


# Resilient and rapid recovery of native trout after removal of a non-native trout

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## Abstract

While the importance of reducing impacts of non-native species is increasingly recognized in conservation, the feasibility of such actions is highly dependent upon several key uncertainties including stage of invasion, size of the ecosystem being restored, and magnitude of the restoration activity. Here, we present results of a multi-year, non-native brown trout (*Salmo trutta*) removal and native Bonneville cutthroat trout (*Oncorhynchus clarkii utah*) response to this removal in a small tributary in the Intermountain West, United States. We monitored trout for 10 years prior to the onset of eradication efforts, which included 2 years of mechanical removal followed by 2 years of chemical treatment. Cutthroat trout were then seeded with low numbers of both eggs and juvenile trout. We monitored demographics and estimated population growth rates and carrying capacities for cutthroat trout from long-term depletion estimate data, assuming logistic population growth. Following brown trout eradication and initial seeding efforts, cutthroat trout in this tributary have responded rapidly and have approached their estimated carrying capacity within 6 years. Population projections suggest a 95% probability that cutthroat trout will be at or above 90% of their carrying capacity within 10 years of the eradication of brown trout. Additionally, at least four age-classes are present including adults large enough to satisfy angling demand. These results demonstrate native trout species have substantial capacity to rapidly recover following removal of invasive species in otherwise minimally altered habitats. While tributaries such as like this study location are likely limited in extent individually, collectively they may serve such as source populations for larger connected systems. In such cases, these source populations may provide additional conservation potential through biotic resistance.

## KEYWORDS

carrying capacity, eradication, fish biomass, invasion, mechanical removal, population growth

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## 1 | INTRODUCTION

While freshwaters represent critical hotspots of biodiversity, they are also among the most highly threatened ecosystems on Earth (Ricciardi & Rasmussen, 2001). According to the World Wildlife Fund (2018), as of 2014, freshwater vertebrate populations have declined by 83% since 1970, at more than double the rate for either terrestrial or marine organisms (Reid et al., 2019). One of the primary threats to freshwater biodiversity globally is proliferation of invasive species (Crutzen, 2006; Dudgeon et al., 2006; Reid et al., 2019). Invasive species present substantial threats to native fishes, through competition for resources, predation by novel predators on naïve prey, spread of disease, hybridization, and ecosystem alterations (Cucherousset & Olden, 2011). As such, invasive species have contributed to the imperiled status of nearly all species and sub-species of native North American trout (Budy et al., 2019). Native cutthroat trout (*Oncorhynchus clarkii* spp.) specifically once had the most extensive distribution of all Pacific trout in North America, but now, of 14 subspecies, two are extinct, five are listed as threatened under the Endangered Species Act, and the remaining all have some recognized legal status of imperilment. Ironically, some of the world's worst invasive fish are non-native trout, many of which are imperiled in their native habitat (Budy et al., 2019; Welcomme, 1992). Brown trout (*Salmo trutta*) are considered one of the world's top 30 worst aquatic invasive species (McIntosh, McHugh, & Budy, 2012) and have been firmly and repeatedly demonstrated to threaten native trout via interference competition and predation (reviewed in McIntosh et al., 2012; Budy & Gaeta, 2017).

In response to well-documented negative impacts of non-native trout and imperiled status of many native trout, there has recently been a surge in efforts to remove these invasive fishes (Budy et al., 2019; Saunders, Budy, & Thiede, 2014). These efforts are either mechanical (e.g., electrofishing; e.g., Shepard, Nelson, Taper, & Zale, 2014) or via chemical toxicants (e.g., rotenone; e.g., McClay, 2000), or some combination of both. Mechanical efforts are often size-selective and are rarely 100% effective (e.g., Walsworth et al., 2020), while chemical toxicant-based removals are expensive, not species-specific, and not always supported by the public (Meronek et al., 1996; Saunders et al., 2014). Furthermore, neither of these removal-based restoration approaches are guaranteed to be effective and questions always remain after removal efforts. These uncertainties include: (a) Will the invasive fish remain absent after removal, or recolonize the site? (b) Will the native species respond positively to removal of invasive fish, or are they limited by another constraint? and (c) How long after

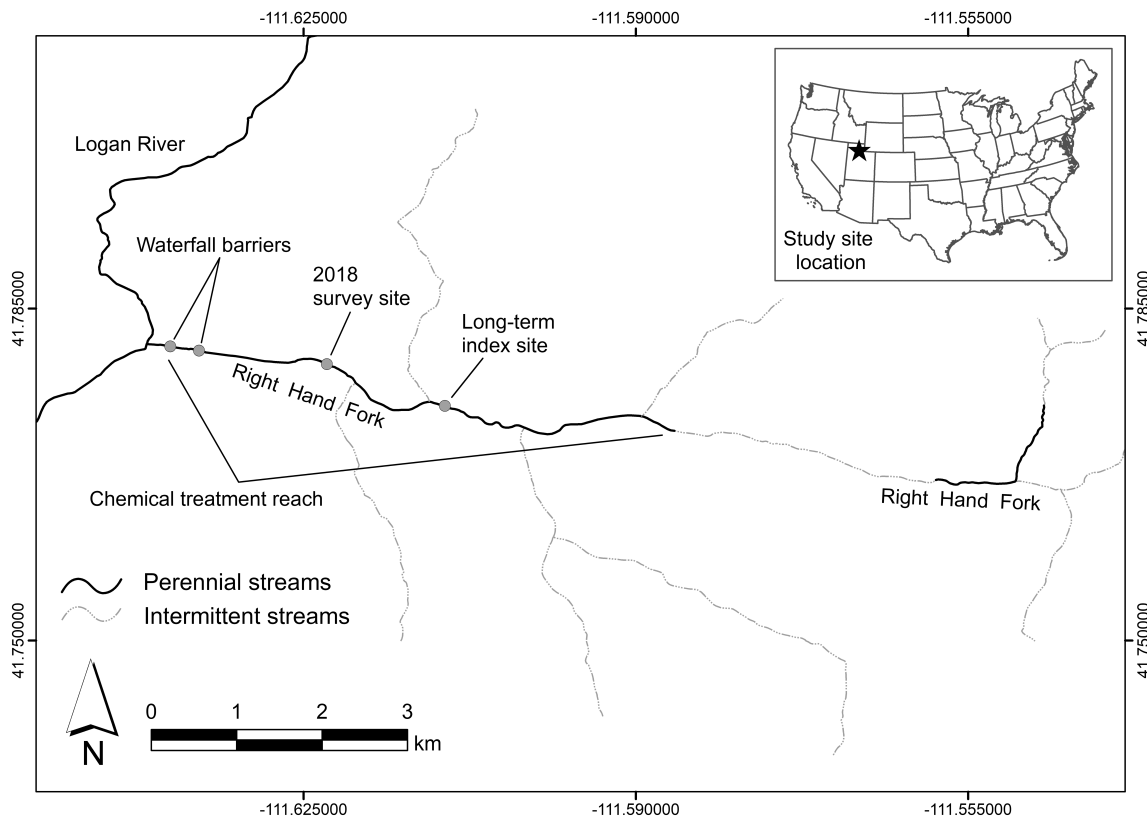
restoration activities can the native species be expected to reach a recovered state without further intervention (a key measure of success)? However, because non-native species removal is rarely thought of in an experimental vein, these actions are rarely designed to properly answer these questions, thus limiting our ability to learn and advance conservation science (*but see* Vredenburg, 2004; Clancey et al., 2019).

Here, we present a long-term study designed to understand the recovery trajectory of a native Bonneville cutthroat trout (*O. c. utah*) population following a multi-year, non-native brown trout removal effort in an important tributary in the Intermountain West, United States (Figure 1). We have been studying the Logan River (Utah, United States) fish community nearly continuously for 18 years, providing a robust long-term data set against which to design experiments and assess the effectiveness of management actions. The Logan River is home to the largest remaining population of Bonneville cutthroat trout (hereafter cutthroat trout), and densities can exceed 3,000 fish per linear km in high elevation reaches (Budy, Thiede, & McHugh, 2007). These relatively rare contemporary high densities occur in high elevation reaches primarily because the habitat is connected and nearly pristine, and non-native trout are rare, except for some very high elevation hot spots. Naturalized brown trout had excluded cutthroat trout in one of the largest and most suitable spawning and rearing tributaries in the lower river, where brown trout achieved some of the highest recorded densities in the world (Budy et al., 2013; Saunders et al., 2014). Brown trout thrived in this tributary due to highly intact, productive habitat, with spring-fed hydrology such that temperatures are near optimal in both summer and winter (Budy, Thiede, McHugh, Hansen, & Wood, 2008). Restoring this tributary for cutthroat trout via brown trout removal offered a rare opportunity to bolster this important metapopulation of cutthroat trout, expand their distribution and density into the lower watershed, better ensure persistence, and learn about the effectiveness of this conservation action.

## 2 | METHODS

### 2.1 | Site description

Our study reach of Right Hand Fork included the lower 5 km perennial reach initiating near the confluence with the Logan River in northern Utah, United States; Right Hand Fork is a tributary draining 65 km<sup>2</sup> of the total 557 km<sup>2</sup> Logan R. watershed (Figure 1). The entire tributary is 12 km, but the upper 7 km has a large



**FIGURE 1** Location of study site in Utah, United States. Map of the study area and treatment reach. Waterfall barriers ( $n = 2$ ), 2018 UDWR survey site, and our long-term index site are also shown

subterranean reach in the middle; downstream fish passage seems unlikely (e.g., high flow events), and upstream passage is likely impossible. The hydrograph in Right Hand Fork is relatively stable and maintained by groundwater inputs in this spring-fed system; mean annual discharges range  $0.19\text{--}0.20\text{ m}^3\text{ sec}^{-2}$ , spring snowmelt flood ranges  $0.22\text{--}0.23\text{ m}^3\text{ sec}^{-2}$ , and dry summer baseflow ranges  $0.16\text{--}0.17\text{ m}^3\text{ sec}^{-2}$  (de la Hoz Franco & Budy, 2005). Limestone geology drives highly productive stream habitats. The mainstem Logan River supports native populations of cutthroat trout and other native fishes, as well as introduced populations of non-native brown trout and some other non-native trout (e.g., a small, localized brook trout [*Salvelinus fontinalis*] population in a headwater tributary and stocked sterile trout lower in the watershed where there are impoundments). Cutthroat trout and brown trout demonstrate divergent distributions in the mainstem Logan River, with brown trout dominating the fish community in the lower reaches of the canyon, while cutthroat trout dominate the river at higher elevations (McHugh & Budy, 2006). Competition from brown trout is currently considered the primary threat to the persistence of the Logan River cutthroat trout population. Since the late

1990s and before cutthroat trout reintroduction, Right Hand Fork only supported naturalized brown trout.

## 2.2 | Data collection

Field sampling and abundance estimation methods are described in detail in Budy et al. (2007). Briefly, the Right Hand Fork fish community was sampled annually in late summer via three-pass electrofishing in a 100 m reach to inform depletion estimates. Each year, we randomly select one of three 100 m reaches including a central index site and a reach 100 m above or below this index site. In 2018, the Utah Division of Wildlife Resources (UDWR) completed a two-pass depletion sample event in a 87 m reach much farther downstream (Figure 1). In addition, there have been multiple other studies where trout abundance and distribution data have been collected, for example, in association with River Styles and habitat delineation (Mohn, 2016), system wide snorkeling (e.g., Meredith, Budy, & Hooten, 2016), and independent Bayesian modeling (LaPlanche, Elger, Santoul, Thiede, & Budy, 2018); these complementary studies provide bookends for assessing the reliability of our density estimates (below).

## 2.3 | Brown trout eradication and cutthroat trout reintroduction

We eradicated brown trout from Right Hand Fork in two phases. First, we mechanically removed 15,425 brown trout via electrofishing in 2009 and 2010 as part of a larger study investigating the potential for biotic resistance (Saunders et al., 2014). We enhanced two natural waterfalls to prevent upstream migration of all fishes, but specifically brown trout, from the mainstem Logan River community. A heavy equipment crew placed boulders on the existing bedrock outcrops to make the drops higher and more abrupt and installed a thick rubber pond liner to prevent water from creating vortices down through the interstitial spaces among the boulders. The barriers now measure 1.75 m and 2.2 m in height. Upstream passage would only be possible in extremely large spring discharge events, and because this tributary is spring fed, it demonstrates a more stable hydrograph than the snowmelt driven hydrograph of the mainstem Logan River (2001–2002 maximum = 12.8–12.1 m<sup>3</sup>/sec (de la Hoz Franco & Budy, 2005); 2015–2017 maximum = 4.6 m<sup>3</sup>/sec, this study). Note, however, that brown trout are autumn spawners and would likely not be trying to ascend the tributary during spring flooding.

In 2012 and 2013, we chemically treated Right Hand Fork with liquid-emulsifiable rotenone to kill any remaining fish in the tributary. Rotenone was deactivated with potassium permanganate dispensed downstream of the lowermost migration barrier. No brown trout have been detected above this barrier in Right Hand Fork since the completion of chemical treatments in 2013. A conservative estimate of the cost of eradication and restocking is US\$25,000; however, that does not include approximately 30 person days per year of volunteer work and in-kind funded labor nor environmental permitting.

We spawned cutthroat trout eggs streamside from a tributary of the upper Logan River and translocated a portion to remote streamside incubators (RSI) in the headwaters of Right Hand Fork, above the section that goes underground during the summers of 2012–2013 (Donaghy & Verspoor, 2000). This reach was above the brown trout population and was not treated with rotenone; it was either fishless or contained only extremely low densities of cutthroat trout. The local angling club (Cache Anglers – Trout Unlimited) maintained RSIs containing 4,000–5,000 eggs until fry emergence. In addition, UDWR reared remaining eggs and released 450 fry into Right Hand Fork in autumn 2013. Then, following a 2014 streamside spawn, UDWR raised and released 2,050 fry later that autumn. No adult cutthroat trout (or other native species) were introduced into the tributary following brown trout removals.

## 2.4 | Age-composition model

As our goal was to recover the cutthroat trout population in Right Hand Fork with a limited source population, we did not extract otoliths for ageing purposes, which would require lethal sampling. Instead, we developed a model to estimate age-composition of cutthroat trout from the observed length-frequency distribution and assuming length-at-age followed a von Bertalanffy growth relationship. For full model details, see Appendix S1.

## 2.5 | Population model

As we expected ecosystem carrying capacity to limit the total biomass of trout capable of being supported by the environment and not the total number of individuals, we converted annual abundance estimates for cutthroat trout to biomass estimates using observed length-frequency data and length-weight regressions developed for Logan River trout (McHugh & Budy, 2006). Lengths of individuals sampled and not measured or not captured but assumed present (by depletion abundance estimators) were estimated by sampling from the observed length-frequency distribution, and their biomass was estimated from the length-weight regressions. We repeated this 1,000 times across each of 1,000 abundance estimates drawn from the distribution of estimated annual abundance to generate uncertainty estimates for total reach biomass in each year.

As cutthroat trout began at extremely low biomass immediately after brown trout removal, we assumed that cutthroat trout populations follow discrete logistic growth dynamics (Hilborn & Walters, 1992), with constant carrying capacity and population growth rates:

$$B_y = (B_{y-1}) \left( 1 + r \left( 1 - \frac{B_{y-1}}{K} \right) \right),$$

$$\ln(\hat{B}_y) \sim \tilde{N} \left( \ln(B_y), \sigma_y^2 \right),$$

where  $B_y$  is the model estimated cutthroat trout biomass in year  $y$ ,  $r$  is the cutthroat trout intrinsic growth rate, and  $K$  is cutthroat trout carrying capacity (kg/km),  $\hat{B}_y$  is the observed cutthroat trout biomass in year  $y$ , and  $\sigma$  is the standard deviation of the natural log of observed cutthroat trout biomass in year  $y$ . Recreational harvest is negligible for both species as local anglers primarily practice catch-and-release (97%) in non-reservoir sections of the Logan River (Budy, Thiede, & Shamo, 2017; Budy, Thiede, & Vatland, 2002). To initialize models, we estimated biomass in the year prior to the first year of

surveys (i.e., cutthroat trout biomass in 2013) as an additional model parameter. Prior distributions used for parameter estimation are presented in Table S1. We fit the population model with AD Model Builder (Fournier et al., 2012), implemented through R Statistical Computing Environment (R Core Team, 2018).

## 2.6 | Projecting time to carrying capacity

We used our population model to simulate forecasts of cutthroat trout population dynamics and estimate how long it would take the population to reach carrying capacity. We ran simulations for 50 years across the range of model uncertainty by sampling parameters from posterior distributions. We then calculated the proportion of carrying capacity of the population in each simulated year to determine how long it will take for the population to approach carrying capacity.

## 3 | RESULTS

### 3.1 | Age composition

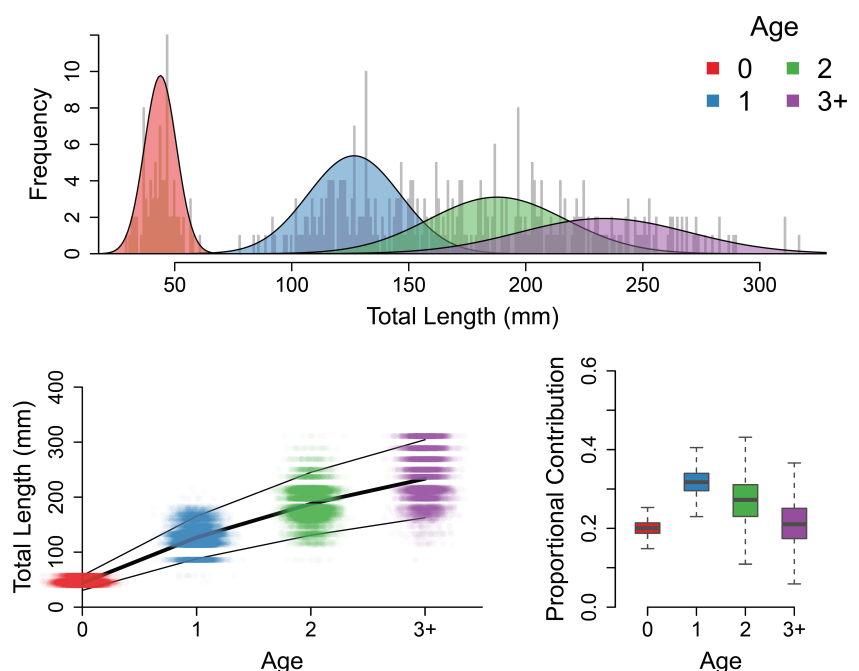
Only 3 years after brown trout removal, at least four age-classes of cutthroat trout appeared to be present in 2016. In 2018, UDWR documented 2,488/km (95% CI = 2,415–2,562) age-1 and older cutthroat trout (size range 73–285 mm) at the lower sample site; age-0 cutthroat trout (size range 31–57 mm) were also present

( $n = 17$  captured and measured but depletion not achieved). By 2019, all distinguishable age-classes were present at the index reach (Figure 2), as is also seen in the broader Logan River meta-population. Just over half of cutthroat trout captured in Right Hand Fork were estimated to be age-0 and age-1 individuals, with remaining individuals being either age-2 and age-3 and older (“3+”; Figure 2). Estimates of proportional contribution of ages-2 and -3+ fish were highly variable due to increased overlap in length-at-age estimates for these older age classes as they approach asymptotic maximum length. Based on von Bertalanffy model estimates, the asymptotic maximum length  $L_{\infty}$  is 368.3 mm (95% CI = 277.0–567.1; Table S1, Figure 2), the Brody growth rate coefficient  $\theta$  is 0.293 (95% CI = 0.165–0.467), and  $t_0$  is  $-0.432$  (95% CI =  $-0.4501 - -0.362$ ).

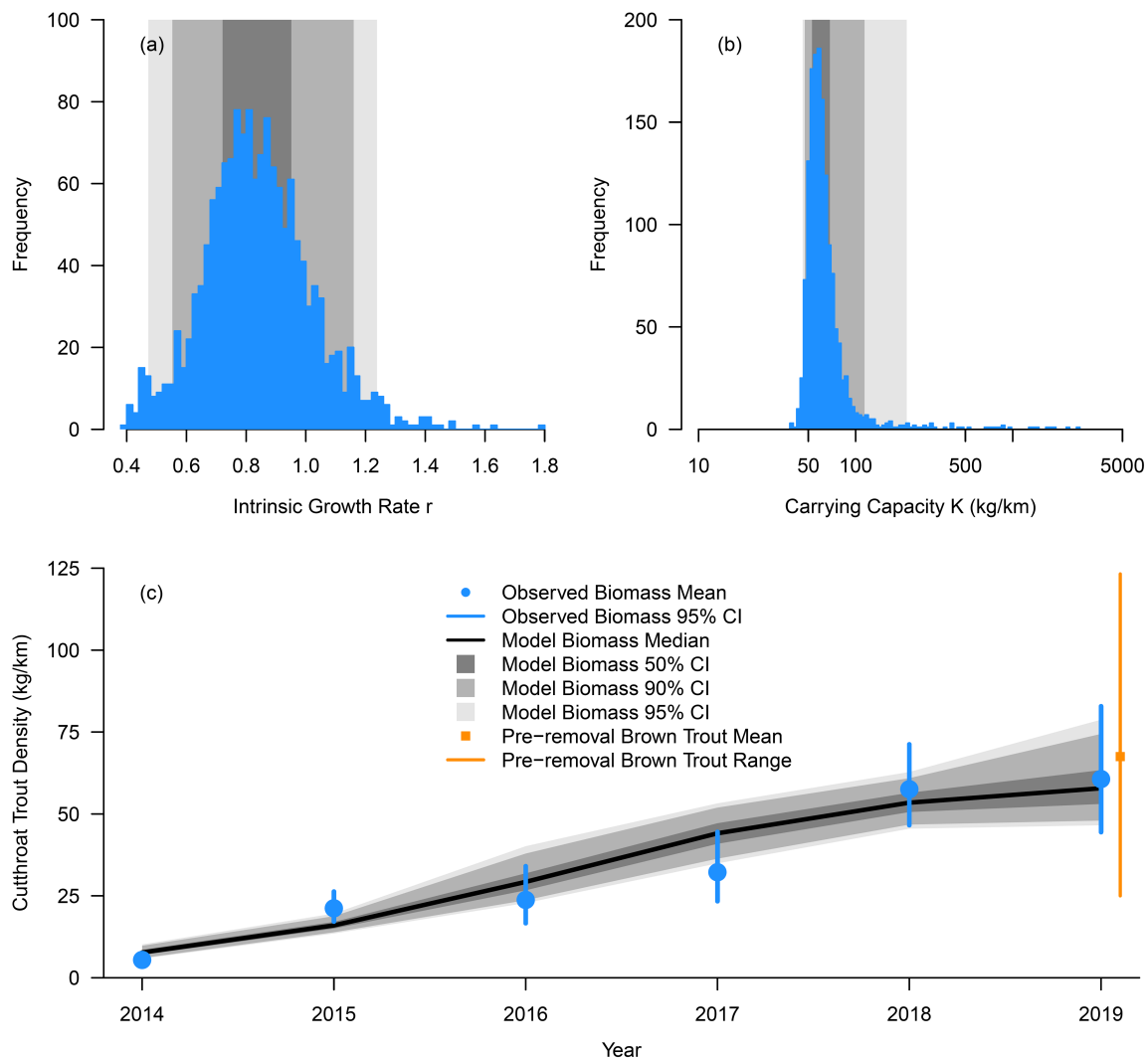
### 3.2 | Population models

The mean intrinsic growth rate estimate for cutthroat trout was 0.84 (median = 0.83, 95% CI = 0.48–1.24; Figure 3a). The mean carrying capacity estimate was 80.1 kg/km, though the posterior distribution was right-skewed (median = 59.2 kg/km, 95% CI = 46.5–209.0 kg/km; Figure 3b). While our estimates of carrying capacity have relatively large uncertainty, the interquartile range of the estimates broadly matches the range of estimated brown trout biomass prior to eradication (Figure 3c). The estimated biomass of the cutthroat trout population in Right Hand Fork increased steadily following brown

**FIGURE 2** (a) Length-frequency histogram (gray bars) with density distributions (colored polygons) for estimates of each age-class of cutthroat trout captured in Right Hand Fork of the Logan River from 2014–2018. “3+” includes trout age-3 and older. (b) von Bertalanffy growth curve estimated from length-frequency data with semi-transparent points indicating lengths at estimated ages of individuals. Each individual fish has multiple points, indicating uncertainty in age-estimates. (c) Age-composition estimates of cutthroat trout in Right Hand Fork. Bold line indicates the median age composition estimate from the MCMC posterior distribution, colored box indicates the interquartile range of MCMC estimates, and the whiskers extend to the most extreme MCMC sample within 1.5\* IQR from the median







**FIGURE 3** Posterior distribution of intrinsic growth rate (a) and carrying capacity (b) parameter estimates, and the time series of estimated cutthroat trout biomass density estimates (c). Shaded polygons represent (in order of increasing darkness) the 95, 90, and 50% credible intervals from the MCMC samples, and orange line indicates the range of brown trout biomass estimates prior to removal efforts. Note the log x-axis in (b)

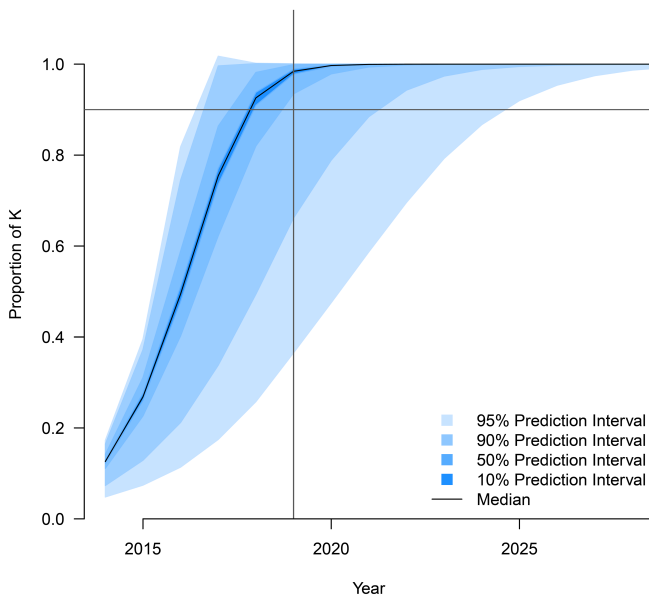
trout eradication in 2013 (Figure 3c), demonstrating a particularly large increase in biomass from 2017 to 2018, before at least temporarily plateauing in 2019.

### 3.3 | Simulations of time to recovery

Our simulation model projections estimate the Right Hand Fork population of cutthroat trout to currently be at approximately 92.8% of their carrying capacity, though the distribution of estimates is variable and highly skewed due to uncertainty in estimates of  $K$  (median = 98.4%, 95% CI = 36.5–100%; Figure 4). Our projection model estimates a 95% likelihood cutthroat trout populations will be at or above 90% of carrying capacity by 2022 (Figure 4).

## 4 | DISCUSSION

In the face of multiple widespread threats, conservation and restoration actions such as invasive species control efforts must be prioritized to target populations and situations with the greatest potential for success and persistence with little future human intervention (Al-Chokhachy et al., 2018; Beechie, Pess, Roni, & Giannico, 2008; Wilson et al., 2011). Here, we demonstrate a rapid recovery of a native trout population after complete eradication of non-native trout from a tributary (Akçakaya et al., 2018). In general, we consider the project a success because brown trout were successfully eradicated and are blocked from reentry/re-establishment. We consider the subpopulation of cutthroat trout to be recovered because they are now successfully reproducing



**FIGURE 4** Estimated proportion of carrying capacity for Right Hand Fork cutthroat trout from simulations across the range of parameter uncertainty. Black line indicates the median estimate, while shaded polygons indicate (in order of increasing darkness) the 95, 90, 50, and 10% prediction intervals. Vertical gray line indicates 2019, the last year with observed data, and the horizontal gray line indicates the 90% threshold

every year with high recruitment success and have a high probability of being at or near carrying capacity within a decade of successful brown trout eradication. In addition, over a relatively short time period, Bonneville cutthroat trout numbers have increased to densities approaching densities of the brown trout sub-population that formerly occupied this tributary, some of the highest densities observed worldwide (Budy et al., 2013). Finally and critically, there are already fishable-sized cutthroat trout available to be targeted by anglers.

Beyond the restoration of a primary sub-population of native and imperiled Bonneville cutthroat trout, there are several additional benefits of this recovery success. Spawning habitat is naturally limited in this watershed (Budy, Seidel, & Roper, 2012), and the addition of Right Hand Fork provides an additional source population, potentially bolstering persistence of the greater meta-population in the face of disturbance (Murphy, Walsworth, Belmont, Conner, & Budy, 2020). Re-establishment of cutthroat trout in Right Hand Fork increases the range of cutthroat trout in the lower portion of the Logan River watershed, expanding the spatial extent and number of sub-populations in this meta-population (UDWR, 2019). Further, while brown trout are one-on-one superior competitors over native cutthroat trout (Budy & Gaeta, 2017; McHugh & Budy, 2006), there is increasing evidence that high

densities of cutthroat trout in the upper portions of the watershed prevent brown trout expansion through biotic resistance (e.g., Moyle & Light, 1996). We do note, however, that if genetic issues (e.g., founder effects or inbreeding depression) were to arise as a consequence of the small number of eggs and fry used to initiate recovery (Beibach, Leigh, Sluzek, & Keller, 2016), this time period may be actually too short to assess full recovery. We believe these genetic issues are unlikely given the Logan River meta-population is very well-mixed genetically (Mohn, 2016), and eggs and fry were taken from multiple locations across multiple years. Nonetheless, we plan to monitor this genetic variability carefully in the future and ripe cutthroat trout from the lower river observed trying to ascend above barriers could also be assisted over and allowed to reproduce in the tributary.

Several other factors contributed to the success of this project, including scale of restoration, lack of additional limiting factors, and stakeholder buy-in. First, the restoration action was completed at a spatial scale that is biologically meaningful yet still logistically feasible. Right Hand Fork provides adequate spawning, rearing, and adult habitat to support a large sub-population of native trout, yet is small enough to allow complete eradication and exclude non-native trout. The native fish restoration literature is replete with studies documenting the general failure of a restoration project to meet intended goals because the scale of action is inadequate (Bernhardt & Palmer, 2011) or conversely unmanageable (Barbour, Allen, Frazer, & Sherman, 2011). Second, this location offered an ideal opportunity to restore native trout because there were no other limiting factors to slow or prohibit recovery (e.g., Clancey et al., 2019). This tributary is affected only by gentle recreational use (hiking, mountain biking) and light livestock grazing (less than five cattle head months/year) leaving the habitat highly intact and connected (internally). Angling pressure is also relatively light, with 0–3 anglers typically encountered on a given day during creel surveys, and 97% of angling is catch and release (Budy et al., 2002, 2017). Additionally, Right Hand Fork is spring fed with little temperature variation and abundant prey resources, providing a stable and productive growth environment for salmonids. Cutthroat trout are capable of rapid growth in the absence of competitors and produce many small offspring whose typically poor survival likely increases in productive environments with few predators and competitors, such as Right Hand Fork after brown trout eradication.

In our study, we believe this combination of factors contributed to a relatively rapid recovery of the subpopulation with high densities of native trout, a diverse age structure, and with individuals demonstrating very rapid growth rates. Directly comparable published studies are

somewhat rare, as stream restoration projects often have multiple objectives, including habitat improvement, flow augmentation, and non-native removal, and many restoration responses are buried in the gray literature. However, Clancey et al. (2019) similarly observed Westslope cutthroat trout (*O. c. lewisi*) populations were deemed rapidly recovered in 3–4 years post non-native removal (based on density and mean size) in a location where ecological conditions were otherwise nearly ideal. Similarly, in Great Smoky Mountains National Park, United States, when brook trout were reintroduced at relatively low densities (39–156 fish/km) after non-native rainbow trout removal, they returned to densities and biomass comparable to the density and biomass of rainbow trout (*O. mykiss*) pre-restoration within 2 years, though their reintroduction included adult, reproductively viable fish (Kanno, Kulp, & Moore, 2013). In another similar non-native brown trout removal to benefit native brook trout, Hoxmeier and Dieterman (2016) observed that native brook trout were slow to respond for the first 3 years, then abundance began to increase nearly exponentially in about Year 4. However, there are multiple examples where removal of non-native fishes had no effect on native fishes, even after long time periods. In a quite infamous case, after 10 years of the removal of non-native fishes in the Colorado River, United States, and millions of U.S. dollars spent (and stocking of multiple species of multiple age classes), there has been no positive response from the highly imperiled endemic fish community (Mueller, 2005). In a study more similar to ours in scale, installation of barriers and removal of non-native trout and stocking had no effect on wild native cutthroat trout in Wyoming, United States, where the authors speculate habitat was limiting and stocked fish exited the area downstream (Novinger & Rahel, 2003). Clearly there are many factors that must be considered when prioritizing conservation actions such as non-native removal, and not all outcomes are predictable or timely.

In our study, the barriers were necessary to prevent brown trout from reinvading; however, the partial isolation of this sub-population (no upstream movement or immigration) that results as an artifact of those barriers is not without issue. Connectivity among sub-populations and the ability to recolonize has been firmly demonstrated to be critical for stream fish populations after disturbances such as drought and wildfire, both of which are increasing in frequency, intensity, and magnitude (Westerling, Hidalgo, Cayan, & Swetnam, 2006; Murphy et al. 2020). However, we have demonstrated herein that if this sub-population were extirpated in the future due to disturbance, it could be rapidly re-established using eggs from nearby tributaries. The lack of genetic differentiation among tributary sub-population in the Logan River

(Mohn, 2016) simplifies this fallback recovery strategy. Further, the geographic configuration and large spatial scale of this watershed makes it unlikely that wildfire would impact all tributaries in one event.

Our project was also a success socio-politically because we sought and earned political and angler support through education, outreach and persistence from the onset of the project (taking five years to achieve). The local angler population was involved from the beginning and demonstrated commitment and ownership by taking the lead on egg incubation and fry dissemination. Finally, we fostered and maintained a tight partnership and shared vision among state and federal governments, and academia (e.g., Clancey et al., 2019). More specifically, this restoration contributes to the goal of the multi-signatory, range-wide Conservation Agreement and Strategy of “ensuring the long-term persistence of Bonneville cutthroat trout within its historic range by coordinating conservation efforts among states, [...], federal management agencies, and other involved parties” (UDWR, 2019). We also note this was a relatively inexpensive restoration action (~US \$25,000). Each of these socio-political and ecological factors set the stage for a highly successful restoration project.

Despite the somewhat limited sampling regime, we believe the broad trends observed in our sampling reach likely reflect the broad population trends in Right Hand Fork. First, we expect trout will disperse among habitats as density increases and per capita resources are less available (e.g., ideal free distribution; Fretwell & Lucas, 1970; Newman, 1993; Grand & Dill, 1997). Second, we have confidence in our estimates of cutthroat trout carrying capacity in Right Hand Fork (median 835.5 fish/km [95% CI of 657.3–2,951.1] because they align well with other related studies in the Logan River as well as comprehensive previous studies in this tributary. LaPlanche et al. (2018) estimated Bonneville cutthroat trout at 1,019 fish/km in the upper Logan River, which is wider and where we believe the population is stable and near carrying capacity (Budy et al., 2007). Saunders et al. (2014) estimated that brown trout densities before removal in Right Hand Fork were > 2,000 fish/km; however, at that time brown trout could theoretically still emigrate into the tributary. The fundamental niches of cutthroat and brown trout overlap directly as do their diets, generally, in this system (Meredith et al., 2014), suggesting that if brown trout thrived, cutthroat also have a good probability of thriving. We do know, however, that brown trout are much more aggressive than cutthroat trout (reviewed in Budy & Gaeta, 2017), which could affect their relative carrying capacities in the same given area.

We also had logistical hurdles to overcome. First, we had to demonstrate to the city of Logan (Utah, United States) these rotenone treatment chemicals are used at



very low concentrations and would remain well below drinking water standards. Second, many anglers prefer and have a deep appreciation for non-native brown trout (Budy & Gaeta, 2017; McIntosh et al., 2012), and we could not guarantee a replacement fishery. Further, there is no hatchery source of native Bonneville cutthroat trout, such that there was no way to stock adult fish, which typically have the greatest probability of surviving and reproducing, as well as providing suitable angling targets most quickly (e.g., Yule, Whaley, Mavrakis, Miller, & Flickinger, 2011). In addition, the State of Utah prohibits the movement of whirling disease positive trout (Utah Admin. Code Rule R58-17 Aquaculture and Aquatic Health). This meant we had to rely on survival of a limited number of streamside spawned eggs and a small number of fry reared from those eggs. In contrast, for example, Clancey et al. (2019) were able to stock 39,000 eggs as part of a large-scale non-native removal project for native Westslope cutthroat trout in Montana, United States. The survival of eggs to age-1 for cutthroat trout in the wild is typically only ~5% (Weaver & Fraley, 1993), and survival of fry to age-1 is typically <40% (range 32–52%; Budy et al., 2007). Thus there was uncertainty that there would even be adequate cutthroat trout to initiate the population, and we anticipated there would be at least 5 years before any adult fish were suitable for angling. Nonetheless, spring-fed conditions and reduced competition resulted in rapid growth rates and high survival of the few stocked eggs and fry. Ultimately, this project offered a viable fishery in only three years.

Finally, although becoming more common, it is rare for restoration projects to be set up *a priori* to advance our understanding of population dynamics of either the invader or recovering native species, and thus overall effectiveness of the action (Chasco et al., 2014; Davis, Chadès, Rhodes, & Bode, 2019; Vredenburg, 2004). Here, we demonstrate the importance of pre-restoration and post-restoration monitoring and long-term data. Ideally, the whole aquatic food web would be monitored (e.g., macro-invertebrates), a monitoring strategy that has recently become more feasible and economical with advances in genomic sampling approaches such as eDNA, for example (Ruppert, Kline, & Rahman, 2019). Nonetheless, from our time-series of brown trout data before removal, we were able to determine that this tributary was nearly ideal for trout and could theoretically support extremely high densities of native species, including successful reproduction. This information was then critical for gaining angler and management agency buy-in. By providing estimates of expected future cutthroat trout dynamics, stakeholder expectations can be set in order to allow sufficient time for the restoration action to have its full effect, staving off impatience that may drive alternative management actions, which may be unnecessary or even

detrimental to achieving conservation objectives. The observed rapid recovery of cutthroat trout demonstrated in this study can benefit other native trout recovery projects and can convince stakeholders they may not have to forego benefits (i.e., lost fishing opportunities following non-native trout extirpation) for a long time before achieving the desired management and conservation objectives are achieved (Walsworth & Schindler, 2016). In the face of multiple and varied threats, conservation actions will be most effective when targeted at systems with the greatest potential for success and independent persistence, as well as opportunities to learn.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

All authors contributed to the manuscript intellectual ideas, study design, and monitoring. P.B. and P.T. were the leads on writing. G.P.T. summarized the data and T.W. completed most of the analyzes. P.B.H., P.D.C., and W.C.S. implemented field study components of the project.



## DATA AVAILABILITY STATEMENT

Data will be made available from the corresponding author upon reasonable request.

## ETHICS STATEMENT

We performed this research ethically under the standardized auspices of Utah State University IACUC Protocol 2022.

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## SUPPORTING INFORMATION

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

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