Centennial Valley Arctic Grayling Adaptive Management Project Annual Report, 2021

27 January, 2022

EXECUTIVE SUMMARY

Arctic grayling (*Thymallus arcticus*) are a freshwater holarctic salmonid that were once widespread throughout the Upper Missouri River (UMR) drainage as a glacial relict population. One of the last endemic grayling populations remaining in the UMR drainage resides in the Centennial Valley (CV) of southwestern Montana. Spawning is largely limited to Red Rock, Corral, Elk Springs, and Odell creeks, with Red Rock Creek likely supporting 80-90% of annual spawning in the CV. It is presumed that most of the grayling population in the CV spends non-breeding portions of the year in Upper Red Rock Lake (Upper Lake). Red Rock Lakes National Wildlife Refuge (Refuge) encompasses Upper Lake, and nearly all of the currently occupied grayling spawning habitat within Red Rock, Elk Springs, and Odell creeks.

The estimated number of grayling in the 2021 Red Rock Creek spawning population was 88 fish (95% CI = 26–176), statistically similar to the previous year ($\hat{N}$ = 138, 95% CI = 82–302; Figure 1). The consistently low grayling abundances experienced since 2016 will likely lead to irreversible losses of genetic diversity annually (Kovach et al. 2021). Suitable habitat the prior winter within Upper Lake (i.e., water depth below the ice $\geqslant$ 1 m and dissolved oxygen $\geqslant$ 4 ppm) reached a minimum during March sampling at an estimated 5 ha. This is $\approx$ 3 ha less suitable winter habitat than experienced during the winter of 2015–2016 that led to the documented decline of spawning grayling from 1131 fish (95% CI = 1069–1210) in 2015 to 214 fish (95% CI = 161–321) in 2016. Area of winter habitat for the current year (2022) was $\approx$ 14 ha in January.

Suitable spawning habitat was quantified in 2021, with an estimated weighted area of suitable habitat (A_t) of 6.1 ha, in Red Rock and Elk Springs creeks (see **METHODS** below for description of variables). Barriers precluding grayling from accessing suitable spawning habitat, i.e., beaver dams, were notched prior to spawning in 2021.

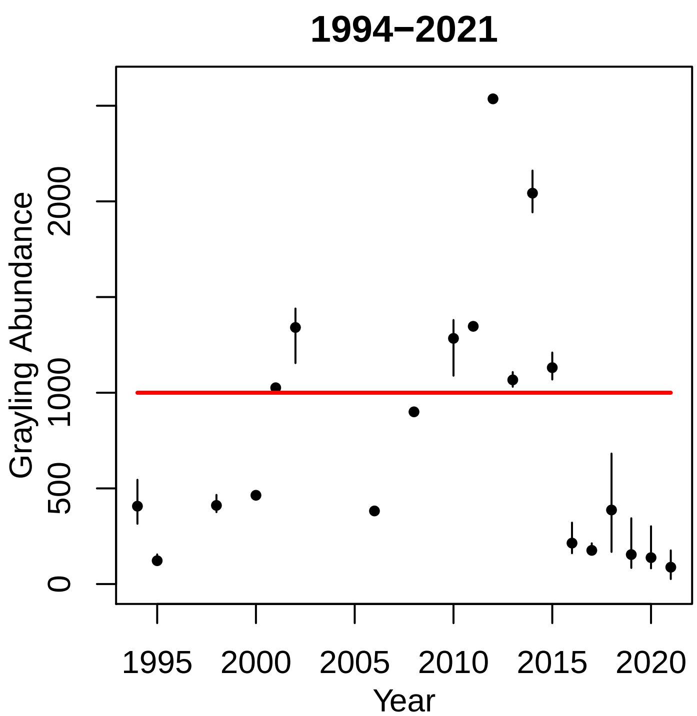

Figure 1. Estimated annual Red Rock Creek Arctic grayling spawning population abundance and 95% confidence intervals (when available), 1994–2021. The red line indicates the current grayling population objective of 1000 fish for Upper Red Rock Lake and tributaries (Warren and Jaeger 2017).

The first management experiment conducted as part of the Adaptive Management Plan (AMP) was reducing abundance of non-native Yellowstone cutthroat trout (*Oncorhynchus* *clarkii bouvieri*). Trout were captured and euthanized at a fish weir and fishing regulations were liberalized to 20 cutthroat trout per day (excluding a stream closure 15 May–14 June) on Red Rock Creek. Both actions were first implemented in 2013; the weir was operated through 2016 and liberalized harvest occurred through 2017. During 2013–2017 a total of 7150 cuttroat trout were removed from Red Rock Creek. Removal efforts peaked in 2014 at 2604 cutthroat removed. The first year a grayling response to cutthroat removal could be quantified was 2016 when the 2013 grayling cohort recruited.

The second management experiment examined the relationship between spawning habitat and grayling recruitment. Suitable habitat available for spawning was increased 2017–2020 by 1) ensuring fish passage at beaver dams ($n > 50$ in 2016) via notching, 2) restoration of an Elk Springs Creek channel that provides direct connection to Upper Lake, and 3) restoration of spawning habitat at the head of Elk Springs Creek. This experiment was undertaken for four years, similar to the cutthroat trout reduction. Increased per capita availability of spawning habitat is hypothesized to increase egg (β) and age-0 fish in-stream (γ) survival; potential recruitment responses from treatments conducted in 2017 and 2018 were quantified in 2020 and 2021, respectively.

The iterative phase of the AMP began in 2021. If grayling spawning population is less than 1000 fish, management action(s) predicted to restore the population to objective will be implemented. Experimental actions (aeration and pulsed-flow from Widgeon Pond) to mitigate the primary population driver, winter habitat, have been unsuccessful to date. Neither action demonstrated the ability to consistently provide suitable oxygen levels for the duration of winter. Additional modeling of pulsed-flow from Widgeon Pond also indicated this action could not provide suitable habitat within Upper Lake throughout winter. Therefore, the most influential secondary population driver, spawning habitat availability, was maximized in 2021 by notching beaver dams to ensure fish passage.

Final engineering design of a tributary point-of-inflow modification will be completed winter 2022 to further clarify the effectiveness, costs, and impacts of this alternative. Fundraising and permitting will be completed during spring of 2022. Project construction can occur once NEPA analysis is completed.

Learning in the context of this project occurs through comparison of model predictions with reality (i.e., predicted grayling population vs. actual grayling population). Each hypothesized driver of grayling population dynamics, i.e., winter habitat, spawning habitat, and non-native fish, is represented by a model structured to estimate the driver's influence on a specific life stage. The *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models predicted 207, 361, and 323 grayling, respectively, in the 2021 Red Rock Creek spawning population. Model weights, i.e., relative support for a model given the data, were 0.576, 0.333, 0.09 for the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models, respectively. The 2022 model-averaged prediction of spawning grayling abundance based on January habitat monitoring is 187 fish; if conditions worsen in Upper Lake this prediction will decline.

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INTRODUCTION

Montana Arctic grayling (*Thymallus arcticus*; hereafter grayling) were patchily distributed throughout the Upper Missouri River (UMR) drainage prior to the mid-1850s. This population declined to about 4% of their perceived historic distribution by the 1990s, which led to formal consideration for listing under the Endangered Species Act (USFWS 2014). One of the last populations of indigenous UMR grayling resides in the Centennial Valley (CV) of southwestern Montana. Grayling were historically distributed among at least a dozen CV streams and three lakes at presumably high abundances (Nelson 1954). Perceived distribution and abundance declined to historic lows sometime between the 1950s and mid-1990s, but have since improved, although large fluctuations in abundance still occur (USFWS 2014, MAGWG in press).

Currently, most of the CV grayling population spawns in Red Rock Creek and spends non-breeding portions of the year in Upper Red Rock Lake (Upper Lake) within Red Rock Lakes National Wildlife Refuge (Refuge; Figure 2). Over the past 70 years numerous hypotheses were posited regarding drivers of the CV grayling population, including 1) reduction and alteration of spawning habitat, 2) predation by, and competition with, non-native fishes, and 3) limited winter habitat. Although these hypotheses have been repeatedly proposed to explain population fluctuations, drivers of the population remain unclear.

Previous and ongoing research has focused on aspects of each hypothesis but has not linked them to demographic responses in grayling, which precludes inference regarding their role as population drivers. Resultantly, the most effective management and conservation approaches for CV grayling remain ambiguous, and selecting management actions can be contentious among and within agencies. This plan seeks to elucidate the relative effect of hypothesized drivers of CV grayling abundance to direct future management of this population. Determining the cause of previous population declines, *per se*, is not the primary issue of grayling conservation and management – finding an effective strategy to achieve population goals and prevent future declines is. In an effort to accomplish this, an adaptive management (AM) approach is being undertaken (Walters 1986). The Centennial Valley Arctic Grayling Adaptive Management Plan (AMP) embraces existing uncertainty regarding drivers of the grayling population in the CV to provide further understanding of important limiting factors and help guide management actions toward those that will have the most direct benefit to grayling.

Due to the initial level of structural uncertainty, and agency conflict regarding that uncertainty, the AMP was divided into two phases – a 'management as experiment' phase that emphasizes learning, i.e., reducing structural uncertainty (MacNab 1983, Walters 1986, Walters and Holling 1990), and an iterative phase. The former was designed to explore grayling population response to hypothesized drivers that could be influenced via management actions. The latter is using the information gained in phase 1 to determine an optimal policy to inform annual management decisions (while still learning, but with less of an emphasis on learning).

STUDY AREA

The Centennial Valley of southwestern Montana is a high-elevation (ca. 2013 m) valley dominated by sagebrush steppe comprising *Artemisia* spp. shrub overstory and native bunchgrass understory (e.g., *Festuca* spp., *Nasella* spp., and *Hesperostipa* spp.). The valley is bounded on the north by the north-south trending Gravelly and Snowcrest mountain ranges and on the south by the east-west trending Centennial Mountains. Extensive wetlands exist throughout the CV, including a large shallow lake/wetland complex encompassed by Red Rock Lakes National Wildlife Refuge (Figure 2). The complex comprises Upper Red Rock, Lower Red Rock, and Swan lakes and associated palustrine emergent marsh dominated by seasonally-flooded sedge (*Carex* spp.). The complex is a remnant of Pleistocene Lake Centennial, a prehistoric lake that was believed to have formerly covered the valley floor to a depth of ca. 20 m (Mumma 2010). Upper Lake, the largest and deepest of the lakes, is ca. 1198 ha with a maximum depth of 2 m. The geologic (Sonderegger 1981; Centennial Valley Historical Society 2006), hydrologic (Deeds and White 1926, MTFWP 1989, MCA 2000), and fisheries (Nelson 1952, Randall 1978, Boltz 2000, Oswald et al. 2008) resources and contemporary administrative status (USFWS 2009) within the Centennial Valley are well described elsewhere.

The Centennial Valley includes all tributaries of the Red Rock River and their associated drainages upstream of Lima Dam (Figure 2). Most Upper Lake tributaries have their origins to the south along the eastern extent of the Centennial Mountains. Red Rock Creek, the largest of these tributaries, originates at an elevation of 2,562 m and flows north and west ca. 21 km to the northeast shore of Upper Lake. Elk Springs Creek originates from a series of springs south of Elk Lake and flows southwest, entering Upper Lake along the northeast shore. Red Rock River exits Upper Lake in the northwest corner, carrying water through the River Marsh and into the northwestern corner of Lower Lake. Red Rock River continues westward through the outlet of Lower Lake, ca.1.5 km west of where it enters the lake, leaving the CV near Lima, MT after passing through the 13 km long Lima Reservoir. Long Creek enters the Red Rock River 17 km downstream of the Lower Lake outlet and just upstream of Lima Reservoir.

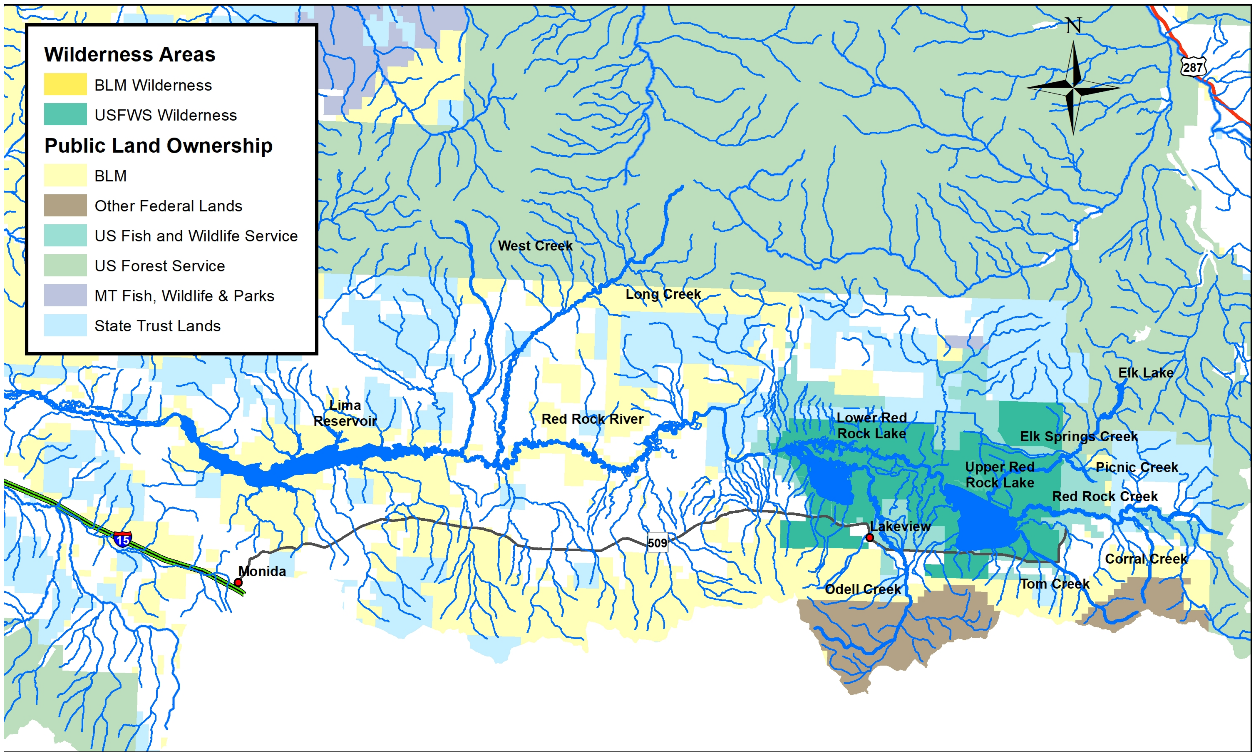

Figure 2. Arctic grayling Adaptive Management Plan study area within the Centennial Valley of southwestern Montana.

METHODS

Models of System Dynamics

Spawning habitat, non-native fishes, and winter habitat have all been identified as potentially important drivers of grayling population dynamics in the upper CV. Each of these hypotheses is translated into a model, or set of models, to link hypothesized drivers and demographic rates.

The annual abundance of spawning grayling is the product of demographic rates ranging from adult survival to the number of eggs deposited per female (fecundity) three years prior. All population models for spawning grayling share a common balance equation that allows prediction of annual abundance as a function of survival and recruitment processes:

$$N_{t+1} = N_t S_t + (F_{t-2}\alpha_{t-2}\beta_{t-2}\gamma_{t-2}\delta_{t-2}\epsilon_{t-1})\theta_t \ (1)$$

The number and survival of adult (i.e., reproductive age) grayling in year t is N_t and S_t, respectively. Assuming recruitment occurs with the age-3 cohort in year $t+1$ (i.e., knife-edge recruitment at age-3), the number of potential age-2 recruits in year t is the product of:

- F_{t-2} – the number of females in the spawning run in year t - 2,
- α_{t-2} – length-specific fecundity rate, year t - 2,
- β_{t-2} – probability of an egg being fertilized and hatching, year t - 2,
- γ_{t-2} – age-0 fish in-stream survival (emergence to September 1^{st}), year t - 2,
- δ_{t-2} – age-0 fish winter survival (September 2^{nd} – May 15^{th}), year t - 2,
- ϵ_{t-1} – age-1 fish survival (May 16^{th} – May 15^{th}), year t - 1, and
- θ_t – age-2 fish survival, year t.

It is assumed that a female that participates in the spawning run will deposit a clutch of eggs. The number of females in the spawning run is calculated as $f_t\hat{N}_t$, where f_t is the proportion of females captured during the spawning run in year t, and $\hat{N}_t$ is the estimated spawning run population corrected for imperfect detection (e.g., Paterson 2013). Length-specific fecundity, α_l, was estimated using data from Lund (1974) and Bishop (1971). Lund provided mean number of eggs and lengths by female length category; Bishop provided length and fecundity data from individuals. One of Bishop's observations (13^{th} observation) was excluded as an outlier. Total fecundity in year t is then $F_t\alpha_l L_t$, where L_t is mean female length in year t. Egg hatchability was taken from Lund's (1974) work in Elk Lake. Hatchability varied from 0.04–0.12; the mean of these values ($\bar{x} = 0.08$) was used for β.

Estimates of demographic rates were taken from published values for fish of similar life history, age, and size when empirical estimates were not otherwise available (Table 1). Maximum and mean survival rate values were obtained for model fitting. Mean Age-2 survival, θ_t, was estimated using the upper confidence interval of annual survival for age-3 Red Rock Creek grayling (Paterson 2013). The upper confidence interval was selected because age-2 fish generally do not incur the risk of predation and physiological demands associated with spawning and, resultantly, likely have higher annual survival than age-3 fish. The maximum Age-2 survival rate was the highest annual adult survival rate estimated from available CMR data. Age-1 annual survival, ϵ_{t-1}, and age-0 winter survival, δ_{t-2}, were calculated by averaging published survival estimates for fish of similar life history, age, or size. Published survival estimates were transformed, when necessary, to account for differences between time intervals of published estimates and parameters of grayling models. Because no published estimates applicable to age-0 in-stream survival, γ_{t-2}, were found, we calculated this rate for all years with adequate data using Equation 1 and the aforementioned age specific rates and solving for γ_{t-2}. Average age-0 in-stream survival was the average of the calculated rates among years and maximum age-0 in-stream survival was the highest annual value calculated.

Table 1. Demographic estimates used for testing competing models of grayling response to winter habitat, spawning habitat, non-native predation, and spring hydrology.

	Average survival rate (maximum survival rate) size range in mm; age range time period applicable to survival rate			
Species	γ_{t-2}	δ_{t-2}	ε_{t-1}	θ_t
Arctic grayling[1,2,3]	**0.014 (0.035)** 15-100; 0-90 d 90 days	**0.25 (0.48)** 100-150; 90 d -1 y .75 year	**0.44 (0.68)** 153-211; 1-2 y 1 year	**0.74 (0.87)** 263-340; 2-3 y 1 year
Bull trout[4]	--	0.23 (0.38) 121-170; 2 y 1 year	--	--
Chinook salmon[5]	--	0.16 (0.48) 61-115; 90 d- 1.2 y 0.95 year	--	--
Bull trout[6]	--	0.09 (0.60) 121-170; 2y 1 year	0.45 (0.85) 171-220; 3y 1 year	--
Brown trout[7]	--	0.26 (0.47) 120-175; 0.5-1 y .75 year	0.43 (0.50) 200-305; 1-3 y 1 year	--

[1]Katzman 1998; [2]Mogen 1996; [3]Paterson 2014; [4]Bowerman, T. and P. Budy 2012; [5]Achord, S., R. Zabel, and B. Sanford 2007; [6]Al-Chokhachy, R. and P. Budy 2008; [7]Dieterman, D.J. and R.J.H. Hoxmeier 2011.

Winter Habitat Model–The influence of winter habitat on the grayling population would likely manifest itself as reduced survival of all-age grayling during years with widespread hypoxic conditions in Upper Red Rock Lake (e.g., Greenbank 1945). If the response of different age-class fish to winter habitat conditions is proportionally constant, e.g., poor winter conditions halve fish survival across all age classes, it is possible to estimate the relationship between all-age survival and winter conditions.

The influence of winter habitat conditions on grayling was quantified based on the minimum amount of winter habitat available between January and March, a period when hypoxic conditions can occur in Upper Red Rock Lake (Gangloff 1996, Davis 2016). Available winter habitat is defined as the area (ha) of water in Upper Red Rock Lake from January to March with $\geqslant$ 4 ppm dissolved oxygen and $\geqslant$ 1 m in depth (Davis 2016). Assuming species-specific density dependence, available winter habitat per fish, W_t (ha fish^{-1}), is related to the area of suitable winter habitat, A_t, and the number of fish that entered the winter period, $N_{w,t}$.

$W_t = \frac{A_t}{N_{w,t}}$ (2)

The estimated number of spawning fish in Red Rock Creek in year t will be used as an index for $N_{w,t}$. Winter habitat will be related to the proportional change in all-age grayling survival using a saturating function (i.e., Holling type-II functional response) by

$P_t = \frac{aW_t}{b+W_t}$. (3)

Parameters a and b determine how the realized proportion of maximum grayling survival is related to winter habitat conditions. Maximum realized proportion of grayling survival is a, and b represents the value of suitable winter habitat to an individual when the proportional change in survival is 50% of a (Hilborn and Mangel 1997). For example, if no reduction to survival occurs $a = 1$, i.e., grayling survive at their maximum age-class rates. To assess if the influence of available winter habitat is density independent, A_t will be substituted for W_t in Equation 3. Figure 3 shows a hypothetical situation where $a = 1$, $b = 0.0185$, and W_t varies from 0 to 0.50 ha fish^{-1}.

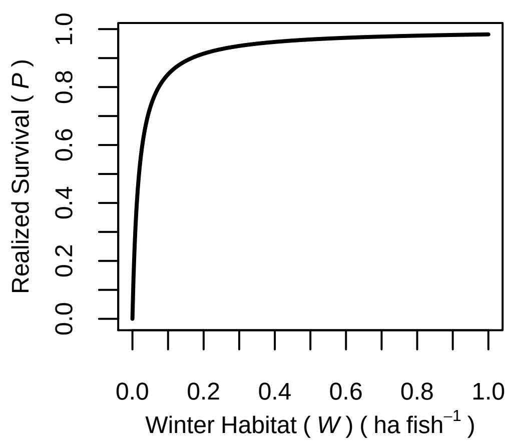

Figure 3. Hypothetical relationship between the realized proportion of maximum grayling survival and the area of suitable winter habitat per fish in Upper Red Rock Lake based on a Holling type-II functional response.

The winter habitat model for grayling population dynamics and observation error, linking survival to winter habitat conditions, would then be:

$N_{t+1} = N_t S_t P_t + F_{t-2}\alpha_{t-2}Y_{t-2}(\delta_{t-2}P_{t-2})(\epsilon_{t-1}P_{t-1})(\theta_t P_t)$, (4)

$N_{obs,t} = N_t V_t$. (5)

The number of adult fish surviving from year t to year t + 1 is the product of the number of adults in year t, maximum annual survival (S_t), and the realized proportion of maximum survival conditional on winter habitat conditions (P_t). The number of potential recruits in year t is the number of age-2 fish, which is the product of the number of females t - 2, length-specific fecundity t - 2, the probability of an egg laid in year t - 2 surviving until its first winter, Y_{t-2}, (the combined probabilities of egg (β) and age-0 stream (γ) survival), and maximum survival of age-0 winter (δ), and age-1 (ϵ) survival for cohort i multiplied by the estimated proportional influence of winter habitat on survival for each respective winter. The number of recruits in year $t + 1$ is the product of the cohort in time t, second year survival (θ_t), and P_t. Substituting in demographic rates assumed fixed and constant (described above), gives the following equation for the winter habitat model

$$N_{t+1} = N_t * 0.74P_t + F_{t-2}\alpha_{t-2} * 0.0112 * (0.48P_{t-2})(0.68P_{t-1})(0.87P_t). \quad (6)$$

There are two components to the likelihood for this model, adult grayling annual abundance and survival. For the latter, apparent survival (ϕ) estimates for 1993–1996 (0.41, 95% CI = 0.24–0.66) and 2010-2013 (0.63, 95% CI = 0.53–0.74) are available (Paterson 2013). Estimates of ϕ will be obtained annually using marked individuals.

Spawning Habitat Model–The relative quality of spawning habitat was hypothesized to influence cohort strength by its influence on egg (β) and age-0 fish in-stream (γ) survival. Low per capita area of suitable spawning habitat would lead to low egg and age-0 fish in-stream survival due to increased intra-specific competition for available spawning habitats, resulting in increased use of low suitability or unsuitable spawning habitat with lower intrinsic rates of egg and age-0 fish in-stream survival. Although degradation of spawning habitat is caused by the same mechanism (sedimentation) that degrades habitat for older fish, survival rates are most likely to be directly influenced in ages that are unable to avoid degraded habitat (i.e., eggs and fry).

The definition of suitable spawning habitat follows Hubert et al.'s (1985) functional relationships between suitability and percent fines and gravels in spawning riffles, where $\leqslant$ 10% fines is considered suitable, 11–50% fines represent linearly declining suitability, and $>$ 50% is unsuitable. Conversely, $\geqslant$ 20% gravel and rubble is considered suitable with $<$ 20% representing a linearly declining suitability (Figure 4). Thus, the most suitable spawning habitat can be characterized by having $\leqslant$ 10% fines and $\geqslant$ 20% gravel and rubble.

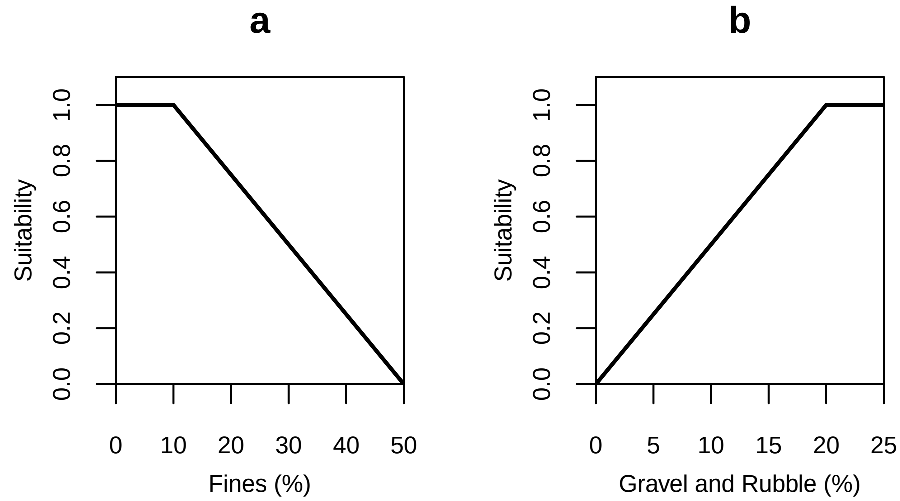

Figure 4. Predicted relationship between suitability of riverine Arctic grayling spawning habitat and a) percent fines (< 3 mm) in spawning areas and downstream riffles, and b) percent gravel and rubble (1.0–20.0 cm) in spawning areas (from Hubert et al. 1985).

The suitability threshold provided by Hubert et al. (1985) predicts the proposed asymptotic relationship between spawning area and recruitment. For example, at low population and high area of suitable spawning habitat, individuals would presumably all utilize the most suitable areas, resulting in maximum egg and age-0 fish in-stream survival, and number of recruits per individual. Further increases in suitable spawning habitat would not result in greater per capita recruitment. However, if population increased, and suitable spawning area per individual decreased, more individuals would spawn in less suitable habitats and an overall decrease in per capita recruitment would result as egg and age-0 fish in-stream survival declined.

Percent fines (particles < 3 mm) and gravel and rubble (1.0–20.0 cm) in riffles were estimated biennially using pebble count surveys. Each stream of interest was divided into reaches based on gross geomorphological characteristics and 1–5 representative sites were selected for sampling within each reach (Warren and Jaeger 2017). At each sampling site, four separate consecutive riffles were sampled following MT DEQ TMDL Sediment Assessment Methods (Kusnierz and Welch 2011). Cumulative percent fines are calculated for each sampled riffle.

Total area of suitable spawning habitat, A_t, was calculated using weighted habitat suitability based on observed percent fines and gravel and rubble following Hubert et al. (1985; Figure 4). Empirical assessment of Arctic grayling egg survival at varying levels of sediment provides support for this approach (Anderson 2019). Riffle area (m^2; *riffle length (m)* $\times$ *riffle bankfull width (m)*) was multiplied by weighted riffle suitability to estimate area of suitable habitat by riffle. Area of suitable riffle habitat was then summed to obtain area of suitable spawning habitat by reach and stream.

To ensure all suitable spawning habitat was available to grayling as part of the current AMP treatment, beaver dams have been notched 2017–2020 to allow fish passage (i.e., probability of passage = 1). During 2013–2016, area of suitable habitat (A_t) was adjusted to account for effects of beaver dams and fragmentation. Habitat backwatered by beaver dams becomes unsuitable for spawning for at least the life of the beaver dam and the number and location of beaver dams varies among years. Each stream was annually surveyed and the total length of beaver dam backwaters was subtracted from each reach length when calculating A_t. The effects of fragmentation can range from incrementally reducing the likelihood of passage past a given location depending on daily conditions to completely precluding passage for that year. If passage is completely prevented then the area of upstream spawning habitat is functionally zero. If the probability of upstream passage is reduced then the area of available habitat is similarly reduced. To correct for the effects of fragmentation the area of suitable spawning habitats upstream of a barrier that prevents passage (i.e., probability of upstream passage is 0.0) was not included in calculation of A_t. Probability of passage at beaver dams was estimated based on assessment of relevant beaver dam characteristics within each reach (Cutting et al. 2019). Calculation of A_t was adjusted by multiplying the area of suitable habitat upstream of a beaver dam by the probability of passage at that dam. The effects of reduced passage probability were cumulatively considered. For example, the calculated value of A_t upstream of three beaver dams would be multiplied by the probability of a fish passing all three dams.

Assuming species-specific density dependence, availability of suitable spawning habitat per fish, H_t (m^2 fish^{-1}), is related to the area of suitable spawning habitat, A_t, and the number of spawning females, F_t

$$H_t = \frac{A_t}{F_t}. \quad (8)$$

Spawning habitat was related to the product of egg and age-0 fish in-stream survival, R_t, using a saturating function (i.e., Holling type-II functional response) (Figure 5) by

$$R_t = \frac{aH_t}{b+H_t}. \quad (9)$$

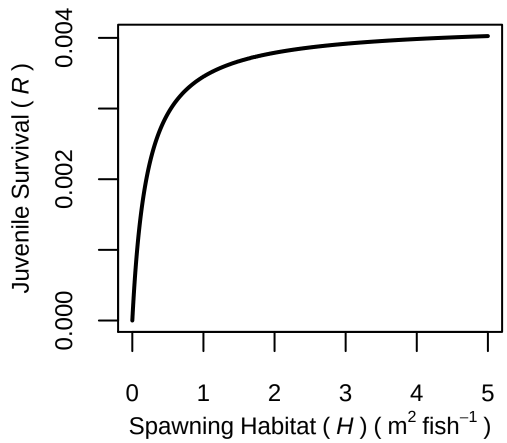

Figure 5. Hypothetical relationship between grayling egg and age-0 fish in-stream survival, R, and area of suitable spawning habitat per female based on a Holling type-II functional response.

Parameters a and b determine how survival of eggs and age-0 fish are related to spawning habitat conditions. Maximum survival is a, and b represents the value of suitable spawning habitat when survival is 50% of a (Hilborn and Mangel 1997).

The spawning habitat model for grayling population dynamics and observation error, linking recruitment to spawning habitat conditions, is:

$N_{t+1} = N_t S_t + F_{t-2}\alpha_{t-2}R_{t-2}\delta_{t-2}\epsilon_{t-1}\theta_t$ (10)

$N_{obs,t} = N_t V_t.$ (11)

Adult grayling survival and total abundance year t, number of females year t - 2 are obtained from sampling. Length-specific fecundity t - 2 was estimated using data from Lund (1974) and Bishop (1971). Age-0 winter (δ), age-1 annual (ϵ), and age-2 annual (θ) fish survival were taken from published estimates for similar-aged salmonids or estimated for this grayling population (Table 1) and assumed to be constant among years. The product of survival estimates resulted in a value of 0.082, i.e., $\approx$ 8% of age-0 fish that reach Upper Lake are predicted to survive through their second winter. There is only a single component to the likelihood for this model, adult grayling annual abundance estimates.

Non-native Fish Model–Non-native Yellowstone cutthroat trout (trout) were hypothesized to reduce survival of a grayling cohort prior to age-2, i.e., reduced age-0 through age-1 survival, via predation. To use the same model structure as the other hypotheses outlined above we considered grayling mortality (1 - survival) instead of survival. This allows grayling mortality to increase rapidly with increasing trout abundance up to a threshold at which mortality approaches an asymptote (Figure 6).

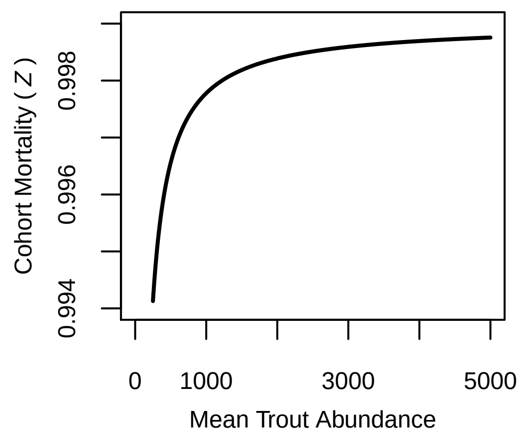

Figure 6. Hypothetical relationship between grayling age-0 and age-1 mortality for a cohort, Z, and concurrent winter abundance of adult Yellowstone cutthroat trout, C_t, based on a Holling type-II functional response.

Mortality of cohort i from hatching to age-1, Z_i (1 - $\gamma_{t-2}\delta_{t-2}\epsilon_{t-1}$), was asymptotically related to mean abundance of adult trout during the cohort's first two years. For example, mortality up to age-2 of a grayling cohort that hatched year t would be related to the mean abundance of adult trout in years t + 1 and t + 2, C_t as

$Z_t = \frac{aC_t}{b+C_t}$. (12)

This results in a balance equation, relating grayling mortality to trout abundance, with the following form:

$N_{t+1} = N_t S_t + F_{t-2}\alpha_{t-2}\beta_{t-2}Z_i\theta_t$. (13)

Adult trout abundance was annually estimated during spawning in Red Rock Creek by adding the number of fish 1) harvested by anglers, 2) removed at the fish weir, and 3) remaining in the system. Adult trout were experimentally removed from Red Rock Creek by culling fish at the weir (2013–2016) and liberalized angler harvest (2013–2017) to generate an adequately broad range of trout abundances to test this hypothesis. Number of fish harvested by anglers was estimated from catch cards corrected for non-reporting (Warren and Jaeger 2017). Cutthroat trout captured at the weir were sexed, length ($\pm$ 1 mm) and weight ($\pm$ 1 g) recorded, uniquely marked with a floy tag and released upstream of the trap (2013–2017). Initial marking occurred in April; trout, marked and unmarked, encountered during electrofishing in May were recorded and used to estimate detection probability ($p = \frac{m}{n}$, where n is the number of trout marked in April and m is the number of marked trout recaptured in May). The number of trout remaining within Red Rock Creek was estimated as $\frac{T}{p}$, where T is the number of trout captured in May. Beginning in 2018, cutthroat trout abundance was estimated via two-pass electrofishing and the Chapman method.

The enumeration of C_t likely provides a minimum estimate of the number of adult trout a given grayling cohort hatched year t was subjected to in years $t + 1$ and $t + 2$. Because trout have a lower likelihood of being detected below Elk Lake Road due to asynchronous timing of their spawning run and electrofishing surveys, the number of fish remaining in the system will be underestimated. Therefore, the aforementioned overall abundance estimates represent an index of trout abundance that is less than actual abundance. It is possible that some adult trout present in the Upper Lake system do not ascend Red Rock Creek for spawning or complete spawning and return to Upper Lake prior to attempts to quantify their abundance. However, C_t is likely proportional to the number of adult trout present each year.

The *Non-native Fish* model does not differentiate between competition and predation, but will quantify the response of grayling to trout population reduction. Evidence for niche overlap between grayling and trout, where the potential for competition exists, occurs when trout are $<$ 450 mm in total length (Cutting et al. 2016). The management action being undertaken, Yellowstone cutthroat trout removal during spawning, is primarily removing larger ($>$ 450 mm) fish, which not only precludes a direct test of competition but also does not allow estimation of trout of the size class that potentially compete with grayling. Lastly, evidence for bottom-up regulation, e.g., low condition factor for either species observed during spawning, is lacking.

Simulations, Predictions, and Model Weighting

Learning in the context of this adaptive management project occurs through the comparison of model predictions with reality (i.e., predicted grayling population vs. actual estimates of grayling population). Hypothesized drivers of grayling population dynamics are each represented by a model that links the driver to a specific life stage. A complete time series of observations (i.e., grayling and trout abundance, habitat characteristics) is needed to fit models so estimates of effects can be obtained and, subsequently, models can be used to make predictions. Delayed maturation of grayling (i.e., recruiting at age 3) results in needing three consecutive years of data to predict the number of grayling in a spawning population. The first time-series of data necessary to make a prediction was available in 2016, which was also the first population estimate that could be used to fit models. However, it is preferable to fit the models using several population estimates. To address this issue in the short-term, we conducted simulations to estimate the influence of each hypothesized driver of grayling population.

We conducted simulations to estimate response of grayling to 1) winter habitat, 2) spawning habitat, and 3) cutthroat trout abundance. For each of the three models we simulated 1000 grayling populations for 15 years, using mean grayling population 1994–2021 ($\hat{\bar{N}} = 767$) as the first three population abundances (i.e., N_t, N_{t+1}, and N_{t+2}; necessary due to assumption of knife-edge recruitment at age-3). For each time step a random value was drawn from a normal distribution ($X \sim N(\mu, \sigma^2)$) defined by the existing mean (μ) and standard deviation (σ) from each variable (Figure 7). The distribution of winter habitat (W_t) was defined by 11 values, with $\mu = 94$ ha, and $\sigma = 140$. We assumed that a minimum of 5 ha was always available in the lake at the mouths of streams and spring heads; this precluded a complete die-off during a winter otherwise predicted to have 0 ha available habitat. Estimates of weighted suitable spawning habitat, 2013–2021, were used to estimate mean (μ) and variance (σ) spawning habitat values for simulations ($A_w \sim N(\mu = 3.99, \sigma = 2.38)$). Finally, cutthroat trout abundance was drawn from $N(\mu = 1093, \sigma = 890)$, constrained to > 500 trout. The *Non-native Fish Model* links mean trout abundance the first two years of a cohort's life (C_t) to mortality during that period (see **Models of System Dynamics** above). Therefore, we used the mean of two randomly drawn trout abundances to estimate C_t.

The common balance equation structure of models with saturating functions linking hypothesized population drivers to grayling demographic rates results in two parameters per model that mathematically describe the non-linear relationship. First, a represents maximum survival for the *Winter Habitat* and *Spawning Habitat* models. For the former, a is multiplied by the survival rate of each age-class to allow the influence of winter habitat to vary from none (i.e., grayling survival is 100% of expected age-class survival rates) to a winterkill event where survival ≈ 0. For the *Spawning Habitat* model, maximum survival of egg (β) and age-0 in-stream grayling (γ), R_t, was set at 0.0042, the product of $\beta = 0.12$ (Lund 1974) and $\gamma = 0.035$ (maximum estimated survival based on back-calculations using existing demographic data). The complement of survival, mortality, is considered in the *Non-native Fish Model.* We set maximum combined mortality for first winter (δ), age-1 (ϵ), and age-2 (θ) grayling as 0.999, which results in a minimum survival of 0.001 for juvenile grayling, excluding mortality during egg and age-0 phases.

The second common parameter, b, defines the value of a given variable when survival is half of a (Hilborn and Mangel 1997) – the larger the value of b, the more sensitive survival is to the variable of interest.

We conducted simulations to estimate b for each model. Our convergence criterion was achieving a long-term simulated grayling population mean ± 10 individuals of the actual grayling mean, 1994–2021 ($\hat{\bar{N}} = 767$). Simulated population means did not include the first three values in the time series as these were set at the current grayling mean, 1994–current (see above).

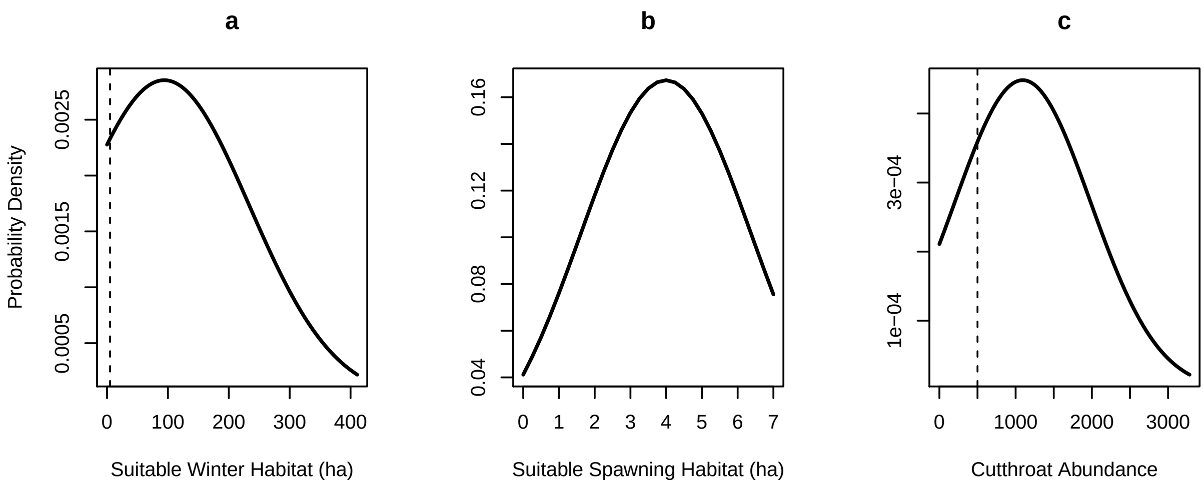

Figure 7. Probability distributions used in grayling simulations to draw random a) minimum amount of suitable winter habitat (ha), b) amount of suitable spawning habitat (ha), and c) abundance of non-native cutthroat trout. Vertical dashed lines represent constraints, i.e., $>$ 5 ha winter habitat and $>$ 500 trout.

Model weights were calculated using Baye's formula, which allows adding new information (i.e., an updated comparison of predicted and observed grayling abundances) to existing information (i.e., existing model weights based on prior comparisons of predicted and observed grayling abundances). The model weight of model i in year $t + 1$ given the observed data (i.e., response), $p_{i,t+1}$, is calculated as the prior model weight ($p_t(model_i)$) multiplied by the probability of the observed data in $t + 1$ given model i ($P(response_{t+1}|model_i)$), divided by the total probability of all the models given the observed data ($\sum j = 1^n p_t(model_j)P(response_{t+1}|model_j)$),

$$p_{i,t+1} = (model_i|response_{t+1}) = \frac{p_t(model_i)P(response_{t+1}|model_i)}{\sum j=1^n p_t(model_j)P(response_{t+1}|model_j)} \quad (14)$$

We used observed values of W_t, A_t, C_t, and $\hat{b}$ from simulations for each model of system dynamics to predict the 2021 grayling spawning population in Red Rock Creek. Prior-year's (2020) model weights were used as model priors. Because enough data are not available to fit models and obtain likelihoods for $P(response_{t+1}|model_i)$, we used the probability of observing 88 grayling in 2021 given each model prediction, assuming a normal distribution with μ = model predicted values and σ = 649 (Figure 8). Model likelihoods based on maximum-likelihood estimation will be used for $P(response_{t+1}|model_i)$ when a sufficient time-series is available for fitting models.

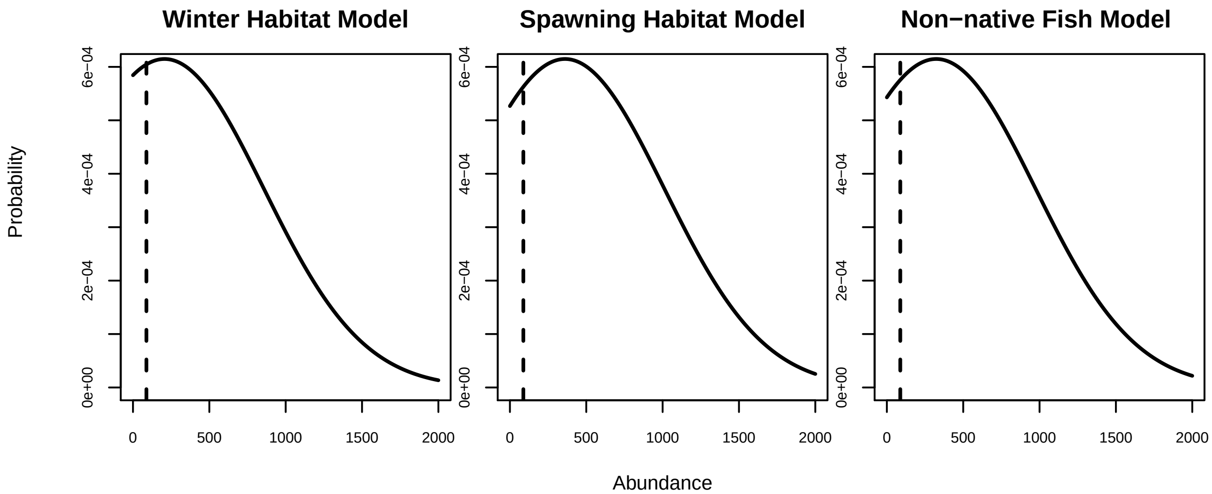

Figure 8. Normal probability density plots for *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models with $\mu = 207$, 361, and 323, respectively. Standard deviation for all plots $= 649$. Vertical dashed lines show the observed grayling spawning population, $\hat{N} = 88$, in 2021.

Abundance and Survival

Grayling and cutthroat trout were captured by mobile anode electrofishing (May and June) and a stationary weir (April–June) from 2013 to 2017 (see Paterson 2013 for further description). Beginning in 2018 only electrofishing surveys occurred. Grayling were uniquely marked with a visual implant (VI) tag, sexed, and length ($\pm$ 1 mm) and weight ($\pm$ 1 g) recorded. We used capture-mark-recapture (CMR) models implemented in program MARK (White and Burnham 1999) using the RMark package (Laake 2013) in R version 3.6.2 (R Development Core Team 2019) to estimate grayling abundance with closed population models and apparent survival (ϕ) with open population models concurrent with operation of the fish weir on Red Rock Creek. After cessation of the fish weir (2018), grayling and cutthroat estimates were obtained using electrofishing data and the Chapman method (Guy and Brown 2007). Apparent survival confounds permanent emigration and mortality; survival will be biased low if adult grayling fidelity to spawning streams is < 1.

RESULTS

Simulations, Predictions, and Model Weighting

Simulations resulted in $\hat{b}$ values of 0.0185, 0.011, and 1.225 for the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models, respectively. These values of b resulted in simulated populations similar to observed dynamics 1994–2021, as measured by population mean during that period. Based on simulation results, the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models predicted 207, 361, and 323 grayling, respectively, in the 2021 Red Rock Creek spawning population (Table 2). Updated model weights based on model predictions were 0.576, 0.333, and 0.09 for *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models, respectively (Table 2). Each model's predicted grayling spawning population for 2022 are provided in Table 2. The 2022 model-averaged prediction of spawning grayling abundance is 187 fish. Annual grayling spawning population estimates and model predictions, 2016–2021, are provided in Figure 9.

Table 2. Arctic grayling spawning abundance model predictions, observed abundance, and relative model weights for 2021, and model predictions for 2022.

Model	2021 Prediction	Observed	Model Weights	2022 Prediction
Winter Habitat	207	88	0.576	172
Spawning Habitat	361	88	0.333	229
Non-native Fish	323	88	0.090	128

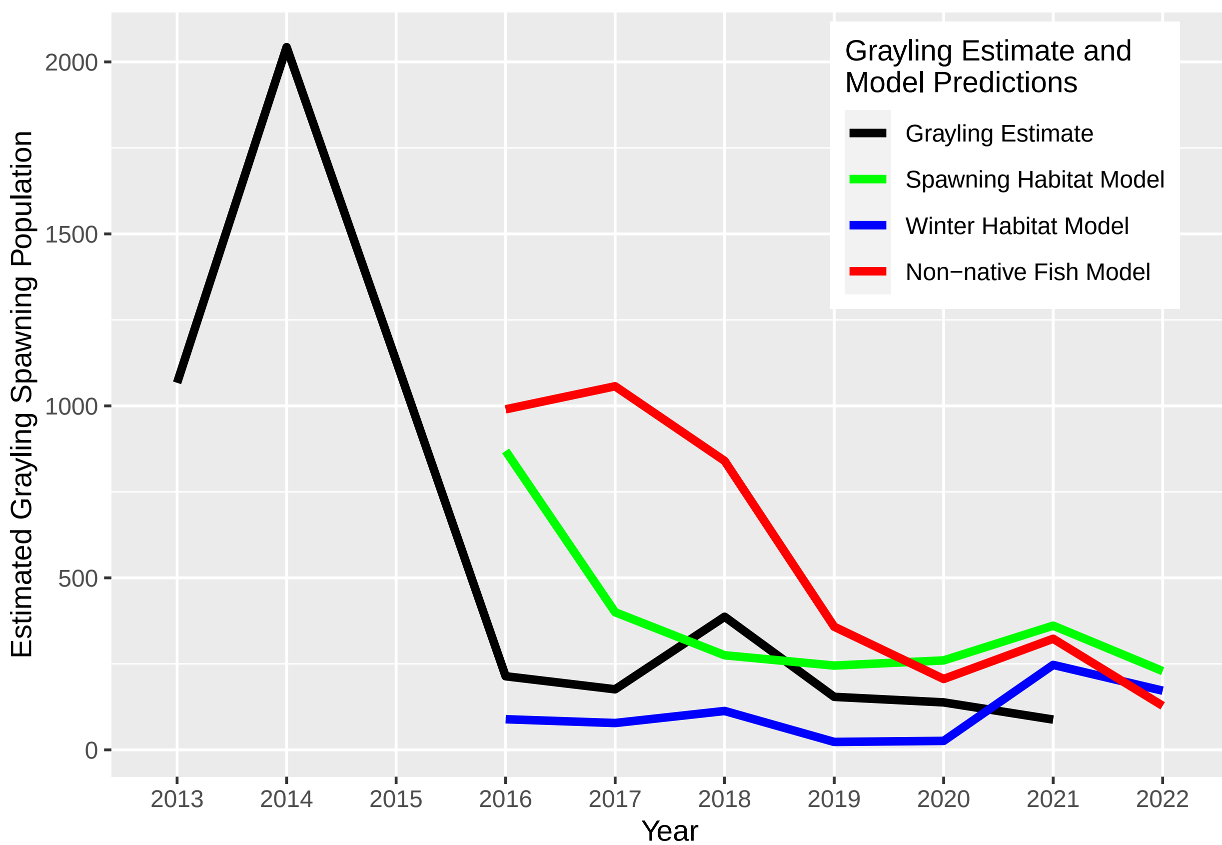

Figure 9. Arctic grayling spawning population estimate and model predictions by year, 2013–2021 and 2016–2022, respectively.

Abundance and Survival

The 2021 Red Rock Creek grayling spawning population was 88 fish (95% CI = 26–176), statistically similar to last year's estimate of 138 grayling (95% CI = 82–302; Figure 10), but significantly less than predicted abundances (Table 2, Figure 9). The lack of congruence between model predictions and observed grayling abundance may represent a depensatory response of breeding-age grayling to repeated years of low abundance (i.e., <400 fish)(Liermann and Hilborn 2001). The 2021 spawning population represents the sixth consecutive year of grayling population below 400 individuals (Figure 10), well below the grayling population objective of 1000 spawning fish (Warren and Jaeger 2017).

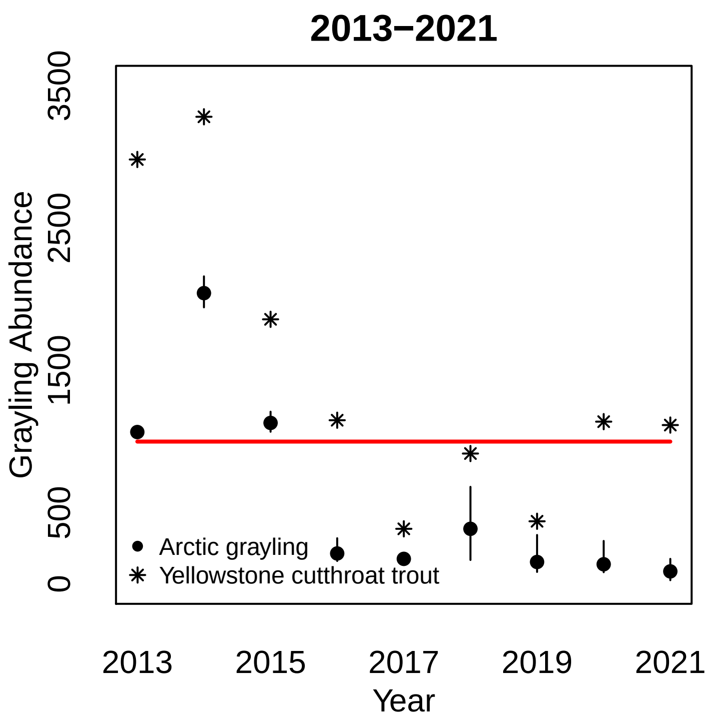

Figure 10. Arctic grayling and Yellowstone cutthroat trout abundance estimates and 95% confidence intervals (grayling only) from Red Rock Creek, 2013–2021. The red line indicates the current grayling population objective of 1000 fish for Upper Red Rock Lake and tributaries (Warren and Jaeger 2017).

The 2021 estimate of genetic variation (average expected heterozygosity) was the lowest value observed in 23 years of monitoring (1998-2021)(Kovach et al. 2019, Kovach et al. 2021). During that period, the population lost an average of 1.5 alleles per locus. The loss of some of that genetic variation is irreversible, as grayling in Upper Red Rock Lake harbor unique genetic variation not found elsewhere among native grayling populations in Montana. Along with demographic declines, estimates of the number of effective breeders demonstrate the population is experiencing an increasingly severe genetic bottleneck. This will further reduce genetic variation and increase the likelihood of inbreeding depression, which together greatly reduces the immediate and long-term probability of persistence for this population. The genetic consequences of this population bottleneck will persist following a population rebound (if one were to occur), emphasizing that each additional year of small population size further erodes the evolutionary legacy and resilience of this population.

Age distribution of the spawning population is inconsistent with the long-term age distribution of the spawning run, with age-2 and age-5 fish the predominant age classes represented (Figure 11). However, given the low number of individuals captured in 2021 (n = 17), this could be an artifact of random chance.

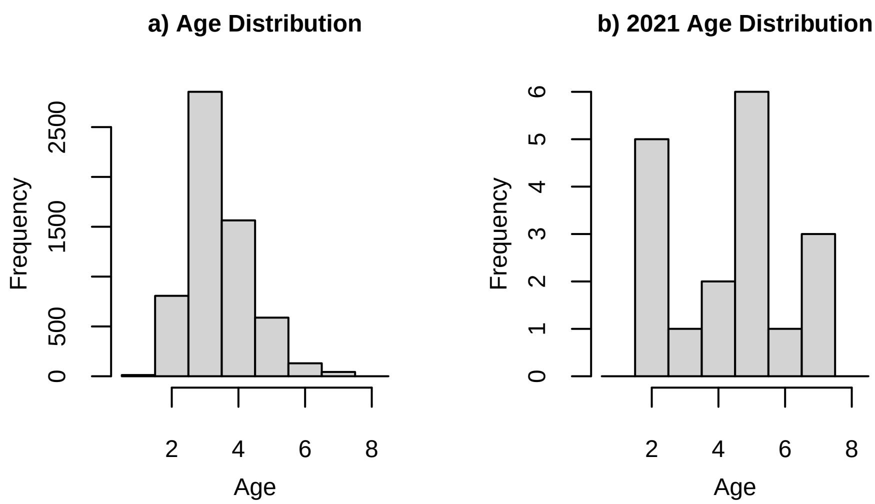

Figure 11. Age distribution of the spawning population of Arctic grayling in Red Rock Creek for a) all years of data (1950–2021, with missing years), and b) 2021.

The estimated spawning population of cutthroat trout was 1116 fish, nearly unchanged from 2020 (1140 fish)(Figure 10). We will continue to learn how grayling respond to the Yellowstone cutthroat trout population and spawning habitat availability as 1) grayling cohorts spawned during low trout abundances and high availability of spawning habitat recruit, and 2) Yellowstone cutthroat trout spawning population recovers.

Winter Habitat

Suitable grayling winter habitat during 2020–2021 in Upper Red Rock Lake was surveyed 12 January, 17 February and 12 March, 2021. Suitable habitat within the lake was lowest during March with $\approx$ 5 ha (Figure 12). The first habitat sampling of the 2021–2022 winter occurred 25 January, 2022; suitable winter habitat was estimated as 14 ha (Figure 12). Winter habitat suitability criteria, i.e., dissolved oxygen and water depth, were both highly variable during the period of record. For example, the area (ha) of Upper Lake with suitable dissolved oxygen and depth were 7–1023 ha, and 8–628 ha, with mean values 310.4 (SD = 314.8) and 162.4 (SD = 187.6), respectively.

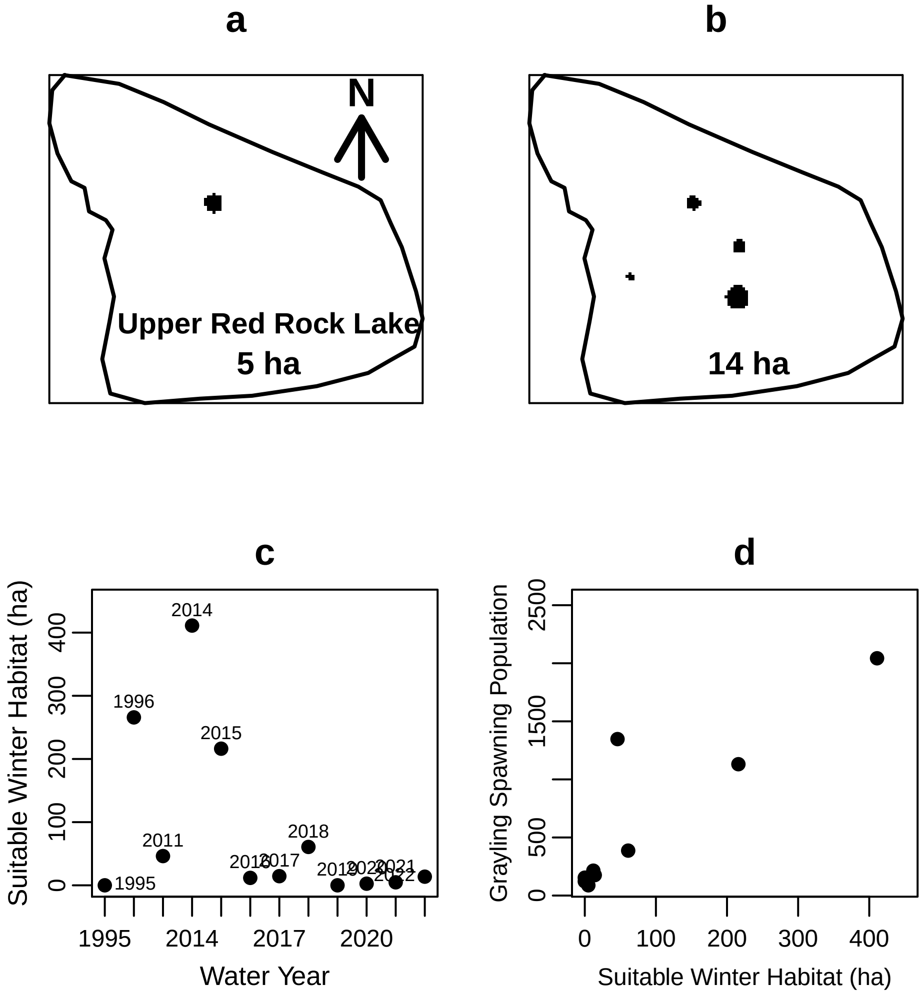

Figure 12. a) Extent of minimum area of suitable Arctic grayling winter habitat in Upper Red Rock Lake, 2021, b) January 2022, c) annual estimate of minimum area of suitable habitat for water years 1995–2022, and d) grayling spawning population as a function of minimum area of suitable winter habitat for years when both were estimated.

Spawning Habitat

Suitable spawning habitat was most recently quantified in 2021, with an estimated weighted area of suitable habitat, A_t, of 6.1 ha in Red Rock Creek (Table 3, Appendix). This was an increase of 16× the area of suitable spawning habitat available during 2016, the nadir of suitable spawning habitat during the AMP. Moreover, area of suitable habitat during the spawning habitat experiment was 12 (2017–2018) and 18 (2019–2020) times more spawning habitat than the lowest amount observed in 2016. Area of suitable spawning habitat in 2019, the most observed during the AMP, was coincident with above average flows on Red Rock

Creek; days above 67% of bankfull discharge ($c67bf = 12$) were 60% of the long-term mean. Fines within riffles are mobilized by stream discharges greater than 67% of bankfull (Mueller et al. 2005), providing a mechanism for the observed improvement in grayling spawning habitat in 2019 (Hubert et al. 1985). All suitable spawning habitat was made available to grayling via beaver dam notching during the spawning habitat AMP experiment. The increased per capita availability of suitable spawning habitat is hypothesized to increase egg (β) and age-0 fish in-stream (γ) survival. Grayling response to increased availability of spawning habitat was first quantified in 2020, when the 2017 grayling cohort recruited. This was the second year spawning habitat manipulations to favor grayling was assessed. Spawning habitat will next be surveyed in 2023.

Although the spawning habitat experiment has concluded, beaver dams are currently being notched to provide unencumbered access to spawning habitat in Red Rock Creek. This is due to the current lack of a management response to address the primary limiting factor of grayling population, winter habitat. Until the latter can be addressed, access to suitable spawning habitat will be maximized to increase grayling recruitment. This management action addresses the second most influential factor affecting grayling population, spawning habitat.

Table 3. Estimated area (ha) of weighted suitable Arctic grayling spawning habitat (Hubert et al. 1985) by year and stream for Red Rock and Elk Springs creeks.

Year	Red Rock Creek	Elk Springs Creek	Total
2013	2.55	0.00	2.55
2014	2.55	0.00	2.55
2015	1.63	0.00	1.63
2016	0.38	0.00	0.38
2017	4.04	0.33	4.37
2018	4.04	0.33	4.37
2019	6.88	0.10	6.98
2020	6.88	0.10	6.98
2021	6.01	0.12	6.13

MANAGEMENT ACTIONS

An alternatives analysis was completed in 2019 to assess costs, logistical and legal feasibilities, and likely effects on grayling of 26 potential winter habitat enhancement approaches (Flynn et al. 2019). Two alternatives, solar aeration and flow augmentation to Elk Springs Creek from Widgeon Pond, were experimentally assessed during the winters of 2019 and 2020, respectively. Aerators did not successfully function throughout the winter, ultimately becoming frozen into the lake ice. Empirical assessment of pulsed-flow demonstrated ambiguous results and additional modeling indicated this action could not provide suitable habitat within Upper Lake throughout winter. Therefore, neither action demonstrated the ability to consistently provide suitable oxygen levels at preferred depths for the duration of winter.

Final engineering design of a tributary point-of-inflow modification will be completed in 2022 to further clarify potential effectiveness, costs, and impacts of this alternative. Fundraising and permitting will be completed during spring of 2022. Project construction can occur once NEPA analysis is completed.

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Appendix. Estimated area (ha) of weighted suitable Arctic grayling spawning habitat (Hubert et al. 1985) in Red Rock and Elk Spring creeks by year and reach.

Creek	Reach	2013	2014	2015	2016	2017	2018	2019	2020	2021
Red Rock Creek	Antelope Creek to Elk Lake Road	1.47	1.47	0.93	0.11	1.26	1.26	3.03	3.03	2.21
Red Rock Creek	Corral Creek to Antelope Creek	0.34	0.34	0.00	0.00	0.59	0.59	0.48	0.48	0.32
Red Rock Creek	Downstream of Battle Creek	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Red Rock Creek	Elk Lake Road to Battle Creek	0.68	0.68	0.70	0.27	0.53	0.53	1.19	1.19	1.18
Red Rock Creek	Hellroaring Creek	0.00	0.00	0.00	0.00	0.44	0.44	0.47	0.47	0.82
Red Rock Creek	Huntsman	0.00	0.00	0.00	0.00	0.10	0.10	0.28	0.28	0.17
Red Rock Creek	Huntsman to Corral Creek	0.06	0.06	0.00	0.00	1.12	1.12	1.43	1.43	1.32
Elk Creek	Forks	0.00	0.00	0.00	0.00	0.11	0.11	0.03	0.03	0.06
Elk Creek	Restoration	0.00	0.00	0.00	0.00	0.22	0.22	0.07	0.07	0.07
	Total	2.55	2.55	1.63	0.38	4.37	4.37	6.98	6.98	6.13