

Centennial Valley Arctic Grayling Adaptive Management Project Annual Report, 2016

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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 populations of endemic adfluvial grayling 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 2016 Red Rock Creek spawning population was 214 (95% CI = 161–321), a 5-fold decline from last year's estimated spawning population ($\hat{N} = 1131$, 95% CI = 1069–1210; Figure 1). Suitable winter habitat within Upper Lake (i.e., water depth below the ice ≥ 1 m and dissolved oxygen ≥ 4 ppm) reached a minimum during February sampling at an estimated 12 ha. This represented the second lowest area of suitable winter habitat measured since 1995 ($n = 7$). Suitable spawning habitat was most recently quantified in 2014–2015, with an estimated total area of suitable spawning habitat (A_{ts}) of 0 ha, and weighted area of suitable habitat (A_{tw}) of 0 ha, in Red Rock and Elk Springs creeks (see **METHODS** below for description of variables). The amount of suitable spawning habitat that was available has yet to be calculated; A_{ts} and A_{ws} will be corrected for 1) availability based on fish passage as a function of barrier (i.e., beaver dam) characteristics and 2) backwatered areas. Hydrology during the 2016 breeding season critical period (i.e., *peak spawning + 188 degree days + 5 weeks*) was characterized using four variables related to stream flows (cubic feet second⁻¹) and temperature (°C) – mean daily discharge ($mdd = 59.6$ cfs), cumulative

degree days from peak emergence to five weeks post-emergence ($cdd = 454.5$), days above bankfull discharge ($cbf = 0$), and days above 67% of bankfull discharge ($c67bf = 3$). These values represent 74%, 110%, 0%, and 16% of the long-term mean values for mdd , cdd , cbf , and $c67bf$, respectively.

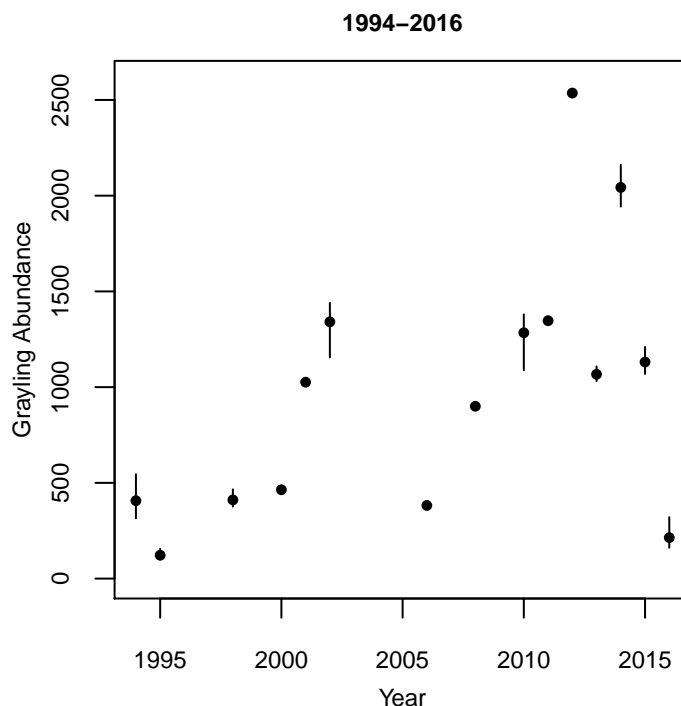


Figure 1. Estimated annual Red Rock Creek Arctic grayling spawning population abundance and 95% confidence intervals, 1994–2016. Confidence intervals are not available for all years prior to initiation of the Adaptive Management Plan.

The first management experiment conducted as part of the adaptive management plan was reducing 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; during 2013–2016 a total of 6973 cutthroat 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 next several years will continue to provide information on the relationship between cutthroat abundance and grayling recruitment.

The second management experiment will explore the relationship between spawning habitat and grayling recruitment. Efforts beginning in 2017 will increase suitable habitat available for spawning by 1) ensuring fish passage at beaver dams ($n > 50$ in 2016) via notching, 2) restoration of an Elk Springs Creek channel that will provide direct connection to Upper Lake, and 3) restoration of spawning habitat at the head of Elk Springs Creek. This experiment will be undertaken for 4–5 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; the first year a possible response could be quantified is 2020, when the 2017 grayling cohort recruits.

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, non-native fish, and spring hydrology, is represented by a model structured to estimate the driver’s influence on a specific life stage. Grayling recruit at age-3, which necessitates having three consecutive years of data to make model-based predictions. 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. Obviously, models cannot be fitted to a single population estimate. We addressed this issue in the short-term using simulations to estimate the influence of each hypothesized driver of grayling population (see **Methods**). Based on simulation results, the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models predicted 89, 869, and 990 grayling, respectively, in the 2016 Red Rock Creek spawning population. Model weights, i.e., relative support for a model given the data, were 0.476, 0.289, 0.235 for the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models, respectively.

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INTRODUCTION

Montana Arctic grayling (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). 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) will embrace existing uncertainty regarding drivers of the grayling population in the CV, 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 active adaptive management phase. The former was designed to explore grayling population response to hypothesized drivers that could be influenced via management actions. The latter will use 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 of the 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.

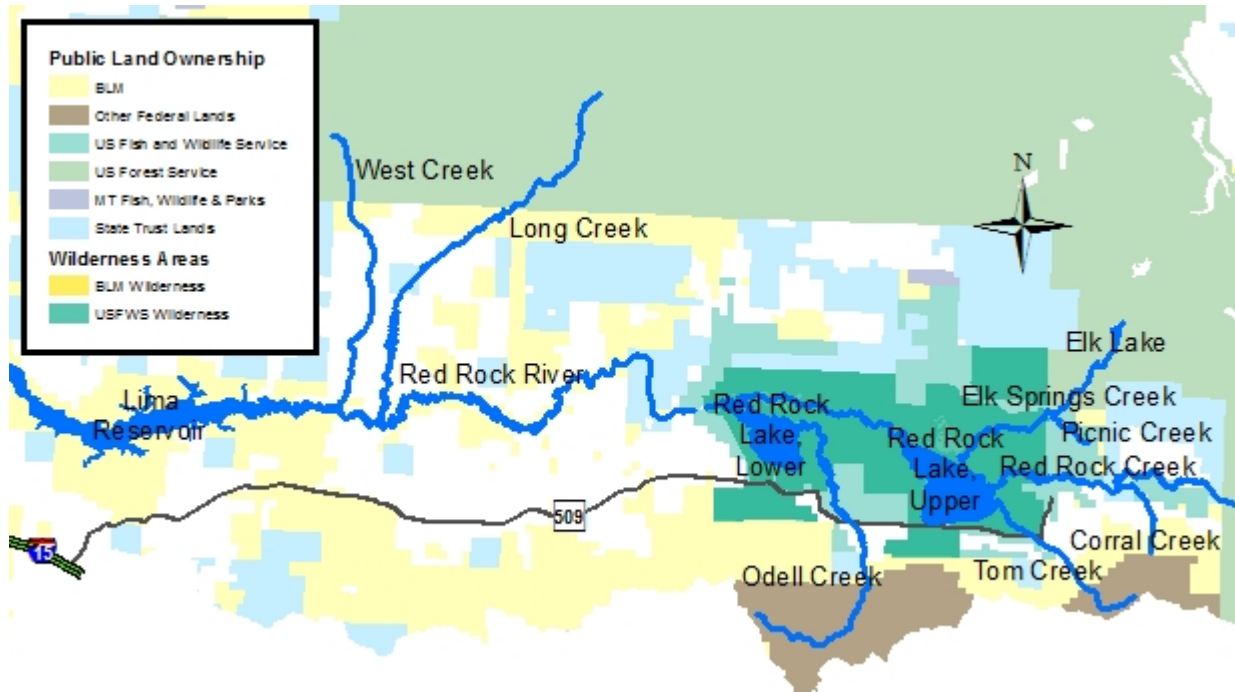


Figure 2. Arctic grayling adaptive management plan study area within the Centennial Valley of southwestern Montana.

METHODS

Grayling Abundance and Survival

Grayling and cutthroat trout were captured by mobile anode electrofishing (May and June) and a stationary weir (April–June) (see Paterson 2013 for further description). Grayling were uniquely marked with a visual implant (VI) tag, sexed, and length (± 1 mm) and weight (± 1 g) recorded. Cutthroat trout captured at the weir were sexed, length (± 1 mm) and weight (± 1 g) recorded, and then euthanized. A subset of male cutthroat trout (100–200) were uniquely marked with a floy tag and released upstream of the trap annually. Cutthroat trout subsequently captured by electrofishing were enumerated, floy-tags recorded, and released.

We used capture-mark-recapture (CMR) models implemented in program MARK (White and Burnham 1999) using the RMark package (Laake 2013) in R version 3.2.2 (R Development Core Team 2016) to estimate abundance with closed population models and apparent survival (ϕ) with open population models. Apparent survival confounds permanent emigration and mortality; therefore survival will be biased low if adult grayling fidelity to spawning streams is < 1 .

Models of System Dynamics

Spawning habitat, non-native fishes, winter habitat, and spring and summer hydrology 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:

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

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 1st), year $t - 2$,
- δ_{t-2} – age-0 fish winter survival (September 2nd - May 15th), year $t - 2$,
- ϵ_{t-1} – age-1 fish survival (May 16th – May 15th), 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 (13th 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. 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.

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, the period of hypoxic conditions experienced during the winter of 1994-1995 (Gangloff 1996). Available winter habitat is defined as the area (ha) of water in Upper Red Rock Lake from January to March with ≥ 4 ppm dissolved oxygen and ≥ 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, $N_{w,t}$, that entered the winter period.

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

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

Species	Average survival rate (maximum survival rate)			
	size range in mm; age range time period applicable to survival rate			
	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	--

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

Figure 1:

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

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

The 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 $a = 1$, $b = 10$, and W_t varies from 0 to 0.50 ha fish⁻¹.

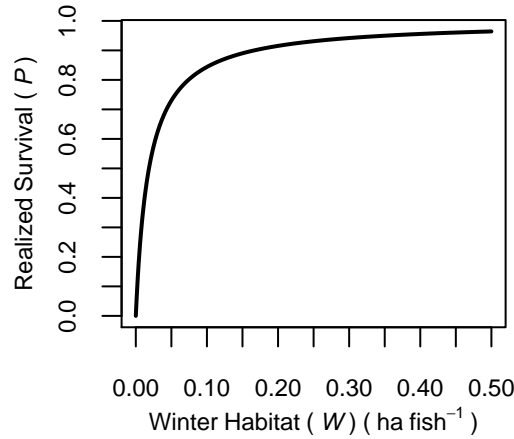


Figure 3. Hypothetical relationship between the realized proportion of maximum grayling survival and the area of suitable winter habitat per fish in Upper Red Rock Lake based on a Holling type-II functional response.

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

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

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

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

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

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 $\leq 10\%$ fines is considered suitable, 11–50% fines represent linearly declining suitability, and $> 50\%$ is unsuitable. Conversely, $\geq 20\%$ gravel and rubble is considered suitable with $< 20\%$ representing a linearly declining suitability (Figure 4). Thus, suitable spawning habitat can be characterized by having $\leq 10\%$ fines and $\geq 20\%$ gravel and rubble.

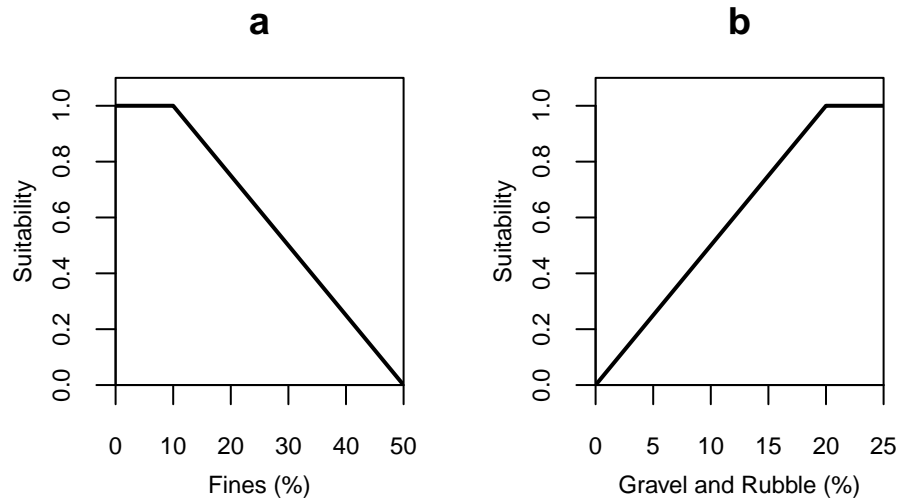


Figure 4. Predicted relationship between suitability of riverine Arctic grayling spawning habitat and a) percent fines (< 3 mm) in spawning areas and downstream riffles, and b) percent gravel and rubble (1.0–20.0 cm) in spawning areas (from Hubert et al. 1985).

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 the 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 will be 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 are sampled following MT DEQ TMDL Sediment Assessment Methods (in press). Cumulative percent fines are calculated for each sampled riffle.

Total area of suitable spawning habitat, A_t , is calculated and modeled considering 1) only habitat that has a suitability of 1.0 (i.e., $\leq 10\%$ fines and $\geq 20\%$ gravel and rubble) and 2) weighted suitability of habitat based on observed percent fines and gravel and rubble following Hubert et al. (1985; Figure 4).

Habitat area per stream with suitability of 1.0, A_{ts} , is riffle area per site with suitability = 1.0, divided by total site length, multiplied by reach length, summed across reaches within a stream (Equation 7).

$$\sum_{i=1}^n \frac{\text{suitablerifflearea}(m^2)}{\text{totalsitelength}(m)} \times \text{reachlength}_i \quad (7)$$

Habitat area per stream with weighted suitability, A_{tw} , differs from A_{ts} in using the product of riffle suitability scores for percent fines and gravel and rubble estimated from the hypothesized suitability relationships of Hubert et al. (1985) instead of classifying riffle habitat as suitable (i.e., suitability = 1) or not (suitability < 1).

Area of suitable habitat (A_t) will also be annually adjusted to account for the 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 will be annually surveyed and the total length of beaver dam backwaters will be 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) will not be included in calculation of A_t . Probability of passage at beaver dams will be estimated based on the results of a study in progress and annual assessment of relevant beaver dam characteristics within each reach each year during the peak spawning period. Calculation of A_t will be 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 will be 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, the availability of suitable spawning habitat per fish, H_t ($m^2 \text{ fish}^{-1}$), 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

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

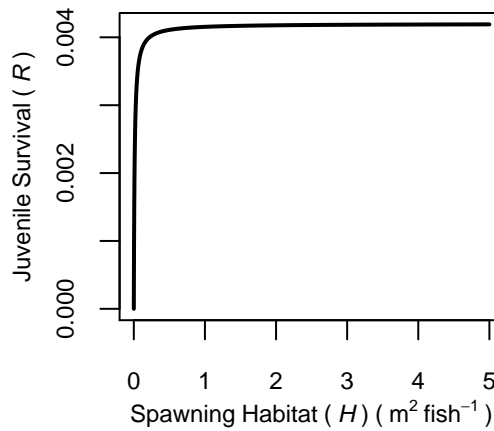


Figure 5. Hypothetical relationship between grayling egg and age-0 fish in-stream survival, R , and the area of suitable spawning habitat per female based on a Holling type-II functional response.

The 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:

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

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

Adult grayling survival and total abundance year t , number of females year $t - 2$, and length-specific fecundity $t - 2$ are obtained from sampling. 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 (i.e., $1 - \text{survival}$) 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).

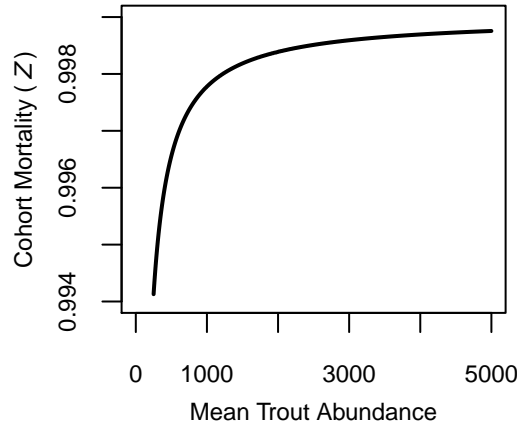


Figure 6. Hypothetical relationship between grayling age-0 and age-1 mortality for a cohort, Z , and concurrent winter abundance of adult nonnative Yellowstone cutthroat trout, C_t , based on a Holling type-II functional response.

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 the 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

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

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

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

Adult trout abundance will be 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 from 2013–2016 by angler harvest and culling fish at the weir 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). Most trout encountered at the weir were enumerated, euthanized, and transported to area food pantries. The number of trout in the spawning run not removed at the weir or by angling was estimated annually. Approximately 100 trout captured at the weir were marked with a uniquely numbered tag (i.e., t-bar anchor Floy tag) and released upstream of the weir. The number of trout, marked and unmarked, encountered during electrofishing was recorded and used to estimate detection probability (i.e., capture efficiency, $\frac{m}{n}$, where m is the number of marked trout recaptured electrofishing and n is the number of trout marked at the weir). The number of trout remaining within Red Rock Creek was estimated as $\frac{T}{p}$, where T is the number of trout captured electrofishing and p is detection probability. Total trout within the spawning run, and Upper Lake the prior winter, was then estimated as *remaining trout + weir trout + harvested trout*. Because trout have a lower likelihood of being detected below the weir 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.

The aforementioned 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 $t + 2$. 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. It is likely that some adult trout that were present during times when a given cohort of grayling was subject to predation die prior to the spawning period. 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 (USFWS upubl. data). 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. Therefore, 2016 was the first year in which we have a time series that could be used to make a prediction. However, due to the time-lag, 2016 also represents the first population estimate that could be used to fit models. Obviously, models cannot be fitted to a single population estimate. 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 1994–2016 ($\hat{N} = 1099$) 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 6 values, with $\mu = 159$ ha, and $\sigma = 166$. 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. A single estimate of weighted suitable spawning habitat was available; we used half that value for μ , and assumed $\sigma = 2$, i.e., $A_{tw} \sim N(\mu = 2.4, \sigma = 2)$. Finally, cutthroat trout abundance

was drawn from $N(\mu = 1205, \sigma = 1014)$, 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, 1994–2016 ($\hat{N} = 1099$). 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).

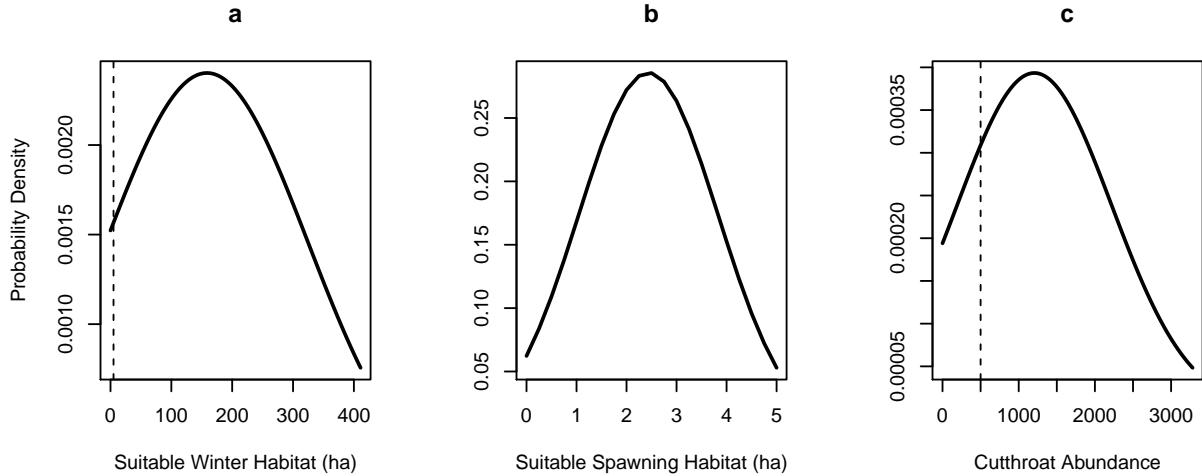


Figure 7. Probability distributions used in grayling simulations to draw random a) minimum amount of suitable winter habitat (ha), b) amount of suitable spawning habitat (ha), and c) abundance of non-native cutthroat trout. Vertical dashed lines represent constraints, i.e., > 5 ha winter habitat and > 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_{ws} (uncorrected for barriers and constant across time), C_t , and \hat{b} from simulations for each model of system dynamics to predict the 2016 grayling spawning population in Red Rock Creek. Equivalent model weights (i.e., an uninformative prior) 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 214 grayling in 2016 given each model prediction, assuming a normal distribution with μ = model predicted values and $\sigma = 645$ (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.

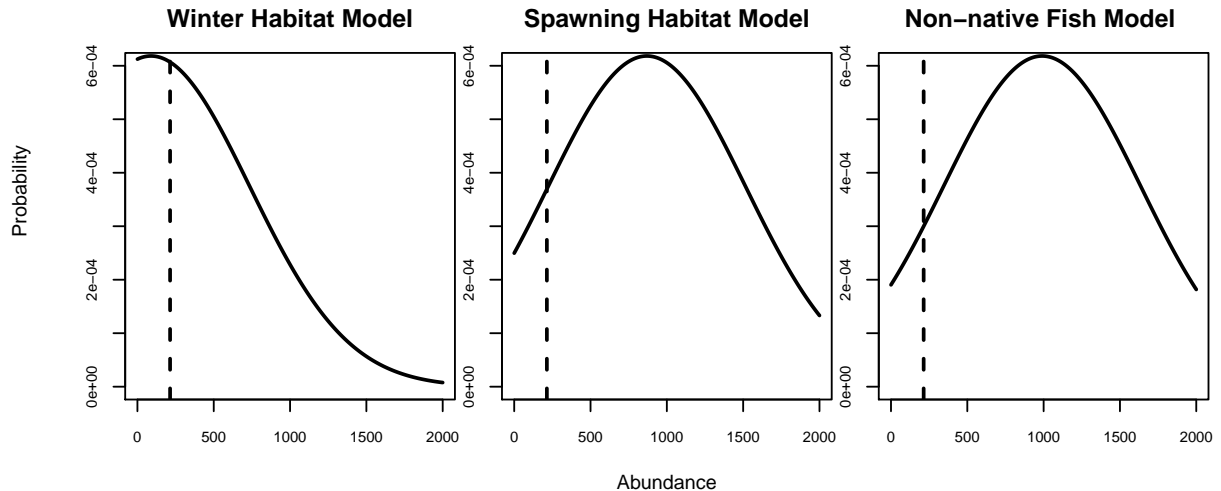


Figure 8. Normal probability density plots for *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models with $\mu = 89$, 869 , and 990 , respectively. Standard deviation for all plots = 645 . Vertical dashed lines show the observed grayling spawning population, $\hat{N} = 214$, in 2016.

We explored grayling response to hypothetical management actions for ameliorating winter conditions experienced during 2016 and 2017. First, to simulate potential aeration effects, we took points sampled in 2016 with suitable depth but deficient oxygen and increased dissolved oxygen values to ≥ 4 ppm. Second, we tested potential benefits of increasing Upper Lake water depth; points too shallow to be suitable, but with adequate dissolved oxygen, were given depths ≥ 1 m. We then calculated area of suitable winter habitat for each hypothetical action and predicted the 2016 grayling spawning population using the *Winter Habitat* model. Last, we conducted these same exercises with 2017 winter habitat data and predicted grayling spawning population for 2017 using observed grayling abundance and winter conditions for 2016.

RESULTS

Grayling Abundance and Survival

The 2016 Red Rock Creek spawning population was 214 (95% CI = 161–321), a 5-fold decline from last year’s estimate of 1131 fish (95% CI = 1069–1210)(Figure 9). The spawning population was predominantly age-3 fish (Figure 10).

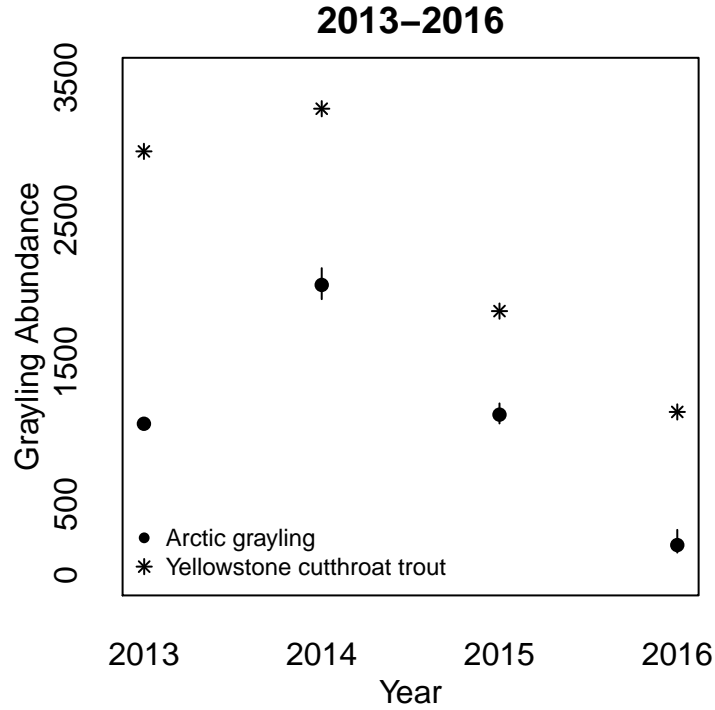


Figure 9. Arctic grayling and Yellowstone cutthroat trout abundance estimates and 95% confidence intervals (grayling only) from Red Rock Creek, 2013–2016.



Figure 10. Age-distribution of the spawning population of Arctic grayling in Red Rock Creek for a) all years of data (1994–2016, with missing years), and b) 2016.

Winter Habitat

Suitable grayling winter habitat in Upper Red Rock Lake reached an annual minimum during the February sampling effort (Figure 11). At that time, suitable habitat was predicted near the mouth of Red Rock Creek (Fig. 11). The estimated area of suitable winter habitat was 12 ha, the second lowest amount of suitable

habitat recorded 1995–2016 ($n = 6$ winters, 17 sampling occasions). The least amount of suitable winter habitat observed was the winter of 1995 (based on the water year starting October 1), the second year of a graduate project investigating grayling winter habitat use and distribution in Upper Lake (Figure 11; Gangloff 1996). 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 11–1023 ha, and 8–628 ha, with mean values 401.9 (SD = 350.4) and 231.7 (SD = 207.7), respectively.

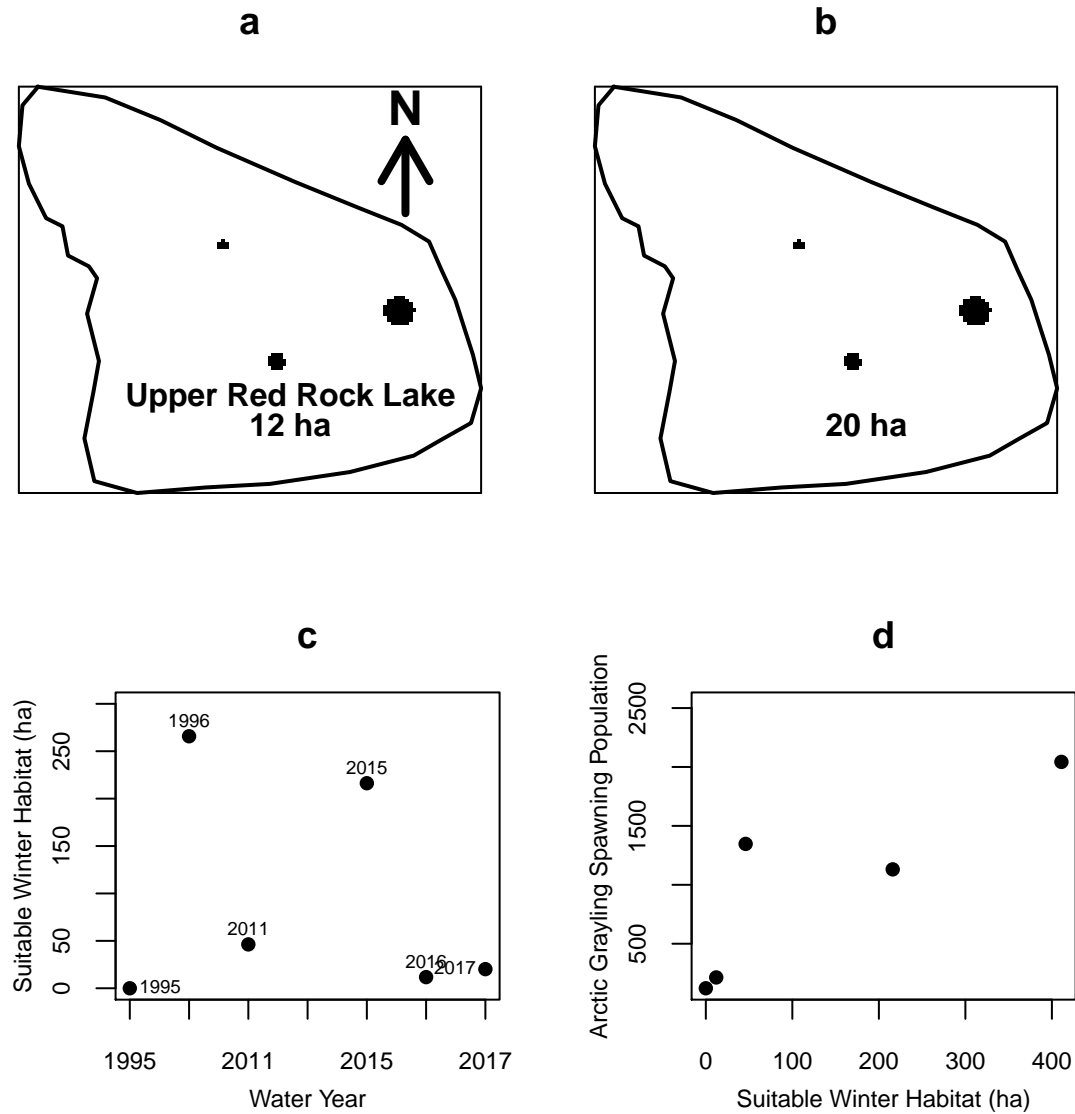


Figure 11. a) Extent of minimum area of suitable Arctic grayling winter habitat in Upper Red Rock Lake, 2016, b) 2017, c) annual estimate of minimum area of suitable habitat for water years 1995–2017, and d) grayling spawning population as a function of minimum area of suitable winter habitat for years when both were estimated.

Spawning Habitat

Suitable spawning habitat was most recently quantified in 2014–2015, with an estimated total area of suitable spawning habitat (A_{ts}) of 0 ha, and weighted area of suitable habitat, A_{tw} , of 0 ha in Red Rock and Elk

Springs creeks. The amount of suitable spawning habitat that was available has yet to be calculated. Ongoing analyses will correct A_{ts} and A_{ws} for availability based on probability of fish passage as a function of barrier (i.e., beaver dam) characteristics.

Spawning habitat will be surveyed in 2017, providing estimates of available spawning habitat concurrent with efforts to make all suitable spawning habitat within Red Rock and Elk Springs creeks available to grayling. The increased per capita availability of suitable spawning habitat is hypothesized to increase egg (β) and age-0 fish in-stream (γ) survival. The first year a possible response could be quantified is 2020, when the 2017 grayling cohort recruits.

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 1994–2016, as measured by population mean during that period. Based on simulation results, the *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models predicted 89, 869, and 990 grayling, respectively, in the 2016 Red Rock Creek spawning population (Table 2). Updated model weights based on model predictions were 0.476, 0.289, and 0.235 for *Winter Habitat*, *Spawning Habitat*, and *Non-native Fish* models, respectively, indicating the *Winter Habitat* model predicted the 2016 spawning run more precisely than the other two models (Figure 8; Table 1). Predicted grayling spawning population for 2017 are provided in Table 2.

Table 2. Arctic grayling spawning abundance model predictions, observed abundance, and relative model weights for 2016, and model predictions for 2017.

Model	2016 Prediction	Observed	Model Weights	2017 Prediction
Winter Habitat	89	214	0.476	91
Spawning Habitat	869	214	0.289	418
Non-native Fish	990	214	0.235	1057

Simulated aeration in 2016 resulted in 376 ha of suitable winter habitat and a predicted grayling spawning population of 777. This is a projected improvement of 365 ha of suitable habitat and 563 grayling beyond what was observed (Table 3, Figure 12). Six sample points had suitable depth but insufficient dissolved oxygen, the criteria used in the simulation. Simulated depth augmentation had less of a positive effect in 2016 than aeration (Table 3), indicating dissolved oxygen was more limiting than depth. Only four sample points had suitable oxygen but insufficient depth. This was reversed in 2017, with depth more limiting than dissolved oxygen. Simulated depth augmentation in 2017 resulted in 628 and 396 ha more suitable winter habitat than no action or aeration (Figure 12). Predicted difference in grayling spawning population between hypothetical actions was small, but both predicted roughly three-fold more grayling than no action (Table 3).

Table 3. Predicted response of winter habitat (Wt) and Arctic grayling spawning abundance (N) the subsequent spring to simulated management actions (aeration and depth augmentation) to ameliorate Upper Red Rock Lake winter conditions 2016 and 2017.

Action	Wt 2016	N 2016	Wt 2017	N 2017
None	8*	214*	10*	63
Aeration	352	708	193	182
Depth Augmentation	289	593	465	195

*Observed, not predicted, values.

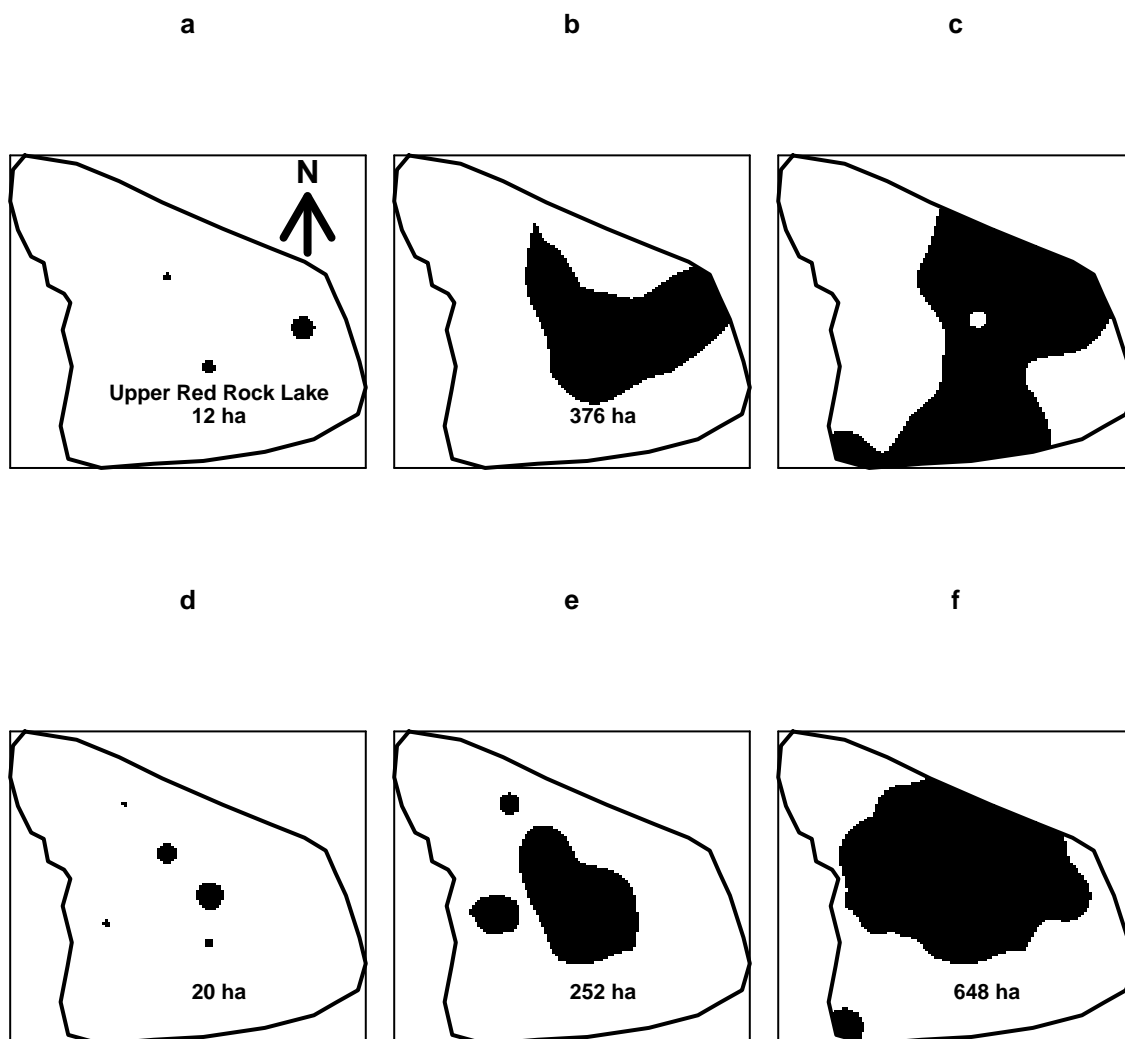


Figure 12. Observed and projected extent of suitable Arctic grayling winter habitat in Upper Red Rock Lake based on hypothetical management actions (aeration and depth augmentation) for 2016 (a = observed, b = aeration, c = depth augmentation) and 2017 (d = observed, e = aeration, f = depth augmentation).

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