PIT-tags can be successfully interrogated) was acquired by measuring inductance and adjusting capacitors on the tuning boards accordingly (Ritter 2015). Passive integrated transponder tag interrogation stations were visited every 2 to 3 weeks to download PIT-tag detection histories. I evaluated PIT-tag reader and antenna efficiency during each site visit and performed maintenance if necessary.

PIT interrogation stations were operated in some combination from spring 2016 to autumn 2018, primarily during spring, summer, and autumn (Figure 5). Inclement weather and topography associated with PIT interrogation station locations prevented me from visiting my PIT interrogation stations for maintenance purposes during winter, which resulted in data gaps (Figure 5). Additionally, the PIT-tag reader installed at the Former Diversion station was relocated to the Historical Channel station in April of 2017 after the PIT-tag reader installed at the Historical Channel station was damaged by water (Figure 5). Finally, animals occasionally damaged equipment associated with PIT interrogation stations, which resulted in data gaps (Figure 5).

PIT Tagging

Arctic Grayling (N = 64), Brook Trout (N = 1,278), and White Suckers (N = 312) were captured and tagged with half-duplex 12- or 23-mm long PIT tags (Biomark, Boise, Idaho) in Elk Springs and Picnic creeks. I tagged fish in Picnic Creek during May 2015 to 2018, and October 2016 to 2018 (Figure 3; Table 3). I tagged fish in the East and West fork and Mainstem 1, 2, 3, 4, and 5 reaches from 2016 to 2018 during May and October, and in the Historical Channel during May 2017 and 2018 after Swan Lake and the Former Diversion were bypassed (Figure 3; Table 3). Fish were not tagged in the Historical Channel during October 2017 and 2018 because of time constraints (Table 3). Fish were also tagged in the East and West fork and Mainstem 1, 2, 3, 4, and 5 reaches in July 2018 (Table 3). Fish were not collected for tagging in Picnic Creek or the Historical Channel in July 2018 because maximum daily water temperatures exceeded 17 °C (Table 3), which in combination with electrofishing would have stressed fish (Columbia Basin Fish and Wildlife Authority 1999).

Fish were collected using a backpack Smith-Root (Vancouver, Washington) LR-20B electrofisher or a boat-based Smith-Root VVP-15B electrofisher. I used a boat-based electrofisher to collect fish in the Picnic Creek, Mainstem 4 and 5, and Historical Channel reaches because stream depths were occasionally deeper than 1 m and could not be sampled with the backpack electrofisher. Electrofishers were operated at voltages of 400 to 600 V DC, frequencies of 30 to 60 Hz, and pulse widths of 3 to 6 µsec to maximize capture probability while minimizing injury to fish (Rosenberger and Dunham 2005). Backpack electrofishing passes were completed by moving in an upstream direction to limit sediment disturbance, which can reduce capture efficiency. A backpack electrofishing crew consisted of an electrofisher operator, two netters, and a person carrying a perforated bucket in the stream channel below the three other crew members for transporting captured fish. Boat-based electrofishing passes were conducted by moving in a downstream direction to maintain orientation of the boat (i.e., parallel with the stream bank). A boat-based electrofishing crew consisted of 4 to 5 people; one person operated the wand anode, one person held the bow of the boat and waded across the reach holding the boat parallel to the current, and two or three people netted stunned fish with dip nets. The person operating the wand anode during backpack and boat-based electrofishing used a zig-zag pattern to cover as much area as possible, and care was taken to ensure that effort was constant among electrofishing passes.

Fish were held in a perforated holding container located outside of the electrical field following capture. Fish were then placed in an anesthetic solution of tricaine methanesulfonate at a concentration of 30 mg/L in stream water, and monitored until motility ceased (Carter et al. 2011). Fish were measured (nearest mm), weighed (nearest g), and implanted with a PIT tag. A PIT tag was inserted ventrally into the abdominal cavity between the pyloric ceca and the pelvic girdle using a hypodermic needle (Columbia Basin Fish and Wildlife Authority 1999; Davis 2016). Fish that measured 60 to 100 mm long were tagged with 12-mm PIT tags and fish ≥ 100 mm in length were tagged with 23-mm PIT tags (Bateman and Gresswell 2006). All tagged Arctic Grayling were also marked with an alphanumeric visual implant tag inserted in adipose tissue behind the left eye to positively identify them as tagged individuals (Steed 2007). All tagged Brook Trout were also marked by trimming their adipose fins. Trimming was favored over complete removal of the adipose fin to encourage regeneration of the adipose fin (Thompson and Blankenship 1997). Moreover, complete excision of the adipose fin reduces swimming efficiency in turbulent streams because it potentially serves as a flow sensor (Buckland-Nicks et al. 2011). All tagged White Suckers were marked by trimming their right pectoral fins. Fish less than 60 mm long were not tagged and were released immediately after weighing and measuring.

Fish Density, Biomass Density, and Size

I used multiple-pass depletion electrofishing to acquire estimates of fish abundance and biomass in selected portions of Elk Springs and Picnic creeks, before and after habitat restoration. The East Fork, West Fork, Picnic Creek, and Mainstem 1, 2, 3, 4, and 5 reaches were sampled in May 2016 before restoration, and again during May 2017 and 2018 after restoration. I also used multiple-pass depletion electrofishing to determine fish abundances and biomasses during autumn, 2016 to 2018; however, these data were not analyzed because restoration actions were implemented during fish sampling in autumn 2016 and precluded collection of comparable pre-restoration data. Restoration actions probably displaced fish temporarily in the Mainstem 1 and 2 reaches, which would bias estimates of fish abundance and biomass in these reaches and therefore limit my ability to draw conclusions regarding the effects of restoration on fish abundance and biomass. The remoteness and high amounts of sediment associated with the Former Diversion, Historical Channel, and Mainstem 6 reaches prevented me from acquiring depletion estimates of fish abundances there (Table 3).

The assumption of population closure for study reaches was met by (1) blocking the upper and lower ends of all reaches with 6.5-mm mesh block nets before sampling; (2) using two netters during sampling to prevent fish from moving downstream; and (3) conducting all electrofishing passes within 4 hours (White et al. 1982). Three or four electrofishing passes were made in the East Fork, West Fork, and Mainstem 1, 2, and 3 reaches (Table 3). Two electrofishing passes were made in the Picnic Creek, and Mainstem 4 and 5 reaches because of an inability to maintain the downstream block net (Table 3). Moreover, bed scouring beneath the block net occurred after the second electrofishing pass in these reaches because substrate consisted of fine sediments.

Fish were placed in holding containers prior to anesthesia and measurement. The lengths (TL; mm) and weights of all captured fish were measured and recorded after each electrofishing pass. After handling, fish were placed in perforated holding containers located in the stream outside of the sampling reach and released about 50 m below the downstream block net after recovery to avoid further exposure to the electrical field.

DATA ANALYSES

I used both before-after and BACI study designs to evaluate the data. Furthermore, data were analyzed using a BACI study design if both restored (impact) and unrestored (control) sampling areas were measured both before and after restoration. I used a before-after study design if only treated areas were measured both before and after restoration. The statistical computer program R, version 3.6.1, was used to analyze all physical habitat, water quality, fish movement, and fish abundance, biomass, and size data (R Development Core Team 2019). Packages used within program R that are not part of the standard R download are listed with each analysis.

Stream Habitat

Physical Habitat

I calculated mean wetted widths and depths, the percentage of stream length consisting of pools, the amount of large woody debris (pieces/m^2), and the proportion of substrates in each size class (fines, gravel, cobble, boulder) in the Mainstem 1 and 2 reaches and compared these values between 2016 (before restoration) and 2017 (after restoration) to determine if restoration improved physical habitat conditions for the three fish species. Increases in depth, percentage of pools, and amount of large woody debris, and decreases in wetted width and proportion of fine substrates were considered physical habitat improvements (Riley and Fausch 1995; Moerke and Lamberti 2003). I was unable to use a BACI design to evaluate changes in physical habitat between pre- and post-restoration years because I did not determine physical habitat conditions in unrestored (i.e., control) reaches both before and after restoration.

Stream Temperature Change

I used a BACI design (Schwarz 2014) to test the hypothesis that summer (from July 2 through August 31) stream temperatures changed as a result of restoration. The before-restoration period was 2015 and 2016 and the after-restoration period was 2017 and 2018. The Picnic Creek station was the control (unrestored), and the Upper ESC and Mainstem 6 stations were impacted (restored). The effects of restoration on mean maximum daily stream temperatures or the average range of daily stream temperatures (i.e., difference between daily maximum and minimum—a measure of thermal stability) were tested using a linear mixed-effects model with one fixed effect and one random effect. The single fixed effect was constructed based on all unique combinations of sampling station and period (before or after restoration), and the single random effect was constructed based on all unique combinations of sampling station and year. A significant fixed effect would indicate that the relative change in either mean maximum daily stream temperatures or the average range of daily stream temperatures between periods (before versus after restoration) differed between the restored and unrestored stations. The linear mixed-effect model was fitted using the lmer function in the lmerTest package (Kuznetsova et al. 2017) in program R (Schwarz 2014). An ANOVA with a Kenward-Roger approximation of the degrees of freedom was applied to the results of the model to acquire the fixed-effect test using the anova function in the car package (Fox and Weisberg 2019) in program R (Schwarz 2014). Mean maximum daily stream temperature and the average range of daily stream temperature for each period (before versus after restoration) and station were estimated in R using the lsmeans function in the lsmeans package (Lenth 2016). I also calculated the estimated BACI contrast (the differential change between the before and after periods) in R using the contrast function in the car package (Fox and Weisberg 2019). The BACI contrast is the difference of the differences between sample period (i.e., before and after restoration) mean maximum daily stream temperatures or average range of daily stream temperatures for each station class (i.e., restored and unrestored stations), and is represented as the following:

$$(\mu_{UA} - \mu_{UB}) - (\mu_{RA} - \mu_{RB}),$$

where μ_{UA} is mean maximum daily stream temperature or average range of daily stream temperature after restoration at the unrestored Picnic Creek station, μ_{UB} is mean maximum daily stream temperature or average range of daily stream temperature before restoration at the unrestored Picnic Creek station, μ_{RA} is mean maximum daily stream temperature or average range of daily stream temperature after restoration at a restored station (Mainstem 6 or Upper ESC), and μ_{RB} is mean maximum daily stream temperature or average range of daily stream temperature before restoration at a restored station (Mainstem 6 or Upper ESC). BACI contrasts provide information about the magnitude of the treatment effect (i.e., restoration) on either maximum daily stream temperature or range of daily stream temperature (Schwarz 2014). BACI contrasts with a Bonferroni correction were constructed to separately test for differences between the Picnic Creek (unrestored) and Mainstem 6 (restored) stations, and between the Picnic Creek and Upper

ESC (restored) stations. A negative contrast value indicated that stream temperature decreased more at the restored station than at the unrestored station. Normality and constant variance were assessed by examining QQ plots of the residuals and residual versus fitted plots.

Dissolved Oxygen Concentration Before and After Restoration: Mainstem 6 Station

I performed a one-factor ANOVA with year as a fixed factor using air temperature data collected from the Lakeview Ridge Snotel site (Site 568; 44°35′N, -111°49′W; https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=568) from June 1 through August 31 to ensure that changes in DO concentration between pre- (2016) and post-restoration (2017 and 2018) years were not driven by air temperature differences.

I compared mean minimum daily DO concentration and the average range of daily DO concentration (i.e., difference between daily maximum and minimum stream temperatures) between pre- (2016) and post-restoration (2017 and 2018) years to determine if restoration improved stream habitat conditions at the Mainstem 6 station during summer (from June 1 through August 31). I performed a one-factor ANOVA with year as a fixed factor to determine if significant differences in mean minimum daily DO concentration and the average range of daily DO concentration existed across pre- and post-restoration years. Additionally, I performed a Tukey-Kramer multiple comparison test to identify statistical differences in mean minimum daily DO concentration and the average range of daily DO concentration between pre- and post-restoration years. Each linear model was fitted using the lm function in the stats package (R Development Core Team 2019). An ANOVA was applied to the results of each model to acquire the fixed-effect tests using the anova function in the car package (Fox and Weisberg 2019) in program R. Tukey-Kramer post hoc tests were performed using the TukeyHSD function in the stats package. Normality and constant variance were assessed for each model by examining QQ plots of the residuals and residual versus fitted plots.

Fish Movement: Inferred Spatial Distributions

Inferred spatial distributions of PIT-tagged fish were evaluated before and after restoration to determine if restoration increased movements of Arctic Grayling, Brook Trout, and White Suckers among different habitat segments in Elk Springs and Picnic creeks. This analysis was conducted using a single data set of relocations. Detections of PIT-tagged fish at each of my PIT interrogation stations were filtered in program R until a relocation was defined as one detection per fish per day (Ritter 2015). PIT-tag numbers detected at each of my PIT interrogation stations were linked to corresponding data collected for each fish during tagging using a database management system in program R.

Spatial distributions were inferred from graphical representations showing the locations of PIT-tagged fish in space and time both before and after restoration. I divided the study area into five locations (below Mainstem 6, Mainstem 6 to Former Diversion, Former Diversion to confluence of Elk Springs and Picnic creeks, above Upper ESC, and above Picnic Creek) for the pre-restoration period and five locations (below Mainstem 6, Mainstem 6 to Historical Channel, Historical Channel to confluence of Elk Springs and Picnic creeks, above Upper ESC, and above Picnic Creek) for the post-restoration period based on the presence of fixed PIT interrogation stations. An encounter history for each tagged fish was constructed using relocations collected by PIT interrogation stations and electrofishing. Using this encounter history, I created a spatio-temporal data set that inferred fish location by day based on physical relocations (i.e., electrofishing captures) and fixed PIT interrogation station operation (Ritter 2015). Inferred spatial distribution is represented by a gradient of fish-days (i.e., the number of days spent in each location per fish). However, not all fixed PIT interrogation stations ran simultaneously. To account for this, location of an individual fish was represented as a fraction when more than one location could not be ruled out (Ritter 2015). For example, if a tagged fish was relocated at Mainstem 6 on June 1 and relocated again at Upper ESC on June 4, but the fixed PIT interrogation station between these two stations (Historical Channel or Former Diversion) was not operational during that time frame, the location of that individual would be represented by 0.5 between Mainstem 6 and Historical Channel (or Former Diversion) and 0.5 between Historical Channel (or Former Diversion) and the confluence of Upper ESC and Picnic Creek (i.e., below the Picnic Creek and Upper ESC stations) on June 2 and 3. In other words, either location of that fish could not be ruled out because the Historical Channel (or Former Diversion) station was not operational. Presence in both locations was therefore represented by equal fractions (Ritter 2015). Additionally, if a fish was relocated on the same station twice between June 1 and June 5, two fish-days were allocated to the stream segment on the downstream side of the antenna and two fish-days were allocated to the stream segment on the upstream side of the antenna because either location of that fish could not be ruled out unless that fish was physically recaptured during electrofishing surveys. This analysis assumes that tagged fish did not die or expel their tags (100% retention of tags) and that fixed PIT interrogation stations had detection efficiencies of 100% (Ritter 2015).

Fish Movement Among Restored and Unrestored Reaches

I estimated immigration of each species into the restored Mainstem 1 and 2 reaches from recapture rates of PIT-tagged fish. Furthermore, I calculated the proportion of fish that migrated from unrestored reaches (West Fork, East Fork, Picnic Creek, and Mainstem 3, 4, and 5) to restored reaches (Mainstem 1 and 2) after restoration, and vice versa. Additionally, I calculated the percentage of fish that were not previously PIT-tagged to determine if they were immigrants from outside of my defined sample reaches.

Fish Density and Biomass Density

Abundance and biomass estimates for each species in the East Fork, West Fork, Mainstem 1, 2, 3, 4, and 5, and Picnic Creek reaches were calculated for fish ≥ 75 mm TL; the size restriction was used to reduce the effects of size-related differences in capture probability among individuals (i.e., small fish are less vulnerable to capture), which can bias estimates of fish abundance (Otis et al. 1978; Buttiker 1992).

Estimates of fish abundance were calculated using the maximum likelihood population estimator (Otis et al. 1978, originally recommended by Zippin 1958) in the deplet function within the fish methods package (Nelson 2017) in program R if three or more electrofishing passes were made. Estimates of fish abundance were calculated using the maximum-weighted-likelihood population estimator (Carle and Strub 1978) in the removal function within the FSA package (Ogle et al. 2020) in program R if only two electrofishing passes were made. Additionally, estimates of fish abundance were calculated by summing the number of fish captured among all electrofishing passes if fish numbers were not depleted during successive electrofishing passes. Abundance estimates of each species in each reach were standardized to density (fish/m^2) by dividing the abundance estimate (fish/reach) by the product of the reach length (m) and average wetted width (m) to account for differences in reach areas.

I estimated biomass ($\widehat{W}$) by summing the weights of fish that were captured among all electrofishing passes with the total weights of non-captured fish as:

$$\widehat{W} = W_{weighed} + \widehat{W}_{non-captured},$$

where $W_{weighed}$ is the sum of the weights of all weighed fish and $\widehat{W}_{non-captured}$ is the predicted weight of fish not captured (Shepard et al. 2013). The predicted weight of non-captured fish ($\widehat{W}_{non-captured}$) was calculated as:

$$\widehat{W}_{non-captured} = (\widehat{N} - n)\overline{w},$$

where $\widehat{N}$ is the abundance estimate, n is the total number of captured fish that were weighed, and $\overline{w}$ is the mean weight of captured fish. Additionally, variance estimates of biomass were calculated using the finite population factor (FPCM) method described by Shepard et al. (2013). The sum of the weights of captured fish was used as the biomass estimate if the total number of fish captured was used as the abundance estimate. Biomass estimates of each species in each reach were standardized to density (g/m^2) by dividing total biomass (g) by the product of the reach length (m) and average wetted width (m) to account for differences in reach areas.

The densities and biomass densities of each species were compared between 2016 (before restoration) and 2017 (after restoration) and between 2016 and 2018 to determine if the densities and biomass densities of each species had changed as a result of restoration using two different methods. The method selected depended on how frequently each species was encountered during each sample year in each of the restored (Mainstem 1 and 2) and unrestored (East and West forks, Mainstem 3, 4, and 5, and Picnic Creek) reaches.

I used a BACI design (Schwarz 2014) to test the hypotheses that Brook Trout densities (fish/m^2) and biomass densities (g/m^2) changed as a result of restoration. Linear models were fitted to test for differences in Brook Trout densities or biomass densities between years 2016 and 2017 and between years 2016 and 2018. The before-restoration period was 2016 and the after-restoration period was either 2017 or 2018. The East Fork, West Fork, Picnic Creek, and Mainstem 3, 4, and 5 reaches were controls (unrestored), and the Mainstem 1 and 2 reaches were impacted (restored). The effects of restoration on Brook Trout densities and biomass densities were tested using a linear model with treatment (restored or unrestored reaches) and period (before or after restoration) as fixed effects. A significant treatment × period interaction would indicate that the relative change in either Brook Trout density or biomass density between periods (before versus after restoration) differed between the restored and unrestored reaches (Schwarz 2014). Each linear model was fitted using the lm function in the stats package in program R

(Schwarz 2014). An ANOVA with a Kenward-Roger approximation of the degrees of freedom was applied to the results of each model to acquire the fixed-effect tests using the anova function in the car package (Fox and Weisberg 2019) in program R (Schwarz 2014). Mean Brook Trout density and biomass density for each period (before versus after restoration) and reach category (restored versus unrestored) were estimated in R using the lsmeans function in the lsmeans package (Lenth 2016). Normality and constant variance were assessed for each model by examining QQ plots of the residuals and residual versus fitted plots. I also calculated the differential change in mean Brook Trout density and biomass density (i.e., the BACI contrasts; Schwarz 2014) and 95% confidence intervals using the contrast function in the car package (Fox and Weisberg 2019). The BACI contrast is the difference of the differences between sample period (i.e., before and after restoration) mean Brook Trout densities or biomass densities for each site class (i.e., restored and unrestored reaches), and is represented as the following:

$$(\mu_{UA} - \mu_{UB}) - (\mu_{RA} - \mu_{RB}),$$

where μ_{UA} is mean Brook Trout density or biomass density after restoration at the unrestored reaches, μ_{UB} is mean Brook Trout density or biomass density before restoration at the unrestored reaches, μ_{RA} is mean Brook Trout density or biomass density after restoration at the restored reaches, and μ_{RB} is mean Brook Trout density or biomass density before restoration at the restored reaches. BACI contrasts provide information about the magnitude of the treatment effect (i.e., restoration) on either Brook Trout density or biomass density (Schwarz 2014).

Before and after restoration differences in the densities and biomass densities of White Suckers and Arctic Grayling between restored and unrestored reaches were not statistically compared using the BACI model because White Suckers and Arctic Grayling were either absent or present in low numbers throughout the entire duration of study; only 86 White Suckers and 64 Arctic Grayling were captured among all reaches throughout the entire duration of study. Instead, I visually compared density and biomass density trends of White Suckers and Arctic Grayling between the restored and unrestored reaches across sample years to determine if substantial differences existed.

Fish Size

I determined if the length distributions of each species in each reach changed after restoration. Length-frequency distributions of individuals of each species captured in the East Fork, West Fork, Mainstem 1, 2, 3, 4, and 5, and Picnic Creek reaches from 2016 to 2018 during spring were constructed by assigning fish lengths to 10-mm bins (because the maximum length of each species was less than 500 mm; Neumann et al. 2012). Additionally, median lengths of Brook Trout were compared between pre- and post-restoration years to determine if median Brook Trout size changed in the restored (Mainstem 1 and 2) and unrestored (East and West forks, Mainstem 3, 4, and 5, and Picnic Creek) reaches after restoration. The median lengths of Arctic Grayling and White Suckers were not compared between pre- and post-restoration years because these species were either absent or present in small numbers in the restored and unrestored reaches during each spring sampling period, 2016-2018.

RESULTS

Stream Habitat

Physical Habitat

Restoration actions administered on Elk Springs Creek changed stream habitats markedly. Habitat modifications reduced mean wetted widths by more than 50% and increased mean stream depths by more than 200% in both of the restored Mainstem 1 and 2 reaches (Table 1). The percent of stream length consisting of pools was more than five times longer after restoration than before restoration in both the Mainstem 1 and 2 reaches (Table 1). The percentages of substrates in each size category were similar before and after habitat modifications in the Mainstem 1 reach (Table 1) but fines decreased from 70% to 33% and gravels increased from 29% to 65% in the Mainstem 2 reach (Table 1). Substrate composition was similar in the Mainstem 1 reach before and after restoration, but gravels were abundant and fines were minimal there prior to restoration. The amount of large woody debris in Mainstem 1 was similar before (0.005 pieces/m^2) and after (0.004 pieces/m^2) habitat modifications, and no large woody debris was observed in Mainstem 2 during the study. Finally, stream rerouting bypassed Swan Lake and reclaimed historical stream habitats (i.e., Historical Channel), which created a direct connection between productive foraging habitats in Upper Red Rock Lake and historical spawning habitats in Picnic Creek and the upper reaches of Elk Springs Creek.

Stream Temperature

Restoration reduced mean maximum daily stream temperature at the restored Mainstem 6 station, and some evidence existed to suggest that restoration reduced mean maximum daily stream temperature at the restored Upper ESC station (Figure 6A, Table 4). Moderate evidence ($T_6 = -3.00$, $P = 0.07$) existed to suggest that the differential change (i.e., BACI contrast) in mean maximum daily stream temperature between restoration periods was significantly different between the Upper ESC (restored) and Picnic Creek (unrestored) stations. Additionally, strong evidence ($T_6 = -5.37$, $P = 0.005$) existed to suggest that the differential change in mean maximum daily stream temperature between restoration periods was significantly different between the Mainstem 6 (restored) and Picnic Creek stations. Mean maximum daily stream temperatures decreased by 1.4 °C (from 15.8 °C to 14.4 °C) at the restored Upper ESC station and decreased by 3.2 °C (from 21.8 °C to 18.6 °C) at the restored Mainstem 6 station following restoration, whereas mean maximum daily stream temperatures increased 1 °C (from 20.4 °C to 21.4 °C) over the same time period at the unrestored station (Picnic Creek). Furthermore, the estimated differential change in mean maximum daily stream temperature between restoration periods was 2.4 °C lower (95% CI = -4.95 to 0.23 °C) at the Upper ESC station than at the Picnic Creek station, and was 4.2 °C lower (95% CI = -6.8 to -1.6 °C) at the Mainstem 6 station than at the Picnic Creek station. The differential decrease in maximum daily stream temperatures between the Mainstem 6 and Upper ESC stations indicates that bypassing Swan Lake and reclaiming the Historical Channel probably had more of an effect on lowering stream temperatures at the Mainstem 6 station than the spawning habitat restoration actions administered near the headwaters of Elk Springs Creek.

Moderate evidence existed ($P = 0.07$) to suggest that the changes in the average ranges of daily stream temperatures between the before (2015 and 2016) and after (2017 and 2018) restoration periods were significantly different among the Mainstem 6 (restored), Upper ESC (restored), and Picnic Creek (unrestored) stations (Figure 6B, Table 4). However, minimal evidence existed to suggest that the differential changes (i.e., BACI contrast) in average ranges of daily stream temperatures between restoration periods was significantly different between the Picnic Creek (unrestored) and Upper ESC (restored) stations ($T_6 = -0.25$, $P = 1.00$), and between the Picnic Creek and Mainstem 6 (restored) stations ($T_6 = -2.25$, $P = 0.20$). Therefore, I conclude that restoration did not reduce the average ranges of daily stream temperatures at the restored Mainstem 6 and Upper ESC stations.

Dissolved Oxygen Concentration Before and After Restoration: Mainstem 6 Station

Mean minimum daily DO concentration increased substantially two years after habitat restoration at the restored Mainstem 6 station. Mean minimum daily DO concentrations at the Mainstem 6 station were significantly different (Figure 7A, Table 5) among the 3 years. DO concentration was slightly lower ($P = 0.003$) one year after restoration in 2017 (mean = 1.3 mg/L) than before restoration in 2016 (mean = 1.9 mg/L); however, mean minimum daily DO concentration was more than three times greater ($P < 0.001$) two years after restoration in 2018 (mean = 7.1 mg/L) than before restoration in 2016 at the restored Mainstem 6 station. A sediment berm formed below the Mainstem 6 station in mid- to late June of 2017, which partially diverted stream flows to Swan Lake and probably lowered DO concentration at the Mainstem 6 station during the summer of 2017. Stream flows between Upper Red Rock Lake and the Historical Channel were unimpeded after the sediment plug dissipated during spring 2018, which probably explains the increase in DO during summer 2018.

The average range of daily DO concentration (i.e., difference between daily maximum and minimum) declined after restoration at the restored Mainstem 6 station. The average range of daily DO concentration at the Mainstem 6 station was significantly different across pre- and post-restoration years (Figure 7B, Table 5). The average range of daily DO concentration was significantly lower after restoration in both 2017 (mean = 3.5 mg/L; $P < 0.001$) and 2018 (mean = 6.8 mg/L; $P < 0.001$) than before restoration in 2016 (mean = 11.78 mg/L).

I did not detect a difference in average daily maximum air temperature ($F_{2, 272}$ = 1.59, $P = 0.20$), average daily mean air temperature ($F_{2, 272}$ = 1.01, $P = 0.37$), and average daily minimum air temperature ($F_{2, 272}$ = 1.17, $P = 0.33$) among pre- (2016) and post-restoration (2017 and 2018) years. Therefore, minimal evidence exists to suggest that changes in DO concentration at the Mainstem 6 station between pre- and post-restoration years were driven by air temperature differences.

Fish Movement: Inferred Spatial Distribution

Longitudinal connectivity between historical spawning habitats in upper Elk Springs and Picnic creeks and foraging habitats in Upper Red Rock Lake was greater for all three species after restoration than before restoration. Prior to restoration, the number of fish-days in the lowermost sections of Elk Springs Creek (below the confluence of Upper ESC and Picnic creeks) and the number of unique detections at the lowermost PIT interrogation stations (Former Diversion and Mainstem 6) were minimal for Arctic Grayling, Brook Trout, and White Suckers (Figures 8-10, Tables 6 and 7). Fish-days in these sections and unique detections at the lowermost PIT interrogation stations (Historical Channel and Mainstem 6) increased for each species after restoration (Figures 8-10), indicating that movements between Upper Red Rock Lake and upper Elk Springs and Picnic creeks increased. However, stream habitats above the Upper ESC station were rarely occupied by Arctic Grayling (Figure 8, Table 6) and White Suckers (Figure 10, Table 6) both before and after restoration, which indicates that these species did not respond positively to the spawning habitat restoration in upper Elk Springs Creek. Whereas my monitoring of pre-restoration movements was limited in this study (less than four months), my findings suggest that all three target species could successfully migrate between Upper Red Rock Lake and upper Elk Springs and Picnic creeks after restoration.

Fish Movement Among Restored and Unrestored Reaches

The majority of Brook Trout and all of the White Suckers captured in the restored Mainstem 1 and 2 reaches after restoration were immigrants from outside of my defined sample reaches. After restoration was complete, 26% of PIT-tagged Brook Trout migrated from unrestored to restored reaches, and only 10% of PIT-tagged Brook Trout migrated from restored to unrestored reaches. Additionally, 77% and 67% of Brook Trout captured in the restored reaches after restoration in 2017 and 2018, respectively, were not previously PIT-tagged, which suggests that they immigrated from areas outside of our defined sample reaches. All of the White Suckers captured in the Mainstem 1 reach after restoration in 2018 were not previously PIT-tagged. However, fish present during previous electrofishing surveys may have been undetected. No PIT-tagged Arctic Grayling were recaptured throughout the duration of my study.

Fish Density and Biomass Density

Brook Trout density (Figure 11) increased substantially two years after habitat restoration (i.e., 2018) in the restored reaches (Mainstem 1 and Mainstem 2) relative to the unrestored reaches (West Fork, East Fork, Mainstem 3, 4, and 5, and Picnic Creek), and Brook Trout biomass density (Figure 12) increased substantially in the restored reaches relative to the unrestored reaches in both years after restoration. Moreover, similar changes in mean Brook Trout density (Figure 11, left panel; Table 8) occurred in the restored and unrestored reaches between 2016 (before restoration) and 2017 (after restoration), which indicate Brook Trout density did not immediately respond to habitat restoration. However, mean Brook Trout densities changed significantly (Figure 11, right panel; Table 8) in the restored reaches relative to the unrestored reaches between 2016 and 2018 (after restoration). The differential change (i.e., BACI contrast) in mean Brook Trout density between 2016 and 2018 was 0.24 fish/m^2 larger (95% CI = 0.17 to 0.31 fish/m^2) in the restored reaches than in the unrestored reaches (Figure 11, right panel). Mean Brook Trout biomass densities increased significantly in the restored reaches relative to the unrestored reaches between 2016 and 2017 (Figure 12, left panel; Table 8), and between 2016 and 2018 (Figure 12, right panel; Table 8). The differential change in mean Brook Trout biomass density between 2016 and 2017 was 5.50 g/m^2 larger (95% CI = 1.01 to 9.98 g/m^2) in the restored reaches than in the unrestored reaches (Figure 12, left panel), and the differential change in mean Brook Trout biomass density between 2016 and 2018 was 23.30 g/m^2 larger (95% CI = 19.10 to 27.60 g/m^2) in the restored reaches than in the unrestored reaches (Figure 12, right panel).

Differences in the densities (Figure 13) and biomass densities (Figure 14) of Arctic Grayling before and after restoration in the unrestored (West Fork, East Fork, Mainstem 3, 4, and 5, and Picnic Creek) reaches were not apparent, and no Arctic Grayling were captured in the restored (Mainstem 1 and 2) reaches throughout the entire duration of study. Therefore, I have no evidence to suggest that restoration resulted in increases in Arctic Grayling densities and biomass densities.

Differences in the densities (Figure 13) and biomass densities (Figure 14) of White Suckers in the restored and unrestored reaches between pre- and post-restoration years were generally not apparent. However, the density and biomass density of White Suckers in the restored Mainstem 1 reach increased after restoration. Furthermore, no White Suckers were captured in Mainstem 1 in 2016 (before restoration) and 2017 (after restoration), but the density and biomass density of White Suckers in Mainstem 1 were 0.006 fish/m^2 (95% CI = 0.005 to 0.007 fish/m^2) and 0.311 g/m^2 (95% CI = 0.270 to 0.351 g/m^2), respectively, in 2018 (after restoration). Additionally, the density of White Suckers in the unrestored reaches (i.e., West Fork, Mainstem 4 and 5, and Picnic Creek) appeared to be greater in 2018 (after restoration) than in 2016 and 2017. However, interpretation of these results necessitates caution because confidence intervals could not be calculated for some density estimates. Furthermore, confidence intervals could not be calculated if all White Suckers were collected during the first electrofishing pass, or if White Suckers were not depleted from a reach during successive electrofishing passes.

Fish Size

Length distributions of some species changed after restoration. Brook Trout longer than 100 mm were more abundant in most reaches after restoration (2017 and 2018) than before restoration (2016) but post-restoration increases were more pronounced in the restored reaches (Mainstem 1 and 2) than in the unrestored reaches (West Fork, East Fork, Picnic Creek, and Mainstem 3, 4, and 5) (Figure 15). Small Brook Trout (≤ 100 mm TL) were uncommon in both the restored and unrestored reaches after restoration. Overland flooding attributable to habitat restoration measures may have caused small Brook Trout to seek out off-channel habitats, which may explain why small Brook Trout were infrequently captured in the restored and unrestored reaches after restoration. Additionally, median Brook Trout lengths were generally longer in both the restored and unrestored reaches after restoration than before restoration (Figure 16; Table 9). Arctic Grayling captured in the Mainstem 4 and Picnic Creek reaches during spring 2016 to 2018 were primarily between 100 and 200 mm long; however, three Arctic Grayling greater than 300 mm long were captured in Mainstem 4 after restoration in 2017 (1) and 2018 (2) (Figure 17). I did not detect clear differences in the size distributions of

White Suckers between pre- and post-restoration years (Figure 18); however, comparisons were limited because White Suckers were observed in only the Mainstem 4 and Picnic Creek reaches both before and after restoration.

DISCUSSION

The effects of restoration actions on physical habitat, water quality, and fish movement, abundance, biomass, and size have been well documented (Riley and Fausch 1995; Merz and Setka 2004; Roegner et al. 2010; Nakamura et al. 2014; Pierce et al. 2014a, 2014b; Shirey et al. 2016) but few if any, investigators have comprehensively evaluated all of these parameters simultaneously. I showed the value of using an integrated combination of methods to gauge the effectiveness of two simultaneously administered habitat restoration projects on physical habitat, water quality, and fish movement, density, biomass density, and size. Furthermore, monitoring each of these parameters simultaneously not only allowed me to determine the effects of restoration on fish populations, but also allowed me to identify potential mechanisms (i.e., changes in temperature, dissolved oxygen concentration, and physical habitat) responsible for eliciting the observed changes.

My study had several limitations. Logistical constraints (e.g., time) and resource limitations (e.g., funding, personnel) prevented me from collecting all of the necessary data needed to draw meaningful conclusions, especially with regard to physical habitat conditions, DO concentrations, and fish movements before and after restoration. I recommend that researchers carefully consider each factor that affects fish assemblages at multiple spatial and temporal scales when designing future management actions and evaluations (i.e., monitoring) thereof.

Physical Habitat

My ability to draw meaningful conclusions regarding the effects of restoration on physical habitat was limited because pre- and post-restoration physical habitat surveys were not completed on unrestored reaches both before and after restoration, thereby precluding rigorous BACI comparisons. However, I observed improvements after restoration. Channel re-meandering similarly reduced stream widths and fine sediments, and increased water depths, the amount of gravel substrates, and the proportion of pool habitats in a small English chalk stream (Champkin et al. 2018). These variables are important features of spawning and foraging habitat for Arctic Grayling, Brook Trout, and White Suckers (Raleigh 1982; Twomey et al. 1984; Hubert et al. 1985). Habitats in the restored Mainstem 1 and 2 reaches responded differently to restoration because creation and removal of McDonald Pond affected the Mainstem 2 reach disproportionately. Furthermore, the formation of McDonald Pond probably increased sedimentation and inundated gravels that were historically present in the restored Mainstem 2 reach.

Stream Temperature Change

Active restoration substantially reduced summer stream temperatures and improved thermal conditions for native Arctic Grayling in my study area; however, further restoration measures aimed at reducing stream temperatures in Elk Springs and Picnic creeks may be required. Maximum daily stream temperatures at the Mainstem 6 station occasionally exceeded 25 °C prior to restoration, and the warmest temperature recorded there was 28.6 °C (my unpublished data). However, temperatures never exceeded 22 °C at the Mainstem 6 station after restoration (my unpublished data). The UILT for Arctic Grayling is 23 °C for fish acclimated from 8.4 °C to 16 °C, and 25 °C for fish acclimated to 20 °C (Lohr et al. 1996). Therefore, thermal conditions were probably more suitable for native Arctic Grayling after restoration than before restoration at the Mainstem 6 station. Similarly, active restoration reduced summer stream temperatures and improved thermal conditions for native Bull Trout (*Salvelinus confluentus*) and Westslope Cutthroat Trout (*Oncorhynchus clarki lewisi*) in the Blackfoot River basin (Pierce et al. 2013; Pierce et al. 2014a, 2014b). Temperature strongly dictates the distribution and abundance of individual species across many spatial and temporal scales (Brannon et al. 2004; Rieman et al. 2007; Wenger et al. 2011; Isaak et al. 2012). However, maximum daily stream temperatures exceeded the UILT of Arctic Grayling at the Picnic Creek station where temperatures exceeded 25 °C both before and after restoration (my unpublished data). These elevated temperatures probably increase stream temperatures in Elk Springs Creek below its confluence with Picnic Creek and are probably caused by warming in two man-made, shallow (< 5 m) impoundments (Widgeon and Culver ponds) located upstream of Picnic Creek. I recommend removal of these ponds and remediation of affected stream habitats to restore the natural thermal regime in Elk Springs and Picnic creeks.

Dissolved Oxygen Concentration

Increases in mean minimum daily DO concentration and decreases in the average range of daily DO concentration after restoration were probably a result of changes in physical and biological processes that produce and consume oxygen. However, conclusions regarding the effects of restoration on DO concentration were limited because we did not monitor DO concentration at a control (unrestored) station both before and after restoration. Information describing the effects of stream restoration on DO concentration is scarce. However, restoration of stream flows through reconnected natural river channels of the Kissimmee River in Florida increased mean monthly DO concentrations from 2.2 to 4.9 mg/L, possibly because of increases in water velocities and reductions in aquatic vegetation and organic matter in the restored channels (Colangelo 2014). Reductions in stream flow and high densities of aquatic vegetation and organic matter result in sustained water column hypoxia (Rose and Crumpton 2006; Colangelo 2007; Bunch et al. 2010). Swan Lake was shallow and relatively stagnant, and aquatic vegetation and organic matter were abundant throughout it. These characteristics probably reduced DO concentrations in Elk Springs Creek because of increases in respiration by aquatic vegetation and sediment oxygen demand and minimal reaeration by stream flows. Channel reclamation probably increased and equilibrated DO concentrations in Elk Springs Creek because aquatic vegetation was minimal and stream flows were unimpeded after the Historical Channel was reclaimed.

Fish Movement

Increases in fish movements among unique segments of Elk Springs and Picnic creeks suggests that restoration improved habitat connectivity, and these increases were probably facilitated by improved water quality conditions in Elk Springs Creek. Elevated temperatures and low DO concentration can affect fish movement. For instance, less than 20% of tagged Brown Trout (*Salmo trutta*) moved when temperatures exceeded 19 °C (Young et al. 2010). Additionally, Chinook Salmon waited to migrate until DO concentration was 5 mg/L or higher (Hallock et al. 1970). Restoration efforts aimed at improving water quality can increase habitat connectivity for fish attempting to migrate between spawning and foraging habitats. Westslope Cutthroat Trout underwent extensive migrations between spawning and foraging habitats after thermal conditions improved as a result of habitat restoration (Pierce et al. 2014a, 2014b).

Physical habitat conditions caused by restoration can attract fish from relatively long distances. Fifty-two percent of Brown Trout and Brook Trout in six northern Colorado streams moved to areas restored using log drop structures (Riley and Fausch 1995). Trout were attracted from relatively long distances, rather than from adjacent sample reaches (Riley and Fausch 1995). The majority of Brook Trout in the restored reaches (Mainstem 1 and 2) immigrated from outside of the impact and control reaches, probably in response to improved physical habitat conditions for spawning and foraging. Furthermore, temperature strongly influences Brook Trout movements, and thermal conditions at the Upper ESC station probably attracted Brook Trout to above this station. For instance, relatively few Brook Trout moved when water temperatures ranged between

14 °C and 17 °C, and Brook Trout moved to cooler water when temperatures exceeded this thermal range within an Appalachian riverscape suggesting that this thermal range was optimal for Brook Trout (Petty et al. 2012). Mean maximum daily stream temperatures at the Picnic Creek and Mainstem 6 stations exceeded the optimal thermal range reported by Petty et al. (2012); however, mean maximum daily stream temperature was within the optimal range for Brook Trout at the Upper ESC station. Therefore, cooler temperatures probably attracted Brook Trout to reaches above the Upper ESC station. Additionally, greater stream depths and percentage of pools in the restored Mainstem 1 and 2 reaches were more favorable than the East Fork, West Fork, Picnic Creek, and Mainstem 3, 4, and 5 reaches after restoration and led to increases in density and biomass density of Brook Trout.

Rerouting Elk Springs Creek effectively bypassed Swan Lake and created a direct connection for adult Arctic Grayling attempting to migrate from Upper Red Rock Lake to upper Elk Springs Creek for spawning purposes. Diverting stream flows into alternative channels can establish direct connections for large (> 300 mm TL), adult Arctic Grayling attempting to migrate between spawning and foraging habitats. Prior to restoration, only juvenile Arctic Grayling (< 200 mm TL) were observed in Elk Springs and Picnic Creeks, and these Arctic Grayling were probably reared in RSIs that were used for artificial supplementation until 2016. However, we collected three large (> 300 mm TL) Arctic Grayling in Elk Springs Creek after restoration. Moreover, these Arctic Grayling ranged from three to six years of age (my unpublished data), which indicates they were mature adults (Mogen 1996). Similarly, excavation of a 3.4 km long artificial stream in the Northwest Territories, Canada, restored watershed connectivity and allowed adult adfluvial Arctic Grayling to migrate between foraging habitats in Kodiak Lake and newly created spawning habitats in the artificial stream (Jones et al. 2003).

I acknowledge that pre-restoration monitoring of fish movements was limited in this study; fish movements were monitored for about three months prior to restoration. Additionally, no historical evidence indicating that fish were using all migratory corridors in Elk Springs and Picnic creeks prior to restoration exists. Nonetheless, I predicted that poor water quality and physical conditions in Elk Springs Creek limited the movement of fish among unique segments of Elk Springs and Picnic creeks prior to restoration and that restoration would improve these conditions and subsequently increase fish movement, which is what I observed.

Fish Density and Biomass Density

Colonization by any organism is influenced by the abundance of colonists, the distance to a source of colonists, the mobility of colonists, the reproductive capabilities of colonists, and food and habitat needs of colonists (Gore 1985; Gore and Milner 1990; Sheldon and Meffe 1995; Moerke and Lamberti 2003; Albanese et al. 2009). Contrary to expectations, Arctic Grayling density and biomass density did not increase as a result of restoration because none were captured in the restored Mainstem 1 and 2 reaches during the study, and pre- and post-restoration differences were negligible in the unrestored (West Fork, East Fork, Mainstem 3, 4, and 5, and Picnic Creek) reaches. Increases in Arctic Grayling density and biomass density may have been prevented by (1) too few

Arctic Grayling in nearby source populations to facilitate colonization of the restored Mainstem 1 and 2 reaches, (2) unsuitable conditions for migrating Arctic Grayling downstream of the restored Mainstem 1 and 2 reaches, (3) the high density of Brook Trout in the restored Mainstem 1 and 2 reaches after restoration that may have caused Arctic Grayling to avoid these reaches, or (4) some combination of these factors. The number of Arctic Grayling captured outside of the restored Mainstem 1 and 2 reaches was low; only 64 individuals were collected from 2015 through 2018, which indicates that Arctic Grayling existed in low numbers in Elk Springs and Picnic creeks. Additionally, the number of Arctic Grayling in Red Rock Creek, the main Arctic Grayling spawning tributary in the Centennial Valley, has declined substantially in the last few years (Warren et al. 2019). Species with low abundance in the regional species pool are unlikely to colonize restored reaches (Stoll et al. 2014). Because the numbers of Arctic Grayling in nearby populations are low, the potential of colonization from nearby source populations is probably limited. Artificial supplementation may be required to bolster Arctic Grayling numbers in Elk Springs and Picnic creeks. Moreover, trout populations did not fully respond for 5-7 years after habitat restoration in Lawrence Creek, Wisconsin (Hunt 1976). Therefore, the density and biomass density of Arctic Grayling in my sample reaches should be monitored for several more years to determine the effects of restoration on Arctic Grayling.

Minimum water depth considered suitable for migrating Arctic Grayling is 12 cm (Hubert et al. 1985). Mean depth in the Mainstem 3 reach, which is located downstream of the restored Mainstem 1 and 2 reaches, was 16.7 cm (range 2–53 cm). However, Arctic Grayling are probably selecting deeper and more suitable stream habitats elsewhere. Moreover, physical habitats below the restored Mainstem 1 and 2 reaches were degraded after the creation of McDonald Pond, which inundated historical Arctic Grayling spawning habitats. Even though McDonald Pond was removed in 2010, habitat quality remained degraded immediately below the restored Mainstem 1 and 2 reaches (e.g., Mainstem 3). Further research is needed to determine if Arctic Grayling are avoiding the shallow, homogenous stream reaches located below the restored Mainstem 1 and 2 reaches. Restoration measures aimed at increasing channel sinuosity, decreasing stream widths, increasing the amount of deep water, reducing the amount of fine sediments, and increasing the amount of suitable spawning gravels in stream reaches affected by the creation of McDonald Pond may be required to establish a population of Arctic Grayling in areas historically used for spawning.

Brook Trout are widely known to displace native salmonids (Shepard 2004; Rieman et al. 2006; McGrath and Lewis 2007). Because Brook Trout density increased substantially in the restored Mainstem 1 and 2 reaches after restoration (see below), competitive interactions between Brook Trout and Arctic Grayling may have prevented the establishment of Arctic Grayling in these reaches. Mechanical removal of Brook Trout in the restored Mainstem 1 and 2 reaches may be required to establish a population of spawning Arctic Grayling.

Increases in the densities and biomass densities of Brook Trout and White Suckers in the restored reaches were not observed until two years after restoration, which indicate delayed responses. Similarly, Brook Trout abundance and biomass increased significantly two years after habitat restoration in Colorado, and increases in Brook Trout abundance and biomass were the result of increases in pool volume and deep habitats (Riley and Fausch 1995). Trout populations did not fully respond for 5-7 years after habitat restoration in Lawrence Creek, Wisconsin (Hunt 1976). Therefore, the density and biomass density of Brook Trout and White Suckers in my sample reaches should be monitored for several more years to determine the full effects of restoration even though densities and biomass densities of both species increased significantly within two years after habitat restoration.

Salmonid abundance increased after streamflow was re-diverted into historical stream habitats, and these increases were attributed to increased connectivity among a variety of diverse stream habitats (Nakamura et al. 2014). Increases in Brook Trout density and biomass density in the restored Mainstem 1 and 2 reaches were probably the result of both increased habitat connectivity and habitat quality.

Increases in Brook Trout density may have been the result of increased survival; however, fish populations were only sampled once prior to restoration, which prevented me from determining pre-restoration survival rates of Brook Trout. Therefore, I recommend monitoring fish populations for at least two years prior to restoration to determine pre-restoration survival rates.

Post-restoration increases in the density and biomass density of Brook Trout are encouraging because these increases suggest that habitat conditions are probably more suitable for Arctic Grayling as a result of restoration. Both Brook Trout and Arctic Grayling prefer clear, cold spring-fed streams with relatively stable water flow and temperature regimes, silt-free rocky substrates in riffle-run areas for spawning, and areas where pool habitats are abundant (Raleigh 1982; Hubert et al. 1985).

Fish Size

The size-class distribution of Brook Trout broadened after restoration, probably as the result of both improved habitat conditions in the restored Mainstem 1 and 2 reaches and increased habitat connectivity. Numbers of large fish are positively related to the volume of deep-water habitat in small streams (Angermeier and Karr 1984; Gerking 1994; Moerke and Lamberti 2003). Channel re-meandering, increases in stream depth and pool habitats, and reduction of stream widths and fine sediments enhanced habitat diversity in restored reaches of Juday Creek in Indiana, and thereby offered more habitat types for a broader range of trout sizes (Moerke and Lamberti 2003). Additionally, Brook Trout dispersed from lakes into streams, and larger individuals were the primary dispersers (Adams et al. 2001). Restoration increased movements of Brook Trout among unique habitat segments in Elk Springs and Picnic creeks, which indicates longitudinal connectivity was greater after restoration than before restoration. Moreover, large Brook Trout (> 200 mm TL) may have immigrated from more productive habitats in Upper Red Rock Lake to habitats in the upper reaches of Elk Springs Creek after Swan Lake was bypassed, which may explain why we observed more large Brook Trout in both unrestored and restored reaches after restoration than before restoration. However, large Brook Trout were potentially migrating to my defined sample reaches from unsampled stream reaches in lower Elk Springs Creek. Further research needs to be conducted to determine if large Brook Trout are migrating from Upper Red Rock Lake to habitats in upper Elk Springs Creek.

CONCLUSIONS

Two restoration actions simultaneously administered on Elk Springs Creek attempted to restore historical Arctic Grayling spawning habitats and improve connectivity between foraging habitats in Upper Red Rock Lake and spawning habitats in upper Elk Springs Creek. I demonstrated that restoration can substantially improve physical habitat and water quality (i.e., temperature and dissolved oxygen concentration), and ultimately improve conditions for native Arctic Grayling and sympatric species. I also demonstrated that a multifaceted management approach can elicit variable, but generally positive, responses from fish assemblages when multiple limiting factors contributing to the loss of robust fish populations are addressed. However, additional restoration measures and long-term monitoring (> 7 years) of fish populations, physical habitat, and water quality should be considered to achieve management goals established by managers tasked with preserving and restoring Arctic Grayling populations in the Centennial Valley. Future management actions should primarily focus on restoring additional habitats degraded by the creation of water impoundments and maintaining connectivity among different habitat types in Elk Springs and Picnic creeks. Additionally, negative interactions with Brook Trout, an invasive species, may be preventing the establishment of Arctic Grayling in the restored Mainstem 1 and 2 reaches. Therefore, managers should consider ways to suppress Brook Trout numbers in Mainstem 1 and 2.

My study had several limitations that limited my ability to draw some meaningful conclusions regarding the effects of restoration on fish assemblages, physical habitat, and water quality. Therefore, I recommend that researchers evaluating management actions carefully consider the resources and time needed, both before and after the management actions, to thoroughly evaluate the effects of restoration on their response variables of interest.

TABLES AND FIGURES

Table 1. Physical habitat characteristics of 11 study reaches on Elk Springs and Picnic Creeks.

Reach	Sample year	Reach length (m)	Mean wetted width (m)	Pools per reach (%)	Mean depth (cm)	Substrate size (% of total)			
						Fines	Gravel	Cobble	Boulder
Unrestored reaches									
West Fork	2016	184	3.3	0	14.9	34	65	1	0
East Fork	2016	113	4.9	0	14.1	12	64	23	1
Mainstem 3	2016	200	7.8	5	16.7	100	0	0	0
Picnic Creek	2018	524	4.1	22	34.5	81	15	4	0
Mainstem 4	2016	200	7.6	16	48.2	100	0	0	0
Mainstem 5	2016	200	7.2	20	40.5	100	0	0	0
Former Diversion	2018	581	3.9	3	45.6	100	0	0	0
Mainstem 6	2018	723	8.9	12	32.4	100	0	0	0
Restored reaches									
Mainstem 1	2016	233	7.5	4	14.1	31	63	6	0
Mainstem 1	2017	318	3.2	21	35.3	36	59	5	0
Mainstem 2	2016	200	7.0	5	16.6	70	29	1	0
Mainstem 2	2017	241	3.1	26	35.4	33	65	3	0
Historical Channel	2018	952	3.6	22	52.6	100	0	0	0

Table 2. Timing of physical habitat surveys conducted in Elk Springs and Picnic creeks, 2016-2018. The before-restoration period was 2016, and the after-restoration period was 2017 and 2018. Time constraints precluded completion of some surveys.

Reach	Reach category	Sampled before	Sampled after
West Fork	Unrestored	X	
East Fork	Unrestored	X	
Mainstem 3	Unrestored	X	
Picnic Creek	Unrestored		X
Mainstem 4	Unrestored	X	
Mainstem 5	Unrestored	X	
Former Diversion	Unrestored		X
Mainstem 6	Unrestored		X
Mainstem 1	Restored	X	X
Mainstem 2	Restored	X	X
Historical Channel	Restored		X

Table 3. Timing and purpose of electrofishing surveys in Elk Springs and Picnic creeks. Asterisks denote samples that were not attempted because water temperatures exceeded 17 °C, which stressed fish. Daggers denote samples that were not attempted because of time constraints. Double daggers denote samples that were not attempted or completed because the remoteness and high amounts of sediment associated with these sampling locations prevented me from doing so.

Study Reach	Sampling dates	Number of electrofishing passes conducted	Sampling purpose
West Fork	May 2016-2018	3-4	Density/PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging
East Fork	May 2016-2018	3-4	Density/PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging
Mainstem 1	May 2016-2018	3-4	Density/PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging
Mainstem 2	May 2016-2018	3-4	Density /PIT-tagging
	October 2016-2018	2	Density /PIT-tagging
	July 2018	1	PIT-tagging
Mainstem 3	May 2016-2018	3-4	Density /PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging

Table 3. Continued

Study reach	Sampling dates	Number of electrofishing passes conducted	Sampling purpose
Picnic Creek	May 2015	2	PIT-tagging
	May 2016-2018	2	Density /PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018*	-	PIT-tagging
Mainstem 4	May 2016-2018	2	Density/PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging
Mainstem 5	May 2016-2018	2	Density/PIT-tagging
	October 2016-2018	2	Density/PIT-tagging
	July 2018	1	PIT-tagging
Historical Channel	May 2017-2018‡	1	Density/PIT-tagging
	October 2017-2018†‡	-	Density/PIT-tagging
	July 2018*	-	PIT-tagging
Former Diversion	May 2016‡	-	Density/PIT-tagging
	October 2016‡	-	Density/PIT-tagging
Mainstem 6	May 2016-2018‡	-	Density/PIT-tagging
	October 2016-2018‡	-	Density/PIT-tagging
	July 2018‡	-	PIT-tagging

Table 4. Results from analysis of variance comparing maximum daily stream temperatures and daily ranges of stream temperatures at restored (Upper ESC and Mainstem 6) and unrestored (Picnic Creek) stations between pre- (2015 and 2016) and post-restoration (2017 and 2018) years.

		Daily maximum		Daily range	
Model terms	df	*F*	*P*	*F*	*P*
Siteperiod	5	60.77	< 0.001	3.85	0.066
Residuals	6				

Table 5. Results from analysis of variance comparing minimum daily DO concentrations and daily ranges of DO concentrations at the restored Mainstem 6 station between pre- (2016) and post-restoration (2017 and 2018) years.

		Daily minimum		Daily range	
Model terms	df	*F*	*P*	*F*	*P*
(Intercept)	1	171.07	< 0.001	1863.82	< 0.001
Year	2	362.55	< 0.001	230.03	< 0.001
Residuals	253				

Table 6. Total numbers of fish-days recorded for each species in unique segments of Elk Springs and Picnic creeks before and after restoration. Fish-days are defined as the numbers of days per fish spent in unique segments (between fixed PIT interrogation stations, below Mainstem 6 station, and above Upper ESC and Picnic Creek stations) of Elk Springs and Picnic creeks before and after restoration. Confluence refers to the confluence of upper Elk Springs and Picnic creeks. The before-restoration period was from May 1 through September 15, 2016, and the after-restoration period was from September 16, 2016, through October 26, 2018.

Species	Restoration period	Location relative to PIT interrogations stations	Fish-days
Arctic Grayling	Before restoration	above Upper ESC	0
		above Picnic Creek	10
		Confluence – Former Diversion	1
		Former Diversion – Mainstem 6	1
		below Mainstem 6	1
	After restoration	above Upper ESC	2
		above Picnic Creek	60
		Confluence – Historical Channel	78.5
		Historical Channel – Mainstem 6	24.5
		below Mainstem 6	22
Brook Trout	Before restoration	above Upper ESC	181
		above Picnic Creek	42
		Confluence – Former Diversion	34
		Former Diversion – Mainstem 6	0
		below Mainstem 6	0
	After restoration	above Upper ESC	8547
		above Picnic Creek	5416
		Confluence – Historical Channel	12650
		Historical Channel – Mainstem 6	2946
		below Mainstem 6	1093
White Suckers	Before restoration	above Upper ESC	0
		above Picnic Creek	28
		Confluence – Former Diversion	12
		Former Diversion – Mainstem 6	8
		below Mainstem 6	1
	After restoration	above Upper ESC	70
		above Picnic Creek	2757
		Confluence – Historical Channel	4131.5
		Historical Channel – Mainstem 6	4297.5
		below Mainstem 6	2427

Table 7. Numbers of unique detections of each species at fixed PIT interrogation stations before and after restoration. A unique detection is defined as one detection per day per individual fish. The before-restoration period was from May 1 through September 15, 2016, and the after-restoration period was from September 16, 2016, through October 26, 2018.

Species	Restoration period	PIT interrogation station	Unique detections
Arctic Grayling	Before restoration	Upper ESC	0
		Picnic Creek	3
		Former Diversion	1
		Mainstem 6	2
	After restoration	Upper ESC	3
		Picnic Creek	38
		Historical Channel	25
		Mainstem 6	11
Brook Trout	Before restoration	Upper ESC	53
		Picnic Creek	48
		Former Diversion	0
		Mainstem 6	0
	After restoration	Upper ESC	948
		Picnic Creek	921
		Historical Channel	162
		Mainstem 6	357
White Suckers	Before restoration	Upper ESC	0
		Picnic Creek	29
		Former Diversion	17
		Mainstem 6	4
	After restoration	Upper ESC	45
		Picnic Creek	502
		Historical Channel	215
		Mainstem 6	302

Table 8. Results from analysis of variance comparing Brook Trout densities (fish/m^2) and biomass densities (g/m^2) in restored (Mainstem 1 and 2) and unrestored (West Fork, East Fork, Picnic Creek, and Mainstem 3, 4, and 5) reaches between 2016 (before restoration) and 2017 (after restoration) and between 2016 and 2018. A significant period:treatment term indicates a restoration effect. Other model terms should not be interpreted.

		Density		Biomass density	
Model terms	df	*F*-value	*P*-value	*F*-value	*P*-value
2016 versus 2017					
(Intercept)	1	0.51	0.490	0.05	0.819
Period	1	3.11	0.103	8.31	0.014
Treatment	1	0.17	0.690	0.46	0.509
Period: treatment	1	3.75	0.077	7.18	0.020
Residuals	12				
2016 versus 2018					
(Intercept)	1	0.34	0.573	0.06	0.811
Period	1	76.05	< 0.001	205.04	< 0.001
Treatment	1	0.11	0.746	0.51	0.489
Period: treatment	1	51.61	< 0.001	141.55	< 0.001
Residuals	12				

Table 9. Median total lengths of Brook Trout measured in the West Fork, East Fork, Picnic Creek, and Mainstem 1, 2, 3, 4, and 5 reaches before restoration in May 2016, and after restoration during May 2017 and 2018. Ranges of median Brook Trout lengths are in parentheses.

	Median length (mm)			Number measured		
Study Reach	2016	2017	2018	2016	2017	2018
West Fork	60 (45-210)	61 (35-143)	154 (107-196)	157	28	51
East Fork	78 (49-336)	194 (65-248)	153 (110-240)	67	19	35
Mainstem 1	67 (48-204)	200 (60-261)	183 (125-376)	122	97	273
Mainstem 2	74 (55-194)	231 (206-265)	185 (130-363)	10	12	168
Mainstem 3	69 (65-72)	221 (203-230)	178 (134-305)	2	3	16
Picnic Creek	170 (63-325)	0	188 (148-214)	16	0	7
Mainstem 4	224 (48-302)	261 (194-338)	216 (152-373)	18	13	32
Mainstem 5	62 (51-72)	277 (277-277)	210 (148-312)	2	1	10

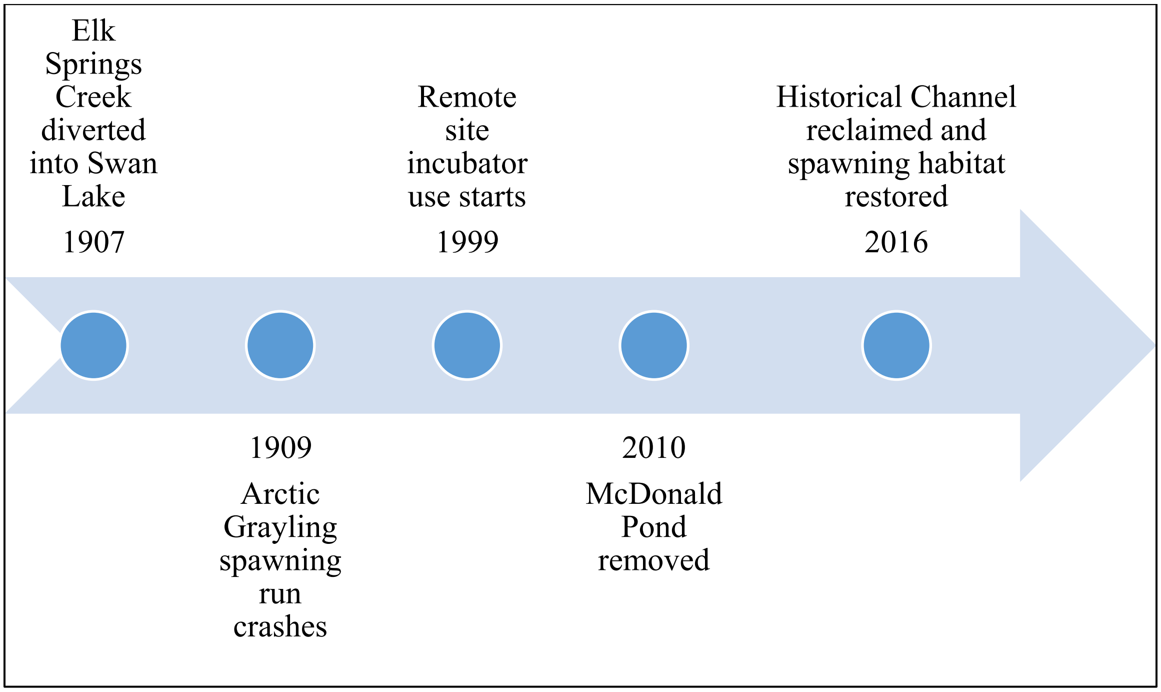

Figure 1. Timeline of Elk Springs Creek historical events.

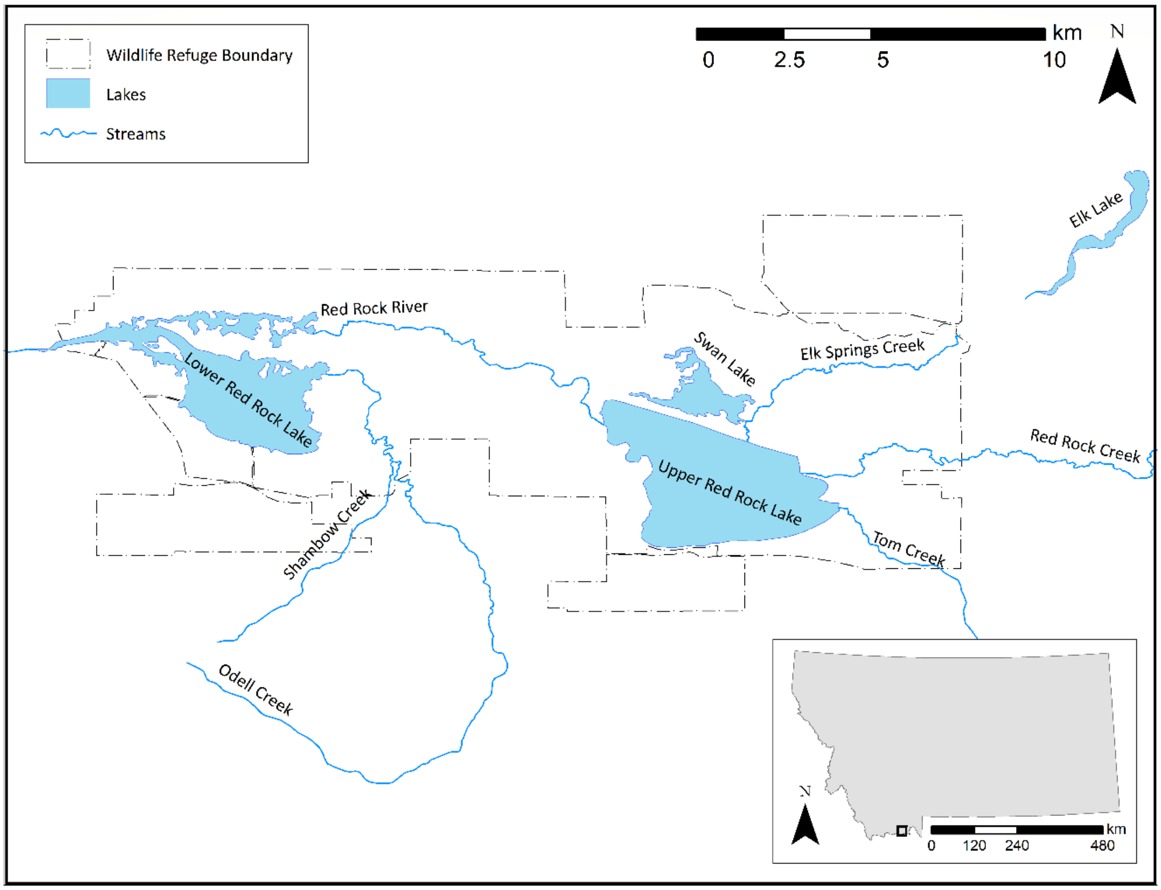

Figure 2. Upper and Lower Red Rock lakes, and their major tributaries.

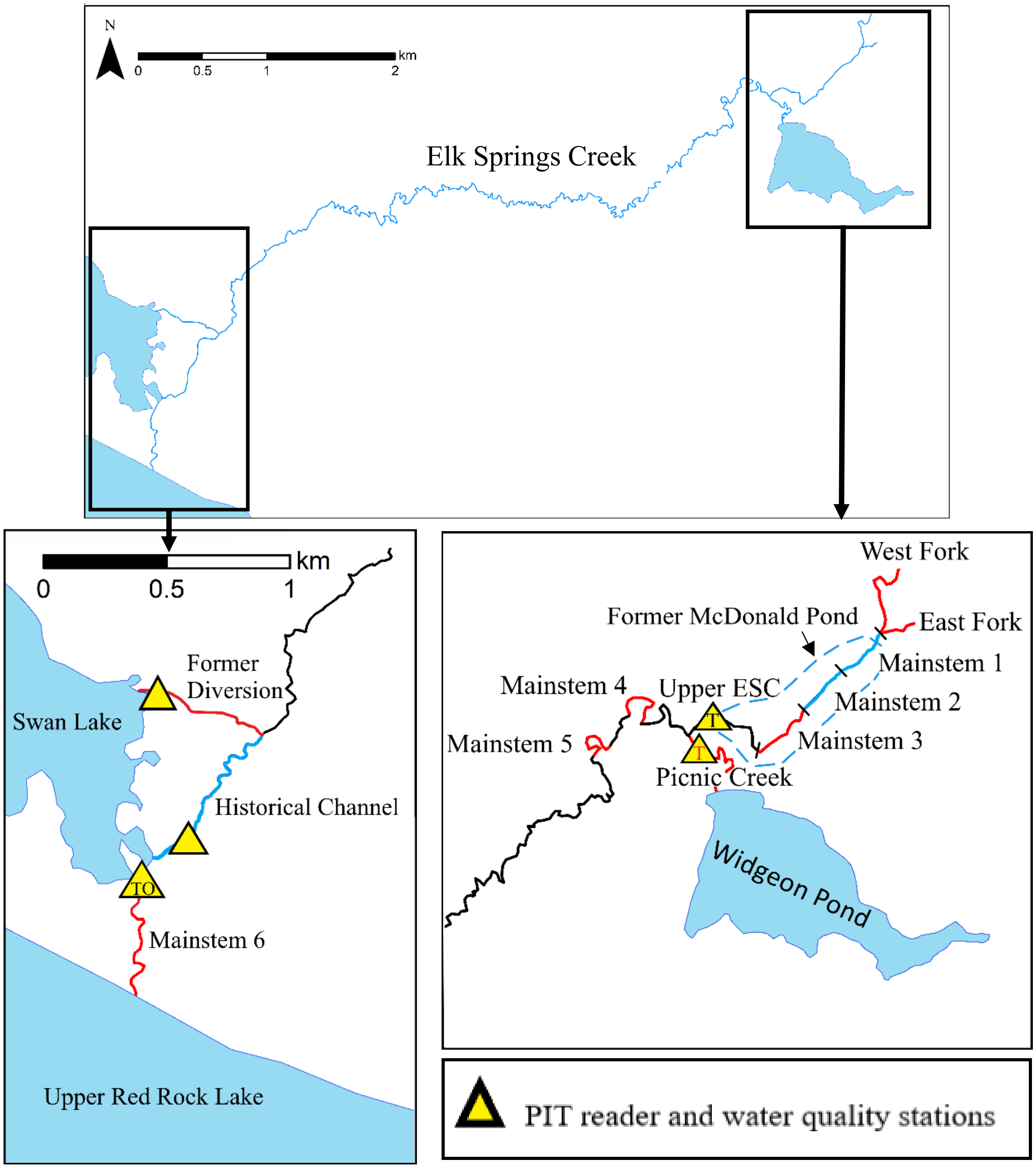

Figure 3. Locations of seven unrestored (red; West and East forks, Picnic Creek, and Mainstem 3, 4, 5, and 6), three restored (blue; Mainstem 1 and 2, and Historical Channel), and the Former Diversion reaches, and PIT interrogation stations and the Picnic Creek, Upper ESC, and Mainstem 6 water quality stations. Black letters on yellow triangles (△) indicate the locations of stream temperature loggers (T) and dissolved oxygen concentration loggers (O) at restored stations (Upper ESC and Mainstem 6) and the red letter on the yellow triangle indicates the location of the stream temperature logger at the unrestored Picnic Creek station.

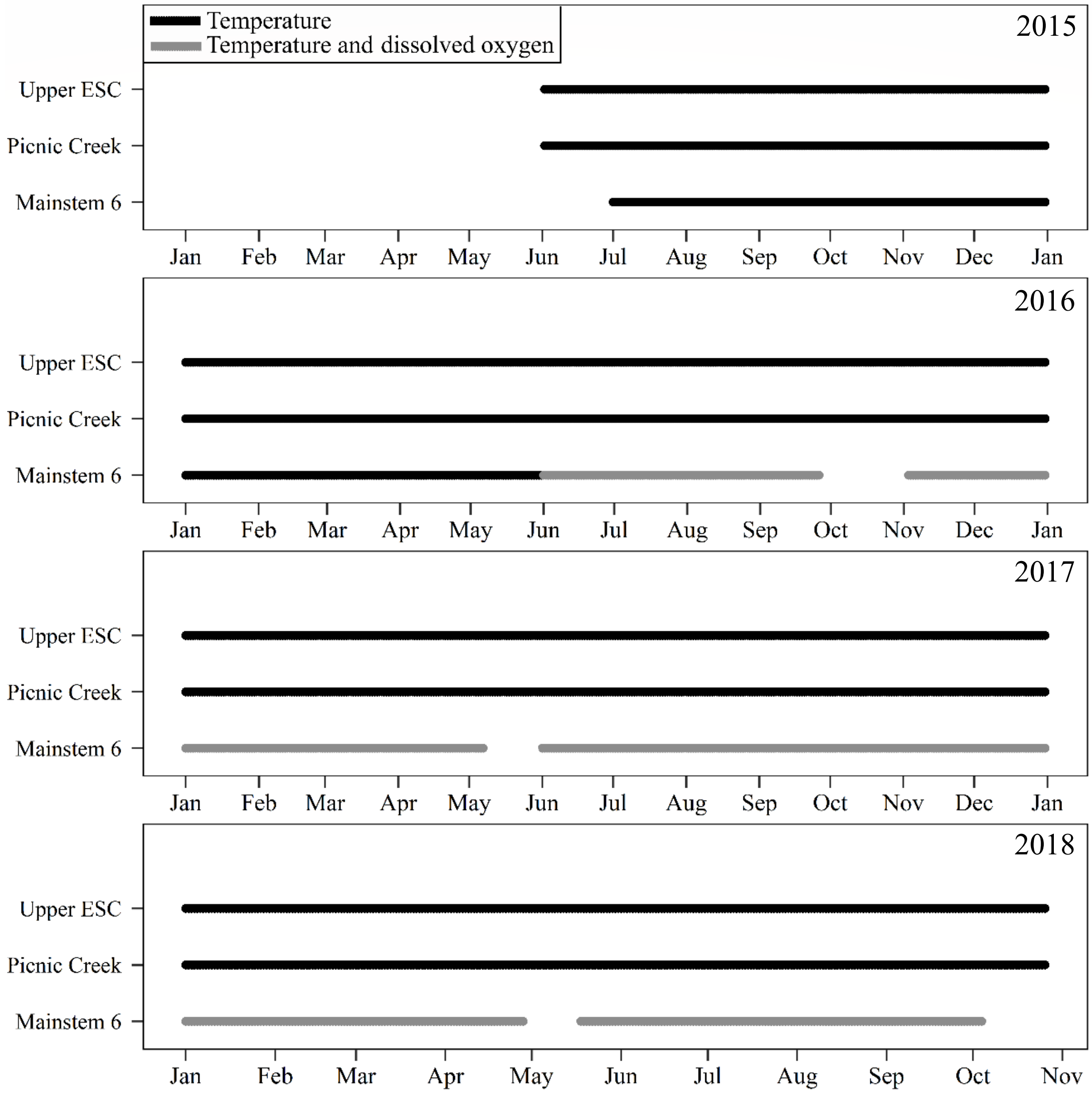

Figure 4. Water quality monitoring times at the unrestored Picnic Creek station and at the restored Upper ESC and Mainstem 6 stations from 2015 to 2018. Solid black lines indicate periods when only water temperatures were monitored, and solid gray lines indicate periods when both water temperatures and dissolved oxygen concentrations were monitored simultaneously.

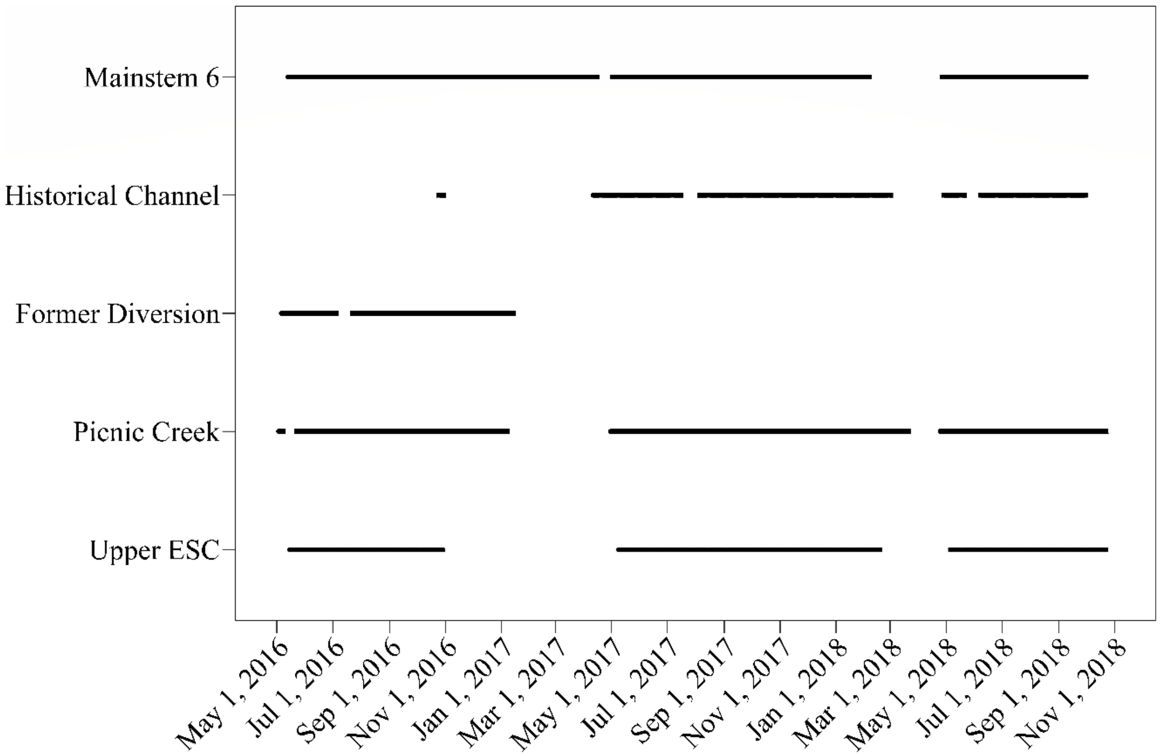

Figure 5. Operation times of fixed PIT interrogation stations in Elk Springs and Picnic creeks.

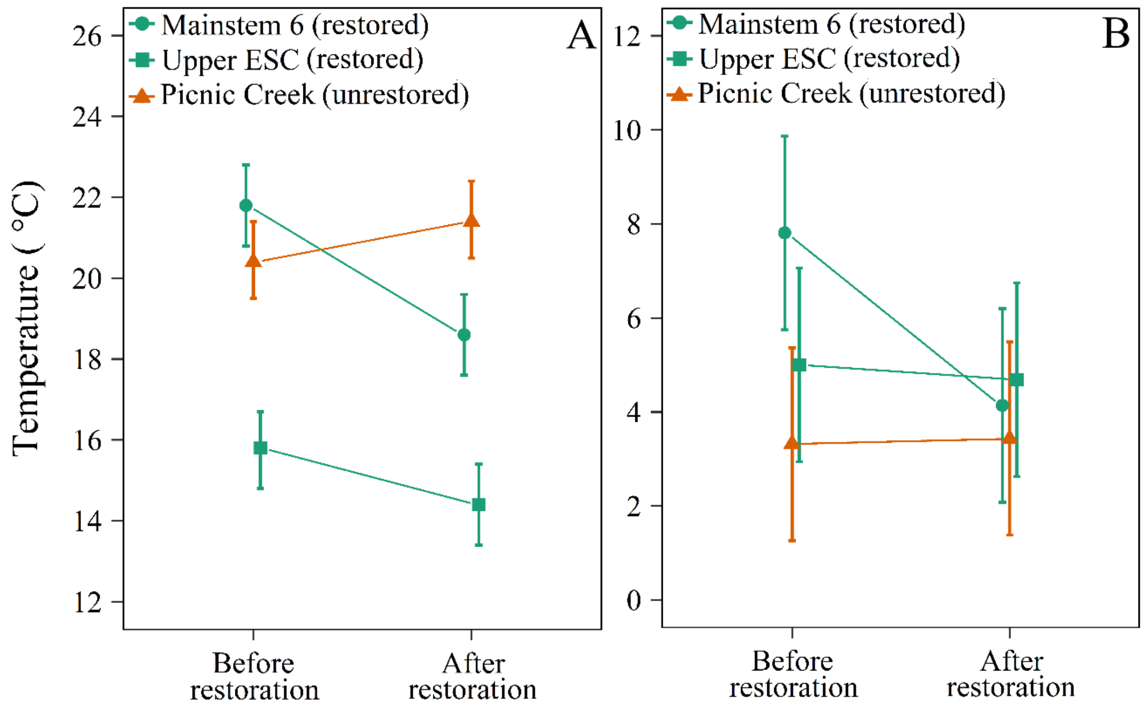

Figure 6. (A) Mean maximum daily stream temperatures at the Mainstem 6 (restored), Upper ESC (restored), and Picnic Creek (unrestored) stations in 2015 and 2016 (before restoration) versus 2017 and 2018 (after restoration), and (B) mean ranges of daily stream temperatures at the Mainstem 6 (restored), Upper ESC (restored), and Picnic Creek (unrestored) stations in 2015 and 2016 (before restoration) versus 2017 and 2018 (after restoration). Error bars indicate 95% confidence intervals.

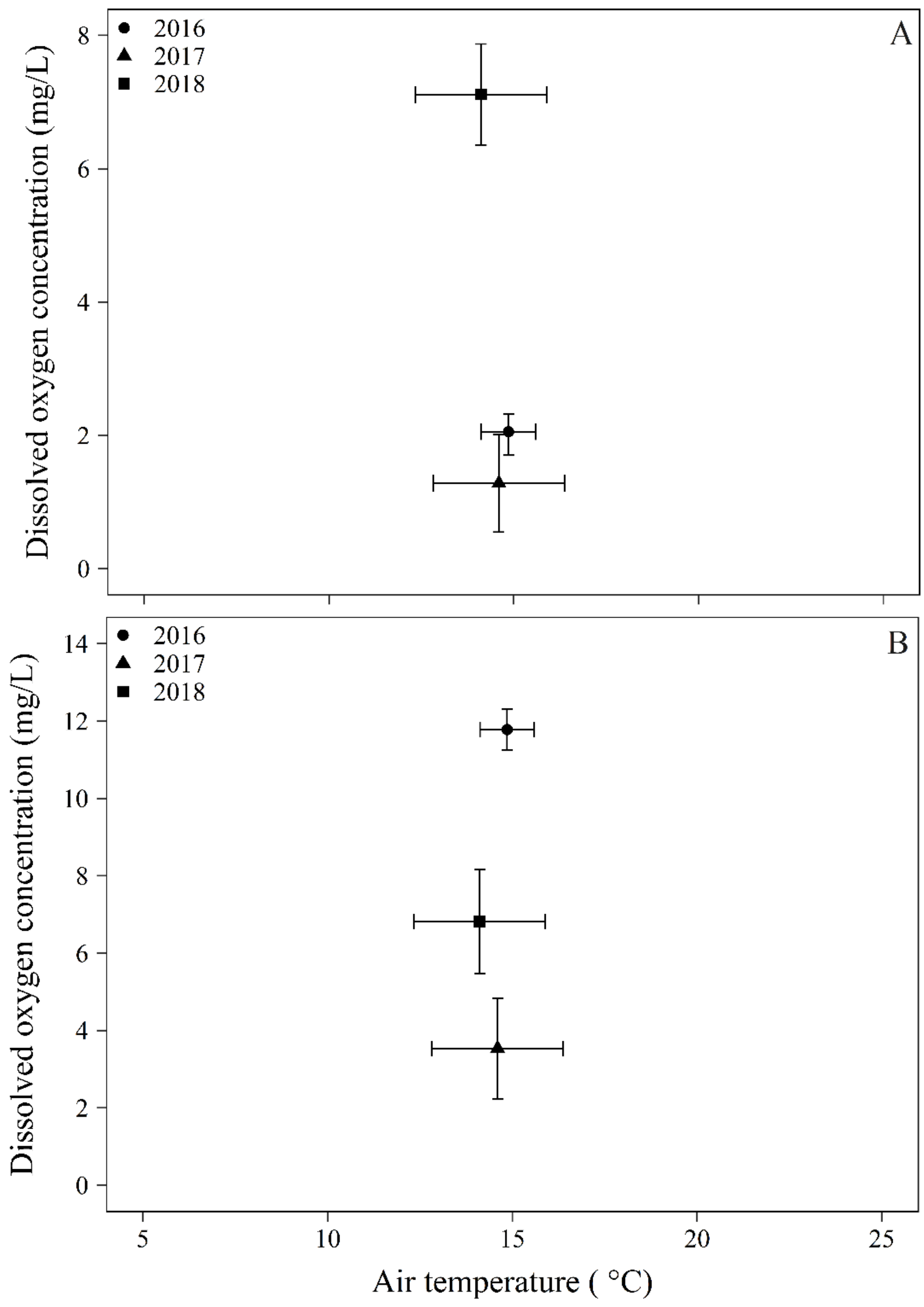

Figure 7. Relationships between (A) mean minimum daily dissolved oxygen concentration at the restored Mainstem 6 station and mean daily air temperature before restoration in 2016, and after restoration in 2017 and 2018, and (B) average daily range of dissolved oxygen concentrations at the restored Mainstem 6 station and mean daily air temperature before restoration in 2016, and after restoration in 2017 and 2018. Error bars indicate 95% confidence intervals.

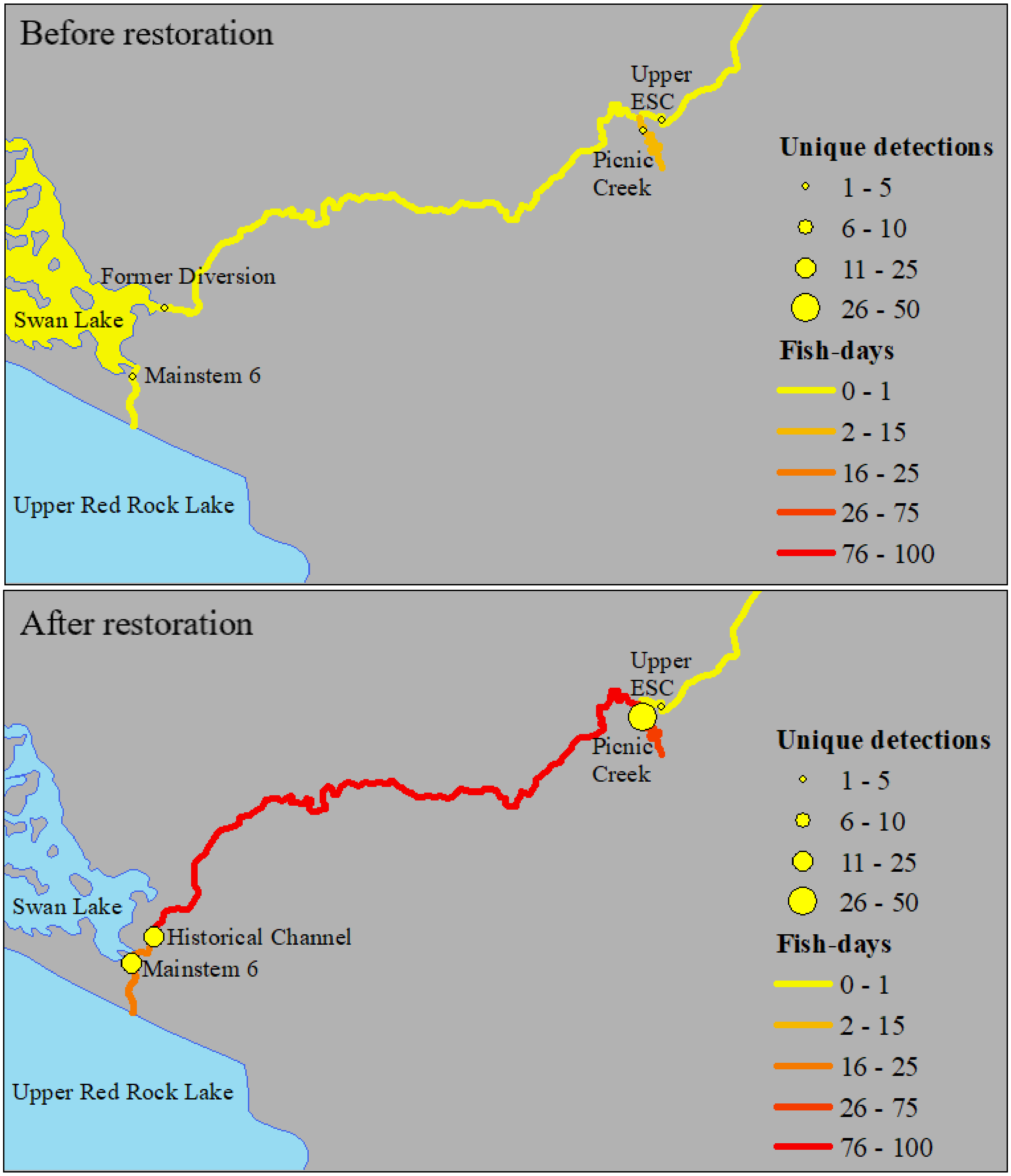

Figure 8. Inferred spatial distributions and numbers of unique detections of Arctic Grayling in Elk Springs and Picnic creeks before (May 1 through September 15, 2016) and after (September 16, 2016, through October 26, 2018) restoration. Fish-days are defined as the total numbers of days per fish spent in unique segments (between fixed PIT interrogation stations, below Mainstem 6 station, and above Upper ESC and Picnic Creek stations) of Elk Springs and Picnic creeks before and after restoration. A unique detection is defined as one detection per day per individual fish; unique detection totals are represented by yellow circles.

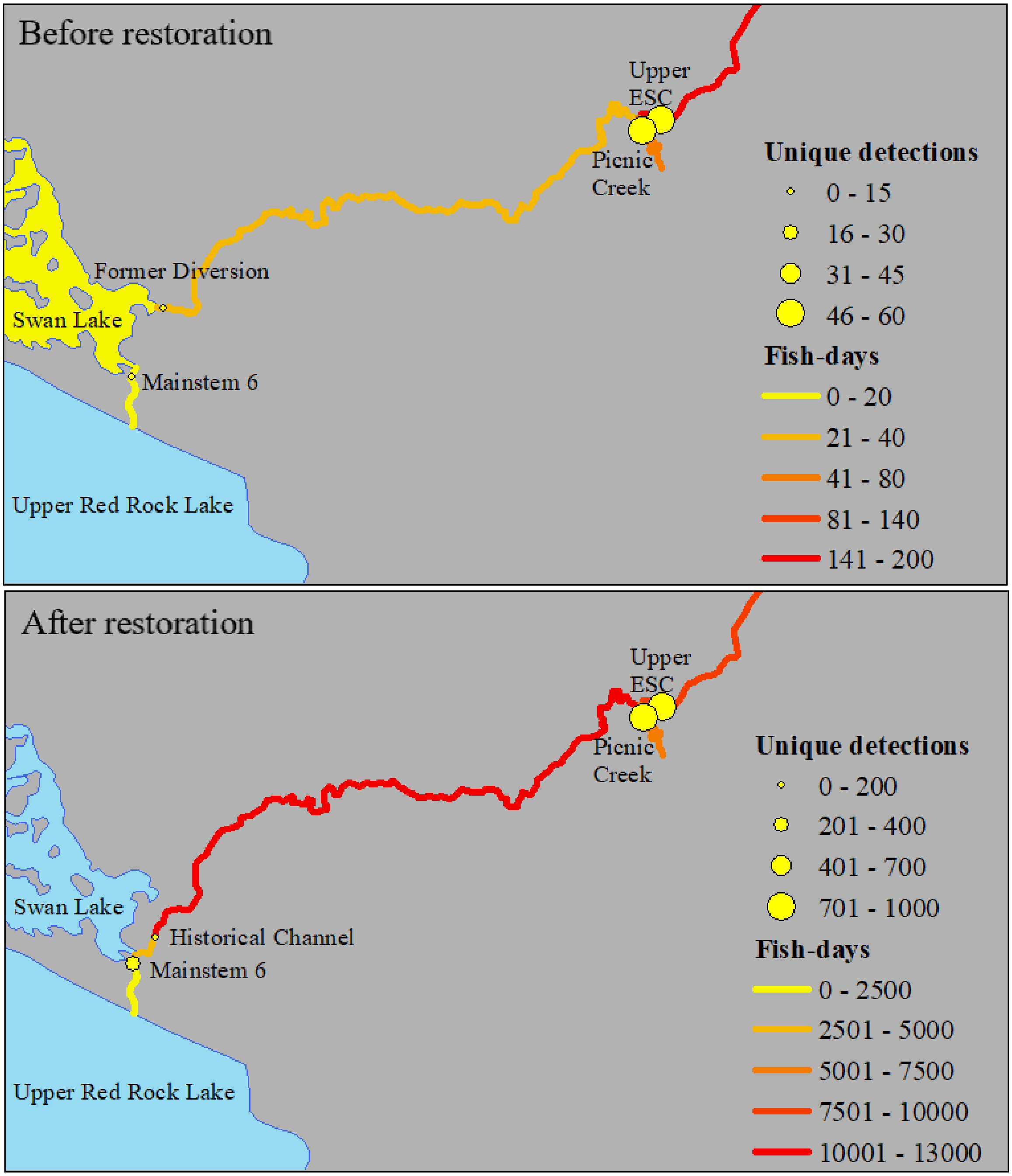

Figure 9. Inferred spatial distributions and numbers of unique detections of Brook Trout in Elk Springs and Picnic creeks before (May 1 through September 15, 2016) and after (September 16, 2016, through October 26, 2018) restoration. Fish-days are defined as the total numbers of days per fish spent in unique segments (between fixed PIT interrogation stations, below Mainstem 6 station, and above Upper ESC and Picnic Creek stations) of Elk Springs and Picnic creeks before and after restoration. A unique detection is defined as one detection per day per individual fish; unique detection totals are represented by yellow circles.

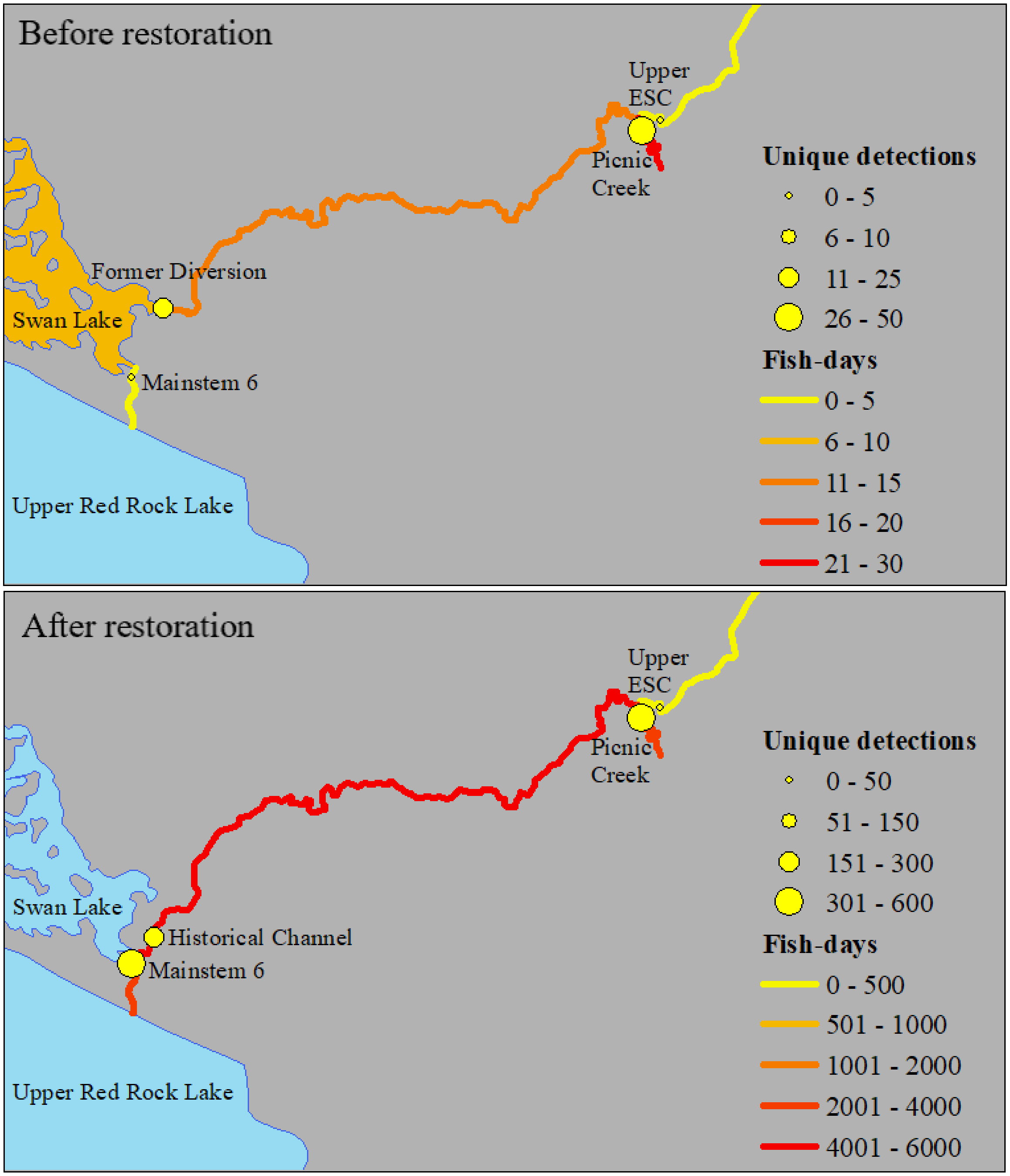

Figure 10. Inferred spatial distributions and numbers of unique detections of White Suckers in Elk Springs and Picnic creeks before (May 1 through September 15, 2016) and after (September 16, 2016, through October 26, 2018) restoration. Fish-days are defined as the total numbers of days per fish spent in unique segments (between fixed PIT interrogation stations, below Mainstem 6 station, and above Upper ESC and Picnic Creek stations) of Elk Springs and Picnic creeks before and after restoration. A unique detection is defined as one detection per day per individual fish; unique detection totals are represented by yellow circles.

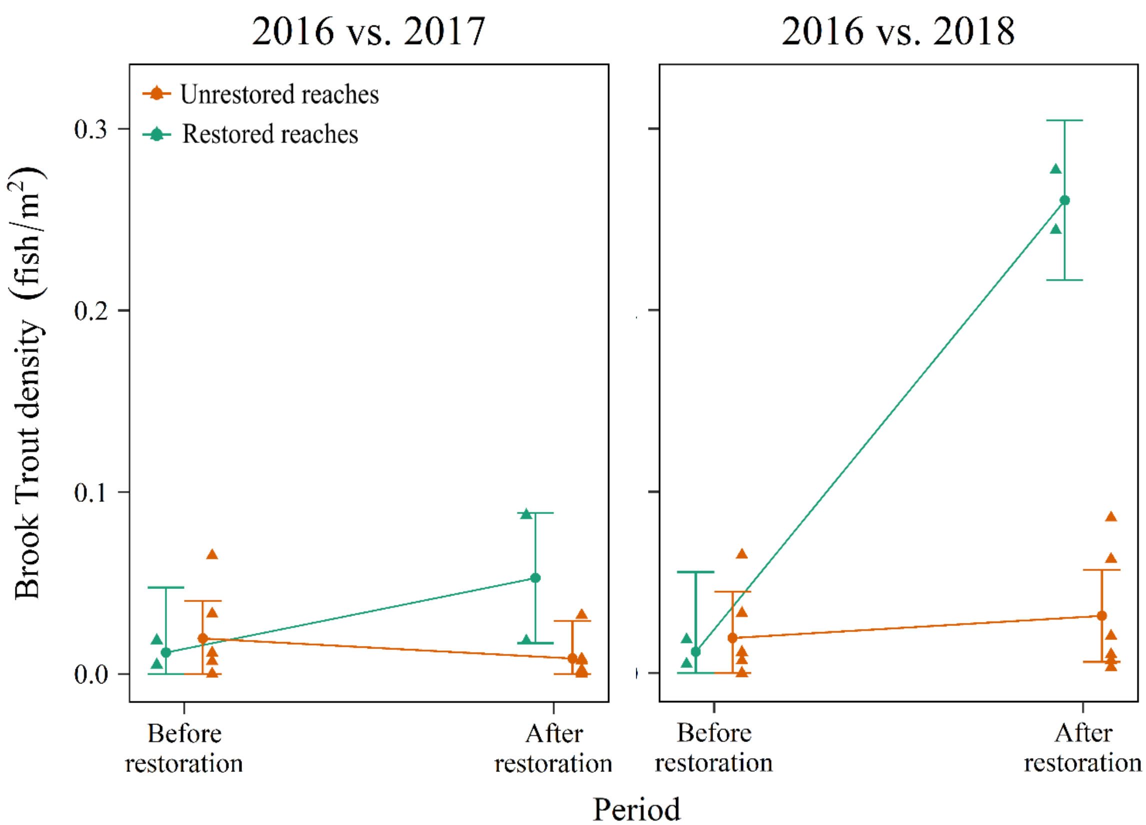

Figure 11. Relationships between Brook Trout numeric densities (fish/m^2) and periods in restored (Mainstem 1 and 2) and unrestored (East Fork, West Fork, Picnic Creek, and Mainstem 3, 4, and 5) reaches in 2016 (before restoration) versus 2017 (after restoration) and 2016 (before restoration) versus 2018 (after restoration). Solid triangles represent Brook Trout density estimates and solid circles represent mean Brook Trout densities for each period in impact and control reaches. Error bars indicate 95% confidence intervals of mean Brook Trout density.

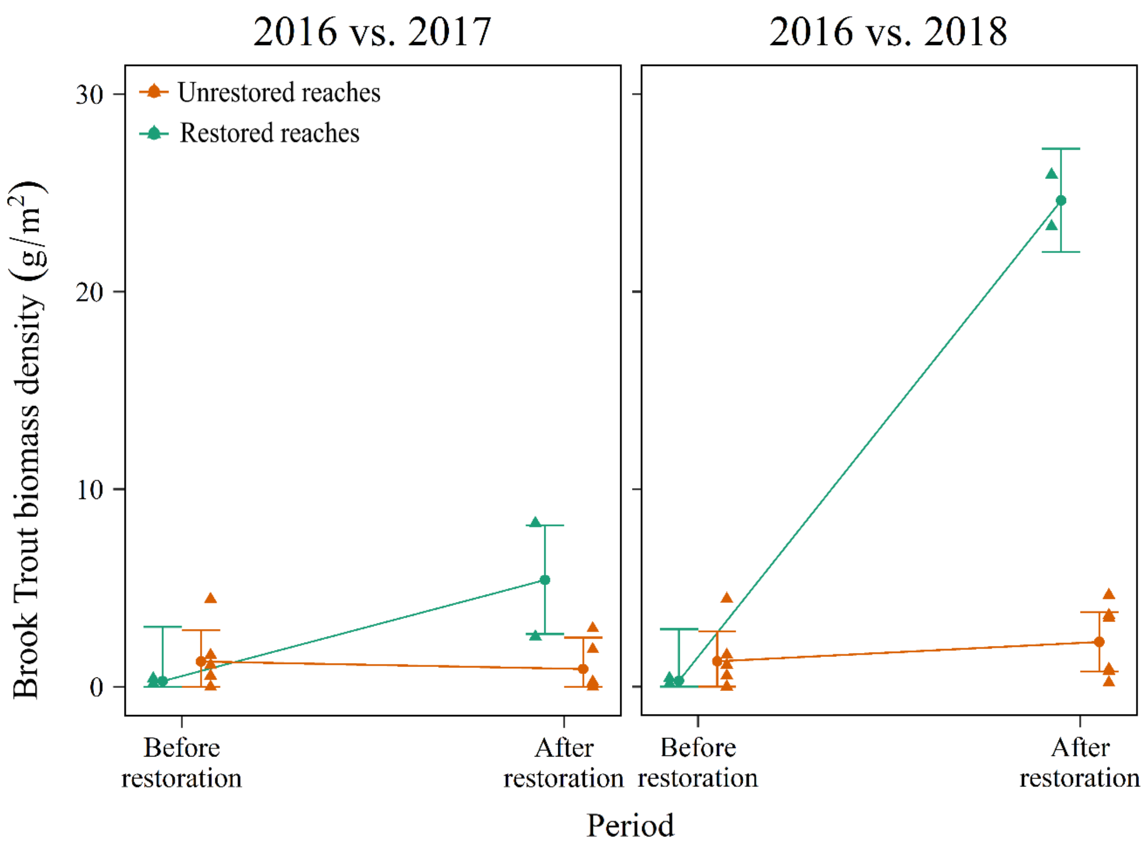

Figure 12. Relationship between Brook Trout biomass densities (g/m^2) and period in restored (Mainstem 1 and 2) and unrestored (East Fork, West Fork, Picnic Creek, and Mainstem 3, 4, and 5) reaches in 2016 (before restoration) versus 2017 (after restoration) and 2016 (before restoration) versus 2018 (after restoration). Solid triangles represent Brook Trout biomass density estimates and solid circles represent mean Brook Trout biomass densities for each period in restored and unrestored reaches. Error bars indicate 95% confidence intervals of mean Brook Trout biomass densities.

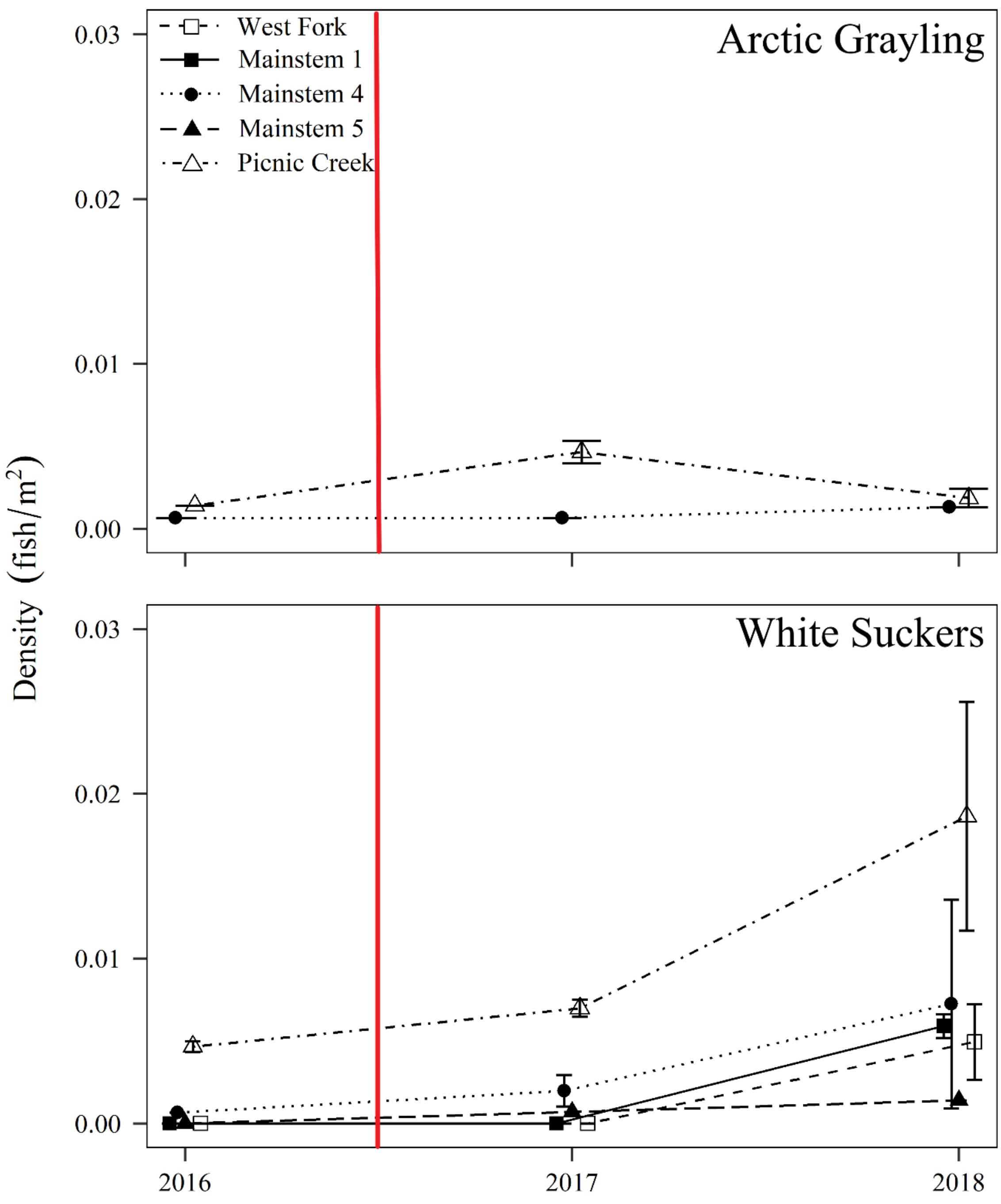

Figure 13. Numeric densities (fish/m^2) of Arctic Grayling in Mainstem 4 and Picnic Creek and numeric densities of White Suckers in West Fork, Mainstem 1, 4, and 5, and Picnic Creek before restoration in May 2016 and after restoration during May 2017 and 2018. No Arctic Grayling were collected in East Fork, West Fork, and Mainstem 1, 2, 3, and 5 and no White Suckers were collected in East Fork, and Mainstem 2 and 3 during the study. Vertical red line indicates timing of restoration.

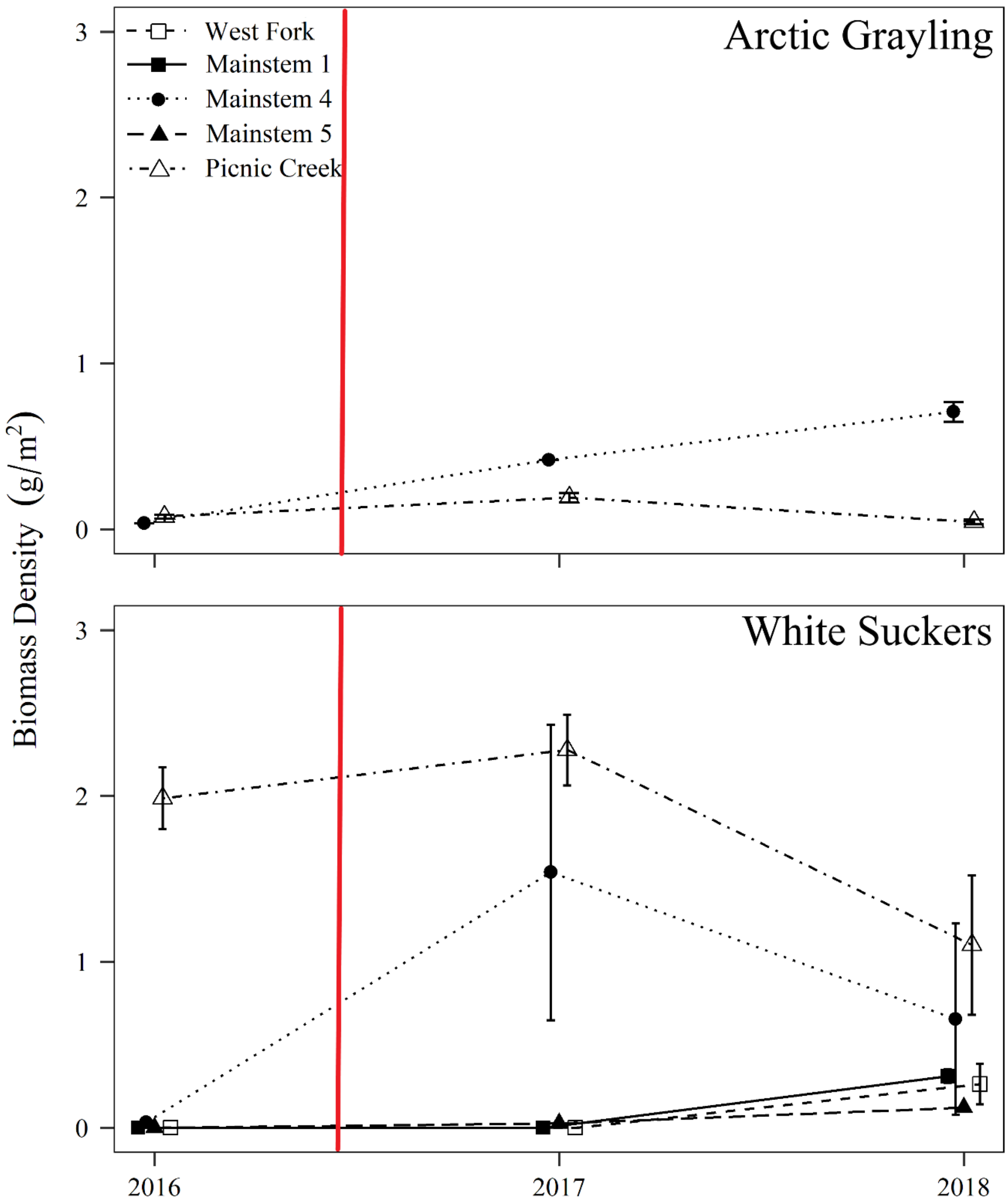

Figure 14. Biomass densities (g/m^2) of Arctic Grayling in Mainstem 4 and Picnic Creek and biomass densities of White Suckers in West Fork, Mainstem 1, 4, and 5, and Picnic Creek before restoration in May 2016 and after restoration during May 2017 and 2018. No Arctic Grayling were collected in East Fork, West Fork, and Mainstem 1, 2, 3, and 5 and no White Suckers were collected in East Fork, and Mainstem 2 and 3 during the study. Vertical red line indicates timing of restoration.

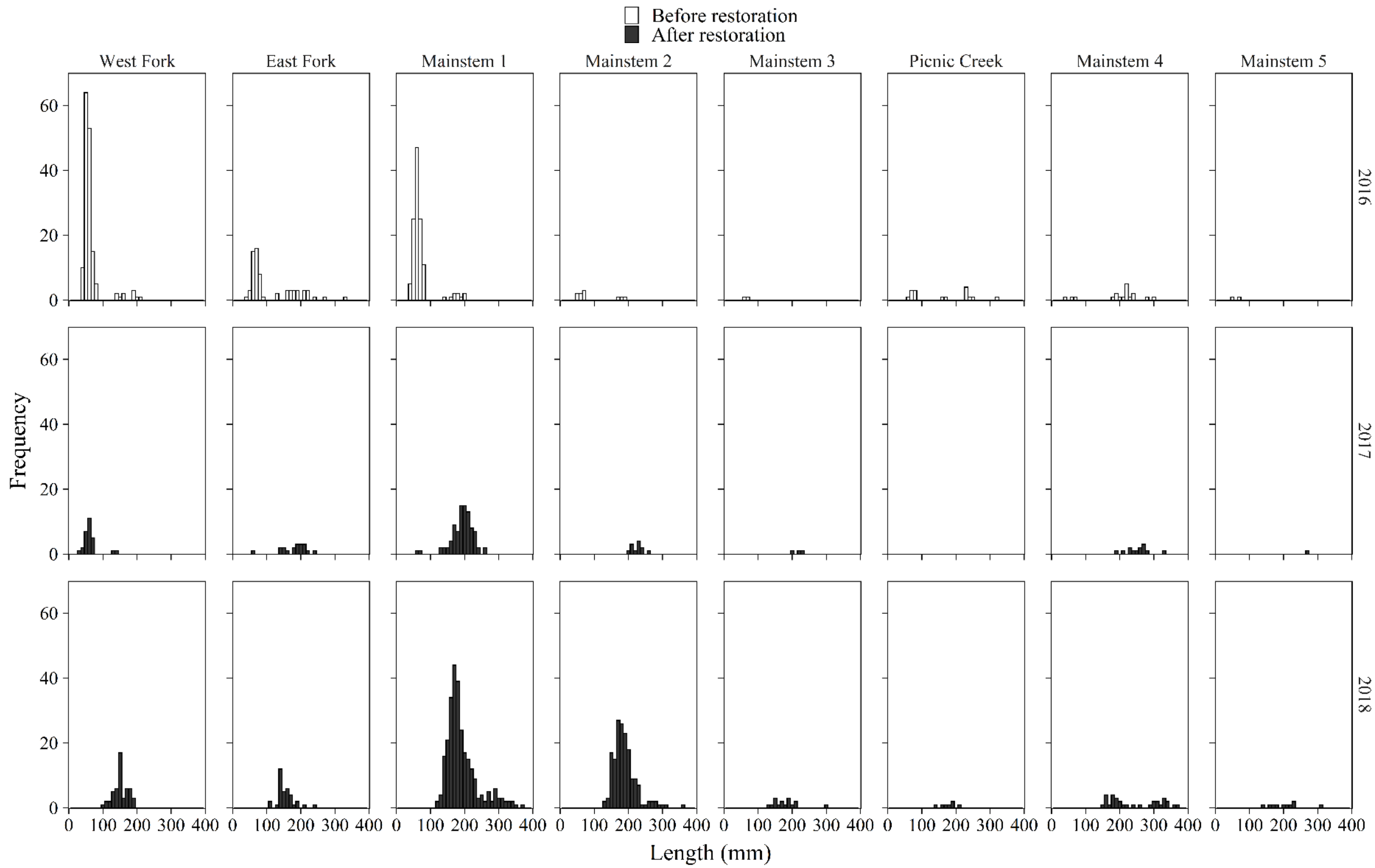

Figure 15. Length-frequency distributions of Brook Trout collected before restoration in May 2016 and after restoration during May 2017 and 2018 in two restored (Mainstem 1 and 2) reaches and six unrestored (West Fork, East Fork, Picnic Creek, and Mainstem 3, 4 and 5) reaches. Open bars represent Brook Trout collected before restoration, and closed bars represent Brook Trout collected after restoration.

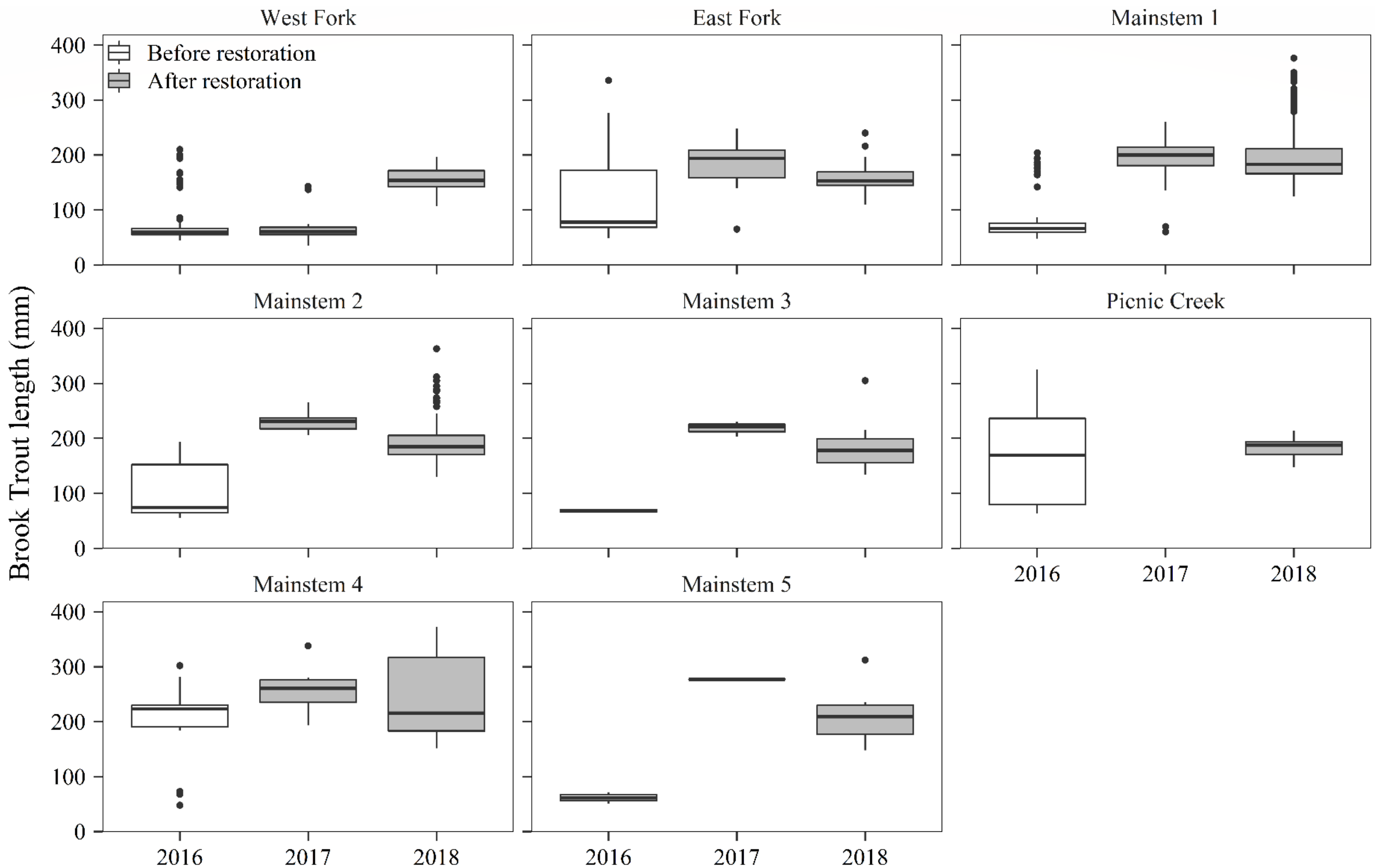

Figure 16. Lengths of Brook Trout collected before restoration in May 2016 and after restoration during May 2017 and 2018 in two restored (Mainstem 1 and 2) reaches and six unrestored (West Fork, East Fork, Picnic Creek, and Mainstem 3, 4 and 5) reaches. Box plots represent the 25th and 75th percentiles and median values. Bars represent the 10th and 90th percentiles. Closed circles represent outliers.

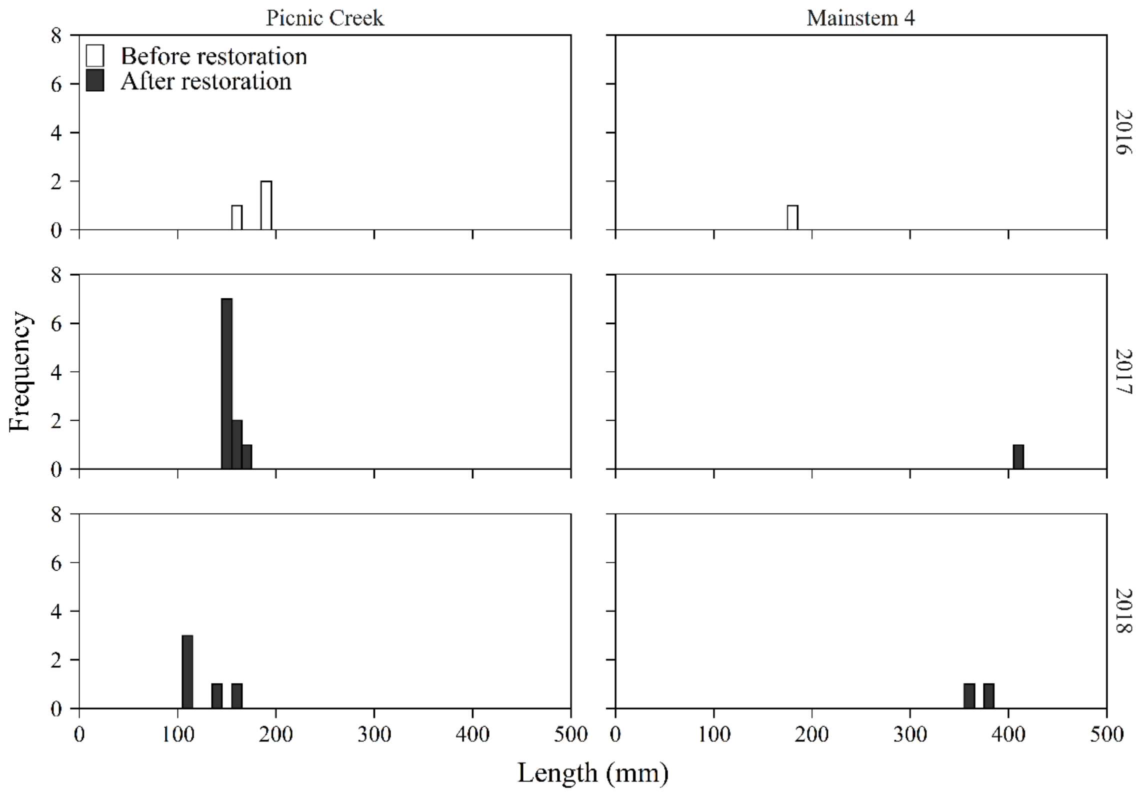

Figure 17. Length-frequency distributions of Arctic Grayling collected before restoration in May 2016 and after restoration during May 2017 and 2018 in two unrestored (Picnic Creek and Mainstem 4) reaches. No Arctic Grayling were captured in the West Fork, East Fork, and Mainstem 1, 2, 3, and 5 reaches during May 2016 to 2018. Open bars represent Arctic Grayling collected before restoration, and closed bars represent Arctic Grayling collected after restoration.

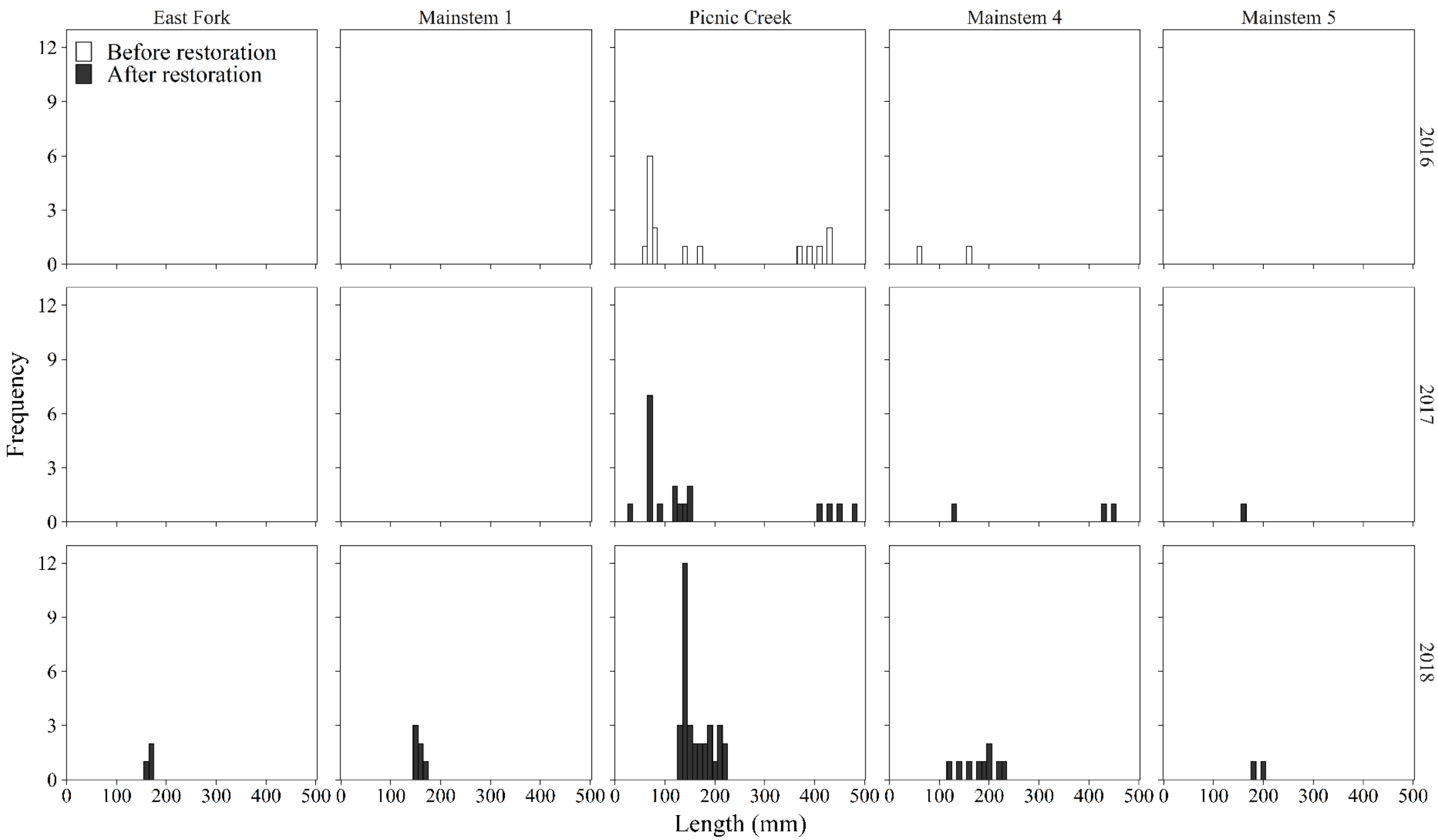

Figure 18. Length-frequency distributions of White Suckers collected before restoration in May 2016 and after restoration during May 2017 and 2018 in one restored (Mainstem 1) reach and four unrestored (East Fork, Picnic Creek, and Mainstem 4 and 5) reaches. No White Suckers were captured in the West Fork, Mainstem 2, and Mainstem 3 reaches during May 2016 to 2018. Open bars represent White Suckers collected before restoration, and closed bars represent White Suckers collected after restoration.

REFERENCES CITED

Adams, S. B., C. A. Frissell, and B. E. Rieman. 2001. Geography of invasion in mountain streams: consequences of headwater lake fish introductions. Ecosystems 4:296-307.

Albanese, B., P. L. Angermeier, and J. T. Peterson. 2009. Does mobility explain variation in colonization and population recovery among stream fishes? Freshwater Biology 54:1444-1460.

Armstrong, J. D., V. A. Braithwaite, and P. Rycroft. 1996. A flat-bed passive integrated transponder antenna array for monitoring behaviour of Atlantic salmon parr and other fish. Journal of Fish Biology 48:539-541.

Armichardy, D. J. 2008. The role of migration in community dynamics in Beaver Lake Basin. Master's thesis. Northern Michigan University, Marquette.

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

Bateman, D. S., and R. E. Gresswell. 2006. Survival and growth of age-0 steelhead after surgical implantation of 23-mm passive integrated transponders. North American Journal of Fisheries Management 26:545-550.

Bednarek, A. T., and D. D. Hart. 2005. Modifying dam operations to restore rivers: ecological responses to Tennessee River dam mitigation. Ecological Applications 15:997-1008.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308:636-637.

Brannon, E. L., M. S. Powell, T. P. Quinn, and A. Talbot. 2004. Population structure of Columbia River basin Chinook Salmon and steelhead. Reviews in Fisheries Science 12:99-232.

Boltz, G. D. 2000. Fisheries investigations on the Red Rock Lakes National Wildlife Refuge. USFWS, Progress Report, Bozeman, Montana.

Buckland-Nicks, J. A., M. Gillis, and T. E. Reimchen. 2011. Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. Proceedings of the Royal Society [online serial]. DOI: 10.1098/rspb.2011.1009.

Bunch, A. J., M. S. Allen, and D. C. Gwinn. 2010. Spatial and temporal hypoxia dynamics in dense emergent macrophytes in a Florida Lake. Wetlands 30:429-435.

Buttiker, B. 1992. Electrofishing results corrected by selectivity functions in stock size estimates of Brown Trout (*Salmo trutta* L.) in brooks. Journal of Fish Biology 41:673-684.

Calles, O., and L. Greenberg. 2009. Connectivity is a two-way street – the need for a holistic approach to fish passage problems in regulated rivers. River Research and Applications 25:1268-1286.

Carter, K. M., C. M. Woodley, and R. S. Brown. 2011. A review of tricaine methanesulfonate for anesthesia of fish. Reviews in Fish Biology and Fisheries 21:51-59.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215-244.

Champkin, J. D., G. H. Copp, C. D. Sayer, H. M. Clilverd, L. George, L. Vilizzi, M. J. Godard, J. Clarke, and A. M. Walker. 2018. Responses of fishes and lampreys to the re-creation of meanders in a small English chalk stream. River Research and Applications 34:34-43.

Colangelo, D. J. 2007. Response of river metabolism to restoration of flow in the Kissimmee River, Florida, U.S.A. Freshwater Biology 52:459-470.

Colangelo, D. J. 2014. Interim response of dissolved oxygen to reestablished flow in the Kissimmee River, Florida, U.S.A. Restoration Ecology 22:376-387.

Columbia Basin Fish and Wildlife Authority. 1999. PIT tag marking procedures manual. Columbia Basin Fish and Wildlife Authority, Portland, Oregon.

Connolly, P. J., I. G. Jezorek, K. D. Martens, and E. F. Prentice. 2008. Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. North American Journal of Fisheries Management 28:402-417.

Davis, M. N. 2016. Winter survival and habitat as limiting factors for Arctic Grayling at Red Rock Lakes National Wildlife Refuge. Master's thesis. Montana State University, Bozeman.

Dean, H. D. 1910. Annual Report to the Commissioner of Fisheries. Bozeman, Montana.

Dence, W. A. 1948. Life history, ecology, and habits of the Dwarf Sucker, *Catostomus commersonii utawana* (Mather), at the Huntington Wildlife Station. Roosevelt Wildlife Bulletin 8:81-150.

Doherty, C. A., R. A. Curry, and K. R. Munkittrick. 2010. Spatial and temporal movements of White Sucker: implications for use as a sentinel species. Transactions of the American Fisheries Society 139:1818-1827.

Eby, L. A., and L. B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River Estuary: context-dependent shifts in behavioral avoidance thresholds. Canadian Journal of Fisheries and Aquatic Sciences 59:952-965.

Fausch, K. D., B. E. Rieman, J. B. Dunham, and M. K. Young. 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conservation Biology 23:859-870.

Fox, J., and S. Weisberg. 2019. An R companion to applied regression, 3rd edition. Sage, Thousand Oaks, California.

Gangloff, M. M. 1996. Winter habitat and distribution of Arctic Grayling in Upper Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana. Master's thesis. Montana State University, Bozeman.

Geen, G. H., T. G. Northcote, G. F. Hartman, and C. C. Lindsey. 1966. Life histories of two species of catostomid fishes in Sixteenmile Lake, British Columbia, with particular reference to inlet stream spawning. Journal of Fisheries Research Board of Canada 23:1761-1788.

Gerking, S. D. 1994. Feeding ecology of fish. Academic Press, San Diego, California.

Gore, J. A. 1985. Mechanisms of colonization and habitat enhancement for benthic macroinvertebrates in restored river channels. Pages 81-102 *in* J. A. Gore, editor. The restoration of rivers and streams: theories and experience. Butterworth, Boston.

Gore, J. A., and A. M. Milner. 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? Environmental Management 14:737-753.

Gowan, C., and K. D. Fausch. 1996. Mobile Brook Trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370-1381.

Gowans, A. R. D., J. D. Armstrong, and I. G. Priede. 1999. Movements of adult Atlantic Salmon in relation to a hydroelectric dam and fish ladder. Journal of Fish Biology 54:713-726.

Hallock, R. J., R. F. Elwell, and D. H. Fry, Jr. 1970. Migrations of adult king salmon, *Oncorhynchus tshawytscha*, in the San Joaquin Delta, as demonstrated by the use of sonic tags. California Department of Fish and Game Fish Bulletin 151.

Hansen, A. G., J. R. Gardner, D. A. Beauchamp, R. Paradis, and T. P. Quinn. 2016. Recovery of Sockeye Salmon in the Elwha River, Washington, after dam removal: dependence of smolt production on the resumption of anadromy by landlocked kokanee. Transactions of the American Fisheries Society 145:1303-1317.

Henshall, J. A. 1907. Culture of Montana Grayling. Annual report to the Commissioner of Fisheries. U.S. Bureau of Fisheries Document No. 628 1-7, Bozeman, Montana.

Henshall, J. A. 1909. Annual Report to the U.S. Fish Commission. Bozeman Fish Hatchery, Bozeman, Montana.

Holden, P. B. 1979. Ecology of riverine fishes in regulated stream systems with emphasis on the Colorado River. Pages 57-74 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum, New York.

Hubert, W. A., R. S. Helzner, L. A. Lee, and P. C. Nelson. 1985. Habitat suitability index models and instream flow suitability curves: Arctic Grayling riverine populations. U.S. Fish and Wildlife Service Biological Report 82(10.110).

Huckins, C. J., and E. A. Baker. 2008. Migrations and biological characteristics of adfluvial coaster Brook Trout in a south shore Lake Superior tributary. Transactions of the American Fisheries Society 137:1229-1243.

Huckins, C. J., E. A. Baker, K. D. Fausch, and J. B. K. Leonard. 2008. Ecology and life history of coaster Brook Trout and potential bottlenecks in their rehabilitation. North American Journal of Fisheries Management 28:1321-1342.

Hunt, R. L. 1971. Responses of a Brook Trout population to habitat development in Lawrence Creek. Wisconsin Department of Natural Resources Technical Bulletin 48.

Hunt, R. L. 1976. A long-term evaluation of trout habitat development and its relation to improving management-related research. Transactions of the American Fisheries Society 105:361-364.

Hunter, C. J. 1991. Better trout habitat: a guide to stream restoration and management. Island Press, Washington, D.C.

Isaak, D. J., C. H. Luce, B. E. Rieman, D. E. Nagel, E. E. Peterson, D. L. Horan, S. Parkes, and G. L. Chandler. 2010. Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network. Ecological Applications 20:1350-1371.

Isaak, D. J., S. Wollrab, D. Horan, and G. Chandler. 2012. Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. Climate Change 113:499-524.

Jones, N. E., and R. W. Mackereth. 2016. Resource subsidies from adfluvial fishes increase stream productivity. Freshwater Biology 61:991-1005.

Jones, N. E., W. M. Tonn, G. J. Scrimgeour, and C. Katopodis. 2003. Productive capacity of an artificial stream in the Canadian Arctic: assessing the effectiveness of fish habitat compensation. Canadian Journal of Fisheries and Aquatic Sciences 60:849-863.

Junge, C., J. Museth, K. Hindar, M. Kraabøl, and L. A. Vøllestad. 2014. Assessing the consequences of habitat fragmentation for two migratory salmonid fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 24:297-311.

Jungwirth, M., S. Muhar, and S. Schmutz. 1995. The effects of recreated instream and ecotone structures on the fish fauna of an epipotamal river. Journal of Fish Biology 7:195-206.

Kaeding, L. R., and G. D. Boltz. 2004. Use of remote-site incubators to produce Arctic Grayling fry of wild parentage. North American Journal of Fisheries Management 24:1031-1037.

Kaya, C. M. 1990. Status report on fluvial Arctic Grayling, *Thymallus arcticus*, in Montana. U.S. Fish and Wildlife Service, Report to Montana Fish, Wildlife and Parks, Helena, Montana.

Kaya, C. M. 1991. Fluvial and lacustrine populations of Arctic Grayling (*Thymallus arcticus*), and implications for the only remaining indigenous population of fluvial "Montana grayling." Canadian Journal of Fisheries and Aquatic Sciences 48:53-59.

Kaya, C. M. 1992. Review of the decline and status of fluvial Arctic Grayling, *Thymallus arcticus*, in Montana. Proceedings of the Montana Academy of Science 1992:43–70.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: tests in linear mixed effects models. Journal of Statistical Software 82:1-26.

Lenth, R. V. 2016. Least-squares means: the R package lsmeans. Journal of Statistical Software 69:1-33.

Liknes, G. A., and W. R. Gould. 1987. The distribution, habitat and population characteristics of fluvial Arctic Grayling (*Thymallus arcticus*) in Montana. Northwest Science 61:122-129.

Lohr, S. C., P. A. Byorth, C. M. Kaya, and W. P. Dwyer. 1996. High-temperature tolerances of fluvial Arctic Grayling and comparisons with summer river temperatures of the Big Hole River, Montana. Transactions of the American Fisheries Society 125:933-939.

Lucas, M. C., and E. Baras. 2001. Migration of freshwater fishes. Blackwell Science, Malden, Massachusetts.

Lucas, M. C., T. Mercer, J. D. Armstrong, S. McGinty, and P. Rycroft. 1999. Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. Fisheries Research 44:183-191.

McCormick, J. H., K. F. Hokanson, and B. R. Jones. 1972. Effects of temperature on growth and survival of young Brook Trout, *Salvelinus fontinalis*. Journal of the Fisheries Board of Canada 29:1107-1112.

McGrath, C. C., and W. M. Lewis, Jr. 2007. Competition and predation as mechanisms for displacement of Greenback Cutthroat Trout by Brook Trout. Transactions of the American Fisheries Society 136:1381-1392.

Merz, J. E., and J. D. Setka. 2004. Evaluation of a spawning habitat enhancement site for Chinook Salmon in a regulated California river. North American Journal of Fisheries Management 24:397-407.

Moerke, A. H., and G. A. Lamberti. 2003. Responses in fish community structure to restoration of two Indian streams. North American Journal of Fisheries Management 23:748-759.

Mogen, J. T. 1996. Status and biology of the spawning population of Red Rock Lakes Arctic Grayling. Master's thesis. Montana State University, Bozeman.

Morita, K., S. H. Morita, and S. Yamamoto. 2009. Effects of habitat fragmentation by damming on salmonid fishes: lessons from White-spotted Charr in Japan. Ecological Research 24:711-722.

Nakamura, F., N. Ishiyama, M. Sueyoshi, J. N. Negishi, and T. Akasaka. 2014. The significance of meander restoration for the hydrogeomorphology and recovery of wetland organisms in the Kushiro River, a lowland river in Japan. Restoration Ecology 22:544-554.

Nelson, G. A. 2017. fishmethods: Fishery science methods and models in R. Available: https://CRAN.R-project.org/package=fishmethods

Nelson, P. H. 1954. Life history and management of the American Grayling (*Thymallus signifer tricolor*) in Montana. Journal of Wildlife Management 18:324–342.

Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637-676 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Northcote, T. G. 1997. Potamodromy in Salmonidae: living and moving in the fast lane. North American Journal of Fisheries Management 17:1029-1045.

Ogle, D. H., P. Wheeler, and A. Dinno. 2020. FSA: fisheries stock analysis. Available: https://github.com/droglenc/FSA

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Paterson, T. J. 2013. Estimation of the abundance and apparent survival of spawning Arctic Grayling in Red Rock Creek; Red Rock Lakes National Wildlife Refuge. Master's thesis. Montana State University, Bozeman.

Peterson, D. P., and W. R. Ardren. 2009. Ancestry, population structure, and conservation genetics of Arctic Grayling (*Thymallus arcticus*) in the upper Missouri River, USA. Canadian Journal of Fisheries and Aquatic Sciences 66:1758-1774.

Petty, J. T., J. L. Hansbarger, B. M. Huntsman, and P. M. Mazik. 2012. Brook Trout movement in response to temperature, flow, and thermal refugia within a complex Appalachian riverscape. Transactions of the American Fisheries Society 141:1060-1073.

Pierce, R., C. Podner, and K. Carim. 2013. Response of wild trout to stream restoration over two decades in the Blackfoot River basin, Montana. Transactions of the American Fisheries Society 142:68-81.

Pierce, R., C. Podner, L. Marczak, and L. Jones. 2014a. Instream habitat restoration and stream temperature reduction in a whirling disease-positive spring creek in the Blackfoot River basin, Montana. Transactions of the American Fisheries Society 143:1188-1198.

Pierce, R., C. Podner, T. Wendt, R. Shields, and K. Carim. 2014b. Westslope Cutthroat Trout movements through restored habitat and Coanda diversions in the Nevada Spring Creek complex, Blackfoot Basin, Montana. Transactions of the American Fisheries Society 143:230-239.

Platts, W. S., and R. L. Nelson. 1988. Fluctuations in trout populations and their implications for land-use evaluation. North American Journal of Fisheries Management 8:333-345.

Poole, G. C., and C. H. Berman. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environmental Management 27:787-802.

Prentice, E. F., T. A. Flagg, C. S. McCutcheon, and D. F. Brastow. 1990. PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. American Fisheries Society Symposium 7:323-334.

R Development Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available: http://www.R-project.org.

Rabalais, N. N., R. J. Diaz, L. A. Levin, R. E. Turner, D. Gilbert, and J. Zhang. 2010. Dynamics and distribution of natural and human-caused hypoxia. Biogeosciences 7:585-619.

Raleigh, R. F. 1982. Habitat suitability index models: Brook Trout. U.S. Fish and Wildlife Service Report FWS/OBS-82/10.24.

Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. Pages 334-475 *in* J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Symposium 17, Bethesda, Maryland.

Reutter, J. M., and C. E. Herdendorf. 1976. Thermal discharge from a nuclear power plant: predicted effects on Lake Erie fish. Ohio Journal of Science 76:39-45.

Rieman, B. E., D. J. Isaak, S. Adams, D. Horan, D. Nagel, C. Luce, and D. Myers. 2007. Anticipated climate warming effects on Bull Trout habitats and populations across the Interior Columbia River Basin. Transactions of the American Fisheries Society 136:1552-1565.

Rieman, B. E., J. T. Peterson, and D. L. Myers. 2006. Have Brook Trout (*Salvelinus fontinalis*) displaced Bull Trout (*Salvelinus confluentus*) along longitudinal gradients in central Idaho streams? Canadian Journal of Fisheries and Aquatic Sciences 63:63-78.

Riley, S. C., and K. D. Fausch. 1995. Trout population response to habitat enhancement in six northern Colorado streams. Canadian Journal of Fisheries and Aquatic Sciences 52:34-53.

Ritter, D. T. 2015. Connectivity in a montane river basin: salmonid use of a major tributary in the Smith River system. Master's thesis. Montana State University, Bozeman.

Rodriguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83:1-13.

Roegner, G. C., E. W. Dawley, M. Whiting, A. Whiting, and D. J. Teel. 2010. Juvenile salmonid use of reconnected tidal freshwater wetland in Grays River, lower Columbia River basin. Transactions of the American Fisheries Society 139:1211-1232.

Rose, C., and W. G. Crumpton. 2006. Spatial patterns in dissolved oxygen and methane concentrations in a prairie pothole wetland in Iowa, USA. Wetlands 26:1020-1025.

Rosenberger, A. E., and J. B. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for Rainbow Trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395-1410.

Roussel, J. M., A. Haro, and R. A. Cunjak. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated PIT technology. Canadian Journal of Fisheries and Aquatic Sciences 57:1326-1329.

Schwarz, C. J. 2014. Analysis of BACI experiments. *In* C. J. Schwarz, editor. Course notes for beginning and intermediate statistics. Available: http://people.stat.sfu.ca/~cschwarz/CourseNotes. (July 2019).

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada, Bulletin 184, Ottawa.

Sestrich, C. M., T. E. McMahon, and M. K. Young. 2011. Influence of fire on native and nonnative salmonid populations and habitat in a western Montana basin. Transactions of the American Fisheries Society 140:136-146.

Sheldon, A. L., and G. K. Meffe. 1995. Short-term re-colonization by fishes of experimentally defaunated pools of a coastal plain stream. Copeia 1995:828-837.

Shepard, B. B. 2004. Factors that may be influencing nonnative Brook Trout invasion and their displacement of native Westslope Cutthroat Trout in three adjacent southwestern Montana streams. North American Journal of Fisheries Management 24:1088-1100.

Shepard, B. B., M. L. Taper, and A. V. Zale. 2013. Improved variance estimates of biomass for stream-dwelling fish calculated using removal estimators. Transactions of the American Fisheries Society 142:841-853.

Shirey, P. D., M. A. Brueseke, J. B. Kenny, and G. A. Lamberti. 2016. Long-term fish community response to a reach-scale stream restoration. Ecology and Society 21(3):11. doi: 10.5751/ES-08584-210311

Smith, O. R. 1947. Returns from natural spawning of Cutthroat Trout and eastern Brook Trout. Transactions of the American Fisheries Society 74:281-296.

Steed, A. C. 2007. Population viability of Arctic Grayling (*Thymallus arcticus*) in the Gibbon River, Yellowstone National Park. Master's thesis. Montana State University, Bozeman.

Stoll, S., J. Kail, A. W. Lorenz, A. Sundermann, and P. Haase. 2014. The importance of the regional species pool, ecological species traits and local habitat conditions for the colonization of restored river reaches by fish. PLoS One 9:e84741.

Teixeira, A., and R. M. V. Cortes. 2007. PIT telemetry as a method to study the habitat requirements of fish populations: application to native and stocked trout movements. Hydrobiologia 582:171-185. doi: 10.1007/s10750-006-0551-z

Thompson, D. A., and H. L. Blankenship. 1997. Regeneration of adipose fins given complete and incomplete clips. North American Journal of Fisheries Management 17:467-469.

Tupper, M., and K. W. Able. 2000. Movements and food habits of Striped Bass (*Morone saxatilis*) in Delaware Bay (USA) salt marshes: comparison of a restored and a reference marsh. Marine Biology 137:1049-1058.

Twomey, K. A., K. L. Williamson, P. C. Nelson, and C. Armour. 1984. Habitat suitability index models and instream flow suitability curves: White Sucker. USFWS, Report 82/10-64, Lafayette, Louisiana.

Unthank, A. 1989. Historical overview of Red Rock Lakes National Wildlife Refuge grayling report. U.S. Fish and Wildlife Service Kalispell Field Station, Creston, Montana.

Vincent, R. E. 1962. Biogeographical and ecological factors contributing to decline of Arctic Grayling, *Thymallus arcticus* Pallas, in Michigan and Montana. Doctoral dissertation. University of Michigan, Ann Arbor, Michigan.

Warren, J., M. Jaeger, A. Gilham, K. Cutting, L. Bateman, T. Paterson, and M. Duncan. 2016. Centennial Valley Arctic Grayling adaptive management project. Annual Report. U.S. Fish and Wildlife Service, Red Rock Lakes National Wildlife Refuge, Lakeview, Montana.

Warren, J., M. Jaeger, A. Gilham, K. Cutting, L. Bateman, T. Paterson, and M. Duncan. 2019. Centennial Valley Arctic Grayling adaptive management project. Annual Report. U.S. Fish and Wildlife Service, Red Rock Lakes National Wildlife Refuge, Lakeview, Montana.

Wenger, S. J., D. J. Isaak, J. B. Dunham, K. D. Fausch, C. H. Luce, H. M. Neville, B. E. Rieman, M. K. Young, D. E. Nagel, D. L. Horan, and G. L. Chandler. 2011. Role of climate and invasive species in structuring trout distributions in the interior Columbia Basin, USA. Canadian Journal of Fisheries and Aquatic Sciences 68:988-1008.

Waite, I. R., and K. D. Carpenter. 2000. Associations among fish assemblage structure and environmental variables in Willamette Basin streams, Oregon. Transactions of the American Fisheries Society 129:754-770.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Report LA-8787-NERP, Los Alamos, New Mexico.

Wilcock, R. J., G. B. McBride, J. W. Nagels, and G. L. Northcott. 1995. Water quality in a polluted lowland stream with chronically depressed dissolved oxygen: causes and effects. New Zealand Journal of Marine and Freshwater Research 29:277-288.

Wolman, M. G. 1954. A method of sampling coarse river-bed material. Transactions of the American Geophysical Union 35:951-956.

Young, R. G., J. Wilkinson, J. Hay, and J. W. Hayes. 2010. Movement and mortality of adult Brown Trout in the Motupiko River, New Zealand: effects of water temperature, flow, and flooding. Transactions of the American Fisheries Society 139:137-146.

Zippin, C. 1958. The removal method of population estimates. Journal of Wildlife Management 22:82-90.

Zydlewski, G. B., G. Horton, T. Dubreuil, B. Letcher, S. Casey, and J. Zydlewski. 2006. Remote monitoring of fish in small streams: a unified approach using PIT tags. Fisheries 31:492-502.