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ARTICLE

Evaluating streamflow and temperature effects on Bull Trout migration and survival with linear spatial capture–recapture models

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Abstract

Objective: In the U.S. Pacific Northwest, climate change is increasing air temperatures, decreasing warm season (April–September) streamflow, and increasing cool season (October–March) streamflow. Warmer water temperatures may alter conditions for migratory coldwater fishes like the Bull Trout *Salvelinus confluentus*. Consequently, an understanding of Bull Trout migration and survival is critical for species conservation and restoration. In the Salmon River basin, Idaho, 1992 and 1993 transpired to be two of the most opposing extreme years among the past three decades for warm season water temperature and streamflow. These extremes provided a unique opportunity to retrospectively compare Bull Trout survival and migration under potential climate change scenarios.

Methods: We evaluated prespawning and postspawning migrations and survival of fluvial Bull Trout that were radio-tagged and tracked from 1992 to 1994. We used a Cormack–Jolly–Seber linear spatial capture–recapture model to simultaneously model the migration and survival of radio-tagged prespawn ($n = 58$) and postspawn ($n = 23$) Bull Trout among weeks and river reaches with streamflow, water temperature, and habitat covariates.

Result: Most individual prespawning migrations were similar among tagged fish, whereas postspawn fish adopted multiple migration and overwintering strategies. Movements of prespawn Bull Trout were larger when (1) weekly average daily maximum streamflow increased and (2) weekly average daily maximum water temperature increased. The model estimated that at least 52% of spawners survived to spawning, and mean weekly prespawning apparent survival was higher in the low-streamflow year (1992) than in the year with higher and more variable streamflow (1993). Survival of 1992–1994 fish during the 38-week postspawning period was intermediate to that in the prespawning period. Detections of prespawn Bull Trout were generally higher at sites with more complex habitats, less large woody debris, and fewer undercut banks.

Conclusion: We found that the prespawn life stage can represent a shorter time frame (14–18 weeks) with increased mortality compared to the longer postspawning period (38 weeks). Bull Trout apparent survival increased with lower streamflow variability, indicating that expected future changes in climate may adversely affect Bull Trout.

†Retired.

KEYWORDS

climate change, fluvial Bull Trout, pre- and postspawning migration, spatial capture–recapture model, streamflow, survival, water temperature

INTRODUCTION

The Bull Trout *Salvelinus confluentus* is a native Pacific Northwest (PNW) char that is listed as threatened under the U.S. Endangered Species Act (Endangered and Threatened Wildlife and Plants 1999) and that has an affinity for cold water (<16°C; Dunham et al. 2003). Like other salmonids, Bull Trout migrate long distances (Power 2002; Starcevich et al. 2012) and have diverse life histories that include both migratory (i.e., fluvial, adfluvial, and anadromous) and resident forms (Guzevich and Thurow 2017). Migratory Bull Trout attain large sizes, live up to 12 years, and may migrate over 300 km to spawning grounds in second- through fourth-order tributaries (Bjornn and Mallet 1964; Guzevich and Thurow 2017; Thurow et al. 2020; Roth et al. 2021). Several months prior to spawning, fluvial migratory Bull Trout ascend natal tributaries (Bahr and Shrimpton 2004), stage either in pools (Starcevich et al. 2012) or in habitats with concealment cover (e.g., undercut banks, vegetated banks, and large woody debris [LWD]; Guzevich and Thurow 2017; Thurow et al. 2020), and may seek thermal refugia (Isaak et al. 2016; Howell 2018). Downstream postspawning movements are generally faster than upstream prespawning migrations (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2012), with larger adults generally migrating rapidly and smaller individuals exhibiting less predictable behavior (Muhlfeld and Marotz 2005; Monnot et al. 2008). High mortality rates (~50%) for migratory postspawn Bull Trout have been reported consistently (Chandler et al. 2001; Hogen and Scarnecchia 2006; Watry and Scarnecchia 2008).

Despite numerous migration studies in Alberta, British Columbia, and the PNW, our understanding of Bull Trout migration, survival, and overwintering remains incomplete (Dare 2006; Starcevich et al. 2012). Research on prespawning and postspawning migrations and overwintering is especially lacking (Roth et al. 2021). For example, we do not know whether the sometimes-extreme water temperatures encountered by Bull Trout during migrations are associated with increased mortality, which may create a survival bottleneck (Cooke et al. 2008). Additionally, Bull Trout are among the most temperature-sensitive freshwater fishes in North America (Selong et al. 2001; Guzevich and Thurow 2017; Thurow et al. 2020; Roth et al. 2021). Therefore, water temperature, stream discharge (Starcevich et al. 2012; Sinnatamby et al. 2018), and variation in both summer and winter water temperatures and streamflow during a given year or multiple years will likely affect migration and survival (Selong et al. 2001; Meyer et al. 2014; Letcher et al. 2015; Roth et al. 2021). For example, the onset of prespawning migration from May to August may be triggered by optimal water temperatures for growth or when streamflows reach a certain threshold (COSEWIC 2012; Letcher et al. 2015; Sinnatamby et al. 2018). Bull Trout are likely vulnerable to the climatic changes that have resulted in increasing air and water temperatures, decreasing warm season (April–September) streamflows, and increasing cool season (October–March) streamflows in the PNW (summarized by Wenger et al. 2011).

Impact statement

An understanding of Bull Trout migration and survival is critical for species conservation and restoration. Results of a spatial capture–recapture model of radio-tagged Bull Trout indicate lower streamflow variability that is expected with future changes in climate may adversely affect Bull Trout.

To our knowledge, there is no published research describing the prespawning and postspawning migration survival and movements of fluvial Bull Trout as related to climatic changes in streamflow and water temperature in unregulated streams. Consequently, in this study, we analyzed a 1990s radiotelemetry data set to understand how streamflow and water temperature extremes influence the prespawning and postspawning migration and survival of fluvial Bull Trout. We hypothesized that fluvial Bull Trout survival and movements could be related to absolute and short-term changes (within weeks) and longer term changes (among weeks) in water temperature and streamflow (Benjamin et al. 2016). We also hypothesized that the encounter rate (hereafter, "detection rate") of prespawn Bull Trout that migrate slowly and conceal before spawning would be positively related to complex habitats and negatively related to habitats with less concealment cover (Rich et al. 2003). Lastly, we hypothesized that survival bottlenecks may be associated with location in the river and/or extreme water temperature during prespawning and postspawning. To examine our hypotheses, we adapted the Bayesian linear spatial capture–recapture (SCR) model from Raabe et al. (2014) to use with radiotelemetry detections to correlate migrations and survival among weeks and river reaches with time, environmental, and habitat covariates.

METHODS

Study system

We radio-tagged and tracked fluvial Bull Trout in the Rapid River and in the Salmon River, Idaho, from White Bird to New Meadows. The Rapid River is an intact and relatively undisturbed fourth-order tributary of the Little Salmon River in west-central Idaho (Figure 1). The densely forested Rapid River watershed drains 31,000 ha within the Payette and Nez Perce National Forests (Guzevich and Thurow 2017). Elevations range from 2540 m in the headwaters to 580 m at the confluence with the Salmon River. Mean stream width is 8 m, and channel morphologies are comprised largely of high-gradient riffles, runs, and other fast-water habitats. The Rapid River flow regime is typical of mountainous central Idaho streams, with peak snowmelt runoff typically occurring in late spring (May–June) and flows decreasing until the onset of fall precipitation. The Little Salmon River originates near New Meadows and flows northward for 83 km to its confluence with the Salmon River at Riggins (Figure 1). The Rapid River is a major tributary that enters 7 km upstream from Riggins. The Little Salmon River watershed drains 133,643 ha of forested and agricultural land. Elevations range from 2743 m in the headwater to 536 m at the confluence. The upper watershed is a broad, low-gradient valley that is used primarily for agriculture. In contrast to the Rapid River, extensive logging, mining, and agriculture have occurred in the Little Salmon River. The Salmon River drains 3.49 million ha of a semi-arid region of central Idaho; it is considered the wildest and most intact river of its size and is one of the longest undammed rivers (including no diversion dams) in the western United States.

The Rapid River supports both resident and fluvial forms of Bull Trout. Resident fish mature at a comparatively smaller size (<25 cm) and complete their life cycle entirely within the Rapid River or its tributaries. Fluvial fish are larger (from >30 to >60 cm) and have a more complex life cycle during which they spawn and rear in the headwaters of the Rapid River or its tributaries and migrate to downstream overwintering habitats in the Little Salmon River and the main-stem Salmon River.

Fish capture and tagging

From April to September 1992–1994, all adult Bull Trout that ascended the Rapid River were captured in a fish trap at a weir that was located 1.5 km upstream from the confluence (Figure 1). The trap was operated by the Idaho Department of Fish and Game (IDFG) Rapid River Hatchery (RRH). Bull Trout were removed from the trap daily and transferred to RRH holding ponds. We selected a subsample of captured Bull Trout for radiotelemetry tag implantation and released the remainder. Radiotelemetry is a prominent method for tracking freshwater fish (Starcevich et al. 2012; Brownscombe et al. 2019; Garavelli et al. 2021). In the years after 1992, we inspected all captured Bull Trout for evidence of prior radio-tagging. All repeat spawners and a subsample of fish that were captured for the first time were held for radio tag implantation.

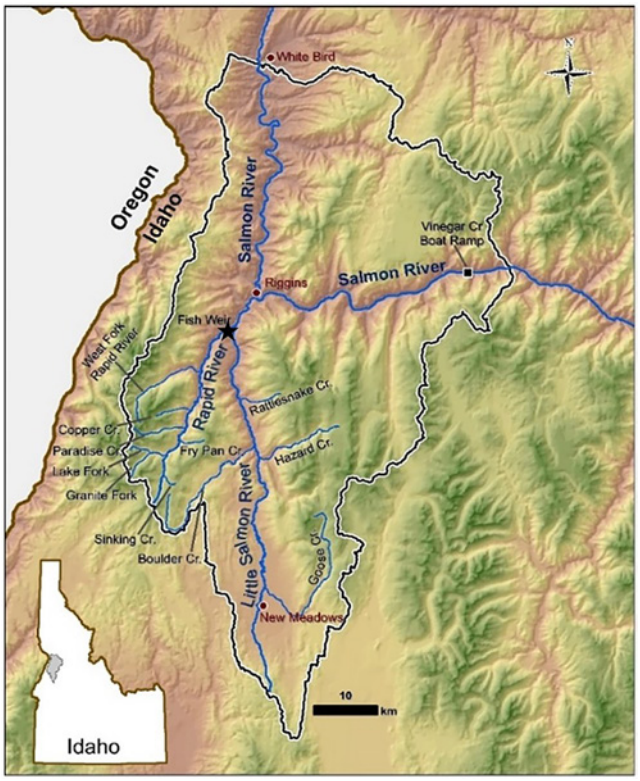

FIGURE 1 The Rapid River and Salmon River study area (blue outline) in western Idaho (colored map), USA (bottom map). Bull Trout were tracked in the Salmon River between Riggins and White Bird and in the Rapid River upstream from Riggins. The black star indicates the location of the Idaho Department of Fish and Game weir.

Prior to and during surgery, we anesthetized selected Bull Trout with tricaine methanesulfonate (MS-222). We measured the total length (mm) and weight (nearest g) of each fish; to reduce tag expulsion, we implanted a tag that was less than 2% of the fish's body weight (Winter 1996). We inserted three radio tag sizes: 35, 45, and 55 mm long, weighing 6, 10, and 20 g, respectively, with diameters from 12 to 20 mm (Advanced Telemetry Systems [ATS]). Each tag emitted a unique frequency between 150.015 and 150.685 MHz. Battery life exceeded 12 months and often approached 24 months. Some recovered tags were subsequently inserted into newly captured fish and were given new identifiers for modeling.

During surgery, we placed fish in a net cradle and constantly aerated their gills with a water bath via a sprayer and bilge pump recirculating anesthetic water. To avoid heat stress, we performed surgeries in a cooled room between 2100 and 1500 hours. We began surgery by making a 20–30-mm incision through the ventral abdominal wall anterior to the pelvic girdle and inserted the external whip antenna posterior to the pelvic girdle. After inserting the tag in the coelomic cavity, we closed the incision with three to four stitches by using a one-half-curved needle and a 4–0 collagen suture. We applied Betadine disinfectant to the incision location before and after surgery and to the antenna exit site. Surgeries were completed by experienced biologists within approximately 5 min. After surgery, a Floy tag (Dell 1968) was inserted into each fish to facilitate visual identification of radio-tagged Bull Trout and to monitor radio tag loss. We held individual fish in a recovery tank before releasing them back into the Rapid River upstream from the RRH water intake. Fish were released either during the same evening as capture or within 24 h of capture. We were unable to determine the sex of migrating fish or to verify their maturity status.

Radio-tracking

We tracked fish in streams ranging from second-order Rapid River headwater tributaries to the eighth-order main-stem Salmon River. Radio-tagged Bull Trout were actively tracked during prespawning (including spawning) and postspawning (including overwintering) from the ground and air by using an ATS Model R2100 receiver equipped with a three-element Yagi directional antenna. Immediately after tagged fish were released, we hiked roadless reaches throughout the Rapid River or until all known alive fish were detected, and we searched for tag signals once every week to 2 weeks (Figure S1 available in the Supporting Information in the online version of this article). Upon detecting a tag, we pinpointed the location by triangulation, listened for the maximum acoustic signal strength, visually observed the signal strength display, and set the display at the lowest possible power gain. During initial surveys, we assessed receiver detection ranges to inform our tracking protocols. When possible, we sought visual contact with the tagged fish and its Floy tag or radio tag antenna and sometimes used snorkeling gear to locate the fish (Thurow 1994). Ground-based surveys were supplemented by aerial tracking from a Cessna 206, with two-element antennae mounted to each wing. Aerial tracking was ground-truthed for accuracy once in 1992 and twice in 1993 before we conducted aerial surveys. An experienced backcountry pilot flew approximately 300 m above the stream channel at 130–150 km/h. We flew the Rapid River, the Little Salmon River, and the main-stem Salmon River and scanned transmitter frequencies at 2-s intervals using a programmable ATS receiver. The point of maximum acoustic signal strength was considered the tagged fish's location, and the aircraft was circled to confirm locations. Locations that were detected aerially or from the ground were marked on detailed topographic maps and used to create a digitized drainage map with Global Positioning System coordinates.

We classified Bull Trout as either prespawn (upstream) or postspawn (downstream) depending on their direction of movement. Although a small number of radio-tagged fish were observed on redds and actively spawning, we were unable to discern whether most of the relocated tagged fish had spawned, so some prespawn or postspawn locations may have been from spawning fish. After the fish had vacated the redds, we continued searching for postspawn fish, either aerially or via ground-based hiking surveys or vehicle-based surveys on roads adjacent to the Little Salmon River and the main-stem Salmon River, at a slightly reduced intensity than during prespawning (Figure S1).

Rapid River habitat covariates

We derived a total of 19 habitat covariates for prespawn fish from data collected in the Rapid River during continuous warm season (April–September) stream surveys by Overton et al. (1993, 1997). Further, we developed reach-level habitat covariates by dividing the study area into a total of 102 reaches, with each reach being approximately 1 km. The Rapid River was divided into 36 reaches, its two headwater tributaries (Lake Fork and Granite Fork) were divided into four reaches each, and the Salmon River was divided into 58 reaches. We assigned prespawn radio-tagged fish relocations to these ~1-km reaches. Bull Trout did not spawn in the Little Salmon River or the Salmon River, and we did not measure habitat covariates in those rivers.

We derived 11 habitat unit covariates for Rapid River reaches by calculating the proportion of channel area comprised of fast- and slow-water habitat types in each ~1-km reach (Table S1 available in the Supporting Information in the online version of this article). Habitat units are discrete geomorphic segments within stream channels categorized by specific habitat types (Overton et al. 1993, 1997). Habitat types were identified by flow patterns and channel bed shape (Hawkins et al. 1993), and boundaries were recognized by changes in channel slope, morphology, substrate, and LWD (Overton et al. 1997). At the coarsest scale, we identified habitats as fast-water or slow-water types. Fast-water habitats included channel units

with moderate to fast current velocities (average velocity >0.30 m/s) in six categories (Overton et al. 1997). Slow-water habitats included channel units defined as "pools" in five categories, which were formed either by scour or damming (Overton et al. 1997). We calculated habitat unit area by multiplying habitat length (measured along the middle of the channel) by the average wetted width across three representative transects equal to 0.25, 0.50, and 0.75 times the length of the habitat unit (Overton et al. 1997). We then calculated the proportion of the reach in each habitat type by dividing by the habitat unit area. We calculated two additional habitat covariates based on the habitat unit data: (1) a habitat unit diversity index, which was calculated by using all habitat types in a reach following Schlosser (1982) and Gorman and Karr (1978); and (2) a pool proportion habitat covariate, which included all pool habitat unit types (Table S1).

We developed five additional covariates using depth, streambank, and LWD data collected by Overton et al. (1993, 1997; Table S1). We calculated average depth by summing nine depth measurements (crews used a rod to probe depths at 0.25, 0.50, and 0.75 times the wetted width of each of the three transects where width was measured) and dividing by 12; at each transect, a measure of zero was included to account for a theoretical depth of zero at the start of each transect (Overton et al. 1993, 1997). For each reach, we calculated average habitat depth and the standard deviation (SD) of habitat unit depths to use as covariates (Table S1).

We calculated a vegetated stable bank covariate as the sum of left and right stable banks divided by the length of the habitat unit per reach. Vegetated stable bank length (m) was visually estimated by crews as the bank length (1) without an exposed bank, bank slipping/slumping, tension cracking/fracture, or erosion; (2) with over 50% of the bank covered by perennial vegetation, roots, cobble-size or larger rocks, or logs (diameter ≥0.1 m); and (3) with a bank angle less than 80° from horizontal.

For each Rapid River reach, we calculated the mean proportion of undercut bank, defined as the bank length that was undercut at least 5 cm and was directly (within 0.1 m) above the water surface, from both the right and left banks (Overton et al. 1997). We summed undercut lengths and divided by the lengths of all habitat units to derive a mean proportion of undercut bank per reach. We calculated reach LWD density as the mean density of LWD (>3 m long ×0.1 m in diameter [measured one-third up from the base]), rootwads, and wood aggregates (see definitions in Overton et al. 1997) across all habitat units per reach (Table S1). We created an additional overhead cover covariate with a principal components analysis of total vegetated stable bank, LWD density, and the proportion of undercut stable bank per reach.

During the postspawning period (August 19–May 12), we recorded few detections in the Rapid River. Although we recorded more detections in the Salmon River, the large river size prevented us from measuring habitat covariates as we did in the Rapid River. In addition, our sampling protocol was slightly different during the postspawning season compared to the prespawning season, when we searched for fish more frequently (Figure S1). Therefore, we analyzed the prespawning and postspawning periods separately. To increase our sample size, we pooled postspawning locations in the Rapid and Salmon rivers from 1992 to 1994.

Weekly streamflow and water temperature covariates

Serendipitously, two of the most extreme warm season water temperatures and streamflows during the past three decades were recorded in 1992 and 1993, as evidenced by several metrics (Figures 2 and 3). Among the years from 1992 to 2018, 1992 had some of the warmest observed May–August maximum water temperatures, in contrast to 1993, which had the coldest maximum water temperatures during the same months (Figure 2). Similarly, over the previous three decades, the Rapid River in 1992 had the lowest observed maximum warm season streamflow in contrast to 1993, which had among the highest maximum streamflows, particularly from May to July (Figure 3). Warm season streamflows during the 1990s were generally higher compared to those in the 2010s (Figure 3). Interestingly, during the postspawning cool season from 1992 to 1994, water temperatures and streamflows were less variable than those observed in the previous three decades, as evidenced by several metrics (Figures 4 and 5).

Consequently, we used hourly water temperatures recorded by a thermograph anchored near the RRH intake, coupled with data from two upstream thermographs, to construct five short- and long-term absolute and delta current and past water temperature covariates for the two prespawning Rapid River models and one postspawning Rapid River model (Figures 2 and 4). The five temperature covariates were (1) weekly maximum hourly water temperature in the current week, (2) average maximum daily temperature in the current week, (3) the 3-day moving average of the maximum daily temperature within a week, (4) average hourly temperature in the current week, and (5) difference (delta) between the previous week's average daily temperature and the current week's average (Figures 2 and 4).

Water temperature records at RRH were missing for prespawning weeks 11–19 in 1992 and prespawning weeks 12–18 in 1993; therefore, we imputed data for those weeks to

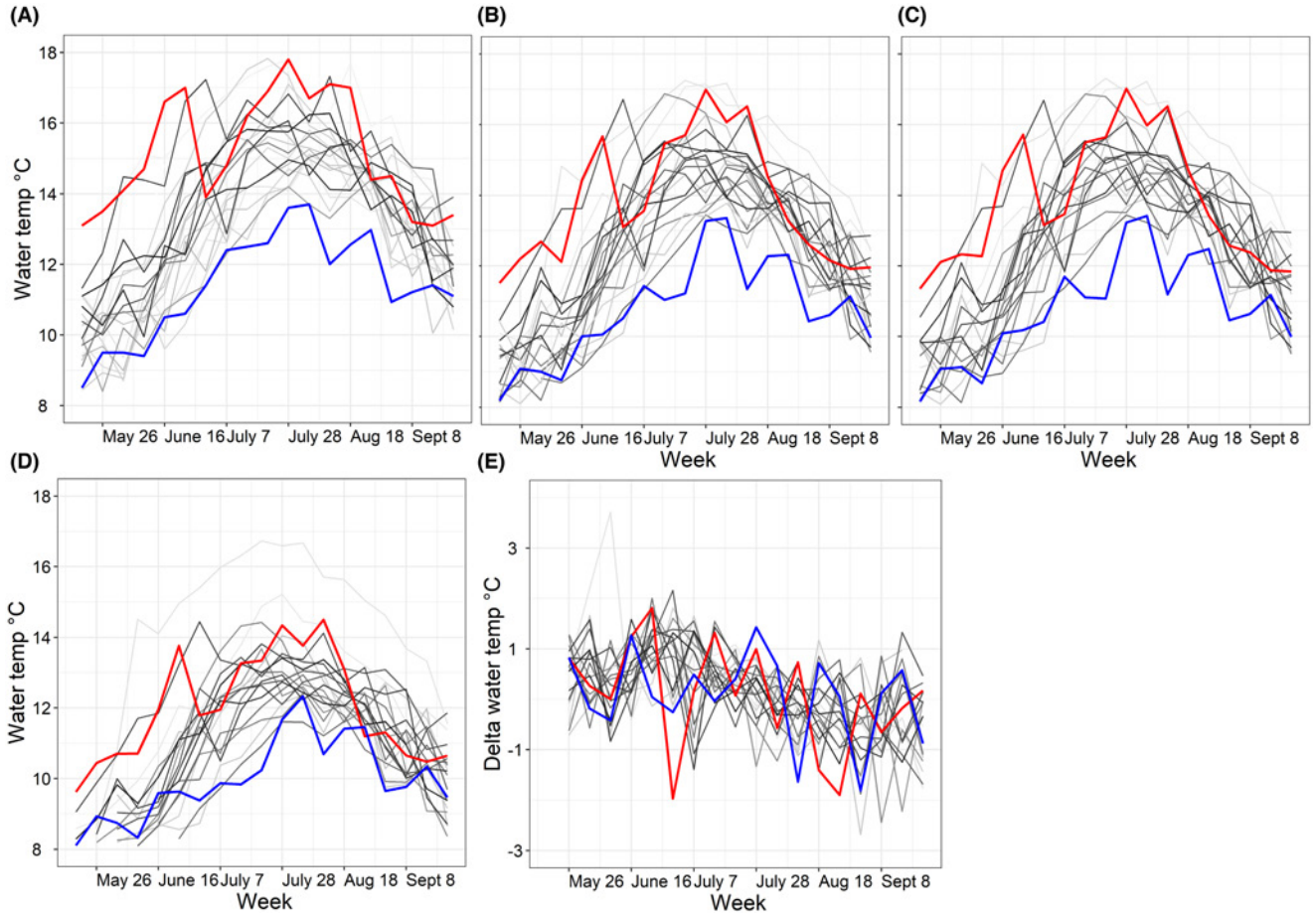

FIGURE 2 Rapid River Hatchery thermographs from May 19 to September 28 in 1992 (red line), 1993 (blue line), and the years 1994–2018 (lighter gray lines represent earlier years; darker gray lines represent later years) without missing data for five water temperature covariates tested in Idaho Bull Trout prespawning models: (A) weekly maximum hourly water temperature (temp; °C), (B) weekly average daily maximum water temperature, (C) weekly 3-day moving average of the maximum daily temperature, (D) weekly average hourly temperature, and (E) difference (delta) between the previous week's average daily temperature and the current week's average.

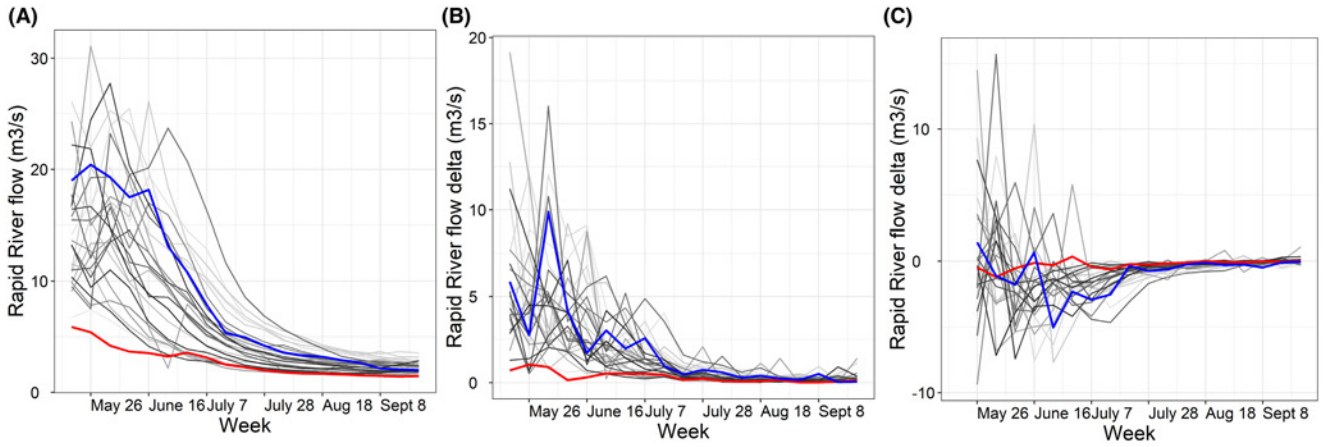

FIGURE 3 Rapid River weekly streamflow (m^3/s; U.S. Geological Survey gauge 13316390) during 18 weeks from May 19 to September 28 in 1992 (red line), 1993 (blue line), and the years 1994–2018 (lighter gray lines represent earlier years; darker gray lines represent later years) used as flow covariates in the Bayesian linear spatial capture–recapture Bull Trout prespawning model: (A) mean weekly streamflow, (B) difference (delta) between maximum streamflow and minimum streamflow in the current week, and (C) difference between the current week's streamflow and the previous week's streamflow.

be used in the prespawning SCR models from the two closest upstream thermographs from the 1990s (1997 and 1999) using the R package simputation (van der Loo 2021). We also used Rapid River thermographs to construct the same weighted water temperature covariates (as described above) to use in our postspawning model (Figure 4). We justified imputing the missing 1992 and 1993 data because water temperature trends were similar over the prespawning and postspawning periods among years throughout the 1990s (Figures 2 and 4).

We used Rapid River streamflows recorded near RRH (U.S. Geological Survey [USGS] gauge 13316390) to construct three different weekly streamflow metrics to use as prespawning streamflow covariates (Figures 3 and 5). The three streamflow metrics were (1) mean weekly streamflow; (2) difference (delta) between the maximum streamflow and minimum streamflow within the current week, where a negative sign denotes decreasing streamflow and a positive sign represents increasing streamflow; and (3) difference between the current week's mean streamflow and the previous week's mean streamflow (Figure 3). We used streamflow recorded in the Salmon River near White Bird (USGS gauge 13317000) to construct the same three streamflow covariates described above for use in a third, separate postspawning model (Figure 5). Because the cool season (October–March) environmental trends were similar among the years studied, we pooled 1992–1994 streamflow data and created a 3-year average weighted by the number of postspawn fish that were tracked in each year (Figure 5).

Spatial capture–recapture modeling

We adapted the Raabe et al. (2014) linear SCR model for use with the Bull Trout radiotelemetry data, where reaches correspond to arrays used in other fish migration studies (Gardner et al. 2010). The linear SCR model uses the basic

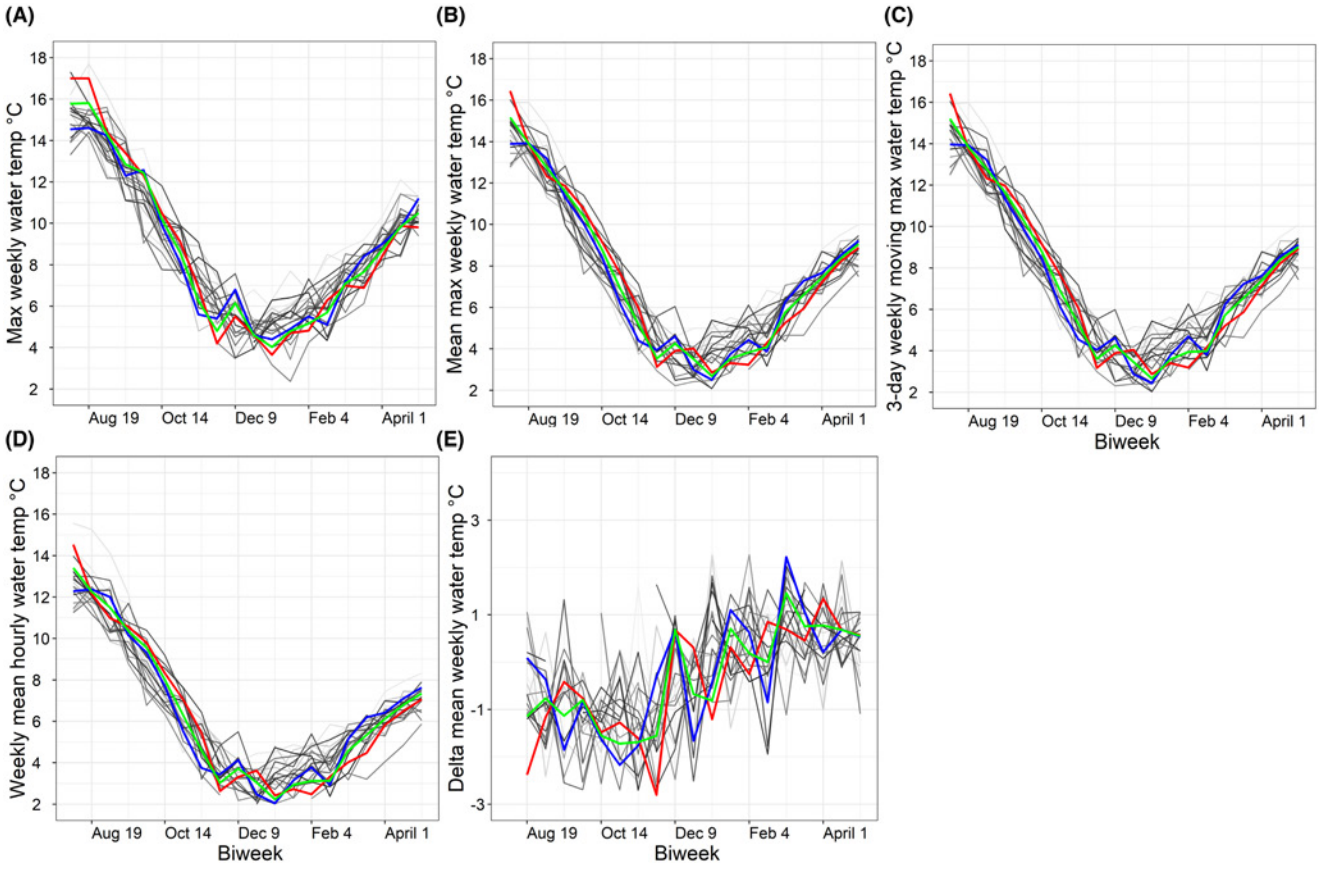

FIGURE 4 Rapid River Hatchery thermographs for 19 weeks from August 12, continuing into the new year, and ending on May 12 for 1992 (red line), 1993 (blue line), and the years 1994–2018 (lighter gray lines represent earlier years; darker gray lines represent later years) without missing data. The average weighted by the proportion of Bull Trout tracked per year (green line) is included. The five water temperature covariates used in the Bull Trout postspawning linear spatial capture–recapture models were (A) weekly maximum hourly water temperature (temp; °C), (B) weekly average daily maximum water temperature, (C) weekly 3-day moving average of the maximum daily temperature, (D) weekly average hourly temperature, and (E) difference (delta) between the previous week's average daily temperature and the current week's average.

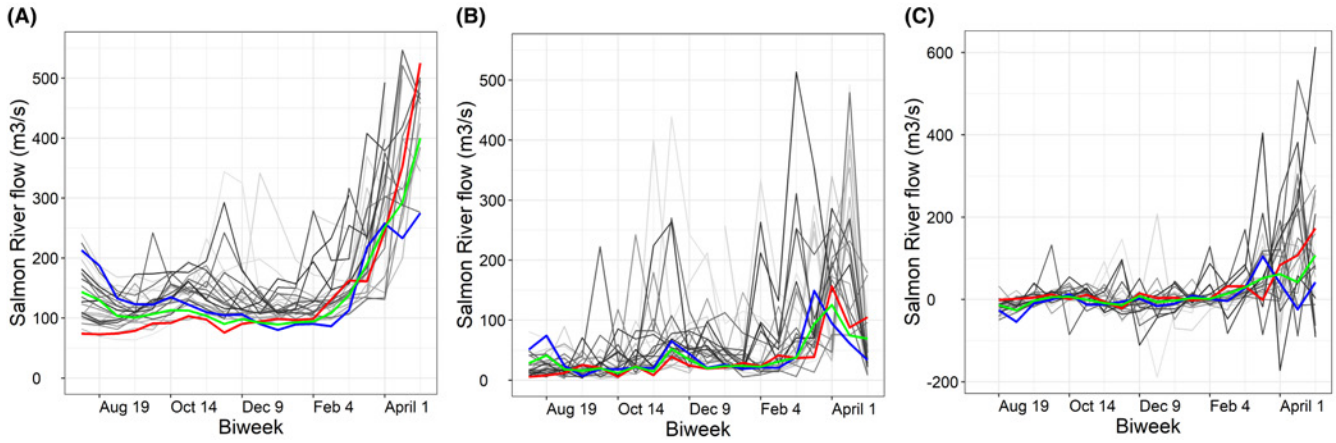

FIGURE 5 Salmon River biweekly streamflow (m^3/s; U.S. Geological Survey gauge 13317000 [Salmon River at White Bird]) from August 12, continuing into the new year, and ending on May 12, used for modeling flow in the Bayesian linear spatial capture–recapture Bull Trout postspawning model. The red solid line represents 1992, the blue line represents 1993, the green line represents the weighted average of 1992 and 1993, and the gray lines represent the years 1994–2018 (lighter gray lines represent earlier years; darker gray lines represent later years) used for flow covariates, including (A) mean weekly streamflow, (B) difference (delta) between maximum streamflow and minimum streamflow in the current week, and (C) difference between the current week's streamflow and the previous week's streamflow.

framework of the Jolly–Seber open SCR model (Gardner et al. 2010) with a Cormack–Jolly–Seber (CJS) formulation that is conditional on first capture. Spatial capture–recapture models offer an efficient, precise, and unbiased method for estimating the spatial scale of detection rates and the effects of environmental covariates on detection rates, movements, and survival simultaneously (Gardner et al. 2010; Raabe et al. 2014; Harris et al. 2021), even for species with low detection rates (Blanc et al. 2013; Royle et al. 2014; Leuenberger et al. 2019).

The Raabe et al. (2014) linear SCR model is an extension of the Gardner et al. (2010) SCR model for migrating stream fishes that requires detection coordinates, capture–recapture histories of marked individuals, and covariates. The main components of the SCR model are an observation model based on detections ($\lambda_{i,j,t}$); a state model ($z_{i,t}$) based on whether the fish was alive and in the river system, was dead, or had emigrated; and latent individual activity (or home range) centers ($S_{i,j}$; Gardner et al. 2010; Raabe et al. 2014). We used the Raabe et al. (2014) SCR model in a Bayesian framework to evaluate the relationship between environmental and habitat covariates and Bull Trout telemetry detection rates, survival, and movement distances over time. We used telemetry data that were collected and based on a sampling design used before the advent of linear SCR modeling (i.e., 2008; Smith et al. 2020); however, because the data were collected for an organism that could only be alive and confined to a small linear area, we believe that the telemetry data met the spatial assumptions of the CJS linear SCR model.

Spatial capture–recapture models require standard open capture–recapture model assumptions, including the following: (1) tagged individuals are representative of the population, (2) tagging does not influence survival, (3) mortality events can be attributed to a specific time period and location, (4) tagged fish are independent, (5) subsequent recaptures do not influence fish status, (6) relocation probability is similar among tagged individuals, and (7) the status of tagged fish is correctly identified (i.e., tags were not lost and dead fish were not interpreted as alive; Williams et al. 2002; Perry et al. 2012). We used Bull Trout telemetry data for our recapture events, and due to large detection ranges, telemetry data often have greater detection probabilities than conventional mark–recapture methods (Perry et al. 2012). Telemetry can be used to detect tagged fish one or more times at specific locations and time periods, thus fulfilling the model assumptions for recapture (Perry et al. 2012). We handled this assumption differently than Raabe et al. (2014) in that we conducted active telemetry over standardized spatial and temporal intervals as opposed to using passive telemetry arrays. Live fish were constrained to remain within the boundaries of the river and therefore had to pass through the river on their migration; hence, we were able to assign passive telemetry detections to a reach or "trap" by dividing the river into reaches as in Leuenberger et al. (2019). Thus, we could model reaches as "count" detectors for which the detection process followed a Poisson distribution, as reaches were spatially fixed and multiple fish could have visited the same reach or multiple reaches multiple times during an occasion

(Royle et al. 2014; Murphy et al. 2021). Assigning detections to "trap areas" in SCR models has been conducted by other researchers recently with camera trap data (Warbington and Boyce 2020), fecal samples at latrines (Murphy et al. 2021), hair traps (Balmori-de la Puente et al. 2023), and water snakes in stream reaches (Leuenberger et al. 2019).

We believe that we met the basic assumptions and requirements of SCR models using telemetry data, with some additional caveats. Our tagged fish satisfied the independence assumption aside from two prespawn fish that did not survive tagging. However, all other fish were later detected at or close to the end of their migration near spawning sites, indicating that these tagged fish were representative of the untagged population, and we simply removed the two tagging mortalities from the data set. The maximum sampling area of receivers was over 1500 m. Given the generally shallow depths (i.e., <2 m) and low conductivity (<60 μS/cm in the study area; Peters et al. 2008) and given that the timing (1 day) of our telemetry methodology was on a much finer scale than the trap location and survival period, observations from fish after they were detected as dead (i.e., not moving or tags recovered) were removed from the data set. We presumed that fish with multiple records from the exact same location were dead, and we assigned the record to the first period in which we observed the fish at that location. Finally, fish recaptures were passive via telemetry and did not influence the status of the fish, and all fish detected throughout the Rapid and Salmon rivers had the same detection probability.

Model specification

To evaluate possible effects of contrasting warm season hydrothermal regimes on Bull Trout prespawning migration and survival and to assess habitat effects on detection rates, we developed two separate 1992 and 1993 prespawning SCR models. We evaluated a third pooled postspawning model for Bull Trout from both the Rapid River and the Salmon River because cool season streamflow and water temperature were similar from 1992 to 1994.

The beginning of each sampling reach (j) was assigned a linear river kilometer (RKM). It was possible for each tagged fish to be detected in any ~1-km reach any number of times during a particular week (Raabe et al. 2014). A prespawn fish's week of entry into the study (f_i) was either (1) its capture at the weir or (2) for a fish tagged in a prior year, its first detection in the first reach. For the 1993 prespawning model, we constructed a binary "maturity" variable to denote newly tagged fish versus fish that were initially tagged in 1992. We also constructed a fish size variable using lengths that were measured at tagging. A postspawn fish's entry into the study occurred in the reach and week in which the fish reversed its direction of movement from upstream to downstream. For time periods after the first entry into the model, the alive state ($z_{i,t}=1$) tracked which fish survived to the next period, defined as $z_{i,t} \sim \text{Bernoulli}(\phi z_{i,t-1})$, where the individual survived to time t with probability ϕ when $z_{i,t-1}$ was equal to 1. We censored fish that were known to be alive (e.g., detected in the following year) but that were not detected in the last period by creating a last vector for all fish in the alive state ($z_{i,t}$). In addition, for postspawn Bull Trout, we censored the fish when we could no longer hear the tag signal because of presumed battery failure prior to the end of the study period. Below, we describe the four component submodels used in the analysis.

Detection submodel

Our Bull Trout detection histories ($y_{i,j,t}$) were counts (number of locations) of individual fish ($i=1, 2, ..., n$) in each ~1-km reach ($j=1, 2, ..., J$) summarized by weekly (prespawning) or biweekly (postspawning) time periods ($t=1, 2, ..., T$; Raabe et al. 2014). Detection histories were conditional on the alive state ($z_{i,t}$) and followed a Poisson distribution, where the parameter λ_0 is the expected number of detections per reach (Raabe et al. 2014). We allowed λ_0 to vary with uncorrelated habitat covariates that we developed from the Overton et al. (1997) surveys by reach (Table S1). We had a few habitat covariates that were correlated ($|r|>0.70$), and we did not test them in the same λ_0 submodels (Moore and McCabe 2005). Specifically, the following sets of covariates were not included in the same model: (1) the principal component of overhead cover and the proportion of vegetated stable bank per reach, (2) the principal component of overhead cover and the proportion of undercut bank per reach, (3) the proportion of the reach in step pool complex habitats and the proportion of the reach in pool habitat, and (4) the SD of the depth of habitat units in the reach and the proportion of the reach in run habitat (Table S2). We also allowed λ_0 to vary with environmental covariates by weekly periods. Likewise, we did not use correlated environmental variables ($|r|>0.70$; Table S2) in submodels (Moore and McCabe 2005). Two streamflow variables were correlated, so the less intuitive variable of the two was eliminated from further analysis; we removed the difference between maximum flow and minimum flow in the week and retained the mean weekly flow. All temperature variables were correlated except the difference between the previous week's average

daily temperature and the current week's average, so we again retained the most intuitive of the correlated variables: weekly average daily maximum water temperature (Table S2). All continuous covariates were standardized to a mean of zero and an SD of 1.0 prior to model fitting. We did not assess interactions among the covariates because our sample sizes were limited.

We used log-linear models to model the environmental effects on weekly or biweekly detection rates and habitat effects on the detection rates of prespawn fish by reach (Equation 1). We also evaluated whether aerial or ground detections affected detection rates by including an individual detection covariate similar to other CJS formulations (e.g., sex; Leuenberger et al. 2019; Murphy et al. 2021) and as suggested by Raabe et al. (2014):

$$\log(\lambda_{0i,j,t}) = \beta_0 + (\beta_{1j} \times Habcov_j) + (\beta_{2t} \times Envcov_t) + (\beta_{3i} \times Indcov_i) \ldots (\beta_n \times cov_{i,j,t\ldots n}), \quad (1)$$

where β_0 is the intercept and $\beta_{1\ldots ni,j,t}$ is the coefficient for a habitat covariate (*Habcov*) by reach (e.g., Shannon–Wiener diversity index), an environmental covariate (*Envcov*) by time (e.g., streamflow or water temperature), or an individual covariate (*Indcov*) by fish (e.g., aerial versus ground detection).

Scale submodel

The scale parameter, sigma (σ), is included in the detection part of the model to quantify the "availability" of a reach to a Bull Trout as the individual moves through time conditional on $S_{i,t}$, the latent activity center (location) of the fish. Scale parameter estimates were included for all fish with a posterior mean z_i greater than zero and were a general regulator of weekly movements for the entire population. We evaluated whether the scale parameter varied with streamflow or water temperature covariates by time period with log-linear models similar to equation 1.

Apparent survival submodel

We allowed apparent survival probability (ϕ) to vary across time periods with water temperature and streamflow by using logistic regression equations (equation 2). We also allowed survival to vary across individuals by fish size and maturity in 1993 only, as 10 fish were recaptured in 1993, whereas all 1992 fish were captured for the first time and of unknown maturity:

$$\text{logit}(\phi_{i,t}) = \beta_0 + (\beta_{1t} \times Envcov_t) + (\beta_{2i} \times Indcov_i) \ldots (\beta_n \times cov_{i,t\ldots n}), \quad (2)$$

where β_0 is the intercept, β_{1t} is the coefficient for an environmental covariate (*Envcov*; e.g., streamflow or water temperature), and β_{2i} is the coefficient for an individual covariate (*Indcov*; e.g., fish size, maturity, or location covariate estimated through the movement submodel).

Movement submodel

We considered potential locations for prespawn fish to range from their Rapid River release point (RKM 62.5) to the Rapid River headwaters (RKM 97; a total of 34.5 RKM), either at the confluence of Sinking Creek or the upper boundaries of the Granite Fork and Lake Fork spawning tributaries (RKM 99.9 and 95.8, respectively). In contrast, postspawn fish could move from the Rapid River headwaters downstream to RKM 1 in the Salmon River—a distance of 95.8 RKM. A Markovian structure informed models of a Bull Trout's previous locations and estimated locations ($S_{i,t}$) when an individual was not detected.

We calculated a weekly population mean location (in RKM) from the posterior mean estimate of all activity centers $S_{i,t}$ for individuals that were estimated to be alive and in the study system (mean z across chains was >0.99). We also calculated the mean number of detections per ~1-km reach for prespawning and postspawning models from the final top models and plotted those relationships.

We used indicator variables to conduct Bayesian model selection for uncorrelated environmental, habitat, and individual covariates for submodels within the three separate prespawning and postspawning models (Kuo and Mallick 1998; Hooten and Hobbs 2015). To do this, we multiplied the coefficient for each covariate in the global (i.e., all covariates) model by a latent binary indicator variable (w; Kuo and Mallick 1998; Royle et al. 2014; Duarte et al. 2020). To evaluate variable importance, we examined the posterior probabilities of the indicator variables, where each unique sequence of indicator variables was a candidate model (Kuo and Mallick 1998; Royle et al. 2014). The best model could include no variables. We based our inferences on the model with the largest weight (i.e., the highest posterior probability density [HPD]; Duarte et al. 2017) and only on top model covariates for which the untransformed 90% credible intervals (CIs) did not overlap zero. Variables with 90% CIs that overlapped zero were removed from the top models. We summarized posterior distributions of estimated parameters (i.e., ϕ, σ, S, and λ_0) in the final reduced models (i.e., variables from the model with highest posterior probability) and covariates with their mean and 90%

CIs to increase computational stability (Gelman and Carlin 2014; Gelman et al. 2014; Kruschke 2014) using the MCMCvis package (Youngflesh 2018). We also extrapolated weekly survival estimates with 90% CIs across all time periods for 1992 and 1993 prespawning and postspawning, a benefit of Bayesian modeling (Yackulic et al. 2020).

We used JAGS (Plummer 2012) and R (R Development Core Team 2021) via the R package rjags to fit our Bayesian linear SCR models (see https://github.com/pjwohner/BullTrout for R code). The Bayesian framework for inference allows the construction of complex models and the use of relatively small sample sizes (Gardner et al. 2010; Hooten and Hobbs 2015). We used diffuse normal distributions (mean = 0, SD = 0.368) for all priors on all parameters; we ran three chains with an adaptive phase of 2000 iterations and a burn-in of 6000 iterations, and we evaluated output from an additional 20,000 iterations. We confirmed chain convergence with the potential scale reduction factor ($\hat{R} < 1.01$) and by visual inspection of trace and density plots of the posterior distributions of all top-level stochastic nodes (Gelman et al. 2008; Royle et al. 2014). All R code and data files used in the analysis can be found on the following public GitHub repository: github.com/pjwohner/BullTrout.

RESULTS

We included 63 radio-tagged Bull Trout in our SCR analyses: 30 fish from 1992, 28 fish from 1993, and 5 fish from 1994 (Table S3; Figure S1). No fish were relocated from the years before 1992, as this was when tagging began. Total lengths of tagged fish ranged from 360 to 630 mm ($\bar{x}$ = 473.7 mm, SD = 64.1), and weights ranged from 475 to 2924 g ($\bar{x}$ = 1155.7 g, SD = 531.4; Table S3). The number of detections per fish ranged from 4 to 21 detections in each model ($\bar{x}$ = 14 detections, SD = 4.13; Table S2). We included 552 ground relocations and 328 aerial relocations in the analysis, totaling 880 detections. Individual mortalities (n = 23) were primarily identified by subsequently recovering tags (n = 21; 91%), while two (9%) dead fish were recovered (Figure S1). Two fish (6%) were never relocated after capture, possibly because of tag failure, and were not included in the analysis. Markov chain–Monte Carlo chains for all parameters and covariates in the two separate 1992 and 1993 prespawning SCR models and the 1992–1994 postspawning SCR model converged on stationary and stable distributions based on examination of trace plots and the potential scale reduction factor. We include weights and proportions from top models selected by indicator model selection in Table S4.

Model scale parameters

The scale parameter mean ranged from 1.24 RKM (90% HPD = 1.12–1.36) in the 1992 prespawning model to 1.40 RKM (90% HPD = 1.30–1.51) in the 1993 prespawning model and 4.00 RKM (90% HPD = 2.43–6.29) in the postspawning model. The lower scale parameter estimates during prespawning indicated that fewer reaches were available for fish to move to from week to week than from biweek to biweek over postspawning (i.e., fish were traveling slower during postspawning considering the longer 2-week time frame). The availability of reaches to fish increased with higher average maximum daily water temperature in the current week within the postspawning model and was not related to environmental covariates in the 1992 and 1993 prespawning models (Figure 6; Table S5).

Detection rate

Detection rate varied by RKM in the prespawning models (Figure 7). Although the CIs overlapped, prespawning detection rates were higher in 1993 ($\bar{x}$ = 0.39, 90% CI = 0.31–0.48) than in 1992 ($\bar{x}$ = 0.32, 90% CI = 0.26–0.39). The detection rate was a constant 0.15 (90% HPD = 0.12–0.17) for 1992–1994 postspawn fish (Figure 6; Table S5) because we examined habitat covariates only in the prespawning models. Three habitat covariates were related to detection rate in the 1992 Rapid River prespawning model, and four covariates were related to detection rate in the 1993 prespawning model (Figure 6). Notably, fish maturity and size were not important in the prespawning model for 1993, during which recaptured fish were also tracked. In both the 1992 and 1993 prespawning detection submodels, the positive relationship between detection rate and habitat diversity had one of the largest and most consistent seasonal effect sizes across both years (Figure 6). Parameter estimates indicated that for every 1-unit increase in the habitat diversity index, prespawn Bull Trout detections increased by a factor of 1.13 and 1.28 for 1992 and 1993, respectively (Table S5). Habitat diversity, as estimated by the Shannon–Wiener diversity index, was higher in upstream reaches (Figure 8). Large wood density had a small and inconsistent effect on detection rate, although the 90% CI overlapped zero in 1993 (Figure 6; Table S5). During the lower flow year (1992), the detection rate was negatively related to the proportion of undercut bank, decreasing by a factor of 1.40 for every 1-unit increase in undercut bank. The 1993 prespawning detection rate was negatively related to the proportion of vegetated stable banks and positively related to habitat units that included steep falls (Figure 6; Table S5).

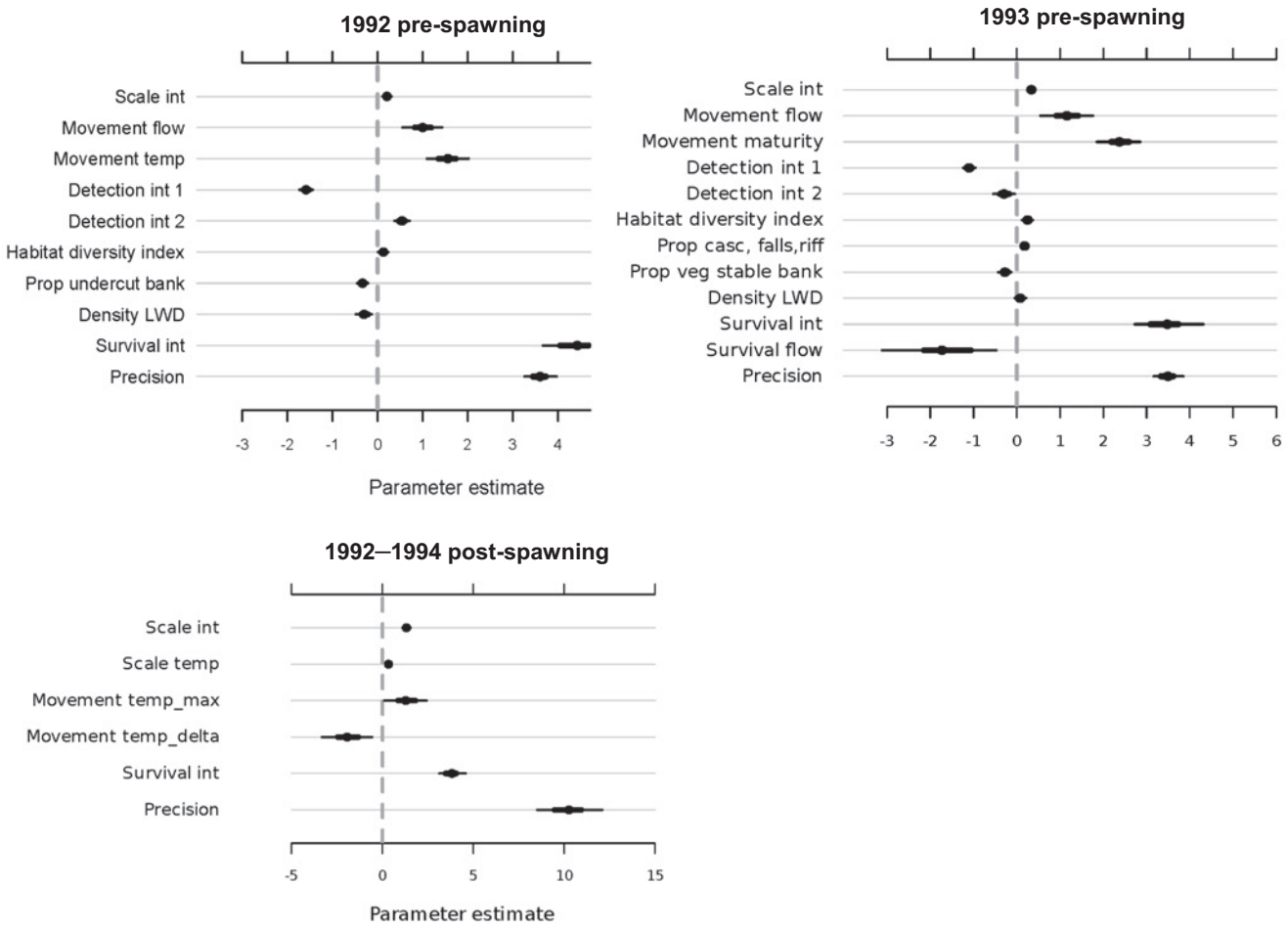

FIGURE 6 Parameter estimates with posterior medians (points) and lower 50% (thick bar) and upper 90% (thin bar) highest posterior density credible intervals for intercepts and covariates from the best approximating prespawning 1992 (low-flow season), prespawning 1993 (season with high and variable flow), and postspawning (August 19–May 12, 1992–1994) linear spatial capture–recapture models for Bull Trout in the Rapid and Salmon rivers, Idaho. Credible intervals that overlap the dashed line representing zero indicate no effect. casc, cascade; int, intercept; LWD, large woody debris; max, maximum; prop, proportion; riff, riffle; temp, temperature; veg, vegetated.

Migration and movement

The average weekly estimated activity centers (locations) for Bull Trout ranged from RKM 58 to RKM 102 for 1992 and 1993 prespawn Bull Trout (Figure 9) and from RKM 1 to RKM 98 for postspawn Bull Trout (Figure 10). The RKM location for average weekly activity centers exhibited a general tendency to (1) increase from spring through late summer as prespawn fish migrated to spawning sites, (2) decrease after spawning in the fall, and (3) remain constant through early spring (Figures 9 and 10). Individual locations were not related to fish size in the 1992 prespawning model, the 1993 prespawning model, or the postspawning model (1992–1994). In the 1993 prespawning model, the fish maturity variable was important and indicated that previously tagged prespawn fish migrated much further upstream (Figure 6; Table S5). Although Bull Trout generally reached the same positions in the river during prespawning in both years (i.e., ~RKM 77–100), they moved further upstream and faster during the warmer year (1992) compared to the colder year (1993; Figure 9).

Most mature prespawn Bull Trout migrated steadily upstream to known spawning sites, where they staged until spawning. However, three smaller-than-average fish (360, 400, and 416 mm) either did not move upstream or moved a very short distance before migrating back downstream past the RRH tagging site. Weekly locations of both 1992 and 1993 prespawn fish further upstream were positively related to the weekly average maximum daily water temperature (Figures 6 and 9). Upstream positions were related to higher mean weekly streamflow in the 1992 prespawning model (Figures 6 and 9).

In contrast to prespawn fish, postspawn Bull Trout had several different migration strategies. Approximately half of the fish rapidly migrated long distances downstream at the beginning of September as maximum temperatures decreased, and these fish then overwintered from RKM 0 to

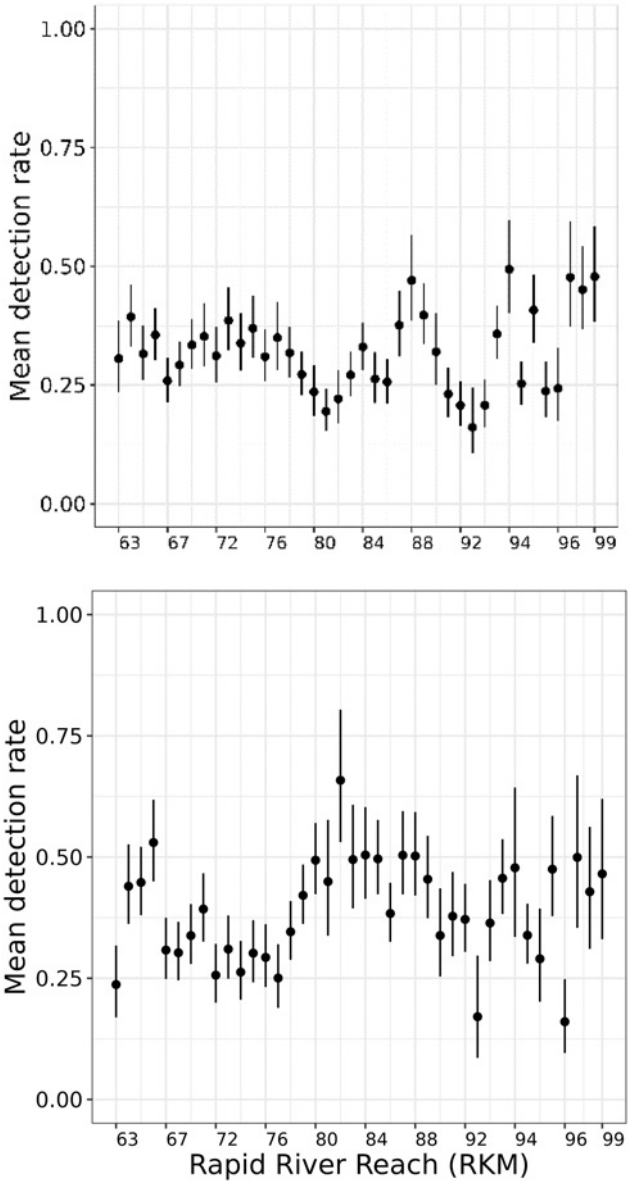

FIGURE 7 Mean estimates of prespawn Bull Trout detection rates (with error bars representing 90% credible intervals) per ~1-km reach from May 26 to September 28 in 1992 (top panel) and 1993 (bottom panel) within the Rapid River, Idaho. RKM, river kilometer.

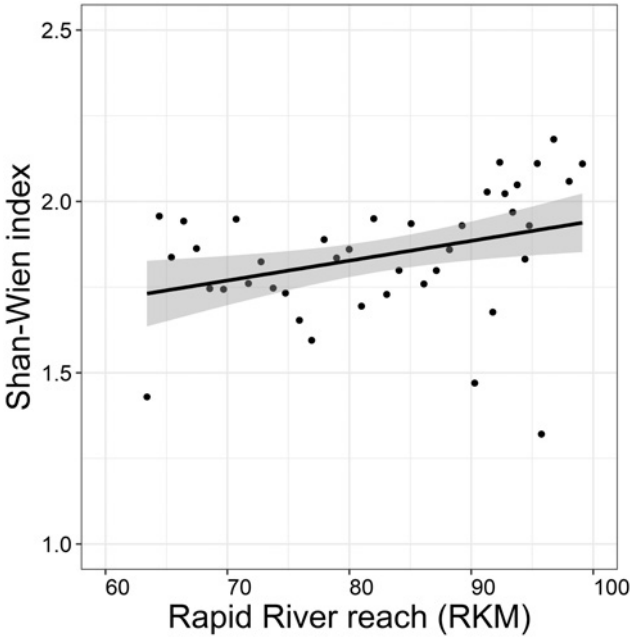

FIGURE 8 Relationship between the Shannon–Wiener (Shan–Wien) index of habitat unit diversity (with 90% credible intervals) and ~1-km reaches in the Rapid River, Idaho. RKM, river kilometer.

RKM 63 in the Salmon River (Figure 10). A second group migrated shorter distances downstream and overwintered near the Rapid River's confluence with the Little Salmon River. A third group of fish exhibited more diverse movements: for example, some fish moved short distances and remained in the Rapid, Little Salmon, or Salmon River, and one fish did not migrate prior to November, well after other postspawn fish had already left the Rapid River (Figure 10).

During postspawning, the movement of tagged fish closely followed the mean weekly maximum daily water temperature as fish moved out of the headwaters and they were generally in their overwintering sites by the onset of the coldest maximum temperatures in November–December (Figures 6 and 10). After December, fish were concentrated from RKM 0 to RKM 63 in the Salmon River, with the highest concentrations being observed at RKM 27–60. Despite increases in daily maximum weekly water temperature, postspawn fish exhibited high fidelity to their overwintering sites either until they were no longer detected or until the following April, when they repeated their upstream migration (Figure 10). Large declines in the current biweekly water temperature relative to the previous biweekly temperature were also related to upstream positions for postspawn fish (Figures 6 and 10).

Survival

The estimated posterior mean of weekly apparent survival for the 1992 (low-streamflow) prespawning period was constant ($\bar{x}$ = 0.988, 90% CI = 0.980–1.000) compared to the mean weekly apparent survival ($\bar{x}$ = 0.966, 90% CI = 0.930–0.987) for 1993 (high and variable streamflow). Extrapolated across the entire multi-week study periods, overall apparent survival was 0.83 (90% CI = 0.74–0.91) for 1992 prespawn fish and 0.64 (90% CI = 0.52–0.76) for 1993 prespawn fish. Mean apparent survival of 1993 prespawn fish generally decreased over time, with fish having lower survival in the final weeks of the prespawning period compared to the beginning weeks (Figure 11). Apparent

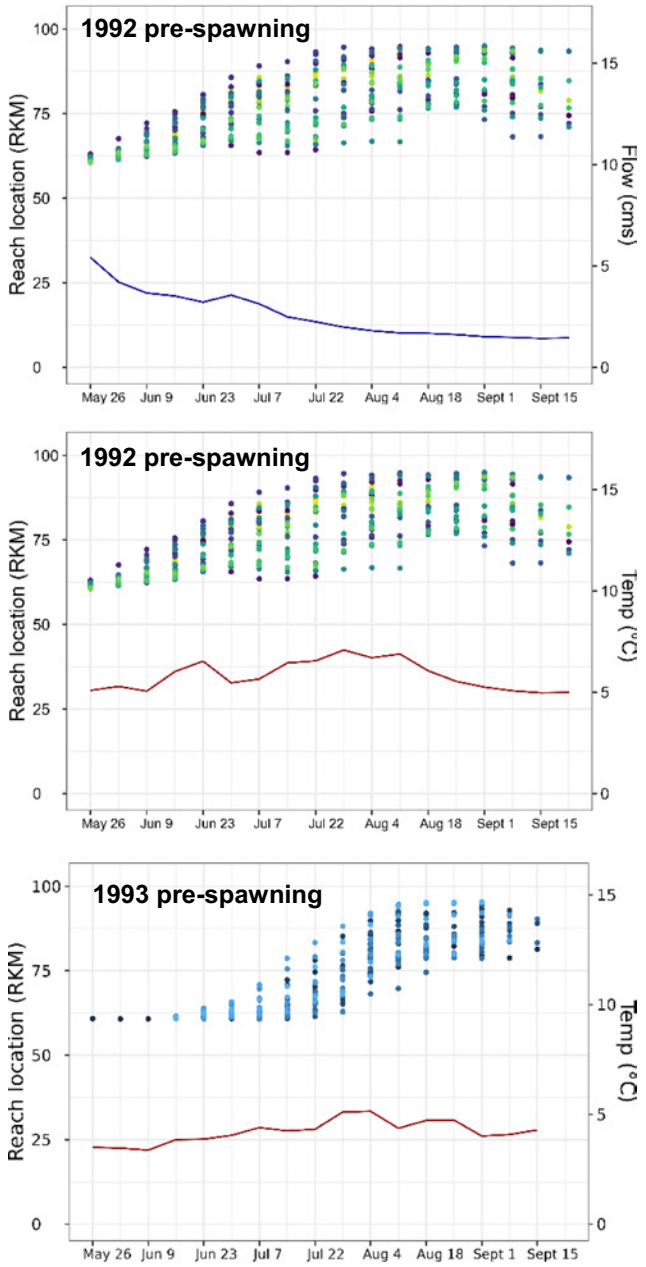

FIGURE 9 Locations of prespawn Bull Trout in the Rapid River from May 19 to September 28 in 1992 ($n = 30$; top and middle panels) and 1993 ($n = 28$; bottom panel) for fish with a high likelihood of being alive ($z > 0.70$) based on the linear spatial capture–recapture model (mean posterior distribution of individual activity centers). Red lines denote weekly average maximum daily water temperature (temp; °C), and the blue line denotes the average weekly streamflow for 1992. River kilometer (RKM) 0 corresponds to 1 km upstream from the confluence of the Salmon River and White Bird Creek, RKM 59.1 corresponds to the confluence of the Rapid River and the Little Salmon River, RKM 63.4 is the capture/tagging/release reach, RKM 90 represents the Rapid River headwaters, and RKM 99.9 is the furthest upstream reach in the Rapid River headwaters. cms, cubic meters per second.

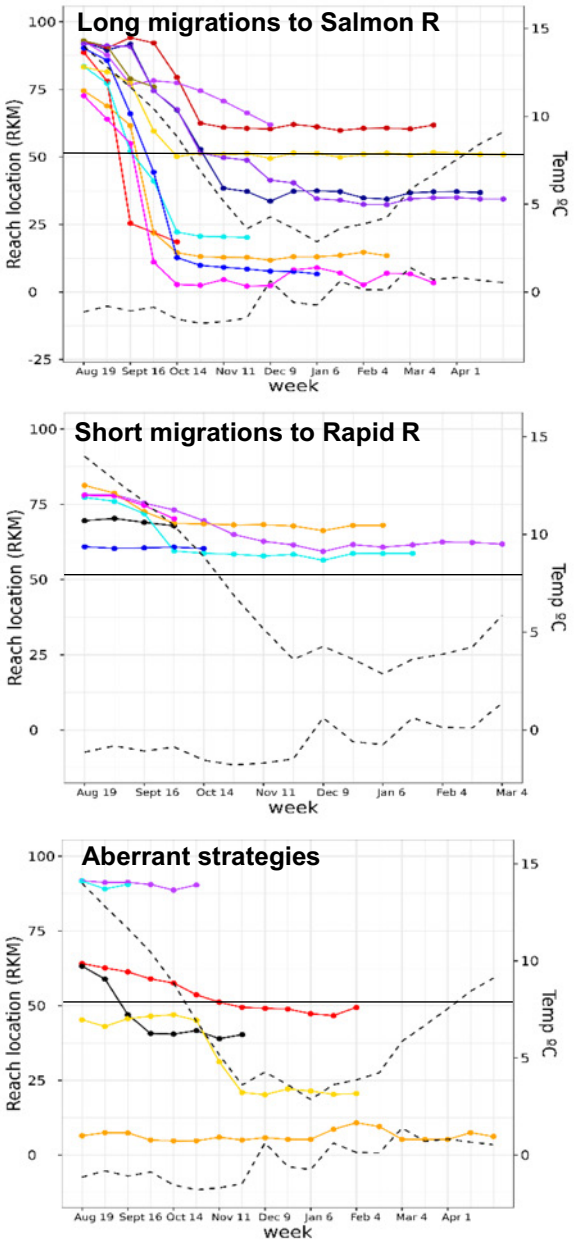

FIGURE 10 Estimated mean biweekly locations of postspawn Bull Trout ($n = 23$) with a high probability of being alive ($z > 0.70$) in the Rapid and Salmon rivers from August 12 to May 12, 1992–1994, based on linear spatial capture–recapture models (mean posterior distribution of individual activity centers). Fish made long migrations from headwater tributaries to overwinter in the Salmon River (top panel), short migrations to winter near the Rapid River confluence (middle panel), and aberrant migrations (bottom panel). River kilometer (RKM) 0 corresponds to 1 km upstream from the confluence of the Salmon River and White Bird Creek, RKM 59.1 corresponds to the confluence of the Rapid River and the Salmon River (solid black line), and RKM 90 represents the Rapid River headwaters. The top black dashed line denotes the average weekly maximum daily water temperature (temp; °C), and the bottom black dashed line denotes the difference (delta) between the current week's water temperature and the previous week's water temperature.

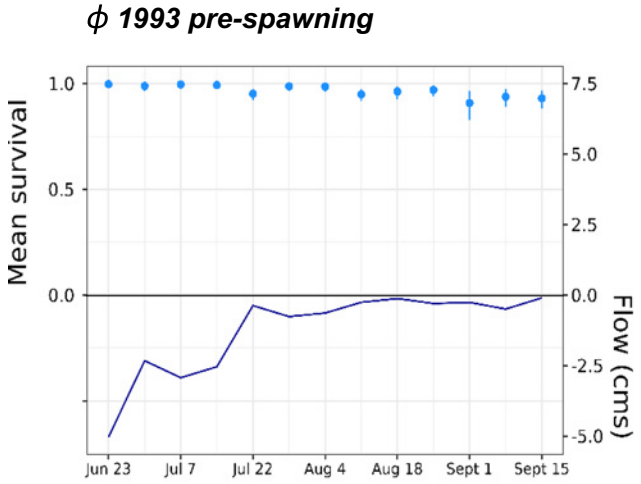

FIGURE 11 Mean posterior distribution (with error bars representing 90% credible intervals) of Bull Trout apparent survival (ϕ) estimates (top of figure) and the difference (delta) between the current week's mean streamflow and the previous week's mean streamflow (blue line) over the same period (bottom of figure) during 1993 prespawning ($n = 28$ fish) in the Rapid River, Idaho, from May 26 to September 28, as estimated from linear spatial capture–recapture models. cms, cubic meters per second.

survival of prespawn fish in 1992 (low-flow season) was not related to water temperature, streamflow metrics, fish size, or maturity. Apparent survival of prespawn fish in 1993 (high and variable streamflow) increased with larger, more negative changes in flow variability (delta) of the current week relative to the previous week (Figure 11).

Mean biweekly postspawning survival was a constant 0.977 (90% CI = 0.96–0.99). Extrapolated across the entire multi-week study period, apparent survival was 0.76 (90% CI = 0.65–0.87) for postspawn fish over 38 weeks.

DISCUSSION

Streamflow and temperature effects

Streamflow and water temperature are the primary drivers of ecological processes in riverine ecosystems (Ouellet et al. 2020). Therefore, it was not surprising that Bull Trout migration and survival were related to these environmental factors. The environmental effects, however, varied between years and with prespawning and postspawning activity. Bull Trout migrated upstream faster (~1 month earlier) during the 1992 season, which was characterized by warmer water temperatures in the Rapid River, compared to 1993, which had colder temperatures, suggesting that fish indeed sought cooler temperatures. Cooler temperatures upstream are likely influenced by groundwater inputs (Somers and McKenzie 2020); with reduced snowpack, groundwater recharge might decline, possibly making upstream locations less hospitable in the future.

Maximum hourly water temperature measured at the Rapid River stream gauge never exceeded lethal temperatures for Bull Trout (i.e., 20.9°C; Selong et al. 2001) in the three decades since 1992. Despite mean weekly maximum water temperatures exceeding 16°C during most of July 1992, survival did not decrease during those times. This is likely because water temperatures were always colder upstream toward the higher elevation headwaters. Prespawn Bull Trout ascended the Rapid River quickly and thereafter occupied tributaries and headwater reaches. Consequently, the actual water temperatures sought by Bull Trout were likely cooler than those represented by our downstream thermograph. Even in warmer years, Rapid River water temperatures likely remain sufficiently cold because the riverscape is at high elevation and is intact, complex, and highly connected (Isaak et al. 2016; Roth et al. 2021). In intact systems with water temperatures in the preferred range for Bull Trout, studies have confirmed that prespawn fish did not use cooler water than was available (Howell et al. 2010).

Bull Trout survival was constant during postspawning even when average maximum daily water temperature at the Rapid River thermograph reached less than 2.7–4.2°C. Bull Trout have a threshold for very cold water, which was estimated (but not confirmed) to be 5.2°C (Selong et al. 2001). Although the 5.2°C value was outside of the temperatures studied by Selong et al. (2001), their 95% confidence interval of peak temperature for age-0 Bull Trout suggested a range of 10.9–15.4°C for maximum growth. The peak growth rates from Selong et al. (2001) decreased sharply above and below this temperature range, falling to 60% of the peak growth rate at 8°C and 18°C, suggesting potential negative consequences from colder water.

In 1992 and 1993, the biweekly mean maximum water temperature during postspawning migrations was generally cooler and streamflow was lower and exhibited less seasonal variability compared to the other years of the previous three decades. Higher fall and winter flows coupled with temperatures below physiological optima may present Bull Trout with swimming performance challenges (Letcher et al. 2015), especially as fish must migrate long distances to the larger and lower elevation Salmon River. The Salmon River likely provides wintering conditions that are less harsh than those in the Rapid River, and it provides more abundant food for large, piscivorous Bull Trout. Although correlated, water temperature may not have been the ultimate driver of cool season survival. The fluvial Bull Trout that we studied complete a rigorous upstream migration that exceeds

80 km in many cases. Fish that stage and spawn in headwater streams lose a considerable amount of their body weight and then must migrate back downstream to overwintering areas. Thus, fish that successfully foraged and recovered body condition likely survived, while those that were unable to feed adequately may not have survived the winter.

Despite the increasing number of investigations on overwintering, knowledge of the winter behavior and ecology of Bull Trout and other native salmonids is incomplete. Our analyses included several factors that were likely to influence the detection rate, survival, and migration of postspawn Bull Trout, but unfortunately we were unable to collect detailed habitat information for Bull Trout overwintering in the Salmon River. Additional years with an expanded set of thermographs and postspawning habitat data would enhance our ability to assess future climate scenarios more accurately.

Our estimates of 14–18-week prespawning survival ($\bar{x}$ = 0.64–0.83) and 38-week postspawning survival ($\bar{x}$ = 0.76) are much higher than annual survival reported for other fluvial and adfluvial Bull Trout populations, which averaged 0.43 (Roth et al. 2021) and ranged from 0.35 to 0.47 (Beauchamp and Tassel 2001; Al-Chokhachy and Budy 2008; Howell et al. 2016; Al-Chokhachy et al. 2019). It is possible that our survival estimates were biased by our treatment of mortality (i.e., we assumed that all recovered tags represented mortalities), as fish can expel their tags while still alive (Summerfelt and Mosier 1984). However, tag retention is generally high in similar fish species (e.g., 0.98 [95% confidence interval = 0.92–1.00] for Sockeye Salmon *Oncorhynchus nerka*; Ramstad and Woody 2003), and fish that expel their tags would serve to negatively bias our survival estimates. Fish that may have died shortly after their tag battery failed would account for positively biased survival; however, all detections of fish that we lost track of due to failed batteries were censored.

We found that the prespawn life stage, especially when fish were staging or spawning, represented a shorter time frame (14–18 weeks) with possible increased mortality compared to the longer postspawning period (38 weeks). Higher prespawning mortality may have been associated with the vulnerability of large Bull Trout to predators (mink, otters, bears, osprey, and eagles) while staging or spawning in small headwater streams. During tracking surveys, we frequently detected Bull Trout larger than 450 mm in water less than 10 cm deep and we recovered radio tags from likely predation events (tags were lying on streambanks). It is also possible that some or all of the recovered tags were in fact expelled tags, which would mean that survival is even higher than we estimated. However, recovered tags were generally discovered in searches for tags that had not changed locations, potentially from predation of tagged fish.

Climate change

We investigated two of the most extreme and contrasting warm seasons recorded in the Rapid River over the past 30 years. From 1992 to 2018, there was not a prespawning season with water temperatures colder than those in 1993, and few prespawning seasons had water temperatures warmer than those in 1992, as recorded by the Rapid River stream gauge. These extreme temperatures are likely related to those seasons having exceptionally low (1992) and moderately high (1993) streamflow. The 1992 and 1993 environmental data for the Rapid River illustrate fluctuations in prespawning water temperature and flow that might be reflective of future PNW climatic conditions (e.g., see predictions by Dalton and Fleishman 2021). Thus, our analyses of 1990s Rapid River data are relevant for assessing the potential effects of climate change.

Climate change is expected to increase cool season (October–March) flows in the form of surface runoff (Dalton and Fleishman 2021), and warming trends are already affecting stream temperatures (Isaak et al. 2010, 2012) and flow regimes (Luce and Holden 2009), with shifts in winter precipitation from snow to rain (Knowles et al. 2006; Brown and Mote 2009). In the PNW, climate change is already reducing snowpack and shifting streamflow timing, hydrology, and thermal regime, with increases in variability and extreme events (Dalton and Fleishman 2021). Warmer water temperature during the warm season (April–September), which is produced by both reduced streamflow and warmer air temperatures from climate change, is expected to become a major issue for coldwater fishes (Letcher et al. 2015; Benjankar et al. 2018).

To elucidate potential effects of climate change on prespawn Bull Trout, we compared survival and migration within and between the 1993 season, with high and variable streamflow, and the 1992 season, with low and stable streamflow. Similar to a central Idaho study by Roth et al. (2021), we found that Bull Trout apparent survival increased with lower streamflow variability and warmer water temperature in low-flow 1992 but not in 1993. As climate change is expected to increase both streamflow variability and water temperature, this is a highly relevant result. We note, however, that our models were restricted to a relatively narrow temperature range that may be exceeded with future climate warming.

Increased survival with warmer water temperatures seems contrary to the preponderance of data confirming that Bull Trout are among North America's most

warm-temperature-sensitive freshwater fishes (Selong et al. 2001; Thurow et al. 2020). However, other factors may be contributing to this contradictory result, such as groundwater reserves that may be significantly more depleted with climate change in mountain aquifers (Meixner et al. 2016). Groundwater is stored over time and is available even in drought years (Meyers et al. 2021), which may have benefited fish during the 1992 low-flow season. Groundwater recharge at high elevations is heavily dependent on snowpack, which is projected to decrease with climate change, resulting in lower groundwater recharge, especially at higher elevations (Meixner et al. 2016; Somers and McKenzie 2020). In turn, lower recharge may lead to lower and warmer base flows during the warm, dry seasons (Meyers et al. 2021).

Multiple studies have reported that the rate of temperature increase within higher elevation, cold headwater PNW streams may be slower than the rate of increase at lower elevations, thus allowing coldwater refugia to persist (Benjamin et al. 2016; Isaak et al. 2016; Howell 2018). Other studies suggest that even if the maximum temperature increases during prespawning are negligible, an earlier onset of temperature increases, as reported by Howell et al. (2016), could negatively influence migration onset and food availability (Arismendi et al. 2013; Isaak and Young 2023). In addition, less snow projected due to climate change may lower groundwater recharge, which would lower groundwater contributions during the summer and result in higher stream temperatures that may not have been experienced by the fish that we tracked in 1992–1994.

If high temperatures affect spawn timing or location, we might expect spawning to occur later in fall or to be concentrated in the uppermost headwater stream reaches (Howell et al. 2010). However, similar to the findings by Howell et al. (2010), many of our tagged fish likely spawned lower in the river, as indicated by the furthest point of movement, where temperatures were warmer during the 1992 warm year. Clearly, additional work is needed to resolve the many ways in which changing temperatures could be important for Bull Trout (Howell et al. 2010).

As climate change alters hydrothermal regimes, Bull Trout survival may also be reduced by invasive species that are currently limited by cold temperatures but that will become more competitive as waters become warmer (Warnock and Rasmussen 2013; Al-Chokhachy et al. 2016). Although invasive Brook Trout *S. fontinalis* have been aggressively managed in the Rapid River (Koenig et al. 2015), they may become increasingly difficult to control in Bull Trout habitat farther downstream in the Salmon River. For example, invasive Smallmouth Bass *Micropterus dolomieu* have become abundant in the Salmon River near Riggins.

Complex habitats

Our results agree with other studies reporting that Rapid River Bull Trout use complex habitats (D'Angelo and Muhlfeld 2013; Guzevich and Thurow 2017). Increased habitat unit complexity provides more opportunities for cryptic Bull Trout to seek concealment cover (e.g., pools, LWD, and undercut banks; Williams et al. 2015; Thurow et al. 2020). Interestingly, fast-water habitat unit types like cascades and runs were positively associated with higher Bull Trout detections by reach in 1993. Despite having less channel complexity, fast-water habitats with turbulence (e.g., high-gradient riffles, cascades, and upper ends of runs) provide overhead concealment cover. This may be particularly important for prespawn fish during the initial stages of their upstream migration, as they make frequent movements and temporarily stage on their way to upstream spawning sites. Undercut banks are also an important feature of complex habitats (Allouche 2002), and we were surprised that undercut banks were associated with fewer detections during the low-flow year. However, this counterintuitive relationship may be an artifact of our field protocols inadequately measuring the importance of undercut banks or may have occurred because the scale of our measurements was very broad over entire reaches.

We found high diversity in prespawning and postspawning migration timing, speed, and distance; the locations of spawning and overwintering sites; and responses to water temperatures and streamflows. This biocomplexity likely increases species persistence by ensuring the broadest capacity for biological adaptation to variable and changing environments (Carlson and Satterthwaite 2011; Sturroch et al. 2019). Future Bull Trout persistence in response to climate change in the Salmon River basin likely depends on conserving the diversity of complex habitats and the diverse life history strategies reported in this paper (Cooke et al. 2008; Schindler et al. 2015).

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no competing interests.

DATA AVAILABILITY STATEMENT

This submission uses novel code with several data files. Our code and data are archived in a permanent public GitHub repository (github.com/pjwohner/BullTrout).

ETHICS STATEMENT

All fish surgeries and sampling were conducted in accordance with Idaho State scientific collection permits: Bull Trout investigations under projects no. F-73-R-15 to F-73-R-18.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.